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Routine metabolic rates of pelagic marine fishes and cephalopods as a function of body mass, habitat temperature and habitat depth

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ABSTRACT

Cephalopods and fishes are major components of marine micronekton and nekton, so an understanding of their physiology and roles in ocean biogeochemistry is important. I compiled the routine respiration rates (50 datasets on 41 cephalopod species; 102 datasets on 90 fish species) from various depth horizons (< 1,300 m) of the world's oceans and analyzed these rates as a function of body mass [wet mass (WM), dry mass (DM), carbon (C) or nitrogen (N)], habitat temperature and habitat depth using multiple regression. Stepwise-regression analyses revealed that body mass was the most important parameter, followed by habitat temperature and habitat depth, and these variables explained 89.7–93.8% and 94.7–95.8%, respectively, of the variance in the respiration data of fishes and cephalopods. The addition of a taxon category (order or family) as a fourth variable improved these correlations only slightly (95.6–95.7% and 95.7–96.2%, respectively). The resultant regression equation showed higher respiration rates in cephalopods than fishes relative to the DM, C or N body mass (by a factor 1.5- to 1.7-fold), but not to the WM body mass. The O:N ratios (respiration/ammonia excretion, by atoms) reported for 6 cephalopods (median:13.2) and 35 fishes (24.2) suggested the predominance of protein as a metabolite in the former and carbohydrate or lipid in the latter. The present results are discussed in light of the methodological constraints and standing hypothesis for the relationship between the metabolic rate and temperature. The empirical models established in the present study can be used to assess the roles of cephalopods and fishes in C and N cycles in pelagic ecosystems based on the organisms' body mass spectra, ambient temperatures and depth distributions.

1. Introduction

Fishes and cephalopods (mostly squids) are major components of micronekton and nekton, and occur throughout a wide depth range in the world's oceans. They are almost exclusively predators and exert strong feeding pressure on zooplankton and other micronekton and nekton. Nevertheless, they have been considered to play only a minor role in the global biogeochemical cycles in the oceans because their biomass is much smaller than that of bacteria and zooplankton (Conover, 1978; del Giorgio and Duarte, 2002). Recent studies, however, suggest that carbon exported downward by the respiration, defecation and mortality of micronektonic fishes and squids that undertake diel vertical migration between the epipelagic and mesopelagic zones can contribute much to the total downward carbon flux, e.g., 26–54% in the western equatorial Pacific Ocean (Hidaka et al., 2001), 15–17% in the northeastern Pacific Ocean (Davison et al., 2013), and 12–32% in the subtropical Atlantic Ocean (Ariza et al., 2015).

Information about metabolism [respiration rates, ammonia excretion rates and O:N ratios (the atomic ratio of the former to the latter)] has proved useful in understanding the energy demands, metabolic substrates and nutritional conditions of marine zooplankton (Ikeda et al., 2000). For marine fishes, respiration data have been compiled for many diverse species (Winberg, 1956; Clarke and Johnston, 1999; Acuña et al., 2011). While these comprehensive datasets have revealed that body mass and temperature are the major predictors of fish respiration rates, habitat depth has emerged as an additional predictor for the respiration rates of mesopelagic and bathypelagic fishes (Torres et al., 1979; Smith and Laver, 1981; Donnelly and Torres, 1988; Torres and Somero, 1988; Cowles and Childress, 1995). Nitrogen metabolism in fishes has been studied intensively in the early life stages over the last two decades (Wright and

Fyhn, 2001; Terjesen, 2008), but nitrogen excretion data are available for only a few species (Wright and Fyhn, 2001; Wood, 2001). Instead of the O:N ratio mentioned above, the molar ratio of ammonia excreted to oxygen consumed (ammonia quotient; Kutty, 1978) or nitrogen excreted to oxygen consumed (nitrogen quotient; Wright and Fyhn, 2001), has been used as an index of protein utilization as a metabolic substrate for fishes. However, the available measurements of these indices are largely based on laboratory-raised/maintained fishes, and information on wild pelagic fishes is limited to the Peruvian anchovy (Whitledge and Packard, 1971), leptocephalus larvae (Bishop and Torres, 1999), and small juvenile fishes (Ikeda, 1974; Ikeda et al., 2011).

Compared with fishes, the respiration data available for pelagic cephalopods are modest (Seibel et al., 1997; Seibel, 2007; Grigoriou and Richardson, 2009; Hirst et al., 2014). Brey (2010) combined a large body of respiration data from diverse aquatic invertebrate taxa including 44 cephalopod species and established an empirical model to estimate the respiration rates as a function of the lifestyle features (i.e., feeding type, mobility type and vision type) and physiological states (fed or starved, and activity level) of these animals, along with the body mass, temperature and water depth as parameters. Brey's (2010) model can be applied to pelagic cephalopods through the proper translation of features such as mobility (as swimmer in contrast with crawler or sessile for benthos), feeding (carnivore) and vision types (with functional eyes). Nevertheless, the application of a general model developed for broad aquatic invertebrates to a specific group (e.g., pelagic cephalopods) may lead to biased results, as accuracy and generality are contradistinctive objectives in predictive models (cf. Brey 2010). Ammonia excretion data and O:N ratio data have been collected for several

pelagic cephalopods in the laboratory and in the field (Ikeda and Bruce, 1986; Hoeger et al., 1987; Segawa and Hanlon, 1988; Boucher-Rodoni and Mangold, 1989).

As a basis for the evaluation of the functional roles of pelagic fishes and cephalopods in the fluxes of carbon and other elements in the ocean, I constructed an empirical model of metabolic rates of pelagic fishes and cephalopods as a function of body mass, habitat temperature, habitat depth and taxon. Such a model was established recently for major marine metazooplankton taxa while excluding cephalopods and fishes (Ikeda, 2014). For my purpose, data from laboratory-raised animals are of limited use. Hatchery fish have higher water content and lipids, and lower ash than wild fish (Love, 1970). Sea bream (*Chrysophrys major*) raised in the laboratory on artificial diets exhibit higher carbon (C) and lower nitrogen (N) compositions than those from the wild (Anraku and Azeta, 1973). By measuring the lipid-class composition of laboratory-raised anchovy (*Engraulis mordax*) larvae under a variety of food regimes, Håkanson (1989) suggested the importance of low food concentrations to obtain larvae that have body composition similar to those of the wild larvae. This suggests the great difficulty in raising fishes with a chemical composition equivalent to fish in the wild. To avoid potential artifacts in the comparison of metabolic rate standardized by body mass, I restricted this analysis to wild-caught individuals.

In the present study, differences in the effects of body mass, habitat temperature and habitat depth on the metabolic rates between pelagic fishes and cephalopods are also explored. Finally, the present results are compared with those of wild pelagic crustaceans to highlight any unique features of the fishes and cephalopods as pelagic taxa.

2. Materials and methods

2.1. *The metabolic data*

The metabolic rate (oxygen consumption rate) of an unfed animal can be classified as "resting," "routine" or "active" metabolism, depending on the activity level. Resting and active metabolism represent the rates at zero and maximum activity levels of animals, respectively, and routine metabolism occurs somewhere between these two extremes. Resting and active metabolism measured under strictly defined conditions interest physiologists. Routine metabolic rates showing normal or spontaneous activity are not well defined but have important implications for ecologists interested in energy expenditure of animals in the field (cf. Steffensen, 2005). In most previous experiments with conventional sealed chamber methods (cf. Ikeda et al., 2000), the swimming activities of small fishes and cephalopods were uncontrolled, and the metabolic data derived from the methods may approach routine rates (Torres et al., 1979; Torres and Somero, 1988; Bishop et al., 2000; Ikeda et al., 2000). Large epipelagic fishes and cephalopods are active swimmers, and the effect of swimming activity on their metabolic rates in terms of "factorial aerobic scope" (the ratio of active metabolism to standard metabolism) is greater than in small-sized ones (Killen et al., 2007). For this reason, routine metabolism, which falls somewhere between standard and active metabolism, of the large-sized fishes and cephalopods is best estimated from the oxygen consumption rate-swimming rate relations established by means of a swim-tunnel respirometer, together with the swimming performance data of animals in the field. For the recent development of radio-acoustic positioning telemetry for tracking squids in the field and estimating routine metabolic rates, see O'Dor (2002). In the present analyses, for species whose swimming velocity in the field is not known, the respiration rate at

140 the optimum velocity to yield the minimum cost of transport (Videler and Nolet, 1990;
141 O'Dor, 2002) was substituted. In contrast to epipelagic fishes and cephalopods, many
142 mesopelagic and bathypelagic species are neutrally buoyant and inactive. Their routine
143 respiration rates have been determined with conventional sealed respirometers using
144 specimens caught *in situ* with submersibles or carefully collected and transported to an
145 onboard laboratory.

146 Body mass units, dry mass (DM), carbon (C) or nitrogen (N) have been used for
147 smaller fishes and cephalopods, in contrast to the almost exclusive use of wet mass
148 (WM) for larger ones. If water content and C and N body compositions are constant
149 within and among the taxon compared, the choice of body mass units does not affect the
150 results of the interspecific comparisons. In fact, however, large among-species
151 variations in water content (% of WM), C and N (both % of DM) have been reported.
152 These values (water content, C and N) range from 74.0 to 92.8, from 31.6 to 57.8 and
153 from 6.4 to14.0, respectively, for 15 pelagic cephalopods (all squids; Clarke et al., 1985;
154 Ikeda and Bruce, 1986; Donnelly et al., 2004; Ikeda, unpublished data) and from 63.6 to
155 93.9, from 18.4 to 55.6 and from 3.5 to16.0, respectively, for 58 pelagic fishes
156 (Whitledge and Packard, 1971; Torres et al., 1979; Torres and Somero, 1988; Donnelly
157 et al., 1990; Bishop et al., 2000; Ikeda et al., 2011). In the present analyses, body mass
158 was expressed as WM, DM, C or N to examine the effects of body mass units on the
159 results and for meaningful between-taxon metabolic comparison (Zeuthen, 1947;
160 Schneider, 1990; Ikeda, 2008; Acuña et al., 2011). For species in which only WM has
161 been reported, DM, C and N were estimated from known predictors, such as whether
162 the cephalopods are from ammoniacal or muscular squid families (Clarke et al., 1985;
163 Ikeda and Bruce, 1986; Ikeda, unpublished data) or according to the habitat depths for

deep-sea pelagic fishes (Childress and Nygaard, 1973). The squid family Bathyteuthidae was classified as ammoniacal by Voight et al. (1994), but in the present study, this family was treated as muscular in terms of the overall body composition (see Seibel et al., 2004). For species in which no such predictors are available, mean values of taxonomically close species or grand mean values for that taxon were substituted**.** The application of the same conversion factor to obtain missing body mass units could violate the conditions required for the regression statistics mentioned below, but no correction was made for this procedure in this study.

Criteria applied for the selection of routine metabolic datasets of pelagic fishes and cephalopods were as follows:

1. Data represent juvenile and adult cephalopods or larval, juvenile and adult fishes collected from the field and used for experiments with a time delay of several hours to several weeks (mostly < 24 h). In the present analyses, the pelagic larvae/juveniles of some demersal fish orders (chiefly Perciformes, Anguilliformes and Scorpaeniformes) were considered. The larvae of many demersal fishes swim slowly without well-developed sensory organs at the start of their pelagic live, but they gain micronektonic features, characterized by functional sensory organs that can detect prey and predators, and they swim well (faster than ambient currents in many cases) at the end of the pelagic period (cf. Leis, 2006).

2. Measurements were made in the absence of food near *in situ* temperatures and at surface hydrostatic pressures (1 atm) in the dark. For deep-sea fishes and cephalopods, the hydrostatic pressure is well established to have small effects on respiration rates over the range that the species encounter in natural habitats (Belman, 1978; Childress, 1995; Seibel., 2007). Exceptions are the data for the deep-sea fish *Cyclothone*

188 *acclinidens* from *in situ* capture (1300 m deep) and incubation using submersibles
189 (Smith and Laver, 1981).
190 3. The O:N ratios were computed from simultaneous measurements of respiration rates
191 and ammonia excretion rates.
192 4. Body mass in terms of WM, DM, C, or N units was extracted together with metabolic
193 data (note: body-mass specific rates without body-mass data are not useful). Body
194 composition (water content, ash, C or N) was obtained using standard methods (Omori
195 and Ikeda, 1984; Postel et al., 2000).
196 On the bases of these criteria, a total of 102 respiration datasets and 42 ammonia
197 excretion datasets were selected for 90 fish species from 15 orders, and 50 respiration
198 datasets and 6 ammonia excretion datasets were selected for 41 pelagic cephalopod
199 species from 6 orders for the present analyses (Tables 1-1, 1-2). When data had been
200 reported in the form of a regression equation of rate against body mass, a value for the
201 rate at the mid-body mass (= geometric mean) was extracted. Datasets for the same
202 species from different locations or from two or more body mass ranges were treated as
203 independent. Study sites of all cephalopods and fishes were plotted on the world map
204 (Fig. 1) to illustrate geographical coverage of the datasets.
205
206 2.2. *Regression models*
207 Multiple regression models used for marine metazooplankton taxa (Ikeda, 2014) were
208 modified for respective analyses. The first model is
209

$$\mathrm{lnR} = \mathrm{a}_0 + \mathrm{a}_1 \times \mathrm{lnBM} + \mathrm{a}_2 \times (1000/\mathrm{Temp}) + \mathrm{a}_3 \times \mathrm{lnDepth} \cdots (1)$$

210

where lnR is the logarithm (base e) of the respiration rate (R: μlO_2 ind^{-1} h^{-1}), lnBM is the logarithm of the body mass (WM, DM, C or N), Temp is habitat temperature (K), and lnDepth is the logarithm of sampling or habitat depth (meters). Next, taxon terms are introduced to the first model as

$$\begin{aligned} \ln R = {} & a_0 + a_1 \times \ln BM + a_2 \times (1000/Temp) + a_3 \times \ln Depth + a_4 \times De \\ & + a_5 \times Ch + a_6 \times Cr + a_7 \times En + a_8 \times Go + a_9 \times Hi \\ & + a_{10} \times Jo + a_{11} \times Ma + a_{12} \times Oc + a_{13} \times Om + a_{14} \times Ps \\ & + a_{15} \times Py + a_{16} \times Se + a_{17} \times Va + a_{18} \times Oc \quad \cdots (2) \end{aligned}$$

for cephalopods, and

$$\begin{aligned} \ln R = {} & a_0 + a_1 \times \ln BM + a_2 \times (1000/Temp) + a_3 \times \ln Depth + a_4 \times Au \\ & + a_5 \times At + a_6 \times Bel + a_7 \times Ber + a_8 \times Cl + a_9 \times Ga \\ & + a_{10} \times Lo + a_{11} \times Mu + a_{12} \times Os + a_{13} \times Pe + a_{14} \times Sc \\ & + a_{15} \times Ste + a_{16} \times Sto + a_{17} \times Te \quad \cdots (3) \end{aligned}$$

for fishes, where De, Ch, En, Go, Hi, Jo, Ma, Oc, Om, Ps, Py, Se, Va, Oc and Cr are abbreviated cephalopod orders/families (Table 1-1), and Au, At, Bel, Ber, Cl, Ga, Lo, Mu, Os, Pe, Sc, Ste, Sto and Te are abbreviated fish orders (Table 1-2) as dummy (binary) variables. For the data from a given taxon, the dummy variable takes a value of 1 if representing the taxon or 0 otherwise. Loliginidae (Lo) for cephalopods and Myctophiforms (My) for fishes, which do not appear in the regression equation, are represented by values of 0 in either case.

