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ZOOPLANKTON ABUNDANCE AT KAVARATTI AND KALPENI ATOLLS IN THE LACCADIVES

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ABSTRACT

Quantitative zooplankton samples were taken and the samples weighed to estimate the biomass potentially available to nourish coral reefs. High biomass values were recorded at the surface by night, particularly at Kavaratti Atoll, where dense swarms of the luminescent ostracod *Cypridina* commonly reached concentrations of the order of 1000 individuals per m^3 . The biomass was greatest seaward of the western (lagoon) reef, (Kavaratti 481 mg/m^3 , Kalpeni 128 mg/m^3), and lowest seaward of the eastern (island) reef (Kavaratti 131 mg/m^3 , Kalpeni 53 mg/m^3). The biomass was depleted en route from ocean to lagoon (Kavaratti 61%, Kalpeni 23%), suggesting that the reef community is nourished by oceanic zooplankton. However, calculations showed that the magnitude of this food supply, as a source of energy, was relatively small compared with the primary production of the reef community as indicated by the oxygen flow method of Sargent and Austin.

INTRODUCTION

The nature of atolls has exercised the imagination of biologists and geologists alike ever since the famous voyage of the "Beagle" when Darwin developed his classical theory of atoll formation. Controversy concerning the origins of the platforms on which atolls stand has now fallen to the lot of the geologist. Biologists have concentrated rather on what has become another classical problem—the "ultimate reason for the flourishing of coral atolls in an empty ocean" (Sargent and Austin, 1954).

The crux of the problem is coral nutrition. Although for over 50 years the matter has been the centre of controversy, corals are still thought to be zooplankton feeders (Yonge, 1930, 1963); however, the plankton near coral reefs has often been

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reported to be sparse (Sargent and Austin, 1949; Odum and Odum, 1955). The remarkable transparency of coral waters is sufficient testimony to the dearth of phytoplankton. Measurements of phytoplankton concentration, pigments, and productivity confirm this (Russell, 1934; Johnson, 1954; Jeffrey, 1968; Qasim, Bhattathiri, and Reddy (in Press). However, there is conflicting evidence on zooplankton abundance. Russell (1934), for example, believes the zooplankton of the Great Barrier Reef lagoon to be equal in abundance to that in North Sea, and other workers (eg. Emery, 1968) report large concentrations of zooplankton near coral reefs, particularly at night.

It is important to know not only whether or not the zooplankton is abundant, but also whether the reef filters zooplankton from the water flowing across it. Motoda (1940) and Johnson (1949, 1954) found more, not less, zooplankton within the lagoon than in surrounding seas. However the question whether oceanic zooplankton provides a net input of energy to the reef must take into account qualitative as well as quantitative changes in the zooplankton of the water flowing across the reef (Emery, 1968).

The present survey was designed to obtain quantitative data relevant to the general problem of coral reef nutrition. Atolls are ideal for such investigations because of their isolation from continental influences. Kavaratti ($10^{\circ}33'N$, $72^{\circ}36'E$) and Kalpeni ($10^{\circ}04'N$, $73^{\circ}38'E$) lie toward the centre of the Laccadive Archipelago, a chain of atolls in the Arabian sea, some 200 miles from the southwest coast of India (Fig. 1). Both are "perfect" atolls (Gardiner, 1903-06) and, like most other atolls in the archipelago, they are orientated along a north-south axis, the lagoon to the west and the island to the east (Figs. 2, 3).

These Indian Ocean atolls lie in the path of the monsoons which blow with tremendous force from the southwest from May to about September and with lesser force from the opposite direction from November to about January (Hydrographic Office, 1961). Thus the windward and the leeward sides of the atoll change from season to season; however, it is the western reefs, exposed to the full fury of the monsoon, that more closely parallels a Pacific windward reef. Living corals are more in evidence on the western reef of Kavaratti than on the western reef of Kalpeni.

There is some information available about circulation in the lagoon at Kavaratti, gathered by the local harbour authorities (Kannan, personal communication). These observations (using floats) show that, irrespective of season, currents generally move in one direction through the shallow lagoon towards the entrance, accelerating en route. The flow is faster on a rising tide, especially during the southwest monsoon, but it rarely exceeds 0.5 m/sec (1 kt). The flow is created by the surf which breaks across the reef and spills into the lagoon. The bulk of this discharges through the "Entrance" which in this respect functions as an "Exit". The atolls of the Laccadives differ from those of the Pacific in that their lagoons are nearly always shallow. The average lagoon depth at both Kavaratti and Kalpeni is not more than two fathoms.

