Food Utilization in *Artemia* for Growth, Reproduction, and Maintenance

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Using marine *Chlamydomonas* as food, the food requirement of bisexual brine shrimp *Artemia franciscana* was estimated in terms of nitrogen in order to assist production. The ingested food was theoretically fractionated to the maintenance, somatic growth and reproduction of nauplius and cyst. While feeding marine chlamydomonad (5 pg N/cell) to the shrimp (L mm), the daily maintenance ration was almost proportional to the cube of body length (2.952) and was 2844 cells/shrimp/day for shrimp of 1 mm length at 28°C. On the basis of ingested food, the somatic food conversion efficiency was 67%. The efficiency of nauplius production was 23% and that of cyst production was 44%, based on the food taken by a pair of shrimps. Including the reproductive products as growth, the gross conversion efficiency was 16% in the groups from which the maintenance ration and somatic conversion factor were obtained, and 24% in the groups from which the reproductive conversion factors were obtained. The reproductive growth per total growth increased with the body length and the feeding rate, and was zero below 5.7 mm in length and 1.0 times the daily maintenance ration.

Key words: *Artemia*, *Chlamydomonas*, nitrogen budget, growth efficiency, maintenance ration

The worldwide expansion of marine fish-seedling production requires large quantities of brine shrimp *Artemia* cysts, from which the nauplii are obtained and used as food. Japan imports considerable quantities of the world's cyst production.^{1,2)} The increasing demand is extending *Artemia* production to many countries, even to places where the shrimp were not originally found. Therefore, further biological information on *Artemia* production is in great demand.

The shrimp can consume a large amount of food relative to body mass, but growth is retarded by overfeeding.³⁾ It is important to determine the optimum feeding regime for effective production, especially for intensive culture. Of the many models available to analyze the energy or mass budget, we employed a mass budget model for individual growth including reproduction using nitrogen as the indicator. Nitrogen is one of the important biological elements which constitute the tissue, and the nitrogen content is reported to be 5 to 10% of the dry weight of shrimp.⁴⁾ The model used assumes that the assimilated food is used to maintain the body, to increase the body mass and to reproduce offspring such as nauplii and cysts of shrimp.

The present paper describes the regression between the maintenance ration and body length, food conversion factors for somatic growth and reproduction of nauplii and cysts, and the ratio of reproductive growth to total growth. These data are fundamental to know the food requirement of the shrimp.

Materials and Methods

Marine *Chlamydomonas* sp. was cultured in Miquel seawater without addition of silicate and used as food in the exponential phase. It contained 5.0 pg N/cell.^{3,4)} The algal concentration was measured by a Bürker-Türk

hemocytometer and the standard error was about 6%. The mean specific growth rate was found to be 0.665/day, which was used to calculate the ration. The stock culture was diluted with GF/C-filtered seawater to prepare the rearing medium.

The San Francisco Bay brine shrimp *Artemia franciscana* (previously *Artemia salina*) was purchased from Metaframe Corporation, Newark, Cal., hatched in seawater at about 28°C, reared under stable light conditions, fed with the marine chlamydomonad, and kept in the medium at ca. 28°C. The body length L was measured under a microscope from the tip of head to the end of furca excluding setae.³⁾ The nitrogen content was estimated from the body length according to the regression for groups including both sexes:⁴⁾

$$L, \text{ mm} \quad \text{N content, ng N/shrimp}$$

$$0.8-6.3 \quad 305.8 L^{2.176} \quad (1)$$

$$6.3- \quad 111.7 L^{2.725} \quad (2)$$

Before starting the feeding experiments, the shrimps were grouped by size and also by sex when they were mature enough for sex identification. A single pair of shrimps of similar size were reared in a beaker to obtain the food conversion factor for reproduction. However, 10 shrimps of similar size were reared in a container to obtain the somatic food conversion factor or daily maintenance ration.

A nauplius was assumed to have 0.1983 µg N/embryo when spawned and a cyst to have 0.3123 µg N/cyst according to Dutrieu.⁵⁾

Estimation of Daily Ration

The daily ration d was estimated by the following equation:^{6,7)}

$$d = C_0 \cdot f \cdot [\exp\{(p - f/V) \cdot t\} - 1] / (p - f/V), \quad \text{and} \quad t = 1 \text{ day} \quad (3)$$

$$= C_0 \cdot V \cdot [\exp(p - f/V) - 1] / (p - f/V - 1) \quad (4)$$

$$= C_0 \cdot V \cdot Cf \quad (5)$$

The definition of all the variables including the above are shown in the Appendix in alphabetical order. The correction factor Cf shown in Table 1 is nearly unity when f/V is kept large enough. The ratio actually ranged from 2.3 to 21.7 (mainly 3.3–21.2). This phenomenon of Cf being almost unity simplified the design of the feeding plan. However, Cf was not assumed to be unity in the final calculation.

The filtering rate f was estimated from the body length L (mm) according to the following regression:³⁾

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Table 1. Correction factor (C_f) to estimate the daily ration by $C_0 \cdot V$ as related to the change in the filtering rate (f) and the specific phytoplankton growth rate (p)

Growth rate p , 1/day	f/V , 1/day								
	2	3	4	5	10	15	20	25	30
	Correction factor (C_f)*								
-1.000	0.633	0.736	0.795	0.831	0.909	0.937	0.952	0.962	0.968
-0.500	0.734	0.831	0.879	0.905	0.952	0.968	0.976	0.980	0.984
-0.200	0.808	0.899	0.938	0.956	0.980	0.987	0.990	0.992	0.993
0.000	0.865	0.950	0.982	0.993	1.000	1.000	1.000	1.000	1.000
0.200	0.927	1.006	1.029	1.033	1.020	1.014	1.010	1.008	1.007
0.500	1.036	1.101	1.108	1.099	1.053	1.034	1.026	1.020	1.017
0.665	1.104	1.160	1.157	1.138	1.071	1.046	1.034	1.027	1.023
0.800	1.165	1.213	1.199	1.173	1.087	1.056	1.042	1.033	1.027
1.000	1.264	1.297	1.267	1.227	1.111	1.071	1.053	1.042	1.034
1.500	1.574	1.554	1.469	1.385	1.176	1.111	1.081	1.064	1.053

Refer Appendix for variables.