227 The data of cephalopods and fishes were pooled, and possible differences in
228 regression coefficients (a_1, a_2 and a_3) and intercepts (a_0) between these two groups were
229 tested by incorporating interaction terms into Model (1). For the data from cephalopods
230 (Ceph), the dummy variable has a value of 1 when representing the cephalopods or 0
231 otherwise. The data for fishes (Fish), which do not appear in the regression equation,
232 take values of 0 in either case:
233

$$\ln R = a_0 + a_1 \times lnBM + a_2 \times (1000/Temp) + a_3 \times lnDepth + a_4 \times Ceph + a_5 \times (Ceph \times lnBM) + a_6 \times (Ceph \times (1000/Temp)) + a_7 \times (Ceph \times lnDepth) \quad \cdots (4)$$

234

235 where *lnBM* , *1000/Temp*, *lnDepth* and *Ceph* are mean-centered lnBM , 1000/Temp,
236 lnDepth and Ceph, respectively, to reduce the effects of multicolinearity among the
237 variables (Aiken and West, 1991). The newly defined coefficients a_5–a_7 and a_4 are
238 useful to judge whether the differences in the slopes and intercepts, respectively, are
239 significant or not between the cephalopods and fishes.
240 On the premise that the effects of body mass, habitat temperature and habitat
241 depth on the metabolism are common across pelagic animal taxa, the respiration rates of
242 fishes and cephalopods were compared with the rates of pelagic crustaceans, which
243 include copepods (109 species), euphausiids (24), amphipods (32), mysids (32) and
244 decapods (43) [selected from metazooplankton datasets in the Supporting materials in
245 Ikeda (2014)], with fishes (Fish) and cephalopods (Ceph) being designated as the
246 dummy variables:
247

$$\ln R = a_0 + a_1 \times \ln BM + a_2 \times (1000/Temp) + a_3 \times \ln Depth + a_4 \times Ceph + a_5 \times Fish \quad \cdots (5)$$

For the data from fishes and cephalopods, the dummy variables take a value 1 or 0 otherwise. The data for the crustaceans, which do not appear in the regression equation, take values of 0 in either case. The same regression model was used for the analyses of O:N ratios among fishes, cephalopods and crustaceans.

As an index of temperature effects, the activation energy (E_a) was calculated from the coefficient a_2 [= $-E_a$/k, where k is the Bolzmann's constant (8.62×10^{-5} eV/K); E_a = $a_2 \times 1000 \times 8.62 \times 10^{-5}$]. Temperature effects on the physiological rates have usually been expressed by Q_{10} instead of E_a. By defining a temperature range (t_1 and t_2, both in ^{o}C), E_a can be converted to Q_{10} (Ivleva, 1980) as follows:

$$Q_{10} = \exp[10 \times E_a/(k \times (273 + t_1) \times (273 + t_2))].$$

Habitat depth (= sampling depth) was represented by mid-range values for discrete samplings. The minimum depth of occurrence (MDO), defined as the depth below which 90% of the population of a given species is distributed (Torres et al., 1979; Donnelly and Torres, 1988; Seibel et al., 1997; Seibel, 2007**),** was assumed equivalent to the habitat depth of the species. The depth of the near-surface collections was assigned 1 m. The attributes of these variables were analyzed simultaneously using a stepwise multiple-regression (forward selection) method (Sokal and Rohlf, 1995).

Independent variables were added and removed at the $p = 0.05$ level; therefore, partial regression coefficients from the resultant equations are all significant ($p \leq 0.05$), unless otherwise noted. The calculations were conducted using a linear regression program in SYSTAT version 10.2.

3. Results

3.1. *Respiration*

Habitat depths ranged from 1 to 1,300 m (for fishes) and 1 to 975 m (for cephalopods), the temperature range was 0.5 to 30°C (fishes) and –0.8 to 30°C (cephalopods), and body mass ranged from 4 to 10,076,000 mgWM (fishes) and 100 to 937,000 mgWM (cephalopods). The entire datasets are summarized as supplemental materials (S1 for cephalopods and S2 for fishes) in Appendix A. All respiration data are plotted against WM, without regard for the differences in habitat temperatures and depths (Fig. 2).

The overall results of the stepwise multiple regressions with Models (1), (2) and (3) showed that for both cephalopods and fishes, the prime predictor of the respiration rates was body mass, followed by habitat temperature, habitat depth and taxon (as judged by standardized partial regression coefficient values, Table 2). Together, these predictors accounted for 89.7–93.8% (adjusted $R^2 = 0.897–0.938$) and 94.7–95.8% (adjusted $R^2 = 0.947–0.958$) of the variances in respiration rates of cephalopods and fishes, respectively, depending on the choice of body mass units with Model (1). The addition of the taxon term to the predictors [Models (2) and (3)] improved the correlation to 95.6–95.7% (adjusted $R^2 = 0.956–0.957$) for cephalopods, and 95.7–96.2% (adjusted $R^2 = 0.957–0.962$) for fishes. Thus, the respiration rates increased

291 with increasing body mass and habitat temperature, but decreased with increasing depth.
292 By the definition of dummy variables, respiration rates of the taxonomic categories for
293 which regression coefficients were not significant ($p > 0.05$, blanks in Table 2) are
294 equivalent to the rates of Loliginidae (Lo) for cephalopods and Myctophiformes (My)
295 for fishes. Among the 16 designated taxonomic categories (families and orders) for
296 cephalopods, Ommastrephidae (OM) and Gonatidae (Go) exhibited consistently higher
297 respiration rates regardless of the choice of body mass units, while Cranchiidae (Cr),
298 Histioteuthidae (His), Vampyroteuchidae (VA), and Octopoda (Oc) exhibited lower
299 respiration rates on the basis of WM units only (the latter three orders/families) or WM,
300 C and N units (Cranchiidae). For the 14 fish orders, those characterized by higher or
301 lower respiration rates varied depending on the choice of body mass units. Lophiiformes
302 (Lo), Osmeriformes (Os) and Stephanoberyciformes (Ste) exhibited lower respiration
303 rates on the basis of WM units, and Lophiiformes (Lo), on the bases of the DM and N
304 units. Anguilliformes (An) was the only order that exhibited higher respiration rates on
305 the bases of the DM, C and N units. Multicolinearity between these variables is
306 considered small, because the variation inflation factors (VIF) of these variables
307 (1.02–3.77 for the cephalopods, 1.07–3.66 for the fishes, both not shown) were < 5 (cf.
308 Kutner et al., 2004). Regardless of the choice of models or body mass units, the
309 coefficient a_1 (the scaling exponent of the body mass effect) was significantly less than
310 unity ($p < 0.0001$). Regarding the effect of habitat temperature, the E_a (eV) calculated
311 from the coefficient a_2 varied depending on the choice of either models or body mass
312 units from 0.482 to 0.681 (equivalent to 1.98–2.62 in terms of Q_{10} between –2 and
313 30^{o}C) for cephalopods and from 0.475 to 0.757 (Q_{10} of 1.96 to 2.91) for fishes.
314 Multiple regression analyses, including interaction terms [Model (4)], revealed

315 that the results varied across body mass units. Judging from the coefficient a_4,
316 cephalopods exhibited higher respiration rates than fishes on DM (by a factor ×1.6), C
317 (×1.7) and N (×1.5) body mass bases, but not on WM body mass basis (Table 3). The
318 coefficient a_7 indicated the decline in respiration rates with increasing habitat depth was
319 greater in cephalopods than in fishes. No significant differences were seen between
320 fishes and cephalopods in the coefficients a_5 (body mass effect) or a_6 (temperature
321 effect).

322 Model (4) was modified to extract the effects of the R of body mass, habitat
323 temperature or habitat depth for cephalopods or fishes by calculating the standardized R
324 (R_{std}), which is free from the effects of the other independent variables. For the effect of
325 body mass (represented by WM):

326

$$\ln R_{std} = a_0 + a_1 \times \ln WM$$

327

328 where $\ln R_{std} = \ln R - a_2 \times$ *1000/Temp* $- a_3 \times$ *lnDepth.*

329 Scatter plots of $\ln R_{std}$ versus lnWM (re-converted from *lnWM;* lnWM = *lnWM* +
330 7.8076, where 7.8076 is the mean lnWM) for cephalopods and fishes are shown in Fig.
331 3A. In the same way, the generalized effects of habitat temperature (1000/Temp =
332 *1000/Temp* + 3.4807) on R_{std} and of habitat depth (lnDepth = *lnDepth* + 2.8220) on R_{std}
333 were analyzed by replacing the *lnWM* on the right side of the equation with *1000/Temp*
334 and with *lnDepth*, respectively. Thus, I obtained scatter diagrams of R_{std} versus habitat
335 temperature and of R_{std} versus habitat depth for cephalopods and fishes (Figs 3B and C,
336 respectively).

337 In terms of the respiration rates of the specimens of the same body mass (DM, C

338 or N), living at identical temperatures and from similar depths, multiple regression
339 analyses revealed that the cephalopods were comparable to the crustaceans, but fishes
340 exhibited slightly reduced rates (0.76-fold) compared with the rates of the crustaceans
341 [Model (5), Table 3]. Model (5) was modified to extract the effects on the R of the body
342 mass by calculating a standardized R (R_{std}), which is free from the effects of habitat
343 temperature and habitat depth. To elucidate the intercept differences of the regression
344 lines of the cephalopods, fishes and crustaceans more clearly, the body N-specific R_{std}
345 (SR_{std}), instead of the R_{std}, was plotted against N on a log-log graph (Fig. 4).
346
347 3.2. *Ammonia excretion and O:N ratio*
348 Habitat depth ranged from 1 to 1,300 m, (mostly between 1–2 m) for fishes and
349 from 1 to 781 m (mostly at 1 m) for cephalopods, the temperature range was 3 to 30^{o}C
350 (fishes) and –0.8 to 27^{o}C (cephalopods), and the body mass (DM) ranged from 1.2 to
351 1,700 mg (fishes) and 26.6 to 202,392 mg (cephalopods)(Appendix A, S1 and S2).
352 Ammonia excretion data (42 values for 35 fishes, and 5 values for 5 cephalopods) were
353 not sufficient to analyze the effects of body mass, habitat temperature and habitat depth
354 by multiple regression methods, so the cephalopod-versus-fish comparison of ammonia
355 excretion was made indirectly using O:N ratios.
356 The O:N ratio ranged from 11.3 to 98.4, with a median of 13.2 for the 6
357 cephalopods, and from 5.9 to 66.4, with a median of 24.2 for the 41 fishes (S1, S2). The
358 former was significantly less than the latter (Mann-Whitney U-test, $p = 0.024$).
359 Multiple-regression analyses of pooled O:N ratio data of cephalopods and fishes
360 of this study and those of crustaceans (Ikeda, 2014) revealed that the effects of body
361 mass, habitat temperature, habitat depth and taxon (fishes or cephalopods) varied

362 depending on the choice of body mass units (DM or C, N) [O:N Model (5), Table 3].
363 Nonetheless, the contribution of the significant variables to the variance was as small as
364 4.4–6.4% (adjusted R^2 = 0.044–0.064). In fact, variance analyses showed no difference
365 in the O:N ratio data among the three taxa ($F = 2.791$, $df = 2,168$, $p = 0.064$). The
366 significant difference seen between cephalopods and fishes was overwhelmed in the
367 broad variance analyses that included crustacean data.
368
369 **4. Discussion**
370 4.1. *Methodological constraints*
371 The metabolic data for fishes and cephalopods listed in Tables 1-1 and 1-2 were derived
372 from experiments on unfed wild animals. Experiments in the absence of food are
373 imperative to determine the rates of respiration and ammonia excretion accurately
374 without corrections for complex uptake/release of oxygen and ammonia by food
375 organisms during experiments (Ikeda et al., 2000), but longer-term starvation of animals
376 may influence their normal metabolism. Specific dynamic action (SDA) is a widespread
377 phenomenon across diverse animals and is interpreted as the energy expended on
378 ingestion, digestion, absorption and assimilation of food (Secor, 2009). The magnitude
379 and temporal variation of SDA are functions of feeding duration and meal size (Secor,
380 2009). SDA accompanies an increase in ammonia excretion rates, but the pattern and
381 magnitude differ greatly from those of respiration rates from one fish to the next (cf.
382 review of Wood, 2001). In a typical study on juvenile rainbow trout fed ad libitum,
383 ammonia excretion increased 6-fold while respiration showed only a 1.7-fold increase in
384 the 2 h after the cession of feeding (Alsop and Wood, 1997).
385 Clearly, the types of natural prey, daily ration and feeding history prior to

