



Title	An approach to integrating specific dynamic action (SDA) with routine metabolism for improved estimation of the realistic metabolism of marine metazooplankton in the field
Author(s)	Ikeda, Tsutomu
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3 An approach to integrating specific dynamic action (SDA) with routine metabolism for
4 improved estimation of the realistic metabolism of marine metazooplankton in the field

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6 Tsutomu Ikeda*

7 16-3-1001 Toyokawa-cho, Hakodate, 040-0065 Japan

8 ikeda.tutomu@sepia.plala.or.jp

9 Tel: +81-138-22-5612

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14 Running head: Estimating metabolic rates of marine metazooplankton in the field

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17 metazooplankton

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25 **Abstract**

26 An increase in respiration (R_{SDA}) associated with food ingestion (I) was estimated from
27 routine rates (R_{routine}) determined in the absence of food with sealed-chamber methods.
28 Based on regression analyses of R_{SDA} on I for metazooplankton in the laboratory, the
29 fraction of I allocated to R_{SDA} was calculated to be 0.10. Likely food ingestion of
30 metazooplankton in the field (I_{field}) was derived from “basic balanced equations” in
31 which parameters such as R_{routine} , laboratory-obtained food absorption efficiency (AE)
32 and gross growth efficiency (K_1) were incorporated (I&M model). Based on
33 differences in AE values, metazooplankton were separated into particle-feeders
34 (herbivores, omnivores) and carnivores and R_{SDA} was computed to be 0.37 times R_{routine}
35 for the former and 0.25 times R_{routine} for the latter. Hence, realistic respiration rates of
36 metazooplankton feeding in the field ($R_{\text{field}} = R_{\text{SDA}} + R_{\text{routine}}$) accounted for 1.37 times
37 R_{routine} for particle-feeders and 1.25 times R_{routine} for carnivores. The increase in
38 ammonia excretion (E_{SDA}) accompanied by SDA in particle-feeders and carnivores was
39 calculated from R_{SDA} coupled with carbon to nitrogen (C:N by mass) ratios of possible
40 natural foods (6.5 for the former and 4.5 for the latter). Results indicated that E_{SDA} is
41 0.080 times R_{SDA} for particle-feeders, and 0.116 times R_{SDA} for carnivores.

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49 **Introduction**

50 To measure the metabolic rates (respiration and excretion) of metazooplankton,
51 traditional “water–bottle” or “sealed–chamber” methods involve incubating
52 field-caught animals in filtered seawater, thereby eliminating the effects of respiration
53 and excretion by prey organisms. From the viewpoints of three categories of metabolic
54 rates defined by swimming activity level, e.g. “standard” (maintenance only or at zero
55 activity), “routine” (uncontrolled activity) and “active” metabolism (enforced activity
56 at a maximum level), the resulting rates are close to routine rates based on the premise
57 that normal or spontaneous swimming activity of the study animals is unaltered (Ikeda
58 et al. 2000; Ikeda 2014a). However, the metabolic rates of metazooplankton may be
59 affected by the absence of feeding. Specific dynamic action (SDA) is the phenomenon
60 by which the metabolic rate increases in association with feeding and is widespread
61 throughout the animal kingdom (see Secor 2009 for review). The major cause of SDA
62 is the cost of protein synthesis from absorbed amino acids (Kiørboe et al. 1985; Thor
63 2000; Secor 2009), with the costs of feeding, digestion and excretion being of minor
64 importance (ca. 1% of SDA) (Kiørboe et al. 1985). The type of natural prey, feeding
65 history, and, most importantly, ingestion rate of metazooplankton in the field must be
66 taken into account prior to conducting experiments so that sealed-chamber metabolic
67 data for wild metazooplankton can be appropriately corrected for wild
68 metazooplankton. However, it is not always possible to define the conditions for wild
69 metazooplankton species at the time of collection.

70 The approach described in this paper is simple but allows for an estimation of
71 the SDA effects on respiration and excretion rates of metazooplankton feeding in the
72 field by combining the sealed-chamber method-derived- routine rates with the

73 laboratory-obtained food absorption efficiency, gross growth efficiency and carbon to
74 nitrogen (C:N) ratios of their natural foods.

75

76 **Methods**

77 **SDA as a function of food ingestion**

78 To evaluate the increase in respiration rate (R) with the increase in the ingestion rate (I),
79 metazooplankton were placed into varying food concentrations (C). The R – I
80 relationship of interest was derived indirectly from parallel experiments of R – C and
81 I – C relationships (Kjørboe et al. 1985; Lampert 1986; Thor et al. 2002), or directly by
82 simultaneous measurements of R and I of the same specimen or batches of specimens
83 (Gaudy 1974; Abou Debs 1984; Ikeda and Dixon 1984). In both cases, oxygen
84 consumption by food organisms during incubation periods was determined and
85 subtracted from the calculation of respiration rates of study metazooplankton. As a
86 version of the former method, the R – I relationship was established based on both
87 parameters integrated over six days for the same specimens reared at two food
88 concentrations (Reeve et al. 1978) (Table 1). The linear R – I relationship that was
89 obtained for a euphausiid *Euphausia superba* (Ikeda and Dixon 1984), a copepod
90 *Acartia tonsa* (Kjørboe et al. 1985; Thor et al. 2002), and a freshwater cladoceran
91 *Daphnia magna* (Lampert 1986) is schematically detailed in Fig. 1. The slope (α) of
92 the regression line of R on I is of special interest to estimate the R_{SDA} ($= R_{\text{field}} - R_{\text{routine}}$)
93 of metazooplankton based on their food ingestion (I_{field}) in the field. To date, a total of
94 12 datasets are available on 1 cladoceran (freshwater), 3 copepods, 1 euphausiid, and 1
95 ctenophore (Table 1). Despite their methodological differences, the 12 datasets were

96 pooled, and a grand mean $\alpha = 0.10 (\pm 0.045, SD)$ was calculated. Thus, the fraction of
97 ingested C allocated to the increase in respiration (R_{SDA} , as CO_2-C) is written as:

$$98 \quad R_{SDA} = 0.10 I \quad (1)$$

99

100 **Ingestion as a function of metabolism**

101 The I can be computed indirectly from the R by accounting for the experimentally
102 determined absorption efficiency (AE , %) and gross growth efficiency (K_1 , %) (Ikeda
103 and Motoda, 1978) (note: AE has been referred to as the “assimilation” efficiency;
104 however, “absorption” efficiency is more appropriate in the context of sequential
105 processes of digestion through the assimilation of ingested food; see Penry 1998).

