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Abstract.—Eighteen species of chaetognaths were identified from shelf waters in the Middle Atlantic Bight. Species composition in the water column and the hyponeuston was nearly identical, but the percent frequencies of the more common cold-temperate species were generally lower in surface collections. Mean surface salinity, weighted for abundance of individual chaetognath species in the hyponeuston collections, varied from 32.6 and 32.8 ‰ for the coastal- and estuarine-inhabiting *Sagitta tenuis* and *Parasagitta elegans*, to 34.8 and 34.9 for the offshore *Pterosagitta draco* and *Krohnitta pacifica*. Weighted mean temperatures ranged from below 14°C for *Mesosagitta minima*, *P. elegans*, and *Serratosagitta tasmanica* to over 24°C for *K. pacifica*. Overall association among Middle Atlantic Bight chaetognaths, measured for the 15 most frequent species in 716 collections by variance ratio, was significantly positive. Association between pairs of species was therefore also largely positive, with the important exception of *Parasagitta elegans*. This species, with a unique regional niche in low salinities and temperatures, was negatively associated ($p < 0.01$) with five warm-water species (*Krohnitta pacifica*, *Ferosagitta hispida*, *Sagitta tenuis*, *Sagitta helenae*, and *Flaccisagitta enflata*). Most species reached maximum abundance at the surface near midnight. Exceptions included *Sagitta helenae*, with daylight maxima, and *Krohnitta pacifica*, *Ferosagitta hispida* and *Serratosagitta serratodentata*, showing crepuscular increases in abundance.

Chaetognatha from the Central and Southern Middle Atlantic Bight: Species Composition, Temperature-Salinity Relationships, and Interspecific Associations*

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Recognition of several chaetognath species along the northeastern coast of the United States is quite recent. Until 1960, only eight species had been identified from shelf waters off the Middle Atlantic states, i.e., the Middle Atlantic Bight from Cape Cod to Cape Hatteras; these were included in Bigelow and Sears (1939): *Eukrohnna hamata*, *Parasagitta elegans*, *Flaccisagitta enflata*, *Serratosagitta serratodentata* (including the then undescribed *Serratosagitta tasmanica*), *Flaccisagitta hexaptera*, *Pseudosagitta maxima*, *Krohnitta subtilis*, and *Pterosagitta draco***.

Deevey (1960), in a study of the Delaware Bay region, added *Ferosagitta hispida*, *Sagitta helenae*, and *Mesosagitta minima* to the list of recognized species. Since her material had been collected three decades earlier (1929–31), it appears that pre-1960 studies had simply failed to distinguish between grossly similar species. *Sagitta tenuis*, *Sagitta bipunctata*, and *Krohnitta pacifica* were added by Grant (1963a, b) to the list of shelf species, and Grant (1967)

later confirmed that the endemic shelf population of “*S. serratodentata*” in this region was actually *S. tasmanica*. Grice and Hart (1962) found other species in slope waters southeast of Long Island, New York, including *Pseudosagitta lyra*, *Mesosagitta decipiens*, and *Solidosagitta planctonis*. Thus, at the close of the 1960s, some 15 species were known from the shelf and the presence of others in surface slope waters suggested their likely occurrence over the shelf as well.

This study of Middle Atlantic Bight chaetognaths is based on an intensive series of collections from the central and southern bight. Presented here are the species composition in hyponeuston and subsurface collections, temperature-salinity-plankton (T-S-P) diagrams for the more common surface species, measurements of interspecific associations among chaetognaths, and a summary of diel abundance in the hyponeuston.

Methods and materials

Chaetognath collections

A transect of six stations (C1-J1, Fig. 1) off southern New Jersey was sampled quarterly for two years, October 1975–August 1977. Two more northerly stations (A2, B5) and a southern transect of four stations (L1-L6) were added in the second survey year

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** Taxonomy in this paper generally follows the revisions of Tokioka (1965) and Kassatkin (1971), but removes *Pseudosagitta lyra* and *P. maxima* from the genus *Flaccisagitta* in agreement with species groupings of Alvarino (1963).

(Grant 1977a, 1979, 1988). Routine collections at each station included paired 60-cm bongo net samplers (202 and 505 μm mesh nets), towed from just below the surface to near, but safely off, the bottom, then back to the surface (so-called double oblique tows; 220 samples), and eight surface layer (upper 10 cm) collections obtained at 3-hour intervals over a 24-hour period (496 samples), using a 1-m wide hyponeuston net (505 μm mesh). Of the 716 collections (Table 1), only 1 bongo and 79 hyponeuston (mostly daytime) collections lacked chaetognaths.

