

A STUDY OF SURFACE ZOOPLANKTON
IN THE CARIBBEAN SEA OFF
JAMAICA.

by

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INTRODUCTION

Despite the tremendous amount of work that has been published on productivity and plankton studies in the North Atlantic and Arctic oceans, investigations in the tropics have been almost entirely restricted to material obtained by research vessels during transects and short cruises, and previous to 1949, there was no long-term undertaking to observe seasonal changes at any one place. The deductions possible from comparison of results from stations spread over wide geographical areas and cruises in different seasons and years, yield a limited picture with large gaps. The problem is rendered even more acute because of the heterogeneity of methods used in these investigations. These facts point up the need for more extensive detailed sampling, and the employment of methods that at least contain some common factor by which comparisons can be easily effected. These are some of the ideas presented by Riley et al (1949) in the preface to a treatise on the quantitative ecology of the plankton of the Western North Atlantic. Their work was an attempt to fill in some of the gaps, co-ordinate and expand knowledge of the conditions affecting production in the tropical and subtropical North Atlantic.

The limited literature then available included the reports on exploration of fauna of the Gulf Stream by Agassiz (1833), the pioneer studies of plankton and hydrography conducted by Bigelow

(1915, 1917 et seq) in the Gulf of Maine and waters adjacent to the northeast coast of the United States; reports on the investigation of the Great Barrier Reef by Farran (1936), Orr (1933), Russell and Colman (1934); studies on the plankton of the Sargasso Sea by Coe (1936) and Riley (1939); the increasing richness of offshore-inshore plankton in the Atlantic by Clarke (1940) and observations on the seasonal distribution of the plankton of the Trivandrum by Menon (1945).

Since then information on tropical hydrographical conditions and plankton abundance and interrelationships have been steadily increasing both in detail and extent. Yet much of the investigation is still centered around the subtropical and near-temperate oceanic regions on the American side of the Atlantic. Moore (1949), Sutcliffe (1960), Hulburt et al (1960), Menzel and Ryther (1960a, 1960b, 1961), Grice and Hart (1962), Deevey (1964), have concentrated efforts on determining nutrient chemistry, primary production, zooplankton composition and cycles in the Sargasso Sea. Lewis (1954), Bsharah (1957), Woodmansee (1958), Owre (1960), Owre and Foyo (1964a) have worked on the zooplankton of the Florida current and some Florida keys. In other areas King and Demond (1953) made studies of the zooplankton abundance of the central Pacific; Hart (1953) on the plankton of the Benguela current; Kohn and Helfrich (1957) on primary organic productivity of a Hawaiian coral reef; Halse (1959) on quantitative aspects of phytoplankton from the equatorial Pacific; Björnberg (1963) on the free living copepods off Brazil and Owre and Foyo (1964b) on a collection of copepods from the Caribbean Sea.

It is generally maintained that production in tropical seas is relatively low and characterised by a more even seasonal distribution

than in higher latitudes, but there are doubts about the total annual size of the production. To quote from Hesse, Allee and Schmidt (1951), "Whether the entire years production of the polar seas is greater than that of the tropics cannot yet be stated with certainty. Hansen is inclined to believe that it is but his evidence is inconclusive". Raymont (1963) believes that production in the tropics considered on a yearly basis may be considerably greater than it would appear at first sight, since the nutrients are more rapidly regenerated at the higher temperatures of tropical regions and thus pass through several cycles during the course of a year. He also states that the factors responsible for the fluctuations in total plankton and for the seasonal breeding of plankton species in tropical waters are difficult to elucidate.

These large areas of doubt and speculation need to be resolved. But knowledge of biological production in the Caribbean seas is even more seriously limited. There are very few and scattered direct determinations of productivity in this area (Steven, Beers, Lewis, (1965); (Steeman Nielson, 1957). On the other hand there is a fairly considerable amount of information on the hydrography and nutrient chemistry of the western tropical North Atlantic and Caribbean sea resulting from the investigations of Jacobson (1929), Iselin (1936), Böhnecke (1936), Rakestraw and Smith (1937), Parr (1938), Seiwel (1938), van Andel and Postma (1954), Barnes (1957), Richards (1958 and 1960), Fuglister (1960), Gade (1961) and Lewis, Brundritt and Fish (1962). These workers have done much to elucidate the physical oceanographic characteristics of these areas, including water movements and origins as well as certain aspects of their chemistry. This sort

of information provides a very good background and reference source for a project aimed at determining quantitative transformation of energy and matter in these areas.

A study of primary productivity in the Caribbean Sea off Jamaica was carried out by Steven between March 1962 and March 1964. Results of this study are contained in a report to the Biology Branch of ONR (1965). In conjunction with the measurements made for the primary productivity determination, surface zooplankton tows were made at each station in order to study the relationship between phytoplankton and zooplankton levels. This joint effort represents the first attempt at getting a comprehensive picture of production at the various trophic levels in this area.

When work was started on the zooplankton studies in September 1963 approximately one half of the monthly collections had already been made. The collections are unique, in that they represent a serial set of samples taken from specific areas over a two year period during which other data relating to productivity were also being determined. This situation presents opportunities for extracting information dealing with long term variations in production at each locality and in particular "on the importance of seasonal climatic variables which might be expected to affect both the low and high productivity waters in a similar manner" (Steven, 1965). This thesis is therefore largely a descriptive discourse on the results of physical measurements and observations made on these collections with the following aims in view :

- a) to determine the composition of the epizooplankton in the areas chosen for study.

- b) to determine the extent, if any, of seasonal climatic variations on the zooplankton.
- c) to elucidate some of the factors responsible for the fluctuations in total plankton and the breeding cycles of some of the plankton species in these tropical waters.
- d) to establish, if possible, relationships between primary and secondary production.

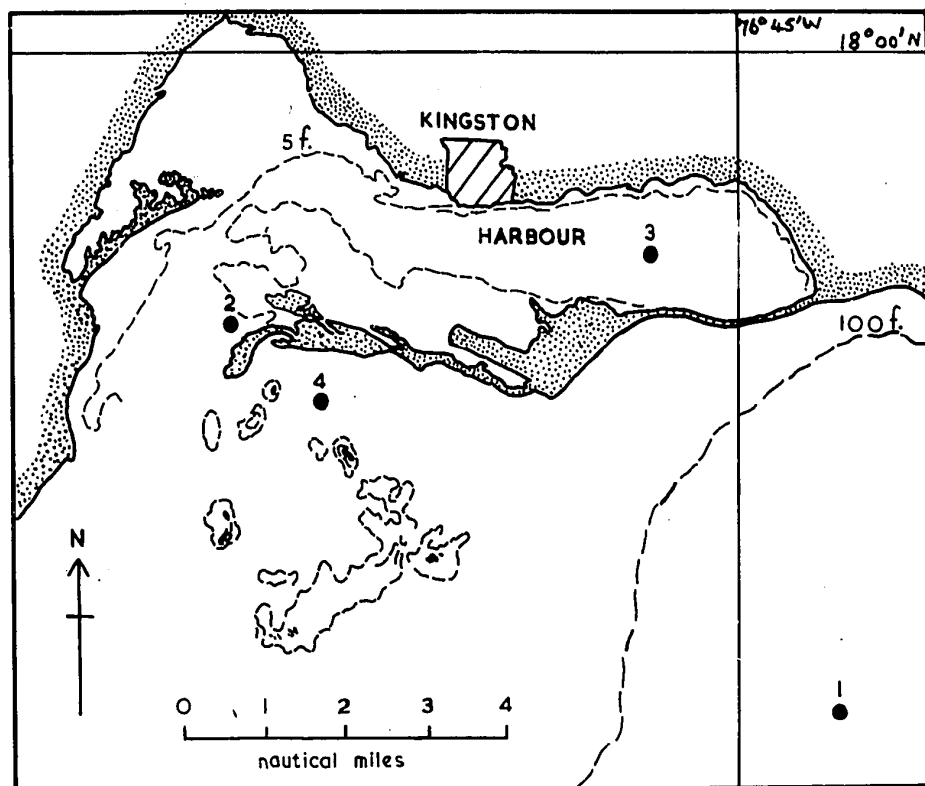


Fig. 1. Map of Kingston harbour and Caribbean sea showing location of stations.

Description of stations.

The stations selected for study are shown in Fig. 1. Kingston harbour is situated on the south coast of Jamaica. Its north shore is dominated by the city of Kingston with its attendant docks and industrial plants. East and west it is bounded by the mainland mass and on the south it is separated from the open sea by a narrow strip of land seldom more than a tenth of a mile across, except at Palisadoes airport. This configuration constitutes an extensive natural harbour 10 miles long and about 1.75 miles wide along most of its length. The harbour mouth lies at the south western corner and though this is about 2 miles wide at the surface, the island shelf extending inwards leaves only a narrow ship channel one-eighth of a mile across and drawing no more than 20-25 m of water, but this widens out in the eastern harbour basin to a relatively uniform depth (30-40m) across most of its width. In the north eastern corner there is a shallow arm of the harbour, Hunts Bay, roughly 2.25 miles long and 2 miles wide. Into this basin, the two rivers - Rio Cobre and Ferry - discharge themselves.

The island shelf slopes off very gently, and in the region of the coral reefs and cays is 30-35 m below the surface. At the 60 m contour this incline terminates at a sheer underwater cliff about 300-400 m deep. From the base of this cliff the ocean floor falls away more gradually (Fig. 2).

Station 1J is situated about 3 miles seaward from this cliff at latitude $17^{\circ} 51.7' N$ and longitude $76^{\circ} 42.9' W$, bearing 6 nautical miles SSE of station 3J. Depth of water here is approximately 900 m.

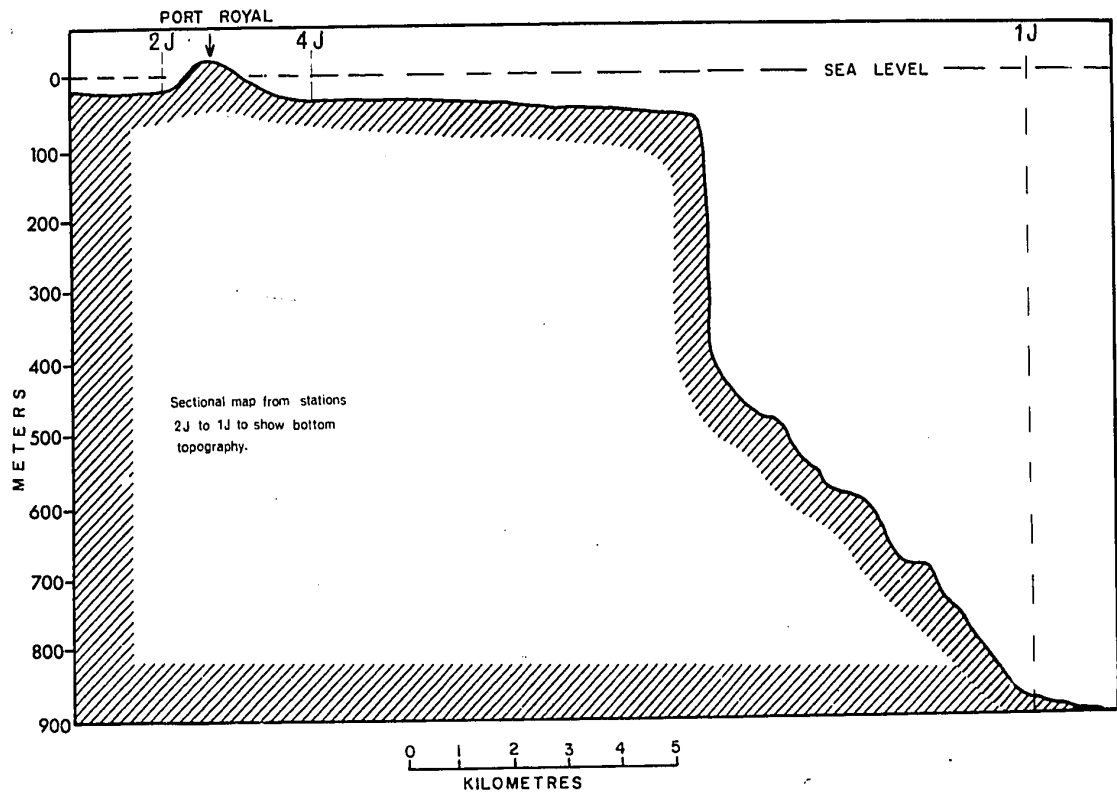


Fig. 2. Depth profile of three of the stations.

Station 4J is situated at latitude $17^{\circ} 55.5' N$ and longitude $76^{\circ} 49.7'$

W in about 35 m of water in the region of the coral reefs and cays.

Station 2J situated just inside the mouth of the harbour at latitude $17^{\circ} 56.4' N$ and longitude $76^{\circ} 50.5' W$, is supported by a water column 15-18 m and is the only area where extensive surface interchange occurs between the harbour waters and the open sea.

Station 3J is situated at latitude $17^{\circ} 57.3' N$ and longitude $76^{\circ} 45.5'$

W in the eastern basin of the harbour midway between Palisadoes road and the mainland. Depth here is approximately 20 m.

Temperature : The ranges of temperature of the surface waters in the several areas of study are small in comparison with conditions encountered in coastal and offshore waters in higher latitudes. Generally the differences between high and low temperatures during two years of observations did not exceed $4^{\circ}C$ and this represents the extent of seasonal difference between "midsummer" and "midwinter". Temperature differences from station to station were also slight as shown by the figures given below.

TABLE 1. Annual variations in temperature and salinity at the four stations.

<u>Station</u>	<u>Temperature $^{\circ}C$</u>	<u>Salinity %.</u>
1J	$26.3^{\circ} - 29.8^{\circ}$	35.22 - 36.22
4J	$27.2^{\circ} - 30.6^{\circ}$	34.56 - 36.25
2J	$27.2^{\circ} - 31.5^{\circ}$	34.40 - 36.20
3J	$27.1^{\circ} - 30.6^{\circ}$	*34.20 - 36.40

* See next page, line 20.

Salinity : As with temperature, variations in salinity from station to station were very small, as reference to the table above will show. Of the four stations 1J maintained the most constant conditions while 3J showed the widest range (2.20%).

Rainfall : The annual average rainfall at Palisadoes Airport (based on data collected from 1942-1957) is 780 mm. and the bulk of this is distributed between the two principal rainy seasons in April to May and September to October; but considerable variations may occur from year to year. Outside of the rainy seasons the flow of the rivers is limited and does not normally reduce the salinity of the harbour below 34‰, and even though there is considerable overflowing during the rainy seasons, salinity determinations throughout the harbour and observations from high ground of the turbid waters (Goodbody, 1961) both indicate that the flood waters usually flow along the western side of the harbour out to sea and do not circulate around the harbour to any great extent. Salinity in the eastern end of the harbour is only seriously affected when heavy rainfall is concentrated over a few days as for example, during the hurricane Flora rains of October 1963 when salinity at the 3J stations was reduced to *30.00‰ for a few days.

Tidal changes are diurnal and normally show a difference of no more than 15 cm. The greatest difference in height at the spring solstice is 30 cm (12 inches).

Water exchange : Water exchange between the open sea and the eastern end of the harbour is extremely limited. It is believed that there must be a bottom current travelling west to east along the ship channel

and upwelling somewhat east of 3J to replace surface water that is blown across the harbour by the prevailing easterly wind and which finds its way out of the harbour in a counter clockwise direction.. It was assumed that at this station, as well as at stations 2 and 4J, because of shallowness and lack of thermal stratification, the water was mixed from top to bottom and a sample from 5 metres characterised the whole water column. At 1J, however, there is, apparently, permanent thermal stratification. A shallow thermocline between 100-200 m and a temperature difference of 3-6° (Steven, 1965), prevented vertical mixing with the relatively nutrient-rich deeper waters.

Transparency : At 1J the water was always tropical-sky blue in colour, at 4J blue-green, but at 2J visibility varied considerably. Sometimes the water was of a dirty green colour with low visibility while at other times, presumably because of the influx of open sea water, visibility extended to the bottom. At 3J the water was generally turbid and greenish in colour. From Secchi-disc readings recorded by Steven and given in Table 2 it can be seen that 2J had the lowest mean visibility and 3J the second lowest while the upper lens of the water increased in depth with distance from the harbour. At 1J the mean depth of transparency was approximately four times as great as the mean depth in the harbour. The conditions at 1J were considered representative of oceanic Caribbean water in the area. On the basis of the above written description, the stations were classified as follows :

1J - offshore or oceanic

4J - island shelf

2J)
) - harbour
 3J)

TABLE 2.

Secchi-disc readings arranged to show variations in
 visibility and mean extinction coefficient 'K'.

Station	1J	4J	2J	3J
	20.50 m	7.00 m	3.50 m	4.50 m
	22.00	9.00	3.50	4.50
	22.50	11.00	4.50	4.50
	23.00	12.30	4.50	6.00
	27.00	13.00	5.00	6.50
	28.00	13.50	5.75	6.75
	28.50	19.50	6.75	7.25
	29.50	22.00	7.00	7.50
	31.75	23.00	7.50	8.00
	39.50	23.50	9.00	8.00
	40.00	24.00	9.00	9.00
				10.50
				12.50
				14.50
Mean	28.38 ± 1.87	16.16 ± 1.79	$6.00 \pm .57$	$7.80 \pm .75$
Mean 'K'	.05	.10	.28	.21

MATERIALS AND METHODS

Collection of samples.

The materials used in this study are all surface samples collected between 0-5 m. The tows were made with a .5 m diameter no. 8 plankton net with a mesh aperture 0.203 mm (86 meshes/inch). Station 1J was occupied on 26 occasions between March 2, 1962 and March 18, 1964. Stations 2, 3 and 4J were occupied on 26 occasions between July 19, 1962 and July 29, 1964. (The stations were numbered in order of first occupation and do not represent a serial order on the map). Samples from 2, 3 and 4J were always collected the same day between 9-12 a.m. Owing to distance, 1J collections were made on another day at about 10:30 a.m. The tows at 1J and at 4J, except on three occasions, were always of 15 minutes duration. At 2J and 3J, however, the nets were often clogged with phytoplankton after only 5 minutes towing, hence the tows were of shorter duration than 15 minutes. From the 3rd February onwards all tows were metered with a G.M. Flow-meter mounted in the mouth of the net.

In order to understand more fully the value of the no. 8 net day surface plankton the following additions were made :

a) Duplicate samples were taken and used to test the replicability of the sampling.

b) On several occasions tows were made with a no. 97* net in order to compute the abundance of smaller forms and younger stages

* = 97 meshes/inch.

that might escape the larger mesh. This provided a good reference to the relative abundance of large and smaller forms.

c) Some night collections were made. These served to determine the question of the extent to which the day surface plankton was representative of total plankton both quantitatively and qualitatively.

d) To supplement observations made on preserved material, special collections were made and examined live. Drawings from these helped greatly in the identification of some specimens, especially of the siphonophores.

Preservation.

The samples, usually of about 1 litre volume but sometimes of 2-3 litres, were fixed with neutralised formalin immediately after collection. Enough formalin was used to bring the liquid to a 5% strength, and this was allowed to stand for at least 24 hours.

Investigations.

All the samples were used first for volume determinations, and from each whole sample small aliquots were taken for counting and identification. Dry weight measurements were done on larger aliquots and the remaining portions of the sample kept for re-determinations where necessary, and as a general reference stock. All quantitative measurements were reduced to average values per unit volume of seawater filtered.

Volumetric determinations.

Supernatant fluid from the sample was drained off by suction. In order to minimise errors caused by retention of water between the

animals, suction was maintained long after the last bubble appeared. The volume of plankton was estimated by the 'Yentsch and Hebard' method, using a G.M. no. 024WA130 plankton volume gauge which had been calibrated previously. Determinations were done on whole samples from 1J and 4J but at 2J and 3J they were usually done on duplicate aliquot subsamples since these volumes were generally too large to be treated as a whole. The samples were then stored in bottles with known volumes of 2% neutralised formalin. Samples from 2J and 3J often contained a high percentage of phytoplankton and debris and large numbers of medusae. The medusae were first removed by straining through a coarse sieve and their volume was determined separately. Separation of zooplankton from phytoplankton was achieved by washing under slight pressure through two thicknesses of no. 8 silk net in a Buchner funnel. The diameter of the silk circles was made approximately 1" greater than that of the funnel in order to avoid over-flushing, and the filtrate from these washings was checked periodically to ensure against loss of zooplankton through the meshes.

Table 3 shows the displacement volumes obtained at the various stages of the procedure and also indicates the high percentage contribution of medusae and phytoplankton. The corrected or final volumes, however, still represent in some instances, zooplankton plus detritus for which no successful means of separation was achieved. Johannes Krey (1960) has suggested several ways of estimating detritus, but very often zooplankton and detritus were so closely bound up in lumps as to defy all practicable means of separation. The method of running sample tests on various species, and estimating total

TABLE 3.

Volumes obtained at various stages of separation.

Station	Date	Crude Vol.	Medusae	Phytoplankton	Zooplankton
3J	19/7/62	429.40 cc	70.00 cc	163.40 cc	196.00 cc
3J	28/3/63	562.64	6.20	158.44	398.00
3J	24/4/63	295.78	70.20	46.88	178.70
3J	1/8/63	89.21	-	54.51	34.70
3J	23/8/63	95.91	-	42.41	53.50
3J	23/3/64	36.77	-	12.17	24.60
3J	28/5/64	255.64	15.00	74.14	165.50
2J	3/12/62	31.40	6.20	9.00	16.20
2J	3/1/63	11.30	5.10	-	6.20
2J	3/2/63	54.00	21.40	-	33.60
2J	19/6/63	38.04	-	26.02	12.02
2J	19/9/63	133.44	107.00	-	26.44
2J	22/10/63	28.50	20.00	-	8.50

volumetric contribution of all species (Grice and Hart, 1962) was not feasible because of the extremely small size of most of the copepods which were the chief constituent of the plankton, and because of the relative scarcity of larger species of crustaceans; the errors involved in using such small samples would be tremendous. The method is more applicable to weight determination (provided a sufficiently sensitive balance is obtainable). The final volumes are shown in Fig. 3. Values for dates before February 1963 were extrapolated on basis of average/min. readings for metered tows.

Dry weights.

The whole sample was quantitatively transferred to a measuring cylinder from which, after thorough shaking and stirring, duplicate aliquot portions were poured into previously weighed sintered-glass crucibles. These portions were drained by suction, washed and then heated in an oven at 60°C for at least one hour, cooled and weighed. The heating, cooling and weighing were repeated until constant weight was obtained. Weights in grams were read off to the fourth decimal; agreement between duplicate subsamples was generally good to the third decimal. Discrepancies could usually be traced to clumps of particulate matter. The results of these determinations are reported in Fig. 4. A summary of all gross quantitative measurements is included in Tables 4 to 7 in the appendix.

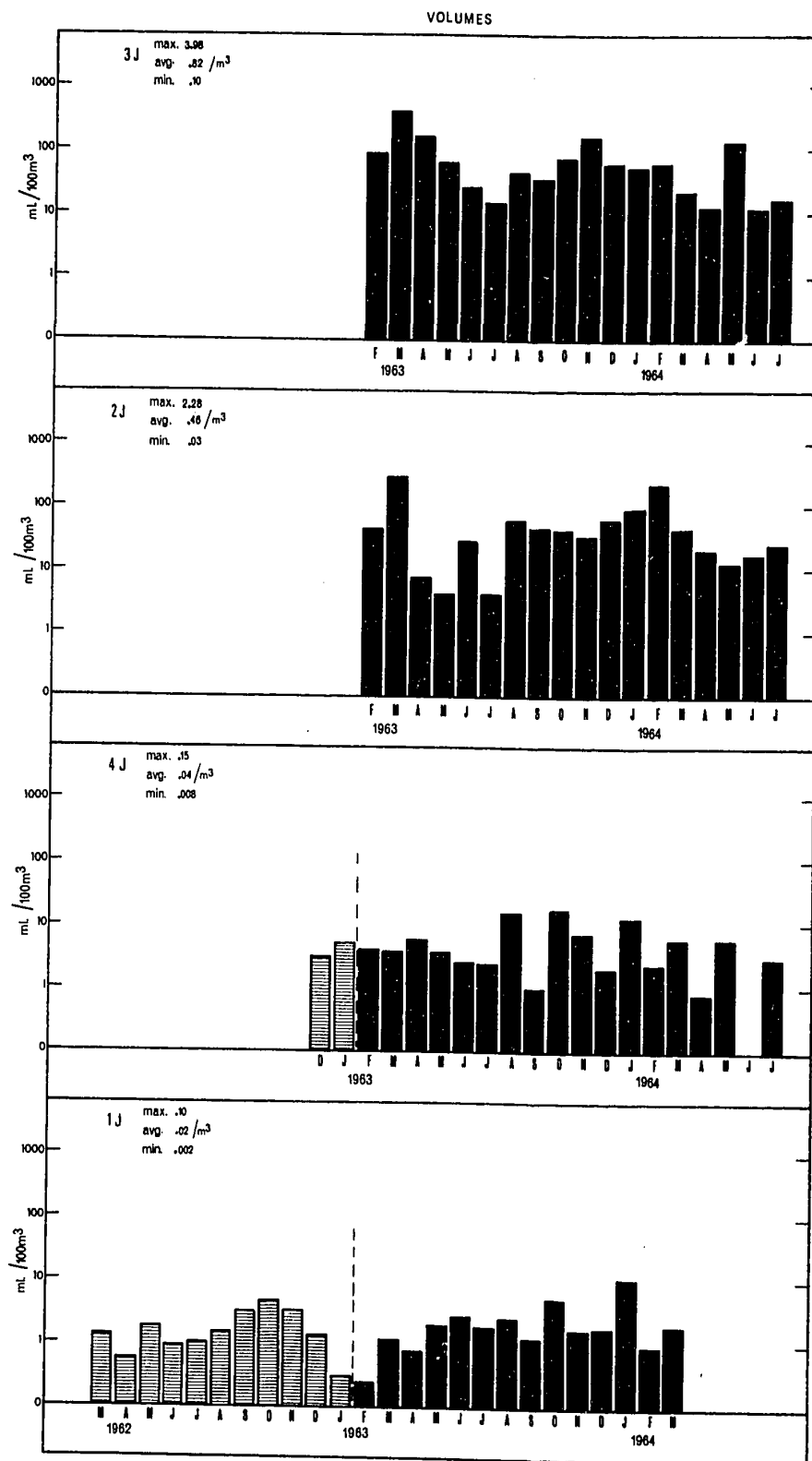


Fig. 3. Estimated monthly volumes - ml/100m³. Solid columns represent directly measured values, horizontal stripes extrapolated values.

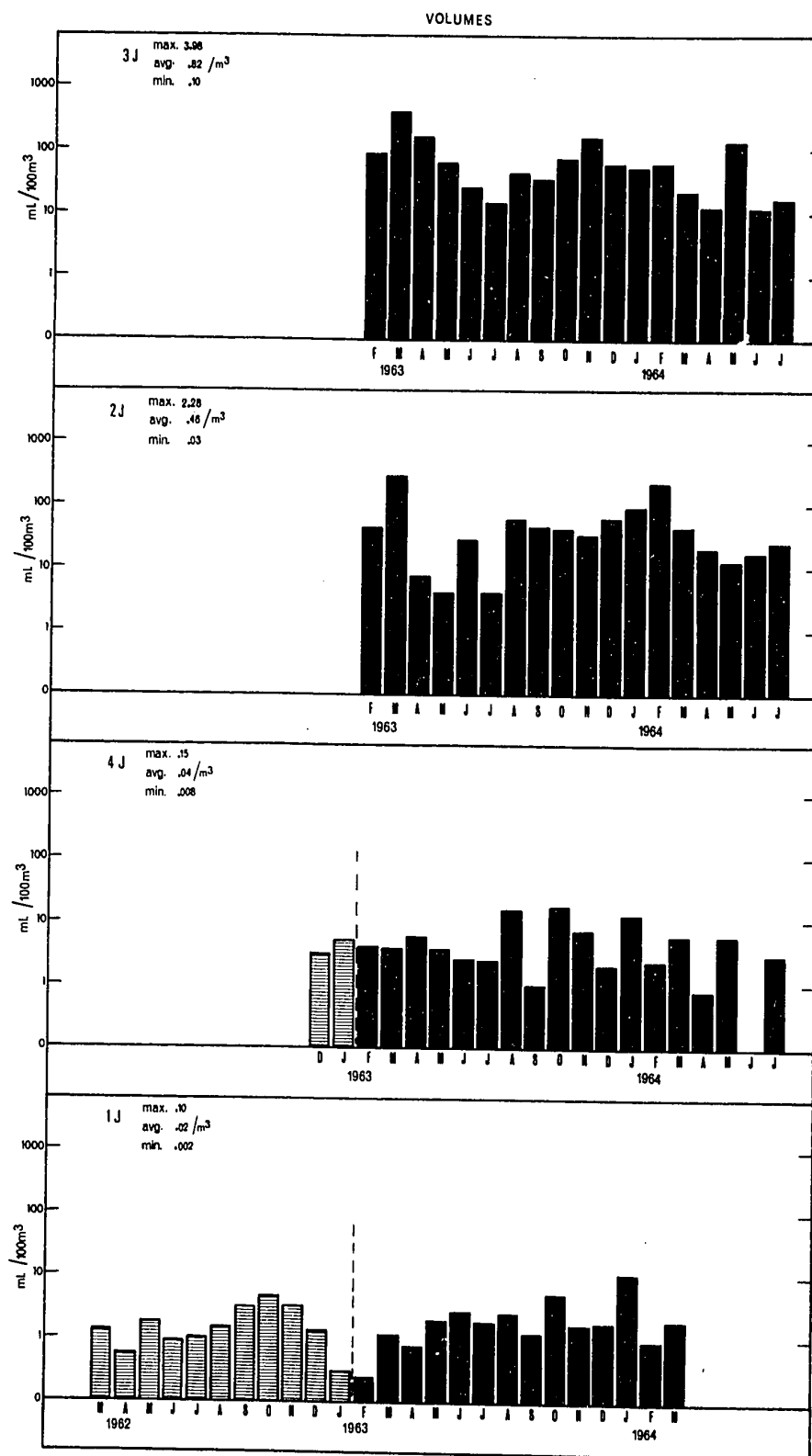


Fig. 3. Estimated monthly volumes - ml/100m³. Solid columns represent directly measured values, horizontal stripes extrapolated values.

