Trophic interactions of chaetognaths, larval fish, and zooplankton in the South Atlantic Bight

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ABSTRACT: Chaetognaths are highly abundant carnivores in marine environments, and feed both on fish larvae and on the same foods as fish larvae. We assessed predation by chaetognaths on winter-spawned fish larvae and on the planktonic food of fish larvae in February 1992, December 1992, and February 1993 off the southeastern U.S. coast. Feeding rates of chaetognaths were calculated from gut content analysis and experimentally determined digestion rates, and combined with estimates of *in situ* densities of predators and prey. Chaetognath and larval fish distributions overlapped temporally and spatially on all dates. Densities of chaetognaths averaged 10 to 67 m^{-3}, and fish larvae averaged 0.1 to 1.8 m^{-3} Only 1 fish larva was found in 6718 chaetognath guts examined. Effects of chaetognath predation on the abundant small prey consumed by the small fish larvae present in December 1992 and February 1993 were negligible (0.3 to 0.7 % consumed d^{-1}). In February 1992, however, chaetognaths consumed up to 44 % d^{-1} of standing stocks of large copepods that also were prey of the large fish larvae present on that date. We conclude that chaetognaths were not important predators of fish larvae during this study, but may, at times, consume substantial amounts of the copepod populations, which are shared by fish larvae.

KEY WORDS: Chaetognaths · Competition · Fish larvae · Ichthyoplankton · Predation · *Sagitta* · Zooplankton · Trophodynamics

INTRODUCTION

Chaetognaths are potentially important both as predators and competitors of larval fish. Chaetognaths are highly abundant in all oceans, often numbering second only to copepods, and are strictly carnivorous (Feigenbaum & Maris 1984). Chaetognaths feed on fish larvae in the laboratory (Kuhlmann 1977), and reports of larvae in the guts of preserved chaetognaths are common in the literature (reviewed in Feigenbaum & Maris 1984, Alvarino 1985, Feigenbaum 1991). Several researchers have speculated that chaetognaths cause significant mortality of fish larvae, based on the great abundances of chaetognaths and the presence of larvae in chaetognath guts (reviewed in Alvarino 1985). Previous information on the effects of chaetognath predation on larval fish is largely qualitative; the present study provides quantitative data.

Copepods are the most important food of both chaetognaths and larval fish. Young chaetognaths begin feeding on small prey such as tintinnids and copepod nauplii, and then progress to copepods and other large prey (Feigenbaum & Maris 1984). Similarly, first feeding larvae of many fish species feed on a variety of organisms, such as copepod nauplii, tintinnids, and mollusc larvae, and subsequently specialize on copepods (Hunter 1981) Several studies showed that chaetognath predation can significantly affect populations of copepods or larvaceans. For example, Sameoto (1973) estimated consumption by *Sagitta elegans* as 36 % of annual secondary production in Bedford Basin, Nova Scotia (Canada), and concluded that chaetognaths were the most important predators of copepods in that location (other examples include Szyper 1978, Kimmerer 1984, Stuart & Verheye 1991).

Predation and starvation are thought to be the main causes of larval fish mortality (e.g. Hunter 1981, Houde 1987). Predation may be the largest direct source of larval mortality (Bailey & Houde 1989). Food limitation

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can kill larvae directly through starvation, but may have more important indirect effects by slowing larval growth rates and increasing predation-induced mortality (Houde 1987, Taggart & Leggett 1987). Chaetognaths previously have not been evaluated as predators and competitors of fish larvae. Our study quantifies the trophic interaction of chaetognath predation on fish larvae and on the zooplankton prey-field of fish larvae off the southeastern coast of the United States during 3 observational periods.

METHODS

Distributions and abundances. Distributions of chaetognaths, fish larvae, and ambient zooplankton were estimated from depth-stratified samples collected in 5 min tows with a 1 m diameter multiple-opening-closing-net system (MOCNESS), from 5 locations in the South Atlantic Bight, during February 1992, December 1992, and February 1993 (Fig. 1, Table 1). Stn 120 (Dec 1992) was sampled approximately every 4 h for a 24 h period to assess diel changes in depth distributions and feeding. Bottom depths ranged from 24 to 34 m, and the entire water column was sampled. The MOCNESS had 333 µm mesh nets, and these samples were preserved in 95% ethanol. Fish larvae of the species *Brevoortia tyrannus* (Atlantic menhaden), *Leiostomus xanthurus* (spot), *Paralichthys dentatus* (summer flounder), *Micropogonias undulatus* (Atlantic croaker), the bothid flounders *Bothus* sp. and *Syacium* sp., and a cynoglossid (tonguefish) from the 333 µm mesh nets were counted, identified, and measured to determine standard length. In Dec 1992 and Feb 1993, 0.25 m² insets of 64 µm mesh were put in each MOC-NESS net to collect chaetognaths and zooplankton. These samples were preserved in a 5% formaldehyde solution.
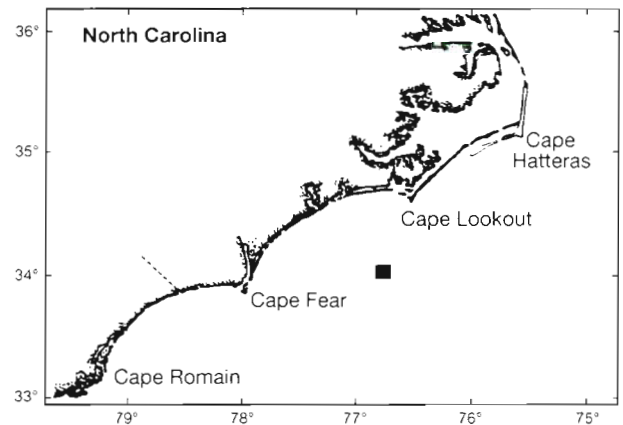

Fig. 1. Study area (■) off the southeastern U.S. coast

Subsamples were taken with a Folsom Plankton Splitter to obtain 100 to 300 chaetognaths from each sample. Chaetognaths were identified to species, counted, and measured to determine standard lengths (distance from the front of the head to the end of the tail, excluding fin) using a CUE-2 image analysis system. Very small chaetognaths and a few damaged specimens could not be identified and were included with 'other' chaetognaths.