Laboratory processing

Collections were divided into successively smaller aliquots for the more numerous taxa, using a sample-splitting device of proven design (Burrell et al. 1974). However, chaetognaths were generally obtained from whole or half samples, unless very abundant.

Data analysis

Collection data were sorted by species, stations, and collection methods. Analysis of the relationship of species abundance to hydrography was limited to hyponeuston collections because subsurface tows were oblique, often traversing multiple layers of different water types. Mean temperatures and salinities of capture in surface-layer collections were calculated for each common chaetognath species, weighting each observed temperature and salinity by the size of catch ($\log N + 1$), where N = total catch in a standard 20-minute hyponeuston net tow at 2.5 knots. Thus,

$$\bar{T} =$$

$$\frac{t_1(\log n_1 + 1) + t_2(\log n_2 + 1) + \dots + t_n(\log n_n + 1)}{(\log n_1 + 1) + (\log n_2 + 1) + \dots + (\log n_n + 1)}$$

$$\bar{S} =$$

$$\frac{s_1(\log n_1 + 1) + s_2(\log n_2 + 1) + \dots + s_n(\log n_n + 1)}{(\log n_1 + 1) + (\log n_2 + 1) + \dots + (\log n_n + 1)}$$

where t_i , s_i , and n_i are the surface temperature, surface salinity, and total catch in each positive collection, respectively.

Presence, absence, and joint occurrences of the 15 most frequent species from both bongo and hyponeuston collections were used in an analysis of association between and among species. As recommended by Ludwig and Reynolds (1988), the significance of association among all 15 species and 716 collections was first tested simultaneously using a variance ratio (VR)

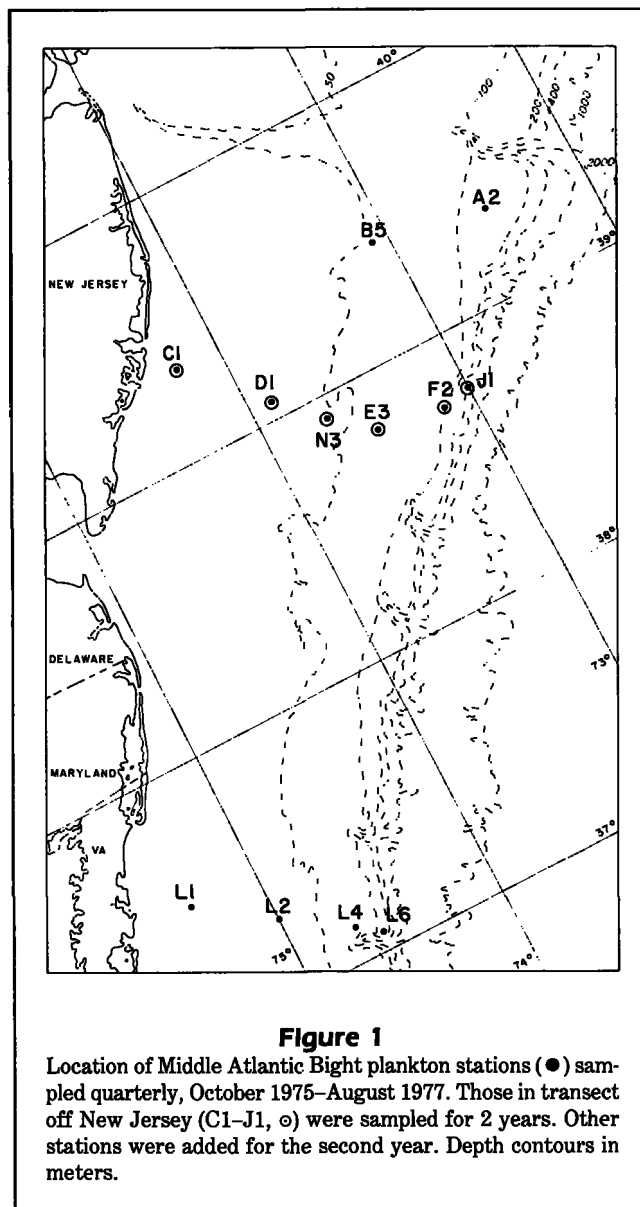


Figure 1

Location of Middle Atlantic Bight plankton stations (●) sampled quarterly, October 1975–August 1977. Those in transect off New Jersey (C1–J1, ○) were sampled for 2 years. Other stations were added for the second year. Depth contours in meters.

derived from a null association model (Schluter 1984). The expected value of VR under the null hypothesis of independence is 1. When $VR > 1$, a positive association of species is indicated; $VR < 1$ indicates a negative association. A test statistic $W = (N)(VR)$ provides a test of significance for deviations from 1. If species are not associated there is a 90% probability that W lies between the chi-square limits:

$$\chi^2_{0.05, N} < W < \chi^2_{0.95, N}$$

Because of the large degrees of freedom in this study (where $N = 716$), critical values of χ^2 were approximated (see Zar 1984, p. 482).