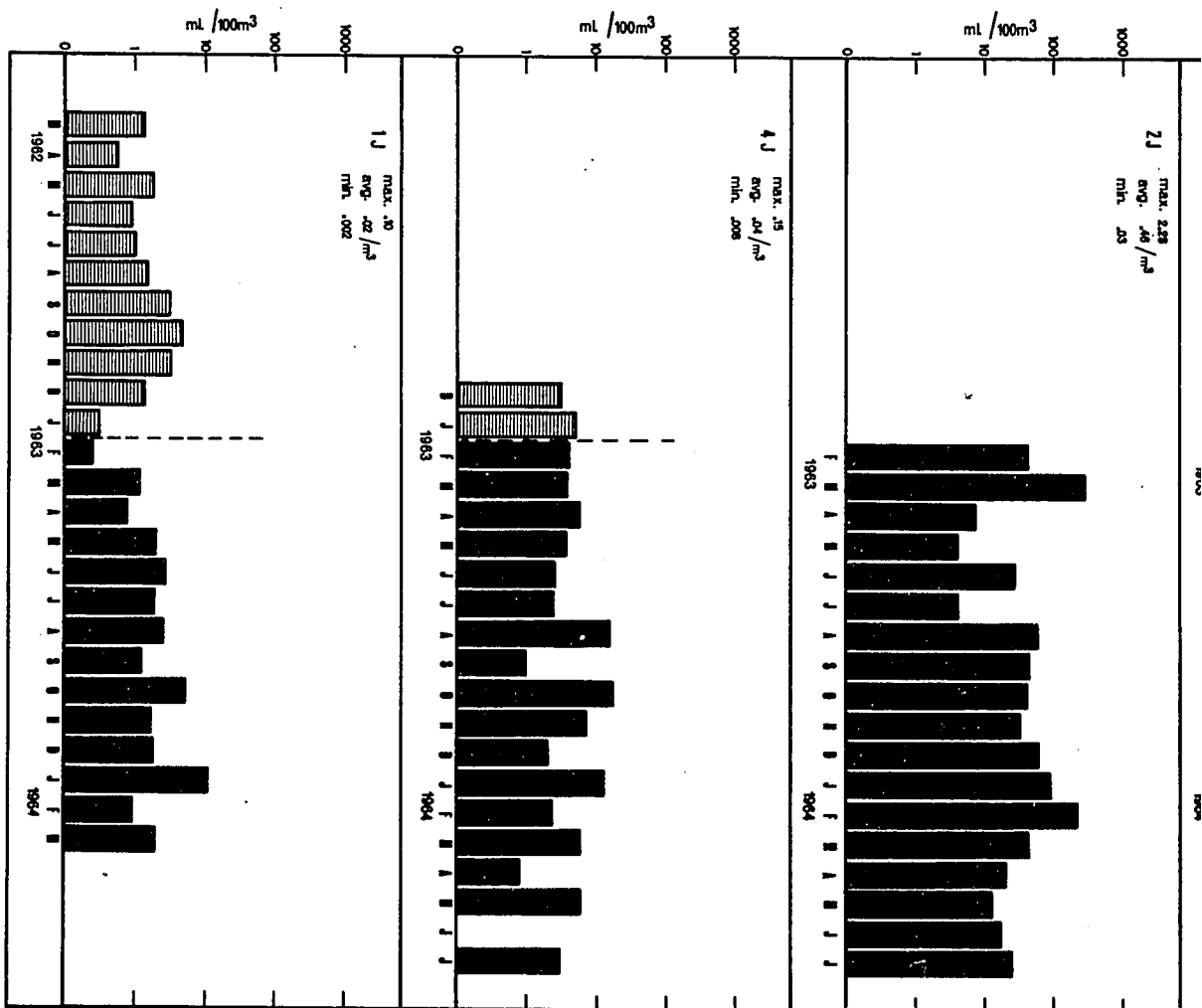
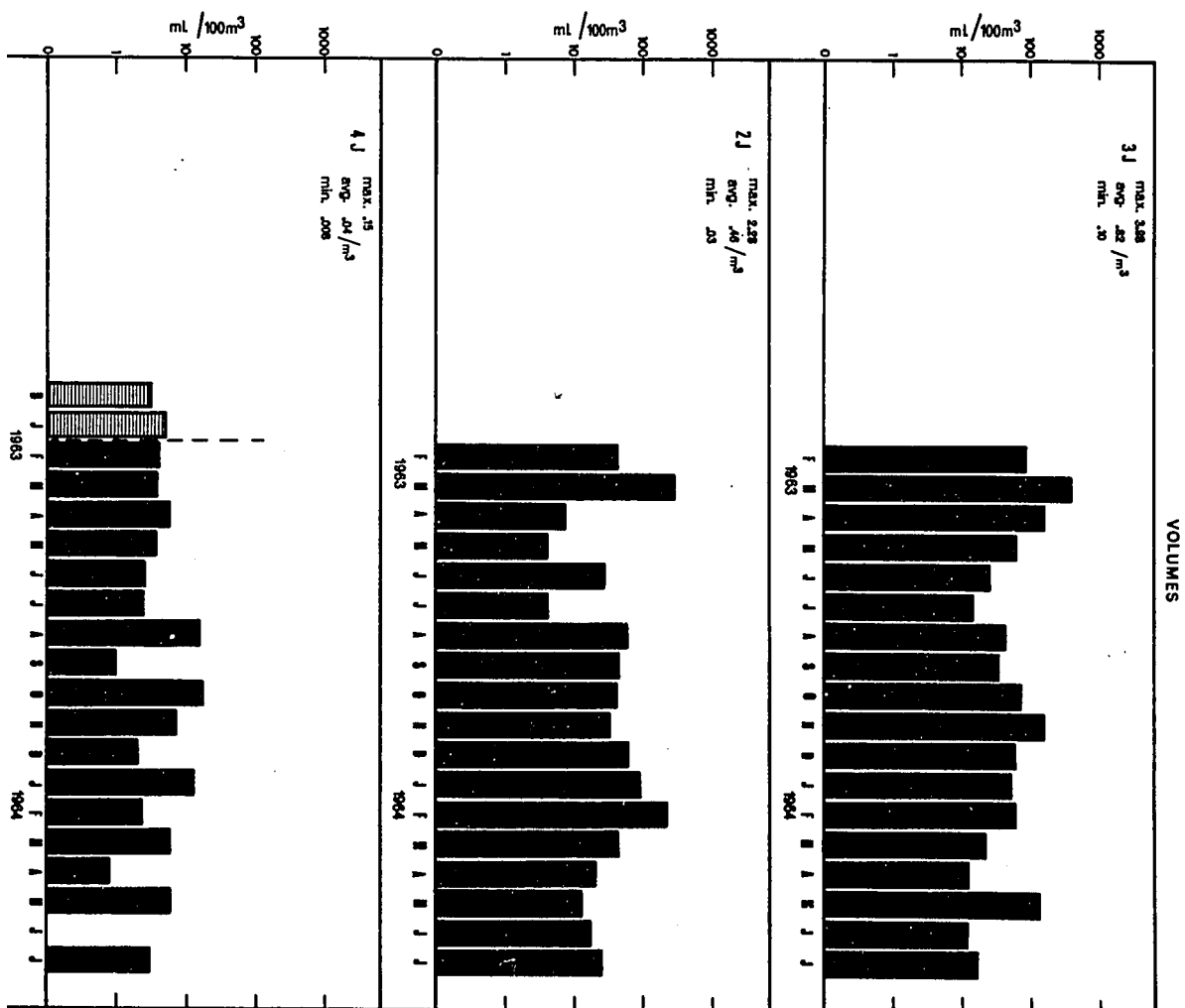


Fig. 3. Estimated monthly volumes - $\text{ml}/100\text{m}^3$. Solid columns represent directly measured values, horizontal stripes extrapolated values.



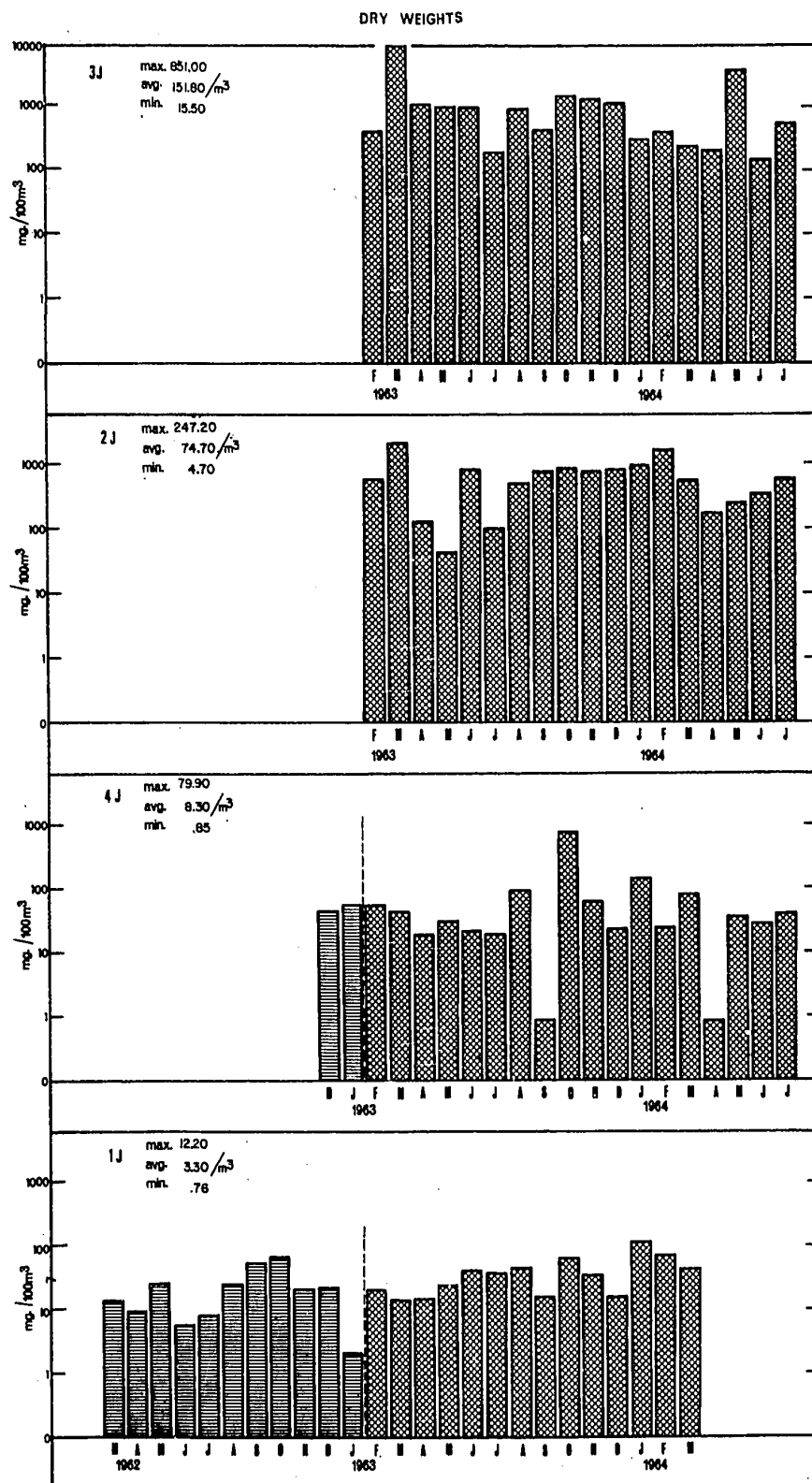


Fig. 4. Estimated dry weight - mg/100³. Cross hatching represents directly measured values, horizontal stripes extrapolated values.

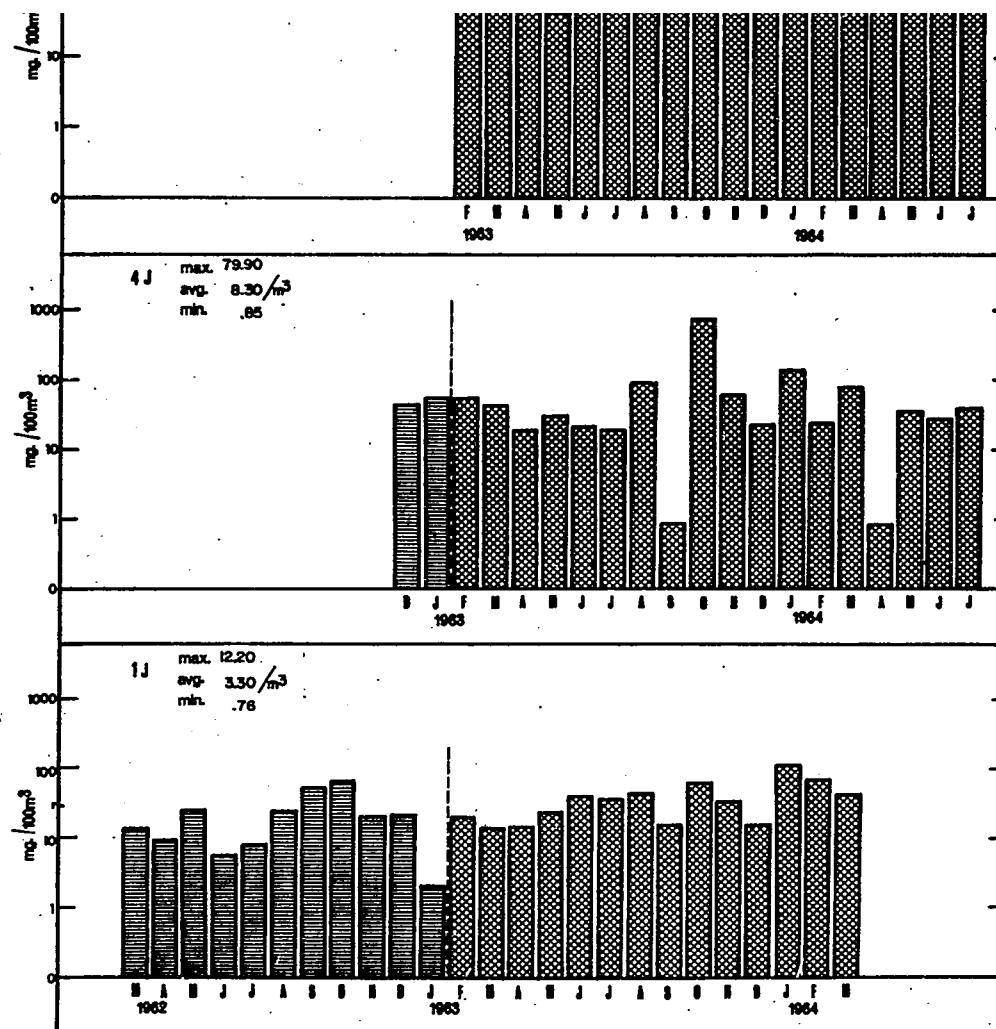
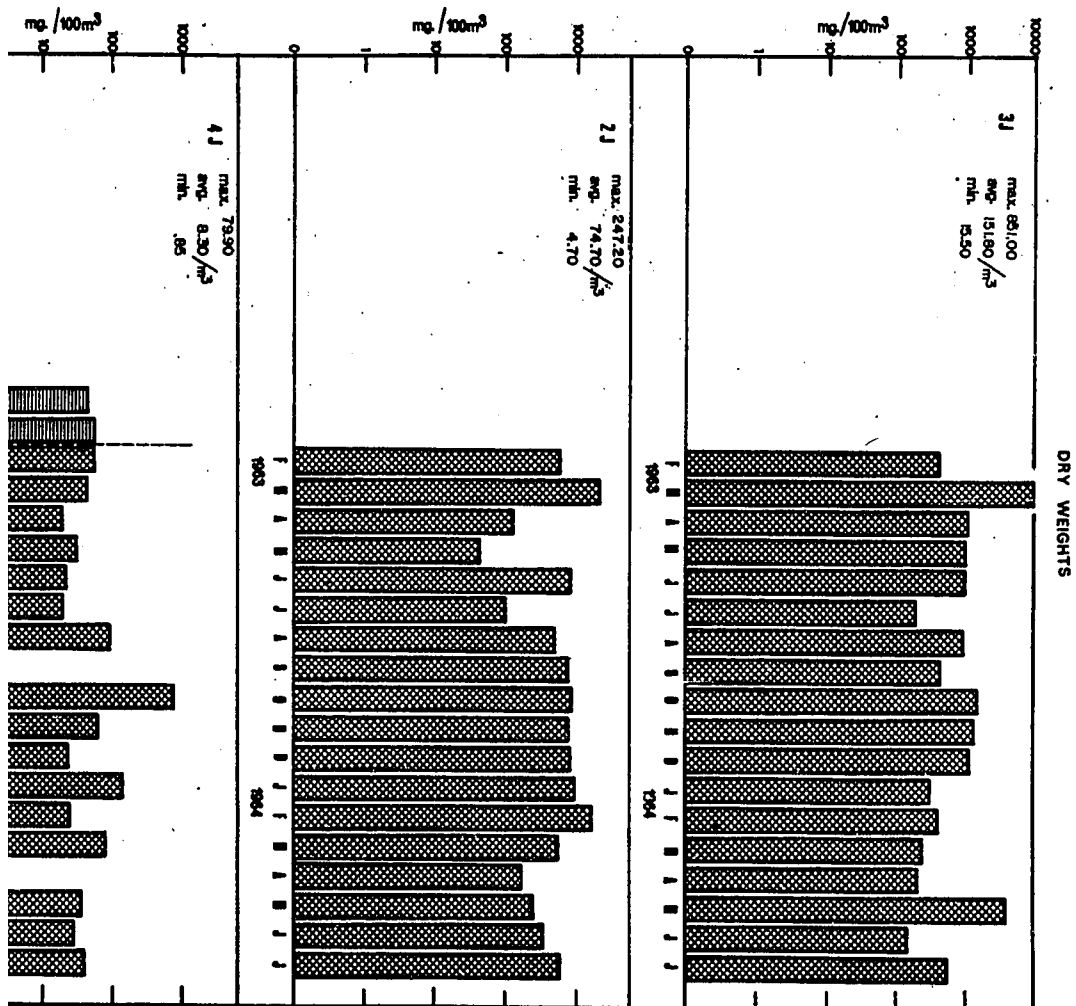


Fig. 4. Estimated dry weight - mg/100³. Cross hatching represents directly measured values, horizontal stripes extrapolated values.



Identification and counting.

The equipment used in sorting and counting consisted of a Zeiss binocular microscope, an adjustable pipette, a specially prepared petri-dish and a Zeiss plankton microscope.

No simple standard treatment was satisfactory for all samples because of differences in the nature of the material, so some groups had to be accorded special treatment as follows :

- i. Large medusae were separated and counted.
- ii Pteropods too large and heavy to be sampled by the pipette method were counted separately.
- iii Rare species occurring in only small numbers were counted in larger samples than common ones.
- iv. Species that were abundant but of small individual size were counted with an Untermyhl plankton microscope.

For all samples the general procedure was as follows : Whole samples were examined and a preliminary sorting into major groups such as copepods, cladocerans, etc. was made. These groups were further broken down into species. The identifications were later checked and in doubtful cases confirmed by specialists.

Counting.

The entire sample was brought to known volume, mixed and stirred with the tip of a pipette which was adjusted to remove exactly 0.5 cc material. This subsample was quickly transferred to a petri-dish; the petri-dish was marked off in units of area $\frac{1}{2}$ cm² and numbered in serial order. The amount of liquid in the 0.5 cm sample was usually just enough to spread over the area and keep the animals moist but

prevent any undue mixing or shifting. Because of the large number of organisms usually occurring in a sample, the distribution of total zooplankton was assumed to be approximately normal. Counting was done on only one species at a time and the total number of each species present in each subsample was recorded on a specially prepared table.

A few groups occurring in very large numbers, for example the copepod Farranula gracilis Geisbrecht and fish eggs, were separated and later counted with a Zeiss Untermühl plankton microscope.

At least two subsamples were counted, and where the total number of animals counted was less than a thousand, additional aliquots were counted until this number was exceeded.

Larger samples of 2 cc or more were scanned for the presence of rarer species. Often too, some species counts were very low - one or two animals per .5 cc and in these cases larger samples were used to check on the abundance of the species throughout the sample.

Pteropods were usually too large for the tip of the pipette used in subsampling and, owing to the high density of their shells, they sank too quickly for a sufficiently representative portion of the population to be taken in a sample. Total counts of pteropods were done therefore on whole samples. Tables 8 to 11 (in appendix) show the species occurring at each station and the estimated density /m³ for each species; and the monthly fluctuations in total plankton numbers at all four stations are shown in Fig. 5.

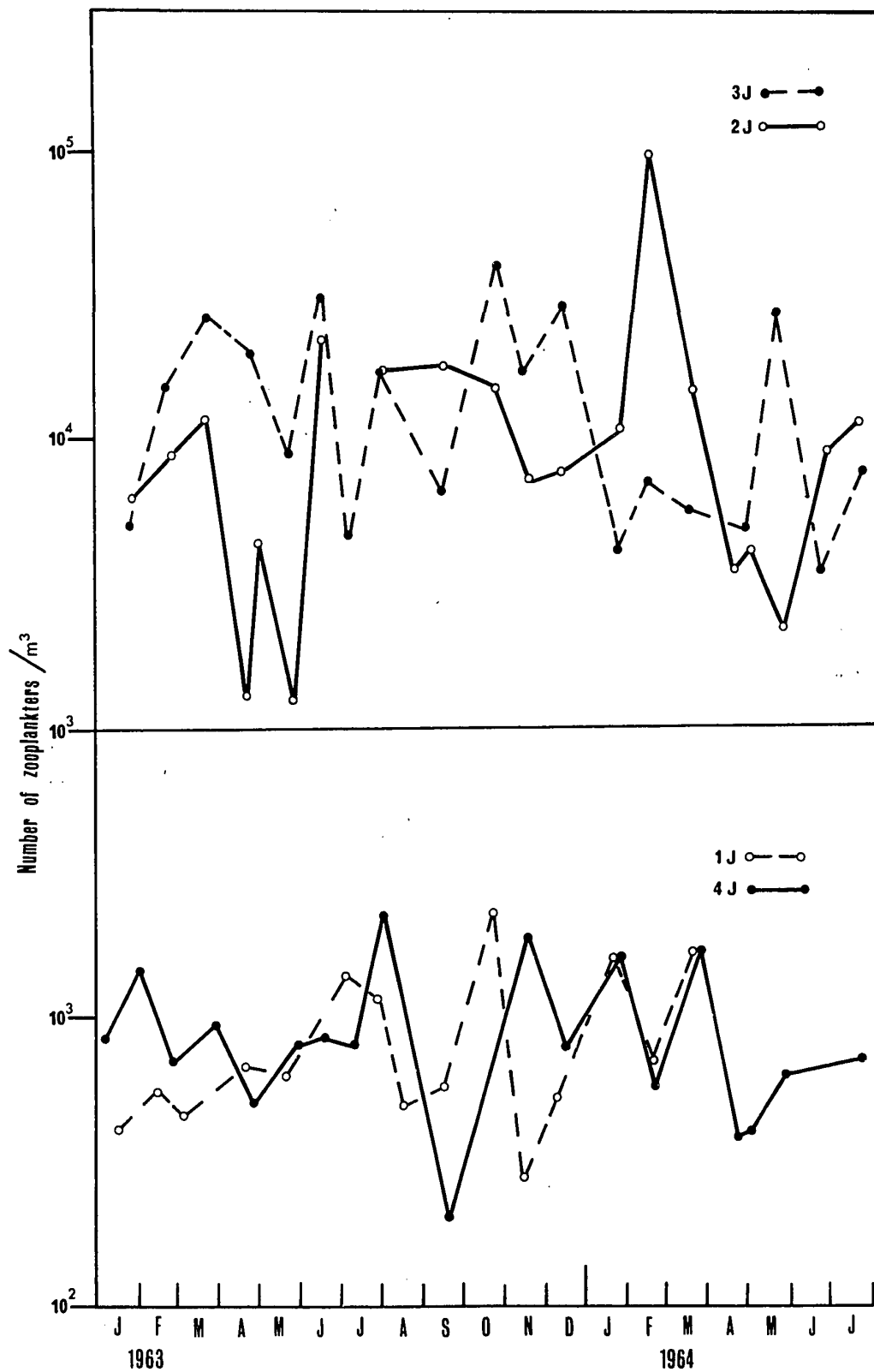


Fig. 5. Monthly fluctuations in total zooplankton numbers at the 4 stations.

Statistical validity of counts.

The reliability of the counting technique was checked by the following method. Five replicate counts of 0.5 cc each were made on one sample from each station. The counts were done at different times and without reference to earlier counts. Eight groups of plankters were selected for the detailed statistical testing. As far as was possible all the sets had the same groups of animals and each set had animals ranging from very low population density to very abundant. For each of these groups the mean, SD, SE, % SE and fiducial limits were calculated at a significance level of 5%. Where actual counts exceeded the theoretical limits obtained, the probability of such counts occurring by chance was also determined. Of the 160 counts, 9 turned out to be below or bordering the significance level chosen, but did not exceed the 10% level. The data are shown in Tables 12 to 15.

High counts were always associated with the presence of debris on which many setose organisms were caught. On the other hand the presence of a few siphonophores or small medusae, by taking up a greater volume, could make an appreciable difference in the number of copepods in a 0.5 cc volume. By way of increasing the discriminatory power of the test at the given significance, and as a counter check on the values obtained on the basis of the 0.5 cc level, determinations were done on larger volumes, e.g. 1-2 cc. In every case the comparisons were very good; for example, for sample 4/5/62 the following figures were obtained :

<u>1 cc volume count</u>	<u>2 cc volume count</u>
Undinula vulgaris 400	790
Farranula gracilis 608	1225

For species like the large coelenterates and pteropods on which total counts were done, there is obviously a smaller margin of error. The discrepancies in counts are therefore due mainly to uneven distribution of animals, which could not be eliminated entirely. From the other parameters calculated however, it can be seen that the means obtained are valid, being in every instance equal to more than $3 \times SD$ (Stanley (38) 1963) or more than the variance, and that % SE became progressively smaller with the increase in the numbers of a species counted. It is claimed therefore, that although randomness of distribution could not be assured, the sampling and counting methods were sufficiently consistent and unbiased to warrant confidence in the resultant approximate totals.

Calculated statistics for determining the validity of the counting method. Five samples of .5cc volume were used for each test.

TABLE 12. Sample of 12/10/62 from Station 1J.

Selected animals	Mean	Fiducial limits		SD	SE	% SE
Copepod A35	661.0	678.25	643.74	13.0	6.71	0.87
Copepod A2	120.0	133.87	102.12	11.6	5.398	4.32
Copepod A1	109.6	119.76	99.44	8.4	3.95	3.48
Fish eggs	106.5	116.42	96.57	8.5	3.86	3.52
Sagitta	40.0	47.19	32.80	6.7	2.79	6.82
G. bulloides	11.2	13.72	8.66	2.1	.98	8.53
Copepod A8	27.0	33.82	20.17	5.7	2.65	9.44
Veligers	68.2	78.07	58.33	8.2	3.84	5.39

TABLE 13. Sample of 1/5/64 from Station 2J.

Selected animals	Mean	Fiducial limits		SD	SE	% SE
Larvacea	166.2	171.22	160.2	4.7	1.9	1.2
Copepod A31	77.4	81.7	72.1	4.0	1.6	2.2
Copepod A35	51.4	57.9	44.8	6.1	2.5	4.9
Fish eggs	46.8	52.2	48.4	5.1	2.1	4.48
Sagitta	29.0	32.1	25.9	2.9	1.2	4.2
Nauplii	25.4	29.13	21.66	3.50	1.4	5.7
Copepod A8	23.2	25.4	20.9	2.1	.9	3.7
Veligers	22.0	25.1	18.9	2.9	1.2	5.4

Calculated statistics for determining the validity of the counting method. Five subsamples of .5cc volume were used for each test.

TABLE 14. Sample of 24/4/64 from Station 4J.

Selected animals	Mean	Fiducial limits		SD	SE	% SE
Larvacea	457.2	475.0	439.3	16.7	6.93	1.5
Copepod A35	292.0	302.2	281.7	9.6	3.9	1.4
Copepod A34	251.4	259.2	243.6	7.3	3.0	1.2
Lucifer	98.8	103.6	93.9	4.5	1.9	1.9
Copepod A8	39.0	43.8	34.2	4.5	1.9	4.8
Copepod A26	24.2	27.8	20.5	3.4	1.4	5.8
Sagitta	21.0	24.1	17.9	2.9	1.2	5.7
Fish eggs	7.4	9.0	5.8	1.5	.6	8.4

TABLE 15. Sample of 24/4/64 from Station 4J

Selected animals	Mean	Fiducial limits		SD	SE	% SE
Veligers	46.2	50.9	41.6	4.43	1.8	3.9
G. bulloides	29.0	30.7	27.3	1.6	.7	2.2
Larvacea	23.0	26.8	19.2	3.53	1.5	6.3
Nauplii	19.2	22.1	16.3	3.0	1.2	6.5
Copepod A8	15.4	16.6	14.2	1.1	.5	3.0
Copepod A35	14.6	17.3	11.9	2.5	1.0	7.1
Fish eggs	13.2	15.1	11.3	1.8	.7	5.6
Sagitta	11.2	12.8	9.6	1.5	.6	2.2

ANALYSIS OF RESULTS

I. Zooplankton composition and spatial distribution.

The species list of identified zooplankters for all areas of study is represented in Tables 8 to 11 in the appendix. This may be considered as composed of the following elements :

1. The copepod population represented by the following orders :
Calanoida, Cyclopoida and Harpacticoida, listed according to their species and numerical abundance.
2. A permanent population of the decapod Lucifer - 2 species.
3. A very considerable population of larvaceans consisting of two species of Oikopleura and one of Fritillaria.
4. Twenty-five species of coelenterates, including 13 species of siphonophores.
5. An appreciable cladoceran population of Penilia with Podon constituting a minor fraction.
6. Three species of chaetognaths.
7. Rarely occurring groups; i.e. groups lacking both constancy and numbers in their occurrence. These include six species of Foraminifera, two species of rotifers, two species of ostracods, five species of amphipods, one isopod, 1 species of Dololium and a cephalochordate, Branchiostoma caribbaeum.
8. Larval forms which showed sporadic maxima in their occurrence. These represent the pelagic stages of several bottom and shore living crustacea (shrimps, cirripedes), gastropods and lamelli-branch veligers, polychaete and echinoderm larvae, fish eggs

and early developmental forms.

