Reprinted from the
AUSTRALIAN JOURNAL OF MARINE AND FRESHWATER RESEARCH

SEASONAL VARIATIONS IN THE INDIAN OCEAN ALONG 110°E.

VI.* MACROPLANKTON AND MICRONEKTON BIOMASS

By M. Legand†

[*Manuscript received July* 28, 1967]

Summary

At about 2230 hr, samples were taken between the surface and approximately 210 m with a 5-ft Isaacs–Kidd midwater trawl (IKMT) at 91 stations.

Samples were divided into four arbitrary categories—gelatinous organisms, small plankton, macroplankton, and micronekton. The last two categories were considered to be typical of the IKMT and were subdivided further. IKMT material is characterized by the dominance in weight of fishes, carids, euphausiids, sergestids, and leptocephali.

Measurements were expressed as dry weight and frequency per standard haul of 10,000 m, and as average organism size. The average dry weight of 14·8 g consisted of one-third fishes, about one-quarter crustacean macroplankton, and one-quarter small plankton.

Between 0 and 200 m meroplanktonic larvae of littoral organisms were concentrated toward the northern and southern extremities of the section. Gelatinous organisms were more abundant by weight in the south while larger crustaceans were more abundant in the extreme north. The distribution of fishes tended to be bimodal. In general, groups with maxima further to the north developed these maxima later in the season. The size of cephalopods, penaeids, and chaetognaths was usually greater in the south. Fishes, euphausiids, and carids were larger in the north. Phyllosomas, stomatopods, and leptocephali (meroplankton), and annelids and pteropods (holoplankton) were larger toward the centre.

In general the highest frequencies and largest biomasses occurred from August to November. There were periods of poverty in the first part of the year. Micronekton biomass was also high in March–April. The seasonal cycle was often clearer in the south, suggesting more marked biological seasons there, and more confused in the centre, suggesting that this region was of an intermediate nature. The seasonal distribution as a whole was bimodal. A main frequency maximum with a smaller average size of organisms was preceded by a secondary frequency maximum with a greater average size of organisms. These two maxima were related, the interval between them being of the order of 6–9 months. This suggests a succession of adults and young individuals.

There were minima in abundance characterizing whole regions and cruises, suggesting that there were large-scale environmental changes, e.g. to the south of 26°S., from mid April to the beginning of June; to the north of 12°30′S., in January to March; and, in particular, from the north towards the centre and south, in September during the richest period of the year. Except for the end of the year, when the distribution was similar from north to south, there were alternate maxima and minima along the section.

Despite similarities in the distribution of the four major categories, their cycles of abundance were out of phase. The development of small plankton was earlier than that of macroplankton and micronekton.

* Part V, *Aust. J. mar. Freshwat. Res.*, 1969, **20**, 77–84.

† Laboratoire d'Océanographie, Centre O.R.S.T.O.M., Nouméa, New Caledonia.

I. Introduction

Data on higher tropic level plankton ("micronekton") caught with the midwater trawl are generally quite recent in the literature. The Isaacs–Kidd midwater trawl was not designed to be a quantitative net, but it is the most convenient for the present type of investigation. Besides the usual causes of variation in the results for the organisms and methods of capture described here, the following must be considered in any statistical evaluation:

(i) Variation in the size of the opening of the net with a frame which is not rigid.
(ii) Variations in the mesh-size along the net.
(iii) The diversified ability of the organisms considered here to escape and avoid the net.
(iv) Our limited knowledge of the behaviour of the net, especially during an oblique haul.

Examination of the results must also consider the effectiveness of the equipment with respect to each category or group of species.

There are other sources of uncertainty:

(i) Our minimal knowledge of the vertical migrations of the species considered, as the maximum depth sampled was 200 m.
(ii) The distance of 120 miles between stations. A series of daytime stations would not have improved this situation as we would then have had two series of results, practically independent and unconnected.
(iii) The time interval between successive stations at identical positions was highly variable: only a month separated the first and last stations at the southern extremity of the section while the most northerly station was occupied twice during a cruise within about 10 days, but with two months between cruises.

In the following sections the general characteristics of the samples and the distribution tendencies observed will be described. The reservations listed in this introduction must be kept in mind throughout the following text when considering the interpretations and conclusions drawn.

II. Methods

(a) Collection of Samples

The net used was a pelagic Isaacs–Kidd midwater trawl (Isaacs and Kidd 1953) of 5 ft (IKMT 5). It was a scaled-down version of the 6 ft midwater trawl (King and Iversen 1962; Aron 1962). The mesh was uniform along the trawl itself, with a stretched measurement of 12 mm. The cod-end was a conical plankton net of 0·5 m mouth diameter and mesh width 0·366 mm. No flowmeter was used.

The collecting procedure was standardized. With the ship's speed at 5 kt, the cable was paid out at 40–50 m/min, and near the end of paying out, speed was reduced to 3 kt. With 700 m of wire out, the net was left for 5 min and then recovered at about 9 m/min, the ship's speed being adjusted around a mean of 3 kt to maintain constant wire tension. Tows were started at about 2140 hr. Usually, it took 15 min to pay out, and about 82 min to recover the net. The maximum depth reached (average 211 m) was recorded by depth meter (Hamon, Tranter, and Heron 1963).

(b) Division of Samples

Samples were preserved in 10% formalin and large organisms removed. They were sorted in the laboratory two or three months after collection. Organisms were first separated into four categories—gelatinous organisms, relatively small organisms (plankton), macroplankton, and micronekton. Displacement volume of each of these categories was determined. Macroplankton and micronekton were further subdivided into groups. Counts were made of the organisms present in these groups and their displacement volumes measured. The criterion for division into groups was often ease of separation. Consequently, the groups might have little taxonomic significance.

