Trophic Interactions among Ctenophores and Copepods in St. Margaret's Bay, Nova Scotia

by

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ABSTRACT

The annual cycles of abundance of the four ctenophore species Pleurobrachia pileus, Bolinopsis infundibulum, Mertensia ovum, and Beroë cucumis were determined in St. Margaret's Bay, Nova Scotia. Populations of all four were markedly variable in both space and time. The maximum volume of Pleurobrachia, 12.4 ml $\cdot$ m^{-2}, occurred in March and this species was present throughout the year. Bolinopsis (maximum 5.7 ml $\cdot$ m^{-2} in May) and Beroë (maximum 5.7 ml $\cdot$ m^{-2} in July) were both absent from October through December. Mertensia, an Arctic species, appeared briefly in May and June (maximum 3.0 ml $\cdot$ m^{-2} in May).

Sampling was done with concentric nets which captured ctenophores and copepods separately. Bolinopsis egested gut contents upon capture but Pleurobrachia retained contents. Of food particles in Pleurobrachia guts 89.6% were adult or stage V copepods, 7.2% were copepodids or nauplii, 2.5% were other crustacea, and 1.6% were non-crustaceous.

Gut contents divided by digestion time gave in situ feeding rates for Pleurobrachia, which rates were related by the equation

$$\text{copepods eaten} \cdot (\text{ml ctenophore})^{-1} \cdot \text{hr}^{-1} = (4.40 \cdot 10^{-5} - 2.45 \cdot 10^{-2}) \cdot \text{adult copepods} \cdot m^{-2}$$

The annual ingestion of copepods by Pleurobrachia is 0.52 g C $\cdot$ m^{-2}. Pleurobrachia captured individuals of the copepod species Temora longicornis and Centropages typicus ten times more frequently relative to their abundances than the third and fourth most commonly caught copepods Pseudocalanus minutus and Oithona similis. Photographic studies of the swimming activities of copepods showed that species with higher horizontal velocities and less recursive paths were more likely to be

caught by Pleurobrachia, whose mode of predation is ambush. Bolinopsis, which swims while feeding, preferentially captures the less active Oithona.

Experiments in a 10 m deep tank showed no evidence of diurnal vertical migrations by either Pleurobrachia or Bolinopsis.

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INTRODUCTION

Ctenophores are often very conspicuous members of the zooplankton. At times these gelatinous animals may be so numerous as to clog nets set for such fish as mackerel and herring. Because the ctenophores are relatively large plankters, often reaching several centimeters long, they together with the true jellyfish of the Cnidaria are the planktonic animals most familiar to fishermen and sailors.

Ctenophoran feeding types

Four species of ctenophores occur in St. Margaret's Bay. The four belong to three orders, corresponding to the three ecologically significant ctenophoran feeding types. Because a basic knowledge of these feeding types is necessary to this exposition, I will provide brief descriptions and schematic diagrams.

The order Cydippida, represented locally by Pleurobrachia pileus and Mertensia ovum, is considered closest to the ancestral stock because members of all other orders of the class Tentaculata pass through a larval stage similar to the adult cydippid (see Figure 1A). The catching apparatus consists of two lateral retractile tentacles which when relaxed may be more than 25 times as long as the body. The tentacles are provided with a curtain of filaments which are armed with "sticky cells", or colloblasts. The colloblasts adhere to any prey which contacts the net, and the jerking of the prey releases the feeding evolution, which begins with simultaneous retraction of the tentacles and rotation of the body in the plane defined by the oral-aboral and tentacular axes. This movement wraps the tentacles in a loose coil which passes over the mouth. Further contraction wipes the tentacles

Figure I A-C

Diagrams of the three most common ctenophoran orders. A, Cydippida (Pleurobrachia pileus). B, Lobata (Bolinopsis infundibulum). C, Beroida (Beroë cucumis).

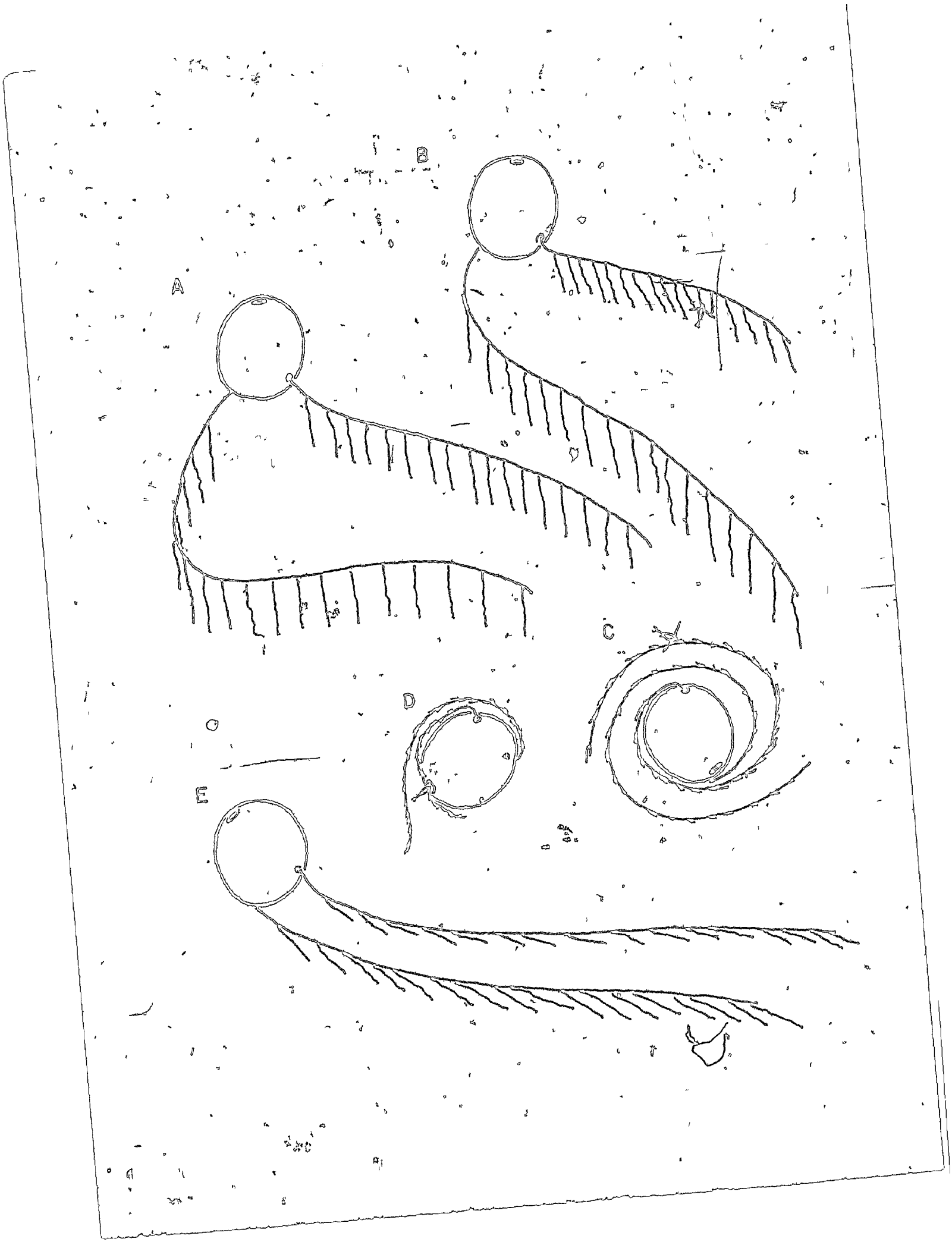
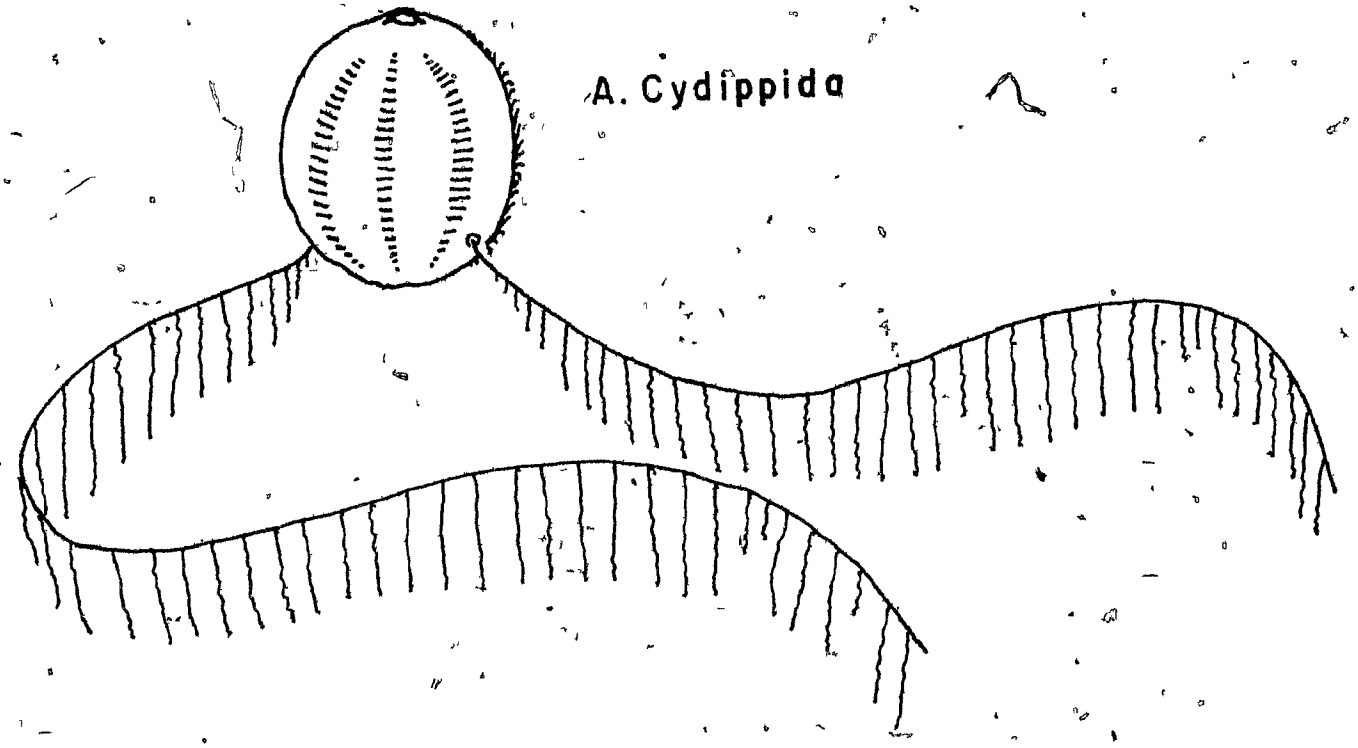
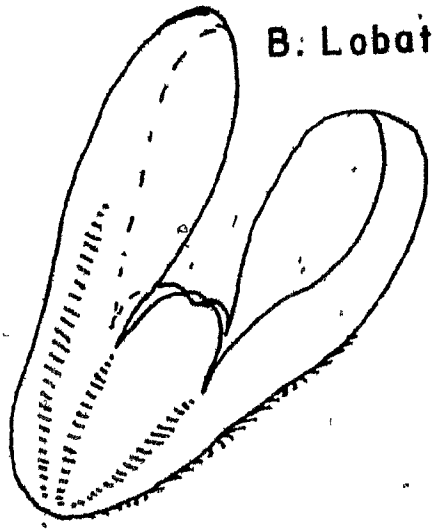
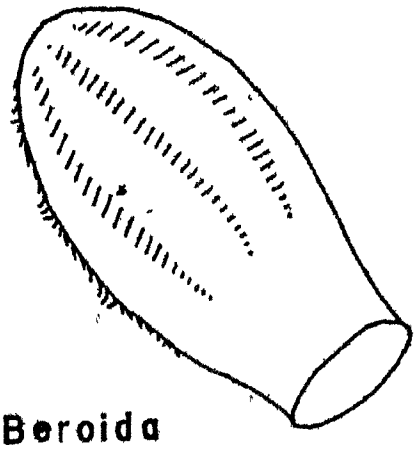

A
B
C
D
E

Figure 2 A-E

Feeding evolution of Pleurobrachia pileus. A, tentacles deployed. B, capture of a copepod. C, rotation. D, ingestion. E, swimming off to redeploy tentacles.


A. Cydippida


B: Lobata


C. Beroida

over the mouth, and prey are picked off and swallowed (Hardy, 1956 and personal observation).

Bolinopsis infundibulum is the local representative of the second order, the Lobata, which have a more complex feeding mechanism. The general form of the body resembles that of a gaping clam (see Figure 1B). When feeding, the animal swims mouth-first, exposing the inner surface of its lobes, or auricles. These channel a flow of water over the four organs of capture, the auricular grooves, which extend outward from the mouth to follow the juncture of the auricles with the body proper. Within the groove, a row of cilia set up a swirling current which drives particles onto a parallel row of small tentacles. Particles captured by the colloblasts of the tentacles are passed over a small ridge into an inner groove, wherein they are conveyed, apparently by cilia, to the mouth (Main, 1928; Nagabushanam, 1959). Thus the Lobata, unlike the Cydippida, can capture passive particles such as eggs, as well as smaller zooplankters. Ctenophores are the largest animals propelled entirely by cilia, and this is a weak mechanism for macroscopic animals. The Lobata are not able to overtake fleeing adult copepods; they apparently owe their success as predators to a combination of transparency and quiet approach. The hunting strategy of Bolinopsis can therefore be described as a combination of the pursuit and ambush modes.

The third common feeding type is seen in the unigeneric class Nuda, of which one species, Beroë cucumis, occurs in St. Margaret's Bay (see Figure 1C). Greve (1970) has shown that this species is an obligate predator on other ctenophores. Individuals of Beroë swim mouth-first in search of prey, which they simply engulf upon encounter.

Precedent studies on the feeding of ctenophores

The fragile appearance and simple organization of ctenophores veil their raptorial natures. Most are predators, and most of their prey are taken from a more complexly organized taxon, the Crustacea. Reports on the feeding habits of ctenophores have occurred sporadically in the literature since Chun in 1880 presented his mainly morphological monograph. Most of the early reports are anecdotal accounts of catching behaviour in aquaria. Lebour (1922, 1923) describes the ability of Pleurobrachia pileus to capture large quantities of zooplankton and larval fish. Mayer (1912), Bigelow (1915, 1926), Nelson (1925), Main (1928), and Nagabushanam (1959) are the major sources of material of this sort.

Often the earlier reports suggest that ctenophores are important as direct predators upon commercially valuable species. Thus Nelson's (1925) interest centered upon the consumption of oyster spat by Mnemiopsis leidyi. Mayer (1912), Bigelow (1924) and Russell (1935) believed that ctenophores might seriously deplete stocks of juvenile fish.

It has often been observed that high concentrations of ctenophores commonly coincide with low concentrations of other zooplankton. This class of observations may be divided into two groups: observations of contemporaneous negative correlation between cetnophores and other zooplankton, and observations of reciprocal changes in abundances from year to year. Among the first class, the best documented is that of Bigelow (1924) who stated that, in the Gulf of Maine, areas where Pleurobrachia pileus was abundant were poor in copepods. Fraser (1961) and Russel (1931) have also stressed the regularity with which an inverse

relationship is found between the abundances of copepods and ctenophores in the northeast Atlantic and North Sea. Lucas and Henderson (1937) asked fishermen to report their catches of herring from individual drift nets along with their observations of jellyfish. The results showed a strong negative correlation between catches of herring and the occurrence of small jellyfish, most of which were presumably ctenophores. They inferred that the cause was not a trophic relationship, but rather that herring avoid concentrations of ctenophores.

Year-to-year reciprocal changes in abundance were best demonstrated by Kamshilov (1960), who showed that in the vicinity of Murmansk, in years in which Bolinopsis and Pleurobrachia were particularly abundant, numbers of Calanus and young euphausiids were below average. The demonstration of reciprocal relations extended two trophic levels above the Bolinopsis-Pleurobrachia: Calanus link. Beroë cucumis, a ctenophore, feeds on Bolinopsis, and is eaten in turn by members of the cod family. Kamshilov's data suggest that in years in which cod are abundant near shore, numbers of Beroë are depressed, the growth of Bolinopsis is released, and standing stocks of copepods are depleted.

Fraser (1962) in his review of the role of ctenophores and salps in zooplankton production and standing crop gave great emphasis to Kamshilov's exemplary study of the annual cycles and feeding relations of ctenophores. These two contributions in the early 1960's mark the end of a period of observation and conjecture, and called the attention of students of the zooplankton to a set of important trophic relationships requiring further quantitative evaluation.

The first of the recent series of quantitative studies on the

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ecology of ctenophores was that of Williams and Baptist (1966) who measured the consumption of O_2 by the lobate ctenophore Mnemiopsis leidyi, and concluded that a 20 ml. individual respires daily the carbon equivalent of the zooplankton in 4 to 100 l. of water from an estuary near Beaufort, North Carolina. Investigators working in the mid-Atlantic states of the U.S.A. have studied this species in some detail, with divergent results. Bishop in 1967 extrapolated laboratory feeding rates of Mnemiopsis leidyi on the copepod Acartia tonsa to the populations of the Patuxent River, an estuary in Maryland. Miller (1970) has pointed out that Bishop found a spuriously high feeding rate, probably because copepod concentrations in the experiments were on average 253 times those in the field.

Miller (1970) gave a less dominant trophic role to Mnemiopsis. He determined feeding rates, extrapolated these to field conditions in the Pamlico River, North Carolina, and found that the feeding of Mnemiopsis could account for 11% of the summer mortality of the dominant copepod species, Acartia tonsa. This could not, however, support laboratory respiration levels. Miller speculated that Mnemiopsis might exploit some additional energy source, such as phytoplankton or detritus.

