PRODUCTION OF TWO PLANKTONIC CARNIVORES (CHAETOGNATH AND CTENOPHORE) IN SOUTH FLORIDA INSHORE WATERS[1]

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ABSTRACT

Seasonal changes in biomass and production of two planktonic carnivores, *Sagitta hispida* Conant and *Mnemiopsis mccradyi* Mayer, were followed in a subtropical inshore marine environment. Production was estimated as the product of mean daily biomass (calculated from the sampled biomass and computed mortality rates) and daily growth rate. The latter was determined from laboratory culture experiments at three temperatures. Seasonal fluctuations of ctenophore biomass and production were much greater than those of chaetognaths. Mean daily production in milligram carbon per square meter was 2.00 and 4.80 for *Sagitta* in Card Sound and Biscayne Bay respectively, and 1.01 for *Mnemiopsis* in Biscayne Bay. The ctenophore was absent from Card Sound, possibly because the zooplankton standing crop was an order of magnitude lower than in Biscayne Bay (excluding ctenophores). Average production/biomass ratios were 0.31 for *Sagitta* and 0.12 for *Mnemiopsis*.

Most production data for zooplankton are restricted to the herbivorous copepods in temperate and cold waters (see review of Mullin 1969; Mullin and Brooks 1970; Riley 1972). Estimates for carnivores are very few and include *Sagitta elegans* (McLaren 1969; Zo 1969; Sameoto 1971) and *Pleurobrachia bachei* (Hirota 1974).

As pointed out by Mullin (1969) there is no simple technique for the measurement of production of natural populations of zooplankton comparable to the relatively routine ^{14}C uptake method for the determination of primary production by phytoplankton. Unlike the phytoplankton, which share a common characteristic of a single trophic level, zooplankton extend over at least two trophic levels, and an individual species may vary its trophic status on the basis of food availability or life history stage. In addition, zooplankton range in size from 20μm or less to 20 cm or more and have widely differing growth and reproduction rates. Attempts to measure total zooplankton production have been made, especially where a single species dominates the population over a period (e.g., Cushing and Vucetic 1963) or where a single group (such as copepods) dominates and is treated as a unit (e.g., Riley 1972), and most recently by relating respiration to temperature and body weight

and applying these data to the plankton biomass of the Kuroshio (Ikeda and Motoda in press).

The data reported below are based on the individual species approach, using experimentally determined growth rates to compute production from environmental biomass estimates for two planktonic carnivores, widely separated phylogenetically but dependent upon the same source of food.

STUDY SITE AND SAMPLING METHODS

The study area consisted of Biscayne Bay and Card Sound which form part of an extensive system of shallow, warm, semiestuarine, and semienclosed interconnected water bodies typical of the coastal region of a large part of Florida. Zooplankton sampling programs were conducted at 4 stations on 28 dates throughout 1971 in Card Sound and at 11 stations on 26 dates from October 1970 to February 1972 in central Biscayne Bay. Detailed reports of these programs were given by Reeve and Cosper (1973) and Baker (1973), respectively.

In both locations, surface tows were made with a metered, ½-m mouth diameter net of 200-μm mesh. In addition, a similar net of 64-μm mesh was used in Card Sound. In Biscayne Bay, a 1-m, 705-μm mesh net with a 14-liter flexible, vinyl cod end was employed to collect ctenophores. It was not used routinely in Card Sound because ctenophores

were not encountered. Zooplankton were thus collected from both locations using two nets (which were towed simultaneously), one of which (the 200-μm mesh) was common to both locations.

An extensive series of samples was collected in Card Sound to check on the adequacy of the 64- and 200-μm mesh $\frac{1}{2}$-m mouth diameter nets in sampling the entire size range of the population of *Sagitta hispida*. In comparisons between a 64- and 35-μm mesh, the size-frequency distribution of the population was not significantly different. Absolute numbers often differed, but this was attributable to the rapid clogging of 35-μm mesh, which rendered flowmeter readings unreliable, and was why this mesh was not used routinely. The 64-μm mesh net, which filtered less than 50% of the volume of water of the 200-μm mesh in the same time, collected fewer of the larger size chaetognaths than the 200-μm mesh, indicating that a greater proportion of the larger animals were avoiding the smaller meshed net. Comparative tests between the 200-μm $\frac{1}{2}$-m diameter net and a 200-μm 1-m net (which filtered 3 times more water) did not indicate that the larger net caught either a larger absolute number, or a higher percentage, of the larger size classes per volume filtered. These data are available by writing to the first author. It appeared, therefore, that the two standard $\frac{1}{2}$-m nets utilized in the sampling program quantitatively collected the entire size range of this species in the surface water.