Altogether there were 114 distinct taxonomic groups of zooplankters, 90 of which were identified at the specific or generic level. Of these there were 87 at 1J, 84 at 4J, 77 at 2J and 66 at 3J.

Copepods.

Of the taxonomic groups listed above the copepods were

- a) represented by most species; b) most abundant numerically;
- c) the largest constant contributors to zooplankton volume at stations 1 and 4J.

The percentage of zooplankton numbers formed by copepods in the hauls from all stations ranged from 8-89% with averages of 57.08% at 1J, 65.40% at 4J, 34.25% at 2J and 43.20% at 3J, and densities ranged from 43.00/m³ to 18,703/m³.

Most of the copepods have a world wide tropical and subtropical distribution and some have a much wider latitudinal range. A record was established for one harpacticoid, Microsetella norvegica Boeck, because its discovery in these waters represents a range extension of 20° latitude. It has a distribution range stretching from the Arctic down the North American Atlantic seaboard and its previously known southern limit was the latitude of Chesapeake Bay - 38° N (Fish, 1955).

Thirty-nine of the 45 species identified were taken at station 1J, but of these only three species had average population densities of more than 100/m³ : Farranula gracilis Geisbrecht (Cyclopoida) 169/m³; Paracalanus aculeatus Geisbrecht (Calanoida) 133/m³; and Undinula vulgaris Dana (Calanoida) 121/m³. These three species were constant in their occurrence, being represented in every haul from the station

from March 1962 through March 1964. Other regularly occurring species were the cyclopoids Corycaeus amazonicus Dahl 12/m³, Oncaea venusta Philippi 12/m³, Oithona plumifera Baird 9/m³, Corycaeus speciosus Dana 11/m³, Miracia efferata Dana 6/m³ and the calanoids Acartia lilljeborgi Geisbrecht 6/m³ and Calocalanus pavo Dana 13/m³. Other species like the cyclopoids Oncaea mediterranea Claus, Macrosetella gracilis Dana, Microsetella norvegica and the calanoids Candacia pachydactyla Dana and Temora stylifera Dana appeared in more than 50% of the hauls but in very low densities. A number of parasitic species (cyclopoids) Caligus species, Copilia mirabilis Dana, Clytemnestrata scutelata Dana, Sapphirina intestinata Geisbrecht, S. auriontens Geisbrecht were also taken, but as is to be expected, their temporal distribution is sporadic and densities are very low. Other rarely occurring species include the larger carnivores like Neocalanus robustior Geisbrecht and the harpacticoids.

The three major contributors to copepod numbers in the 4J area are the same as at 1J, but here Paracalanus aculeatus is not only the most abundant (417/m³) but more than three times the average population density at 1J. Undinula vulgaris becomes slightly more numerically important here (128/m³) while the average density of Farranula gracilis decreases to 74/m³. Playing a secondary role in numerical importance are again species like Calocalanus pavo (39/m³), Oncaea mediterranea Claus (37/m³), Corycaeus amazonicus (25/m³), Oncaea venusta (23/m³), while other species only poorly represented at 1J come into importance - Corycaeus latus Dana (39/m³), Temora turbinata Dana (26/m³), Oithona nana Geisbrecht (23/m³) and Centropages furcatus Dana

($17/m^3$). Yet again other species which were never taken at station 1J, but which become more numerically abundant shorewards, made low-density sporadic appearances at 4J, for example Temora turbinata, Labidocera scotti Geisbrecht, Eucalanus subcrassus Geisbrecht and Calanopia americana Dahl.

Species number range is from 7 (February 1964) to 24 (February 1963), quite similar to that at 1J, and as at 1J, occasional population bursts are limited to only a few species at a time, emphasizing the purely local nature of factors affecting population size.

The two harbour stations can conveniently be treated together because they show such a marked similarity in species distribution and population size. The inshore species collected number 18 and of these 9 species together account for more than 90% of the copepod population. The average monthly densities of these 9 species range from $92/m^3$ for Eucalanus subcrassus to $1797/m^3$ for Paracalanus aculeatus at 2J, and $101/m^3$ for Acartia lilljeborgi to $2605/m^3$ for Paracalanus aculeatus at 3J.

The copepod percent fraction of the total zooplankton at these two stations, however, is much less than that at the shelf and oceanic stations, being on an average only 34.25% at 2J and 43.20% at 3J. This difference is accounted for both by relatively large populations of shallow water forms like Penilia avirostris as well as the larger numbers of bottom living forms whose larvae significantly augment zooplankton numbers.

Cladocerans.

Two cladocerans, Podon sp. and Penilia avirostris were taken in the hauls. Podon sp. occurred occasionally in small numbers at 1 and 4J stations. It was taken on 15 occasions at 1J (62.5%) and had an average density of $6/m^3$. Podon sp. was taken 5 times at station 4J, but appeared on only 2 occasions inshore. It therefore appears to be more characteristic of Caribbean offshore waters.

Penilia avirostris Dana on the other hand, is characteristic of the shallower inshore water, maintaining an average density of $1856/m^3$ (11.30%) at 3J, and having its focal concentration, $6475/m^3$ (32.90%) at 2J. Although the population densities were so high, Penilia avirostris was not a constant contributor. It disappeared from the stations completely for periods of one to three months at both stations. This situation is discussed under 'Breeding'.

Penilia avirostris, therefore, makes the largest numerical contribution of any single species, and, if the medusae are excluded, probably the largest volumetric contribution as well at 2J. At 3J Penilia avirostris is third in order of numerical significance and probably of volumetric importance as well.

Larvacea.

Three species of larvacea were identified, all of which were distributed throughout the area of study. Fritillaria sp. was the least abundant and the most unpredictable in occurrence. It was taken most often at 3J in 50% of the hauls with a density range from 15 to 499/m³ and its density decreases steadily offshore, achieving an average of 7/m³ at station 1J.

Of the two species of Oikopleura, Oikopleura I was most abundant and regular in its occurrence at 2J, where it achieved an average density of 812/m³. Oikopleura II was concentrated at 3J where its average density was 4272/m³ and where it ranked second only to the copepods (6654/m³) in numerical importance. It was also very constant in occurrence at 4J but here its average population density was 139/m³. Table 16 below gives an indication of the distribution of the larvacea.

TABLE 16. Showing the estimated range in population densities of three species of Larvacea.

	3J			2J			4J			1J		
	Max	Min	Av/m ³	Max	Min	Av/m ³	Max	Min	Av/m ³	Max	Min	Av/m ³
Oikopleura I	503	24	186	4540	38	812	188	27	81	116	1	25
Oikopleura II	22835	10	4272	2779	25	593	556	8	139	84	1	15
Fritillaria sp.	499	15	205	643	10	156	13	6	8	20	1	7
Total			4663			1561			228			47

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Total			4663			1561			228			47

Chaetognaths

Three species of chaetognaths were present - the relatively large Sagitta enflata Grassi (up to 3.6 cm), S. serratadentata Krohn (1-1.5 cm) and Khronita subtilis Grassi (1-1.5 cm). All three species occurred quite regularly at stations 4 and 1J while S. enflata was much more common in the harbour where it constitutes an important element of the zooplankton, as represented below :

TABLE 17. Average density /m³ of the chaetognaths.

Stations	3J	2J	4J	1J
<u>S. enflata</u>	501	114	6	2
<u>S. serratadentata</u>	235	82	17	13
<u>Khronita subtilis</u> only 3 occurrences		46	11	5
Total % contribution	3.70	1.34	1.38	1.57

On the basis of numerical abundance S. enflata was by far the largest contributor, 60.4%, to the chaetognath population, Sagitta serratadentata contributing 33.6% while Khronita subtilis comprised a very small fraction - 6%. Partly because of a large contribution made by S. enflata, chaetognaths were 5-15 times more abundant in harbour than in shelf and oceanic waters, but it should be noted that low density figures of S. serratadentata and Khronita subtilis obtain from a constant population while at 3J the population is characterised by a much less regular occurrence with occasions of high incidence. As is the case with the larger carnivorous copepods

and amphipods, daytime hauls at 1J do not fairly sample the chaetognath population. Night tows indicate that the populations of these species is on the average 3.5 larger than day hauls.

Although there was considerable temporal fluctuation, no obvious seasonal variations could be detected in the populations of chaetognaths. Population peaks occurred at different periods in different years and population blooms rarely concurred in even two of the species. The three species named above are typical members of the plankton of the tropical and subtropical North Atlantic and may be expected to occur at any time. (See Grice and Hart (1962), Moore (1949), Deevey (1952)).

It has been suggested, (Stone, 1966) that the number of S. enflata is a good indicator of variation in size of standing crop in an area. Whether or not this statement applies significantly to the special food of S. enflata or to the zooplankton in general, it is a postulate that fits quite easily in the present circumstances of generally higher production inshore at 3J.

Coelenterates.

Six of the 25 species of coelenterates listed, Eirene sp., Aequorea macrodactyla Brandtse, Eutima, Octorchis, Cosmetira and Carybdea xaymacana Conant and sometimes Liriope scutigera were relatively large measuring more than an inch in diameter. These were regularly sorted and measured separately. Their numbers were extremely small in comparison to their volumetric measurements hence their volumes have not been taken into account for purposes of comparison. Their very high contributions by volume are indicated in Table 2. However, smaller members of these same species passing through sieve of mesh size .2 cm were included in both volume and counts. Other Hydromedusae like Liriope mucroranta Gegenbaur, Eucheolita sp. and Obelia whose medusae are of semi-microscopic size were included in volume determination and counts.

The larger medusoid forms mentioned above occurred more abundantly in the harbour stations, Eirene, for example, occurring almost exclusively at 2J where a mean concentration of $12.6/\text{m}^3$ would represent an increase of 12.6 cc to average volume at this station (mean volume without medusae = $.46 \text{ cc}/\text{m}^3$). Reference to Table 10 in the appendix will show this as well as the fact that other species of genera Liriope, Eucheolita, Octorchis and Eutima are distributed around 2 and 3J and occur only occasionally at 4J.

Siphonophores.

Thirteen species of siphonophores were present. These occurred much more regularly at the shelf (4J) station and deep water (1J)

station than at the two harbour stations, but sporadic occurrences inshore were characterised by much higher concentrations. Many of these species found are typically warm water species, among them Abylopsis eschscholtzii Huxley and A. tetragona Otto, Eudoxides spiralis Bigelow, Dyphyes dispar Chamisso and D. bojani Chun, Lensia subtiloides and Chelophyes appendiculata, and, according to Grice and Hart (1962), Bigelow and Sears (1939) are more characteristic of Sargasso sea waters. Grice and Hart also maintain that in general there is a paucity of siphonophore species in neritic waters and that there is an offshore deep water distribution of this group of animals. This observation was not paralleled in this area. Eleven species were sampled at some time during the study at 2J and thirteen at 4J station, but only eight at each of the two extreme stations.

It has already been stated that this study was concerned mainly with day surface plankton and night tows suggest that the majority of carnivores remain below sampling depth in the daytime and rise to feed at night. Since the siphonophores are notorious carnivores, this might account for their fewer species occurrence in the daytime plankton at 1J.

In résumé therefore it may be seen that though the density of small medusoid forms and siphonophores was small in comparison to the copepods and they therefore make only a small percent numerical contribution, the smallest is large (approximately 5 times) in comparison to the average size of the copepods, so their volumetric fraction was quite large, and as a group was most important at station 1J where their percent displacement volume would rank them comparatively high in an environment where the total mass is small.

Eucarids.

The euphausiids and sergestids were the only adult eucarids represented in the epizooplankton. There were 5 species of euphausiids but only two were common in the daytime plankton and the larger populations appeared inshore. Euphausiid I was most abundant and regular in occurrence at 2J. It occurred in 56% of the samples and had an average population density of $346/\text{m}^3$. This figure was considerably weighted by a dense occurrence of $2421/\text{m}^3$ in June 1963. This bloom was not repeated in any of the collections and for the other months the density figures ranged from 28 to $595/\text{m}^3$. Euphausiid II was taken only five times and its mean monthly density was less than $1/\text{m}^3$. Euphausiid II occurred frequently at stations 3 and 4J, in both instances in more than 70% of the tows and the mean monthly densities were 236 and $5/\text{m}^3$ respectively. At station 1J both species occurred frequently but in very small numbers, averaging together less than $1/\text{m}^3$ in daytime plankton. In the night tows however, these species were three times more abundant than in day hauls and in addition three other species were represented. Although euphausiids contribute only 1.03% at 2J and 0.75% at 3J of zooplankters, yet considering their size (mean value 15 mm) in relation to copepods, they added quite significantly to the displacement volume. Even at 4J they ranked as the sixth most numerous animals and likewise would make fair percent contribution to zooplankton volume. At 1J, however, their paucity in numbers renders their contribution negligible both numerically and volumetrically.

The sergestid component comprised two species of the genus Lucifer. L. faxoni Borradaile is, according to Hansen (1919), a typical coastal

or inshore species and as such it appeared in these collections. It had its highest incidence at 2J. It was also quite common at 3J but its seaward extension appeared to end at 4J. At all these stations both adults and the various larval stages were taken. The average densities of the adults were respectively $172/\text{m}^3$ at 3J, $504/\text{m}^3$ at 2J and $2/\text{m}^3$ at 4J. These figures represent .88%, 2.73% and .05% respectively of zooplankton numbers at the three stations. If the larval stages are added these figures would be increased to 2.92% (3J), 12.11% (2J) and .50% (4J). The importance of L. faxoni as a component of the zooplankton can therefore be assessed from these figures.

L. typus Milne-Edwards, easily distinguished from L. faxoni by its much longer eye stalks, is described as a typical oceanic species, was taken only at 1J in both day and night hauls. However, it was more abundant at the surface at night. Average density for daytime was less than $1/\text{m}^3$.

Amphipods.

Five species of amphipods were identified, but only three species - Brachyscelus cruscum Spence Bate, Hyperia atlantica Vosselev and Glossocephalus milne-edwardsii Bovallius were represented in the daytime plankton. B. cruscum and G. milne-edwardsii are both characteristic of tropical Atlantic waters; Hyperia atlantica is as well, and it was the most abundant of the three in these Caribbean waters but even so it was extremely sparse, less than $2/\text{m}^3$ at 1J. The distribution of amphipods seemed to have its shoreward limit at station 2J. All three of the above mentioned groups were taken in daytime hauls at 1J, and in increased

abundance in the night time hauls. In addition, Eusirus longipes and one unidentified species were taken in the night time hauls. The amphipods as a group therefore, made no significant contribution either volumetrically or numerically to the zooplankton at any of the stations.

Other groups.

Two pteropods, Creseis acicula and Limacina sp. occurred irregularly at 4J and 1J where samples occasionally contained high populations. C.acicula was found only twice at 3J and three times at 2J.

Beside the taxa mentioned above seven other groups were present in small numbers. These will be mentioned in order of numerical importance.

There were 10 species of Foraminifera but of these only Globigerina bulloides d'Orbingy occurred in appreciable numbers and that only at 1J (23/m³) and 4J (33/m³). The other species of foraminifers identified were evident mainly in general examination of portions larger than the aliquot samples used for counting. It is possible, however, that because of heaviness of the skeletons, these settled too quickly to be taken in the small subsamples.

The other adult members of the plankton are comprised of two species of rotifers, two parasitic isopods, two ostracod species taken only at 1J and one annelid, Loima sp., small populations of which were found at all stations. There was also one species of Dololium and one of the cephalochordate Branchiostoma caribbaeum which was found only in the harbour (stations 2 and 3J).

Larval forms

The plankton contained numerous free-swimming larvae of bottom living or sessile forms of echinoderms, molluscs, annelids, crustacea as well as fish eggs and early developmental forms.

Decapod nauplii, zoeae, megalopa : Porcellanid and Carcinus zoeae made only infrequent appearances at 1J but Carcinus zoeae were almost always found at 4J. They were more abundant at the harbour stations. Decapod nauplii were found at all stations and the phyllosoma larva of Panulirus was taken on two occasions at 1J. As mentioned before the various stages of the larvae and pre-adult of Lucifer faxoni made quite an appreciable numerical contribution to the epifauna of stations 2, 3 and 4J - 9.38%, 2.04% and .45% respectively. Barnacle nauplii and cyprids were numerous at 3J and 2J but few were found in the shelf and offshore populations.

Veligers : Gastropod and lamellibranch veligers were found in relatively large numbers at all stations with the highest density at 2J station $726/\text{m}^3$ (4%), followed by 3J with $388/\text{m}^3$. More than thirty distinct groups were separated but owing to lack of information about the adult stages no further identification could be attempted.

Polychaete larvae which were also not identified were relatively abundant, particularly at the harbour stations. Mean population densities were as follows :

1J	4J	2J	3J
$3/\text{m}^3$	$10/\text{m}^3$	$38/\text{m}^3$	$100/\text{m}^3$

Echinoderm larvae were common both in numbers and occurrence at stations 1J, 4J and 2J, but very rare at 3J.

The other larval forms mentioned above were relative rarities and included such forms as Sipunculid larva, larvae of Lingula and Phoronis, Müllers larva of Maricolan polycladida, Polyzoan cyphonaute larva and ascidian tadpoles.

Fish eggs and larvae. Fish eggs in various stages of development were always in relatively great abundance at 1J. In fact, they were the second most abundant constituent of the plankton ($236/\text{m}^3$) and as such constituted 28.71% of zooplankton numbers and a considerable fraction of displacement volumes for this station. At 4J a much lower average density of $79/\text{m}^3$ represents 4.53% of zooplankton numbers for this station. The higher average values of $396/\text{m}^3$ at 3J and $305/\text{m}^3$ at 2J are derived from a much more sporadic distribution in time, and represent a much less significant percent contribution at these stations - 0.47% and 1.72% respectively.

The total percent numerical contributions at the four stations may be derived from Table 18 which also shows the shoreward decreasing importance of fish eggs and larvae and the increasing importance of larvae of bottom living forms.

TABLE 18

Showing the percentage contribution by the major groups to the zooplankton of the four stations.

Station	1J	4J	2J	3J
Copepods	57.08	65.40	34.25	43.20
Cladocerans	0.33	0.27	32.90	11.30
Larvacea	4.19	8.05	6.31	24.11
Larvae: nauplii	3.00	8.18	13.14	8.04
veligers etc.				
Fish eggs	28.71	4.53	1.72	0.47
Decapods				
Lucifer	< 1	< 1	2.73	0.89
Euphausids	< 1	< 1	1.03	0.75
Chaetognaths	1.57	1.38	1.34	3.70
Coelenterates	< 1	< 1	2.77	1.52
	94.89	88.03	96.17	93.97
Others	5.11	11.97	3.83	6.03

II. Comparison of four stations.

The results described in the previous section may be conveniently summarised under the following headings :

Gross measurements.

a. Plankton volumes.

Three main facts appear on examination of the data :

- i) The size of the standing crop varied greatly but with little or no relation to climatic seasonality.
- ii) The amplitude of monthly variations is approximately the same for all stations - about an order of magnitude of difference.
- iii) The harbour waters support a zooplankton population at least an order of magnitude greater than that of shelf and offshore waters.

There is, in fact, a gradient in average displacement volumes. There were generally larger quantities of zooplankton at 3J (or harbour basin) with progressively lesser amounts at 2J (or harbour mouth), 4J (shelf or coral reef) and 1J (oceanic) giving mean values of .82, .46, .04, .02 cc/m³ respectively. The reverse gradients 1J, 4J, 2J and 3J therefore give ratios of 1 : 2 : 23 : 41 for displacement volumes.

b. Dry weights. The quantitative relationship is repeated in the dry weight measurements (Fig. 4), the average values for each station again giving ratios of 1 : 2.5 : 22.5 : 46.

c. Numerical abundance. In concordance with volume and dry weight relationships, considerably larger numbers of zooplankters were encountered at 2 and 3J than at 1 and 4J, but the gradation is not completely duplicated. Average /m³ density ratios are 1 : 2 : 20.3 : 18.6.

General examination of the plankton showed, and reference to the

tables of results will indicate that the generally and relatively high standing crop in the harbour will be attributed proximately to the following :

- i) Much greater population density of common species of copepods, e.g. Paracalanus aculeatus 2605/m³ at 3J (c.f. 169/m³ at 1J).
- ii) The occurrence in larger numbers of species of copepods of much larger size (mean size ratio 5:1) for example Eucalanus subcrassus, Centropages furcatus, Temora turbinata, as well as other taxa such as Penilia, Oikopleura, Sagitta and Lucifer.
- iii) The much greater abundance of meroplanktonic forms.

At 3J larger volumes seem to be linked directly to high densities of Larvacea (4663/m) and copepods (6654/m) and to a lesser extent to chaetognaths, while at 2J cladocerans and larvae made very significant contributions (see Table 17). This does not altogether explain the apparent breakdown in concordance between numerical abundance and the other measurements.

An interesting feature of all the quantitative aspects is, with the exception of the numerical ratios, the correspondence in the order of magnitude difference for all the measurements both those determined for chemistry and primary productivity, as well as those determined for standing crop. This correspondence is diagrammatically expressed in Fig. 6.

Species diversity, abundance and spatial distribution.

The species list for the four stations comprise 114 different taxa of zooplankters. Groups that were identified only at the order or generic level, such as larvae of decapods, cirripedes, molluscs and polychaetes, undoubtedly comprised many species and this would greatly extend the species list. There is therefore a great variety of species occupying

tables of results will indicate that the generally and relatively high standing crop in the harbour will be attributed proximately to the following :

- i) Much greater population density of common species of copepods, e.g. Paracalanus aculeatus 2605/m³ at 3J (c.f. 169/m³ at 1J).
- ii) The occurrence in larger numbers of species of copepods of much larger size (mean size ratio 5:1) for example Eucalanus subcrassus, Centropages furcatus, Temora turbinata, as well as other taxa such as Penilia, Oikopleura, Sagitta and Lucifer.
- iii) The much greater abundance of meroplanktonic forms.

At 3J larger volumes seem to be linked directly to high densities of Larvacea (4663/m) and copepods (6654/m) and to a lesser extent to chaetognaths, while at 2J cladocerans and larvae made very significant contributions (see Table 17). This does not altogether explain the apparent breakdown in concordance between numerical abundance and the other measurements.

An interesting feature of all the quantitative aspects is, with the exception of the numerical ratios, the correspondence in the order of magnitude difference for all the measurements both those determined for chemistry and primary productivity, as well as those determined for standing crop. This correspondence is diagrammatically expressed in Fig. 6.

Species diversity, abundance and spatial distribution.

The species list for the four stations comprise 114 different taxa of zooplankters. Groups that were identified only at the order or generic level, such as larvae of decapods, cirripedes, molluscs and polychaetes, undoubtedly comprised many species and this would greatly extend the species list. There is therefore a great variety of species occupying

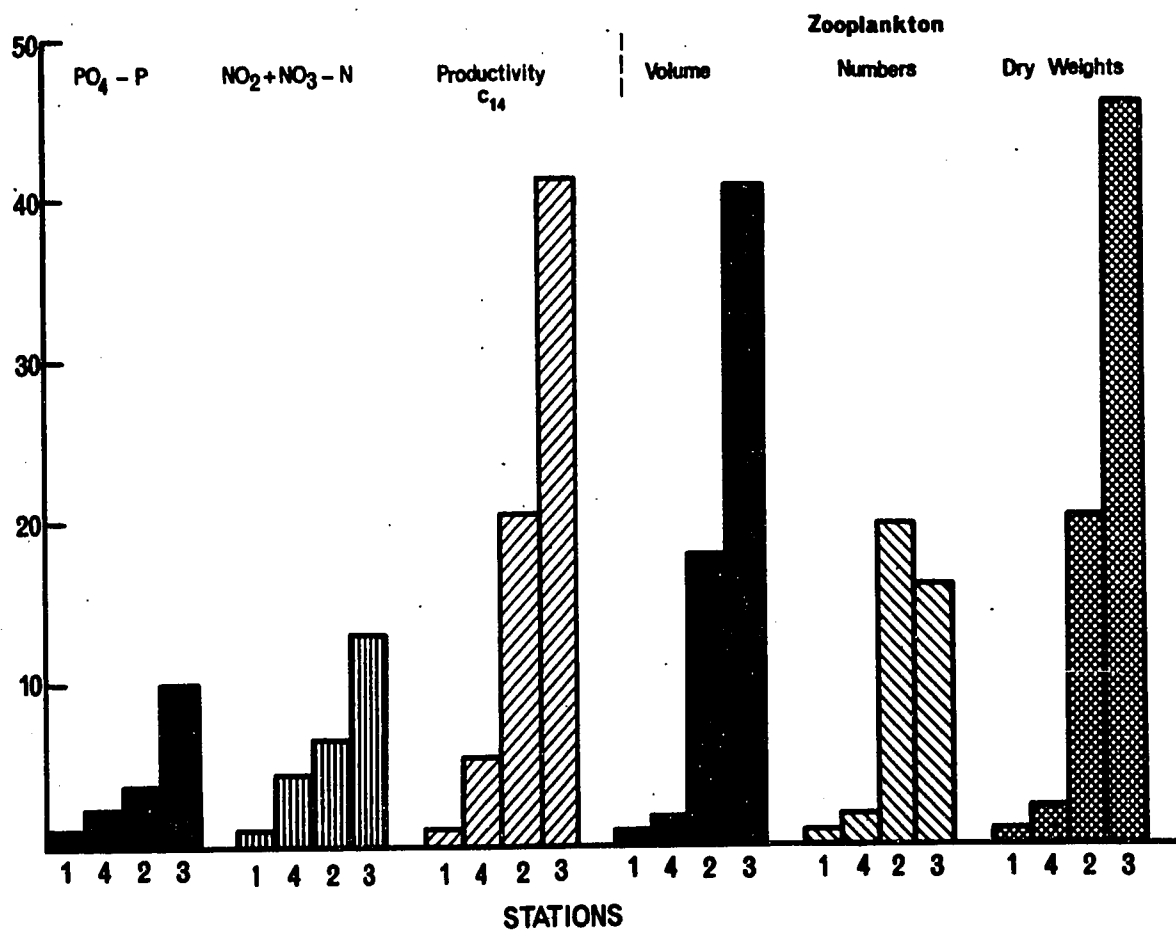


Fig. 6. Histogram of ratios of determinations of nutrient, primary productivity and standing crop levels.

the surface waters over a relatively short distance (cf. Grice and Hart-transect from Bermuda to New York).

The spatial distribution of some groups, especially pelagic larvae, is quite understandable on the basis of what is known of the benthic fauna. Many species of gastropods, sedentary annelids, lamellibranchs and cirripedes and echinoderms are abundant in the coral reefs which surround 4J, and in the harbour. The densities of larval forms again demonstrate the 1-3J gradient. The paucity of pelagic larval forms at 1J could presumably be accounted for on the premise that the greater depth there severely limits the density of benthic fauna.

Some of the free-living adult forms like Penilia avirostris and Lucifer faxonii are also well known characteristic inshore shallow-water forms and their absence from 1J serves further to characterise this station as a deep water oceanic station. It is in the copepod population that the main contrasts are highlighted. Some formal statements can therefore be made concerning the distribution of copepods in so far as they serve to characterise their areas of occurrence.

Harbour stations 2 and 3J.

The similarity in species composition at these two stations has already been mentioned. The copepod population in harbour consists of 18 species, only nine of which made significant percent contributions to the total population. Of the other nine species, 3 are parasitic and were taken only rarely, 3 were characteristic of 4 and 1J and their very rare occurrences were interpreted as being indicative of the influx of offshore waters. Of the other three, Labidocera scotti is a subsurface dweller, or at least negatively phototactic, and the other

two probably are as well, and therefore were taken only occasionally. Of the nine constant copepod zooplankters only three - Paracalanus aculeatus, Corycaeus amazonicus and Oithona plumifera - have parallel occurrence at all stations and their population densities serve well to underscore the trend of inshore-offshore decreasing population sizes. The other six species appear to be limited to the harbour and, with the exception of Acartia lilljeborgi maintain their highest densities at 3J. However, the populations at the two stations seem to fluctuate independently of each other, and the two stations further distinguish themselves from one another by the peculiar features such as the distribution of some non-copepod species. Species such as Penilia avirostris, Lucifer faxoni, Acartia lilljeborgi and Eirene sp. have their focal concentrations at 2J and spatial distribution tapers off toward 3 and 4J. (2J and 4J are undoubtedly areas of mixing between the two extreme stations, but mixing is probably much greater at 2J).

Oceanic 1J.

With 39 species, station 1J has the most heterogeneous community but population sizes are very small, the three most abundant average less than the three least populous species in harbour. Most of the harpacticoids and cyclopoids occurred at this station. Of the three regularly occurring and most abundant species only Undinula vulgaris and Paracalanus aculeatus are calanoids. U. vulgaris has a size range of 2-2.5 mm, P. aculeatus and Farranula gracilis are both smaller, ranging from .8-1.1 mm. There are many more species of the Pontellids and the other large carnivorous calanoids but their daytime densities are very small, in every case less than one per m^3 ; even if these populations were

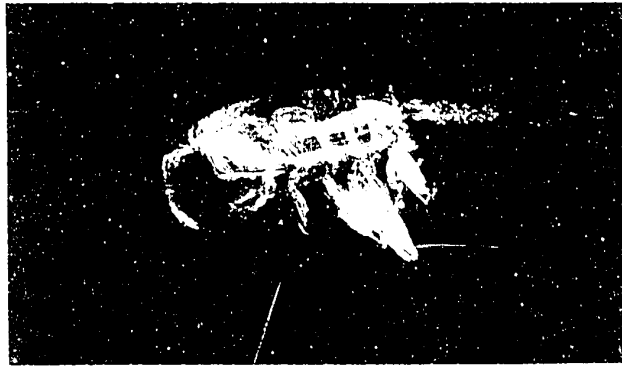
multiplied by 3.5 (night to day tows ratio) they could still rate as being very sparse. This situation is in contrast to the harbour population which is concentrated in a small number of species of copepods of relatively large size and very large population size. The copepods bulking in the zooplankton at the harbour stations range from .8 mm-4m with large populations in the 2-3 mm range. The size range of copepods is given in Figures 7a and 7b.