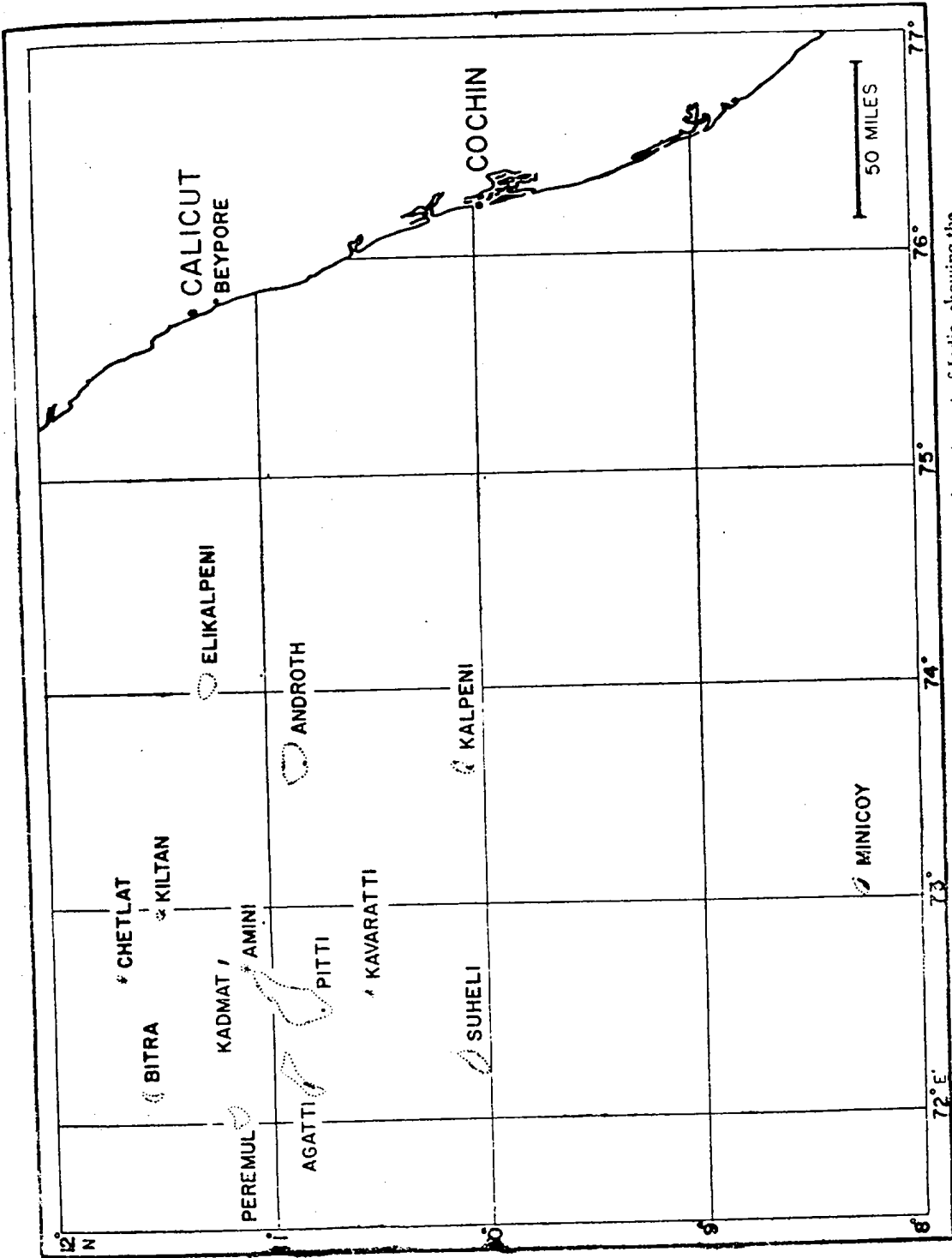


FIG. 1. The Laccadive Archipelago with respect to the south-west coast of India, showing the relative positions of Kavaratti and Kalpeni Atolls.

