

STUDIES ON THE PHYTOPLANKTON OF THE WEST COAST OF INDIA. PART IV. MAGNITUDE OF THE STANDING CROP FOR 1955-1962, WITH OBSERVATIONS ON NANOPLANKTON AND ITS SIGNIFICANCE TO FISHERIES *

By R. SUBRAHMANYAN, ** and A. H. VISWANATHA SARMA ***

Central Marine Fisheries Research Institute

INTRODUCTION

It is well known that net collection of plankton made for quantitative studies on the standing crop does not give a correct picture, for lack of such data as quantity of water filtered, speed of haul and degree of clogging of the bolting silk meshes. Further, another source of error is the unknown quantity of minute organisms, the *nanoplankton*,¹ that readily pass through the meshes of even the finest woven bolting silk which are not reckoned and the consequent distorted picture obtained about the abundance of the larger organisms. These and other methodological aspects, as well as the importance of nanoplankton, have been pointed out and discussed by several workers, Allen, 1919; Atkins, 1945; Bernard, 1939, 1952, 1954, 1956, 1958a, b; Bernard and Fage, 1936, 1958; Bernard and Lecal, 1960; Braarud, 1958; Cole and Knight-Jones, 1949; Goldberg, Baker and Fox, 1952; Gross, 1937; Harvey, 1950; Hentschel, 1932, 1933; Hulbert, Ryther and Guillard, 1960; Knight-Jones, 1951; Knight-Jones and Walne, 1951; Krey, 1958; Lohmann, 1901, 1908; Riley, 1939, 1941a; Smayda, 1965; Steemann Nielsen, 1938; Steemann Nielsen and Jensen, 1957; Utermöhl, 1931; Wood and Davis, 1956; Yentsch and Ryther, (1959), and also by Subrahmanyam (1959) for the West Coast of India. The only account of nanoplankton for the Indian Ocean region appears to be by Bernard and Fage (1958) and Bernard and Lecal (1960) who estimated its abundance in the Indian Ocean. Many of these workers give evidence to show that the photosynthetic activity of nanoplankton may contribute to the bulk of the organic production in parts of the oceans and state that its importance in the economy of the sea has perhaps been greatly underestimated. But, a few (Ballantine, 1953; Cushing, 1955) consider them insignificant and argue that their contribution to organic production is far less than that by diatoms.

The importance of nanoplankton lies in this that it might form the main source of food for the minute zooplankters as also the larvae of the planktonic, pelagic and benthic animals as many of these cannot ingest the larger organisms such as the many setaceous diatoms (Atkins, 1945; Bruce, Knight and Parke, 1940; Clarke

* Published with the permission of the Director, Central Marine Fisheries Research Institute, Mandapam Camp, India.

** Present address : C.M.F.R. Sub-Station, Ernakulam-6, S. India.

*** Present address : Indian Ocean Biological Centre, Ernakulam-6, S. India.

¹ Lohmann (1903) first applied the term *nanoplankton* to that portion of the plankton which passes through the pores of a fine plankton net, which includes the smaller Diatoms, Dinoflagellates, Silicoflagellates, Microflagellates, Coccolithophores, Protozoa and Bacteria, the majority of which are autotrophic in nature.

and Gellis, 1935 ; Clarke and Zinn, 1937 ; Cole, 1936, 1939 ; Fuller and Clarke, 1936 ; Hanuška, 1949 ; Raymont and Gross, 1942 ; Thorson, 1946, 1950).

Detailed studies based on net collections of the phytoplankton of the Malabar Coast on the West Coast of India have been already reported (Subrahmanyam, 1958b, 1959 ; Subrahmanyam and Sarma, 1960). It was deemed desirable to attempt an accurate measurement of the total standing crop by measuring the pigment in a known quantity of sea-water, as this would, in addition to giving an indication of the error involved in sampling the crop using the net in this area, would also give a quantitative assessment of the smaller organisms that pass through the meshes of the bolting silk and their seasonal fluctuations. No such observations are available for Indian waters nor an account for any area elsewhere covering a number of years.

METHODS

The routine plankton collection stations situated at 4 F-, 10 F- and 20 F- areas in a perpendicular section off Calicut on the West Coast of India were sampled once a week for the present studies. Equal quantities of water were collected from surface, middle and bottom layers using a Casella Bottle and immediately after returning to the Laboratory, a measured quantity of water from each sample was filtered for pigment estimations. 10-20 l of water were at first filtered through No. 16 bolting silk and 5 l of the filtrate was refiltered through Whatman Filter Paper No. 542. From 1958 onwards Collodion Filter Plates were used in the place of Whatman paper and filtration was carried out in the Gimesi Plankton-Filter with the aid of a vacuum pump. Before refiltration, the nanoplanktonic organisms in the filtrate were first concentrated by adding 5 ml of 1% solution of $K_2Al(SO_4)_2$ per litre of sea-water with pH 8.0 (*vide* Atkins and Parke, 1951). The supernatant liquid was decanted off after the flocculent mass had settled to the bottom. The pigment was extracted separately from the sediment on the bolting silk disc as well as Filter Plates with 80% Acetone for 24 hours in the dark at room temperature and estimated colorimetrically using Harvey's colour standards (Harvey, 1934). The value of both reckoned together gives the total standing crop. The phytoplankton content in a M^3 of the water column was calculated from this, assessing the water samples from the three depths as a whole, equal volumes of which had been taken for filtration.

