

Feeding by Chaetognatha: Aspects of Inter- and Intra-Specific Predation

S. Pearre, Jr.

Department of Oceanography, Dalhousie University, Halifax, Nova Scotia B3H 4J1, Canada

ABSTRACT: Predation on chaetognaths by their own or other species – loosely termed ‘cannibalism’ – increases with the size of the predator species. It is also affected by abundance, although the relationship is less clear from the data available at present. For both of these relationships, as previously shown for prey size selection, head width is a better measure of predator size than length. The proportion of chaetognaths in the diets increases exponentially with predator size and at a rate greater than predicted by a random feeding model; large-headed chaetognath species appear to be primarily predators of small-sized species. The cost-benefit ratio, calculated by Kerr’s (1971) model, heavily favors selection of chaetognath-sized particles over copepod-sized particles by large chaetognaths, and the levels of cannibalism achieved appear to maintain overall food-gathering efficiency approximately constant over a wide range of chaetognath sizes. The model is consistent with Darwinian evolution of inter- and intraspecific predation among large species.

INTRODUCTION

While copepods have generally been found to be numerically dominant among the gut contents of field-preserved Chaetognatha, larger species and stages have been found to contain a variety of larger prey items. These include Larvaciae, fish larvae and even euphausiids, but by far the most common seem to be chaetognaths of their own or other species, usually detected as chaetae (grasping jaws) and sometimes also eyes or soft tissue. As it is usually difficult to identify such remains to species, all predation by chaetognaths on chaetognaths, whatever the species, has been casually called ‘cannibalism’ in the literature. For lack of a better term I will herein use ‘cannibalism’ in the same sense, i.e. a (generally unknown) combination of inter- and intra-specific predation. Purely intra-specific predation will be called ‘true cannibalism’.

Cannibalism in chaetognaths was probably first recorded by Thomas Scott (1893) who found it in ‘*Sagitta*’ (probably *S. elegans* Verrill) in Scottish waters. Alvarino (1975) and Nagasawa and Marumo (1976a) listed a number of studies showing cannibalism in various species, and more have been reported since. Reports on the food of 31 planktonic chaetognath species have shown cannibalism in 24 and it seems

likely in all. Stone (1969) noted that larger species were more cannibalistic than small ones, although Alvarino (pers. comm.) feels that *S. enflata* Grassi, a medium-sized species, is the most cannibalistic of all. Feigenbaum (1979) estimated that cannibalism becomes an increasingly important carbon source for *S. enflata* as it matures. I have estimated that true cannibalism can provide a major energy source for large *S. elegans*, especially in times of food shortage (Pearre, 1981*). In an unpublished presentation (Pearre, ms 1976) I considered the relation of chaetognath species size to their degree of cannibalism. This paper enlarges that work, and attempts to explain the observed variations in cannibalism.

The data utilized in this study are listed in Table 1. Where data could be conveniently subdivided by areas and dates (Rakusa-Suszczewski, 1969; Pearre, 1970), these were entered separately.

THE MODEL

Mature chaetognaths grow larger than copepods, their numerically dominant prey. Mean prey size increases with chaetognath predator size (Pearre, 1980a) so it follows that in plankton size classes up to the size of large adult chaetognaths, there is an increase in the numbers of chaetognaths relative to copepods. Thus it might be expected *a priori* that,

* See Erratum p. 43

Table 1. Data on inter- and intra-specific predation by chaetognaths of the genera *Sagitta*, *Eukrohnia* and *Pterosagitta*

No.	Species	Mean length (mm)	Number examined	Number of chaetognaths in diet	Total prey	% cannib.	Number of chaetognaths per m ³	Source
1.	<i>S. bipunctata</i>	9.4	2,756	16	240	6.7	3.0	Stone (1965)
2.	<i>S. elegans</i>	7.4	2,777	20	755	2.7	262.4	Pearre (1970; July)
		8.5	4,048	22	749	4.0	76.0	Pearre (1970; Dec.)
		10.0	3,820	19	1699	1.2	n.d.	Feigenbaum (ms 1979)
		10.6	2,923	19	1059	1.8	8.4	Sullivan (1977)
		10.7	7,827	12	1331	0.9	13.2	Rakusa-Suszczewski (1969)
		13.4	3,673	15	956	1.6	n.d.	Rakusa-Suszczewski (1969)
		12.0	5,749	7	723	1.0	4.8	Rakusa-Suszczewski (1969)
		9.0	10,564	61	2067	3.0	13.6	Rakusa-Suszczewski (1969)
		10.3	4,709	10	612	1.6	17.4	Rakusa-Suszczewski (1969)
		7.3	469	3	214	1.4	8.2	Pearre (1974)
3.	<i>S. enflata</i>	10.4	1,436	39	1071	3.6	24.9	Pearre (1976)
		10.7	14,544	39	374	10.4	3.0	Stone (1965)
		6.8	5,677	94	1593	5.9	2151	Szyper (1976)
		16.5	3,088	28	535	5.2	0.4	Feigenbaum (1979)
		7.1*	2,199*	423*	944*	44.8*	233*	Piyakarnchana (1965)
4.	<i>S. friderici</i>	6.2	1,700	2	334	0.6	8.2	Pearre (1974)
		8.8	1,131	3	135	2.2	24.9	Pearre (1976)
		12.6	3,244	3	41	7.3	3.0	Stone (1965)
5.	<i>S. hexaptera</i>	17.1	3,103	33	107	30.8	3.0	Stone (1965)
6.	<i>S. lyra</i>	13.4	1,295	20	42	47.6	3.0	Stone (1965)
7.	<i>S. minima</i>	4.7	6,734	1	470	0.2	8.2	Pearre (1974)
8.	<i>S. robusta</i>	9.6	1,468	10	44	22.7	3.0	Stone (1965)
9.	<i>S. serratodentata</i>	8.5	7,034	2	168	1.2	3.0	Stone (1965)
10.	<i>S. setosa</i>	6.5	1,000	1	61	1.6	12.3	Rakusa-Suszczewski (1969)
		8.4	3,058	20	337	5.9	35.1	Rakusa-Suszczewski (1969)
		5.3	2,165	20	907	2.2	27	Mironov (1960)
11.	<i>E. hamata</i>	10.0	3,791	4	434	0.9	8.4	Sullivan (1977)
12.	<i>P. draco</i>	5.9	600	3	66	4.6	n.d.	Newbury (1978)
		6.4	5,860	42	337	12.5	3.0	Stone (1965)

* Piyakarnchana's (1965) data not included in the regression due to methodological differences (see text). n.d.: no data available

given either random or constant selection, the proportions of chaetognaths in chaetognaths' diets should increase as larger size classes are examined. Assuming that the usual exponential survivorship curve applies to both a chaetognath population (Sameoto, 1971a; Szyper, 1976) and the associated copepod community, an exponential relation of size class to proportion of chaetognaths in the environment is expected. Data supplied by O'Connell (1971), for southern California waters can be fitted by exponential curves for both copepod and chaetognath fractions. From these, the proportions of chaetognaths increase as:

$$S_p = 21.1 e^{0.45w} \quad (1)$$

where $S_p = \frac{\text{number of chaetognaths per cubic meter}}{\text{number of copepods plus chaetognaths per cubic meter}}$

(expressed as arcsine transform); w = plankton width class (mm)

Breder and Coates (1932) noted that true cannibalism increases with population density. Piyakarnchana (1965) found this to be true in a dense population of small *Sagitta enflata* in Kaneohe Bay, Hawaii. The exact form of the density-dependence is not obvious, however. In the usual patchy environment encounter probability is likely to depend on the logarithm of the

density (Barnes, 1952; Cassie, 1962), so this seems the most reasonable, simple model.

