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Feeding and metabolism of the siphonophore *Sphaeronectes gracilis*[1]

Jennifer E. Purcell[2] and Patricia Kremer[3]

Department of Biological Sciences and the Marine Science Institute, University of California, Santa Barbara, CA 93106, and [3]Allan Hancock Foundation, University of Southern California, Los Angeles, CA 90007, USA

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Abstract. The *in situ* predation rate of the siphonophore *Sphaeronectes gracilis* was estimated from gut content analysis of hand-collected siphonophores and from laboratory data on digestion rates of prey organisms. At daytime prey densities of 0.25 copepods l^{-1}, *S. gracilis* was estimated to consume 8.1 – 15.4 prey day^{-1} siphonophore^{-1}. From data on abundances of siphonophores and copepods, *S. gracilis* was estimated to consume 2 – 4% of the copepods daily. In laboratory experiments, ingestion rates averaged 13.8 prey day^{-1} siphonophore^{-1} at prey densities of 5 copepods l^{-1} and 36.9 at 20 copeods l^{-1}. This was equivalent to a specific ingestion rate (for both carbon and nitrogen) of ~17% day^{-1} and 45% day^{-1}, respectively, while specific ingestion *in situ* was only 2% day^{-1}. Ammonium excretion averaged 0.095 μg-at siphonophore^{-1} day^{-1} at 5 prey l^{-1}, and 0.162 at 20 prey l^{-1}. The specific respiration (carbon) and specific excretion (nitrogen as ammonium) were calculated to be 3% day^{-1} at the lower experimental food level, and 5% day^{-1} at the higher food level.

Introduction

Interest in the ecological importance of gelatinous marine zooplankton has been increasing in recent years. Several studies have used one of four of the possible approaches in estimating the prey consumption by chaetognaths, ctenophores, siphonophores, and medusae. The most direct approach is to determine gut contents of freshly-collected predators, digestion times, and population densities of both predator and prey organisms. This approach has been taken for the chaetognath *Sagitta enflata* (Szyper, 1978), for ctenophores of the genus *Pleurobrachia* (Anderson, 1974; Sullivan and Reeve, 1982), and for some siphonophore species (Purcell, 1981a,1981b,1982).

In other studies, natural predation rates have been extrapolated from laboratory feeding rates and combined with *in situ* predator and prey abundances to estimate the ecological impact of ctenophores of the genus *Mnemiopsis* (Miller, 1970; Reeve *et al.*, 1978; Kremer, 1979; Reeve, 1980b). Predation rates for ctenophores and chaetognaths have also been calculated by relating carnivore production and growth efficiencies to estimates of herbivorous zooplankton production (Hirota, 1974; Reeve and Baker, 1975). These calculations generally maximize the predation rates because they are based on growth rates of well-fed laboratory populations.

Metabolic measurement of energetic demands of the predators have been

[1]Contribution from the Catalina Marine Science Center No. 66.

[2]Present address: Dept. of Biology, University of Victoria, Victoria, B.C., Canada V8W 2Y2.

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used to calculate minimum ingestion rates. This approach has been taken for chaetognaths (Sameoto, 1972; Kotori, 1976), and for the siphonophore *Agalma okeni* (Biggs, 1976a,1976b). Additional metabolic studies of gelatinous zooplankters include Kremer (1976,1977) on the ctenophore *Mnemiopsis leidyi*; Ikeda (1974) and Biggs (1977) on a variety of oceanic ctenophores, siphonophores, and hydromedusae; and Kruger (1968) on the respiration of scyphomedusae.

Only a few studies have attempted to approximate energy or carbon budgets for the soft-bodied predators. Such studies include work by Sameoto (1972) on chaetognaths, and Miller (1970), Hirota (1972), Kremer (1976), and Reeve *et al.* (1978) on ctenophores. Here we present a combination of field and laboratory results for the neritic siphonophore *Sphaeronectes gracilis* (Claus, 1873), and estimate *in situ* feeding rates, its predation impact upon copepod populations, and the importance of predation by *S. gracilis* relative to other gelatinous predators. Estimates of carbon and nitrogen budgets, and growth efficiencies are calculated for the first time for a species of siphonophore.

