スケトウダラ稚仔消化管中の動物プランクトン重量の推定

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Estimation of Zooplankton Weight in the Gut of Larval Walleye Pollock (*Theragra chalcogramma*)[1),2),3)]

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Abstract

Mensuration formulae are applied to estimate the volume and weight of individual zooplankton occurring in the gut of larval walleye pollock (*Theragra chalcogramma*), based on the assumption that copepod and euphausiid eggs are spherical in shape, copepod nauplii are ellipsoid, copepod copepodites are a combination of ellipsoid and cylindrical, and euphausiid furciliae are a combination of two cylinders. By measuring the diameter of eggs, the length of carapace, metasome, urosome or abdomen, the volumes of these zooplankton are estimated. The weight is approximated by multiplying the volume by the specific gravity of sea water.

The food and feeding habits of larval fish have been examined in relation to the survival strategy affecting the strength of year-class (BHATTACHARYYA 1957, SYSOEVA & DEGTEREVA 1965, MARAK 1974, DE MENDIOLA 1974). It has been generally accepted that in numerical comparison the relative importance of the major food organisms changes with the fish size. MARAK (1960) has pointed out that the numbers of the food items are not a true indication of the relative amount of food in the gut as the volume of food organisms differ greatly by species. To demonstrate the prey-predator size preference and changes in food compositions at different times and in different regions, BAINBRIDGE & MCKAY (1967), LAST (1978a-c) and CONWAY (1980) have introduced the biomass proportion as method of comparison by converting the numbers of food items in the gut into the wet weights. In these studies, the wet weights of zooplankton were derived mainly from BOGOROV's (1959) standardized weight values of various zooplankton. It is likely that biomass estimates represented by the wet weight of food organisms are preferable to numerical estimates in assessing the relative importance of each type of food in temporal and spatial comparisons of the feeding intensity. However, it is inevitable that unless the volume and weight of the zooplankton in the gut are actually measured, the interpretation of the relative importance of the respective food organisms will be inaccurate.

The analysis of food contents are expected to provide information to assess the energy transfer from lower trophic levels to larval fish. Little attention, however, has been paid to quantitative analysis of gut contents in larval fish. This is primarily due to the difficulty in measuring the weight of food organisms in the gut because of the small size of the prey, consisting mainly of copepod eggs, nauplii and copepodites. Table 1 is representative of the

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TABLE 1. GUT CONTENTS (IN NUMBER) DISSECTED FROM 50 LARVAL WALLEYE POLLOCK. SAMPLES WERE COLLECTED FROM 30-M DEPTH AT LAT. 57°14′N AND LONG. 162°25′W IN THE SOUTHEAST BERING SEA ON JUNE 24, 1980.