Vertical distribution of *S. hispida* Conant in the 3-m water column was investigated on six dates during the year using both towed nets and a pump as described by Reeve and Cosper (1973). There was considerable variability in vertical distribution between sampling dates, due in part to variability in incident radiation and water turbidity, but it was estimated that the numbers per cubic meter from surface hauls should be multiplied by a factor of 1.54 to obtain a mean water column density per cubic meter in the 3-m deep water column. This factor was very close to the 1.45 calculated for the plankton as a whole, by Reeve and Cosper (1973). As noted previously (Reeve and Walter 1972), *S. hispida* has the ability to attach itself to substrates in the laboratory and lays its eggs on surfaces in clumps. It does not attach significantly until near maturity and even then, most of the population is usually to be found swimming in the water column in aquaria. We believe that the biomass estimates of our plankton samples were not biassed downwards due to this

behavioral pattern, as eggs are usually laid at night while the plankton samples were taken during the day, and the vertical sample series gave no indication of a higher proportion of older animals nearer the bottom. On the other hand, comparisons of the size-frequency distribution of a population sampled with a towed net and with an Okelmann sledge lightly skimmed across the bottom, which is an effective means of sampling the benthic *Spadella*, usually yielded a few mature individuals in the larger size classes which were absent from the net. The sledge, however, only provided a qualitative sample and it was not possible to adjust the biomass of Table 1 to take these few animals into account. Our biomass estimates are, therefore, slightly underestimated on this account. No estimates of egg numbers were made, since *Sagitta hispida* does not deposit them in the water column, but attaches them to objects on the bottom.

Ctenophores presented different sampling problems. Lobate ctenophores, such as the genus *Mnemiopsis*, tend to break up easily in nets and are rapidly disintegrated in the usual fixatives. Baker (1973) reported that transference of individual, newly hatched larvae by pipette from one beaker to another would result in the disappearance without a trace of over 90% of these 200-μm diameter animals. It was futile, therefore, to attempt to assess the numbers of eggs or the smallest larvae from net tows, and probably some of size class A (0.8-4.4 mm) were also fragmented beyond recognition. Even so, the pattern of distribution of biomass between the size classes (Table 1) suggests that the fraction contributed by the smallest unsampled or inadequately sampled members of the population is small. It may be presumed that animals in the larger size classes were not avoiding nets, since *Mnemiopsis* is a weak swimmer with no rapid escape behavior, and hence were sampled adequately. No feasible method was devised of making tows near the bottom of this shallow water column with a 1-m mouth diameter net, and pumps were impractical for sampling ctenophores. The only indication we have that *Mnemiopsis* does not exhibit any marked vertical layering are observations by scuba.

Analysis of Samples

The chaetognaths of the preserved samples (all of which belonged to the species *S. hispida*) were

TABLE 1.—Summary of biomass and production data for *Sagitta* and *Mnemiopsis* by size class averaged over the entire survey period.

		Sagitta — Size class (live length)								Mnemiopsis — Size class (live volume)				
		A <2.5	B 2.5–3.7	C 3.8–4.9	D 5.0–6.2	E 6.3–7.4	F 7.5–8.7	G 8.8–9.9	H 10.0–11.3	A 0.021	B 0.052	C 0.92	D 15.0	E 28.0
Numbers per cubic meter		87.4	66.0	33.3	13.7	3.32	0.40	0.031	0.008	2.90	1.50	0.225	0.157	0.075
Mean duration (days)		12	4.7	2.8	2.7	1.7	2.0	5.5	9	8.7	2.0	17	10	16
Ash-free dry weight per organism (µg)		2.18	10.1	29.5	71.2	132	218	349	531	19.7	507	12,100	140,000	278,000
Ash-free dry weight per size class (µg/m³)		191	667	982	975	438	87.2	10.8	4.2	57.0	761	2,730	22,000	20,900
Daily net production (µg ash-free dry wt/m³)		72.5	244	289	290	63.1	13.1	0.78	0.17	60.9	452	936	1,800	1,860
P/B		.38	.37	.29	.30	0.14	0.15	0.07	0.04	1.1	0.59	0.34	0.08	0.09
Growth	21	0.25	0.25	0.25	0.25	0.25	0.25	0.083	0.044	0.50	0.50	0.21	0.069	0.069
Coefficient	26	0.35	0.35	0.35	0.35	0.35	0.35	0.074	0.044	0.78	0.78	0.23	0.071	0.071
	31	0.41	0.41	0.41	0.41	0.41	0.11	0.041	0.007	0.65	0.65	0.23	0.069	0.069
Mortality	21	<0.01	<0.01	0.15	0.40	0.85	1.5		0.3	<0.01	1.8	<0.01	0.08	0.08
Coefficient	26	<0.01	<0.01	0.55	0.30	3.5	2.0			<0.01	1.1	0.03	0.08	0.07
	31	<0.01	<0.01	0.90	2.0	4.0				<0.01	0.76	0.05	0.069	0.09

counted and measured in the laboratory. The Card Sound samples from the four stations were pooled for each net on each sampling date in proportion to the filtered volumes they represented (Reeve and Cosper 1973). Aliquots of each pooled sample were taken such that they contained between 50 and 100 organisms. The total body length of each animal was measured (see Reeve 1970). The entire sample was examined for mature animals. The lengths were tabulated in 1-mm preserved length size classes (see next section for conversion to live length). Since two values were obtained for each size class from the Card Sound samples (i.e., one for each mesh size) the larger number was taken as the correct one, on the assumption that the smaller value was due either to avoidance by larger animals of the 64-µm mesh, or escape of the smaller animals through the 200-µm mesh.

