Marine Biology 68, 15–23 (1982)

MARINE BIOLOGY

Energetics of *Euphausia pacifica.* II. Complete Carbon and Nitrogen Budgets at 8° and 12 °C Throughout the Life Span

R. M. Ross

Marine Science Institute, University of California at Santa Barbara; Santa Barbara, California 93106, USA

Abstract

Complete carbon and nitrogen budgets at 8° and 12 °C over the life span of *Euphausia pacifica* were constructed from data published in the foregoing publication. The relative magnitudes of physiological functions such as metabolism and growth for the different life history stages were compared. The carbon net growth efficiency (NGE) for *E. pacifica* increased to a maximum of 60 to 74% at Calyptopis 3 (a larval stage) and then decreased rapidly to a level of 10 to 12% for adults. The cumulative amount of assimilated carbon or nitrogen in reproductive products was equal to that in growth. The cumulative net production efficiency (tissue plus molts plus reproductive products) is 24 to 29%, and is slightly higher for nitrogen than for carbon. For juveniles and adults, the largest proportion (40 to 65%) of assimilated material is used in metabolism, and is about 10% higher at 8° than 12 °C. The difference between measured and predicted ingestion (the sum of metabolism, leakage, defecation, growth, molting and reproduction) probably results from poorly understood aspects of zooplankton physiology (e.g. the effect of body weight on leakage). Nitrogen budgets at 8 °C for furcilia balanced the best, with deviations of less than 10%. In general, predicted ingestion was increasingly less than measured ingestion as body weight and temperature increased. Possible omissions or errors in assumptions or methods that may cause the imbalances are discussed.

Introduction

The processes underlying secondary production in the oceanic ecosystem can be clarified by considering the transfer or flow of material through individual organisms or the single-species populations constituting the ecosystem. In the present paper, equations describing relationships between body weight and physiological processes (derived from Ross, 1982) are used to construct material budgets. These budgets (1) describe the flow of carbon and nitrogen through an average individual *Euphausia pacifica* over its life span, and (2) characterize this euphausiid as a converter of food to carbon and nitrogen production. Since the rates of material transfer and nutrient cycling in zooplankton populations may ultimately be integrated with rates of transfer for other components of the ecosystem, the materials measured should be common and important to all components of the ecosystem. Carbon is a traditional indicator of organic matter, and nitrogen is often the limiting nutrient in the oceanic ecosystem. The effect of temperature on the utilization of these materials was determined by comparing material budgets for 8° and 12 °C, which are within the environmental range encountered by *E. pacifica* in Puget Sound, Washington, the source of the experimental euphausiids (Hulsizer, 1971). Since budgets were constructed for the entire life span of *E. pacifica,* the relationships and relative importance of the various physiological functions such as metabolism and growth were compared for all life history stages.

In a budget where all gains and losses are accurately estimated, the input equals the output. One of the main objectives of this study was to examine the accuracy or completeness of the relationships derived for these gains and losses. All known inputs and outputs were either measured or calculated from literature values to avoid the almost universal practice of measuring most parameters and deducing the remainder by difference (Richman, 1958; Corner *et al.,* 1967; Lasker *et al.,* 1970; Harris, 1973; Mootz and Epifanio, 1974; Logan and Epifanio, 1978; and others). Such deduction is unsatisfactory, since all errors of measurement are incorporated into the unmeasured gain or loss, and no indication is available from the material balance about the validity of the methods and assumptions used. In the present study, measured ingestion and predicted ingestion were compared to show the accuracy of the material budgets.

0025-3162/82/0068/0015/$ 01.80

Although most previous budgets have been calculated using the difference approach, complete budgets have been constructed for adults of a deposit-feeding amphipod (Hargrave, 1971) and a barnacle (Wu and Levings, 1978), and for all life history stages of *Calliopius laeviusculus*, a carnivorous amphipod (Dagg, 1976). The material budgets in the present study are the first complete budgets for all life history stages of a long-lived oceanic zooplankter.

Materials and Methods

Dagg (1976) presented a complete equation for a budget for a crustacean:

$$\text{ingestion} = \text{growth} + \text{reproduction} + \text{molting} + \text{metabolism} + \text{leakage} + \text{defecation}.$$

Expressions for all the budget parameters except leakage were derived (in terms of carbon and nitrogen) for *Euphausia pacifica* kept in the laboratory at 8° or 12 °C under conditions of excess ration (Ross, 1982). The larvae were reared in the laboratory and never experienced food deprivation. Because ingestion rates were lower in fall and early winter than in spring and summer, even when maintained on excess food (Ross, 1979), fall and winter individuals were probably in a quiescent state. I wished to calculate material budgets for individuals under optimal food conditions; therefore I used only data from laboratory-reared larvae, and juveniles and adults collected in the spring and summer to derive the equations describing the relationships between each budget parameter and body weight.

Webb and Johannes (1967) emphasized that zooplankton may release significant amounts of dissolved organic carbon; such leakage can be measured as a fraction of respiration (Dagg, 1976), or excretion, or as the release of organic materials such as urea and amino acids (Jawed, 1969). Ammonia comprised 82.56% of the total nitrogen excreted by adult *Euphausia pacifica* starved for 24 h prior to experimentation (Jawed, 1969), and this proportion was not affected by temperature. Although Dagg (1976) found neither a temperature nor a body-weight effect on the ratio of organic carbon leakage to respiration of the amphipod *Calliopius laeviusculus*, leakage in feeding individuals was about one-third more than that in starved individuals. When constructing the present budgets, I assumed that carbon and nitrogen leakage constituted the same fraction of metabolic loss, and that the fraction was constant at all body weights and both temperatures. I increased the ratio of leakage to excretion found for non-feeding *E. pacifica* by Jawed (1969) by the same feeding factor as that found by Dagg (1976), estimating leakage of a feeding individual to be 28.7% of respiration and excretion. All respiration and excretion expressions were multiplied by 1.287 to obtain total metabolic loss (Table 1).

