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Aspects of the nutritional ecology of Sagitta tenuis (Chaetognatha) in the lower Chesapeake Bay

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ASPECTS OF THE NUTRITIONAL ECOLOGY OF SAGITTA TENUIS (CHAETOGNATHA) IN THE LOWER CHESAPEAKE BAY

A Thesis

Presented to

The Faculty of the School of Marine Science

The College of William and Mary in Virginia

In Partial Fulfillment

of the Requirements for the Degree of

Master of Arts

by

Michael F. Canino

1981

APPROVAL SHEET

This thesis is submitted in partial fulfillment of
the requirements for the degree of
Master of Arts in Marine Science

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DEDICATION

This work is dedicated to Richard and Diane Kallerman and their children for their support and affection over the years.

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ABSTRACT

The nutritional ecology of *Sagitta tenuis* in the lower Chesapeake Bay was examined by laboratory measurements of digestion time and gut content analysis of preserved specimens. Gut clearing times, measured at 21°C and 25°C, were highly variable and did not appear to be affected by differences in temperature. There was an apparent increase in digestion time as a function of the number of food items ingested. The overall digestion time was 69.2 minutes.

Copepods accounted for 92% of total chaetognath diet and usually occurred as single items in the gut. *Sagitta tenuis* exhibited a diel variation in feeding intensity, in that the fraction of the sampled population containing food was significantly higher at night than during the day. Large *S. tenuis* consumed more prey per individual than smaller ones regardless of the time of day.

Daily food rations, expressed as the number of prey consumed per chaetognath per day, were calculated for six size classes of *S. tenuis*. These rations ranged from 3.12 to 8.70 prey and increased with increasing chaetognath size. Specific daily rations, as fractions of body dry weight, carbon and nitrogen consumed per chaetognath per day, were estimated from length-weight relationships and the chemical content of *S. tenuis*. Specific daily rations decreased with increasing chaetognath size, indicating young animals ingested a higher proportion of their body weight per day than mature individuals.

Comparisons of chaetognath and prey abundances suggest *S. tenuis* is a minor seasonal predator in the lower Chesapeake Bay ecosystem. Chaetognath distribution and numerical density appear to be largely controlled by the local hydrography.

ASPECTS OF THE NUTRITIONAL ECOLOGY OF _SAGITTA_ _TENUIS_ (CHAETOGNATHA) IN THE LOWER CHESAPEAKE BAY

GENERAL INTRODUCTION

The phylum Chaetognatha is an ubiquitous group of holoplanktonic carnivores of major trophic importance in most marine ecosystems (Reeve, 1970; Steele and Frost, 1977). Their numerical abundance is often second only to that of copepods, their primary prey (Grice and Hart, 1962; Alvariño, 1965). Taxonomic and distributional studies comprised the bulk of earlier research on chaetognaths (*e.g.* Hyman, 1949; David, 1955; Alvariño, 1965), but their role as higher trophic level consumers has received limited attention, primarily because of difficulties in the capture and maintenance of laboratory populations (Lebour, 1922; Parry, 1944; Murakami, 1966). As plankton predators, an understanding of their nutritional ecology is vital to the development of trophodynamic models of plankton communities (Petipa *et al.*, 1970; Steele and Frost, 1977).

Research on the feeding habits and diet of chaetognaths has generally followed two lines of investigation: laboratory observations of feeding and examination of the gut contents of preserved specimens. Quantitative aspects of feeding behavior with regard to food type and density are ideally measured in a controlled laboratory environment, as has been done with copepods (*e.g.* Paffenhoffer, 1971; Nival and Nival, 1976). In practice, chaetognaths are easily damaged by conventional zooplankton sampling gear or cannot be induced to feed in the laboratory (*e.g.* Fraser, 1969). Early reports of laboratory food consumption by chaetognaths were largely qualitative descriptions of ingestion and digestion (Parry, 1944; David, 1955). *Sagitta hispida*, an epiplanktonic neritic species, has been intensively studied by Reeve (1964, 1966) and co-workers for a number of years. The successful culture of *S. hispida* (Reeve, 1970; Reeve and Walter, 1972a) and its apparent hardiness in the laboratory, have enabled observations of feeding and diet throughout its development. With the exception of some limited observations of feeding by *S. enflata* (Feigenbaum, 1977; Reeve, 1980), *S. setosa* (Kuhlmann, 1977), and *S. elegans* (Kuhlmann, 1977; Feigenbaum, 1979b; Reeve, 1980), little experimental work has been attempted with live chaetognaths.

The traditional alternative to laboratory studies has been gut analyses of preserved specimens (*e.g.* Mironov, 1960; Nagasawa and Marumo, 1972, 1976; Pearre, 1973, 1974) from which most information on chaetognath diet and feeding behavior has been derived. The main advantage of this method is a 'naturalness' lacking under laboratory control and duplication (Reeve, 1980). Dietary analyses are subject to a number of interpretive problems. The two most important difficulties concern the artifactual effects of collection or preservation and the accurate identification of partially digested prey items. Chaetognaths may 'feed' indiscriminately in the plankton net (Cosper, 1973; Feigenbaum, 1979a) or defecate upon fixation (Reeve, 1980), thus introducing unnatural prey into or excluding natural prey from the apparent diet. Food remnants in the gut may go undetected (Sullivan, 1980) or unidentified prey items may not constitute a representative fraction of identified gut contents, affecting calculation of prey electivities (Pearre, 1974).

In several studies, gut content analyses have been combined with laboratory estimations (Szyper, 1978) or observations (Nagasawa and Marumo, 1972; Newbury, 1978; Feigenbaum 1979a) of digestion times to predict food rations for chaetognaths. The feeding models rely upon accurate measurement of gut clearing rate, a process that appears to be highly variable in many species. Differences in the size (Kuhlmann, 1977; Szyper, 1978) or number of ingested food items can result in significant differences in their gut residence time. In addition, digestion may vary with chaetognath age (Reeve, 1980) or temperature (Feigenbaum, personal communication). Despite this problem, combined measurements of digestion times and gut contents are probably more useful than laboratory feeding observations alone for determining daily rations. The ingestion rates exhibited by starved laboratory specimens exposed to high prey densities often exceed those predicted from field collections (Reeve, 1980; personal observation) and perhaps represent maximum rates never achieved simultaneously by the entire population in nature.

The Chesapeake Bay lacks an endemic chaetognath fauna but there are winter-spring and summer-fall assemblages recruited from adjacent continental shelf waters (Grant, 1977). Sagitta tenuis Conant 1896, a neritic inshore species, numerically dominates the summer-fall chaetognath group. During September, this species represents locally the entire phylum, accounting for nearly 99% of sampled individuals.

Mean population densities may reach several hundred individuals per cubic meter (Grant, 1977), suggesting that *S. tenuis* is an important seasonal predator in the lower Bay zooplankton community whose nutritional ecology was unknown.

Aspects of the feeding behavior and diet of *S. tenuis* were investigated through laboratory observations and gut content analysis of field collected specimens. The main objectives of this study were threefold and are presented as separate sections in the text. A description of length-weight relationships and chemical contents of *S. tenuis* are presented in Section I. These measurements allow conversion of population length-frequency distributions into units of biomass, *i.e.* carbon and nitrogen. Section II is a laboratory study of gut clearing by *S. tenuis* as a function of temperature and number of prey consumed. In Section III, the dietary composition and feeding behavior of *S. tenuis* in the lower Chesapeake Bay are examined from preserved gut contents. From the results of these sections, a daily ration (in terms of number of prey consumed per day) and a specific daily ration (expressed as the weight of food consumed per predator weight per day) are calculated for *S. tenuis*. Throughout the study observed results are related to those for other chaetognaths, particularly *S. hispida* and *S. enflata*, two species best known in a nutritional sense and that occur with *S. tenuis* over most of the southeastern Atlantic coast (Pierce, 1953, 1958; Deevey, 1960; Owre, 1960; Grant, 1963a, 1963b).

SECTION I. LENGTH-WEIGHT RELATIONSHIPS AND CHEMICAL COMPOSITION OF *SAGITTA TENUIS*

INTRODUCTION

The chemical composition of zooplankton has been widely utilized to evaluate productivity and biogeochemical cycling in pelagic marine ecosystems. In theory, the trophodynamics of plankton communities or life histories of individual species may be described by their equivalent weights, usually in terms of dry weight, carbon, or nitrogen per unit volume. Prior studies of zooplankton chemical contents have followed major taxonomic divisions with most research centered on the herbivorous macrocrustacea (*e.g.* Curl, 1962; Omori, 1969).

The phylum Chaetognatha is a homogeneous group of planktonic carnivores found in many marine and neritic environments. Despite the gross physical similarities of chaetognaths, different species exhibit considerable variation in their weights and chemical contents. Some gravimetric and compositional data have been reported for tropical and subtropical chaetognaths (Beers, 1966; Reeve *et al.*, 1970; Reeve and Baker, 1975; Szyper, 1976; Newbury, 1978; Feigenbaum, 1979a), mostly for the epiplanktonic *Sagitta hispida* and *S. enflata*.

Sagitta tenuis is the dominant summer-fall chaetognath species in the lower Chesapeake Bay. It is a regular seasonal component of this ecosystem, occurring in greatest numbers during September (Grant, 1977). Although the numerical abundance of *S. tenuis* often exceeds those of ctenophores and hydromedusae (Price, personal communication), two major holoplanktonic predators, its nutrition and trophic importance have not been investigated. Comparisons of food rations relative to predator size are best presented in terms of a specific daily ration. This ration (expressed as unit weight of food ingested per unit weight of predator per day), can be used as a general index of the energetic requirements of a predator.

A series of laboratory measurements were initiated to determine the weights and chemical contents of *S. tenuis* of different sizes. The objective was to provide conversion factors of chaetognath size-frequency distributions to dry weight, carbon, or nitrogen, the most common measures of biomass for plankton. The length-weight relationships and chemical composition of *S. tenuis* are reported for the first time. In conjunction with estimates of feeding rates and diet presented later in this study, this information will quantify some aspects of the nutritional ecology of *S. tenuis* in the lower Chesapeake Bay.

METHODS AND MATERIALS

Live S. tenuis were captured from the pier at the Virginia Institute of Marine Science by tows with a 1/2 m, 202 μm mesh plankton net. The cod end was rinsed into a bucket containing seawater and stored at room temperature prior to use, usually less than an hour later. Only live, healthy, and unfed animals were used for weight determinations. Chaetognath total length (tip of head to base of trunk excluding caudal fin) was measured with an ocular micrometer to the nearest 0.1 mm.

Specimens were weighed individually to the nearest 0.1 μg on a Perkins-Elmer AD-2 electrobalance. A single chaetognath was dipped in glass-distilled water to remove external salts then transferred to a pre-weighed, pre-ashed glass fiber filter for wet weight determination. Samples were dried overnight at 60°C and reweighed. Filter and specimen were then combusted at 500°C for 5 hours and weighed a final time for ash weight. Ash-free dry weights were computed as the weight loss during combustion. Blank filters were subjected to the same treatments as experimental filters and showed no appreciable weight loss.

Analyses for total body carbon and nitrogen were performed on S. tenuis species grouped into four size classes: 2.0 to 4.0 mm, 4.0 to 6.0 mm, 6.0 to 8.0 mm, and 8.0 to 10.0 mm. Chaetognaths were measured and rinsed, as described above, then placed into the appropriate size category. Specimens were dried for 24 hrs at 60°C, ground, and stored in a dessicator until analysis. Triplicate samples from each size class were analyzed for total body carbon and nitrogen in a Perkins-Elmer 240B Elemental Analyzer. Ash-free dry weight and ash weight were obtained as percentages of sample dry weight.

RESULTS

Nearly 100 individual weight determinations were used to describe length-weight relationships in *Sagitta tenuis*. Simple linear regressions and geometric mean functional regressions of weight on total length are summarized in Table 1. Linear regressions of these data are illustrated in Figures 1, 2 and 3.

Dry weight ranged from 5.6% to 26.2% of wet weight with a mean value of 12.5 ± 3.2%. The percentage decreased slightly with increasing chaetognath size, indicating that larger animals contained proportionally more water than smaller ones. Ash-free dry weight averaged 68% of dry weight and was highly variable, ranging from 31.0 to 83.3%. Although the coefficient of determination (r^2) for the length:ash-free weight regression is high, the small amount of inorganic ash left after combustion and repeated handling of sample filters probably contributed to the observed variation, particularly in specimens less than 5 mm in length. The mean ash content of the chaetognath size classes used for CHN analyses was 7.75% of dry weight. A slight but nonsignificant increase of ash with increasing chaetognath size was observed. Subtracting ash weight from sample weight in each chaetognath size category indicates ash-free dry weight averaged 92.25% of dry weight, a percentage exceeding regression estimates over most of the size range examined. According to the

Table 1. Length-weight relationships for *Sagitta tenuis* 2 to 9 mm in length. Weight (in μg) = a x $(TL)^b$; where, TL = chaetognath total length (in mm).