Station 4J.

This station distinguishes itself from 1J in two main ways :

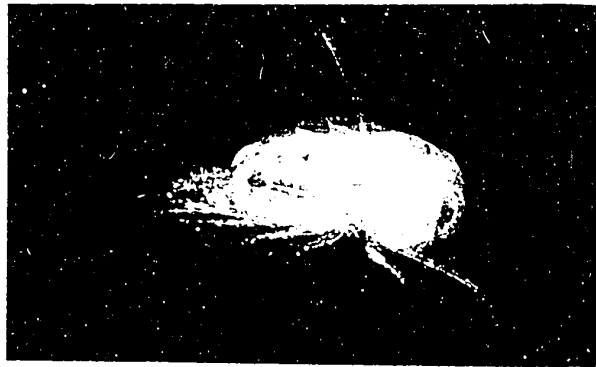
- a) In the high population densities of species like Undinula vulgaris and Paracalanus aculeatus, that are common to both stations and also in more species and larger population densities of larval forms.
- b) It appears to form the seaward limit of the spatial distribution of many inshore species like Lucifer faxonii, Penilia avirostris and Acartia lilljeborgi, as well as the shoreward limit to some characteristic oceanic forms.

1 mm



50.

Euchaeta
marina male



Undinula
vulgaris female



Pontellina
plumata male



Paracalanus
aculeatus female



Oncaea
venusta male

Fig. 7. Size range of copepods.

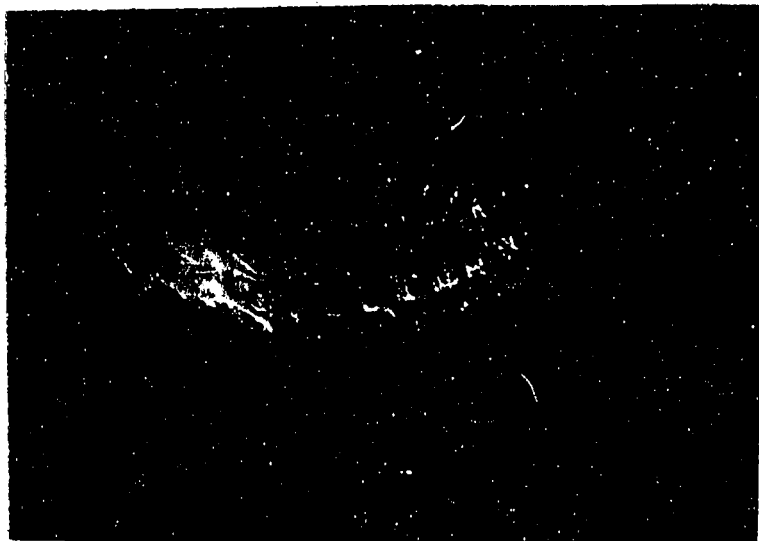
1 mm



Pontellopsis
regalis female



Pontella
securifer male



Neocalanus
robustior female

1 mm

Fig. 7b. Size range of copepods.

BREEDING

The reproductive activity of the various adult species of the zooplankton lacks synchronization and seasonal regularity. For many species breeding appears to take place all the year round with periods of intensified activity. To begin again with the copepods, there is evidence that most of the species are continuous breeders or at least have protracted breeding periods. Of the 40 free living species, 15 occur only infrequently - some obviously bottom living forms - and though taken in various stages of development do not provide enough connected evidence for a description of their breeding habits and cycles, but their occurrence is sufficiently randomly distributed in time to emphasize independence of climatic seasonality. The other twenty-five species display breeding patterns of the type described above.

Other non-copepod zooplankters display reproductive habits of the same categories as described for the copepods and observations and results for some selected species are discussed in the following pages.

Method.

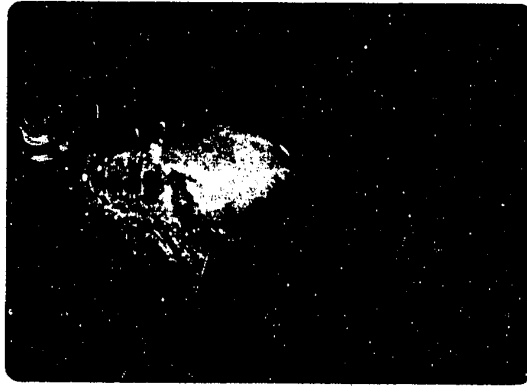
The patterns of reproductive activity were determined, as in other cases, on replicate counts. The entire sample was well shaken and a subsample of unspecified quantity pipetted into the counting dish. From each sample 100 specimens of the species under consideration were counted into cohorts of 10; of these only the adults in breeding condition were recorded. The total of these counts gives percent and the average of the replicate counts was the final accepted figure. Differences in counts ranged from 0-5%. It should be pointed out here that the method

of percent breeding individuals only serves to demonstrate the relative abundance of breeding individuals. Periods of maximum reproductive activity could be calculated from the absolute number of breeding individuals per unit volume of water, but since species population sizes and densities vary so greatly it was found inconvenient to represent variations on any one scale. The percentage basis was found most applicable to both large and small populations.

In non-ovigerous copepods a breeding state can be distinguished by several other features. For example, females of Undinula vulgaris, a non-egg bearing species, develop an opacity around the two terminal spines on the last metasomal segment. This opacity is more pronounced on the right spine and is further characterised by two reddish brown spots. The male then carries a specially modified fifth leg in a lowered position. It is with this leg that the spermatophores are transferred and attached to the right terminal spine of the female. In every female observed in this condition from one to five spermatophores were observed attached to this right spine. Well developed ovaries can also be seen through a transparent body, as for example in Eucalanus subcrassus.

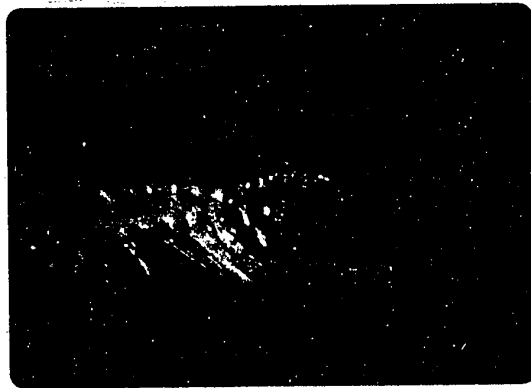
Candacia pachydactyla advertises its breeding state by an intensification of dark brown colour in pereipods, setae and thoracic terga as well as at the tip of the right terminal thoracic spine. Figs. 8a and 8b illustrate the breeding symptoms of some species of the copepods investigated. Any one or combination of these conditions in addition to nauplius stages in the medium is diagnostic of a period of active breeding. On the basis of these results the species investigated were grouped in the following categories :

54.



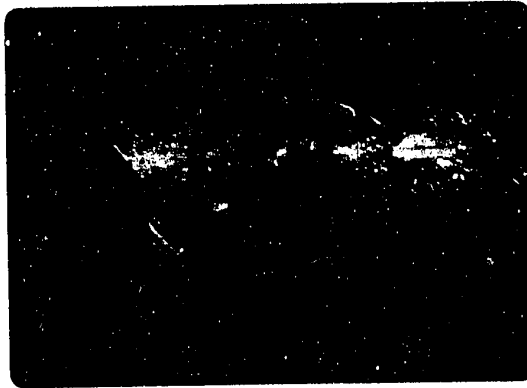
1.

x 16



2.

x 30

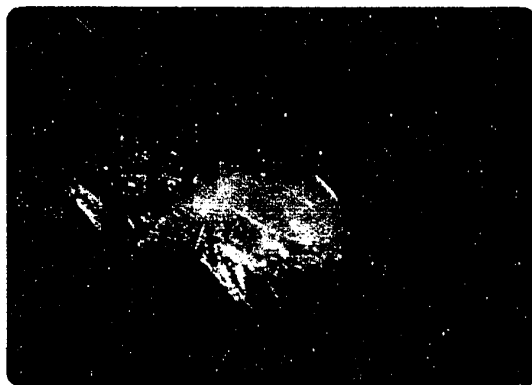


3.

x 20

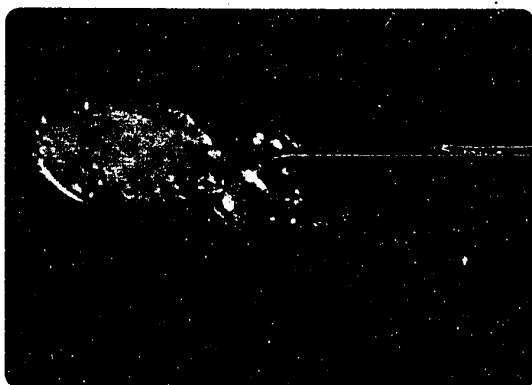
Fig. 8 a. Breeding conditions in some copepods.
1. Undinula vulgaris female with spermatophores.
2. Miracia efferata female with egg sac.
3. Euchaeta marina female with egg sac.

55.



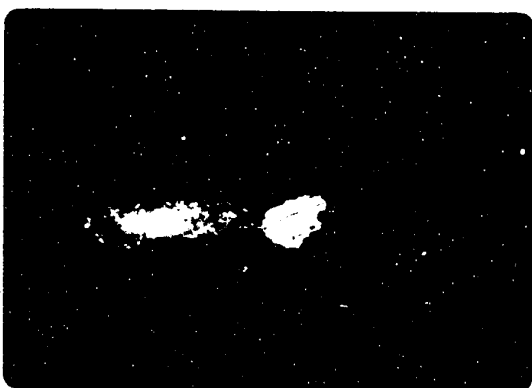
1.

x 50



2.

x 50



3.

x 60

Fig. 8b. Breeding conditions of some copepods.
1. Oncaea venusta female carrying male.
2. O. venusta female with young egg sac.
3. Corycaeus amazonicus female with egg sac.

Continuous breeders

Paracalanus aculeatus : It is known that this species holds spermatophores and egg sacs for a very short period, and egg sacs are easily lost in captivity (Coker and Gonzalez, 1960; Russell and Colman, 1934). Only very few adults with eggs were found in the preserved samples but immature stages and females in breeding condition were found throughout the year at all stations, and the maturation period is thought to be of approximately a month's duration. The long sampling intervals precluded the possibility of defining the period more exactly, but the repeated sequence of abundance of early larval stages followed by a large crop of adults in the succeeding month may reasonably indicate a cycle of breeding. At times this sequence, accompanied by a gradual population increase was particularly noticeable at 2J. This observation is supported by the findings of Gonzalez and Coker (1960) on the species in Puerto Rican waters. The fact that P. aculeatus is able to maintain dominance and a persistent adult population at all stations, suggests a survival advantage which could very well be a short maturation period combined with maintenance of a constant reproductive state. Russell et al (1934), working on the zooplankton off the Great Barrier Reef, found a similar situation for the same species of copepod but noticed a distinct falling-off of numbers from September to January. A similar falling-off period was noticed in this study, the decrease being more noticeable from November to January. It is reasonable to conclude, therefore, that for this species there is at least a rapid succession of broods with some intensification at particular periods of the year.

Farranula gracilis : Males and/or females with sperm sacs were taken in every sample; females with egg sacs were less frequent. It was

difficult to distinguish the nauplii of this species from those of four *Corycaeus* species to which it is closely related, hence evidence of its reproductive habits must depend on the presence of adults bearing either sperm sacs or eggs. Also of importance in deciding on a long or continuous breeding period is the fact of the continual presence of adults. These small copepods have very small life spans so there must be rapid replacement to maintain a constant adult population. There was also evidence of local intensification in breeding.

The histogram in Fig. 9a depicts the percentage of adults in breeding condition from month to month. It is obvious that at any sampling time there was a high percentage of the population in this condition; the average was 90.5% with a minimum of 67.5%. At 4J (Fig. 9b) the picture was similar to that at 1J; at any time of the year from 50-96% of the adult population displayed an obvious breeding condition.

Corycaeus species : (C. latus Dana, C. americanus M.S. Wilson, C. amazonicus, C. speciosus) all display similar habits of continuous or protracted breeding. Other species comprising the group of continuous breeders are Oncaea venusta, O. mediterranea (cyclopoids), Oithona plumifera and Oithona nana. Gonzalez and Coker find the cyclopoids O. nana and O. simplex as well as the harpacticoid Euterpina acutifrons Dana to be perennial breeders. Figs. 10a and b give the percent population of Oncaea venusta in breeding condition at stations 1 and 4J. Fig. 11 represents the percent breeding of Oithona nana at the 3J station. Of the calanoid species, Undinula vulgaris and

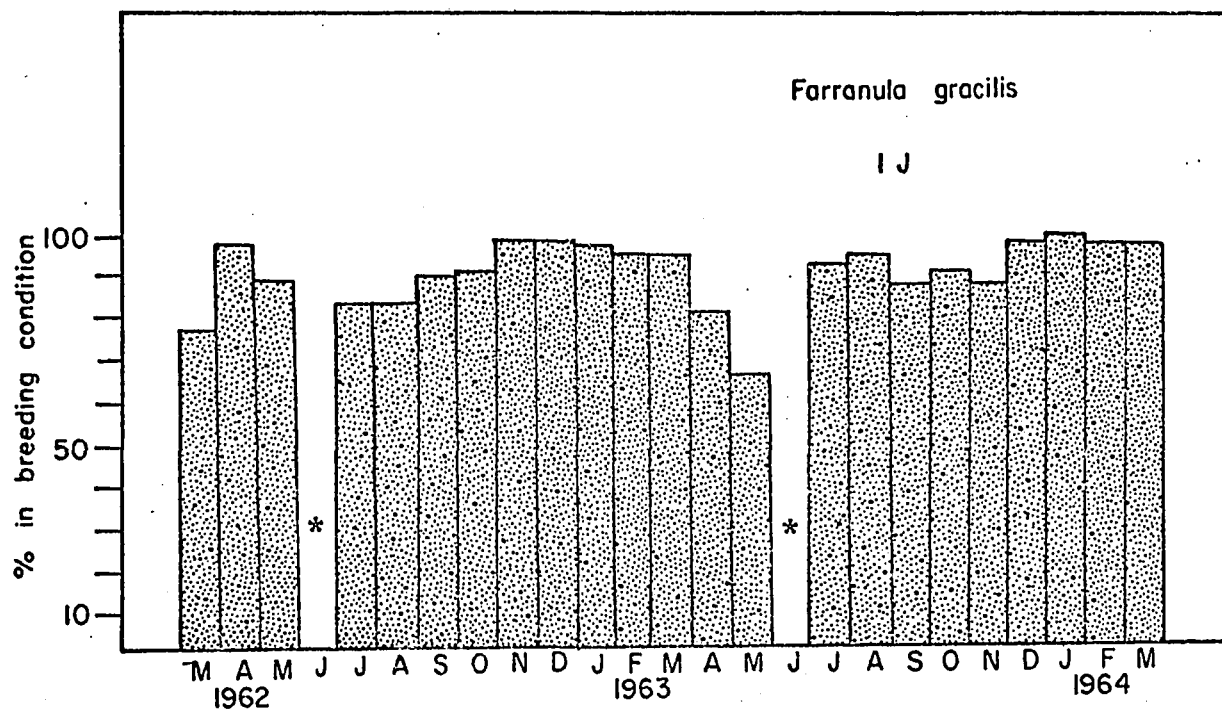


Fig. 9a.

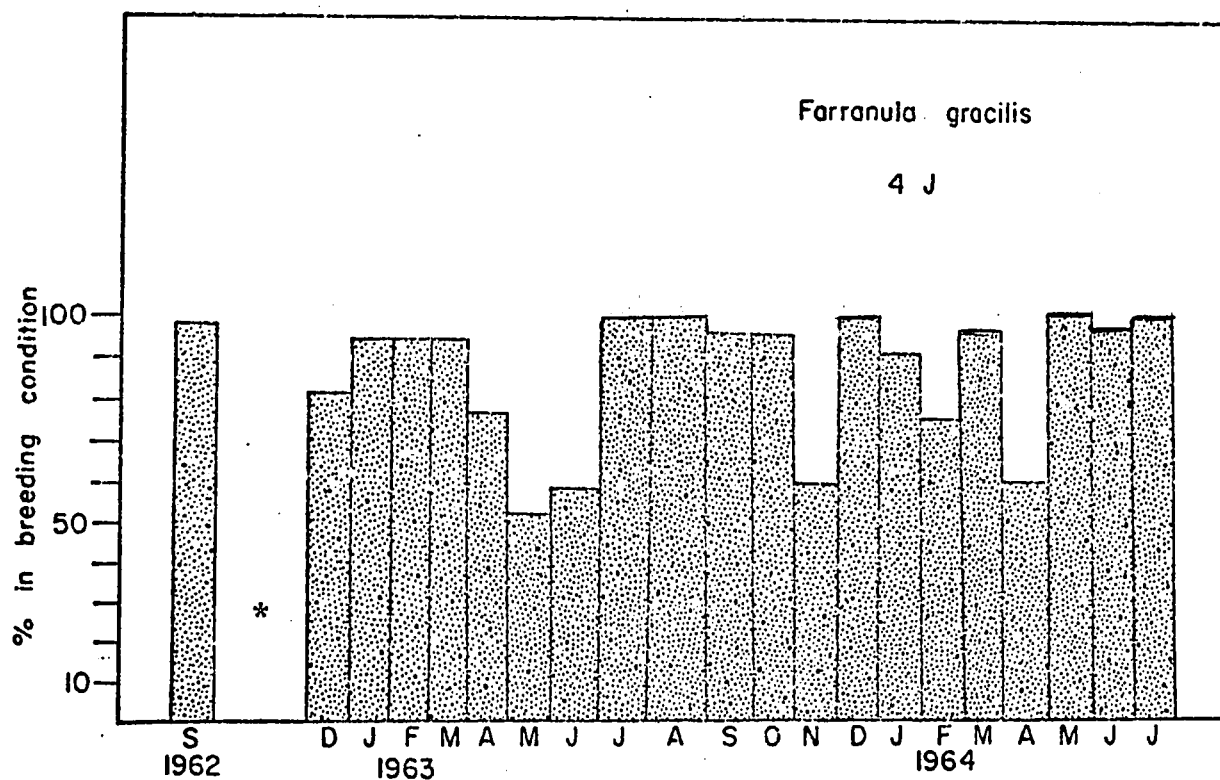


Fig. 9b.

Fig. 9a-9b. Breeding activity of *Farranula gracilis* expressed as % of population in breeding condition each month.
* means no sample was taken on that date.

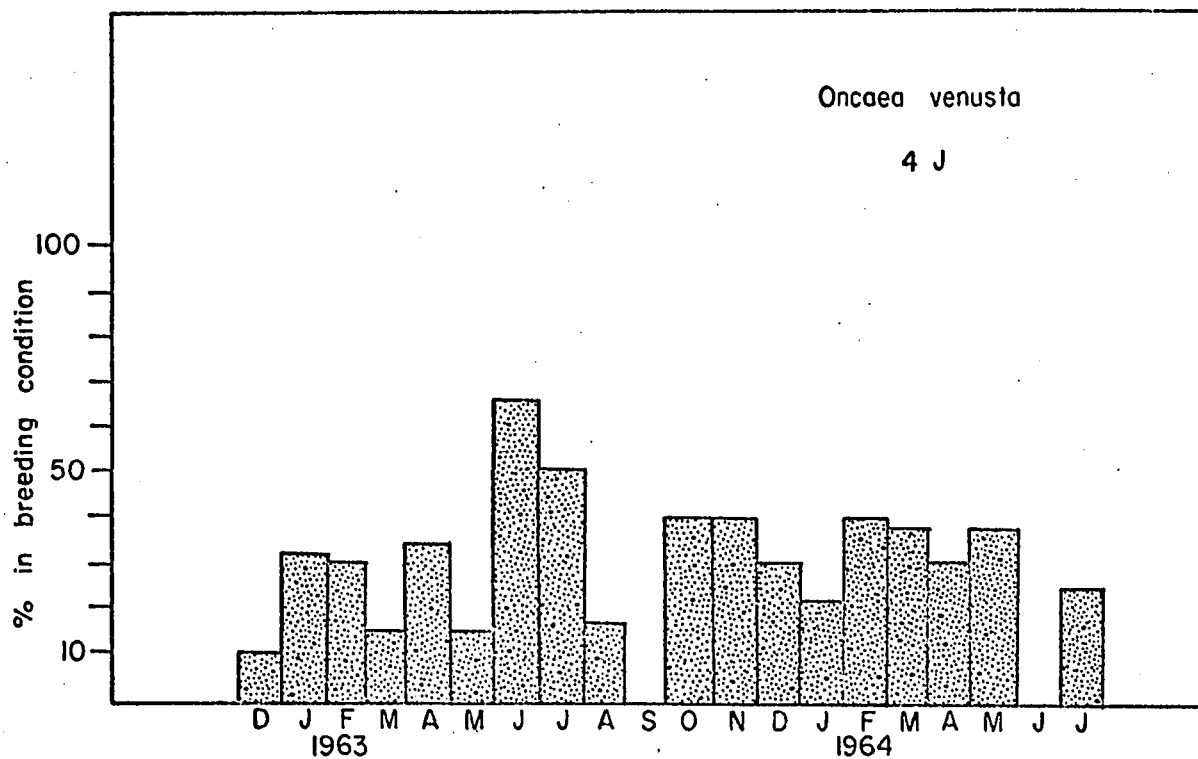


Fig. 10a.

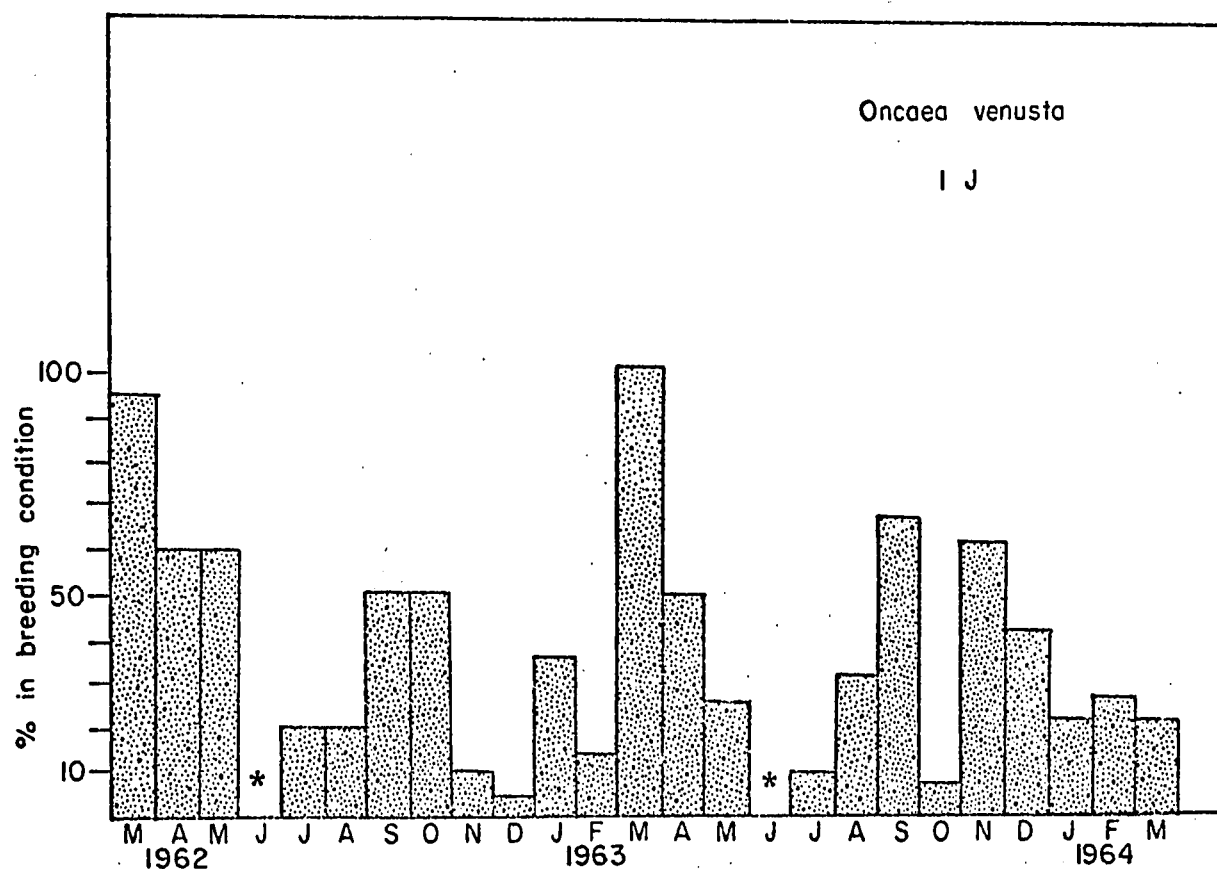


Fig. 10b.

Figs. 10a-10b. Breeding activity of *Oncaea venusta* expressed as % of population in breeding condition each month.
* means no sample was taken on that date.

Centropages furcatus also seem to breed continuously but with a longer maturation period. The two Temora species, Acartia lilljeborgi, Calanopia americana and Euchaeta marina Prestandrea being of more sporadic occurrence did not provide enough connected evidence of continuous breeding but adults in a reproductive state and juvenile stages were sufficiently randomly distributed over the months to indicate lack of periodic seasonality, and suggest at least protracted periods of breeding. One calanoid, Eucalanus subcrassus had a nauplius and other juvenile stages sufficiently distinctive to be easily separated from the others. Nauplii and other juvenile stages were taken in almost every sample. This indicates a rather rapid succession of generations and a short maturation period. Eucalanus subcrassus is one of the biggest copepods of the area and, since copepods show determinate growth, would be expected to take longer to mature.

Euchaeta marina, a comparatively large predatory calanoid, carries an egg sac of about 10 large eggs (see fig. 8a) and probably takes as much as six weeks to mature; the data, however, are insufficient to make this an incontestable conclusion.

Species with sporadic breeding periods.

The evidence derived from the data suggests that the species Miracia efferata (Fig. 12) and Oithona plumifera have sporadic breeding habits with breeding periods lasting from one to three months. This is, however, not necessarily true. These species were taken in only small numbers and in some months no specimens were found at all. Whether or not the population had disappeared or merely migrated below the sampling area cannot be ascertained. For this reason these two species are

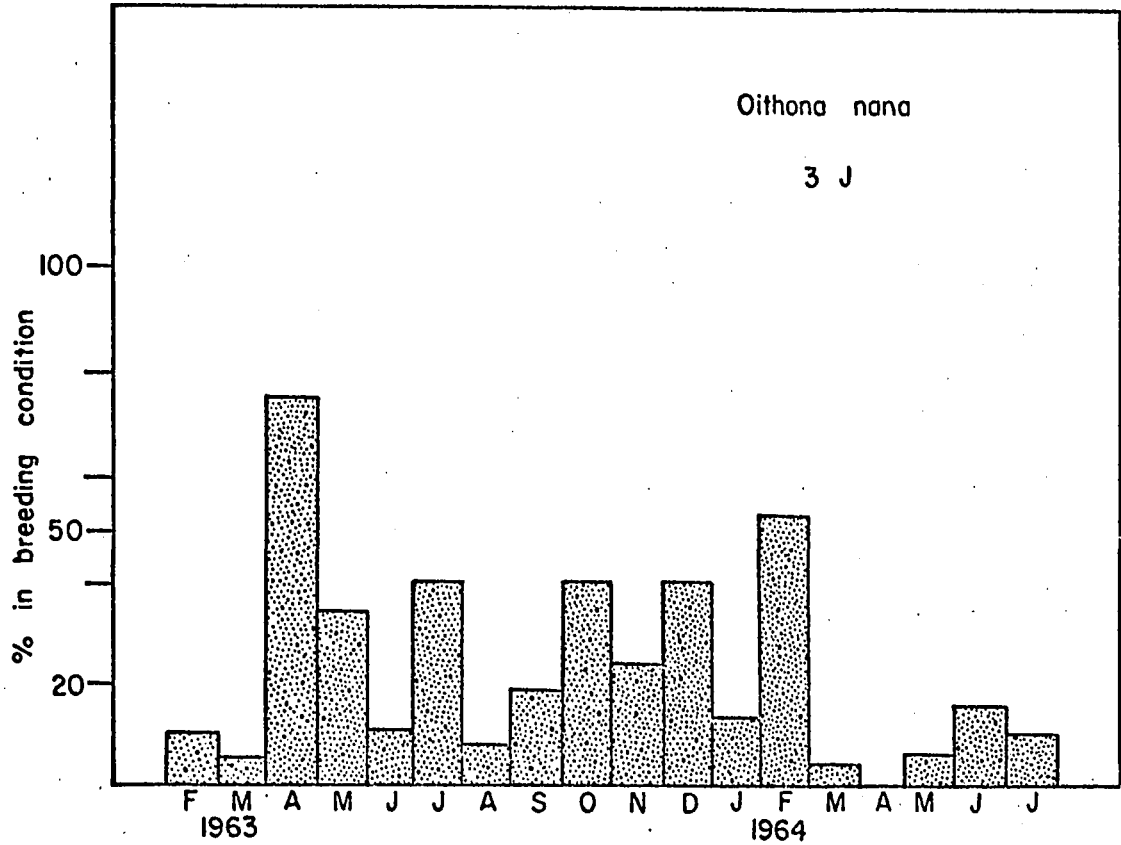


Fig. 11. Breeding activity of *Oithona nana* expressed as % of population in breeding condition each month.