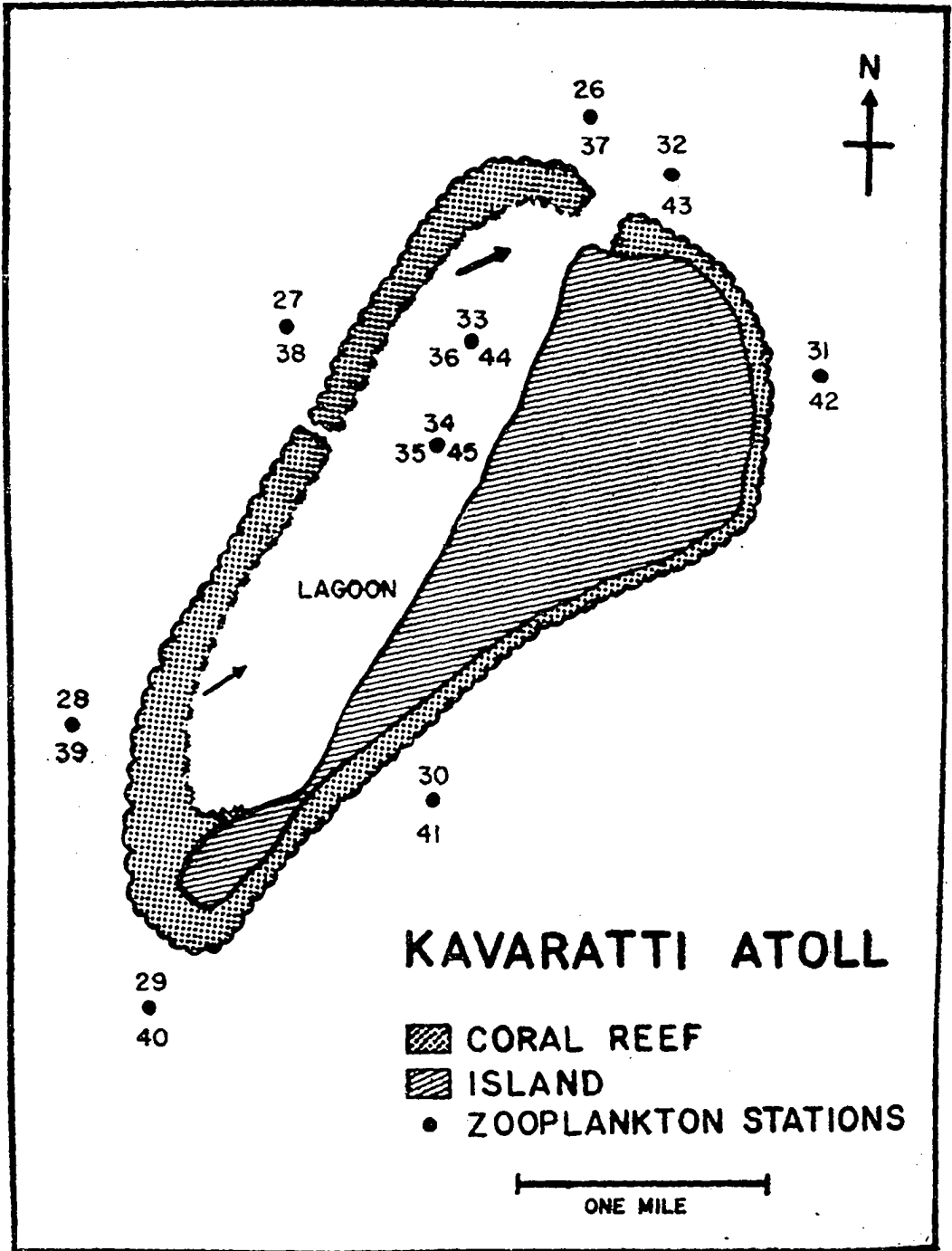


FIG. 2. Kavaratti Atoll showing the relative location of Island, Lagoon, and Reef, and the position of the sampling stations.