Regression design	parameter	intercept(a)	slope(b)	std. err of regression	95% c.i. on b	r^2	n
Linear regression	wet weight	1.08	3.28	0.08	b ± 0.17	0.9469	98
	dry weight	0.28	2.84	0.07	b ± 0.13	0.9460	99
	ash-free dry weight	0.79	3.20	0.10	b ± 0.23	0.9050	99
Geometric mean functional regression	wet weight	-0.22	3.61	0.08			98
	dry weight	-0.68	3.01	0.07			99
	ash-free dry weight	-1.25	3.54	0.10			99

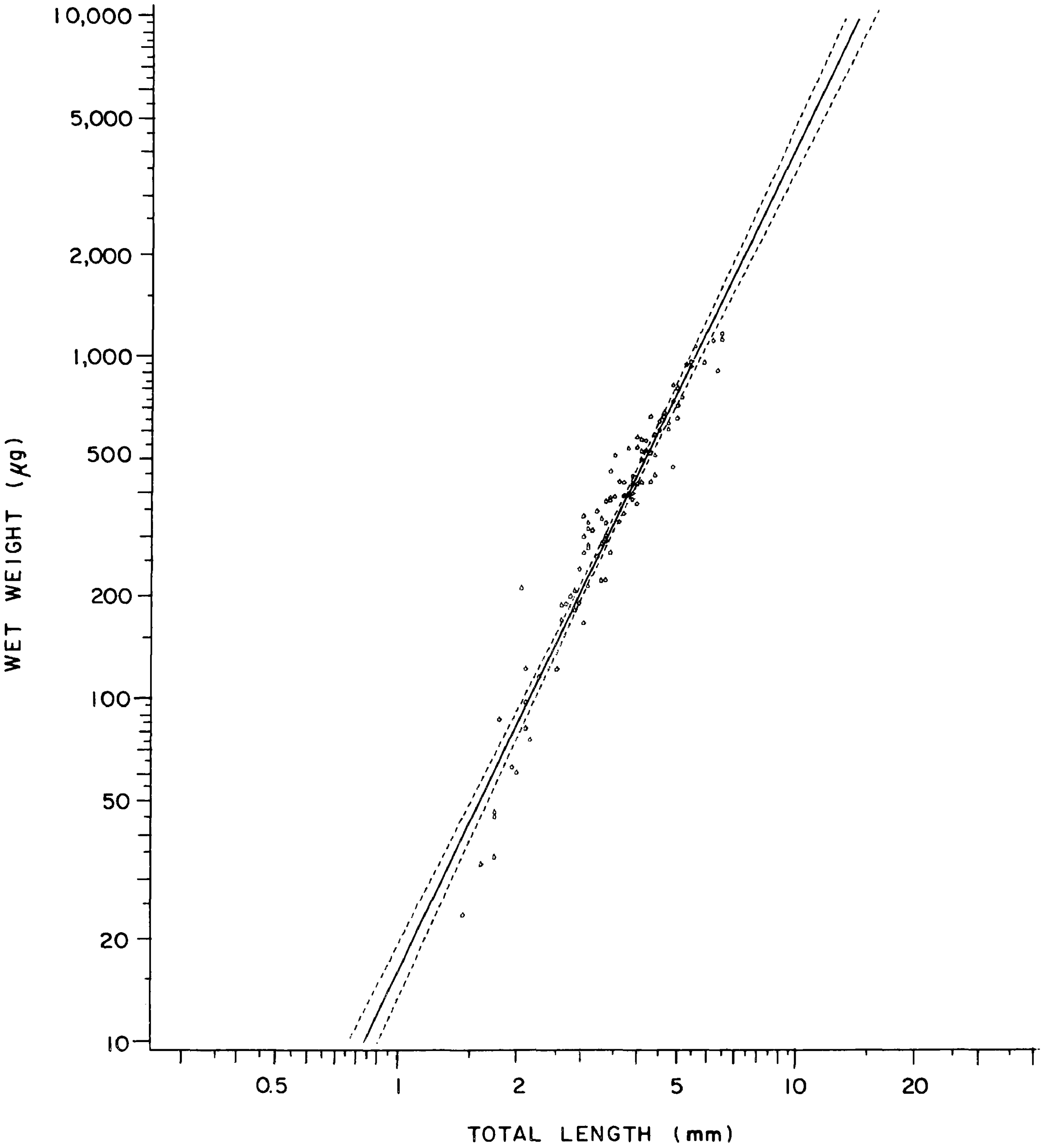


Figure 1. Wet weight versus total length for Sagitta tenuis. Dashed lines represent 95% confidence interval around the mean.

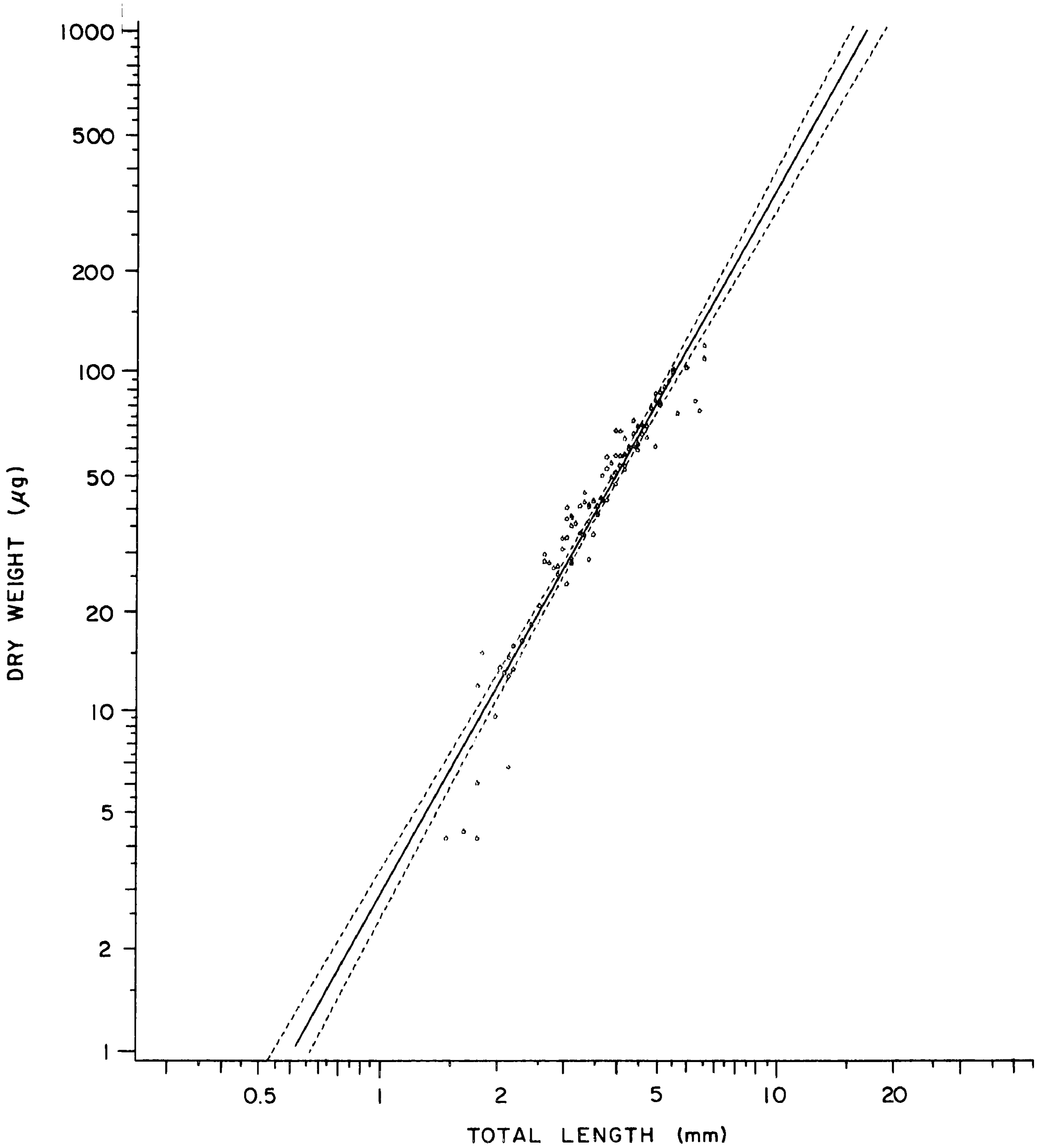


Figure 2. Dry weight versus total length for Sagitta tenuis. Dashed lines represent 95% confidence interval around the mean.

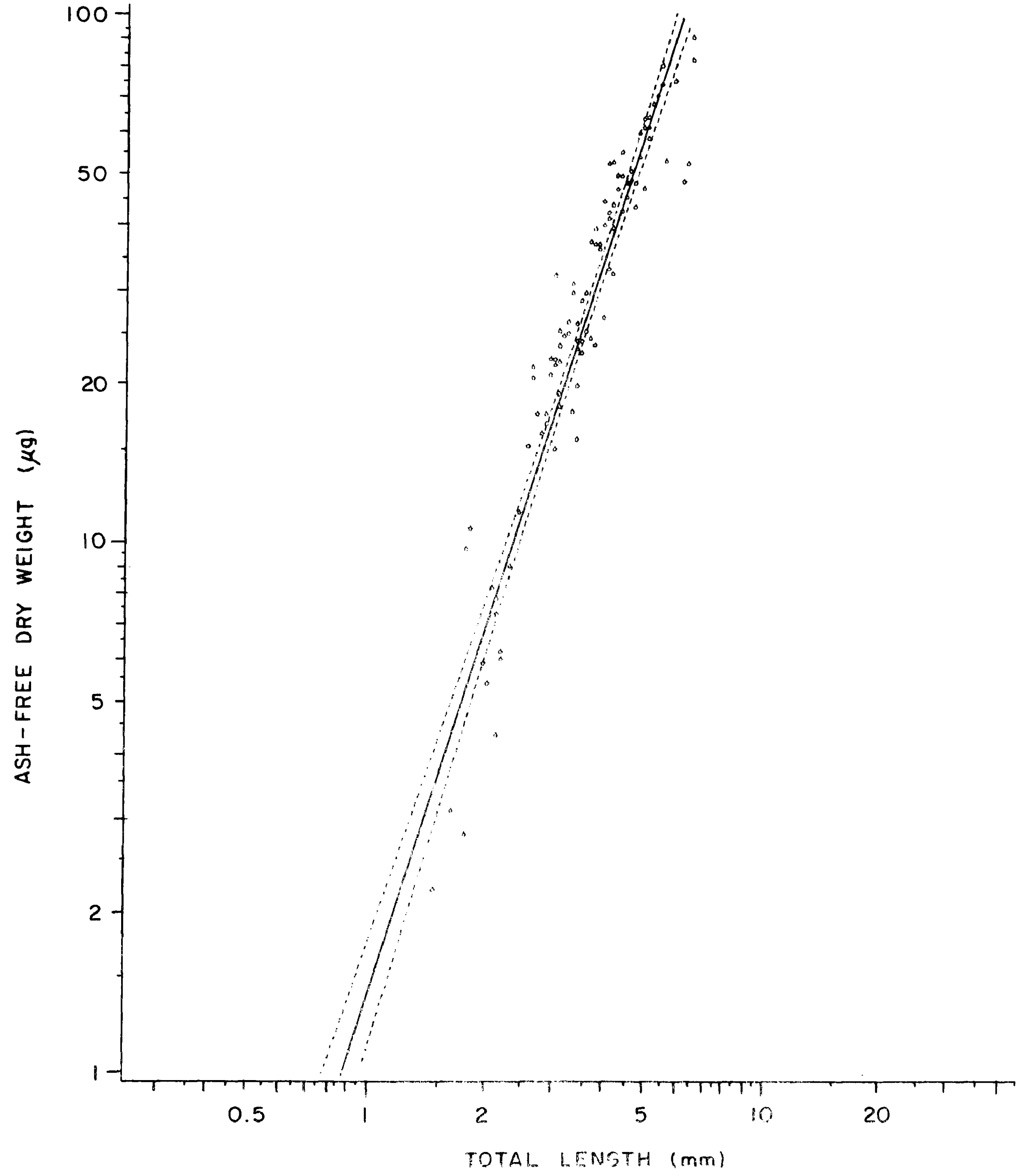


Figure 3. Ash-free dry weight versus total length for <u>Sagitta tenuis</u>. Dashed lines represent 95% confidence interval around the mean.

regression equations (Table 1), ash-free weight would equal 90% or more of body dry weight only in specimens greater than 9.0 mm in length. As mentioned earlier, errors associated with weighing small individuals may be largely responsible for the discrepancy between observed and predicted values.

Total body carbon and nitrogen as percentages of dry weight for all samples combined were 36.82% and 10.64%, respectively (Table 2). Relative concentrations of both elements increased in size classes larger than 6 mm, a length roughly delineating the onset of sexual maturity. Pooled values for the two largest and two smallest size classes showed mean carbon and nitrogen contents were significantly greater in larger specimens than in smaller ones (for carbon, $t = 2.660$, $0.01 < p < 0.025$; for nitrogen, $t = 12.07$, $0.001 < p < 0.01$). The mean carbon:nitrogen ratio for all size classes was 3.43.

Table 2. Nitrogen, carbon, and ash content of <u>Sagitta</u> <u>tenuis</u> as a percentage of dry weight.

Chaetognath size class (mm)	2.1-4.0	4.1-6.0	6.1-8.0	8.1-10.0
% N	10.4	10.6	11.0	11.6
	9.5	9.8	11.3	11.5
	10.1	8.9	11.5	11.5
mean	10.0	9.8	11.3	11.5
mean of pooled size classes	9.9		11.4	
% C	32.1	33.3	40.9	40.7
	32.7	31.4	39.7	40.8
	33.4	35.6	39.7	41.5
mean	32.7	33.4	40.1	41.0
mean of pooled size classes	33.1		40.5	
% ash	6.4	7.4	7.8	9.0
	7.9	7.7	7.3	8.0
	7.2	8.0	8.2	8.1
mean	7.2	7.7	7.8	8.4

DISCUSSION

The morphometry and chemical composition of S. tenuis are comparable to those reported for other Sagitta (Beers, 1966; Reeve, 1970; Reeve and Baker, 1975; Szyper, 1976; Newbury, 1978; Feigenbaum, 1979a). Some existing literature and the results of this study are summarized in Table 3. Dry weight:wet weight (DW/WW), ash-free dry weight:dry weight (AFDW/DW), and carbon:nitrogen ratios are calculated for 6 mm individuals from reported data where indicated for comparison with S. tenuis of equal size.