For qualitative studies, the organisms in 5 l of the filtrate after filtering through the bolting silk disc (without adding any preservatives) were concentrated by continuous centrifugation in an International Centrifuge at maximum rotation speed for 30 minutes and examined.

RESULTS AND DISCUSSION

1. *Quantitative studies on nanoplankton and net phytoplankton.*

The results of studies carried out at the 10 F Station over a period of eight years from 1955 to 1962 are presented in Fig. 1 (The trends at the other two stations are very similar and, therefore, are not discussed here.) The seasonal fluctuation shows a peak during the south-west monsoon months every year, but the intensity varies from year to year. In terms of monthly averages, the highest values for the total standing crop obtained were 171,000 Pigment Units (PPU)/ M^3 (September,

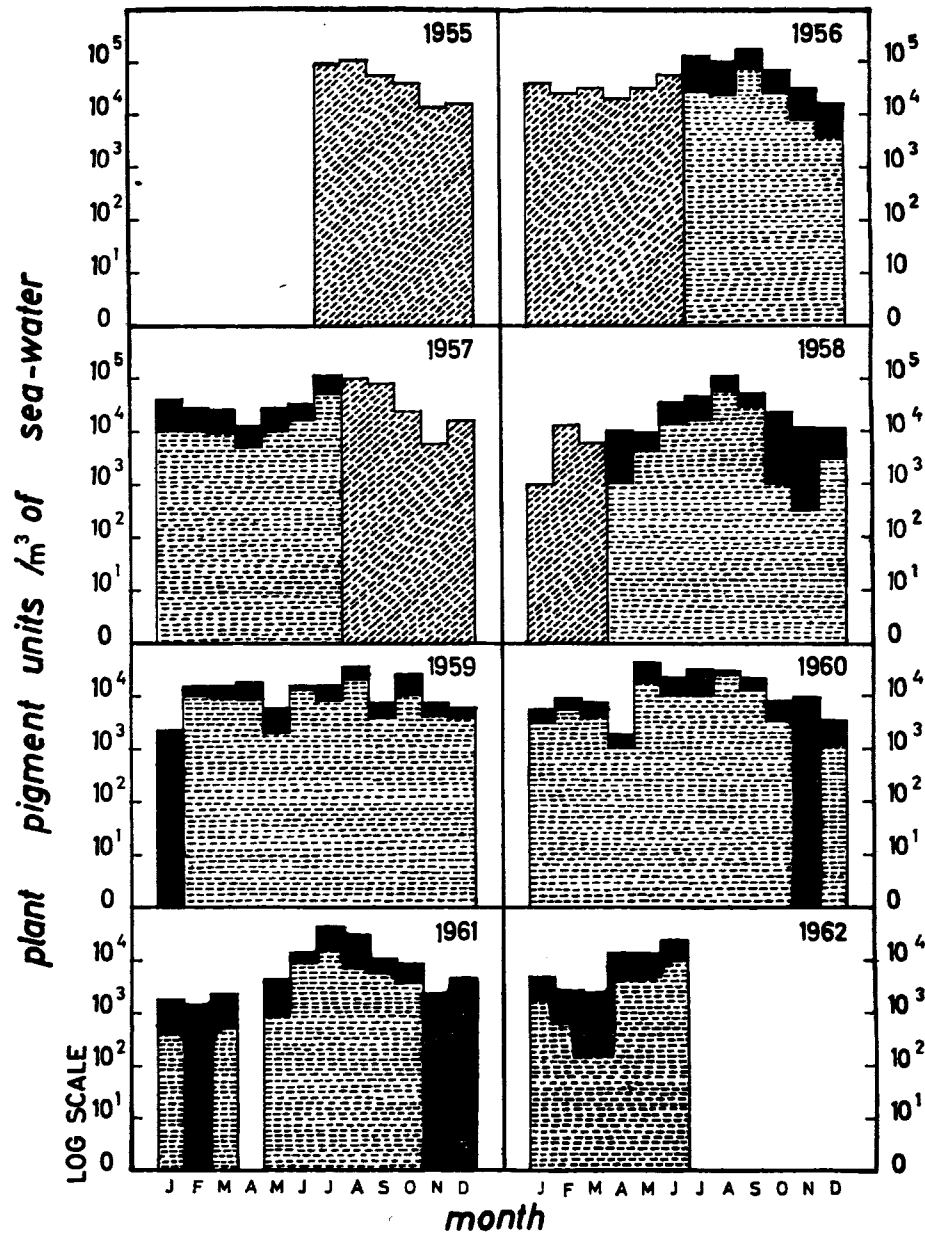


FIG. 1. Seasonal fluctuation of the total standing crop of phytoplankton in terms of Plant Pigment Units/ M^3 of sea water. The horizontally hatched portion indicates the nanoplankton and the dark portion the net plankton. The obliquely hatched portion shows the total standing crop for the period July 1955 to June 1956 and August 1957 to March 1958 when the nanoplankton could not be separately estimated.