Gelatinous Organisms—Category 1

The category contained medusae, salps, siphonophores, pyrosomas, and similar organisms. These were usually broken and it was therefore impossible to make an accurate analysis of them.

Relatively Small Organisms (Plankton)—Category 2

In allotting organisms to this category, an arbitrary separation was made, depending on whether the organisms were considered to be characteristic of IKMT 5, or of standard plankton nets, such as the one used as a cod-end. Certain groups, for example annelids, pteropods, chaetognaths, and fish larvae, should have been included in this category, and not sorted separately. However, because they were easy to separate, each of these was counted and measured as a whole and placed in either the third or fourth category.

Macroplankton and Micronekton—Categories 3 and 4

These two categories can be considered to characterize samples taken by the IKMT. They are more or less artificial, the distinction between them, i.e. their respective abilities to swim, being quite arbitrary.

Micronekton was first restricted to fishes and cephalopods, but, by an almost opposite point of view, fish larvae and young cephalopods were added: these are intrinsically planktonic but represent an index of future micronekton.

The macroplanktonic and micronektonic categories were divided into the following groups:

Macroplankton

Holoplanktonic organisms.—Non-Crustacea: annelids, pteropods, heteropods, and chaetognaths. Crustacea: phronimids, various amphipods, euphausiids, carids, sergestids, and penaeids.

Meroplanktonic organisms.—Stomatopod larvae and phyllosomas.

Micronekton

Fishes, leptocephali, fish larvae (other than leptocephali), gelatinous cephalopods (all the transparent forms—mostly cranchiids), and non-gelatinous cephalopods (all non-transparent forms).

(*c*) *Determination of Volumes and Weights*

Wet volumes were measured, keeping the conditions and duration of the measurement as constant as possible. Excess water was removed by hand shaking the plankton for 10 min in a nylon filter of the same mesh as the cod-end of the trawl. The plankton was then placed in a graduated cylinder containing a known volume of water, and the difference between this known volume and the new reading gave the wet volume. The significance of these values varied from one station to another depending on the sample composition. In several groups the water content was very different. For example, chaetognaths might have been a major part of the volume of the sample but only a minor part of its dry weight. A similar situation existed as regards salps and medusae. This tended to give particular values an exaggerated importance and might falsely suggest peaks in abundance. Consequently, all values were expressed in dry weight equivalents.

Instead of measuring dry weights directly, the need to keep samples intact for further description made it necessary to use conversion coefficients. These were determined on subsamples, one for each leg of the cruise. The values so obtained were sufficiently similar, within a particular group, to permit the use of a mean annual conversion coefficient. Subsamples were dried to constant weight. The coefficients used to convert the wet volumes to dry weights are given following the results in each of the cruise reports (CSIRO Aust. 1965*a*, 1965*b*, 1965*c*, 1965*d*, 1966, 1967).

The meanings attached to the various terms used for measures of volume or weight of the material studied are defined as follows:

Biomass.—Weight of the living organisms, as though it were measured immediately after capture, after complete drying of the interstitial water, but before the onset of any dehydration processes or deterioration of the tissues.

Wet weight.—Weight of a sample preserved in formalin, weighed after drying the sample according to the method described for wet volume.

Wet volume.—Volume of a sample preserved in formalin for at least two months, measured by displacement, as described above.

Dry weight.—Weight of a sample dried in an oven for 24 hr at 60°C (mean of several consecutive weights. measured immediately after removal of the sample from the oven, with short intervals of desiccation between weighings).

Estimated biomass.—76% of the wet weight. This figure was arrived at by comparing the wet weights of samples of fishes and crustaceans dried in the filter as described above, before and after washing in 95% alcohol; it was found that the weight was reduced by 24% by the alcohol wash, and this has been arbitrarily taken to be a measure of the excess interstitial water. It has been used here in an attempt to eliminate the over-estimation of the wet weight owing to the insufficient removal of interstitial water during the drying process.

There is no practical method of measuring the real biomass of plankton. The results obtained in practice are approximations to this ideal value, valid only with reference to the stated conditions of measurement. The only merit of the estimated biomass value is that it is the *minimal* estimate of the real biomass. excluding all the usual causes of over-estimation.

The action of formalin is a known cause of underestimation of the biomass (Ahlstrom and Thraikill 1963). Preservation in formalin causes a decrease of the wet weights and wet volumes of the sample, a decrease which varies according to the biological composition of the samples. It varies from half or nearly half of the original weight for gelatinous organisms, to only a few parts per hundred for the large crustaceans. According to our own measurements, this decrease takes place mainly in the first hours of fixation, and by the end of a month, further treatment with formalin no longer causes an appreciable decrease in weight or volume. Consequently the action of formalin cannot be corrected for precisely, and measurements made before fixation cannot be compared with measurements made after a month or two of formalin treatment.

The ideal would have been to express the results in carbon content. This would have given a common base for all trophic levels, including the phytoplankton, but it was not possible to do this in this study.

(*d*) *Calculation of Volume of Water Sampled*

The results of all hauls, classed by categories, have been published (CSIRO Aust. 1965*a*, 1965*b*, 1965*c*, 1965*d*, 1966, 1967). To take into account differences in sampling duration between stations, all results were corrected to values for a "standard haul". The length of the standard haul was calculated (from mean ship's speed and mean sampling duration) to be approximately 10,000 m.

It would have been preferable to calculate the results as a function of volume of water sampled, but this was not done for the following reasons.

