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

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17 Running head: Metabolism of zooplankton and hyperbenthos

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19

20 **Abstract:** Rates of oxygen consumption (R) and ammonia excretion (E) of a total of 22
21 species of zooplankton and hyperbenthos, which weighed 0.0012 to 26.7 mg dry mass
22 (DM), from inshore and slope waters of the Great Barrier Reef were determined at *in*
23 *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
24 from 0.00051 to 15.9 $\mu\text{g NH}_4\text{-N ind.}^{-1} \text{ h}^{-1}$. Stepwise regression analyses in which the
25 differences in body mass are taken into account revealed that zooplankton and
26 hyperbenthos exhibited comparable R , but the latter showed lower E than the former.
27 As a result, the atomic ratio of R to E (O:N) of hyperbenthos (geometric mean: 52.5)
28 was greater than that (15.1) of zooplankton. No appreciable differences were evident in
29 C and N composition of the bodies between zooplankton-hyperbenthos; total carbon
30 (C) ranged from 18.0 to 47.2% of DM and total nitrogen (N) from 2.4 to 12.7% of DM,
31 with C:N ratios of 3.1–7.5. Judging from C and N composition, protein was the major
32 component of body organic matter of both zooplankton and hyperbenthos. In terms of
33 N-specific R and N, the present zooplankton data are comparable to those published on
34 tropical zooplankton and small fishes with similar body N. Compared with
35 zooplankton, lower specific E s and higher O:N ratios of hyperbenthos were interpreted
36 to reflect their partial or entire dependence on diets characterized by lower N
37 composition (detritus).

38

Introduction

39

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

49 Information about oxygen consumption, ammonia excretion rates and resultant
50 O:N (as $\text{NH}_4\text{-N}$) ratios of zooplankton has proved to be useful to provide a wide
51 perspective for understanding their energy demand, metabolic balance and nutritional
52 condition (cf. Ikeda et al. 2000). Data sets on these metabolic parameters for tropical
53 marine zooplankton are presently available for copepods (Ikeda 1974, Gaudy &
54 Boucher 1983), ctenophores (Kremer et al. 1986), salps (Cetta et al. 1986) and
55 "gelatinous" zooplankton including siphonophores, hydromedusae, scyphomedusae,
56 heteropods and pteropods (Biggs 1977). However, no comparable data sets are
57 currently available for the hyperbenthos, with the notable exception of those in the
58 deep benthic boundary layer (1,300–2,600 m deep) of the East Pacific (Smith 1982,
59 1985).

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

63 zooplankton, small teleost fishes and benthic animals from tropical regions to explore
64 unique features, if any, of the metabolism and body composition of the zooplankton
65 and hyperbenthos in this study.

66

67

Materials and methods

68 Sampling

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

85

86 Metabolic measurements

87 Within 2–4 hours of collection, oxygen consumption and ammonia excretion
88 rates were measured simultaneously by a sealed-chamber method (Ikeda et al. 2000).
89 The specimens were rinsed briefly 3–4 times with filtered seawater and an individual
90 or a batch of individuals was placed into glass bottles (60, 100, 300 or 550 mL capacity
91 depending on the size of specimens) filled with filtered seawater. Control bottles
92 without specimens were prepared concurrently. In a typical experiment with six
93 experimental bottles, two control bottles were prepared before the first experimental
94 bottle and two after the last experimental bottle. All bottles were incubated for 2–12 h
95 in the dark at near *in situ* temperatures (23 to 30°C). At the end of the incubations,
96 duplicate 15 mL (or 70 mL for larger capacity bottles) and 5 mL (or 10 mL) water
97 samples were siphoned out for the measurements of dissolved oxygen and ammonia,
98 respectively. Dissolved oxygen and ammonia were determined by the Winkler titration
99 method and the phenol-hypochlorite method, respectively (Strickland & Parsons 1972).
100 Based on replicate measurements on homogenous samples, the precision expressed as
101 coefficient of variation (CV) was 0.2% for dissolved oxygen determinations and 6%
102 for ammonia determinations in this study. Specimens left in experimental bottles were
103 rinsed briefly with a small amount of distilled water, blotted on a filter paper to remove
104 water adhering to the body, weighed (wet mass, WM) and frozen for experiments
105 conducted at AIMS. At sea, the specimens were rinsed briefly with a small amount of
106 distilled water, blotted on the filter paper then stored at –20°C, and the frozen
107 specimens were weighed (WM) in the laboratory after the cruise. For some small
108 crustaceans, weighing of frozen specimens could not be done.