In general we predict that if chaetognath prey are selected randomly, constantly, or with a linearly size-dependent bias, the proportion of chaetognaths in the diet should increase as some exponential function of predator size and as the logarithm of the abundance.

MATERIALS AND METHODS

Field Methods

Sagitta elegans Verrill was collected by the author at 7 depths near the deepest part of Bedford Basin, Nova Scotia (Table 2). Sampling was done at various times through the diel cycle on July 17–18 and December 12–13, 1967. Due to high abundance in July, only 1/8 of the samples were used; in December the whole samples were counted. All chaetognaths which could be found under the dissecting microscope were removed, measured, and examined for gut contents; the range found was from about 1.2 mm (newly hatched) to 33 mm. Further details of collection and handling are given in Pearre (1973, 1980a).

Sagitta minima Grassi, *S. enflata* Grassi, and *S. friderici* Ritter-Zahony (believed by Dallot, 1978, to be

instead *S. setosa* Müller) were obtained from 2 sets of samples taken by F. Vives and J. M. San Feliu, of the Instituto de Investigaciones Pesqueras, Castellón, Spain. Further details of these samples and their treatment can be found in Pereiro (1972) and Pearre (1976).

Other data were obtained from the literature or via personal communication from the authors. For comparison, an outline of field methods used is given in Table 2.

Laboratory and Statistical Methods

A number of workers have shown that chaetognaths feed more intensively at night (Parry, 1944; Mironov, 1960; Reeve, 1964; Rakusa-Suszczewski, 1969; Nagasawa and Marumo, 1972; Pearre, 1973, 1974; Szyper, 1978; Feigenbaum, 1979; Sullivan, 1980). According to Sullivan (1980), feeding intensity is also dependent on total food available. Environmental temperature can affect both rate of food intake (Reeve, 1966; Pearre, 1974, 1976) and rate of digestion (Mironov, 1960; Nagasawa and Marumo, 1972; Feigenbaum, ms 1979).

The variability introduced by these environmental factors made it necessary to express the degree of

cannibalism by the proportions of chaetognaths among all diet items rather than by the simple frequency of chaetognath prey. These proportions were normalized by the arcsine transformation (Sokal and Rohlf, 1969) to permit statistical manipulation and testing.

Feigenbaum (1977, 1979) did not report the abundance of chaetognaths in his study area. A value for this (0.4 m^{-3}) was assumed from Bsharah's (1957) study in the same area. For all studies, the mean abundance of potential prey chaetognaths in the water column was estimated as the total abundance of all species found throughout the sampled water column.

Piyakarnchana's (1965) study, featuring extremely high estimates of cannibalism, has been omitted from the general analysis because of criticisms of the methodology (Szyper, 1976). However, some of the findings have been useful for comparative purposes.

Mean head widths of Stone's populations of chaetognaths were provided in his thesis (Stone, 1965). Mean head widths of chaetognaths in other studies were estimated from mean lengths and head width/total length ratios derived from observation and photomicrographs or camera lucida drawings (Pearre, 1980a). These refer only to bristles in non-expanded position. A list of these ratios and the number of separate ratios used to obtain each is given in Table 3; literature sources can be supplied by the author.

Table 2. Field methods used in various studies (chronological order)

No.	Source	Sampling area	Net mouth (cm)	Mesh (mm)	Depth (m)	Tow method	Season	Time
1	Mironov (1960)	Sevastopol Bay, Black Sea	n.d.	n.d.	n.d.	n.d.	Au	DN
2	Piyakarnchana (1965)	Kaneohe Bay, Hawaii	46.5	0.285	sfce	h	Sp, Su, Au, Wi	D, DN
3	Stone (1965, 1969)	Agulhas C. S. Africa	70 100	0.53+0.3 ³ 4+2 ³	150 150	v h, o	Sp, Su, Au	D
4	Rakusa-Suszczewski (1969)	North Sea Irish Sea Engl. Channel	~70	~0.33	32-148	v	Su, Au	D, DN
5	Pearre (1970, 1973)	Bedford Basin, Canada	12.7 ¹	0.24	70	h	Su, Wi	DN
6	Pearre (1974)	W Mediterranean Sea	36.5	0.25, 0.18, 0.10 ³	94	h	Sp	DN
7	Pearre (1976)	W. Mediterranean Sea	36.5	0.25, 0.18, 0.10 ³	78	h	Sp, Su, Au, Wi	D
8	Szyper (1976, 1978)	Kaneohe Bay, Hawaii	50 0.35	0.33 .035+0.33 ⁴	6.8	v	Sp, Su, Au, Wi	D, DN
9	Feigenbaum (1977, 1979)	Florida C.	100	1.62	50 or 100	v	Wi, Sp	DN
10	Sullivan (1977, 1980)	Sta. 'p', N. Pacific Ocean	70 ²	{ 0.33 ⁵ 0.18	500	h	Su	D, N
11	Newbury (1978)	Near Hawaii	70 ²	{ 0.20 ⁵ 0.18	300	o	Su	D

n.d.: no data supplied – Net mouth: 1 Clarke-Bumpus net; 2 Bongo net – Mesh: 3 different sections on one net; 4 concentric nets; 5 separate nets on Bongo frame – Tow method: h horizontal tows, generally with closing nets; v vertical tows; o oblique tows – Season: Sp spring; Su summer; Au autumn; Wi winter – Time: D daylight; N night; DN multiple set in 24 h; D, N one each in 24 h

Table 3. Head width/body length ratios estimated for chaetognath predator species of the genera *Sagitta*, *Eukrohnia* and *Pterosagitta*

Species	Head-width/ body length	Number of determi- nations	Number of authors
<i>S. bipunctata</i>			
Quoy & Gaimard	0.0676	12	10
<i>S. elegans</i> Verrill	0.0517	22	12
<i>S. enflata</i> Grassi	0.0758	24	13
<i>S. iriderici</i> Ritter-Zahony	0.0710	6	6
<i>S. hexaptera</i> d'Orbigny	0.0619	16	11
<i>S. lyra</i> Krohn	0.0745	8	7
<i>S. minima</i> Grassi	0.0460	10	8
<i>S. robusta</i> Doncaster	0.0977	10	6
<i>S. serratodentata</i> Krohn	0.0586	15	4
<i>S. setosa</i> J. Müller	0.0540	13	7
<i>E. hamata</i> Möbius	0.0618	12	8
<i>P. draco</i> (Krohn)	0.1169	14	13

Regressions were weighted for the number of each species examined. Four regression models were tested: linear-linear, linear-logarithmic ('log'), log-linear ('exponential') and log-log ('power'). Model I regressions (Sokal and Rohlf, 1969) were calculated on proportion of cannibalism vs. either mean length or mean head width. For these all data on any given species were grouped. Model I multiple regressions were calculated using chaetognath prey abundance as an extra factor. For these, each study or part of a study for which abundance estimates were available was included separately. Significances of the simple regressions were calculated as 2 tailed 'Student's-t' tests. Multiple regressions were treated as recommended by Snedecor and Cochran (1956) to obtain partial regressions on each variable as well as overall 'F' values. In tables and text, significance of the null hypothesis is denoted by the following convention (Sokal and Rohlf, 1969):

- = 0.05 > P > 0.01
- = 0.01 > P > 0.001
- = P < 0.001

The value of cannibalism to predator chaetognaths was approached by estimation of carbon value of

chaetognath prey and other prey, the latter assumed to be of copepod size and carbon content. This required estimation of mean sizes of each as functions of predator size, and from those, carbon weights.