* $C_f = f/V \cdot \exp(p - f/V) / (p - f/V)$.

$$f = 4.989 L^{1.751}, \quad \text{ml/shrimp/day} \quad (6)$$

Mean initial food concentration C_0 (Tables 2 and 3) and mean specific algal growth rate ($p = 0.665/\text{day}$) were used in the calculation. The rearing media including controls without *Artemia* were changed daily and the body length was measured when the shrimp were transferred to a new container.

Design of Feeding Experiment

The assimilated food is considered to contribute to maintenance of the body, individual or somatic growth and reproduction such as production of nauplii or cysts, as shown by the following equation:

$$a' \cdot R = A + gm \cdot G + yn \cdot Yn/2 + yc \cdot Yc/2 \quad (7)$$

where a' is the apparent assimilation efficiency (here a' is normally assumed to be unity), R the ration in a certain period T or Ta , M the maintenance ration during the period T , gm the food conversion factor (food per growth) for somatic growth G , yn the factor for the naupliar production Yn , and yc the factor for cyst production Yc . Yn and Yc are the spawn per pair as shown in the Appendix.

Estimation of Daily Maintenance Ration

At a fixed daily ration $d1$, shrimps were reared and the body length was measured daily. If growth was confirmed to stop at body length $L1$, $d1$ was considered to be the daily maintenance ration for the shrimp of body length $L1$ as shown in Fig. 1. The daily ration was then increased to $d2$ by decreasing the rearing density, i.e. increasing V . When the shrimp attained another steady size $L2$, another daily maintenance ration was obtained as $d2$ in the same way. The daily maintenance ration m_i for each group of shrimps between these sizes was estimated by interpolation using the allometric growth of the group (log-log plot). Another kind of daily maintenance ration m_r was obtained from the regression line shown in Fig. 4 (Eqs. (10) and (11)).

Estimation of Somatic Food Conversion Factor

The simplest way of estimation is described at first, though several kinds of estimation were carried out. As shown in Fig. 1, the daily maintenance ration m_i for a group is estimated from the body length growth curve. The integrated difference ($d2 - m_i$) over period T is considered to be the surplus food for the somatic or individual growth before the shrimp starts to reproduce, and is shown by the shaded area in Fig. 1. Assuming that a' is unity, the ratio of all the surplus food ($Rm_i = A - M_i$ in Table 2) to the somatic growth G is defined here as the somatic food conversion factor gm_i in terms of nitrogen, i.e., $gm_i = Rm_i/G$ in Table 2. This mean is gm_{i1} in Table 4 (cf. Appendix for details of the variables).

The second estimation method used the ratio gm_r for each group, M_r , instead of M_i :

$$gm_r = (A - M_r)/G = Rm_r/G \quad (8)$$

as shown in Table 2. This mean is gm_{r1} in Table 4.

The third and fourth estimates of gm were the weighted means of gm_i

Fig. 1. Experimental design to estimate the daily maintenance ration and food conversion factor in *Artemia*.

Solid circles are the body length of shrimp and the solid line is the growth curve. Broken lines are the fixed daily rations and the shaded area is the ration which contributes to the growth of shrimp. $L1$ and $L2$ are the steady length attained at the daily ration of $d1$ and $d2$, respectively.

and gm_r , respectively, i.e., the ratios of mean ration over maintenance to mean somatic growth. These are gm_{i2} and gm_{r2} in Table 4.

The fifth and sixth estimations were made by multiple regression using data Rm_i and Rm_r including the groups which reproduced. These are gm_{ir} and gm_{rr} in Table 4.

The seventh estimate of gm_3 used to estimate the reproductive food conversion factor was obtained from the regression of gm_i vs. body length L as shown in Fig. 5 assuming that the factor changed with body size.

These factors are shown below (cf. Appendix):

$$gm_{i1} = \text{Mean}(gm_i), \quad gm_i = Rm_i/G = (A - M_i)/G;$$

$$gm_{r1} = \text{Mean}(gm_r), \quad gm_r = Rm_r/G = (A - M_r)/G;$$

$$gm_{i2} = \Sigma Rm_i / \Sigma G;$$

$$gm_{r2} = \Sigma Rm_r / \Sigma G;$$

$$gm_{ir} \text{ by multiple regression of } Rm_i(G, Yc, Yn) \text{ and } Rm_r(G, Yc, Yn);$$

$$gm_{rr} \text{ by multiple regression of } Rm_r(G, Yc, Yn); \text{ and}$$

$$gm_3 \text{ by regression of } gm_i(L).$$

Estimation of Reproductive Food Conversion Factor

A fixed daily ration was given to each pair of shrimps throughout the experiment. However, the ration differed among the pairs. Ry_x , the ration over maintenance and somatic growth, is considered to contribute to the production of nauplii Yn and/or cysts Yc : $A - M - gm_x \cdot G$ where the suffix x denotes the estimation method as shown in Table 4 and the Appendix. The component of Ry_x for Yn_x divided by Yn_x is defined to be the reproductive food conversion factor ym_x , and yc_x is also defined in the same way. These were estimated by the multiple regression described in the next section (Statistical analysis). However, there are many ways of estimating M and gm_x as shown above. Using the ration over maintenance Rm_i is a compromise when using methods ir , $ri1$, or $ri2$ (cf. Table 4 and the end of the above section), i.e., Rm_i for groups 1–17 and Rm_r for groups 18–35. The estimate gm_3 was also used in the same way, in which only Ry_{r3} in Table 3 was used as the dependent variable.

Another problem is the choice of period Ta during which the ration directly contributes to the production of nauplii and/or cysts. Shrimp usually spawn every 3 days in the optimum conditions at the temperature. This interval is the reproductive cycle. The oocytes pass out from the ovary to the brood pouch (ovisac) 2 or 3 days before being spawned and are inseminated. The embryos develop there into nauplii or cysts which are covered by the shell secreted by shell glands in the inner wall of the brood pouch. Assuming that the materials for reproduction are accumulated over a longer period than the reproductive cycle (2 or 3 days per cycle) and that the brood size (number of young produced per brood) is stable, then the surplus ration for reproduction per brood is equal to the increase in the surplus in a cycle except the initial cycle as shown in Fig. 2. In this figure, ry is the maximum food surplus for reproduction per brood and n is the number of reproductive cycles in accumulating materials for a brood:

$$ry = ry/n \cdot \left(\sum_{j=1}^n j - \sum_{j=1}^{n-1} j \right) = ry/n \cdot n \quad (9)$$

Statistical Analysis

Letting the surplus food for somatic growth and/or reproduction be the

Fig. 2. Schematic diagram of estimating the ration which contributes to reproduction.