In a second paper, Bishop (1968) compared the feeding of two ctenophores of different feeding types, Pleurobrachia bachei and Bolinopsis microptera. The concentrations were within the natural range, and Bishop successfully distinguished the feeding success of the two species on two copepod species, Pseudocalanus minutus and the much larger and more robust Epilabidocera amphitrites. Both ctenophore species

captured more Pseudocalanus than Epilabidocera. Bolinopsis, a lobate ctenophore, was particularly unsuccessful at capturing the larger copepod, but took nauplii of Pseudocalanus more frequently than did the cydippid ctenophore, Pleurobrachia.

Fraser (1970) presented a thorough review of the literature on the occurrence and habits of Pleurobrachia pileus and with it an enumeration by species of the gut contents of Pleurobrachia taken in plankton tows from the northern North Sea in 1965 - 1968. His work laid to rest the idea that Pleurobrachia preys extensively upon the eggs or larvae of fish or shellfish, for 80% to 97% of the included prey were Crustacea, mostly copepods. He did not, unfortunately, relate the gut contents to ambient prey concentrations.

The work of Kamshilov and Fraser was extended by Greve (1970, 1971), who had notable success in characterizing the maximum growth rates of both Pleurobrachia pileus and Bolinopsis infundibulum as well as the minimum size and age at which Pleurobrachia may reach reproductive maturity, 5.5 mm diameter at about 35 days old. This rapid maturation helps to explain the sudden and unpredictable appearance of swarms of this species. Greve (1970) also investigated the selective feeding of the specialized ctenophores Beroë cucumis, which takes mostly Bolinopsis, and Beroë gracilis, which preys exclusively upon Pleurobrachia. The success of Greve's laboratory experiments is a consequence of his development of the "planktonkreisel" (Greve, 1968), an aquarium whose bottom is covered by a sand filter, through which water is drawn and gently recirculated by an air-lift pump. This device was so successful that he was able to rear plankters as delicate as Pleurobrachia from egg to egg. He supported

his laboratory research with field observations on these four species in the German Bight of the North Sea, where he found a year-to-year reciprocal relationship between the abundance of Beroë gracilis and Pleurobrachia.

This was the foundation upon which I began my work. While it was in progress, a parallel enquiry appeared when Hirota (1973) presented a study on the quantitative natural history of Pleurobrachia bachei in La Jolla Bight, California. This species is very similar to Pleurobrachia pileus; Mayer (1912) considered the two to be synonymous, and they are separated mainly on the basis of their habitat ranges. Pleurobrachia bachei extends into much warmer waters in the Pacific than does Pleurobrachia pileus in the Atlantic.

Hirota found Pleurobrachia bachei to be a very abundant species. Its numbers reached 1,000 $\cdot$ m^{-2} off southern California in August. Its annual production of organic matter which Hirota calculated from laboratory rates of growth and reproduction along with field measurements of populations, was 5.4 g $\cdot$ m^{-2}, which is a surprisingly high estimate for a single species at the third trophic level. It is, however, supported by an approximate energy budget which states that 60% of ingested energy is converted into soma and 7% into eggs.

This has been a brief historical review of work on the ecology of ctenophores, with increasing emphasis toward the present. Thorough reviews of earlier work are available in Fraser (1970) and Kamshilov (1960). In the remaining few pages of the Introduction I will attempt to display the unifying goal which motivated my several courses of approach to understanding the natural history of ctenophores, especially

Pleurobrachia pileus, in St. Margaret's Bay.

Objectives of this study

The method I chose to measure the feeding of ctenophores in the field is conceptually simple. Gut contents divided by residence time gives the instantaneous feeding rate. When I had measured natural feeding rates, I sought to comprehend the relations between predators and prey in terms of spatial distribution and motion.

The hunting strategies of planktonic predators may be analysed for the purposes of this exposition into two modes: pursuit and ambush. The cydippids, like most true jellyfish, are pure ambush predators. Their placement relative to concentrations of potential prey is their most important adaptable behavioral attribute. Therefore the sampling program was designed, not only to produce estimates of the populations, but also to test the hypothesis that zooplanktonic species are distributed at random with respect to one another. Additional laboratory experiments were required to distinguish interspecific tropisms from joint responses to environmental conditions. Cassie (1959, 1960, 1963) has presented a statistical treatment of zooplankton samples from a mixing zone between oceanic and harbor water, and shown that most of the variability in species abundances can be related to physical parameters. This frequently-cited work demonstrates that in such a heterogeneous zone, populations remain identified with their parent water-masses, but it says little of the joint distributions of species under ordinary circumstances.

The swimming activity of prey leads directly to their ambush by the cydippids, and must also influence the feeding of the relatively sluggish

lobates. It follows that the natural movement of potential prey is important to ctenophoran feeding. While the review articles of Banse (1964) and Bainbridge (1961) demonstrate that there is a copious literature on the vertical migrations of zooplankton, and Bainbridge (1952) and Gauld (1966) have given qualitative descriptions of the smaller scale excursions of copepods, there are no quantitative measures of these local activities. I have provided a few such measurements and will show that they lend robustness to my field observations.

The study area

The major sampling program was conducted in St. Margaret's Bay, Nova Scotia. This is a body of water 9 miles (14.4 km) long by 5.5 miles (10.2 km) wide, with a mean depth of 19 fathoms (35 m). It mixes with the waters of the Scotian Shelf through a mouth 2.5 miles (4.0 km) wide with a controlling depth of 23 fathoms (42 m). When the larger study of which this work forms a part was initiated, it was hoped that the planktonic populations of the Bay were to some extent conservative. This hope was soon broken. Sharaf El Din, Hassan, and Trites (1970) showed that the water in the Bay is replaced several times per year. In an extreme case, reported by Platt, Dickie, and Trites (1970), the water at 10 m in the Bay was apparently replaced in one day, between 24 June and 25 June, 1969. Heath (1973 a,b) has shown that at least three flushing mechanisms operate in the Bay. Tidal excursions and a net cyclonic circulation together give flushing times of 5-10 days in the upper layer and 10-30 days in the lower layer. Wind-driven reciprocal two-layered fluctuations give separately - calculated flushing times of 11 days in the upper layer and 13 days in the lower layer.

MATERIALS AND METHODS

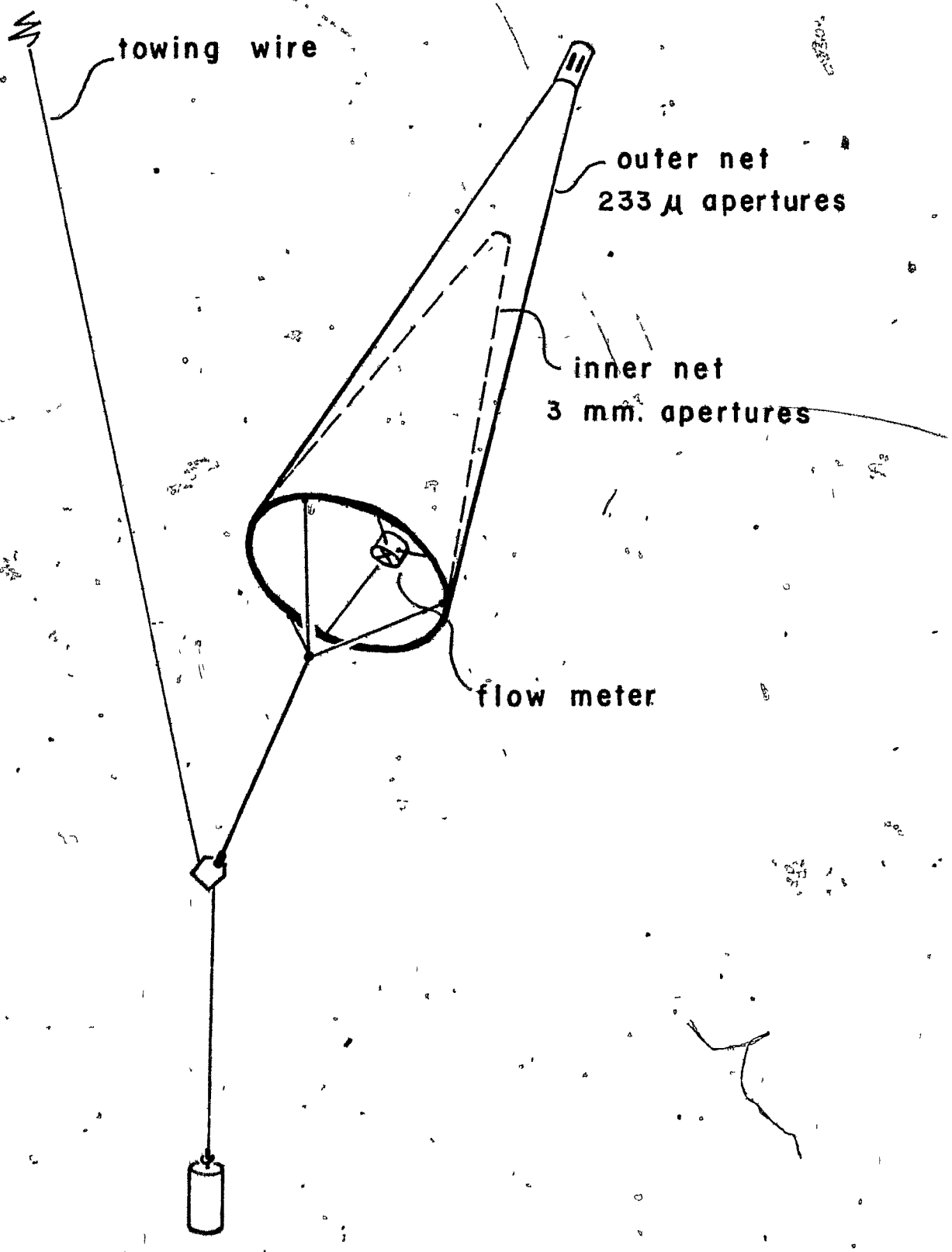
Sampling technique

All quantitative zooplankton samples in this study were made with vertical tows of a metered 0.75 m diameter ring net designed to collect ctenophores and their prey separately. Separation was necessary because in preliminary observations of lumped tows, Pleurobrachia gorged on immobile prey and detritus. Figure 2 is a drawing of the net. An inner net of hexagonal knit mesh, aperture size 3 mm, captured all but the smallest ctenophores while passing virtually all potential prey. The outer net was a standard nylon monofilament net of #6 mesh (233μ apertures). This captured adult copepods efficiently but was too coarse to retain quantitatively either nauplii or small copepodids. Very young copepods formed an insignificant part of the diet of the ctenophores.

The net was attached to the towing wire approximately 2.5 m above the approximately 35 kg weight. A rope pennant and three-part bridle, total length about 2.0 m formed the only attachment between net and wire. The net was thus free to fish both going down and coming back up. Descent rate was about 0.5 $m \cdot sec^{-1}$. When the weight hit bottom, the wire was checked and a delay of 10 seconds was counted to allow the net to sink to the limit of its pennant and the ring to capsize before hauling. Ascent rate was about 0.5 $m \cdot sec^{-1}$ but was not well controlled from tow to tow because tows were made at the idle speed of the gasoline-powered hoisting engine, and this speed varied with the condition of the engine and weather. The action of the net during this evolution was observed over the rail in shallow water on a calm day.

Figure 3

Concentric plankton nets for the separate collection of ctenophores and their prey.


towing wire
outer net
233 μ apertures
inner net
3 mm. apertures
flow meter

The net did not collapse or evert through the ring when the weight hit bottom.

The meter readings were highly variable because in the vicinity of 0.5 m · sec $^{-1}$ the calibration of the meter was strongly speed-dependent. Therefore a single filtering efficiency, the ratio of meter readings for five hauls of the complete net from 50 m to the surface to meter readings for five similar hauls of the ring and meter alone, was used to correct all samples. Each count of a vertical sample was multiplied by the factor 1.51 to give numbers per square meter of sea surface. This factor was calculated as follows:

$$\text{factor} = (\text{efficiency} \cdot 2 \cdot \text{mouth area of net})^{-1}$$

$$= (0.745 \cdot 0.884)^{-1} = 1.51 .$$

The net never appeared to be clogged with plankton.

It is necessary in any quantitative study of gut contents to demonstrate that all items which are in the gut at capture, and only those items, are present at enumeration. The behaviour of Pleurobrachia and of Bolinopsis were tested for this criterion in March, 1971. In each trial one animal was dipped from the surface layer with a 250 ml beaker. The trauma of capture was simulated by gently pouring the animal plus its surrounding water into a second vessel. The individual was held for about one minute, during which time further agitation was supplied by the motion of the collecting craft, a rowboat. The animal and its surrounding water were preserved separately in 7% formalin sea water. Ten of each species were taken, plus a control series of ten dummy dips. The copepodan contents of each fraction were enumerated and are presented here in Table 1. Student's "t" test was applied to the

hypothesis, "Water surrounding captured animals contained as many copepods as did the control series." The hypothesis is rejected for Bolinopsis water minus control ($t_{18} = 3.747$; $0.01 > p > 0.1$), but not for Pleurobrachia ($t_{18} = 0.411$; $0.7 > p > 0.6$). In fact, some Bolinopsis extruded their gut contents in a sticky stream which made quantitative collection difficult. From that time on, Bolinopsis gut contents were not regularly enumerated, nor were any digestion times determined for that species.

Field program - annual cycles

A square grid of nine stations at 0.5 mile intervals was laid out in the center of the Bay. Each station was sampled between the hours of 0830 and 1330 with the concentric nets on each of 25 sampling occasions between 29 October, 1970 and 25 October, 1971. There were thus 225 plankton samples. A bathythermograph cast was made at the central station on each sampling day.

The #6 net sample was preserved in 7% formalin sea water. The coarse net sample was washed into a finger bowl, and the non-ctenophores added to the #6 net sample. At stations 1, 2, 3, 7, 8, and 9, the ctenophores were separated by species, counted, blotted, and the total volume for each species measured by displacement of water in an appropriate size of graduate cylinder. At stations 4, 5, and 6, each individual ctenophore was dipped from the net on a wire mesh ladle four cm in diameter, blotted through the ladle on a pad of paper towels, its volume measured, and preserved separately in 7% formalin sea water. When there were more than ten ctenophores in a tow, a subsample of ten was taken to represent the tow. The measuring and preservation was performed in less than ten

	$\bar{X}$	$V_{\bar{X}}$	t	D.F.	p
A. *Pleurobrachia* guts	2.800	0.7289			
B. *Pleurobrachia* water	0.200	0.0178			
C. (A) - (B)	2.600	0.7600			
D. *Bolinopsis* guts	0.800	0.1956			
E. *Bolinopsis* water	3.400	0.8044			
F. (D) - (E)	-2.600	0.8933			
G. Dummy dips	0.300	0.0233			
H. (B) - (G)	-0.100		0.4110	18	0.7>p>0.6
I. (E) - (G)	3.1		3.7471	18	0.01>p>0.001

Table 1. Test for egestion of gut contents of ctenophores upon capture. Each mean represents the number of copepods in ten determinations.

minutes per tow. The ctenophores had to be measured immediately after capture because they shrink or even disintegrate when preserved. Table 2 shows the reactions of Bolinopsis and Pleurobrachia to several standard fixative solutions chosen from Baker (1958) but made up with filtered sea water rather than distilled water. The most effective of these solutions was the most common, formalin/sea water. In this, entire Pleurobrachia remained intact, as did the guts of Bolinopsis.

The plankton samples were counted in the laboratory under a dissecting microscope. A subsample of at least 250 individuals, and usually more than 400 individuals was isolated by sequential halving of the sample with a Folsom splitter. Larger items such as members of the genus Calanus, medusae, and large Sagitta were counted at about the third split (1/8 of the whole sample) while smaller items were counted at greater attenuation in order to reduce the labor of counting. The guts of the individually preserved ctenophores were dissected out, opened, and their contents enumerated.

Most copepods were identified with the descriptions provided by Rose (1933). The exceptions were Eurytemora herdmani, for which Grice (1971) was used, and the three Calanus species, which were distinguished on the basis of size according to Grainger (1963).

The errors of the sampling and counting method were evaluated from data representing five replicate tows taken between 0930 and 1050 on 24 June, 1972, which was a fair day with winds less than five knots. Each tow was split and counted twice. The raw counts for several abundant categories, and for revolutions of the flow meter, are shown in Table 3A.

Fisher's coefficient of variation, $\frac{s}{\bar{x}}$, for the flow meter readings

NAME	Ethanol	Picric acid	Mercuric chloride	Formal-dehyde	Acetic acid	Nitric acid	Results: Bolinopsis 1 Day	Bolinopsis 1 Week	Pleurobrachia 1 Day	Pleurobrachia 1 Week
Bouin	--	1.2%	--	11%	5.6%	--	Broken	Disintegrated	Broken	Disintegrated
Gilson	6.5%	2.2%	--	--	--	1.3%	Broken	Disintegrated	Broken	Disintegrated
Formalin	--	--	--	7%	--	--	Shrunken	Partially Disintegrated	Intact	Intact Volume loss 20%
Mercuric/ Acetic	--	--	6.8%	--	5.3%	--	Intact, fragile	Broken	Intact	Intact, mesogela liquid
Ethanol	20%	--	--	--	--	--	Disintegrated	Disintegrated	Intact	Intact, fragile

Table 2. Reactions of Pleurobrachia and Bolinopsis to several standard fixative solutions chosen from Baker (1958) but made up with filtered sea water.

is 0.022, showing that the volume filtered per tow was essentially constant.

Fisher's coefficient of dispersion, $\frac{V}{\bar{X}}$, is 6.2 for Mertensia and 13.8 for Bolinopsis. When particles are distributed at random, the expectation for $\frac{V}{\bar{X}}$ is one. The departure from unity may be assigned a probability under the hypothesis of random distribution by entering a table of variance ratios at $n_1 = 4$, $n_2 = \infty$. Both species show a departure from the hypothetical expectation whose probability is much less than 0.01. Even when tows are made as closely together as possible, ctenophores show a clumped distribution.