Calculations of volume filtered depend upon the following assumptions—that the trawl worked, during paying out and hauling in, in proportion to the speed of the winch and the ship; that the maximum mouth opening was maintained during the whole operation; and that all the water passing through a defined section of the net was filtered. Making these assumptions, maximal and minimal values of the volume of water filtered can be given. From these, maximal and minimal values for the concentration of organisms in the water column sampled by the trawl can be estimated. For a standard haul (10,000 m) the maximal volume would be $10,000 \times 1 \cdot 929 \text{ m}^2 = 19,290 \text{ m}^3$ of water (Aron 1960), using the maximum mouth opening.

The volume of water filtered by the cod-end can be estimated from its mouth area ($0 \cdot 197 \text{ m}^2$), and the distance towed (10,000 m). From this volume (1970 m^3), which is the minimal volume of water filtered, maximal values can be estimated for the concentration of organisms in the water column sampled by the trawl, by assuming that organisms have been retained only by the cod-end. This means that the results per standard haul would need to be divided by approximately 20 to obtain a minimal estimate of the concentration of organisms per 1000 m^3, and by approximately 2 to obtain a maximal estimate of their concentration per 1000 m^3. The former figure would be more accurate for the larger and better swimmers among the organisms collected, e.g. large fishes and cephalopods. The latter figure would be more accurate for the plankton category and for such groups as chaetognaths, heteropods, and pteropods. In other cases, the real value would lie between these two extremes.

III. Results

(a) Average Composition

(i) General Variability of Results as a Function of the Nature of the Organisms

Figure 1 shows the results of hauls for each category as a frequency distribution of stations as a function of the dry weights. The scatter of the results increases distinctly from small planktonic organisms to micronektonic organisms, as the mean

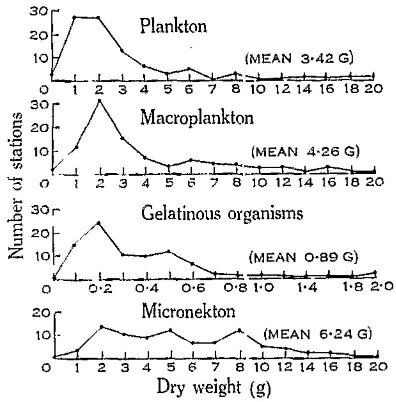

Fig. 1.—Frequency distribution of station mean dry weights. The mean of all stations is given in brackets.

dry weight increases from 3·42 g to 6·24 g (excluding the gelatinous category). The variability of the mean results for the categories is shown in Table 1. This shows that for all the calculated means, the largest mean is four times larger than the smallest

Table 1

Variability of IKMT 5 categories

Dry wt. in mg

	Plankton	Macroplankton	Micronekton	Gelatinous Organisms
	*Seasonal Variability in the Mean**			
Traverse	Sept. 1962	Aug. 1962	Oct. 1962	Aug. 1962
Maximum mean	6291	7747	9431	940
Traverse	Jan. 1963	Feb. 1963	Jan. 1963	Apr. 1963
Minimum mean	1620	2106	4467	231
Ratio max./min.	3·9	3·6	2·1	4·1
	Geographic Variation in the Mean†			
Station position	9°S.	9°30′S.	9°S.	32°S.
Maximum mean	10,140	9343	9315	1072
Station position	27°S.	27°S.	21°S.	30°S.
Minimum mean	2359	2358	4923	271
Ratio max./min.	4·3	4·0	1·9	4·0

* Extreme values chosen from means for 12 traverses during the year.

† Extreme values chosen from means for nine stations.

mean for the planktonic categories, and only twice as large for micronektonic organisms. Even looking at the individual values rather than the means, this general difference persists.

Thus the micronekton samples show evidence of more stable biomasses and numbers, both chronologically and geographically, than do the plankton. This stability might be due to these organisms having either generally longer life cycles or slower responses to environmental changes.

TABLE 2

COMPOSITION OF IKMT 5 SAMPLES

Categories and Groups		Mean % of Sample Dry Wt.
Gelatinous organisms		3·4
IKMT 5 plankton		23·9
Micronekton		
Fishes		34·3
Leptocephali		3·8
Fish larvae		3·1
Non-gelatinous cephalopods		1·6
Gelatinous cephalopods		0·5
	Total	43·3
Macroplankton		
Carids		10·1
Euphausiids		5·2
Sergestids		4·9
Pteropods		2·6
Chaetognaths		2·3
Amphipods (except phronimids)		1·3
Penaeids		1·3
Stomatopod larvae		1·2
Heteropods		0·3
Phronimids, annelids, phyllosomas		0·3
	Total	29·5

(ii) *Mean Composition of Samples*

Table 2 shows the mean composition of the samples, expressed as percentage dry weight of the various components. Figure 2 compares the mean composition in numbers and dry weights of the macroplankton and the micronekton groups (the other categories were not counted).

Table 3 shows that gelatinous organisms have a water content greater than 90% of the estimated biomass. The category includes not only salps, pyrosomes, medusae, etc., but also chaetognaths, leptocephali, transparent crustaceans (e.g. phyllosomas and phronimids), annelids, and gelatinous cephalopods. The water content of plankton and micronekton was less than 85%. The less planktonic groups (e.g. fishes, fish larvae, and large cephalopods) had a water content of only 70–80%. Since carids with eggs have a relatively higher dry weight than carids without eggs, when only the latter are considered the four principal macroplanktonic groups of crustaceans have a water content of 81–83%.