106 According to the “basic balanced equation” for fish energetics (Winberg 1956):

$$107 \quad (AE/100) \times I = P + R$$

$$108 \quad K_1 = P \times 100/I$$

109 where P is growth (plus egg production for metazooplankton). This then leads to:

$$110 \quad I = 100 \times R / (AE - K_1) \quad (2)$$

111 Ikeda and Motoda (1977) used AE and K_1 values of 70% and 30%, respectively.

112 However, for the present study, 79 AE and 50 K_1 datasets were compiled across 13
113 metazooplankton taxa (Supplemental materials, S1) to obtain updated values. To
114 compare the values for different feeding types, the taxa were separated into
115 particle-feeders (herbivores and omnivores) and carnivores. Arcsine transformation of
116 the data was performed because both AE and K_1 are proportions (%) (Sokal and Rohlf
117 1995), followed by a Student t -test. This revealed that the differences between the
118 means of these two groups were significant for AE ($t = 3.106, df = 77, p = 0.003$) but
119 insignificant for K_1 ($t = 0.881, df = 48, p = 0.383$) (Fig. 2). The mean ($\pm SD$) and

120 median AE were 69 (± 18)% and 71%, respectively, for particle-feeders, and 83 (± 16)%
 121 and 90%, respectively, for carnivores. The mean and median K_1 pooled from these two
 122 feeding-type groups were 30% (± 13) and 28%, respectively. Substituting these values
 123 into Eq. (2) obtained the following:

$$124 \quad I = 100 \times R / (69 - 30) = 2.6R \quad (3 - 1)$$

$$125 \quad I = 100 \times R / (83 - 30) = 1.9R \quad (3 - 2)$$

126 for particle-feeders [Eq. (3-1)] and carnivores [Eq. (3-2)], respectively. Ikeda and
 127 Motoda (1978) represented R by the routine respiration (R_{routine}) obtained from using a
 128 sealed chamber method. However, in the present study, R was more precisely defined
 129 as $R = R_{\text{routine}} + R_{\text{SDA}}$ to estimate I in the field (I_{field}), which obtained the following:

$$130 \quad I_{\text{field}} = 2.6 \text{ or } 1.9(R_{\text{routine}} + R_{\text{SDA}}) \quad (4)$$

131 Substituting Eq. (4) into Eq. (1):

$$132 \quad R_{\text{SDA}} = 0.10 \times (2.6 \text{ or } 1.9) \times (R_{\text{routine}} + R_{\text{SDA}}) \quad (5)$$

133 Rearranging for R_{SDA} , we finally obtained:

$$134 \quad R_{\text{SDA}} = 0.37R_{\text{routine}} \quad (6 - 1)$$

$$135 \quad R_{\text{SDA}} = 0.25R_{\text{routine}} \quad (6 - 2)$$

136 for particle-feeders [Eq. (6-1)] and carnivores [Eq. (6-2)], respectively. Assuming that
 137 AE and K_1 are independent of each other, the propagation of error (SD) for the
 138 coefficient of 0.37 [Eq. 6-1)] and 0.25 [Eq. (6-2)] were computed as ± 0.19 ($df = n - 3$
 139 $= 121$) and ± 0.12 ($df = 76$), respectively, and their respective 95% CI values were
 140 $-0.01 - 0.74$ and $0.02 - 0.48$. To facilitate a comparison of R_{SDA} derived from the
 141 maximum ingestion rate (I_{max} ; see below), Eqs. (6-1) and (6-2) are hereafter referred
 142 to as the ‘‘I&M model’’.

143

144 **Maximum ingestion as a function of body mass and temperature**

145 By fitting I and C data into Holling type II and Ivlev models, Kiørboe and Hirst (2014)
146 calculated the maximum specific ingestion rate (MSI_{max} ; $\mu\text{gC mgC}^{-1}\text{h}^{-1}$ at 15°C). By
147 definition, MSI_{max} is no longer affected by an increase in C . They reported MSI_{max} as a
148 function of M (mgC) for five individual metazooplankton taxa, including calanoid
149 copepods, non-calanoid copepods, euphausiids, chaetognaths and tunicates (hereafter
150 the “K&H model”):

151
$$MSI_{max} = aM^b \quad (n = 10 - 72, R^2 = 0.04 - 0.77) \quad (7)$$

152 where the constants a (-0.19 to 1.99) and b (-0.56 to 0.28) vary depending on the
153 metazoan taxon. To consider I_{max} ($\mu\text{LO}_2 \text{ h}^{-1}$) at $T^\circ\text{C}$, Eq. (7) can be rewritten as:

154
$$I_{max} = aM^{b+1} \times [22.4/(12 \times RQ) \times Q_{10}^{[(T-15)/10]} \quad (8)$$

155 where $RQ = 0.97$ (protein metabolism; assigned by the present author) and $Q_{10} = 2.8$
156 (Kiørboe and Hirst, 2014). Substituting Eq. (8) into Eq. (1) obtains the following:

157
$$R_{SDA} = 0.10 \times aM^{b+1} \times [22.4/(12 \times RQ) \times Q_{10}^{[(T-15)/10]} \quad (9)$$

158 From Fig. 1, $R_{SDA} = R_{max} - R_{routine}$ is derived from the K&H model and is expected to
159 be greater than $R_{SDA} = R_{field} - R_{routine}$ derived from the I&M model [Eqs. (6-1, 6-2)].

160

161 **Ammonia excretion in association with the SDA**

162 The increase in ammonia excretion (E_{SDA}) associated with R_{SDA} can be calculated by
163 defining the C:N ratios (γ , by mass) of natural food for particle-feeders and carnivores,
164 assuming that ammonia is the sole end-product of organic N components of food.