The pooled 200-µm Biscayne Bay samples were treated similarly. The numbers of *S. hispida* in Biscayne Bay were estimated by adjusting the numbers in each size class in the 200-µm net to total number on the basis of ratios computed for the 64- and 200-µm counts from Card Sound.

Analysis of ctenophore samples from the 1-m net presented special difficulties, because there was no known satisfactory method of preservation of lobate ctenophores. Following Miller (1970) analysis was performed on deck immediately after recovery of the net (see Baker 1973). The contents of the cod end were emptied into a stack of wire sieves of arbitrarily chosen decreasing mesh sizes (25-, 12.5-, 6.25-, 3.0-, and 0.7-mm mesh openings) immersed in seawater. The ctenophores from each sieve, except the smallest, were transferred to a graduated cylinder and the total volume of organisms retained by each sieve measured. The average volume per individual retained in each sieve was determined either by counting the total number of animals in each sieve or, in the case of the larger animals, by direct volume displacement of randomly selected individual ctenophores. It was impractical to follow this routine with the smallest animals (0.7-mm sieve) since their total volume was too small to be measured accurately. Instead, they were resuspended in seawater, transferred to plastic bags, and returned to the laboratory where they were counted. No attempt was made to assess the number and hence production of ctenophores smaller than 0.7 mm in diameter.

Conversion of Raw Data to Other Units

The shrinkage in length of *S. hispida* with Formalin[3] preservation was estimated by measuring over 100 live animals from a freshly caught 200-μm mesh sample, and repeating this 10 and 420 days following preservation of that collection in a 5% formaldehyde solution buffered with methenamine, which was the standard preservative for all plankton samples. The degree of shrinkage was judged by the extent of the downward shift in the peak of the length/frequency histogram. Half the total shrinkage (12.5% of the original length) occurred within the first 10 days. Assuming a linear rate of shrinkage after day 10, and preservation time of the samples before analysis varying from 1 to 9 mo, the degree of shrinkage was computed to be 20% with a range of $\pm$ 3.5%. This mean estimate was used to adjust size classes from preserved to live length.

Live length was converted to dry weight using the relationship obtained from a linear regression analysis of more than 40 separate weight determinations of animals over their entire size range. Animals to be weighed were rinsed in isotonic ammonium formate and dried at 60°C. The ash-free (i.e., organic) dry weight was previously determined to be 90.7% of the dry weight (Reeve et al. 1970). The mean carbon and nitrogen content of *S. hispida* was determined by a Perkin-Elmer elemental analyzer to be 44.9% with a standard error of $\pm$ 1.0% and 11.9% $\pm$ 0.2% of the ash-free dry weight from 23 separate estimations over its entire size range. The raw biomass units for ctenophores were obtained in terms of live volume. Over 100 separate determinations of animals over their entire size range were made for wet (drained), dry (at 60°C), and ash (at 500°C) weights. Live volume was approximately numerically equal to wet weight (1.000 ml = 0.958 $\pm$ 0.002 g standard error). Dry weight was 4.43% $\pm$ 0.40% of wet weight and ash-free dry weight was 21.90% $\pm$ 0.15% of dry weight.

Eighteen separate determinations of carbon and nitrogen content of *Mnemiopsis mccradyi* Mayer were made which yielded unusually low values 8.72% $\pm$ 0.06% and 2.32% $\pm$ 0.07% of the ash-free dry weight of carbon and nitrogen respectively. A value of 44.9% carbon was reported for *Sagitta* (above), and Curl (1962) quoted values for various planktonic crustaceans between 44 and

52%. Even his value for *Mnemiopsis* sp. was considerably higher at 20.6%. Hirota (1974) assumed a 50% carbon content of organic weight for *Pleurobrachia bachei* in his calculations, because analysis by wet combustion with acid dichromate was unsuccessful due to problems with chloride ion interference (J. Hirota, pers. commun.).

We considered the possibility that our analyses were also yielding incorrect results and tested three possible sources of error: a) interference in the analysis by the unusually large amount of inorganic salts present in the ctenophore tissue, b) errors of dry weight determination, and c) errors of ash weight determination. Mixtures of bovine serum albumin (5-15%) and sodium chloride did not reduce the theoretical yield of carbon when combusted in the elemental analyzer. Since, however, the dried ctenophore material was a more intimately bound complex of organic and inorganic substances, which might be more resistant to complete combustion, potassium persulfate was added to promote complete oxidization (see Strickland and Parsons 1968). No increase in carbon yield was achieved by this method. The reliability of dry and ash weight determinations affects the reliability of the carbon value since the numbers so obtained are used in its computation. The possibility of any significant loss of organic matter during drying at 60°C was checked by performing carbon analyses on freeze-dried material. The previously derived mean value remained unchanged. Finally, ash weights were determined at a temperature 100°C lower than previously. Slightly higher ash weights resulted, which in turn slightly increased the computed carbon level to 10.3% of the ash-free dry weight. Since any significant source of error in this determination has so far eluded us, we report production values below for ctenophores and chaetognaths in terms of ash-free dry weight for direct comparison and in terms of the analyzed carbon. Mullin (pers. commun.), on the basis of unpublished observations, suggested that the weight lost on ashing may be largely "bound" water, and that in *Pleurobrachia bachei*, at least, only about 12% of the ash-free dry weight is organic matter. This suggests that comparisons based on carbon content are more valid than those based on "organic" or ash free-dry weight.

