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Metabolism and chemical composition of small teleost fishes from tropical inshore waters

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ABSTRACT

Rates of oxygen consumption (R: μl O_2 (individual)$^{-1}$ h^{-1}), and ammonia excretion (E: μg NH_4-N (individual)$^{-1}$ h^{-1}) of 29 species of small teleost fishes (1-400 mg dry mass (DM)) from inshore waters of the Great Barrier Reef were determined at *in situ* temperatures (25-30^{o}C). Regression analyses revealed that R (6.7-1296) and E (0.28-64.2) were correlated with body mass, but the ratio of R to E (O:N; 17-104 by atoms) was not. Water content of fish bodies ranged from 66.0 to 81.4% of wet mass (WM), and ash content from 11.9 to 28.6% of DM. Total carbon (C) and total nitrogen (N) composition varied from 36.2 to 44.4% and from 8.3 to 12.8% of DM, respectively, resulting in C:N ratios of 3.1-4.7. Fractions of inorganic C and N were small (0.04-0.33% and 0.01-0.15% of DM, respectively). Combining R and E data with those of body CN composition, daily metabolic losses were estimated to be 4.3-18.6% for body C and 0.8-9.1% for body N. With regard to predictive models for R for fishes, the present results fit that of Bochdansky and Leggett (2001) rather than those of either Winberg (1956) or Clarke and Johnston (1999). On a body mass basis expressed by N, values for R were consistent with those of Ikeda's (1985) model for epipelagic zooplankton, but values for E were 70% lower, suggesting somewhat reduced E relative to R in fishes as compared with zooplankton. Three out of the 29 fishes exhibited markedly high metabolic O:N ratios together with high body C:N ratios, which was interpreted as an adaptation to N-limited detritus nutrition.

INTRODUCTION

Fish are regarded as one of the integral components of marine ecosystems, but they are considered to play only a minor role in global biogeochemical cycles because of their smaller biomass and lower specific physiological rates relative to those of bacteria, micro- and mesozooplankton (Conover 1978, del Giorgio and Duarte 2002). Nevertheless, fish are significant in some regions; for example, in upwelling systems, anchoveta are not only the major consumer of phytoplankton but also a major nutrient regenerator for phytoplankton (Whitledge and Packard 1971, McCarthy and Whitledge 1972, Whitledge 1978, 1982). In some reef systems characterized by high productivity but low nutrient concentrations in ambient water, nutrients excreted by resident fish aggregations are quickly utilized by nearby corals or benthic macrophytes (Meyer et al. 1983, Meyer and Schultz 1985, Bray et al. 1986).

Information about metabolism (oxygen consumption and ammonia excretion rates, O:N ratios) and body chemical composition (water content, ash and carbon and nitrogen composition) has proved to be useful to provide a wide perspective for understanding the energy demand, metabolic balance and nutritional condition of marine zooplankton (cf. Ikeda et al. 2000). For fish, oxygen consumption data have been accumulated on diverse species from the world's oceans (Winberg 1956, Post and Lee 1996, Clarke and Johnston 1999, Bochdansky and Leggett 2001 and literatures therein). While nitrogen metabolism in fish has been studied intensively on the early life stages during the last two decades (Wright and Fyhn 2001, Wood 2001, Finn et al. 2002, Terjesen 2008), nitrogen excretion data are limited (Cockcroft and Preez 1989, Wright and Fyhn 2001, Wood 2001). The atomic ratio of oxygen consumption rate to ammonia excretion rate (O:N ratio) has been used extensively as an index of protein

64 utilization as a metabolic substrate in zooplankton (Mayzaud and Conover 1988, Ikeda
65 et al. 2000). A similar index, the molar ratio of ammonia excreted to oxygen
66 consumed (ammonia quotient; Kutty 1978) or nitrogen excreted to oxygen consumed
67 (nitrogen quotient; Wright and Fyhn 2001) has been used for fishes, but the available
68 measurements of these indices are largely based on laboratory-raised/maintained fishes
69 and information about wild fishes is largely limited to the Peruvian anchovy (Whitledge
70 and Packard 1971).
71 Vinogradov (1953) compiled data, including water, ash content and carbon and
72 nitrogen, on the composition of various parts of fishes. Love (1970) summarized
73 detailed data of water, ash and proximate composition of fishes in relation to their
74 nutritional state. Because of the large body size of fishes in general, carbon and
75 nitrogen composition data on the whole body of fishes are few and often limited to their
76 early life stages; grunion *Leuresthes tenuis* from La Jolla, California (May 1971), sea
77 bream *Chrysophrys major* from the coasts of Kyushu, southern Japan (Anraku and
78 Azeta 1973), herring *Clupea harengus* from Firth of Clyde (Ehlrich 1974a), plaice
79 *Pleuronectes platessa* from Scotland (Ehrlich 1974b), and walleye pollock *Theragra*
80 *chalcogramma* in the Bering Sea (Harris et al. 1986), with the notable exception of all
81 life stages of silvery lightfish *Maurolicus muelleri* in the Japan Sea (Ikeda 1996). For
82 fishes living low latitude seas, Beers (1965) analyzed water content, carbohydrate and
83 CNP composition on mixed fish/fish larvae collected with a plankton net off Bermuda.
84 The present study aims to fill the gaps in our knowledge about metabolic and
85 body compositional characteristics of larval and early juvenile teleost fishes in tropical
86 regions. In this study, the term “larvae” is used broadly; not only to the end of the
87 attainment of full external morphological characters, but also to the loss of temporary

specialization to pelagic life (cf. Leis and Rennis 1983). The results are compared with those of marine zooplankton and larger fishes to elucidate unique features of tropical fishes, if any.

MATERIALS AND METHODS

Fish sampling

In order to minimize physical damage of fish specimens, most sampling was made with a light-trap (37 cm × 37 cm × 82 cm), deployed along the jetty of the Australian Institute of Marine Science (AIMS) located at Cape Ferguson, North Queensland, during the period September 2009 and April 2010. For a basic design and the advantages of light-traps for the collection fishes, see Meekan et al. (2001). The light-trap was submerged just under the surface water in the evening and recovered in the next morning. Fish thus collected were sorted and placed into plastic buckets filled with fresh seawater and transported to a constant temperature room. Additional sampling was done on board RV Cape Ferguson around coastal reefs off Townsville (19^{o}S) and Mackay (20^{o}S) by means of a scoop net when fishes were aggregating under an artificial light at night. Some (1-5) specimens were preserved in 5% formalin-seawater solution for later identification. Seawater for experiments was collected from the sampling sites of each fish, e.g. near the AIMS jetty (land-based experiments) or from 2 m depth with 10 liter Niskin bottles (shipboard experiments), filtered through GF/F filters, and well oxygenated prior to use.

Metabolic measurements

Within 2 hours of collection, oxygen consumption and ammonia excretion rates were measured simultaneously by a sealed-chamber method (Ikeda et al. 2000). The

fish were rinsed briefly 3-4 times with filtered seawater and transferred individually to glass bottles (100, 300, 500 or 1000 ml capacity depending on the size of specimens) filled with filtered seawater. Control bottles without fish 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 1-5 h in the dark at near *in situ* temperature (25 to 30˚C) to obtain significant differences in the concentrations of dissolved oxygen and ammonia between control and experimental bottles. At the end of the incubations, the condition of each fish was checked briefly, then duplicate 15 ml (or 70 ml for larger capacity bottles) and 10 ml water samples were siphoned out for the measurements of dissolved oxygen and ammonia, respectively. Fishes with regular operculum movements, whether resting on the bottom of bottles, suspended or gently swimming in the water column, were regarded as “normal” in this study. Dissolved oxygen and ammonia were determined by the Winkler titration method and the phenol-hypochlorite method, respectively (Strickland and 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 determination in this study. Metabolic rates of fishes thus determined without control of their activities are considered to represent “routine” metabolism (cf. Fry 1971). Fish 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.