386 experiments need to be taken into account for better extrapolation of laboratory
387 measurements to wild animals. In practice, the inability to define those conditions for
388 wild fishes and cephalopods at the time of collection hinders an appropriate correction
389 of the measured rates. When analyzing SDA data from 56 fishes and 1 cephalopod
390 (octopus), Secor (2009) concluded that the maximal increase in routine respiration rates
391 by SDA averaged 2.36 (± 0.07, 1SD) and 3.00 times, respectively, the rates of
392 non-feeding animals. Thus, a factor of 2× or 3× may be taken as the maximum for the
393 routine respiration rate of wild fishes and cephalopods engaging in feeding for 24 hours
394 daily, but the factor would be much less for fishes or cephalopods that feed only at
395 night.
396
397 4.2. *Effects of body mass*
398 Interspecific basal or standard metabolic rate allometries of organisms from a
399 broad variety of taxa and of many different sizes (bacteria to large mammals) have been
400 documented to be a power function of body mass with an exponent of 0.75
401 (Hemmingsen, 1960). Since West et al. (1997) provided a theoretical foundation (fractal
402 network theory) for this empirical 3/4 power law, the theory has been contested
403 regarding the validity of its mathematical and methodological bases (Kozłowski and
404 Konarzewski, 2004, 2005) and verification with the data (Isaac et al., 2010 and
405 literatures therein). While the debate is not settled, alternative analytic theories that are
406 free from the constraint of a fixed scaling exponent have also been proposed (Agutter
407 and Tuszynski, 2011; Hirst et al., 2014).
408 For fish metabolism, the scaling exponent of the empirical models proposed by
409 Winberg (1956) and Clarke and Johnston (1999) is interesting to the present study for

two reasons. One, these references contain comprehensive datasets of diverse fishes of a broad variety of body sizes (87–870,000 mg WM for the Winberg model, and 400–3,000,000 mg WM for the Clarke and Johnston model), which is comparable to the present study (body mass range; 4.1–10,076,000 mgWM, Appendix A, S2). Two, they adopted the same regression model used in the present study (linear regression of the logarithm of respiration rate on the logarithm of body mass). The model of Acuña et al. (2011) also addressed a broad body mass range (0.01–10,000,000 mgWM) of fishes. However, the resultant model of Acuña et al. (2011) is not an empirical one in the strict sense because they made the temperature correction by adopting a hypothetical temperature coefficient (E_a = 0.65 eV, or Q_{10} = 2.5 for the temperature range of –1.8 to 30^{o}C). The Winberg (1956) model predicts “routine metabolism” (normal activity), and the Clarke and Johnston (1999) model predicts “standard” or “resting” metabolism (no activity) of fish. The scaling exponent of WM is 0.81 (95% CI: 0.79–0.83) for marine fish in the Winberg model, and is 0.80 (0.687–0.930) in the Clarke and Johnston model, and is intraspecifically and interspecifically consistently in both studies. The scaling exponents of WM derived from Models (1) and (3) in the present analyses [0.885 (95% CI: 0.843–0.925) and 0.893 (0.855–0.931)] are greater than in the two previous studies, but did not differ significantly from that of the Clarke and Johnston model because the 95% CI ranges overlap partially each other. The greater exponent of the present study may have been due to the inclusion of the data of larval fish, of which respiration rates are disproportionally lower than the rates of juvenile/adult fishes (Post and Lee, 1996). Bochdansky and Leggett (2001) analyzed the relations between the routine respiration rate and body mass of larval and juvenile fishes (25 species) with a WM range of 0.06–600,000 mg. The results of their analyses demonstrated a gradual decrease in the

scale exponents with WM from approximately 1.0 to 0.6 along with the increase in body mass; thus the overall pattern of the change in the exponents may be curvilinear, rather than linear, on a log-log plot. Notably, despite the non-linear relation between the routine metabolism and body mass, the relation overlapped greatly with the linear model of Winberg (1956) mentioned above. Thus, discrepancies in the scaling exponents with body mass in fishes in the present results and with those of the other workers may have been caused by the confounding effects of body mass range [inclusion of the data on smaller fishes (this study) or not (the other studies)], species [solely pelagic species or pelagic larvae/juveniles of demersal species (this study) or a mixture of pelagic and demersal species (the other studies)], ecology [shallow and deep water species (this study) or shallow water species only (the other studies)], and respirometry [well defined routine metabolism data by swimming speed for large species (this study) versus routine metabolism data with no swimming speed data or standard metabolism (the other studies)].

For pelagic cephalopods, available information about the relation between metabolism and body mass is limited to Seibel (2007), who listed scaling relations between the routine respiration rate and the WM of eight families (0.77–0.98, with a mean of 0.80). Grigoriou and Richardson (2009) modeled the routine metabolism of laboratory-raised cuttlefish (*Sepia officinalis*); however, their data do not meet the selection criteria established in the present study, so no meaningful comparison can be conducted. As the only comparable interspecific data, the mean scaling exponent with WM (0.80), derived by Seibel (2007) and mentioned above, does not differ significantly from the present results [0.779 (95% CI: 0.644–0.914) from Model (1), and 0.738 (0.639–0.837) from Model (2), Table 2)].

458

459 4.3. *Effects of temperature*

460 Clarke (1987) differentiated intraspecific Q_{10} from interspecific Q_{10}; the former
461 represents the adjustment of an organism to a new temperature in the laboratory
462 (acclimation), and the latter, the evolutionary adjustment of an organism's physiology to
463 the environment (adaptation). Acclimated (intraspecific) Q_{10} is interpreted as reflecting
464 the acute thermodynamic effect of temperature, and the adapted (interspecific) Q_{10}, as
465 an evolutionary optimization of each species ["evolutionary trade-off" (ET) hypothesis,
466 Clarke and Fraser, 2004]. Clarke and Fraser (2004) developed the ET hypothesis from
467 their compilation of the resting respiration data for 69 teleost fishes from a global range
468 of habitat temperatures spanning 40^{o}C (acclimated Q_{10} = 2.40 > adapted Q_{10} = 1.83,
469 Clarke and Johnston, 1999). By comparison, Gillooly et al. (2001) proposed a
470 "universal temperature dependence" (UTD) hypothesis based on the relation between
471 resting metabolic rates adjusted to 1 g WM and temperature for a broad suite of
472 organisms, including unicells, plants, invertebrates and vertebrates, and they concluded
473 that the magnitude of the effect of temperature on the rates was relatively constant and
474 expressed by the activation energy (E_a) of 0.6–0.7 eV, which is equivalent to Q_{10} =
475 2.3–2.7 for the temperature range of –2 to 30^{o}C [the quantitative range they accept
476 within their UTD hypothesis (Gillooly et al., 2001, 2006)]. Thus, the UTD hypothesis is
477 based on the notion of a biochemical mechanism (Boltzmann kinetics) common within-
478 and between-species, thereby implying that acclimated Q_{10} = adapted Q_{10} = 2.3–2.7 (cf.
479 Clarke, 2006).

480 The Winberg model for fish metabolism mentioned above adopted an empirical
481 "normal curve" to adjust the data at 20^{o}C to a given temperature and, thereby, is not

482 comparable to the present results. In this regard, the temperature response of the Clarke
483 and Johnston model is based on the data of fishes from diverse thermal regimes of –2 to
484 40^{o}C; thereby the results of that model can be compared with the present results (–2 to
485 30^{o}C). The resultant temperature response of fish metabolism normalized by WM in
486 terms of Q_{10} by Clarke and Johnston is 1.83 (computed over the temperature range
487 0–30^{o}C), which is close to 2.02 [95%CI: 1.68–2.42, Model (1) based on body WM) or
488 1.96 [1.66–2.30, Model (3) based on body WM] in the present study. Thus, the present
489 results favor the ET hypothesis rather than the UTD hypothesis.
490 No information is available on the adapted Q_{10} for the pelagic cephalopods at
491 present. The present analyses of data from 41 cephalopods from diverse thermal
492 regimes (–0.8 to 29.5^{o}C) yielded a mean Q_{10} of 2.62 [95% CI: 1.56–4.38, Model (1)
493 based on body WM) or 2.07 [1.43–3.01, Model (2) based on body WM], but wide 95%
494 CI ranges makes it difficult to discern whether the data fit the ET hypothesis or the UT
495 hypothesis.
496
497 4.4. *Effects of habitat depth*
498 A rapid reduction in metabolic rates with increasing habitat depth of the pelagic fishes
499 and cephalopods has been established based on the comprehensive data by Torres et al.
500 (1979) and Seibel et al. (1997), respectively. These depth-related changes in metabolic
501 rates are consistent with *in situ* observations from submersibles that deeper-living fishes
502 and cephalopods are inactive and often neutrally buoyant (or “lethargic”; Vecchione and
503 Roper, 1991 and literatures therein). Their feeding strategies of these deeper-living
504 organisms, so called “sit-and-wait” behavior, appears advantageous in terms of energy
505 saving for life in the food-poor deep sea, where encounter rates with prey are extremely

low. The bodies of many deeper-living fishes are characterized by higher water content, less muscle (or protein or N) and a less ossified skeleton (or ash) than observed in shallow-living counterparts (Denton and Marshall, 1958; Childress and Nygaard, 1973). With the exception of the higher water content (Fig. 1 in Childress et al., 2008), comparable body composition data of fishes are not available for deeper-living cephalopods. Notably, these body composition features of the deeper-living fishes and cephalopods are not the only cause of the reduction in metabolic rates with increasing depth, as significant reductions still occur in respiration with habitat depth regardless of body mass unit (WM, DM, C or N) examined in the fishes and cephalopods in the present study (Table 2).

Seibel et al. (1997) noted that the depth-related decline in WM-specific respiration rates was greater in cephalopods than in fishes. The present results from Model (4), in which the data were pooled for the cephalopods and fishes, suggest a similar difference (Fig. 3C). This difference suggests the presence of a cephalopod family characterized by extremely high respiration rates, such as the shallow-living Ommastrephidae [cf. coefficient a_{13} of Model (2), Table 2], which influenced the coefficient a_3 of Model (1) of the cephalopods and a_7 of Model (4) (Table 3).

For the progressive decline of respiration rates in the deeper-living pelagic animals, the “visual-interactions hypothesis” (Childress, 1995) and the “predation-mediated selection hypothesis” (Ikeda et al., 2006) have been offered. These hypotheses both interpret the phenomenon as being a result of lowered selective pressure for high activity at depth because of the decrease in visual predators in the dark. However, these two hypotheses are different in that the former applies strictly to micronekton with functional eyes (Childress et al., 2008), whereas the latter applies to

micronekton and zooplankton either with or without functional eyes (Ikeda, 2008). The negative effects of habitat depth have been confirmed in the empirical respiration model of aquatic invertebrates regardless of the presence or absence of functional eyes (Brey, 2010). Because fishes and cephalopods possess functional eyes and both exhibited a decline in metabolism downward regardless of the body mass units examined (Table 2), the present results analysis cannot distinguish between these competing hypotheses.

4.5. *O:N ratios*

Clearly, available ammonia excretion or O:N ratio data for either wild cephalopods or wild fishes are extremely limited in terms of being able to analyze the effects of body mass, habitat temperature and habitat depth (Appendix A, S1and S2). Nevertheless, O:N ratios have been demonstrated to show little variation in comparisons of those parameters and are quite stable across various metazooplankton taxa (Ikeda, 2014).

The atomic ratio of the respiratory oxygen consumption rate to ammonia-nitrogen excretion rate (O:N ratio) is 7 when only protein is metabolized and is calculated to be 21 or 13 when protein-and-lipid or protein-and-carbohydrate, respectively, are catabolized in equal quantities simultaneously (Table 10.3 in Ikeda et al., 2000). The O:N ratios greater than 21 are indicative of lipid or carbohydrate predominance in the metabolite. The large variations in the O:N ratios of the 35 fishes (5.9–66.4; median, 24.2) suggest broad food habits (carnivores, omnivores, or herbivores). The median O:N ratio (24.2) implied the predominance of a lipid or carbohydrate-oriented metabolism in general. Because in most studies, the fishes were placed in filtered seawater without providing food for the 1-5 h of the experiments (see “Materials and methods” Section), thereby lowering the contribution of protein as a metabolite, the results of this study are

554 consistent with previous results (14-36% of the total metabolites) on nonfed rainbow
555 trout, the Nile tilapia, sockeye salmon and others [see review of Wood (2001)].
556 According to Wood (2001), the major metabolite in fish fed to satiation is protein, but in
557 nonfed fish, it is lipid followed by protein or carbohydrate.

558 Cephalopods are exclusive carnivores (Boyle and Rodhouse, 2005). In support of
559 the anticipated low O:N ratios of cephalopods, the squid *Loligo forbesi* and the octopus
560 *Octopus maya* that were raised from eggs in the laboratory and fed well-defined
561 protein-rich diets (copepods, shrimp larvae and mysids) showed O:N ratios of 8–23 and
562 9.0–15.0, respectively (Segawa and Hanlon, 1988). In the present study, the O:N ratios
563 of cephalopods, with the exception (98.4) of a deeper-living cirrate octopod
564 *Stauroteuthis syrtensis* (code: C40, Table 1), were also low (11.3–17.2, S1). As a
565 cephalopod species, the anomalously high O:N ratio of *S. syrtensis* has been explained
566 by their feeding on the lipid-rich copepod *Calanus finmarchicus* (Jacoby et al., 2009).