Bold lines show the sum of materials which are accumulated and metabolized for reproduction, and thin lines show those for each spawning or reproduction. Figures 2A and 2B show the case where the materials for reproduction are accumulated and metabolized over two reproductive cycles ($n=2$) and over three cycles ($n=3$), respectively. Materials for reproduction are shown in units of ry (material for reproduction per brood per pair). For further details, see the text.

dependent variable and G , Yc , and Yn be the independent variables, multiple regression was applied to the partly normalized data in order not to degrade the accuracy of the matrix calculation.⁸⁾ The regression equation was assumed to pass through the origin.⁹⁾ However, the log-log regression between the daily maintenance ration and body length was not assumed to pass through the origin. The regression equation (12) was obtained by eye at first to determine the asymptote with the help of the coefficient of determination (R^2). Equation (13) was also obtained in the same way.

The standard errors (SE) of the ratios, gm_{i2} and gm_{r2} , were calculated according to the formula given by Kuno.¹⁰⁾

Results

Daily Maintenance Ration vs. Body Length

Figure 3A shows examples of the growth curves with the first and second cessations of growth. Some of the data are also shown in Table 2. In several cases, however, only the initial cessation was observed and those data were also used for the analysis.

A straight line was fitted to the log-log plot of the daily maintenance ration mL and body length L as shown in Fig. 4:

$$m_r = 2844 \cdot L^{2.952} \quad (N=61) \text{ cells/shrimp/day} \quad (10)$$

and

$$= 14.22 \cdot L^{2.952} \text{ ng N/shrimp/day} \quad (11)$$

The standard error of the exponent 2.952 was 0.1373 and that of $\log_{10} 2844$ was 0.0851.

The logarithmic slope for each group $Slpi$ ranged from 2.13 to 4.14, and the mean was 3.015 as shown in Table 2.

Somatic Food Conversion Factor

Table 2 shows the data of non-spawners which ceased growth two times in the rearing experiment. There were 17 groups. The largest mean body length was 6.23 mm. The surplus food for growth was estimated as Rm_i or Rm_r for each group. The factor $gm_i (= Rm_i/G)$ ranged from 0.40 to 3.07 and the mean was 1.292 ($= gm_{i1}$ in Table 4), while the weighted mean was 1.489 ($= gm_{i2}$ in Table 4) which was the ratio of the sum of Rm_i to the sum of G . The factor gm_i increased with body size (Fig. 5, $r \neq 0$, $p < 0.01$). The regression was obtained as follows:

$$\log_{10}(Rm_i/G - 0.384) = -16.266/L^2 + 0.798, \quad (12)$$

where L is the body length in mm. The coefficient of determination due to regression was 0.777. The estimates from the regression are shown as gm_3 in Tables 2, 3, and 4. However, the distribution of the square root of this ratio (Rm_i/G) was almost symmetric.

As shown in Table 2, the factor $gm_r (= Rm_r/G)$ ranged from -2.12 to 4.29 and the mean was 1.520 ($= gm_{r1}$ in Table 4), while the weighted mean was 2.095 ($= gm_{r2}$ in Table 4). The above factors were obtained only by using the data of non-spawners which did not reproduce during the experiment.

Two other factors were estimated from the multiple regression using all the data including data for groups which reproduced: Rm_i and/or Rm_r was the dependent variable and G , Yc , and Yn were the independent variables. These are gm_{ir} and gm_{rr} in Table 4, i.e., $gm_{ir} = 1.122$ and $gm_{rr} = 1.833$.

The gross conversion factor was found to be 6.1 ($= 16.4\%$) for groups 1–17 as shown at the bottom of column

Table 2. Feeding and growth of *Artemia* which did not reproduce in the rearing experiment to estimate the somatic food conversion factor