Materials and Methods

Field collections

Specimens of the siphonophore *S. gracilis* (Suborder Calycophorae) were collected within a mile offshore of the Catalina Marine Science Center on Santa Catalina Island, CA between April 17, and May 14, 1980. Siphonophores were collected in hand-held jars during SCUBA dives at 10 – 15 m depth between 0830 and 1030 h. Hand-collected *S. gracilis* to be examined for gastrozooid contents were preserved at depth by divers by injecting formalin into the collecting jar. In the laboratory, the gastrozooids of the siphonophores were mounted on slides with coverslips. Newly budded gastrozooids lack distinct tentacles and probably are not involved yet with feeding, therefore only gastrozooids having well developed tentacles were counted from these preparations. Prey remains could be identified in the semi-transparent gastrozooids at 100 x – 200 x magnification and were measured according to cephalothorax (metasome) length (70 – 80% of total length for copepods).

Plankton samples were taken with 0.75 m diam, 250 μm mesh net immediately following siphonophore collection and at several other times during the day and night. The net was allowed to fall mouth down to a maximum depth of 35 m, depending upon boat drift, and was then hauled vertically back to the surface (total volume filtered = 31 m^3). Siphonophore densities, as well as densities of potentially competing zooplankers (i.e., chaetognaths, ctenophores, and medusae) were determined from whole samples. Copepod densities were determined from subsamples made using a Folsom plankton splitter. Siphonophores were removed from these preserved tows and examined for prey which had been consumed. Hand-collected specimens were compared to siphonophores collected by net between 0830 and 1030 h to check for damage and for evidence of feeding while in the net. Siphonophores collected by net at various times were compared to determine diel variations in feeding. The size distributions and proportions of the common orders of copepods available in the environment were determined

from vertical tows with a 0.5 m diam, 70 μm mesh net. Electivity indices were calculated from the proportions of prey types consumed and the proportions available in the environment according to Chesson (1978).

Laboratory experiments

Feeding. Hand-collected siphonophores were maintained for a total of 48 h at temperatures of 13 – 14°C individually in 4-l clear plastic (polycarbonate) containers. Twelve hours after the siphonophores were collected, calanoid copepods (0.7 – 0.8 mm cephalothorax length) were individually counted, then added to each experimental container at concentrations of 5 and 20 copepods l^{-1}. Prey were collected from the sites of siphonophore collection, and were prepared for laboratory experiments by first siphoning water containing active zooplankton through 420 μm mesh netting to remove large zooplankton, and then siphoning off water through 149 μm mesh netting to concentrate calanoid copepods of nearly uniform size. Therefore copepods used in the feeding experiments were the same as those available to siphonophores *in situ* in the size range of ~149 – 420 μm. These containers were covered by black plastic to minimize phototactic responses of the siphonophores (which swam downward in light) and of the copepods.

In order to maintain fairly constant prey densities, the siphonophores were transferred every 12 h to containers with fresh seawater and prey at the initial concentrations. The unconsumed prey were preserved and later counted. Counts on controls (containers with prey but without siphonophores) averaged 6.1 ± 1.3 prey l^{-1} (N = 8) at the lower food level and 21.5 ± 3.3 prey l^{-1} (N = 9) at the higher level. Ingestion rates were computed for three successive 12 h periods from the difference in initial (average of controls) and final prey concentrations. Ten siphonophores were kept at each food concentration, and the experiment was repeated several days later.

Metabolism. After siphonophores were kept for 36 h at the two experimental prey concentrations, metabolic measurements were made on these experimental animals. Preliminary observations of ammonium release over time had confirmed that the excretion rate was constant over several hours. Therefore it was possible to make an accurate assessment of the metabolic rate using incubations with a single end point determination. Glass stoppered bottles (60 – 65 ml) were filled with filtered water (GFC Honeycomb 0.5 μm retention) siphoned from a well-mixed carboy. Experimental bottles each held two siphonophores while control bottles contained filtered water only. After 5 h, duplicate 5 ml aliquots were taken for ammonium (modified from Solorzano, 1969). Additional simultaneous measurements of ammonium and oxygen were made using higher densities of siphonophores in larger bottles (280 ml) to establish the atomic ratio between oxygen and ammonium nitrogen. Oxygen concentrations were measured by Winkler titration (Strickland and Parsons, 1972) in subsamples transferred into 60 ml BOD bottles with a plastic syringe fitted with plastic tubing. Samples were also taken from these incubations for preliminary estimates of release of dissolved organic nitrogen using the U-V oxidation method (Armstrong *et al.*, 1966).