The five categories at the top of Table 3A were counted in duplicate, and the raw counts within each category were subjected to an analysis of variance, with the result shown in Table 3B. The data have not been transformed because the items of greatest interest are the differences within species among replicate counts, and these are likely to be normally distributed. In three of the five cases, those of Sagitta, Oithona and Pseudocalanus, the among tows variation within species was significantly greater than that which could be attributed to counting error. Catches of Sagitta were particularly variable. This may be due to aggregation, or to the fact that during the day the large individuals of this species lie very close to the bottom (Pearre, 1970) and catches are strongly influenced by topography and the closeness of approach of the net to the bottom.

The coefficient of variation between duplicate counts ranges from 0.17 to 0.27, bracketing Winsor and Clarke's (1940) lowest value, 0.226. I have chosen 0.25 as a representative value for the coefficient

Tow	1		2		3		4		5	
Replicate	a	b	a	b	a	b	a	b	a	b
Sagitta, large	14	15	15	8	20	13	36	29	7	3
Pseu'cal adult	23	16	19	25	23	29	28	26	12	14
Pseu'cal juv.	125	99	91	164	147	180	238	186	135	158
Oithona	12	18	11	12	14	10	30	24	20	31
Calanus glac.	38	34	22	25	32	38	40	36	56	28
Mertensia	5		5		0		13		15	
Bolinopsis	12		21		36		12		42	
Revolutions	500		510		510		530		520	

Table 3A. Two raw counts of seven categories of zooplankton in five tows taken in close sequence on 24 June, 1972.

	SS	DF	MS	VR	p	$\frac{s}{\bar{x}}$
Sagitta						
Tows	832	4	208	12.68	0.01	0.90
Duplicates	82	5	16.4			0.25
Total	914					
Pseu'cal. adult						
Tows	254	4	63.5	4.92	0.05	0.37
Duplicates	64.5	5	12.9			0.17
Total	318.5					
Pseu'cal. juv.						
Tows	11,924.6	4	2,981.15	2.89	0.15	0.36
Duplicates	5,163.5	5	1,032.7			0.21
Total	17,088.1					
Oithona						
Tows	448.6	4	112.15	5.36	0.05	0.58
Duplicates	105	5	21.00			0.25
Total	553.6					
Calanus glac.						
Tows	382.4	4	95.6	1.11	0.20	0.28
Duplicates	430.5	5	86.1			0.27
Total	812.9					
Total within species	19,687.1					
Total between species	136,627.08					
Total	156,314.18					

Table 3B. Analysis of variance of the data from the replicate samples taken on 24 June, 1972.

of variation associated with the counting method. Whenever two determinations differ by two standard deviations they may be considered different at the 0.05 level of probability. Therefore whenever two counts by this method differ by at least 0.5 times the mean they may be considered different.

Soon after the initiation of the program it became apparent that the average weight of the adult copepods on each sampling occasion would be required. From 25 February on, small subsamples of the preserved #6 net hauls from stations 4, 5, and 6, were removed within a few hours after the tows were made. The subsamples were transferred to distilled water and inspected under a dissecting microscope. The first 100 adult copepods encountered were removed, blotted on filter paper, dried at 60° C for one hour, and weighed as a group. Average weights for the first six sampling occasions were determined from single samples taken within five days of the corresponding date in the following year.

Digestion times

Digestion of copepods by Pleurobrachia was observed directly through the transparent bodies of the ctenophores. The most decisive event in the process was the collapse of the exoskeleton of the prey. The interval between capture of a ctenophore and the collapse of the last prey was taken as a measure of digestion time. The same criterion was used in counting gut contents: collapsed prey were ignored.

Digestion times were measured at selected numbers of copepods per ctenophore gut in the field and in the laboratory at temperatures between 2° C and 4° C. The laboratory animals were acclimated to the experimental temperature for 24 hours before the experiments were begun

in 1,300 l capacity tanks of gently flowing sea water innoculated with enough copepods, mostly Temora, Pseudocalanus and Acartia, to keep the prey concentration at about 100 • l^{-1}. In other respects the laboratory procedure was similar to that used in the field. The ctenophores were dipped gently from the surface with a finger bowl and examined immediately under an 8X hand lens. Those with gut contents were held at the temperature of the parent population and re-inspected at 15-minute intervals. Digestion time was recorded as the interval between capture and the mid-point in time between the last observation of an intact exoskeleton and the first of no intact exoskeleton.

Vertical distributions

Two series of day/night horizontally stratified plankton tows were made to evaluate the diurnal feeding pattern of the ctenophores. Metered concentric nets were used in this series as in the vertical hauls, except that a messenger-operated opening and closing device permitted the tows to be taken within selected depth intervals. The intervals were chosen to represent lower water layers, thermocline with associated layers, and surface. Each tow lasted 10 min at 2.0 to 2.5 knots. The sets of three tows were repeated at dawn, noon, dusk and midnight on two days in the spring of 1972. The meters worked well; the readings for five vertical calibration hauls at this speed had a coefficient of variation of 0.018.

The vertical distribution studies in the field were supplemented with a series of experiments run in the spring of 1972 in the tower tank of the Dalhousie Aquatron. This tank is 10.7 m deep by 3.7 m in diameter, is lined with polyvinyl chloride, and has viewing ports at approximately 0.7 m depth intervals.

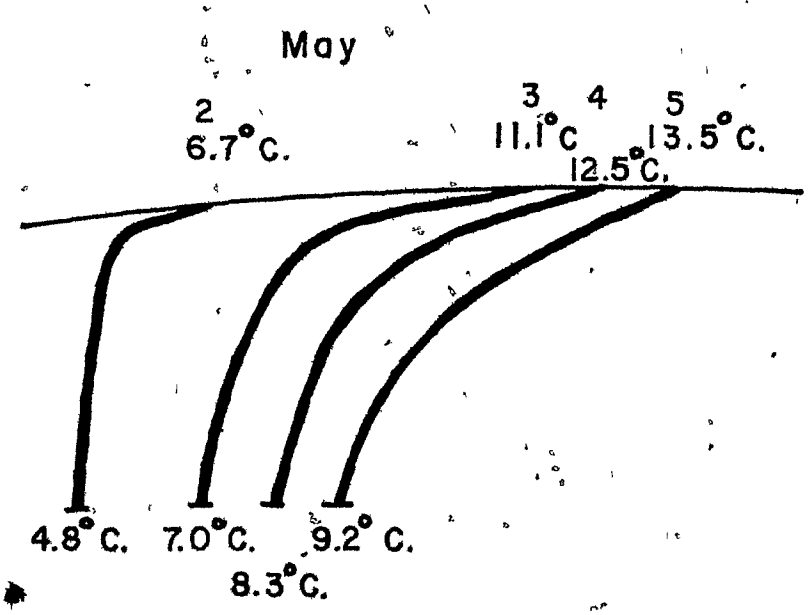
A bathythermograph cast was taken in the tank at the beginning and end of each experiment. A series of four casts was taken in May, 1972 to assess the changes in temperature structure to be expected. After the first day's rapid heat exchange between tank and water, a shallow thermocline was established (see Figure 3). The temperature structure was a vertically compressed version of that which had been found in St. Margaret's Bay on 11 May, 1972 (see Figure 4). The rapid change was followed by a slower drift toward ambient temperature.

The design of the tank experiment was such as to allow a multiple regression equation to be calculated for the dependence of mean population depth of the ctenophores on light, mechanical disturbance, and availability of food in the given regime of temperature and salinity. This statistical treatment was used with some success by Moore (1949) on the vertical distribution of siphonophores, but was abandoned in this study because no reversible reaction to any of the three manipulatable parameters could be demonstrated in preliminary experiments.

Plankton for these experiments was captured at the mouth of Halifax Harbor with a #6 mesh (233μ apertures) net for copepods and a #00 mesh (1.02 mm apertures) net for ctenophores. The cod ends of the nets were 1 liter glass jars, and tows lasted no longer than 5 minutes to minimize damage to the animals. Copepods and Pleurobrachia were transported to the laboratory with negligible mortality in covered polyethylene buckets completely filled with sea water to eliminate free surface. Mertensia ovum and Beroë cucumis also survived satisfactorily if carefully handled, but Bolinopsis caught in nets suffered unacceptable damage. On no sampling occasion were Bolinopsis abundant enough at the surface to make it seem

Figure 4

Temperature structure of water in the tower tank, 2 - 5 May, 1972.


May
2
6.7° C.
3
11.1° C
4
12.5° C.
5
13.5° C.
4.8° C.
7.0° C.
8.3° C.
9.2° C.

profitable to hand-dip the 100 or so individuals which would have been required for an experiment in the tower tank. The animals were held in the laboratory in tanks of gently-running sea water which ran out through a sand filter on the bottom. Animals were transferred to the surface of the water in the tower tank in buckets of sea water. Ctenophores could be counted individually, but the copepodan inoculum was measured by filtering three bucketsful through a #6 seive and multiplying the average count by the number of bucketsful transferred.

Illumination was varied in a 12 hours light/12 hours dark cycle by switching on and off the overhead mercury vapor lamps.

A semi-quantitative estimate of ctenophore populations at various depths in the tank was made by visual inspection through the viewing ports. At each port, a one-minute scan was made in a prescribed manner. During dark periods, a battery-operated hand lantern with a red-passing filter was used in the scan. Ten minutes' illumination with this lantern produced no observable change in the behaviour of any of three Pleurobrachia; but upon sudden exposure to the unfiltered light, two of the three individuals promptly dived about 1 m before redeploying their tentacles.

In order to evaluate the sampling error of this technique, one "day" and one "night" count were replicated three times, with a five-minute rest between counts. Using the lantern, a count of 8 was replicated exactly. By "day" the result was 11.7 ± 2.2. The means are not comparable because they were estimated by different methods. In fact it was much harder to recognize ctenophores under uniform illumination than under the beam of the lantern.

Horizontal distributions in aquaria

The existence of active responses of Pleurobrachia and Bolinopsis to the presence of their copepod prey, and of Beroë to Pleurobrachia and Bolinopsis was tested for in a series of experiments run in the laboratory in aquaria with porous partitions. The materials used in these aquaria were restricted to plate glass 5 mm thick, silicone rubber sealant ("RTV - 108", General Electric Company), clear acrylic plastic, nylon plankton mesh, and neoprene "O" rings. Each aquarium was "aged" in running sea water for at least a week before its first use.

In early experiments two separate aquaria were used, one for predators and one for prey. The aquaria communicated through 3 cm diameter holes bored in their sides. A sandwich of two "O" rings with #6 mesh cemented between them was placed between the aquaria over the holes, and the two aquaria were bound together with elastic cord. When no distributional responses appeared, the area of communication was increased by cementing a partition of mesh in the center of a 24 cm x 24 cm x 48 cm aquarium, perpendicular to the long axis.

Aquaria were washed between runs with detergent, rinsed with tap water, 0.1 N. HCl, and distilled water, and air dried. All seawater used in these experiments was filtered through glass fiber filters (Whatman GF/C) and aged one week before use.

In order to control temperature and isolate the aquarium from light and mechanical disturbances, it was placed in a covered plywood box lined with 2.5 cm of styrofoam. Coolant from a constant temperature bath was pumped through a heat exchanger on the inside of one wall of the box. Although there was no feedback control on temperature, it was

possible to achieve a steady-state temperature within 0.5° C of the intended value by adjusting the temperature of the bath. In initial trials of the apparatus a crystal of the vital stain methylene blue was dropped to the bottom of the water in the aquarium after an equilibration period of one hour. The dye diffused into the water much more rapidly in the horizontal than in the vertical direction. After two hours its distribution was apparently homogeneous in horizontal planes but had a strong vertical gradient. Thus there was evidence of stratification, but not of large convection currents.

Photographs recorded the positions of the ctenophores at 24 minute intervals. A motor-driven "Nikon F" 35 mm camera equipped with a 55 mm "Micro Nikkor" lens was mounted inside the box. Photographs were made on Kodak High Speed Infrared Film 2481, and the subject was lit from the side with electronic flash illumination. The camera and flash were triggered by an automatic timer. The flash was filtered through a Kodak "Wratten 87" filter, which passes almost no light of wavelengths less than 740 nm (Anonymous, 1968). The information contained in the negative was extracted by projecting the image at an appropriate scale with a photographic enlarger and counting the numbers of ctenophores in the half of the test chamber nearest the partition and in the farther half. In order to ensure independence of the counts in any run, the positions of the ctenophores in the frame taken previously to the one being counted were marked on a sheet of paper placed on the easel of the enlarger. The frame of immediate interest was then projected in register with the previous image. Only those animals were counted which could be seen to have moved between frames.

The null hypothesis that animals were distributed equally between the left and right halves of the test chamber was tested by calculating the probability of the random occurrence of as bad or worse a fit to the hypothesis, first within individual frames, and then for the sums of frames in a run. The probabilities were calculated as the sums of the appropriate terms of a binomial expansion whose terms are $\frac{j!}{(j-r)!} p^r (1-p)^{(j-r)}$ where p is the hypothetical probability of an individual falling into the category in which r actually occurred, and j is the total number of individuals. The χ^2 distribution is inappropriate to these data because it is a continuous distribution while the data are discrete, and although the discrepancy is small for large numbers, it becomes unacceptably large when the expectation in any class is less than five (Fisher, 1925).

Swimming of copepods

The local excursions of copepods were also measured by photography. For this purpose the apparatus used in the distribution studies was modified slightly to allow the timer to fire the flash several times during one exposure of the film. During different runs of the experiment there were from four to seven flashes per exposure, and the interval between flashes was from one to seven seconds. For the shorter intervals the recycling time of the electronic flash unit was reduced by replacing the standard 500 μfd condenser with a 150 or 30 μfd condenser. Two large plastic Fresnel lenses placed between the flash unit and the aquarium condensed the flash into an approximately parallel-rayed beam slightly smaller in cross section than the aquarium. This minimized light scattering from the walls of the aquarium.

The photographs were taken horizontally through the square faces of the 22 cm by 30 cm by 30 cm aquarium. A smaller aquarium, a cube 15 cm on each edge, was used for some trials involving smaller copepods. Some experiments were run at sea in relatively clam weather, and for these the aquaria were fitted with tops provided with 1 cm inside diameter standpipes at diagonally opposite corners. The aquaria were filled and the animals introduced through these standpipes, which were then sealed with corks. The only free surfaces of water in the aquaria were those in the standpipes immediately below the corks.

The aquaria were filled with sea water taken from Halifax Harbor or St. Margaret's Bay no longer than a week before the experiment. The water was warmed to 5° C above the experimental temperature, shaken vigorously, and cooled back to the experimental temperature. This procedure gave water slightly undersaturated with gases which would not form bubbles on the walls of the aquaria. The water was filtered through a "Nitex" seive, aperture size 88 μ, but the smaller particles were not removed because normal swimming and feeding in most herbivorous calanoid copepods are closely related (Gauld, 1966) and feeding ceased in both of the species investigated by Parsons, LeBrasseur, and Fulton (1967) when phytoplankton concentrations fell below a lower threshold.

From 5 to 25 animals of a single species were selected from a fresh plankton tow for each run. Individuals of the genera, the adults of which are about 1 mm long, (Oithona, Pseudocalanus, Acartia, Temora, Centropages) were chosen under a dissecting microscope. Larger copepods (Tortanus, Metridia, Calanus) could be selected without visual aids by their colors and swimming patterns.

The photographic negatives were projected as for the distribution studies, and the vertical and horizontal components of each excursion were measured for each animal for which an unambiguous sequence of positions could be identified. It was assumed that the horizontal components of motion were distributed equally over directions, and therefore that motions in the horizontal direction perpendicular to the camera's optical axis were equal to those parallel to the axis. It was also assumed that the average density of animals was homogeneous within horizontal layers. Therefore the errors resulting from the fact that animals might be nearer to the camera or farther away are equally distributed about 0 and do not bias the results.

The averages were calculated of the absolute values of excursion lengths in both the vertical and horizontal directions for each category of copepods whose movements were studied. This statistic was chosen because the root mean square displacements, which at first seemed more attractive, might lead one to form an invalid analogy with the statistical mechanical model of molecular diffusion. This analogy is wrong because the time intervals chosen in this study are of necessity small relative to the time at which successive excursions would become uncorrelated in direction (Okubo, 1972). Thus it is possible to characterize the species by average displacement over a given time, but not to use these data to calculate fluxes from the familiar equation of diffusion.

RESULTS

General cycle of the zooplankton

In order to provide a background for the discussion of feeding by ctenophores, I have presented in Figure 5 a summary of the general cycle of the zooplankton in St. Margaret's Bay. The corresponding plankton counts are tabulated in the Appendix. There are several prominent features. In the spring and summer, concentrations of four of the five most abundant genera of copepods were quite low relative to their winter concentrations. Of the five, only Oithona similis was more abundant in spring than in winter. Temora longicornis and Pseudocalanus minutus both showed a minor increase in late March and April, around the time of the spring phytoplankton bloom in St. Margaret's Bay (Platt and Irwin, 1968), but the most striking event in the year was a spectacular increase in copepod populations in the fall, with the rise to dominance of the non-endemic copepod Centropages typicus. The plot of bathythermograph results in Figure 6 shows that a profound hydrographic event occurred during the increase. From 26 August to 17 September, 1971, the depth of the thermocline plunged from 5 to 40 m while the surface temperature rose from 13.6° C to 15.3° C. This trend continued until at least 25 October when warm waters reached almost to the bottom.

A second, less dramatic, influx of non-residents occurred in May, when late copepodids of Calanus glacialis and Calanus hyperboreus appeared in the Bay. These species are indicators of Arctic water (Grainger, 1963) as is the ctenophore which appeared with them, Mertensia ovum (Mayer, 1912; Huntsman, Bailey and Hachey, 1954). These results confirm the survey of the zooplankton of St. Margaret's Bay

Figure 5

Abundance of common zooplanktonic species in St. Margaret's Bay, October 1970 to October 1971.