The results indicate the biochemical composition of S. tenuis is more like that of S. hispida than that of S. enflata, the two other species occurring in the lower Chesapeake Bay during late summer and fall (Grant, 1977). Gross morphology of S. tenuis and S. hispida are similar (Suarez-Caabro, 1955; Tokioka, 1955) both are small, rigid, and negatively bouyant, though S. hispida is more robust than S. tenuis. In contrast, S. enflata is large, often exceeding 20 mm, flaccid, and appears to be neutrally bouyant (Cosper, 1973; Feigenbaum, 1979a).

The similarity of DW/WW ratios estimated for 6 mm S. tenuis and S. enflata is misleading. The exponent for the length:dry weight regression (Table 1) is intermediate to those given by Szyper (1976)

Table 3. A comparison of gravimetric and chemical analyses of chaetognaths. Abbreviations used are: WW = wet weight; DW = dry weight; AFDW = ash-free dry weight; AW = ash weight; C = carbon; N = nitrogen

Study	Species	Size (mm)	% DW/WW	% AFDW/DW	% AW/DW	% C/DW	% N/DW	% C/N
Beers (1966)	chaetognaths	unknown	6.8			28.3	7.84	4.2
Omori (1969)	*S. nagae*	17.9 - 19.3			4.2	43.5	11.1	3.90
	S. nagae and *S. elegans*		12.8		4.5	45.6	10.9	4.2
Reeve *et al.* (1970)	*S. hispida*	5.0 - 9.0	17.0	90.7	8.6		14.1	
Reeve and and Baker (1975)	*S. hispida*	2.0 - 11.5				44.9		3.2**
Szyper (1976)	*S. enflata*	3.0 - 13.0		56.0*		19.6	5.3	3.7**
Feigenbaum (1979a)	*S. enflata*	6.0 - 20.0	11.5*			17.7	4.8	3.7**
This Study	*S. tenuis*	2.0 - 10.0	11.7*	69.3*	7.75	36.8	10.6	3.43

* Calculated for 6 mm individuals from regression equations.

** Calculated from reported mean values.

and Feigenbaum (1979a) for two populations of *S. enflata* with different mean lengths. The former study was confined to smaller specimens which have a higher DW/WW ratio than larger ones. Feigenbaum (1979a) used mostly large Gulf Stream *S. enflata* for weight determinations and noted that predicted dry weights may be less accurate for smaller sizes. In his study, dry weight declined from 11.5% of wet weight for a 6 mm individual to 5.6% for a 20 mm chaetognath, a percentage close to the 6.8% reported by Beers (1966) for subtropical chaetognaths as a group. The DW/WW ratios for specimens larger than 20 mm approach those reported for other gelatinous zooplankton such as hydromedusae (4.3%), siphonophores (4.0%) (Beers, 1966), and ctenophores (4.3%) (Baker, 1973). According to regression estimates, dry weight declines from 15.0% of wet weight for a 4 mm *S. tenuis* to 8.6% for a 10 mm adult. Reeve *et al.* (1970) found dry weight in *S. hispida* to average 17% of wet weight over a size range similar to the one examined in this study.

The ratio of ash-free dry weight to dry weight is generally lower in 'watery' zooplankton because of dilution by inorganic salts contained in species with low dry weight:wet weight ratios. The predicted AFDW/DW ratio for a 6 mm *S. tenuis* exceeds that for a *S. enflata* of equal size by 13.3% (Table 3). At 10 mm in length, the AFDW/DW ratio for *S. enflata* has decreased to 47.8% while that for *S. tenuis* has increased to 91.0%. As mentioned earlier, predicted ash-free dry weights may be underestimated, particularly for small individuals. Residual ash from CHN analyses averaged 7.75% of dry weight indicating the remaining 92.25% was ash-free dry weight, a percentage realized only by large *S. tenuis* from regression equation estimates. *Sagitta hispida* has an ash content comparable to *S. tenuis* (Reeve *et al*., 1970) and the assumption that the ash-free dry weights are similar seems justified.

Total body carbon and nitrogen percentages of dry weight in *S. tenuis* are about twice those of *S. enflata* and roughly two-thirds the concentrations found in planktonic crustaceans (Curl, 1962; Beers, 1966; Jawed, 1969). In contrast, the contents in *S. enflata* are similar to those for cnidarians (Curl, 1962) and siphonophores (Beers, 1966). The carbon:nitrogen ratio (3.45) in this study is somewhat lower than other reported values. Reeve *et al*. (1970) reported that *S. hispida* 5 to 9 mm in length contained 14.1% nitrogen on a dry weight basis. Later, Reeve and Baker (1975) found that carbon averaged 44.9% of dry weight over a slightly larger size range, a content similar to that of boreal and temperate species (Omori, 1969). Combining the two values yields an estimated C/N ratio of 3.2, indicating that *S. tenuis* and *S. hispida* tend to contain proportionally more nitrogen than *S. enflata*.

Mean carbon and nitrogen contents are appreciably greater in larger *S. tenuis* than in smaller ones. Individuals over 6 mm in length all represent maturity stages II and III in Grant's (1977) classification. The relative increases of these elements with chaetognath size probably reflect the presence of reproductive tissues, most likely the larger masses of maturing or ripe ova, in mature *S. tenuis*. The calculated C/N ratio for individuals less than

6 mm long is 3.3 and rises to 3.6 for larger chaetognaths. Eggs generally have increased lipid levels associated with yolk. This fact would tend to raise C/N ratios in sexually mature specimens.

SECTION II. LABORATORY FEEDING AND DIGESTION TIMES OF *SAGITTA TENUIS*

INTRODUCTION

The measurement of digestion time is of primary importance for zooplankton feeding models and calculation of food ration. Feeding in *Sagitta* has been described as a discontinuous 'batch' process (Reeve *et al*., 1975; Cosper and Reeve, 1975; Szyper, 1976, 1978; Feigenbaum, 1977) that may be advantageous in patchy food regimes. Gut transparency and the formation of discrete fecal pellets in chaetognaths enable direct observations from ingestion to defecation.

Historically, planktonic chaetognaths have been difficult to maintain under laboratory conditions (Parry, 1944; Murakami, 1966; Fraser, 1969). Although the benthic genus, *Spadella*, can be cultured for laboratory work (John, 1933;/see Ghirardelli, 1968), attempts to collect and rear populations of *Sagitta* were largely unsuccessful. Technical improvements for collection and the first culture of an epiplanktonic species (Reeve, 1970; Reeve and Walter, 1972a) have yielded more accurate information on the feeding and diet of *Sagitta hispida* throughout its life cycle.

There appears to be a large natural variability in the gut clearance times of chaetognaths. Nagasawa and Marumo (1972) summarized previously recorded digestive intervals for seven species ranging from 40 minutes to over 6 hours. Prey type, relative prey size, and temperature may all influence this process. Large soft-bodied prey, *i.e.* fish larvae, have been observed to take longer to digest than copepods (Kuhlmann, 1977). Szyper (1976) reported a similar qualitative difference for *S. enflata* feeding on copepods and *Oikopleura*. Reeve (1980) found an apparent increase in the digestion time of *S. hispida* as a function of the number of copepods ingested. Gut clearing rates may also be somewhat dependent upon temperature. Feigenbaum (1977) noted that the 2°C difference between his and Szyper's (1976) study may have been partly responsible for the threefold difference in reported digestion time. Feigenbaum (1979b) has also observed an average digestion time of 10.24 hours for *S. elegans* feeding at 0°C. This is far longer than the 2.45 hours for specimens at 15°C recorded by Kuhlman (1977).

Feeding and digestion in *S. tenuis* were observed at two discrete temperatures. A third experimental temperature was originally planned to approximate the normal range encountered by *S. tenuis* but sufficient numbers of chaetognaths could not be obtained. If temperature directly effects gut clearing rate, ration estimates from field collections can be refined for seasonal or geographic temperature variation.

METHODS AND MATERIALS

Live chaetognaths were caught in a 1/2 m, 333 μm mesh plankton net terminating in a 7 liter plexiglass cod end. Four or five animals were isolated in a gallon jar containing 35 μm filtered seawater and starved for 24 hours at constant experimental temperature and simulated diurnal photoperiod in an incubator. Only transparent, vigorous specimens were used; damaged individuals usually died within several hours after capture.

Ingestion and gut clearance rates were measured at two temperatures: 21°C and 25°C. In each experiment, five or six *S. tenuis* were placed individually in fingerbowls containing 35 μm-filtered seawater. Prey organisms, consisting of freshly caught zooplankton retained on a 202 μm mesh net, were introduced at densities exceeding 500 individuals per liter. Adult and late stage copepodid *Acartia tonsa* comprised 85 to 90% of the prey items. Juvenile mysids, decapod zoea, and other copepods were present in minor variable quantities.

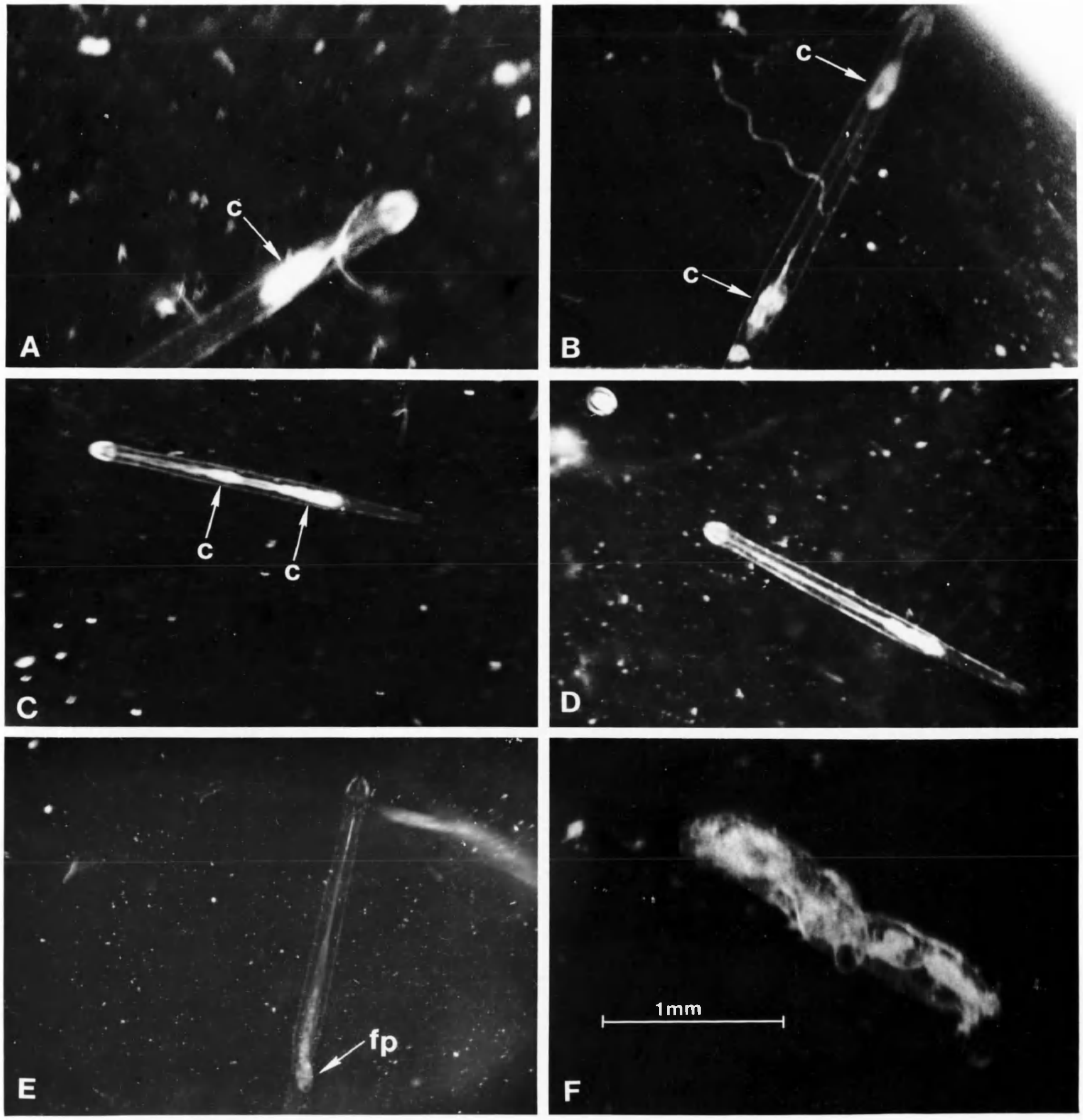
Each chaetognath was observed under low magnification for 15 minutes and the times to prey ingestion recorded. Animals which fed during this interval were then isolated in fingerbowls without food and checked at 10 minute intervals until defecation. Temperature was held constant to within 1°C by returning fingerbowls to the incubator between microscope examinations. If ingestion or defecation was not directly observed, the digestion time was taken to be as the midpoint between observations, usually less than 5 minutes. Chaetognath total length was measured to the nearest 0.1 mm with an ocular micrometer and the number of prey ingested was recorded for each specimens.