Ingestion (I_C or I_N) expressions multiplied by the assimilation efficiency (AE) gave the expressions for assimilation rate (Table 1). Defecation was measured to determine assimilation efficiency, but when comparing measured and predicted ingestion, defecation was calculated as the difference between ingestion and assimilation $(1.00 - (AE_C \text{ or } AE_N)/100) \times (I_C \text{ or } I_N)$.

Table 1. *Euphausia pacifica*. Equations used in calculating carbon and nitrogen budgets at 8 ° and 12 °C; weight (W) in μg carbon or nitrogen, rates in μg d^{-1}

Physiological rate	8 °C	12 °C
	Carbon	
Assimilation	$0.202\ W^{0.910}$	$0.328\ W^{0.910}$
Total metabolic loss		
$< 165\ \mu g$	$0.220\ W^{0.839}$	$0.291\ W^{0.839}$
$> 165\ \mu g$	$0.198\ W^{0.810}$	$0.257\ W^{0.810}$
Growth		
$< 12.5\ \mu g$	$-0.057 + 0.124\ W$	$-0.315 + 0.198\ W$
$> 12.5\ \mu g$	$0.156\ W^{0.617}$	$0.261\ W^{0.617}$
Molting		
$< 12.5\ \mu g$	$(8.80\ W - 11.42)^a$	$(8.73\ W - 7.60)^a$
$> 12.5\ \mu g$	$0.011\ W^{0.853}$	$0.021\ W^{0.805}$
Reproduction		
$> 685\ \mu g$	$12.20 + 6.16\ W^a$	
$> 665\ \mu g$		$20.37 + 10.29\ W^a$
	Nitrogen	
Assimilation	$0.100\ W^{0.959}$	$0.153\ W^{0.959}$
Total metabolic loss	$0.075\ W^{0.925}$	$0.094\ W^{0.925}$
Growth		
$< 3.5\ \mu g$	$-0.042 + 0.151\ W$	$-0.048 + 0.170\ W$
$> 3.5\ \mu g$	$0.097\ W^{0.609}$	$0.160\ W^{0.609}$
Molting		
$< 3.5\ \mu g$	$(6.47\ W - 2.16)^a$	$(6.35\ W - 1.43)^a$
$> 3.5\ \mu g$	$0.0067\ W^{0.853}$	$0.0119\ W^{0.805}$
Reproduction		
$> 183\ \mu g$	$2.39 + 4.11\ W^a$	
$> 166\ \mu g$		$3.98 + 6.86\ W^a$

[a] $\times 10^{-3}$

For three parameters, more than one equation was necessary to represent the relationship between body weight and rate. The use of one equation for larvae and another for juveniles plus adults to calculate carbon total metabolic loss (Table 1) decreased the sum of squares about the regression(s) for the entire size range. The gills are not fully developed in the larvae, so their respiratory behavior may be different from adults. For both growth and molting, the slope of the body weight-rate curve is steeper for naupliar and calyptopis stages than for furcilia, juveniles and adults, and the relationship is linear instead of allometric, probably because the body undergoes a fundamental change in shape when molting from Calyptopis 3 to Furcilia I (Ross, 1982).

Reproduction occurs only in the last half of the life cycle of *Euphausia pacifica* (Table 2). Reproduction is zero for individuals less than 685 or 655 μg C and less than 183 or 166 μg N at 8° and 12 °C, respectively. Production was calculated as the sum of growth, molting, and reproduction (i.e., all material that an organism produces), whether retained in the body or released.

I calculated both daily and cumulative budgets using the expressions in Table 1. A daily budget was constructed from Calyptopis 1 to the time when an adult released all its reproductive products: 365 d from hatching to complete gamete release at 8 °C and 219 d at 12 °C. On 8 or 4 d (8° or 12 °C, respectively) after hatching, the content of carbon (2.78 μg) and nitrogen (0.66 μg) (Ross, 1979) of a Calyptopis 1 was used to solve each equation. The calculated growth was added to the original weight for that day to give the rates for the euphausiid for the next day. Calyptopis 1 was chosen as the starting point because it is the first feeding stage. Although ingestion is zero for naupliar stages, the rest of the parameters are positive, implying that these early stages lose weight. However, the early stages do not lose weight, so the first few days of the life cycle are omitted from this budget. The cumulative budget was calculated by summing the daily budgets, giving (1) total carbon or nitrogen invested in assimilation, (2) total metabolic loss, and (3) production at four time periods during the life cycle (late furcilia, the transition from juvenile to adult, adults with reproductive products just beginning to mature, and adults close to the end of their life span). I expressed the imbalance in both daily and cumulative budgets as the percentage deviation of measured from predicted ingestion:

$$\text{Imbalance} = 100\% \, \frac{\text{(predicted ingestion)}}{\text{(measured ingestion)}} \times 100.$$

Predicted ingestion was calculated as the sum of measured metabolic losses, defecation and measured production of tissue, molts and reproductive products. In the subsequent discussion, respiration, excretion, leakage, defecation, growth, molting and reproduction, refer to the respective rates, except when I refer not to rates but to the cumulative budgets for total carbon and nitrogen invested in the parameter.

I analyzed the partitioning of assimilated material among total metabolic loss, growth, molting, and reproduction for any changes related to temperature, body weight or material. Since assimilation efficiency remained constant in this study, the same patterns of increase and decrease in response to the three variables will be seen in gross and net growth, and production and metabolic efficiencies, although the absolute value of the net efficiency is 3 to 4% higher. Within a given species, partitioning of material into the different physiological functions is best compared in terms of net efficiencies, removing any variability caused by differences in the assimilation efficiencies due to species or food type. In this study, total metabolic loss, net growth, molting and reproduction efficiencies were calculated for both daily and cumulative budgets.