Growth Rates

Growth rates of populations of the ctenophore

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[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

and chaetognath were determined in the laboratory using larvae hatched from wild adults according to methods detailed by Reeve and Walter (1972) for *S. hispida* and Baker and Reeve (1974) for *M. mccradyi*. Three separate populations of the chaetognath and two of the ctenophore were grown at each of three temperatures (21°, 26°, 31°C), which corresponded to the mean monthly minimum, annual mean, and mean monthly maximum temperatures (to the nearest 1°C) off the laboratory dock in Biscayne Bay over 11 yr (unpubl. records). Food was provided in the form of naturally occurring zooplankton of suitable size (see previously cited information on culture technique), consisting mostly of the copepods *Acartia tonsa* and *Paracalanus parvus*, maintained at a level such that no more than 50% were grazed down over 24 h.

Growth rates were measured as length increase to avoid sacrificing any members of the populations and the data converted to ash-free dry weight as previously described. Total length of *Mnemiopsis* was measured from the aboral to the oral pole (or tip of the oral lobes in adults) as described in detail by Baker (1973).

Production Calculation

The method of calculating production was that employed by Mullin and Brooks (1970) and Hirota (1974), where for each size class an exponential coefficient of daily growth (G) and mortality (M) is obtained from laboratory growth rate and field size-frequency data.

The growth coefficients were computed from the slope of the line relating the logarithm of increase in ash-free dry weight and age (Figure 1) following Crisp (1971). Data from each rearing experiment were combined for each species at the specified temperature. For *S. hispida*, the semilogarithmic relationship is linear over most of its size range until growth levels off at maturity (Reeve and Walter 1972). The termination of the linear (i.e., constant exponential growth) phase was arbitrarily set at 20, 25, and 30 days at 31°, 26°, and 21°C respectively, and the slope of the line calculated by linear regression analysis. At each temperature, slopes at two points beyond the linear phase were required, and these were derived by extrapolation on the basis of the remaining data points and other (unpubl.) data on lengths of
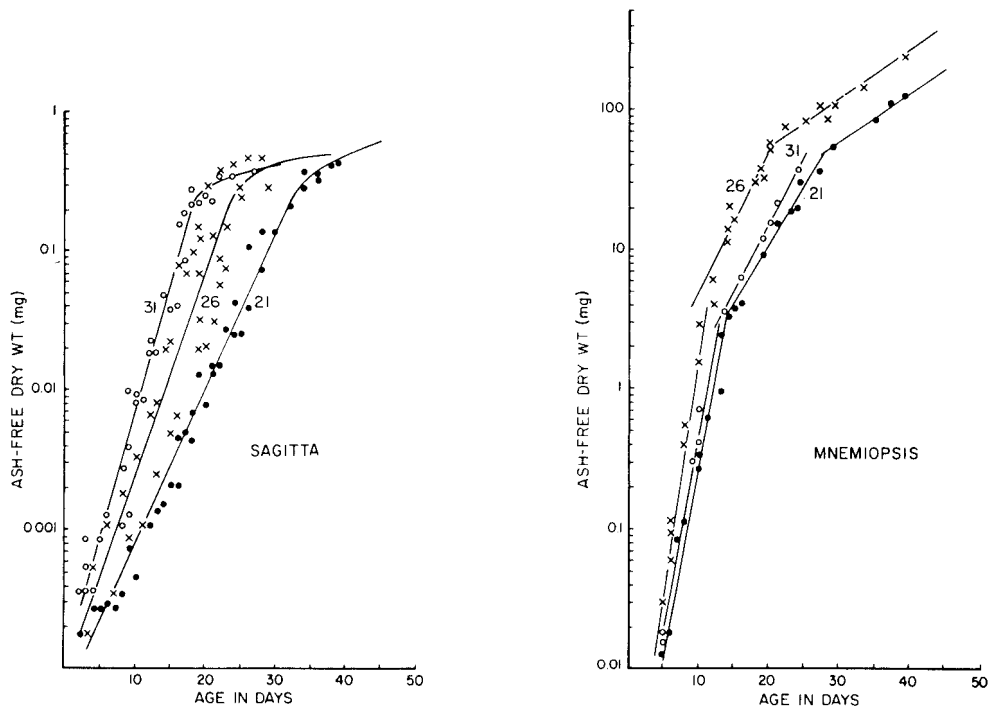

FIGURE 1.—Growth rate of *Sagitta* and *Mnemiopsis* at three different temperatures.

animals older than those surviving in these experiments. The potential errors in such a procedure are minimal, because the coefficients are tending towards zero and the biomass involved in the two largest size classes is only a small percentage of the total.