Carbon Value of Prey Copepods

As well as being numerically dominant among prey of chaetognaths, copepods usually have been thought to contribute the largest fraction of nutrition (Feigenbaum, 1979; Pearre, 1981). The carbon value of non-chaetognath prey was estimated as though entirely copepods (Table 4). Equation 4-A, embodying data on 2984 prey items, closely resembles the equation derived from Reeve and Walter's (1972) experimental study on feeding of *Sagitta hispida*, $H = 0.282 P^{0.602}$. The difference in multipliers is at least partly attributable to the very great head size of this species (Pearre, 1980a).

Carbon Values of Prey Chaetognaths

Size of prey vs. size of predator: the data from July samples (Pearre, 1981) were weighted by 8 to account for subsampling. Significance was computed by a 't' test for groups, d.f. = 35.

Carbon content vs. chaetognath length: the genus *Sagitta* contains about ¾ of the known chaetognath species, with *Eukrohnia* being next largest. There are 2 basic body types among *Sagitta*: individuals which are active muscular hunters (= 'rigid' forms) and others which are less muscular, more water-filled ambush predators ('flaccid' forms). Fortunately, carbon data are available for both types (*S. hispida* and *S. enflata*, Table 5) as well as *S. elegans*, which in appearance is intermediate. Dry weight as a function of length is reported for one species of *Eukrohnia*, and a carbon to dry weight determination for another. These were combined to approximate the carbon/length relation for this genus, and then all 4 relationships were combined to yield a 'generalized chaetognath' (Eq. 5-B).

Table 4. Estimators for carbon contribution of non-chaetognath prey (as copepods)

No.	Equation	Source	Remarks
4-A	$H = 0.483 P^{0.629}$	All field data combined Pearre (1980a)	$n = 484$ (size groups) $r^2 = 0.424$ •••
4-B	$W_w = 1.56 H^{2.88}$	Pearre (1980b)	General relationship for copepods
4-C	$W_D = 0.154 W_w^{1.08}$	Pearre (1981)	General relationship for copepods
4-D	$W_C = 484.2 W_D^{1.028}$	Data of Ikeda (1974)	$n = 109$ $r^2 = 0.995$ •••

H: prey body width (mm); P: predator head width (mm); W_w : live wet weight (mg); W_D : dry weight (mg); W_C : carbon weight (μ g)

Table 5. Estimators for carbon contributions of chaetognaths (genera *Sagitta* and *Eukrohnia*) among prey

No.	Equation	Source	Remarks
5-A	$L_H = 0.520 L_p^{0.900}$	Combined July and December data, cannibalism of <i>Sagitta elegans</i> , Pearre (1981)	$n = 39, r^2 = 0.600^{***}$
	$W_C = 0.039 L^{2.96}$	Modified from McLaren (1969)	<i>S. elegans</i> , recalculated as geometric mean regression, adjusted for 15% methodological underestimation (Copin-Montegut and Copin-Montegut, 1972)
	$W_C = 0.057 L^{2.83}$	Szyper (1976)	<i>S. enflata</i> (flaccid)
	$W_C = 0.120 L^{3.28}$	Data of Reeve and Baker (1975)	<i>S. lispida</i> (rigid)
	$W_C = 0.116 L^{3.00}$	Matthews and Hestad (1977) ($W_{D/L}$) Ikeda, (1974) (W_C/W_D)	<i>E. hamata</i> <i>E. fowleri</i>
5-B	$W_C = 0.0724 L^{2.719}$	Combination, above 4 equations	„Generalized chaetognath“
5-C	$P/L_p = 0.0733$	This paper	Head width for „generalized chaetognath“

W_C : carbon weight (μg); L : total length excluding tail fin (mm); L_H : prey chaetognath length (mm); L_p : predator chaetognath length (mm); P : predator chaetognath head width (mm)

Chaetognath head width vs. length: values of this ratio, measured by myself or from literature sources, were themselves averaged for 39 species of *Sagitta*, 4 *Eukrohnia*, 2 *Krohnia*, and 1 each of *Heterokrohnia* and *Pterosagitta* (Eq. 5-C).

RESULTS

Relation of Cannibalism to Size and Abundance

The best fit multiple regression for cannibalism as a function of both predator size and chaetognath abundance was:

$$C_s = 1.531e^{2.431P} \cdot U^{0.455} \quad (2)$$

with $n = 26, r^2 = 0.67, F = 23.0^{***}$

C_s = arcsine transformation of the numerical proportion of chaetognaths among diet items; P = mean head width of predators (mm); U = total number of chaetognaths per cubic meter.

The partial regression on head width alone was highly significant ($t = 6.72^{***}$), accounting for 66 % of the variance. The partial regression on abundance had $t = 2.90^{**}$ but accounted for only 12 % of the variance. The sums of r^2 values for size and abundance total more than the overall r^2 , indicating lack of orthogonality. This probably is because smaller species tend to be more abundant in nature, and is a statistical anomaly of studies involving cannibalism. The multiple regression using length instead of head widths was not significant ($F = 2.45$). The partial regression on length alone was barely significant ($t = 2.14^*$).

After applying Szyper's (1976) corrections for abundance, Piyakarnchana's (1965) data on the relation of *Sagitta enflata* abundance to cannibalism can be fitted to a power curve as:

$$C_s = 9.24 U^{0.237}, m = 12, t = 3.32^{**}$$

Equation 2 evaluated at the mean predator head width in Piyakarnchana's study ($P = 0.53$ mm) yields a similar result:

$$C_s = 5.56 U^{0.455}$$

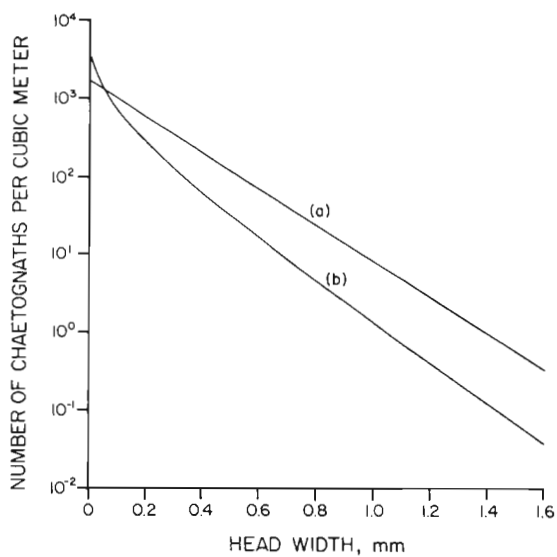


Fig. 1. Combinations of chaetognath abundances and size at which 50 % of the diet is expected to be chaetognaths, (a) by numerical abundance, (b) by carbon contribution

Equation (2) can be used to predict combinations of predator size and prey abundance at which 50 % of the diet items are chaetognaths (Fig. 1a). The value of cannibalistic feeding to the predator chaetognath species cannot be judged by numerical proportions alone. Following Feigenbaum (1979) I have estimated proportions of carbon contributed by cannibalism, as described in Tables 4 and 5 ('Methods').

Equations 4-A, 4-B, 4-C, and 4-D (Table 4) can be combined to estimate the carbon value of an average copepod prey to a chaetognath of size (head width) P :

$$W_c = 11.39 P^{2.001} \quad (3)$$

Similarly, Equations 5-A, 5-B, and 5-C (Table 5) can be combined to estimate the value of a typical chaetognath prey to a chaetognath of size P :

$$W_c = 88.21 P^{2.719} \quad (4)$$

Assuming equal handling costs, it is clear that a cannibalistic encounter is likely to be much more valuable, especially for a large predator chaetognath. These results can be substituted into Eq. (2) to yield combinations of predator size and prey abundance at which cannibalism supplies 50 % of the dietary carbon

(Fig. 1b). As expected, this line diverges from (a) as predator size increases.