Chemical composition

In the laboratory, frozen fish were freeze-dried, then oven dried at 60^{o}C overnight to remove residual water for the estimation of dry mass (DM) and water content. The dried specimens were pooled by species then finely ground with a ceramic mortar and pestle. For some species, specimens were separated by size or experimental temperatures (e.g. the same species used in experiments conducted on different dates where *in situ* temperatures were dissimilar). Powdered samples were used for analysis of total CN composition with an elemental analyzer (TruSpec CN Determinator, LECO Corp. USA) using ethylenediaminetetraacetic acid (EDTA) as a standard. Inorganic C:N composition was analyzed with powdered samples incinerated in a muffle furnace at 450^{o}C overnight (>12 h). For ash determination, weighed fractions of powdered samples were incinerated at 450˚C overnight and reweighed. All measurements were made 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 wet mass (WM), whereas the contents of ash, carbon and nitrogen were expressed as percent of dry mass (DM).

Daily metabolic losses in body C and N

Combining oxygen consumption (R) and ammonia excretion (E) data with body C and N compositions, daily metabolic losses in body C (DMC: % of body C) and N (DMN: % of body N) can be estimated. R data were converted to CO_2-C assuming that the dominant metabolic substrate of fishes in feeding is protein (cf. Wood 2001, Finn et al. 2002) and ammonia is only end-product of protein; $DMC = R \times 0.97 \times 24 \times (12/22.4) \times 10^{-3} \times 100$ (mg body C)$^{-1}$, where 0.97 is the respiratory quotient (RQ) for

160 protein metabolism characterized by ammonia as the sole end-product (Gnaiger 1983),
161 24 is the number of hours d^{-1}, 12/22.4 is the C mass in 1 mol of CO_2 (22.4 l) and 10^{-3} is
162 to convert μg to mg. Similarly, $DMN = E \times 24 \times 10^{-3} \times 100$ (mg body N)$^{-1}$, where 24
163 and 10^{-3} are the same as defined for DMC.

164 **Statistical treatment of the data**

165 Means ± one standard deviation (1SD) were given throughout the text and tables.
166 For analyzing the effects of body mass (X_1) and temperature (X_2) on metabolic rate (Y),
167 the regression model used for marine epipelagic zooplankton (Ikeda 1985) was adopted;
168 $\ln Y = a_0 + a_1 \ln X_1 + a_2 X_2$, where a_0 (intercept), a_1 and a_2 are coefficients. Student
169 t-test was used to judge significance of the coefficient at $p = 0.05$ unless otherwise noted.
170 For the comparison of R or E of fishes observed with those predicted from the models
171 of previous workers, the Wilcoxon signed ranks test was used. All these calculations
172 were conducted using SYSTAT version 10.2.
173

174 **RESULTS**

175 **Oxygen consumption and ammonia excretion**

176 Of 29 fish species belonging to 22 families studied, 18 species were common
177 coral reef fishes of the Great Barrier Reef province (Table 1). The results of
178 *Caracanthus* sp. and *Neomyxus* sp. were separated into two size groups, and those of
179 *Ambassis* sp., *Hypoatherina* sp., *Lethrinus* sp and *Monocanthus* sp. were divided into
180 two temperature groups, yielding a total of 35 datasets. The range of fish body masses
181 was 6.3-1786 mg for WM and 1.24-395 mg for DM. Experimental temperatures were
182 adjusted to the range of temperatures observed in the field (25 to 30^{o}C). Oxygen
183 saturation of experimental bottles at the end of experiments varied considerably

(49-97%, with a mean of 80%), but was well above the 15-33% of critical oxygen saturation of coral reef fishes (Nilsson and Östlund-Nilsson 2006). R and E varied from 6.73 to 1296 μl O_2 (individual)$^{-1}$ h^{-1} and from 0.28 to 64.2 μg NH_4-N (individual)$^{-1}$ h^{-1}, respectively (Table 2). Preliminary analysis using the multiple regression model ($\ln Y = a_0 + a_1 \ln X_1 + a_2 X_2$, see "Statistical treatment of the data" section) assigning X_1 and X_2 to be DM and temperature, respectively, showed that the coefficient a_1 was highly significant (t-test, df = 32, $p < 0.01$) for both oxygen consumption and ammonia excretion rates) but a_2 was not significant (t-test, df = 32, $p > 0.60$ for R, and $p > 0.90$ for E). From these results, X_2 was ignored and R and E of the fishes were expressed as a function of X_1 ($R^2 = 0.9270$, df = 33, $p < 0.01$ and $R^2 = 0.8156$, df = 33, $p < 0.01$, respectively, Fig. 1).

O:N ratio

Based on apparent nitrogen quotient (NQ) in which nitrogen is represented by ammonia only, Finn and Ronnestad (2003) proposed a set of equations to calculate mass fraction of protein catabolized simultaneously with carbohydrate (Kp) or lipid (K*p*) in fish; $K_p = 3.221(NQ) + 2.571(NQ)^2 + 4.064(NQ)^3$, and $K_p = 8.069(NQ) - 25.267(NQ)^2 + 36.732(NQ)^3$. When only protein is metabolized in fish, the NQ is 0.24 which is equivalent to O:N = 8.2 (= 2/0.24) since NQ = 2 /O:N. In this way, O:N ratios for a fish catabolizing protein and carbohydrate or lipid of equal amounts at the same time are calculated as 14.6 or 25.0 (mid-point: 20). Then, O:N ratios of 8-20 may be used as an index of protein-oriented metabolism and the ratios of >20 as lipid/carbohydrate oriented metabolism.

O:N ratios of the fishes in this study ranged from 17.3 to 104 with a mean of 38.3 (± 22.0, SD) (Table 2), suggesting lipid/carbohydrate oriented metabolism. O:N

208 ratios were found to be independent of body mass (R^2 = 0.0124, df = 33, p > 0.05, Fig.
209 1).

210 **Water, ash and elemental composition**

211 Across the 35 datasets, water content varied from 66.0 to 81.4% with a mean
212 of 76.5% (± 3.6) of WM, and ash content from 11.9 to 28.6% with a mean of 17.8% (±
213 3.3) of DM (Table 3). The ranges of total C and N composition were 36.2-44.4% with
214 a mean of 41.2% (± 1.8) of DM and 8.3-12.8% with a mean of 11.4% (± 1.0) of DM,
215 respectively, yielding C:N ratios of 3.1-4.7 with a mean of 3.6 (± 0.4)(by mass).
216 Fractions of inorganic C and N in the total were small, ranging from 0.04 to 0.33% with
217 a mean of 0.14% (± 0.07) and from 0.01 to 0.15% with a mean of 0.05% (± 0.03) of
218 DM, respectively (Table 3).

219 From the information about elemental CN composition of typical protein (C;
220 52.9%, N; 17.3%), carbohydrate (C; 44.4%, N; 0%) and lipid (C; 77.6%, N; 0%) in
221 Gnaiger and Bitterlich (1984), the proportion of protein in organic matter (=ash free
222 DM) can be estimated. For organic matter composed of protein alone a C:N ratio = 3.1
223 (= 52.9/17.3) is computed, and for organic matter of which one half is composed by
224 protein and the other half by lipid, a C:N ratio = 7.5 (= ((52.9 + 77.6)/2)/17.3) can be
225 used. Carbohydrate in fishes has been reported as <1% of DM (Beers 1956) or < 2%
226 of ash-free DM (Childress and Nygaard 1973) and is therefore omitted in this
227 calculation.