165 When $I = I_c$ (μgC), Eq. (1) obtains:

166
$$R_{SDA}(\mu\text{LO}_2) = 0.10 \times I_c \times 22.4/(12 \times RQ)$$

167 $E_{\text{SDA}}(\mu\text{gN}) = 0.10 \times I_c / \gamma,$

168 where $22.4/(12 \times RQ)$ is used to convert μgC into μLO_2 . From these,

169
$$\text{O/N (by atoms)} = (R_{\text{SDA}}/11.2)/(E_{\text{SDA}}/14)$$

170
$$= [(22.4/(12 \times RQ)) \times 14/11.2] \times \gamma \quad (10)$$

171 where 11.2 and 14 are factors for converting μLO_2 and μgN , respectively,
 172 into μg -atoms, and $RQ = 0.97$ (protein metabolism; Gnaiger 1983). Natural food items
 173 of the particle-feeders are phytoplankton, protozoans and/or detritus (=particulate
 174 matter) for which $\gamma = 6.5$ was adopted in this study [most data fall between 6 and 7;
 175 Ohman and Snyder (1991), Sin et al. (1998), Geider and LaRoche (2002) and literature
 176 therein]. For carnivores which feed on various metazooplankton taxa, $\gamma = 4.5$ was
 177 adopted [most data fall between 4 and 5; Kiørboe (2013) and Ikeda (2014b)] [note: $\gamma =$
 178 5.7, which is derived from the Redfield ratio (C:N:P molar ratio = 106:16:1), for
 179 “plankton” falls within the mid-range of the two values adopted]. Substituting the γ
 180 values into Eq. (10), we obtain an O/N ratio = 15.7 for particle-feeders and 10.8 for
 181 carnivores. From the O/N ratio thus obtained, a possible increase in ammonia excretion
 182 (E_{SDA} ; μgN) can be assessed from R_{SDA} (μLO_2) as:

183
$$(R_{\text{SDA}} / 11.2) / (E_{\text{SDA}}/14) = 15.7 \text{ or } 10.8 \quad (11)$$

184 Rearranging Eq. (11) for E_{SDA} , we obtained:

185
$$E_{\text{SDA}} = 0.080R_{\text{SDA}} \quad (12-1)$$

186
$$E_{\text{SDA}} = 0.116R_{\text{SDA}} \quad (12-2).$$

187 for particle-feeders [Eq. (12-1)] and carnivores [Eq. (12-2)], respectively.

188

189 **Results and Discussion**

190 R_{SDA} and E_{SDA} values were estimated using the I&M model [Eqs. (6-1), (6-2), (11-1)]

191 and (11–2)] for eight arbitrarily selected metazooplankton species (five particle-feeders
192 and three carnivores) from Table 1 in Ikeda et al. (2000), for which R_{routine} (0.056–30.4
193 $\mu\text{LO}_2 \text{ ind.}^{-1}\text{h}^{-1}$) and E_{routine} (0.005–2.93 $\mu\text{gN ind.}^{-1}\text{h}^{-1}$) had previously been determined
194 (Table 2). The resulting R_{SDA} and E_{SDA} values were then added to R_{routine} and E_{routine} ,
195 respectively, to obtain realistic metabolic rates (R_{field} and E_{field}) for each species feeding
196 freely in the field. The R_{field} and E_{field} values thus obtained accounted for 1.37 (95% *CI*:
197 0.99–1.74) times the value of R_{routine} , and 1.30–1.74 (0.98–2.49) times the value of
198 E_{routine} for particle-feeders, and 1.25 (1.02–1.47) times the value of R_{routine} , and
199 1.12–1.40 (1.01–1.77) times the value of E_{routine} for carnivores. Because SDA has
200 differential effects on R_{routine} and E_{routine} , realistic O:N ratios decreased or increased in
201 varying degrees from the original values of 5.1–31.5.

202 As expected, the resultant R_{SDA} ($= R_{\text{max}} - R_{\text{routine}}$) values from the K&H model
203 based on I_{max} data were greater than those ($= R_{\text{field}} - R_{\text{routine}}$) from the I&M model for
204 all particle-feeders, but the reverse was the case for two carnivores (*Sagitta elegans*
205 and *S. enflata*) (Table 3). Since R_{routine} data (Table 3) of these two chaetognaths are
206 similar to those of other chaetognaths when considering species-specific differences in
207 body mass, temperature and distribution depth (Ikeda and Takahashi 2012), and *AE* or
208 K_1 of this taxon do not deviate appreciably from those of other metazooplankton taxa
209 (S1), overestimation of R_{SDA} values for the two chaetognath species derived from the
210 I&M model is thought to be unlikely. Considering the present paucity of I_{max} data on
211 various carnivorous metazooplankton taxa other than chaetognaths, an accumulation of
212 data is needed to resolve the disparity between the two models for carnivorous
213 metazooplankton.

214 Secor (2009) analyzed R_{SDA} data for more than 250 animal species with different
215 habitats (terrestrial, freshwater and marine), life forms (sedentary, swimming and
216 flying), and phylogenies (invertebrates, fishes, amphibians, reptiles, birds and
217 mammals, including humans) and found a significant relationship between R_{SDA} and I
218 for each group. Using data from that paper, the present author re-analyzed the
219 relationship between R_{SDA} and I for “invertebrates” (body mass = 0.01 to 750 g,
220 temperature = -0.65°C to 30°C), which yielded the following:

$$221 \quad \log_{10}R_{\text{SDA}} = 0.956\log_{10}I - 1.071 \quad (n = 29, R^2 = 0.876)$$

222 The R^2 value indicates that 88% of the variance in R_{SDA} can be attributed to I alone.
223 Since the slope did not differ significantly from unity (95%CI = 0.816–1.096; $p > 0.05$)
224 this equation can be simplified as:

$$225 \quad \log_{10}R_{\text{SDA}} = \log_{10}I - 1.071,$$
$$226 \quad \text{or } R_{\text{SDA}} = 0.085I \quad (13)$$

227 where the SD of the coefficient (0.085) is ± 0.035 . Originally, Eq. (12) was expressed as
228 an energy unit (kJ), but it can be converted to oxygen units (μLO_2) based on the
229 oxycaloric equivalents ($1\text{kJ} = 49.8 \times 10^3 \mu\text{LO}_2$; Gnaiger 1983). Considering that
230 entirely different sources of the data were analyzed in Secor (2009) and in this study,
231 the resultant slopes [0.10, Eq. (1) vs. 0.085, Eq. (13)] of the $R_{\text{SDA}}-I$ relation were
232 remarkably similar to each other, which suggests that the cost of SDA is 9–10% of the
233 ingestion by metazoans.