567 An O:N ratio of the cephalopod *Cranchia* sp. (code: C10) in S1 [original data; 1.5
568 (± 0.6 SD, N = 5), Ikeda, unpublished data], which is well below the theoretical
569 minimum (7, mentioned above) and omitted in the regression analyses, deserves
570 attention. The family Cranchiidae is known as an ammoniacal squid with a very large
571 coelom filled with ammonia chloride-rich fluid to achieve nearly neutral buoyancy in
572 seawater (Denton et al., 1969; Voight et al., 1994). Hence, that the ammonia determined
573 is highly likely the sum of that excreted as the end-product of protein catabolism and
574 also that stored in the coelom and leaked during the experiment, though the origin of the
575 latter is not clear (Denton et al., 1969).

576

577 4.6. *Cephalopods versus fishes*

578 For valid metabolic comparison between taxa, a common effect of independent
579 variables, such as body mass, habitat temperature and habitat depth needs to be
580 demonstrated or be assumed (otherwise, the conclusion varies depending on the choice
581 of the value of the variables). For metabolic comparison between the pelagic
582 cephalopods and fishes, the effects of body mass and habitat temperature were
583 demonstrated to be the same [the coefficients a_5 and a_6 of Model (4) were not
584 significant, Table 3]. Then, assuming the same effect of habitat depth, the resultant
585 regression equation showed higher respiration rates of the cephalopods than the fishes
586 on DM, C or N body mass basis (by a factor 1.5- to 1.7- fold), but not on the basis of
587 WM body mass [Model (4), Table 3]. The difference in results due to the choice of body
588 mass units (DM, C or N versus WM) may reflect the higher body water content [85.2 (±
589 6.4 SD, N = 50) % of WM, calculated from the data in Appendix A, S1] of cephalopods
590 than in fishes [78.1(± 8.6, N = 102) calculated from the data in Appendix A, S2], and a
591 large scatter of the cephalopod data associated with the regression of respiration rates on
592 WM (adjusted R^2 = 0.897, Cephalopod Model 1, Table 2) compared with those with the
593 regressions of the rates on DM, C or N (adjusted R^2 = 0.932–0.938).
594 The data from pelagic fishes and cephalopods can be put into a wider perspective
595 if compared with marine pelagic crustaceans, which include the predominant
596 components of the zooplankton and micronekton taxa, such as copepods, euphausiids,
597 amphipods, mysids and decapods (Fig. 4). The results of multiple regression analyses
598 based on DM, C and N body mass units [Respiration Model (5), Table 3] showed that
599 the routine respiration rates of the cephalopods and the crustaceans were similar, but the
600 fishes exhibited slightly lower rates (by a factor of 0.76×) than these two taxa. The
601 present results are not consistent with those of Acuña et al. (2011), who compared the

602 relations between temperature-corrected (at 15^{o}C) routine respiration rate and body
603 mass (expressed as WM or C) of pelagic crustaceans and fishes and found no significant
604 differences between the two taxa. The fish data used in the analyses of Acuña et al. are
605 from shallow-living pelagic and demersal species (in contrast to a mixture of shallow-
606 and deeper-living pelagic species or pelagic stages of demersal species in the present
607 study), and the temperature corrections are substituted by the hypothetical value of E_a =
608 0.65 eV, or Q_{10} = 2.5 [in contrast to the empirical one of E_a = 0.495 eV (or Q_{10} = 2.0)
609 on the basis of WM or E_a = 0.634 eV (or Q_{10} = 2.4) on the basis of C, cf. the coefficient
610 of a_2 of Model (4), Table 3]. These differences in the ecology of the fishes from which
611 metabolic data were derived and in the standardization methods for the temperature
612 might account for the dissimilar conclusions between these two studies. In light of the
613 great lack of data on the metabolic rates and chemical composition of pelagic
614 cephalopod and fish species living in the deep sea, an accumulation of data is needed to
615 validate and improve the models in the future. Therefore, the role of cephalopod and
616 fish communities in C and N cycles in the oceans can be assessed more precisely by
617 knowing their body mass spectra, ambient temperatures and depth distributions.
618 As a general conclusion, the present results offer a broad choice of body mass
619 units to predict the routine respiration rates of pelagic fishes and cephalopods living in
620 various depth horizons of the world’s oceans. In addition to body mass, habitat
621 temperature and habitat depth, the information on taxonomy will improve the precision
622 of the predictions. When information on the taxonomy is not available, DM, C or N,
623 rather than WM, would be the choice of body mass units to yield better predictions.
624 While similar analyses were not possible for ammonia excretion rates because of the
625 limited data available, ammonia excretion rates can be predicted indirectly from the

626 respiration rates combined with the median O:N ratios (13.2 for cephalopods and 24.2
627 for fishes, cf. Section 4.5.). Taking into account the effects of habitat temperature and
628 habitat depth, a comparison of the present results with pelagic crustaceans at an
629 equivalent body mass showed that fishes respired at slightly lower rates than
630 crustaceans, but no difference was found between cephalopods and crustaceans.
631

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637

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Table 1-1. A list of cephalopods of which routine metabolic data were analyzed. Some pecies were separated into 2 or more groups depending on collection sites or body sizes. Abbreviations of orders or families in parenthese denote dummy variables designated in multiple regression analyses.

Superorder	Order	Family	Genus and species	Code	Collection site	Date	Reference
Decapodiformes	Decapodiformes (De)	Bathyteuthidae	*Bathyteuthis abyssicola*	C1	Off Hawaii, USA	Sep 1992-Sep 1996	Seibel et al. (1997)
		Chtenopterygidae	*Chtenopteryx sicula*	C2	Off Hawaii, USA	Sep 1992-Sep 1996	Seibel et al. (1997)
	Myopsida	Loliginidae (Lo)	*Loligo forbesii*	C3	Off Roscoff, France	Jan 1986	Boucher-Rodoni and Mangold(1989)
			Lolliguncula brevis	C4-1	Chesapeake Bay, USA		Bartol et al.(2001)
			Lolliguncula brevis	C4-2	Chesapeake Bay, USA		Bartol et al.(2001)
			Lolliguncula brevis	C4-3	Chesapeake Bay, USA		Bartol et al.(2001)
			Lolliguncula brevis	C4-4	Chesapeake Bay, USA		Bartol et al.(2001)
			Lolliguncula brevis	C4-5	Chesapeake Bay, USA		Bartol et al.(2001)
			Lolliguncula brevis	C4-6	Chesapeake Bay, USA		Bartol et al.(2001)
			Lolliguncula brevis	C4-7	Galveston Bay, Texas, USA		Segawa and Hanlon (1988)
			Sepioteuthis lessoniana	C5	Pacific coast of central Japan		Segawa (1991)
	Oegopsida	Chiroteuthidae (Ch)	*Chiroteuthis calyx*	C6	Off California, USA	Sep 1992-Sep 1996	Seibel et al. (1997)
			Chiroteuthis imperator	C7	Off Hawaii, USA	Sep 1992-Sep 1996	Seibel et al. (1997)
			Planctoteuthis oligobessa (formerly *Valbyteuthis oligobessa)*	C8	Off California, USA	Sep 1992-Sep 1996	Seibel et al. (1997)
		Cranchiidae (Cr)	*Cranchia scabra*	C9	Off California, USA	Sep 1992-Sep 1996	Seibel et al. (1997)
			Cranchia sp.	C10	Prydz Bay, Antarctica	Jan 1985	Ikeda,unpublished data
			Galiteuthis glacialis	C11-1	Weddell Sea, Antarctica	Nov-Dec 1993	Donnelly et al. (2004)
			Galiteuthis glacialis	C11-2	Weddell Sea, Antarctica	Nov-Dec 1993	Donnelly et al. (2004)
			Galiteuthis phyllura	C12	Off California, USA	Sep 1992-Sep 1996	Seibel et al. (1997)
			Helicocranchia pfefferi	C13	Off California, USA	Sep 1992-Sep 1996	Seibel et al. (1997)
			Leachia dislocata	C14	Off California, USA	Sep 1992-Sep 1996	Seibel et al. (1997)
			Leachia pacifica	C15	Off Hawaii, USA	Sep 1992-Sep 1996	Seibel et al. (1997)
			Liocranchia valdivia	C16	Off Hawaii, USA	Sep 1992-Sep 1996	Seibel et al. (1997)
			Megalocranchia fisheri	C17	Off Hawaii, USA	Sep 1992-Sep 1996	Seibel et al. (1997)
		Enoploteuthidae (En)	*Abraliopsis felis*	C18	Off California, USA	Sep 1992-Sep 1996	Seibel et al. (1997)
			Abraliopsis pacificus	C19	Off Hawaii, USA	Sep 1992-Sep 1996	Seibel et al. (1997)
			Enoploteuthis higginsi	C20	Off Hawaii, USA	Sep 1992-Sep 1996	Seibel et al. (1997)
		Gonatidae (Go)	*Gonatus onyx*	C21	Off California, USA	Sep 1992-Sep 1996	Seibel et al. (1997)
			Gonatus pyros	C22	Off California, USA	Sep 1992-Sep 1996	Seibel et al. (1997)
		Histioteuthidae (Hi)	*Histioteuthis heteropsis*	C23-1	Off California, USA	Sep 1992-Sep 1996	Seibel et al. (1997)
			Histioteuthis heteropsis	C23-2	Off California, USA	Sept 1975	Belman (1978)
			Histioteuthis hoylei	C24	Off California, USA	Sep 1992-Sep 1996	Seibel et al. (1997)
		Joubiniteuthidae (Jo)	*Joubiniteuthis portieri*	C25	Off Hawaii, USA	Sep 1992-Sep 1996	Seibel et al. (1997)
		Mastigoteuthidae (Ma)	*Echinoteuthis famelica (* formerly *Mastigoteuthis famelica)*	C26	Off Hawaii, USA	Sep 1992-Sep 1996	Seibel et al. (1997)
		Octopoteuthidae (Oc)	*Octopoteuthis deletron*	C27	Off California, USA	Sep 1992-Sep 1996	Seibel et al. (1997)
			Octopoteuthis nielseni	C28	Off Hawaii, USA	Sep 1992-Sep 1996	Seibel et al. (1997)
		Ommastrephidae (Om)	*Dosidicus gigas*	C29	Gulf of California/Eastern tropical Pacific	May-Jun 2006, Jun 2007, Oct-Nov 2007	Rosa and Seibel (2010)
			Illex illecebrosus	C30-1	St. Margaret's Bay Nova Scotia, Canada	Aug-Nov 1982, 1983	Webber and O'Dor (1985)
			Illex illecebrosus	C30-2	Coast of Halifax, Nova Scotia, Canada		Hoeger et al.(1987)
			Sthenoteuthis oualaniensis	C31	Tropical Indo-Pacific Ocean	1961-1990	Shulman et al.(2002)/Zuyev et al. (2002)
			Sthenoteuthis pteropus	C32	Tropical Atlantic Ocean	1961-1990	Shulman et al.(2002)/Zuyev et al. (2002)
		Psychroteuthidae (Ps)	*Psychroteuthis* sp.	C33	Prydz Bay, Antarctica	Nov 1982	Ikeda and Bruce (1986)
		Pyroteuthidae (Py)	*Pterygioteuthis microlampas*	C34	Off Hawaii, USA	Sep 1992-Sep 1996	Seibel et al. (1997)
	Sepiida	Sepiolidae (Se)	*Heteroteuthis hawaiiensis*	C35	Off Hawaii, USA	Sep 1992-Sep 1996	Seibel et al. (1997)
Octopodiformes	Vampyromorpha	Vampyroteuthidae (Va)	*Vampyroteuthis infernalis*	C36	Off California, USA	Sep 1992-Sep 1996	Seibel et al. (1997)
	Octopoda (Oc)	Amphitretidae	*Eledonella pygmaea*	C37	Off Hawaii, USA	Sep 1992-Sep 1996	Seibel et al. (1997)
			Japetella diaphana	C38	Off Hawaii, USA	Sep 1992-Sep 1996	Seibel et al. (1997)
			Japetella heathi	C39	Off California, USA	Sep 1992-Sep 1996	Seibel et al. (1997)
		Cirroteuthidae	*Stauroteuthis syrtensis*	C40	NW Atlantic Ocean	Sep 2004	Jacoby et al. (2009)
		Octopodidae	*Octopus rubescens* (juv.)	C41	Off California, USA	Sep 1992-Sep 1996	Seibel et al. (1997)

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Table 1-2. A list of teleost fishes of which routine metabolic data were analyzed. Some pecies were separated into 2 or more groups depending on collection sites or body sizes. Abbreviations of orders in parenthese denote dummy variables designated in multiple regression analyses. Note: Fishes are pelagic species or pelagic larvae/juveniles of demersal species (Ikeda 1974, Smith and Brown 1983, Morris and North 1984, Ikeda et al. 2011).