1956) while the lowest were 1,000 PPU/M³ (January, 1958). Individual estimations indicate much wider fluctuations ranging from 400 PPU/M³ (25-4-1960) to 248,000 PPU/M³ (28-7-1955 and 24-7-1956). The monsoon bloom of phytoplankton was richest and most sustained during 1956 (May to October) and of shortest duration during 1959 and 1961 (June to August). On seasonal basis, the standing crop varied from 1,300-248,000 PPU/M³ during the south-west monsoon season which is the phytoplankton dominant period, and 500-75,000 PPU/M³ during the north-east monsoon season. This trend of fluctuations fully confirms those obtained by the employment of the net in this area and has been discussed in detail by Subrahmanyam (1958b, 1959) and, Subrahmanyam and Sarma (1960). Earlier, Subrahmanyam (1959), using similar methods, estimated the magnitude of the total standing crop of phytoplankton in terms of plant pigments and organic carbon per M² of sea surface and stated that 'the high plankton content of the water obtained by the water sample method is striking compared with the lower values for the net samples, where, obviously, a large number of minute organisms escape through the meshes of the net.' The rate of organic production in this area, indicates a very similar trend in the seasonal fluctuation as reported here (Sarma, Unpublished).

The nanoplankton portion was separately estimated from July 1956 onwards; the pigment values for net and nanoplankton samples are given in Table I. The highest values for nanoplankton were recorded in September 1956 (96,000 PPU/M³), while the highest values for the net portion were recorded in July 1956 (103,520 PPU/M³). The nanoplanktonic portion was not detectable in any of the estimations during January 1959; November 1960; and February, November and December of 1961. During the period of the present study, nanoplankton fluctuated from 0-120,000 PPU/M³ during the south-west monsoon season, and 0-35,000 PPU/M³ during the north-east monsoon season. Net plankton content varied from 300-216,000 PPU/M³ for the whole period. On percentage basis, nanoplankton constituted 85% of the crop in August 1960, and 84% in June 1959 in terms of Plant Pigment Units. In most of the estimations, it formed 30-50% of the crop, while on 8-6-1959 it contributed to 96% of the standing crop. The same was the case when the net was hauled through a *Gymnodonium* bloom on one occasion in November 1959. The seasonal fluctuations in the nanoplankton on percentage basis of the total standing crop is shown in Fig. 2. It is seen that except for two peaks in June and September, the percentage in terms of PPU/M³ remains almost constant throughout the year.

These studies show that, on the basis of overall average of the Plant Pigment Units, the nanoplankton constitutes about 40% of the total standing crop and this should be considered as the minimum error to be expected in the sampling with a net in this area. It is generally accepted that the standing crop of nanoplankton in the tropical waters is richer than at higher latitudes. Sverdrup, Johnson and Fleming (1942) state that this portion of the plankton may constitute as much as a third or more of the total mass of plankton at some seasons and certain areas, while according to Steemann Nielsen, in the open warm oceans nanoplankton (< 40 μ) may sometimes contribute upto almost 100% of the standing crop (average 94%). Bernard (1958a) states that calcareous flagellates constitute 75-96% of the phytoplankton volume in the Mediterranean Sea. According to Yentsch and Ryther (1959), at Vineyard Sound, the nanoplankton contributes to 92% of the total chlorophyll, 91% of total cell numbers and 98% of the photosynthesis. Hulbert, Ryther and Guillard (1960) estimated that it was at least 100 times more numerous than the larger phytoplankton and that the biomass of the two groups would be the same. They state that the photosynthetic activity of this group may be far more important than that of the larger cells.

It was not possible to make any quantitative estimations of the nanoplankton organisms by cell counts. However, in comparison with the larger organisms in terms of quantum of pigment extracted, the nanoplankton number must be enor-

