

Feeding Rate of the Chaetognath *Sagitta enflata* in Nature^{a, b}

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The feeding rate of the chaetognath *Sagitta enflata* in its natural environment, Kaneohe Bay, Hawaii, was estimated from the frequency of animals in preserved samples having food in their guts, and from the average digestion times for live animals in the laboratory. The average feeding rate was estimated at 7.4 prey items per *Sagitta* per day; the chaetognath population sampled by 0.33 mm mesh removed about 4800 prey/m³ from the waters of the Bay daily.

The prey consisted mainly of: small copepods, too numerous and productive to be much affected by the predation; *Oikopleura*, whose populations could be seriously affected; and *Sagitta* itself, with a rate of cannibalism about 17% of the population per day.

Like some other chaetognaths, *Sagitta enflata* here is caught with food in the gut more frequently at night (36% of the population) than during the day (23%). The usual batch of food in the gut consists of one prey item (96% of the time), which is cleared from the gut in about one hour. The clearing time does not depend on the size of the predator, because larger animals digest their larger prey at a greater rate per unit of mass than the small animals do.

The daily ration of *Sagitta* amounts to 70% of its body content of nitrogen, and 111% of the body content of phosphorus. The relationships of the N/P ratios of planktonic organisms, their food, and their excretion products may be a consistent feature of marine ecosystems, and may help to explain some aspects of nutrient cycling.

Introduction

Laboratory experiments have shown that chaetognaths are capable of rapid ingestion rates, exceeding 60% of their own body weight per day, when food is plentiful (Reeve, 1964.) Some species under some conditions, however, do not feed at all in the laboratory (Fraser, 1969).

Because chaetognaths are often a major component of the carnivorous zooplankton in marine waters, it would be useful to have estimates of their feeding rates in nature. Few

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such estimates are available. The purpose of the work presented here is to derive estimates of the feeding rate in the natural environment for the chaetognath *Sagitta enflata* from the southern basin of Kaneohe Bay, Hawaii, and to examine the estimation method used.

Other aspects of chaetognath feeding behavior, and their impact on the prey, have been studied. Selection of prey by species and by size have been demonstrated (Reeve & Walter, 1972; Pearre, 1973). Pearre also inferred a diel feeding cycle from the daily pattern of gut contents in preserved *Sagitta*, as did Nagasawa & Marumo (1973).

Feeding rates in nature have been estimated for fishes from information on the fullness of the gut and laboratory-determined digestion rates. The basic approach taken in such methods, and some of the problems involved, were discussed by Eggers (1977). Briefly, the fullness of the gut at a given time is the net result of the opposing processes of ingestion and the passing of the food beyond the stomach region. With information on the feeding pattern of the animals (for example, whether or not it is continuous), the capacity of the gut and its fullness at the time of capture, and the rate at which food is processed, a reasonably simple mathematical relation can be used to describe the rate of ingestion that must have been necessary to produce the observed condition of animals in a sample. Such methods, rather than direct feeding experiments, are used at least partly because the process of digestion is regarded as less subject than feeding to the influence of the experimental conditions. In both cases, animals must be kept in the laboratory, but digestion is at least partly isolated from the experimental environment, in the gut of the animal.

Estimating feeding rates from gut contents and digestion rates is particularly appropriate for chaetognaths because their feeding behavior, involving detection and pursuit of prey, is more complex than filter-feeding, and so is more subject to influence of the experimental conditions (discussed by, for example, Anraku, 1964), and less amenable to attempts to describe it with models as a mechanical process (Steele & Mullin, 1977). Also, digestion in the partly-transparent chaetognaths is visible from outside the animal, and it has been shown to take place in batches, rather than continuously (Reeve, Cosper & Walter, 1975).

A method of this sort was implicit in the estimate by Nagasawa & Marumo (1973) that *Sagitta nage* in the coastal waters of Japan ingested about 38% of its body weight per day during their study.