228 **Daily metabolic losses in body C and N**

229 Body C and N were represented by total C and N, since the fractions of inorganic
230 C and N in the total were very small (Table 3). Resultant DMC and DMR values were
231 4.3-18.6% with a mean of 10.0% (±3.3) and 0.8-9.1% with a mean of 3.3% (±1.9),

232 respectively (Table 2).

233

234 **DISCUSSION**

235 **Metabolic comparison**

236 While fishes show considerable variation in systematics, morphology, ecology
237 and body size, their oxygen consumption rates (R; μl O_2（individual)$^{-1}$ h^{-1}) are known to
238 be governed ultimately by body mass and metabolic models are based on various
239 concepts, assumptions and data sources. Among many models being published, those
240 of Winberg (1956), Clarke and Johnston (1999), and Bochdansky and Leggett (2001)
241 were selected to compare with the present results because these references contain
242 comprehensive datasets of diverse fishes. The models of Winberg (1956) and Clarke
243 and Johnston (1999) are characterized by body mass (WM: mg) and temperature (t: ^{o}C)
244 as independent variables, and that of Bochdansky and Leggett (2001) by body mass
245 only.

246 The Winberg (1956) model predicts “routine metabolism” (normal activity) from
247 the formula $R = R_{20}\ q^{-1} = (1.37 \times WM^{0.79})\ q^{-1}$, where R_{20} is R at 20^{o}C and q is Q_{10} to
248 convert R_{20} to R at t^{o}C or vice versa (Table 1 in Winberg 1956). The Clarke and
249 Johnston (1999) model predicts “standard” or “resting” metabolism (no activity) from
250 the formula $\ln R' = 0.8 \times \ln(WM/1000) + (15.7 - 5.0 \times 1000/(273.2 + t)) - 0.8 \times \ln(50)$,
251 where R’ is mmol O_2 (individual)$^{-1}$ h^{-1}. R’ is doubled (“routine” metabolism
252 = ”standard” metabolism × 2, cf. Bochdansky and Leggett 2001) and finally converted
253 to R (μl O_2 (individual)$^{-1}$ h^{-1}); $R = (\exp R') \times 2 \times 22.4 \times 1000$. While Winberg’s (1956)
254 and Clarke and Johnston’s (1999) analyses used juvenile and adult fishes, Bochdansky
255 and Leggett’s (2001) analysis included larval fishes in addition to juvenile and adult

256 fishes. In contrast to the two models mentioned above, their model has only one
257 variable (= body mass) since temperature was shown to be not important relative to
258 body dry mass (DM: mg). Their model is written as; $\log_{10}R = (1000/24) \times \log_{10}(1/(A$
259 $+ B))$, where $A = 1/10^{(-3.71 + \log_{10}DM)}$ and $B = 1/10^{(-2.40 + 0.67 \times \log_{10}DM)}$.
260 Predicted Rs from these three models are plotted against observed Rs (Fig. 2) and the
261 differences between the two were tested by the Wilcoxon signed ranks test (null
262 hypothesis: Rs predicted match those observed). The null hypothesis was rejected for
263 Rs predicted by the Clarke and Johnston model ($p < 0.001$) and the Winberg model ($p <$
264 0.05); the former yielded Rs 1.8 times and the latter 1.6 times greater than those
265 observed. On the other hand, the null hypothesis was accepted for Rs predicted by the
266 Bochdansky and Leggett model ($p > 0.95$). This result may be due to the fact that the
267 body mass of fishes of this study (6.3-1,786 mg WM or 1.24-395 mg DM, Table 2) only
268 partially overlap those (87-870,000 mg WM) of Winberg (1956) and those
269 (400-3,000,000 mg WM) of Clarke and Johnston (1999); but fall well within those
270 (0.001-100,000 mgDM) of Bochdansky and Leggett (2001). In addition, metabolic
271 rate-body mass relationships of larval fishes, which may be disproportionally lower than
272 those of juvenile/adult fishes (Post and Lee 1996), are taken into account in the
273 Bochdansky and Leggett (2001) model but not in the Winberg (1956) and Clarke and
274 Johnston (1999) models.
275 All the fishes used in the present study are small pelagic species (or pelagic stages
276 of benthic species), as a consequence of the methods of collection (light-trap and
277 scoop-net, see “Materials and Methods” section). Ammonia is well documented as the
278 major form of dissolved nitrogen excreted by diverse animal taxa which occur as marine
279 zooplankton (Ikeda et al. 2000). Consequently, it is of interest to compare the present

metabolic data on fishes with those of marine epipelagic zooplankton measured using similar sealed chamber methods. In terms of DM, the entire body mass range of the epipelagic zooplankton analyzed by Ikeda (1985) was 0.002-400 mg to which the DM range of fishes of this study overlaps perfectly. Body N mass (N: mg) and temperature (t: ^{o}C) data of each fish in Table 2 were substituted for the global model for oxygen consumption rates (R: μl O_2 (individual)$^{-1}$ h^{-1}) or ammonia excretion rates (E: μg NH_4-N (individual)$^{-1}$ h^{-1}) of epipelagic zooplankton, i.e. lnR = -1.7412 + 0.8505 × lnN + 0.0636 × t and lnE = -0.9657 + 0.836 × 1lnN + 0.0656 × t (Ikeda 1985). N instead of DM is used as a unit of body mass to reduce variation originating from diverse body composition among animal taxa (Ikeda 1985). Wilcoxon signed ranks test revealed that Rs predicted from the model were similar to those observed ($p > 0.25$), but Es from the model were significantly different from those observed ($p < 0.001$)(Fig. 3). Overall, the observed E was 70% of that predicted, implying that fishes with equivalent body N mass to zooplankton consume oxygen at the same rate but excrete less ammonia than zooplankton under similar thermal regimes.

Metabolic O:N ratios

The O:N ratios (17-104) of the 29 fishes of this study implied the predominance of lipid/carbohydrate-oriented metabolism. Taking into account that the fishes were placed in filtered seawater (starved) for 1-5 h during experiments in this study (see "Materials and methods" Section), lower contribution of protein as a metabolite is consistent to the previous results (14-36% of the total metabolites) on nonfed rainbow trout, the Nile tilapia, sockeye salmon and others (see review of Wood 2001). According to Wood (2001), the major metabolite in fish fed to satiation is protein but in nonfed fish this is lipid followed by protein or carbohydrate.