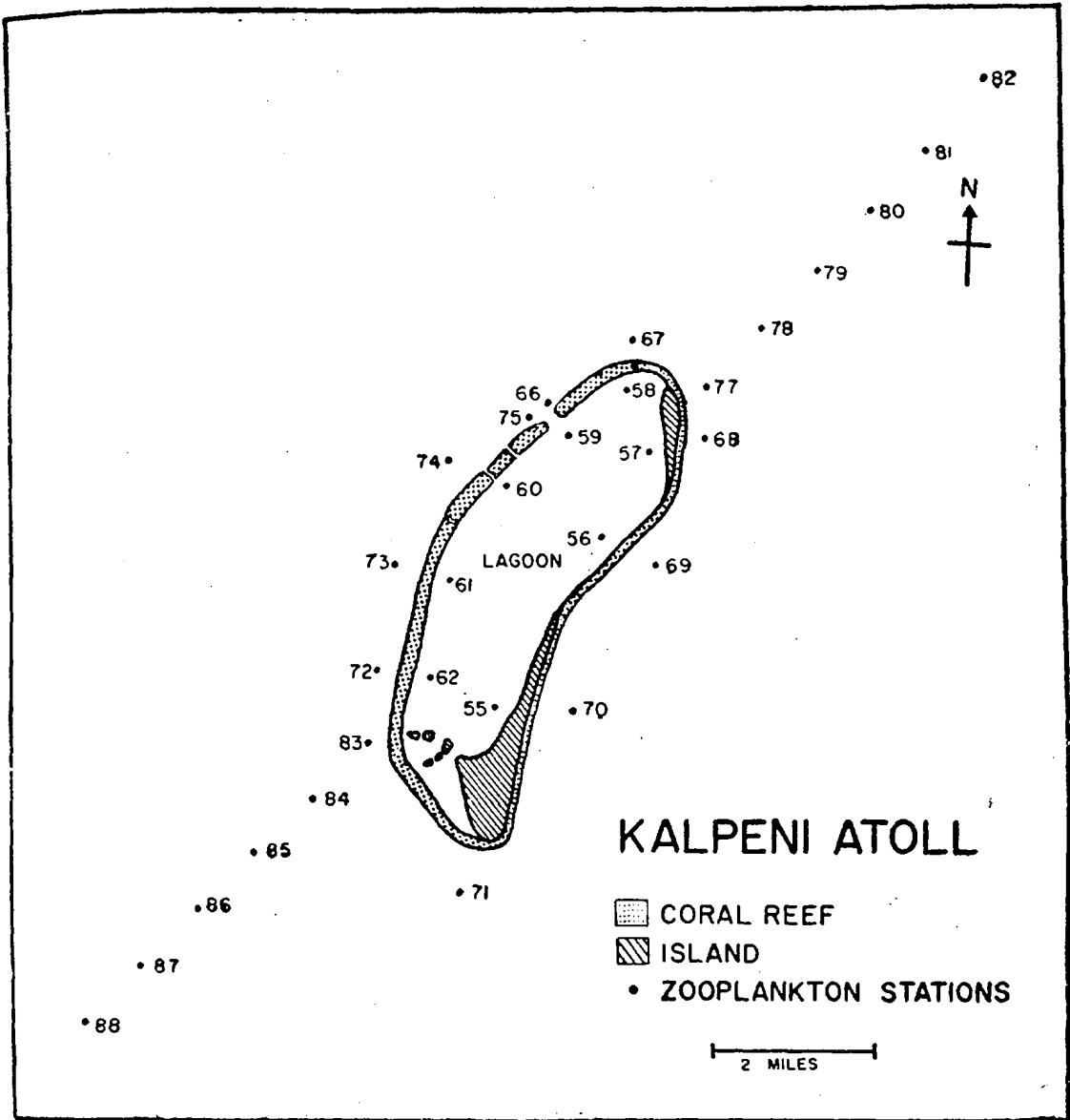


FIG. 3. Kalpeni Atoll showing the relative location of Islands, Lagoon, and Reef, and the position of the sampling stations.

This could explain why the circulation pattern differs from that described by Von Arx (1948) for Bikini and Rongelap in the Marshalls where average depths exceed 20 fathoms.

Nothing is known about the currents *around* these atolls except that they are complex and variable and apparently bear little relation to the oceanic circulation round about (Captain Nair, Personal communication).

METHODS

Two surveys were made (Figs. 2, 3) one at Kavaratti (20-22, October, 1968), the other at Kalpeni (21-27, December, 1968). At Kavaratti the sea was calm and there was little wind. By December, at Kalpeni, the northeast monsoon had developed some force. Changing wind conditions during the latter survey placed first the west and then the east side of the atoll in the lee.