Sagitta enflata is the dominant planktonic carnivore in the sewage-enriched ecosystem of the southern part of Kaneohe Bay, a subtropical marine embayment. *Sagitta* appears to be a major link in the transfer of matter and energy to fishes in the bay, and a potentially large influence on the dynamics of some of its preferred prey (Szyper, 1976). The animal rarely fed when confined in vessels in the laboratory, and then only in relatively large containers with abundant food present. An indirect method of estimating its ingestion rates was needed.

Methods

Samples for analysis of *Sagitta*'s diet were taken in vertical hauls from near the bottom of the bay (about 13 m) with a conical net of 0.33 mm mesh. The plankton was immediately preserved in the field by emptying the cod-end bucket into a glass jar containing sufficient formalin to make the final formalin concentration about 2% upon mixing with the sample. The total time from the start of the haul to preservation was always less than two minutes. When the vertical hauls brought in the usual large catches, the material was split, and the animals in a subsample were measured and examined for gut contents, as described in detail by Hirota & Szyper (1976) and Szyper (1976). Two diel series of samples were taken and handled in this manner, as were the initial samples on the days of the experiments to be described below.

Live animals for observation and experiment were taken in short surface hauls (two to 10 min) with a net of 0.33 mm mesh. The boat was allowed to drift during the hauls when the wind speed was sufficient, or was otherwise kept under way at minimum speed. The catch was diluted with surface bay water in a bucket, and returned to the laboratory.

Preliminary observations of digestion were made by pipetting live animals from the catches into finger bowls containing filtered seawater. The animals were examined under a dissecting microscope at intervals of 5–10 min until they had emptied their guts. The chaetognaths were then measured with an ocular micrometer, and the identity of food items was noted.

Estimates of the complete digestion time were made on subsamples of the natural population. Aliquots of about 100 ml, containing 20 to 200 *Sagitta*, were dipped from the live catches and diluted in glass jars containing 800 ml filtered seawater. The jars were incubated without stirring at ambient air temperatures (24–26 °C, similar to the water temperatures on the days of the experiments). Sets of up to 24 jars were prepared simultaneously in the field; two or three jars were immediately preserved as described above, at the beginning of each experiment. Two or three jars were preserved at intervals of ten to 30 min until the ends of the experiments. The preserved chaetognaths were then measured and examined for gut contents.

Results and discussion

Analysis of preserved samples

Sagitta enflata in Kaneohe Bay, like the other species studied by Nagasawa & Marumo (1973) and by Pearre (1973), contained food items more frequently at night than during the day, with periods of relatively rapid transition at dawn and dusk (Figure 1). The percent containing food was rather constant during the day (23%, S.D.=4), and at night (36%, S.D.=5). These means are similar to those observed by Pearre (1973), but somewhat higher than the results of Nagasawa & Marumo (1973).

Of all *Sagitta* having food in the gut, 95.7% contained only one item; nearly all the other fed animals had two items. Fewer than 3% of all food items were seen forward of the rear-most portion of the gut, which suggests that food is rapidly moved to the rear of the gut after ingestion. Observations of live animals confirmed this: one item near the head of a freshly captured animal was moved to the rear in 30 s, another in less than 2 min. Reeve, Cosper & Walter (1975) also observed rapid transfer of food to the rear gut in *S. hispida*. They noted that the percentage of food items in a forward position is therefore a poor indicator of feeding (or lack of feeding) in the cod-ends of nets, because even the food eaten during the haul might well be found at the rear of the gut at the time of preservation. It was fortunate that, in Kaneohe Bay, a sufficiently large sample of chaetognaths could be taken in very short hauls, thereby minimizing the problem of animals feeding in the net. There remains, however, the possibility of slight 'contamination' of the food items seen in preserved *Sagitta*.