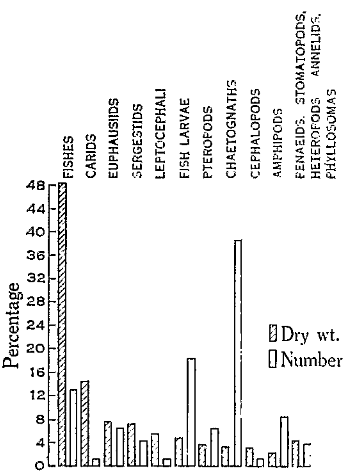

Fig. 2.—Composition of macroplankton and micronekton as a % of their mean dry weight per haul (10·5 g) and as a % of their mean number of organisms per haul (865).

TABLE 3

MEAN CHARACTERISTICS OF ORGANISMS IN IKMT 5 SAMPLES

Groups and Categories	Water Content in % of the Estimated Biomass	Mean Individual Weight	
		Dry Weight (mg)	Estimated Biomass (mg)
Gelatinous organisms	99·0		
Heteropods	98·4	4·5	288
Phyllosomas	95·8	8·4	200
Phronimids	94·1	2·8	47
Annelids	92·5	4·6	61
Chaetognaths	92·1	1·2	15
Leptocephali	92·1	79·0	1100
Gelatinous cephalopods	91·3	15·0	171
IKMT 5 plankton	84·4		
Amphipods except phronimids	83·9	4·1	25
Sergestids	83·0	23·0	135
Small non-gelatinous cephalopods	82·2	64·0	360
Euphausiids	81·3	15·0	80
Penaeids	81·3	29·0	155
Fish larvae	79·1	3·3	16
Stomatopods	78·1	24·0	110
Large non-gelatinous cephalopods	76·9		
Fishes	76·8	47·0	203
Carids	70·4	179·0	605
Pteropods (thecosomas, with shell)	59·7	8·3	21
Pteropods (thecosomas, without shell)	86·8	2·2	17

Taken as a whole, the average sample had a water content of 88·7%. For a mean sample dry weight of 14·8 g, the estimated biomass would therefore be 131 g.

(*b*) *Geographic Variation* (*Dry Weight*)

A general representation of the biology of the region is given by the latitudinal variation in the annual mean dry weight of the four main categories (Fig. 3). With the exception of gelatinous organisms, there was a distinct maximum at 9°–12°S. There

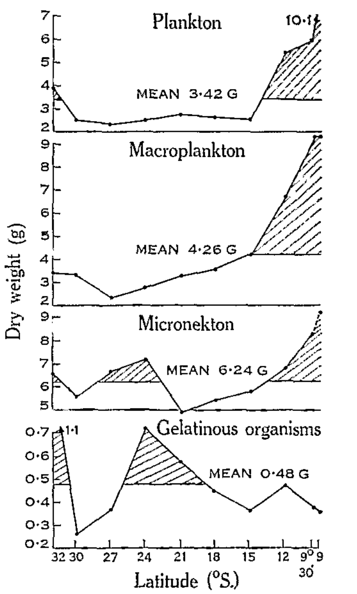

Fig. 3.—Variations with latitude of the annual mean dry weights per haul of the four categories. Hatched areas show values greater than the means for the whole section.

was also a general increase towards 32°S., particularly with gelatinous organisms. For micronektonic and gelatinous organisms there were further peaks at 27°S. and 24°S. Therefore, the distributions seem to be of three main types—maxima in the south (gelatinous organisms), a distinct maximum in the north with a weaker one at 24°S. (micronekton), and a single distinct maximum in the far north (plankton, macroplankton).

Table 4 gives the annual mean dry weights of the various groups, for the regions to the north and to the south of 20°S., and the ratios between values for the two regions. On the basis of these ratios the groups have been separated into four classes.

Almost all the groups which had their maximum annual mean concentration in the south were gelatinous (Table 4), and the water content of the samples decreased towards the north (Table 5). In Table 5 the groups have been classed according to the latitude position of the observed maximum in the annual mean. (The similarity between this classification and that of Table 4 should be noted.) This variation is illustrated in Figure 4. If biomass had been used instead of dry weight, this distribution of the groups would be even more apparent.

TABLE 4

COMPARISON OF MEAN DRY WEIGHTS (mg) OF SAMPLES OF THE GROUPS N. AND S. OF 20°S.

Group	Annual Mean Dry Weight (mg)		
	North of 20°S.	20°S. and South of 20°S.	Ratio N./S.
Leptocephali	345	728	0·47
Phronimids	12	21	0·57
Pteropods	288	458	0·63
Chaetognaths	256	368	0·70
Gelatinous organisms	424	537	0·79
Gelatinous cephalopods	64	71	0·90
Various amphipods	174	191	0·91
Fish larvae	417	423	0·99
Phyllosomas	20	20	1·00
Heteropods	29	27	1·07
Annelids	16	14	1·14
Fishes	5241	4530	1·16
Non-gelatinous cephalopods	249	186	1·34
Stomatopods	202	145	1·39
IKMT 5 plankton	3975	2684	1·48
Penaeids	255	125	2·04
Sergestids	915	428	2·14
Carids	2109	802	2·63
Euphausiids	1205	329	3·67
Total sample	16196	12087	1·34