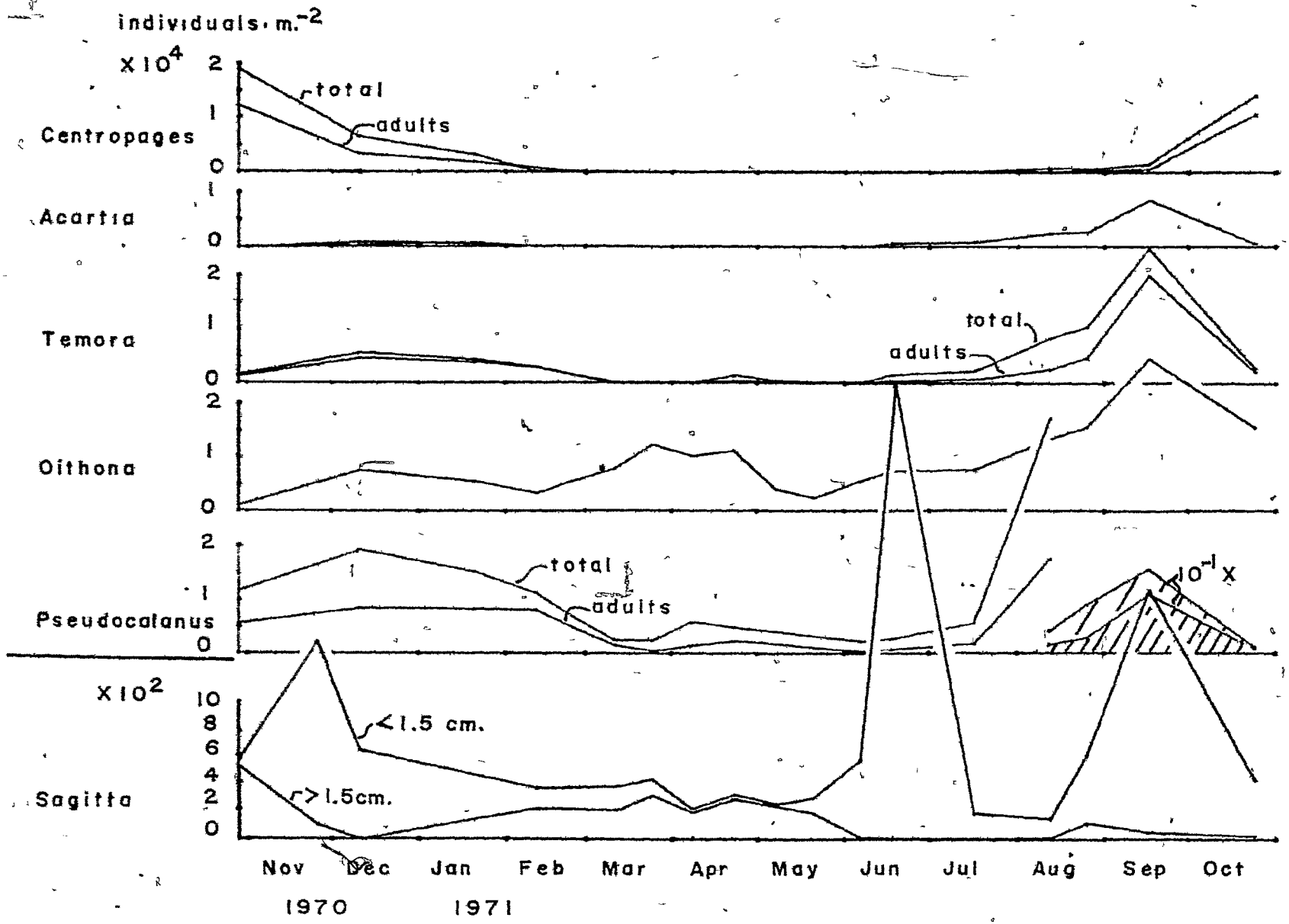
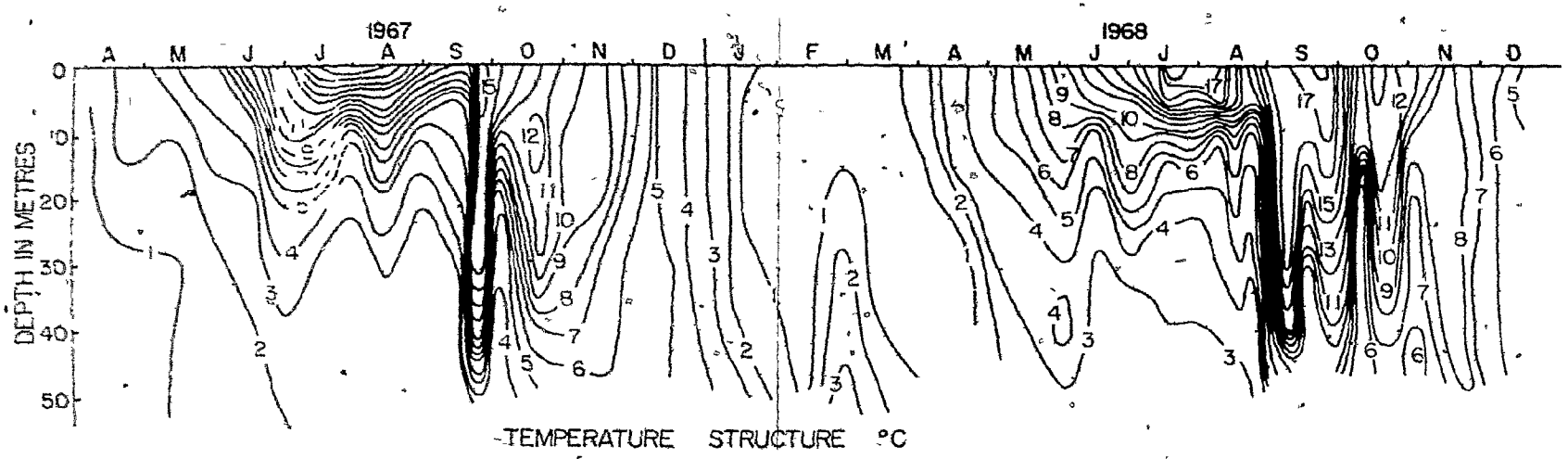
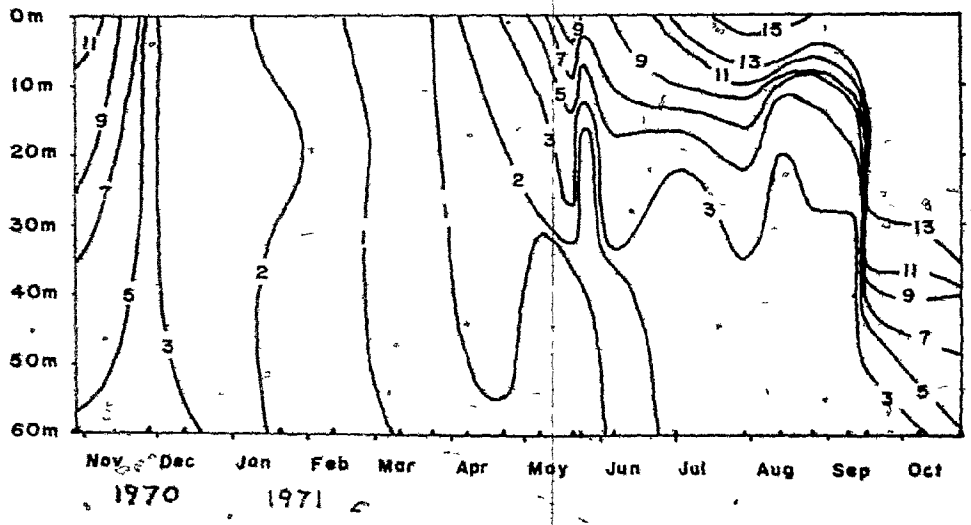

individuals · m.-2
X10^4
2
1
0
total
adults
Centropages
Acartia
Temora
Oithona
Pseudocalanus
10-1 X
X10^2
10
8
6
4
2
0
<1.5 cm.
>1.5cm.
Sagitta
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
1970
1971

Figure 6

Depths of selected isotherms in St. Margaret's Bay, October 1970 to October 1971, displayed with Heath's (1973) figure showing temperature structure in 1967-1968.



TEMPERATURE STRUCTURE °C



reported by Paranjape and Conover (1973) for the period January, 1968 to April, 1971.

The major competitor with the ctenophores Pleurobrachia, Bolinopsis and Mertensia for zooplanktonic crustacea is the chaetognath Sagitta elegans (Sameoto, 1971, 1972). Large Sagitta were abundant throughout the winter of 1970-1971. A strong pulse of reproduction began in May and reached its peak in June, at which time there were many small juveniles, but the adult population had declined to near zero.

The distribution of the populations of ctenophores over the year can be projected against this background of natural history. Figure 7 shows the volumes per square meter of each of three species through the year.

Pleurobrachia was most abundant in March and April. The small average sizes of individuals in June and July reflect the high numbers of young individuals present then. This cohort did not develop into a conspicuous summer population; the summer peak in volume was small.

The volumes per tow of Bolinopsis were more variable but showed a similar overall pattern. Again a spring pulse of reproduction occurred, this time in May, but by June most of these animals had disappeared from the Bay.

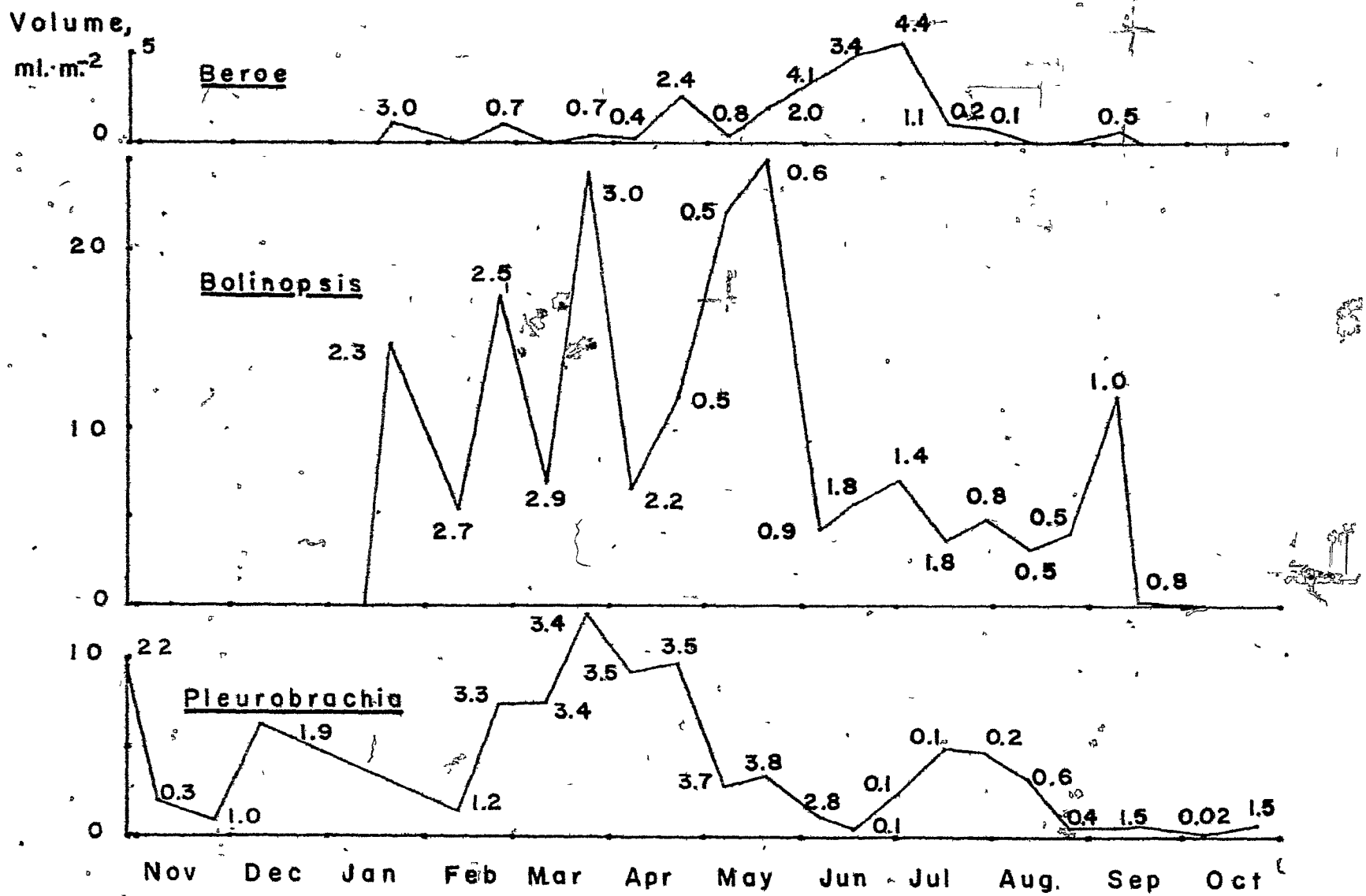
Beroë was absent during the fall and early winter. Its volume increased through the late spring to a peak at the end of June.

Feeding of ctenophores - prey taken

The results from the enumeration of gut contents show that the predation pressures of Pleurobrachia and Bolinopsis are very differently distributed among copepodan species. Although the counts of the gut contents of Bolinopsis are not useful for calculating feeding rates, they

Figure 7

— Abundances of Fleurobrachia pileus, Bolinopsis infundibulum and Beroë cucumis in St. Margaret's Bay, October 1970 to October 1971. The numbers over the data points are average volumes per individual in ml.


Volume,
ml·m⁻²
Beroe
5
0
3.0
0.7
0.7
0.4
2.4
0.8
4.1
2.0
3.4
4.4
1.1
0.2
0.1
0.5
Bolinopsis
20
10
0
2.3
2.7
2.5
2.9
3.0
2.2
0.5
0.5
0.6
0.9
1.8
1.4
1.8
0.8
0.5
1.0
0.8
Pleurobrachia
10
0
2.2
0.3
1.0
1.9
1.2
3.3
3.4
3.4
3.5
3.5
3.7
3.8
2.8
0.1
0.1
0.2
0.6
0.4
1.5
0.02
1.5
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug.
Sep
Oct

may be used to show the relative numbers of each species ingested, if the assumption is made that egestion is random among species. Table 4 shows the contents of Pleurobrachia and Bolinopsis at stations 4, 5, and 6 for the six dates in the late winter and spring of 1971 when both ctenophoran species were abundant. A scan of the columns indicates that Temora and Oithona were the most frequently consumed food items.

If the ctenophores consumed items at random from the water column, for increasingly large samples the ratios among prey species in the gut would approach those among potential prey species at large. The probability of a departure from this hypothetical expectation as great or greater than that observed can be calculated by summing the appropriate terms of binominal expansion. On 25 February, the probability that Bolinopsis feeding at random would have taken no Temora among 4 (Temora plus Oithona) items is 0.40; but the probability that Pleurobrachia would have taken no Oithona among 8 items is $2.9 \cdot 10^{-6}$. On the other occasions when both Temora and Oithona were present in significant numbers a similar result can be shown. On 12 February, the probability of 0 Temora among the food of Bolinopsis is 0.144, but the probability of 1 or 0 Oithona among the 13 items counted in Pleurobrachia guts is $1.0 \cdot 10^{-3}$. A similar treatment for Oithona and Pseudocalanus in Bolinopsis on 12 February shows a departure whose probability is 0.23 in favor of Oithona, while on the same date the probability is $1.3 \cdot 10^{-6}$ that the departure in Bolinopsis guts in favor of Temora over Pseudocalanus could have risen at random. Bolinopsis is thus a rather generalized feeder, showing a weak preference for Oithona. But Pleurobrachia in the same conditions takes Temora much more frequently

Bolinopsis

Date	Number Caught	Total Volume	Contents	Contents ml ctenophore	Prey · m^{-2}
12 Mar. 71	6	20.4	4 O	0.196	15,900
25 Mar. 71	16	54,5	11 O	0.202	24,700
			1 Am	0.018	--
12 Feb. 71	10	25.4	3 O	0.118	6,500
			3 Ps	0.118	16,200
25 Feb. 71	10	22.0	4 O	0.182	11,200
			1 A	0.045	--
			1 ?	0.045	--
8 Apr. 71	10	25.4	3 O	0.118	6,500
			3 Ps	0.118	16,200
23 Apr. 71	18	11.5	2 O	0.174	22,500
			3 H	0.261	--
			1 Am	0.087	--
			1 N	0.087	--
			1 Po	0.087	--

Pleurobrachia

Date	Number Caught	Total Volume	Contents	Contents ml ctenophore	Prey · m^{-2}
12 Mar. 71	10	39.1	9 O	0.230	15,900
			1 T	0.026	--
			1 Ps	0.026	2,800
25 Mar. 71	9	54.0	12 O	0.222	24,700
			1 N	0.018	--
			1 Cy	0.018	--
12 Feb. 71	5	6.6	12 T	1.818	5,900
			1 Ps	0.152	16,200
			1 O	0.152	6,500
25 Feb. 71	3	17.9	8 T	0.443	2,900
8 Apr. 71	10	34.1	1 O	0.029	20,400
			1 N	0.029	--
			1 Cy	0.029	--
23 Apr. 71	8	19.9	2 Cy	0.102	--
			1 O	0.052	22,500
			1 N	0.052	--

Table 4. Gut contents of Pleurobrachia and Bolinopsis taken at stations 4, 5, and 6 on the six occasions when both were abundant. Key: O = Oithona similis, T - Temora longicornis, Ps - Pseudocalanus minutus, A - Acartia longiremis, Am - Amphipod, N - nauplius, Cy - cypris, Po - Polychaete, Pt - Pteropod.

than it takes either Oithona or Pseudocalanus.

I have watched Beroë cucumis from St. Margaret's Bay capture both Pleurobrachia and Bolinopsis in aquaria. This contrasts with the situation in the North Sea, where Greve (1970) demonstrated the very strong preference of Beroë cucumis for Bolinopsis, while a second species, Beroë gracilis, fed exclusively on Pleurobrachia. I have also seen the ectoparasitism which Greve describes for Beroë gracilis on Pleurobrachia performed by Beroë cucumis on Pleurobrachia, most notably on 21-22 January, 1969, when a 2.3 mm long Beroë cucumis remained attached by its mouth to a 1.1 cm long Pleurobrachia for a full day. Bolinopsis was present in the aquarium when the attack began. When the pair were separated there was a wound on the Pleurobrachia at the point of attachment.