234 In the present study, carnivores were found to have a higher AE than
235 particle-feeders (herbivores, omnivores) (83% vs. 69%, respectively) (Fig. 2), which
236 may be due to differences in the proportion of inorganic components in their foods, e.g.
237 algal diets that are characterized by hard shells (such as small diatoms) or high ash

238 contents, which have been associated with low AE values in copepods (Conover
239 1966a; Abe et al. 2013) and tunicates (Anderson 1986; Paffenhöfer and Köster 2005).
240 As an alternative explanation, differences in AE values between particle-feeders and
241 carnivores may be due to dissimilar protein (or N) contents of their foods, which has
242 been demonstrated on fishes (Pandian and Marian 2005). The AE values compiled in
243 the present study (S1) were obtained from laboratory studies, so the quality and
244 quantity of prey are likely to have differed from what would be encountered in the field.
245 However, it is interesting to note that Conover (1966b) collected samples of
246 metazooplankton feces ($n = 26$) in the field and determined a mean AE value of 63%
247 (median: 71%), which does not differ appreciably from the values that were obtained
248 for particle-feeders (69% and 70%, cf. Fig. 2).

249 There was no significant difference in K_1 between particle-feeders and
250 carnivores in this study (Fig. 2), with the mean value (30%) being much lower than the
251 possible maximum K_1 value of 35–50% for metazoans, as was proposed by Calow
252 (1977). Any differences in K_1 that might exist between the different feeding types of
253 metazooplankton were blurred by the large scattering of values around the means. Like
254 the AE values mentioned above, the K_1 values compiled in the present study (S1) were
255 obtained almost exclusively from laboratory studies. As exceptions, Butler et al. (1969,
256 1970) calculated the K_1 values of wild *C. finmarchicus* from the N:P ratios of food
257 particulate matter and *C. finmarchicus* that were collected in the field, which were
258 combined with the N:P ratios of soluble excreta by *C. finmarchicus* that were
259 determined in laboratory experiments. Resultant K_1 values for wild *C. finmarchicus*
260 growing from eggs to adults were 33% in N and 28% in P (Butler et al. 1969) and *C.*
261 *finmarchicus* at C5 and C6 were 27% in N and 17% in P (Butler et al. 1970),

262 respectively. These results from wild *C. finmarchicus* support the view that the mean
263 K_1 (30%) obtained in the present study is realistic for wild metazooplankton.

264 In a review of the gross growth efficiency ($= K_1$) of marine and freshwater
265 protozooplankton (nano/microflagellates, dinoflagellates and ciliates) and
266 metazooplankton (rotifers, cladocerans and copepods) taxa, Straile (1997) concluded
267 that K_1 was insignificantly influenced by the temperature, prey-predator weight ratio
268 and taxon groups but was affected by the food concentration; thus, mean and median
269 values of 20–30% were calculated across these taxonomic groups. As metazooplankton
270 taxa, the mean and median K_1 values calculated by Straile (1997) for cladocerans (27%
271 and 28%, respectively) and copepods (26% and 22%, respectively) appear to be
272 somewhat low compared with the respective values for particle-feeders in the present
273 study (29% and 27%, respectively; Fig. 2). Since different suites of species, units and
274 methods used to calculate K_1 across various studies, I used one datum (mean or
275 median) per diet or measuring unit, disregarding the effects of food concentration. Also,
276 I treated values for the same species obtained from different studies as an independent
277 dataset for this study (S1) to minimize any bias caused by different sample sizes for
278 each metazooplankton species. By contrast, Straile (1997) adopted different criteria for
279 data selection and reduction to analyze the effects of several potential factors
280 mentioned above on the K_1 of each taxon group. Considering the large errors around
281 the mean and median K_1 values of the taxa (Straile, 1997; Fig. 2) and feeding-types
282 (this study; Fig. 2) as well as the nature of comparisons, some differences between the
283 two studies may be of marginal importance.

284 In conclusion, realistic respiration rates ($R_{\text{routine}} + R_{\text{SDA}}$) of metazooplankton
285 feeding under field conditions can be estimated from R_{routine} , which was determined in

286 the absence of feeding, multiplying by 1.37 for particle-feeders and 1.25 for carnivores.
287 Similarly, the increase in ammonia excretion rates (E_{SDA}) can be calculated from R_{SDA}
288 by multiplying 0.080 for particle-feeders and 0.116 for carnivores. It can be argued that
289 the assumptions that were made and the use of overall means or medians for the $R-I$
290 relationship, AE , K_1 and food C:N ratio mask important species-specific metabolic
291 features of metazooplankton species. However, considering enormous complexity of
292 metazooplankton assemblages in terms of taxonomy, size, food habits and habitats and
293 the lack of feasible approaches to assess their metabolic rates under field conditions,
294 the I&M model may be an acceptable compromise between crude “general”
295 metazooplankton approximations and highly intensive species-by-species approach.
296 Therefore, the approach used in this study could contribute to our better understanding
297 of the realistic dynamic roles of metazooplankton in the carbon cycle and energy flow
298 in pelagic ecosystems.

299

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302

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305

306 **Data availability**

307 All AE and K_1 data are presented in Online Resource (S1). Online data are
308 acknowledged at appropriate points of the Methods section.

309

310 **Compliance with ethical standards**

311 **Conflict of interest**

312 The author declares that there are no conflicts of interest.

313

314 **Ethical approval**

315 Ethical approval was not required for this work.

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Table 1. Regression statistics of respiration rates (R as $\text{CO}_2\text{-C}$) of six metazooplankton species on ingestion rates (I). When the original units of R and I were different, they were converted to common units for regression analyses. C6F = Copepodid 6, female.