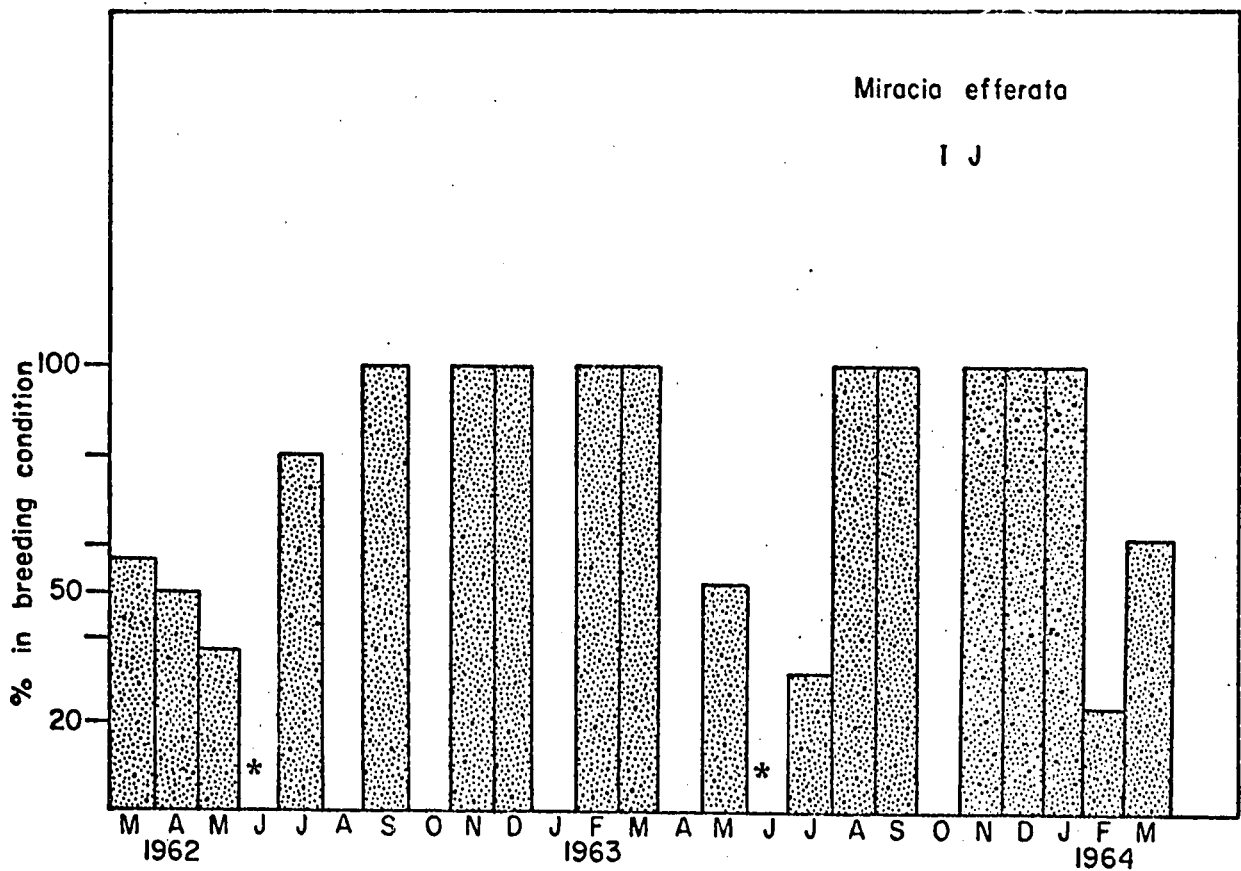


Fig. 12. Breeding activity of *Miracia efferata* expressed as % of population in breeding condition each month.
* means no sample was taken on that date.

tentatively placed among those with sporadic breeding periods, but they might well be continuous breeders. A point in evidence is served by the case of Oithona nana at stations 3J and 2J. Whereas O.nana produced adults in breeding condition for 14 consecutive months at 3J, as shown in Fig. 11, the data provide evidence of several peaks of breeding activity of shorter durations during those same 14 months at 2J. It is suggested elsewhere that 2J is subjected to lateral water exchanges that serve to vitiate normal expected sequences.

It might be of some significance that the copepods maintaining a high percent productive rate also maintain a high average population density, for example, Paracalanus aculeatus, U. vulgaris and F. gracilis. The species with low productive rates or sporadic breeding habits constitute only a small percentage of the total copepod population.

Breeding in some non-copepod species.

Larvacea : The developmental history of the larvacea was difficult to follow mainly because of the problem of identifying the eggs and distinguishing the early stages of the three genera present. The older stages and adults were readily recognised by differences in the width and relative lengths of the tails. Because Oikopleura II was most abundant and regular in its occurrence at 3J it was assumed that most of the juveniles belonged to this species. The six month period from August 1962 to February 1963 seems to show a two month periodicity in breeding. A large crop of adults in one month, a few adults and some juveniles in the next, followed again by a large crop of adults; but from March to July both adults and juveniles were present every month. (During this period adults of Oikopleura I were present and in small

numbers only, in February - May, and those of Fritillaria, also in small numbers, in February, May, June and July.) From August to December the two month rhythm seemed to have been restored, but a good crop in January preceded total absence in February, and a small number in March; an apparent disappearance in April was followed by large numbers in May.

Cladocera.

Penilia avirostris : The samples from 2 and 3J provided good evidence of the reproductive activity of this species. The data are presented as absolute population numbers for 3J and as a percentage histogram for 2J.

From the data in Table 19 and Fig. 13, it was concluded that the developmental period for the species is very short, probably two weeks : in four weeks, May 1-28, 1964 the population had increased sevenfold. This feat was twice duplicated in the period 28/10/63 to 16/12/63. The animal broods six to seven young at a time, and the young mature so rapidly that they themselves begin production of parthenogenic eggs even before they leave the parent's brood pouch. Apparently in the period of prolific reproduction a new batch of eggs is deposited in the pouch every five to seven days (Davis, 1955), and propagation will take place at any time provided the right conditions are in operation. The population builds up rapidly to a peak and either declines slowly or disappears suddenly. From what is known of cladoceran biology (Wickstead, 1965) these periods of low density or apparent disappearance are preceded by the production of males and resting stage eggs. In more temperate latitudes population growth and size is closely linked with food supply and climatic conditions, but in the present survey no significant positive

TABLE 19.

Absolute densities and population changes for the cladoceran Penilia
avirostris at station 3J from February 1963 to July 1964.

Date	Density/m ³	Observations
3/2/63	758	Most with eggs
26/2/63	643	Most with eggs
28/3/63	1182	Few with eggs
26/4/63	1849	Few with eggs
27/5/63	1059	Most with eggs and young
19/6/63	3266	Some with eggs
9/7/63	384	Few with eggs
1/8/63	132	Few with eggs
23/8/63	91	Few with eggs
19/9/63	0	
28/10/63	495	Most with eggs
18/11/63	2733	Most with eggs
16/12/63	12856	Few with eggs
24/1/64	0	
21/2/64	3298	Most with eggs
23/3/64	1821	Few with eggs
23/4/64	0	
1/5/64	427	Most with eggs
28/5/64	2860	Most with eggs
29/6/64	767	Few with eggs
27/7/64	469	Some with eggs

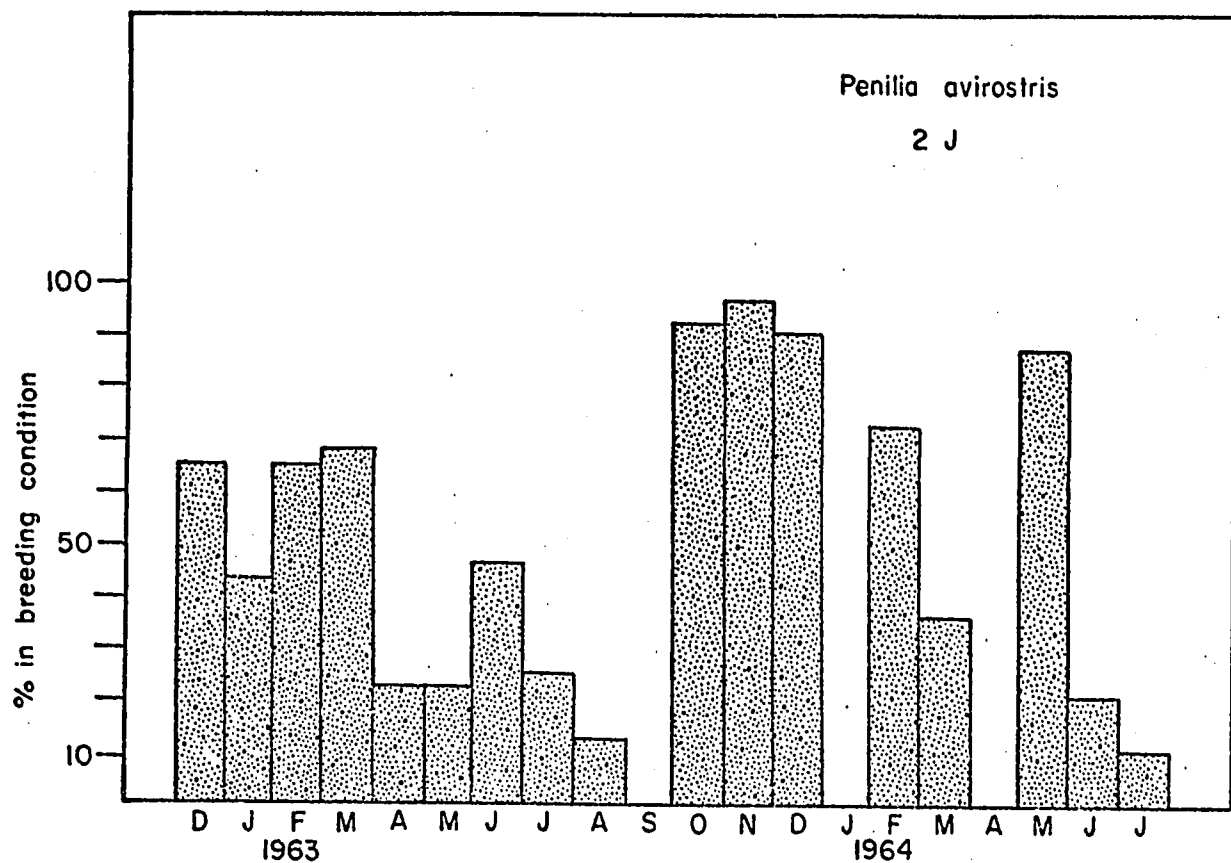


Fig. 13. Breeding activity of *Penilia avirostris* expressed as % of population in breeding condition each month.

correlation between abundance of Penilia and phytoplankton population size could be demonstrated. However the availability of food does not necessarily fluctuate with general phytoplankton abundance. Moreover, even slight imbalances in optimal environmental conditions result in the disappearance of all but scattered individuals.

This pattern of reproductive activity was similar to that of the species at station 2J where it was more abundant.

Chaetognaths : There appears to be only sketchy information on the life span or maturation period of Sagitta in tropical seas. Direct observations have been done on different species in different temperature belts. From the evidence Redfield and Beale (1940) have concluded that breeding, and presumably growth rate, are controlled by the physical characteristics of the water, particularly by temperature. The number of generations produced each year increases with distance from the poles (Owre, 1960). Dunbar (1941) worked out a two year life span for S. elegans in arctic and subarctic waters, each generation producing one brood a year. Towards the southern boundary of its distribution in the temperate region, S. elegans produces five or more broods per year; though this was not specifically stated, the conclusion to be drawn is that the life span is correspondingly shorter.

Various schemes have been suggested for determining the stage of maturity of chaetognaths (Thomson, 1947; Pierce, 1951; Colman, 1959; Ghirardelli, 1961a, 1961b, quoted by Alvarino). It is generally agreed that the testes ripen and expel their contents some little time before the ovaries; and in the more comprehensive scheme of Ghirardelli the most sexually ripe individual (Stage IV) is characterised by tail regions devoid of sperm and ova fully developed, of a polygonal shape, and with

small granulations around the nuclei. For the purposes of this study Ghirardelli's stage IV was accepted as the only reliable evidence of breeding condition.

Sagitta enflata : There is also some question as to whether the animals die upon once producing eggs (Dunbar, 1941). Stone (1966), however, concluded they are apparently iterparous; some species spawn once per year, others, including S. enflata, spawn several times or continuously throughout the year, depending on the animal's geographical location. The results of this survey concur with Stone's findings: the breeding period may be long or short but without any obvious rhythm or being restricted to any particular time of the year. For instance, at 3J S. enflata was taken with mature eggs in eleven consecutive months from February 1963. At 2J S. enflata was taken with stage IV eggs from December 1962 through March 1963 and in odd months after that. The combined results from these and the other two stations provide a picture of continuous breeding.

Continuous breeding can be produced either by closely succeeding or overlapping generations or by individuals in a protracted breeding condition. If the first method applies, then variations between generations should show up in the monthly samples, that is, in any one generation variations in length of mature individuals should be less than the month to month variations. The size of stage IV egg bearing adults in any one sample varied greatly from 12 to 33 mm. Stone also found a similar range in length classes of breeding individuals of S. enflata (7 to 20 mm) in the Agulhas current off South Africa. This wide range in sizes suggests that there might be different age classes among adults and that the animals may continue growing and breeding for

protracted periods. Owre (1960) also accepted the differences in length classes of S. bipunctata off Miami as evidence of several cycles of reproduction. Alvarino (1965) advises caution in such assertions because the location of Miami admits of immigration from several regions where maturity is reached at a different size range. This criticism is hardly admissible for the sheltered harbour waters of the 3J station.

Breeding stages for the other two species of chaetognaths were sporadically distributed in time at any one station but combined data strongly indicated that mature ovigerous individuals could be sampled from the area during any month of the year.

Decapods.

Lucifer faxonii : This species also appears to be a continuous breeder. Since L. faxonii occurred in such large numbers at stations 2 and 3J and was spatially separated from L. typus (at 1J), the larval forms found at the harbour stations were assumed to be those of L. faxonii; these could readily be arranged in serial order to provide a complete life history of the species. Eggs could only be identified with certainty when carried by the adult female - those found loose in the sample were indistinguishable from those of S. enflata and other animals. However, the slightly older egg with nauplius larva could be separated easily, as also the free metanauplius and other stages. Nauplius and metanauplius were never taken in large numbers but in view of the great abundance of the later stages it could be assumed that there was a rapid transition from these earlier stages - probably no more than 24 hours (Brooks, 1882).

At 2J females in berry and males and females with spermatophores were observed in June, October and December of 1963, and in April and June of 1964 but zoea, mysis, mastigopus and adult stages were taken in every haul from December 1962 to November 1964. At 3J ovigerous females were observed in June, July, August, and December of 1962, in April and October of 1963, and in January, February, March and May 1964. Again all stages from zoea to adult were present in every haul from April 1962 to November 1964.

On the basis of this evidence of egg bearing adults, breeding would seem to be sporadic with no recognisable pattern in temporal distribution. It is possible that egg bearing periods of short duration were missed and that the indifferent mixture and abundance of later developmental stages

represented overlapping generations. Moreover, the continued abundance of both juvenile and adult stages strongly suggests a steady input of new individuals.

On combining data from the two harbour stations it turns out that females in berry were taken in every month of the year except August, September and November.

RELATIONSHIPS BETWEEN PRIMARY AND
SECONDARY PRODUCTION

As stated in the introduction, one of the aims of this study is to establish, if possible, relationships between primary and secondary production. The dynamics of any ecological system is always more difficult to determine than the effects of the system, and the question of the productivity of tropical waters relative to temperate and Arctic boreal waters cannot be satisfactorily resolved until the dynamics of these tropical systems are understood.

During the process of counting the zooplankton, an apparent inverse relationship between zooplankton numbers and phytoplankton density was observed, that is, whenever the sample looked like a thick green soup there were relatively fewer animals to be counted, and these were mainly larval forms. A clean, clear sample was generally associated with high concentration of zooplankters, especially copepods. These observations were similar to the findings of Marshall and Orr (1930) in Loch Striven, Moore (1949) in the North West Atlantic, and Harvey et al (1935) off Plymouth. This reciprocity of relations in phytoplankton-zooplankton populations was most obvious at the 3J station. Some attempt will therefore be made to elucidate the nutrient-phytoplankton-zooplankton relationships. For this purpose use will be made of the results of nutrient chemistry and primary productivity measurements determined by Steven et al (1965) concurrently with the zooplankton measurements. The results for all four stations are summarised and reproduced in Table 20 though this section is primarily concerned with results from

TABLE 20.

Average values and standard errors of nutrient chemistry and primary productivity measurements at stations 1-4J (reproduced from ONR report, .Beers et al, 1965).

	n	1J	n	4J	n	2J	n	3J
C ₁₄	20	2.84	26	15.32	26	58.23	26	117.52
mg/m ³ /day		.74		3.20		8.01		21.0
Chlorophyll <u>a</u>	20	0.10	25	0.28	25	0.85	25	1.88
mg/m ³		0.01		0.02		0.06		0.19
Phytoplankton	20	32.2	22	58.5	22	136.7	21	1351.0
cells/L x 10 ³		7.8		14.1		17.1		288.0
Phosphate-P	18	0.023	26	0.054	26	0.084	26	0.232
ugA/L		0.003		0.005		0.006		0.091
Nitrite-N	19	0.012	26	0.036	26	0.056	26	0.155
ugA/L		0.002		0.012		0.018		0.057
Nitrate-Nitrite-N	18	0.12	25	0.53	26	0.78	26	1.14
ugA/L		0.02		0.15		0.27		0.355
Silicate-Si	18	1.57	26	2.55	25	3.49	26	10.70
ugA/L		0.09		0.24		0.28		1.93

station 3J.

The annual range in surface temperature is small, 26.1 to 29.8°. In salinity too the amplitude of change was small; the yearly range is from 34.2 to 36.4‰. Marked decrease in salinity following flood rains was usually accompanied by an increase in nutrient concentrations and a drop in both plant and animal numbers, but recovery was rapid and marked by phytoplankton blooms.

Because there are such slight station-to-station and monthly differences in the temperature, salinity and radiant energy, these conditions can be regarded as constant or non-significant fixed level environmental factors. It is in the nutrient levels that significant temporal-spatial changes are most obvious.

Nutrient chemistry. The concentrations of inorganic nutrients were generally low throughout the year in comparison to values obtained for temperate and arctic latitudes, but they show the same offshore-inshore gradient as the other parameters studied, i.e. 1J 4J 2J 3J. At 2J there was on the average 2.2x as much silicate 3.6 x PO_4 -P and 6.5x $\text{NO}_3 + \text{NO}_2$ -N as at 1J, while at 3J the corresponding ratios are 6.8, 9.5 and 10 respectively. The effects of these higher nutrient concentrations are reflected in higher production levels. The results for 3J, being subject to slightly wider variations, depict this most clearly. Figure 14 is a graphic representation of the results for two nutrient substances and of the phytoplankton counts. The points that emerge from this comparison are :

- a) the ratio of nitrogen to phosphorous is about 5:1, i.e. less than the expected value of 8:1 (Raymont).

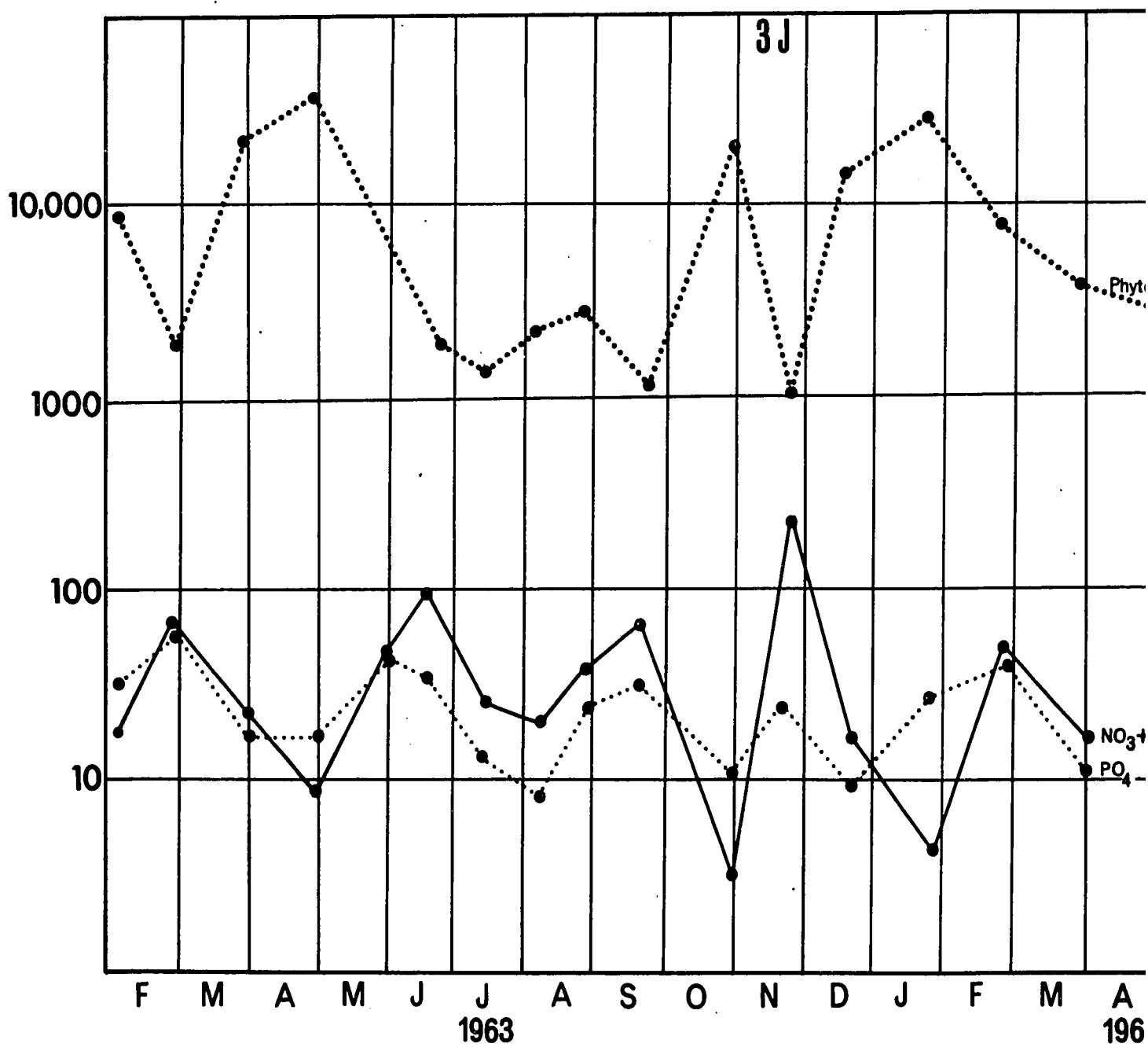


Fig. 14. Estimated monthly fluctuations in NO₃+NO₂ and PO₄ in mg/m³ and phytoplankton in cells/m³.

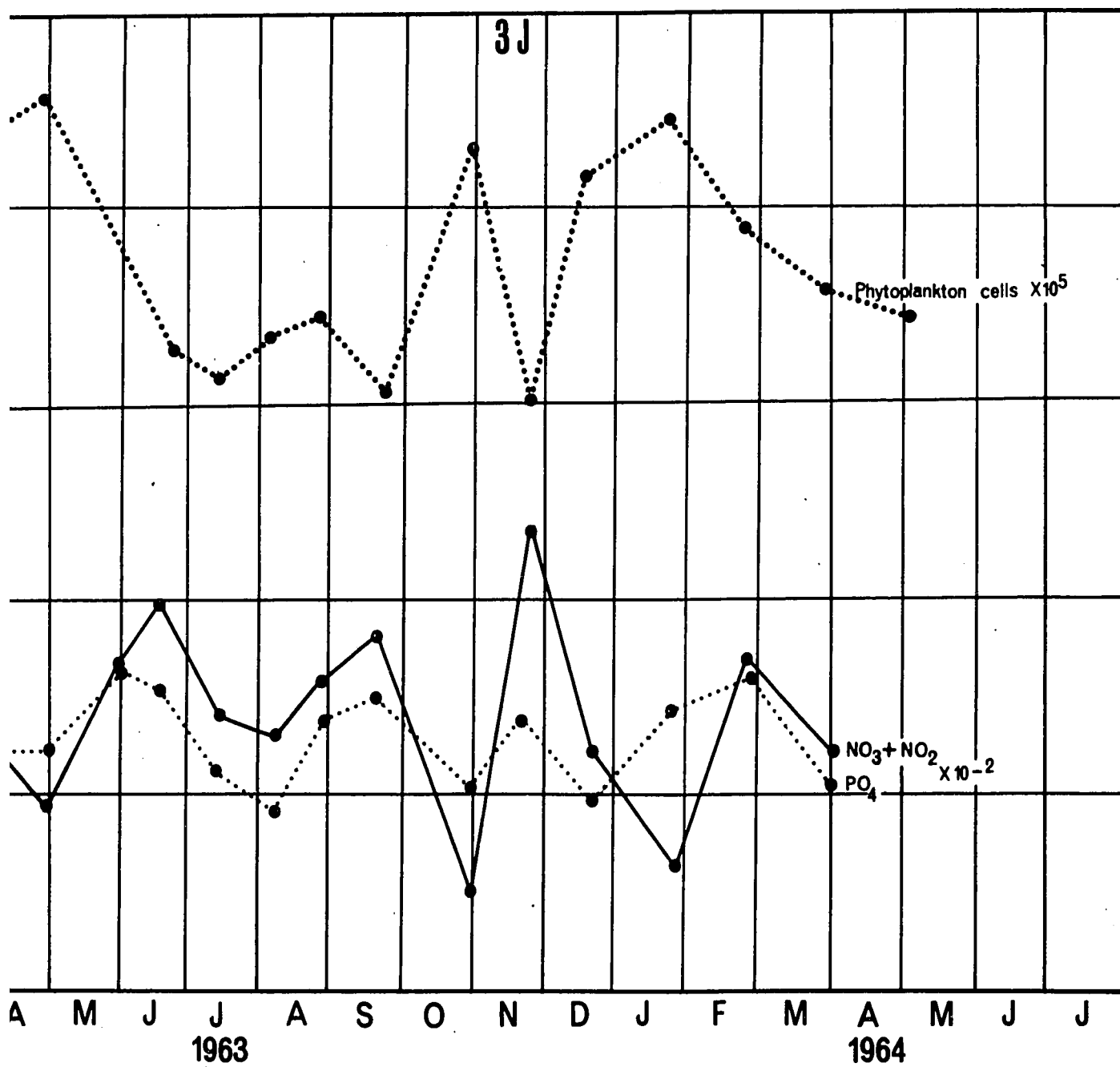


Fig. 14. Estimated monthly fluctuations in NO₃+NO₂ and PO₄ in mg/m³ and phytoplankton in cells/m³.

- b) The monthly fluctuation in the concentrations of the two substances are coincident, which suggests a coupled cycle of utilisation.
- c) Phytoplankton concentrations vary inversely with N and P.

It is a generally accepted belief that nutrients, especially the nitrates, limit production in the tropics. To explain more fully the idea of nutrient-phytoplankton-zooplankton relationship, a brief recapitulation of the conceptual model as proposed by Marshall and Orr, Buzzati-Traverso and others (Bogorov, 1958) will be made here.

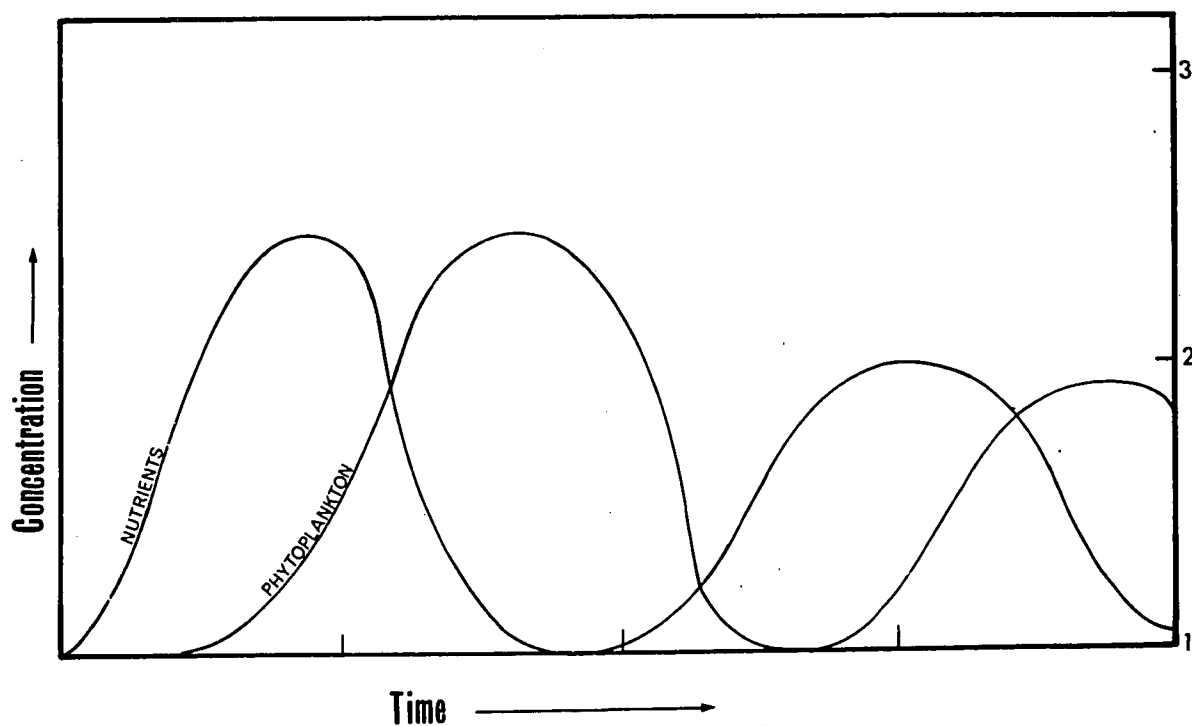


Figure 15. Classical model of temporal relationships between nutrients and phytoplankton concentration.

The classical model (Fig. 15) for the relation that exists between nutrient material and phytoplankton bloom is one that produces an alternation of positive and negative correlations. A bloom is triggered by the sudden availability of nutrient substances and the coincidence of optimal light and temperature conditions. The peak of the bloom (i.e. when $\frac{dP}{dt} = 0$, according to the Fleming equation quoted by Raymont) is achieved when the nutrient material is exhausted or the rate of depletion of the phytoplankton balances out the rate of reproduction of the cells. The rising zooplankton population, which at this time exhibits a positive correlation with the phytoplankton population, reaches its peak at some time interval after that of the phytoplankton. When the zooplankton peak is reached the phytoplankton is already on the decline. Indeed the zooplankton numbers might yet be at their height when the phytoplankton production is at its lowest ebb. The inevitable wane in zooplankton sets in, and, depending on the rate of factors of regeneration of nutrient substances, the two troughs in production might coincide, and then the cycle repeats itself.