Group #	C_0	V ml	T day	$L1$ mm	$L2$ mm	f ml	d	A $\mu\text{g N}$	M_i $\mu\text{g N}$	M_r $\mu\text{g N}$	G $\mu\text{g N}$	$Slpi$	Rm_i $\mu\text{g N}$	Rm_r $\mu\text{g N}$	gm_i	gm_r	gm_3	Used somatic conversion factor					
																		1.292	1.489	gm_3	1.520	2.095	gm_3
1	83.7	2	17	3.18		38	174	38.4	28.8	18.5	5.9	2.125	9.6	20.0	1.621	3.371	1.018	2.0	0.8	3.6	11.0	7.6	13.9
	83.7	5			4.90	81	436																
2	83.7	2	16	3.20		38	174	36.2	28.4	18.2	5.7	2.213	7.8	18.0	1.352	3.140	1.014	0.3	-0.8	1.9	9.3	6.0	12.2
	83.7	5			4.87	80	441																
3	83.7	2	17	3.39		42	174	38.4	28.3	19.1	5.4	2.504	10.1	19.3	1.892	3.608	1.095	3.2	2.2	4.3	11.2	8.1	13.5
	83.7	5			4.90	81	436																
4	83.7	2	18	3.32		41	174	40.6	30.1	20.3	5.8	2.317	10.5	20.3	1.828	3.522	1.087	3.1	2.0	4.3	11.5	8.2	14.0
	83.7	5			4.95	82	438																
5	33.5	2	12	2.75		29	70	11.3	8.9	7.6	3.5	2.707	2.3	3.6	0.6662	1.041	0.6186	-2.2	-2.9	0.2	-1.7	-3.7	1.5
	33.5	5			4.00	57	194																
6	33.5	2	11	2.50		25	71	10.3	8.2	6.2	3.3	2.216	2.2	4.2	0.6472	1.243	0.5282	-2.2	-2.8	0.4	-0.9	-2.8	2.4
	33.5	5			3.80	52	180																
7	33.5	10	14	5.08		86	366	55.2	39.5	33.2	5.1	4.140	15.8	22.0	3.068	4.285	2.280	9.1	8.1	4.0	14.2	11.3	10.3
	33.5	20			6.10	118	781																
8	33.5	10	14	4.80		78	369	55.4	41.6	31.1	5.8	3.369	13.8	24.3	2.375	4.181	2.124	6.3	5.1	1.5	15.4	12.1	11.9
	33.5	20			6.00	115	783																
9	33.5	10	14	5.06		85	367	55.0	42.3	36.2	6.0	3.623	12.6	18.8	2.121	3.159	2.324	4.9	3.8	-1.2	9.8	6.3	5.0
	33.5	20			6.23	123	779																
10	13.4	2	14	2.18		20	29	5.3	4.5	4.9	2.2	2.558	0.9	0.4	0.4048	0.1859	0.4195	-1.9	-2.4	0.0	-2.9	-4.2	-0.5
	13.4	5			3.20	38	77																
11	13.4	2	16	2.25		21	29	6.0	4.7	6.6	2.8	2.171	1.3	-0.6	0.4714	-0.2054	0.4475	-2.3	-2.8	0.1	-4.8	-6.4	-1.8
	13.4	5			3.46	44	73																
12	13.4	10	12	4.07		58	152	19.4	14.9	16.3	3.7	3.543	4.5	3.1	1.226	0.8354	1.401	-0.2	-1.0	-0.6	-2.5	-4.6	-2.1
	13.4	20			5.00	84	315																
13	13.4	10	14	3.95		55	153	22.5	17.9	19.0	4.3	3.022	4.6	3.5	1.074	0.8117	1.373	-0.9	-1.8	-1.3	-3.0	-5.5	-2.4
	13.4	20			5.05	85	321																
14	13.4	10	12	4.07		58	152	19.4	15.2	16.3	3.4	3.729	4.2	3.1	1.207	0.8901	1.381	-0.3	-1.0	-0.6	-2.2	-4.1	-1.7
	13.4	20			4.95	82	315																
15	5.4	10	10	3.55		46	62	6.5	5.1	9.0	2.7	3.680	1.4	-2.6	0.5122	-0.9534	0.9539	-2.1	-2.6	-1.2	-6.6	-8.2	-5.1
	5.4	20			4.35	65	131																
16	5.4	10	11	3.60		47	62	7.1	5.3	10.0	2.5	3.610	1.8	-2.9	0.6973	-1.152	0.9713	-1.5	-2.0	-0.7	-6.8	-8.2	-5.4
	5.4	20			4.35	65	123																
17	5.4	10	13	3.88		54	61	8.4	6.1	14.4	2.8	3.724	2.3	-6.0	0.8012	-2.122	1.186	-1.4	-1.9	-1.1	-10.3	-11.9	-9.3
	5.4	20			4.65	74	120																
Mean	34.4	9.6	13.8	3.58		63	252	25.6	19.4	16.9	4.2	3.015	6.2	8.7	1.292	1.520	1.189	0.8	0.0	0.8	2.4	0.0	3.3
SE	5.1	1.2	0.6	0.22	0.21	5	36	4.5	3.4	2.3	0.3	0.168	1.2	2.5	0.185	0.488	0.143	0.8	0.8	0.5	2.1	1.9	1.9
Food/Growth								6.143					1.489	2.095	1.292	1.520	var.						

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Refer Appendix for variables.

Table 3. Feeding, growth, and reproduction of *Artemia* which reproduced in the rearing experiment to estimate the reproductive food conversion factors

Group #	C_0	V ml	Ta day	$L1a$ mm	$L2a$ mm	f ml	d	R $\mu\text{g N}$	M_r $\mu\text{g N}$	G $\mu\text{g N}$
18	83.7	60	13	6.95	7.70	163	5800	377.0	68.3	7.1
19	83.7	60	10	8.00	8.50	201	5837	291.9	69.4	5.8
20	83.7	80	6	7.76	8.60	198	7670	230.1	43.8	9.6
21	83.7	20	10	6.60	7.10	145	1842	92.1	41.4	4.2
22	83.7	40	3	6.54	6.80	138	3891	58.4	11.5	2.1
23	83.7	20	16	6.11	7.05	135	1851	148.1	60.5	7.2
24	83.7	40	13	6.90	7.68	162	3866	251.3	67.2	7.3
25	83.7	20	17	6.77	7.30	152	1830	155.5	79.2	4.7
26	83.7	20	3	6.57	7.00	143	1843	27.6	12.2	3.6
27	83.7	80	3	6.63	7.06	145	7231	108.5	12.7	3.6
28	83.7	80	5	7.54	8.08	182	7570	189.2	30.7	5.7
29	83.7	10	13	6.50	6.50	132	881	57.3	46.4	0.0
30	83.7	20	6	6.87	7.28	153	1830	54.9	27.9	3.6
31	83.7	80	6	7.30	7.30	162	7412	222.4	30.2	0.0
32	83.7	10	6	5.82	6.00	112	889	26.7	16.6	1.0
33	83.7	60	11	7.10	7.40	160	5796	318.8	56.1	2.8
34	83.7	40	10	6.95	7.54	160	3877	193.9	47.1	5.5
35	83.7	40	14	6.48	7.11	143	3885	272.0	60.1	5.2
Mean	83.7	43	9.2	6.86	7.33	155	4100	170.9	43.4	4.4
SE		6	1.1	0.13	0.15	5	575	25.2	5.2	0.6