Order	Genus and species	Code	Collection site	Date	Reference
Anguilliformes (An)	*Ariosoma balearicum*, leptocephalus larvae	F1	E. Gulf of Mexico	1990-1996	Bishop and Torres (1999)
	Gymnothorax saxicola, leptocephalus larvae	F2	E. Gulf of Mexico	1990-1996	Bishop and Torres (1999)
	Ophichthus gomesii, leptocephalus larvae	F3	E. Gulf of Mexico	1990-1996	Bishop and Torres (1999)
	Paraconger caudilimbatus, leptocephalus larvae	F4	E. Gulf of Mexico	1990-1996	Bishop and Torres (1999)
Atheriniformes (At)	*Hypoatherina* sp.	F5-1	GBR inshorewater, Australia	Oct 2009	Ikeda et al. (2011)
	Hypoatherina sp.	F5-2	GBR inshorewater, Australia	Dec 2009	Ikeda et al. (2011)
Beloniformes (Bel)	*Cypselurus* sp.	F6	Tropical W Atlantic Ocean	Jan 1972	Ikeda (1974)
	Scomberesocidae sp.	F7	Oshoro Bay, Hokkaido, Japan	Jul 1970	Ikeda (1974)
Beryciformes (Ber)	*Anoplogaster cornuta*	F8-1	Off S. California, USA	Jul 1970, Feb 1971	Meek and Childress (1973)
	Anoplogaster cornuta	F8-2	Off S. California, USA	1974-1975	Torres et al. (1979)
	Anoplogaster cornuta	F8-3	E. Gulf of Mexico	Jun 1981-Jul 1985	Donnelly and Torrres (1988)
Clupeiformes (Cl)	*Brevoortia tyrannus*	F9	Narragansett Bay, R.I., USA		Durbin et al. (1981)
	Engraulis capensis	F10	Off Cape Town, S. Africa		James and Probyn (1989)
	Engraulis ringens	F11-1	Costa Rica Dome, off Peru		Whitledge and Packard (1971)
	Engraulis ringens	F11-2	Off Peru, S. America		Villavicencio (1981)
	Herklotsichthys sp.	F12	GBR inshorewater, Australia	Oct 2009	Ikeda et al. (2011)
	Sardinops sagax (formaly *S. caerulea*)	F13	Off California, USA	Oct-Dec 1960, 1961	Lasker (1970)
Gadiformes (Ga)	*Melanonus zugmayeri*	F14	Off S. California, USA	1974-1975	Torres et al. (1979)
Lophiiformes (Lo)	Caulophrynidae sp.	F15	Off Oauhu, Hawaii		Cowles and Childress (1995)
	Melanocetus johnsonii	F16	Off Oauhu, Hawaii	Jul 1983-Jul 1986	Cowles and Childress (1995)
	Oneirodes acanthias	F17	Off S. California, USA	1974-1975	Torres et al. (1979)
	Oneirodes sp.	F18	Off Oauhu, Hawaii		Cowles and Childress (1995)
Mugiliformes (Mu)	*Neomyxus* sp.	F19-1	GBR inshorewater, Australia	Apr 2010	Ikeda et al. (2011)
	Neomyxus sp.	F19-2	GBR inshorewater, Australia	Apr 2010	Ikeda et al. (2011)
Myctophiformes (My)	*Diaphus mollis*	F20	E. Gulf of Mexico	Jun 1981-Jul 1985	Donnelly and Torrres (1988)
	Diaphus theta	F21	Off S. California, USA	1974-1975	Torres et al. (1979)
	Electrona antarctica	F22	Scotia-Weddell Sea	Nov-Dec 1983, Mar 1986	Torres and Somero (1988)
	Gymnoscopelus braueri	F23	Scotia-Weddell Sea	Nov-Dec 1983, Mar 1986	Torres and Somero (1988)
	Gymnoscopelus opisthopterus	F24	Scotia-Weddell Sea	Nov-Dec 1983, Mar 1986	Torres and Somero (1988)
	Lampanyctus nobilis	F25	E. Gulf of Mexico	Jun 1981-Jul 1985	Donnelly and Torrres (1988)
	Lampanyctus regalis	F26	Off S. California, USA	1974-1975	Torres et al. (1979)
	Lampanyctus ritteri	F27	Off S. California, USA	1974-1975	Torres et al. (1979)
	Lepidophanes guentheri	F28	E. Gulf of Mexico	Jun 1981-Jul 1985	Donnelly and Torrres (1988)
	Myctophum affine	F29	E. Gulf of Mexico	Jun 1981-Jul 1985	Donnelly and Torrres (1988)
	Parvilux ingens	F30	Off S. California, USA	1974-1975	Torres et al. (1979)
	Scopelengys tristis	F31	Off S. California, USA	1974-1975	Torres et al. (1979)
	Stenobrachius leucopsarus	F32	Off S. California, USA	1974-1975	Torres et al. (1979)
	Tarletonbeania crenularis	F33	Off S. California, USA	1974-1975	Torres et al. (1979)
	Triphoturus mexicanus	F34	Off S. California, USA	1974-1975	Torres et al. (1979)
Osmeriformes (Os)	*Bajacalifornia burragei*	F35	Off S. California, USA	1974-1975	Torres et al. (1979)
	Bathylagus antarcticus	F36	Scotia-Weddell Sea	Nov-Dec 1983, Mar 1986	Torres and Somero (1988)
	Bathylagus milleri	F37	Off S. California, USA	1974-1975	Torres et al. (1979)
	Bathylagus ochotensis	F38	Off S. California, USA	1974-1975	Torres et al. (1979)
	Bathylagus wesethi	F39	Off S. California, USA	1974-1975	Torres et al. (1979)
	Sagamichthys abei	F40	Off S. California, USA	1974-1975	Torres et al. (1979)
Perciformes (Pe)	*Abudefduf vaigiensis*	F41	GBR inshorewater, Australia	Jan 2010	Ikeda et al. (2011)
	Ambassis sp.	F42-1	GBR inshorewater, Australia	Nov 2009	Ikeda et al. (2011)
	Ambassis sp.	F42-2	GBR inshorewater, Australia	Dec 2009	Ikeda et al. (2011)
	Amblyeleotris sp.	F43	GBR inshorewater, Australia	Dec 2009	Ikeda et al. (2011)
	Amblygobius sp.	F44	GBR inshorewater, Australia	Feb 2010	Ikeda et al. (2011)
	Ammodytes sp.	F45	SW coast of Hokkaido, Japan	May 1971	Ikeda (1974)
	Apogon sp.	F46	GBR inshorewater, Australia	Jan 2010	Ikeda et al. (2011)
	Callionymus sp.	F47	Oshoro Bay, Hokkaido, Japan	Jun 1970	Ikeda (1974)
	Chiasmodon niger	F48	Off Oahu, Hawaii		Cowles and Childress (1995)
	Coryphaena hippurus	F49	Arabian Sea	1987	Waller (1989)
	Cubiceps whiteleggii	F50	Arabian Sea	1987	Waller (1989)
	Euthynnus affinis	F51	Off Oahu, Hawaii	Jul-Aug 1997	Sepulveda and Diskson (2000)
	Galeoides sp.	F52	Tropical E Pacific Ocean	Feb 1972	Ikeda (1974)
	Gerres sp.	F53	GBR inshorewater, Australia	Jan 2010	Ikeda et al. (2011)
	Katsuwonus pelamis	F54	Off Hawaii		Gooding et al. (1981)
	Leiognathus sp.	F55	GBR inshorewater, Australia	Jan 2010	Ikeda et al. (2011)
	Lethrinus sp.	F56-1	GBR inshorewater, Australia	Dec 2009	Ikeda et al. (2011)
	Lethrinus sp.	F56-2	GBR inshorewater, Australia	Jan 2010	Ikeda et al. (2011)
	Lutjanus carponotatus	F57	GBR inshorewater, Australia	Dec 2009	Ikeda et al. (2011)
	Mullidae sp.	F58	GBR inshorewater, Australia	Dec 2009	Ikeda et al. (2011)
	Neopomacentrus bankieri	F59	GBR inshorewater, Australia	Nov 2009	Ikeda et al. (2011)
	Notothenia rossii	F60	Cumberland East Bay, South Georgia	Feb-Mar 1982	Morris and North (1984)
	Omobranchus sp.	F61	GBR inshorewater, Australia	Jan 2010	Ikeda et al. (2011)
	Pelates quadrilineatus	F62	GBR inshorewater, Australia	Apr 2010	Ikeda et al. (2011)
	Pomacentrus sp.	F63	GBR inshorewater, Australia	Sep 2009	Ikeda et al. (2011)
	Pseudocaranx dentex (formaly *Longirostrum delicatissimus*)	F64	Tropical W Atlantic Ocean	Jan 1972	Ikeda (1974)
	Scomber japonicus	F65	Off S. California, USA	May-Aug 1998	Sepulveda and Diskson (2000)
	Scomberoides lysan	F66	GBR inshorewater, Australia	Jan 2010	Ikeda et al. (2011)
	Scomberomorus queenslandicus	F67	GBR inshorewater, Australia	Jan 2010	Ikeda et al. (2011)
	Selaroides leptolepis	F68	GBR inshorewater, Australia	Jan 2010	Ikeda et al. (2011)
	Siganus sp.	F69	GBR inshorewater, Australia	Dec 2009	Ikeda et al. (2011)
	Sphyraena sp.	F70	GBR inshorewater, Australia	Jan 2010	Ikeda et al. (2011)
	Terapon sp.	F71	GBR inshorewater, Australia	Apr 2010	Ikeda et al. (2011)
	Thunnus alalunga	F72	Off California, USA	Jul, Aug 1981	Graham and Laurs (1982)
	Thunnus albacares	F73-1	Off Hawaii	Aug 1990-Sep 1991	Dewar and Graham (1994)
	Thunnus albacares	F73-2	Off Hawaii	Aug 1990-Sep 1991	Dewar and Graham (1994)
	Upeneus tragula	F74	GBR inshorewater, Australia	Dec 2009	Ikeda et al. (2011)
Scorpaeniformes (Sc)	*Caracanthus* sp.	F75-1	GBR inshorewater, Australia	Apr 2010	Ikeda et al. (2011)
	Caracanthus sp.	F75-2	GBR inshorewater, Australia	Apr 2010	Ikeda et al. (2011)
	Hexagrammos otakii	F76	Oshoro Bay, Hokkaido, Japan	Jun 1970	Ikeda (1974)
	Sebastolobus altivelis	F77	Off S. California, USA	Mar 1982	Smith and Brown (1983)
Stephanoberyciformes (Ste)	*Melamphaes acanthomus*	F78	Off S. California, USA	1974-1975	Torres et al. (1979)
	Scopelogadus mizolepis bispinosus	F79	Off S. California, USA	1974-1975	Torres et al. (1979)
	Poromitra crassiceps	F80	Off S. California, USA	1974-1975	Torres et al. (1979)
Stomiiformes (Sto)	*Argyropelecus aculeatus*	F81	E. Gulf of Mexico	Jun 1981-Jul 1985	Donnelly and Torrres (1988)
	Aristostomias scintillans	F82	Off S. California, USA	1974-1975	Torres et al. (1979)
	Borostomias panamensis	F83	Off S. California, USA	1974-1975	Torres et al. (1979)
	Cyclothone acclinidens	F84-1	Off S. California, USA	Jun 1979	Smith and Laver (1981)
	Cyclothone acclinidens	F84-2	Off S. California, USA		Smith and Laver (1981)
	Cyclothone acclinidens	F84-3	Off S. California, USA		Smith and Laver (1981)
	Cyclothone microdon	F85	Scotia-Weddell Sea	Nov-Dec 1983, Mar 1986	Torres and Somero (1988)
	Gonostoma elongatum	F86	E. Gulf of Mexico	Jun 1981-Jul 1985	Donnelly and Torrres (1988)
	Stomias atriventer	F87	Off S. California, USA	1974-1975	Torres et al. (1979)
	Stomias danae	F88	Off Oauhu, Hawaii		Cowles and Childress (1995)
Tetraodontiformes (Te)	Monacanthidae sp.	F89-1	GBR inshorewater, Australia	Jan 2010	Ikeda et al. (2011)
	Monacanthidae sp.	F89-2	GBR inshorewater, Australia	Feb 2010	Ikeda et al. (2011)
	Ranzania laevis, Ostracion boops stage	F90	Subtropical N. Pacific Ocean	Mar 1972	Ikeda (1974)

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Table 2. Regression statistics of pelagic cephalopods and fishes derived from stepwise (forward selection, $P_{in} = P_{out} = 0.05$) multiple regression analysess of routine respiration rates (R: μl O_2 $individual^{-1}$ h^{-1}) on body mass [BM, in terms of wet mass (WM), dry mass (DM), carbon (C) or nitrogen (N), all mg], habitat temperature (Temp, K) and habitat depth (Depth, m) [Model (1)], and plus 16 orders/families for cephalopods [Model (2)], or 15 orders for fishes [Model (3)]. Model (1): $\ln R = a_0 + a_1 \times \ln BM + a_2 \times 1000/Temp + a_3 \times \ln Depth$, Model (2): $\ln R = a_0 + a_1 \times \ln BM + a_2 \times 1000/Temp + a_3 \times \ln Depth + a_4 \times De + a_5 \times Ch + a_6 \times En + a_7 \times Go + a_8 \times Hi + a_9 \times Jo + a_{10} \times Ma + a_{11} \times Oc + a_{12} \times Om + a_{13} \times Ps + a_{14} \times Py + a_{15} \times Se + a_{16} \times Va + a_{17} \times Oc + a_{18} \times Cr$, and Model (3): $\ln R = a_0 + a_1 \times \ln BM + a_2 \times 1000/Temp + a_3 \times \ln Depth + a_4 \times Au + a_5 \times At + a_6 \times Bel + a_7 \times Ber + a_8 \times Cl + a_9 \times Ga + a_{10} \times Lo + a_{11} \times Mu + a_{12} \times Os + a_{13} \times Pe + a_{14} \times Sc + a_{15} \times Ste + a_{16} \times Sto + a_{17} \times Te$. For Models (2) and (3), the dummy variable of a given taxon takes a value 1 if representing the taxon or 0 otherwise, whereas Loliginidae (Lo) for cephalopods and Myctophiformes (My) for fishes, which do not appear in the regression equation, take values of 0 in either case. For the abbreviations of the other taxa, see Tables 1-1 and 1-2.