Because coral polyps are expanded mainly at night, this is generally considered to be the time they feed on zooplankton (Yonge, 1930, 1963). With this in mind, zooplankton sampling was restricted to the hours of darkness; on both surveys there was little moon and bioluminescence was conspicuous. Zooplankton tows were made only at the surface because it is the surface water which washes over a reef bringing potential food and nutriment to the reef community.

On each survey, samples were taken both within the lagoon and around the atoll. The Kavaratti stations (Fig. 2) were worked on two successive nights. The first series (Oct. 20) was made while the tide was rising, the second (Oct. 21-22) while the tide was falling. The Kalpeni survey (Fig. 3) extended for a period of seven days and consisted of three series of samples. The first series (Dec. 21) was made within the lagoon in a counterclockwise circuit. The second series (24 Dec.) was made around the atoll in a clockwise circuit, the stations being located, so far as possible, opposite the stations in the lagoon (Fig. 3). The third series (Dec. 27) consisted of a pair of seaward traverses extending five miles to the northeast and five miles to the southwest of the atoll. Further details about the surveys are given in Appendix 1 and 2. Relevant tidal data for the nearby Port of Beypore (Fig. 1) are given in Appendix 3.

The nets used on both surveys were a modification of the WP 2 net (Fraser, 1968). They differed from the WP 2 net in that the mouth was square and the frame was towed by a two-leg bridle from opposite corners so that there was little obstruction to the flow of water through the mouth (Fig. 4). From the same corner-pivots was suspended a 10 kg weight. Within the net-mouth was a flowmeter located a little below the horizontal diagonal. Flowmeters were calibrated in a swimming pool before the investigation.

The net used at Kavaratti (HT net) was made of nylon gauze with a mesh width of 0.2 mm and was fitted with a Rigosha flowmeter. The net used at Kalpeni (LB Net) was made of nylon gauze with a mesh width of 0.33 mm and was fitted with a TSK flowmeter. Otherwise the nets were identical. The difference in the gauzes would result in smaller organisms being taken at Kavaratti than at Kalpeni (Vannucci, 1968) and, probably, slightly larger catches.