Fish No.	Fish size (TL: mm)	Zooplankton[1)]										
		CE	CN	CC	*OS*	*AT*	*AL*	*CM*	*PC*	EE	EC	EF
1	4.6						(empty)					
2	5.2	—	18	—	—	—	—	—	—	—	—	—
3	5.5	—	13	—	—	—	—	—	—	—	—	—
4	4.9	—	9	—	—	—	—	—	—	—	—	—
5	4.7	—	3	—	—	—	—	—	—	—	—	—
6	6.2	—	19	—	—	—	—	—	—	—	—	—
7	4.1						(empty)					
8	4.9	1	1	—	—	—	—	—	—	—	—	—
9	6.3	—	21	—	—	—	—	—	—	—	—	—
10	6.2	—	15	—	—	—	—	—	—	—	—	—
11	5.9	—	6	—	—	—	—	—	—	—	—	—
12	6.3	—	8	—	—	—	—	—	—	—	—	—
13	7.3	—	15	—	—	—	—	—	—	—	—	—
14	5.5	—	12	—	1	—	—	—	—	—	—	—
15	6.5						(empty)					
16	7.2	—	23	—	—	—	—	—	—	—	—	—
17	9.3	—	60	1	1	—	—	—	2	—	—	—
18	8.3	2[2)]	43	1	4	—	—	—	1	—	—	—
19	16.4	53	—	—	—	—	—	—	10	—	—	5
20	15.0	—	7	—	3	—	—	1	2	1	—	—
21	12.5	2[2)]	4	—	3	1	5	—	2	—	—	—
22	10.7	—	25	6	—	—	12	—	—	—	—	—
23	7.8	—	6	1	—	—	1	—	—	—	—	—
24	7.6	—	37	1	—	—	—	—	1	—	—	—
25	8.5	—	11	1	2	—	—	—	—	1	—	—
26	8.9	—	26	1	2	—	2	—	—	—	—	—
27	8.3	1	63	—	1	—	—	—	—	2	—	—
28	11.4	—	16	1	—	—	1	—	1	—	—	—
29	10.1	—	18	4	2	—	1	—	3	2	—	—
30	9.4	—	30	6	2	—	1	—	—	—	—	—
31	9.3	—	28	—	2	—	1	—	—	—	—	—
32	10.1	—	29	—	1	—	—	—	1	2	—	—
33	10.4	—	32	4	1	—	—	—	4	—	—	—
34	8.3	2	92	—	—	—	—	—	—	—	—	—
35	10.6	28	32	—	4	—	2	1	2	—	—	—
36	7.5	—	30	—	—	—	—	—	—	—	—	—
37	5.9	—	12	—	—	—	—	—	—	—	—	—
38	9.4	1	23	2	1	1	2	—	—	—	—	—
39	15.1	85	—	—	3	1	2	—	8	—	1	2
40	13.8	—	—	—	—	7	5	—	1	—	—	—
41	14.5	60	8	2	2	—	—	—	6	—	—	—
42	12.8	2[2)]	1	7	5	1	2	—	—	—	—	—
43	11.4	2[2)]	4	1	2	2	3	—	2	—	—	—
44	11.7	27	—	—	—	—	—	—	10	—	—	—
45	12.7	4[2)]	11	2	5	—	4	—	1	—	—	—
46	9.8	27	29	3	—	—	—	—	2	—	—	—
47	13.2	9	3	7	1	1	5	—	—	—	—	—

TABLE 1. (CONTINUED)

Fish No.	Fish size (TL: mm)	Zooplankton[1] CE	CN	CC	*OS*	*AT*	*AL*	*CM*	*PC*	EE	EC	EF
48	13.2	—	11	12	—	3	10	—	—	—	—	—
49	14.3	—	—	3	3	—	—	1	—	—	—	—
50	14.0	14	4	—	—	—	—	—	13	—	—	—

[1] Abbreviations: CE: Copepod egg, CN: Copepod nauplius, CC: Calanoid copepodite, *OS*: *Oithona similis*, *AT*: *Acartia tumida*, *AL*: *Acartia longiremis*, *CM*: *Calanus marshallae*, *PC*, *Pseudocalanus* sp., EE: Euphausiid egg, EC: Euphausiid calyptopis, and EF: Euphausiid furcilia.
[2] Egg cluster of *Oithona similis* containing ten or eleven eggs. —: did not occur.

type of raw data associated with larval fish food studies. The problem is how to treat these organisms, which differ greatly in number and size in a quantitative manner, in terms of their energy contribution to the larvae.

Wet weights of zooplankton have been measured based on direct weighing, displacement methods or geometrical computations (NAKAI 1942, LUBNY-GERTSYK 1953, NAKAI & KUDOH 1967, OMORI 1969, IKEDA 1972 and CONWAY 1980). Several regression equations have been established for the length-weight relationships in copepods (KAMSHIROV 1951, PERTSOVA 1967, KRYLOV 1968) and euphausiids (MAUCHLINE & FISHER 1969). PEARRE (1980) reviewed the methods for estimating copepod wet weight from linear dimensions. SCHNACK (1972) and UYE (1982) reported length-dry weight regressions for several zooplankton species, with species specific coefficients of slope.

Although these measurements and equations estimate the volume and weight of meso- and macrozooplankton, few data are available for microzooplankton which dominate the prey of larval fish. LUBNY-GERTSYK (1953) calculated the weight of several microzooplankton including copepod and euphausiid nauplii by applying geometric formula of a right circular cylinder to the shape of these organisms. In the study of standing stocks of microzooplankton, BEERS & STEWART (1967) made volume estimates based on two dimensional measurements of the various zooplankton and approximation of their shape to standard geometric configurations. In their study, copepods were considered to be double cylinders (cephalothorax and abdomen) with the abdomen length and width assumed to be one-third of the measurements for total length and width. Nauplii were regarded as simple cylinders, and the crustaceans, such as ostracods, were considered ellipsoids.