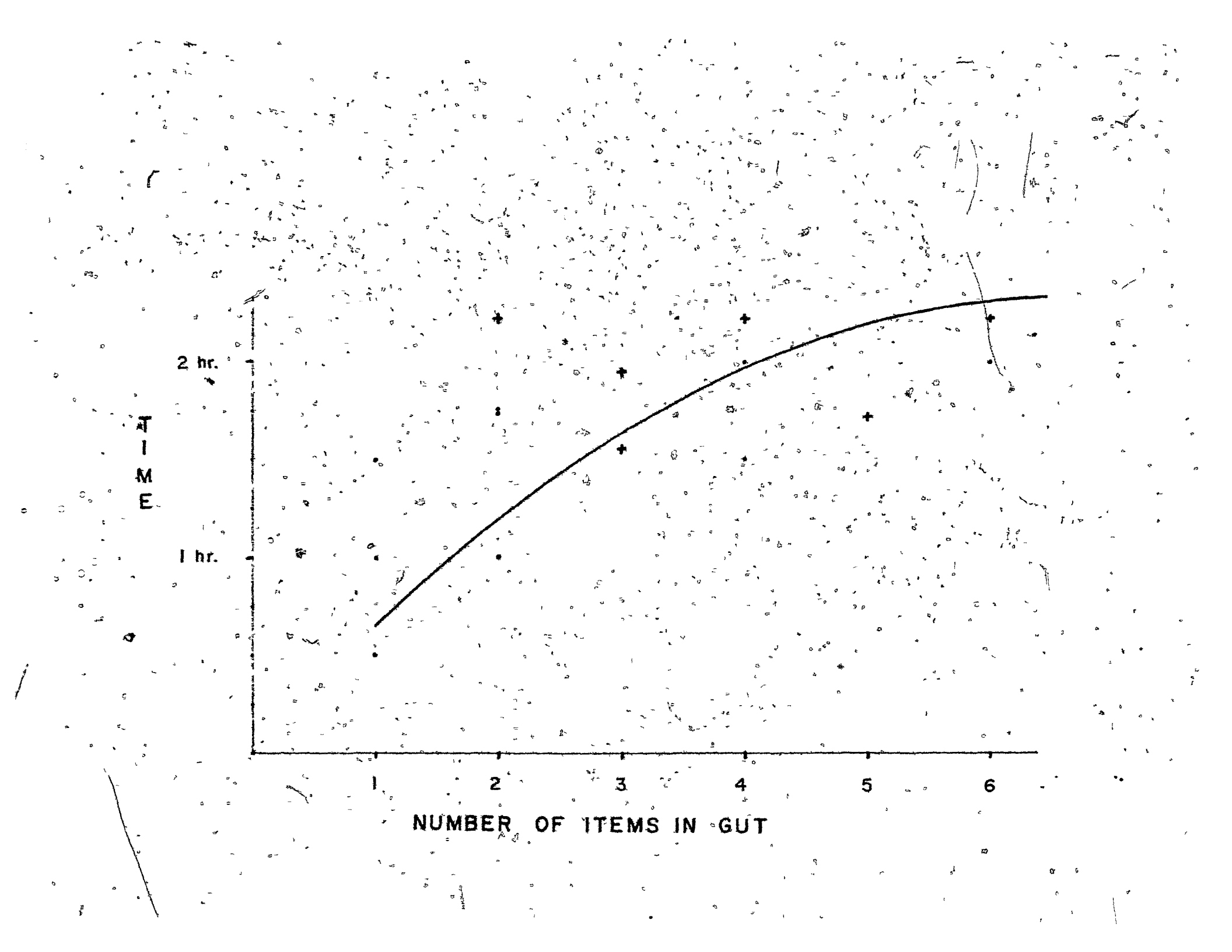
Feeding of Pleurobrachia - digestion time

In order to convert gut contents to feeding rate, a determination of the digestion time of copepods by Pleurobrachia was made on 27 April, 1972. The prey were mostly Temora, with some Pseudocalanus and Acartia. Sea surface temperature was 3.0° C and the temperature of incubation, 3.5° C. The nine observations on freshly-caught ctenophores were supplemented by six observations on ctenophores which had been held for a week in the laboratory at 5° C. The laboratory determinations were made on 5 April, 1974 at 4.5° C.

The results together with a fitted second degree polynomial are shown in Figure 8. The fact that the line rises to the right does not necessarily indicate that the time from ingestion to collapse of an individual food item increases with increasing gut loading. What is measured here is the time from capture of the ctenophore to the collapse

Figure 8

Time in hours from capture of individual Pleurobrachia to collapse of the exoskeleton of the last food item to be digested. The values for various gut loadings at capture are fitted with a second degree polynomial curve. Crosses represent field-caught animals; dots, animals taken from holding tanks.


TIME
2 hr.
1 hr.
1
2
3
4
5
6
NUMBER OF ITEMS IN GUT

of the last item to be digested. Thus if the [redacted] from ingestion to collapse were constant at T, for a ctenophore containing one item the "age" of that item in the gut previous to capture is equally probably any time from 0 to T, and the probability that is "older" than t, that is, that it will collapse within T-t, is $\int_0^t p(t)dt = \frac{t}{T}$. For a ctenophore containing two items the probability that both are "older" than t, in other words that neither will remain after T-t is $\frac{t^2}{T^2}$, for three items $\frac{t^3}{T^3}$, and so on. Figure 9 is a plot of these functions for $0 < n < 15$ food items in the gut. The times are connected, below which half the observations should lie.

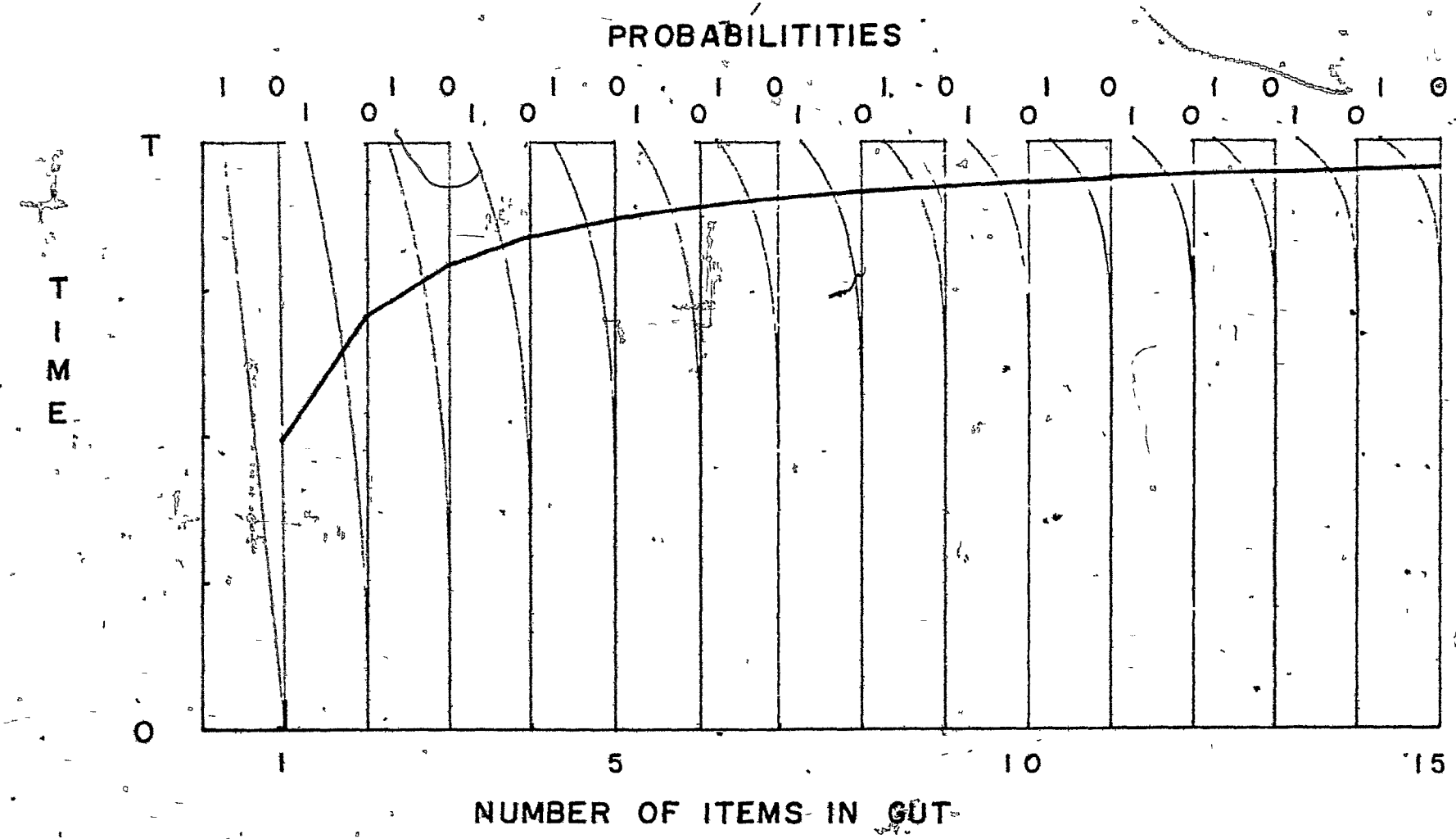
The plot of the data at hand is indistinguishable from this theoretical distribution. Therefore the simplest assumption was made, that digestion time is independent of gut loading. Digestion time was calculated from the hypothetical distribution, which gives median digestion times as a fraction of T for any number of items in the gut, together with the observed average digestion times for animals with 3, 4, 5, and 6 items in the gut. For example, half the ctenophores which when sampled contained four copepods in various stages of digestion might be expected to complete the digestion of the last item at 0.841 times the complete interval between capture by the ctenophore and collapse of the prey's exoskeleton (see Figure 9). One ctenophore was observed to complete its digestion of four items in 2.0 hr, giving a single estimate of digestion time as $\frac{2.0}{0.841} = 2.38$ hr. The average of eight estimates is 2.26± 0.10 hr.

Feeding rate of Pleurobrachia

The plot of the volume-specific feeding rate of Pleurobrachia on

Figure 9

Theoretical time from capture of a ctenophore to collapse of the last food item in the gut, assuming the total digestion time of an individual prey item is constant at T.


PROBABILITIES
1.0 1.0 1.0 1.0 1.0 1.0 1.0 1.0 1.0 1.0
1.0 1.0 1.0 1.0 1.0 1.0 1.0 1.0 1.0
T
TIME
O
1
5
10
15
NUMBER OF ITEMS IN GUT

copepod density (Figure 10A) is based on plankton tows taken at stations 4, 5, and 6 on all those occasions when more than five items were found in Pleurobrachia guts. The points are rather widely scattered, but Figure 10B shows that the variance can be substantially reduced by plotting feeding rate versus adult copepods only. This is so because of all food particles enumerated, 7.2% were nauplii or juvenile copepods, 2.5% were other crustacea, 1.6% were non-crustaceous, and 89.6% were adult copepods. The regression equation, $\frac{\text{copepods eaten}}{\text{ml ctenophore} \cdot \text{hr}} = 4.40 \cdot 10^{-5} - 2.45 \cdot 10^{-2}$ adult copepods $\cdot m^{-2}$ is an adequate predictor of the feeding rate of Pleurobrachia on copepods in St. Margaret's Bay.

For each sampling occasion during the annual cycle the appropriate value from this regression equation is multiplied by the volume of Pleurobrachia present (Figure 11A) to give the numbers of copepods consumed by Pleurobrachia (Figure 11B). This in turn is multipled by the average dry weight of adult copepods (Figure 11C) to give the annual cycle of consumption of copepods by Pleurobrachia in dry weight (Figure 11D). The integral of this curve over the year, plus a small increment for the four days by which the sampling cycle is short of one complete year, is $0.522\ g \cdot m^{-2} \cdot yr^{-1}$.

When the data which gave rise to Figure 10 are plotted separately for each of the four most abundant copepod species, several components of the overall relationship between feeding rate and prey concentration are separated. Figure 12A to D shows these component relationships. The regression slopes indicate that on any given day an individual of either Temora longicornis or Centropages typicus is approximately ten times more likely to be captured by Pleurobrachia than is one of Pseudocalanus minutus

Figure 10

Volume specific feeding rate of Pleurobrachia plotted against (A) total copepods • m^{-2} and (B) adult copepods • m^{-2}.

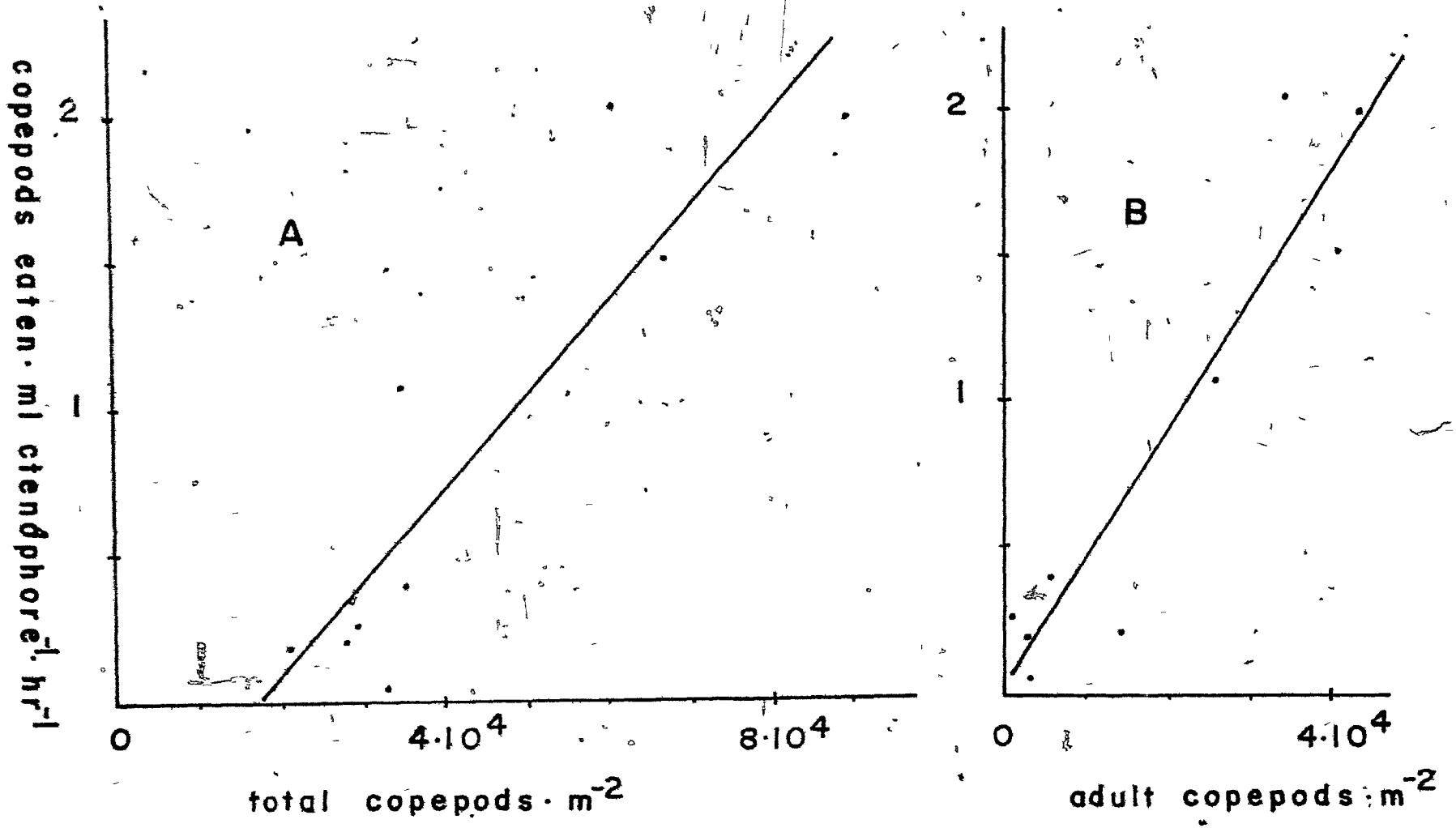

copepods eaten · ml ctenophore^{-1} · hr^{-1}
2
1
A
0
4·10^4
8·10^4
total copepods · m^{-2}
2
1
B
0
4·10^4
adult copepods · m^{-2}

Figure 11

Development of the calculation of the annual ingestion of copepods by Pleurobrachia. (A) abundance of Pleurobrachia through the year. (B) number of copepods consumed by Pleurobrachia. (C) average dry weights of adult copepods. (D) dry weight of copepods consumed by Pleurobrachia.