After removing the chaetognaths, the remaining zooplankton sample was sieved through a 500 µm mesh. Organisms from the >500 µm fraction were counted, identified to major taxa, and measured using the CUE-2 system. The <500 µm fraction was diluted and subsampled with the Folsom Plankton Splitter to obtain 100 to 300 organisms to count, identify, and measure.

All statistical analyses were done using Statistical Analysis Systems (SAS) software (SAS Institute Inc., Cary, NC, USA). Analysis of Variance (ANOVA) was used to test for differences in densities and lengths of

Table 1. Station data for MOCNESS samples. Chaetognaths and zooplankton were collected from 333 µm mesh nets in Feb 1992, and from 64 µm mesh insets in Dec 1992 and Feb 1993. Fish larvae were collected from 333 µm mesh nets on all dates. Densities averaged over all depths

Stn	Date	Latitude (N)	Longitude (W)	Time (h)	T (°C)	Bottom depth (m)	Mesh size (m)	Density (no. m⁻³) Chaet.	Fish larvae
107	1 Feb 92	34° 04.10'	76° 45.7'	11:45	15	31	333	43.6	0.9
109	1 Feb 92	34° 03.05'	76° 45.5'	17:00	15	34	333	48.3	1.5
110	1 Feb 92	34° 02.97'	76° 45.6'	19:00	15	32	333	66.9	1.8
120	17 Dec 92	34° 03.0'	76° 45.0'	11:35	22	24	64	19.1	0.2
120	17 Dec 92	34° 03.0'	76° 45.0'	17:00	22	34	64	40.8	0.3
120	17 Dec 92	34° 03.0'	76° 45.0'	20:45	22	32	64	33.1	0.4
120	18 Dec 92	34° 03.0'	76° 45.0'	00:45	22	30	64	10.0	0.1
120	18 Dec 92	34° 03.0'	76° 45.0'	04:45	22	31	64	16.3	1.0
120	18 Dec 92	34° 03.0'	76° 45.0'	08:30	21	32	64	37.6	0.3
227	12 Feb 93	34° 04.00'	76° 47.0'	18:30	18	25	64	55.3	0.5

fish larvae and chaetognaths among dates. Kolmogorov-Smirnov statistics were used to test for differences in depth and length frequency distributions (Kim & Jennrich 1970).

Gut content analysis. Prey items in the guts of chaetognaths and fish larvae were identified and measured after excision from the guts using insect pins. The prosome length of copepods and the total length of other measurable zooplankters was measured using the CUE-2 system. Soft-bodied organisms such as larvaceans were not measured. Although prey diameter is thought to limit the size of prey consumed both by chaetognaths and larval fish (Pearre 1980, Hunter 1981), prey length was used in this study because it was difficult to measure diameters of partially digested prey. ANOVAs were used to test for differences in numbers of prey ingested by chaetognaths and fish larvae among stations, among depths within stations, and with time of day. Comparisons of least squares means were made using the Bonferroni approach (Tarone 1990).

Ambient zooplankton and prey in the guts of fish larvae and chaetognaths were categorized by major taxa. Prey that were not common to both chaetognaths and fish larvae were classified as 'other' prey. Sample-size-independent percent similarities (reviewed in Kohn & Riggs 1982) were calculated as an index of diet overlap of chaetognaths and larval fish. Prey preferences were assessed using Pearre's (1982) electivity index. ANOVA was used to test for differences in prey size among dates.

Digestion rates. Digestion rate experiments were conducted at sea using chaetognaths collected in Dec 1992 and Feb 1993. Surface temperature was recorded at each station. Because chaetognaths are delicate and difficult to maintain and feed in the laboratory, we used a method that minimized handling. Chaetognaths were collected in series of very short (<1 min) vertical net tows (5 to 10 m), using conical plankton nets. Samples were examined immediately over a light table, and chaetognaths with prey were isolated in 1 l jars filled with 64 µm filtered seawater, and maintained at the temperature of collection. Initial time of isolation, prey position in the gut, and prey type were recorded. Chaetognaths were observed in the jars at 15 min intervals until prey were egested or could no longer be seen in the gut. Then the chaetognaths were examined with a dissecting microscope for prey remnants, identified, and measured using an ocular micrometer. Regressions of these digestion times versus temperature for each species were used to estimate digestion times in the field from ambient temperatures. Estimated digestion times were multiplied by 2, to allow for digestion that may have occurred before the observations began, as recommended by Feigenbaum (1991).

Feeding rates. The mean number of prey per chaetognath (NPC) was determined at each station for the predominant chaetognath species *Sagitta enflata*, *S. helenae* and *S. hispida*, and for 'other species'. Prey in the foregut and undigested prey were excluded from the analysis because they probably were consumed in the net (Baier & Purcell 1997 this issue). NPCs were multiplied by 2 to account for prey loss due to gut evacuation during sampling and preservation (Baier & Purcell 1997).

NPCs from the 24 h station at different times of day were compared using ANOVA. The 24 h station samples were assigned to day (08:30 to 17:00 h) or night (20:45 to 04:45 h). Sunrise was just before 07:00 h on all dates, while sunset was at approximately 17:35 h on the February dates and at 16:53 h in Dec 1992. The ratio of mean night NPC to day NPC (1.96) from the 24 h station was used to adjust daily feeding rates at stations where only day or night samples were collected.