Relative strength of the association between pairs of species was measured using 2×2 contingency tables and Hurlbert's (1969) coefficient of interspecific association (C_s), as corrected by Ratliff (1982) for errors resulting from lack of absolute association (Pielou 1977). Yates' correction of chi-squared calculations was applied for low expected frequencies (Bailey 1981).

Results

Species composition

Eighteen species (11 genera) of chaetognaths were identified, 17 in both surface hyponeuston and subsurface bongo net collections (Tables 2 and 3). Compositional differences in the two lists were limited to the rarest species: *Sagitta bipunctata* was found only in hyponeuston collections, while *Pseudosagitta maxima* was restricted to subsurface collections. After adjustment for the 80 collections devoid of chaetognaths (79 surface and 1 subsurface collections), the percent frequencies of the most common cold-temperate species (*Serratosagitta tasmanica*, *Parasagitta elegans*, and *Mesosagitta minima*) were found to be much lower in surface collections. Warm-water chaetognaths (*Flaccisagitta enflata*, *Sagitta helenae*, *Pterosagitta draco*, *S. tenuis*, *Serratosagitta serratodentata*, *Ferosagitta hispida*, and *Krohnitta pacifica*) were either equally frequent in the two types of collections or more frequent in the hyponeuston.

Temperature-salinity-abundance relationships

The chaetognaths were collected in a wide range of temperatures (2.2–26.6°C) and salinities 27.7–36.0‰ (Table 4). Weighted means of surface salinities measured at the time of hyponeuston collections were very similar among all common surface species, ranging from 32.6 and 32.8‰ for *Sagitta tenuis* and *Parasagitta elegans*, respectively, to 34.9‰ for *Kroh-*

Table 1

Number of zooplankton collections obtained during eight seasonal cruises in the Middle Atlantic Bight, 1975–77.

Cruise	Dates	Subsurface		Surface	Total
		60-cm bongo nets 202 μ m	505 μ m	1-m hyponeuston net 505 μ m	
1	23–29 Oct 75	6	6	48	60
2	5–16 Feb 76	6	6	48	60
3	8–16 Jun 76	6	8	52	66
4	31 Aug–9 Sep 76	6	7	48	61
5	5–28 Nov 76	22	21	75	118
6	20 Feb–6 Mar 77	21	21	75	117
7	17–28 May 77	21	21	75	117
8	19–29 Aug 77	21	21	75	117
Total		109	111	496	716

Table 2

Percent frequency of chaetognath species occurrence in hyponeuston collections from eight quarterly cruises, 1975–77.

	Cruise:								Total
	1	2	3	4	5	6	7	8	
Number of collections:	48	48	52	48	75	75	75	75	496
<i>Serratosagitta tasmanica</i>	50.0	43.8	48.1	33.3	66.7	61.3	17.3	21.3	42.5
<i>Flaccisagitta enflata</i>	18.8	—	1.9	81.2	77.3	34.7	24.0	73.3	41.9
<i>Parasagitta elegans</i>	35.4	85.4	92.3	14.6	6.7	16.0	58.7	14.7	37.3
<i>Mesosagitta minima</i>	2.1	22.9	—	—	50.7	30.7	2.7	9.3	16.5
<i>Sagitta helenae</i>	4.2	—	—	8.3	24.0	18.7	20.0	8.0	11.9
<i>Ferosagitta hispida</i>	—	—	—	35.4	21.3	—	1.3	14.7	9.1
<i>Pterosagitta draco</i>	2.1	8.3	—	16.7	8.0	17.3	6.7	—	7.5
<i>Sagitta tenuis</i>	—	—	—	31.2	20.0	—	1.3	2.7	6.7
<i>Krohnitta pacifica</i>	—	—	—	—	—	—	9.3	24.0	5.0
<i>Serratosagitta serratodentata</i>	—	—	—	4.2	4.0	6.7	2.7	8.0	3.6
<i>Flaccisagitta hexaptera</i>	—	10.4	—	10.4	2.7	6.7	—	—	3.4
<i>Krohnitta subtilis</i>	—	—	—	4.2	1.3	2.7	1.3	1.3	1.2
<i>Mesosagitta decipiens</i>	—	—	—	2.1	—	6.7	—	—	1.2
<i>Pseudosagitta lyra</i>	—	2.1	—	—	—	4.0	—	—	0.8
<i>Eukrohnia hamata</i>	—	2.1	—	—	—	2.7	—	—	0.6
<i>Sagitta bipunctata</i>	2.1	—	—	—	—	—	1.3	—	0.4
<i>Solidosagitta planctonis</i>	—	—	—	—	—	—	1.3	—	0.2