Digestion rates were measured on siphonophores kept for 7 h in filtered sea-

water in order to clear their gastrozooids of prey. The siphonophores were allowed to feed at high copepod densities for 1 h, and then were removed to containers of filtered water. Some siphonophores were preserved initially and others at 1 h intervals. Gastrozooids were examined microscopically as previously described, to determine when gastrozooids were cleared of prey remains.

Results and discussion

Field collections

The specimens of *S. gracilis* collected in this study had one rounded swimming bell 6 – 8 mm in diameter and a chain of gastrozooids 17 – 60 units long (mean 38.5 ± s.d. 9.6 gastrozooids siphonophore^{-1}) which would extend < 10 cm. This siphonophore was abundant throughout this study in the waters off Santa Catalina Island, and has been observed in surface neritic waters off Santa Barbara, CA in spring and fall months (Purcell, personal observations). This same species has been reported from tropical and sub-tropical regions (Totton, 1965), as well as from Monterey Bay, CA during July (Bigelow and Leslie, 1930), and from the Mediterranean (Carré, 1969).

Of 39 siphonophores that were hand-collected during the day, 88.5% had captured from 1 to 6 prey organisms and 3.9% of the gastrozooids contained prey (Table I). Prey included naupliar through adult stages of copepods, and measured 0.1 mm to 0.9 mm in a cephalothorax length. *S. gracilis* consumed small copepod prey, a typical diet of siphonophore species which have small gastrozooids and which swim rapidly to extend their tentacles (Purcell, 1981c).

Siphonophores collected by net showed artifacts attributable to that method of collection. The gastrozooids from the distal part of the chain had broken off, therefore those siphonophores had an average of only half as many gastrozooids as the hand-collected specimens, and gut contents were consequently reduced (Table I). Feeding by the siphonophores during collection in the net was evidenced by partially ingested prey (copepods and larvaceans). These prey totalled 7% of the consumed prey and were not included in the percentages in Table I.

It was possible to collect siphonophores at night only by net. Daytime and nighttime feeding estimates from net-collected siphonophores were very similar (Table I), even though copepod densities at night (517.0 ± 283.6 m^{-3}, 6 tows) averaged twice those in the day 257.9 ± 152.5 m^{-3}, 12 tows). At prey densities representative of natural conditions, feeding rates of siphonophores and ctenophores increase linearly with increasing prey densities (e.g., Reeve *et al.*, 1978; Purcell, 1982). Therefore, we would have expected greater feeding by

Table I. Summary of *in situ* predation by *Sphaeronectes gracilis* determined from analysis of gastrozooid contents.

Collecting method	Time	No. of siphonophores	No. of gastrozooids	% of siphonophores with prey	% of gastrozooids with prey
jar	day	39	1500	88.5	3.9
net	day	168	2801	26.4	2.2
net	night	98	1909	28.3	2.5

S. gracilis at night when prey densities were greater. The failure to observe that trend very likely is attributable to the distal gastrozooids breaking off during net collection of the siphonophores.

An estimate of daily feeding was calculated based upon the average of 1.5 prey found in each hand-collected siphonophore during the day. Digestion experiments on *S. gracilis* indicated that prey 0.4 – 0.9 mm in cephalothorax length remained in the gastrozooids 4 – 6 h before egestion, while prey <0.4 mm required 2 – 4 h for digestion. Daily ingestion by *S. gracilis* was estimated using the following equation

$$\text{Ingestion} = \sum_{0.1}^{9.0} P\,(\text{NPS})\,\frac{24\text{ h}}{D}$$

where P = percentage of prey consumed (in 0.1 mm size intervals), NPS = average number of prey in each siphonophore, and D = digestion time in hours. Daily ingestion at daytime prey densities of 0.25 copepods l^{-1} was estimated to range between 8.1 – 15.4 copepods d^{-1}, depending on the range of digestion times. An estimated removal rate of 7 – 14 prey $d^{-1}\,m^{-3}$ was calculated based on a day-night average of 0.9 *S. gracilis* m^{-3}. At prey densities of 387.4 prey m^{-3} (day-night average), 1.9 – 3.6% of the prey populations would be consumed by *S. gracilis* daily. This is probably a minimum estimate since daytime feeding rates of *S. gracilis* were applied for nighttime as well.