304 Presently available information about O:N ratios on wild marine fishes is limited
305 to the Peruvian anchovy (*Engraulis ringens*) (Whitledge and Packard 1971) and four
306 juvenile fishes (*Cypselurus* sp., *Galeoides* sp., *Longirostrum delicatissimus*, *Ranzania*
307 *laevis*) from the epipelagic zones of tropical Indian Ocean and subtropical Pacific Ocean
308 (Ikeda 1974). All these previous O:N ratio data (13-22), determined with similar
309 sealed chamber methods to the present study, were at the lower range of data collected
310 in the present study (17-104). Apart from differences in fish species studied, the
311 discrepancy between this study and those of previous workers may partly be attributed
312 to the dissimilar diets of fishes living in tropical inshore waters (this study) and those in
313 offshore waters (the previous study) as discussed below.
314 Of the 29 fishes studied, *Chaetodon rainfordi* (CHR), *Chromis viridis* (CHA) and
315 *Scatophagus* sp. (SCA) are characterized by anomalously greater metabolic O:N
316 (74-104) and body C:N ratios (4.3-4.7) compared with those of the other fishes (Fig. 4).
317 As well as the feeding conditions discussed above, food quality (specially N
318 composition) has been documented to affect O:N ratios of various marine zooplankton
319 (Ikeda et al. 2000) and marine benthic animals (Mukai et al. 1989). While main diets
320 of most fishes used in this study are considered to be relatively N-rich zoobenthos,
321 zooplankton and/or nekton (Hiatt and Strasburg 1960, Russell 1983), these three fishes
322 have small and/or squat bodies that may not be well suited to capturing agile prey.
323 According to Grant (1987), these three fishes in the waters around Australia are known
324 to feed on algae or seaweeds (*C. rainfordi* and *C. viridis*) or detritus (*Scatophagus* sp.),
325 all characterized by extremely low N composition (1-2% of DM, Tenore 1983, Duarte
326 1990). In these three fishes, dietary N may be used preferentially to build body protein
327 by using energy derived largely from lipid/carbohydrate oriented metabolism. In

328 addition to lower metabolic O:N ratios, lower body C:N ratios (Fig. 4) may be a trait of
329 life modes of these fishes caused by N-limited food nutrition. Considering the high
330 diversity and flexibility of diets of tropical fishes (Hiatt and Strasburg 1960, Russell
331 1983, Blaber 1997), combined with abundant detritus in the tropical inshore water
332 environments (Qasin and Sankaranarayaran 1972, Alongi and Christoffersen 1992), it is
333 conceivable that some fishes other than these three species of this study may ingest
334 N-poor diets opportunistically, contributing to the higher O:N ratios of this study as
335 compared with those (13-22) of the previous studies of Whitledge and Packard (1971)
336 and Ikeda (1974). The Peruvian anchovy and four fishes studied by Whitledge and
337 Packard (1971) and Ikeda (1974), respectively, were both from offshore waters, and
338 feeding on phytoplankton (the Peruvian anchovy) or zooplankton (the four fishes).
339 According to Tenore (1988) phytoplankton is more N-rich as compared with seaweeds
340 or vascular plants.

341 **Chemical composition and daily metabolic losses in body C and N**

342 The chemical composition of fish changes during development (Love 1970).
343 For example, the water and ash content of silvery lightfish (*Maurolicus muelleri*)
344 growing from larvae to mature adults decreases from 77 to 69% of WM and from 26 to
345 11% of DM, respectively, while C increases from 34 to 54% of DM due to accumulation
346 of lipid around the digestive tract, gonads and liver (Ikeda 1996). The chemical
347 composition of fish living in deep-sea is known to be different greatly from those living
348 in shallow waters in the ocean (Childress and Nygaard 1973). Bearing these in mind,
349 previous results on late larval or early juvenile fishes from shallow waters and with
350 similar body mass to those of the present study are compared in Table 4. As an
351 exception from these criteria, “fish/fish larvae” data of which body mass is unknown are

352 included in Table 4. Interestingly, C, N and C:N ratio data on grunion, sea bream,
353 lanternfish, herring, plaice and walleye pollock, all from higher latitude seas, and
354 “fish/fish larvae” from a low latitude sea (off Bermuda) overlap those of the 29 fishes of
355 the present study. However, the water content of 82-87% of herring and 84.2-88.1% of
356 “fish/fish larvae”are much higher than 66.0-81.8% of the 29 fishes in the present study.
357 Higher water content of herring and “fish/fish larvae” may imply their life stages being
358 earlier than those of the 29 fishes since the water content of newly hatched larvae is
359 high (89-90%) and declines rapidly with development (Ehlrich 1974a,b). This is
360 especially true for “fish/fish larvae” which were caught with a plankton net (Beers
361 1956). Ash content of 5.4-10.0% of grunion (May 1971), 7.5-9.7% of herring (Ehlrich
362 1974a) and 9.3-10.0% of plaice (Ehlrich 1974b) were less than the 29 fishes in the
363 present study (11.9-28.6% of DM). The lower ash content of these three fishes may
364 partly be due to the use of combustion temperatures (500-600^{o}C) higher than that
365 (450^{o}C) of this study or species-specific compositional characteristics of each fish. In
366 general, the effect of geographical position (that is, habitat temperature) is not
367 detectable in the chemical composition data of larval and early juvenile fishes compared
368 in Table 4.
369 As a component of bones, otolithes and scales in fishes, inorganic C (as
370 $CaCO_3$-C) has been reported as 0.4-5% of dried ash for several teleost fishes
371 (Vinogradov 1953). If one assumes that the ash content of fishes is 18% of DM (the
372 mean of the 29 fishes of the present study), these inorganic C values are equivalent to
373 0.1-0.9% of DM, similar to the present results (0.04-0.33%; Table 4). This indicates
374 that the respective contribution of inorganic C and N to the total C and N is insignificant
375 for the 29 fish species of the present study and possibly for the other teleost fishes.

376 With regard to inorganic N composition detected, NH_4 may be a possible source.

377 On the premise that the C:N ratio is 3.1 for organic matter composed of protein
378 alone and 7.5 for organic matter composed of equal amount of protein and lipid (see
379 “Water, ash and elemental composition” section), the protein composition of the 29 fish
380 species with C:N ratio = 3.1-4.7 of the present study is calculated as 73-99%. If one
381 omits the three isolated data characterized by high C:N ratios (4.3-4.7, Fig. 4) out of the
382 29 fish species (e.g. C:N = 3.1-4.0), the percentage of protein for the organic matter is
383 re-calculated as 83-99%. Thus, the C:N ratio data indicate that protein is the almost
384 exclusive component of body organic matter of the 29 fish species. The same
385 calculation revealed that the percentage of protein is 70-95% for the six fishes plus
386 “fish/fish larvae” with C:N = 3.3-5.0 in Table 4. It must be noted that the proportion of
387 protein thus estimated will vary depending on the degree of deviation of C and N
388 composition of protein and lipid from that given by Gnaiger and Bitterlich (1984), but
389 no precise information is available for tropical fish larvae material.

390 Daily metabolic losses in body N (DMN: 0.8-9.1%, with a mean of 3.3%) were
391 consistently less than the losses in body C (DMC: 4.3-18.6% with a mean of 10.0%) in
392 the 29 fish species in the present study (Table 2). Fishes are known to excrete not only
393 ammonia but also urea as the end products of protein metabolism (Wright and Fyhn
394 2001, Wood 2001). Therefore, part of the reason why DMN is lower than DMC may
395 be that urea-N which was not measured in this study. However, omission of urea in
396 our calculation of DMN is not sufficient to explain the low observed DMN, since
397 urea-N seldom exceeds 40% of ammonia-N in most marine teleosts, with the exception
398 of unusual fishes that excrete urea as the major nitrogenous excreta (Wood 2001).
399 Lower DMN than DMC is a general feature of marine zooplankton living in various

400 regions of the world ocean (Ikeda 1974, Ikeda and Mitchell 1982).

401 There are no comparable data for DMC and DMN for marine teleosts, with one
402 notable exception. Whitledge (1982) determined N excretion (ammonia and urea) and
403 N composition of the body for the near-bottom fish *Diplodus senegalensis* (weighing
404 27-29 g DM) in the upwelling region off northwest Africa, and calculated DMN as
405 1.2-1.5% (0.9-1.1% when only ammonia excretion is considered) at 15^{o}C. From the
406 E-DM relationship at 25-30^{o}C (median: 29^{o}C) established in this study (Fig. 1),
407 combined with a Q_{10} = 2 for E-temperature relationship established for marine
408 zooplankton (Ikeda 1985), DMN for *D. senegalensis* is computed as 1.1-1.2%, which is
409 close to the value (0.9-1.1%) obtained by Whitledge (1982).