Datasets	Regression model	Regression statistics	Body Mass (BM) unit							
			WM		DM		C		N	
Cephalopods	(1)	*N*	50		50		50		50	
		Adjusted R^2	0.897		0.932		0.938		0.932	
		Coefficient (std error; std coeff)								
		a_0	28.326	(7.456; 0.000)	24.248	(6.097; 0.000)	24.461	(5.820; 0.000)	26.142	(6.078; 0.000)
		a_1	0.779	(0.067; 0.582)	0.855	(0.056; 0.648)	0.868	(0.054; 0.664)	0.856	(0.056; 0.651)
		a_2	−7.903	(2.102; −0.304)	−6.534	(1.724; −0.252)	−6.424	(1.650; −0.247)	−6.527	(1.734; −0.251)
		a_3	−0.365	(0.083; −0.337)	−0.293	(0.067; −0.271)	−0.261	(0.064; −0.241)	−0.282	(0.067; −0.261)
	(2)	Adjusted R^2	0.956		0.956		0.957		0.957	
		Coefficient (std error; std coeff)								
		a_0	21.848	(5.321; 0.000)	21.917	(5.062; 0.000)	24.714	(4.886; 0.000)	23.146	(5.028; 0.000)
		a_1	0.738	(0.049; 0.551)	0.762	(0.049; 0.577)	0.793	(0.049; 0.607)	0.761	(0.049; 0.579)
		a_2	−5.983	(1.517; −0.230)	−5.739	(1.442; −0.221)	−6.452	(1.386; −0.248)	−5.594	(1.442; −0.215)
		a_3	−0.290	(0.062; −0.268)	−0.269	(0.056; −0.249)	−0.223	(0.055; −0.206)	−0.262	(0.055; −0.242)
		a_4								
		a_5								
		a_6	−1.030	(0.240; −0.151)	−0.461	(0.227;−0.067)			−0.528	(0.226; −0.077)
		a_7								
		a_8	1.231	(0.434; 0.088)	1.158	(0.423; 0.083)	1.134	(0.419; 0.081)	1.100	(0.422; 0.079)
		a_9	−0.782	(0.370; −0.068)						
		a_{10}								
		a_{11}								
		a_{12}								
		a_{13}	1.322	(0.336; 0.145)	1.340	(0.332; 0.147)	1.290	(0.332; 0.142)	1.346	(0.331; 0.148)
		a_{14}								
		a_{15}								
		a_{16}								
		a_{17}	−1.710	(0.632; −0.088)						
		a_{18}	−1.086	(0.308; −0.119)						
Fishes	(1)	*N*	102		102		102		102	
		Adjusted R^2	0.947		0.958		0.952		0.948	
		Coefficient (std error; std coeff)								
		a_0	19.491	(2.491; 0.000)	27.667	(2.249; 0.000)	30.767	(2.451; 0.000)	32.748	(1.586; 0.000)
		a_1	0.885	(0.021; 1.119)	0.881	(0.018; 1.109)	0.870	(0.020; 1.112)	0.869	(0.020; 1.084)
		a_2	−5.770	(0.752; −0.310)	−7.833	(0.678; −0.421)	−8.515	(0.737; −0.457)	−8.777	(0.468; −0.472)
		a_3	−0.261	(0.032; −0.314)	−0.114	(0.028; −0.137)	−0.088	(0.031; −0.105)	(−0.186*)	
	(3)	Adjusted R^2	0.957		0.962		0.958		0.961	
		Coefficient (std error; std coeff)								
		a_0	18.592	(2.281; 0.000)	26.083	(2.305; 0.000)	27.634	(2.436; 0.000)	25.735	(2.332; 0.000)
		a_1	0.893	(0.019; 1.129)	0.885	(0.018; 1.115)	0.879	(0.019; 1.124)	0.879	(0.018; 1.097)
		a_2	−5.519	(0.688; −0.297)	−7.374	(0.692; −0.396)	−7.599	(0.731; −0.408)	−6.691	(0.697; −0.360)
		a_3	−0.232	(0.030; −0.278)	−0.124	(0.030; −0.149)	−0.131	(0.031; −0.157)	−0.094	(0.030; −0.112)
		a_4			0.551	(0.261; 0.045)	1.056	(0.275; 0.087)	1.212	(0.265; 0.099)
		a_5								
		a_6								
		a_7								
		a_8								
		a_9								
		a_{10}	−1.181	(0.269; −0.097)	−0.570	(0.250; −0.047)			−0.651	(0.253; −0.053)
		a_{11}								
		a_{12}	−0.521	(0.219; −0.052)						
		a_{13}								
		a_{14}								
		a_{15}	−0.753	(0.301; −0.054)						
		a_{16}								
		a_{17}								

*p = 0.064

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Table 3. Regression statistics derived from stepwise (forward selection, $P_{in} = P_{out} = 0.05$) multiple regression analyses for the differences in the effects of body mass [BM, in terms of wet mass (WM), dry mass (DM), carbon (C) or nitrogen (N), all mg], habitat temperature (Temp, K) and habitat depth (Depth, m) on routine respiration rates of pelagic cephalopods and fishes [Model (4)], and for the differences in routine respiration rates and O:N ratios between pelagic cephalopods, fishes and crustaceans [Model (5)]. Pelagic crustacean data are from Ikeda (2014). Model (4): $\ln Y = a_0 + a_1 \times \mathit{lnBM} + a_2 \times \mathit{1000/Temp} + a_3 \times \mathit{lnDepth} + a_4 \times \mathit{Ceph} + a_5 \times (\mathit{Ceph} \times \mathit{lnBM}) + a_6 \times (\mathit{Ceph} \times \mathit{1000/Temp}) + a_7 \times (\mathit{Ceph} \times \mathit{lnDepth})$, Model (5): $\ln Y = a_0 + a_1 \times \ln BM + a_2 \times 1000/Temp + a_3 \times \ln Depth + a_4 \times Ceph + a_5 \times Fish$. Variables in *italic* denote those mean-centered to reduce the effects of multicolinearity between the variables.

Datasets	Dependent variable, Y	Regression model	Regression statistics	Body Mass (BM) unit							
				WM		DM		C		N	
Cephalopods + Fishes	Respiration	(4)	*N*	152		152		152		152	
			Adjusted R^2	0.928		0.950		0.947		0.944	
			Coefficient (std error; std coeff)								
			a_0	5.600	(0.056; 0.000)	5.594	(0.047; 0.000)	5.589	(0.048; 0.000)	5.604	(0.049; 0.000)
			a_1	0.872	(0.022; 0.986)	0.870	(0.018; 0.965)	0.861	(0.019; 0.966)	0.859	(0.019; 0.949)
			a_2	–5.743	(0.732; –0.292)	–7.356	(0.653; –0.374)	–7.912	(0.669; –0.402)	–7.315	(0.686; –0.372)
			a_3	–0.309	(0.033; –0.340)	–0.171	(0.028; –0.188)	–0.141	(0.029; –0.155)	–0.131	(0.030; –0.144)
			a_4	(0.063*)		0.456	(0.110; 0.085)	0.537	(0.112; 0.100)	0.389	(0.116; 0.072)
			a_5								
			a_6								
			a_7	–0.162	(0.046; –0.080)	–0.134	(0.039; –0.066)	–0.108	(0.040; –0.053)	–0.185	(0.041; –0.091)
Cephalopods + Fishes + Crustaceans	Respiration	(5)	*N*			589		589		589	
			Adjusted R^2			0.973		0.970		0.974	
			Coefficient (std error; std coeff)								
			a_0			22.118	(1.019; 0.000)	23.731	(1.071; 0.000)	23.996	(0.993; 0.000)
			a_1			0.862	(0.007; 0.913)	0.866	(0.008; 0.911)	0.865	(0.007; 0.916)
			a_2			–6.069	(0.296; –0.220)	–6.315	(0.311; –0.229)	–6.055	(0.289; –0.219)
			a_3			–0.174	(0.011; –0.159)	–0.188	(0.012; –0.172)	–0.140	(0.011; –0.128)
			a_4								
			a_5			–0.279	(0.070; –0.033)	–0.281	(0.073; –0.033)	–0.270	(0.068; –0.032)
Cephalopods + Fishes + Crustaceans	O:N	(5)	*N*			171		171		171	
			Adjusted R^2			0.044		0.064		0.064	
			Coefficient (std error; std coeff)								
			a_0			3.035	(0.049; 0.000)	2.919	(0.065; 0.000)	2.919	(0.065; 0.000)
			a_1			0.043	(0.014; 0.249)				
			a_2								
			a_3					0.056	(0.020; 0.226)	0.056	(0.020; 0.226)
			a_4			–0.527	(0.252; –0.174)				
			a_5					0.326	(0.103; 0.250)	0.326	(0.103; 0.250)

910 *p = 0.444

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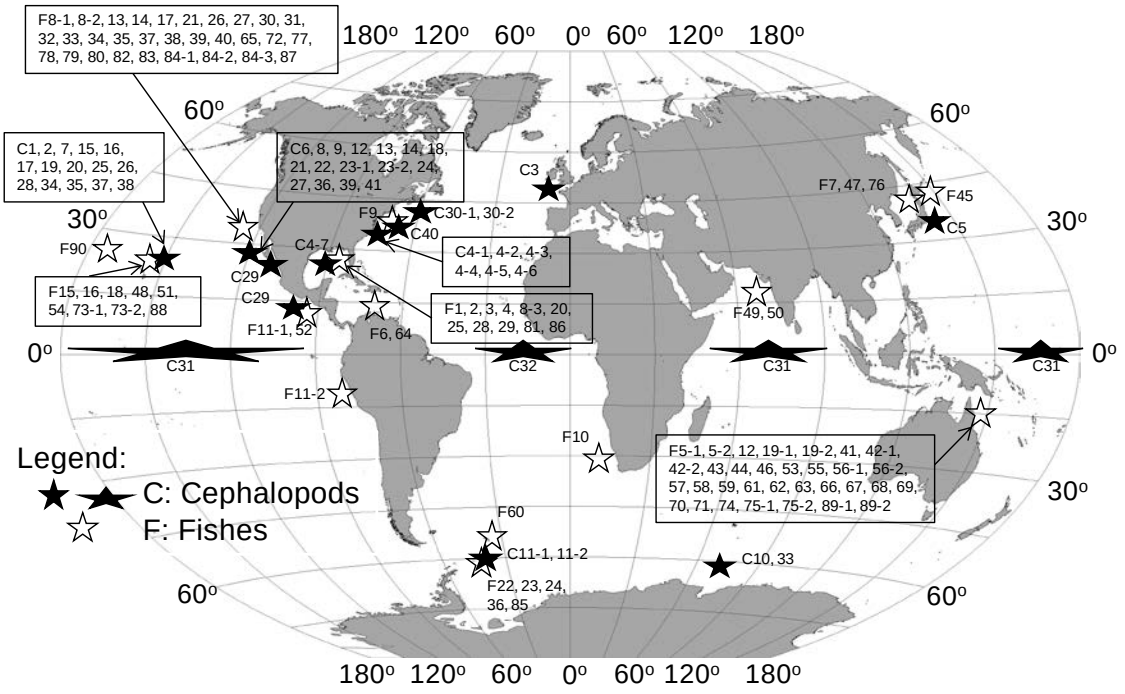

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915 Fig.1. Study sites of routine metabolic rates of pelagic cephalopods and fishes. The

916 character and associated number alongside the symbol correspond to the code of each

917 cephalopod and fish species in Tables 1-1 and 1-2, respectively.

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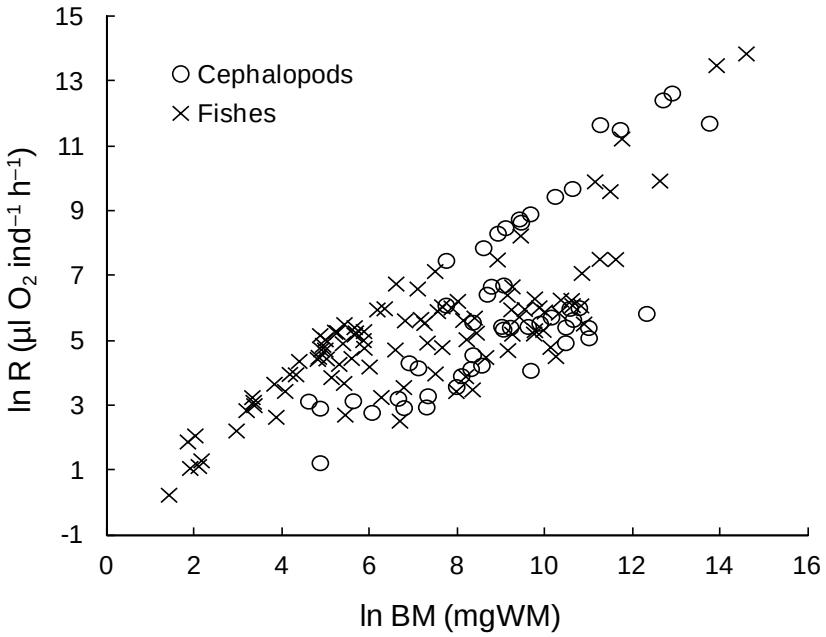

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931 Fig. 2. Scatter diagram of the routine respiration rates (R) versus the body mass (BM)

932 for cephalopods (41 species) and fishes (90 species) from widely different habitat

933 temperatures (–0.8 to 30°C) and habitat depths (1 to <1,300 m) of the world's oceans.