Results

Carbon and nitrogen budgets at 8° and 12 °C are presented for 4 sizes of larvae (two calyptopis and two furcilia), early and late juveniles, and early, mid- and late-adults (Tables 2 and 3) of *Euphausia pacifica*. The calculated daily carbon and nitrogen budgets did not balance equally well at all weights and temperatures. The budgets for the furcilia stages balanced the best, with the difference between measured and predicted ingestion being usually less than 10%. In general, predicted ingestion declined with respect to measured ingestion as body weight and temperature increased. However, during the early larval or calyptopis stages, predicted ingestion was greater than measured by 12 to 101%; the imbalances were greater for larger calyptopis relative to smaller ones and for nitrogen relative to carbon. Except for the calyptopis stages, the balance for the nitrogen budgets was within 10% for the first half of the life span at 8 °C and within 15% at 12 °C; better than the balance for the carbon budgets, which was within 25 to 30%.

The percentage of the measured cumulative ingestion predicted by the cumulative budgets (Table 4) followed the same trends as the daily budgets. Near the end of the life span, the cumulative predicted ingestion was 78 and 69% of cumulative measured carbon ingestion at 8° and 12 °C, respectively (90 and 82% for nitrogen).

The daily energetic efficiencies and the imbalance of the budget varied with age or weight of the organism, temperature, and the material analyzed (Figs. 1–4). During the calyptopis stages, net growth and molting efficiencies increased with weight, but the imbalance also increased. The net growth efficiency (NGE) was at times greater than 100% for the 8 °C nitrogen budget (a theoretical impossibility). At 12 °C, the NGE was less and so was the imbalance. The NGE for calyptopis carbon was (1) much lower than that for nitrogen and (2) more variable at 12 °C (29 to 60%) than at 8 °C (56 to 74%). The proportion of the assimilated material invested in metabolism, net metabolic loss efficiency (NML), decreased slightly during the calyptopis stages: 5 to 10% for carbon and a few percent for nitrogen.

During the furcilia stages, both NGE and NML decreased for all temperatures and materials. The NGE decreased more for nitrogen (55 to 30%) than for carbon (30 to 18%), with no apparent temperature effect. The imbalance was usually under ±15% for both materials. Nitrogen NML during the furcilia stages was fairly stable, decreasing only slightly. Net molting efficiency decreased initially, but was stable during most of the furcilia phase.

During the juvenile phase, NGE decreased at a much slower rate than during the furcilia stages. The nitrogen NML was very stable, and lower by about 10% at 12° than at 8 °C. The nitrogen balance was fairly good at both temperatures, predicted ingestion usually deviating by less than 18% from measured. The carbon NML, however, decreased to about 50% at 8 °C, slightly higher than at 12 °C where the decrease was slower. The imbalance was

Table 2. *Euphausia pacifica.* Daily carbon budgets at 8° and 12 °C: age, weight, rates of assimilation (Assim), total metabolic loss (Meta), growth (Grow), molting (Molt) and reproduction (Repr) and percent deviation (% dev) of measured from predicted ingestion = total metabolic loss plus defecation plus growth, molting and reproduction, whereby the amount of carbon in defecation is calculated by [measured assimilation/(assimilation efficiency/100)] minus (measured assimilation)

Life phase	Age	Weight	Rate (μg C d^{-1})					% dev
	(d)	(μg)	Assim	Meta	Grow	Molt	Repr	
8 °C								
Calyptopis	8	2.78	0.51	0.52	0.29	0.01	0	+49
	21	11.06	1.80	1.65	1.32	0.09	0	+57
Furcilia	42	33.91	4.99	4.23	1.37	0.22	0	+13
	84	124.29	16.27	12.58	3.06	0.67	0	0
Juvenile	105	198.55	24.91	14.39	4.08	1.00	0	-18
	147	417.20	48.96	26.25	6.45	1.89	0	-24
Adult	168	565.94	64.62	33.61	7.79	2.45	0	-26
	252	1 469.94	154.03	72.81	14.04	5.53	21.25	-21
	336	2 954.25	290.71	128.15	21.60	10.04	30.40	-28
12 °C								
Calyptopis	4	2.78	0.83	0.69	0.24	0.02	0	+12
	14	8.83	2.38	1.81	1.43	0.07	0	+32
Furcilia	28	33.18	7.94	5.49	2.26	0.35	0	+2
	56	136.85	28.83	18.04	5.43	1.10	0	-12
Juvenile	70	225.29	45.38	20.68	7.38	1.65	0	-28
	98	491.74	92.33	38.93	11.95	3.08	0	-34
Adult	112	675.67	123.29	50.35	14.54	3.98	27.32	-18
	154	1 462.73	248.98	94.13	23.42	7.42	35.42	-29
	196	2 654.53	428.26	152.53	33.83	11.98	47.69	-35

Table 3. *Euphausia pacifica.* Daily nitrogen budgets at 8° and 12 °C: age, weight, rates of assimilation, total metabolic loss, growth, molting and reproduction and percent deviation of measured from predicted ingestion = total metabolic loss plus defecation plus growth, molting and reproduction; further details and abbreviations as in Table 2

Life phase	Age	Weight	Rate (μg N d^{-1})					% dev
	(d)	(μg)	Assim	Meta	Grow	Molt	Repr	
8 °C								
Calyptopis	8	0.66	0.07	0.05	0.06	0.002	0	+52
	21	2.65	0.26	0.19	0.36	0.02	0	+101
Furcilia	42	9.14	0.84	0.58	0.37	0.04	0	+16
	84	33.64	2.91	1.94	0.83	0.13	0	0
Juvenile	105	53.63	4.56	2.98	1.10	0.20	0	-5
	147	112.06	9.24	5.90	1.72	0.38	0	-12
Adult	168	151.56	12.34	7.80	2.06	0.49	0	-14
	252	389.10	30.47	18.66	3.67	1.08	3.99	-9
	336	774.14	58.94	35.25	5.57	1.95	5.57	-15
12 °C								
Calyptopis	4	0.66	0.10	0.06	0.06	0.003	0	+23
	14	2.10	0.31	0.19	0.31	0.01	0	+56
Furcilia	28	8.19	1.15	0.66	0.58	0.06	0	+11
	56	34.65	4.58	2.50	1.39	0.21	0	-9
Juvenile	70	57.21	7.42	3.97	1.88	0.31	0	-15
	98	124.88	15.68	8.17	3.03	0.58	0	-21
Adult	112	171.38	21.24	10.95	3.67	0.75	5.16	-3
	154	368.99	44.31	22.26	5.85	1.39	6.51	-16
	196	665.57	78.01	38.42	8.38	2.23	8.55	-22