The siphonophores *S. gracilis* and *Muggiaea atlantica* were second to chaetognaths in abundance of the soft-bodied carnivorous zooplankton, and far outnumbered ctenophores and hydromedusae. The average abundances of these zooplankters in 12 daytime and 6 nighttime tows during May 1980 were as follows (Mean No. 10 m^{-3} ± s.d.): *S. gracilis* (asexual polygastric colonies) 8.3 ± 4.6, (sexual monogastric eudoxids) 6.3 ± 5.4; *M. atlantica* (polygastric) 6.2 ±3.7, (monogastric) 17.3 ± 11.5; medusae 4.6 ± 1.7; ctenophores (*Pleurobrachia bachei*) 2.5 ± 1.5; chaetognaths (*Sagitta* spp) 87.4 ± 17.8. The importance of siphonophores and other tentaculate predators may be underestimated if only numerical abundance is considered, since the volume of water each would influence is far greater than that influenced by an individual chaetognath. Ctenophores always captured more prey than chaetognaths over a wide range of prey densities (Reeve, 1980a). A daily ratio of 2 prey day^{-1} is representative for several species of chaetognaths (Mironov, 1960; Nagasawa and Marumo, 1972; Kuhlmann, 1977; Feigenbaum, 1979). We combined this estimated feeding rate with chaetognath abundance and calculated that the chaetognaths would remove ~18 copepods $m^{-3}\,d^{-1}$, a value approximately twice the predation rate calculated for *S. gracilis*, much less than the 10-fold difference in abundance. Of 10 *M. atlantica* examined, none had any prey remains, so it was impossible to estimate its importance.

Electivity indices were calculated for 3 size categories of prey, and for copepods of 3 subclasses and nauplii (Table II). Digestion times by siphonophores increase with increasing prey size (Purcell, 1981b, 1982), which would increase the proportion of large copepods in the gastrozooids. The propor-

tions of prey sizes found in the gastrozooids were adjusted to avoid this bias by assuming that digestion times for small, medium and large prey were 2, 4, and 6 h, respectively. In spite of these extreme corrections, selection was negative for small prey and was positive for large prey (Table II). This trend was demonstrated in the siphonophores *Rosacea cymbiformis* and *M. atlantica*, and may be related to greater encounter rates with large copepods having greater swimming speeds and body diameters than small copepods (Purcell 1981b, 1982). Calanoid, cyclopoid, and harpacticoid copepods were consumed in proportion to their respective availabilities in the environment, while selection for nauplii was negative (Table II). No corrections for digestion were made among these prey types since no data on the respective rates of digestion were available.

Laboratory experiments

Feeding. Daily prey ingestion measured in the laboratory at 5 and 20 copepods l^{-1} averaged 13.8 and 36.9 prey d^{-1} siphonophore^{-1}, respectively (Table III). Results for the two replicate experiments, run more than one week apart, were very similar, although ingestion in the second set (B) was somewhat lower at both prey levels. The results show that a 4-fold increase in prey density resulted in a 3-fold increase in daily ingestion.

At laboratory prey densities of 5 prey l^{-1}, *S. gracilis* consumed only 1–2 times more prey than siphonophores *in situ* where prey densities were only 5% of those in the laboratory. This discrepancy could be due to inhibition of feeding in

Table II. The percentage of prey available and prey consumed by *Sphaeronectes gracilis*, and calculated electivity indices for copepod prey according to size and to type (nauplii and 3 copepod subclasses).