The proportions of prey in chaetognath guts (all species combined) that represented potential prey of fish larvae (% FP) were determined using 3 criteria. Prey types were excluded from the feeding effect calculations if they (1) were not found in fish larvae gut contents, (2) were outside of the size range consumed by larvae, or (3) could not be identified. The portion of the ambient zooplankton that represented potential prey of fish larvae on each date was determined by the same criteria. These percentages were applied to ambient zooplankton densities to obtain the densities of prey available to fish larvae (FP m^{-3}).

Feeding rates were calculated for each station and chaetognath species using an equation modified from Bajkov (1935): Feeding rate = (NPC/D) × T, where feeding rate is the number of prey ingested per chaetognath during each time period, NPC is the number of prey per chaetognath, D is the digestion time in hours, and T is the time period in hours. For each of the six 24 h samples, T = 4 h; for all other samples, day T = 10 h and night T = 14 h. Daily feeding rates (prey chaetognath^{-1} d^{-1}) for each station and species were obtained by summing the feeding rates for those periods. The %FP then was applied to obtain feeding rates of chaetognaths on potential prey of fish larvae.

Feeding effects. The numbers of prey consumed m^{-3} d^{-1} by each chaetognath species were calculated by multiplying the daily feeding rate by the mean density for each species on each day. These values were then summed to yield the total number of prey consumed per day for all chaetognaths at each station (P m^{-3} d^{-1}). The percentages of prey standing stocks consumed daily by chaetognaths = (P m^{-3} d^{-1}/FP m^{-3}) × 100.

RESULTS

Distributions and abundances

Chaetognath and larval fish distributions overlapped on all dates and at all stations, and chaetognaths were always much more abundant (10 to 67 m^{-3}) than fish larvae (0.1 to 1.8 m^{-3}; Table 1). Chaetognath densities were highest in Feb 1992 and 1993 (Fig. 2A). *Sagitta enflata* was the most abundant chaetognath species, followed by *Sagitta helenae* (Fig. 2A). Other species included *Serratosagitta serratodentata*, *Sagitta minima*, *Pterosagitta draco*, *Krohnitta* sp., *Sagitta tenuis*, *Sagitta hexaptera*, and *Sagitta bipunctata*. About 30% of chaetognaths in Dec 1992, compared with only 7% in Feb 1993, were unidentified juveniles (included with other species, Fig 2A) that were too small to be sampled quantitatively by the 333 µm mesh net used in Feb 1992. Fish larvae of the target species were much less abundant than other species and densities were greatest in Feb 1992 (Table 1, Fig. 2B).

At the 24 h station (Dec 1992), chaetognaths and fish larvae were distributed throughout the water column at all times. The depth distributions of chaetognaths and larval fish appeared to be roughly similar at each sampling time, except at 04:45 h; however, the distributions were significantly different at all times except 11:30 h and 17:00 h (Kolmogorov-Smirnov statistic, p < 0.05, Fig. 3). Fish larvae were distributed more towards the surface at 04:45 h, which was significantly different from the distributions at other times of day (Kolmogorov-Smirnov statistic, p < 0.05), whereas chaetognaths were distributed more towards the bottom then than at other sampling times.

Diel patterns and diet

Diel patterns. Chaetognaths fed most actively at night while fish fed mainly during daylight hours (Fig. 4). The mean number of prey per chaetognath
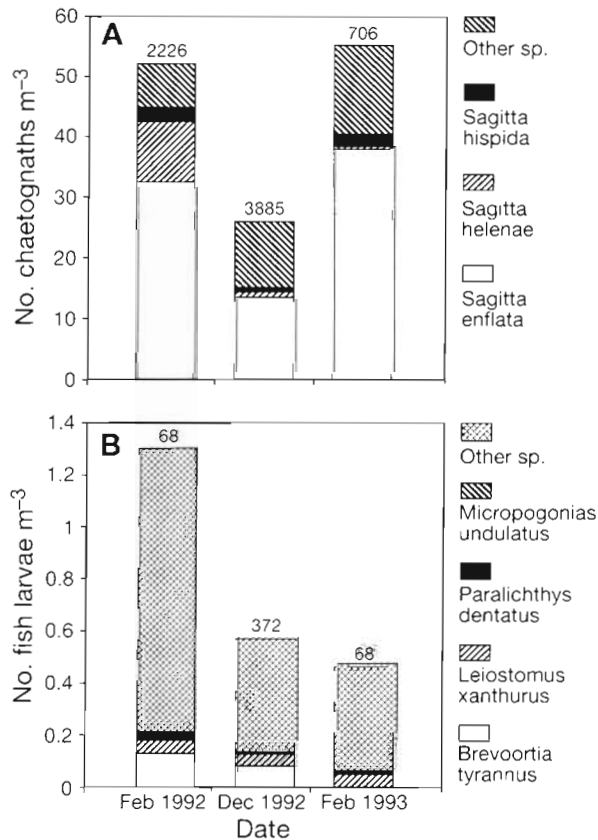