Table 4. *Euphausia pacifica.* Cumulative carbon and nitrogen budgets at 8° and 12 °C; age, cumulative amount of element in assimilation (Assim), total metabolic loss (Meta) and production (Prod) and percent of measured ingestion accounted for by predicted ingestion where total metabolic loss plus production plus defecation = amount of carbon or nitrogen in defecation calculated by [measured assimilation/(assimilation efficiency/100)] minus (measured assimilation)

Life phase	Age	Budget parameter (μg)			Predicted ingestion
	(d)	Assim	Meta	Prod	(%)
		Carbon			
8 °C					
Late furcilia	84	512	416	146	108
Juvenile-adult	168	3 671	2 186	716	83
Eggs maturing	252	12 588	6 564	3 261	82
Late adult	336	30 986	14 917	7 545	78
12 °C					
Late furcilia	42	260	179	86	101
Juvenile-adult	98	3 008	1 473	609	75
Eggs maturing	154	12 229	5 107	3 214	74
Late adult	210	32 877	12 569	7 946	69
		Nitrogen			
8 °C					
Late furcilia	84	88	60	38	110
Juvenile-adult	168	679	440	182	93
Eggs maturing	252	2 419	1 519	733	94
Late adult	336	6 111	3 749	1 644	90
12 °C					
Late furcilia	42	38	22	21	110
Juvenile-adult	98	491	263	148	86
Eggs maturing	154	2 104	1 084	702	87
Late adult	210	5 844	2 935	1 675	82

the inverse of this decrease in the carbon NML: 18 to 24% at 8 °C and 28 to 34% at 12 °C.

During the adult phase most efficiencies were stable or slowly decreased as follows – NGE: 11 to 7% for carbon, 17 to 9% for nitrogen, with no apparent temperature effect; net molting efficiency: 3 to 4% for carbon and nitrogen, slightly higher (0.5%) for carbon and at 8 °C; net production efficiency: 24 to 10%, slightly higher at 12° than 8 °C. Nitrogen NML remained constant at both temperatures, but carbon NML continued to decrease. For the nitrogen budgets, the imbalance was only 3% at the beginning of the adult phase and, even at the end of the life span, remained less than 25 and 20% at 12° and 8 °C, respectively. But the imbalance was over 16% for the carbon budgets of early adults and increased to over 30% toward the end of the life span.

The cumulative energetic efficiencies (Table 5) followed the same pattern as the daily energetic efficiencies. The cumulative NGE decreased rapidly in the first half of the life span, and then became constant. Almost 10% of cumulative measured assimilation was invested in carbon growth, 12% in nitrogen growth, and an equal percentage in reproduction, by the end of the life span. Of the three production terms, the smallest amount of cumulative measured assimilation was invested in molting, 3.0 to 3.6%. Therefore, based on measured assimilation, the cumulative net production efficiency was slightly higher for nitrogen (29%) than for carbon (24%) (Table 5). For the three production terms, the difference between the energetic efficiency calculated from measured and predicted assimilation was usually less than 4%. However, the amount of assimilated carbon used for metabolism dif-

Table 5. *Euphausia pacifica.* Cumulative energetic efficiencies for carbon and nitrogen budgets at 8° and 12 °C: age, percentage of measured (meas) and predicted (pred) assimilation in total metabolic loss, growth, molting and reproduction

Life phase	Age	Metabolic loss		Growth		Molting		Reproduction	
	(d)	meas	pred	meas	pred	meas	pred	meas	pred
				Carbon					
8 °C									
Late fucilia	84	81.4	74.0	24.3	22.1	4.3	3.9	0	0
Juvenile-adult	168	59.5	75.3	15.6	19.7	4.0	5.0	0	0
Eggs maturing	252	52.1	66.8	11.8	15.1	3.8	4.8	10.4	13.3
Late adult	336	48.1	66.4	9.6	13.2	3.6	5.0	11.1	15.4
12 °C									
Late furcilia	42	68.8	67.6	28.8	28.3	4.2	4.1	0	0
Juvenile-adult	98	49.0	70.7	16.7	24.1	3.6	5.2	0	0
Eggs maturing	154	41.8	61.4	12.1	17.8	3.2	4.8	10.9	16.0
Late adult	210	38.2	61.3	9.7	15.5	3.0	4.8	11.5	18.4
				Nitrogen					
8 °C									
Late furcilia	84	68.1	61.1	38.4	34.4	4.9	4.4	0	0
Juvenile-adult	168	64.8	70.8	22.5	24.6	4.3	4.6	0	0
Eggs maturing	252	62.8	67.4	16.2	17.4	3.9	4.1	10.2	11.0
Late adult	336	61.4	69.5	12.8	14.4	3.6	4.1	10.6	12.0
12 °C									
Late furcilia	42	57.0	50.9	49.8	44.4	5.2	4.7	0	0
Juvenile-adult	98	53.6	64.0	25.9	31.0	4.1	5.0	0	0
Eggs maturing	154	51.5	60.7	17.8	20.9	3.5	4.1	12.1	14.2
Late adult	210	50.2	63.7	13.6	17.3	3.1	4.0	11.9	15.1