It must be realised that the extent of the phytoplankton bloom is limited by minimal concentration of any one of the vital substances (Liebig Minimum Law quoted by Hardy, 1962); that the rate of exhaustion and replenishment will be subject to variation of factors other than the rate of cell multiplication, that is, their concentration is determined by a combination of biological transformation and physical translocation in much the same way as the phytoplankton crop is controlled; and that the ideal relationship between the two nutrients and phytoplankton would be a phased periodic function.

At a cursory glance the data presented graphically in Fig. 14 do not correspond to the type of relationship expressed in Fig. 15.

This is a very important result of these investigations. The relationship expressed in Fig. 15 is representative of conditions of high latitudes which are exposed to more pronounced extremes of seasonal variations and where energy cycles encompass relatively wide time intervals. The type of data presented in Fig. 14 reflect a telescoping of seasonal extremes and energy cycles. The cycles of production here are much smaller and more numerous over any year period than those for higher latitudes and there is no way of determining from the data at what points in the respective cycles the absolute figures represented here were taken.

This sort of data is not subject to any simple mathematical manipulation. No meaningful correlation coefficient can be extracted. In any case, each increase and subsequent decrease does not in any sense fit a normal frequency distribution or a binomial or Poisson distribution, so that the product-moment coefficient methods are inapplicable. One could perhaps, perform a periodogram analysis on both nutrients and plankton and then carry out some sort of chi-squared test to see if the two periodic functions are the same, but with somewhat random variations in wave-length and amplitude, such an analysis would be formidable, and the whole operation would be statistically doubtful. In theory this problem is a case of the classical "Volterra fluctuations", but since the fluctuations are not isochronous and have varying amplitude, a Volterra analysis would be so mathematically formidable that one could scarcely attempt it. One presumes that the periodic fluctuations in nutrients and the effect of the one upon the other would produce a curvilinear relationship.

A close approximation of this relationship is depicted in Fig. 16

Phytoplankton / total Phosphorous

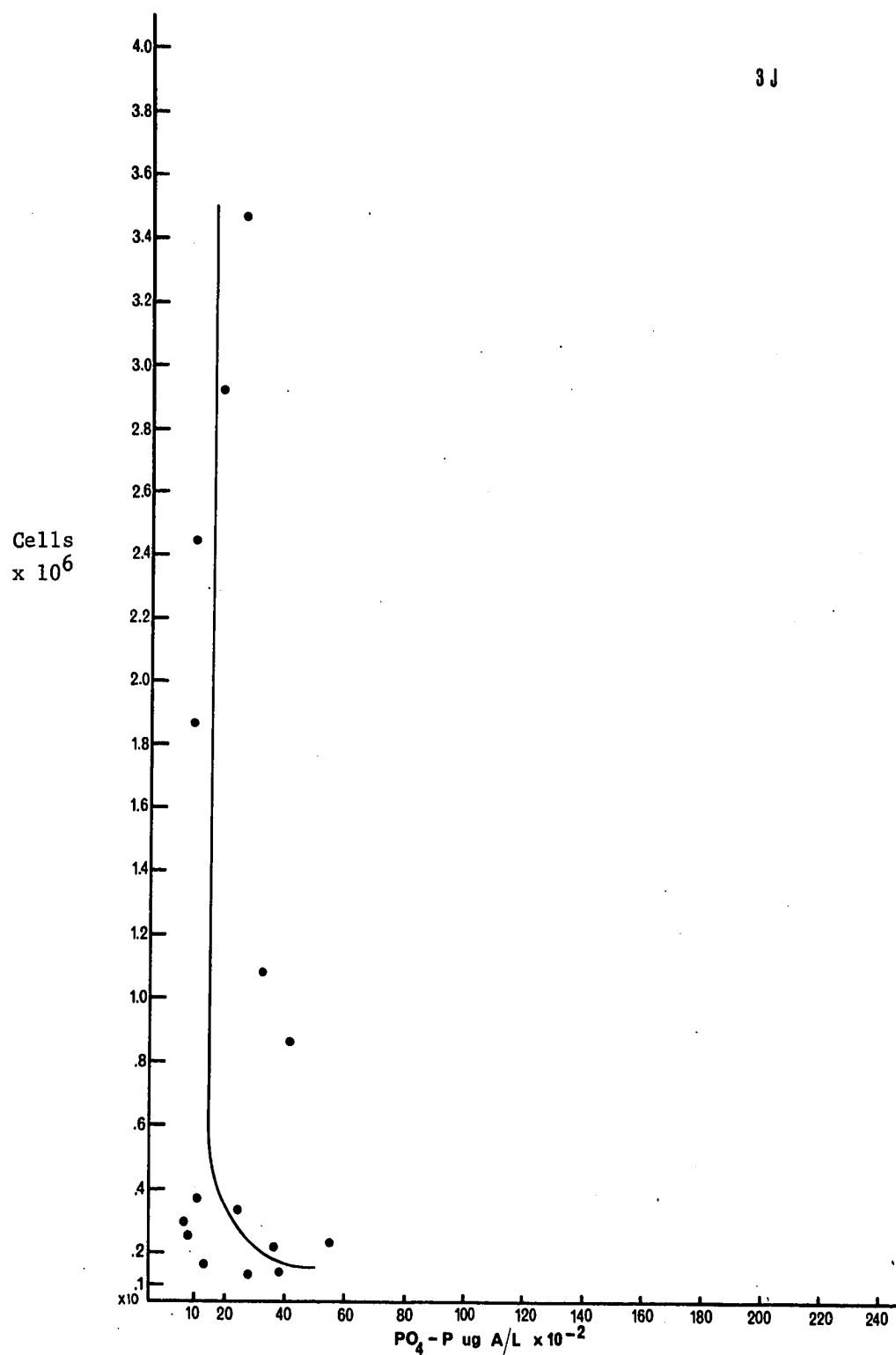


Fig. 16. Plot of phytoplankton cells $\times 10^6$ as a function of phosphate-phosphorous in mg/m^3 . $\mu\text{g A/L} = \text{mg/m}^3$.

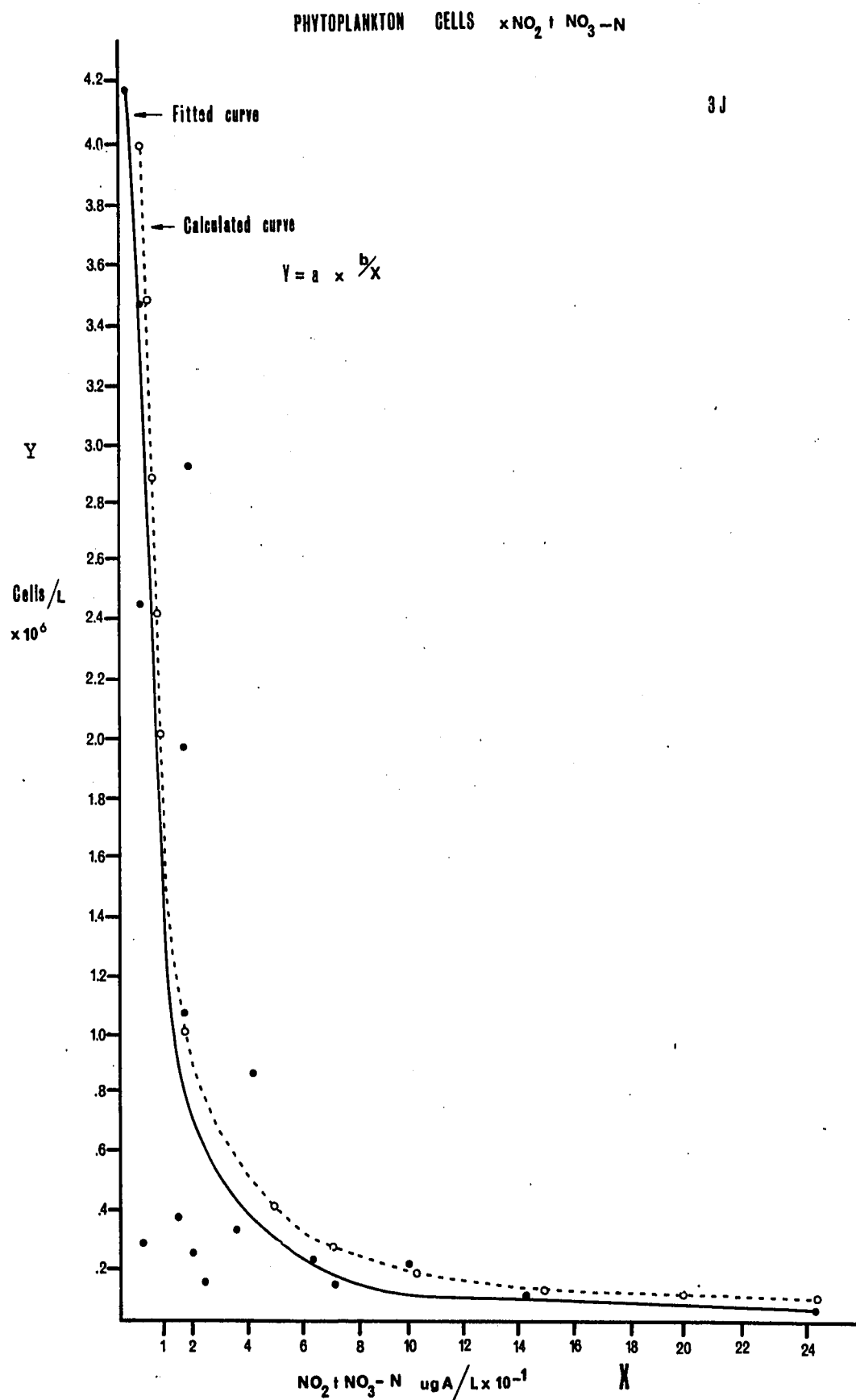


Fig. 17. Plot of phytoplankton cells as a function of total nitrogen measured in mg/m^3 . $\mu\text{gA/L} = \text{mg/m}^3$.

and Fig. 17, which are plots of phytoplankton numbers as a function of phosphate-phosphorous and total nitrogen at 3J. The similarity of the two regression lines on the same function serve to reinforce the observation that there is a common factor regulating the concentration of both these nutrient substances. The curvilinearity of both lines also suggests a direct relationship that could best be represented by the equation $y = a + \frac{b}{x}$, where y = phytoplankton numbers, a = minimal value of nutrients supporting pulse or minimal value for phytoplankton numbers and x = nutrient concentration.

It was not possible to work out minimal concentration figures, but the observed minimal values for both phytoplankton and nutrients were substituted instead. For the phytoplankton, this value turns out to be 1000 cells per litre at the 3J station. Substituting this for a in the equation $y = \frac{b}{x}$, and setting the value for b as 200 (this is an approximate value derived from a rough solution of the equation) the broken curve in Fig. 17 is obtained. The broken line represents the calculated curve, while the continuous line is the best fit to the raw data. The group of points in the lower left hand corner representing low concentrations of both substances may be explained by the lag-oscillations in the system. If this is accepted and also that the fitted curve is a fairly good solution to the equation, then it is reasonable to assume that a correlation, (though not necessarily a causal relationship) exists between nutrient and phytoplankton levels, and that the variations in time sequences and amplitude are due to the interaction of a host of biotic and environmental parameters.

Phytoplankton-zooplankton relationships.

Since the copepods are the dominant group of animals at all four stations and all the species taken in large numbers are mainly herbivorous, they may be treated as the primary exploiters of the plankton. The cyclic changes in copepod densities and food abundance are represented in Figs. 18 and 19. Fig. 18 shows the generally inverse correlation between total copepod numbers and primary production as determined by C_{14} uptake. In Fig. 19 phytoplankton densities are plotted against the density of a single species; Paracalanus aculeatus is a small, surface-loving phytophagous calanoid which is especially numerous at 3J. The species has shown itself at both harbour stations to be very sensitive to environmental changes. Changes in its population size are therefore probably a good index to the interrelationships of these two trophic levels.

The relationship between primary production and copepod numbers as shown in Figs. 18 and 19 is clearly not like the model but essentially similar to that adduced for nutrient-phytoplankton levels. Departures from the model may be attributed most proximately to :

- a) sampling intervals which were too widely spaced in relation to the growth cycles and therefore missed subtle refinements in the system. It is recognised that if these intervals were shortened the graph picture could be altered either way.
- b) copepods are not the only phytophagous forms : others, for example cladocerans, larvacea and decapod larvae are abundant, and inclusion of these would raise the animal numbers graph on the page. However, the copepod population is subject to predation by other members of the

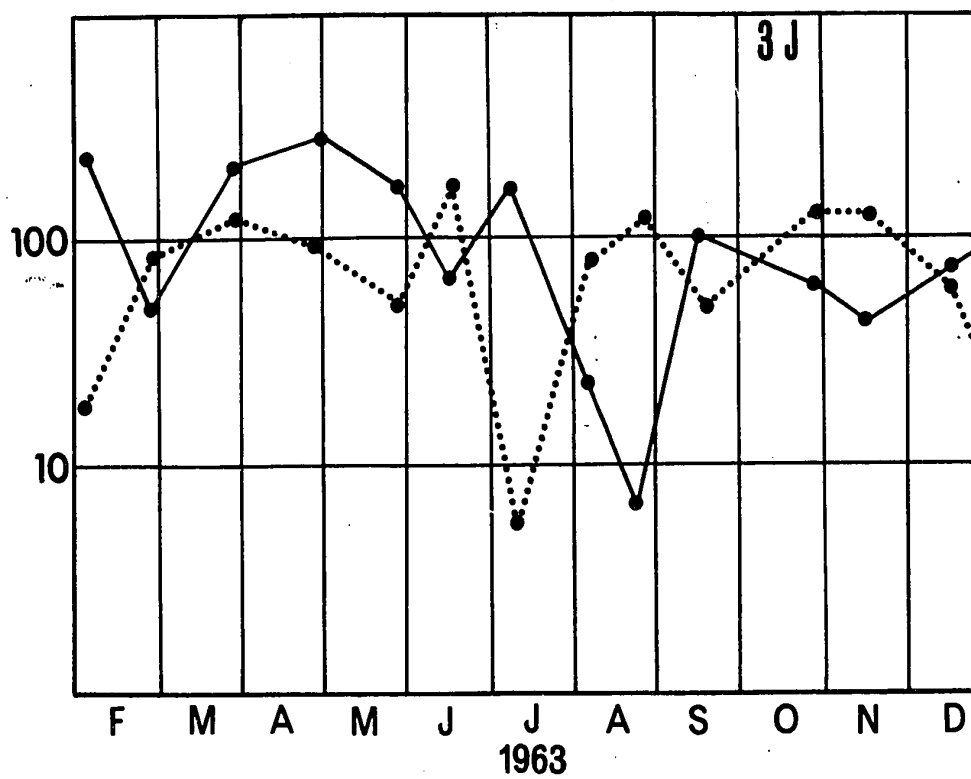


Fig. 18. Showing the generally existing between primary production mg/m^3 uptake and the primary grazer copepod density m^3 .

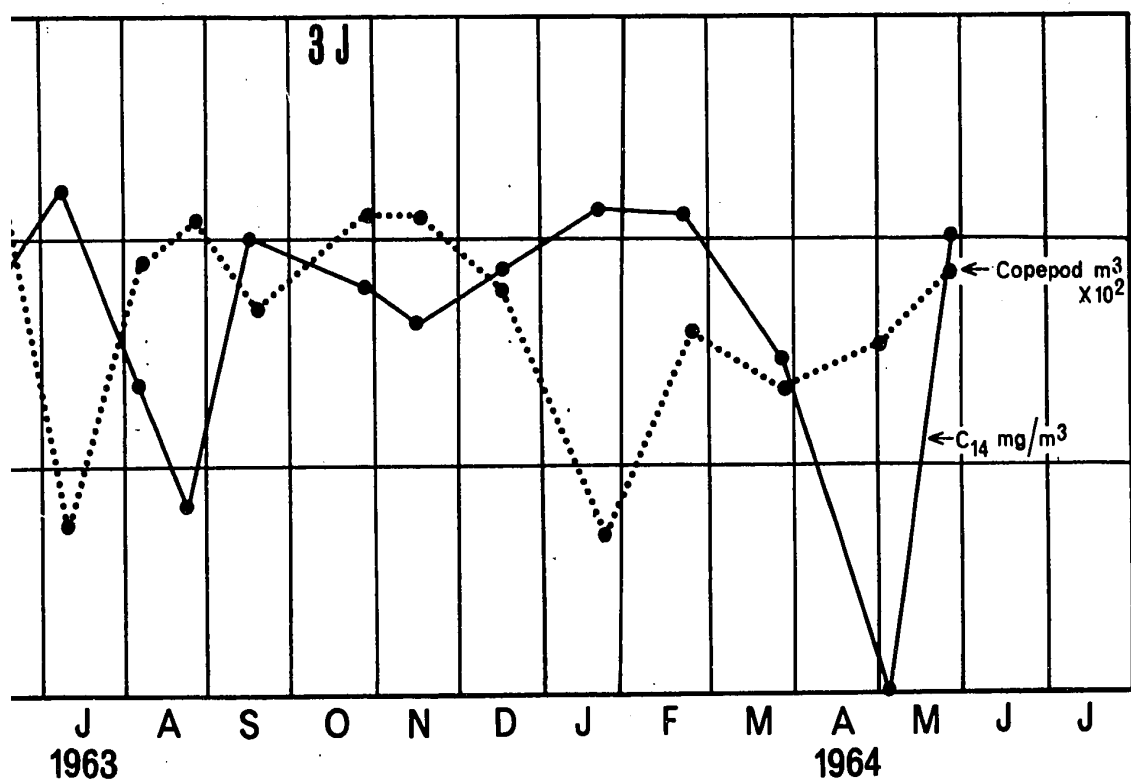


Fig. 18. Showing the generally inverse relationship existing between primary production determined by C₁₄ mg/m³ uptake and the primary grazers represented by copepod density/m³.

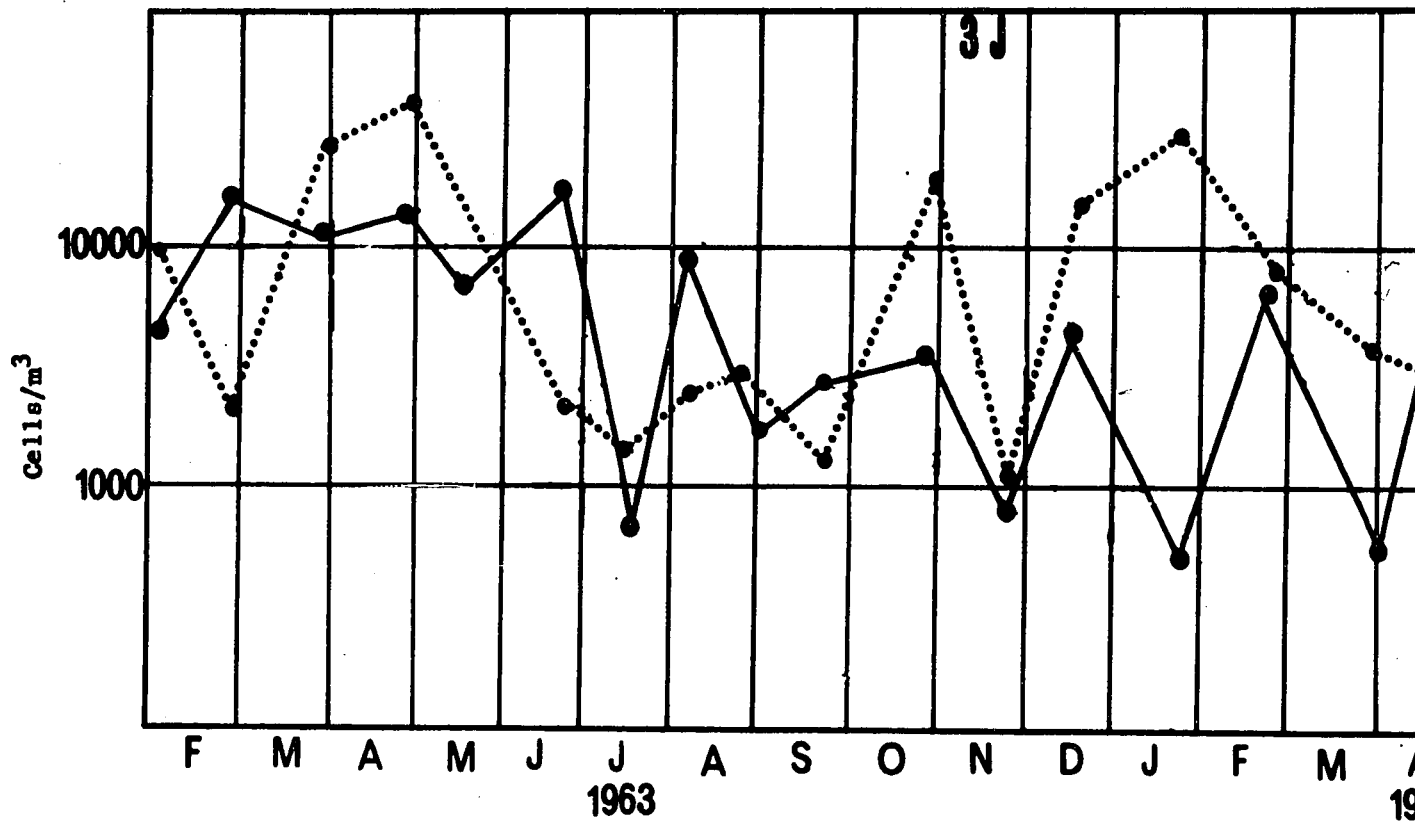


Fig. 19. Temporal relationship between phytoplankton abundance and density of *Paracalanus aculeatus*, a phytophagous copepod used as an index to secondary production. The two distributions are adjusted to show relative fluctuations in density.

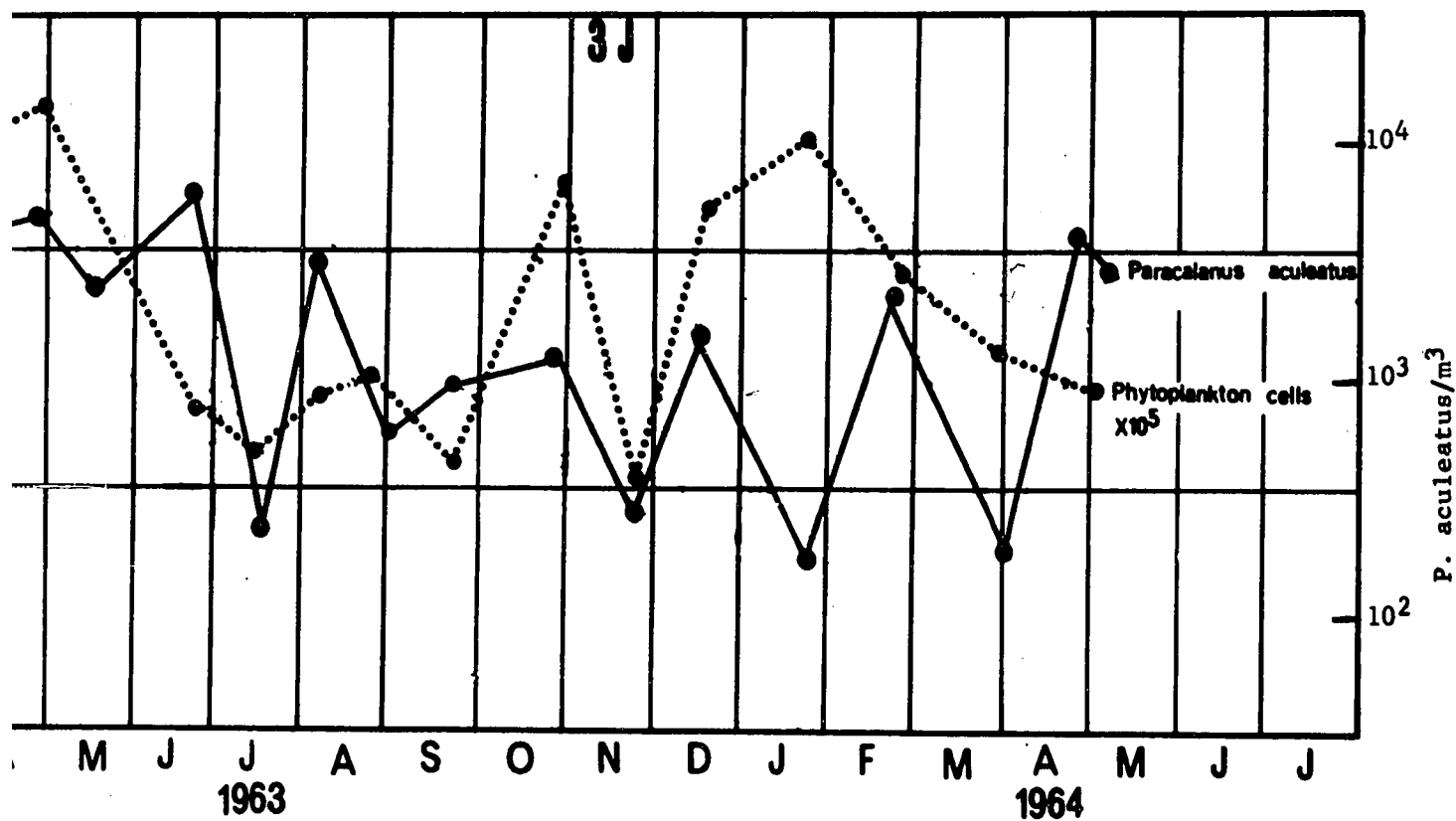


Fig. 19. Temporal relationship between phytoplankton abundance and density of *Paracalanus aculeatus*, a phytophagous copepod used as an index to secondary production. The two distributions are adjusted to show relative fluctuations in density.

holoplankton, notably Sagitta species, coelenterates and other copepods. Only if all these factors could be properly adjusted would the true picture emerge.

Despite these departures, however, it is maintained that fairly good approximation of the ideal model is achieved at 3J.

Conditions at other stations.

This picture of extended relationships between nutrient levels and the two levels of trophism is not so obvious at 2 and 4J. The values quoted in Table 20 show that none of the observed facts agrees with the expected results; the nitrogen-phosphorous ratio at each station is more than 8:1 (Raymont, 1963); the quantities present vary randomly with respect to one another and with primary production. These findings are not surprising. It has already been mentioned that these two stations, especially 2J, are areas of great mixing and, in the words of Raymont "The concomitant changes in nutrient and diatom density often cannot be followed in the open sea, since mixing processes obliterate the relationship".

At 1J where production at all levels is lowest, the picture in summary appears to be one of a low grade continuous production with small oscillations and a rapid turnover of nutrient materials by organisms in a constant reproductive state. The average nutrient values at 3J are about ten times that at 1J, yet both primary production, and secondary production as measured by zooplankton volumes, weight and species counts, are approximately 40 times as great as they are at 1J. The nutrient concentrations that obtain at 1J are obviously above the

dilution minimal for the support of a phytoplankton population. Yet species populations of both the flora and fauna at 1J are relatively so very small. It is likely that when the concentrations of nutrients together reach the limits necessary to set off a phytoplankton pulse, the total amount of substances, singly or combined, is insufficient to sustain the bloom through a period long enough for the maturation of the juvenile stages of the fauna. There might, therefore, be a high juvenile physiological mortality and, in that case, there would not be enough individuals to take advantage of the next bloom. These results, along with those of the breeding habits, indicate a very complex nutrient-phytoplankton-zooplankton relationship.

DISCUSSION

Volumes

Comparison with volumes in other areas.

Because of differences in methods used in collection, treatment of material and presentation of results, it is not easy to effect comparisons of available quantitative data. Many authors merely record the number of individuals/m³ of water, some per unit time of tow, some differentiate stages of development, whereas others consider only adults. Many authors indicate total weight or total volume/m³, whereas others refer this value to the water below one m² at the surface (Bogorov, 1958). The volumes of zooplankton recorded here are in reference to the number of cubic meters towed. The tows were timed but the time values are valid only at 1 and 4J stations. The mean volumes of zooplankton in cc/m³ of water filtered are as follows :

	1J		4J		2J		3J
	Caribbean Sea		Shelf		Harbour head		Harbour basin
	.02		.04		.46		.82
Ratio	1	:	2	:	23	:	41

Clarke in 1940 reported ratios of 1:4:16 for the Sargasso Sea, slope and shelf of the American seaboard and Grice and Hart in 1962 obtained ratios of 1:4:12 for the same areas. The mean volume value obtained by Grice for the Sargasso Sea is the same as that obtained here for

the Caribbean Sea - $.02 \text{ cc/m}^3$ at 1J and this value is of the same order of values reported by Clarke for the European side of the Atlantic Ocean and Baltic sea - $.01-.02 \text{ cc/m}^3$. In the Gulf Stream displacement volume determinations yield similar values, $.02-.03 \text{ cc/m}^3$. Bsharah (1957) has reported two- to three-fold increase in zooplankton in the upper 600 m of the Florida current off Miami in the period March to June, and he thinks this constitutes a seasonal peak for the area. The mean values derived from 26 monthly samples from Barbados (Beers, Steven and Lewis, 1965) is $.12 \text{ cc/m}^3$. This is six times average values obtained by other workers in the tropical North Atlantic. The composition of the Barbados plankton has not been determined but Clarke included salps in his volume determinations while Grice excluded salps (which he found unusually abundant) from his measurements. However, it is believed that Orinoco River and Amazon River drainage contribute to an increased fertility in the Barbados area of the Caribbean. All volume measurements obtained in this study exclude the larger medusae that otherwise make harbour values even higher.

The values estimated for 3J are more strictly comparable to those derived by Deevey (1952) for Block Island Sound, but for the purposes of comparison with results obtained by Grice and Hart, Clarke and St. John (1958 quoted by Grice) the two harbour stations are classified as neritic waters.

Temporal variations in volumes in the neritic Jamaican waters are of a much lower order than those in the area of Grice's study. The highest value obtained for a single tow by Grice was 13.64 cc/m^3 and minimum value was $.12 \text{ cc/m}^3$. This gives a variation ratio of 1:129.

Despite this wide variation, mean values for all neritic areas was .24 cc/m³. At 3J the highest (washed) value was 3.98 cc/m³ and the lowest .10 cc/m³ (which represents a variation factor of 1:40) and mean value was .82 cc/m³. These values attest to the high productivity of Kingston Harbour waters; on the average they were 4.5 to 5.75 times those of slope and 1.5 to 4 times those of the shelf waters in the area of Grice's study.

