Selective predation and its impact on prey of *Sagitta enflata* (Chaetognatha)

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ABSTRACT: Feeding by a natural population of the chaetognath *Sagitta enflata* in southern Kaneohe Bay, Hawaii, was studied over 1 yr. Detailed examination of gut contents led to refinements of previous estimates of ration and of impact on prey. *S. entflata* fed at or near its maximum rate of 10 to 12 prey d^{-1} at food concentrations of over 150 prey l^{-1}. Specific daily ration in terms of nitrogen was 32 %. Chaetognaths apparently select for prey size, with *Oikopleura longicauda* and adult copepods preferred over smaller prey. Predation on copepod populations removes a substantial fraction of production, but *Oikopleura* populations can usually grow more rapidly than *S. enflata* can consume them. Cannibalism provides a minor part of the diet and usually removes only a small fraction of production.

INTRODUCTION

Numerous studies of chaetognath predation have appeared in the literature, most of them on *Sagitta enflata*, *S. hispida* and *S. elegans* (Reeve, 1964, 1966, 1970, 1980; Pearre, 1974, 1976; Szyper, 1978; Feigenbaum, 1979; Sullivan, 1980). Most of these studies have been concerned with prey selection and feeding rates, and few of them have addressed the effect of predation on prey populations.

Predatory zooplankton have been shown in some instances to have a significant impact on prey populations (e.g. Rippingdale and Hodgkin, 1974; Lonsdale, 1981). In particular, the literature on fresh water zooplankton is replete with examples of predatory effect on prey morphology (Kerfoot, 1977), size (Brooks and Dodson, 1965), species composition (Gehrs and Robertsen, 1975), and abundance (McQueen, 1969). In marine waters examples are fewer, but it is clear that voracious, fast growing predators such as ctenophores can decimate prey populations (Harris et al., 1982). It is likely that other abundant planktonic predators such as chaetognaths can remove a substantial fraction of prey production each day; based on considerations of energetics, Sameoto (1972) concluded that *Sagitta elegans* consumes 100 % of copepod production in winter and early spring.

In this paper I report a study of the feeding of *Sagitta enflata* in Kaneohe Bay, Hawaii. Previous work by Szyper (1976, 1978, 1981) described feeding rates, daily ration and excretion. Here I enlarge upon those studies to consider ambient prey abundance, prey species and size selection, and proportion of prey consumed, based on detailed examination of gut contents and prey abundances. Pearre (1974), Reeve et al. (1975), Szyper (1978) and Reeve (1980) discuss the assumptions implicit in the use of gut content analysis for feeding studies. I then calculate the proportions of prey biomass consumed and compare them to estimated production.

METHODS

Samples were taken monthly during 1976 at a station near the center of the southern basin of Kaneohe Bay (Station SE; Smith et al., 1981: Fig. 16) having a water depth of about 14 m. Vertical hauls were taken with a paired net sampler (Clutter, 1973) consisting of a 0.5 m diameter, 0.33 mm mesh conical net (macroplankton) and a 0.35 m mouth diameter, 0.035 mm mesh net with a reducing cone and a 0.33 mm mesh pre-filter (microplankton). The sampler was hauled at about 75 cm s^{-1} with a power winch from 1.5 m off the bottom to the surface. Volumes filtered were determined from distance hauled and net efficiencies of 100 % for the macroplankton net and 70 % for the microplankton

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net, determined with a flow meter. The contents of the macroplankton net cod end were immediately fixed with buffered formaldehyde. Total time from start of the haul to preservation was usually less than 30 s, and always less than 1 min. Allowing animals to feed or defecate in the cod end for such a short time should make these sources of error negligible; Szyper (1978) reported times for passage of ingested food to the rear of the gut of 30 s to 2 min. The contents of the microplankton net cod end were preserved more slowly, hence chaetognaths in this net were not used for gut content analysis.

Six pairs of hauls were taken at 4 h intervals to cover a 24 h period. Because of time constraints I did not process all samples. For 7 sampling dates, I examined subsamples of both replicate hauls from each time period for the 'food containing ratio' (FCR; Feigenbaum, 1979), the proportion of animals containing food (expressed here as a percentage). I also examined one of the pair of hauls for identification of prey and for macroplankton and microplankton abundance. For 2 of the remaining months, complete sets of FCR data were obtained; otherwise, only 1 night sample was analysed for prey identification and for macroplankton and microplankton abundance.