This paper utilizes simple mensuration formulae to estimate the volume and weight of individual microzooplankton found in the gut of larval walleye pollock, *Theragra chalcogramma* (PALLAS).

Materials and Methods

A total of 50 gut samples from larval walleye pollock (4.1 to 16 mm total length), fixed with 5% buffered formalin solution, were examined (Table 1). Alimentary canal was dissected with surgical needles and its contents was placed on a glass slide and stained with a solution of methylene blue and lactic acid. The size of almost all food organisms found in each gut was measured with an ocular meter under a microscope. The precision of measurement was 0.02 mm. The characteristic measurement was different for each type of prey (Fig. 1). Egg

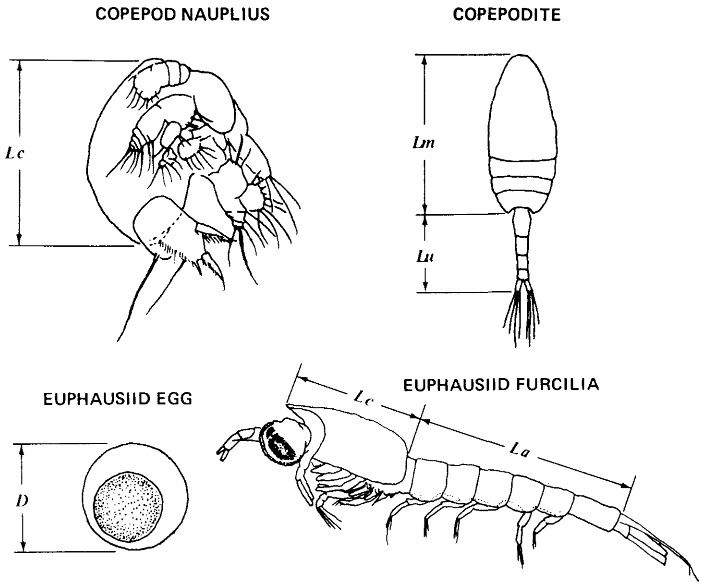

Fig. 1. Representative measurement for various zooplankton which were observed in the gut of larval walleye pollock. *Lc*: carapace length, *Lm*: metasome length, *Lu*: urosome length, *D*: diameter, and *La*: abdomen length.

diameter was measured for copepod and euphausiid eggs. Carapace length was measured for copepod nauplii. In addition, to make clear the dimensional relations, width and depth were also measured on several individuals. The length of metasome and urosome was used as the characteristic measurement of copepod copepodites. To find the length-width relations and volume proportions of metasome to the volume of the whole body, the width of metasome and urosome was also measured on the several sample of copepods which were collected with plankton nets. In this case, the width of the urosome was estimated as the mean of the largest width of the genital segment and the shortest width of the anal segment. For the furcilia stage of euphausiids, length and depth of carapace and abdomen were measured. The volume of zooplankton was calculated from mensuration formulae for the volumes of spheres, ellipsoids and right circular cylinders. The weight of a particular zooplankton species was calculated by multiplying the estimated volume by the specific gravity of sea water (1.025) in the southeast Bering Sea (NISHIYAMA & HARYU 1981). The possible effect of shrinkage due to the formalin fixative was not taken into account.

Results

Copepod and Euphausiid Eggs

Since the shape of the copepod and euphausiid eggs is essentially spherical (Fig. 1), the volume of the egg (Ve) can be easily calculated by measuring the diameter of the egg (D) with the following formula:

$$Ve=1/6 \cdot (\pi D^3)\,. \qquad (1)$$

Copepod Nauplii

The shape of copepod nauplii in dorsal, lateral and ventral views is elliptical (Fig. 1). Therefore, the volume of the nauplii (Vn) can be given by the formula of an ellipsoid (Fig. 2B):