During the diel series of samples represented in Figure 1(b), a duplicate sample from each sampling time was held without preservation until return to the laboratory, and was preserved about 20–30 min after collection. The per cent of animals with food decreased in almost all cases, indicating that small losses, rather than gains from stress-induced feeding, may have taken place during the capture and preservation times of less than 2 min for field-preserved samples.

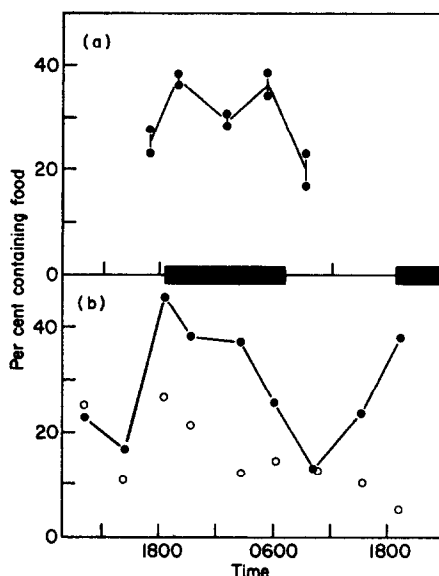


Figure 1. The diel cycle of feeding by *Sagitta enflata* in Kaneohe Bay. The dark bars indicate hours between sunset and sunrise; closed circles represent samples preserved in the field; open circles represent duplicate samples returned to the laboratory before preservation. (a) 6-7 February 1974. (b) 27-28 March 1974.

The length-frequency (l-f) distribution of the *Sagitta* population sampled with 0.33 mm mesh is basically unimodal, with the peak at about 4 mm length, the shortest length captured quantitatively by the net. The l-f distribution of the animals in a sample containing food never differed significantly from the l-f distribution of all the animals in the same sample (0.05 level, K-S test). This indicates that *Sagitta* of all sizes were equally likely to contain food, and so the per cent of the population with food represents the average per cent of the time an individual animal may be expected to contain food.

The diet of *Sagitta enflata*, while occasionally including a wide variety of prey (Piyakarnchana, 1965; Szyper, 1976), is heavily dominated by a few major zooplankton groups (Table 1). Observations of live *Sagitta* showed that the ciliates were not digested normally. Apparently too small to stimulate peristaltic action of the gut, the ciliates remained in one place or else 'swam' erratically back and forth in the lumen. The passage of larger items appeared to clear ciliates from chaetognath guts, but even if they were digested, they are too small to be of food value to any but the smallest *Sagitta* which passed through the mesh and were not captured. Since ciliates are very abundant in the southern part of Kaneohe Bay (about 1000/l, Hirota & Szyper, 1976), larger *Sagitta* could ingest them with other prey or with its accompanying water. For this reason, the diet of *S. enflata* was re-calculated for the second column of the table, ignoring the ciliates.

Preliminary observations of digestion

The process of digestion in *S. enflata* was similar to the sequence observed by Reeve *et al.* (1975). Freshly-taken food items were quickly moved to the rear of the gut, where they were moved slightly back and forth, or rotated slowly, until defecation. While *S. hispida*, studied by Reeve *et al.*, was often seen with more than one food item, and would capture more than

TABLE 1. Frequency of major food items in the diet of *Sagitta enflata* in Kaneohe Bay, with their content of nitrogen and phosphorus

Item	Per cent of diet	Per cent ignoring ciliates	N-content ($\mu\text{g}/\text{animal}$)	P-content ($\mu\text{g}/\text{animal}$)
Copepods	38.3	53.0	0.031 ^a	0.00261 ^b
Ciliates	27.8	—	—	—
<i>Oikopleura</i>	21.1	29.2	0.716	0.0768
<i>Sagitta</i>	5.9	8.2	1.17	0.0678
Others	6.9	9.6	0.355 ^c	0.0326

^a Calculated from the data of Bartholomew (1973).^b Calculated from the N/P ratio of mixed small zooplankton in Kaneohe Bay (Szyper *et al.*, 1976).^c Weighted average, based on the identified items.

one item in succession in the laboratory when starved, it appears that the habits of *S. enflata* differ in this respect. One item is the usual batch in the gut, despite the high abundance of food items in Kaneohe Bay (Hirota & Szyper, 1976).