Metazooplankton	Diet	T°C	Original unit		Common unit	$R = \alpha I + \beta$		Reference
			R	I		α (95%CI)	p for $\alpha = 0$	
Particle-feeder								
<i>Daphnia magna</i>	<i>Scenedesmus acutus</i>	20	$\mu\text{gC mgDM}^{-1} \text{h}^{-1}$	$\mu\text{gC mgDM}^{-1} \text{h}^{-1}$			0.11–0.17 ^b	Lampert (1986)
<i>Acartia tonsa</i> C6F	<i>Tetraselmis impellucida</i>	20	$\mu\text{gC ind.}^{-1} \text{d}^{-1}$	$\mu\text{gC ind.}^{-1} \text{d}^{-1}$	adjusted ^d		0.19 (0.13–0.25)	Thor et al. (2002)
	<i>Dunaliella tertiolecta</i>	20	$\mu\text{gC ind.}^{-1} \text{d}^{-1}$	$\mu\text{gC ind.}^{-1} \text{d}^{-1}$			0.06 (0.002–0.12)	
<i>Acartia tonsa</i> C6F	<i>Rhodomonas baltica</i>	18	$\text{ngC } \mu\text{gDM}^{-1} \text{d}^{-1}$	$\text{ngC } \mu\text{gDM}^{-1} \text{d}^{-1}$			0.071 (0.053–0.089)	Kjørboe et al. (1985)
<i>Calanus helgolandicus</i>	<i>Lauderia borealis</i>							
	<i>Skeletonema costatum</i>		$\mu\text{LO}_2 \text{ ind.}^{-1} \text{d}^{-1}$	$\mu\text{gOM ind.}^{-1} \text{d}^{-1}$			0.049 (0.024–0.074) ^c	Gaudy (1974)
	<i>Phaeodactylum tricornutum</i>							
<i>Temora stylifera</i> C6	<i>Hymenomonas elongata</i>	16	$\mu\text{gC ind.}^{-1} \text{d}^{-1}$	$\mu\text{gC ind.}^{-1} \text{d}^{-1}$			0.15 (0.10–0.20)	About Debs (1984)
<i>Euphausia superba</i>	<i>Chaetoceros calcitrans</i>	–0.5	$\mu\text{LO}_2 \text{ mgWM}^{-1} \text{h}^{-1}$	$10^6 \mu\text{m}^3 \text{ ind.}^{-1} \text{h}^{-1}$	$\mu\text{gC mgWM}^{-1} \text{h}^{-1}$		0.072	Ikeda and Dixon (1984)
	<i>Phaeodactylum tricornutum</i>	–0.5	$\mu\text{LO}_2 \text{ mgWM}^{-1} \text{h}^{-1}$	$10^6 \mu\text{m}^3 \text{ ind.}^{-1} \text{h}^{-1}$	$\mu\text{gC mgWM}^{-1} \text{h}^{-1}$		0.054	
	<i>Thalassiosira eccentrica</i>	–0.5	$\mu\text{LO}_2 \text{ mgWM}^{-1} \text{h}^{-1}$	$10^6 \mu\text{m}^3 \text{ ind.}^{-1} \text{h}^{-1}$	$\mu\text{gC mgWM}^{-1} \text{h}^{-1}$		0.13	
	<i>Fragilariaopsis vanhaurkii</i>	–0.5	$\mu\text{LO}_2 \text{ mgWM}^{-1} \text{h}^{-1}$	$10^6 \mu\text{m}^3 \text{ ind.}^{-1} \text{h}^{-1}$	$\mu\text{gC mgWM}^{-1} \text{h}^{-1}$		0.10	
	<i>Artemia nauplii</i>	–0.5	$\mu\text{LO}_2 \text{ mgWM}^{-1} \text{h}^{-1}$	$10^6 \mu\text{m}^3 \text{ ind.}^{-1} \text{h}^{-1}$	$\mu\text{gC mgWM}^{-1} \text{h}^{-1}$		0.086	
Carnivore								
<i>Pleurobrachia piteus</i>	natural copepods	13	$\text{gC ind.}^{-1} (6\text{d})^{-1}$	$\text{gC ind.}^{-1} (6\text{d})^{-1}$			0.14 (–0.10–0.29)	Reeve et al. (1978)
Grand mean 0.104								
						SD:	0.045	
						N:	12	

^a R expressed in μLO_2 was converted to μgC as, $\text{O}_2 \times 0.97 (\text{RQ}) \times 1222.4$; I in organic matter (OM): μg to μgC as $\text{OM} \times 0.5$, and volume (V : μm^3) to μgC as $0.38 \times V^{0.85}$ for diatoms (Montagnes and Franklin, 2001) and $0.064 \mu\text{gC/V}$ for *Artemia* nauplii (Ikeda, unpublished).

^bOriginal α expressed as $R_{\text{SDA}}/\text{Assimilation}$ was converted R_{SDA}/I by using $AE = 71\%$ (Nielsen and Olsen 1989)

^cData on the three alga were combined

Table 2. SDA effects (mean \pm 95%CI) on metabolic rates of eight metazooplankton species. (1) The rates of routine respiration (R : $\mu\text{L O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$) and ammonia excretion (E : $\mu\text{g N ind.}^{-1} \text{ h}^{-1}$) and O:N ratios (by atoms), (2) the effects of SDA on R , E and O:N ratios, and (3) the difference between realistic R ($= R_{\text{field}}$) and E ($= E_{\text{field}}$) of these species free-feeding in the field and R_{routine} and E_{routine} respectively.

	(1) Routine			(2) SDA effect			(3) = (1) + (2)			(3)/(1)		
	R	E	O:N	R (Eqs. 6-1.2)	E (Eqs. 12-1.2)	O:N	R	E	O:N	R	E	O:N
Metazooplankton ^a												
Particle-feeders (herbivores, omnivores)												
Calanoid copepods												
<i>Acartia australis</i>	0.056	0.0054	13.0	mean +95%CI -95%CI	0.020 0.041 0.000	0.002 0.003 0.000	0.076 0.097 0.056	0.007 0.009 0.005	13.6 14.0 12.9	1.37 1.74 0.99	1.30 1.61 0.99	
<i>Calanus finmarchicus</i>	0.328	0.013	31.5	mean +95%CI -95%CI	0.120 0.243 -0.003	0.010 0.019 0.000	0.448 0.571 0.325	0.023 0.032 0.013	24.8 22.0 31.8	1.37 1.74 0.99	1.74 2.49 0.98	
<i>Neocalanus cristatus</i>	1.67	0.164	12.7	mean +95%CI -95%CI	0.61 1.24 -0.01	0.049 0.099 -0.001	2.28 2.91 1.66	0.213 0.263 0.163	13.4 13.8 12.7	1.37 1.74 0.99	1.30 1.60 0.99	
Euphausiids												
<i>Euphausia pacifica</i>	16.1	0.781	25.8	mean +95%CI -95%CI	5.89 11.91 -0.13	0.471 0.953 -0.010	21.99 28.01 15.97	1.25 1.73 0.77	22.0 20.2 25.9	1.37 1.74 0.99	1.60 2.22 0.99	
Tunicates												
<i>Salpa thompsoni</i>	12.0	0.806	18.6	mean +95%CI -95%CI	4.39 8.88 -0.10	0.351 0.710 -0.008	16.39 20.88 11.90	1.16 1.52 0.80	17.7 17.2 18.6	1.37 1.74 0.99	1.44 1.88 0.99	
Carnivores												
Chaetognaths												
<i>Sagitta elegans</i>	1.41	0.345	5.1	mean +95%CI -95%CI	0.35 0.67 0.02	0.041 0.078 0.003	1.76 2.08 1.43	0.39 0.42 0.35	5.7 6.1 5.2	1.25 1.47 1.02	1.12 1.22 1.01	
<i>Sagitta enflata</i>	1.67	0.12	17.4	mean +95%CI -95%CI	0.41 0.79 0.03	0.048 0.092 0.003	2.08 2.46 1.70	0.17 0.21 0.12	15.5 14.5 17.2	1.25 1.47 1.02	1.40 1.77 1.03	
Ctenophores												
<i>Mnemiopsis leidyi</i>	30.35	2.93	12.9	mean +95%CI -95%CI	7.53 14.39 0.52	0.873 1.669 0.060	37.88 44.74 30.87	3.80 4.60 2.99	12.4 12.2 12.9	1.25 1.47 1.02	1.30 1.57 1.02	

^aselected from Table 1 in Ikeda et al. (2000).