$$Vn=4/3 \cdot (\pi abc)\,, \qquad (2)$$

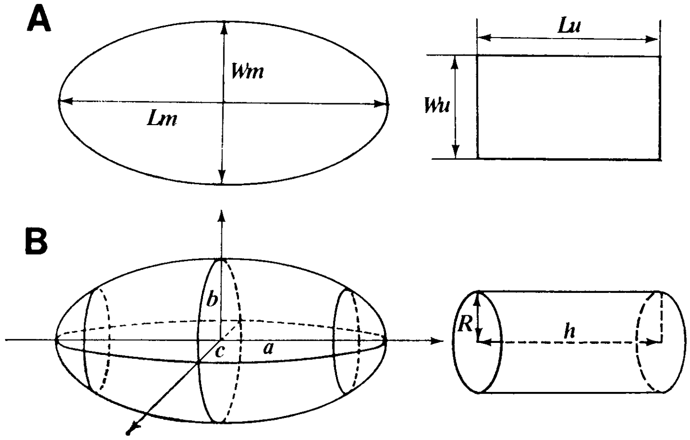

Fig. 2. A. Schematic dorsal views of metasome and urosome of calanoid copepod. *Lm*: metasome length, *Wm*: metasome width, *Lu*: urosome length, and *Wu*: urosome width. B. Dimensional view of an ellipsoid and right circular cylinder. *a*: semimajor axis, *b* and *c*: semiminor axes, *h*: the altitude, and *R*: the radius of base.

where a, b and c are semiaxes. The semimajor axis is a with b and c being semiminor axes. Thus, when the relation among a, b and c is known, we can calculate the volume by measuring semimajor axis a, instead of using the measurements of each semiaxes.

Table 2 represents the measurements of the length, width and depth of copepod nauplii in the gut of larval walleye pollock. The resultant mean length-width and length-depth ratios ($\pm$ one standard deviation) are 1.84 ($\pm$0.21) and 1.91 ($\pm$0.28) respectively. A statistical test indicates that the difference of the means of these two ratios is not significant at the 95% level ($t=0.596$, $0.5<P<0.6$). To compare these values with those of intact specimens, the length-width ratios of copepod nauplii 40–120 μm in width were determined from samples collected in the Bering and Chukchi Seas in the summer of 1978 (TANIGUCHI, personal communication). Figure 3 illustrates these length-width ratios, ranging from 1.6 to 2.4, with

TABLE 2. LENGTH (L), WIDTH (W), DEPTH (D) AND THEIR RATIOS OF COPEPOD NAUPLII OBSERVED IN THE GUT OF LARVAL WALLEYE POLLOCK.

Sample No.	Length (mm)	Width (mm)	Depth (mm)	L/W	L/D
1	0.28	0.12	0.18	2.33	1.56
2	0.30	0.18	0.18	1.67	1.67
3	0.26	0.14	0.12	1.86	2.17
4	0.18	0.10	—	1.80	—
5	0.24	0.12	—	2.00	—
6	0.24	0.12	—	2.00	—
7	0.24	—	0.12	—	2.00
8	0.24	0.13	—	1.85	—
9	0 26	0.16	—	1.63	—
10	0.30	0.17	0.14	1.73	2.14
11	0.22	0.14	—	1.57	—
12	0.18	0.10	—	1.80	—
13	0.22	0.12	—	1.75	—
14	0.26	0.14	—	1.75	—
15	0.28	0.16	—	1.75	—
16	0.26	0.12	—	2.17	—