Fig. 2. Densities and species compositions of (A) chaetognaths and (B) larval fish on 3 sampling dates. Numbers above bars represent no. of chaetognaths examined (A), and no. of fish larvae measured and used for gut content analysis (B). Chaetognaths were examined from 333 µm mesh samples in Feb 1992 and from 64 µm mesh samples on the other dates. All fish larvae in 333 m samples were identified
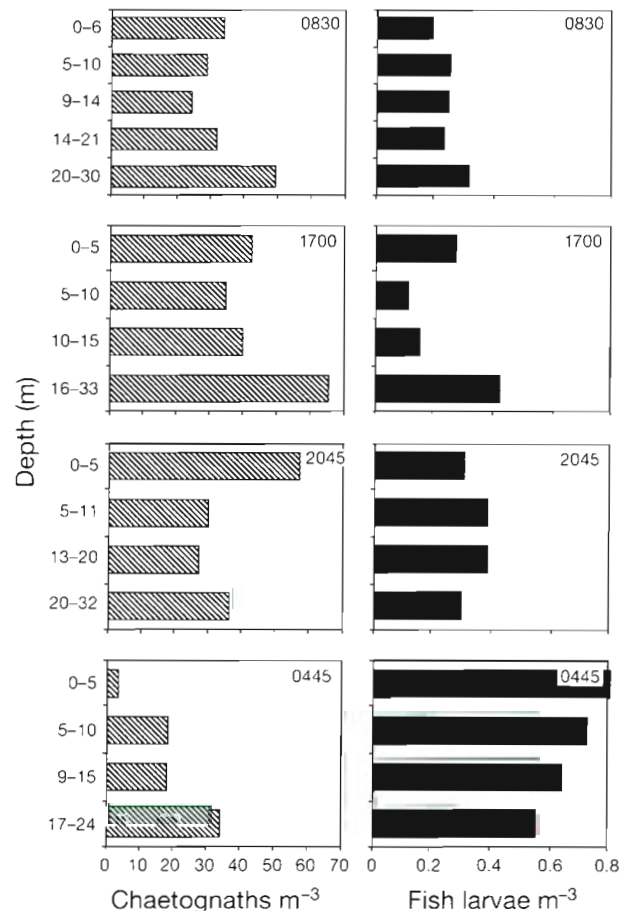

Fig. 3. Depth distribution in relation to time of day for chaetognaths (hatched bars) and fish larvae (solid bars) at the 24 h station in Dec 1992. Distributions at 11:30 h (not shown) were similar to those at 08:30 and 17:00 h. Distributions at 00:45 h are not shown because the net dragged the bottom
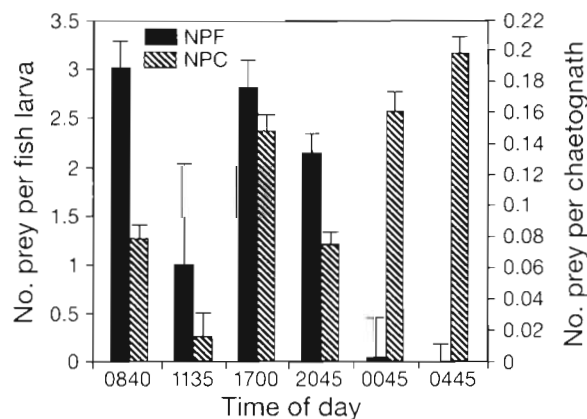
Fig. 4. Comparison of feeding by chaetognaths (NPC, before adjusting for prey loss) and fish larvae (NPF) in relation to time of day in Dec 1992. Variance shown as ±1 standard error. Data averaged over entire water column except at 04:45 h, when the 25 to 31 m sample is missing. No. of chaetognaths and larvae examined shown in Fig. 2

(NPC, not adjusted for prey loss) was significantly greater at night (0.089 ± 0.006) than during the day (0.045 ± 0.008). Heavy feeding by chaetognaths at 04:45 h coincided with markedly different vertical distributions of chaetognaths and larval fish (Fig. 3). The number of prey per fish larva (NPF) was significantly higher during the day (2.87 ± 0.33) than at night (1.02 ± 0.17) (p < 0.001; Fig 4). Active feeding of both fish larvae and chaetognaths occurred at dusk (17:00 h).

Prey types. Only 1 of the 6817 chaetognaths examined from all samples contained a fish larva. Copepods were the most important prey items of chaetognaths on all dates, accounting for 42% of the diet in Dec 1992, 44% in Feb 1993, and nearly 90% in 333 μm mesh samples from Feb 1992. The chaetognaths collected in 64 μm mesh nets were smaller than those collected in 333 μm mesh

nets, and contained a greater diversity of prey, including some microzooplankton. Copepod nauplii (20%) and tintinnids (18%) were important prey items of chaetognaths in Dec 1992. In Feb 1993, copepod nauplii and larvaceans each accounted for 20% of total prey.

Although it represented only a small proportion of the fish larvae in the samples (Fig. 2), *Leiostomus xanthurus* contained most of the prey found in Feb 1992 (100%), Dec 1992 (97%) and Feb 1993 (81%). Copepods were the most important prey of fish larvae in Feb 1992 (100%) and 1993 (68%; Table 2). In Dec 1992 tintinnids (51%) outnumbered copepods (22%) as prey items, and such small prey items as invertebrate eggs were found only on this date.

Chaetognaths were more selective than fish larvae for prey type (Table 2). In both Dec 1992 and Feb 1993, chaetognaths selected for copepods and larvaceans, and in Feb 1993 tintinnids were selected for as well. By contrast, fish larvae consumed most prey types in proportion to their ambient densities (selection was not significantly different from zero) (Table 2). Electivities for Feb 1992 were not calculated since small ambient prey were not sampled quantitatively.

Prey sizes. The prey sizes consumed by chaetognaths were similar to those consumed by larval fish (Fig. 5A, B, C). Both consumed prey in approximate proportion to the sizes available in Dec 1992. In Feb 1993, however, relatively few small (<0.25 mm) prey were eaten by chaetognaths or fish larvae, while a disproportionately large percentage of prey in the 0.25 to 0.50 mm size class was consumed.