RESULTS

The feeding behavior and digestive process in Sagitta tenuis resemble those described for other planktonic chaetognaths. In this study, copepods were the only prey item ingested. Attacks were observed only while prey were actively moving within several millimeters of the chaetognath's head. Prey were usually caught by the cephalothorax, quickly manipulated by the gasping spines, and ingested headfirst. One unsuccessful capture attempt was observed in which a S. tenuis grasped a copepod by the urosome and was unable to properly orient it for ingestion.

The sequence of digestion in S. tenuis is depicted in Figure 4. Although the resolution is sometimes poor, these photographs serve to illustrate the location and general appearance of food during digestion. Ingested prey move quickly down the gut by peristaltic contraction of the gut wall, usually reaching the anus between 6 and 10 minutes after capture. Multiple prey were incorporated into a single bolus that remained in the posterior gut until defecation (Figs. 6D and 6E). Prey copepods became increasingly compacted and transparent during digestion, providing a reference for later evaluation of gut contents from field collections. The fecal pellets produced by S. tenuis were clearly surrounded by a peritrophic

Figure 4. The sequence of digestion for a *Sagitta tenuis* 9.6 mm in length ingesting two prey items. A - 25 seconds after ingestion of first copepod; B - 3 minutes and 25 seconds after ingestion of first copepod; the chaetognath has just ingested a second copepod; C - 10 minutes and 55 seconds after ingestion of first copepod; note peristaltic contraction of gut wall; D - 32 minutes and 15 seconds after ingestion of first copepod; both prey are incorporated into a single food bolus; E - defecation 78 minutes and 15 seconds after ingestion of first copepod; note transparency of fecal pellet; F - fecal pellet containing remains of two copepods; exoskeletal outlines are visible within the pellet: c = copepod; fp = fecal pellet.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1mm
F

membrane (Fig. 11F) like that described for S. hispida by Cosper (1973), Cosper and Reeve (1975), and Reeve et al. (1975).

A high percentage of chaetognaths (71.2%) fed during experimentation. The percentage of S. tenuis feeding and digestion times versus the number of prey consumed are illustrated in Figure 5. Chaetognaths ingested from 0 to 5 food items at both experimental temperatures and a higher proportion of animals consumed single prey at 21°C than at 25°C.

Although each observation may be viewed as a single experiment, comparisons of data pooled by temperature or the number of prey consumed are not amenable to conventional statistical treatments. The experimental design did not randomize the feeding regimes; i.e., chaetognaths were not offered specific numbers of food items. For that reason, pooled gut clearing times (Figs. 5 and 6) are presented as graphic trends and subsequent analyses do not have strict statistical validity.

Digestion Times Versus Temperature

Digestion times were pooled to examine the effects of temperature and single versus multiple prey ingestion (Fig. 6). There was no apparent correlation between chaetognath length and gut clearing time at either experimental temperature regardless of the number of prey ingested (Kendall's Tau Test, Hollander and Wolfe, 1973; $p > 0.2$ in all cases). The average digestion time for all experiments combined is 69.2 minutes (Fig. 6A). Mean digestion times at 21°C and 25°C were

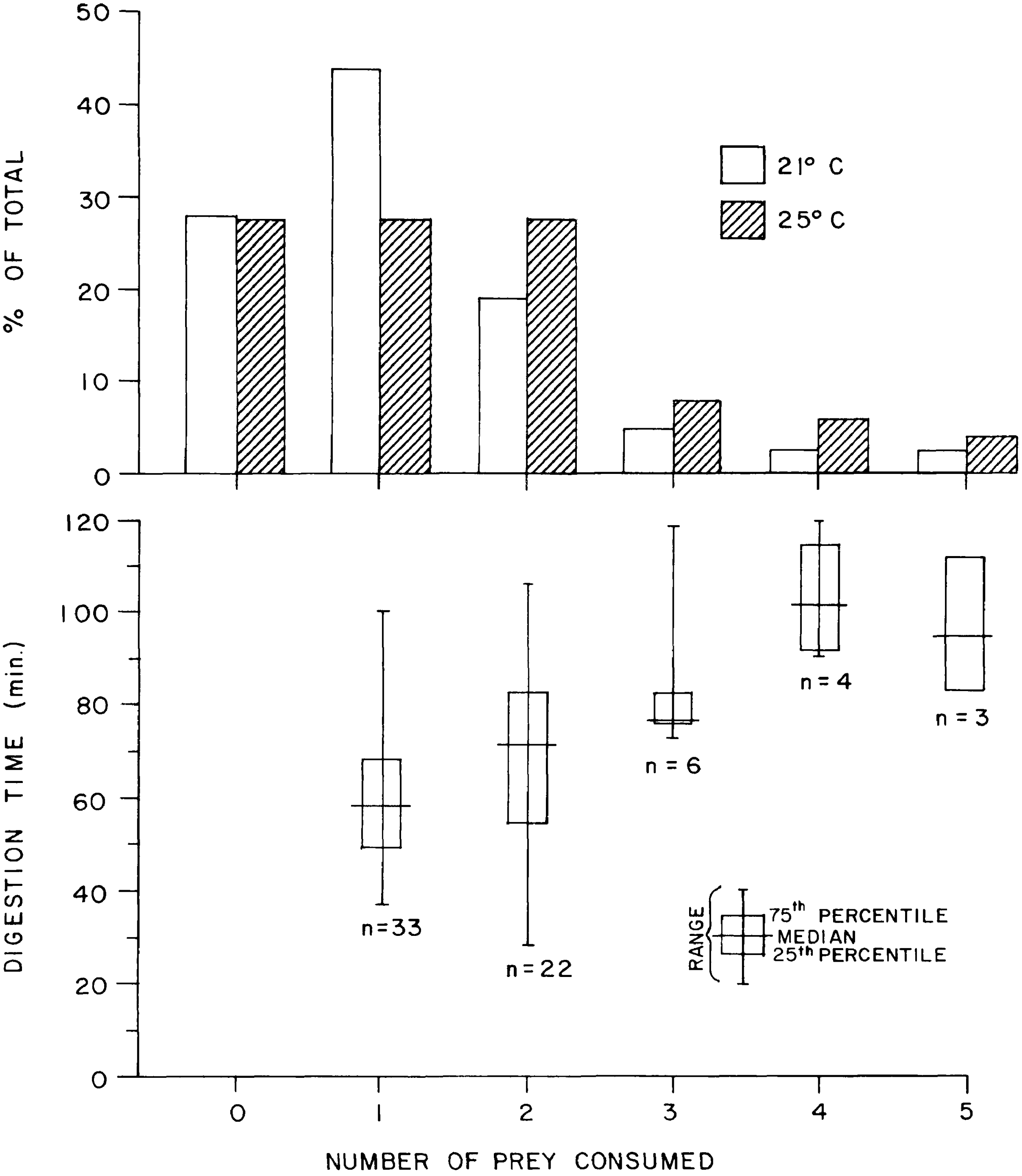

Figure 5. The percentages of Sagitta tenuis feeding during experimentation and digestion time versus the number of prey consumed.

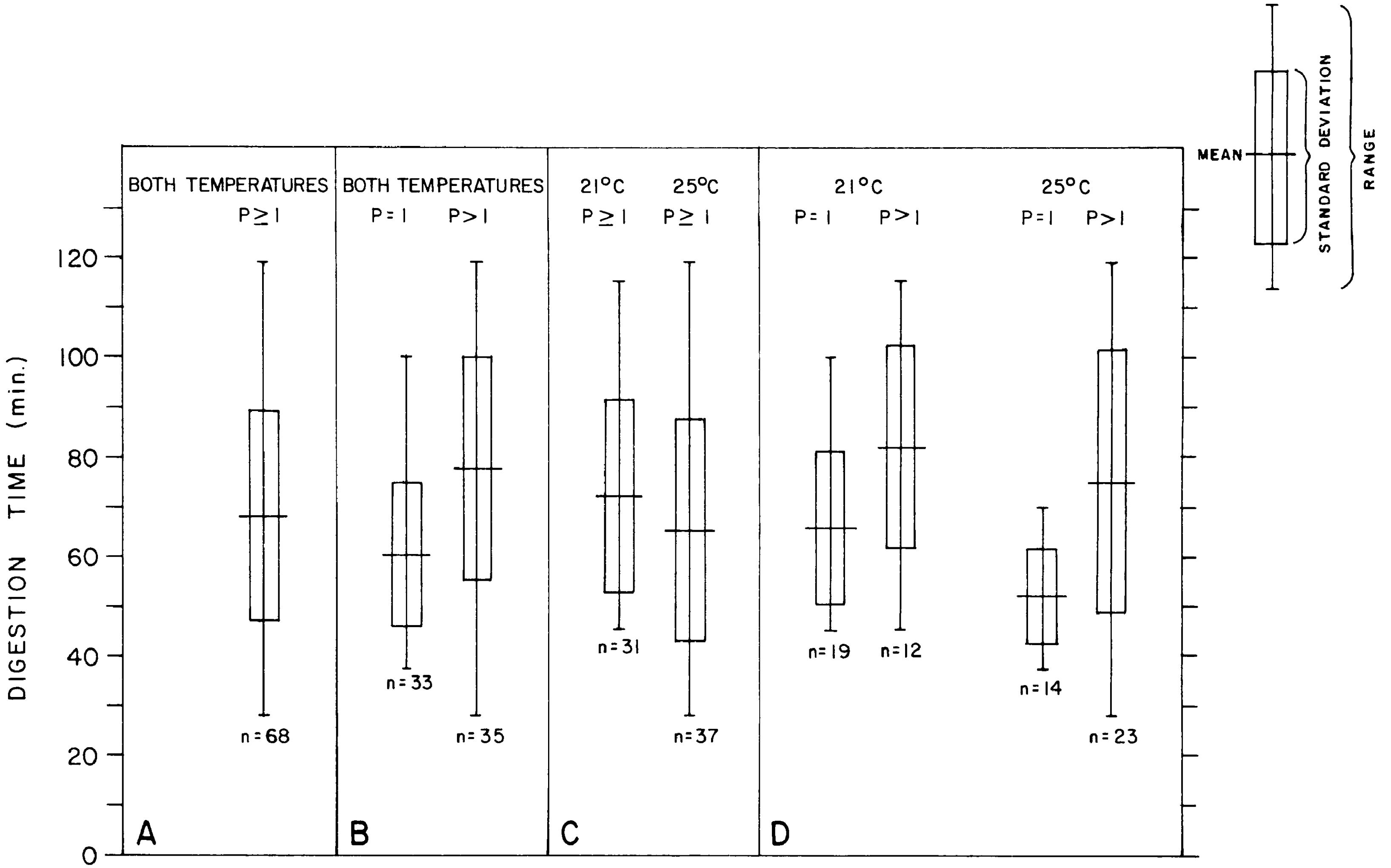

Figure 6. Digestion times for *Sagitta tenuis* pooled by experimental temperature and the number of prey consumed P=1, single prey consumed; P>1, two or more prey consumed.

not appreciably different (t-test, $t = 1.34$; $0.1 < p < 0.2$) and the variability of gut clearing seemed unaffected by differences in temperature ($F = 1.36$; $p < 0.05$).

Digestion Times Versus Number of Prey Consumed

Ingestion of multiple prey apparently increased the duration and variability of digestion. Mean digestion time was longer for chaetognaths consuming more than one prey (Fig. 6D) at both temperatures ($t_{21°C} = 2.50$; $0.005 < p < 0.01$; $t_{25°C} = 3.48$; $0.001 < p < 0.005$). Variation in digestion rate was also increased at 25°C ($F = 6.17$; $0.01 < p < 0.05$) but not at 21°C ($F = 1.78$; $p > 0.20$) by multiple prey ingestion. The two extreme observations of digestion time, 28 and 119 minutes, were for *S. tenuis* that had consumed two and three prey, respectively. If experimental temperatures are pooled (Fig. 6B), the differences in sample variation are still apparent ($F = 2.31$; $0.01 < p < 0.05$). The mean digestion time for single and multiple prey ingestion (pooled temperatures) are 60.1 and 77.3 minutes, respectively.

DISCUSSION

The feeding behavior of *Sagitta tenuis*, like that of other chaetognaths, appears to be a stereotyped response to specific prey vibrations over a limited distance (Feigenbaum and Reeve, 1977). Although experimental conditions were not controlled during observation, the requirement for motile prey in close proximity to elicit chaetognath response was evident in this study. *Sagitta tenuis* was not directly observed to feed on dead prey items even though these were frequently encountered during the feeding period. Reeve (1964, 1966) reported that *S. hispida* would not consume particulate detritus, several species of phytoplankton, or thermally killed zooplankton in the laboratory but readily ingested live zooplankton and *Artemia* nauplii. Kuhlmann (1977) investigated ichthyoplankton predation by *S. elegans* and *S. setosa* and found fish eggs and yolk-sac larvae were not eaten; the young fish remain motionless most of the time and apparently go undetected.

Vibration perception by chaetognaths is a mechanoreceptive function of the 'stiff cilia' (Horridge and Boulton, 1967) or 'hair fans' (Feigenbaum, 1978) distributed over the external epithelium. Horridge and Boulton (1967) were able to induce the benthic *Spadella cephaloptera* to attack a vibrating glass probe from a distance of 1 to 3 mm. A peak response was noted in the frequency range reported for copepod swimming (Newbury, 1972). Feigenbaum (1977) repeated this work with *S. hispida* and *Spadella schizoptera* and found the attack distance to be similar but with no clear frequency preference for copepods even though they are the most common prey in the diet. In the present study, attacks were observed only when copepods swam to within several millimeters of the chaetognath's anterior end. Prey approaching the mid-body or caudal area were not seized and caused a rapid swimming (escape?) response by *S. tenuis*.