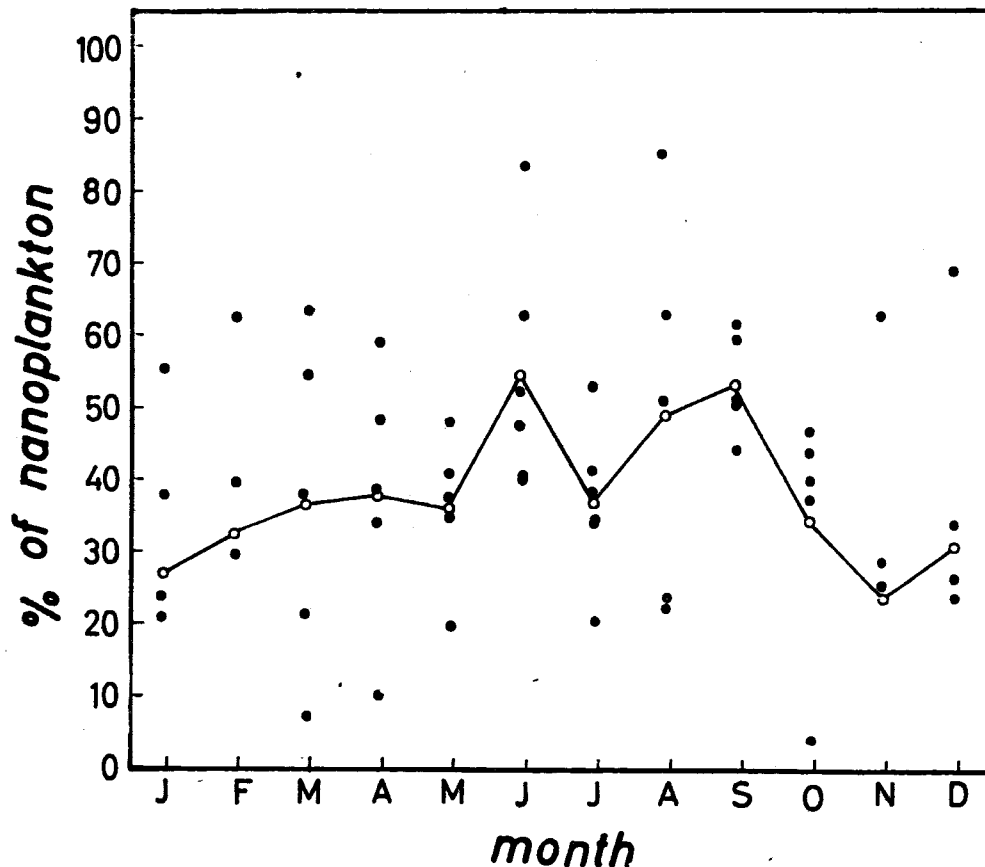


FIG. 2. Seasonal fluctuation of nanoplankton on percentage basis of the total Plant Pigment Units/M³ of water. The curve with white circles indicates the overall monthly averages for the period of study; the black dots indicate the individual monthly average value.

mous, as each cell, because of its minute size, would contain only a very small quantity of pigment; in other words, the pigment in one diatom cell of average dimensions would be equivalent to that in several of the nano-flagellates. The importance of taking the cell size into consideration while comparing pigment units with cell counts has been stressed by Harvey *et al.* (1935), Mare (1940) and others. For this purpose, Yentsch and Ryther (*l.c.*) have calculated the relative chlorophyll content of several species of nanoplankton.

The net phytoplankton in terms of Plant Pigment Units showed pronounced seasonal trends in its fluctuations, with the values gradually rising from February onwards until the peak of the south-west monsoon bloom is attained by July, from whence it steadily fell, touching the minimum in December followed by a minor

secondary peak in the following January. In comparison with this, the trend of seasonal fluctuations of the nanoplankters was not as marked; however, the Plant Pigment values were usually quite high during the south-west monsoon season and very poor during the north-east monsoon months. This is to be expected because of the shorter span of life-cycles of the constituent microflagellates. The only controlling factor in their fluctuation would appear to be the environmental conditions as pointed out by Subrahmanyam (1959) for larger phytoplankters, particularly certain nutrients which are essential for their growth, which get locked up in the bottom sediments as a result of calmer state of the sea. It is also quite interesting that the bloom of nanoplankters always lags behind that of larger phytoplankters, usually occurring only after the latter has begun to wane. Thus, during the primary and secondary blooms, nanoplankton touches the peak in terms of Plant Pigment Units in the months of August and February after the net phytoplankton has already attained the peak in July and January respectively. Birge and Juday (1922), who were perhaps the first to make a quantitative assessment of the biomass of nanoplankton (in freshwaters), found that it did not show any marked trends in seasonal fluctuations. Observations of Yentsch and Ryther (*l.c.*) show that cell numbers do not follow any uniform seasonal trend, but chlorophyll exhibits three major peaks, although the fluctuations were not as pronounced when compared with that of net phytoplankton.

It is possible that the standing crop of zooplankton and shoaling fishes in the inshore areas might be responsible for the depletion of nanoplankton by grazing during the north-east monsoon season. Elsewhere we (Subrahmanyam and Sarma, 1960) have pointed out that a similar trend exists for the net phytoplankton also. The nanoplankton could be a crucial factor regulating the survival rate of fish larvae, as these small plankters are likely to constitute a major portion of their diet. This would also throw some light on the prospects of future fish harvests resulting from that year's recruitment. It would be of great interest to recall here that many workers have employed microflagellates for feeding fish larvae in rearing them in the laboratory and met with success.

2. Qualitative nature of nanoplankton.

Qualitative analysis of nanoplankton was carried out on a few occasions during June-October period of 1959 to 1961.² For this purpose the organisms were concentrated by centrifugation or on the Gimesi Plankton-Filter and examined. The following organisms were recorded.

Bacillariophyceae: *Bacterosira fragilis* Gran, *Chaetoceros filiformis* Meunier, *C. socialis* Lauder, *Cocconeis* spp., *Corethron hystrix* Hensen, *Coscinodiscus excentricus* Ehrenberg, *C. sublineatus* Grunow, *Coscosira polychorda* Gran, *Cyclotella meneghiniana* Kützing, *Detonula confervacea* (Cleve) Gran, *Diploneis* sp., *Fragilaria oceanica* Cleve, *Leptocylindrus danicus* Cleve, *L. minimus* Gran, *Mastogloia* sp., *Melosira sulcata* (Ehrenberg) Kützing, *Navicula* spp., *Nitzschia closterium* (Ehrenberg) W. Smith, *N. panduriformis* Gregory, *N. seriata* Cleve, *Pleurosigma carinatum* Donkin, *Skeletonema costatum* (Greville) Cleve, *Schroederella delicatula* (Peragallo) Pavillard, *Thalassiosira decipiens* (Grunow) Jörgensen, *T. nana* Lohmann, *Triceratium alternans* Bailey, and *T. reticulatum* Ehrenberg.

Dinophyceae: *Amphidinium* sp., *Ceratium teres* Kofoid, *Cochlodinium* spp., *Dinophysis acuminata* Clap. et Lachm., *Exuviaella compressa* Ostenfeld, *Glenodinium*

² The nature of net plankton and species concerned are given in Subrahmanyam and Sarma (1960).