The time required for clearing the gut by animals containing food when captured does not indicate the full digestion time, because ingestion was not observed. The average time, however, provides a minimum expected time for complete digestion, and the longer times may well be near the true value. The mean of the fourteen completed observations of gut-clearing time in such live animals was 0.78 h (s.d. = 0.47 h). Larger *Sagitta* contained larger prey than small *Sagitta* did, as expected (Reeve & Walter, 1972). Among chaetognaths of similar size, larger prey items (*Oikopleura*, other chaetognaths) remained in the guts longer than small prey (copepods), despite the resistant exoskeletons of the latter. Considering the similar-sized copepod prey, large *Sagitta* cleared them from the gut more rapidly (0.2 to 0.3 h) than small *Sagitta* did (0.6 to more than 1 h).

Since large chaetognaths take larger prey, but digest a given amount of food more rapidly, their digestion time for a batch in the gut need not be longer than the time taken by a smaller chaetognath to digest its smaller prey. The natural prey-selection and the greater digestive capacity of large *Sagitta*, in terms of food mass, act to smooth out differences in digestion times for animals of different sizes. There was in fact no significant correlation ($P > 0.50$) between *Sagitta* length and gut-clearing time in these observations, when prey size is ignored. In the samples represented by the open circles in Figure 1(b), in no case did the 1-*f* distribution of the remaining animals with food differ from the population distribution, nor from the distribution of animals with food in the field-preserved samples. That is, the gut-clearing rate does not depend on the size of the feeder, given the natural size-selection of prey.

Digestion experiments

In confined subsamples of the *Sagitta* population, the per cent containing food decreased with time as shown in Figure 2. If the animals cannot or do not feed during the experiment, 'p' should reach zero in the time taken for gut-clearing by the last animals to feed before capture. The non-digested ciliates mentioned earlier accounted for nearly all the animals with items in their guts after more than an hour of incubation. The incidence of ciliates in the guts decreased slightly during incubation, probably because they were forced out with

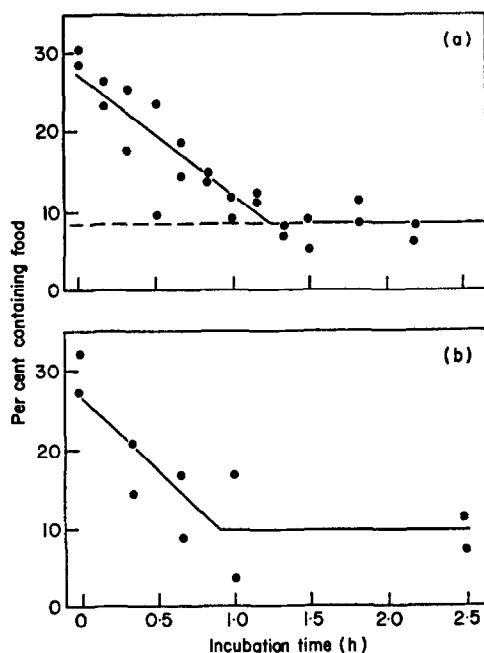


Figure 2. Gut-clearing by confined subsamples of the *S. enflata* population. Each point represents the per cent of animals with food in a jar containing 20 to 200 *Sagitta*. The equations for the fitted lines are: (a) decreasing line $y = 27.3 - 15.2x$; base line $y = 8.4$; (b) decreasing line $y = 27.0 - 19.7x$; base line $y = 9.6$.

the remains of larger prey, but the rate of this decrease (slope) was not significant at the 0.05 level. The expected base level of p was therefore drawn at the mean level of ciliates (8.4%) for the experiment represented in Figure 2(a). The decreasing line in the figure was fit to all points up to and including the earliest sample without food items in the guts other than ciliates. The lines intersect at about 1.2 h, the estimated average digestion time of the population on the day of the experiment.