Macroplankton samples were subsampled when necessary with a Folsom splitter and the macroplankton were counted. I then selected a minimum of 100 chaetognaths at random by taking successive small aliquots, and counted and removed the animals containing prey. Individuals with prey only in the forward third of the gut or protruding from the mouth were not considered to contain food; these prey were usually large *Sagitta enflata* or *Oikopleura longicauda*. I further subsampled the fed chaetognaths at random to obtain at least 40 individuals, measured them, and examined their gut contents. Prey were identified insofar as possible to species and, for copepods, life stage. Often the identification of copepods was based on individual body parts such as mandible blades (Sullivan, 1980) or segments of swimming feet. A regression of trunk length against fecal pellet length for *O. longicauda*, after Shelbourne (1957), was used to estimate trunk length. Length of *S. enflata* as prey was estimated when possible through regressions of total length against either head width or, when to head was distorted, distance between the eyes.

I determined nitrogen content of chaetognaths from lengths using a relationship reported by Szyper (1976). Nitrogen content of copepods was estimated from Kimmerer (1983) and Newbury and Bartholomew (1976), while that of *Oikopleura longicauda* was estimated from trunk length using data in Alldredge (1976) and Beers (1966) and assuming 30 % ash (Kimmerer, unpubl. for mixed Kaneohe Bay zooplankton). Nitro-

gen content of minor prey taxa was taken from Peterson (1975). Specific daily ration was then computed from the feeding rate and mean nitrogen content of predators and prey for each sampling date.

For the 30–31 January samples I also measured empty chaetognaths for overall population size distributions. In all other samples I sorted empty animals into those larger and smaller than 10.6 mm.

For each sample examined I calculated FCR and the number of prey per chaetognath (NPC; Feigenbaum, 1979); this is the product of FCR and the average number of prey per fed chaetognath, which I will call NPFC. Feeding rates were estimated by the method of Nagasawa and Marumo (1972), using the gut clearance time of about 1 h estimated by Szyper (1978). This method assumes the same average gut clearance time for all predator sizes and prey species (Szyper, 1978; Harris et al. 1982; Sullivan and Reeve, 1982).

Subsamples of the preserved microplankton samples were taken with a Stempel pipette and several hundred metazoans counted. Protists were not counted; they are only occasionally found in *Sagitta enflata* stomachs. The ciliates reported by Szyper (1978) in the guts of *S. enflata* were not included in the counts as they do not appear to be food for the chaetognaths.

I based selectivity calculations on all identifiable prey for a given sampling data, and mean abundances from all plankton samples from that date. I therefore used Ivlev's (1961) index of electivity; Pearre's (1982) index is preferable but applies only to raw count data.

In chaetognaths containing multiple prey the proportion of pairs of the same species was tested against the proportion expected by chance. The expected proportion of identical pairs in 2 prey items is:

$$\frac{\Sigma n_i \, (n_i - 1)}{N \, (N - 1)} \tag{1}$$

where n_i = frequency of prey i; $N = \Sigma n_i$ for all identified prey. The expected proportions of identical pairs or triplets in 3 prey items are calculated similarly.

RESULTS

Length frequency distributions were similar to those reported by Szyper (1976) with a median of 5.3 mm and a range of 1.4 to 14.6 mm. Chaetognaths smaller than 4 mm were not sampled quantitatively by the macroplankton net. The distributions were divided into 10 length classes, each containing approximately the same number of individuals, for subsequent analysis. These length classes and the numbers of fed and empty chaetognaths in each class from the January samples are shown in Table 1. Size class 10 (> 10.6 mm)

Table 1. *Sagitta enflata*. 30–31 January 1976 samples. FCR expressed as percentage vs length class

Length class	Length interval (mm)	Count in 30 January samples: Full	Empty	FCR
1	<3.00	27	31	47
2	3.00– 3.65	33	44	43
3	3.66– 4.10	40	70	36
4	4.11– 4.60	34	47	42
5	4.61– 5.25	30	57	34
6	5.26– 6.00	36	61	37
7	6.01– 7.10	27	37	42
8	7.11– 8.60	21	30	41
9	8.61–10.60	19	26	42
10	>10.60	63	18	78

as 5. The frequency of multiple prey was significantly greater by night than by day (Chi-square test, $p < 0.001$). The number of prey per chaetognath containing food (NPFC) was 1.09 for daytime samples and 1.18 at night. The mean NPFC increased with size from 1.05 for the smallest size class to 1.33 for the largest class (Rank correlation coefficient = 0.96, $p < 0.01$). Identical taxa among multiple prey were significantly more common than expected (Z-test) for pairs in 2 prey ($p < 0.0001$) and pairs in 3 ($p = 0.02$) but not triplets in 3 prey items ($p = 0.08$).