TABLE I
 Comparison of the Magnitude of the Standing Crop of Net Phytoplankton and Nanoplankton

Month	Net Phytoplankton Nanoplankton	Plant Pigment Units/M ³ of Sea-water										
		1955	1956	1957	1958	1959	1960	1961	1962			
January	Net Phytoplankton	—	(39,400)*	30,750	(1,000)	2,330	2,430	1,520	2,920			
	Nanoplankton	—	—	10,000	—	0	3,050	420	1,800			
February	Net Phytoplankton	—	(24,750)	16,250	(15,500)	5,000	3,350	1,430	1,750			
	Nanoplankton	—	—	10,750	—	10,000	5,680	0	750			
March	Net Phytoplankton	—	(31,250)	15,750	(5,500)	5,400	3,380	1,770	2,130			
	Nanoplankton	—	—	9,750	—	9,480	4,100	500	170			
April	Net Phytoplankton	—	(19,100)	7,800	8,750	8,930	750	—	8,500			
	Nanoplankton	—	—	5,000	1,000	8,500	1,100	—	4,500			
May	Net Phytoplankton	—	(31,250)	16,500	4,550	3,620	25,150	3,400	8,110			
	Nanoplankton	—	—	10,000	4,200	2,000	17,750	850	4,730			

June	Net Phytoplankton	—	15,330	20,330	2,450	11,220	4,830	13,860
	Nanoplankton	(60,000)	17,000	13,670	12,630	10,300	8,330	9,460
July	Net Phytoplankton	(90,500)	103,520	31,140	7,200	20,500	26,200	—
	Nanoplankton		27,200	16,290	8,100	10,850	16,250	—
August	Net Phytoplankton	(107,000)	83,000	53,710	12,390	4,400	21,630	—
	Nanoplankton		24,000	56,430	20,810	24,800	6,880	—
September	Net Phytoplankton	(54,750)	96,000	20,170	3,480	8,250	5,900	—
	Nanoplankton		75,000	29,170	3,600	13,000	6,000	—
October	Net Phytoplankton	(38,000)	41,600	22,000	15,030	4,200	4,400	—
	Nanoplankton		24,400	1,000	9,950	3,230	3,830	—
November	Net Phytoplankton	(13,250)	23,000	11,330	2,700	9,050	2,270	—
	Nanoplankton		7,750	330	4,500	0	0	—
December	Net Phytoplankton	(15,800)	11,800	8,500	1,900	2,230	4,600	—
	Nanoplankton		3,600	3,000	4,150	1,130	0	—

* Figures in brackets indicate total standing crop for those months for which the net phytoplankton and nanoplankton portions were not separately estimated.

lindemanni Lefevre, *G. pilula* (Ostenfeld) Schiller, *G. trochoideum* Stein, *Gonyaulax minima* Matzenauer, *G. scrippsae* Kofoid, *Goniodoma polyedricum* (Pouchet) Jörgensen, *Gymnodinium marinum* Saville-Kent, *G. splendens* Lebour, *Gymnodinium* spp., *Gyrodinium citrinum* Kofoid, *Gyrodinium* spp., *Oxytoxum gladiolus* Stein, *O. scolopax* Stein, *Peridinium africanum* Lemmermann, *P. bulla* Meunier, *P. inconspicuum* Lemmermann, *P. minutum* Kofoid, *P. pedunculatum* Schütt, *Phalacroma rotundatus* (Clap. et Lachm.) Kof. et Mich. *Prorocentrum dentatum* Stein and *P. micans* Ehrenberg.

Chlorophyceae : *Carteria* sp., and *Chlamydomonas* sp.

Coccolithineae : *Coccolithus pelagicus* (Wallich) Schiller.

Euglenineae : *Euglena* sp.

Myxophyceae : *Merismopedia* sp.

Most of these organisms have already been recorded from the West and East Coasts of India (Subrahmanyam, 1946, 1958a; Subrahmanyam and Sarma, 1960). Bernard and Lecal (1960), however, could not find any nanoplanktonic diatoms in the central Indian Ocean area, presumably because the collections were not spread over any length of time. Yentsch and Ryther (1959) found that the main constituents of nanoplankton at Vineyard Sound were diatoms.

Diatoms predominated during June-August period when the net catches were also abounding in larger diatom cells, while during September-October, Dinophyceae became very abundant. It is known that in the open seas Dinophyceae succeed diatoms in their abundance. Because of the abundance of these smaller Dinophyceae, the rate of organic production during September-October did not show a proportionate decrease, in relation to the sudden fall in the standing crop of net phytoplankton (Sarma, Unpublished). These smaller forms were, however, absent in formalin-preserved water samples, as they disintegrate quickly.

3. Sampling efficiency of bolting silk and of different filters.

Selective sampling of the standing crop made by the bolting silk net was also evident on some occasions. On 16-6-1960 the nanoplankton sample abounded in small 2-3 celled chains of *Leptocylindrus minimus* cell-breadth, 1.5-2.5 μ) and *Detonula confervacea* (cell-breadth, 7.5 μ) while these species were very rare in the net collections made the same day. Nanoplankton contributed to 85.5% of the total pigment on that occasion. *Skeletonema costatum* chains were abundant both in the net collections and in the nanoplankton sample on 31-7-1961. However, the chains in the net collections were on the average 200-300 μ long and over 15 μ broad, while those in the nanoplankton sample were only 3-4 cells long and less than 8 μ broad. Similarly, on 3-8-1961, *Leptocylindrus danicus* cells in the nanoplankton collections were 4-8 μ broad and 10-22 μ long, while larger cells, mostly over 15 μ broad and 75 μ long, predominated the net collections. This occurrence of distinct size groups together in the same water mass is interesting and perhaps represent two or more different generations.