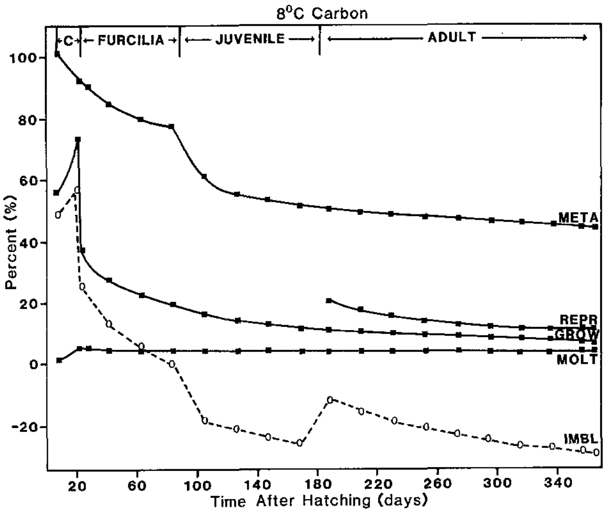

Fig. 1. *Euphausia pacifica.* Daily efficiencies (as percent of assimilated carbon) of growth (GROW), molting (MOLT), reproduction (REPR), and total metabolic loss (META), and the imbalance (IMBL, % measured ingestion not accounted for) of the carbon budget at 8 °C. C: calyptopis

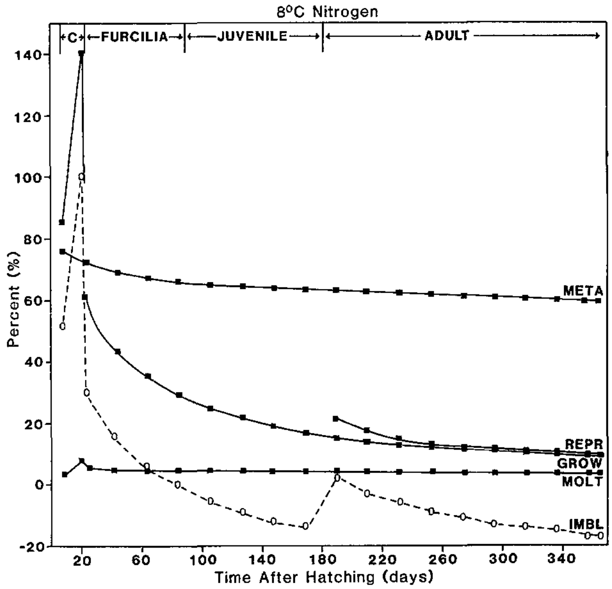

Fig. 3. *Euphausia pacifica.* Daily efficiencies (as percent of assimilated nitrogen) of the nitrogen budget at 8 °C. Abbreviations as in Fig. 1

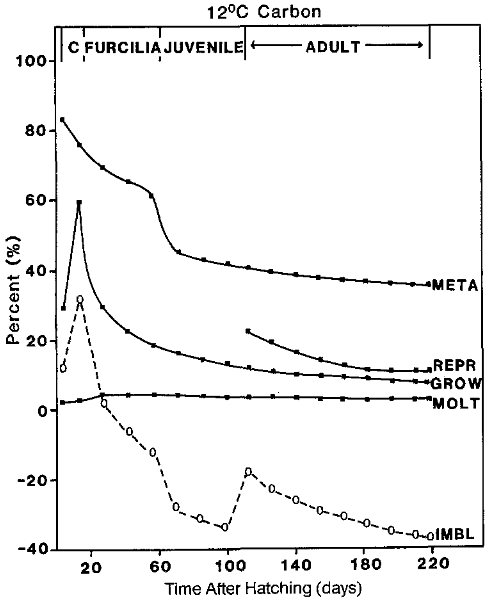

Fig. 2. *Euphausia pacifica.* Daily efficiencies (as percent of assimilated carbon) of the carbon budget at 12 °C. Abbreviations as in Fig. 1

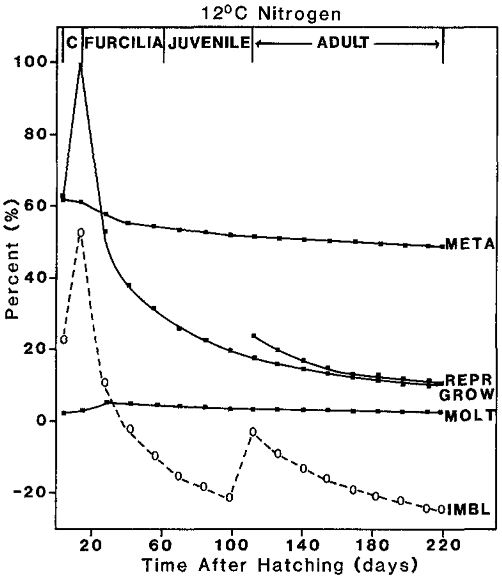

Fig. 4. *Euphausia pacifica.* Daily efficiencies (as percent of assimilated nitrogen) of the nitrogen budget at 12 °C. Abbreviations as in Fig. 1

fered by as much as 23%, depending on whether measured or predicted cumulative assimilation was used. Cumulative NML based on measured assimilation was always less than that for predicted assimilation, but the difference was substantially greater for carbon budgets than for nitrogen budgets due to the greater imbalance. Since predicted assimilation incorporated any errors that existed in all the equations for production and total metabolic loss, I feel that the energetic efficiencies based on measured assimilation were the better estimates. For juveniles and adults, between 40 and 65% of assimilation appeared to be used for metabolism, by far the largest portion of assimilation going to any one budget parameter. The proportion of assimilated material used in metabolism was 10% lower at 12° than at 8 °C; in growth and reproduction slightly higher (0.1 to 3%) at 12 °C. The percentage of assimilation used in molting did not appear to change with temperature.

Discussion

Because most of the parameters were described with an allometric equation, the budgets would have balanced only if all weight-specific coefficients were the same or compensated for each other, which was not true for *Euphausia pacifica* (Ross, 1982). The coefficients for assimilation and total metabolic loss of nitrogen were close to 1, and significantly larger than those for molting and total metabolic loss of carbon; the coefficient for growth was lowest of all.