The *Mnemiopsis* growth curves were treated differently because their slopes decreased progressively with age. In order to facilitate computation of the required slopes, the curves were divided into segments, the junctions of which were assigned by visual inspection to be at 3- and 50-mg ash-free dry weight. The slopes of the individual segments A, B, and C were individually calculated from the population mean points within them by linear regression analysis. Unlike *S. hispida*, where growth rate is proportional to temperature between 21° and 31°C, *M. mccradyi* grows faster at 26°C than at either end of the range. Survival was poor at 31°C, populations dying out by the 25th day. Since no points exist from which to compute a slope for segment C at 31°C, it was taken to be the same as that for the 21°C experiments, since segments A and B at the two temperatures are almost identical.

Sampling dates were divided into three groups on the basis of the proximity of the ambient water temperature to 21°, 26°, and 31°C so that growth coefficients derived for these temperatures could be applied to the standing stock data. Similarly, mean mortality coefficients were derived for the three temperature ranges by averaging the numbers of animals in each size class over the sampling dates in each temperature range. These mean numbers were used to obtain mean ratios of Y/X (as did Mullin and Brooks 1970) where X and Y are the numbers of the earlier and later of two successive size classes. This ratio, and the duration of development in each of the two successive size classes, enables calculation of the exponential coefficient of daily mortality between the two size classes using computer-generated tables. We recognize that this procedure is an approximation which probably oversimplifies actual conditions by making unproven assumptions regarding constancy of mortality rate with time and between adjacent size classes, yielding a single value for m rather than a measure of its possible range (see Fager 1973).

The duration of development in each size class at each temperature range was estimated from the arbitrarily defined limits of each size class and the laboratory growth rate data.

Net production of a size class on a given sampling date, taking into account animals which die before the end of the day, is the product of the mean biomass and the daily exponential coefficient of growth for that temperature range. The day is assumed to start at the time of sampling, and the mean biomass ($\overline{WN}$) of that size class over the subsequent 24 h is obtained by application of the relationship given by Mullin and Brooks (1970) which utilizes the initial biomass, growth, and mortality coefficients. The initial biomass (WN in ash-free dry weight) is the product of sampled numbers (N) and mean ash-free dry weight (W) of an individual organism of that size class. Summing the production values for each size class provides an estimate of the total net production of the population on that day. No attempt was made to estimate egg production in either species.

Net production was determined for chaetognaths of the Card Sound population only; values quoted below for the Biscayne Bay population are estimated by applying the mean population production/biomass ratio for Card Sound to estimated total biomass in Biscayne Bay. An estimate of annual production is obtained by taking each sampling date as the midpoint of each sampling period, summing the product of daily production and number of days in that sampling period, and summing the total production for each sampling period and adjusting for 365 days. In the ctenophore population, which was sampled for 17 mo, and passed through two biomass peaks which Baker (1973) considered to be an annual winter event (Table 2), two values were computed (see Table 3), one for 365 days from the beginning and one for 365 days up to the end of the sampling program.

Results and Discussion

Seasonal Changes

Summaries of the population dynamics and production data are contained in Tables 1 and 2, computed as detailed above from tabulations by sampling date and size class. Figure 1 contains the laboratory growth rate data. The standing stock and production data are summarized in Tables 1 and 2, and are derived from the Card Sound population of *Sagitta* and the Biscayne Bay population of *Mnemiopsis*, since these populations had been the most effectively sampled. For each size class (Table 1) averaged over the entire

TABLE 2.—Summary of biomass and production data by sampling data averaged over all size classes.

	Sagitta				Mnemiopsis		
Date	Biomass mg ash-free dry wt/m³	Production mg ash-free dry wt/m³/day	P/B	Date	Biomass mg ash-free dry wt/m³	Production mg ash-free dry wt/m³/day	P/B
1/06/71	3.82	0.95	.25	10/12/70	18.02	2.64	.15
1/23/71	2.86	0.62	.22	10/23/70	135.59	12.12	.09
2/06/71	2.94	0.74	.25	11/20/70	314.31	27.80	.09
2/16/71	7.09	1.44	.20	12/15/70	81.97	6.92	.09
3/05/71	3.68	0.94	.26	1/15/71	18.31	2.09	.11
3/19/71	1.56	0.40	.26	2/15/71	23.56	2.35	.10
4/02/71	4.89	1.28	.26	3/12/71	5.46	0.67	.12
4/16/71	4.10	0.96	.23	4/08/71	20.34	1.63	.08
4/30/71	11.98	3.11	.26	5/07/71	17.77	1.49	.08
5/14/71	5.53	1.77	.32	6/03/71	0.22	0.04	.18
5/28/71	2.50	0.69	.28	7/01/71	0.87	0.12	.14
6/11/71	4.46	1.54	.35	7/26/71	0.17	0.01	.06
6/25/71	1.24	0.46	.37	8/25/71	—	—	—
7/09/71	1.58	0.60	.38	9/17/71	0.06	<0.01	.06
7/23/71	0.10	0.04	.40	9/30/71	0.58	0.09	.16
8/06/71	0.56	0.23	.41	10/14/71	1.29	0.14	.11
8/20/71	0.25	0.10	.40	10/28/71	3.27	0.64	.20
9/03/71	0.48	0.19	.40	11/12/71	8.86	1.30	.15
9/09/71	0.62	0.24	.39	11/24/71	6.80	1.07	.16
9/14/71	6.03	2.26	.37	12/02/71	56.55	6.14	.11
9/21/71	2.00	0.66	.33	12/20/71	20.89	2.16	.10
9/28/71	3.47	1.24	.36	1/06/72	200.35	15.66	.08
10/14/71	4.85	1.67	.34	1/21/72	103.59	7.38	.07
10/26/71	6.06	2.23	.37	2/03/72	7.69	0.75	.10
11/09/71	0.99	0.37	.37				
11/23/71	3.93	0.97	.25				
12/07/71	5.21	1.27	.23				
12/15/71	1.16	0.30	.26				