	Prey available (%)	Prey consumed (%)		Electivity $\alpha = 0.333$
		In the gastrozooids	Adjusted for digestion	
Prey size (mm)				
0.10–0.39	66.4	63.8	74.2	0.291 –
0.40–0.79	32.5	30.4	23.6	0.189 –
0.80–1.00	1.1	5.8	2.2	0.520 +
Prey type				$\alpha = 0.250$
Nauplii	26.7	17.0		0.159 –
Calanoids	62.9	71.6		0.285 =
Harpacticoids	7.0	7.5		0.268 =
Cyclopoids	3.4	3.9		0.287 =

Available prey were collected with a 0.5 m diameter, 70 μm mesh net. The percentages of prey consumed were based on 79 measurable prey from daytime hand- and net-collected siphonophores. Prey consumed are given according to the % found in the gastrozooids, and are also adjusted for digestion, assuming that the digestion times for small, medium, and large prey were 2, 4, and 6 h, respectively. No adjustments were made among prey types. Electivity indices were based on the adjusted % of prey consumed. Electivity values (which lie betwen 0 and 1) greater than α indicate positive selection (+), less than α indicate negative selection (–), and similar to α indicate no selection (=).

laboratory containers, as dicussed by Reeve (1977). The time spent feeding in the 4-l containers may have been reduced since *S. gracilis* retracted its gastrozooid chain and tentacles after coming into contact with the container walls. Also, the siphonophores sank to the container floor and ceased feeding after capturing several of the large, negatively-buoyant prey used in the laboratory experiments. Patches of high prey density may be important to siphonophore feeding *in situ*. Specimens of *S. gracilis* were seen by divers mainly below 10 m depth, at or below the thermocline, while net tows averaged copepod and siphonophore densities over 30 m depth. Thus, prey densities measured by net tows may not have reflected prey densities which actually were encountered by siphonophores.

Metabolism. There was a clear effect of food availability on ammonium excretion by *S. gracilis* in both replicate experiments (Table III). When the prey concentration was increased 4 times, the average excretion rate increased 1.7 times. These results are comparable to findings for other carnivorous zooplankton. An increase in ammonium excretion of 1.7 times was measured for the ctenophore *Mnemiopsis mccradyi* as food availability increased from 5 to 50 copepods per liter at 21°C (Kremer, 1982). Slightly less than a 3-fold difference in metabolic rate was measured for another ctenophore, *Pleurobrachia bachei*, held at prey concentrations of 10 and 100 copepods per liter (data used in Reeve *et al.*, 1978), and a maximum range of a factor of three was observed between the metabolic rate of fed (or freshly collected) and starved animals (Conover and Lalli, 1974; Mayzaud, 1976; Ikeda, 1976).

Direct measurements of oxygen changes for the experimental animals were too

Table III. Ingestion, and excretion, for *Sphaeronectes gracilis* in two replicate experiments (A and B).

		Prey concentration (No. l^{-1})	
		5	20
Ingestion	A	16.5 ± 10.3	42.4 ± 32.9
(No. of prey day^{-1} siph.$^{-1}$)	B	11.1 ± 9.8	31.5 ± 29.4
	average	13.8 ± 10.1	36.9 ± 31.2
Excretion	A	0.098 ± 0.023	0.180 ± 0.014
(μg-at NH_4-N day^{-1} siph.$^{-1}$)	B	0.091 ± 0.021	0.148 ± 0.051
	average	0.095 ± 0.021	0.162 ± 0.041

Ten siphonophores were used at each prey concentration in each replicate. Values are expressed as mean ± s.d.

variable and small to be reliable in calculating respiration rates. Therefore, estimates for respiration for the experimental animals were derived using an oxygen to nitrogen atomic ratio of 11.6:1. This value was based on a linear regression of oxygen respired with ammonium excreted ($r = 0.81$) for an independent set of laboratory fed siphonophores. This ratio was similar to other O:N measurements for other gelatinous carnivores, including two species of ctenophores (Kremer, 1977, 1982) and another siphonophore, *Rhizophysa eysenhardti* (Kremer, unpublished results).