Numerical abundance.

Density of zooplankters per unit volume from each of the four stations appears to be higher than values obtained by Grice and Clarke for higher latitudes on both sides of the Atlantic. The highest value of 2401/m³ obtained from neritic waters by Grice and Hart in July of 1961 was less than the lowest value for the 3J station - 3878/m³ for June of 1964. The values from 3J are much closer to those reported for sheltered estuarine waters in the region of New York. Deevey's (1952) estimates for Block Island Sound, based on a no. 10 net collection varied between 5000/m³ and 34,000/m³. At 3J the range in densities was 3878 to 40,967/m³ with an average of 15,799/m³.

It has been established that partially enclosed inshore waters normally support high zooplankton populations; among the benefits accruing from such enclosed systems might be mentioned the limitation of high tidal movement and water exchange in so far as this serves to limit dilution of high nutrient concentrations accruing from land effect.

Station 2J numbers are even more impressive by comparison with those quoted above. The mean density value is 16,722/m³ with minimum and maximum of 1,389 and 106,612/m³ respectively. The variation factor is 89; but this maximum density which so heavily weights the average

value is more than three times the next nearest number, and was due almost entirely to a phenomenal population burst of the cladoceran Penilia avirostris which comprised 85% of the zooplankters for that haul.

The numerical abundance of zooplankters at 1J was not so variable. Minimum, mean and maximum values are 145, 823 and 2445 respectively, giving a variation factor of 16. However, these figures are much higher than those obtained by Grice in the Sargasso Sea, minimum $18/m^3$ and maximum $128/m^3$. Fish (1954) reported a yearly average of $239/m^3$ zooplankters in the Sargasso Sea at a station off Bermuda. According to his data the total number of zooplankters varied from $15/m^3$ to $600/m^3$ with a well defined augmentation period in May-June. Although the variation at 1J was less dramatic, there was a significant increase in numbers in October of each year which may be associated with the local wet season for reasons already discussed. Other peaks in numbers occurred in June and July of 1963 and January and March 1964.

Seasonality.

The apparent lack of seasonal pattern in the fluctuation of variables seems almost to be the theme of these observations and results. Reference to Fig. 3a shows that at 3J there appeared to be a gradual increase in plankton volumes during the late "summer" months and "autumn" of 1963, followed by a gradual decline during the "winter" months and "spring". A similar development can be noted for station 2J only that here the peak in standing crop, as measured by volumes, is somewhat displaced on the time axis, occurring in February 1964 and the decline continues until June (1964). Unfortunately, the high density

of phytoplankton and easy clogging of the nets at 2 and 3J made tows taken before February 1963 very unreliable for comparative studies, but at stations 4 and 1J it was possible, on the basis of average meter-wheel readings for metered tows to extrapolate values for the non-metered tows. As the resultant mean displacement volume was unaffected by inclusion of the unmetered tows their inclusion for comparative purposes was considered defensible.

	4J	1J
Average displacement volume for metered tows	= .0432	.0212 cc/m ³
Average displacement volume including non-metered tows	= 0.431	.0212 cc/m ³

At 1J these extrapolated values provide for the period March 1962 to March 1963, a picture similar to that found in the harbour; for the period 1963-64 this picture breaks down completely and the peak in standing crop (and indeed a record value) for this station for the period under study was in January 1964. At 4J fluctuations in volumes are so completely randomly distributed in time as not even to give a semblance of seasonality.

The same randomness is apparent in both species abundance and population densities. At station 1J, in January and February of 1963 low volumes were associated with low copepod species abundance (10 in each case) and low species population, average 43/m³ and 103/m³ respectively. The sample for January 1964 contained 16 species of copepods of which Undinula vulgaris (380/m³) and Farranula gracilis (404/m³) were the highest percent contributors. A very high volume measurement .104 cc/m³ was associated with this population outburst. Again in October

of 1962 nineteen species contributed to a copepod population whose total mean density was $1574/m^3$. To this population three species alone contributed 91.8% - Paracalanus aculeatus with $1085/m^3$, Farranula gracilis $188/m^3$ and Undinula gracilis $173/m^3$.

Again in October 1963 the total copepod density at this station was $2067/m^3$. The highest single contributor was Farranula gracilis $826/m^3$. Five other species had densities of more than $100/m^3$ and mean species density was $172/m^3$.

Thus it may be seen that there is no obvious consistent pattern in the occurrence of the species or the size of their individual population. High copepod densities may be due to concurrent population burst of a few species or to the cumulative effect of a relatively large number of small populations.

Since the four stations under study are subject to identical climatic variations, it would be reasonable to expect that the effects of such variations would express themselves in coupled oscillations in some measurable attribute of standing crop. The fact that the oscillations at four stations are neither coupled nor phased along the time axis strongly suggests that climatic conditions can be regarded as steady state environmental factors, and that the factors determining production are of very local nature.

In the Sargasso Sea Grice (1962) could find little evidence of seasonal fluctuations, though admitting his observations were widely spaced in time (monthly observations). Clarke (1940) also found no seasonal fluctuations in samples from the Sargasso Sea. But Moore (1949) reported maximum zooplankton volumes in May to June and minimum

in October, in waters off Bermuda. Results obtained by Menzel and Rhyther (1961) from a station 15 miles off Bermuda corroborated Moore's findings. Their results were extracted from three years collections taken fortnightly. The results derived by Lewis (1965) from monthly collections over three years from a station near Barbados give some indication of seasonal productivity. On the basis of dry weight measurements reproduced in Table 21, three distinct maxima could be detected in the late "winter" (January-February) of three successive years, and although there is not a good correlation between dry weight and volumes, (owing, no doubt, to changes in zooplankton composition) these peaks are reflected in the volume measurements as well. There also appears to be a subsidiary maximum in midsummer; this is quite clearly marked in July of 1963 and less distinctly so in July of 1962. But there are too many gaps in the collections to establish the authority of such conclusions. From the data available it is difficult to distinguish between real "peak" and "trough" periods. For instance, the period October to November of 1962 was marked by a "trough" in production, whereas yields for the corresponding period in 1963 were hardly distinguishable from those of the so-called high-producing period of January to February of the same year. The amplitude of variation in both volume and dry weight measurements from this station is of the order of 12-15 (compare 129 for North Atlantic), so the seasonal pattern becomes somewhat blurred in a series of randomly ranging samples.

In a previous paper Lewis et al (1962) had worked out from a series of semimonthly 30 minute tows, marked, seasonal variation in catch volumes, with peaks occurring in the summer of each year of investigation (1959 and 1960) and definite troughs in the winter months.

The abundance of zooplankton in terms of volume and dry weight
at Station 1B off Barbados (reproduced from ONR report, Beers et al, 1965).

<u>Station Number</u>	<u>Date</u>	<u>Volume Displacement (CC/m³)</u>	<u>Dry Weight (mg/m³)</u>
1	28 November, 1961	0.25	8.97
2	14 December, 1961	0.16	6.01
3	17 January, 1962	0.43	22.62
4	22 February, 1962	-	-
5	21 March, 1962	0.08	3.51
6	18 April, 1962	0.05	2.13
7	22 May, 1962	-	-
8	18 June, 1962	0.04	2.61
9	5 July, 1962	0.10	3.98
10	23 October, 1962	0.03	3.29
11	28 November, 1962	0.03	2.15
12	29 December, 1962	0.06	2.98
13	30 January, 1963	0.17	10.83
14	27 February, 1963	0.18	4.61
15	27 March, 1963	0.13	6.14
16	25 April, 1963	0.10	3.27
17	28 May, 1963	-	-
18	10 July, 1963	0.24	9.17
19	9 August, 1963	0.04	1.77
20	27 September, 1963	0.14	5.56
21	24 October, 1963	0.13	3.60
22	28 November, 1963	0.08	4.72

Table 21 - continued

<u>Station Number</u>	<u>Date</u>	<u>Volume Displacement (CC/m³)</u>	<u>Dry Weight (mg/m³)</u>
23	6 January, 1964	0.07	6.91
24	13 February, 1964	0.19	13.88
25	12 March, 1964	-	-
26	16 April, 1964	0.12	8.55
27	14 May, 1964	0.06	2.37
28	18 June, 1964	-	-
29	14 July, 1964	-	-
30	20 August, 1964	0.08	2.49
31	14 September, 1964	-	-
32	15 October, 1964	0.05	2.81

The seasonal influence could be detected in all the major taxa except the copepods. This is in contradiction to the conclusions drawn from results obtained 1962 to 1964. Timed tows, even supposing the plankton remained constant, would vary with the speed of the boat and the direction of the wind. To effect any real comparison of the data, correction would need to be made for these variables.

Coker and Gonzalez (1960) working in S. Puerto Rican waters on a problem similar to the Jamaican one also could detect no overall seasonality. In a two year period of study two autumn maxima and two spring minima were discerned for two species, Oithona simplex and Euterpina acutifrons, but for this result they have not ruled out the possibility of mere coincidence. Menon (1945) reported that on the Trivandrum coast of India copepods become abundant in October and that a regular succession of maxima occurs from December to March for Oithona, Acartia and Paracalanus. Temora however is rare from December to February, but becomes abundant from April to May. The harpacticoid, Euterpina, reaches its maximum somewhat later in July. From the study of areas in the Indian Ocean 1935-38, D.B. Sundara (quoted by Bogorov) could find no conspicuous maxima during the years, but states that a certain increase in the zooplankton corresponding to the 'biological spring' corresponds to the calendar winter.

Thus the results vary somewhat but underscore the tendency towards a more even seasonal distribution of zooplankton in the lower latitudes.

Species distribution.

On resuming discussion of the question of increasing sparsity of species shorewards it is pertinent here to note that Grice and Hart found a similar situation in their transect study from New York to the Sargasso Sea. Implicit in their discussion is the idea that the large differences in numbers of species stemmed from the fact of climatic differences in the waters sampled, that the decrease of species inshore is a logical consequence of its higher latitude. They quoted the ideas of Fischer (1960) and Dunbar (1960) as supporting evidence for the idea that diversity of species in tropical waters is the product of a long-term environmental stability and niche diversification. But here in a completely tropical setting, over a short horizontal distance, with relatively stable environmental conditions and negligible latitudinal difference of only a few minutes the same pattern is repeated. Coker and Gonzalez (1960) also found the same situation in a transect study off S. Puerto Rico - 21, 17 and 13 copepods. It may be argued that the more limited areal extent of 3J does not offer as much scope for niche diversification, in other words space would be a limiting factor. This has to be considered against the fact that the total population of the numerous species offshore is only a small portion of the total population of a few species inshore. Grice and Hart think that intraspecific competition is more important in population regulation.

Density of species at the zooplankton level may be controlled more immediately by interspecific competition at the phytoplankton level. In the equilibrium condition suggested for tropical waters the most immediately important variable is nutrient material. With a large

number of phytoplankton species all needing the same basic substances, phytoplankton species population sizes will be limited most proximately by the supply of these substances. If in turn animal species are very specialised in their feeding habits (cf. Deevey 1960 for two species of copepods found in the Sargasso Sea near Bermuda) a large number of species with small populations will be the result. In areas where a large number of variables are important (such as temperature, salinity plus nutrients) each variable as it passes to optimum value will alter the direction of change in the others so that there will be either a succession of species with varied or graded requirements or the dominance of a few species with a wide range of tolerance for change in the values of the determinants. When the number of variables is limited to one, there are two likely situations arising out of diversity of species at the plant level (a) many species with specialised food preferences capable of coexisting without successions; (b) few species with generalised food habits. The long term environmental stability postulated by the many authors provides the ideal milieu for speciation and, if the specific differences are related to feeding habits, the situation at 1J becomes very likely. Only by evolution of specialisation are several closely allied species able to occupy and exploit a single habitat (Hartley, 1953). Tentatively, this argument (a) seems to apply to the open ocean, as represented by 1J. With small variations of community factors except in nutrients and a large number of phytoplankton organisms (38 species - as many as the free living copepods) depending equally on the same inorganic substances a considerable number of zooplankton species have evolved. The full potential of the plant level

of production is not expressed in absolute amounts at any one time because the phytoplankton is being removed from the surface waters approximately as fast as it is produced by zooplankton grazing and by redistribution of the population. Menzel and Rhyther (1960-61) have found in their studies of plankton near Bermuda that nearly 100% of the production is used by the zooplankton. A significant point emerging from the population statistics of the area is that percentage of carnivorous species (siphonophores, chaetognaths, amphipods, euphausiids and carnivorous copepods) is much higher at 1J than at 3J. Even small cyclopoid copepods such as Oithona, seem to be graspers of either detritus or animals (see also Coker and Gonzalez, 1960). This suggests that as fast as energy is fixed at one level it is transferred to the next higher trophic level and there is little or no wastage. This equilibrium situation reinforces environmental equilibrium to characterise the situation at 1J as a very stable ecosystem.

The second pathway to stability seems to be the one operative at 3J. According to Dunbar (1960) the supply of nutrient salts in tropical waters is limited to (1) regeneration within the euphotic layer and (2) to such quantities as can enter any given area from outside by horizontal transport. These two sources have to maintain the equilibrium against constant loss from the system of salts contained in detritus which sinks out of the photosynthetic area before it is mineralized. Owing to the shallowness of the water and the 'convective' mixing caused by the upwelling of bottom current at 3J, the stability of the system as far as nutrients are concerned, is enhanced. Dunbar also discussed the effect of greatly varying environmental oscillations (temperature, salinity, etc.).

Of the areas studied 3J was subject to the greatest salinity variations. It has been suggested that these variations make the harbour waters a more vigorous environment. Goodbody (1961) has discussed mass mortality of fauna in the mangroves off Kingston harbour resulting from heavy rainfall concentrated over a few days and the concomitant fall in salinity. But such dilutions extend only to about 67 cm. below the surface and quickly drain off to the open sea. Against this may be advanced the conclusions of Coker and Gonzalez (1960) that breaks caused by rare occurrences such as severe storms or heavy rainfall change the plankton picture for only brief periods at a time and that their in-harbour station maintains a high degree of stability throughout the year. An increased stability is also associated with land drainage (Riley, 1947), and of the four stations 3J benefits most directly from land drainage. For these reasons, the stability of inshore waters is possibly greater than that of offshore, altogether permitting a high degree of exploitation of material resources. With greater environmental stability, less energy is required for regulatory activities, that is those which counter the challenges offered by environment, therefore more energy is allocated for net productivity, that is growth and production, with the result that larger populations are supported (Connel and Orias, 1964).

The zooplankton community at 3J contrasts with that of 1J by having a larger number of obligate herbivores. All the copepods except the pontellids (4 species occurring in very small numbers and only occasionally) are herbivores and this list is supplemented by other species occurring in large numbers such as larvacea, cladocerans,

the decapod Lucifer and veliger larvae. An equally large number of phytoplankton species occurs inshore as offshore.

McArthur (1956) has suggested that the number of possible pathways of energy flowing through a food web is a good measure of its stability. A small number of species each eating a wide variety of other species could have the same community stability as a large number of species each with a fairly restricted diet. These two stations would appear therefore to represent stable ecosystems of different types.

Though the foregoing might provide plausible explanations for the stability of the two areas under discussion it does not satisfactorily explain the exclusion of species from the respective areas. It could be that 1J (oceanic) station has reached its maximum diversity but that seems unlikely when it is compared with the 268 species of the Sargasso Sea to which it is comparable in so many other respects.

Coker and Gonzalez (1960) concluded from their study of Bahia Fosforescente (an enclosed area very similar to the Kingston harbour) that although inshore abundance of food could insure greater propagation other factors incumbent on the reproduction and survival of the species might make the environment too highly competitive. Moreover the consequent high multiplication rate of the successful copepods could intensify competition faced by other groups.

Summary and conclusions.

1. Quantitative zooplankton samples and hydrographic data were collected monthly at four stations located in the oceanic, shelf, harbour mouth and harbour basin waters of the Caribbean sea off Jamaica from March 1962 to July 1964.
2. All measurements were higher for the harbour stations than for the shelf and oceanic stations.
3.
 - a) The mean displacement volume. (cc/m^3) for each area was oceanic (1J) .02; shelf (4J) .04; harbour mouth (2J) .46; harbour basin (3J) .82; thus establishing an offshore-inshore gradient of ratios 1 : 2 : 23 : 41.
 - b) Dry weight measurements followed a similar trend to the volumes. Mean values were, in the order quoted above, 3.30, 8.28, 74.72 and 151.82 mg/m^3 , giving ratios of 1 : 2.5 : 22.5 : 46.
 - c) Zooplankton numbers were much larger at the harbour stations than at the shelf and oceanic stations but did not quite duplicate the ratios of the other two determinations. Mean values per m^3 were oceanic 823; shelf 1600; harbour mouth 16722; harbour basin 15797; giving ratios of 1 : 2 : 20.3 : 18.6.
3. The species composition of the taxa identified were as follows :

Copepods	45, including 5 parasitic species.
Coelenterates	22, 10 medusae and 12 siphonophores.
Foraminifera	6
Amphipoda	4
Larvacea	3
Chaetognaths	3
Cladoceran	2
Euphausiids	2
Sergestids	2
Pteropods	2

4. Eighty-seven species were identified from oceanic waters, 84 from shelf, 77 from harbour mouth and 66 from harbour basin. Copepods were the most important constituent of the zooplankton in all areas but most important at the shelf and oceanic stations. Of secondary numerical importance were fish eggs at 1J, larvae at 4J, cladocerans at 2J and Larvacea at 3J.

5. There are no obvious patterns of successions. Much of the same kind of organisms make up the plankton community at all times of the year. In the open water the number of species of copepods having any prominence is very small. Proportions of the several kinds vary from time to time but in no cyclical fashion that has been observed.

6. Considerable fluctuations occurred in all quantitative measurements from all stations - more than an order of magnitude in each case - but the overall variations showed no distinct seasonal pattern. Some few species like Penilia avirostris showed peculiar cycles of occurrence

but the cycles appeared to be independent of climatic variations or successions. Most of the copepods and nearly all the other leading species maintain an active reproductive state throughout the year.

7. The zooplankton population at the oceanic station was characterised by a larger numerical percentage of carnivores. The generally low abundance of phytoplankton coupled with large number of faunal species with small populations indicate that an efficient relationship exists between producers and consumers in these tropical waters. By contrast, at 3J where nutrient values were always higher, phytoplankton densities were always higher than at 1J, despite much higher populations densities and higher percentage composition of obligate herbivores. It is reasonable to assume that at 3J phytoplankton production was not limited at the grazing level.

8. Since climatic and hydrographic conditions throughout the area are subject to such slight spatial and temporal variations, the much higher levels of energy fixation and transfer demonstrated at all trophic levels at 3J may be attributed to better nutrient supply. This conclusion would tend to confirm the belief that nutrient supply is the most operative limiting factor to production in tropical areas.

9. The tentative conclusion about the harbour as a home for zooplankters is that despite the greater abundance of food, conditions there inhibit the multiplication and survival of several species found in the open sea.

10. For copepods, conditions at all these stations and especially

at 1J, favour the multiplication of species with small individual size.

11. A significant result of this study is that energy cycles in the tropical waters off Jamaica are of short duration and undergo numerous oscillations during the year. The oscillations seem to be of a shorter wave-length than monthly periods. A climatic effect operates only in so far as it increases the supply of nutrients, for example seasonal rainfall and river outflow.

12. A more complete understanding of the system would require serial observations of shorter time intervals - weekly or twice weekly observations. A month of daily observations would help to delimit more clearly growth and energy cycles and would serve as a good reference point when considering large scale variations from a seasonal point of view.

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APPENDIX

Tables 4-7 comprise gross quantitative data from each of the four stations. In Tables 4 and 5 values above the dotted line were extrapolated from average meter-wheel readings obtained after February 1963. In Tables 6 and 7 entries under Vol/100m³ marked with an asterisk represent final measurements after the various processes of separation had been accomplished.

Tables 8-11 represent the estimated monthly densities of the species occurring at each station. A + entry indicates the species density of less than 1/m³.

The survey at 1J covered a longer period and so data in this form had to be accommodated on larger tables.

In some instances samples were collected on two separate dates in a month (see Tables 4-7); for convenience in constructing tables only the means of these values are entered in tables in the appendix, though they are used as separate entries for small tables in the text and in the construction of diagrams. Those months for which the mean of two collections is given in the tables are indicated by asterisks.

TABLE 4.
Estimated quantitative data

Station 1J

Net No. 8.

Depth of tow 0-5 m.

Date	Duration	Revs.	Total vol.	Vol./100m ³	Dry wt./m ³	No. animals/m ³
2/3/62	15 mins	-	4.50	2.40	2.62	528
28/3/62	" "	-	1.15	0.60	0.92	145
19/4/62	" "	-	1.15	0.60	0.96	519
4/5/62	" "	-	5.00	2.70	2.69	878
30/5/62	" "	-	1.70	0.90	0.55	499
11/7/62	" "	-	1.90	1.00	0.76	396
2/8/62	" "	-	1.00	0.50	0.76	710
23/8/62	" "	-	4.30	2.30	4.42	796
17/9/62	" "	-	6.00	3.20	5.36	940
12/10/62	" "	-	8.80	4.70	6.78	1882
15/11/62	" "	-	6.00	3.20	2.02	350
13/12/62	" "	-	2.76	1.50	2.22	522
18/1/63	" "	2560	0.45	0.33	0.22	419
18/2/63	" "	3570	0.45	0.24	1.99	587
18/3/63	" "	3550	2.00	1.06	2.61	466
19/4/63	" "	3665	1.50	0.77	1.65	693
20/5/63	" "	4590	4.70	1.93	2.44	647
2/7/63	" "	3370	4.90	2.74	4.22	1450
29/7/63	" "	2700	2.80	1.95	3.84	1193
19/8/63	" "	4620	6.00	2.46	4.43	505
16/9/63	" "	3810	2.20	1.09	1.66	568
22/10/63	" "	2530	5.60	4.17	6.52	2445
13/11/63	" "	4190	3.40	1.53	3.28	276
13/12/63	" "	4060	4.00	1.85	1.74	586
22/1/64	" "	2840	15.80	10.48	12.21	1754
19/2/64	" "	2520	1.20	0.90	7.05	701
18/3/64	" "	3300	3.60	2.05	4.45	747

TABLE 5.

Estimated quantitative data

Station 4J		Net No. 8.			Depth of tow 0-5 m.	
Date	Duration	Revs	Total Vol.	Vol./100m ³	Dry wt /m ³	No. animals/m ³
28/9/62	15 mins	—	3.90	2.12	5.59	1136
3/12/62	" "	-	6.30	3.42	4.46	787
3/1/63	" "	-	9.90	6.04	5.56	864
3/2/63	" "	3128	7.00	4.22	8.35	1542
26/2/63	" "	2858	5.90	3.89	2.77	2736
28/3/63	" "	2445	4.90	3.77	4.33	1962
15/4/63	" "	4225	13.60	6.06	2.05	2219
26/4/63	" "	3070	3.00	1.84	1.68	629
27/5/63	" "	3840	7.30	3.58	3.09	1834
19/6/63	" "	2860	3.80	2.50	2.17	894
9/7/63	" "	1600	2.00	2.34	1.84	839
1/8/63	5 mins	900	4.10	8.58	14.51	2319
23/8/63	15 mins	2880	1.40	0.92	4.51	1200
19/9/63	" "	3080	1.50	0.92	0.95	769
28/10/63	5 mins	1030	8.40	15.36	79.89	2525
18/11/63	15 mins	3000	11.60	7.28	6.27	1728
17/12/63	" "	2840	2.80	1.86	2.27	1719
24/1/64	" "	2550	16.40	12.11	16.37	3587
21/2/64	" "	2750	2.90	1.99	2.52	1918
23/3/64	5 mins	860	2.50	5.50	8.02	1395
24/4/64	15 mins	2290	1.00	0.82	0.84	507
1/5/64	" "	1665	3.20	3.69	3.71	1661
28/5/64	" "	2280	6.60	5.45	2.77	1752
29/6/64		-	-	-	-	-
24/7/64	" "	2070	3.00	2.73	3.76	1930

TABLE 6.

Estimated quantitative data

Station 2J

Net No. 8.

Depth of tow 0-5 m.

Date	Duration	Revs	Total Vol.	Vol./100m ³	Dry wt./m ³	No. animals/m ³
3/12/62	15 mins	-	16.00			
3/1/63	" "	-	6.20			
3/2/63	" "	1850	33.60	34.20	58.88	6896
26/2/63	7.5 mins	920	25.24	51.67	66.32	9586
28/3/63	5 mins	330	40.00	228.31	247.26	34086
26/4/63	15 mins	1610	6.50	7.60	14.95	1389
27/5/63	10 mins	2170	3.50	3.04	4.67	4800
19/6/63	5 mins	640	12.02	38.26	89.01	24471
9/7/63	" "	630	1.10	3.29	11.30	-
1/8/63	" "	530	18.00	63.97	92.54	18714
23/8/63	" "	520	2.10	7.06	18.45	-
19/9/63	" "	790	26.44	63.03	85.77	19900
28/10/63	" "	385	8.50	41.59	93.15	16645
18/11/63	" "	1010	18.94	35.32	81.84	7666
16/12/63	" "	1195	32.40	51.06	91.35	8433
24/1/64	" "	670	26.00	73.10	111.38	11480
21/2/64	" "	370	34.40	175.08	183.82	106612
23/3/64	" "	780	20.00	48.30	61.34	17093
24/4/64	" "	450	4.60	19.25	18.52	3673
1/5/64	" "	470	2.50	10.02	35.11	4570
28/5/64	" "	850	6.00	13.29	21.23	2311
29/6/64	" "	320	3.00	17.65	38.49	9047
22/7/64	" "	1280	17.60	25.89	66.03	12600

TABLE 7.

Estimated quantitative data

Station 3J

Net No. 8.

Depth of tow 0-5 m.

Date	Duration	Revs	Total vol.	Vol./100m ³	Dry wt./m ³	No. animals/m ³
17/4/62	15 mins	-	7.60			
27/6/62	" "	-	19.80			
19/7/62	" "	-	429.40			
13/8/62	" "	-	4.60			
28/9/62	" "	-	34.50			
3/12/62	" "	-	40.77			
3/1/63	" "	-	13.44			
3/2/63	5 mins	740	4.20	10.29	46.30	15198
26/2/63	3(5 mins)	1790	89.40	94.06	35.17	15191
28/3/63	10 mins	237	70.00	398.00*	851.04	28384
26/4/63	4.5 mins	280	38.00	178.70*	116.00	22907
27/5/63	5 mins	1070	33.52	58.99	106.79	9307
19/6/63	" "	490	6.00	23.06	100.50	14776
9/7/63	" "	460	2.50	10.23	19.87	4641
1/8/63	" "	380	18.00	34.70*	60.99	18483
23/8/63	" "	1010	51.00	53.50*	125.82	13177
19/9/63	" "	1140	24.12	39.85	43.52	7032
28/10/63	" "	285	13.00	89.50	149.27	40967
18/11/63	" "	930	99.70	200.47	136.20	18379
16/12/63	" "	250	10.00	75.33	120.90	31076
24/1/64	" "	355	13.10	69.50	31.91	4296
21/2/64	" "	580	22.50	73.10	39.83	7703
23/3/64	" "	610	12.21	24.60*	23.95	6052
1/5/64	" "	750	8.00	20.09	20.55	5150
28/5/64	" "	180	23.00	165.50*	357.68	34233
29/6/64	" "	650	5.10	14.78	15.56	3878
28/7/64	" "	465	5.20	21.13	52.96	8160

TABLE 8.

Copepods	1962										1963			
	M	A	* M	J	J	* A	S	O	N	D	J	F	M	
Farranula gracilis	83	245	333	15	22	81	69	188	74	33	28	43	1	
Paracalanus aculeatus	5	44	16	62	19	19	83	1085	75	38	4	4		
Undinula vulgaris	80	28	217	2	34	189	534	173	107	20	4	45		
Corycaeus amazonicus	2	3	2	34	4	10		40	6	6	2	4		
Oncaea venusta	5	3	27	2	4	7	11	21	3	2		7		
Oncaea mediterranea	2	2	12	2		2		9	2	5	1			
Acartia lilljeborgi			1	3		7		2						
Corycaeus speciosus	2		6	3		7			2	1	1			
Macrosetella gracilis	2	1	15	9	2	10	22	4						
Oithona plumifera	3	1	2	15	9	10	2	4	7	1	1	6		
Calocalanus pavo	2	2	5	12	5	8	12	2		4	1	2		
Miracia efferata	2	2	2		3		2		1	5		1		
Microsetella norvegica	+	+	+	+	+		+	+	+			+		
Corycaeus latus		+	+	+	+	+		+	+					
Labidocera acutifrons		+	+	+	+			+	+					
Labidocera mimocera					+				+			+		
Labidocera nerii			+		+	+		+			+			

TABLE 8.

Station 1J

	1963												1964			
	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	Avg.
13	28	43	158	35	38	48	213	103	197	826	57	207	404	185	259	169
18	4	4	95	253	58	76	38	2	16	364	10	13	4	9	328	133
20	4	45	74	18	143	82	171	136	43	461	2	18	380	24	23	121
6	2	4	7	6	3	17	17	6		50	9	21	18	9	8	12
2		7	2	9	13	38	4	8	5	56	4	36	17	5	2	12
5	1		8		7	1	12	9			2	258	6	6	1	18
			3	10			1	2	1	1	1		7	1	22	6
1	1				8	12	33	14	11	57	7	11	13	2	5	11
			2		1	2	2		2	10	2		4	1	6	5
1	1	6	16	7	6	11	4	9	8	34	4	42	7	4	2	9
4	1	2	11	4	22	16	6	2	22	122	1	39	2	10	2	13
5		1	4		5	3	34	2	2		1	1	1	1	8	6
		+	+	+			+	+		+	+		+		+	
			+			+					+		+			
				+		+							+			
		+			+			+					+			
	+		+		+		+			+			+			

TABLE 8 - continued

Copepods	1962										1963		
	M	A	* M	J	J	* A	S	O	N	D	J	F	M
Labidocera													
aestiva		+			+		+		+	+		+	
Candacia													
pachydactyla	+	+	+	+	+	+	+		+			+	
Temora													
stylifera	+	+	+	+	+	+	+	+	+	+		+	
Pontellina													
plumata	+	+	+				+			+		+	+
Pontella													
securifer	+						+					+	
Pontellopsis													
regalis	+				+			+			+		+
Neocalanus													
robustior			+			+			+	+	+	+	+
Euchaeta													
marina	+		+	+		+		+		+			+
Scolecithrix													
danae	+		+		+			+		+	+	+	
Oithona													
nana			+		+	+		+					+
Copila													
mirabilis	+	+	+			+			+			+	
Caligus													
sp.			+			+						+	
Sapphirina													
intestinata	+	+	+				+				+		
Sapphirina													
auriontens	+						+				+		
Clytemnestrata													
scutellata		+					+				+		
Harpacticus													
gurneyii			+				+	+	+	+		+	
Longipeda													
helgolandica	+			+		+	+		+		+	+	+

TABLE 8 - continued

Station 1J.