Mean lengths of chaetognath prey in Dec 92 (0.33 ± 0.32 mm) were significantly different (p < 0.001) from Feb 1992 (0.95 ± 0.94 mm) and Feb 1993 (0.52 ± 0.42 mm; Fig. 5A, B, C). The differences in prey sizes reflected significant differences in chaetognath lengths

Table 2. Composition of prey items in the diet of larval fish from 333 μm mesh nets, and chaetognaths, and ambient densities (averaged over depths and times) of prey retained by 64 μm mesh net. Indices of prey selection (C) were calculated according to Pearre (1982). 'Other' prey include rare prey such as amphipods, mysids, and chaetognaths. Asterisks denote statistical significance, *p < 0.05, **p < 0.005

Date		Copepods	Nauplii	Ostra-cods	Tintin-nids	Molluscs	Larva-ceans	Uniden-tified	Other
Dec 1992	No. m⁻³	2851	2436	1128	2554	475	332	0	2103
	[a]No. larva⁻¹	0.306	0.043	0.048	0.715	0.271	0.018	0.008	0
	[a]No. chaet.⁻¹	0.025	0.012	0.001	0.011	0.001	0.005	0.015	0.005
	Larvae C	−0.008	−0.005	−0.011	+0.002	+0.011	−0.022*	−	−
	Chaet. C	+0.043**	−0.046**	−0.063**	−0.045**	−0.095**	+0.113**	−	−
Feb 1993	No. m⁻³	4724	6146	1421	420	135	338	0	338
	[a]No. larva⁻¹	1.618	0.059	0.397	0.088	0.118	0.103	0	0
	[a]No. chaet.⁻¹	0.052	0.023	0.004	0.013	0	0.024	0.003	0.001
	Larvae C	+0.003	−0.006	+0.006	+0.015	+0.023*	+0.016*	−	−
	Chaet. C	+0.026**	−0.024**	−0.040**	+0.071**	−0.126**	+0.077**	−	−

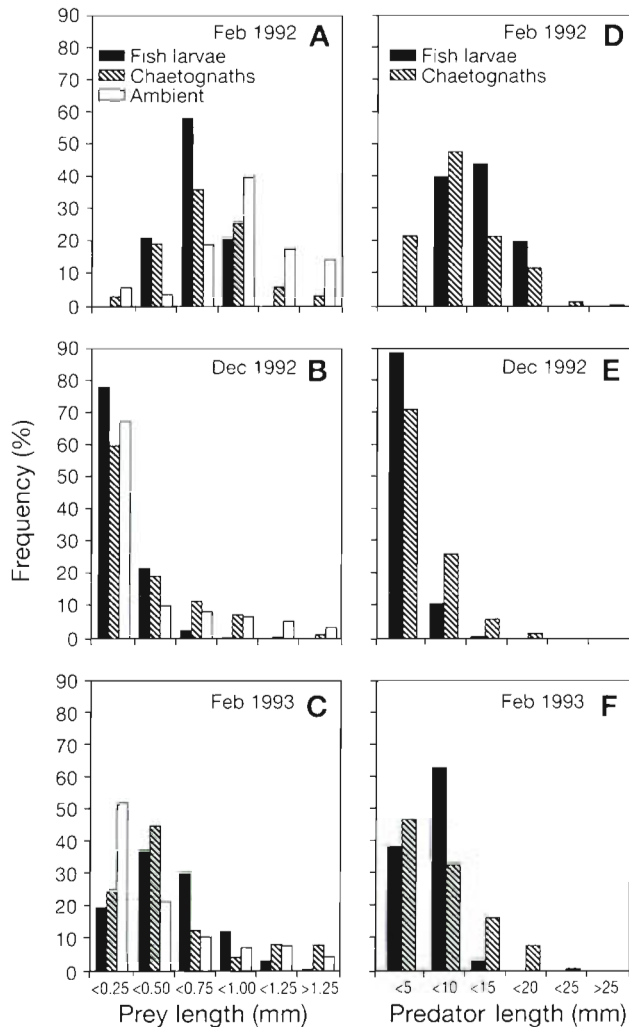[a]Not adjusted for prey loss during sampling and preservation

Fig. 5. (A, B, C) Length frequencies of prey in gut contents of chaetognaths and fish larvae, and of ambient zooplankton, and (D, E, F) length frequencies of chaetognaths and fish larvae on 3 sampling dates. All fish larva data are from 333 μm mesh net samples. Chaetognaths and zooplankton are from 333 μm mesh nets in Feb 1992, and from 64 μm mesh nets in Dec 1992 and Feb 1993. Numbers of ambient zooplankton examined shown in Table 3

among dates: Dec 1992 (4.48 ± 0.06 mm), Feb 1992 (8.82 ± 0.085 mm), and Feb 1993 (6.90 ± 0.15 mm) (p < 0.001, Fig. 5D, E, F). Differences in net mesh size cannot explain these observed size differences; Dec 1992 and Feb 1993 samples were from 64 μm mesh, and Feb 1992 samples were from 333 μm mesh.

Mean prey sizes of larval fish also differed significantly among sampling dates: Feb 1992 (0.62 ± 0.13 mm), Dec 1992 (0.18 ± 0.13 mm), and Feb 1993 (0.49 ± 0.26 mm) (p < 0.001; Fig. 5A, B, C). As with chaetognaths, these prey sizes reflected significantly different fish larvae lengths among dates (p < 0.001, Fig. 5D, E, F). All fish larva data are from 333 μm mesh samples; hence the smaller fish sizes in Dec 1992 and Feb 1993 do not reflect sampling with fine-mesh insets.

The lengths of the fish larvae sampled were greater than the lengths of the largest prey consumed by chaetognaths on all dates. The maximum prey size consumed by chaetognaths was 6.61 mm in Feb 1992, at which time fish larvae averaged 11.85 ± 0.24 mm in length. In Dec 1992, when fish larvae averaged 3.74 ± 0.12 mm, the maximum size of prey in chaetognath guts was only 1.64 mm. In Feb 1993, larval fish averaged 5.86 ± 0.24 mm and the maximum size of prey consumed by chaetognaths was only 1.61 mm.

Considering both types and sizes of prey, chaetognath and larval fish diets overlapped to the greatest extent (88%) in Dec 1992 (Table 3). The percentage of ambient zooplankton that represented potential prey of larval fish also was highest (82%) on that date. The percentage of potential fish prey in chaetognath gut contents (~60%), and in the ambient zooplankton (35 to 40%), was similar in Feb of both years.

Feeding rates and effects

Digestion rates. The temperatures in our study were lower than in other studies of *Sagitta enflata* and *S. hispida*, and digestion times were longer (Table 4).