Comparison of the qualitative composition of the net- and nano-plankton samples from the same water mass somewhat on the lines of Yentsch and Ryther (*l.c.*) gave clear indications of selective sampling of the crop by the net. The efficiency of retention by the net of large genera like *Bacteriastrum*, *Biddulphia*, *Chaetoceros*, *Coscinodiscus*, *Fragilaria*, *Rhizosolenia* and *Ceratium* were found to be very high (in many cases 100%). Retention coefficient for species like *Leptocy-*

linrus danicus, *Nitzschia seriata* and *Skeletonema costatum*, although chain-forming, was roughly estimated to be only about 50%. Species of *Cocconeis*, *Diploneis*, *Mastogloia*, *Amphidinium*, *Cochlodinium*, *Goniodoma*, and *Oxytoxum* were found to be not retained at all by the net. The retention of genera like *Coscinosira*, *Navicula*, *Thalassiosira*, *Glenodinium*, *Gymnodinium* and *Peridinium* was only a matter of chance depending on cell dimensions which varies considerably from species to species and within the species.

The efficiency of Collodion filters and Whatman filter paper No. 542 used in the present study was compared. On five occasions, equal quantity of sea-water (5 l) was filtered simultaneously through No. 21 bolting silk, No. 542 Whatman paper and Collodion filter plates for direct comparison and the results are given in Table II. Except on one occasion the Collodion filter plates were found to retain, on the average, 5.6% more pigment than the Whatman paper. The bolting silk was only about 37% efficient when compared with the Collodion filter.

TABLE II

Comparison of straining efficiency of different filters

Date	PPU/M ³ of Sea-water		
	Bolting Silk No. 21	Whatman Paper No. 542	Collodion Filter Plate
4-6-1959 ..	1,800	23,900	28,000
10-8-1959 ..	29,300	67,000	68,500
20-8-1959 ..	31,500	95,000	99,500
14-6-1960 ..	15,800	32,000	31,500
14-7-1960 ..	19,000	35,000	38,000

A number of accounts (Atkins and Parke, 1951; Graham, 1943; Harvey, 1950; Korringa and Postma, 1957; Riley, 1941a, b; Steele, 1956) deal with the efficiency of various types of filters, papers as well as membrane filters and it would appear that Gradocol Collodion membranes and Whatman No. 542 filter paper are some of the more efficient ones.

The present account also shows that, although there is a possibility of the microflagellates escaping through the pores of the filter paper, this error is only very negligible for this area. On one occasion, 500 ml of sea-water from near the shore was filtered through No. 542 Whatman paper and the filtrate was then continuously centrifuged at 4000 rpm for one hour. The sediment, on examination showed two biflagellate phyto-organisms which could not be identified. The possibility of the loss of smallest plants when Whatman filter paper No. 542 is used is mentioned by Steele (*l.c.*) also.

In conclusion, it may be stated that the present investigation further confirms the earlier observations of one of us (Subrahmanyam, 1959) that the magnitude of the standing crop of phytoplankton along the south-west coast of India is of a very high order and the area is an extremely fertile region for phytoplankton production. The proportion of fish landed to organic production derived on basis of net plankton was found to be extremely low; and, if the nanoplankton dealt with here is also taken into consideration, the ratio of fish landed will be further reduced. It

would, therefore, appear that there is a vast scope for further increased exploitation of commercial fisheries in this region as has already been pointed out (Subrahmanyan, *l.c.*).

SUMMARY

The magnitude of the total standing crop of phytoplankton/ M^3 of the water column was estimated by Harvey's Plant Pigment Extraction method for Calicut, on the south-west coast of India for 8 years from 1955-1962. Its fluctuations showed that the peak is attained during the south-west monsoon months (May to September). The nanoplankton and net plankton portions were separately estimated and it was found that on the basis of overall averages the former constituted 30-50% of the total standing crop and that it did not show any pronounced seasonal trends compared with that of the latter. Qualitative composition of the nanoplankton showed 58 species, mainly 27 diatoms and 26 Dinophyceae. The net collections and nanoplankton samples were compared and the selective sampling by the net analysed. The efficiency of retention by the net of several species are discussed. Comparing the filtration efficiency of different filters, it was found that Collodion filters are 5.6% more efficient than Whatman No. 542 paper, while bolting silk was only 37% efficient when compared with Collodion filters. The importance of nanoplankters as food for fish larvae and its possible significance in their survival rate and thereby to their recruitment to a fishery is indicated. The results further confirmed that the magnitude of the standing crop of phytoplankton on the south-west coast of India is of a very high order, thereby holding out a vast scope for increased exploitation of commercial fisheries.

ACKNOWLEDGEMENT

We thank Dr. S. Jones, for his keen interest and encouragement during these investigations.