109

110 **Chemical composition**

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

125

126 **Multiple regression analysis**

127 Designating the body mass, temperature and life modes (zooplankton or
128 hyperbenthos) as independent variables, the attributes of these variables to oxygen
129 consumption and ammonia excretion rates were analyzed by using stepwise multiple
130 regression (Sokal & Rohlf 1995). Linear regression models adopted were; $\ln Y = a_0 +$
131 $a_1 \ln X_1 + a_2 X_2 + a_3 X_3$, where Y is oxygen consumption rate or ammonia excretion rate,
132 X_1 is body mass (DM, C or N), X_2 is temperature, and X_3 is a dummy variable on the
133 life mode (zooplankton or hyperbenthos). The dummy variable is defined as 0 for
134 zooplankton and 1 for hyperbenthos. Independent variables are added if $p \leq 0.05$ and

135 removed if $p \geq 0.10$. The calculation was conducted using SYSTAT J 10.2.

136

137 **Metabolic data for tropical zooplankton**

138 To facilitate analysis of metabolic features of zooplankton and hyperbenthos,
139 published data on tropical zooplankton were combined with the present data. The data
140 for a chaetognath *Sagitta hispida* (Reeve et al. 1970), six copepods (Gaudy & Boucher
141 1983), four ctenophores (Kremer et al. 1986), four salps (Cetta et al. 1986), and three
142 size-groups of “gelatinous” zooplankton (Biggs 1977) were selected since rates of
143 oxygen consumption (R) and ammonia excretion (E) were determined simultaneously
144 in these studies and yielded O:N ratios comparable to those of the present study.
145 Predicted relationships between body mass (DM and N) and oxygen consumption rate
146 (R), ammonia excretion rate (E) and O:N ratios of “general zooplankton” at the mean
147 experimental temperature of this study (27°C) from the “global zooplankton model”
148 (Ikeda 1985), which was established by analyzing a comprehensive collection of data
149 on diverse zooplankton taxa from the world oceans, were computed. The data on 29
150 small teleost fishes, which comprise a mixture of different life modes (planktonic,
151 hyperbenthic and micronektonic) (Ikeda et al. 2011a) were also selected on the basis
152 that ammonia is the major end product of protein metabolism (Wright & Fyhn 2001) as
153 is the case for zooplankton (Table 5). Experimental procedures in measuring R and E in
154 these previous studies are similar (sealed chamber method) though the collection
155 method of the test animals differed; nets (Reeve et al. 1970, Ikeda 1985, this study),
156 light traps (Ikeda et al. 2011a, this study) and SCUBA (Biggs 1977, Cetta et al. 1986,
157 Kremer et al. 1986).

158 DM body masses of the chaetognaths and copepods were converted to N masses

159 by multiplying by 0.062 (Beers 1964) and 0.11 (Ikeda 1974), respectively. Since *R* and
160 *E* data of salps were given as a function of body length or body C only, *R* and *E* at a
161 mid-body C range (1 mg) were computed and body C was converted to DM or N first
162 by using conversion factors of C:DM = 0.08 (Madin et al. 1981) and C:N = 4.4 (Cetta
163 et al. 1986). Protein biomass of “gelatinous” zooplankton was converted to DM by
164 using a conversion factor of DM = 2 × Protein, and N = 0.08 × DM (Postel et al. 2000).
165 Thus, body mass data of each species or size group were standardized to DM and N
166 (Table 5).

167

168 **Results**

169 **Oxygen consumption and ammonia excretion**

170 Zooplankton including two decapods, one amphipod, three euphausiids, one
171 stomatopod larva, five copepods, three chaetognaths and one cephalopod, and
172 hyperbenthos including two decapods, two amphipods, one mysid and one ostracod
173 were studied (Table 1). Among 16 species classified as zooplankton, *Acetes sibogae*
174 *australis* Colefax has been observed to be distributed only in the surface layer of
175 shallow coastal waters and can be regarded as either zooplankton or hyperbenthos. The
176 copepod *Macrosetella gracilis* (Dana) is reported to be associated with the colonial
177 cyanobacterium *Trichodesmium* preferentially to other phytoplankton (O’Neil 1998).
178 Hyperiid amphipod *Oxycephalus* spp., including *O. clausi* Bovallius, are known to be
179 loosely associated with ctenophores (Laval 1980). The squid *Ideosepius pygmaeus*
180 Steenstrup is characterized by having an adhesive organ located on the posterior part of
181 the dorsal mantle side for attachment during the day to the lower leaf surfaces of sea
182 grasses or algae for camouflage (Boletzky et al. 2005). Despite these divergent life

183 modes from those of typical zooplankton, all of them have been regarded as
184 “zooplankton” in the past and we followed this practice in the present analyses. The
185 results for the decapod *Leptochela* sp. were separated into two size groups.