nitta pacifica (Table 4). Weighted mean temperatures, on the other hand, varied widely among species, from 12.9°C for *Mesosagitta minima* to 24.2°C for *K. pacifica*. Species occurring infrequently at the surface and excluded from Table 4 were those residing at greater depths, with surface occurrences mostly restricted to low winter temperatures. Relationships between surface abundance of common species and the two physical factors were further examined by plotting average daily catch (8 collections at 3-hour intervals) in standard hyponeuston collections, defined previously (Grant 1988) as 1-m neuston nets towed at 2.5 knots for 20 minutes; the sampler used typically fished the upper

10 cm of the sea surface so would more accurately be called a 'hypo-neuston' net. Temperatures and salinities measured during collections containing chaetognaths were averaged at each positive station (Figs. 2 and 3).

Flaccisagitta enflata, *Sagitta tenuis*, *Ferosagitta hispida*, and, to a lesser extent, *S. helenae* and *Pterosagitta draco* were absent or uncommon in temperatures less than about 9°C (Figs. 2, 3), while few *Parasagitta elegans*, *Mesosagitta minima*, and *Pterosagitta draco* were found in warmest temperatures. *Serratosagitta tasmanica* was present in a very wide range of both temperature and salinity. Numbers of *Pterosagitta draco* were reduced in lower salinities as well as low temperatures; occurrences were in salinities higher than 34‰ except in the summer of 1976. *Sagitta helenae* and *Mesosagitta minima* were more frequent and numerous in higher salinities, while *S. tenuis* was absent from salinities greater than 35‰. Other species in Figures 2 and 3 were captured in various salinities.

Interspecific association

Before examining association between pairs of species, the data were first tested for overall association using a matrix of the presence or absence of the 15 most common chaetognaths in 716 collections. Schluter's (1984) index of overall association (VR here, as in Ludwig and Reynolds 1988) for these 15 species was 2.108, indicative of a net positive association among the species. The null hypothesis of no association was rejected ($W = 1509$; 90% probability $654.9 < W < 779.3$).

Among paired-species associations, most statistically significant coefficients ($P < 0.05$) were positive (Table 5). Significant negative associations ($C_8 = -0.15$ to -0.73) were limited to six pairings of various species with *Parasagitta elegans* and the pair *Sagitta tenuis*–*Mesosagitta minima*. The sole significant positive association of *P. elegans* ($P < 0.05$) was with *Serratosagitta*

Table 3

Percent frequency of chaetognath species occurrence in subsurface bongo collections from eight quarterly cruises, 1975–77.