An earlier experiment, performed before the problem of the ciliates was understood, showed a similar pattern [Figure 2(b)]. Since ciliate food items were not distinguished from others, the baseline was drawn through the mean of the last four points. The lines intersect at about 0.9 h, the digestion time estimate for that date. Without detailed knowledge of the factors affecting the population's average digestion time, it is reasonable to suppose that *S. enflata* in this environment clear their guts in about 1 h after feeding. This estimate is consistent with the average clearing time of about 0.8 h for the preliminary observations of individuals, which is known to be an underestimate. The preliminary observations could not be treated like the experimental data because *Sagitta* sometimes fed in containers as large as the bucket in which the catch was brought to the laboratory, especially when the food concentrations were extremely high in the container.

As mentioned earlier, the size of an animal does not appear to affect its average gut-clearing time. If animals of a particular size digested their food more rapidly than others, the decrease in ' p ' in the experiments just described would be curvilinear. The same would be true if significant feeding took place during incubation. Curvilinear fits to the sets of data points shown in Figure 2 showed greater residual variation than the two-line descriptions used here.

Very few non-ciliate food items, none identifiable, were seen in *Sagitta* samples preserved after the time of intersection of the lines in these experiments. The lack of feeding in the jars probably results from the reduced tendency of *Sagitta* to feed in the light (Pearre, 1973), and from the proximity of vessel walls, which could interfere with the darting pursuit behavior of the animals, which covers several centimeters at a time. Szyper *et al.* (1976) believed that *Sagitta* could have fed when confined for their excretion experiments, but those were conducted in vessels with at least twice the diameter of the jars used here, and more potential food in the water.

The feeding model

Given the percentage p of animals in a preserved sample with food in their guts, and the average digestion rate b batches per animal per hour, the feeding rate f batches per animal per hour is estimated as $f=b/p$. If all animals are equally likely to have a food item when caught, the percentage p is the same as the percentage of time the average animal spends with food in the gut. This equivalence, though not expressed by Nagasawa & Marumo (1973), is necessary if the model is to be valid. The 1- f tests discussed above support the equivalence in the present case.

When it is applicable, this method for estimating the feeding rates of zooplankton in nature could add value to the already extensive observations of the diets of chaetognaths. The results of its use are probably best interpreted in terms of the broad ecological impact of an animal's feeding activity, rather than the physiology of feeding by individuals.

It is necessary to minimize, or at least deal with, the possibility that the gut contents of preserved plankton have been affected by the collecting time or method. Short hauls, when a large enough plankton collection can be obtained with them, should be preferred in order to minimize 'contamination' of the gut contents by feeding in the net. It follows that the contamination problem will be less severe in areas of high plankton concentration.

The likelihood of all members of a population to have an equal chance of containing food at a given sampling time is enhanced by the demonstrated ability of zooplankton, including chaetognaths, to select food by size and by other criteria. But higher metabolic rates in smaller members of a population, or different vertical-migration patterns of predators and prey of various sizes, could act against the equal-chance assumption.

The largest simplifying assumption of the model is that there is a single average digestion rate for all members of the population. The idea is reasonable as a first approach because of the tendency of larger predators to take larger prey, and the ability of larger animals to digest food at a greater rate per unit of mass. Still, it is most likely to be true for animals that process their food in batches, rather than continuously. Eggers (1977) pointed out that many applications of the gut-fullness and digestion-time approach to feeding in fishes include expressions for exponential decrease in gut contents when feeding ceases. Some rather detailed knowledge of the digestive process of any animal under study by this method is needed. The length-frequency tests applied here for this purpose may be useful to evaluate the uniform digestion-time assumption for other fairly transparent, raptorial-feeding zooplankters.