—: not measured

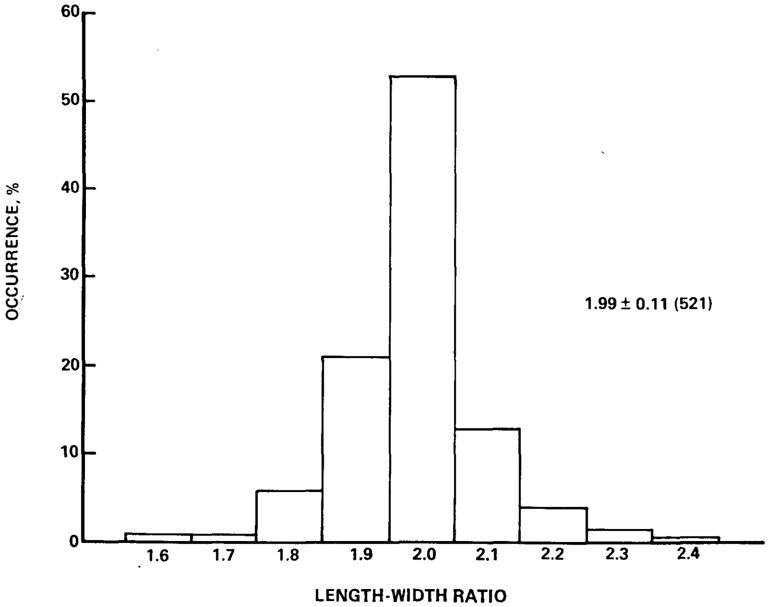

Fig. 3. Frequency distribution of length-width ratios of copepod nauplii which were taken from the Bering and Chukchi Seas in summer 1978 (TANIGUCHI, unpublished). Mean±one standard deviation (number of sample) is given in the figure.

a mean of 1.99. These results allow the assumption that the average length-width ratio of copepod nauplii in the study area is 2:1, and the same ratio is appropriate for the length-depth ratio. Thus, the dimensions of copepod nauplii can be measured in terms of carapace length (Lc) and width (Wc) and depth (Dc) with $Lc=2a$, $Wc=2b$, and $Dc=2c$. Since the assumed ratios of $Lc:Wc:Dc$ are 2:1:1, formula (2) can be replaced by the following equation requiring only the measurement of Lc:

$$Vn=1/24 \cdot (\pi Lc^3)\,. \qquad (3)$$

Copepod Copepodites

The body of copepod copepodites can be regarded as the composite form of the metasome and urosome. The shape of the metasome is elliptical in dorsal and lateral views, and that of the urosome is a right circular cylinder (Fig. 2A). Therefore, the volume of the body can be approximated by the sum of the volume of an ellipsoid and a cylinder. The formula is then given as follows:

$$Vc=4/3 \cdot (\pi abc)+\pi R^2 h\,, \qquad (4)$$

where Vc is the volume of copepod copepodites, a is the semimajor axis, b and c are semi-minor axes, R is the radius of the base and h is the altitude of a right circular cylinder (Fig. 2B). The first term of the formula (4) is the volume of the metasome and the second term is the volume of the urosome. We can assume that the width and depth of the metasome are the same, but the length varies by species of zooplankton. Thus, the first term of formula (4) becomes $4/3 \cdot (\pi ab^2)$. The dimensions of copepod copepodites can be expressed in terms of metasome length (Lm), metasome width (Wm), metasome depth (Dm), urosome length (Lu) and urosome width (Wu). Equating these measurements to the parameters in formula (4), we have $a=Lm/2$, $b=Wm/2$, $Lu=h$, and $R=Wu/2$.

$$Vc=4/3 \cdot \{Lm/2 \cdot (Wm/2)^2\pi\}+1/4 \cdot (Lu\,Wu^2\pi)\,. \qquad (5)$$

If Wm can be expressed in terms of Lm, and the volume relation between metasome and urosome is known, formula (5) will be given in a simpler form, omitting the calculation of the second term. The metasome length-width ratios (k) and the volume proportion of the metasome to the whole body (m) are measured and given as specific values (Table 3). By

TABLE 3. MEAN LENGTH-WIDTH RATIOS AND VOLUME PROPORTION OF METASOME TO THE WHOLE BODY IN COPEPODS.

Species	Length-width ratio (k)	Metasome to whole body (m)
Oithona similis adult & copepodites	2.50	0.93
Calanus marshallae C II	2.89	0.94
Calanus marshallae C I	2.67	0.94
Acartia longiremis adult & copepodites	2.69	0.95
Acartia tumida adult & copepodites	2.65	0.80
Pseudocalanus sp. adult & copepodites	2.81	0.97

using these parameters, the formula (5) is expressed in a single term requiring only the measurement of Lm:

$$Vc=\{Lm/6\cdot(Lm/k)^2\pi\}/m\,. \qquad (6)$$

Euphausiid Furcilia

The body of euphausiid furcilia can be regarded as a combination of two cylinders of carapace and abdomen (Fig. 1). Therefore, the volume of the euphausiid furcilia (Vf) can be estimated by the following formula:

$$Vf=Vfc+Vfa\,, \qquad (7)$$

where Vfc is the volume of the carapace and Vfa is the volume of the abdomen. When we

TABLE 4. SIZE AND ESTIMATED WEIGHT OF ZOOPLANKTON WHICH OCCURRED IN THE GUT OF LARVAL WALLEYE POLLOCK.