Once ingested, prey items are quickly pushed to the posterior gut by peristaltic contraction of the intestine. Food passage may be very rapid, as little as 8 seconds in duration for *S. hispida* (Cosper, 1973). This process usually lasted 6 to 12 minutes for *S. tenuis*, comparable to times reported for *Spadella cephaloptera* (Parry, 1944) and *Sagitta elegans* (Kuhlmann, 1977). All prey copepods were swallowed headfirst, apparently as protection against urosomal spines (Nagasawa and Marumo, 1972).

The location of prey in the gut during digestion is an important consideration for evaluating the extent of cod end feeding in field collected samples. Eliminating those items not found in the posterior gut may exclude recently ingested prey depending upon the length of the haul and subsequent fixation. Similarly, if the food bolus traverses the length of the gut during normal digestion, natural prey items may be eliminated from analyses. During these experiments, prey remained in the posterior gut until defecation without movement in the intestine (Cosper, 1973) or undergoing "more limited movements" as Reeve *et al.* (1975) described for *S. hispida*. As digestion proceeded, urosomal segments of prey copepods often 'telescoped' into cephalothoracic segments as interior tissues were digested away, leaving only the exoskeletal outlines visible at defecation. The fecal pellets produced by *S. tenuis* are at least superficially identical to those reported for *S. hispida* (Cosper, 1973; Cosper and Reeve, 1975; Reeve *et al*., 1975). They are slightly opaque, sticky, and covered with a peritrophic membrane having a distinct tail on the end emerging last from the anus. Based on observations on the entire digestive process and criteria from Feigenbaum, (1979a and personal communication), the state of digestion for food items could be evaluated as early, intermediate, or late. These categories will be discussed in a later section on gut content analyses of *S. tenuis*.

Digestion times for different chaetognath species, some without temperature observations, range from less than 1 to over 11 hours (Nagasawa and Marumo, 1972; Reeve and Walter, 1972a; Cosper and Reeve, 1975; Kuhlmann, 1977; Szyper, 1976; Feigenbaum, 1979a; Reeve, 1980). Those for tropical and subtropical *Sagitta* generally range from 2 to 4 hours, considerably longer than the overall mean of 69 minutes observed in these experiments. The only comparable value, reported by Szyper (1976) for *S. enflata* at 25°C, was indirectly obtained by a different methodology. In his study the percentage of fed animals in a laboratory population, isolated from further feeding, decreased linearly over time to a base level (represented by non-digestible-ciliates in the gut). A regression line fitted to these percentages over time intersected the base level at 0.99 hours. This contrasted with a directly observed digestion time of 3.17 hours at

23°C (Feigenbaum, 1979a) for larger S. enflata feeding on similar prey. The small temperature difference between the studies did not likely influence digestion times since the 4°C difference examined in this study was apparently insignificant.

Chaetognaths exhibit some predator/prey size specificity (Mironov, 1960; Rakusa-Suszczewski, 1969; Reeve and Walter, 1972a; Pearre, 1974, 1976, 1980; Szyper, 1978; Sullivan 1980) which may partially explain variation in digestion rate. Reeve and Walter (1972a) studied the selection of prey sizes in S. hispida and found young chaetognaths ingested proportionally larger prey than adults. Pearre (1980) summarized morphometric data for six species of Sagitta and their prey. He found the relationship of prey size selection is best described by a power curve of chaetognath head width to prey width. These studies show that larger chaetognaths generally select larger food items which may take longer to digest.

Gut clearing time may also be related to chaetognath size although conclusive laboratory evidence is lacking. Szyper (1978) stated that larger S. enflata have a greater digestive capacity than smaller individuals, i.e. they process a food item of a given size more quickly. This tends to offset the lengthening effect on digestion caused by selection of larger prey and leads to a more uniform digestion time for the population. In his study, the length-frequency distribution of fed chaetognaths did not change during digestion, indicating all individuals digested food at nearly the same rate. However, Reeve (1980) found an apparent increase in digestion time with increasing size in _S_. _hispida_. Chaetognaths 6 mm in length took twice as long to clear the gut as 1 mm specimens, apparently because they selected larger prey items. The assumption of greater digestive capacity with increasing chaetognath size and its relationship to prey size selection have yet to be experimentally verified. Feigenbaum (1979b) found no significant relationship between digestion time and the ratio of chaetognath weight:prey weight in _S_. _elegans_.

The quantity of food ingested, either as multiple prey or a single large prey, would seem to be the single greatest determinant of gut clearing rate. The resulting bolus presents less surface area to volume and would be expected to take longer to digest fully. Larger, soft-bodied prey have longer gut residences than crustacean prey despite exoskeletal hard parts of the latter. Szyper (1976) reported a qualitative increase in digestion time for _S_. _inflata_ feeding on _Oikopleura_ rather than copepods. During this study I observed a 10.4 mm long _S_. _tenuis_ cannibalize another 6.8 mm in length (after digestion). Digestion lasted 2.43 hours at 21°C, much longer than for single copepod prey (Figure 6B).

Ingestion of several small prey also lengthened digestion times. Prey sizes were not measured but late copepodite and adult stages of _Acartia_ _tonsa_ retained on the 202 μm mesh represent a fairly limited spectrum of prey sizes. The mean digestion time for _S_. _tenuis_ feeding on multiple prey is nearly 30% longer than for those consuming a single food item. Some additional evidence of gut clearing as a function of the number of prey ingested is provided by two specimens of *S. hispida* that were incidentally caught with *S. tenuis* and tested during this study. Digestion times for *S. hispida* 10.7 mm and 10.9 mm in length were 0.88 (1 prey, 25°C) and 2.29 hours (2 prey, 21°C), respectively. These are considerably shorter than digestion times reported for this species by Cosper (1973) and Cosper and Reeve (1975). They selected only those animals consuming three or more copepods during a 15 minute feeding period as a source for fecal pellets. Their reported digestion times of 3 to 4 hours probably overestimated those found in natural populations where chaetognaths usually consume one prey item at a time. Reeve (1980) later found a positive relationship between gut clearing time and number or weight of ingested prey. His values of digestion time for one and two prey items consumed by *S. hispida* are close to those observed in this study.

Nearly all studies of laboratory feeding of chaetognaths, including this one, show feeding rates in excess of those indicated from field collections. *Sagitta hispida* feeds actively in the laboratory, often ingesting four or more copepods at a time (*e.g* Cosper, 1973). Starvation effects and high prey densities used to induce laboratory feeding produce short term ingestion rates that, while not considered superfluous, are probably unnaturally high even for the 'batch feeding' mode of *Sagitta*. I have observed a starved *S. tenuis* consume six copepods within several minutes, a number not matched in the gut of any field collected specimen.

Because the feeding regimes of controlled laboratory environments are artificial, caution should be used when extrapolating observed results to chaetognath populations in nature. Digestion times obtained from laboratory specimens should be based upon the same prey types and numbers indicated from field collections.

SECTION III. ASPECTS OF FEEDING AND NUTRITIONAL ECOLOGY OF *SAGITTA TENUIS* IN THE LOWER CHESAPEAKE BAY

INTRODUCTION

Most information on the diet and feeding of chaetognaths has been derived from gut content analyses of preserved specimens. Copepods are recognized as the major prey constituent in nearly all studies (see Nagasawa and Marumo, 1976; Szyper, 1978; Newbury, 1978; Feigenbaum, 1979a; Sullivan, 1980). Other prey species, including cladocerans, tintinnids, appendicularians, larval fish, and other chaetognaths may be of seasonal or local importance.

Despite the natural transparency of chaetognaths and their habit of swallowing prey whole, gut contents may not accurately reflect the actual diet. Chaetognaths have been observed to 'feed' indiscriminately, grasping juvenile fish, large salps, or inanimate objects when confined at high densities in the net or exposed to preservative (Cosper, 1973; Feigenbaum, 1977). For this reason, undigested items in the anterior gut or mouth are usually considered artifacts of collection and not counted in dietary analysis. In addition, normal digestive processes themselves may confuse interpretation of preserved gut contents. Unidentified prey remains may not represent the same species proportions or size distributions as those identified if digestion selectively renders certain prey unrecognizable. Small, soft-bodied prey may go completely undetected or dissolve during preservation, lowering the observed frequency in the diet. Sullivan

(1980) found prey remains in 30% of apparently empty guts in *S. elegans*, suggesting cursory examination of chaetognaths may bias estimated diet towards digestion-resistant forms with recognizable hard parts.

Most species of *Sagitta* exhibit some diel rhythm in feeding rate as evidenced by the proportion of sampled individuals with food in the gut. The percentage of individuals containing food to total individuals usually ranges between 5% and 30% in daytime collections and often is significantly higher at night; the FCR (food containing ratio) is fairly consistent despite high variability in estimated prey abundance (Rakusa-Suszczewski, 1969; Reeve, 1970; Nagasawa and Marumo, 1972; Szyper, 1976; Sullivan, 1980). Reeve (1964) reported that *S. hispida* would feed more actively under nocturnal laboratory conditions than diurnal conditions.

Sagitta tenuis is a seasonal planktonic carnivore in the lower Chesapeake Bay. This geographic area represents nearly the northernmost limit of its range (Grant, 1963a). Its apparent tolerance of reduced salinity enables *S. tenuis* to penetrate further into the estuary and establish far greater numerical abundance than other summer-fall species. The growth and distribution of *S. tenuis* populations seems to be dependent upon suitable hydrographic conditions, particularly temperature and salinity, that occur during summer and fall (Grant, 1977; Jacobs, 1978; Canino, unpublished data). After its initial recruitment in June or July, *S. tenuis* breeds continuously in the Bay, reaching maximum densities during September

(Grant, 1977). Declining water temperatures during late fall retard maturation of adults and no overwintering population remains in the lower Bay (Grant, 1977).

The numerical densities attained by *S. tenuis* populations suggest it may be an important seasonal component in the lower Chesapeake Bay ecosystem. Grant (1977) found mean September densities of 161 m^{-3} and 78 m^{-3} during 1971 and 1972, respectively. A maximum of 666 individuals m^{-3} was recorded at one station. Peak abundance of *S. tenuis* occurs at a time when planktonic crustacean biomass is declining from high August levels (Jacobs, 1978). Chaetognath populations typically undergo a similar decline a month or two later. The trophic impact of *S. tenuis* on these dwindling prey stocks and the factors controlling abundances of both predator and prey are not well understood.

The dietary composition and feeding behavior of *S. tenuis* in the lower Chesapeake Bay are described here from gut analyses of preserved collections. The results are combined with those of earlier sections of this study regarding chemical composition and digestion time to predict a daily ration (number of prey consumed/chaetognath/day) and specific daily ration (weight of prey consumed/chaetognath weight/day) for this species. These food rations are compared with those of other species, particularly *S. hispida* and *S. enflata*, which occur seasonally with *S. tenuis* in the lower Bay.

METHODS AND MATERIALS

Field Collections

Zooplankton samples were collected over a two day period from August 23 to August 25, 1978 as part of the Lower Bay Zooplankton Monitoring Program of the Virginia Institute of Marine Science. Station locations (Figure 7) were chosen randomly prior to the cruise, usually ten each for day and night sampling. Stepped oblique tows from near bottom to surface were made with 60 cm bongo nets (202 μm and 333 μm mesh Nitex). Tows were of approximately 5 minutes duration, depending upon the degree of mesh clogging by ctenophores and hydromedusae. Typically, from 50 m^3 to 200 m^3 were sampled by each net. In addition, a one meter neuston net (WHOI-type) with 333 μm mesh sampled the upper 12 cm of the water column for a 10 minute tow. Collections were concentrated and preserved in an 8% buffered formalin seawater solution.