410 As a general conclusion, we demonstrated the importance of body mass to define
411 R and E of tropical fish larvae, and resultant relationships were comparable to the
412 R-body mass relationships of fish and marine zooplankton by choosing appropriate
413 body mass units (WM, DM or N). Somewhat reduced specific E of the fish larvae was
414 evident as compared with marine zooplankton of equivalent body mass. As judged by
415 body C:N ratio, protein is the predominant biochemical compound regulating
416 metabolism in tropical fish larvae but this conclusion needs more detail study. A close
417 association of N-poor diet (detritus) with anomalously high metabolic O:N ratios and
418 body C:N ratios found in some fish larvae warrant further investigation for better
419 prediction of E and N composition from the body mass data only. By knowing body
420 mass composition data of fish populations in a tropical system, their roles in carbon and
421 nitrogen mineralization in the system can be estimated from the R- and E-body mass
422 relationships established in this study (Fig. 1).

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Figure captions

Fig. 1. Relationships between dry mass (DM) and oxygen consumption rates (R) (top), ammonia excretion rates (E)(middle) and oxygen consumption rate to ammonia excretion rate ratios (O:N, by atoms)(bottom). Data points represent the means of 35 data sets on 29 fish species in Table 2. Regression lines and statistics are superimposed.

Fig. 2. Comparison of oxygen consumption rates (R_{obs}) observed with those (R_{pred}) predicted from fish metabolism models of Clarke and Johnston (1999)(top), Winberg (1956)(middle) and Bochdansky and Leggett (2001)(bottom), based on their body mass (mg WM (individual)$^{-1}$ and temperature data for the former two models and body mass only for the last model. Data points represent the means of 35 data sets on 29 fish species in Table 2. To facilitate comparison, 1:1 line superimposed. Null hypothesis (H_o) and the results of Wilcoxon signed ranks test are shown. See text for details

Fig. 3. Comparison of oxygen consumption rates (R_{obs}) observed with those (R_{pred})(top), and ammonia excretion rates (E_{obs}) observed with those (E_{pred}) predicted (bottom), both from marine epipelagic zooplankton metabolic models of Ikeda (1985) based on their body mass (mg N (individual)$^{-1}$) and temperature data. Data points represent the means of 35 data sets on 29 fish species in Table 2. To facilitate comparison, 1:1 line superimposed. Null hypothesis (H_o) and the results of Wilcoxon signed ranks test are shown. See text for details.

Fig. 4. Relationship between metabolic O:N ratios (by atoms) and body C:N ratios (by mass) of 29 fish species (Table 2). Vertical and horizontal lines through

means denote ±1SD. Three isolated data sets (species code: CHR, SCA, CHA) are enveloped by a light shade. Predicted metabolic O:N ratios when protein (PRO) contributed 100% and 50% of total metabolites, and predicted body C:N ratios when protein occupied 100%, 80% and 70% of body organic matter are superimposed by horizontal and vertical hatched lines, respectively. See text for details.

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Table 1. Sampling data of juvenile and early juvenile fishes. Within species the data were separated into two body mass groups for *Caracanthus* sp. and *Neomyxus* sp., and two temperature groups for *Ambassis* sp., *Hypoatherina* sp., *Lethrinus* sp. and *Monocanthus* sp.

Species code	Scientific name	Common name	Family	Sampling site	Sampling method
AB	*Abudefduf vaigiensis**	Seargeant-major	Pomacentridae	Cape Ferguson coast	Light-trap
AM1	*Ambassis* sp.	Glassy	Ambassidae	Cape Ferguson coast	Light-trap
AM2	*Ambassis* sp.	Glassy	Ambassidae	Cape Ferguson coast	Light-trap
AE	*Amblyeleotris* sp.*	Goby	Gobiidae	Cape Ferguson coast	Light-trap
AG	*Amblygobius* sp.*	Goby	Gobiidae	Cape Ferguson coast	Light-trap
AP	*Apogon* sp.*	Soldierfish/Cardinalfish	Apogonidae	Cape Ferguson coast	Light-trap
CA1	*Caracanthus* sp.*	Croucher	Caracanthidae	Cape Ferguson coast	Scoop net
CA2	*Caracanthus* sp.*	Croucher	Caracanthidae	Cape Ferguson coast	Scoop net
CHA	*Chaetodon rainfordi**	Northern butterflyfish	Chaetodontidae	Cape Ferguson coast	Light-trap
CHR	*Chromis viridis**	Blue puller	Pomacentridae	off Townsville	Light-trap
G	*Gerres* sp.*	Silverbelly	Gerreidae	Cape Ferguson coast	Light-trap
HE	*Herklotsichthys* sp.	Tropical herring	Clupeidae	off Mackay	Scoop net
Hy1	*Hypoatherina* sp.*	Silverside/Whitebait	Athernidae	off Mackay	Scoop net
HY2	*Hypoatherina* sp.*	Silverside/Whitebait	Athernidae	off Townsville	Light-trap
LEI	*Leiognathus* sp.	Ponyfish	Leiognathidae	Cape Ferguson coast	Light-trap
LET1	*Lethrinus* sp.*	Sweetlip	Lethrinidae	Cape Ferguson coast	Light-trap
LET2	*Lethrinus* sp.*	Sweetlip	Lethrinidae	Cape Ferguson coast	Light-trap
LU	*Lutjanus carponotatus**	Stripey	Lutjanidae	Cape Ferguson coast	Light-trap
MO1	Monacanthidae sp.*	Leatherjacket	Monananthidae	Cape Ferguson coast	Light-trap
MO2	Monacanthidae sp.*	Leatherjacket	Monananthidae	Cape Ferguson coast	Light-trap
MU	Mullidae sp.*	Goatfish	Mullidae	Cape Ferguson coast	Light-trap
NM1	*Neomyxus* sp.	Mullet	Mugilidae	Cape Ferguson coast	Scoop net
NM2	*Neomyxus* sp.	Mullet	Mugilidae	Cape Ferguson coast	Scoop net
NP	*Neopomacentrus bankieri**	Damselfish	Pomacentridae	Cape Ferguson coast	Light-trap
O	*Omobranchus* sp.*	Blenny	Blenniidae	Cape Ferguson coast	Light-trap
PE	*Pelates quadrilineatus*	Trumpeter	Terapontidae	Cape Ferguson coast	Scoop net
PO	*Pomacentrus* sp.*	Damselfish	Pomacentridae	off Mackay	Scoop net
SCA	*Scatophagus* sp.	Butterfish	Scatophagidae	Cape Ferguson coast	Light-trap
SL	*Scomberoides lysan*	Queenfish	Scombridae	Cape Ferguson coast	Light-trap
SQ	*Scomberomorus queenslandicus*	School mackerel	Scombridae	Cape Ferguson coast	Light-trap
SE	*Selaroides leptolepis*	Smooth-tailed travally	Carangidae	Cape Ferguson coast	Light-trap
SI	*Siganus* sp.*	Spinefoot	Siganidae	Cape Ferguson coast	Light-trap
SP	*Sphyraena* sp.*	Sea-pike	Sphyraenidae	Cape Ferguson coast	Light-trap
T	*Terapon* sp.	Trumpeter	Teraponidae	Cape Ferguson coast	Scoop net
U	*Upeneus tragula**	Blackstriped goatfish	Mullidae	Cape Ferguson coast	Light-trap

625 * coral reef fish (cf. Leis and Rennis 1983)