1963														1964				Station 13.
	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	Avg.	
+	+		+				+				+		+					
+			+					+	+			+	+					
+	+		+			+	+	+	+				+			+		
	+		+	+	+	+		+										
			+				+					+			+			
		+		+			+		+						+			
+	+	+	+	+	+		+	+		+	+	+		+	+			
		+		+		+		+		+						+		
		+	+			+	+		+		+				+			
				+	+	+	+		+							+		
+			+				+							+				
			+					+								+		
			+						+							+		
						+												
+	+		+	+	+		+	+	+	+	+	+		+		+		
+			+	+	+	+	+	+			+							

121

TABLE 8 - continued

	1962										1963				
	M	A	* M	J	J	* A	S	O	N	D	J	⁺ F	M	A	M
<u>Copepods</u>															
Schizopera															
sp.				+			+		+		+		+		
Robertsonia															
knoxii		+		+					+				+		
Phyllothalestris															
mysis		+		+				+			+				
Rhyncothallestris															
rufocincta		+		+				+			+			+	
<u>Siphonophores</u>															
Abylopsis															
tetragona		3		+	1	1	1		1		1		2	2	
Abylopsis															
eschscholtzii	1			1	1			+			1		9		
Dyphyes															
appendiculata	+			+		+		+		+		+	+	+	
Sulculeolaria															
sp.	+		+			+		+			+				
Chelophyes															
appendiculata							+			+				+	
Eudoxides															
spirales	+				+			+		+				+	
Dyphyes															
dispar	+			+			+		+			+		+	
Lensia															
subtiloides					+				+		+		+	+	
<u>Odd groups.</u>															
Tanais sp.	+	+				+		+				+			
Parasitic isopod															
(unidentified)			+		+			+			+				
Globigerina															
bulloides	5	1	9	1	12	7	22	11	1	111	+	2	5	+	

TABLE 8 - continued

Station 1J

1963													1964			
D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	Avg.
	+		+						+					+		
			+			+							+		+	
	+				+			+							+	
	1		2	2		4		+	+	+		+		+		
	1		9		1		+	9		+		3		+		
+		+	+	+			+				+		+			
	+					+								+		
+				+				+							+	
+				+	+							+		+		
		+		+											+	
	+		+	+	+		+			+		+				
		+					+				+		+			
	+				+								+			
111	+	2	5	+	+	57	20	14	24	66	7	16	10	31	17	23

TABLE 8 - continued

	1962										1963				
	M	* A	M	J	J	* A	S	O	N	D	J	F	M	A	
Orbulina															
universa	+	+			+	+	+		+	+	+	+		+	
Dololium															
sp.	+	+		+	+		+		+			+		+	
Quinqueloculina															
sp.	+		+		+		+			+		+			
Textularia															
sp.		+		+		+		+	+		+	+		+	
Planorbulina															
sp	+	+		+		+		+		+	+			+	
Loimia															
sp			+			+		+	+	+	+	+			
<u>Cladocerans</u>															
Podon															
sp.	1		1				1		5	2		1	1		
Penilia															
avirostris		+								+		+	+		
<u>Larvacea</u>															
Oikopleura															
sp. I	2	13	2	4	1	71	32	19	5			11	42	10	
Oikopleura															
sp. II			10			21				14	3				
Frittilaria															
sp.			12			20				2					
<u>Chaetognaths</u>															
Sagitta															
enflata		+	2			4			+	+		2	+		
Sagitta															
serratodentata	6	2	28	2	5	11	7	59	54	29	9	5	1		
Krohnitta															
subtilis	2	4		4		4	7	2	2	+			2		
<u>Decapods</u>															
Lucifer															
typus			+		+		+	1		+		2			

BLE 8 - continued

Station 1J

1963													1964				Station 13	
	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	Avg.		
+	+	+		+		+		+	+				+		+			
		+		+	+		+	+		+		+		+	+			
+		+			+		+					+	+		+			
	+	+		+		+		+		+		+	+					
+	+			+		+		+	+	+	+				+			
+	+	+		+	+		+		+			+						
2		1	1		3			10	5	38	2	1	+	5	2	6		
+		+	+	+									+		+			
		11	42	10	15	42	46	6	12	88	1	16	21	25	116	25		
14	3				2	17	12	1	4	5	1	6	36		84	15		
2					2		2					1			2	7		
+		2	+	+	2		2		+					2		2		
29	9	5	1	1	1	4	4	21	9	28	2	2	7	20		13		
+			2	2		9		6		2	7			2	16	5		
+		2		2	1		1	4	1	2	1	+		+	+			

TABLE 8 - contin

		1962										1963		
		M	A	* M	J	J	* A	S	O	N	D	J	F	
<u>Euphausiids</u>														
sp.	I		1			+			+		+		+	
sp.	II			+				+				+		
<u>Amphipods</u>														
Brachyselsus														
crusculum			+					+		+		+		
Hyperia														
atlantica		+		+			+			+		+	+	
<u>Pteropods</u>														
Creseis														
acicula		+		+		+	2	2	32	+		+	4	
Limacina														
sp.			+		+	+	7		+			+		
<u>Larval forms</u>														
<u>Porcellanid</u>														
zoea				+		+		+			+			
Other														
zoea		2	13	1	1	1	2	2	9	2	3	2	1	
<u>Squillid</u>														
larva		+	+			+	+				+		+	
<u>Decapod</u>														
nauplii		+			+	+		+		+	+	+		
<u>Phyllosoma</u>														
larva							+				+			
<u>Gastropod</u>														
veligers		6	1	28	8	15	75	60	65	12	+	+	+	
<u>Lamellibranch</u>														
veligers		+	+	2	2	+	13		+	4		+		
<u>Polychaete</u>														
larvae		+	3	6	3	1	+	1	12	4			2	
<u>Echinoderm</u>														
larvae		5	4	+	+	1	1	2	+	+	1		3	

TABLE 8 - continued

1963													Station 1J			
D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	Avg.
+		+	+		+		+		+	+			+			
	+			+			+		+				+		+	
	+		+	+								+			+	
	+	+	+	+		+			+	+				+		
	+	4	+	2		+		+		2		+		2		
	+		+		4	1		+								
+				+						+	+		+	+	+	
3	2	1	1	2	1	1	1	22	2	1	2	+	2	+	+	3
+		+		+		+	+				+			+		
+	+		+		+		+	+		+	+	+	+	2	+	
+			+					+						+		
+	+	+	+	1	6	9	19	35	3	8	2	+	2	1	112	23
	+		5	2	2	2	29	+	2	2	+	+		+	42	8
		2	2	1	2	+	+	+	+	+	+	+	+		+	3
1		3	1	2	6	+	+	+	+		+	+	10	1	9	3

TABLE 8 - cont:

	1962										1963	
	M	A	* M	J	J	* A	S	O	N	D	J	F
<u>Larval forms</u>												
Sipunculid larva	+			+	+		+	+	+			+
Maricolan larva			+	+	+	+	+		+		+	+
Cyphonaute larva	+		+			+		+	+	+	+	+
Ascidian tadpole	+			+		+		+		+		
Cirripede larvae	+			+	+		+			+		+
Fish eggs and larvae	272	228	149	75	290	450	111	161	92	285	257	449

8 - continued

Station 1J

963

1964

J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	Avg.
	+		+	+	+		+						+		
+	+		+				+	+		+	+			+	
+	+	+	+		+		+		+				2	2	2
		+							+					+	
	+			+			+				+		+		
257	449	28	291	298	62	352	240	25	128	33	138	448	33	575	236

TABLE 9.

Sta

Copepods	1963											1964		
	* F	M	* A	M	J	J	* A	S	O	N	D	J	F	M
Paracalanus aculeatus	826	317	2446	286	43	24	253	132	748	990	307	266	211	22
Undinula vulgaris	53	24	157	8	31	77	768	2	380	66	17	431	162	20
Farranula gracilis	52	89	221	115	15	72	175	5	53	71	20	44	21	20
Corycaeus latus	15	28	92	18	2	7	379		48	11		32	9	1
Calocalanus pavo	13			3	43	73	64		35	231	7	27		2
Oncaea mediterranea	8	23	24		9		156				1	204		
Temora turbinata	3	2	6	46	51		2	2		50	86	15		
Corycaeus amazonicus	9	10	70	26	7	13		23	90	53	8		9	
Oncaea venusta	6	18	39	1		2	69	1	31	41	3	219	3	1
Oithona nana	61	14	9		5			1	11	21			77	1
Centropages furcatus	1	7	13	22	1	2	5	1	59	121	1			
Acartia lilljeborgi	25	11	28	11	1					17		5		
Oithona plumifera	5	2	7	6	12	21	7	1		71				
Macrosetella gracilis	1	1			1		40		5			27		
Corycaeus speciosus	9	2	11		1	2	7			2		10		
Temora stylifera	1		2	6	3					27	9			
Eucalanus subcrassus	3			18			2			41	1			

TABLE 9.

Station 4J.

I								1964							Avg.
	J	J	* A	S	O	N	D	J	F	M	A	* M	J	J	
286	43	24	253	132	748	990	307	266	211	226	24	95	86	68	417
8	31	77	768	2	380	66	17	431	162	207	14	53	69	68	128
115	15	72	175	5	53	71	20	44	21	204	12	82	21	148	74
18	2	7	379		48	11		32	9	12	7	7	2	35	39
3	43	73	64		35	231	7	27		26	9	17	8	18	39
	9		156				1	204		1	48	50	1	8	37
46	51		2	2		50	86	15						69	26
26	7	13		23	90	53	8		9		25	10	1	17	25
1		2	69	1	31	41	3	219	3	16	1	43	4	1	23
	5			1	11	21			77	19	8	14	10	49	23
22	1	2	5	1	59	121	1			25	4	10			17
11	1					17		5		16		7	7		15
6	12	21	7	1		71				13	7	43	4	6	11
	1		40		5			27		10		12		11	6
	1	2	7			2		10				3		1	
6	3					27	9								
18			2			41	1								

TABLE 9 - continued

[illegible]

TABLE 9 - continued

Station 4J

	1963							1964							
	* F	M	* A	M	J	J	* A	S	O	N	D	J	F	M	A
<u>Cladocerans</u>															
Podon															
sp.	+	+		+		+	+			19		15	+		6
Penilia															
avirostris	1	2	2	61		2		2		+	+	+		+	
<u>Larvacea</u>															
Oikopleura															
sp. I		50		50	51	+		85	145		63		188	27	42
Oikopleura															
sp. II	66	44	78	35	140	270	448	8	199	468	110	155	78	556	36
Frittilaria															
sp.	6				7				6	13				10	
<u>Chaetognaths</u>															
Sagitta															
enflata	7	+	+	1				+	+	11	3	7	2	2	20
Sagitta															
serratodentata	8	6	22	10	29	3	14	2	3	69	5	4	3	38	1
Krohnitta															
subtilis	19	14	11	9	8	2				9	4	4	23	15	
<u>Decapods</u>															
Lucifer															
faxoni	+		+	5		+		1		+		+			3
<u>Euphausiids</u>															
sp. II	8	2	9	1	+	+	17		1	16	4		2	9	+
<u>Amphipods</u>															
Brachyscelus															
crusculum		+		+			+	10		+		+		+	
Hyperia															
atlantica			+	+	+		+	+				+	+		
Glossocephalus															
milne-edwardsi				+			+		+				+		

TABLE 9 - continued

Station 4J

1964													
J	* A	S	O	N	D	J	F	M	A	* M	J	J	Avg.
+	+			19		15	+		6	3		2	
2		2		+	+	+		+		+	+		
+		85	145		63		188	27	42		91		81
270	448	8	199	468	110	155	78	556	36	224	441	24	139
			6	13				10					8
		+	+	11	3	7	2	2	20	9	2	+	6
3	14	2	3	69	5	4	3	38	1	12	10	12	17
2				9	4	4	23	15					11
+		1		+		+			3			6	2
+	17		1	16	4		2	9	+	3	+	3	5
	+	10		+		+		+	+		1		
	+	+				+	+			+			
	+		+				+						

TABLE 9 - continued

	1963							1964						
	* F	M	* A	M	J	J	* A	S	O	N	D	J	F	M
<u>Siphonophores</u>														
Abylopsis														
tetragona	2		+			+		+		+	+		+	
Abylopsis														
eschscholtzi	2			3				+		+		+		
Dyphyes														
appendiculata		+		+	+		+		+		+	+	+	+
Sulculeolaria														
sp.			+		+	+		+	+				+	
Chelaphyes														
appendiculata	+				2	5			1				+	
Eudoxides														
spiralis		+		+	+		+			+		+		+
Dyphyes														
dispar	1	2			1				33			+		
Dyphyes														
bojani	1				6			+		1				+
Lensia														
subtiloides			+	+		+		+		+			+	
Agalma														
sp.			+					+						+
<u>Medusae</u>														
Aglaura														
hemistoma	+			+					+					
Liriope														
mucroranta	+				+					+				+
Eirene														
sp.		+							+			+		
<u>Odd Groups</u>														
Globigerina														
bulloides	3	11	28	67	1	43	39	113	5				19	2
Dololium														
sp.	+			2		+	+				+	+		
Loimia														
sp.				7	2			1		1		+		

*

1964

1964														Avg.
J	* A	S	O	N	D	J	F	M	A	* M	J	J		
	+	+		+	+		+			+				
		+		+		+				2	4	5		
+		+	+		+	+	+	+			+			
+	+	+	+				+			+				
2	5		1				+		2		1			
+		+		+		+		+	+					
1			33			+				3				
6		+		1				+						
	+	+		+			+		1	2				
		+						+						
			+						+		+			
+				+				+	+	+				
1	43	39	113	5			19	2	48	43	41	39	33	
	+	+			+	+				+				
2			1		1	+			+					

TABLE 9 - continued

1963												1
	* F	M	* A	M	J	J	* A	S	O	N	D	
<u>Pteropods</u>												
Creseis												
acicula	6		4	6		+			44		+	
<u>Larval forms</u>												
Lucifer												
faxoni	+	2		5		1		+		9	6	
Porcellanid												
zoea	+	1	+	+		+		+	5	2		
Carcinus												
zoea	47	2	6	1	+	+	+	1	2	9	7	
Other												
zoea	4	6	2	14	+	2	+	1	+	2	1	
Decapod												
nauphlii	+	+		+			+	+	+	+		
Gastropod												
veligers	18	2	314	105	134	8	52	5	7	32	25	
Lamellibranch												
veligers				6	7	13	+		5	1	+	
Polychaete												
larvae	3	+	+	2	3	3				24	4	
Echinoderm												
larvae	4	1			2	1			2			
Maricolan												
larva	+	+				+	+		+			
Cyphonaute												
larva	+			+	+			+			+	
Ascidian												
tadpole	+	+	+					+	+			
Cirripede												
larvae	+				+					+		
Fish eggs												
and larvae	12	2	104	9	443	123	227	10	13	35	125	

BLE 9 - continued

Station 4J

1964												Avg.
* A	S	O	N	D	J	F	M	A	* M	J	J	
		44		+			+			+		
	+		9	6		+			6	+		
	+	5	2		+		4	2	+	1	6	
+	1	2	9	7	26	6	7	3	11		6	8
+	1	+	2	1		1	1	+	1	+	1	3
+	+	+	+		+		+		+	+	+	
52	5	7	32	25	55	19	80	74	20	35	43	56
+		5	1	+	+	+	22		3		89	
			24	4	26	3		3	31		+	10
		2			92	42		7	3	10	7	15
+		+			+		+			+		
	+			+						+	+	
	+	+			+				+			
			+					+			+	
227	10	13	35	125	266	51	242	29	72	34	38	79

TABLE 10

	1963											1
	F*	M	A	M	J	J	*A	S	O	N	D	
Paracalanus aculeatus	969	4594	240	132	1998		3340	1437	1551	111	335	1
Acartia lilljeborgi	461	371	27	36	9752		27	200	491	2001	204	
Corycaeus americanus	778	1427	181	260	769		3153	393	684	811	551	1
Centropages furcatus	156	628	77	94	1259		3234	403	920	28	357	
Temora turbinata	314	856		23	269		1563	2010	1499	225	223	
Oithona nana	290	1883	54	57	259		239		396		4	
Corycaeus amazonicus	600	1225	35	93	461		310	507	780	353		
Euterpina acutifrons	160	257			86			64	652	11	13	
Eucalanus subcrassus	129	770	82	19	67		53	21	11	17	4	
Oithona plumifera		37	10		280		40			60		
Harpacticus gurneyi		+		+					+			
Miracia efferata	+				+			+		+		
Corycaeus latus		+			+						+	
Oncaea mediterranea							+			+		
Temora stylifera	+	+					+					
Labidocera acutifrons					+					+		
Macrosetella gracilis	+						+				+	
Corycaeus speciosus	+	+					+			+		

TABLE 10

Station 2J

						1964							
J	* A	S	O	N	D	J	F	M	A	* M	J	J	Avg.
	3340	1437	1551	111	335	1953	4979	1931	744	1900	3858	3689	1797
	27	200	491	2001	204	317	37	183		27	26		897
	3153	393	684	811	551	1406	2270	1844	200	488	168	300	849
	3234	403	920	28	357	314	1208	821	284	285	150	3655	782
	1563	2010	1499	225	223	146	1711		17			41	694
	239		396		4			10		45	2799	235	507
	310	507	780	353				203	301	104	97	241	361
		64	652	11	13	30	299	50	13	1483	212	34	240
	53	21	11	17	4	40	37	19	9	59	221	65	92
	40			60				10		30		40	70
			+				+			+			
		+		+				+					
					+				+				
	+			+						+			
	+					+				+			
				+		+			+				
	+				+								
	+			+			+				+		

TABLE 10 - continued

[illegible]

TABLE 10 - continued

	1963											1964	
	* F	M	A	M	J	J	* A	S	O	N	D	J	F
<u>Coelenterates</u>													
<u>Siphonophores</u>													
Abylopsis													
tetragona	+	+					+			+			+
Abylopsis													
eschscholtzi	+	+					+				+		+
Dyphyes													
appendiculata	+	+		+			+		+		+		
Sulculeolaria													
sp.		+		+			+		+		+		+
Chelaphyes													
appendiculata	+			+					+		66		+
Eudoxides													
spiralis				+			362		+	+		18	
Dyphyes													
dispar				+			+		11		33		
Lensia													
subtiloides	+		+				+			+			+
Dyphyes													
bojani			+				+						+
<u>Medusae</u>													
Eirene													
sp.	2	106	9	5	5			21	4	4		5	4
Eutima													
sp.	+	91		6	38				6		+		5
Aequorea													
macrodactyla	+		+		+		+		+	+		+	
Eucheolita													
sp.	+	91	+		+		33		4	1	7		48
Liriope													
mucroranta			4	+			+			+			+
Liriope													
scutigera				+	+		+				+		

TABLE 10 - continued

Station 2J

1964						Station 2J							Avg.
J	* A	S	O	N	D	J	F	M	A	* M	J	J	
	+			+			+			+			
	+				+		+			+			
	+		+		+								
	+		+		+		+		+				
			+		66		+	29				+	
	362		+	+		18				12		+	
	+		11		33								
	+			+			+	10			7	9	
	+						+			9			
		21	4	4		5	4	26		22	16	3	13
			6		+		5	16		4	+		
	+		+	+		+		+	+				
	33		4	1	7		48	16		6	6		
	+			+			+				7		
	+				+			+		+		+	

TABLE 10 - continued

	1963											1964
	* F	M	A	M	J	J	* A	S	O	N	D	J
<u>Larval forms</u>												
Lucifer												
faxoni	231	57	76	26	80		43	3369	1668	83	2259	4343
Porcellanid												
zoea	4	8		2	28		63	57	+	+		+
Carcinus												
zoea	188	82		+	+			+			+	
Other												
zoea	+	2311	60	194	641		2878	1501	78		33	50
Decapod												
nauplii	+	+	+	+	+		+	+	+	+	+	
Gastropod												
veligers	484	52	+	28	9		1680	106	1666	441	29	
Lamellibranch												
veligers	155	+	+	10	+		2431	74	83	55	+	
Polychaete												
larvae	4	+	+	3	+		+	+	+	44	71	146
Echinoderm												
larvae	14	22	+	14			107	128	+		10	36
Lingula												
larva	+	+	+	+	+			+		+	+	
Phoronis												
larva	+		+				+	+		+		+
Maricolan												
larvae	+	+	+	+			+					10
Cyphonaute												
larvae	+	+					13	86		18		+
Cirripede												
larvae	759	+	+	95	567		268	307	1016		77	354
Fish												
eggs	25	93	30	400	48		25	1051				111
Ascidian												
tadpoles	+	+		+	+			+			+	

ABLE 10 - continued

Station 2J

1964												
* A	S	O	N	D	J	F	M	A	* M	J	J	Avg.
43	3369	1668	83	2259	4343	1901	5505	208	22	344	659	1913
63	57	+	+		+	+	154	33	11	+	47	42
	+			+		+		23	28	153		
2878	1501	78		33	50	842		204	45	21	358	656
+	+	+	+	+		+		+	+	+	+	
1680	106	1666	441	29			212	120	162	35	376	408
2431	74	83	55	+			244		21		100	318
+	+	+	44	71	146	10	7	5	22	132	+	38
107	128	+		10	36	10	4	3	6	+	+	35
	+		+	+			+				+	
+	+		+		+			+				
+					10	36	290	+		+		
13	86		18		+			+			+	
268	307	1016		77	354		1144	87	71	53	856	411
25	1051				111			53	400	303	64	305
	+			+				+	+	+	+	

TABLE 11

SI

Copepods	1963							1964						
	* F	M	A	M	J	J	* A	S	O	N	D	J	F	I
Paracalanus aculeatus	4273	4255	4438	2661	6463	250	3602	820	1421	389	2199	159	2429	
Temora turbinata	479	561	721	348	2956	229	1999	4476	2842	11986	1684	4674		
Oithona nana	235	1832	1664	392	1372	12	562	5099	38	2644	30	707	66	
Corycaeus americanus	367	2541	444	974	5965	106	264	165	2809	170	527	159	305	
Corycaeus amazonicus	327	1359	1177	451	551	57	446	347	796		30		377	
Centropages furcatus	143	1063	1331	158	834	70	155	53	892	109	798	40	71	
Euterpina acutifrons	46	118	111		67		98	6	2875	36	408			
Eucalanus subcrassus	249	206	166	249	343	16	82	59	163	182	166	33	45	
Acartia lilljeborgi	60		111	4	182	37			364	79	105	19	26	
Corycaeus latus	223				303		214							
Harpacticus gurneyi			+				+				+			
Miracia efferata	+				+					+				
Oncaea mediterranea			+					+					+	
Temora stylifera	+	+				+							+	
Labidocera scotti	+					+		+			+			
Macrosetella gracilis		+					+						+	
Corycaeus speciosus		+					+		+		+			

TABLE 11

Station 3J

1964														
J	J	* A	S	O	N	D	J	F	M	A	* M	J	J	Avg.
6463	250	3602	820	1421	389	2199	159	2429	197	4759	1351	423	3670	2605
2956	229	1999	4476	2842	11986	1684	4674					6	65	2426
1372	12	562	5099	38	2644	30	707	66	667	216	793	2144	678	971
5965	106	264	165	2809	170	527	159	305	756	331	1151	101	57	885
551	57	446	347	796		30		377		552	1412	333	163	579
834	70	155	53	892	109	798	40	71	15	138	680	159	186	362
67		98	6	2875	36	408				8	418	9	688	178
343	16	82	59	163	182	166	33	45	26	60	366	116	599	177
182	37			364	79	105	19	26		10	314	6		101
303		214												
		+				+							+	
+					+				+					
			+					+					+	
	+							+						
	+		+			+			+				+	
		+						+				+		
		+		+		+				+				

TABLE 11 - continued

	1963											1964
	* F	M	A	M	J	J	* A	S	O	N	D	J
<i>Oithona</i>												
<i>plumifera</i>	+	+			+					+		
<u>Cladocerans</u>												
<i>Penilia</i>												
<i>avirostris</i>	702	1182	1849	1059	3267	385	112		496	2734	12858	
<i>Podon</i>												
sp.	+		+								+	
<u>Larvacea</u>												
<i>Oikopleura</i>												
sp. I	503		+	24	+		+	+		+		+
<i>Oikopleura</i>												
sp. II	650	4669	7360	249	2521	1948	5385	75	22835	516	5109	3302
<i>Frittilaria</i>												
sp.	37			83	15	151		+			499	
<u>Chaetognaths</u>												
<i>Sagitta</i>												
<i>enflata</i>	+	2304	+	1029	484	45	413	137	165	279	26	53
<i>Sagitta</i>												
<i>serratodentata</i>	+	827	1516	75	53	8	33	11			15	
<i>Krohnitta</i>												
<i>subtilis</i>	489										10	
<u>Decapods</u>												
<i>Lucifer</i>												
<i>faxoni</i>	176	1063		83	15	86	115	99		370	60	29
<u>Euphausiids</u>												
sp. II	6	59				16	26	+			377	
<u>Amphipods</u>												
<i>Hyperia</i>												
<i>altantica</i>		+				+						

TABLE 11 - continued

Station 3J

* A	1964											
	S	O	N	D	J	F	M	A	* M	J	J	Avg.
112		496	2734	12858		3298	1832		2860	768	470	1856
+	+		+	+	+				33			186
385	75	22835	516	5109	3302		102	374	15591	736	624	4272
	+			499			350		239	420	219	205
413	137	165	279	26	53	208	296	326	1604	52	291	501
33	11			15					30	17	4	235
				10						3		
115	99		370	60	29	65	118		34	84	71	172
26	+			377		+	15	10	1743	32	73	236
										+		

TABLE 11 - continued

	1963											1964			Stat:
	* F	M	A	M	J	J	* A	S	O	N	D	J	F	M	
<u>Siphonophores</u>															
Abylopsis															
tetragona	+						+			+			+		
Abylopsis															
eschscholtzii	+		+		+		+			+	226			138	
Dyphyes															
appendiculata	15	13	+		38			17		+		+	+		
Sulculeolaria															
sp.	+	+			+		+	+		+	+	+		+	
Chelaphyes															
appendiculata	6	+		+	89		+	11	165	18				41	
Eudoxides															
spirales	+				+	+					+			+	
Dyphyes															
dispar	+		+			+				+	+		+		
Lensia															
subtiloides	+	+			+				198				7	15	
Dyphyes															
bojani		+		+	+	+	+		+			+		+	
Agalma															
sp.				+						+			+		
<u>Medusae</u>															
Eirene															
sp.	+	+		+			+			+				+	
Aequorea															
macrodactyla				+		+	+		+			+			
Eutima															
sp.		+			+		+				+			+	
Liriope															
mucroranta	5	2		605	7	1		+			+	+		+	
Liriope															
scutigera	+			+						+					
Aglaura															
hemistoma	+	+				+			+			+	+	+	
Aeginura															
incisa				+					+					+	

TABLE 11 - continued

Station 3J

							1964							
J	J	* A	S	O	N	D	J	F	M	A	* M	J	J	Avg.
		+			+			+			+			
+		+			+	226			138		89			
38			17		+		+	+			+			
+		+	+		+	+	+		+			+		
89		+	11	165	18				41	3	104			
+	+					+			+					
	+				+	+		+						
+				198				7	15				57	
+	+	+		+			+		+			+		
					+			+			+			
		+			+				+		+			
+	+	+		+		+	+		+		+			
7	1		+			+	+		+	104		+		
					+					+				
	+			+			+	+	+	+				
				+					+					

TABLE 11 - continued

	1963										
	* F	M	A	M	J	J	* A	S	O	N	D
<u>Larval forms</u>											
Lucifer											
faxoni	6	59			16	26	115	71	26		376
Porcellanid											
zoea	10	10	10	8		8	38	5		18	30
Carcinus											
zoea		59	25	75	38		7	165	33	24	30
Other											
zoea	2120	4609	591	229	476	883	181	84	539	528	249
Decapod											
nauplii	+		+	+	+	+	+		+	+	+
Gastropod											
veligers	10	59	1	27	200	8	66	11	693	72	30
Lamellibranch											
veligers	+	59			38		297		+	+	
Polychaete											
larvae	9		157	265	292	66	45	6	264	18	105
Echinoderm											
larvae				39			+		727	6	
Branchiostoma											
caribbeaum				11							
Lingula											
larva	+				+				+	+	
Phoronis											
larva	+		+			+		+		+	+
Maricolan											
larvae	+			+		+			+		+
Ascidian											
tadpoles	+	+	+	+		+	+		+		+
Cirripede											
larvae	624	59	25		92				66	+	524
Fish eggs											
and larvae	72	108	+	+	514	102	2362	16	11	66	45

TABLE 11 - continued

Station 3J

						1964							
	* A	S	O	N	D	J	F	M	A	* M	J	J	Avg.
26	115	71	26		376	10	79	15	10	1744	32	73	235
8	38	5		18	30	27	4			34	20	8	18
	7	165	33	24	30		1		9	75	24	11	49
33	181	84	539	528	249	859	411	1059	16	25	145	1891	828
+	+		+	+	+			+		+			
8	66	11	693	72	30	+	+	62	1	802	101	24	223
	297		+	+		+		25		383	269	79	164
56	45	6	264	18	105	20	+	+	+	18	5	138	100
	+		727	6									
								46					
			+	+				+					
+		+		+	+	+						+	
+			+		+	+		+		+			
+	+		+		+		+		+	+	+		
			66	+	524		+		+		14	52	185
12	2362	16	11	66	45	+	+	236	+			113	396