As expected when all weights are usually represented by one equation, the best balance occurred in the middle of the weight range, for furcilia and juveniles. The budget for the calyptopis stages had the worst balance. Either assimilation was underestimated or growth overestimated in the late calyptopis stages, as a nitrogen NGE of over 100% would only be possible if total metabolic loss was zero. An overestimation of growth is less likely than errors in estimating assimilation, since growth during the calyptopis stages was determined by subsampling the population, a method with only minor errors due to contamination and machine error. However, the linear equation describing growth for the calyptopis gives higher growth rates for late calyptopis and early furcilia than the allometric equation for furcilia, juveniles and adults, suggesting that growth could be overestimated for the late calyptopis stages by the present equations, and that growth in this transition between calyptopis and furcilia may be neither linear nor allometric, but a complex mixture.

The balance of the budget may have been affected by the assumptions that neither assimilation efficiency nor leakage were affected by body weight. Existing data support these assumptions, but larval stages were not used in the assimilation efficiency experiments. If very small individuals have slightly higher assimilation efficiencies (as has been found for other organisms by Lawton, 1970) then assimilation was underestimated for young stages, and the weight-specific coefficient would decrease. Such a decrease would tend to (1) decrease assimilation estimates for larger individuals, (2) increase estimates for smaller individuals, and (3) improve the balance for both calyptopis and adults. The very early larvae may also still be depending to some extent on yolk reserves, a food input not measured in the ingestion experiments.

In a study of the effect of weight on leakage in an amphipod, Dagg (1976) found no difference in the ratio of leakage to respiration in late larvae and juveniles, although he did not use large adults of reproductive age. It seems possible that individuals approaching the end of their life may become physiologically less efficient and less able to retain dissolved organic substances. If the organic fraction of total metabolic loss is greater for older individuals, then the coefficient for total metabolic cost will increase, also improving the balance for both calyptopis and adults.

For furcilia, juveniles and adults, the carbon budgets did not balance as well as the nitrogen budgets; both total metabolic loss and growth for carbon had significantly lower weight-specific coefficients than carbon assimilation, causing an increasing divergence of predicted from measured ingestion as the body weight increased. Although molting also had a coefficient less than that for assimilation, the production of molt carbon was only 3.5 to 5.0% of assimilation, and is unlikely to be an important factor in the imbalance.

Since the coefficient for total metabolic loss differs significantly for the carbon and nitrogen budgets, I feel these equations are the source of the differences in the balances found for the two materials. The ratios of carbon and nitrogen leakage to respiration and excretion, respectively, were assumed to be the same, and to remain constant throughout the life of *Euphausia pacifica.* This ratio of leakage to metabolic loss was estimated from literature on nitrogen excretion. The ratio of carbon leakage to respiration may differ from the ratio of nitrogen leakage to excretion; alternatively, there may be a stronger effect of body weight on carbon than nitrogen leakage. Because the carbon : nitrogen ratio of the euphausiids is less than that of the phytoplankton (Ross, 1979), and because nitrogen is probably the limiting nutrient in the ocean (Checkley, 1980), it is probable that the ratio of carbon ingested to carbon used differs from the ratio of nitrogen ingested to nitrogen used. This excess carbon may be released as leakage, increasing the fraction of organic carbon metabolic loss.

The growth-rate equation was based on measurements of euphausiids collected from Port Susan, Washington, USA (see preceding paper). It was not likely that inaccuracies in the equation caused part of the imbalance. If the equation was correct, the maximum size of an individual in Port Susan (8° to 12 °C at depth, where the euphausiids are found much of the time) should be close to that predicted by accumulating daily growth with the 8 °C growth rate equation for 1 yr, or about 18 mm. In Port Susan, the average adult size was 18 mm by late June at about 15 mo old. However, during the late fall and early winter months in Port Susan, the euphausiids grow very slowly (Hulsizer, 1971). After subtracting the 3 to 4 mo of low food conditions, the yearly growth of individuals in the field and as predicted by the growth equation were very close.

Originally, I thought that all production and loss parameters had been measured and only inaccuracies in the relationships between body weight and the parameters, and not omission of a parameter, would cause any imbalance. However, in the calculation of ingestion and assimilation rates I assumed that none of the phytoplankton cell contents were lost during the feeding process because the cells were small enough to be eaten whole. Lampert (1978) found that even if algae were swallowed whole, up to 4% of carbon ingestion could be lost as part of the feeding process. In the present study, this loss of dissolved organic matter may be a minor factor contributing to the imbalance.

The budgets balance better at 8° than 12 °C because the increase in total metabolic loss due to temperature ($Q_{10} \simeq 2.0$) was not enough to offset the increase in assimilation ($Q_{10} \simeq 3.0$). Possible causes of the differences in Q_{10} could be an increase in the organic fraction of net metabolism with temperature or the possibility that the small experimental vessels used in the respiration and excretion experiments restricted euphausiid activity. In a study of the effect of activity on the metabolism of the sea bass, activity was found to increase respiration about twice as much as excretion, but this difference was less at the lower temperature (Muravskaya and Belokopytin, 1975). Reeve (1977) found that the degree of confinement affects almost every physiological parameter. If confinement were a factor and affected respiration more than excretion, both the Q_{10} and the absolute value for carbon metabolic loss might increase if the euphausiid were given more room to swim. The improvement in the balance of the carbon budgets, especially at 12 °C, would be greater than the balance for nitrogen.