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Table 2. Summary of oxygen consumption and ammonia excretion rates of 29 larval and early juvenile fishes, calculated metaolic O:N ratios and daily metabolic losses in body C and body N. For species code, see Table 1. Values are mean ± SD of N replicates. ND:no data

Species Code	Expt T (^oC)	N	Body mass (mgWM individual^{-1})	Body mass (mgDM individual^{-1})	Oxygen consumption rate (μlO_2 individual$^{-1}h^{-1}$)	Ammonia excretion rate (μgN individual$^{-1}h^{-1}$)	O:N ratio (by atoms)	Daily metabolic loss (% of bodyC)	Daily metabolic loss (% of bodyN)
AB	29	3	477.7 ± 208.8	114.64 ± 53.35	395.7 ± 163.3	55.85 ± 42.30	17.5 ± 17.1	10.6 ± 1.3	9.13 ± 6.05
AM1	28	6	265.9 ± 81.3	64.13 ± 19.80	88.4 ± 24.6	4.37 ± 1.09	25.5 ± 4.6	4.3 ± 0.4	1.43 ± 0.29
AM2	29	5	355.3 ± 101.4	87.68 ± 25.69	121.2 ± 31.2	3.52 ± 1.23	44.5 ± 6.4	4.4 ± 0.3	0.82 ± 0.10
AE	29	2	58.3 ± 2.3	10.87 ± 0.91	32.0 ± 3.4	1.05 ± 0.19	38.5 ± 2.8	8.9 ± 0.2	1.87 ± 0.18
AG	30	6	47.6 ± 20.5	9.96 ± 4.49	14.4 ± 5.9	0.94 ± 0.65	22.2 ± 5.5	4.6 ± 0.8	1.83 ± 0.49
AP	30	6	7.5 ± 2.0	1.54 ± 0.42	8.1 ± 1.6	0.42 ± 0.09	24.4 ± 2.2	18.6 ± 2.7	5.91 ± 0.84
CA1	28	6	6.3 ± 0.9	1.24 ± 0.20	6.7 ± 1.1	0.28 ± 0.12	34.9 ± 13.3	15.9 ± 1.9	5.15 ± 2.56
CA2	28	3	28.4 ± 9.7	5.67 ± 2.15	22.9 ± 7.4	0.66 ± 0.23	43.9 ± 9.6	12.0 ± 1.3	2.66 ± 0.35
CHA	29	5	169.9 ± 59.1	52.56 ± 17.06	113.1 ± 25.9	2.08 ± 0.64	74.0 ± 32.1	7.2 ± 1.0	1.25 ± 0.51
CHR	29	6	31.9 ± 2.3	9.17 ± 0.68	36.2 ± 1.9	0.45 ± 0.10	104.4 ± 20.1	11.2 ± 0.7	1.25 ± 0.26
G	29	2	74.7 ± 19.7	15.39 ± 4.06	53.5 ± 22.3	1.56 ± 0.13	43.6 ± 21.3	11.1 ± 1.8	2.09 ± 0.71
HE	27	4	129.6 ± 68.6	41.22 ± 18.77	179.1 ± 90.0	8.33 ± 2.36	27.0 ± 10.3	12.2 ± 2.2	4.39 ± 2.25
Hy1	26	6	182.3 ± 70.8	55.57 ± 21.44	199.5 ± 50.8	5.00 ± 3.36	66.0 ± 34.4	10.6 ± 1.8	2.05 ± 1.58
HY2	29	3	225.3 ± 49.7	60.79 ± 11.96	251.6 ± 47.0	6.10 ± 2.54	57.9 ± 25.3	11.8 ± 1.3	2.09 ± 0.91
LEI	29	4	145.5 ± 30.4	35.32 ± 6.88	114.8 ± 22.4	5.74 ± 1.50	25.4 ± 3.5	10.1 ± 0.8	3.03 ± 0.26
LET1	29	9	150.3 ± 27.7	35.59 ± 6.23	87.3 ± 18.4	4.98 ± 2.22	24.2 ± 7.3	7.5 ± 0.7	3.00 ± 0.87
LET2	30	6	122.9 ± 16.6	29.54 ± 4.01	85.9 ± 15.5	2.82 ± 1.95	49.4 ± 20.9	8.5 ± 0.8	2.00 ± 1.17
LU	29	6	292.1 ± 24.0	69.45 ± 8.43	195.2 ± 37.9	19.24 ± 11.98	17.3 ± 10.9	8.5 ± 1.3	6.10 ± 3.67
MO1	29	3	217.9 ± 31.3	45.92 ± 5.49	139.7 ± 15.4	4.83 ± 2.87	46.5 ± 26.8	8.9 ± 0.2	2.17 ± 1.19
MO2	30	10	285.7 ± 76.9	59.26 ± 17.33	182.8 ± 52.6	11.01 ± 8.31	30.9 ± 17.7	9.4 ± 2.0	4.05 ± 3.18
MU	29	3	80.4 ± 26.9	18.38 ± 6.29	80.8 ± 16.9	5.13 ± 1.91	20.8 ± 4.6	14.0 ± 2.4	5.23 ± 0.67
NM1	28	16	27.6 ± 4.0	6.10 ± 0.85	26.4 ± 5.6	2.14 ± 1.88	21.7 ± 10.2	12.7 ± 1.8	7.10 ± 5.34
NM2	28	4	45.7 ± 9.1	14.97 ± 4.35	39.9 ± 13.2	2.84 ± 0.80	17.7 ± 4.8	8.7 ± 3.9	4.76 ± 2.31
NP	28	6	347.8 ± 58.7	87.50 ± 14.46	153.7 ± 26.8	9.74 ± 3.16	20.6 ± 3.5	5.6 ± 0.5	2.33 ± 0.46
O	30	6	24.2 ± 6.9	5.90 ± 1.74	17.7 ± 2.5	0.38 ± 0.06	60.0 ± 12.9	9.4 ± 1.3	1.43 ± 0.43
PE	28	6	19.2 ± 1.8	3.94 ± 0.42	9.4 ± 0.6	0.49 ± 0.11	24.9 ± 4.9	7.0 ± 0.4	2.56 ± 0.41
PO	25	3	ND		15.27 ± 0.69	54.1 ± 16.1	2.14 ± 0.92	34.1 ± 12.8	10.7 ± 3.4	2.98 ± 1.32
SCA	29	4	90.4 ± 7.5	24.30 ± 2.69	71.6 ± 25.5	0.97 ± 0.31	93.3 ± 20.4	9.0 ± 2.7	1.03 ± 0.39
SL	30	2	565.1 ± 352.8	132.5 ± 85.8	410.9 ± 432.2	29.52 ± 34.62	21.3 ± 6.7	8.0 ± 4.9	3.33 ± 2.82
SQ	29	3	733.7 ± 68.3	142.1 ± 16.1	880.8 ± 164.4	18.20 ± 8.20	66.4 ± 20.5	18.2 ± 1.4	2.38 ± 0.83
SE	29	4	1786 ± 278	394.8 ± 64.1	1296 ± 206.5	64.23 ± 9.99	26.2 ± 8.2	10.5 ± 2.9	3.16 ± 0.53
SI	29	6	352.1 ± 51.5	77.83 ± 16.28	203.0 ± 31.4	13.95 ± 3.44	19.4 ± 6.1	8.2 ± 1.2	3.96 ± 1.35
SP	29	6	125.8 ± 41.1	25.31 ± 9.01	91.7 ± 29.4	6.43 ± 4.50	22.8 ± 10.0	10.9 ± 2.1	4.91 ± 2.67
T	28	6	28.9 ± 3.7	5.77 ± 0.74	20.6 ± 3.9	0.59 ± 0.34	50.9 ± 18.3	10.8 ± 1.3	2.11 ± 1.07
U	29	6	284.4 ± 47.7	71.21 ± 13.52	229.0 ± 41.6	15.05 ± 6.16	21.4 ± 7.6	10.3 ± 1.0	4.42 ± 1.44