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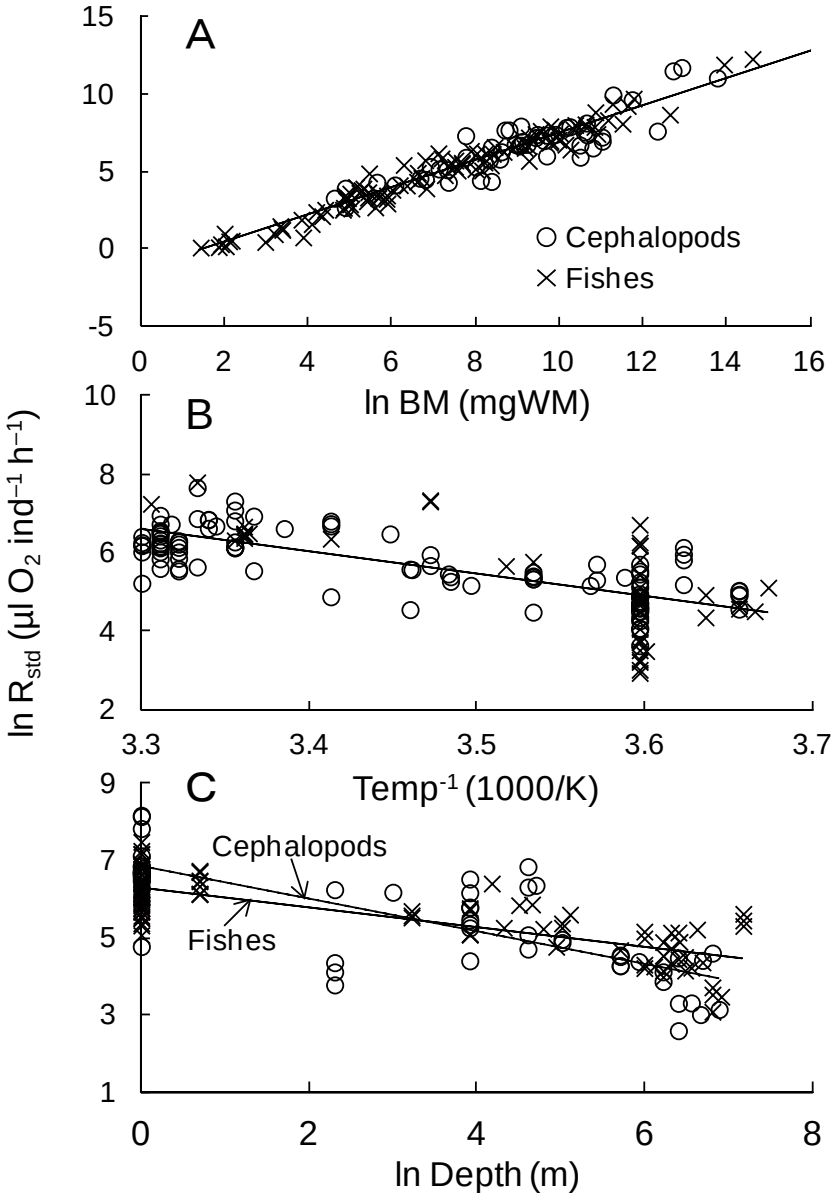

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937 Fig. 3. Scatter diagram of the standardized routine respiration rates (R_{std}) versus the (A)
938 body mass (BM), (B) habitat temperature ($Temp^{-1}$) and (C) habitat depth (Depth) for
939 cephalopods and fishes. The superimposed regression line represents the pooled data
940 of the cephalopods and fishes (solid line) for panels A and B or cephalopods (hatched
941 line) and fishes (dashed line) separately for panel C.

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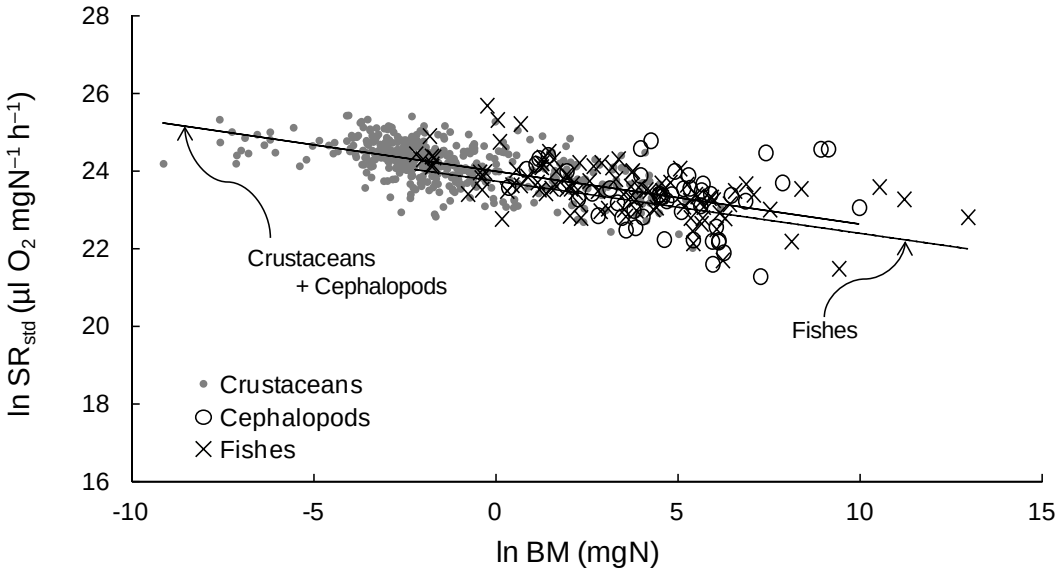

Fig. 4. Scatter diagram of the standardized N-specific routine respiration rates (SR_{std}) versus the body mass (BM) for cephalopods (this study), fishes (this study) and crustaceans (copepods, euphausiids, amphipods, mysids and decapods, cf. Ikeda 2014) from widely different habitat temperatures (–1.7 to 30°C) and habitat depth (1 to 4000 m) of the world's oceans. Note that the superimposed regression lines of the cephalopods and crustaceans overlap but that the regression line of the fishes lies below it.

Appendix. A

S1. Habitat depth, experimental temperature, body mass [Wet mass (WM), dry mass (DM), carbon (C) or nitrogen (N) units], routine respiration (R, and swimming velocity in terms of body length (L) s^{-1} at the measurement in parenthesis for some species), ammonia excretion (E), respiration/ammonia excretion (O:N) and body composition (water, ash, C and N) of cephalopods. For cephalopod species codes see Table 1-1.

Species	Depth	Temp	Body mass				R	E	O:N	Water	Ash	C	N
code	(m)	(°C)	mgWM	mgDM	mgC	mgN	(μlO_2 $ind^{-1}h^{-1}$)	(μgN $ind^{-1}h^{-1}$)	(by atoms)	(%WM)	(%DM)	(%DM)	(%DM)
C1	800	5	19600	2117	768	222	259			78.4[a]	10.7[a]	44.9[a]	10.5[a]
C2	50	5	4240	916	411	96.2	267			78.4[a]	10.7[a]	44.9[a]	10.5[a]
C3	1	11.3	937000	202392	90874	21251	124153 (at 2L s^{-1})	15873	11.4	78.4[a]	10.7[a]	44.9[a]	10.5[a]
C4-1	1	24.5	2310	499	224	52	1799 (at 0.5-1.5L s^{-1})			78.4[a]	10.7[a]	44.9[a]	10.5[a]
C4-2	1	24.5	7500	1620	727	170	4161 (at 0.5-1.5L s^{-1})			78.4[a]	10.7[a]	44.9[a]	10.5[a]
C4-3	1	24.5	12250	2646	1188	278	6465 (at 0.5-1.5L s^{-1})			78.4[a]	10.7[a]	44.9[a]	10.5[a]
C4-4	1	24.5	15750	3402	1527	357	7561 (at 0.5-1.5L s^{-1})			78.4[a]	10.7[a]	44.9[a]	10.5[a]
C4-5	1	24.5	27700	5983	2686	628	12968 (at 0.5-1.5L s^{-1})			78.4[a]	10.7[a]	44.9[a]	10.5[a]
C4-6	1	24.5	41100	8878	3986	932	16544 (at 0.5-1.5L s^{-1})			78.4[a]	10.7[a]	44.9[a]	10.5[a]
C4-7	1	24.25	8942	1931	867	203	4937			78.4[a]	10.7[a]	44.9[a]	10.5[a]
C5	1	25	5400	1166	524	122	2660	548	11.3	78.4[a]	10.7[a]	44.9[a]	10.5[a]
C6	300	5	38880	4199	1524	441	409			89.8[b]	17.9[b]	36.3[b]	10.5[b]
C7	300	5	14940	1614	586	169	234			89.8[b]	17.9[b]	36.3[b]	10.5[b]
C8	900	2	25400	2743	996	288	313			89.8[b]	17.9[b]	36.3[b]	10.5[b]
C9	10	5	35390	3822	1387	401	230			89.8[b]	17.9[b]	36.3[b]	10.5[b]
C10	600	-0.2	1473	120	39.5	13.8	19.5	(14.3)[c]	(1.5)[c]	91.8	20.2	32.8	11.5
C11a	50	0.5	424	30.4	11.0	3.2	16.5			92.8	22.3	36.3[b]	10.5[b]
C11b	50	0.5	772	65.8	23.9	6.9	25.5			91.5	16.3	36.3[b]	10.5[b]
C12	300	5	5190	561	203	58.9	70.9			89.8[b]	17.9[b]	36.3[b]	10.5[b]
C13	300	5	880	95	34.5	10.0	19.1			89.8[b]	17.9[b]	36.3[b]	10.5[b]
C14	10	5	3270	353	128	37.1	51.3			89.8[b]	17.9[b]	36.3[b]	10.5[b]
C15	50	5	1520	164	59.6	17.2	27.6			89.8[b]	17.9[b]	36.3[b]	10.5[b]
C16	500	5	2920	315	114	33.1	36.6			89.8[b]	17.9[b]	36.3[b]	10.5[b]
C17	10	5	47900	5173	1878	543	418			89.8[b]	17.9[b]	36.3[b]	10.5[b]
C18	50	5	990	214	96.0	22.5	76.3			78.4[a]	10.7[a]	44.9[a]	10.5[a]
C19	50	5	1220	264	118	27.7	65.3			78.4[a]	10.7[a]	44.9[a]	10.5[a]
C20	50	5	6470	699	254	73.4	810			89.8[b]	17.9[b]	36.3[b]	10.5[b]
C21	100	5	2300	497	223	52.2	453			78.4[a]	10.7[a]	44.9[a]	10.5[a]
C22	100	5	8580	1853	832	195	842			78.4[a]	10.7[a]	44.9[a]	10.5[a]
C23-1	150	5	9990	1079	392	113	228			89.8[b]	17.9[b]	36.3[b]	10.5[b]
C23-2	1	5	4250	459	167	48.2	97.8			89.8[b]	17.9[b]	36.3[b]	10.5[b]
C24	150	5	8510	919	334	96.5	215			89.8[b]	17.9[b]	36.3[b]	10.5[b]
C25	500	5	41850	4520	1641	475	291			89.8[b]	17.9[b]	36.3[b]	10.5[b]
C26	375	5	4060	438	159	46.0	63.7			89.8[b]	17.9[b]	36.3[b]	10.5[b]
C27	100	5	8190	885	321	92.9	235			89.8[b]	17.9[b]	36.3[b]	10.5[b]
C28	100	2	130	14	5.1	1.5	3.5			89.8[b]	17.9[b]	36.3[b]	10.5[b]
C29	1	20	12755	2755	1237	289	5854			78.4[a]	10.7[a]	44.9[a]	10.5[a]
C30-1	1	15	400000	86400	38794	9072	315336 (at 1.5L s^{-1})			78.4[a]	10.7[a]	44.9[a]	10.5[a]
C30-2	1	15	325000	70200	31520	7371	254800 (at 1.5L s^{-1})		15	78.4[a]	10.7[a]	44.9[a]	10.5[a]
C31	1	29.5	122474	24495	10998	2572	102348 (at 2L s^{-1})			80	10.7[a]	44.9[a]	10.5[a]
C32	1	27	77460	15492	6956	1627	118780 (at 2L s^{-1})			80	10.7[a]	44.9[a]	10.5[a]
C33	20	-0.8	276	64.6	37.3	4.1	23.7	1.72	17.2	76.6	8.3	57.8	6.4
C34	50	5	130	28.1	12.6	2.9	18.8			78.4[a]	10.7[a]	44.9[a]	10.5[a]
C35	110	5	5880	1270	570	133	634			78.4[a]	10.7[a]	44.9[a]	10.5[a]
C36	600	5	223400	13404	4866	1407	350			94	17.9[b]	36.3[b]	10.5[b]
C37	975	5	15880	953	346	100	60.5			94[d]	17.9[b]	36.3[b]	10.5[b]
C38	700	5	59490	3569	1296	375	227			94[d]	17.9[b]	36.3[b]	10.5[b]
C39	600	5	35190	2111	766	222	142			94[d]	17.9[b]	36.3[b]	10.5[b]
C40	781	4.7	59910	3210	494	86.7	165.0	2.10	98.4[e]	94.3		15.4	2.7
C41	10	10	100	21.6	9.7	2.3	23.4			78.4[a]	10.7[a]	44.9[a]	10.5[a]

[a] A mean from 5 muscular squids (Clarke et al. 1985 , Ikeda and Bruce 1986)

[b] A mean from 9 ammoniacal squids for water and ash (Clarke et al. 1985, Donnelly et al. 2004, Ikeda unpublished data), and from 8 ammoniacal squids for C and N (Clarke et al. 1985, Ikeda unpublished data)

[c] Assumed as an artifact (see Discussion)

[d] Substituted by the data of *Vampyroteuthis infernalis*

[e] Calculated by the present author

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S2. Habitat depth, experimental temperature, body mass [Wet mass (WM), dry mass (DM), carbon (C) or nitrogen (N) units], routine respiration (R, and swimming velocity at the measurement in trms of body length (L) s^{-1} or cm s^{-1} in parenthesis for some species), ammonia excretion (E), respiration/ammonia excretion (O:N) and body composition (water, ash, C and N) of fishes. For fish species codes see Table 1-2.