186 Across a total of 22 species, body masses ranged from 0.0012 mgDW for
187 *Oithona nishidai* McKinnon to 26.7 mgDM for *I. pygmaeus*. Oxygen concentration in
188 experimental bottles at the end of the experiments was >80% of that of control bottles.
189 Oxygen consumption (R) and ammonia-N excretion (E) rates varied from 0.0048 to
190 118.3 $\mu\text{L O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$ and from 0.00051 to 15.9 $\mu\text{g NH}_4\text{-N ind.}^{-1} \text{ h}^{-1}$, respectively
191 (Table 2).

192 Stepwise multiple regression analyses revealed that among the three independent
193 variables (body mass, temperature and life modes), significant variables were body
194 mass only for R , but body mass and life mode for E (Fig. 1, Table 3). In the analyses of
195 E , *Leurolebris* sp. was identified as an outlier and was therefore removed. The choice
196 of body mass unit (DM, C or N) had little effect on the results of this analysis. The
197 variables identified as significant attributed 95–98% of the variance of R and 94–95%
198 of the variance of E (Table 3).

199

200 **O:N ratio**

201 The atomic ratio of oxygen consumption rate to ammonia-nitrogen excretion rate
202 (O:N ratio) has been used as an index of the proportion of protein in total metabolites
203 in marine zooplankton (Mayzaud & Conover 1988, Ikeda et al. 2000). When only
204 protein is metabolized, the O:N ratio is 7 (Table 10.3 in Ikeda et al. 2000). When
205 protein and lipid or carbohydrate is catabolized in equal quantities at the same time,
206 O:N ratios are calculated as 21 or 13. Hence, O:N ratios of 7–17 (mid-point of 21 and

207 13) may be used as an index of protein-oriented metabolism and the ratios of >17 as
208 lipid/carbohydrate-oriented metabolism.

209 O:N ratios ranged from 7.7 to 46.1 (geometric mean 15.1) for zooplankton and
210 from 17.1 to 341 (52.5) for hyperbenthos (Fig. 2), suggesting protein-oriented
211 metabolism on average for the former and lipid/carbohydrate-oriented metabolism for
212 the latter. Regression analyses of O:N ratios on body mass (DM) showed that the ratios
213 were independent from body mass ($R^2 = 0.029$, $p = 0.525$ for zooplankton, and $R^2 =$
214 0.162 , $p = 0.729$ for hyperbenthos). The differences in the mean O:N ratios between
215 zooplankton and hyperbenthos were highly significant (Mann-Whitney U -test, $p =$
216 0.002), which remained unchanged even if the isolated datum (341) of *Leuroleberis* sp.
217 was excluded (U -test, $p = 0.004$).

218

219 **Water, ash and elemental composition**

220 Across 17 zooplankton species, the range of variation was 62.6–91.1% (mean:
221 78.5%) for water contents, 7.3–43.0 % (16.8) for ash, 25.5–47.2% (38.7) for C and
222 6.2–12.3% (10.3) for N, with C:N ratios of 3.1–4.7 (3.8) (Table 4). For 6 hyperbenthic
223 species, the range of variation was 51.1–76.0% (64.2) for water content, 14.2–58.8%
224 (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
225 3.3–7.5 (4.2). Significant differences between zooplankton and hyperbenthos were
226 seen only in ash (U -test, $p < 0.05$), and this conclusion was unaffected by the
227 presence/absence of the anomalous datum for *Leuroleberis* sp. from hyperbenthos data
228 sets.

229

230 **Comparison with other zooplankton data**

231 Published data (Table 5) on tropical zooplankton and small fishes were
232 converted first to DM-specific R and E and plotted against DM on a log-log graph (Fig
233 3A, C), and compared with the 95% CI belt of pooled zooplankton and hyperbenthos
234 data (DM-specific R) or with zooplankton data only (DM-specific E) from this study
235 (Fig. 3). While most of the data fall within or close to the 95% CI belt, both
236 DM-specific R and E data for ctenophores and only the E data for hyperbenthos and a
237 part of the small fish data scatter below the lower 95% CI limit. In terms of N-specific
238 R and E , the low values for ctenophore data plotted well within the 95% CI, but this
239 was not the case for the hyperbenthos and some small fishes (Fig. 3B, D). Preliminary
240 calculation of C-specific R and E yielded estimates close to N-specific R or E and
241 somewhere between DM-specific and N-specific R and E ; therefore the results were
242 not shown.

243 The published O:N data for tropical zooplankton and small fishes (Table 5) fall
244 within the 95% CI (5.7–43.3) belt of those of zooplankton from this study (Fig. 4),
245 with the exception of part of the hyperbenthos data in this study and 13 out of 35 data
246 points for small fishes (Ikeda et al. 2011a) which scattered above the upper 95% CI.