Zooplankton	No. indiv. measured	Size range (mm)	Weight (μg)	Reference (μg)
Copepod eggs	265	0.07-0.22	0.18- 5.7	1.8(0.15 mm)[1]
Copepod nauplii	841	0.10-0.30	0.13- 3.5	5(0.4 mm)-7[2], 2-5[3]
Calanoid copepodites	65	0.30-1.10	2.0 - 98.5	
Calanus C I	5	0.50-0.86	9.3 - 47.1	
Calanus C II	3	0.48-0.68	8.2 - 23.3	
Calanus C I or C II	3	0.50-0.88	9.3 - 50.5	
Calanus C III	3	0.42-1.34	5.5 -164.5	
Oithona similis eggs	109	0.06-0.07	0.12- 0.18	0.03(0.042 mm)[1]
Oithona similis copepodites	2	0.44-0.48	7.9 - 10.2	
Oithona similis[5]	43	0.30-0.54	2.5 - 14.5	7(0.8 mm)[2,3]
Oithona similis female	5	0.42-0.50	6.8 - 11.5	7(0.76 mm)[4]
Oithona similis male	3	0.46-0.52	9.0 - 13.0	
Acartia longiremis C IV	1	0.48	8.6	10[2], 12(0.71 mm)[4]
Acartia longiremis[5]	33	0.40-1.20	5.0 -134.9	51(1.15 mm)[3]
Acartia longiremis female	6	0.94-1.20	64.8 -134.9	50[2], 30(0.95 mm)[4]
Acartia longiremis male	15	0.78-0.96	37.0 - 69.1	50[2], 26(0.95 mm)[4]
Acartia tumida C V	1	1.02	101.4	
Acartia tumida[5]	8	0.80-1.30	38.1 -163.8	
Acartia tumida female	5	1.12-1.32	104.8 -171.5	
Acartia tumida male	3	0.90-1.20	54.4 -128.8	
Calanus marshallae C I	1	0.80	41.0	
Calanus marshallae C IV	1	2.30	871.2	
Pseudocalanus sp. eggs	139	0.12-0.13	0.9 - 1.2	0.9(0.12 mm)[1]
Pseudocalanus sp. C III	1	0.56	12.3	10[2], 40[3], 24(0.77 mm)[4]
Pseudocalanus sp. C IV	1	0.70	24.0	10[2], 60[3], 32(0.98 mm)[4]
Pseudocalanus sp.[5]	38	0.50-1.32	8.8 -161.2	80[3]
Pseudocalanus sp. female	26	0.94-1.32	58.2 -161.2	100[2], 109(1.5 mm)[4]
Pseudocalanus sp. male	4	0.72-0.92	26.2 - 54.6	80[2]
Euphausiid eggs	8	0.18-0.42	3.1 - 39.8	39(0.42 mm)[1], 20[2,3]
Euphausiid furcilia	7	2.24-3.22	76.5 -209.1	150[2]

[1] CONWAY (1980)—North Atlantic; [2] LUBNY-GERTSYK (1953)—Bering and Okhotsk Seas; [3] BOGOROV (1959)—Barents Sea; [4] PERTSOVA (1967)—White Sea; [5] Adult and copepodites

measure the carapace length (Lc), the carapace depth (Dc), the abdomen length (La) and the abdomen depth (Da), then formula (7) can be replaced by the following equation:

$$Vf=(Dc/2)^2\pi Lc+(Da/2)^2\pi La\,. \qquad (8)$$

The results of the weight estimation of the zooplankton in the gut of larval walleye pollock are given in Table 4. A comparison with available data given by previous authors indicate that the present values fall in almost the same ranges, with few exceptions. The weight of copepod nauplii reported by LUBNY-GERTSYK (1953) is slightly higher than that of this study. The values of female and male *Acartia longiremis* in this study are greater than those of PERTSOVA (1967). The discrepancy in the weight of several species between the present results and the existing data might be caused by seasonal and geographic variability. It must be mentioned that the wide range of zooplankton sizes within each life history stage results in a significant difference in the weight in several types of zooplankton. The maximum: minimum ratio was 32 in copepod eggs, 27 in copepod nauplii, 49 in calanoid copepodites and 27 in *Acartia longiremis*. These can be compared with smaller ratios in *Oithona similis* (6), *Pseudocalanus* sp. (18) and euphausiid furcilia (3). Although the species of copepod nauplii and copepodites have not been identified in this study, the wide size range suggests that the copepod nauplii and copepodites found in these larval walleye pollock guts are a mixed sample of different broods or different species.