Published budgets for aquatic organisms usually include one parameter calculated by difference and/or ignore one or more parameters (usually leakage). However, Dagg (1976) calculated complete carbon and nitrogen budgets at three temperatures for the entire life cycle of the carnivorous amphipod *Calliopius laeviusculus*. He found that the imbalance in both the carbon and nitrogen budgets increased as body weight increased, that predicted ingestion was usually less than that measured, and that the balance was better at the lowest temperature. Thus, Dagg (1976) is in general agreement with the present study. His imbalances for carbon and nitrogen, respectively, ranged from 12 to 100%, and from 37 to 228%; however, in *Euphausia pacifica,* nitrogen balances were better than carbon and the cumulative imbalances were less than 30%. The other complete energy or material budgets that exist for aquatic organisms are limited to one temperature or to one life history stage. Wu and Levings (1978) constructed an energy budget for three groups of adult *Balanus glandula,* and assumed that the loss of dissolved organic matter was not important; the maximum difference between measured and predicted ingestion was 16.2%. Using the adult amphipod *Hyalella asteca,* Hargrave (1971) found predicted ingestion was only 2.9% less than measured. Solomon and Brafield (1972) and Kay and Brafield (1973), both using high rations, found balances within 6 to 24% for the freshwater fish *Perca fluviatilis* and the nereid polychaetae *Neanthes virens,* and Fischer (1972) found that predicted and measured ingestion varied by 1 to 17% in the grass carp *Ctenopharyngodon idella.* Thus, the balance between measured and predicted ingestion appears to be better for energy or material budgets when one considers only one individual or a group of individuals of similar size. Since a budget for the entire life cycle of an animal uses one or two relationships to describe each parameter for the entire weight range of the animal, small changes in the intercepts or weight-specific coefficients can change the balance. Hargrave (1971) pointed out that a difference in ingestion of 2.5 μg animal^{-1} h^{-1} (a change of only 10%) will alter the balance considerably.

Net and gross growth efficiencies usually decrease progressively with increasing age and size in aquatic organisms (Reeve, 1963; Paloheimo and Dickie, 1966). However, the gross growth efficiency of young American lobster (*Homarus americanus:* Logan and Epifanio, 1978) and the net production efficiency of the amphipod *Calliopius laeviusculus* (Dagg, 1976) increased during early development, reached a plateau, and then fell off in the later stages. Calow (1977) reviewed the conversion efficiencies (growth and production efficiencies) of heterotrophic metazoans, and postulated that, in general: (1) maximum net efficiencies of 50 to 80% are found in postnatal organisms; (2) during development, there is probably an initial period when the efficiency rises as the various physiological systems become totally functional – this falls to zero as the organism matures to a non-growing adult. Net production efficiency appeared to increase initially in *Euphausia pacifica* during the naupliar and calyptopis stages, but did not drop to zero, since *E. pacifica* continues to grow throughout its adult life.

Although temperature affects the NGE of *Daphnia pulex* (Lampert, 1977; Kersting, 1978), neither the NPE of *Calliopius laeviusculus* (Dagg, 1976) nor *Euphausia pacifica* (present study) appeared to vary significantly with temperature. Since the Q_{10}s of the physiological functions involved in calculating the growth and production efficiencies were about the same, no temperature effect was expected.

The proportion of assimilated materials metabolized increases (Lasker, 1966; Lasker *et al.,* 1970; Clutter and Theilacker, 1971; Dagg, 1976) or decreases with increasing body size (Harris, 1973; Mootz and Epifanio, 1974). I found NMLs for *Euphausia pacifica* that fall within the range of values for crustaceans found by other investigators (Dagg, 1976). The carbon NML, however, was less than the 88.2% (based on predicted assimilation) found by Lasker (1966) for specimens of *E. pacifica* weighing more than 1 mg. I found a cumulative carbon NML based on predicted assimilation of 66.4% at 8 °C and only 48% for measured assimilation.

Interpreting the energetic efficiencies calculated for *Euphausia pacifica* is difficult because the budgets did not always balance well. Despite the problems of interpretation, it is clear that in the larval stages up to 70% of assimilated food can be incorporated into new tissue and molts, dropping to 24–29% in mature reproducing adults. Lasker (1966) found that the cumulative net production efficiency (NPE) for carbon for *E. pacifica* under 1 mg dry weight was 25.8% but was 11.8% for individuals over 1 mg dry weight; both values are less than the NPEs found in the present study.

Construction of a complete material budget for an organism over its entire life cycle is useful, since it permits one to discover whether assumptions are correct and whether methods provide unbiased results. Areas of imbalance should be explored for omissions of loss factors or possible inaccuracies in the equations describing the various parameters due to incorrect assumptions or methodological bias. The following four areas in this study merit further investigation: (1) the assumption that assimilation efficiency does not vary with weight; (2) the assumptions that leakage is a constant proportion of metabolism and does not vary with weight, and that it constitutes the same fraction for carbon and nitrogen; (3) the loss of prey cell contents during ingestion; (4) the effect of confinement on respiration and excretion and the interaction of activity with temperature.

The imbalances found also warn that one can reach erroneous conclusions if one uses measured physiological rates to predict a rate that is not measured and calculates efficiencies based on this predicted rate. The predicted rate and the efficiency will include all the errors in the measured rates in addition to any omitted physiological functions. Vidal (1980), in an extensive study on the respiration and growth of *Calanus pacificus,* predicted that (1) rates of assimilation and probably ingestion, in comparison to rates of metabolism and growth, should decrease relatively quickly with increasing body weight, and (2) the slopes of the lines would vary with temperature. Neither the present study nor Dagg's (1976) work on *Calliopius laeviusculus* verify Vidal's predictions. The difference between the two coefficients found in the present study for ingestion and respiration was opposite to the trend predicted by Vidal (1980).

Acknowledgements. I would like to express my appreciation to B. W. Frost, T. S. English and L. B. Quetin for support and advice throughout this study, and to N. D. Holland for editorial advice. I also thank N. Kachel and D. Somerton for help in programming, and D. Thoreson and J. Yen for help in collecting euphausiids. Discussions with my colleagues J. Vidal, J. Yen, L. B. Quetin and M. Dagg were valuable at various points in the study. This research was part of a Ph. D. dissertation submitted to the University of Washington, Seattle. Facilities for the preparation of the manuscript were provided by the Australian Institute of Marine Science.