Because of the great superiority of head width (size) over abundance as a predictor I felt justified in comparing cannibalism to size alone. This permitted use of some data sets which did not have information on abundance, and combination of all sets by species (Fig. 2). As expected, the best fit regression was again an exponential,

$$C_s = 2.012 e^{2.473 P} \quad (5)$$

$n = 12, r^2 = 0.767, t = 6.28^{***}$

This regression becomes virtually identical to the multiple regression (Eq. 2) at a mean chaetognath abundance of 4.6 per cubic meter. Fig. 2 shows that, as predicted by Stone (1969), larger species are more cannibalistic than small ones. This will be treated further under 'Discussion'.

Sources of Error

Factors Affecting the Estimate of Numerical Proportion of Chaetognaths in the Diet

Although cannibalism increases with species size, the largest individuals within a species are not necessarily the most cannibalistic. Both Szyper (1978) and Feigenbaum (1979) found cannibalism to be essentially invariant with size in *Sagitta enflata*. Mironov's (1960) data, however, show cannibalism peaking at 4-5 mm in populations of *S. setosa* ranging to more than 10 mm. Rakusa-Suszczewski (1969) reported reduced cannibalism by *Sagitta setosa* and *S. elegans* of the smallest and largest size classes. My results on *S. elegans* in Bedford Basin and *S. minima*, *S. friderici* and *S. enflata* in the Mediterranean Sea show no statistically supportable trends among life stages. The simplest explanation for low observed cannibalism in young stages is the difficulty of recognizing very young-stage prey. Newly-hatched chaetognaths lack the chaetae by which chaetognath prey are usually identified (Kotori, 1979; Nagasawa and Marumo, 1979), and so are never recognized among prey of any predators. These stages suffer high mortality (McLaren, 1969; Sameoto, 1973; Zo, 1973) and it is likely that cannibalism accounts for some of this. On the other hand, low observed levels of cannibalism among large stages can be a statistical artefact: larger individuals tend to be scarcer, and so if the expectation of cannibalism is less than 0.5, the probability of finding chaetognath prey compared to others decreases as size increases. The overall effect of both artefacts is probably a general underestimation of cannibalism.

Data from samples spanning several seasons or a

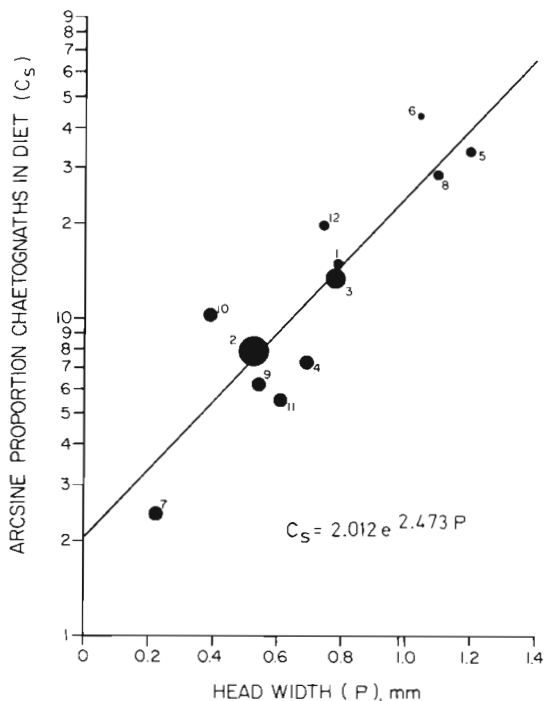


Fig. 2. Arcsine transformation of numerical proportion of chaetognaths in the diet as a function of predator (genera *Sagitta*, *Eukrohnia* and *Pterosagitta*) head width alone; all data from Table 1 grouped by species, and numbered as in Table 1, by alphabetic rank. Areas of circles surrounding points are proportional to number of specimens examined. 1 *S. bipunctata*; 2 *S. elegans*; 3 *S. enflata*; 4 *S. friderici*; 5 *S. hexaptera*; 6 *S. lyra*; 7 *S. minima*; 8 *S. robusta*; 9 *S. serratodentata*; 10 *S. setosa*; 11 *E. hamata*; 12 *P. draco*

year were presented by authors 2, 3, 5, 7 and 8 (Table 2). Among the remainder, studies from areas of low seasonality (9, 10, 11) are probably most valuable.

Regardless of seasonality, there may be diel variability. Multiple samples during 24 h (Authors 1, 5, 6 and 9) are probably best, followed by single day and night samples (10) and mixed sets (2, 4, 8).

Finally, although rates of digestion of various prey seem not to differ markedly (Kuhlmann, 1977; Feigenbaum, 1979; Szyper, 1978; Sullivan, 1980) the criteria used for judging legitimately ingested prey can affect the results. Due to the possibility of extra feeding in nets or convulsive grasping as preservative is added, most authors now apply criteria of position in the digestive tract and/or partial digestion to distinguish 'real' prey. It is not known what criteria were applied in some older studies.

Estimates of Prey Abundance

The estimates of abundance of chaetognaths are very approximate. Different studies are made with different types of sampling gear (Table 2); these sample small chaetognaths (~ 1.0–1.5 mm at hatching) with differing efficiencies. Worse, some workers are uninterested in young stages, which are difficult to identify to species (but see Nagasawa and Marumo, 1976b) and do not even attempt to enumerate them. Compounding this problem are the different vertical distributions of different species and life stages, and the generally unknown depth of most feeding activity, which also varies between species and stages (Pearre, 1973, 1974; Sullivan, 1977).

The approach made in this paper has been to ignore the difficulty of different sampling techniques, and to employ mean abundances through the water column sampled (or vertical range of all species), although these may differ from the abundances at the actual feeding depth.

Errors Affecting Regression on Carbon Contribution of Chaetognath Predation

The accumulated variance in the power relations cannot be simply estimated.

The relation of chaetognath prey size to predator size is obtained from only 1 species (*Sagitta elegans*) in a single area. Relatively small errors in the coefficient of this power curve (Eq. 5-A) could seriously affect the overall estimate of carbon contribution of chaetognath prey.

Non-chaetognath prey are all assumed to be copepods or of copepod size. Although almost all

studies have found copepods to be numerically dominant, many other types of prey have been found (Nagasawa and Marumo, 1976a; Alvarino, 1975). Szyper (1978) and Feigenbaum (ms, 1979) have found lower cannibalism than expected from the general relation (Eq. 2) combined with heavy predation on appendicularians, suggesting a substitution when appendicularians are abundant.

Problems Associated with Characteristics of Regression

Prey selection has been assumed to be random or constant. Selective feeding would not invalidate the model but would complicate the model's interpretation. This will be discussed further in the next section.

Proportions of chaetognaths in the diet are being equated to numbers rather than proportions of chaetognaths in the water column. This was necessary because of a scarcity of data on the abundances of other prey in the water column, but it probably puts limits on the goodness of fit of the overall regression. It may be possible to regard the multiplier of Eq. 2 as having dimensions of

$$\left(\frac{\text{m}^3}{\text{potential prey}}\right)^{0.445}$$

i.e., roughly the square of the inverse of the potential prey abundance.

DISCUSSION

Effective Predator Size

Head width, as an approximation of chaetognath mouth size, has been considered by several authors to be a better predictor of prey size than body length (Reeve and Walter, 1972; Pearre, 1974, 1980a, 1981; Tungate, 1975). The results of correlating both head width and length with proportion of chaetognath prey strongly support head width as the appropriate measure of predator size for chaetognath food selection studies.