sampling period, the mean numbers, live length (or volume for *Mnemiopsis*), ash-free dry weight per organism, and ash-free dry weight per size class are tabulated. The mean net daily production of each size class (per cubic meter) averaged over the entire period using the information on daily rates of growth and mortality and the average duration of each size class (over the three temperatures) is also provided.

Seasonal changes in production reflected those of biomass generally as indicated in the production/biomass ratios (Table 2), which varied between 0.20 and 0.41 (mean, 0.31) for *Sagitta* and 0.059 and 0.20 (mean, 0.12) for *Mnemiopsis*. The ratios were highest in *Sagitta* in the summer when growth rates were maximum, but biomass and production was at its lowest. In *Mnemiopsis*, which also exhibited minimum summer biomass and production levels, the ratio tended to be low relatively, as was growth rate. This summer low point of biomass and production is a confirmation of the experience of some nine seasons of observation by the first author and is characteristic of the 200-μm net plankton of Card Sound and Biscayne Bay as a whole (for a discussion of which, see reviews of Reeve and Cosper 1973 and Reeve in press).

Throughout the rest of the year the chaetognath biomass of Card Sound and Biscayne Bay fluctuated much less widely than that of the ctenophores in Biscayne Bay. The biomass of *Sagitta* ranged (excluding July-September) between 1- and 12-mg ash-free dry wt/m³ in Card Sound and an estimated 2- and 20-mg ash-free dry weight in Biscayne Bay, whereas for ctenophores the range was 0.2 to 314 mg/m³. The mean annual biomass of *Sagitta* in Card Sound and Biscayne Bay was 3.36- and 8.04-mg ash-free dry wt/m³ and for *Mnemiopsis* in Biscayne Bay was 25.2- to 42.5-mg ash-free dry wt/m³ (reckoning 12 mo from the date of the first sample or 12 mo prior to the date of the last sample).

The range of net daily production rate in terms of ash-free dry weight for *Sagitta* at the surface from Card Sound and *Mnemiopsis* from Biscayne Bay was 0.04 to 3.1 and < 0.01 to 27.8/m³, respectively. Table 3 contains production estimates on an annual basis computed for surface and average water column (for *Sagitta* only) as ash-free dry weight and carbon per cubic meter. For *Mnemiopsis*, carbon production is computed both on the basis of the carbon content of *Sagitta* and the experimentally determined carbon content for *Mnemiopsis*. Daily production estimates per cubic meter and per square meter are also computed in terms of experimentally determined carbon content. As noted above, the two values in each case for *Mnemiopsis* incorporate successive annual production peaks.

TABLE 3.—Mean annual and daily production of the *Sagitta* populations of Card Sound and Biscayne Bay and *Mnemiopsis* population of Biscayne Bay.

	Annual production				Daily production	
	mg ash-free dry wt/m³		mgC/m³			
	Surface	Average water column	Carbon 44.9%	Carbon by analysis	mgC/m³	mgC/m²
Sagitta						
Card Sound	357	542	244	244	0.67	2.00
Biscayne Bay	855	1,200	584	584	1.60	4.80
Mnemiopsis						
Biscayne Bay	695/1,409		312/633	60.6/123	0.17/0.34	0.50/1.01

Details of methods for the calculation of production for populations with continuous breeding occur in Winberg (1971) and Crisp (1971). They are essentially similar to the method used here and by Mullin and Brooks (1970) and Hirota (1974) except that no adjustment is made to the sampled biomass (WN) to compute the mean biomass ($\overline{WN}$) during the 24 h immediately following the taking of the sample. This additional step, which we also performed, requires considerable extra effort (depending on the number of size classes and sampling dates involved) as well as access to computer services. In these warm waters, however, where growth and mortality rates may be less variable than in regions of more pronounced seasonality, the increase in W tends to cancel out the decrease in N, the difference between WN and $\overline{WN}$ for *Sagitta* and *Mnemiopsis* being less than 10% (93 and 108%, respectively).

Mortality coefficients tended to increase progressively with age in *Sagitta* and with increasing temperature. These environmental observations correspond to the conditions of laboratory cultures with respect to temperature, but in cultures young animals tend to die off more rapidly than juveniles and immature animals (Reeve and Walter 1972). A variety of interacting factors, including differences in predation pressure and food adequacy, may be responsible. In the ctenophore population the pattern of mortality is uniformly low except in size class B which corresponds to the time of change from tentaculate larva to lobate adult. The unmeasurable mortality of size group A can be partly attributed to sampling inefficiency, though this was shown not to be the case for *Sagitta* (see above).