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Table 3. Comparison of the SDA effects on routine respiration rates (R_{SDA} : $\mu\text{LO}_2 \text{ ind.}^{-1} \text{ h}^{-1}$) of metazooplankton species derived from R_{routine} in this study (I&M model), and maximum ingestion rates (I_{max}) as a function of body mass (M) and temperature (T) by Kiørboe and Hirst (2014) (K&H model). The mean and 95%CI were given to the results from the I&M model (see Table 2). ND = no data.

Metazooplankton ^a	T (°C)	M (mgC) ^b	(1) R_{routine}	Model	(2) R_{SDA} (95%CI)	(2)/(1)
Particle-feeders (herbivores, omnivores)						
Calanoid copepods						
<i>Acartia australis</i>	24.5	0.0039	0.056	I&M	0.020 (0.000–0.041)	0.37
				K&H	0.077 ^c	1.38
<i>Calanus finmarchicus</i>	0.1	0.215	0.328	I&M	0.120 (-0.003–0.243)	0.37
				K&H	0.156 ^c	0.48
<i>Neocalanus cristatus</i>	6.3	0.792	1.67	I&M	0.61 (-0.01–1.24)	0.37
				K&H	0.84 ^c	0.50
Euphausiids						
<i>Euphausia pacifica</i>	10.2	5.36	16.1	I&M	5.9 (-0.1–11.9)	0.37
				K&H	6.4 ^c	0.40
Tunicates						
<i>Salpa thompsoni</i>	-1	5.39	12	I&M	4.4 (-0.1–8.9)	0.37
				K&H	26.0 ^c	2.17
Carnivores						
Chaetognaths						
<i>Sagitta elegans</i>	-0.3	1.73	1.41	I&M	0.35 (0.02–0.67)	0.25
				K&H	0.04	0.03
<i>Sagitta enflata</i>	25	0.249	1.67	I&M	0.41 (0.03–0.79)	0.25
				K&H	0.25	0.15
Ctenophores						
<i>Mnemiopsis leidyi</i>	20	5.08	30.4	I&M	7.5 (0.5–14.4)	0.25
				K&H	ND	

^aselected from Table 1 in Ikeda et al. (2000).

^bconverted from mgDM by referring original data source.

^cK&H > I&M

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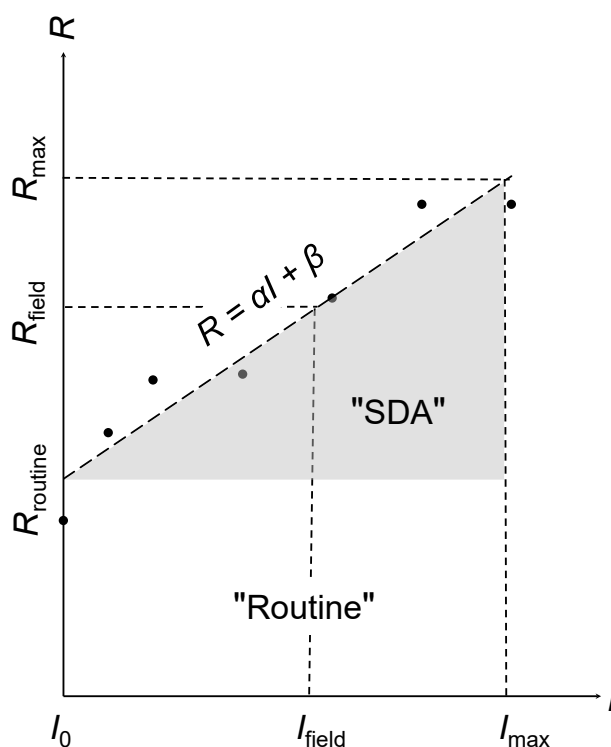
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456 **Fig. 1.** Schematic presentation of the increase in respiration rate (R) in response to the
457 increase in ingestion rate (I) of metazooplankton (based on Ikeda and Dixon 1984;
458 Kiørboe et al. 1985; Lampert 1986; Thor et al. 2002). From the regression line of R on
459 I (broken line), R of metazooplankton feeding in the field ($R_{\text{field}} = R_{\text{routine}} + R_{\text{SDA}}$) can
460 be estimated by knowing its ingestion rate in the field (I_{field}). Routine and maximum
461 metabolic rates (R_{routine} and R_{max}) are R at no-feeding (I_0) and maximum ingestion (I_{max}),
462 respectively. The area under the broken line minus R_{routine} (“Routine”) represents SDA
463 (“SDA” shaded gray).

