

Digestion Rates and Assimilation Efficiencies of Siphonophores Fed Zooplankton Prey*

J. E. Purcell**

Biology Department, Woods Hole Oceanographic Institution; Woods Hole, Massachusetts 02543, USA

Abstract

Digestion times and assimilation efficiencies are critical factors used in calculations of carbon and nitrogen budgets. Digestion times of natural copepod prey differed significantly among 4 genera of siphonophores ($P < 0.001$), from a minimum of 1.6 h to a maximum of 9.6 h. Assimilation efficiencies, in contrast, were uniformly high; 87 to 94% for carbon and 90 to 96% for nitrogen. Nitrogen assimilation was consistently greater than carbon assimilation. Assimilation efficiencies calculated according to dry weight substantially underestimated assimilation of carbon and nitrogen, while calculations using ash-free dry weights and ash-free to dry weight ratios approached values for carbon assimilation. These values are appreciably higher than most of the assimilation efficiencies previously measured for a few other planktonic carnivores. These results indicate very efficient digestion of food by siphonophores in oceanic environments where prey densities are low.

Introduction

Much recent research has attempted to measure quantitatively the trophic importance of planktonic consumers. This type of research involves determinations of the ingestion and metabolism of the zooplankters, and is directed toward estimation of carbon and nitrogen budgets. Estimates of ingestion can be made from the numbers of prey captured by predators *in situ*, divided by the digestion times. These estimates of ingestion then must be multiplied by the assimilation efficiencies before they are figured into the carbon and nitrogen budgets of the predators.

Siphonophores are colonial, holoplanktonic cnidarians found throughout the world's oceans. They often are the most abundant carnivorous gelatinous macrozooplankters in subtropical surface waters of the North Atlantic Ocean (Biggs *et al.*, 1981; Purcell, personal observation). Siphonophores have multiple, small stomachs (gastrozooids) which ingest individual prey organisms. This characteristic makes them particularly amenable to gut analyses and to measurements of digestion rates, because prey are ingested whole and contained individually within each gastrozooid. Prey are then egested as coherent waste that can be recovered quantitatively for gravimetric studies of assimilation. Data have been gathered on the natural feeding, digestion, and metabolism of some species (Biggs, 1976, 1977 a, b; Purcell, 1980, 1981 a, b, c, 1982; Purcell and Kremer, 1983), yet assimilation efficiencies have not been measured. Assimilation efficiencies have been measured previously for only a few other species of soft-bodied predators: the pteropod *Clione limacina*, the chaetognath *Sagitta hispida*, and the ctenophores *Mnemiopsis mccradyi* and *Pleurobrachia bachei* (Conover and Lalli, 1974; Cosper and Reeve, 1975; and Reeve *et al.*, 1978, respectively). I report here the digestion times and assimilation efficiencies of 4 genera of siphonophores fed natural copepod prey.

Material and Methods

The experiments were conducted during February and May, 1982 in the Sargasso Sea (approximately Lat. 30°N; Long. 77–78°W and Lat. 34°N, Long. 73°W, respectively) and in the Gulf Stream (approximately Lat. 32°N, Long. 78°W to Lat. 36°N, Long. 72°W and Lat. 33°N, Long. 77°W to Lat. 36°N, Long. 73°W). Surface water temperatures were 21° to 22° C in February, and 24° to 25° C in May. Siphonophores were collected in $\frac{1}{4}$, $\frac{1}{2}$, or 1-l clear glass jars by divers at 5- to 25-m depth. Small specimens were maintained on shipboard in the collection

* Contribution no. 5298 from the Woods Hole Oceanographic Institution

** Present address: Department of Biology, University of Victoria; Victoria, British Columbia V8W 2Y2, Canada

jars and larger ones were transferred to 4-l clear plastic containers. The siphonophores were kept at 21° to 22 °C, and used in experiments for no more than 24 h.

Active copepods collected in plankton nets were transferred individually to the containers where they were captured by the siphonophores. The time of prey ingestion was recorded, and individuals were checked at 0.5- to 1.0-h intervals to determine if the prey had been egested. The digestion time is the length of time between ingestion and egestion of prey.