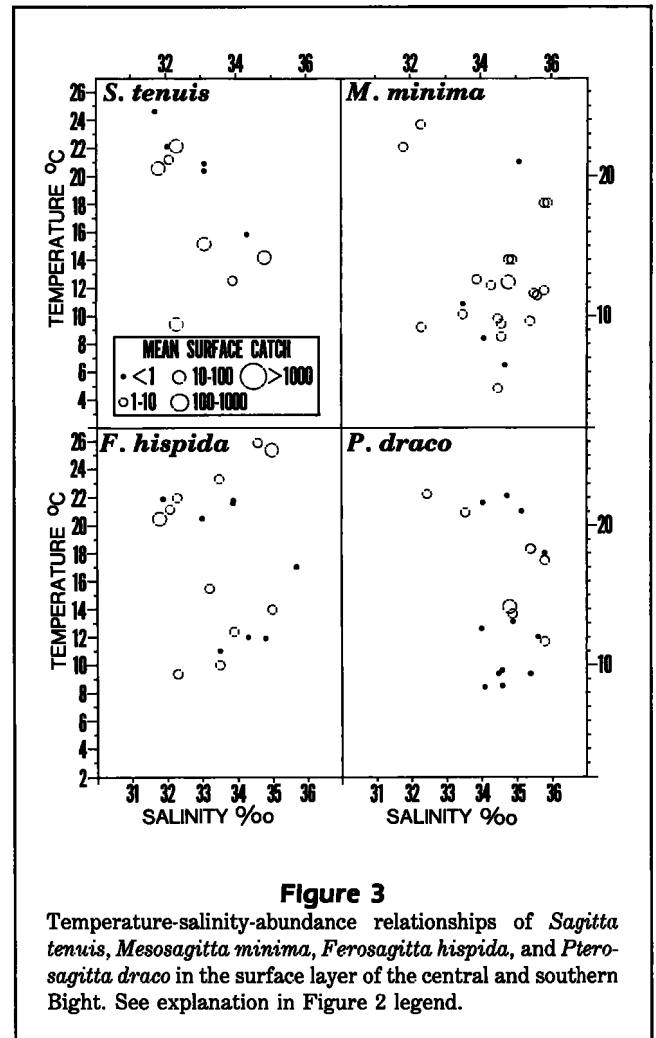
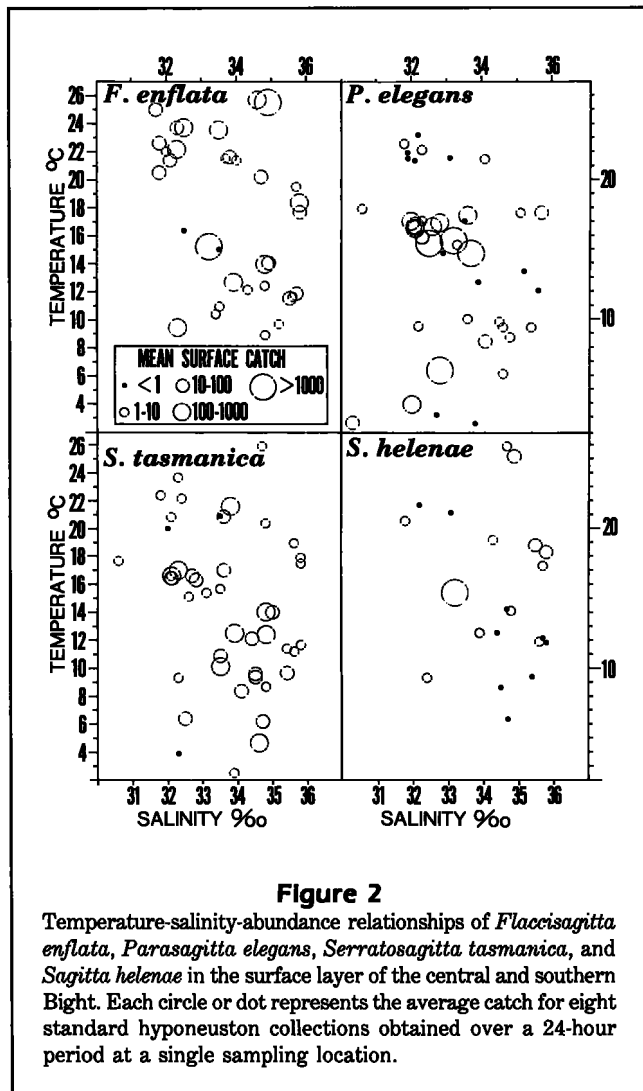
	Cruise:								Total
	1	2	3	4	5	6	7	8	
Number of collections:	12	12	14	13	43	42	42	42	220
<i>Serratosagitta tasmanica</i>	100.0	75.0	78.6	84.6	95.3	95.2	21.4	85.7	77.3
<i>Parasagitta elegans</i>	91.7	91.7	100.0	61.5	25.6	52.4	98.6	90.5	70.9
<i>Flaccisagitta enflata</i>	33.3	8.3	—	76.9	72.1	50.0	14.3	92.9	50.9
<i>Mesosagitta minima</i>	8.3	33.3	7.1	30.8	65.1	69.0	14.3	64.3	45.4
<i>Sagitta helenae</i>	—	—	—	—	18.6	26.2	14.3	9.5	13.2
<i>Eukrohnia hamata</i>	—	8.3	14.3	15.4	16.3	23.8	9.5	2.4	12.3
<i>Flaccisagitta hexaptera</i>	16.7	33.3	14.3	30.8	11.6	7.1	2.4	2.4	10.0
<i>Pterosagitta draco</i>	—	—	7.1	15.4	7.0	14.3	9.5	2.4	7.7
<i>Sagitta tenuis</i>	—	—	—	38.5	11.6	2.4	—	4.8	5.9
<i>Serratosagitta serratodentata</i>	—	—	—	—	2.3	2.4	4.8	16.7	5.0
<i>Pseudosagitta lyra</i>	—	8.3	—	—	4.7	7.1	7.1	2.4	4.5
<i>Krohnitta subtilis</i>	—	—	—	—	—	14.3	—	7.1	4.1
<i>Ferosagitta hispida</i>	—	—	—	23.1	7.0	—	—	4.8	3.6
<i>Krohnitta pacifica</i>	—	—	—	—	—	—	2.4	11.9	2.7
<i>Mesosagitta decipiens</i>	—	—	—	—	2.3	9.5	—	2.4	2.7
<i>Solidosagitta planctonis</i>	—	—	—	—	—	4.8	—	—	0.9
<i>Pseudosagitta maxima</i>	—	—	7.1	—	—	2.4	—	—	0.9

Table 4

Weighted means and ranges of temperature and salinity from surface collections at capture of the more frequent hyponeustonic chaetognaths, all cruises combined.