*Impact of *Sagitta's* predation on the community*

Assuming 12 h each of day and night, and using the model $f=b/p$, it can now be estimated that *Sagitta enflata* in the southern basin of Kaneohe Bay ingests ($1 \text{ batch/h} \times 0.23$ of population having food $\times 12 \text{ h}$) = 2.8 batches of food during an average daylight period. Since

about 4% of batches of food in the guts consist of two items, the average batch contains 1.04 items. Multiplying the batches per day by the items per batch corrects the daytime feeding rate to 2.9 items per animal per daylight period. The night feeding rate is $(1 \text{ batch/h} \times 1.04 \text{ items/batch} \times 0.36 \text{ of the population with food} \times 12 \text{ h}) = 4.5 \text{ items per animal per night}$, the daily total adding to 7.4 items/animal.

In 1973–75, the average abundance of *S. enflata* caught on 0.33 mm mesh in the southern basin was 646 animals/m³ (Szyper, 1976). This population was capable, according to the feeding rate estimates, of capturing about 4800 prey/m³/day. The relative prey proportions shown in Table 1 indicate that about 2500 of the prey were post-naupliar microcopepods, 1400 were *Oikopleura*, and about 400 were *Sagitta*.

The small copepods are so abundant (about $3 \times 10^4/\text{m}^3$) and so productive (Newbury & Bartholomew, 1976) that they are probably little affected by *Sagitta*'s predation. In contrast, the effect on the several species of *Oikopleura* could be a major one. The estimate of the number eaten per day is greater than the average standing stock estimated by Peterson (1975). His estimate, however, does not include small animals passing the 0.33 mm mesh, which in the case of *Oikopleura*, is a significant part of the stock. These plankters have not been sufficiently studied to permit an estimate of *Sagitta*'s impact on their ability to attain reproductive age and size. The *Sagitta* eaten by their own kind seem to constitute a very high percentage of the stock, when only the catch of the 0.33 mm mesh is considered. In fact, *S. enflata* less than 4 mm long pass through this mesh, and the animals of this size constituted about 70% of the population during the sampling period, although they held a much smaller percentage of the total biomass. The small chaetognaths are not capable of cannibalism, because of the minimum head diameter of the animal, and the limited mouth size of shorter animals. The larger *Sagitta*, then, are responsible for all the cannibalism that takes place, and some of the animals eaten are small individuals that pass through the large mesh. Considering all sizes of *Sagitta* in the environment, the cannibalism amounts to about 17% of the total population per day.

The daily ration of Sagitta in terms of nitrogen and phosphorus

From the chemical composition of *Sagitta* and its prey (Szyper, 1976; Hirota & Szyper, 1976), and from the relative frequencies of the various prey in the diet (Table 1), *Sagitta*'s daily ration of nitrogen can be calculated at 70% of its own body content per day. In terms of phosphorus, the daily ration is 111% of body weight. The difference between N and P results from the prey being richer in P relative to N than the predators are, as Szyper *et al.* (1976) reported for mixed plankton in Kaneohe Bay. The same relationship holds between *Calanus* and its phytoplankton food in British waters (Butler, Corner & Marshall, 1969). The different estimates of *Sagitta*'s ration relative to its body weight in terms of the two elements shows that estimates of material turnover can depend on the material chosen, for a given test animal. Coper & Reeve (1975) discussed similar problems in estimating assimilation efficiencies.

Since *Sagitta* constructs body tissue with an N/P ratio higher than that of its food, it must be excreting the 'excess' P, and so the N/P ratios of its waste products must be lower than the ratios in both the body tissues and the food (see Ketchum, 1962). If such trends in N/P ratios are common properties of marine food chains, the observed rapid cycling of P relatively to N may be partly explained in this way: relatively more P than N is returned to soluble form at each trophic-level transfer, thus shortening the time of the P cycle relative to that of N.

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