Predictive Regressions

Despite the differences in areas, seasons and other sources of variation discussed above, the data form a remarkably coherent set (Fig. 2). As predicted by the model (see 'Introduction') the degree of inter- and intra-specific predation ('cannibalism') is strongly influenced by the size of the predator chaetognath

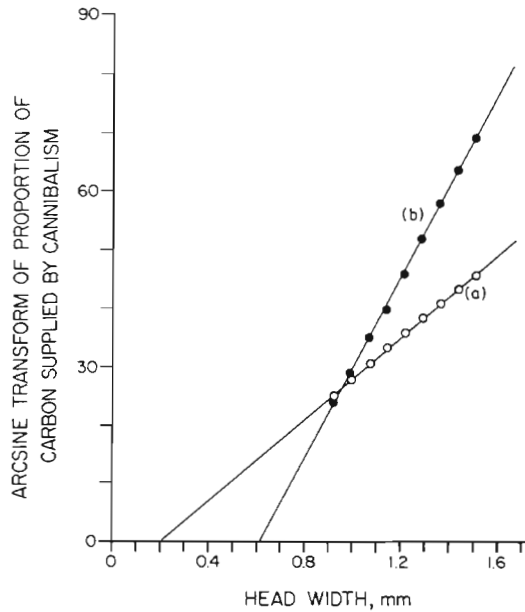


Fig. 3. Proportion of carbon contributed by chaetognath prey as a function of size. (a) Feigenbaum's (1979) model for *Sagitta enflata* off Miami, transformed to head width and arcsine: $-\circ- C_s = -6.97 + 35.1 P$; $r^2 = 0.999$; (b) Eq. 2 (mixed species) evaluated at same sizes as Feigenbaum's model, for abundance $U = 0.4 \text{ m}^{-3}$ (see text for details): $-\bullet- C_s = 48.0 + 77.8 P$; $r^2 = 0.999$

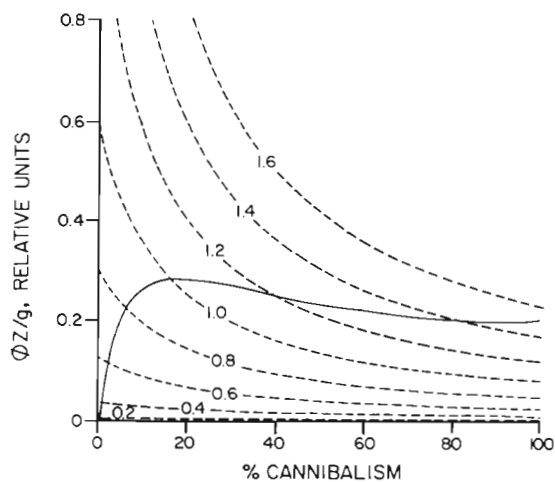


Fig. 4. Relative cost/benefit ratio for feeding at various chaetognath sizes, as a function of proportion of chaetognaths in the diet. Z assumed proportional to $(\text{weight})^{5/3}$ (Kerr, 1971). Dashed lines: Expected variation of $\Phi Z/g$ for various chaetognath sizes (head widths). Solid lines: Achieved $\Phi Z/g$ if cannibalism function follows Eq. 5. See text for derivation

species. Chaetognath abundance was also found to be of significant influence, though not completely independent of size. There can be little doubt that abundance does affect cannibalism: Szyper's (1978) superabundant but very small *Sagitta enflata* ate virtually the same proportion of chaetognaths as Feigen-

baum's (1979) very large but scarce ones in a mixed population (Table 1). However, the contribution of abundance to the variance of the multiple regression was small, probably due partly to the poor comparability of the abundance estimates. Because of this the simpler and very similar regression of proportion of cannibalism vs. size alone is probably the more useful at the present state of knowledge. This allows easy comparison by species, and shows that *S. enflata*, which has a reputation for being especially cannibalistic (Suarez-Caabro, 1955; Alvarino, 1975; Furnestin, 1957; Venter, 1969), actually lies near the middle and in almost exactly the position which would be predicted for its head width. Its cannibalistic reputation probably derives mainly from 2 factors. First, it is one of the largest of the very common and ubiquitous species. Except for Stone's (1965, 1969) study little quantitative work has been published on species of greater mean head size. Second, among large chaetognaths, it is one of the most transparent in preservative, which is especially valuable for the identification of soft-bodied prey.

However, while the form of the relation of cannibalism to head width was exponential, as suggested by the model (see 'Introduction'), the rate of increase with size was much greater than that suggested by the random or constant selection model applied to the single available data set (2.47 : 0.45, from Eqs. 5 and 1, respectively). Although the magnitudes of these exponents are both subject to question, they suggest a tendency to cannibalistic feeding over and above the random model, and varying as:

$$C_s \propto (S_p)^{5.5} \quad (6)$$

where C_s = arcsine transform of proportion of chaetognath in the diet; S_p = arcsine transform of proportion of chaetognaths in width Class P.

The relationships for the numerical proportions of cannibalism are robust relative to the proportions of carbon, due to the many approximations in the latter. However, Feigenbaum's (1979) model for *Sagitta enflata* in the Gulf Stream provides some comparisons. These are plotted in Fig. 3 in arcsine form with those derived from evaluation of Eq. 2 at a chaetognath abundance of 0.4 m^{-3} (Bsharah, 1957) using the appropriate transformations to copepods and chaetognath carbon equivalents (Eqs. 3 and 4). Feigenbaum's estimates are similar at small head sizes, but fall considerably lower at large ones. This is primarily because he found a constant rate of cannibalism with size (5.2%) and assumed that prey chaetognaths were mainly *S. enflata*, which have a lower carbon content than the mixed species model (Table 5).

The regression plane transformed to carbon (Fig. 1b) suggests that many of the larger chaetognath species

obtain more than half of their carbon from chaetognath prey, and are thus mainly secondary carnivores as suggested by Stone (1965). This conclusion is not surprising: large carnivorous fish mainly eat smaller ones; carnivorous copepods seem to prefer smaller herbivorous species (Ambler and Frost, 1974; Phillips, 1976; Båmstedt and Holt, 1978); large shell-less pteropods specialize in feeding on smaller herbivorous species (Lalli, 1970, 1972), and large ctenophores (*Beroe* spp.) specialize on the smaller copepod grazing species (Greve, 1970). An evolutionary origin of such complexes may be true cannibalism, with subsequent selection for dimorphism (P. J. Wangersky, pers. comm.). Whatever the origin, the existence of this trophic diversity among chaetognaths should somewhat lower estimates of their impact on world copepod populations (c.f. Reeve, 1970).

Effects on Predators

Kerr (1971) formalized Dahl's (1926) hypothesis that consumption of large particles should increase growth efficiency in fish. Kerr's Eq. 8 can be reduced to:

$$K = \beta - \alpha \left(\frac{Z}{g}\right)$$

where K = growth per unit ration; Z = cost of acquisition of a food item; g = weight of a food item; $\beta = p - \alpha m$

with p = assimilation efficiency; m = food utilization cost; $\alpha = \alpha_T / (\alpha_T - \alpha_R - \alpha_S)$ and α_T = coefficient of total metabolism in the equation $T_T = \alpha_T W^\gamma$

where T_T = total metabolism; W = weight of the organism; α_R = coefficient of 'spontaneous activity'; α_S = coefficient of standard metabolism; γ = fitted constant.

According to Kerr (1971), Z for fish should be proportional to (weight)^{5/3}, because it is governed by acceleration. For animals which operate at very low Reynolds numbers, mass terms become unimportant. Although no studies have been published on the energetics of swimming or acceleration in chaetognaths, even estimates of migrating speeds of *Sagitta elegans* from Hardy and Bainbridge (1954), Pearre (1973) and Terazaki and Marumo (1979), and of *S. hispida* (Feigenbaum and Reeve, 1977) yield Reynolds numbers in the 'intermediate range', 25–150. Estimates derived from maximum speed/length ratios of anguilliform fish (Webb, 1975) yield Reynolds numbers of up to around 2000 for large chaetognaths in burst swimming. Thus it seems reasonable to use Kerr's formulation as an estimate of ΦZ where Φ is the unknown proportionality constant.