Species	Number of collections	Temperature (°C)		Salinity (‰)	
		\bar{T}	Range	\bar{S}	Range
<i>Krohnitta pacifica</i>	25	24.24	17.0–26.6	34.89	31.6–36.0
<i>Serratosagitta serratodentata</i>	18	21.25	8.1–26.6	34.57	31.7–35.9
<i>Ferosagitta hispida</i>	45	20.15	9.4–25.9	33.56	31.7–35.7
<i>Flaccisagitta enflata</i>	209	18.57	8.1–26.6	33.68	31.5–36.0
<i>Sagitta helenae</i>	58	16.76	6.3–26.6	34.38	31.7–36.0
<i>Pterosagitta draco</i>	37	15.87	8.1–22.3	34.75	32.4–35.9
<i>Sagitta tenuis</i>	33	15.83	9.1–24.6	32.59	31.7–34.8
<i>Flaccisagitta hexaptera</i>	17	14.00	8.4–22.3	34.56	33.1–35.8
<i>Serratosagitta tasmanica</i>	211	13.46	2.3–25.9	33.72	30.5–36.0
<i>Parasagitta elegans</i>	186	13.39	2.2–24.1	32.82	27.7–35.8
<i>Mesosagitta minima</i>	82	12.94	4.4–24.3	34.42	31.8–35.9

tasmanica. Highest positive coefficients included associations among (1) the other most frequent chaetognaths, *Serratosagitta tasmanica*, *Mesosagitta minima*, and *Flaccisagitta enflata* ($C_8 = 0.18$ to 0.27); (2) deeper-living or outer shelf chaetognaths *Flaccisagitta hexaptera*, *Eukrohnia hamata*, *Pseudosagitta lyra*, *Mesosagitta decipiens*, and *Krohnitta subtilis* ($C_8 = 0.11$ to 0.30); and (3) the seasonal warm-water species *K. pacifica*, *Serratosagitta serratodentata*, *Ferosagitta hispida*, and *Sagitta tenuis* ($C_8 = 0.09$ to 0.26). *Sagitta helenae* and *Pterosagitta draco* shared positive associations with all three groups.



Diel distribution at the surface

Most of the chaetognaths commonly occurring in the surface layer reached peak densities near midnight (Table 6). *Flaccisagitta enflata*, *Krohnitta pacifica*, *Sagitta tenuis*, *Mesosagitta minima*, *Ferosagitta hispida*, and *Pterosagitta draco* all were caught in maximum numbers at that hour. Peak numbers of *Parasagitta elegans* and *Serratosagitta tasmanica* occurred somewhat earlier, but they were abundant throughout hours of darkness. There are also suggestions of dusk or dawn (or both) increases in abundance for *K. pacifica*, *F. hispida*, and *Serratosagitta serratodentata*.

Unlike any of the other chaetognaths, *Sagitta helenae* was decidedly more abundant at the surface in daylight hours, with 31.0 and 32.8% of total catches occurring around 1500 and 0900 hours, respectively.

Discussion

Eighteen species of chaetognaths are found in continental shelf waters of the Middle Atlantic Bight, including the 15 species on record after the 1960s plus the present records of three species previously known only from surface slope waters (Grice and Hart 1962). More recent studies of chaetognaths in this region have been restricted to estuaries (Grant 1977b, Sweatt 1980, Canino and Grant 1985) or to oceanic waters (Cheney 1985a,b). All of the western North Atlantic species labeled epipelagic or mesopelagic by Cheney (1985b) have been collected in shelf waters, so the present list appears reasonably complete. The composition of Middle Atlantic Bight chaetognath collections from hyponeuston and subsurface plankton tows was nearly identical. There were no frequent or abundant species unique to the hyponeuston, and all but the rarest species from subsurface shelf waters were taken at least occasionally from the surface layer. However,