Feeding rates for the 9 mo with complete data are presented in Table 2 with *Sagitta enflata* abundance and specific daily ration. Feeding rates were positively related to total prey abundance (Fig. 1; $r_s = 0.63$, $p < 0.05$); nauplii were excluded from this figure

Table 2. *Sagitta enflata*. Abundance (m^{-3}) in macroplankton samples, feeding rate (prey *Sagitta*$^{-1}$ d^{-1}), and percent specific daily ration, for months with complete FCR data

	Jan	Feb	Mar	Apr	Jun	Jul	Aug	Sep	Nov
Abundance	100	540	500	290	980	1470	1080	1760	860
Feeding rate	11.6	8.4	8.3	7.3	10.1	10.0	11.9	11.0	12.3
Specific daily ration	27	23	32	35	38	36	18	40	29

contained relatively more fed individuals than other size classes; in all months, FCR for chaetognaths in Size Class 10 was on the average 55 % higher than for those in the smaller size classes.

FCR was greater by night than by day, at 44 ± 9 % (SD) and 29 ± 9 % (SD) respectively (t-test on arc-sine transformed data, $p < 0.01$). The day–night difference was 24 % on sampling dates near the new moon and 11 % on other dates (two-way ANOVA, $p < 0.05$ for lunar stage x day-night interaction term after arc-sine transformation).

Multiple prey were found in 11 % of the predators; most of these contained 2 prey but some had as many

Table 3. *Sagitta enflata*. Feeding rate (prey *Sagitta*$^{-1}$ d^{-1}) and specific daily ration (% d^{-1}) as a function of length class

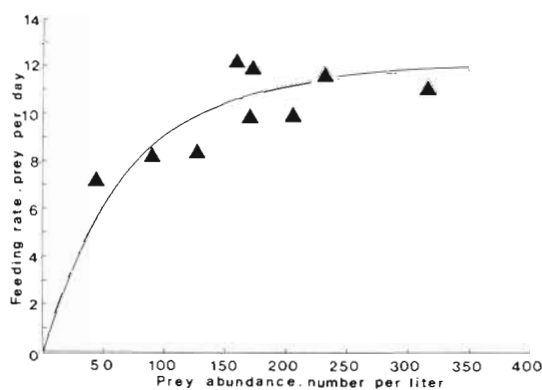| Length class	Feeding rate	Specific daily ration
1	8.8	210
2	8.6	156
3	8.9	94
4	9.2	73
5	9.1	55
6	9.4	43
7	9.4	28
8	9.7	22
9	11.1	15
10	18.8	20

Fig. 1. *Sagitta enflata*. Feeding rate as a function of abundance of prey in plankton excluding nauplii. Ivlev curve, fitted by eye, has the equation: $y = 12(1 - e^{-0.14x})$

because of their vast abundances and minor contribution to prey (see below). The median feeding rate was 10.1 prey *Sagitta*$^{-1}$ d^{-1}. Feeding rates were positively related to length class ($r_s = 0.96$, $p < 0.001$) while the reverse was true for specific daily ration (Table 3; $r_s = -0.96$). Size Class 10 had a higher specific daily ration than Size Class 9 ($p < 0.05$, sign rank test on monthly values).

Of the prey items 78 % were identified to some taxonomic level. Of these, 60 % were copepods, mainly of 4 species: *Oithona simplex*, *O. nana*, *Acrocalanus inermis*, and *Euterpina acutifrons*. *Oiko-*

pleura longicauda comprised 20 % of the diet, and copepod nauplii 8 %. Relative frequencies of prey varied with predator size (Fig. 2). *O. longicauda, A. inermis* and *E. acutifrons* were more abundant in large chaetognaths (rank correlation coefficient, $p < 0.01$)

and *O. nana* and copepod nauplii less abundant ($p < 0.0001$). Minor prey combined in 'other' in Fig. 2 included *S. enflata* (2 %), eggs, barnacle larvae, tintinnids, *Lucifer chacei* and caridean larvae, *Evadne tergestina*, unidentified crustaceans, diatoms and silicoflagellates.