The prey remains were egested in coherent pellets, each containing the remains of one copepod. Each waste pellet was collected intact with a pipette 0 to 0.5 h after egestion, dipped in distilled water to remove salt, and transferred to a piece of pre-ashed, pre-weighed aluminum foil. The samples were stored in a desiccator and later dried at 60 °C for 24 h. Some samples were ashed at 500 °C for 2 h; others were analysed for carbon and nitrogen contents using a Perkin-Elmer elemental analyser. Dry weights and ash weights were measured $\pm 1 \mu\text{g}$ on a Cahn Electrobalance. These methods were also applied to intact copepods of the same species. The percentages of food assimilated (% A) by the siphonophores were calculated from the means of dry weight, ash-free dry weight, carbon, and nitrogen of intact prey and of egested prey remains according to the following formula: $\% A = [(I-E)/I] \times 100$, where I = mean quantity ingested and E = mean quantity egested. Assimilation also was calculated according to the mean ratio of ash-free dry weight to dry weight in intact prey and in their egested remains according to the method of Conover (1966).

Results

The siphonophores *Forskalia edwardsi*, *F. tholoides*, *Rosacea cymbiformis*, *R. flaccida*, and *Diphyes dispar* were collected during February in the Sargasso Sea and in the

Gulf Stream, the species of *Forskalia* being particularly abundant in both locations. All of these species were collected in May, with *D. dispar* and the additional siphonophore *Stephanophyes superba* being encountered frequently. The two species in the genus *Forskalia* are nearly identical in appearance and behavior, as are the two species of *Rosacea*. No differences were seen in the results of this study for species within each genus. Therefore data will be presented by genera, and siphonophores referred to by their generic names.

Copepods compose 80 to 100% of the prey of these siphonophores in oligotrophic waters, and all consume some large copepods such as those used in this study (Purcell, 1981a, c, in preparation). Table 1 gives the lengths, dry and ash-free dry weights, carbon and nitrogen contents of intact, unpreserved copepods used in the digestion and assimilation experiments.

Each digestion rate measurement is accurate within 0.25 h for *Stephanophyes*, and within 0.5 h for the other 3 genera. Digestion times required for the different copepod species were comparable within each siphonophore genus (Table 2). The rates of digestion were not clearly related to differences in copepod size within the limited size range used in the experiments.

The rates of digestion by all of the siphonophore genera were significantly different from one another (for all pairwise comparisons $P \ll 0.001$, single-classification analysis of variance (ANOVA), Sokal and Rohlf, 1969) (Table 2). *Stephanophyes* digested prey most rapidly (mean 1.6 h), and *Rosacea* digested prey most slowly (mean 9.6 h). *Forskalia* and *Diphyes* displayed intermediate digestion rates, and although their rates were most similar to one another (means 4.1 and 5.8 h, respectively), the difference was significant ($P \ll 0.001$).

Copepod species in the genus *Candacia* are known prey of these 4 siphonophore genera (Purcell, 1981c, personal observation). The dark brown pigmentation of *C. ethiopica* made it obvious within the siphonophore

Table 1. Weights and organic contents of copepods used in digestion and assimilation experiments. Means + SD were calculated when >2 measurements were made. The number of measurements (No.) = (dry and ash-free; C and N)

Copepod species	No.	Cephalothorax length (mm)	Dry weight (μg)	Ash-free weight (μg)	Ratio of ash-free to dry weight	C (μg)	% C	N (μg)	% N	C/N
<i>Candacia ethiopica</i> ^{a,b}	(9;7)	1.7 \pm 0.2	195.3 \pm 82.0	172.2 \pm 84.0	0.84 \pm 0.07	68.7 \pm 19.6	39.7 \pm 2.7	21.6 \pm 6.2	12.5 \pm 0.9	3.2 \pm 0.2
<i>Undinula vulgaris</i> ^a	(5;9)	2.0 \pm 0.2	189.6 \pm 47.3	172.7 \pm 42.3	0.91 \pm 0.03	88.9 \pm 21.5	43.3 \pm 5.0	27.5 \pm 2.0	13.9 \pm 3.0	3.2 \pm 0.8
<i>U. vulgaris</i> ^b	(0;4)	2.1	169.2 \pm 2.8	—	—	62.8 \pm 2.1	37.2 \pm 1.6	18.6 \pm 1.7	11.0 \pm 1.1	3.4 \pm 0.2
<i>Euchaeta marina</i> ^a	(7;2)	2.5 \pm 0.7	683.7 \pm 180.9	590.0 \pm 152.2	0.86	120.1	38.5	37.4	11.8	3.3
<i>Labidocera</i> and <i>Pontella</i> ^b	(0;7)	2.7	223.9 \pm 93.0	—	—	83.4 \pm 42.6	36.2 \pm 5.5	23.2 \pm 12.0	10.2 \pm 1.3	3.5 \pm 0.3