Dietary Analysis

In the laboratory, whole samples were examined for large and rare taxa, then successively split to smaller aliquots to enumerate numerous zooplankton groups. The stations, gear, aliquot, and time of collection for samples examined in this study are listed in Table 4. Where low numbers of chaetognaths appear from fractional

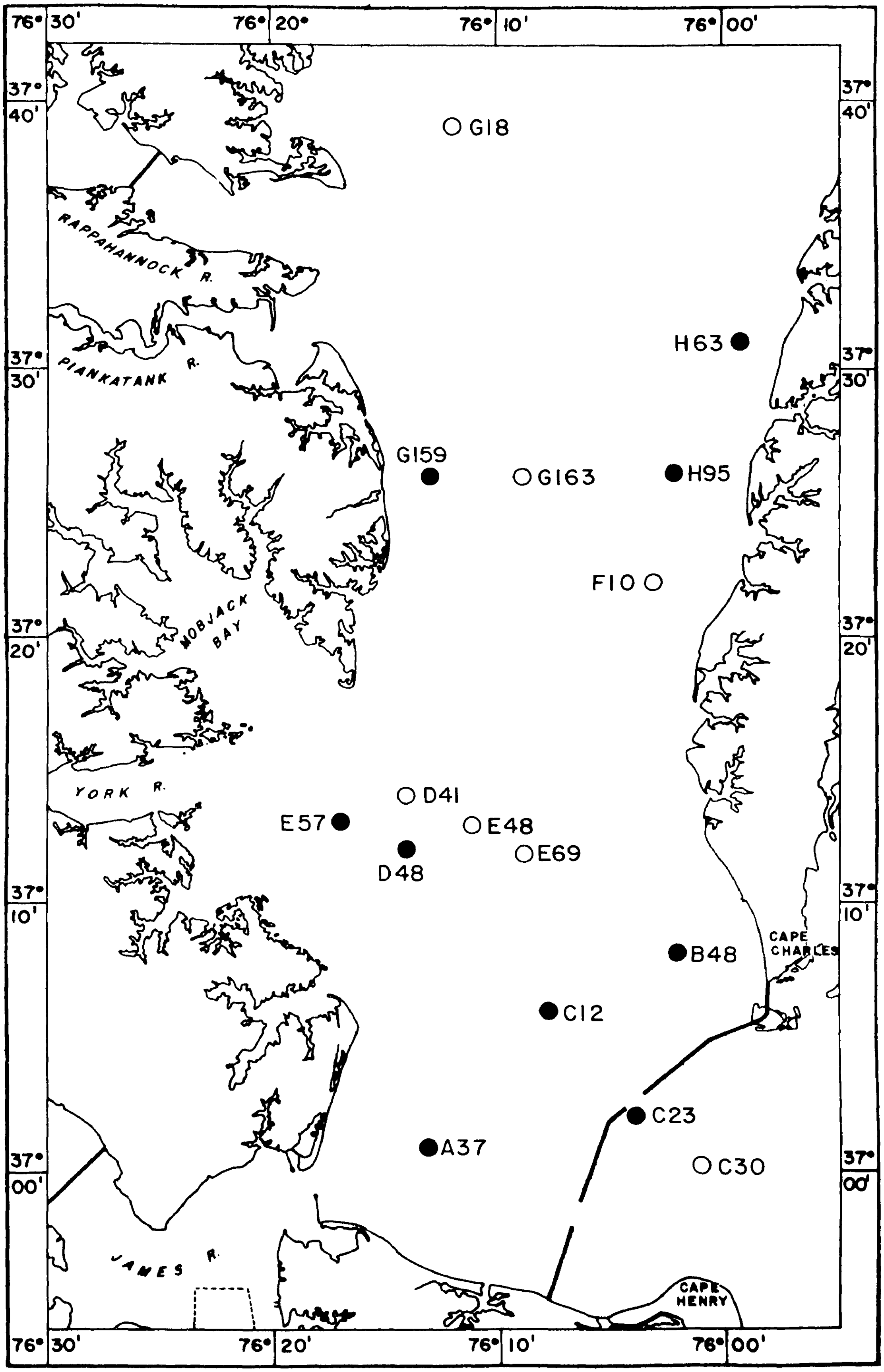

Figure 7. Stations sampled during LBZMP-04 cruise August 23-25, 1978. Open circles, day stations; dark circles, night stations.

Table 4. Sampling date, time of collection, gear and number of *S. tenuis* examined in this study. See text for gear descriptions.

Station	Date	Time (EST)	Gear	Aliquot	n
D41	23 Aug. 78	1920	B202	1/8	12
G18	"	0945	B333	1/4	42
G163	"	1200	B333	1/1	60
F10	"	1440	B333	1/1	55
			B202	1/1	54
E48	"	1740	B333	1/1	103
E69	"	1840	B333	1/1	108
			B202	1/1	104
C30	"	0820	B333	1/1	147
			B202	1/8	24
			Total Day Stations		709
D48	23 Aug. 78	2030	B333	1/1	39
E57	"	2130	B333	1/16	33
G59	"	0200	B202	1/1	20
H95	"	0340	N333	1/1	54
			B202	1/16	12
H63	"	0430	B333	1/1	84
A37	24 Aug. 78	2315	N333	1/1	83
			B333	1/1	156
C12	25 Aug. 78	0100	N333	1/1	28
			B333	1/1	134
B48	"	0230	N333	1/1	30
			B333	1/1	154
C23	"	0435	B333	1/32	44
			B202	1/32	53
			Total Night Stations		924
			Total All Stations		1633

splits, larger aliquots were not available for gut content analyses. Chaetognaths were identified and the stage of maturity estimated (Grant, 1977). Total length (excluding caudal fin) was measured to the nearest 0.1 mm using a dissecting microscope with ocular micrometer at 20X magnification. The gut was dissected from each specimen and examined for prey items. If food was present, the bolus was gently teased apart with fine dissecting pins to identify the number and type of ingested prey. Food items were assigned to one of five prey categories: copepod, cladoceran, chaetognath, unidentified crustacean, or unidentified 'other'. The prosomal length of prey copepods was measured to the nearest 0.02 mm when they could be removed from the gut intact. Chaetognath head width (at widest point with hooks in the closed position) was also measured to the nearest 0.02 mm on all undamaged specimens containing food.

Prey items were judged to be in early, intermediate, or late stage digestion based upon their position, transparency, and compaction in the gut. Criteria for these classifications were based on information from Sullivan (1977), Feigenbaum (1979a and personal communication), and prior observations of digestion in *S. tenuis*. These stages are described for copepods, the item most frequently encountered in the guts:

Early Stage: prey opaque and not compacted; eyespot usually still visible and musculature intact; prey often located in anterior gut or mouth;

Intermediate Stage: prey in posterior gut; exoskeleton fairly transparent with remnants of internal organs visible; some degree of exoskeletal compaction evident particularly if several prey in gut.

Late Stage: prey in posterior gut and completely transparent; no internal organs visible; prey compacted, often with urosomal segments 'telescoped' into cephalothoracic segments.

Sagitta tenuis were divided into 1 mm size categories. The percentage occurrence of food, total numbers of ingested prey, prey types, and stage of digestion of prey items were recorded for each chaetognath size class.

The prosomal length of prey copepods was used to examine prey size selectivity of *S. tenuis*. In cases of multiple prey ingestion, each prey measurement was treated as an independent observation; that is, each prosome length (Y) was paired with headwidth (X) regardless of the number of prey ingested. A linear regression of logarithmic values of copepod prosomal length on chaetognath head width for 252 prey items showed no significant correlation ($r^2 = 0.10855$) of prey to predator size. Pearre (1980) found prey selection by six species of *Sagitta* was best described by the equation $H = aP^b$; where H is the maximum width of the prey (mm); P is chaetognath head width (mm); and a and b are fitted constants. In this study the prosomal length rather than width was used in regression comparisons, and best fit ($r^2 = 0.10689$; $a = 0.2$, $b = 0.1$) for 25 pairs of coefficients, each ranging from 0.1 to 1.0, was no better than the linear regression of log transformed values.

Daily Ration and Specific Daily Ration

Daily food rations, expressed as the number of prey consumed/chaetognath/day, were calculated for each size class of _S. tenuis_ by the equation:

$$R = \frac{NPC\ (24)}{D}$$

where

R = daily ration

NPC = number of prey per chaetognath

D = digestion time in hours

The daily ration of _S. tenuis_, expressed as number of prey/chaetognath/day, was estimated from NPC values and the gut clearing rate. This method, first described by Bajkov (1935) for daily consumption by fish, has been subsequently used for predicting chaetognath rations (Nagasawa and Marumo, 1972, 1976; Szyper, 1978; Newbury, 1978; Feigenbaum, 1979a). Assuming that feeding rates are constant throughout the day, the daily ration was calculated from the average number of prey per chaetognath in each size class and a mean digestion time of 1.00 hour for a single copepod prey (Section II). If diel variation in feeding intensity was evident, half-daily rations were calculated by substituting 12 hours into the ration equation with mean daytime and nighttime NPC values and summing for a total daily ration.

Specific daily rations, in terms of the weight of prey consumed/chaetognath/day, were calculated for each size class of _Sagitta tenuis_. Several simplifying assumptions were made to account for unidentified or unmeasurable components in the diet. First, all prey items were considered to be the copepod _Acartia_ _tonsa_, for reasons explained in the Results section. Secondly, a mean prey weight was used in all calculations of specific daily ration. Although there was a trend for larger chaetognaths to ingest larger prey, the relationship was not predictive enough to improve ration estimates. The mean prosomal length of prey copepods was used to predict a mean prey weight. Assuming a 5 to 1 prosome length: total length ratio for _A_. _tonsa_ (Conover, 1956), a mean prey length was derived. A mean prey dry weight was calculated according to Heinle's (1966) length-weight regression equation for copepodid and adult stage _A_. _tonsa_.

Chaetognath dry weights were calculated from the midpoint of each size category (_e.g_. 4.5 mm for the 4.0 to 4.9 mm size class) using the predictive linear regression derived earlier in this study (Table 1). Carbon and nitrogen percentages of dry weight were 33.1% and 9.9%, respectively, for _S_. _tenuis_ less than 6 mm in length and 40.5% and 11.4% for larger specimens (Table 2). Copepod prey were assumed to have carbon and nitrogen contents of 41.6% and 9.6% of dry weight (Beers, 1966).

RESULTS

Collections from the different nets were pooled by station. The length-frequency distributions of chaetognaths captured by each were not significantly different (Mann Whitney test, $p > 0.05$ in all cases). The smallest size class (3.0 to 3.9 mm), most likely affected by mesh differences, and the largest (10.0 to 10.9 mm), were eliminated from analysis due to insufficient numbers of _S. tenuis_.

From the 1578 chaetognath guts examined, 351 prey items were recovered. Ten prey items (2.8%), judged to be in early stage digestion were not considered in dietary analyses. Of the total sampled population, 284 _S. tenuis_ had food in their guts, yielding an overall food containing ratio of 0.217. The mean number of prey per chaetognath (NPC) was 0.239, slightly higher than the FCR due to multiple prey ingestion by some chaetognaths; 260 chaetognaths (16.5%) contained 1 food item; 20 (1.3%) had 2 prey; 3 (0.2%) had 3 prey, and 1 specimen (0.06%) contained 4 prey items. Most (89.4%) of the food items were judged to be in an advanced stage of digestion. Prey classified in the intermediate stage comprised the remaining 10.6% and appeared with greater frequency in larger chaetognath size classes. When prey in the intermediate stage of digestion occurred with late stage items, they were usually not included in the same food bolus, indicating the fecal pellet membrane had probably formed prior to their ingestion.

The diet of S. tenuis was uniform with copepods accounting for 91.8% of total gut contents. Unidentified crustacea and 'other' prey constituted 2.9% and 4.4% of the total, respectively. Cladocerans and other chaetognaths were minor contributors to the diet, together totaling less than 1%. The percentage occurrence of these prey in the guts of each chaetognath size class are listed in Table 5. Copepods fragmented during digestion or dissection (13.8%) were not measured but simply listed. The percentage of copepods in the guts increased with increasing chaetognath size with a general trend toward ingestion of larger copepods. Corresponding decreases in the unidentified crustacean and 'other' categories suggest prey in the guts of large S. tenuis were more easily identified than those in small specimens.

Diel variation in feeding rate by S. tenuis was examined by comparison of FCR and NPC values in day and night samples (Table 6). Nearly all S. tenuis with food in daytime collections had a single prey item; the FCR and NPC values were identical except for the 8.0-8.9 mm size class. An ANOVA test, weighted by the numbers of individuals in each size class, showed the mean NPC values were significantly different ($F_{day} = 51.19$, $0.001 < p < 0.005$; $F_{night} = 25.77$, $0.005 < p < 0.01$). The FCR and NPC values were transformed to arcsin values (Sokal and Rohlf, 1969). Mean $\arcsin\sqrt{FCR}$ and $\arcsin\sqrt{NPC}$ were significantly greater at night than during the day ($t_{FCR} = 4.53$, $0.001 < p < 0.005$; $t_{NPC} = 2.28$, $0.01 < p < 0.05$). The variances of $\arcsin\sqrt{NPC}$ values did not differ significantly between day and nighttime samples ($F = 2.12$, $0.2 < p < 0.5$).

Table 5. Percentages of various dietary constituents for six size classes of Sagitta tenuis

S. tenuis size class (mm)	no. examined	copepod size class*				cop. frag.	total	unid. crust.	unid. other	clad.	chaet.	state of digestion	
		0.2	0.4	0.6	0.8							Inter.	Late
4.0-4.9	149	35.3	41.2			5.9	82.3	5.9	11.8			5.9	94.1
5.0-5.9	260	28.3	28.3	10.9		19.5	87.0	4.3	6.5		2.2	6.5	93.5
6.0-6.9	400	13.3	37.4	22.7		16.0	89.3	4.0	5.3	1.3		9.3	90.7
7.0-7.9	448	4.3	42.5	28.7	2.1	16.0	93.6	2.1	4.3			13.8	86.2
8.0-8.9	258	2.4	53.7	33.0		6.1	95.1	2.4	1.2	1.2		17.1	82.9
9.0-9.9	63		55.6	33.3	3.7	3.7	96.1		3.7			11.1	88.9

* Copepods in the 0.2 mm size class have prosomal lengths between 0.2-0.39 mm, etc.