In the plankton samples post-naupliar copepods comprised 34 %, *Oikopleura longicauda* 4 %, and *Sagitta enflata* 1 % of the total numbers, while copepod nauplii made up 61 %. Median electivity indices were significantly different from zero and positive ($p < 0.05$, sign rank test) for *O. longicauda* (0.68), *S. enflata* (0.52), total post-naupliar copepods (0.40), *Acrocalanus inermis* (0.39), *Oithona simplex* (0.28) and *Euterpina acutifrons* (0.79) and negative for copepod nauplii (−0.71). Electivity indices varied between day and night, but the above trends held for both periods.

If nauplii are excluded from both diet and abundances, the proportions of common prey more closely reflect proportions in the plankton samples (Table 4).
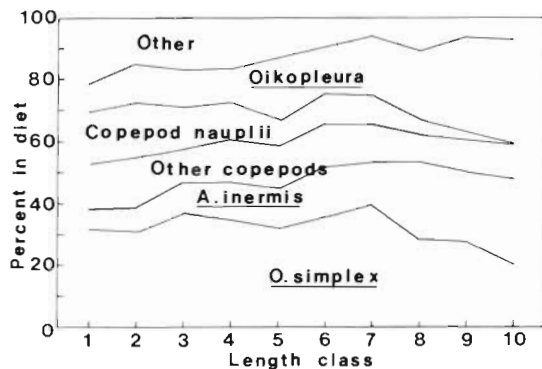

Fig. 2. *Sagitta enflata*. Relative abundance of common prey taxa in guts as a function of length class. See Table 1 for size ranges in each length class

Table 4. *Sagitta enflata*. Proportions of common prey in diet and in plankton, with nauplii excluded

	Jan	Feb	Mar	Apr	Jun	Jul	Aug	Sept	Nov
Oikopleura longicauda									
Percent in diet	13	23	41	35	29	23	5	7	6
Percent in plankton	6	5	14	26	10	9	2	4	2
Oithona simplex									
Percent in diet	46	33	19	15	40	31	50	38	44
Percent in plankton	47	28	42	22	44	35	54	43	29
Acrocalanus inermis									
Percent in diet	28	41	13	15	16	20	16	15	17
Percent in plankton	8	27	13	17	12	24	15	13	11
Sagitta enflata (all size classes)									
Percent in diet	0.7	0	2.8	1.2	2.0	1.9	7.9	6.5	0.5
Percent in plankton	0.5	2.0	1.4	1.4	1.4	2.8	1.6	1.7	0.9

Table 5. *Sagitta enflata*. Numbers of copepodites and adults of *Acrocalanus inermis* and *Oithona simplex* in guts of *S. enflata* in each length class

Length class	*A. inermis*			*O. simplex*		
	Copepodite	Adult	% Adult	Copepodite	Adult	% Adult
1	6	1	14	17	25	60
2	6	3	33	23	22	49
3	10	5	33	29	25	46
4	9	15	62	24	44	65
5	17	9	35	31	31	50
6	16	16	50	29	38	57
7	14	13	48	33	48	59
8	34	23	40	18	47	72
9	41	24	37	19	58	75
10	27	49	64	12	41	77
Total	180	158	47	235	379	62

Table 6. *Sagitta enflata*. Consumption rates (m^{-3} d^{-1}) of common prey, percent consumed daily, and percent of copepod nitrogen consumed daily by chaetognaths in macroplankton and by all chaetognaths. Median values underlined

	Jan	Feb	Mar	Apr	Jun	Jul	Aug	Sep	Nov
Consumption Rates									
Oikopleura longicauda	150	970	1600	670	2600	4200	6000	<u>1200</u>	580
Oithona simplex	530	1400	730	290	3600	<u>2800</u>	5700	6600	4200
Acrocalanus inermis	320	<u>1700</u>	510	290	1500	3100	1800	2600	1700
Sagitta enflata	10	0	<u>110</u>	30	180	260	900	1130	50
Percent Consumed									
Oikopleura longicauda	1.1	13.9	12.3	5.2	<u>12.4</u>	26.3	200.0	8.6	19.3
Oithona simplex	0.5	3.8	1.9	2.6	<u>3.9</u>	4.5	6.0	4.8	9.0
Acrocalanus inermis	1.6	5.2	4.3	3.4	<u>6.0</u>	7.5	6.7	6.1	9.4
Sagitta enflata	0.7	0	8.6	3.5	6.0	<u>5.4</u>	31.9	20.9	3.2
Percent Nitrogen Consumed Macroplankton *Sagitta*									
Oithona simplex	0.7	6.9	4.4	5.0	<u>7.0</u>	7.6	13.8	7.9	14.0
Acrocalanus inermis	2.2	<u>10.2</u>	16.4	6.2	11.9	14.4	9.9	8.4	18.1
Sagitta enflata	0.8	0	3.1	1.2	2.5	<u>2.4</u>	11.6	8.7	0.8
All *Sagitta*									
Oithona simplex	4.3	29.0	13.8	18.0	16.1	29.5	24.6	<u>20.3</u>	20.8
Acrocalanus inermis	3.5	12.4	19.1	7.4	15.1	17.5	<u>12.4</u>	10.9	19.8