Species	Depth	Temp	Body mass				R	E	O:N	Water	Ash	C	N
code	(m)	(°C)	mgWM	mgDM	mgC	mgN	(μO_2 $ind^{-1}h^{-1}$)	(μgN $ind^{-1}h^{-1}$)	(by atoms)	(%WM)	(%DM)	(%DM)	(%DM)
F1	50	25	721	44.1	11.0	1.9	115.0	26.9	5.9	93.9[a]	39.4[a]	25.0[a]	4.4[a]
F2	50	25	400	29.5	5.4	1.0	68.0			92.6[a]	41.2[a]	18.4[a]	3.5[a]
F3	50	25	200	16.5	4.03	0.776	73.7			91.8[a]	47.0[a]	24.4[a]	4.7[a]
F4	50	25	224	17.4	5.2	1.1	40.9	3.3	15.9	92.2[a]	36.6[a]	29.8[a]	6.3[a]
F5-1	1	26	182	55.6	24.7	6.78	199.5	5.00	66.0	69.1	16.2	44.4	12.2
F5-2	1	29	225	60.8	26.7	7.17	251.6	6.10	57.9	72.9	15.7	43.9	11.8
F6	2	26.4	133	30.5	12.1	3.33	115.6	6.58	22.0	77.1[b]		41.2[b]	11.7[b]
F7	2	15.9	6.68	1.53	0.66	0.17	2.97	0.179	20.7	77.1[b]		43.2	11.2
F8-1	650	5	40233	4023	1674	368	530			90.0[c]		41.6[c]	9.1[c]
F8-2	550	5	50900	7635	3177	698.2	1222			85.0	22.5	41.6	9.1
F8-3	600	7	17368	1962	852.9	154.6	555.8			90.1[c]	27.3[c]	43.5[c]	7.9[c]
F9	1	20	302000	104000	42866	12168	21119 (at 0.5L s^{-1})			65.6[d]		41.2[b]	11.7[b]
F10	1	16	10400	3328	1747	499	807 (at 1.85L s^{-1})			68.0[e]		52.5[e]	15.0[e]
F11-1	1	15	7424	1700	700	272	1849	106	21.7	77.1[b]		41.2[b]	16.0
F11-2	1	15	12600	4032	2117	605	3871(at 2.33L s^{-1})			68.0[e]		52.5[e]	15.0[e]
F12	1	27	130	41.22	18.34	5.15	179.1	8.33	27.0	66.0	14.5	44.5	12.5
F13	1	25	68700	14496	6741	1826	20622			78.9[f]		46.5[f]	12.6[f]
F14	550	5	31500	4922	2163	388	536			84.4[c]		43.9[c]	7.9[c]
F15	900	5	28100	2670	1081	222	94			90.5[c]		40.5[c]	8.3[c]
F16	800	5	30163	2865	1161	238	358			90.5[c]		40.5[c]	8.3[c]
F17	900	5	4200	400	162	33.2	33.6			90.5	19.3	40.5	8.3
F18	900	5	53400	5073	2055	421	256			90.5[c]		40.5[c]	8.3[c]
F19-1	1	28	27.6	6.10	2.64	0.73	26.4	2.14	21.7	77.8	15.3	43.2	11.9
F19-2	1	28	45.7	14.97	5.94	1.54	39.9	2.84	17.7	77.1	16.2	39.7	10.3
F20	90	20	168	45	21.7	3.50	49.1			73.3[d]	21.4[c]	48.4[c]	7.9[c]
F21	1	10	2100	711	372	42.1	437			66.1	9.0	52.3	5.9
F22	50	0.5	4600	1530	676.3	93.0	193.2			66.7	9.2	44.2[g]	6.1[g]
F23	150	0.5	12200	4126	1973	249	317.2			66.2	8.0	47.8[g]	6.0[g]
F24	150	0.5	19200	5955	3147	346	422.4			69.0	8.3	52.8[g]	5.8[g]
F25	120	7	3670	774	372.5	61.0	157.8			78.9[c]	19.1[c]	48.1[c]	7.9[c]
F26	500	5	2900	399	178	34.8	31.9			86.3	18.4	44.7	8.7
F27	75	10	2100	616	327	45.6	124			70.6	9.7	53.0	7.4
F28	105	20	1292	305	147.1	24.0	295.9			74.5[c]	23.1[c]	48.3[c]	7.9[c]
F29	1	14	1900	509	251.0	40.1	376.2			71.1[c]	23.1[c]	49.3[c]	7.9[c]
F30	700	5	9400	848	360	66.8	113			91.0		42.5[a]	7.9[a]
F31	650	5	49800	7596	4226	532	448			84.7	7.9	55.6	7.0
F32	25	10	4400	1460	807	89.2	308			66.8	10.1	55.3	6.1
F33	1	13	1400	386	157	39.4	260			72.4[c]	19.6	40.8	10.2
F34	25	10	9300	2674	1332	203	623			71.2	9.4	49.8	7.6
F35	1000	5	24900	2767	1095	218	125			88.9		39.6[c]	7.9[c]
F36	400	0.5	10400	1337	423.6	118	187.2			87.1	21.0	31.7[g]	8.8[g]
F37	550	5	41100	5319	2488	458	452			87.1	14.8	46.8	8.6
F38	1	10	3400	938	462	73.9	286			72.4[c]		49.3[c]	7.9[c]
F39	25	10	1500	250	98.4	26.5	143			83.3	19.3	39.3	10.6
F40	600	5	5700	724	261	81.0	91.2			87.3	20.6	36.1	11.2
F41	1	29	478	115	47.5	12.8	395.7	55.85	17.5	76.2	17.8	41.4	11.2
F42-1	1	28	266	64.1	26.0	7.50	88.4	4.37	25.5	75.9	20.6	40.6	11.7
F42-2	1	29	355	87.7	34.9	10.2	121.2	3.52	44.5	75.4	20.5	39.8	11.6
F43	1	29	58.30	10.90	4.46	1.34	32.0	1.05	38.5	81.4	17.6	41	12.3
F44	1	30	47.60	9.96	4.04	1.16	14.4	0.94	22.2	79.2	20.5	40.6	11.6
F45	2	7.3	4.12	0.94	0.43	0.11	1.30			77.1[b]		45.5	11.3
F46	1	30	7.50	1.54	0.56	0.17	8.10	0.42	24.2	79.6	14.9	36.2	11.3
F47	2	16	8.65	1.98	0.79	0.18	3.76			77.1[b]		40.0	9.0
F48	750	5	76600	13328	6238	946	1887			82.6[c]		46.8[c]	7.1[c]
F49	1	27	900	183	75	21	283 (at 2cm s^{-1})			79.7[d]		41.2[b]	11.7[b]
F50	65	27	1200	244	101	29	755 (at 4cm s^{-1})			79.7[h]		41.2[b]	11.7[b]
F51	1	24	127000	36830	15174	4309	77328 (at 1.5L s^{-1})			79.7[g]		41.2[b]	11.7[b]
F52	2	26.4	191.7	43.9	17.5	4.79	197	13.6	18.1	77.1[b]		39.8	10.9
F53	1	29	74.7	15.39	6.17	1.94	53.5	1.56	43.6	79.4	18.4	40.1	12.6
F54	1	23.5	1962000	568980	234420	66571	1009197 (at 2.1L s^{-1})			71.0[d]		41.2[b]	11.7[b]
F55	1	29	146	35.3	14.2	4.52	115	5.74	25.4	75.7	16.4	40.1	12.8
F56-1	1	29	150	35.6	14.6	3.88	87.3	4.98	24.2	76.3	19.0	40.9	10.9
F56-2	1	30	123	29.5	12.6	3.25	85.9	2.82	49.4	76	20.3	42.5	11
F57	1	29	292	69.5	28.8	7.71	195	19.24	17.3	76.3	18.7	41.5	11.1
F58	1	29	80.4	18.38	7.46	2.33	80.8	5.13	20.8	77.2	15.6	40.6	12.7
F59	1	28	348	87.5	34.5	9.89	153.7	9.74	20.6	74.8	24.1	39.4	11.3
F60	1	3	3000	2163	967	288	516				72.1[h]	44.7[h]	13.3[h]
F61	1	30	24.2	5.90	2.43	0.67	17.7	0.38	60.0	75.6	17.6	41.1	11.4
F62	1	28	19.2	3.94	1.68	0.46	9.4	0.49	24.9	79.5	11.9	42.6	11.6
F63	1	25	65.0	15.27	6.38	1.73	54.1	2.14	34.1	76.5	13.8	41.8	11.3
F64	2	28.4	139	31.7	12.6	3.46	133.0	11.58	14.4	77.1[b]		39.8	10.9
F65	1	24	97300	28217	11625	3301	15265 (at 1.5L s^{-1})			79.7[i]		41.2[b]	11.7[b]

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F66	1	30	565	132.5	50.5	16.2	410.9	29.52	21.3	76.8	16.6	38.1	12.2
F67	1	29	734	142.1	60.1	17.9	880.8	18.20	66.4	80.7	14.0	42.3	12.6
F68	1	29	1786	394.8	157.9	49.4	1296	64.2	26.2	77.9	21.1	40.0	12.5
F69	1	29	352	77.8	31.3	8.79	203.0	13.95	19.4	78	20.4	40.2	11.3
F70	1	29	126	25.3	10.8	3.09	91.7	6.43	22.8	80	16.5	42.5	12.2
F71	1	28	28.9	5.77	2.39	0.66	20.6	0.59	50.9	80	13.6	41.4	11.5
F72	1	17	10076000	3597132	1482635	420864	2227500 (at 1.3L s^{-1})			64.3[d]		41.2[b]	11.7[b]
F73-1	1	25	1100000	315700	130123	36937	745515 (at 2L s^{-1})			71.3[d]		41.2[b]	11.7[b]
F73-2	1	25	2170000	622790	256696	72866	1071386 (at 2L s^{-1})			71.3[d]		41.2[b]	11.7[b]
F74	1	29	284	71.2	28.0	8.05	229.0	15.05	21.4	75	20.2	39.3	11.3
F75-1	1	28	6.3	1.24	0.53	0.13	6.7	0.28	34.9	80.4		42.6	10.7
F75-2	1	28	28.4	5.67	2.39	0.64	22.9	0.66	43.9	80.2	16.7	42.1	11.2
F76	2	14.1	8.13	1.86	0.76	0.17	3.16			77.1[b]		40.7	9.1
F77	608	5.7	1800	360	146.5	32.8	54.9			80.2		40.7[j]	9.1[j]
F78	400	5	17400	2175	1188	171	209			87.5		45.4[c]	7.9[c]
F79	450	5	3600	525	207	46.5	50			85.4	18.7	39.3	8.9
F80	400	5	17100	2239	777	207	188			86.9	26.2	34.7	9.2
F81	165	20	2609	521	248.3	41.0	420			80.0[c]	23.5[c]	47.7[c]	7.9[c]
F82	500	5	21100	3527	1567	277.9	211			83.3[c]		44.4[c]	7.9[c]
F83	500	5	110250	19940	9340	1165	1874			81.9	15.3	46.8	5.8
F84-1	1300	3	230	52.9	23.0	4.25	15.4			77.0	17.2[c]	43.6[c]	8.0[c]
F84-2	1300	3	524	121.4	52.9	9.75	26.6			76.8	17.2[c]	43.6[c]	8.0[c]
F84-3	1300	3	875	178.9	77.9	14.4	36.1	2.79	16.2	79.5	17.2[c]	43.6[c]	8.0[c]
F85	500	0.5	800	291	143.6	17.4	12.8			63.6	8.0	49.4[g]	6.0[g]
F86	140	14	10192	1205	577.3	94.9	397			88.2[c]	27.4[c]	47.9[c]	7.9[c]
F87	300	5	21850	4174	1955	295	371			80.9	13.9	46.8	7.1
F88	400	5	13800	2636	1234	187	402			80.9[c]		46.8[c]	7.1[c]
F89-1	1	29	218	45.9	19.7	5.19	140	4.83	46.5	78.9	16.2	42.8	11.3
F89-2	1	30	286	59.3	24.8	6.81	183	11.01	30.9	79.4	17.1	41.8	11.5
F90	2	22.4	7.29	1.67	0.63	0.16	9.11	0.81	14.1	77.1[b]		41.2[b]	11.7[b]

[a] After Bishop et al. (2000), combined with C and N composition data of protein and lipids in Gnaiger and Bitterich (1984). The data of F3 is the mean of those of the other three species

[b] Substituded by the mean values of tropical fishes (Ikeda et al. 2011)

[c] Calculated from the data given by Childress and Nygaard (1973) a function of habitat depth (X m) for water (Y = 0.0218X + 72.39) and C (Y = –0.0097X + 49.28) but substituted by a grand mean for N (7.9)

[d] After "Mass conversion" in Fishbase (Froese and Pauly 2014)

[e] After James (1988)

[f] Substituted by the data of *Engraulis japonica* (Omori 1969)

[g] After Donnelly et al. (1990), combined with C and N composition data of protein and lipids in Gnaiger and Bitterich (1984)

[h] Calculated from the data of *Notothenia coriiceps* in Fishbase (Froese and Pauly 2014)

[i] Substituted by the data of *Coryphaena hippurus*

[j] Substituted by the data of *Hexagrammos otakii*

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