247

248 Discussion

249 Metabolic comparison

250 While no significant differences were detected in R -body mass relationships
251 between zooplankton and hyperbenthos, the latter showed significantly lower E than
252 zooplankton with equivalent body masses (Fig. 1). Choice of body mass units (DM, C
253 or N) did not affect this conclusion (Table 3). This result implies that different life
254 modes (planktonic or hyperbenthic) affect ammonia excretion but not oxygen

255 consumption by these animals. Coull & Vernberg (1970) observed similar or higher
256 DM-specific R s of a hyperbenthic harpacticoid *Longipedia helgolandica* (Klie), as
257 compared with a planktonic harpacticoid *Euterpina acutifrons* (Dana) at comparable
258 temperatures. Ivleva (1980) compiled published R -body mass data of planktonic,
259 hyperbenthic and benthic crustaceans from tropical waters and noted no appreciable
260 differences among them. Thus, the present results of R -body mass relationships of
261 zooplankton and hyperbenthos are consistent with those reported by Coull & Vernberg
262 (1970) and Ivleva (1980). There is no information yet about comparisons of E of
263 zooplankton and hyperbenthos. Smith (1982) determined R and E simultaneously and
264 calculated O:N ratios (4–30) for mixed benthopelagic plankton (= hyperbenthos)
265 predominated by the scyphomedusa *Poralia rufescens* Vanhöffen living at a depth of
266 1,300 m off Southern California. However, direct comparison of his results with those
267 of hyperbenthos of the present study is difficult because possible predation among
268 hyperbenthos cannot be ruled out during his experiments with mixed species.

269 In Fig. 3, DM-specific R and E data for ctenophores, which scattered below the
270 lower 95% CI range, fell well within the 95% CI range in terms of N-specific R and E .
271 In contrast, DM-specific R of salps, which fell within the 95% CI range, shifted above
272 the upper 95% CI range in terms of N-specific R . The same pattern, though much
273 modulated, was seen in the specific R of gelatinous zooplankton and specific E of the
274 same salps. As compared with other zooplankton, higher N (or protein)-specific R and
275 E of salps and gelatinous zooplankton have been explained by gentle capture of test
276 animals and immediate incubation *in situ* by SCUBA divers (Biggs 1977, Cetta et al.
277 1986). The rapid decline in R and E after capture is a phenomenon that has been
278 observed in early studies on zooplankton metabolism, and interpreted as a result of

279 complex interactions between capture stress (which is highest at capture) and
280 starvation effects (which increase with time after capture)(Ikeda et al. 2000). The result
281 of interactions between these factors could vary across diverse zooplankton taxa
282 characterized by dissimilar body size, behavior, swimming activity and nutrition, and
283 no single method to overcome the problem is presently available.

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

290

291 **O:N ratio**

292 Higher O:N ratios (lipid-oriented metabolism) have been documented for large
293 grazing copepods living in high latitude seas; the copepods deposit a large amount of
294 energy reserves (lipids) in the body as part of their life history traits for coping with a
295 long food-scarce winter (Conover & Corner 1968, Ikeda 1974, Mayzaud & Conover
296 1988, Ikeda et al. 2000). However, this explanation is not applicable for higher O:N
297 ratios of hyperbenthos, since there is no indication of large amounts of lipids in the
298 body as judged by their C and N composition data (see “chemical composition” section
299 below). For some small fishes that exhibited high O:N ratios, Ikeda et al. (2011a)
300 interpreted that this was a reflection of their partial or entire dependence on diets such
301 as benthic algae, seaweeds or detritus, all characterized by extremely low N
302 composition (1–2% of DM, Tenore 1983, 1988, Duarte 1990) in contrast to N-rich

303 phytoplankton and zooplankton (3–12% or more of DM, Parsons et al. 1961, Mayzaud
304 & Martin 1975, Ikeda 1974, Verity et al. 1992).

305 While no information about the diet of the hyperbenthos used in this study is
306 presently available, it is conceivable that their diets are likely to include N-poor
307 detritus because of their close association to the bottom. There is ample evidence to
308 support this interpretation – high metabolic O:N ratios associated with low N
309 composition of diets – in some benthic animals. Mukai & Koike (1984) compared O:N
310 ratios of two mud shrimps and noted that one (*Callinassa japonica* Stimpson) feeding
311 on mud showed a significantly higher ratio (48) as compared with that (20) of the other
312 (*Upogebia major* (de Haan)) feeding on phytoplankton. As typical deposit feeders,
313 tropical sea cucumbers *Holothuria atra* Jaeger and *H. scabra* Jaeger exhibit O:N ratios
314 of 32 and 44, respectively (Mukai et al. 1989), both of which are much higher than the
315 mean of 15.8 observed for zooplankton in the present study.