Table 6. The food containing ratio, number of prey per chaetognath and daily ration for six size classes of *Sagitta tenuis*. FCR = food containing ratio; NPC = number of prey per chaetognath; R = daily ration in number of prey consumed/chaetognath/day

Chaetognath size class (mm)	Number with prey	Number w/o prey	FCR	Number of prey items	NPC	1/2 R	Total R
DAY							
4.0-4.9	10	97	0.093	10	0.093	1.12	3.12
5.0-5.9	21	131	0.138	21	0.138	1.66	3.43
6.0-6.9	21	141	0.130	21	0.130	1.56	4.28
7.0-7.9	25	122	0.170	25	0.170	2.04	4.79
8.0-8.9	15	67	0.183	17	0.207	2.48	6.91
9.0-9.9	4	11	0.267	4	0.267	3.20	8.70
		mean	0.163	mean	0.167		
NIGHT							
4.0-4.9	7	35	0.167	7	0.167	2.00	
5.0-5.9	24	84	0.222	25	0.231	2.77	
6.0-6.9	52	186	0.218	54	0.227	2.72	
7.0-7.9	62	239	0.206	69	0.229	2.75	
8.0-8.9	51	125	0.290	65	0.369	4.43	
9.0-9.9	20	28	0.417	22	0.458	5.50	
		mean	0.253	mean	0.280		

Arcsin$\sqrt{\text{NPC}}$ values were regressed on the midpoint of each chaetognath size class (Fig. 8) and the following relationships were obtained:

$$\text{daytime arcsin}\sqrt{\text{NPC}} = 6.73 + 2.45\ (\text{TL})$$

$$\text{nighttime arcsin}\sqrt{\text{NPC}} = 7.94 + 3.39\ (\text{TL})$$

where

NPC = mean number of prey/chaetognath

TL = chaetognath total length in mm

The regression statistics for these equations are presented in Table 7. The slopes of the regression lines for daytime and nighttime samples were both significantly different than 0 ($F = 60.38$; $p << 0.001$; $F_{night} = 22.04$, $0.005 < p < 0.01$) and not significantly different from each other ($t = 0.08$, $p > 0.4$). These results indicated that a larger fraction of the chaetognath population will contain food at night. In addition, larger S. tenuis tend to ingest more prey per individual than small ones regardless of the time of day.

The daily rations for each S. tenuis size class are given in Table 6. Since the mean of NPC values was significantly larger at night, half-daily rations were computed from day and night NPC values and summed for a total daily ration. As expected, rations for mature chaetognaths are substantially greater than those for small ones. Mean day and night NPC values for the entire population were 0.167 and 0.280, respectively, yielding an overall daily ration of 5.36 prey/chaetognath/day.

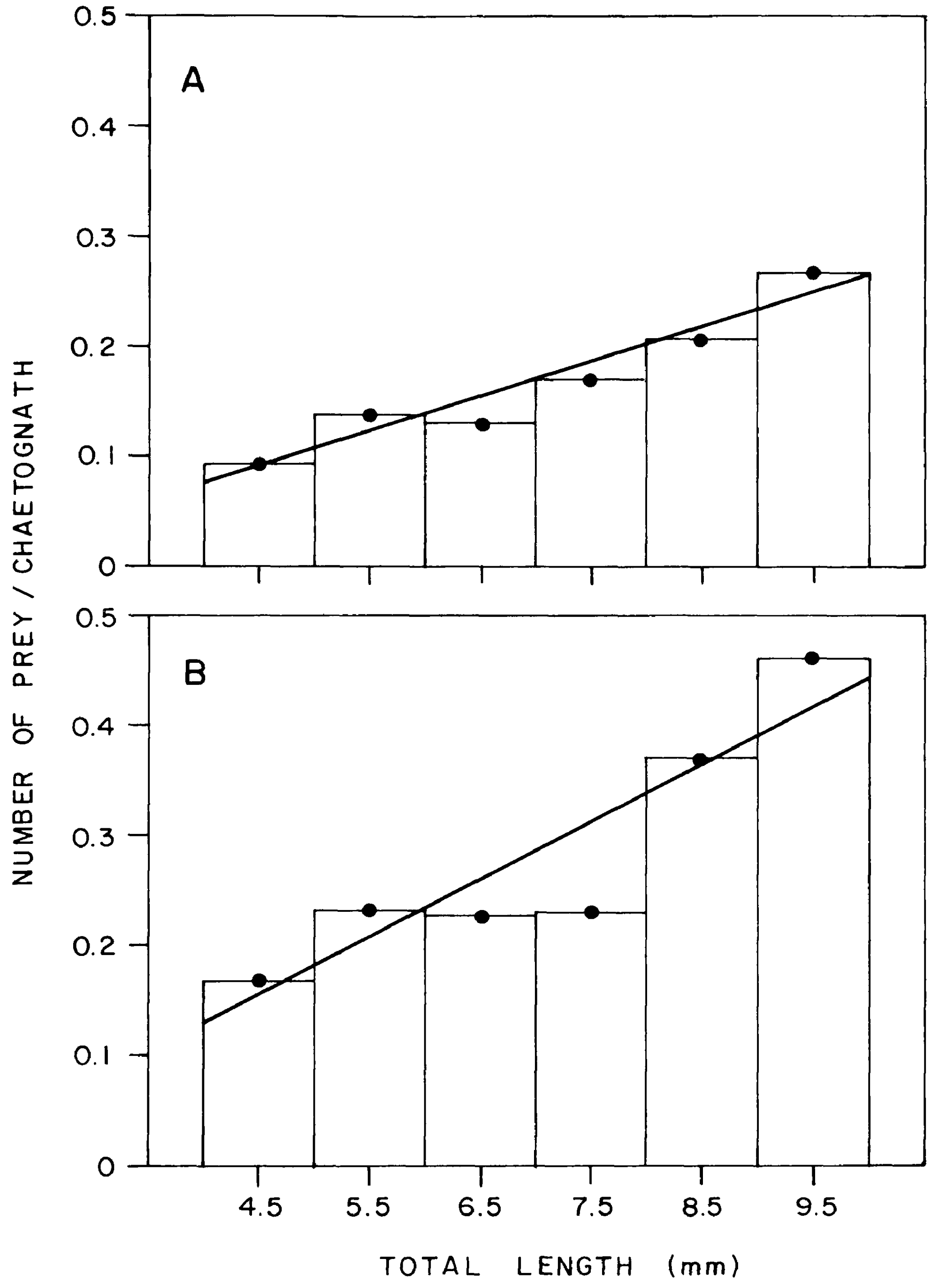

Figure 8. Histograms of the number of prey per chaetognath (NPC) for each *Sagitta tenuis* size class. A linear regression of NPC on chaetognath length is based on the midpoints of the size classes. A, daytime collections; B, nighttime collections.

Table 7. Regression statistics for $\arcsin\sqrt{NPC}$ against total length of *Sagitta tenuis* from daytime and nighttime samples.

	a	b + 95% c.i.	std. err. of regression	$S_{y \cdot x}$	r^2	n
Day NPC	6.727	2.45 ± 0.87	0.25	1.07	0.938	6
Night NPC	7.944	3.39 ± 0.72	0.73	3.04	0.919	6

Specific daily rations for *S. tenuis* were based upon an average dry weight for copepod prey. Gut content analysis showed that copepods were nearly the only dietary constituent for large *S. tenuis* but represent a lower fraction in the diet of small chaetognaths. Few prey identifications were made in this study due to the advanced digestion of most food items. *Acartia tonsa* was the only copepod species recognized among the few prey items judged to be in the intermediate stage of digestion. This species numerically dominated the crustacean zooplankton at the stations sampled. A mean prey dry weight of 4.14 μg was calculated from the mean prosomal length (0.60 mm) of copepods found in the guts (Table 5). This copepod weight is similar to the mean of 4.03 μg dry weight for adult and copepodid stages of *A. tonsa* reported by Heinle (1966).

The specific daily ration, in terms of dry weight, ranged from 0.214 for the 9.0 to 9.9 mm size class to 0.644 for the 4.0 to 4.9 mm size class with a mean value of 0.358 (Table 8). The specific rations for carbon and nitrogen exhibit similar decreases with chaetognath size, averaging 0.412 and 0.327, respectively. Abrupt declines from the 5 to 6 mm size categories reflect differences in calculated carbon and nitrogen content of *S. tenuis* and inaccurately portray what is probably a more gradual decrease.

Table 8. Specific daily rations of dry weight, carbon and nitrogen for six size classes of *Sagitta tenuis*. All rations are based on a mean copepod weight of 4.14 g. DW = dry weight; C = carbon weight; N = nitrogen weight; SDR = specific daily ration

Size class (mm)	*S. tenuis* composition			Ration composition			SDR = ration composition / predator composition		
	DW (μg)	C (μg)	N (μg)	DW (μg)	C (μg)	N (μg)	DW	C	N
4.0-4.9	20.07	6.64	1.98	12.92	5.37	1.24	0.644	0.809	0.626
5.0-5.9	35.52	11.75	3.51	18.34	7.63	1.76	0.516	0.649	0.501
6.0-6.9	57.12	23.16	6.51	17.72	7.37	1.70	0.310	0.318	0.261
7.0-7.9	85.81	34.79	9.77	19.83	8.25	1.91	0.231	0.237	0.195
8.0-8.9	122.49	49.67	13.95	28.61	11.90	2.75	0.234	0.240	0.197
9.0-9.9	168.07	68.15	19.14	36.02	14.98	3.46	0.214	0.220	0.181

DISCUSSION

The gut contents of *Sagitta tenuis* were homogeneous with respect to the type of ingested prey. Nearly all identified food items were copepods, as expected, occurring in the gut as single prey items. This is consistent with prior dietary studies of *Sagitta* (see Nagasawa and Marumo, 1976 for review; Szyper, 1978; Feigenbaum, 1979a; Sullivan, 1980). The extent to which gut analyses accurately describe the diet depends upon several assumptions which may not have been strictly met in this study. Pearre (1974) lists the following criteria necesary if gut contents are to reflect truly the actual diet:

a) Digestion is uniform in duration for all prey items.

b) All prey in chaetognath guts are equally identifiable.

c) Ingested but unidentified prey remains represent the same species and proportions of species as those which were identified.

Digestion times for *S. tenuis* feeding on copepods and a discussion of factors influencing this process were presented in Section II. No observations were attempted for soft or hard-bodied microzooplankton, a size fraction that may be of considerable importance for juvenile chaetognaths (Murakami, 1966; Mironov, 1960; Reeve, 1970; Reeve and Walter, 1972a).

The percentage contribution of copepods to the diet increased with increasing chaetognath size. Corresponding decreases in the unidentified crustacean and 'other' categories suggest that all prey items were not equally recognizable, especially in the smaller size classes. Large copepods selected by large *S. tenuis* aided identification but their percentage increase does not simply reflect redistribution of unidentified prey frequencies. Some fraction of the unidentified 'other' prey may have been parasites. In some specimens, spherical, opaque objects, resembling detached ova, were found in the gut lumen. During morphometric analyses (Section I) small flatworms, approximately 75 to 130 μm in length, were observed swimming in the gut or body cavity of live *S. tenuis*. One individual was dissected out and tentatively identified as *Derogenes* sp., a digenetic trematode having *Sagitta* as an intermediate host (Szypek, personal communication). Preserved specimens of *Derogenes* sp. may have been the amorphous objects mislabeled as prey.

Cladocerans and other chaetognaths were an insignificant part of the diet. Only two cladocerans, both *Penilia avirostris*, were found in the guts of two chaetognaths. Cladocerans were present in only 13 of the 24 collections examined in this study. At stations where they occurred, cladoceran densities averaged roughly 0.1% of those of *Acartia tonsa*. However, at three stations, *Penilia avirostris* was the third most abundant crustacean zooplankter. The reason for their low incidence in the diet of *S. tenuis* is unknown. Pearre (1974) found cladocerans to be regular dietary components in three Mediterranean species of *Sagitta*.

The virtual absence of cannibalism in *S. tenuis* is surprising considering the population densities reached in the lower Chesapeake Bay and the high incidences of cannibalism observed in other chaetognath species (Stone, 1969; Rakusa-Suszczewski, 1969; Szyper, 1978; Feigenbaum, 1979). Boltovsky (1975) reported several instances of cannibalism among *S. tenuis* and *S. enflata* populations in the western South Atlantic. The ecological importance of intraphyletic or intraspecific predation is not well understood although it appears to be a significant energy source for some chaetognath populations (Stone, 1969; Szyper, 1978; Feigenbaum, 1979a). The relationship of cannibalism to relative abundance of other prey species is obscure (Szyper, 1976). It may occur in *S. hispida* if two individuals of a different size seize each other during cross fertilization (Reeve and Walter 1972b). *Sagitta tenuis* is probably not food limited during its seasonal occurrence in the Chesapeake Bay. It breeds prolifically during this period and whether cannibalistic behavior is reduced by frequent encounters with other prey species or suppressed by a specific recognition/inhibition response is unknown. Feigenbaum and Reeve (1977) found that two species of *Spadella* kept in the laboratory were rarely cannibalistic.

The observed variations in the gut contents of *S. tenuis* indicate feeding patterns consistent with those of other chaetognath species (Reeve, 1964; Pearre, 1973, 1974, 1980; Nagasawa and Marumo, 1976; Szyper, 1978; Feigenbaum, 1979a). In general, large chaetognaths ingested greater numbers of prey than small individuals. The FCR and NPC values become most divergent in the large chaetognath size classes at night (Table 6). The number of prey in each 'batch' ingested by S. tenuis rose steadily from 1.0 prey/batch in the 4.0 to 4.9 mm size class to a maximum of 1.3 prey/batch in the 8.0 to 8.9 mm category. In addition, a greater percentage of these were in an intermediate stage of digestion which suggests large S. tenuis were feeding more actively than small ones. Szyper (1976) found the food containing ratio to be independent of chaetognath size in S. inflata. Feigenbaum (1979a) later reported that FCR increased with increasing size in a Gulf Stream population of this species.