TABLE 5

LATITUDINAL VARIATION IN THE COMPOSITION OF IKMT 5 SAMPLES

Figures in bold, principal maximum; italicized figures, secondary maximum

Group	% of Mean Annual Dry Weight of Sample at Latitude (°S.)									
	32°	30°	27°	24°	21°	18°	15°	12°	9°30′	Group Mean
Pteropods, chaetognaths	10·2	**10·5**	3·8	3·7	*8·6*	4·7	3·0	3·5	2·6	4·9
Gelatinous organisms, leptocephali, gelatinous cephalopods	*12·6*	5·6	9·5	**17·3**	11·3	7·0	6·4	4·2	3·7	7·7
Phronimids, fish larvae, non-gelatinous cephalopods	*5·9*	4·9	**6·7**	**6·7**	4·4	5·6	4·1	4·0	3·4	4·8
Annelids, phyllosomas, various amphipods	2·8	**3·7**	1·2	1·2	1·2	1·2	1·1	1·3	*2·1*	1·5
Stomatopods, fishes, heteropods	33·2	41·2	**46·8**	37·2	38·6	37·3	*38·7*	30·5	30·3	35·7
IKMT 5 plankton	*25·9*	22·1	20·1	18·9	24·0	22·0	20·0	**28·2**	25·2	23·9
Penaeids, sergestids, carids, euphausiids	9·3	12·0	12·1	15·0	12·0	22·2	26·5	28·5	**32·8**	21·5

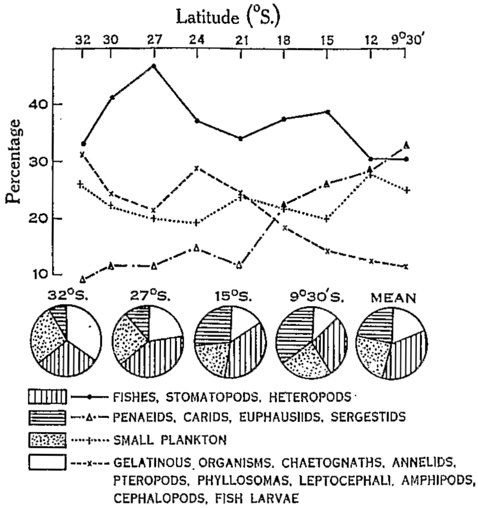

Fig. 4.—Variations with latitude of the annual mean composition of the IKMT samples.

Variation in size of organisms with latitude is given in Table 6 for the groups considered as holoplanktonic. Cephalopods, chaetognaths, and penaeids were larger

TABLE 6

VARIATION WITH LATITUDE OF SIZE OF INDIVIDUAL ORGANISMS IN IKMT 5 SAMPLES

Values in italics, maximum

Group	Individual Dry Weight in mg (Annual Mean)		
	South of 26°S.	24°30′–15°S.	North of 12°30′S.
Gelatinous cephalopods	*14*	10	8
Non-gelatinous cephalopods	*60*	49	34
Penaeids	*30*	26	22
Chaetognaths	*1·5*	1·2	0·6
Annelids	2·5	*4·7*	3·9
Pteropods	5·4	*9·0*	5·3
Fishes	37*		56*
Carids	117	168	*189*
Sergestids	16	17	*21*
Euphausiids	11	12	*14*
Heteropods	6	4	*7*
Phronimids	1·4	1·4	*1·8*
Various amphipods	*3·1*	2·9	2·9

* Fishes were considered for only two zones, with 20°S. as the only boundary.

in the south; annelids and pteropods were larger in mid latitudes; heteropods, fishes, and the majority of large crustaceans (Caridae, Sergestidae, Euphausiacea) were larger in the north.

TABLE 7

SEASONAL VARIATION OF % OF TOTAL DRY WEIGHT OF GROUPS

Values in bold type, principal maximum; values in italics, secondary maximum

Groups	% of Total Dry Weight for each Traverse												
	Aug. 1962	Sept. 1962	Oct. 1962	Nov. 1962	Jan. 1963	Feb. 1963	Mar. 1963	Apr.–May 1963	May–June 1963	June–July 1963	July 1963	Aug. 1963	Group Mean
Annelids, phyllosomas, various amphipods	0·6	1·4	**2·5**	**2·5**	1·6	1·2	0·9	1·2	1·3	1·3	1·3	*2·1*	1·5
Pteropods, chaetognaths	*6·2*	3·6	4·8	**8·6**	**7·1**	4·0	2·8	3·4	3·8	3·7	3·4	*6·5*	4·9
Gelatinous organisms, leptocephali, gelatinous cephalopods	7·0	*8·1*	6·3	6·6	8·9	**16·1**	**10·4**	7·9	6·6	6·1	6·1	5·6	7·7
Phronimids, non-gelatinous cephalopods, fish larvae	*5·6*	3·5	4·3	*6·4*	3·8	**5·5**	**6·1**	4·2	**5·9**	3·0	3·8	*5·4*	4·8
Stomatopods, fishes, heteropods	28·2	26·0	*34·9*	26·0	*37·2*	34·3	34·8	**51·7**	41·8	43·0	39·8	41·2	35·7
Penaeids, sergestids, euphausiids	*12·2*	8·0	*12·7*	*12·1*	13·0	10·7	7·8	9·4	**13·5**	**14·7**	**41·1**	6·9	11·4
Carids	**13·6**	7·9	9·2	7·3	*11·5*	4·6	7·5	7·1	11·3	11·2	**15·0**	**13·6**	10·1
IKMT 5 plankton	**26·6**	**41·2**	**25·3**	**30·4**	16·7	23·4	*29·7*	15·1	15·8	17·2	16·8	17·8	23·9

(*c*) *Seasonal Variation and Total Variations* (*Dry Weights*)

Figure 5 shows that very marked maxima were observed for each of the four categories between August and October or November. Distinct minima occurred between December and February; these were followed by much less marked secondary maxima between February and July. Minima and secondary maxima occurred at different times for the different categories.