316 Relevant here, higher O:N ratios (51–180) have also been observed for
317 carnivorous phyllosoma larvae, a common member of tropical zooplankton (Ikeda et al.
318 2011b). The same line of explanation by low N diets cannot be applied for the
319 phyllosomas, since higher O:N ratios of phyllosomas were also the case for larvae
320 raised in the laboratory provided N-rich foods (*Artemia* larvae, fresh blue mussel). As
321 an alternative, Ikeda et al. (2011b) considered that the higher O:N ratios of
322 phyllosomas were due to a species-specific feature such as the preferential utilization
323 of diet N to synthesize body protein rather than for fuel metabolism. Phyllosomas are
324 different from “general zooplankton” and hyperbenthos of the present study in that
325 they have much reduced *R* as well as lower body N contents.

326

327 **Chemical composition**

328 While ash was the only component that showed a significant difference between
329 zooplankton and hyperbenthos (Table 4), this requires more data on a wide array of
330 species in the light of high inter-species variations within each group. The present
331 results of C and N composition for 7 out of 9 animal groups (decapods, amphipods,
332 mysids, euphausiids, stomatopod alima larvae, copepods and chaetognaths) are in good
333 agreement with those of the respective groups reported from tropical or subtropical
334 seas by previous workers (Ikeda 1974, Gorsky et al. 1988). No C and N composition
335 data is available for ostracods or cephalopods from tropical waters. However, the C
336 and N values of three mesopelagic ostracods from the western subarctic Pacific
337 (39.8–50.8% and 7.8–9.4%, respectively; Kaeriyama & Ikeda 2004) were much higher
338 than the present results for *Leuroleberis* sp. The inorganic fraction (CaCO_3 -C) of total
339 C in zooplankton is thought to be minor (Curl 1962), but may be substantial in
340 calcareous ostracods such as *Leuroleberis* sp. as judged by their high ash content
341 (58.8%). Assuming that ash is solely composed of CaCO_3 (1 mole = 100 g), C and N
342 composition of ash-free DM (= organic matter) of the ostracod is estimated as 26.6%
343 (= $(18.0 - 12 \times 0.588)/0.412$) and 5.8% (= $(2.4 - 0.0 \times 0.588)/0.412$), respectively,
344 yielding a C:N ratio = 4.6. For squids, the present results for *Ideosepius pygmaeus* fall
345 within the ranges of 74–91% for water content, 10.3–20.1% for ash, 31.6–43.0% for C
346 and 9.6–14.0% for N, with C:N ratios of 2.8–4.1 for 11 oceanic squids from the
347 Northeast Atlantic (Clarke et al. 1985).

348 While zooplankton living in high latitude seas are often characterized by high C
349 composition (up to 70% of DM) and C:N ratios (up to 10) due to the accumulation of
350 C-rich lipids as mentioned above, those in low latitude seas do not deposit lipids in the

351 body and C composition (< 40% of DM) and C:N ratios (3–4) are much lower than
352 those of their high latitude counterparts (Ikeda 1974, Båmstedt 1986). Analyzing
353 biochemical composition data on 182 zooplankton species (mostly crustaceans),
354 Ventura (2006) calculated average C and N composition of protein to be 52.8% and
355 16.0%, and lipids (represented by triacylglycerol) to be 77.3% and 0%. With these
356 results, the C:N ratio is calculated as 3.3 for protein alone and 8.1 for organic matter
357 composed of equal amounts of protein and lipid. Carbohydrate in tropical zooplankton
358 has been reported to be <1% of DM (Beers 1966) and is therefore omitted in this
359 calculation. From this criterion, organic matter of all zooplankton (mean C:N = 3.8,
360 Table 4) and hyperbenthos (3.7, excluding *Leuroleberis* sp.) from the present study is
361 characterized by the predominance of protein.

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

373

374

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519 **Figure captions**

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

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

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

543 zooplankton and hyperbenthos (ZP+HB 95% CI) for A) and B), and from
544 zooplankton data only (ZP 95% CI) for C) and D).

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

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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
	Atyidae 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 tricuspida</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
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).

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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 mutica</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 0.006	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 nishidae</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>Sagitta bedoti</i> f. <i>minor</i>	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>Sagitta 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>Sagitta</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>Atyidae</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	7	10.3 \pm 16.5	45.2 \pm 75.8	1.9 \pm 2.1	22.6 \pm 9.3
<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

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				R^2 (Adjusted R^2)
				$\ln Y = a_0 + a_1 \ln X_1 + a_2 X_2 + a_3 X_3$				
				a_0	a_1	a_2	a_3	
O ₂ consumption rate	DM	23	0		0.898	0.027	-0.365	0.954
		23	1		0.912		-0.366	0.976
		23	2	1.073	0.895			0.950 (0.947)
	C	23	0		0.898	0.026	-0.234	0.970
		23	1		0.911		-0.233	0.968
		23	2	1.978	0.901			0.984 (0.966)
	N	23	0		0.882	0.069	-0.180	0.978
		23	1		0.875	0.068		0.977
		23	2	3.21	0.909			0.987 (0.974)
NH ₄ -N excretion rate*	DM	22	0		0.955	-0.051	-1.108	0.950
		22	1	-1.305	0.929		-1.090	0.949 (0.944)
	C	22	0		0.951	-0.070	-1.053	0.952
		22	1	-0.427	0.916		-1.030	0.950 (0.945)
	N	22	0		0.939	-0.045	-1.069	0.952
		22	1	0.787	0.917		-1.054	0.952 (0.947)