REFERENCES

- ALLEN, E. J. 1919. A contribution to the quantitative study of plankton. *J. Mar. biol. Ass. U.K.*, 12: 1-81.
- ATKINS, W.R.G. 1945. Autotrophic flagellates as the major constituent of the oceanic phytoplankton. *Nature, Lond.*, 156: 446-7.
- , AND PARKE, M. 1951. Seasonal changes in the phytoplankton as indicated by chlorophyll estimations. *J. Mar. biol. Ass. U.K.*, 29: 609-18.
- BALLANTINE, D. 1953. Comparison of the different methods of estimating nanoplankton. *Ibid.*, 32: 129-47.
- BERNARD, F. 1939. Étude sur les variations de fertilité des eaux Méditerranéennes. Climat et nanoplancton à Monaco en 1937-38. *J. Cons. int. Explor. Mer.*, 14: 228-41.
- . 1952. Fertilité marine et nanoplancton. *Océanogr. Méditer.*, No. 2, *Vie et Milieu*, 60-71.
- . 1954. Vents, courants et fertilité marine au large de l'Algérie. *Bull. Soc. d'Hist. Nat. Afr. Nord.*, 45: 82-88.
- . 1956. Eaux Atlantiques et Méditerranéennes au large de l'Algérie. II. Courants et nanoplancton de 1951 à 1953. *Ann. Inst. Océanogr.*, 31: 231-334.

- . 1958a. Données récentes sur la fertilité élémentaire en Méditerranée. *Rapp. Cons. Explor. Mer.*, **144** : 103-08.
- . 1958b. Comparaison biologique du nanoplankton estival entre les détroits de Gibraltar de Sicile, l'Algérie et la Tripolitaine. *Rapp. Proc. Verb. Reun.*, **14** : 149-55.
- , AND FAGE, L. 1936. Recherches quantitatives sur le plancton Méditerranéen. *Bull. Inst. Océanogr. Monaco*, No. 701, 1-20.
- , AND ———. 1958. Comparaison de la fertilité élémentaire entre l'Atlantique tropical africain, l'Océan Indien et la Méditerranée. *C. R. Sean. Acad. Sci.*, **247** : 2045-48.
- ; AND LECAL, J. 1960. Plancton unicellulaire récolté dans l'Océan Indien par le *Charcot* (1950) et le *Norsel* (1955-56). *Bull. Inst. Oceanogr. Monaco*, No. 1166, 1-59.
- BIRGE, E. A. AND JUDAY, C. 1922. The inland lakes of Wisconsin. The Plankton. Part I. Its quantity and chemical composition. *Wis. Geol. Nat. Hist. Surv., Bull.*, **64** : 1-222.
- BRAARUD, T. 1958. Counting methods for determination of the standing crop of phytoplankton. *Rapp. Cons. Explor. Mer.*, **144** : 17-19.
- BRUCE, J. R., KNIGHT, M. AND PARKE, M. W. 1940. The rearing of oyster larvae on an algal diet. *J. Mar. biol. Ass. U.K.*, **24** : 337-74.
- CLARKE, G. L. AND GELLIS, S. S. 1935. The nutrition of Copepods in relation to the food cycle of the sea. *Biol. Bull. Woods Hole*, **68** : 231-246.
- * ———, AND ZINN, D. J. 1937. Seasonal production of zooplankton off Woods Hole, with special reference to *Calanus finmarchicus*. *Ibid.*, **73** : 464-87.
- COLE, H. A. 1936. Experiments in the breeding of oysters (*Ostrea edulis*) in tanks, with special reference to the food of the larvae and spat. *Fish. Invest. Lond.*, Ser. II, **15** (4).
- . 1939. Further experiments in the breeding of oysters in tanks. *Ibid.*, **16** (4).
- , AND KNIGHT-JONES, E. W. 1949. Quantitative estimation of marine nanoplankton. *Nature, Lond.*, **164** : 694.
- CUSHING, D. H. 1955. Production and pelagic fishery. *Fish. Invest. Lond.*, Ser. II, **18** (7).
- FULLER, J. L. AND CLARKE, G. L. 1936. Further experiments on the feeding of *Calanus finmarchicus*. *Biol. Bull. Woods Hole*, **70** : 308-20.
- GOLDBERG, E. D., BAKER, M. AND FOX, D. L. 1952. Microfiltration in oceanographic research. I. Marine sampling with the molecular filter. *J. Mar. Res.*, **11** : 194-204.
- GRAHAM, H. W. 1943. Chlorophyll-content of marine plankton. *Ibid.*, **5** : 153-60.
- GROSS, F. 1937. Notes on the culture of some marine plankton organisms. *J. Mar. biol. Ass., U.K.*, **21** : 753-68.
- HANUSKA, L. 1949. Hydrobiologie de l'écluse à Vrané Sur la Vltava I. (Contribution au jugement biologique des eaux superficielles). *Vestník Československé Zoologické Společnosti*, **13** : 69-93.
- HARVEY, H. W. 1934. Measurement of phytoplankton population. *J. Mar. biol. Ass., U.K.*, **19** : 761-73.
- . 1950. On the production of living matter in the sea off Plymouth. *Ibid.*, **29** : 97-138.
- , COOPER, L. H. N., LEBOUR, M. V. AND RUSSEL, F. S. 1935. Plankton production and its control. *Ibid.*, **20** : 407-41.
- HENTSCHEL, E. 1932. Die biologischen Methoden und das biologische Beobachtungsmaterial der 'Meteor' Expedition. *Wiss. Ergebn. dtsh. Atlant. Exped. 'Meteor'*, **10** : 1-274.