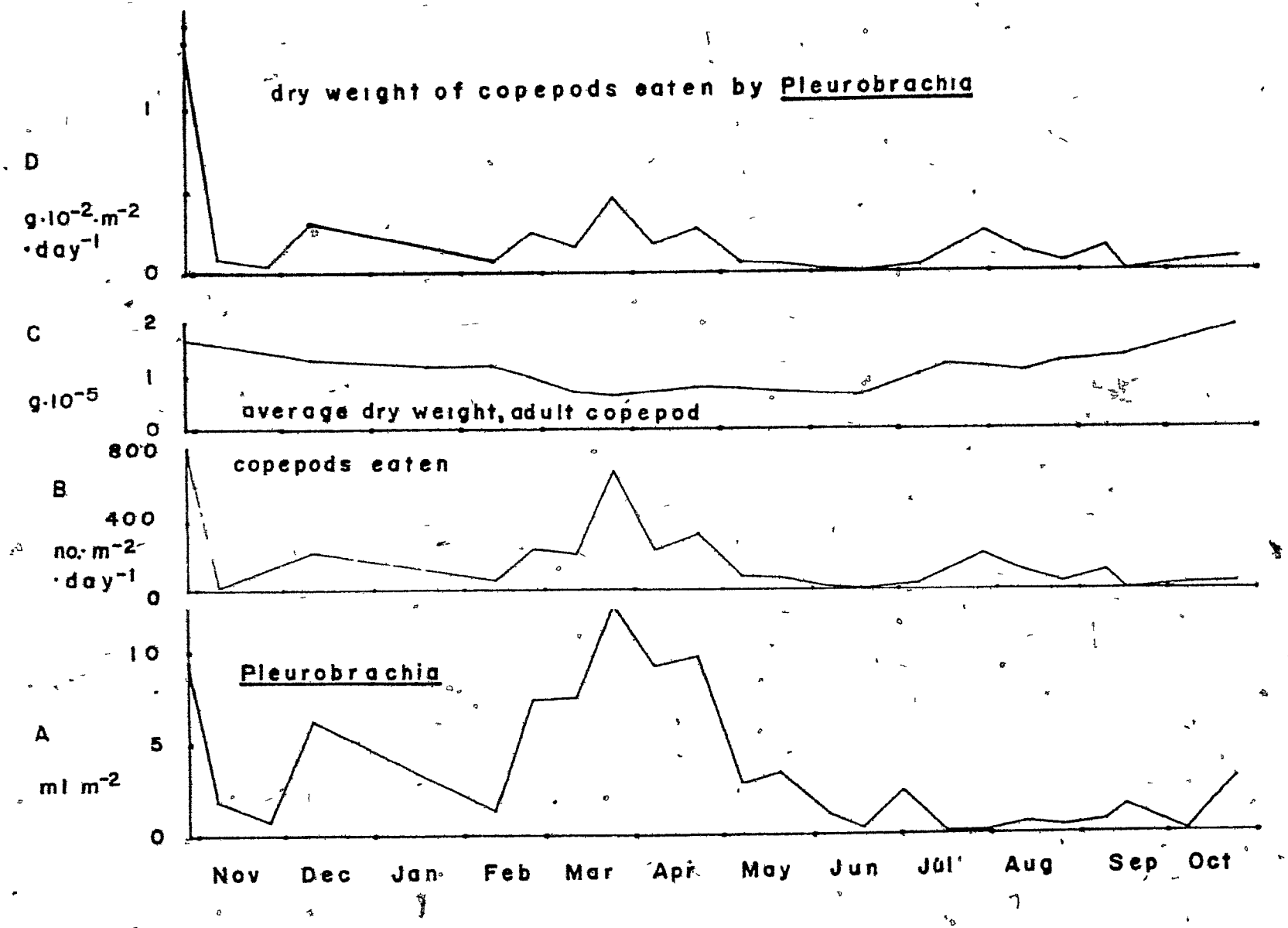
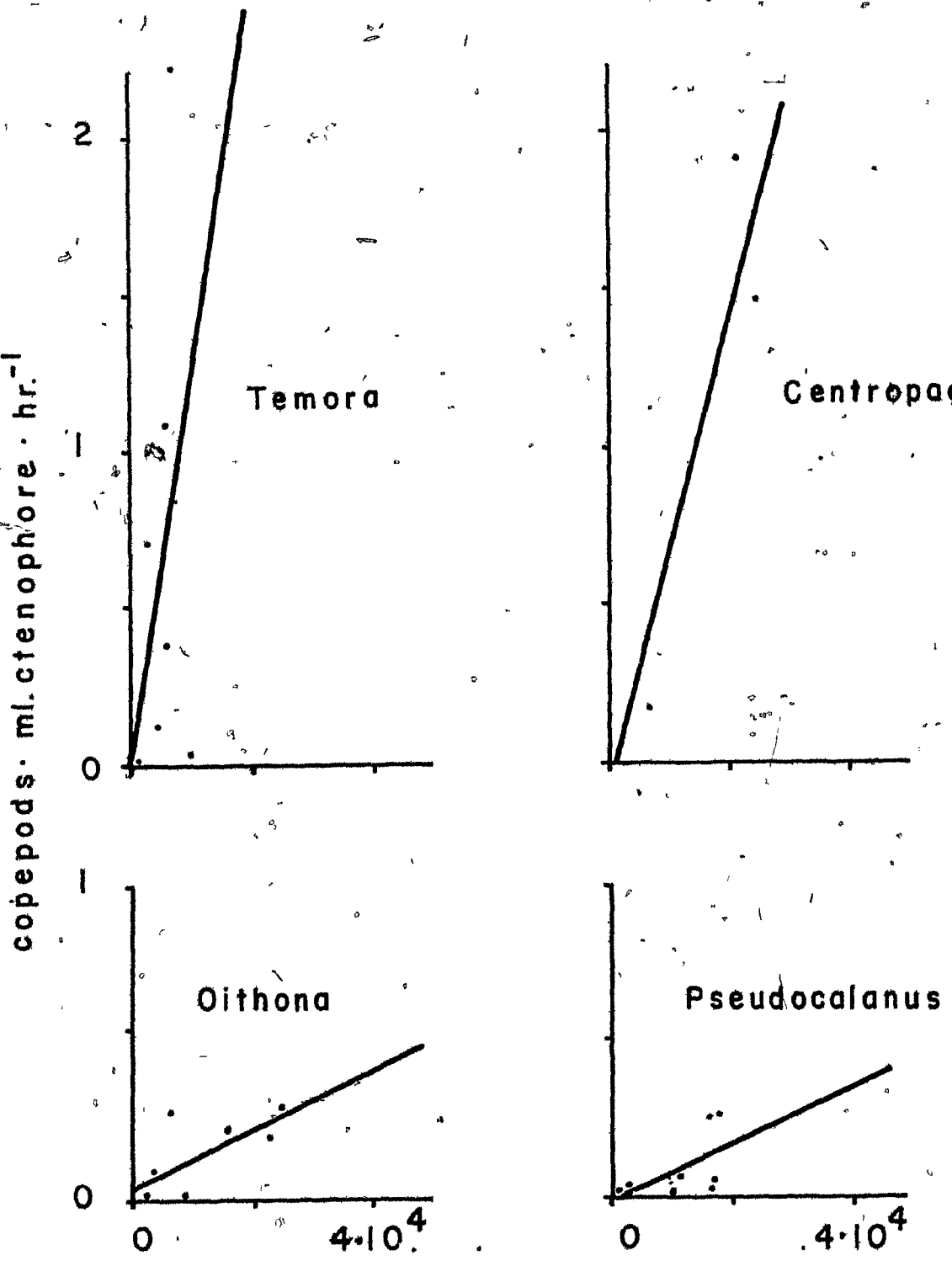

dry weight of copepods eaten by Pleurobrachia
D
g·10⁻²·m⁻²·day⁻¹
1
0
C
g·10⁻⁵
2
1
0
average dry weight, adult copepod
800
B
400
no.·m⁻²·day⁻¹
0
copepods eaten
10
A
ml m⁻²
5
0
Pleurobrachia
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct

Figure 12

Species components of the diet of Pleurobrachia. Feeding rate versus concentration of potential prey for each of the four most abundant copepodan species in St. Margaret's Bay, which are (A) Temora longicornis, (B) Oithona similis, (C) Centropages typicus and (D) Pseudocalanus minutus.


copepods · ml. ctenophore · hr.$^{-1}$
2
1
0
Temora
Centropages
1
0
Oithona
Pseudocalanus
0
$4 \cdot 10^4$
0
$.4 \cdot 10^4$

or Oithona similis. In the discussion this result will be fused with those presented below on vertical distributions and copepod swimming patterns to give a unified account of the predation of Pleurobrachia on copepods.

Vertical distributions - field studies

On 27-28 April and 11-12 May two series of vertically stratified tows were taken in order to examine the vertical distributions of ctenophores and to survey for the presence of a diurnal feeding rhythm. Three depth intervals were sampled: 60 m to 25 m, 25 m to 5 m, and 5 m to surface. Each oblique tow lasted 10 minutes at constant engine revolutions, giving a horizontal path length of 0.4 miles by radar. While the #6 net tow was preserved and the coarse net fraction processed, the sampling vessel returned to the initial position, so that tows were stacked vertically. Four such sets were taken on each day, one near dawn, one near noon, one near dusk, and one near midnight.

Examination of the data from 11-12 May showed that the species composition of the sets changed so much over the day, that a comparison between times of day would be hopelessly confused with the comparison between the populations sampled. That block of data will not be discussed further.

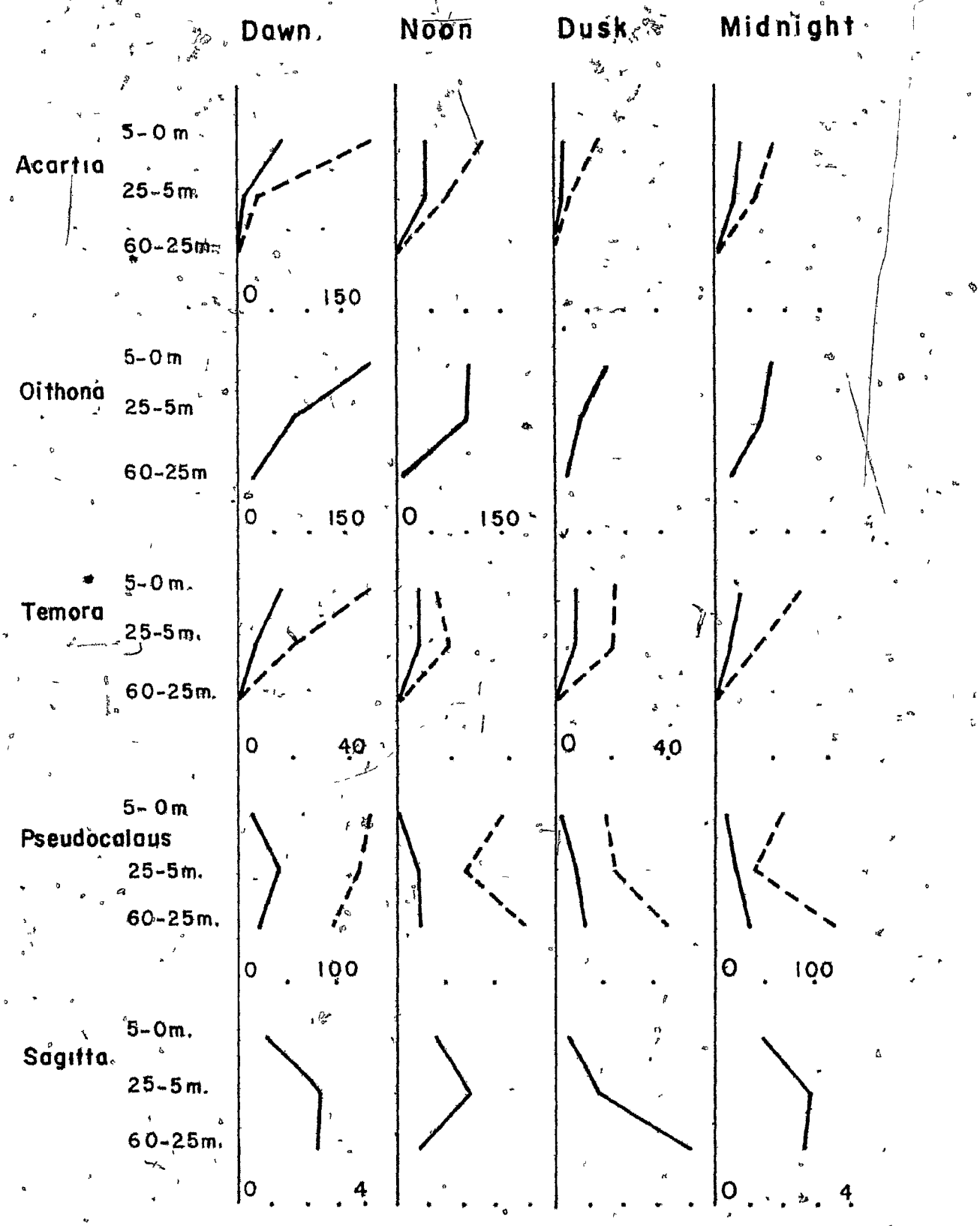
The data representing ctenophores taken on 27-28 April are shown in a condensed form in Table 5. Pleurobrachia occurred in similar numbers in the upper two samples at all times, but only one individual was found below 25 m. Bolinopsis also preferred the upper layers, although a few were found below 25 m. Figure 13 shows the vertical distributions of the four copepod species commonly taken as prey, and of a competitor with

Tow	Time	Depth, m.	Pleurobrachia		Bolinopsis	
			Number	Volume	Number	Volume
1.1	0515	65-25	0	--	0	--
1.2	0542	25-5	6	18.8	1	0.2
1.3	0608	5-0	3	10.1	0	--
2.1	1126	65-25	1	2.1	0	--
2.2	1200	25-5	4	15.1	0	--
2.3	1237	5-0	3	8.9	4	3.7
3.1	1854	65-25	0	--	1	3.8
3.2	1923	25-5	3	7.4	10	31.3
3.3	1955	5-0	5	15.9	5	14.7
4.1	1128	65-25	0	--	3	4.2
4.2	0019	25-5	6	18.3	6	22.1
4.3	0052	5-0	6	19.1	1	2.0

Table 5. Ctenophores taken in vertically stratified tows, 27-28 April, 1972.

Figure 13

Vertical distributions of the four dominant copepodan species and of Sagitta elegans at four times of day on 27 April, 1972.


Dawn
Noon
Dusk
Midnight
Acartia
Oithona
Temora
Pseudocalaus
Sagitta
5-0 m
25-5m
60-25m
0
150
40
100
4
Individuals · m.-3
adults
total

Pleurobrachia and Bolinopsis, Sagitta elegans. The representation displays the haul-to-haul variability as well as changes in vertical distributions. Acartia longiremis and Oithona similis are both surface dwelling species, but there was some indication that populations of both were displaced slightly downward at noon. Temora longicornis is also a surface species, and migrated downward during the day. The population center of Pseudocalanus was always deeper than those of the other copepods. Adult Pseudocalanus were excluded from the surface at noon but juveniles could be found there all day. At dusk many large Sagitta apparently invaded the lower sampling zone. These animals had probably lain near the bottom during daylight, as has been shown by Pearre (1970) for large Sagitta in nearby Bedford Basin.

These results show that Oithona, Temora and Acartia are continuously available to Pleurobrachia and Bolinopsis; but Pseudocalanus, particularly as adults, is not. These facts are reflected in the infrequent occurrence of Pseudocalanus in the gut contents of Pleurobrachia, and also in the lack demonstrable diurnal differences in the feeding success of Pleurobrachia. The latter assertion is supported by reducing Table 3 to Table 6, in which the observed "crop" from the guts of Pleurobrachia is compared with that which might be expected if the prey were uniformly distributed over both time and ctenophore volume. This comparison gives a non-significant χ^2 of 0.92 ($p \sim 0.8$). The hypothesis of uniform feeding rate through the day can not be rejected on the basis of these data.

Vertical distributions - laboratory studies

In the spring of 1972 and again in the spring of 1973 a series of studies was run in the Dalhousie Aquatron's 10.7 m deep tank to determine

Time	Number of Pleurobrachia Caught	Combined Volume, ml	Particles in gut	Particles / ml Pleurobrachia	Expected	(Observed-Expected)^2 / Expected
Dawn	9	28.9	25	0.865	22.2	0.353
Noon	9	26.1	17	0.651	20.1	0.478
Dusk	8	23.3	19	0.816	17.9	0.068
Midnight	12	37.4	28	0.749	28.8	0.022
Total	38	115.7	89	0.769		0.921

$\chi^2 = 0.921$; $p \sim 0.8$

Table 6. Gut contents of Pleurobrachia at four times of day on 27 April, 1971, with χ^2 test of the hypothesis that gut contents are uniformly distributed through the day. Expected values are those which would have been found had particles been distributed uniformly over volume of ctenophores.

whether ctenophores migrate vertically, and if so which stimuli control their position in the water column. The stimuli which could be manipulated were prey concentration, light, and mechanical agitation of the water. Temperature was uncontrolled; it increased through each experiment. The results for the four experiments in which there were more than 20 ctenophores are shown in Table 7. All the ctenophores used were larger than 1.0 cc and these could be seen across the 3.7 m diameter of the tank with little difficulty. At each census at least half the ctenophores in the water were counted, although counts were somewhat higher during the dark period, when the red hand-lantern was used.

In April, Pleurobrachia remained at the surface despite the application of all the available stimuli. All individuals sighted were oriented upward, and many repeatedly bumped the surface or kept their mouths appressed to the surface film. They stayed up for the full duration of the experiment, which was terminated after five days, when the surface temperature was 15° C.

In the May experiment, a few Pleurobrachia remained at the surface for one day, but thereafter the entire population was found near the bottom. Individuals of Bolinopsis distributed themselves rather evenly.

In June, both Pleurobrachia and Mertensia dove to the bottom within a few hours after their transfer to the tank. After two days, a few of each species rose to about 2 m off the bottom, but none was sighted higher.

In July, Pleurobrachia behaved as it had in May and June: it swam directly to the bottom. Bolinopsis was again available, and as in June

4 April, 1973		Shallow	Medium	Deep	Comments
5 April	0900				Fill tank at 4.0° C. Lights on 0900, off, 2100. Introduce 20 large Pleurobrachia.
	1200	12	0	0	
	1400				Add 300 m^3 plankton tow.
	2300	7	0	0	
6 April	1200	14	0	0	Twelve at surface.
	2400	5	0	0	
7 April	1200	12	0	0	Agitate surface ½ hr.
	1230	13	0	0	
	2400	6	0	0	
8 April	1200	14	0	0	Eleven at surface.
	2400	9	0	0	
9 April	1200	13	0	0	
10 April	1200	10	0	0	Ten at surface. Three had bubbles, seven in good condotion. Terminate experiment, temperature 15° C.

---

22 May, 1973 — Fill tank.

1200 — Add 25 Bolinopsis, 20 Pleurobrachia.