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

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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 WW)	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	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
aima 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. minor	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
Atyidae 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>	70.1 \pm 2.7 (7)	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)
p for Ho: ZP = HP (U -test)	0.048	0.017	0.181 ^{NS}	0.284 ^{NS}	0.813 ^{NS}
p for Ho: ZP = HP (U -test)*	0.129 ^{NS}	0.034	0.376 ^{NS}	0.554 ^{NS}	0.941 ^{NS}

* *Leuroleberis* sp. data excluded.

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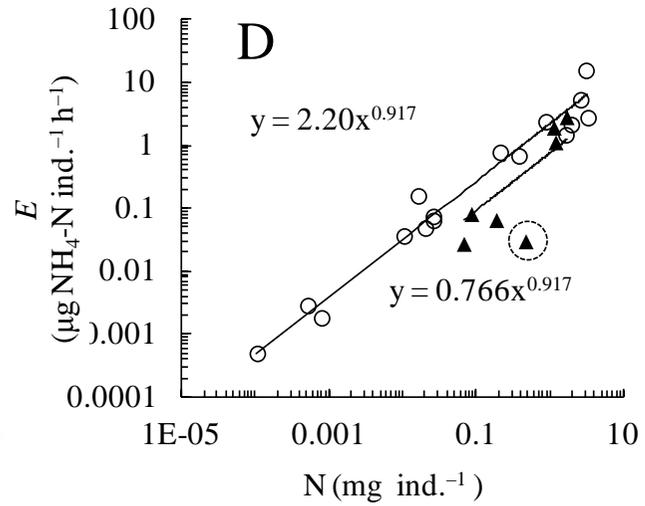
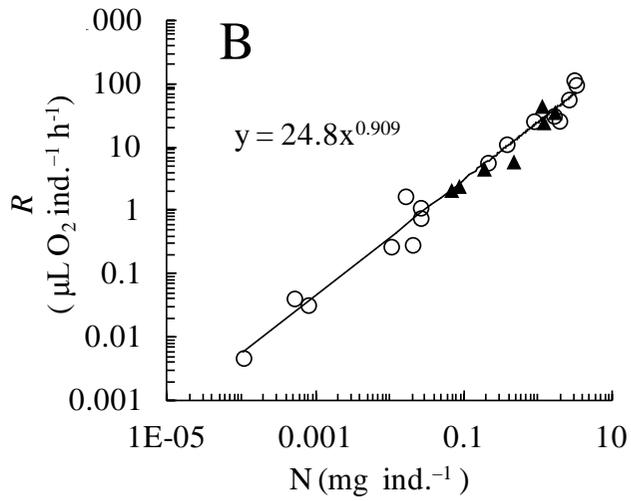
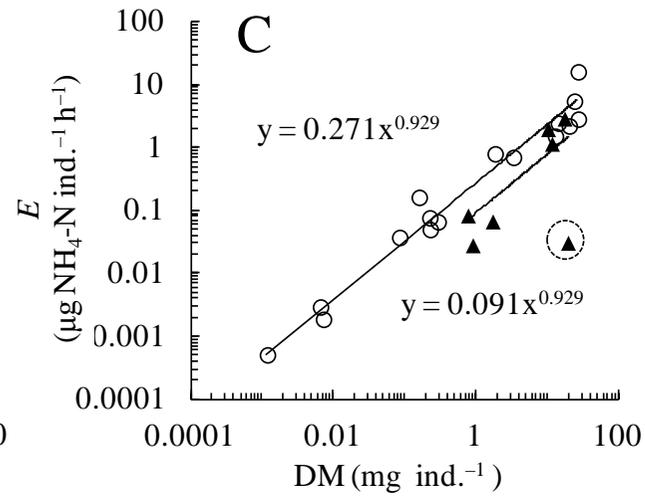
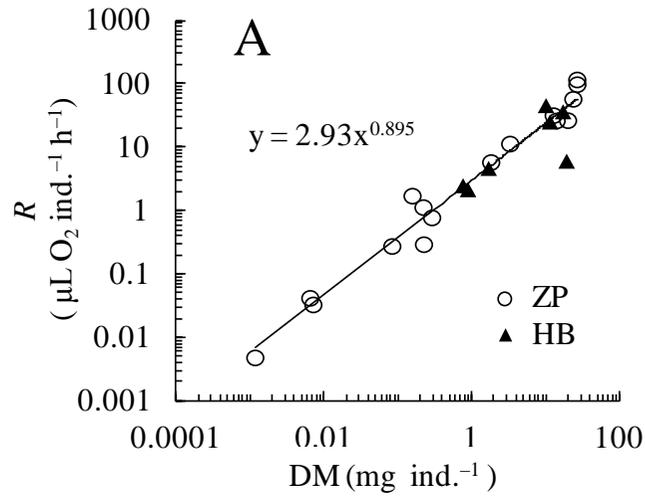
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Table 5. Summary of rates of oxygen consumption (R) and ammonia excretion (E) and O:N ratios of zooplankton and small fishes from tropical seas and those of "general zooplankton" predicted from the "global zooplankton model" at 27°C. It is noted that 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 ($\mu\text{LO}_2 \text{ ind.}^{-1}\text{h}^{-1}$)	E ($\mu\text{gN ind.}^{-1}\text{h}^{-1}$)	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	Gaudy & Boucher (1983)
	<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>Cosmocalanus (=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	Kremer et al. (1986)
	<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>Beroe ovata</i> Bruguère			76	0.749	20.6	2.40	10.7	
Salps	<i>Cyclosalpa affinis</i> (Chamisso), agg	21–28	BL, C	12.5	0.227	27.5	1.43	24.0	Cetta et al. (1986)
	<i>Pegea confoederata</i> (Forskål), agg			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	
Gelatinous zooplankton*	39 species	23–29	protein	1.0	0.08	13.5	0.78	21.6	Biggs (1977)
				10	0.8	70	5.25	16.7	
				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	Reeve et al. (1970)
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	Ikeda et al. (2011a)
"General zooplankton"		27	DM	0.001–500		$2.921 \times \text{DM}^{0.7886}$	$0.2208 \times \text{DM}^{0.7616}$	$16.53 \times \text{DM}^{0.027}$	Ikeda (1985)
		27	N	0.0001–50		$31.77 \times \text{N}^{0.8505}$	$2.238 \times \text{N}^{0.8361}$	$17.74 \times \text{N}^{0.0144}$	