^a February cruise

^b May cruise

Table 2. Time between ingestion of copepods and egestion of waste by four genera of siphonophores. The number of measurements for which means \pm SD were collected appear in parentheses. Temperature = 21° - 22° C

Copepod species	Digestion Time (h)			
	<i>Stephanophyes</i>	<i>Forskalia</i>	<i>Diphyes</i>	<i>Rosacea</i>
<i>Candacia</i>	1.9 \pm 0.5 (15)	4.6 \pm 0.8 (22)	5.8 \pm 1.4 (20)	9.7 \pm 3.4 (14)
<i>Undinula</i>	1.8 \pm 0.2 (12)	3.3 \pm 0.5 (16)	4.4 (2)	9.6 \pm 1.1 (5)
<i>Euchaeta</i>	—	3.3 \pm 1.0 (4)	—	7.0 (1)
<i>Undinula</i> , large	2.8 (2)	4.5 \pm 0.9 (6)	—	—
<i>Labidocera</i> and <i>Pontella</i>	1.25 \pm 0.46 (29)	3.5 (2)	—	—
Overall mean	1.6 \pm 0.5 (60)	4.1 \pm 1.0 (50)	5.8 \pm 1.4 (22)	9.6 \pm 2.9 (20)

Table 3. Weights and organic contents of *Candacia ethiopica* remains egested by siphonophores. Assimilation was calculated from these values and those in Table 1 for intact *C. ethiopica* copepods. The numbers of measurements in parentheses = (dry and ash-free weights; C and N)

Species	Dry weight	Ash-free weight	Ratio of ash-free to dry weight	C	N
<i>Stephanophyes</i> (0; 5)					
waste (μ g)	—	—	—	5.2 \pm 2.9	0.8 \pm 0.8
assimilation (%)	—	—	—	92.4	96.3
<i>Forskalia</i> (21; 18)					
waste (μ g)	48.4 \pm 20.4	24.2 \pm 10.8	0.47 \pm 0.10	9.1 \pm 2.4	1.6 \pm 0.9
assimilation (%)	74.2	86.0	83.4	86.8	93.0
<i>Diphyes</i> (0; 19)					
waste (μ g)	—	—	—	3.9 \pm 2.2	1.5 \pm 1.1
assimilation (%)	—	—	—	94.3	93.1
<i>Rosacea</i> (3; 6)					
waste (μ g)	44.7 \pm 25.3	18.4 \pm 7.3	0.47 \pm 0.15	6.4 \pm 1.8	1.3 \pm 1.3
assimilation (%)	80.4	89.3	83.4	90.7	94.0

Table 4. Percentage assimilation by siphonophores calculated from ash-free to dry weight ratios, and carbon and nitrogen contents of intact prey (Table 1) and of egested prey remains. The values are means \pm SD of assimilation calculated for 3 or more prey species. The number of waste pellets measured (No.) = (ash-free/ dry weight; C and N)