Table 5

Number of occurrences (integers along the diagonal), coefficients of association (Hurlbert's C_8 , right side of diagonal), and their statistical significance (** $P < 0.01$ and * < 0.05 , respectively; blank = not significant, $P > 0.05$, left side of diagonal) for chaetognaths collected during eight seasonal cruises in the Middle Atlantic Bight, 1975-77. Both subsurface and surface layer collections are included ($N = 716$); the three rarest species are excluded.

	pac	ser	his	ten	hel	dra	enf	min	tas	ele	ham	hex	lyr	dec	sub
<i>Krohnitta pacifica</i>	31	0.26	0.09	0	0.13	0.05	0.05	0	-0.09	-0.73	0	-1.00	0.04	0	0
<i>Serratosagitta serratodentata</i>	**	29	0.13	0	0.11	0.06	0.05	0.04	0.01	-0.19	0	0.04	0.05	0	0.05
<i>Ferosagitta hispida</i>	**	**	53	0.21	0	0.12	0.08	0.02	0.01	-0.64	-0.54	0.02	-1.00	0.02	0.03
<i>Sagitta tenuis</i>			**	46	0.09	0.07	0.08	-0.48	-0.18	-0.59	0	0	-1.00	0	0.02
<i>Sagitta helenae</i>	**	**		**	88	0.21	0.15	0.12	0.03	-0.40	0.06	-0.34	0.03	0.03	0.05
<i>Pterosagitta draco</i>		**	**		**	54	0.07	0.15	0.06	-0.22	0.13	0.09	0.05	0.08	0.09
<i>Flaccisagitta enflata</i>	**	**	**	**	**	**	322	0.22	0.18	-0.46	0.03	0.02	0.01	0.02	0.02
<i>Mesosagitta minima</i>		**	*	**	**	**	**	182	0.27	-0.15	0.08	0.08	0.05	0.03	0.04
<i>Serratosagitta tasmanica</i>		*		*	**	**	**	**	381	0.08	0.03	0.04	0.02	0.01	0.02
<i>Parasagitta elegans</i>	**	**	**	**	**	**	**	*	*	341	0.01	0	0	-0.27	0
<i>Eukrohnia hamata</i>					**	**	**	**	**		30	0.30	0.25	0.12	0.11
<i>Flaccisagitta hexaptera</i>						**	**	**	**		**	39	0.11	0.09	0.03
<i>Pseudosagitta lyra</i>		*				*	*	**	**		**	**	14	0.27	0.18
<i>Mesosagitta decipiens</i>						**	**	**	**		**	**	**	12	0.18
<i>Krohnitta subtilis</i>					**	**	**	**	**		**	**	**	**	15

there were apparent temperature-related differences in the percent frequency of chaetognath species in the two habitats. Cold-temperate species were less frequent at the surface than in the underlying water column, while warm-temperate or subtropical species were either equally frequent in the two habitats or more frequent in the hyponeuston.

The idea for T-S-P diagrams apparently originated with Pickford's (1946) study of the cephalopod *Vampyroteuthis*, and was first applied to chaetognaths by Bary (1959, 1963). T-S-P diagrams have since been used to relate abundance of chaetognaths to hydrography by numerous authors, including Sund (1961, 1964), Aurich (1971), Kotori (1976), Michel and Foyo (1976), O'Brien (1977), Nagasawa and Marumo (1982), and Andreu (1984). *Flaccisagitta enflata*, abundant in the Middle Atlantic Bight in warmer temperatures (averaging 18.6°C) and in various salinities (<32 to 36‰), occurred throughout the temperature and salinity ranges sampled by Nagasawa and Marumo (1982) and was apparently limited only by depth in the Caribbean (Michel and Foyo 1976). Sund (1961) also recorded *F. enflata* from 13-28°C and 32.6-35‰. T-S-P diagrams for *Para-*

Table 6

Diel distribution of the more common chaetognaths in hyponeuston collections. Data from 24-hour stations only, combined from eight seasonal cruises, 1975-1977.

	Hours (EST)								Total N
	1200	1500	1800	2100	2400	0300	0600	0900	
	----- (% of total) -----								
<i>Flaccisagitta enflata</i>	10.6	8.9	7.9	11.1	25.7	10.4	13.8	11.6	89,807
<i>Parasagitta elegans</i>	2.3	1.7	1.2	37.4	26.8	19.5	7.8	3.3	87,093
<i>Serratosagitta tasmanica</i>	1.3	1.3	6.7	30.3	27.9	23.5	6.2	2.8	16,283
<i>Sagitta helenae</i>	18.9	31.0	2.5	1.6	10.5	1.8	0.8	32.8	15,073
<i>Krohnitta pacifica</i>	3.5	10.3	11.8	2.5	34.0	1.9	23.0	13.1	2,573
<i>Sagitta tenuis</i>	0.5	0.9	10.3	13.7	45.2	18.2	7.9	3.3	2,283
<i>Mesosagitta minima</i>	0.9	1.4	2.4	8.9	60.4	13.6	7.5	4.9	1,383
<i>Ferosagitta hispida</i>	1.0	4.6	23.4	14.6	26.6	12.9	16.9	0	628
<i>Serratosagitta serratodentata</i>	0.2	2.9	28.2	8.3	0.7	3.4	56.2	0	411
<i>Pterosagitta draco</i>	0	0	1.7	11.9	32.2	27.1	26.3	0.8	118