		Pleurobrachia			Bolinopsis			
		S	M	D	S	M	D	
	1400	10	5	0	20	0	2	
	2400	5	2	3	6	4	3	
23 May	1500	2	4	7	5	7	0	
	2400	0	0	9	3	2	4	
25 May	1500	0	0	15	4	0	8	
	2400	0	0	11	4	3	6	
26 May	1500	0	0	10	6	2	4	Terminate.

17, June, 1972

		Pleurobrachia			Mertensia			
		S	M	D	S	M	D	
	1700							Tank filled, 5.4° C.
	2100							Add 20 Pleurobrachia, 50 Mertensia.
	2200	0	3	12	6	10	13	
	2400	0	0	8	0	0	6	Some of each species on bottom.
18 June	0900	0	0	12	0	0	12	
	1500	0	0	10	0	0	9	
19 June	2400	0	0	5	0	0	7	Three Mertensia about 2 m. off bottom.
24 June	1200	Terminate experiment. Surface Temperature 17.1° C, bottom 12.3° C.						

10 July, 1972

Fill tank at 10.5° C. Lights on 0900, off 2100.

		Pleurobrachia			Mertensia			
		S	M	D	S	M	D	
11 July	1200							Add 50 Pleurobrachia, 95 Bolinopsis.
	1400	27	5	2	33	6	0	
12 July	0100	3	15	5	12	7	0	Add contents of 420 m^3 plankton tow.
	1500	0	6	11	15	6	8	
13 July	0100	0	0	10	18	5	12	
	1500	0	0	6	12	6	18	
14 July	0100	0	0	15	18	5	20	Terminate.

Table 7. Vertical distribution of ctenophores in a 10.7 m deep tank.

it occupied all three depth zones in the tank.

Two statements summarize the work on the vertical distributions of captive populations of ctenophores in the tower tank. First, none of the tested species exhibited any in-phase diurnal migrations under the conditions of these experiments. Second, Pleurobrachia seemed to switch its preferred position from the upper surface to the bottom of the tank some time between April and May.

Horizontal distributions in aquaria of ctenophores relative to their prey

This switch in behavior was also noted in laboratory experiments on horizontal distributions in aquaria, the results of which are shown in Table 8. Four runs using Bolinopsis and Beroë have been omitted because these species usually stuck in the corners of the aquaria soon after the beginning of a run. Pleurobrachia exhibited no significant deviations from random distribution between the left (nearer the prey) and right halves of the aquaria. Although the temperature was controlled at 6° C in all 6 runs and other conditions were kept constant, the proportion of animals at the bottom increased with the approach of summer.

Swimming of copepods

The photographic records of the sequential positions of copepods yielded estimates of the net swimming speeds between flashes. The data allow clear distinctions to be made between the fields of motion characteristic of the four species for which adequate records were obtained. A comparison can thus be made between the swimming of potential prey and the feeding of ctenophores.

Date	Contents of Left Chamber	Left	Right	Moved	On Bottom	Above Bottom	Total	Probability
5 April	Blank	16	19	35	10	40	50	0.37
	mostly *Temora*	18	14	32	7	43	50	0.30
6 April	Blank	18	12	30	13	37	50	0.18
	Temora, Acartia	31	24	55	32	68	100	0.21
17 May	Blank	8	12	20	19	31	50	0.25
	Eurytemora, Acartia	23	13	36	11	39	50	0.067
20 May	Blank	9	9	18	27	23	50	0.59
	Acartia	7	4	11	30	20	50	0.27
9 June	Blank	5	3	8	40	10	50	0.36
	Eurytemora, Acartia	3	1	4	44	6	50	0.31
12 June		4	3	7	42	8	50	0.38
	Total Blanks	60	58	118				
	Total Experimentals	82	56	138				

$$\chi_1^2 = 2 \cdot \frac{13^2}{69} = 2.45;\ p \sim 0.10$$

Table 8. Distribution of *Pleurobrachia* between left and right halves of aquaria. Prey are presented behind a #6 mesh screen at the left.

Figure 14 shows the two - dimensional distributions of distances and directions travelled between flashes. Only one quadrant is shown because the direction of travel could not always be deduced, and so all measurements of excursions had to be reduced to absolute values. The positions of Temora were recorded at 4.8 second intervals, with 7 flashes per exposure. The positions of the other three species were recorded at 7 second intervals, also with 7 flashes per exposure. The mean net displacements between flashes in the horizontal and vertical directions are represented as dark bars. These displacements are under-estimates of the distances travelled, for the true paths are undoubtedly curved, although they are represented here as straight lines. To the right of the scatter diagrams, but on a reduced scale, are the sequences of positions from which the data were drawn.

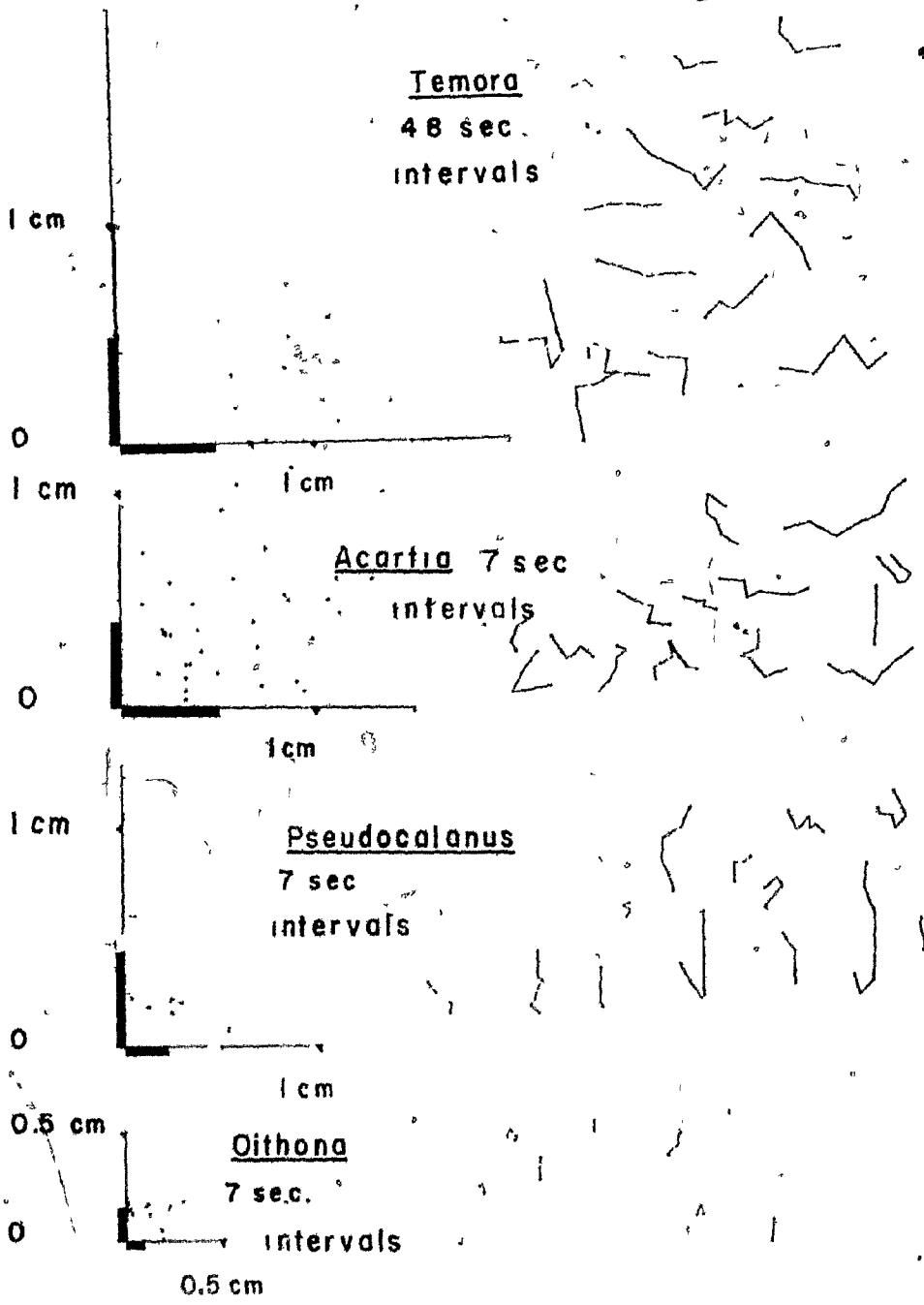
All the experiments which contributed to this section were run in March and April, 1974, at 6° C, using adult female copepods.

Temora longicornis was by far the most active species with a mean net velocity of 0.137± 0.010 cm • sec^{-1} in the horizontal and 0.101± 0.011 cm • sec^{-1} in the vertical. It swims smoothly and continously, propelled mainly by rapid strokes of the second antennae (Gauld, 1966), and its path is less recursive than those of the other three species.

Pseudocalanus minutus is also a smoothly-swimming species, but its path is quite different from that of Temora. Although it occasionally swims in loops, its undisturbed movement is usually similar to the "hop and sink" motion described by Bainbridge (1952) for Calanus. Periods of vertical ascent alternate with passive sinking. Several of these recursive movements can be seen in "J" - shaped paths in Figure 13, and

Figure 14

Swimming excursions of female Temora longicornis, Acartia longiremis, Pseudocalanus minutus, and Oithona similis. Each excursion is plotted as an absolute value, and the average horizontal and vertical components of movement are represented by dark bars. The sequences of positions from which the scatter diagrams were prepared are represented in reduced scale to the right.


Temora
48 sec.
intervals
1 cm
0
1 cm
1 cm
Acartia 7 sec
intervals
0
1 cm
1 cm
Pseudocalanus
7 sec
intervals
0
1 cm
0.5 cm
Oithona
7 sec.
intervals
0
0.5 cm

they are also reflected in the larger vertical component of velocity, 0.0614 ± 0.005 cm $\cdot$ sec^{-1} versus 0.0314 ± 0.003 cm $\cdot$ sec^{-1} in the horizontal direction.

Acartia longiremis swims in a jerky, zigzag course. The horizontal component of its motion is 0.0356 ± 0.003 cm $\cdot$ sec^{-1}, somewhat larger than the vertical component, 0.0281 ± 0.002 cm $\cdot$ sec^{-1}. Its path is not so open as that of Temora, but it contains a larger translational component than does that of Pseudocalanus.

Oithona similis swims in abrupt, discontinuous jerks. The records of its movements are not entirely satisfactory because most individuals lay passively on the bottom of the aquarium, occasionally leaping a few millimeters into the bulk water only to sink again. The few animals which did swim freely leapt upward vigorously from time to time, but spent most of their time drifting slowly downward. The net velocities measured here as 0.013 ± 0.002 cm $\cdot$ sec^{-1} in the horizontal and 0.022 ± 0.002 cm $\cdot$ sec^{-1} in the vertical probably represent mostly the sinking phase.

DISCUSSION

Importance of ctenophores in the trophic structure of St. Margaret's Bay

The central purpose of this study was achieved: a value has been calculated for the annual consumption of copepods by Pleurobrachia in St. Margaret's Bay. This value is 0.52 g of copepod dry weight per year, which may be converted to its enthalpy equivalent by multiplying by 2.29 kcal $\cdot$ g^{-1}, the average of the monthly means of caloric content of St. Margaret's Bay zooplankton reported by Platt and Irwin (1968). This product, 1.2 kcal $\cdot$ m^{-2} $\cdot$ yr^{-1} is about one fifth of the 6.2 kcal $\cdot$ m^{-2} $\cdot$ yr^{-1} which Sameoto (1972) has determined as the ration necessary to support the respiration plus production of the most important consumer of copepods in the Bay, the chaetognath Sagitta elegans. If the feeding rate of Bolinopsis were similar to that of Pleurobrachia, the two together would take about two fifths as many copepods as does Sagitta.

The feeding rate calculated here for Pleurobrachia pileus is lower than most previous estimates, and does not support the more dramatic statements about the voracious nature of the species. Bishop (1968) determined a feeding rate of 1.7 Pseudocalanus per hour for 0.4 ml Pleurobrachia bachei, which is equivalent to 4.5 copepods $\cdot$ hr^{-1} $\cdot$ ml of ctenophore $^{-1}$ at a concentration of $2.5 \cdot 10^5$ copepods $\cdot$ m^{-3}. If this concentration extended 5 m from the surface, it would have been equivalent to $1.25 \cdot 10^6$ copepods $\cdot$ m^{-2}, at which concentration my regression line gives 66 copepods $\cdot$ ml of ctenophore $\cdot$ hr^{-1}. Bishop's ctenophores were probably fed past satiation. An earlier study by Bishop (1967) on the feeding of the lobate ctenophore Mnemiopsis leidyi contains internal evidence of satiation for there is a "knee" in the plot of

feeding rate versus prey concentration at about 15 copepods $\cdot$ l^{-1} of ctenophore (see Figure 15), beyond which value feeding rate rises less rapidly with prey concentration. Greve (1970) used an initial prey concentration of $7.5 \cdot 10^5$ copepods $\cdot$ m^{-2} in his laboratory study on the growth of Pleurobrachia. This concentration is about two powers of ten higher than the general average in temperate neritic waters. He states that the results should not be applied to the calculation of feeding rates in nature.

The gut-contents method

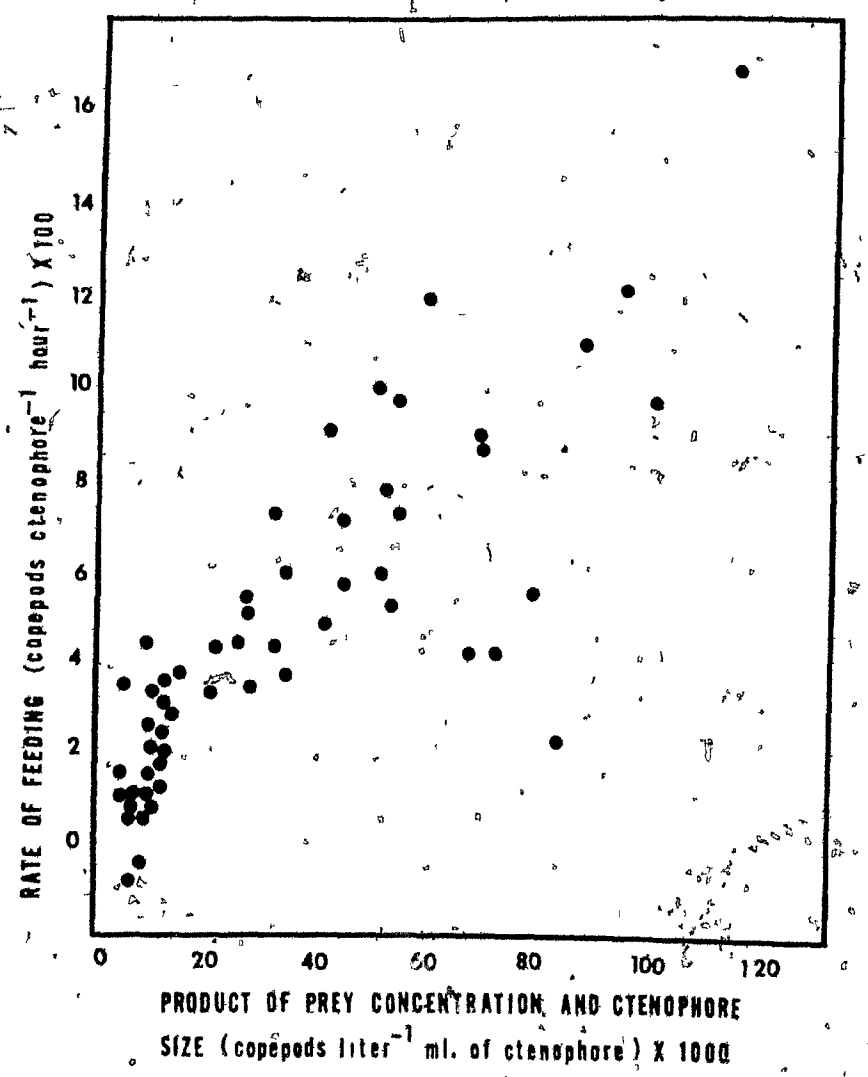
The gut-contents method has important advantages over the more usual studies of the feeding rates of zooplankton, which depend upon counting food in an experimental chamber before and after exposure to predation. The effect of confinement on animals which do not often meet solid surfaces, together with the high concentrations used in such experiments make them doubtful simulations of nature. Although Mullin (1966) has stated that most zooplankton void their gut contents upon capture, Petipa, Pavlova and Mironov, 1966, used the method extensively in their study of the food web in planktonic communities of the Black Sea. There must be many more situations to which the gut contents method is applicable. Where its assumptions can be met, it is the nearest to a completely in situ method of those which provide measures of predation and grazing. The fact that the subject species are completely free in the environment allows the interplay between their distributions in space to have its natural expression in the results.

Annual cycle of zooplankton abundances

The general cycle of the zooplankton showed several unexpected

Figure 15

Feeding of Mnemiopsis leidyi at various prey concentrations, reproduced from Bishop (1968) Figure 1.


RATE OF FEEDING (copepods ctenophore^{-1} hour^{-1}) X 100
16
14
12
10
8
6
4
2
0
0
20
40
60
80
100
120
PRODUCT OF PREY CONCENTRATION AND CTENOPHORE SIZE (copepods liter^{-1} ml. of ctenophore) X 1000

features. April, when the spring phytoplankton bloom can be expected, was a month of decreasing abundance of zooplankton. With the exception of Oithona among the dominant copepodan species, numbers remained low throughout the summer, despite the fact that the rate of primary production during the summer remains at about one third of the annual maximum. Temora showed the most marked spring decline, and it is reasonable to ascribe the decrease to predation by Pleurobrachia, whose average size and volume per tow increased as the abundance of Temora declined. Sagitta ripened and reproduced somewhat later.