Group #	Yn $\mu\text{g N}$	Yc $\mu\text{g N}$	Rm_r $\mu\text{g N}$	gm_3	Ry_{r1} $\mu\text{g N}$	Ry_{r2} $\mu\text{g N}$	Ry_{r3} $\mu\text{g N}$	Ry_{ri1} $\mu\text{g N}$	Ry_{ri2} $\mu\text{g N}$	Ry_{ri2a} $\mu\text{g N}$
Used somatic conversion factor										
					1.520	2.095	gm_3	1.292	1.489	1.489
18	0.0	247.8	308.7	3.511	298.0	293.9	283.9	299.6	298.2	298.2
19	0.0	195.7	222.5	4.009	213.7	210.3	199.2	215.0	213.8	213.8
20	0.0	135.5	186.3	3.975	171.7	166.1	148.1	173.0	172.0	172.0
21	0.0	63.7	50.7	3.213	44.3	41.9	37.2	45.2	44.4	44.4
22	0.0	35.6	46.9	3.092	43.7	42.5	40.4	44.2	43.7	43.7
23	34.1	39.6	87.6	3.030	76.7	72.6	65.9	78.4	77.0	77.0
24	59.9	62.4	184.1	3.491	173.0	168.8	158.6	174.6	173.2	173.2
25	35.5	12.2	76.3	3.333	69.2	66.5	60.7	70.3	69.3	69.3
26	12.5	0.0	15.4	3.170	10.0	8.0	4.1	10.8	10.1	10.1
27	26.2	0.0	95.8	3.210	90.3	88.2	84.2	91.1	90.4	55.7*
28	33.3	0.0	158.6	3.786	149.9	146.6	137.0	151.2	150.1	137.7*
29	4.0	0.0	10.9	2.974	10.9	10.9	10.9	10.9	10.9	10.9
30	6.5	0.0	27.0	3.358	21.5	19.4	14.8	22.3	21.6	21.6
31	41.2	0.0	192.2	3.497	192.2	192.2	192.2	192.2	192.2	147.0*
32	3.2	0.0	10.1	2.535	8.6	8.1	7.7	8.9	8.7	8.7
33	64.4	0.0	262.7	3.466	258.5	256.9	253.0	259.1	258.5	258.5
34	92.6	0.0	146.8	3.463	138.4	135.3	127.8	139.7	138.6	138.6
35	113.2	0.0	211.9	3.177	203.9	200.9	195.3	205.1	204.1	204.1
Mean	29.3	44.0	127.5	3.350	120.8	118.3	112.3	121.8	120.9	115.8
SE	8.1	17.6	21.9	0.084	21.5	21.4	20.9	21.6	21.5	21.4

Refer Appendix for variables.

* The correction due to the assimilation efficiency was made on these groups as shown in Discussion (p. 501R), since they ingested a very large amount of food.

A in Table 2. The factor for groups 18–35 (Table 3) was 4.2 (=24.0%) including the spawn as growth.

Reproductive Food Conversion Factors

There are two kinds of factors, i.e., a factor for nauplius production (yn_x in Table 4) and a factor for cyst production (yc_x in Table 4). Table 3 shows the data on the groups which spawned in the experiment. There were 18 groups. The smallest mean body length was 5.82 mm when the initial spawning was observed. The surplus food for reproduction was estimated as Ry_x shown in Table 3, while the suffix x

was $ri1$, $ri2$, $ri2a$, or others. However, these were very similar to each other despite the difference in gm_x , probably because the somatic growth in the rearing experiment was small (12%) compared to the reproduction. The factors were obtained by multiple regression, using the surplus food only for reproduction (Ry_x) and also for all the growth including reproduction (Rm_r). These are shown in the upper part of Table 4, and the mean (except $r3$) of yn_x was 4.383 (=22.8%) and that of yc_x was 2.258 (=44.3%).

Groups 18–22 spawned only cysts. The ratio of weighted mean of Ry_x to that of Yc was obtained as yc_x (≈ 2.3)

Fig. 3. Examples of growth curves of *Artemia franciscana* in the experiment.

Figure 3A is for groups 9, 12, and 1 from the top. Figure 3B is for groups 21, 24, and 29 from the top. Solid circles are observed body length, lines are growth curves fitted by eye, and solid circles in Fig. 3B are used to estimate the ration which contributed to reproduction. Arrows in Fig. 3A show the time when the ration was changed, and those in Fig. 3B the time of reproduction observed. The numerals below the lines (Fig. 3B) are the number of cysts produced and those above the lines are the number of nauplii produced.

Table 4. Comparison of food conversion factors estimated by various methods (x)

Based data		Food conversion factors for				Coefficient of determination R ²
Dependent variable(s) for <i>y_n</i> & <i>y_c</i>	Method x (for <i>gm_x</i>)* ¹	Somatic growth <i>gm_x</i>	Nauplii production <i>yn_x</i>	Cysts production <i>yc_x</i>	Ratio <i>yn/yc</i>	
Food used/growth (estimate ± standard error, df)						
Estimated mainly by the regression						
<i>Rm_i</i> & <i>Rm_r</i>	ir	1.122 ± 0.303, 32	4.438 ± 0.055, 32	2.292 ± 0.030, 32	1.936	0.835
<i>Rm_r</i>	rr	1.833 ± 0.307, 32	4.352 ± 0.055, 32	2.237 ± 0.030, 32	1.945	0.828
<i>Ry_{r1}</i>	r1	1.520 ± 0.488, 16	4.386 ± 0.047, 33	2.261 ± 0.025, 33	1.940	0.829
<i>Ry_{r2}</i>	r2	2.095 ± 0.452, 16	4.313 ± 0.047, 33	2.217 ± 0.025, 33	1.945	0.826
<i>Ry_{r3}</i>	r3 (3)	<i>gm₃</i> , 14	4.154 ± 0.132, 16	2.092 ± 0.068, 16	1.986	0.645
<i>Ry_{ri1}</i>	ri1 (i1)	1.292 ± 0.185, 16	4.416 ± 0.046, 33	2.279 ± 0.024, 33	1.938	0.836
<i>Ry_{ri2}</i>	ri2 (i2)	1.489 ± 0.187, 16	4.390 ± 0.046, 33	2.264 ± 0.024, 33	1.939	0.835
Mean (except r3)		1.558 ± 0.321	4.383 ± 0.049	2.258 ± 0.026	1.941	0.832
Mean (all)		1.558 ± 0.321	4.350 ± 0.056	2.235 ± 0.030	1.947	0.805
<i>Ry_{ri2a}</i> ^{*2}	ri2a (i2a)	1.489 ± 0.187, 16	4.209 ± 0.116, 33	2.272 ± 0.061, 33	1.853	0.742
<i>yn_x</i> and <i>yc_x</i> estimated independently						
<i>Ry_{r1}</i>	r1	1.520	5.460	2.274	2.400	
<i>Ry_{r2}</i>	r2	2.095	5.370	2.226	2.413	
<i>Ry_{r3}</i>	r3 (3)	<i>gm₃</i>	5.171	2.090	2.474	
<i>Ry_{ri1}</i>	ri1 (i1)	1.292	5.495	2.294	2.396	
<i>Ry_{ri2}</i>	ri2 (i2)	1.489	5.464	2.277	2.400	
Mean (except r3)		1.599	5.446	2.267	2.403	
Mean (all)		1.599	5.392	2.232	2.416	
<i>Ry_{ri2a}</i> ^{*2}	ri2a (i2a)	1.489	5.000	2.277	2.195	

Refer Appendix for variables.