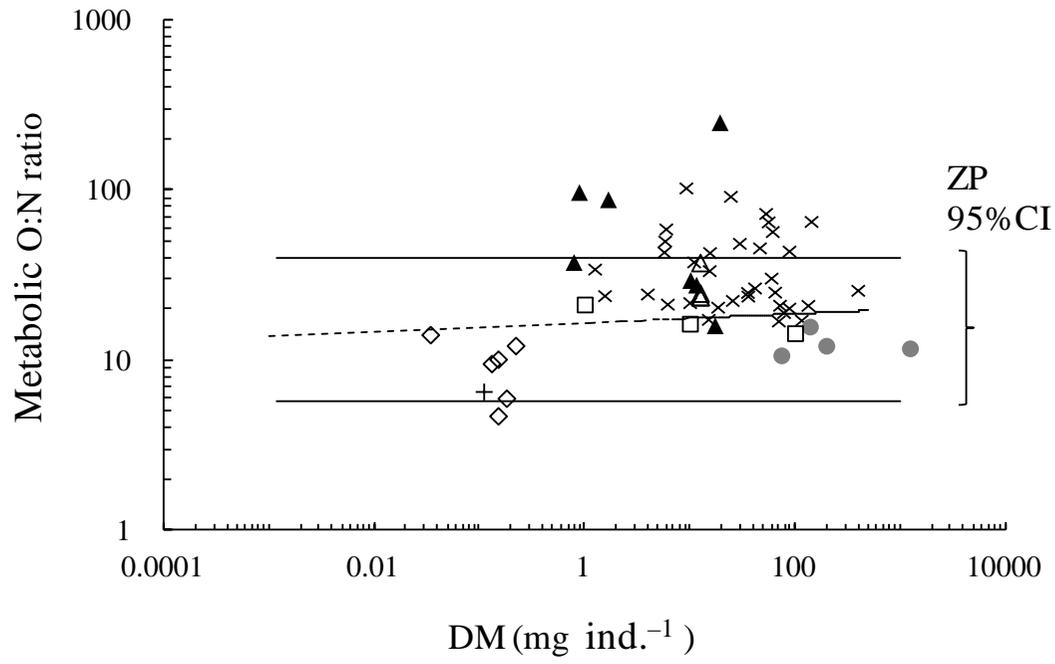
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*siphonophores, hydromedusae, scyphomedusae, ctenophores, heteropods, pteropods and thaliaceans