The fall increase in zooplankton is remarkable, yet difficult to explain. There are at least three possible causes, of which the simplest is local production. Platt and Irwin (1968, 1970) have shown that primary production in St. Margaret's Bay often remains relatively high through the summer and fall. Nutrients are probably replenished by vertical mixing caused by the two-layered fluctuating flow which Heath (1973) has shown to be a prominent local hydrographic feature. This reciprocal flow has a period of about four days and is wind-driven; when atmospheric disturbances pass at about four day intervals the mixing effect should be particularly strong. The primary production must support at least part of the general increase in copepods between July and September. During this period the ratio of juvenile to adult copepods reaches its annual maximum, indicating active reproduction.

The second probable cause is advection. From 10 September to 17 September, 1971, the thermocline plunged from 8 m to 40 m while the surface temperature rose from 13.6° C to 15.3° C. During that period the average change in the heat content of the water column

to 60 m was +4700 cal · cm $^{-2}$ · day $^{-1}$. The average incident radiation between 1000 and 1400 on eight days in late August and September of 1968 and 1969 was 18.9 cal · cm $^{-2}$ · hr $^{-1}$ (Platt and Irwin, 1970). If the daily radiative flux into the Bay were 10 times this value, and neglecting all losses of heat, the observed gain is still 25 times greater than insolation. There must have been a large incursion of surface water, together with its plankton. At this time Centropages typicus and Paracalanus parvus both appear in significant numbers, and Temora and Pseudocalanus approach their peak abundances.

The fall hydrographic event occurs annually in St. Margaret's Bay and other bays along the coast of Nova Scotia (Sharaf El Din, Hassan and Trites, 1970; Heath, 1973). In 1967 the incursion gave way within a week to pre-existing conditions, but in 1968 and especially 1971, the change persisted for a month or more. While Heath (1973) has demonstrated the presence of two-layered surges, this lingering change must be maintained by a different mechanism for it persists after the wind stress is removed.

The third possible cause of the fall increase is release from predation. Numbers of Sagitta, the most important predator on copepods, were at an annual low in July and August. The mackerel Scomber scombrus, an abundant planktivorous fish, appears in St. Margaret's Bay in June on its northward migration. Some remain in the Bay for the summer, but the majority of the population continue northward to spawn in the Gulf of St. Lawrence. All of the fish withdraw southward in September-October (Sette, 1950; MacKay, 1967).

Time of maximum abundance of Pleurobrachia

The seasonal maximum in the abundance of Pleurobrachia in St. Margaret's Bay occurs in March-April, earlier than in the other areas for which adequate records exist. Pleurobrachia is most abundant in the Gulf of Maine in August-September (Bigelow, 1924), in Scottish waters in October-December (Fraser, 1970) and in the North Sea in May-June (Greve, 1971). Pleurobrachia bachei is most abundant off California in August (Hirota, 1973). In St. Margaret's Bay, Pleurobrachia does show a summer pulse of reproduction, but this population does not grow to large size here probably because stocks of its preferred species are low during the summer.

The fields of motion of copepods and the feeding of ctenophores

It is common practice to describe departures in ratios among food items in gut contents from the same ratios among potential prey at large in terms of Ivlev's index of electivity (Ivlev, 1961). I have not used this statistic because it implies that the predator or grazer makes a choice between equally available food items. This study investigates differential availability; it attempts to demonstrate that feeding rates in ctenophores are a consequences of the spatial strategies of potential prey.

The feeding success of ctenophores on different species of copepods in the natural mixture can be related to the vertical distributions and swimming patterns of the copepods. It is especially clear that this should be so for Pleurobrachia, which depends on the activity of its prey to effect captures. The feeding rate of Pleurobrachia should be given by the product of the area of capturing net and the flux of copepods. If

measurements were available of this net area and of the excursions of copepods over time intervals sufficiently long that their initial and final directions were uncorrelated, it would be possible to predict the collision rate of predator and prey. In the absence of such measurements some insight can be gained from a comparison of the shorter term excursions of copepods with their relative capture rates.

Pleurobrachia is a resident of the upper water layers and has little opportunity to prey upon Pseudocalanus, whose population center of mass lies deeper. The small-scale motions of Pseudocalanus are mostly vertical and its path doubles back on itself, further reducing the probability of capture by Pleurobrachia. These behavioral attributes account for the small role of Pseudocalanus in the diet of Pleurobrachia.

Members of the genus Calanus also swim in the "hop and sink" pattern, and they were not found in Pleurobrachia guts in St. Margaret's Bay, where they were at times moderately abundant. This observation contrasts with that of Fraser (1970) who found Calanus spp. to be the second most frequent item in Pleurobrachia guts, and the dominant one by volume. Calanus is more abundant in the more oceanic waters around Scotland than in St. Margaret's Bay, and this may account for a part of the discrepancy. In addition, some of the Calanus in Fraser's samples may have been eaten while the plankton were concentrated in the net or in a jar awaiting preservation.

The swimming pattern of Temora contrasts strongly with that of Pseudocalanus. It is more open and much faster, especially in the horizontal direction. Temora stays in the upper waters with Pleurobrachia, which captures it much more frequently relative to its abundance than

any of the other potential prey except Centropages. Greve (reported in Conover, 1970) found Pleurobrachia and Temora to be strongly interactive in the North Sea. Temora is also a favorite food of Sagitta, whose hunting strategy seems to be to wait motionlessly for prey to pass, when the vibrations of the prey trigger the feeding response, as Horridge and Boulton (1967) have shown for Spadella. Temora's swimming pattern exposes it to large volumes of water, and thus more prey but also more predation.

Centropages is also a very active omnivorous species which inhabits the surface layers. Although I have no quantitative measurements of its swimming, it appears to have a large horizontal component of motion and an open path. Pleurobrachia catches Centropages with a frequency relative to its abundance similar to that for Temora.

Acartia has a horizontal mean velocity about one half that of Temora. It is a surface animal and is caught by Pleurobrachia at a rate intermediate between those for Temora and Pseudocalanus.

Oithona was particularly inactive in the laboratory experiments, and it is less frequently caught by Pleurobrachia than are any of the other common copepodan species. It forms, however, the largest fraction of the diet of Bolinopsis. Bolinopsis seeks out its prey rather than waiting for it, but is a slow swimmer. It is probably the passivity of Oithona which makes it available to Bolinopsis.

The swimming patterns of copepods can be divided tentatively into two groups. The true filter feeders, Pseudocalanus and Calanus, have recursive paths. This pattern has been described as "lingering" in Cladocera by Strickler (1969). The encounter feeders and carnivores, Acartia, Temora, Centropages and Tortanus, exhibit increasingly open and

rapid swimming in the approximate order of the proportion of larger particles in their diets.

The most general conclusion which can be drawn from this study on the feeding of ctenophores is a fortuitous one. It is that the behavior of individual planktonic species, in this example the field of motion of copepods, exerts a decisive force in directing the flow of energy among the paths of the trophic network.

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APPENDIX

This section is a list of the numbers per sample of the common species of copepods, plus Sagitta elegans and Cladocera. Only those samples are included which were used in the calculations. For some dates, the average value for stations 4, 5 and 6 was obtained manually by pooling equivalent splits from each of the three samples. These columns of data are headed "pool".

Key to abbreviations

a	adult
Ac. claus.	Acartia clausi
Ac.long.	Acartia longiremis
Cal. fin.	Calanus finmarchicus
Cal. glac.	Calanus glacialis
Cal. hyp.	Calanus hyperboreus
Cent. typ.	Centropages typicus
Cent. ham.	Centropages hamatus
Euryt.	Eurytemora herdmani
J	juvenile
Metridia	Metridia longa plus Metridia lucens
Oithona p.	Oithona plumifera
Oithona s.	Oithona similis
Paracalanus	Paracalanus parvus
Mic. pus.	Microcalanus pusilus
Pseu'cal	Pseudocalanus minutus
Sagitta	Sagitta elegans
Tort. disc.	Tortanus discaudatus

Date	29 Oct	9 Nov	26 Nov	11 Dec			12 Feb		
Station	pool	pool	pool	4	5	6	4	5	6
Pseu'cal. j	7,500	6,300	2,800	10,000	11,000	18,700	2,600	6,300	1,800
Pseu'cal. a	6,800	6,100	5,900	7,900	12,000	11,300	8,300	14,300	7,000
Temora j	300	900	500	1,800	1,500	500	–	100	–
Temora a	1,700	1,800	1,500	7,200	7,200	3,100	5,200	4,400	1,280
Ac: long. a	–	700	500	2,300	500	300	100	30	100
Ac. claus.a	–	–	1,300	–	–	500	–	30	–
Acartia j	–	500	300	–	–	–	–	–	–
Oithona s.	1,400	2,500	3,800	4,600	5,900	16,900	3,300	6,900	1,800
Oithona p.	300	–	300	–	–	300	–	–	–
Cent. typ.a	8,500	8,700	6,900	3,600	4,100	3,300	–	–	–
Cent. ham.a	6,500	4,100	300	–	–	–	–	–	–
Cent. j	8,500	7,800	8,700	4,900	2,600	5,300	–	–	–
Paracalanus	1,700	1,100	300	–	–	–	–	–	–
Metridia	–	–	–	60	200	30	–	30	4
Cal. fin.IV-VI	–	100	700	1,000	700	1,000	30	20	30
Cal. glac. IV-VI	–	–	–	–	–	–	20	–	–
Cal. hyp. IV-VI	–	–	–	–	–	–	–	–	–
Calanus j	–	–	–	–	–	–	–	800	–
Tort. disc.	–	–	–	–	–	300	20	30	10
Cladocera	700	–	–	–	–	–	–	–	–
Sagitta 1.5	30	680	1,100	–	–	–	100	100	40
Sagitta 1.5 Euryt.	90 300	60 –	60 –	300 –	300 –	500 –	100 –	150 –	200 –

Date		12 Mar			25 Mar			8Apr		
Station		4	5	6	4	5	6	4	5	6
Pseu'cal.	j	900	1,000	1,500	3,600	1,300	2,000	6,700	4,000	5,900
Pseu'cal.	a	700	1,800	2,700	–	500	1,000	2,000	800	2,400
Temora	j	–	–	–	–	100	–	200	–	–
Temora	a	–	60	100	–	–	–	–	–	–
Ac.long.	a	100	–	–	–	–	–	–	–	–
Ac. claus.	a	–	–	–	–	–	–	–	–	–
Acartia	j	200	60	–	–	–	100	500	400	100
Oithona s.		8,400	6,800	14,100	20,200	8,600	17,000	12,500	12,900	13,600
Oithona p.		–	–	–	–	–	–	–	–	–
Cent. typ.	a	–	–	–	–	–	–	–	–	–
Cent. ham.	a	–	–	–	–	–	–	–	–	–
Cent.	j	–	–	–	–	–	–	–	–	–
Paracalanus		–	–	–	–	–	–	–	–	–
Metridia		–	–	–	300	–	–	–	–	–
Cal. fin.	IV-VI	20	10	20	20	20	10	10	30	40
Cal. glac.	IV-VI	–	–	20	30	10	–	–	–	–
Calanus	I-III	–	60	–	–	–	–	–	200	500
Tort. disc.		20	–	10	–	–	–	–	–	–
Euryt.		–	–	–	–	–	–	–	–	–
Mic. pus.		–	–	–	700	–	300	–	–	–
Cladocera		–	–	–	–	–	–	–	–	–
Sagitta	1.5	80	100	140	100	60	50	10	10	30
Sagitta	1.5	180	140	120	200	230	160	100	170	100
Cal. hyp.	IV-VI	–	–	–	10	10	–	–	4	–

Date		23 Apr			7 May			21 May		
Station		4	5	6	4	5	6	4	5	6
Pseu'cal.	j	4,600	2,400	2,400	3,900	4,300	17,200	2,500	2,900	2,300
Pseu'cal.	a	3,800	2,900	1,800	1,800	500	2,800	200	600	600
Temora	j	1,300	3,100	2,300	400	400	1,200	100	100	100
Temora	a	500	–	300	–	60	–	–	–	
Ac. long.	a	–	–	–	–	–	100	100	400	200
Ac. claus	a	–	–	–	–	–	–	–	–	–
Acartia	j	–	–	–	–	–	–	100	200	100
Oithona s.		13,800	5,800	4,300	6,800	4,800	7,800	2,900	3,700	3,800
Oithona p.		–	–	–	–	–	–	–	–	–
Cent. typ.	a	–	–	–	–	–	–	–	–	–
Cent. ham.	a	–	–	–	–	–	–	–	–	–
Cent. J		–	–	–	–	–	–	–	–	–
Paracalanus		–	–	–	–	–	–	–	–	–
Metridia		–	–	–	–	–	–	–	–	–
Euryt.		–	–	–	–	–	–	–	–	–
Cal. fin.	IV-VI	60	20	70	–	–	–	100	200	60
Cal. glac.	IV-VI	–	–	–	20	160	180	90	240	80
Cal. hyp.	IV-VI	–	–	–	30	30	40	10	110	70
Calanus	I-III	3,600	2,200	400	1,500	3,000	3,700	500	800	1,600
Tort. disc.		–	–	10	–	–	–	–	–	100
Mic. pus.		–	–	–	–	–	–	–	–	–
Cladocera		–	–	–	–	–	–	–	–	–
Sagitta	1.5	10	30	20	20	–	20	50	150	20
Sagitta	1.5	150	260	140	180	150	120	70	190	90

Date		4 Jun			18 Jun			16 Jul		
Station		4	5	6	4	5	6	4	5	6
Pseu'cal.	j	4,000	1,200	1,900	1,500	4,100	2,000	4,000	5,600	4,700
Pseu'cal.	a	300	100	400	600	1,000	500	1,500	3.600	1,700
Temora	j	100	100	100	900	1,400	1,800	2,800	2,000	1,200
Temora	a	–	–	30	400	600	1,000	600	1,300	600
Ac. long.	a	–	100	–	–	100	700	800	1,000	600
Ac. claus	a	–	100	100	200	–	300	–	500	–
Acartia	j	100	100	100	–	200	300	–	300	600
Oithona s.		10,000	5,900	6,900	9,900	9,900	7,700	9,600	10,000	8,700
Oithona p		–	–	–	–	–	–	–	–	–
Cent. typ.	a	–	–	–	–	–	–	–	–	–
Cent. ham.	a	–	–	–	100	–	–	–	–	–
Cent.	j	–	–	–	–	–	–	–	–	–
Paracalanus		–	–	–	–	–	–	–	–	–
Metridia		–	–	–	–	–	–	–	–	–
Euryt.		–	–	–	–	–	–	–	–	–
Cal. fin. IV-VI		–	–	10	90	110	100	30	40	20
Cal. glac. IV-VI		20	10	10	–	–	–	–	–	–
Cal. hyp. IV-VI		10	–	10	–	–	–	–	–	–
Calanus I-III		4,000	200	400	100	100	–	600	1,000	600
Tort. Disc.		–	–	60	–	–	–	–	–	–
Mic. pus.		–	–	30	–	–	–	–	–	–
Cladocera		–	–	–	4,000	–	–			
Sagitta 1.5		440	200	400	380	2,200	3,300	140	130	90
Sagitta 1.5		10	–	60	–	–	–	–	–	–

Date		13 Aug			26 Aug			17 Sep	
Station		4	5	6	4	5	6	5	6
Pseu'cal.	j	31,200	12,800	52,700	93,200	50,400	87,600	63,500	50,200
Pseu'cal.	a	21,500	13,800	29,700	45,600	28,200	36,600	148,500	123,900
Temora	j	5,100	4,100	12,300	6,700	5,400	8,700	10,200	2,000
Temora	a	2,000	3,100	4,600	7,700	2,600	7,700	30,700	18,400
Ac. long.	a	500	500	–	2,600	1,500	2,800	6,000	8,000
Ac. claus.	a	–	–	–	–	–	1,300	–	–
Acartia	j	3,500	2,000	2,500	500	1,000	1,800	7,000	1,000
Oithona s.		16,400	10,200	23,000	21,400	13,600	22,300	42,000	27,700
Oithona p.		2,000	–	–	–	–	–	–	–
Cent. typ.	a	–	1,000	1,000	500	–	–	3,000	3,000
Cent.ham.	a	–	500	–	–	–	–	–	–
Cent.	j	–	–	–	500	–	–	1,000	–
Paracalanus		–	–	–	–	–	–	1,000	2,000
Metridia		–	–	10	30	10	20	–	–
Euryt.		500	–	–	–	–	300	–	–
Cal. fin. IV-VI		130	80	140	400	160	430	290	130
Cal. glac. IV-VI		–	–	–	–	–	20	–	–
Cal. hyp. IV-VI		–	–	–	10	–	–	–	–
Calanus I-III		1,000	500	3,100	–	500	1,300	–	–
Tort. disc.		10	10	–	–	–	300	60	–
Mic. pus.		–	–	–	–	–	–	–	–
Cladocera		24,600	17,900	19,500	2,600	4,100	1,000	33,800	7,200
Sagitta 1.5		80	130	80	260	280	350	1,100	1,100
Sagitta 1.5		–	10	20	20	–	30	50	20

Date		25 Oct.		
Station		4	5	6
Pseu'cal.	j	4,300	800	7,200
Pseu'cal.	a	12,300	10,500	10,200
Temora	j	800	300	1,000
Temora	a	3,300	2,300	2,600
Ac. long.	a	800	–	1,000
Ac. claus	a	–	–	–
Acartia	j	300	–	1,500
Oithona	s.	12,500	16,600	27,700
Oithona	p.	–	300	1,000
Cent. typ.	a	14,100	13,800	11,300
Cent.ham.	a	–	–	–
Cent.	j	6,100	4,100	3,100
Paracalanus		5,400	7,800	5,100
Metridia		–	10	30
Euryt.		–	–	–
Cal. fin.IV-VI		160	140	140
Cal. glac. IV-VI		–	–	–
Cal. hyp. IV-VI		–	–	–
Calanus I-III		–	–	–
Tort. disc.		–	10	10
Mic. pus.		–	–	–
Cladocera		500	–	–
Sagitta	1.5	140	210	400
Sagitta	1.5	10	10	20