*¹: When x's for gm and for yc and yn are different, both are shown as stated.

*²: After correction of the assimilation efficiency in Method ri2. For further explanation see the text (Discussion, p. 501R).

Fig. 4. Daily maintenance ration of *Artemia franciscana* related to body size.
The area of circles is proportional to the number of data (≤ 4).
The solid line is the regression line.

for the cyst-producing groups. Groups 26–35, on the other hand, produced only nauplii. Similarly, yn_x (≈ 5.4) was obtained from the nauplius-producing groups. These are shown in the lower part of Table 4.

Although the total offspring produced by a pair differed among the groups, the mean standard deviation of brood size in each pair was 27.8%.

Ratio of Reproductive Products to Total Growth

The growth is composed of somatic growth G and reproductive growth $(Yn + Yc)/2$. The ratio (Y) of reproductive products to total growth was affected by the body size (age) and feeding rate: The simple correlation coefficients of $(Yc + Yn)/(2 \cdot G + Yc + Yn)$ vs. body length and vs. dn/m_r (the ratio of daily ration to daily maintenance ration) were 0.892 and 0.672 (for groups 1–35), respectively (Fig. 6).

When the ratio of all spawn to total growth is expressed as Y , body length as L mm and the ratio dn/m_r as X , the regression equation were obtained as follows:

$$Y = 1.197 - 0.348(L - 5.73)^{-0.2045} \cdot (X - 1)^{0.0059},$$

$$L > 5.73 \quad \text{and} \quad X > 1 \quad (13)$$

$$Y = 0, \quad L \leq 5.73 \quad \text{or} \quad X \leq 1 \quad (14)$$

Assuming that the regression line passes through the point

Fig. 5. Somatic food conversion factor (gm_i) related to body length.
The area of circles is proportional to the number of data (≤ 2).
The line is the regression line, from which gm_3 was estimated.

Fig. 6. Ratio of reproductive growth to total growth related to body length.

The reproductive growth ($Yn + Yc$) is the sum of spawns per pair during the experiment and the total growth is the sum of somatic (G) and reproductive growth. The area of circles is proportional to the number of data (≤ 2). Solid circles were used to estimate the regression equation (13), open circles were not used. The regression line is for a feeding rate of three maintenance rations ($X = 3.0$), which was the mean.

($L = 5.73$, $X = 1$), then the coefficient of determination due to regression was 0.954 for all the original data (groups 1–35) and 0.250 for the spawners data (groups 18–35). However, the coefficient was 0.668 for the log-transformed spawners.

This shows that a well-fed large shrimp uses more food for reproduction than somatic growth. However, the effect of the daily ration is small.

Discussion

The critical food concentration is known to be $41\text{--}233 \times 10^3$ cells/ml for the used shrimp.³⁾ Unfortunately, however, the initial food concentration exceeded this sometimes in the rearing experiment. The period of maximum ingestion ranged from 0 to 5 h in most cases, but that in group 27 was 13 h sometimes. This maximum feeding might introduce an error in the estimation of ration, because the used formula (3) is only applicable when the food concentration is less than the critical value. Fortunately, however, it introduced a positive error of less than 5%,⁷⁾ because the daily specific growth rate of food was 0.665 per day and was less than the standard error of food concentration estimation. Furthermore, the difference between the actual and the estimated filtering rates is not considered to introduce a large error as shown in Table 1.

Although it appears confusing, the models of the energy budget and the mass budget are slightly different.¹¹⁾ Even among mass budget models, there are some differences according to the products, processes and methods involved, which makes it difficult to compare data directly. Therefore, it is important to define the used model accurately. Our main concerns were the maintenance ration, somatic growth and reproduction. The maintenance ration was assumed to vary with the body size under a fixed condition. The other food conversion factors were assumed to be constant irrespective of body size at first, though some models for cattle and sheep assume that the somatic conversion factor increases with body size.¹²⁾ However, it is very difficult to determine how much of the ration contributes to the somatic growth and how much contributes to the reproductive growth separately, because the reproductive organs start to develop earlier than the initial reproduction. This might influence the somatic conversion factor such that the factor increases with body size (cf. Fig. 5). Additionally, the maximum size of groups 1–17 (non-spawners) was larger than the minimum size of spawners (groups 18–35). This implies that the biological minimum size may also change with age (cf. Fig. 6 and the last part of **Discussion**).

The gross conversion efficiency obtained here (16 and 24% in Tables 2 and 3) was similar to values already reported.^{3,13–22)} Although the efficiency is easy to obtain, it is greatly affected by the feeding rate due to the subtraction of maintenance cost. However, the factors (*gm*, *yc*, and *yn*) in our model are not affected under the definition used.

The somatic food conversion factor *gm* includes not only the materials which are composed of somatic mass increment but also the metabolic cost for growth, such as the energy loss and excretion over the maintenance. The cost of molting is also included: the shed shell, for example, is considered to be similar to excreta. The time delay between the mass and length growth was ignored here. However, this delay was so small that it did not introduce a large error in the calculation (cf. Fig. 3). Two other factors (*yn* and *yc*) are similar, the materials for new-born and also the metabolic cost for reproduction including those made by males.

The specific daily maintenance ration increased with the size of shrimp as shown in Fig. 7, ranging from 5 to 35%/day. The specific nitrogen excretion rate was reported to range from 6 to 22%/day for the shrimp of 4–10 mm

Fig. 7. Specific daily maintenance ration related to body size.

Specific maintenance ration (*smr*, specific daily maintenance ration, %/day) is plotted against body length *L*. The area of circles is proportional to the number of data (≤ 3). The broken line is the regression line directly obtained from the data shown here: $smr = 4.698 \cdot L^{0.767}$. The solid rectilinear line is obtained from the regression lines (Eqs. (1), (2), and (11)): $smr = 4.650 \cdot L^{0.776}$ ($L \leq 6.3$) and $smr = 12.73 \cdot L^{0.227}$ ($L > 6.3$).

Fig. 8. Ratio of daily maintenance ration (*mL*) to daily nitrogen excretion rate (*N-Excrtn*) related to body length.