Ikeda & McKinnon Fig. 1

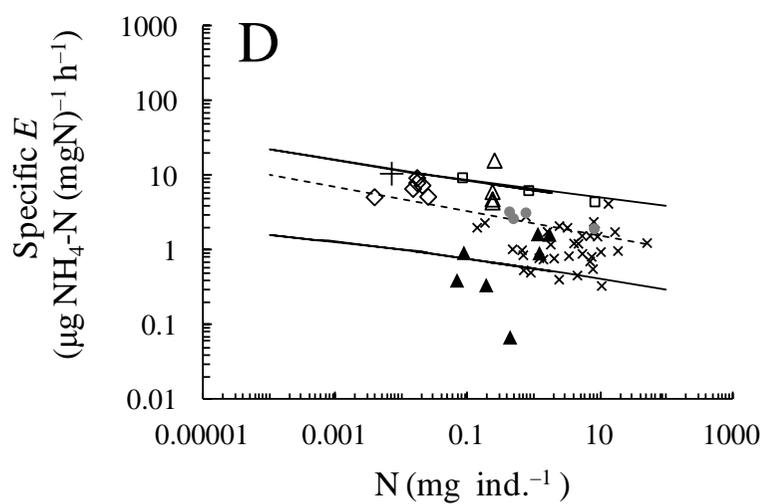
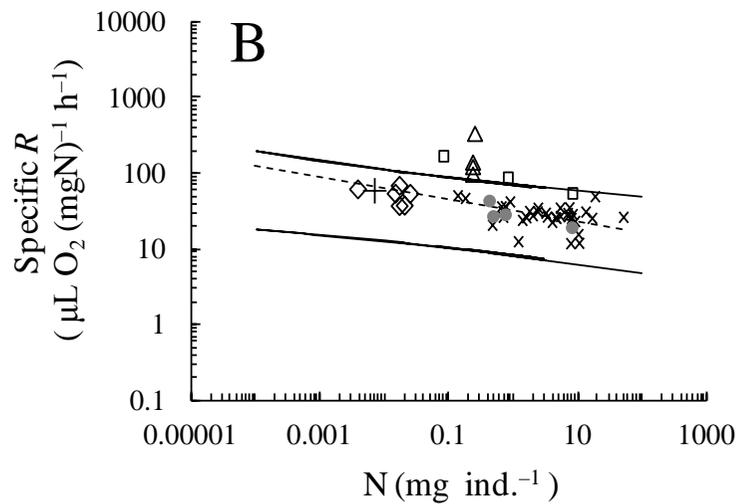
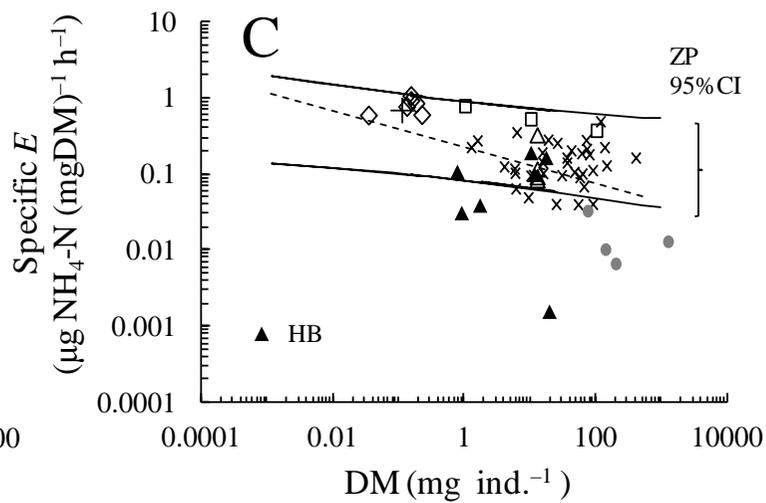
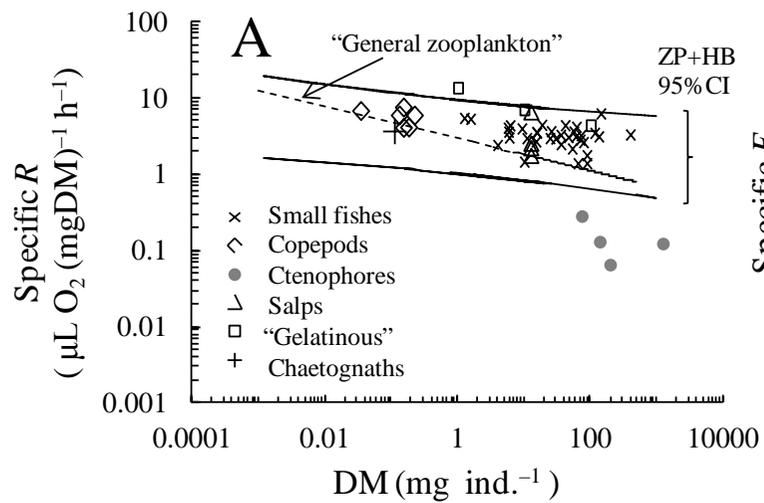
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Ikeda & McKinnon Fig. 4



Ikeda & McKinnon Fig. 3