Fig. 5 shows how $\Phi Z/g$ should vary as a function of percent of chaetognaths in the diet for predator

chaetognaths of different sizes (dashed lines). Superimposed on this is a plot of how $\Phi Z/g$ should have varied among the chaetognaths examined if cannibalism followed Eq. 5. These curves were derived by calculation of mean prey size as varying proportions of chaetognaths and copepods, each with size varying as functions of predator size as in Eqs. 3 and 4.

It is clear that Z/g becomes very unfavorable for large chaetognaths unless a considerable proportion of the diet consists of chaetognath-sized particles. The 'realized' curve seems to indicate that increased cannibalism does in fact act to keep Z/g relatively constant among large chaetognaths. In the absence of better data on metabolic expenditures for prey capture it is not possible to evaluate Φ (the proportionality constant) directly. However, with $\alpha > 1$, $p \approx 0.72$ (Sameoto, 1972), and m around 0.15 (S. R. Kerr, pers. comm.) Z/g should have a maximum value of 0.2 to 0.5. Judging from the inflection point in Fig. 5, Φ may not be much different from 1. An alternative way of presenting this model is to calculate the form of the energetic benefit as a function of predator size, i.e. the difference between $\Phi Z/g$ for copepods alone and $\Phi Z/g$ including cannibalism. Although a complicated function, this closely fits a power function as:

$$\frac{\Delta \Phi Z}{g} = 0.23 P^{5.69}; r^2 = 0.998 \dots$$

evaluated at $0.1 \leq P \leq 1.6$ incremented by 0.1.

From Eq. 6, this is remarkably close to the power function required to match the observed to randomly expected rates of increase of cannibalism with predator size. It therefore seems reasonable to propose that feeding energetic considerations provide both the necessary and sufficient driving mechanism for the evolution of increasing ability of larger chaetognath species to consume chaetognath prey.

Non-Random Predation

Both the estimated energetic bonus from cannibalism and the strong exponential increase with size suggest active selection of chaetognaths over copepods, yet the direct evidence for this is ambiguous. From Nagasawa and Marumo's (1972) data on *Sagitta nagae*, chaetognaths were eaten in greater proportion than their abundance, but the large-meshed net used probably undersampled copepods. Mironov's (1960) data appear to show a strong selection for *S. setosa* in Sevastopol Bay but complete absence of chaetognath predation in the open Black Sea. None of my data on *S. minima*, *S. friderici*, or *S. enflata* in the western Mediterranean Sea or true cannibalism in *S. elegans* in Bedford Basin show statistically significant preference

for either copepods or chaetognaths (contingency \times^2 test or Fisher's exact test, as appropriate). If selection of chaetognaths is random, the chance of finding compound cannibalism – one specimen inside another which is in turn inside a third – should be equal to the square of the overall probability of cannibalism. A single such case occurred among 42 recorded instances of true cannibalism by *S. elegans* in Bedford Basin. With a total of 1502 prey, the number of cases expected from random selection was 1.17.

Perhaps the lack of demonstrated selection of chaetognaths results simply from the lack of studies on large species. Stone's (1965, 1969) data unfortunately do not include copepod abundances.

Population Effects of True Cannibalism

Despite the energetic and competitive advantages to the individual from predation on its own species, true cannibalism can be disadvantageous if it results in eating one's own offspring or if it seriously reduces the probability of finding a mate (Fox, 1975). Despite this, Fox (1975) quoted studies showing that walleye pike dominates the mortality of its young stages. Davies (1949) and Kovalyov and Kudrin (1973) have found that cannibalism is at times the major food source for adult marine fish. According to Borutskii (1960), among *Chaoborus* larvae – which appear to be freshwater ecological equivalents of chaetognaths (Giguère and Dill, 1979) – true cannibalism accounted for about one-half of the annual production and constituted virtually the only source of both food and mortality in winter.

It is difficult to estimate the overall impact on most chaetognath populations, as daily consumption (a rate) is not properly comparable to standing stock (Mironov, 1960), and there are few available estimates of chaetognath production. Among the larger net-size fraction of *Sagitta enflata* in Kaneohe Bay, Hawaii, Szyper (1976) estimated that there was a mean daily nitrogen production of about $560 \mu\text{g m}^{-3}$ over a year's cycle. If predator size was related to prey size as in Eq. 5-A, cannibalism would crop about $117 \mu\text{g m}^{-3}$ or 21 % of production. Sameoto (1973) estimated that *S. elegans* in Bedford Basin produced $29.6 \text{ K cal m}^{-2} \text{ y}^{-1}$. From July and December samples I estimated that the mean daily value of cannibalism was $0.243 \text{ cal. m}^{-3}$ (Pearre, 1981). On a yearly basis, this would be equivalent to cropping about 8.7 % of production, compared to Sameoto's (1973) estimate that *Sagitta* crops about 36 % of copepod production. The figure for cropping of chaetognaths is almost certainly conservative, as their biomass approximates that of copepods in late winter and early spring (Sameoto, 1971b).

Predation on one's own species may be a useful

means of density-dependent population regulation in times of food stress (Cushing, 1971; Fox, 1975; Lane, 1979). Even a reduced population of well-nourished individuals may have better net reproductive potential than a larger number of malnourished ones (Fox, 1975). Szyper (1976) felt that this might explain the positive correlation which he found between reproductive rate and mortality of *Sagitta enflata* in Kaneohe Bay. Fox (1975) has argued that in unpredictable environments true cannibalism may be selected against at the population level, because cannibalistic species would lower their collective reproductive fitness. This is probably compensated for in some groups by growth advantages described above: in many groups (fish, crustaceans, chaetognaths) fecundity increases as a power function of size. Thus the increased growth efficiency allowed by cannibalism at large sizes may mean that the total number of eggs produced by a cannibalistic population may decline much less than does the number of spawning individuals. From Stone's (1965) data, egg number in *S. enflata* increases as $(\text{length})^{2.76}$. If this species crops 21 % of production in Kaneohe Bay (above), an increase of only 9 % in mean mature size could maintain total egg production. McLaren (1963) found that the egg number in mature *S. elegans* increases as $(\text{length})^{2.08}$. If the *S. elegans* population in Bedford Basin crops 10 % of its production (above) the total egg production could be maintained by about a 5 % increase in mean mature size. This mechanism would reinforce Darwinian selection for cannibalism rather than contradicting or limiting it.

CONCLUSIONS

(1) As in prey-size selection, head width of chaetognath predators is the best predictor of the degree of cannibalism.

(2) Both prey abundance and predator size affected cannibalism, but with currently available data, predator size is a much better predictor. Large species may be primarily predators on smaller ones.

(3) Cannibalism or predation on chaetognath-sized objects may be energetically necessary for existence of large species, and at almost all predator size increases feeding efficiency.

(4) Although true cannibalism can reduce the number of reproducing individuals in a population, the energetic advantages may allow equivalent total reproductive effort. Because this consists of increased success for the individual, cannibalism in many aquatic animals may be strongly favored in selection.

Acknowledgements. The beginnings of this work were parts of a thesis, and were supported by NSF grant GB 4676 to C. M. Boyd. Research on other species was done at the

Instituto de Investigaciones Pesqueras in Barcelona, Spain, and I would particularly like to thank B. Andréu (the director) and F. Vives for valuable aid. Besides my own data, many literature sources were tapped, and D. L. Feigenbaum, T. K. Newbury, J. H. Stone, and B. K. Sullivan have been particularly helpful in supplying unpublished details of their work. I would also like to thank A. Alvariño for identification of *Sagitta friderici* and for encouraging me to do the project. Last but not least, I would like to thank S. R. Kerr for a critical review of the manuscript and many helpful suggestions.