The area of circles is proportional to the number of data (≤ 3). The broken line shows a ratio of unity.

length and decreased as the shrimp grew in contrast to the above rate.⁴⁾ The slopes of the log-log plot of the rates and body length were different ($p < 0.001$, *t*-test). Although it is not clear at present, this might be caused from the definition itself. The daily maintenance ration does not include the metabolic cost for growth, but the observed excretion rate might include the cost.⁴⁾

The ratio of daily maintenance ration to daily nitrogen excretion rate⁴⁾ is shown in Fig. 8. Although this ratio must have been larger than unity, it actually ranged 0.48–3.01 for all the shrimps (1.5–7.0 mm) and 0.58–3.01 for larger shrimps (4.0–7.0 mm) whose nitrogen excretion rate was obtained.⁴⁾ The mean for larger shrimps was 1.598 ± 0.1153

(SE, $N=35$). This can be used to estimate the real assimilation efficiency as $1/1.598$ ($=62.6\%$), though it was assumed to be unity initially as shown in **Materials and Methods**. However, this estimate must be an underestimate because the rates were different in the character as described above. Even so, the estimate is similar to those reported on an amphipod,¹⁹⁾ isopod,¹⁹⁾ and copepods.¹⁸⁻²¹⁾

The somatic conversion factor was estimated directly by six methods as shown in Table 4, and varied considerably. Additionally a seventh estimate gm_3 was also obtained from the regression equation (12) in Fig. 5 as shown in Tables 2 and 3. It is very difficult to select one of these factors because the coefficients of determination due to regression and the other factors (yn_x and yc_x) were very similar except the seventh estimate. The last estimate gm_3 was obtained by fitting a line to the independently-obtained gm_i without considering the theoretical nature of gm_i . Although the correlation between gm_i and body length L was statistically significant ($p<0.01$) and the coefficient of determination due to regression was 0.777, one of the theoretical weak points in the regression is that gm_i approaches 0.384 (<1) when the shrimp is small. This means that the sum of newly-formed tissue and the metabolic cost is less than the material (nitrogen) in the food. Even if we neglect food sources other than chlamydomonad, the neglected food would further reduce the estimate of daily maintenance ration because exactly the same rearing medium was used to estimate the daily maintenance ration and the somatic food conversion factor gm_i . This asymptote (<1) is reasonable when the bodily nitrogen estimated from the body length is overestimated and/or when the nitrogen content in chlamydomonad is underestimated. However, the data of bodily nitrogen of the shrimp (2–4 mm) were on or above the regression line,⁴⁾ and the nitrogen content in the phytoplankton ranged from 4.0 to 5.9 pg per cell.³⁾ It is therefore difficult to consider overestimation of bodily nitrogen and underestimation of algal nitrogen to give the asymptote. Even though the somatic conversion factor increased with body size as in cattle and sheep,¹²⁾ the observed conversion factor gm_i less than unity is considered here to be data with a mean larger than unity. So the seventh set of data is ignored here.

Of the remaining six sets of data, the standard errors of gm_{i1} and gm_{i2} were similar to each other and significantly smaller than the others ($p<0.05$, F -test). The ratio gm_{i2} is the ratio of mean ration over maintenance to mean somatic growth, while gm_{i1} is a simple mean of the ratio (gm_i) for each group. Although the standard errors were almost same, gm_{i2} is adopted here as the better estimate because it is the weighted mean of gm_i . The somatic food conversion efficiency is estimated to be $1/1.489$ ($=67.2\%$). This is slightly larger than those of a copepod *Acartia tonsa* (44% ingested C),²²⁾ chub mackerel (18–30% wet weight base),²³⁾ plaice, sole and perch (25–47% ingested N and 28–49% assimilated N),²⁴⁾ but slightly smaller than that of carp (74% assimilated energy, 92% assimilated N).^{24,25)}

The above selection of the estimation method automatically chooses the reproductive conversion factors yn_{i2} and yc_{i2} ; 4.390 (22.8% in efficiency) and 2.264 (44.2% in efficiency), respectively. These are significantly larger than gm_{i2} (somatic conversion factor, $p<0.05$, t -test). Since the factors shown in the lower part of Table 4 were obtained

by ignoring the data of the groups which produced both nauplii and cysts, they are not adopted here, but are fairly similar to the upper data.

Some shrimps (#27, 28, and 31) shown in Table 3 fed so well that the daily ration to bodily nitrogen was larger than unity. This fact might reduce the assimilation efficiency to 68, 94, and 80% respectively, according to Fig. 2 in our another paper.²⁶⁾ When this correction was applied to the data, yn_{i2} and yc_{i2} changed to 4.209 ($=yn_{i2a}$) and 2.272 ($=yc_{i2a}$) as shown in Table 4. However, since the coefficient of determination was reduced by 10%, we ignored the correction here.

The egg production efficiency of a copepod *Acartia tonsa* (39% ingested C and 84% assimilated C)²⁰⁾ was similar to the yc_{i2} obtained here. However, even the data on laying hens did not reveal the metabolic cost for egg production.^{12,27)} Although the nitrogen content per nauplius was smaller than that per cyst including shell,⁵⁾ the food needed to produce a nauplius was larger than the other. It is very difficult to understand the cause of this. After fertilization, the embryo which will become a cyst develops to the later stage of gastrula within the shell in the ovisac.²⁸⁾ The other develops to a nauplius within the thin membranes in the ovisac. If the latter stays in the ovisac and is nourished by the mother even after fertilization, or if the ovoviviparous nauplius has more nitrogen than the oviparous embryo (since no data are available on the nitrogen content in the ovoviviparous new-born nauplius), then this explains the difference between the factors.

As is natural, somatic growth leads to reproductive growth. The smallest spawner was 5.82 mm in length (cf. Table 3) and the largest mean length of non-spawner (cf. Table 2) was 5.645 mm. Hence, the body length of 5.73 mm was employed as the minimum size of reproductive shrimp in the regression calculation. However, this is an arbitrary value, because the largest non-spawner was 6.23 mm as shown in Table 2, and 8.62 mm in the experiment.⁶⁾ The biological minimum may therefore also depend on age. However, at the body length around this there are many kinds of deflection in the allometric growth, namely 3.6 mm in the maximal ingestion rate,³⁾ 4.0 mm in segmentation,²⁹⁾ 5.0 mm in gut content volume,¹⁾ 5.8 mm in dry body weight⁴⁾ and 6.3 mm in nitrogen content.⁴⁾ The similar intercept in feeding rate normalized to the daily maintenance ration was 1.00 (Fig. 6), because below this feeding rate the shrimp hardly maintained their own body and above this level the largest shrimp might only use the food for reproduction but not for somatic growth.