Table 3. Types and size ranges of prey in diets of larval fish on 3 dates, used to determine the proportion of potential prey of larval fish (FP) in chaetognath diets and in ambient zooplankton. N: number of prey examined from fish guts. Number of prey examined from chaetognath guts and from ambient zooplankton shown in parentheses. Number of fish larvae and chaetognaths examined shown in Fig. 2. Overlaps of fish larva and chaetognath diets by prey type only are given in brackets

Date	N	Prey types	Prey lengths (mm) Min.	Max.	% FP in chaet. guts	% FP ambient
Feb 1992	60	Copepods [91%]	0.36	0.89	63.3 (268)	40.7 (5785)
Dec 1992	533	Tintinnids, copepods, molluscs, ostracods, nauplii, larvaceans, eggs [48%]	0.02	0.91	88.4 (505)	82.2 (14617)
Feb 1993	168	Copepods, ostracods, larvaceans, tintinnids, molluscs, nauplii [58%]	0.04	1.54	60.0 (146)	34.9 (2141)

Table 4. Digestion time (D), temperature (T), number of observations (N), and methods from the literature and from this study for *Sagitta enflata, S. helenae,* and *S. hispida.* Lab: fed in lab; *in situ*: prey consumed *in situ*, observed digestion times multiplied by 2. Regr.: proportion of chaetognaths with prey regressed on the time to preservation

| Species	D (min)	T (°C)	N	Prey	Method	Source
S. enflata	40	–	1	Chaet.	Lab	Grey (1930)
	60	24–26	–	Natural	Regr.	Szyper (1978)
	190.2 ± 48.6	23	13	Copepods	Lab	Feigenbaum (1979)
	166.7 ± 33.1	21–25	15	Natural	*in situ*	This study
	253.5 ± 94.0	16–20	8	Natural	*in situ*	This study
	433.2 ± 152.8	12–15	5	Natural	*in situ*	This study
S. helenae	176.7 ± 42.7	21–24	21	Natural	*in situ*	This study
	275.5 ± 82.8	16–20	32	Natural	*in situ*	This study
	352.1 ± 120.4	12–15	18	Natural	*in situ*	This study
S. hispida	60–120	21	250	Natural	Lab	Reeve (1980)
	180–240	–	–	Copepods	Lab	Cosper & Reeve (1975)
	272.5 ± 52.1	13	11	Natural	*in situ*	This study
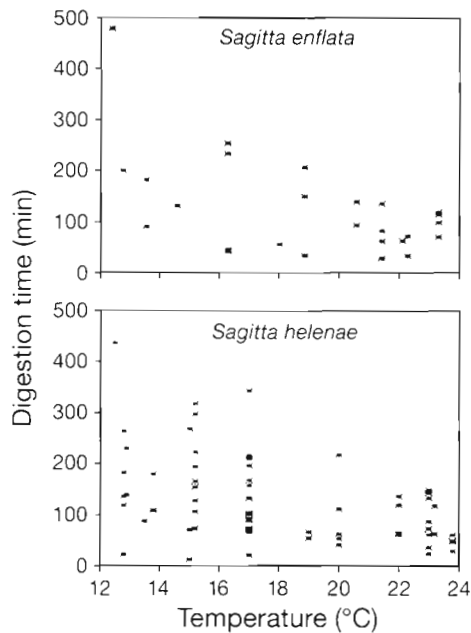
Fig. 6. *Sagitta enflata* and *S. helenae.* Relationship of digestion time (in min, before multiplying by 2) to temperature. Regression equation for *S. enflata*: $D = 2(371.42 - 12.34T)$, $R^2 = 0.302$ (p < 0.003); for *S. helenae*: $D = 2(282.70 - 11.27T)$, $R^2 = 0.202$ (p < 0.0001)

Increased temperature significantly reduced digestion times of *S. enflata* and *S. helenae* (Fig. 6). Linear regressions of digestion times with temperature gave better fits than logarithmic regressions and so were used to estimate digestion times for the feeding rate calculations.

Feeding rates. The numbers of prey per chaetognath (NPC) differed significantly among stations (p < 0.001) but not among depths within stations, so feeding rates for each station were averaged over all depths (Table 5). *Sagitta enflata* had low individual feeding rates compared with *S. helenae* and *S. hispida*, but because of its high densities, *S. enflata* consumed the most zooplankton at all but one station (Table 5).

Feeding effects. Chaetognaths removed considerable portions (12.3 to 44.4 % d^{-1}) of the standing stock of larval fish prey in Feb 1992, but not on other dates (0.3 to 0.7 % d^{-1}, Table 6). The most important factor determining the effect of chaetognath predation was the density of available prey. The relatively large larval fish present in Feb 1992 fed exclusively on copepods between 0.36 and 0.89 mm in length. These copepods were present in the environment in much lower densities than the microzooplankton, small copepods, and other prey that predominated in larval diets in Dec

Table 5. Chaetognath feeding rates as number of prey consumed chaetognath^{-1} d^{-1} (P c.$^{-1}$ d^{-1}); chaetognath densities (c. m^{-3}) averaged over all depths and times; and number of prey consumed m^{-3} d^{-1} by chaetognaths (P m^{-3} d^{-1})

Date	Stn	Sagitta enflata			Sagitta helenae			Sagitta hispida			Other species		
		P c.$^{-1}$ d^{-1}	c. m^{-3}	P m^{-3} d^{-1}	P c.$^{-1}$ d^{-1}	c. m^{-3}	P m^{-3} d^{-1}	P c.$^{-1}$ d^{-1}	c. m^{-3}	P m^{-3} d^{-1}	P c.$^{-1}$ d^{-1}	c. m^{-3}	P m^{-3} d^{-1}
Feb 92	107	0.99	30.0	29.7	2.74	3.8	10.3	0.83	3.0	2.4	2.45	6.9	17.0
	109	0.41	28.0	11.5	0.91	8.9	8.1	2.13	2.8	6.0	0.62	8.6	5.3
	110	1.01	38.8	39.1	2.08	19.8	41.2	0.87	1.1	1.0	0.70	7.2	4.9
Dec 92	120	1.14	13.3	15.1	0.98	1.0	1.0	4.23	0.8	3.5	0.31	10.9	3.4
Feb 93	227	0.86	37.7	32.5	4.21	0.6	2.4	2.53	2.1	5.2	0.24	14.9	3.5