Problems of Measuring Growth Rate

In animals such as copepods, with life history stages marked by recognizable and abrupt changes (i.e., molts), division of the cycle into parts may be accomplished on the basis of some biologically meaningful criteria. Both chaetognaths and ctenophores exhibit more gradual transformation from newly hatched larva to mature adult, and size class separation is based on arbitrary limitations such as preserved length or sieve size. The only real validity of the particular size classes used here is that they represent a progression from the youngest to the oldest animals. Factors such as variability of size of animals of the same age at different temperatures and imprecision of raw measurements (larger ctenophores may pass through a mesh slightly smaller than their diameter by their own weight deforming their shape) tend to blur the sharpness of the line separating one size class from the next. The arbitrary choice of size classes resulted in large variations in the durations of development of each size class. In *Sagitta* the mean duration (i.e., averaged over the three experimental temperatures) of the initial size class was 12 days, shortening to 2 days as length increased rapidly, and increasing to 9 in the last size class as a final length was approached in the adult. In *Mnemiopsis* size class durations proved to be even more erratic (see Table 1).

On the basis of the definitions used by Reeve (1970) for *S. hispida*, the larval, juvenile, immature, and mature stages correspond approximately to size classes A and B, C and D, E and F, and G and H, respectively. For *M. mccradyi* the tentaculate larva extends to size class C and the first eggs are also produced by size class C animals (29 mm and larger).

The most satisfactory way to determine growth and mortality in a population is to follow the increase in size and decrease in numbers of a cohort of the population over successive sampling dates by inspection of size-frequency histograms (Winberg 1971; Crisp 1971). In warmer waters, although biomass may fluctuate widely, breeding

tends to extend over most or all of the year and distinct cohorts can rarely be identified.

Growth rate, therefore, was measured in the laboratory, and in as large a volume as practical (30-70 liters). No attempt was made to simulate natural food levels. There were various reasons for this. Mean annual zooplankton concentrations of the 200-μm mesh, which is the food source of older *Sagitta* and *Mnemiopsis* (Reeve and Walter 1972; Baker 1973), were of the order of magnitude of 1 organism/liter, an impractically low concentration to work with in these volumes. It is certain that any environmental concentration estimated from a net tow is an average of several small-scale patches of higher and lower density. We have some information from direct observation by scuba (unpubl. data) that patch densities at least an order of magnitude greater occur, as well as information (also unpubl. data) that both *Sagitta* and *Mnemiopsis* can ingest food several times faster following a period of starvation than they do under conditions of a constant supply of food. *Sagitta* is capable, under certain conditions, of ingesting within 1 to 2 min all the food it consumes in 24 h under conditions of continuous abundant food supply.

Despite the fact that feeding habits and environmental food concentrations are poorly understood at present, it is clear that for carnivorous zooplankton, at least, maintaining a continuous supply of food at mean environmental concentrations in small-scale experimental conditions, would be as artificial as maintaining a continuous abundant supply, even though there must obviously be a relationship between total food supply and production in the environment. The latter method does provide a standard (i.e., maximum) growth rate. When better data become available on the interrelationships of feeding, food supply, and growth rate, the production estimates computed on that basis can be revised downward. At present, there is little information available to even guess to what extent these growth rates and hence production estimates are overestimations. Hirota (1974) reported surprisingly little difference in growth rates of *Pleurobrachia* in experiments at food concentrations ranging between 1 and 350 μgC/liter, but pointed out that in the 70-m^3 tank in which the low food concentration occurred, food organisms were not uniformly distributed because some species were concentrated at the surface during the day. In Card Sound and Biscayne Bay the mean annual con-

centration of food from the 200-μm net (the size range fed to adult *Sagitta* and postlarval *Mnemiopsis* in our experiments) was 0.8 and 8.1 μgC/liter. Taking into account all organisms down to a 20-μm retaining mesh those figures would be increased by a factor of 5 (Reeve and Cosper 1973).

Production Comparisons

Sameoto (1971) obtained a value for the net production of *S. elegans* in Nova Scotia waters (ranging in temperature approximately from 0.5° to 14°C) of 200 mgC/m^2 per yr in a 50-m water column, and McLaren (1969) reported a similar range of values for this species from Ogac Lake on Baffin Island (49-196 and 318). Those authors estimated production/biomass ratios between 1.0 and 2.1 on an annual basis. These figures compare with annual net production of *S. hispida* in Card Sound and estimated in Biscayne Bay of 730 and 1,750 mgC/m^2 per yr and production/biomass ratio of 109 on an annual basis. With a mean annual biomass two orders of magnitude lower, therefore, *S. hispida* in Card Sound exceeds the net production of *S. elegans* in St. Margaret's Bay, Nova Scotia by virtue of its rapid growth rate and short generation time. The disparity would be even greater on a cubic meter basis because Card Sound is comparatively shallow.