These data help us to construct a feeding program for the shrimp based on the assimilation efficiency and other data.

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Appendix

Variables list in alphabetical order

Variable	Definition/Explanation
$A = a' \cdot R$	assimilated ration, $\mu\text{g N/shrimp}$
a'	apparent assimilation efficiency, normally assumed here to be unity (<i>cf.</i> Discussion)
C_0	initial food concentration in algal suspension, which was same both in the experimental and in the control without any grazer, thousand <i>Chlamydomonas</i> cells/ml
C_f	correction factor for daily ration (Table 1)
d	daily ration, thousand <i>Chlamydomonas</i> cells/shrimp/day
$d1$	daily ration at the initial level, thousand <i>Chlamydomonas</i> cells/shrimp/day
$d2$	daily ration at the second level, thousand <i>Chlamydomonas</i> cells/shrimp/day
dn	daily ration, $\mu\text{g N/shrimp/day}$ ($=0.005 \text{ d}$)
f	daily filtering rate, ml/shrimp/day
G	somatic (or individual) growth in a period T or Ta , $\mu\text{g N/shrimp}$
gm	food conversion factor for somatic (or individual) growth (food/growth)
$gm_3 = 10^{(-16.266/L^2 + 0.798)} + 0.384$	gm estimated by the regression between gm_i and L (Eq. (12))
$gm_i = Rm_i/G$	gm in each rearing experiment on a group
$gm_{i1} = \text{Mean}(gm_i) = 1.292$	simple mean of gm_i
$gm_{i2} = \Sigma Rm_i / \Sigma G = 1.489$	weighted mean of gm_i
$gm_{ir} = 1.122$	gm obtained as a multiple regression coefficient by letting G , Yc , and Yn be independent variables and Rm_i for groups 1–17 and Rm_r for groups 18–35 be dependent one
$gm_r = Rm_r/G$	gm , using m_r to estimate Rm_r
$gm_{r1} = \text{Mean}(gm_r) = 1.520$	simple mean of gm_r
$gm_{r2} = \Sigma Rm_r / \Sigma G = 2.095$	weighted mean of gm_r
$gm_{rr} = 1.833$	gm obtained as a multiple regression coefficient by letting G , Yc , and Yn be independent variables and Rm_r be dependent one
gm_x	gm estimated by the method of x ($x = 3, i, r, i1, i2, \dots$)
j	appropriate interger in calculation
L	body length, mm
$L1$	body length at the initial growth cessation, mm
$L2$	body length at the second growth cessation, mm
$L1a$	body length at the first spawning in the experiment, mm
$L2a$	body length at the last spawning in the experiment, mm
M	total maintenance ration in a period T or Ta , assuming that a' is unity, $\mu\text{g N/shrimp}$
M_i	M estimated by each rearing experiment on a group, $\mu\text{g N/shrimp}$
M_r	M estimated by using the regression equation (Eq. (11)), $\mu\text{g N/shrimp}$
mL	observed daily maintenance ration of a L mm long shrimp, $\mu\text{g N/shrimp/day}$ unless stated
m_i	daily maintenance ratio of a given size of shrimp estimated by log–log interpolation in each rearing group, $\mu\text{g N/shrimp/day}$

m_r	daily maintenance ration of a given size of shrimp estimated by log-log regression between m_i and L (Eq. (11)), $\mu\text{g N/shrimp/day}$ unless stated	$Slpi = \log(mL2/mL1)/\log(L2/L1)$	slope for each rearing group
n	number of reproductive cycles during which the material for a brood is accumulated	$smr = mL/\text{body N}$	specific daily maintenance ration, %/day
p	specific daily growth rate in chlamydomonad, 1/day	T	period between growth cessations, day
R	total ration in a period of T or Ta , $\mu\text{g N/shrimp}$	Ta	period between the first and last spawning in the reproductive experiment, day
R^2	coefficient of determination due to regression	t	single (or short-term) experimental feeding period (≈ 1 day), day
$Rm_i = A - M_i$	surplus food over maintenance, $\mu\text{g N/shrimp}$	V	volume of experimental suspension, ml/shrimp
$Rm_r = A - M_r$	similar as above	$X = dn/m_r$	daily ration relative to the maintenance ration
$Ry_{i1} = Rm_i - gm_{i1} \cdot G$	surplus food for reproduction in a period Ta , $\mu\text{g N/shrimp}$	x	suffix to indicate the method of estimation such as 3, i, i1, i2, ir, r, $\dots$: they are attached to gm_x , Ry_x , yc_x , and yn_x
$Ry_{i2} = Rm_i - gm_{i2} \cdot G$	similar as above	$Y = (Yc + Yn)/(2 \cdot G + Yc + Yn)$	reproductive component in total growth, spawn/total growth
$Ry_{i3} = Rm_i - gm_{i3} \cdot G$	similar as above	Yc	cysts production in a given period of Ta , $\mu\text{g N/pair}$
$Ry_{r1} = Rm_r - gm_{r1} \cdot G$	similar as above	yc	food conversion factor for cysts production (food/cyst)
$Ry_{r2} = Rm_r - gm_{r2} \cdot G$	similar as above	yc_x	yc estimated by the method x ($x = 3, i, r, i1, i2, \dots$)
$Ry_{r3} = Rm_r - gm_{r3} \cdot G$	similar as above	Yn	nauplii production in a given period of Ta , $\mu\text{g N/pair}$
$Ry_{ri1} = Rm_r - gm_{i1} \cdot G$	similar as above	yn	food conversion factor for nauplii production (food/nauplius)
$Ry_{ri2} = Rm_r - gm_{i2} \cdot G$	similar as above	yn_x	yn estimated by the method x ($x = 3, i, r, i1, i2, \dots$)
$Ry_{ri2a} = Rm_r - gm_{i2} \cdot G$	similar as above, assuming that a' in some groups was not unity (<i>cf.</i> p. 501R)		
Ry_x	surplus food for reproduction estimated by the method x as shown above, $\mu\text{g N/shrimp}$		
ry	food for reproduction per brood per pair, used as a unit in Fig. 2		