sagitta elegans have been plotted by Bary (1963), who included the species in his "coastal (neritic) group," by O'Brien (1977) for populations to the west of Ireland, and by Kotori (1976) with ranges of temperature and salinity close to those in the present study. All agree in showing higher occurrence and abundance in colder water and an apparent tolerance for reduced salinity. Although the ranges of surface salinity in which Middle Atlantic Bight species were found were very similar, it is noteworthy that the five species with the lowest weighted means were the same five species recorded from within Chesapeake Bay (Grant 1977b) and in approximate inverse order of their estuarine abundance (*Sagitta tenuis*, $\bar{x} S = 32.6‰$ and the most

abundant, to *Serratosagitta tasmanica*, $\bar{x} S = 33.7\%$, the rarest in Chesapeake Bay). Aurich (1971) includes the only other known T-S-P diagram of *S. tasmanica*, used for a display of habitat differences with *S. serratodentata*. Michel and Foyo (1976) and Nagasawa and Marumo (1982) provided T-S-P diagrams for both *Mesosagitta minima* and *Pterosagitta draco*. Middle Atlantic Bight T-S-P diagrams agree with their depiction of greater abundance at higher salinities for these two species. Finally, Michel and Foyo's (1976) T-S-P diagram of *Ferosagitta hispida* shows a few occurrences at lower temperatures (13–17°C), but most at 27–28°C and in a broad range of salinities.

Association among the Middle Atlantic Bight species was generally positive, both in the multispecies case and between pairs of species. *Parasagitta elegans* provided an important and consistent exception, evidenced by its highly significant ($P < 0.01$) negative associations with five warm-water species: *Krohnitta pacifica*, *Ferosagitta hispida*, *Sagitta tenuis*, *Flaccisagitta enflata*, and *Sagitta helenae*. Although both *P. elegans* and *S. tenuis* occur abundantly in coastal and estuarine waters in the Chesapeake region, they do so in opposite seasons, hence their negative association. The sole significant ($P < 0.05$) positive association of *P. elegans* was with *Serratosagitta tasmanica*, and it appears to occupy a niche of low temperatures and salinities in this region, not unlike that of *Aidanosagitta crassa* in the East China Sea (Matsuzaki 1975). Highly significant positive associations were shared by (1) the endemic and abundant shelf species *Serratosagitta tasmanica*, *Mesosagitta minima*, and *Flaccisagitta enflata*, (2) the warm-water species *Krohnitta pacifica*, *Serratosagitta serratodentata*, *Ferosagitta hispida*, and *Sagitta tenuis*, and (3) the offshore, shelf-edge species *Flaccisagitta hexaptera*, *Eukrohnia hamata*, *Pseudosagitta lyra*, *Mesosagitta decipiens*, and *Krohnitta subtilis*. Three of the latter species comprised Matsuzaki's (1975) "Kuroshio water" species group.

Pearre (1973) determined that extensive diurnal migration takes place with *Parasagitta elegans*, perhaps related to feeding. Data in the present study on the diurnal distribution of the species in the hyponeuston also indicates a strong upward migration at night; numbers caught were about an order of magnitude higher at night than in daylight. Several other species showed similar sharp increases in abundance during darkness, including *Serratosagitta tasmanica*, *Krohnitta pacifica*, *Sagitta tenuis*, *Mesosagitta minima*, and *Pterosagitta draco*. Some were more abundant at dawn or dusk, or, in the case of *Flaccisagitta enflata* and *Sagitta helenae*, were present in considerable numbers in daylight. Among these species, Nagasawa and Marumo (1982) found evidence for diurnal migration in *F. enflata*, *P. draco*, and *K. subtilis*, none for *K.*

pacifica, and mixed evidence for *M. minima* and *F. hexaptera*. However, in the present comparison of day and night hyponeuston collections, only a short migration would be required to populate and depopulate the surface layer diurnally. Such fine-scale diurnal movements likely do occur within the surface mixed layer, but are most difficult to measure.

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