Table 6. Effects of chaetognath predation on available prey of larval fish. P m^{-3} d^{-1}: Number of prey consumed m^{-3} d^{-1} by all species of chaetognaths; FP m^{-3} d^{-1}: number of potential fish prey (determined from percentages in Table 3) consumed by all species of chaetognaths; FP m^{-3}: density of ambient FP. Feb 1992 estimates based on samples collected in 333 μm mesh nets; all others collected in 64 μm mesh nets

Date	Stn	T(°C)	P m^{-3} d^{-1}	FP m^{-3} d^{-1}	FP m^{-3}	% available FP consumed d^{-1}
Feb 92	107	15	76.9	48.5	109.4	44.4
	109	15	40.0	25.3	206.2	12.3
	110	15	111.3	70.5	303.5	23.2
Dec 92	120	22	29.6	26.2	8376.0	0.3
Feb 93	227	18	56.3	33.8	5808.0	0.7

1992 and Feb 1993. Therefore, although chaetognaths consumed only slightly fewer prey per day in Dec 1992 and Feb 1993 than in Feb 1992, their estimated impacts were negligible on the highly abundant microzooplankton prey populations present on those dates.

DISCUSSION

Predation on fish larvae

Only 1 fish larva was found in the 6817 chaetognaths examined, compared with hundreds of other prey organisms. We believe that chaetognaths were not important predators of fish larvae during this study because various factors may have reduced the likelihood of such predation. Specifically, the impact of predators depends on the temporal and spatial overlap of predator and prey, the individual vulnerability of fish larvae to each predator taxon, and the availability of alternative prey (Bailey & Houde 1989).

Temporal and spatial overlap. Although chaetognath and larval fish distributions overlapped on all dates and at all stations, the peak spawning period of *Brevoortia tyrannus*, *Leiostomus xanthuras*, and *Micropogonias undulatus* may have coincided with seasonally low abundances of adult chaetognaths. These fish species spawn most intensively during winter over the mid- and outer continental shelf of North Carolina (Govoni & Pietrafesa 1994), and peak spawning activity of *B. tyrannus* in 1992 was in December (L. Crowder pers. comm.). Chaetognath abundances in our study were about half as high in Dec as in Feb samples, and others have found that adult populations of many chaetognath species are low during the winter (e.g. Owre 1960, Cheney 1985, Terezaki 1993).

Fish larvae may reduce the risk of predation by avoiding the depth strata occupied by their predators (Frank & Leggett 1985). Menhaden *Brevoortia tyrannus*

make a shallow migration to the surface to fill their swim bladders, allowing the larvae to rest at the surface at night (Hoss et al. 1989). In our study, many larval fish, particularly *B. tyrannus*, were near the surface during the night, when chaetognaths were more abundant in deeper water. By being less active at night, fish larvae also may reduce detection by chaetognaths, which locate prey by mechanoreception and feed more at night (reviewed in Feigenbaum 1991).

Vulnerability of fish larvae. Even when populations of predators and fish larvae overlap, subtle differences in the predator-prey size ratio can affect larval mortality (Purcell 1985, Bailey & Houde 1989). During our study, many chaetognaths were too small to consume fish larvae when larvae were small enough to be vulnerable. Early winter appeared to be a breeding period for chaetognaths as well as for larval fish. We found that juveniles measuring <5 mm were a major component (30%) of the chaetognaths sampled in Dec 1992, during the peak spawning period of *Brevoortia tyrannus*, compared with only 7% in Feb 1993. Both laboratory and field studies have shown that only fish larvae within a limited size range are vulnerable to chaetognath predation. Kuhlmann (1977) found that fish larvae of several species were susceptible to chaetognath predation only after the larvae began to swim actively (1 d) and before they became too large or strong to be consumed (10 d). Alvarez-Cadena (1993) found that small herring *Clupea harengus* larvae (5 to 9 mm) accounted for up to 7% of the prey of *Sagitta elegans*, but found no predation on larvae larger than 16 mm.

Availability of alternative prey. The most important reason for low predation rates by chaetognaths on fish larvae during this study probably was the scarcity of fish larvae relative to other available prey. Fish larvae densities averaged only about 1 m^{-3} overall. Other prey types were 10^2 to 10^3 times more numerous. Also, chaetognaths may have preferred other prey types to fish larvae (Kuhlman 1977).

Predation on food sources of larval fish

Predation by chaetognaths could limit the food resources of fish larvae, possibly leading to starvation. Houde (1994) noted that the small size, high metabolic demand, and high required ingestion rates of marine fish larvae make starvation probable if food resources are limited. Several studies indicate that some larvae are starving, or that growth is slowed by food limitation (e.g. O'Connell 1980, Theilacker 1986, Buckley & Lough 1987, Robinson & Ware 1988, Hovenkamp 1990, Canino et. al. 1991, Hovenkamp & Witte 1991)

Food limitation may indirectly contribute to fish larvae mortality via several mechanisms. Low food levels

can slow larval growth rates, thus increasing the amount of time that fish larvae are vulnerable to predation (Houde 1987). Unfed larvae were less able to escape from predators than fed larvae (Bailey & Yen 1982, Purcell et al. 1987). Encounters with predators may increase if larvae swim more in search of scarce prey (Munk & Kiørboe 1985). The cumulative indirect effects of food limitation may be even more important in the long term than the direct effects of predation (Taggart & Leggett 1987).