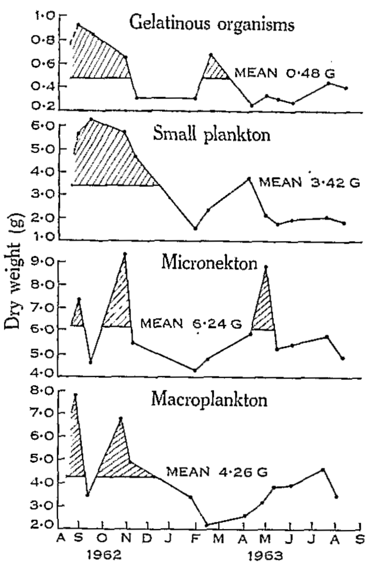

Fig. 5.—Seasonal variations of mean dry weights per haul for the whole section. Hatched areas show values greater than the means for the whole period.

Table 7 shows the seasonal variations in greater detail; a group classification has been used comparable to that in Table 5. The distribution of maxima shows a maximal influence of the gelatinous organisms from October to March, of the macroplankton from April to July, and of the IKMT plankton from August to October. Fishes represent half of the total dry weight in April, IKMT plankton 40% of the total in September, large macroplanktonic crustacea about one-third in July, and gelatinous organisms one-quarter in February.

Comparing Tables 5 and 7 shows that the more northerly is the position of the group's maximal influence, the later in the seasonal cycle is the appearance of this maximum. But only the general means, valid for the observations made at 2230 hr between 0 and 200 m, are considered here, and the preceding descriptions are valid only within these limits.

Figures 6–9 show details of the observed distributions, and at the same time give the dry weights per category for each station. They confirm the trends which have been described above. Moreover, in September 1962 a very sudden and very extensive region of low biomass occurred, for all except the gelatinous organisms.

(*d*) *Seasonal and Geographical Variations of Number of Organisms per Group*

(i) *Numerical Variation of Macroplanktonic and Micronektonic Organisms*

A complete synthesis of the results can be made only after a detailed study of the cycles of all species collected. Some of these studies are under way, but will probably never be complete. Nevertheless, it is interesting to try to identify more

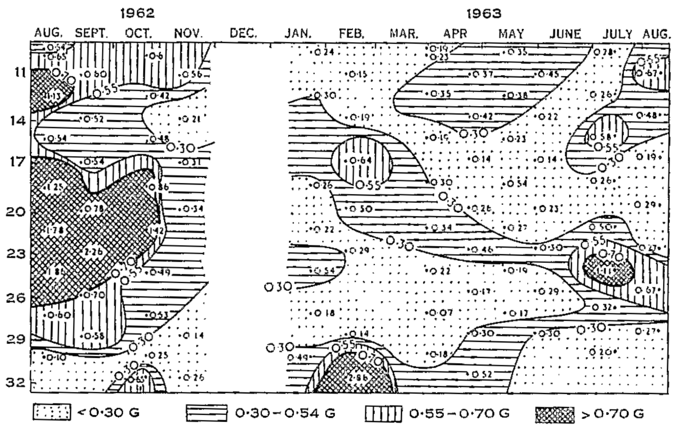

Fig. 6.—Gelatinous organisms. Contours of the dry weight per haul (g) as a function of latitude and time.

precisely the general features of the distribution at the level of the "groups", which represent biological entities that are less heterogeneous than the "categories". Also, biomass or dry weight values include the effects of both growth cycles and abundance variations. It is interesting to consider these two factors separately by referring to the

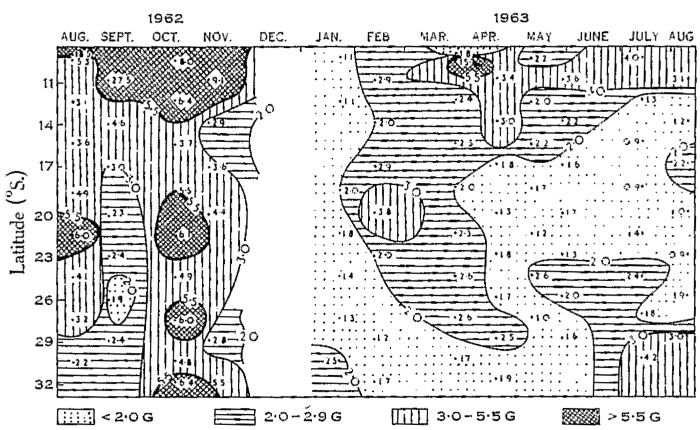

Fig. 7.—Plankton. Contours of the dry weight per haul (g) as a function of latitude and time.

number of organisms collected by groups, and to their individual mean weights (dry weights divided by total number).

The distribution in time of the mean frequencies observed for each traverse of the section has been considered in each of three zones. The southern zone of the section is defined as extending from 32° to 26°S., the central zone from 24°30′ to 14°S., and the northern zone from 12°30′ to 9°S. Not all the groups were considered in this way: for fish and fish larvae, whose distribution was distinctly bimodal, a division into more than two zones would have completely falsified reality, and 20°S. was chosen as the only boundary; euphausiids, on the other hand, had a very marked northern maximum, but this peak commenced very clearly at a more southern station than that

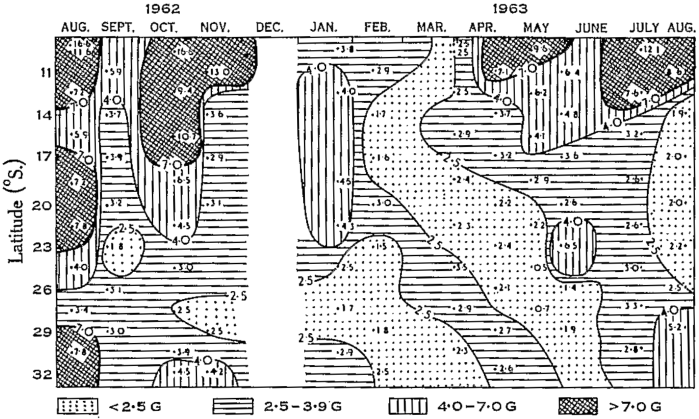

Fig. 8.—Macroplankton. Contours of the dry weight per haul (g) as a function of latitude and time.

observed for the other groups; in this case the northern zone was defined as extending from 15°30′ to 9°S. Altogether, 14 groups were studied in the north and south zones, and 12 in the centre, and this represents 40 annual distributions.