Species	No.	Ratio of ash-free to dry weight (%)	C (%)	N (%)
<i>Stephanophyes</i>	(0; 32)	—	92.4 \pm 3.8	90.7 \pm 6.8
<i>Forskalia</i>	(37; 31)	87.8 \pm 4.8	89.5 \pm 3.7	94.2 \pm 3.6
<i>Diphyes</i>	(0; 19)	—	94.3	93.1
<i>Rosacea</i>	(3; 13)	83.4	88.2 \pm 11.2	90.5 \pm 7.6

gastrozooids, and therefore an ideal prey type for these experiments. The efficiencies with which the 4 siphonophore genera assimilated *Candacia* copepods are given in Table 3. Assimilation efficiencies were calculated from the mean values of dry weight, ash-free dry weight, carbon and nitrogen for intact *Candacia* (Table 2), and the mean values of *Candacia* remains egested by the siphonophores (Table 3). Carbon was assimilated with 87 to 94% efficiency and nitrogen with 93 to 96% efficiency. Calculations of assimilation from dry weights gave low values in comparison, while ash-free dry weights gave good approxi-

mations of carbon assimilation. The ash-free dry weight to dry weight ratio method underestimated assimilation efficiencies of carbon by 3 to 7%.

Egested waste was collected following the digestion rate measurements; therefore assimilation data were accumulated for the different copepods and siphonophores in similar proportions to the digestion data in Table 2. No differences were apparent in the efficiency with which the various copepods species were assimilated. Therefore assimilation efficiencies were calculated using individual copepod species and then averaged within each siphonophore genus (Table 4). Assimilation efficiencies did not differ among siphonophore genera (carbon, $P < 0.75$; nitrogen $0.5 < P < 0.75$, ANOVA). Overall, assimilation of carbon was 87 to 94%, and assimilation of nitrogen always was greater (except for *Stephanophyes*) at 90 to 96%. Although prey digestion rates differed dramatically among the 4 siphonophore genera, assimilation efficiencies were uniformly high.

Discussion

The body of data on the feeding, digestion, and metabolism of gelatinous zooplankton has been accumulating in recent years. From analysis of the gut contents of the

various predators (e.g. Purcell, 1981a) in combination with digestion rates, it should be possible to estimate the quantities of natural prey consumed by gelatinous predators. In the present study, digestion rates were determined using large copepods, and therefore probably represent maximum times. Digestion times measured by Biggs (1976) for the same siphonophore genera fed *Artemia* sp. nauplii are roughly similar to the present results, except that Biggs' times for *Stephanophyes* are much longer. Small, neritic species of siphonophores digested small copepods in 2 to 4 h at 10° to 12°C (Purcell, 1982; Purcell and Kremer, 1983). Copepods are the major prey of most species of siphonophores, but other prey organisms are also important (e.g. Purcell, 1981a). Digestion rates of other natural prey by *Forskalia* (crab zoea larvae, shrimp larvae, fish larvae, and chaetognaths) were 4 to 7 h (Purcell, unpublished data), similar to those measured for copepods (4 to 7 h). Digestion of fish larvae by the siphonophore *Rhizophysa eysenhardti* required 3 to 7 h at 23°C (Purcell, 1981b). These digestion rates by siphonophores are comparable to those measured for some chaetognaths (3 to 4 h, Cosper and Reeve, 1975; 1 to 2 h at 21°C, Reeve, 1980), and for some oceanic ctenophores at 21°C (L. P. Madin, personal communication). By comparison, digestion by some neritic ctenophores is very rapid; *Pleurobrachia bachei* digested large copepods in an average of 46 min at 20°C (Hirota, 1974), and *Mnemiopsis mccradyi* digested copepods in 1 h at 26°C (Reeve, 1980).

Digestion rates of the 4 siphonophore genera tested in this study were correlated with their respiration rates as measured by Biggs (1977b) (Table 5). Siphonophores with higher respiration rates digested prey more rapidly. In contrast, differences in the respiration rates are not clearly related to differences in the activity of the siphonophores. *Stephanophyes* is the most active swimmer of the 4 genera, *Forskalia* and *Rosacea* display little activity, and *Diphyes* is sluggish, but capable of rapid swimming bursts for escape and spreading the tentacles for feeding. Respiration rates may best reflect metabolic processes in gelatinous organisms which spend most of the time drifting passively in the water. The 4 genera of siphonophores had significantly different digestion rates, yet they showed no appreciable differences in assimilation efficiencies. This may reflect differences in enzyme functions as well as differences in metabolic rates.