In our study, we did not establish that fish larvae were food limited. We evaluated the importance of chaetognaths as potential competitors of fish larvae by examining the effects of chaetognath predation on the specific types and sizes of prey consumed by fish larvae. Predation effects were determined from the degree of dietary overlap of chaetognaths and fish larvae, the consumption capacity of chaetognaths, and the abundances of available prey.

Dietary overlap. The diets of chaetognaths and larval fish overlapped considerably on all dates. The prey types and sizes changed among dates, apparently reflecting the trophic ontogenies (changes in diet with growth) of both fish larvae and chaetognaths. Our results were consistent with studies showing that chaetognaths (Sullivan 1980, Kimmerer 1984, Stuart & Verheye 1991, Gibbons 1992) and fish larvae (Economou 1991) consume larger prey over a greater size-range as they grow.

Feeding rates. Feeding rate estimates for chaetognaths were low in this study, as compared with studies in the laboratory and studies using ≤2 min tows (Szyper 1978, Kimmerer 1984; Table 7). Prey losses during our long tow durations may have been greater than estimated (Baier & Purcell 1997). Temperatures

were generally lower during this study than during other studies of *Sagitta enflata* and *S. hispida*, and digestion times were accordingly longer (Table 4), which contributed to low feeding rates. Low feeding rates also could be due to the relatively low prey densities, especially as compared with those used in laboratory studies (reviewed in Feigenbaum & Maris 1984).

Differences in feeding rates among dates may be explained in part by differences in chaetognath species and sizes. For example, because of its high individual feeding rates, *Sagitta helenae* consumed as much prey as *S. enflata* in Feb 92, even though densities of *S. enflata* were twice as great (Table 5). Feeding rates have been shown to be positively related to chaetognath length (e.g. Feigenbaum 1979, Kimmerer 1984) and to be lower in immature chaetognaths (Øresland 1987). In Dec 1992, when chaetognaths were small and 30% were juveniles, NPCs were lower than on the Feb dates, despite the high abundance of microzooplankton prey in Dec (Table 5).

Feeding effects. Abundances of the different prey consumed by larval fish on each date was the most important factor determining the potential effects of chaetognaths on prey populations. Chaetognaths would only have affected the food resources of fish larvae in Feb 1992, when fish larvae were larger than on other dates, and specialized on large copepods. Although chaetognath and larval fish diets overlapped on all dates, the small, diverse prey that larvae consumed in Dec 1992 and Feb 1993 were too abundant to be affected by chaetognath predation. To our knowledge, no other studies have evaluated the potential for competition between chaetognaths and fish larvae; however, some have examined predation effects on popu-

Table 7. Feeding rates of chaetognaths, as number of prey chaetognath^{-1} d^{-1} (P c.$^{-1}$ d^{-1}). Modified from Feigenbaum (1991)

Species	Location	T (°C)	P c.$^{-1}$ d^{-1}	Source
Sagitta enflata	Laboratory	21	10.0	Reeve (1980)
	Kaneohe Bay, Hawaii	–	10.1	Kimmerer (1984)
	Kaneohe Bay, Hawaii	24–26	7.4	Szyper (1978)
	Florida Current	–	2.2	Feigenbaum (1979)
	Virginia Shelf	25	1.3	Bushing & Feigenbaum (1984)
	South Atlantic Bight	22	1.1	This study
	South Atlantic Bight	18	0.9	This study
	South Atlantic Bight	15	0.8	This study
Sagitta helenae	South Atlantic Bight	22	1.0	This study
	South Atlantic Bight	18	4.2	This study
	South Atlantic Bight	15	1.9	This study
Sagitta hispida	Laboratory	24	5–60	Reeve (1964)
	Laboratory	26	23.7	Reeve (1970)
	Laboratory	21	14.1	Reeve (1970)
	Laboratory	16	10.8	Reeve (1970)
	South Atlantic Bight	22	4.2	This study
	South Atlantic Bight	18	2.5	This study
	South Atlantic Bight	15	1.3	This study

lations of copepods and other zooplankton. Szyper (1978) found that small copepods in Kaneohe Bay, Hawaii, were too numerous (3×10^4 m^{-3}) to be much affected by chaetognath predation, but larvacean populations were significantly reduced. Kimmerer (1984) found that chaetognaths removed 4 to 12% of copepod standing stock daily, but speculated that effects on specific size groups could be much greater, since the chaetognaths were size-selective. Stuart & Verheye (1991) found that *Sagitta friderici* removed 1.0 to 5.3% of copepod standing stock off South Africa.

Chaetognath predation has been shown to have the greatest effects on copepod populations during periods of low copepod production. Sameoto (1973) estimated that *Sagitta elegans* consumed only 1% of yearly copepod production, but up to 50% of winter production. Øresland (1990) found that daily predation by *Eukrohnia hamata* on copepods in Antarctic waters was 0.03 to 0.06% of the standing stock, and estimated that this predation could reduce copepod populations by about 12% in winter, when most copepods do not reproduce. Unfortunately, we are not aware of any estimates of copepod production for the South Atlantic Bight. Copepod abundances, reproduction, and growth rates are low in winter on the inner shelf (Pomeroy et al. 1993), but zooplankton rate processes are high throughout the year on the outer shelf (Verity et al. 1993). The sampling stations in our study were located over the mid-shelf, and may be influenced by both inner- and outer-shelf processes.

Chaetognaths were not important predators of fish larvae during this study, and had a negligible effect on the abundant microzooplankton prey of the small fish larvae present in Dec 1992 and Feb 1993; however, predation by chaetognaths removed as much as 44% of standing stocks of the large copepods that the relatively large fish larvae preyed on in Feb 1992. Because of the great abundance of chaetognaths, their predation on copepod populations may, at times, be a major factor affecting prey available to larval fish.

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