Recent work was partially funded by a grant to the author from the Chesapeake Bay Foundation.

Erratum

In my paper 'Feeding by Chaetognatha: Energy Balance and Importance of Various Components of the Diet of *Sagitta elegans*' (Mar. Ecol. Prog. Ser. 5: 45–54, 1981)

- Equation 2, relating gut-clearance time to temperature on both p. 46 and in the Appendix (p. 52), should read:

$$t_D = 10.24 e^{-0.0953T}$$

- References to 'Station' or 'State', p. 47, Column 2, Paragraph 2, Lines 15–17 should read 'Stage' and indicate the maturity stages of the chaetognaths.

LITERATURE CITED

- Alvariño, A. (1975). Depredadores planctonicos y la pesca. Mem. 11 Simposio latinoamericano sobre Oceanografía Biológica 1975: 139–160
- Ambler, J. W., Frost, B. W. (1974). The feeding behavior of a predatory copepod *Tortanus discaudatus*. Limnol. Oceanogr. 19: 446–451
- Båmstedt, U., Holt, M. R. (1978). Experimental studies on the deepwater pelagic community of Kjorsfjorden, western Norway. Prey-size preference and feeding of *Euchaeta norvegica* (Copepoda). Sarsia 63: 225–236
- Barnes, H. (1952). The use of transformations in marine biological statistics. J. Cons. perm. int. Explor. Mer 18: 61–71
- Borutskii, E. V. (1960). The fishery forage base. Akad. nauk. SSSR, Tr. Inst. Morf. Zhiv. im. A.N. Severtsova 13: 5–61 (Trans. IPST Cat. Nr 842).
- Breder, C. M., Coates, C. W. (1932). A preliminary study of population stability and sex ratio of *Lebistes*. Copeia 1932 (3): 147–155
- Bsharah, L. (1957). Plankton of the Florida Current. V. Environmental conditions, standing crop, seasonal and diurnal changes at a station forty miles east of Miami. Bull. mar. Sci. Gulf Carib. 7: 201–251
- Cassie, R. M. (1962). Frequency distribution models in the ecology of plankton and other organisms. J. anim. Ecol. 31: 65–92
- Copin-Montegut, C., Copin-Montegut, G. (1972). Comparison between two processes of determination of particulate organic carbon in sea water. Mar. Chem. 1: 151–156
- Cushing, D. H. (1971). The dependence of recruitment on parent stock in different groups of fishes. J. Cons. perm. int. Explor. Mer 33: 340–362
- Dahl, K. (1926). Undersökningar vid Tunhövdjorden angående fiskens näringsförhållanden före och efter regleringen. Svenska VattenkrFör. Publ. 185: 1–19
- Dallot, S. (1978). Sur la présence du Chaetognate planctonique *Sagitta setosa* Müller 1847, dans les eaux neritiques de Castillón. Invest. Pesq. 42: 33–52
- Davies, D. M. (1949). Preliminary investigations on the foods of South African fishes with notes on the general fauna of the area. Investl. Rep. Div. Sea Fish. Un. S. Afr. Vol. 11: 1–36
- Feigenbaum, D. L. (1977). Nutritional ecology of the Chaetognatha with particular reference to external hair patterns, prey detection, and feeding. Ph. D. thesis, University of Miami, USA
- Feigenbaum, D. (1979). Daily ration and specific daily ration of the chaetognath *Sagitta enflata*. Mar. Biol. 54: 75–82
- Feigenbaum, D. (ms. 1979). Low temperature feeding by the chaetognath, *Sagitta elegans*, in Vinyard Sound, Massachusetts. A. Meet. Am. Soc. Limnol. Oceanogr. Abstr. (unpubl.)
- Feigenbaum, D. L., Reeve, M. R. (1977). Prey detection in the Chaetognatha: response to a vibrating probe and experimental determination of attack distance in large aquaria. Limnol. Oceanogr. 22: 1052–1058
- Fox, L. R. (1975). Cannibalism in natural populations. In: Johnson, R. F., Frank, P. W., Michener, C. D. (eds.) Ann. Rev. Ecol. Syst. 6: 87–106
- Furnestin, M.-L. (1957). Chaetognathes et zooplancton du secteur Atlantique marocain. Rev. Trav. Off. Pêches marit. 21: 1–356
- Giguère, L. A., Dill, L. M. (1979). The predatory response of *Chaoborus* larvae to acoustic stimuli, and the acoustic characteristics of their prey. Z. Tierpsychol. 50: 113–123
- Greve, W. (1970). Cultivation experiments on North Sea ctenophores. Helgoländer wiss. Meeresunters. 20: 304–317
- Hardy, A. C., Bainbridge, R. (1954). Experimental observations on the vertical migrations of plankton animals. J. mar. biol. Ass. U.K. 33: 409–448
- Ikeda, T. (1974). Nutritional ecology of marine zooplankton. Mem. Fac. Fish. Hokkaido Univ. 22: 1–97
- Kerr, S. R. (1971). Analysis of laboratory experiments on growth efficiency of fishes. J. Fish. Res. Bd Can. 28: 801–808
- Kotori, M. (1979). Morphology of *Sagitta elegans* (Chaetognatha) in early larval stages. J. oceanogr. Soc. Japan 31: 139–144
- Kovalyov, S. M., Kudrin, B. D. (1973). Soviet investigations on capelin in the northwest Atlantic in 1971 and 1973. Intern. Comm. for Northwest Atlantic Fisheries, Redbook 1973, Part III: 121–126
- Kuhlmann, D. (1977). Laboratory studies on the feeding behavior of the chaetognaths *Sagitta setosa* J. Müller and *S. elegans* Verrill with special reference to fish eggs and larvae as food organisms. Meeresforsch. 24 (3/4): 163–171
- Lalli, C. M. (1970). Structure and function of the buccal apparatus of *Clione limacina* (Phipps) with a review of feeding in gymnosomatous pteropods. J. exp. mar. Biol. Ecol. 4: 101–118
- Lalli, C. M. (1972). Food and feeding of *Paedocione doliiformis* Danforth, a neotenous gymnosomatous pteropod. Biol. Bull. mar. biol. Lab., Woods Hole 143: 392–402
- Lane, P. A. (1979). Vertebrate and invertebrate predation on freshwater zooplankton communities. Nature, Lond. 280: 391–393
- McLaren, I. A. (1963). Effects of temperature on growth of zooplankton, and the adaptive value of vertical migration. J. Fish. Res. Bd Can. 20: 685–727
- McLaren, I. A. (1969). Population and production ecology of zooplankton in Ogac Lake, a landlocked fiord on Baffin Island. J. Fish. Res. Bd Can. 26: 1485–1559