Table 3. Water content, ash, total C and N composition, C:N ratio and inorganic C and N composition of 29 larval and early juvenile fishes. Values are mean ± SD (the number of replicates of each fish is as in Table 2) for water and mean for others. For species code, see Table 1. ND: no data. For species code, see Table 1

Species code	Water (% of WM)	ASH	Total C (% of DM)	Total N	C:N (by mass)	Inorg C (% of DM)	Inorg N
AB	76.2 ± 0.8	17.8	41.4	11.2	3.7	0.13	0.06
AM1	75.9 ± 1.1	20.6	40.6	11.7	3.5	0.13	0.01
AM2	75.4 ± 0.4	20.5	39.8	11.6	3.4	0.17	0.03
AE	81.4 ± 0.8	17.6	41	12.3	3.3	ND	ND
AG	79.2 ± 0.7	20.5	40.6	11.6	3.5	0.33	0.15
AP	79.6 ± 0.3	14.9	36.2	11.3	3.2	ND	ND
CA1	80.4 ± 0.4	ND	42.6	10.7	4	ND	ND
CA2	80.2 ± 0.9	16.7	42.1	11.2	3.8	ND	ND
CHA	68.8 ± 1.0	28.6	38.8	8.3	4.7	0.09	0.03
CHR	71.2 ± 0.6	17.9	44.1	9.4	4.7	0.16	0.06
G	79.4 ± 0.0	18.4	40.1	12.6	3.2	0.07	0.04
HE	66 ± 9.6	14.5	44.5	12.5	3.5	0.1	0.04
Hy1	69.1 ± 4.2	16.2	44.4	12.2	3.6	0.12	0.03
HY2	72.9 ± 1.1	15.7	43.9	11.8	3.7	0.13	0.03
LEI	75.7 ± 0.4	16.4	40.1	12.8	3.1	0.1	0.03
LET1	76.3 ± 0.6	19	40.9	10.9	3.8	0.13	0.04
LET2	76 ± 0.8	20.3	42.5	11	3.9	0.13	0.04
LU	76.3 ± 1.0	18.7	41.5	11.1	3.8	0.12	0.04
MO1	78.9 ± 0.6	16.2	42.8	11.3	3.8	0.06	0.07
MO2	79.4 ± 0.8	17.1	41.8	11.5	3.7	0.06	0.04
MU	77.2 ± 0.2	15.6	40.6	12.7	3.2	ND	ND
NM1	77.8 ± 0.7	15.3	43.2	11.9	3.6	0.23	0.11
NM2	77.1 ± 1.0	16.2	39.7	10.3	3.9	0.22	0.06
NP	74.8 ± 0.4	24.1	39.4	11.3	3.5	0.12	0.04
O	75.6 ± 0.4	17.6	41.1	11.4	3.6	ND	ND
PE	79.5 ± 0.5	11.9	42.6	11.6	3.7	0.31	0.1
PO	ND	13.8	41.8	11.3	3.7	ND	ND
SCA	73.2 ± 0.8	22.1	40.7	9.5	4.3	0.13	0.12
SL	76.8 ± 0.7	16.6	38.1	12.2	3.1	ND	ND
SQ	80.7 ± 0.4	14	42.3	12.6	3.4	0.04	0.03
SE	77.9 ± 0.2	21.1	40	12.5	3.2	0.1	0.04
SI	78 ± 1.5	20.4	40.2	11.3	3.6	0.1	0.04
SP	80 ± 0.5	16.5	42.5	12.2	3.5	0.15	0.06
T	80 ± 0.4	13.6	41.4	11.5	3.6	0.25	0.08
U	75 ± 1.0	20.2	39.3	11.3	3.5	0.09	0.04

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Table 4. Comparison of water content, ash, C and N composition and C:N ratios of feeding larvae or early juvenile teleost fishes from various locations. ND: no data

Common name	Scientific name	Location	Specimens	Body mass (mg DM individual^{-1})	Water (% of WM)	Ash (% of DM)	C (% of DM)	N (% of DM)	C:N (by mass)	Reference
Grunion	*Leuresthes tenuis*	La Jolla, California	Wild	0.4-38	ND	5.4-10.0	43.1-47.1	10.5-11.3	4.0-4.4	May (1971)
Sea bream	*Chrysophrys major*	Southern Japan	Wild	17-1981	78-79	ND	39-43	11.3-12.2	3.3-3.8	Anraku and Azeta (1973)
Lanternfish	*Tarletonbeania crenularis*	off South California	Wild	92-275	77.1	19.6	40.8	10.2	4	Childress and Nygaard (1973)
Herring	*Clupea harengus*	Firth of Clyde	Lab-raised	0.5-23	82-87	7.5-9.7	40.2-44.3	10.9-12.2	3.6-3.9	Ehlrich (1974a)
Plaice	*Pleuronectes platessa*	Scotland	Lab-raised	1.1-2.2	ND	9.3-10.0	43.8-44.6	11.3-11.6	3.8-3.9	Ehlrich (1974b)
Walleye pollock	*Theragra chalcogramma*	Gulf of Alaska	Wild	1-950	ND	8.7-16.8	34.5-55.1	10.0-13.9	3.4-5.0	Harris et al. (1986)
"Fish/fish larvae"	mixed species	off Bermuda	Wild	ND	84.2-88.1	ND	32.6-41.7	8.3-10.7	3.5-4.2	Beers (1965)
Small early juvenile/larval fishes	29 species, see Table 1	Great Barrier Reef inshore waters	Wild	1.24-395	66.0-81.4	11.9-28.6	36.2-44.4	8.3-12.8	3.1-4.7	This study

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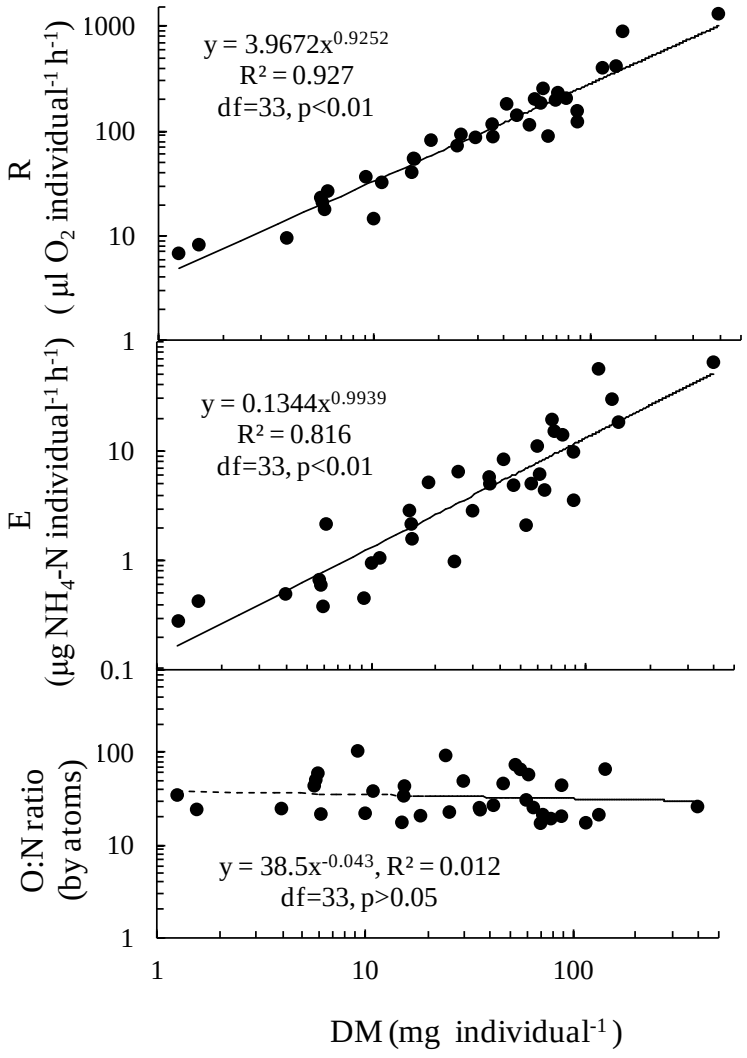