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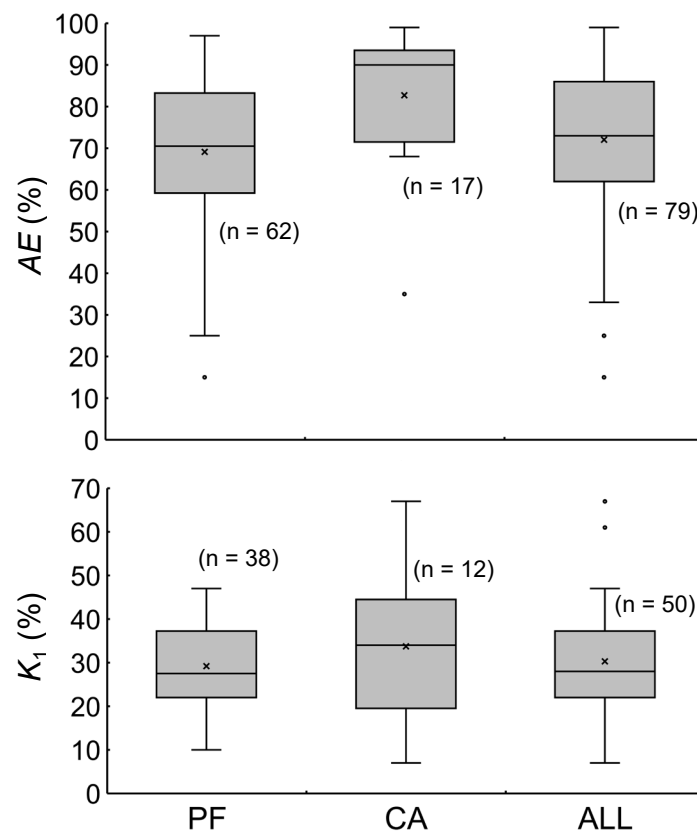
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481 **Fig. 2.** Box-and-whisker plots of AE and K_1 of marine metazooplankton, grouped as
482 particle-feeders (PF), carnivores (CA) and all combined (All), as listed in S1. Crosses
483 denote the mean value, the central line of the box represents the median of the
484 distributions and the upper and lower box limits are the 25% and 75% quartiles of the
485 data, respectively. The whiskers cover the 5–95% percentiles of the data.

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S1. *AE* and *K₁* of various food organisms by marine metazooplankton species. *AE* has been determined gravimetrically [DM, C, N, P or ash-free dry mass (AFDM) or energy content (Cal) of diet ingested and feces], from the ratios of nutrients (C, N) and non-nutrients (ash, Cr, Ge or pigments) of diet and feces, or by incorporation of diet labeled with radio-active isotopes (¹⁴C, ³²P, ³⁵S or ⁶⁸Ge). *K₁* has been calculated on various units (C, N, P, Cal or DM). AFDM = organic matter (OM). For copepods, Naupliar (N) and Copepodid (C) stages were noted wherever available. Metazooplankton was separated into particle-feeders (PF) and carnivores (CA).

Metazooplankton	Feeding-type	Temp (°C)	Food organism ^a	<i>AE</i> (%)	Method	<i>K₁</i> (%)	Units	Ref ^b
Copepods								
<i>Acartia clausi</i> C6F	PF	22	natural phyto assemblages	40–80 (60)	¹⁴ C			1
<i>Acartia tonsa</i> N2–C6	PF	16–18	Diat, Dino, Pym, Chlo			44	C	2
<i>A. tonsa</i> C6	PF	20	Diat	15–50 (33)	C			3
			Fla	94–99 (97)	C			
			Cilia	83–95 (89)	C			
<i>A. tonsa</i> C6F	PF	20–22	coral mucus	47	AFDM/DM ratio			4
				68	C/DM ratio			
				36	N/DM ratio			
<i>A. tonsa</i> C6	PF	18	Chrypt	51–81(62)	C	39–49 (43)	C	5
				60–95 (73)	N	40–49 (43)	N	
<i>A. tonsa</i> C6F	PF	18	Dino, Pym, Chlo	29–61(45)	¹⁴ C/ ³¹ Cr ratio	9–37 (19)		6
<i>Calanus finmarchicus</i> C6F	PF	10–20	Diat	55–99 (87)	³² P			7
			Dino	47–99 (89)	³² P			
			Fla	26–99 (82)	³² P			
<i>Calanus finmarchicus</i> C6F	PF	(10–20)?	Diat	60–75 (68)	¹⁴ C			8
			Fla	53–78 (67)	¹⁴ C			
<i>Calanus finmarchicus</i> N1–C5	PF	10	Diat	54–68 (62)	N	34	N	9
	PF	10				14	N	
<i>Calanus finmarchicus</i> /C. <i>helgolandicus</i> egg–C6	PF	12	natural phyto assemblages			21–38 (33)	N	10
						19–35 (28)	P	
<i>Calanus finmarchicus</i> /C. <i>helgolandicus</i> C5, C6	PF	6–18	natural phyto assemblages	62	N	27	N	11
				77	P	17	P	
<i>Calanus finmarchicus</i> /C. <i>helgolandicus</i> C6F	PF	0.5	Diat	74	⁶⁸ Ge/ ¹⁴ C ratio			12
<i>Calanus finmarchicus</i> /C. <i>helgolandicus</i> C2–C5	PF	10	Diat, Chlo, Pym			36	N	13
<i>Calanus helgolandicus</i> C6F	PF	10	natural phyto assemblages	74–91 (83)	OM			14
<i>Calanus helgolandicus</i> C6F	PF	10	barnacle (<i>Elminus</i>) naupl	80–90 (95)	N	–29–52 (47)	N	15
<i>Calanus helgolandicus</i> N1–C6	PF	10, 15	Diat			34–35 (35)	C	16
<i>Calanus helgolandicus</i> N2–C6	PF	15	Diat, Dino			17–33 (24)	OM	17
						19–30 (23)	C	
						18–33 (25)	Cal	
<i>Calanus hyperboreus</i> C4, 5	PF	2–5	Diat	44–65 (55)	DM or Cal	4–36 (21)	DM	18
						5–50 (30)	Cal	
<i>Calanus hyperboreus</i> C6F	PF	4	Dino	39–86 (69)	AFDM/DM ratio			19
				64–85 (72)	OM			
<i>Calanus hyperboreus</i> C6F	PF	2–11	Diat, Dino, Chlo	40–87 (64)	AFDM/DM ratio			20
<i>Calanus hyperboreus</i> C6F	PF	3	Diat	84–88 (86)	³¹ S/ ¹⁴ C ratio			21
<i>Calanus pacificus</i> C6F	PF	12	Diat	69–85 (77)	C/Chl a ratio			22
				74–93 (84)	N/Chl a ratio			
<i>Calanus pacificus</i> C5, C6F	PF	15	Diat	96–97 (97)	¹⁴ C	40–50 (45)	C	23
<i>Chiridius armatus</i> C6F	PF	6	Artemia naupl mixed zoopl	81–95 (90)	AFDM/DM ratio			24
				91–97 (95)	AFDM/DM ratio			
<i>Eucalanus bungii</i> C5	PF	3	Diat	34–65 (57)	AFDM/DM ratio			25
<i>Eucalanus hyalinus</i> C6F	PF	20	Diat	92–95 (94)	C, N			26
<i>Metridia longa</i>	PF	5	Diat	54–57 (56)	AFDM/DM ratio			27
<i>Metridia lucens</i>	PF	5	Diat, Dino, Chlo, Artemia naupl	35–97 (70)	AFDM/DM ratio			27
<i>Neocalanus cristatus</i> C5	PF	3	Diat, Dino, Raph	45–66 (57)	AFDM/DM ratio			25
<i>Neocalanus cristatus</i> C5	PF	5–7 (6)	natural phyto assemblages	54–86 (75)	¹⁴ C	5–60 (40)	C	28
<i>Neocalanus plumchrus</i> C5	PF	6–12 (9)	natural phyto assemblages	83–86 (85)	¹⁴ C	4–42 (22)	C	28
<i>Neocalanus flemingeri</i> C5	PF	3	Diat	44–66 (62)	AFDM/DM ratio			25
<i>Oithona davisae</i> N1–C3	PF	20	Dino	65–86(78)	C	17–28(22)	C	29
<i>Paracalanus parvus</i> C6F	PF	18	Diat, Dino			33–42 (38)	N	30
						13–45 (27)	C	
<i>Pseudocalanus elongatus</i> N1–C6	PF	12.5	Diat			14–18 (15)	C	31
<i>Rhincalanus nasutus</i> N1–C6	PF	10, 15	Diat			30–45 (37)	C	16
<i>Temora longicornis</i> C6F	PF	10	Diat	52–98 (77)	³² P			32
<i>Temora longicornis</i> N1–C6	PF	12.5	Diat			17–27 (23)	C	31
<i>Temora stylifera</i> C6F	PF	16	Diat	80	C			33
		16	Diat	79	N			
		16	Pym	71	C			
		16	Pym	66	N			
Cladocerans								
<i>Penilia avirostris</i> adult	PF	22	natural phyto assemblages	30–70 (50)	¹⁴ C			1
Mysids								
<i>Metamysidopsis elongata</i> F	PF	14–20	Artemia naupl	59–91 (75)		26	Cal	34
<i>Mysidium integrum</i>	PF	20–22	coral mucus	44	AFDM/DM ratio			4
				57	C/DM ratio			
				55	N/DM ratio			
Euphausiids								
<i>Euphausia superba</i> , larva (C1–F6)	PF	0	Diat, Artemia naupl			30	DM	35
						46	C	
						45	N	
<i>Euphausia pacifica</i>	PF	7–16	Artemia naupl	46–95 (84)	¹⁴ C	6–46 (26)	C	36
<i>Euphausia pacifica</i> furcicilia–late adult	PF	8, 12	Diat	81	C	24	C	37, 38
				86	N	27–29 (28)	N	
<i>Meganyctiphanes norvegica</i>	PF	13.5	Artemia juv	74–92 (84)	AFDM			39
Amphipods								
<i>Themisto japonica</i>	CA	7	Artemia naupl			27 ^b		40
Decapods								
<i>Lucifer chasei</i> , Protozoa–adult	PF	ca. 25	Diat, Artemia naupl	8–22 (15)	³⁵ S	7–14 (10)	Cal	41
<i>Sergia similis</i> PZ1–PL4	PF	10–15	Diat, Pym, Rot, Artemia naupl			10–50 (32)	C	42
Pteropods								
<i>Clione limacina</i>	CA	15	<i>Spiratera</i>	83–98 (97)	C, N balance	47–76 (61)	C	43
				98–99 (99)	N	49–78 (67)	N	