Most of these annual distributions are bimodal; this has made it possible to summarize cycles for each region using three parameters: position in time of the

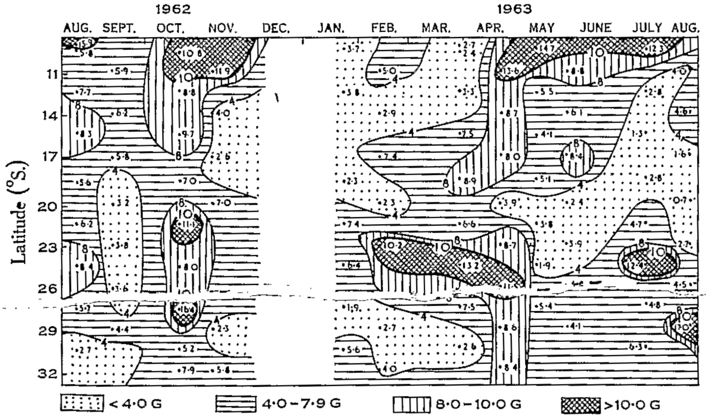

Fig. 9.—Micronekton. Contours of the dry weight per haul (g) as a function of latitude and time.

principal annual maximum, of the secondary maximum, and of the principal annual minimum. However, seven of the 40 distributions were multimodal at the level of the secondary maximum; in these seven cases, the secondary maximum has been chosen more or less arbitrarily, but since the proportion of these cases is small, they do not alter the conclusions which follow (Fig. 10):

(1) The principal maxima are mainly concentrated (29 out of 40) in the August–November period. This is particularly clear in the south and the north (for 11 and 12 of the groups studied, respectively); it is less so in the centre (6 out of 12 groups, mainly in the August–September period), where a greater spreading through the year is observed. In the south, 7 of the 11 groups have their maxima in August–September; in the north, 8 out of the 12 have their maxima in October–November.

(2) Figure 10 suggests that there could be a positive relationship between the positions in time of the principal and secondary maxima observed for the different groups in the three zones. This suggests that they are not independent of each other, and that they reflect two main phases of the cycles of the dominant species of the groups. A space of 2–9 months separates principal and secondary maxima (in more than three-quarters of the cases, this is 6–9 months). For the 40 distributions studied, 15 secondary maxima were observed in the April–June period, seven in August, and 12 in October–November.

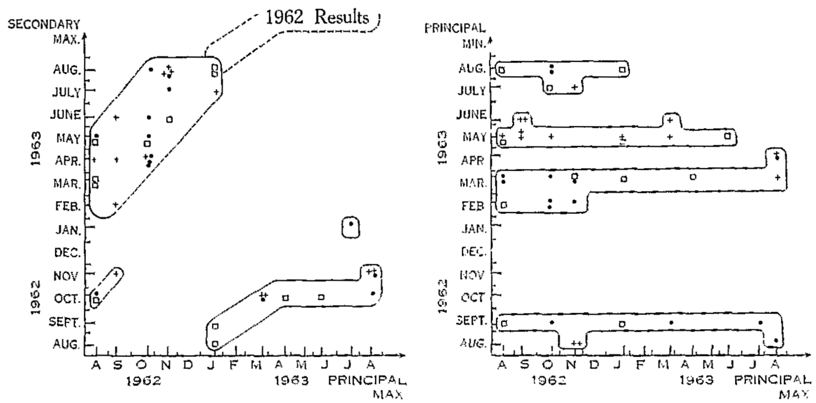

Fig. 10.—Relationship between dates of occurrence of secondary and principal maxima, and between dates of occurrence of annual minimum and principal maximum. + Observed south of 26°S. □ Observed between 25°30′S. and 15°S. ● Observed north of 12°30′S.

(3) Figure 10 suggests that there was no apparent relationship between periods of maximal numerical abundance and periods of minimal numerical abundance, but rather that these periods of minimal frequency are actual discontinuities in the annual trend of the quantitative distributions, affecting the greater proportion of the groups simultaneously. Nine minima were observed out of 14 groups tested, in May–June in the southern zone (3 minima in central zone for the same period). Seven minima were observed in 14 groups in February–March (4 minima in central zone, and 1 in the south, for the same period). Finally a third unfavourable period occurred after July, particularly in August–September: 5 minima in the central zone, 6 in the northern zone, and 3 in the southern zone.

Once again there is greater heterogeneity of distributions in the central zone, a clear alternating of periods of poverty between the north and the south from February to June, and the September low in the middle of the richest period, particularly in the north and centre.

In summary, although some of the points presented earlier in this paper conform to this scheme (Table 7), the mean numerical abundances seem to suggest better than the biomasses that, although the periods of maximal frequency can effectively reflect the seasonal cycles of the dominant species, the minimal frequencies actually correspond to invasions of conditions which are unfavourable to a large proportion of the groups. These groups might have moved away from the region in the waters which they inhabited, or they might have sunk. It might also have happened that their nocturnal migration towards the surface did not reach the depth sampled. This would apply to the periods February–March in the north, May–June in the south, and September mainly in the north and centre.