Ikeda et al. Fig. 1

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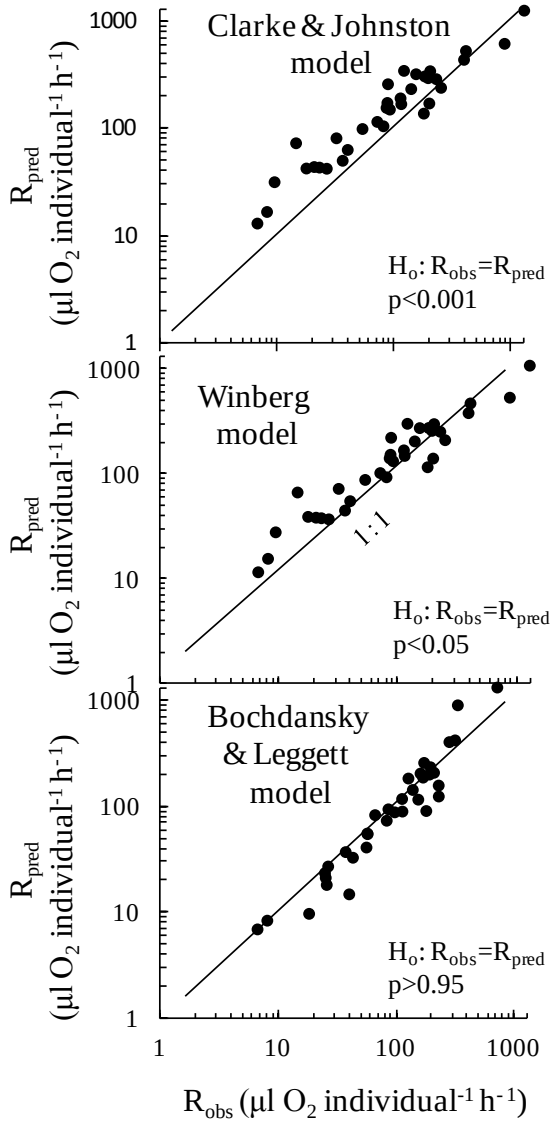

Ikeda et al. Fig. 2

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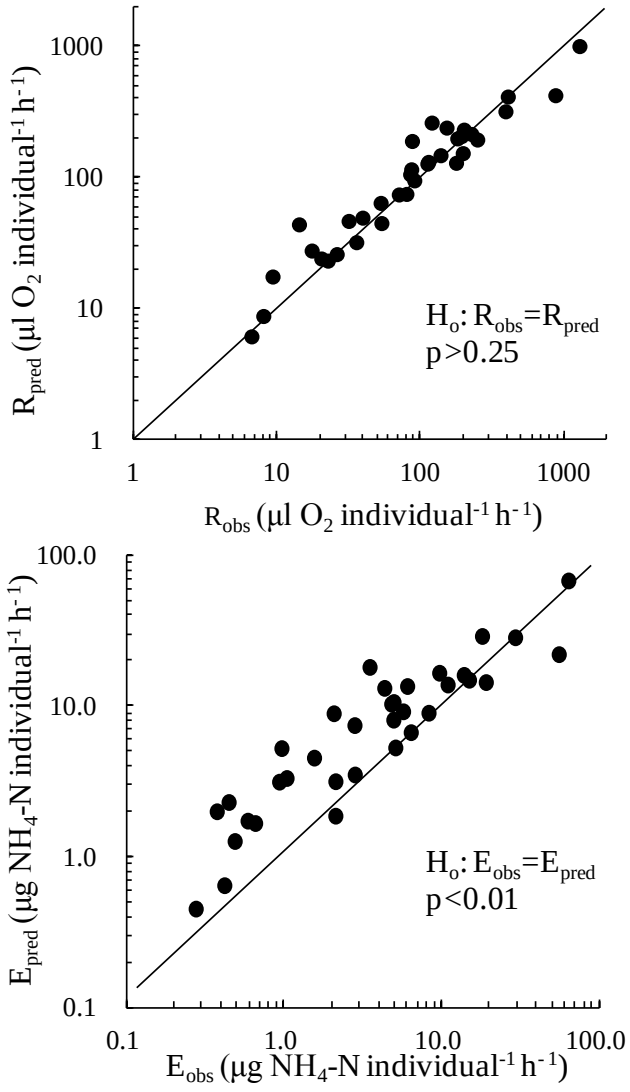

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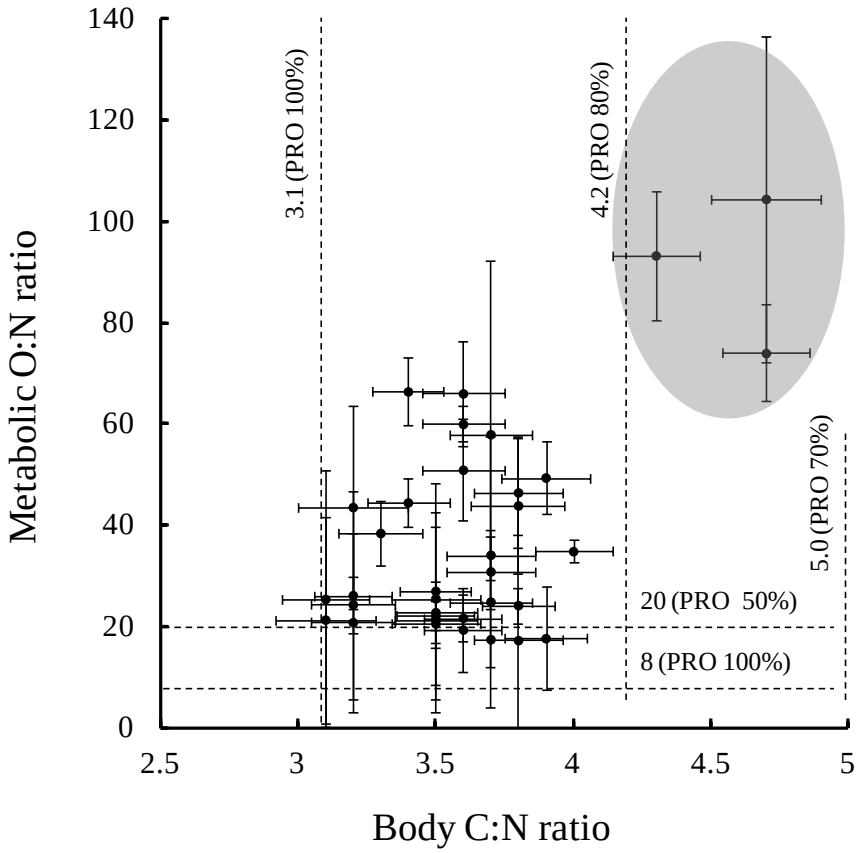
Ikeda et al. Fig. 3



Ikeda et al. Fig. 4