The nocturnal feeding rate of S. tenuis is nearly twice that of daytime feeding. This diel pattern is not always consistent within a species and may be coupled to prey distributions and vertical migration. Mironov (1960) found no daily feeding cycle for S. setosa in the Bay of Sevastopol although this species apparently fed more intensively by night than by day in the western North Sea and Irish Sea (Rakusa-Suszczewski, 1969). Nagasawa and Marumo (1976) reported two distinct feeding patterns for S. nagae in Suruga Bay; chaetognaths in the surface waters fed more intensively at night while those occupying bottom layers fed more actively during the day. Feeding in both groups was not correlated with prey abundance. The estimated numbers of natural prey populations, however, are generally not good measures of the densities available to the predator because of patchy distributions and therefore often show no relationship to feeding (Pearre, 1974; Szyper, 1976).

Sagitta elegans, a strong vertical migrator, exhibited higher nocturnal feeding rates in several different studies (Rakusa-Suszczewski, 1969; Pearre, 1973; Sullivan, 1980). Sullivan (1980) found feeding was unrelated to prey abundance or time of day in the juvenile *S. elegans* population which remained in the upper 25 m of the water column. Mature individuals occupied deeper water and exhibited greater vertical migration. The feeding intensity of adult chaetognaths, as evidenced by food containing ratios, increased with respect to prey abundance and time of day. Although migration was better correlated with temperature than with prey abundance, large *S. elegans* were absent from the surface waters during the day after feeding there at night. Sullivan suggested that visible reproductive structures in the adults may make them vulnerable to predation by visual predators near the surface.

Crypsis in planktonic communities is largely based on transparency (Zaret, 1972; Zaret and Kerfoot, 1975), chaetognaths with food in the gut may be subjected to increased predation pressure because of their enhanced conspicuousness. Pearre (1973) suggested that *S. elegans* may feed principally at night in order to avoid visual predators. Several explanations may be suggested for the diurnal variation of food containing ratios. Chaetognaths of a particular size may feed at a nearly constant rate while some proportion of fed individuals are selectively removed by predators during the day. Stenson (1980) reported differential fish predation on two species of *Chaoborus* larvae, whose appearance and feeding behavior closely resemble those of chaetognaths, in response to the degree of pigmentation and vertical migrations. Alternatively, reduced daytime feeding is a behavioral response to minimize vulnerability to visual predators. Vertical migration may be adaptive by allowing chaetognaths to follow prey distributions or as a predator avoidance mechanism. Zaret and Suffern (1976) found the migration of the copepod, Diaptomus gatunensis, was primarily a strategy to avoid fish predation. In addition, an energetic advantage may be gained by moving to cooler depths after feeding near the surface at night (McLaren, 1963).

The daily ration of S. tenuis is comparable to those for other subtropical chaetognaths. The food ration for the population (5.4 prey/chaetognath/day) is intermediate between those derived from experimental feeding of S. hispida (R = 10.0; Reeve, 1980) and S. enflata (R = 2 to 3; Feigenbaum, 1977). It also lies between the daily ration estimate of 2.2 for large Gulf stream S. enflata (Feigenbaum, 1979a) and the predicted ration of 7.4 for the smaller Kaneohe Bay population (Szyper, 1978). The proportions of S. enflata containing food were comparable in both studies. Large differences in digestion time (0.99 versus 3.17 hours), however, resulted in three-fold differences in predicted daily food consumption.

The specific daily rations calculated in Table 7 declined steadily with increasing chaetognath size. This trend reflects, in part, the higher metabolic requirements of young which have been shown for chaetognaths (Mironov, 1960; Szyper, 1978; Feigenbaum, 1979a; Reeve, 1980), the ctenophore genus Mnemiopsis (Kremer, 1975;

Reeve, 1980), and the copepod *Calanus helgolandicus* (Paffenhoffer, 1971). Declining specific rations in large chaetognaths also reflects increasing predator weight:prey weight ratios, and is exaggerated in the present study by use of a mean prey weight. *Sagitta tenuis* 4.0 to 4.9 mm long, for example, consumed no prey copepods with prosomal lengths greater than 0.6 mm. The mean prey weight (based on 0.6 mm prosomal length) may have inflated specific ration estimates for this size class. Reeve (1964) found that adult *S. hispida* consumed a maximum specific ration of 64.4% of its body dry weight per day feeding on *Artemia* nauplii. This level is attained only by the smallest *S. tenuis* examined in this study. Newly hatched *S. hispida* may ingest up to 20 times their body dry weight per day (Reeve, 1980). Nagasawa and Marumo (1972) reported a specific daily dry weight ration of 0.376 for *S. nagae*. Their calculation of daily ration was too large by a factor of two, however, and the corrected specific ration should be 0.189 (Feigenbaum, 1979a). Kuhlmann (1976) estimated a daily ration of 1.8 prey/chaetognath/day for *S. elegans* feeding in the laboratory which represented about 4% of body dry weight per day.

The mean specific carbon ration in this study is about 40% higher than that for *S. enflata* 12 to 20 mm long (Feigenbaum, 1979). *Sagitta tenuis* consumes, on the average, more than twice the number of prey that *S. enflata* does but contains proportionally more carbon. In contrast, nitrogen rations estimated for *S. enflata* in Kaneohe Bay (Szyper, 1978), where size classes overlap, are nearly 140% greater than those in the present study. Ration estimates by Szyper (1978) perhaps best illustrate the inaccuracy associated with use of a mean prey weight. Specific daily rations for nitrogen were based on a mean weight for prey chaetognaths which comprised 8.2% of the total diet. The nitrogen ration for 4 mm individuals (2.037) indicates they fed on prey chaetognaths much larger than themselves.

The advanced stage of digestion for 88% of the food items in the guts of *S. tenuis* suggests that the criteria followed in this study did not adequately characterize the digestive stages on a temporal scale. Dividing the digestive process into 'early', 'intermediate' or 'late' stages implies they are of somewhat equal duration. If so, more prey items should have been found in the intermediate stage of digestion.

The compaction and fragmentation of prey in the gut may also preclude rigorous accuracy in their measurement. Until a more predictive index of prey size selection in chaetognaths is developed, perhaps such as 'best fit' models of morphometric parameters (Pearre, 1980), the observed trends in food rations may be more meaningful than the actual values.

GENERAL DISCUSSION

Despite the gross physical similarities of planktonic chaetognaths, the chemical composition and morphometry of several *Sagitta* species exhibit significant variation that appears generally related to nutritional ecology and observed laboratory behavior. *Sagitta hispida* and *S. enflata* may be considered representative of 'rigid' and 'flaccid' morphometric types, respectively. The former has a relatively high dry weight:wet weight ratio (17%) and high carbon and nitrogen contents. *Sagitta hispida* is an active, negatively bouyant species that feeds readily in the laboratory (Reeve, 1964; Reeve and Walter, 1972a). Its maximum daily ration (10 prey/chaetognath/day) (Reeve, 1980) is among the highest predicted for the several chaetognaths studied to date.

In contrast, *S. enflata* exemplifies a tumid, watery chaetognath. Morphometric and biochemical parameters approach those of other gelatinous zooplankton taxa (Curl, 1962; Beers, 1966). The few laboratory observations on this species (Cosper, 1973; Feigenbaum, 1979a) indicate it is neutrally bouyant and rather passive. Daily rations for large *S. enflata* (Feigenbaum, 1979a) are about one-third of the maximum ration predicted for *S. hispida* (Reeve, 1980), perhaps reflecting lower nutritional requirements. Another flaccid species, *Pterosagitta draco*, has an estimated ration of one prey item per day (Newbury, 1978). However, Reeve (1980) reported a maximum daily ration of 10 prey/chaetognath/day for *S. enflata* based upon laboratory feeding.

Sagitta tenuis is a 'rigid' chaetognath though less massive than *S. hispida* of similar size. Carbon and nitrogen contents, on a dry weight basis, are slightly less than for *S. hispida* but the dry weight:wet weight ratios for 6 mm *S. tenuis* and *S. enflata* are nearly identical. The daily ration predicted for *S. tenuis* (5.3 prey/chaetognath/day) in this study is intermediate between those for small (Szyper, 1976) and large (Feigenbaum, 1977) individuals of *S. enflata* based upon field collections. Although prey weight is a more accurate indicator of ration than prey number, gut analyses indicate the nutritional requirements of *S. tenuis* lie roughly between those for *S. enflata* and *S. hispida*.

An examination of daily rations and recorded abundance suggests *Sagitta tenuis* is of minor trophic importance in the lower Chesapeake Bay. The large copepod standing stocks and high turnover rates during its seasonal occurrence (Bowman, 1961; Heinle, 1966; Jacobs, 1978) seem to belie any large impact on prey populations. Correlations of predator and prey abundances were not made by station in this study, but some general inferences may be drawn from mean densities recorded in this and other surveys.

At all 16 sampling sites, *Acartia tonsa* was the numerically dominant copepod species with a mean abundance of 3159 individuals m^{-3}. *Sagitta tenuis* averaged 9 m^{-3} at the same stations.

Assuming 6.0 mm as a mean length for the chaetognaths and a mean copepod dry weight of 4.14 μg, *S. tenuis* biomass is 3.7% of the standing stock of *A. tonsa*. The specific daily ration for this size class (Table 8), if applied to the entire population, indicates *S. tenuis* removes about 1.2% of the copepod biomass daily.

The samples in this study were not taken during September, the month of peak chaetognath abundance. Reports by Grant (1977) and Jacobs (1978) from the same area suggest *S. tenuis* does not consume more than several percent of copepod standing stocks. Jacobs (1978) found *A. tonsa* comprised 97.1% and 95.4% of total copepods in September surveys of the lower Bay during 1971 and 1972, respectively. Grant (1977) reported mean *S. tenuis* densities of 161 m^{-3} and 78 m^{-3} for the same collections. I applied a mean weight and production estimate for adult and copepodite *A. tonsa* (Heinle, 1966; Tables 6 and 7) to the abundance data. Based on previous calculations, *S. tenuis* consumed from 1% to 4% of copepod biomass each day, representing approximately 5% to 15% of daily production. These rough estimates are comparable to the predicted consumption of 6.1% of copepod production by *S. enflata* in the Gulf Stream and 12% for the chaetognath community there as a whole (Feigenbaum, 1977). Reeve and Baker (1975) estimated that 100% of copepod production in Card Sound could be removed by *S. hispida*, an area where Reeve (1966) had previously attributed an August paucity of that species to declining macroherbivore stocks below densities of 200 m^{-3}. It is unlikely that *S. tenuis* is ever food limited during its seasonal tenure in the lower Chesapeake Bay. Copepod densities rarely fall below 1000 m^{-3} from

June through November (Jacobs, 1978), and chaetognath populations seem to obtain maximum food rations at fairly low ambient food concentrations (Reeve, 1980).

Although chaetognaths are undoubtedly important predators in many marine ecosystems, the nutritional ecology of most *Sagitta* populations is still not well understood. Evidence presented in this study indicates that the seasonal trophic impact of *S. tenuis* on macrozooplankton populations is less than that of other planktonic carnivores, such as *Mnemiopsis* (Burrell, 1968; Miller and Williams, 1972; Heinle, 1974; Reeve and Walter, 1978). It is hoped that the data given herein for *S. tenuis* will also provide a basis for evaluating its trophic importance where it occurs as a permanent resident of the zooplankton community.

CONCLUSIONS

1. The length-weight relationships and chemical content of *Sagitta tenuis* were similar to those of other 'rigid' type chaetognaths. Dry weight averaged 12.5% of wet weight and the percentage decreased with increasing chaetognath size. Mean carbon and nitrogen percentages of dry weight were 36.8% and 10.6%, respectively. The content of these elements were proportionally higher in chaetognaths longer than 6 mm, perhaps reflecting the presence of reproductive structures in mature animals.

2. Gut clearing times of *S. tenuis* in the laboratory were variable and showed no apparent relationship with chaetognath length or temperature. Digestion time, in general, seems to be related to the amount of food consumed. There was an apparent increase in digestion time for chaetognaths as a function of the number of prey consumed at both experimental temperatures. Mean digestion times for a single and multiple prey items were 1.00 hr and 1.29 hr, respectively.

3. Copepods were the major dietary component for *S. tenuis* and accounted for 92% of the total food items consumed. There was a general trend for large chaetognaths to select larger prey items

than small ones and most animals contained a single food item at a time. Cladocerans, other chaetognaths, and unidentified crustacean taxa were minor contributors to the total diet.

4. *Sagitta tenuis* exhibits a diel variation in feeding intensity. The fraction of the sampled population containing food in the gut was higher at night than during the day. The mean number of prey ingested per chaetognath generally increased with chaetognath size in both daytime and nighttime samples.

5. The daily ration of *S. tenuis*, in terms of the number of prey consumed/chaetognath/day, increased from 3.12 for chaetognaths in the 4.0-4.9 mm size class to 8.7 for those 9.0-9.9 mm in length. The specific daily rations, expressed as fractions of body dry weight, carbon or nitrogen ingested/chaetognath/day, decreased by a factor of three between the largest and smallest sizes examined in this study. While large *S. tenuis* ingest more prey items, young chaetognaths consume proportionally more in terms of weight.

6. *Sagitta tenuis* does not appear to be a major holoplanktonic carnivore in the lower Chesapeake Bay ecosystem. Extrapolation of predicted daily rations to mean densities of chaetognath and copepod populations indicates *S. tenuis* probably consumes no more than several percent of copepod standing stocks each day during its seasonal occurrence. The distribution and abundance of this species in the lower Bay seem more dependent upon abiotic factors than upon the availability of food.

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