Literature Cited

Calow, P.: Conversion efficiencies of heterotrophic organisms. Biol. Rev. *52,* 385–409 (1977)

Checkley, D. M., Jr.: The egg production of a marine planktonic copepod in relation to its food supply: laboratory studies. Limnol. Oceanogr. *25,* 430–446 (1980)

Clutter, R. I. and G. H. Theilacker: Ecological efficiency of a pelagic mysid shrimp: estimates from growth, energy budget, and mortality studies. Fish. Bull. U.S. *69,* 93–115 (1971)

Corner, E. D. S., C. B. Cowey and S. M. Marshall: On the nutrition and metabolism of zooplankton. V. Feeding efficiency of *Calanus finmarchicus.* J. mar. biol. Ass. U.K. *47,* 259–270 (1967)

Dagg, M. J.: Complete carbon and nitrogen budgets for the carnivorous amphipod, *Calliopius laeviusculus* (Krøyer). Int. Revue ges. Hydrobiol. *61,* 297–357 (1976)

Fischer, Z.: The elements of energy balance in grass carp (*Ctenopharyngodon idella* Val.). Part II. Fish fed with animal food. Polskie Archwm Hydrobiol. *19,* 65–82 (1972)

Hargrave, B. T.: An energy budget for a deposit-feeding amphipod. Limnol. Oceanogr. *16,* 99–103 (1971)

Harris, R. P.: Feeding, growth, reproduction and nitrogen utilization by the harpacticoid copepod, *Tigriopus brevicornis.* J. mar. biol. Ass. U.K. *53,* 785–800 (1973)

Hulsizer, E.: A study of the reproductive cycle of *Euphausia pacifica* at two stations in Puget Sound, 1968–1969, 33 pp. M. S. thesis, University of Washington 1971

Jawed, M.: Body nitrogen and nitrogenous excretion in *Neomysis rayii* Murdock and *Euphausia pacifica* Hansen. Limnol. Oceanogr. *14,* 748–754 (1969)

Kay, D. G. and A. E. Brafield: The energy relations of the polychaete *Neanthes* (= *Nereis*) *virens* (Sars). J. Anim. Ecol. *42,* 673–692 (1973)

Kersting, K.: Some features of feeding, respiration and energy conversion of *Daphnia magna.* Hydrobiologia *59,* 113–120 (1978)

Lampert, W.: Studies on the carbon balance of *Daphnia pulex* de Geer as related to environmental conditions. III. Production and production efficiency. Arch. Hydrobiol. (Suppl.) *48,* 336–360 (1977)

Lampert, W.: Release of dissolved organic carbon by grazing zooplankton. Limnol. Oceanogr. *23,* 831–834 (1978)

Lasker, R.: Feeding, growth, respiration and carbon utilization of a euphausiid crustacean. J. Fish. Res. Bd Can. *23,* 1291–1317 (1966)

Lasker, R., B. J. Wells and A. D. McIntyre: Growth, reproduction, respiration and carbon utilization of the sand-dwelling harpacticoid copepod, *Asellopsis intermedia.* J. mar. biol. Ass. U.K. *50,* 147–160 (1970)

Lawton, J. H.: Feeding and food energy assimilation in larvae of the damselfly *Pyrrhosome nymphula* (Sulz.) Odonata: Zygoptera). J. Anim. Ecol. *39,* 669–689 (1970)

Logan, D. T. and C. E. Epifanio: A laboratory energy balance for the larvae and juveniles of the American lobster *Homarus americanus.* Mar. Biol. *47,* 381–389 (1978)

Mootz, C. A. and C. E. Epifanio: An energy budget for *Menippe mercenaria* larvae fed *Artemia* nauplii. Biol. Bull. mar. biol. Lab., Woods Hole *146,* 44–55 (1974)

Muravskaya, Z. A. and Yu. S. Belokoptyin: Effect of moving activity on the nitrogen excretion and oxygen consumption in the pickerel. Biol. Morya, Vladivostok *5,* 39–44 (1975)

Paloheimo, J. E. and L. M. Dickie: Food and growth of fishes. III. Relations among food, body size, and growth efficiency. J. Fish. Res. Bd Can. *23,* 1209–1248 (1966)

Reeve, M. R.: Growth efficiency of *Artemia* under laboratory conditions. Biol. Bull. mar. biol. Lab., Woods Hole *125,* 133–145 (1963)

Reeve, M. R.: The effect of laboratory conditions on the extrapolation of experimental measurements to the ecology of marine zooplankton. V. A. review. *In:* Symposium on warm water zooplankton, pp 528–537. Goa, India: National Institute of Oceanography 1977

Richman, S.: The transformation of energy by *Daphnia pulex.* Ecol. Monogr. *28,* 273–291 (1958)

Ross, R. M.: Carbon and nitrogen budgets over the life of *Euphausia pacifica,* 260 pp. Ph. D. dissertation, University of Washington 1979

Ross, R. M.: Energetics of *Euphausia pacifica.* I. Effects of body carbon and nitrogen and temperature on measured and predicted production. Mar. Biol. 68, 1–13 (1982)

Solomon, D. J. and A. E. Brafield: The energetics of feeding, metabolism and growth of perch (*Perca fluviatilis* L.). J. Anim. Ecol. *41,* 699–718 (1972)

Vidal, J.: Physioecology of zooplankton. IV. Effects of phytoplankton concentration, temperature, and body size on the net production efficiency of *Calanus pacificus.* Mar. Biol. *56,* 203–211 (1980)

Webb, K. L. and R. E. Johannes: Studies of the release of dissolved free amino acids by marine zooplankton. Limnol. Oceanogr. *12,* 376–382 (1967)

Wu, R. S. S. and C. D. Levings: An energy budget for individual barnacles (*Balanus glandula*). Mar. Biol. *45,* 225–235 (1978)

Date of final manuscript acceptance: December 24, 1981.
Communicated by: N. D. Holland, La Jolla