Proportions of *Oikopleura longicauda* in the diet and in the water were positively related (r_s = 0.93, $p < 0.01$), as were those for *Oithona simplex* ($r_s = 0.73$, $p < 0.05$). No such relationship existed for *Acrocalanus inermis* or *Sagitta enflata*, in part because of their narrow ranges of relative abundance.

The size of the predator was reflected in the size of the prey for copepods and *Sagitta enflata* as prey. Proportions of adult *Acrocalanus inermis* and *Oithona simplex* (Table 5) were positively correlated with chaetognath length class (rank correlation coefficient, $p < 0.05$, both species). Adults comprised 47 % of all *A. inermis* and 62 % of all *O. simplex* in chaetognath guts, compared with 19 and 39 % respectively in plankton samples. The size of *S. enflata* as prey also increased with predator size for the 18 prey chaetognaths measured (r_s = 0.66, $p < 0.0025$). Mean chaetognath prey length was 50 % of the predator length.

Sizes of *Oikopleura longicauda* as prey, however, did not vary with predator size ($r = 0.03$ for $N = 179$). The median trunk length of *O. longicauda* consumed was 0.35 mm; trunk lengths in Kaneohe Bay plankton range between 0.07 and 1.1 mm.

Consumption rates on individual prey taxa and proportions of prey populations consumed daily (Table 6, top) show considerable variability. Median values for daily percent consumption were 3.9 for *Oithona simplex*, 6.1 for *Acrocalanus inermis*, 12.4 for *Oikopleura longicauda* and 6.0 for *Sagitta enflata*. Because detailed information was available for body nitrogen content of individual copepods and chaetognaths the

consumption rates can be expressed in terms of nitrogen (Table 6). A greater proportion of copepod nitrogen was consumed than copepods numbers, reflecting differences between the size distributions of prey and of ambient populations. Consumption of *S. enflata* nitrogen was somewhat lower than consumption of numbers, about 3 %, because the chaetognaths consumed were small.

Although the size class of chaetognaths caught in the microplankton net was not examined for prey, it is possible to estimate their predatory impact by the use of data from Size Class 1. This size class consumed relatively few copepods, but because of the large numbers of small chaetognaths the effect of this predation is large (Table 6, bottom).

DISCUSSION

FCR and NPFC values were higher than those reported by Szyper (1978) or Feigenbaum (1979) for *Sagitta enflata*. Feeding rates are therefore correspondingly higher: 10.1 prey $Sagitta^{-1}$ d^{-1} vs 7 (Szyper) and 1.7 to 2.9 (Feigenbaum). As indicated by Feigenbaum (1979) feeding rate increased with increasing predator size.

Feeding in chaetognaths does not satiate in the sense of Holling (1966), but the feeding rate does reach a plateau at a high food concentration. Apparently, *Sagitta enflata* was feeding at or near its maximum rate

of 10 to 12 prey $Sagitta^{-1}d^{-1}$ during most of 1976. Reeve (1980) reported a maximum feeding rate for the large form of S. enflata of 10 prey $Sagitta^{-1}d^{-1}$ where the chaetognaths were offered over 100 copepods l^{-1}. He concluded that chaetognaths rarely become satiated in nature and that feeding rate should increase linearly with the food concentrations normally seen in the ocean. In Kaneohe Bay the food abundance was near its historical maximum in 1976 (Smith et al., 1981) and well above the values summarized by Reeve (1980).

Nighttime feeding rates for Sagitta species are often higher than daytime rates (e.g. Pearre, 1973; Szyper, 1978; Harris et al. 1982; this study) but not always (Feigenbaum, 1979). Diel vertical migration patterns have been implicated in day–night feeding differences (e.g. Harris et al., 1982) and the finding of a higher day–night difference during the new moon suggests such a mechanism. No data on vertical migration of Kanehoe Bay zooplankton are available.