Hydrozoans								
<i>Cladonema californicum</i>	CA	18	Artemia naupl	50–80 (71)	C, N	21–40 (32) 22–43 (36)	C N	44
Siphonophores								
<i>Aurelia aurita</i> ephyra	CA	15	Rot, Artemia naupl, Cirriped larvae	64–74 (68)	C	13–20 (17)	C	45
<i>Aurelia aurita</i> adult	CA	15	Artemia naupl, Acartia	33–37 (35)	C	8–12 (10)	C	45
Siphonophores								
<i>Stephanophyes superba</i>	CA	21–22	Copepods	92	C			46
				91	N			
<i>Forskalia</i> spp.	CA	21–22	Copepods	90	C			
				94	N			
<i>Diphyes disper</i>	CA	21–22	Copepods	94	C			
				93	N			
<i>Rosacea</i> spp.	CA	21–22	Copepods	88	C			
				91	N			
Ctenophores								
<i>Pleurobrachia bachei</i>	CA	13	Copepods (mostly Acartia)	52–75 (68)	C, N	3–11 (7)	C, N	47
<i>Mnemiopsis mccladyi</i>	CA	26	Copepods (Acartia)	57–83 (72)	C	20–45 (37)	C	48
Chaetognaths								
<i>Sagitta hispida</i>	CA	16–26	Artemia naupl		N	19–50 (36)	N	49
<i>Sagitta hispida</i>	CA	24–26	Copepods	54–97 (80)	DM			50
<i>Sagitta crassa</i>	CA	18–26	Copepods (Acartia)			28	DM	51
	CA	19–24	Copepods, polychaete larvae	56–93 (83)	DM			52
<i>Sagitta nagae</i>	CA	20–22	Copepods (Acartia, Oithona)			47	DM	53
Appendicularians								
<i>Oikopleura vanhoeffeni</i>	PF	–1.2 to 4.5	Diat	42–83 (67)	⁶⁸ Ge/ ¹⁴ C ratio			12
Tunicates								
<i>Cyclosalpa bakeri</i>	PF	10–12	natural plankton assemblages	61	C/pigment ratio	14	C	54
				71	N/pigment ratio	16	N	
<i>Doliolleta gegenbauri</i> (gonozoid)	PF	20	Diat, Dino, Fla	51–73 (62)	C			26
				54–81 (68)	N			
<i>Doliolum denticulatum</i> (gonozoid)	PF	22	natural plankton assemblages	20–50 (25)	¹⁴ C			1
<i>Salpa fusiformis</i> (blastozoid)	PF	13–22	Diat, Fla	32–64 (48)	AFDM/DM ratio			55

^aChlo: Chlorophytes, Chrys: Chrysophytes, Cilia: Ciliates, Chrypt: Cryptophytes, Cya: Cyanobacteria, Diat: Diatoms, Dino: Dinoflagellates, Fla: flagellates, Raph: Raphidophytes, Pym: Prymnesiophytes, Rot: Rotifers.

^bcalculated from $K_2 = 30$, assuming AE=90.7% of the benthic-pelagic amphipod *Calliopius laevisculus* fed copepods [Dagg MJ (1976) Int Revue ges Hydrobiol 61: 297–357].

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