Siphonophores in this study assimilated copepod carbon and nitrogen with efficiencies of about 90% or greater. A value of approximately 90% might be expected since copepod exoskeletons, which are not digested, contain about 10% of the total carbon (Mullin and Brooks, 1967). Assimilation of larval fish by the siphonophore *Rhizophysa eysenhardti* was reported incorrectly in Purcell (1981b). Assimilation recalculated from the data therein according to the ash-free dry weight to dry weight ratio method equals 97.8%. *Forskalia* assimilated newborn guppies with 94.3 and 95.4% efficiency for carbon and nitrogen, respectively (Purcell, unpublished data). These results are comparable to those on carnivorous benthic marine inverte-

Table 5. The relationships among the rates of digestion and respiration for siphonophores. Digestion times are from Table 2

Species	Digestion		Respiration	
	Time (h)	Rank	Rate ^a	Rank
<i>Stephanophyes</i>	1.6	1	14, 22	1-2
<i>Forskalia</i>	4.1	2	17, 20	1-2
<i>Diphyes</i>	5.8	3	12, 17	3
<i>Rosacea</i>	9.6	4	8, 8	4

^a From Biggs (1977b). Mean rates for siphonophores of 2 size classes; 0.1-1.0 and 1.1-10.0 mg protein, expressed in $\mu\text{l O}_2$ (mg protein-h)⁻¹

brates, which typically show assimilation efficiencies >90% (Conover, 1978).

The remains of copepod prey were collected quantitatively in this study, therefore the data provide a test of the ratio method of estimating assimilation efficiencies (Conover, 1966), which was designed for use when waste collection cannot be quantitative. The critical assumption of the ratio method, that the inorganic fraction is unaffected during digestion, was shown to be false for some crustaceans (Forster and Gabbott, 1971; Lasenby and Langford, 1973); consequently, the ratio method would underestimate true assimilation (additionally, Cosper and Reeve, 1975). The ratio method underestimated carbon assimilation in the present study by 3 to 7%, which suggests that some inorganic material was lost during digestion or assimilated by the siphonophores.

These assimilation efficiencies for siphonophores are higher than reported for most of the few carnivorous zooplankters which have been tested previously. Reeve *et al.* (1978) reported assimilation of copepods (according to dry weight) by the ctenophores *Mnemiopsis mccradyi* and *Pleurobrachia bachei* to be 74% and 19 to 74%, respectively. The gymnosome pteropod *Clione limacina* assimilated its thecosome pteropod prey with 94.7 and 99.0% efficiency for carbon and nitrogen, respectively (Conover and Lalli, 1974). Cosper and Reeve (1975) measured assimilation for the chaetognath *Sagitta hispida* at 80 to 82% (dry and ash-free dry weights of copepod prey). Euphausiids fed *Artemia* sp. nauplii assimilated 84% of the carbon contents (Lasker, 1966), and mysids assimilated 85% of the organic weight of *Daphnia* (Lasenby and Langford, 1973).

The lower assimilation efficiencies reported for some of these planktonic carnivores are probably due to two factors. First, some were measured according to dry weight, which was shown in the present study to underestimate carbon and nitrogen assimilation. Second, the predators may have introduced organic matter into the waste. Chaetognaths and crustaceans produce a membrane around the waste pellet, and lobate ctenophores, in particular, use much mucus in the feeding process. It seems likely that the actual assimilation by these predators could be as great as that measured for siphonophores. On

the other hand, these other predators are species from neritic environments where food availability is much greater; therefore efficient assimilation of food may not be as critical for them as for species from oceanic environments. The results of this study indicate very efficient digestion of prey by siphonophores from environments having low prey abundances.

Acknowledgements. I thank Dr. L. P. Madin for the opportunity to participate in W.H.O.I. cruises. I am especially grateful to L. P. Madin, C. M. Cetta, D. C. Caron, G. Dietzmann, and several others who assisted in the collection of specimens. I also thank Dr. J. M. Teal, N. Corwin, and J. P. Clarnier for making the CHN analyser available for my use, and Dr. G. D. Grice for identifying the copepods. Drs. L. P. Madin, A. L. Alldredge, and P. Kremer critically read the manuscript. This research was supported by a postdoctoral fellowship from the Woods Hole Oceanographic Institution to the author and by NSF Grant OCE-80-24441 to L. P. Madin.

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Date of final manuscript acceptance: January 22, 1983.

Communicated by S. K. Pierce, College Park