At our lower experimental food concentration, the ammonium excretion rates were comparable to rates observed for freshly-collected animals and equivalent to 0.015 μg-at NH_4 d^{-1} mg d.w.$^{-1}$. The corresponding respiration rate was calculated to be about 2 μl O_2 d^{-1} mg d.w.$^{-1}$. There have been very few studies of siphonophore metabolism with which we can compare our results. Biggs (1977) reported respiration and ammonium excretion of several species of oceanic siphonophores only in terms of animal protein. We have used his protein to carbon conversion (Biggs, 1976b) and our estimates of elemental carbon, and calculated that our excretion rates are about a factor of two lower than his lowest rates at 26°C. Even if we assume a generous Q_{10} to compensate for the difference in temperature, our results are still at the low end of his range. Our estimates for respiration were also considerably lower than those measured by Nival *et al.* (1972) for the small calycophoran siphonophores *Abylopsis tetragona* and *Chelophyes appendiculata* at 15°C. These different results are not obviously related to size or activity of the siphonophores, and may be due to differences in methods and handling.

Carbon and nitrogen budgets

Since the results of our two experimental runs were similar, the data were pooled for overall calculations of the amount of carbon and nitrogen which were ingested and metabolized at the two food concentrations (Table IV). The average dry weight of the copepod prey was 5.5 ± 0.5 μg (2.13 ± 0.21 μg C and 0.71 ± 0.09 μg N). The average dry weight of the siphonophores was 6.27 ± 1.2 mg (~4.3% of wet weight). As with other gelatinous forms, such as ctenophores, the carbon and nitrogen were only small percentages of the dry weight (2.83%, 180.3 ± 44.3 μg C; and 0.71%, 51.3 ± 12.0 μg N, respectively). In order to calculate carbon from respired oxygen, we assumed an R.Q. (Δmol CO_2/Δmol O_2) of 0.8, a value typical of carnivores (Mayzaud, 1976).

The specific ingestion or daily ration (% of body carbon ingested per day) and specific metabolism were similar for both carbon and nitrogen (Table IV). This is a direct result of similar C:N ratios (by weight) which were measured for the copepods (3.87), siphonophores (3.98), and metabolism (4.0). At the lower food concentration (5 l^{-1}), the siphonophores ingested on average ~17% of their body carbon and nitrogen per day, while at the higher food level (20 l^{-1}), this increased to ~45%, a tripling of ingestion in response to a 4-fold increase in the food concentration. At the lower food level, ~3% per day of the body carbon and nitrogen were respired or excreted as ammonium, increasing to 5% at the higher food level. Siphonophores ingested ~5.5 times more carbon and nitrogen

than necessary to meet metabolic demands at the low food level, and ~9 times more at the high food level. By contrast, Reeve *et al.* (1978) found for the ctenophore *Pleurobrachia bachei* for a prey density of 10 copepods l^{-1}, nearly half the ingested nitrogen was excreted as ammonium, and only at the high prey level of 100 copepods l^{-1} did the ingestion ratio exceed six.

Preliminary data showed that ammonium constituted only about half the total nitrogen released by the siphonophores (NH_4/N total = 0.60 + 0.31 (s.d.) n = 11). Although based on only a few samples with widely variable results, these measurements agreed well with other values for release of organic nitrogen (DON) by ctenophores (Kremer, 1977,1982). If this organic excretion is considered in this calculation, then the metabolic demand would approximately double, and surplus ingestion would decrease accordingly.

The growth efficiencies [(ingestion x assimilation efficiency) – metabolism] were calculated to be ~72% at 5 prey l^{-1} and 79% at 20 prey l^{-1} for both carbon and nitrogen from data in Table IV, and by assuming 90% assimilation efficiency as determined for other siphonophore species (Purcell, in preparation). These results do not take into consideration the release of dissolved organic compounds. If this additional metabolic drain is approximately equal to the excreted ammonium and respired carbon, then the growth efficiency would be expected to be ~54% at 5 l^{-1} and 67% at 20 l^{-1}. These estimates are comparable with 48–76% growth efficiency measured for the carnivorous pteropod *Clione limacina* at 15°C (Conover and Lalli, 1974), but are high compared to 35% measured for the chaetognath *Sagitta hispida* (Reeve, 1970) and 10.6% for the ctenophore *Pleurobrachia bachei* (Reeve *et al.*, 1978).