Specific daily ration (nitrogen) for the Sagitta enflata population was around 30 %, less than half of the value reported by Szyper (1978). The difference is attributable to a lower incidence of cannibalism in my data, as well as lower estimates of nitrogen content of the prey based on more detailed estimates of prey size. As with Feigenbaum's (1979) results the SDR decreased with chaetognath size, but it increased again in Size Class 10. This increase, if not spurious, can be explained.

Size Class 10 consists mainly of mature individuals, which may require additional food for reproduction. If, as suggested by Reeve (1964), maximum feeding rate is that needed for maximum growth, then one would expect to see a greater SDR in mature chaetognaths only when feeding is near maximum.

The incidence of cannibalism in my samples is much lower than reported by Szyper (1978) or Feigenbaum (1979) for this species. Cannibalism in Feigenbaum's samples may have resulted from the long time interval between the start of his tows and preservation, 15 to 30 min. Szyper's samples were collected by the same methods as mine, though, and preserved nearly as quickly. The higher incidence of cannibalism may have resulted from a lower abundance of alternative prey, as suggested by the lower feeding rate; prey abundance data were not collected in Szyper's study.

Differences in electivities among prey species can occur through: (1) species selection; (2) size selection; (3) patterns of co-occurrence; (4) differential detection ranges; or (5) differential capture probabilities. Evidence from this study is consistent with selection by species or, more likely, size. The 2 copepods with the highest electivities, Acrocalanus inermis and Euterpina acutifrons, have respectively the highest and lowest swimming speeds, while the smaller Oithona species have intermediate swimming speeds (own obs.). Furthermore, differential capture probabilities cannot explain the apparent selection for later life stages. This selection could result from longer detection ranges for the larger stages, but chaetognaths attack an acoustic signal at a fixed range regardless of amplitude (Feigenbaum and Reeve, 1977). The most reasonable alternative explanation of the observed electivities is co-occurrence, particularly in the vertical direction (Pearre, 1973; Harris et al. 1982). Kaneohe Bay is shallow and strongly wind mixed, though (Smith et al. 1981); furthermore, the observed electivities did not change much by day vs night, when one might expect vertical movements to change co-occurrence patterns. Co-occurrence patterns also offer a very unlikely explanation of the increase in frequencies of preferred prey and of adults with predator size, or of the occurrence of identical prey pairs.

Thus selection, whether by species or size, is the most parsimonious explanation of the observed results. That the preferred prey are also the larger prey suggests that prey size accounts for most if not all of the selection. Further experimental work on food selection by chaetognaths is clearly needed.

Szyper (1978) concluded that the impact of Sagitta enflata predation on copepod populations was small because of their vast numbers, while that on S. enflata itself was intermediate and on Oikopleura longicauda, substantial. My data show similar results in terms of numerical abundance: Sagitta predation removed, on the average, 12, 5, 4 and 6 % d^{-1} of the populations of O. longicauda, S. enflata, Oithona simplex and Acrocalanus inermis. Nevertheless, the estimated impact on these populations is likely to be rather different when actual prey sizes are considered (Sullivan and Reeve, 1982; Harris et al. 1982).

Sagitta enflata removed up to 18 % and 14 % d^{-1} of the nitrogen of Acrocalanus inermis and Oithona simplex, respectively. When estimated consumption rates of the small size class, Sagitta are included, the maximum consumption rates were 20 % for A. inermis and 29 % for O. simplex, with medians of 12 and 20 %, respectively. Specific production rates of A. inermis in southern Kaneohe Bay are around 28 % d^{-1} (Kimmerer, 1983), and those for O. simplex are likely to be similar (Newbury and Bartholomew, 1976). Thus, S. enflata is capable of cropping a substantial proportion of copepod production at some times of the year.

The impact on Oikopleura longicauda is probably somewhat less. Appendicularians are capable of doubling their biomass daily (Fenaux, 1976) but their growth is episodic (King, 1982). Daily consumption of O. longicauda during August was about twice their abundance, but for most of the remaining months it was low.

The impact of cannibalism on *Sagitta enflata* populations can be estimated by assuming gross growth efficiency of 36 % (Reeve, 1970), which implies a median specific growth rate of about 11 % d^{-1}. The consumpiton of *S. enflata* nitrogen was quite variable but approached this value only twice, suggesting that cannibalism normally has little effect on the *S. enflata* population.

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