Hirota (1974) quoted a value for net annual production of the ctenophore *Pleurobrachia bachei* in waters off California (ranging in temperature approximately from 12.5° to 20°C) of 5,415 mg ash-free dry weight/m^2 per yr, and a daily production/biomass ratio of 0.02. These figures compare with an annual net production of *M. mccradyi* in Biscayne Bay of 2,086 to 4,227 mg ash-free dry weight/m^2 per yr and a production/ biomass ratio of 0.12. As in the previous comparison, annual production of different species in different regions is surprisingly similar on a water column (square meter) basis. The growth rate of *M. mccradyi*, however, is some 5 times faster, and its production is supported by a water column depth of 3 m rather than in excess of 40 m in the case of *Pleurobrachia bachei*.

The 10-fold difference in the mean annual standing stock of 200-μm mesh zooplankton between Card Sound and Biscayne Bay (and in phytoplankton pigment) is probably a reflection of the poor water exchange and limited land drainage into Card Sound as compared with Biscayne Bay (Reeve and Cosper 1973). These

differences in plankton biomass are accompanied by differences in biomass for both *Sagitta* and *Mnemiopsis*. In surface net tows from the 200-μm mesh, the biomass of the chaetognath in Biscayne Bay is 2.4 times that in Card Sound. The ctenophore is totally absent from Card Sound (except for rare isolated individuals). Baker (1973), relating stations with low plankton standing stock to low ctenophore levels in Biscayne Bay, suggested that the Card Sound plankton could not support a ctenophore population.

Since the waters of Card Sound are contiguous with those of Biscayne Bay to the north, and neritic waters to the east, where ctenophores are often abundant, the phenomenon of their exclusion from Card Sound can hardly be a physical one. A possibility is that chaetognaths are more efficient in collecting food at lower densities than are ctenophores.

It is of interest that the seasonal variations of biomass and production of the ctenophore populations both in Biscayne Bay and off California are extreme, to the extent that in both cases the months of peak production account for about two-thirds of the annual total. In the case of *S. hispida* this value is about one-fifth. There is probably some correlation between this extreme population instability of *M. mccradyi* and the suggestion above that its absence from Card Sound is related to its inefficiency in collecting food at low concentrations compared to *S. hispida*. The dry weight of other zooplankton from the 200-μm mesh net in Card Sound (Reeve and Cosper 1973) never exceeds the minimum value in central Biscayne Bay (Baker 1973).

It is possible to get a rough estimate of the relationship between production of *S. hispida* and *M. mccradyi* and the rest of the zooplankton by utilizing the standing stock data for that period in the two reports referred to immediately above. The mean annual dry weight of zooplankton (excluding ctenophores and corrected for detritus) was 2.02 and 5.28 mg/m^3 in the 200- and 64-μm mesh net respectively in Card Sound and 19.8 mg/m^3 in the 200-μm mesh net in central Biscayne Bay. Assuming the ratio between 64- and 200-mesh plankton in Card Sound is applicable to Biscayne Bay, and the ash-free dry weight is the same percentage of dry weight as determined for *S. hispida*, the mean annual ash-free dry weight in Card Sound and central Biscayne Bay was 6.62 and 64.9 mg/m^3 respectively. Since it appears that even the youngest larvae of *Mnemiopsis* and *Sagitta* do not utilize food organisms much smaller than those retained by the 64-μm mesh, and since neither carnivore appears to be able to utilize other sources of potential food such as detritus or phytoplankton (Reeve and Walter 1972; Baker and Reeve 1974), the plankton biomass quoted above is the only source of nutrition for these carnivores. If a production/biomass ratio the same as that determined for *S. hispida* is applied to these biomass figures, the net production available to these carnivores is 2.05- and 20.1-mg ash-free dry weight/m^3 per day. Since these figures are for surface waters, they may be related to the equivalent values for *Sagitta* and *Mnemiopsis* derived earlier. The daily net production of *S. hispida* in Card Sound and Biscayne Bay is then 47.7 and 11.7% of the production of potential food in those areas. For *M. mccradyi* in Biscayne Bay it was 9.5 or 19.2% depending on which production peak was included (see above). The total percentage for the two species is then 47.7 for Card Sound and 21.2 or 30.9 for central Biscayne Bay. If the ratio of production to food ingested is taken to be 50% on the basis that immature animals are responsible for most of the production, and would have higher growth efficiencies than the 30-40% range for adults quoted by Reeve (1972), then the chaetognaths in Card Sound appear to utilize all the rest of the zooplankton above 64 μm. For Biscayne Bay, the chaetognaths and ctenophores together utilize between 40 and 60% of the available food. As explained earlier, these are overestimated because the growth rates were maximum growth rates, but they do support the contention that there is little potential food reserve in Card Sound for other carnivores, and that *Sagitta* is more efficient in competing for the available supply. This is in agreement with the fact that in Card Sound, its population was as high as 42% of that in central Biscayne Bay, while for larger decapod larvae, fish larvae, and ctenophores (the other major first-order plankton carnivores) the values were approximately 25, 25 (see Reeve in press), and 0%.

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