- HENTSCH, E. 1933. Allgemeine Biologie des Südatlantischen Ozeans. Erste Lieferung. Das pelagial der Obersten Wasserschicht. *Ibid.*, 11 : 1-168.
- HULBERT, E. M., RYTHER, J. H. AND GUILLARD, R. R. L. 1960. The phytoplankton of the Sargasso Sea off Bermuda. *J. Cons. int. Explor. Mer.*, 25 : 115-28.
- KNIGHT-JONES, E. W. 1951. Preliminary studies of nanoplankton and ultraplankton systematics and abundance by a quantitative culture method. *Ibid.*, 17 : 140-55.
- , AND WALNE, P. R. 1951. *Chromulina pusilla* Butcher, a dominant member of the ultraplankton. *Nature, Lond.*, 167 : 445-46.
- KORRINGA, P. AND POSTMA, H. 1957. Investigations into the fertility of the Gulf of Naples and adjacent water lakes, with special reference to shellfish cultivation. *Publ. Staz. Zool. Napoli*, 29.
- KREY, J. 1958. Chemical methods of estimating standing crop of phytoplankton. *Rapp. Cons. Explor. Mer.*, 144 : 20-27.
- LOHMANN, H. 1901. Ueber das Fischen mit Netzen aus Mullergaze No. 20 zu dem zwecke quantitativer Untersuchungen des Auftriebs. *Wiss. Merresuntersuch. Kiel*, 5 : 47-67.
- . 1903. Neue Untersuchungen über den Reichtum des Meeres an Plankton und über die Brauchbarkeit der verschiedenen Fangmethoden. *Ibid.*, 7 : 1-86.
- . 1908. Untersuchungen zur Feststellung des vollständigen Gehaltes des Meeres an Plankton. *Ibid.*, 10 : 131-370.
- MARE, M. F. 1940. Plankton production off Plymouth and mouth of English Channel in 1939. *J. Mar. biol. Ass. U.K.*, 24 : 461-82.
- RAYMONT, J. E. G. AND GROSS, F. 1942. On the feeding and breeding of *Calanus finmarchicus* under laboratory conditions. *Proc. roy. Soc. Edinb.*, 61B : 267-87.
- RILEY, G. A. 1939. Plankton Studies. II. The Western North Atlantic, May-June, 1939. *J. Mar. Res.*, 2 : 145-62.
- . 1941a. Plankton Studies. III. Long Island Sound. *Bull. Bingham oceanogr. Coll.*, 7 (3) : 1-93.
- . 1941b. Plankton Studies. IV. Georges Bank. *Ibid.*, 7 (4) : 1-73.
- SMAYDA, T. J. 1965. A quantitative analysis of the phytoplankton of the Gulf of Panama. II. On the relationship between C¹⁴ assimilation and the diatom standing crop. *Inter-Amer. Trop. Tuna Comm., Bull.*, 9 : 467-531.
- STEELE, J. H. 1956. Plant production in the Fladen Ground. *J. Mar. biol. Ass. U.K.*, 35 : 1-33.
- STEEMANN NIELSEN, E. 1938. Ueber die Anwendung von Netzfängen bei quantitativen Phytoplanktonuntersuchungen. *J. Cons. int. Explor. Mer.*, 13 : 197-205.
- . AND AABYE JENSEN, E. 1957. Primary Oceanic Production. The autotrophic production of organic matter in the Oceans. *Galathea Rep.*, 1 : 49-136.
- SUBRAHMANYAN, R. 1946. A systematic account of the marine plankton diatoms of the Madras coast. *Proc. Indian Acad. Sci.*, 24 B : 85-197.
- . 1958a. Phytoplankton organisms of the Arabian Sea off the West Coast of India. *J. Indian bot. Soc.*, 37 : 435-41.
- . 1958b. Ecological studies on the marine phytoplankton on the West Coast of India. *Mem. Indian bot. Soc.* 1 : 145-51.
- . 1959. Studies on the phytoplankton of the West Coast of India, Parts I and II. *Proc. Indian Acad. Sci.*, 50 B : 113-87 ; 189-252.

- , AND SARMA, A. H. V. 1960. Studies on the phytoplankton of the West Coast of India. Part III. *Indian J. Fish.*, 7 : 307-36.
- SVERDRUP, H. U., JOHNSON, M. W. AND FLEMING, R. H. 1942. *The Oceans, Their Physics, Chemistry and General Biology*, New York.
- THORSON, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the Sound (oresund). *Medd. Komm. Havundersg. Kbh. Plankton*, 4 (1) : 1-523.
- 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.*, 25 : 1-45.
- UTERMÖHL, H. 1931. Neue wege in der quantitativen Erfassung des Planktons. (Mit besonderer Berücksichtigung des Ultraplanktons). *Verh. Int. Ver. Limnol.*, 5 : 567-96.
- WOOD, E. J. F. AND DAVIS, P. S. 1956. Importance of smaller phytoplankton elements. *Nature, Lond.*, 177 : 438.
- YENTSCH, C. S. AND RYTHER, J. H. 1959. Relative significance of the net phytoplankton and nanoplankton in the waters of Vineyard Sound. *J. Cons. int. Explor. Mer.*, 24 : 231-8.