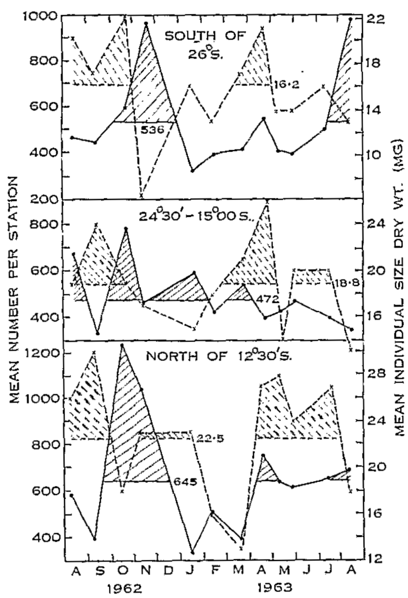

Fig. 11.—Seasonal development of individual size (×———×) and total numbers per haul (●———●) of macroplankton and micronekton, chaetognaths excluded, for the three zones along the section. Hatched areas show values greater than the mean for the whole period.

(ii) *Variation of Individual Size in relation to Variations in Frequency*

Since the study of the size of the organisms can be valid only at the species level, we shall restrict ourselves to discussion of some overall indications which can be inferred from Figure 11. The general mean size of the organisms was calculated for each passage across the section, in each of the three zones. The mean size was obtained by dividing total dry weight of the organisms counted by their total number. The mean for each traverse of each region is indicated on the figure but the numbering for chaetognaths has been left out. Although the chaetognaths sometimes represent up to 50% of the number, their dry weight is such a low percentage that they would have masked the size development of all the other groups, whose frequencies are much more comparable among themselves, and whose individuals are of a much greater dry weight.

Figure 11 shows that in October in the south, and in September in the north, the maximal size precedes the principal maximum in number by about a month. This maximum coincides with the minimal size in the south, and with decreasing sizes elsewhere. Another size peak commencing in April is particularly notable in the north, and corresponds to a secondary increase in numbers.

The situation in all the regions can be summarized as a negative size-frequency relationship from August to January, and a positive relationship from February to July. This permits the speculation that the first maximum signifies a concentration of juveniles, the following phases corresponding to a continuously increasing concentration of adults.

IV. Discussion

Variations of Cycles in relation to the Supposed Trophic Levels of the Organisms under Consideration

The different approaches used in the preceding paragraphs have demonstrated certain general characteristics of the organisms collected in this region by the IKMT 5, and certain general features of their distribution as a function of time or latitude. These characteristics as well as the distributions might well be suspect. The data reflect only the situations between 0 and 200 m, at an hour of the diurnal cycle which was chosen because it was supposed to correspond to a maximal concentration at the surface. But this is doubtless not true of all the organisms, for all the regions traversed, in all seasons. The observed seasonal or geographical fluctuations could in fact correspond with fluctuations in abundance as suggested or simply with variations in the depths occupied by the species in the course of their diurnal migration, or again, movement away of the water masses which previously occupied the section.

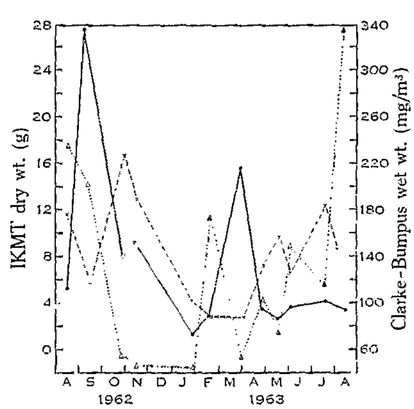

Fig. 12.—Comparison of the seasonal development of IKMT plankton (●———●), IKMT macroplankton (×———×), and Clarke–Bumpus night plankton (△———△) at stations of maximal abundance at the northern end of the section.

One of the most important points which requires study is a comparison of the time and space cycles in relation to the trophic levels of the organisms. Figure 12 is the nearest approach we can make to this problem. The samples taken by a small-mesh, small net like the Clarke–Bumpus, used during the same cruises, would show a much greater percentage of herbivores and short life cycle organisms than the IKMT samples. It is to be expected that the plankton category of the IKMT samples would be the only one to include a certain proportion of short life cycle organisms, and perhaps herbivores. In contrast, the micronekton category comprises mainly organisms of a much longer cycle (1 or more years), and the adult forms at least could certainly only be primary or secondary carnivores.

However, Figure 12 shows that in the rich zone at the northern extremity of the section, the times of occurrence of the peaks and lows in each category follow one another in the following order: Clarke–Bumpus plankton, IKMT plankton, IKMT macroplankton, with a lag of more than a month between each one. The annual cycles of the macroplankton and of the micronekton coincide rather well. There is very little difference between the sizes of the two annual peaks for each of these two categories.

Comparable successions in time were already seen in Figure 5 and Table 7.

On the basis of purely geographic, non-seasonal surveys, Vinogradov and Voronina (1962) and King (1958) established that there were spatial gaps between peak abundance of different planktonic trophic levels. From this, they assumed that the corresponding temporal gaps were 63–88 days (Vinogradov and Voronina, Indian Ocean), and 43–97 days (King, Pacific Ocean).

Figure 12 gave some direct but imprecise measurement of the temporal gap between CBS plankton and IKMT macroplankton. This was 2–3 months, and thus agreed reasonably with the assumptions of Vinogradov and Voronina, and King.

The 2–3 month temporal gap between CBS plankton and IKMT macroplankton could be explained by the effect of current velocities at different depths on organisms with different cycle lengths and vertical distribution.

These differences are an important aspect of the different distributions of planktonic trophic levels and their relationships. Positive or negative correlations between prey and predator could often be explained in this way.

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