The field collected siphonophores were estimated to consume 8–15 prey d^{-1},

Table IV. Ingestion and metabolism for *Sphaeronectes gracilis* at two experimental food concentrations (T = 13°C).

	Prey concentration (no. l^{-1})	
	5	20
Carbon		
ingestion (μg d^{-1} siphonophore^{-1})	29.5	78.6
respiration (μg d^{-1} siphonophore^{-1})	5.3	9.0
specific ingestion (% d^{-1})	16.4	43.6
specific respiration (% d^{-1})	3	5
ingestion/respiration	5.6	8.7
Nitrogen		
ingestion (μg d^{-1} siphonophore^{-1})	7.8	20.95
NH_4 excetion (μg N d^{-1} siphonophore^{-1})	1.3 ± 0.3	2.3 ± 0.6
specific ingestion (% d^{-1})	17.5	47.1
specific excretion (NH_4, % d^{-1})	3	5
ingestion/excretion (NH_4)	5.8	9.4

Means are for 2 replicate experiments, 20 siphonophores in each. Standard deviations of the means are presented for measured rates of excretion, which were measured directly.

apportioned among size categories as in Table II. We converted the lengths of prey to dry weights using the relationship derived from *Acartia clausi* (Durbin and Durbin, 1978), and converted dry weights to carbon and nitrogen using 40% C and 10% N measured for our experimental prey. The calculated range for ingestion by the siphonophores *in situ* was 2.6–4.1 μg C siphonophore^{-1} day^{-1} and 0.8–1.1 μg N siphonophore^{-1} day $^{-1}$. These estimates are 7–11 times lower than the ingestion rates at the lower experimental food concentration (Table IV), a specific ingestion of only 2% d^{-1}. The difference between the experimental and *in situ* ingestion rates was much greater when carbon and nitrogen were taken into account due to the large size of experimental prey, than when only the number of prey was considered.

Freshly collected siphonohores excreted ammonium at a rate comparable to that in the lower experimental food level, therefore calculated ingestion would not quite meet metabolic demands of the siphonophores. We suggested earlier than the nighttime ingestion rate *in situ* probably was greater than that in the daytime, but this factor was not included in the calculation since conclusive evidence was lacking. With increased (twice daytime rates) feeding at night, daily ingestion (3.9–6.2 μg C and 1.2–1.6 μg N) could meet metabolic demands, leaving a little excess for growth.

With data collected in the present study, it is possible to compare three different approaches used to estimate prey consumption. (1) From gut content analysis, we estimated that 8.1–15.5 prey day^{-1} siphonophore^{-1} or 2.5–4.1 μg C day^{-1} siphonophore^{-1}, were consumed. We believe that the feeding estimates calculated in this way are the most reliable. (2) Metabolic measurements at the lower prey concentration in laboratory experiments indicate that 5.3 μg C day^{-1} siphonophore^{-1} would be needed to balance metabolism of the siphonophore. The estimate of minimum carbon ingestion is similar to estimates based on gut contents in this case and for *M. atlantica* (Purcell, 1982), but ingestion far exceeded metabolism for two other siphonophore species (Purcell, 1981a,1981b). From metabolic measurements, it is impossible to make adequate estimates of the number of prey captured *in situ*, unless the size distribution of captured prey is known. (3) If we assume a linear relationship between feeding rate and prey density, we can calculate the expected feeding rate at average field prey densities (0.25 l^{-1}) from a linear regression based on feeding rates in the laboratory at prey densities of 5 and 20 l^{-1}, and by assuming that no feeding occurs at 0 prey l^{-1}. From this method, we estimate that approximately 0.5 prey day^{-1} siphonophore^{-1}, would be consumed at 0.25 prey l^{-1}. This field feeding estimate projected from laboratory results is many times lower than actual prey capture *in situ*. Similarly, extrapolation of *in situ* feeding from laboratory results predicted inadequate feeding for survival of some ctenophores and chaetognaths (Miller, 1970; Reeve, 1980a), and gut content analysis yielded higher feeding estimates than did clearance rate experiments (Sullivan and Reeve, 1982). All of the results suggest caution in extrapolating laboratory feeding rates to field conditions.

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