Discussion

The present approach to the estimation of zooplankton volume permits the calculation of the weight of individual zooplankton by applying mensuration formulae. The advantage of this approach is that the volume is easily calculated by measuring only the diameter of eggs, and the length of the carapace, metasome, urosome or abdomen. Then, the weight can be estimated by multiplying the volume by the known specific gravity of sea water. The present method simplifies the procedure for the measurement of the weight of small zooplankton which occur in the gut of larval fish. In turn, this allows the quantitative comparison of feeding intensity.

The simplified mensuration formulae exclude the measurement of several body parts of zooplankton, such as antennae, feeding appendages, swimming legs and so on. The exclusion of these measurements may underestimate the actual volume of zooplankton. However, since these parts of the zooplankton in this study are believed to compose only minor proportion of the body volume or weight, it is unlikely that the exclusion will cause a significant error in calculating the volume or weight.

The digestion process may diminish the size of zooplankton found in the gut. However, in the larval walleye pollock gut, chitinous integument remains intact for a relatively long time, thus error in calculation is expected to be minimal. Nevertheless, to obtain closer values, the validity of the present methods awaits future evaluation by examining in detail the effects of these factors.

TABLE 5. FREQUENCY OCCURRENCE OF COPEPOD NAUPLII BY SIZE AND ESTIMATED WEIGHT IN THE GUT OF 10 WALLEYE POLLOCK LARVAE FROM TABLE 1. THE FISH NUMBER IS ARRANGED IN ORDER THAT THE ESTIMATED WEIGHT CAN BE COMPARED IN A PAIR OF FISH WITH A SIMILAR NUMBER OF COPEPOD NAUPLII.

Carapace length (mm)	Fish Number A		B		C		D		E	
	2	6	3	14	4	12	9	16	10	13
0.10	—	1	—	—	—	—	—	—	—	—
0.12	—	—	—	—	—	—	—	—	—	—
0.14	1	1	1	—	2	1	2	2	1	—
0.16	—	2	1	3	—	1	3	6	2	—
0.18	5	2	—	3	3	1	5	5	5	4
0.20	3	4	5	5	1	2	5	5	5	1
0.22	5	—	1	—	1	1	4	2	2	4
0.24	3	3	2	—	2	1	1	2	—	4
0.26	—	4	—	1	—	1	1	1	—	1
0.28	—	2	2	—	—	—	—	—	—	1
0.30	1	—	1	—	—	—	—	—	—	—
Total No.	18	19	13	12	9	8	21	23	15	15
Estimated weight (μg)	23.2	27.7	20.4	11.4	9.1	9.3	21.1	21.7	13.3	22.1

Our data indicate that a wide variability in the size of zooplankton results in a wide difference in weight, particularly for copepod nauplii and calanoid copepodites. Since these organisms are the most important food items for larval fish at the early life stages, this difference in size deserves considerable attention. Table 5 shows examples of the size frequency distribution, number and estimated weight of copepod nauplii in 10 guts selected from the first 16 larvae in Table 1. Two of them are arranged as pairs in which the total number of copepod nauplii is similar or the same. It is apparent that in pairs C and D, the weight of nauplii is not different between the two larvae; however, in pair A the weight is slightly higher in No. 6 fish than in No. 2 fish. In striking contrast, the estimated weight differs considerably between the two individuals in pairs B and E. Further, if we use an average weight of copepod nauplii (=1.82 μg calculated from Table 4), such differences in weight as found in pairs B and E will not be recognized. Thus, the average weight of a particular zooplankton species does not ensure its general usefulness in quantitative analyses of food intake in larval fish. Ignoring the variation of zooplankton weight will result in erroneous estimation of energy content in larval guts.

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