- Matthews, J. B. L., Hestad, L. (1977). Ecological studies on the deepwater pelagic community of Korsfjorden, western Norway: Length/weight relationships for some macroplankton organisms. *Sarsia* 63: 57–63
- Mironov, G. N. (1960). Feeding of plankton predators II. Feeding of *Sagitta*. (Russ.) *Trudy sevastopol' biol. Sta.* 13: 78–88
- Nagasawa, S., Marumo, R. (1972). Feeding of a pelagic chaetognath, *Sagitta nageae* Alvarino in Suruga Bay, central Japan. *J. oceanogr. Soc. Japan* 28: 181–186
- Nagasawa, S., Marumo, R. (1976a). Further studies on the feeding habits of *Sagitta nageae* Alvarino in Suruga Bay, central Japan. *J. oceanogr. Soc. Japan* 32: 209–218
- Nagasawa, S., Marumo, R. (1976b). Identification of young chaetognaths based on the characteristics of eyes and pigmented regions. *Bull. Plankton Soc. Japan* 23: 96–106
- Nagasawa, S., Marumo, R. (1979). Identification of chaetognaths based on the morphological characteristics of hooks. *La Mer (Bull. Soc. franco-japonaise d'océanog.)* 17: 14–24
- Newbury, T. K. (1978). Consumption and growth rates of chaetognaths and copepods in subtropical oceanic waters. *Pacif. Sci.* 32: 61–78
- O'Connell, C. P. (1971). Variability of near-surface zooplankton off southern California, as shown by towed-pump sampling. *Fish. Bull. U.S.* 69: 681–697
- Parry, D. A. (1944). Structure and function of the gut in *Spadella cephaloptera* and *Sagitta setosa*. *J. mar. biol. Ass. U.K.* 26: 16–36
- Pearre, S., Jr. (1970). Light responses and feeding behavior of *Sagitta elegans* Verrill. Ph. D. thesis, Dalhousie University, Canada
- Pearre, S., Jr. (1973). Vertical migration and feeding in *Sagitta elegans* Verrill. *Ecology* 54: 300–314
- Pearre, S., Jr. (1974). Ecological studies of three west-Mediterranean chaetognaths. *Investigación pesq.* 38: 325–369
- Pearre, S., Jr. (1976). A seasonal study of the diets of three sympatric chaetognaths. *Investigación pesq.* 40: 1–16
- Pearre, S., Jr. (ms. 1976). Cannibalistic feeding by Chaetognatha. A. Meet. Am. Soc. Limnol. Oceanogr. Abstr. (unpubl.)
- Pearre, S., Jr. (1980a). Feeding by Chaetognatha: the relation of prey size to predator size in several species. *Mar. Ecol. Prog. Ser.* 3: 125–134
- Pearre, S., Jr. (1980b). The copepod width-weight relation and its utility in food-chain research. *Canadian J. Zool.* 58: 1884–1891
- Pearre, S., Jr. (1981). Feeding by Chaetognatha: energy balance and importance of various components of the diet of *Sagitta elegans*. *Mar. Ecol. Prog. Ser.* 5: 45–54
- Pereiro, J. A. (1972). Ciclo anual de los quetognatos epiplanctónicos de los aguas de Castellón. *Boln. Inst. esp. Oceanogr* 153: 3–23
- Phillips, D. G. (1976). The biology of the predatory calanoid copepod *Tortanus discaudatus* (Thomson and Scott) in a New Hampshire estuary. Ph. D. thesis, University of New Hampshire, USA
- Piyakarnchana, T. (1965). The plankton community in the southern part of Kaneohe Bay, Oahu, with special emphasis on the distribution, breeding season, and population fluctuation of *Sagitta enflata* Grassi. Ph. D. thesis, University of Hawaii, USA
- Rakusa-Suszczewski, S. (1969). The food and feeding habits of Chaetognatha in the seas around the British Isles. *Polskie Arch. Hydrobiol.* 13: 213–232
- Reeve, M. R. (1964). Feeding of zooplankton, with special reference to some experiments with *Sagitta*. *Nature, Lond.* 20: 211–213
- Reeve, M. R. (1966). Observations on the biology of a chaetognath. In: Barnes, H. (ed.) *Some contemporary studies in marine science*. Hafner, New York, pp. 614–630
- Reeve, M. R. (1970). The biology of Chaetognatha. I. Quantitative aspects of growth and egg production in *Sagitta hispida*. In: Steele, J. H. (ed.) *Marine food chains*. Oliver and Boyd, Edinburgh, pp. 168–189
- Reeve, M. R., Baker, L. D. (1975). Production of two planktonic carnivores (chaetognath and ctenophore) in south Florida inshore waters. *Fish. Bull. U.S.* 73: 238–248
- Reeve, M. R., Walter, M. A. (1972). Conditions of culture, food-size selection, and the effects of temperature and salinity on growth rate and generation time in *Sagitta hispida* Conant. *J. exp. mar. Biol. Ecol.* 9: 191–200
- Sameoto, D. D. (1971a). Life history, ecological production, and an empirical mathematical model of the population of *Sagitta elegans* in St. Margaret's Bay, Nova Scotia. *J. Fish. Res. Bd Can.* 28: 971–985
- Sameoto, D. D. (1971b). Macrozooplankton biomass measurements in Bedford Basin, 1969–1971. *Fish. Res. Bd Can., Tech. Rep.* 282: 1–238
- Sameoto, D. D. (1972). Yearly respiration rate and estimated energy budget for *Sagitta elegans*. *J. Fish. Res. Bd Can.* 29: 987–996
- Sameoto, D. D. (1973). Annual life cycle and production of the chaetognath *Sagitta elegans* in Bedford Basin, Nova Scotia. *J. Fish. Res. Bd Can.* 30: 333–344
- Scott, T. (1893). The food of *Sagitta*: additional note. *Ann. Scot. nat. Hist.* 2: 120
- Snedecor, G. W., Cochran, W. G. (1956). *Statistical methods*, Iowa State College Press, Ames, Iowa
- Sokal, R. R., Rohlf, F. J. (1969). *Biometry: the principles and practice of statistics in biological research*, W. H. Freeman, San Francisco
- Stone, J. H. (1965). The Chaetognatha community of the Agulhas Current: its structure and related properties. Ph. D. thesis, University of Cape Town, South Africa
- Stone, J. H. (1969). The Chaetognatha community of the Agulhas Current: its structure and related properties. *Ecol. Monogr.* 39: 433–463
- Suarez-Caabro, J. A. (1955). Quetognatos de los mares cubanos. *Mem. Soc. cubana Hist. nat. 'Felipe Poey'* 22: 125–280
- Sullivan, B. K. (1977). Vertical distribution and feeding of two species of chaetognaths at Weather Station P. Ph. D. thesis, Oregon State University, USA
- Sullivan, B. K. (1980). *In situ* feeding behavior of *Sagitta elegans* and *Eukrohnia hamata* (Chaetognatha) in relation to the vertical distribution and abundance of prey at ocean station 'P'. *Limnol. Oceanogr.* 25: 317–326
- Szyper, J. P. (1976). The role of *Sagitta enflata* in the southern Kaneohe Bay ecosystem. Ph. D. thesis, University of Hawaii, USA
- Szyper, J. P. (1978). Feeding rate of the chaetognath *Sagitta enflata* in nature. *Estuar. coast. mar. Sci.* 7: 567–575
- Terazaki, M., Marumo, R. (1979). Diurnal vertical migration of *Sagitta elegans* Verrill in the western North Pacific Ocean. *Bull. Plankt. Soc. Japan* 26: 11–18
- Tungate, D. S. (1975). The distribution and abundance of chaetognaths and the ctenophore *Pleurobrachia pileus* in the southern North Sea in 1968 and their importance as predators of plaice eggs and larvae. *Min. Agric., Fish., Food, Fish. Lab. Tech. Rep.* 18: 1–31
- Venter, G. E. (1969). The pilchard of South West Africa (*Sardinops ocellata*): the distribution of some chaetognaths

and their relation to hydrographical conditions, with special reference to the South West African region of the Benguela Current. Investl. Rep. mar. Res. Lab. S.W. Afr. 16: 4-73

Webb, P. W. (1975). Hydrodynamics and energetics of fish propulsion. Bull. Fish. Res. Bd Can. 190: 1-158

Zo, Z. (1973). Breeding and growth of the chaetognath *Sagitta elegans* in Bedford Basin. Limnol. Oceanogr. 18: 750-756

This paper was presented by Professor P. J. Wangersky; it was accepted for printing on August 25, 1981