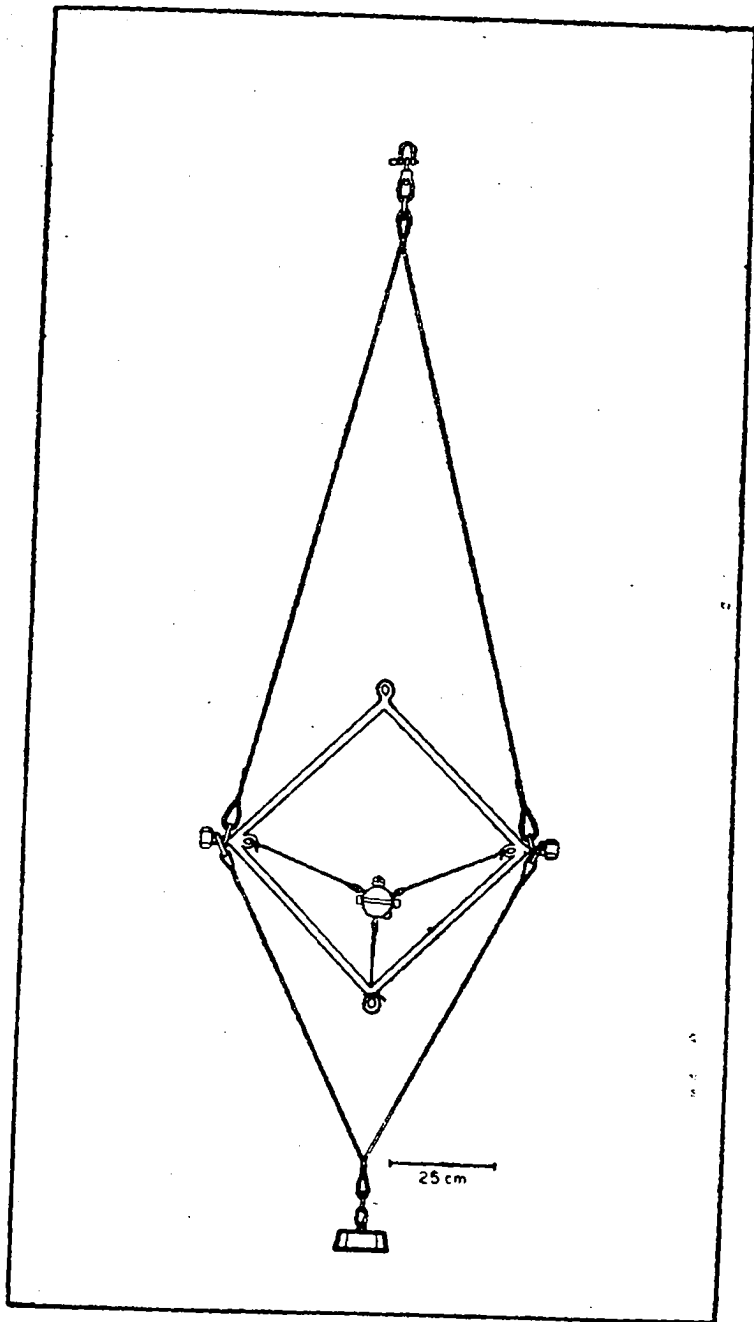


FIG. 4. Front view of the sampler used during the Laccadives investigations.

On both surveys, towing speed was standardized at 1 m/sec (2Kt). An analysis of the flowmeter records shows that the mean velocity of flow through the net mouth was 0.97 m/sec. (Standard deviation 0.15 m/sec) during the Kavaratti survey and 1.12 m/sec (standard deviation 0.37 m/sec) during the Kalpeni survey. At Kavaratti the net was usually towed for two minutes (Appendix 1), and at Kalpeni for five minutes (Appendix 2). Little clogging of the net was noticed on either survey.

The samples were fixed in seawater containing 4% formaldehyde buffered with 1% hexamine. On receipt at the laboratory 1-2 weeks after collection, the samples were halved with the Lea Plankton Splitter (McEwen *et al*, 1954). One half was weighed directly on a balance using a light styrene weighing dish with a base of nylon gauze (mesh width 0.03 mm). Catches too large for accurate determination in the standard weighing dish were further subsampled prior to weighing. Aliquots for counting were taken by withdrawing a column of known volume from the plankton sample. Detailed examination of the samples is being continued.

RESULTS

The results of the Kavaratti survey are recorded in Appendix 1 and those of the Kalpeni survey in Appendix 2. Table 1 shows the mean zooplankton biomass and concentration of *Cypridina* in the lagoon of these two atolls and in various regions of the surrounding sea. Table 2 gives the ratios of zooplankton abundance at Kavaratti relative to that at Kalpeni. Table 3 gives the ratios of zooplankton biomass in the sea surrounding Kavaratti and Kalpeni relative to that within the lagoon.

TABLE 1. *Nocturnal zooplankton biomass and Cypridina concentration in the lagoons at Kavaratti and Kalpeni Atolls, and in the surrounding sea*

Position	Biomass (mg/m ³)		<i>Cypridina</i> No/m ³	
	Kavaratti	Kalpeni	Kavaratti	Kalpeni
Lagoon	189	99	595	< 1
Sea:				
"Entrance"	322	118	690	"
Western	481	128	975	"
Eastern	131	53	124	"
NE Traverse	—	143	—	< 1
SW Traverse	—	4069	—	1.7

TABLE 2. *Nocturnal zooplankton abundance at Kavaratti (October 1968) relative to that at Kalpeni (December 1968). Mesh width of Kavaratti net, 0.20 mm Kalpeni net 0.33 mm.*

Position	Biomass		<i>Cypridina</i>	
	Kavaratti	Kalpeni	Kavaratti	Kalpeni
Lagoon	2.1	1.0	562	1.0
Sea:				
"Entrance"	2.7	1.0	4929	1.0
Western	3.8	1.0	4063	1.0
Eastern	2.5	1.0	775	1.0

The biomass recorded was in general 2-3 times as great at Kavaratti as at Kalpeni (Tables 1 and 2). This could be due in part to the fact that the Kavaratti net was made of finer gauze (mesh width 0.2 mm) than the Kalpeni net (mesh width 0.33 mm). The greater part of the difference, however, is probably due to the dense swarm of *Cypridina* which occurred only at Kavaratti (Table 1).

At both atolls there was far more zooplankton in the seas off the western (lagoon) reef than in the seas off the eastern (island) reef (Table 1). At Kavaratti the ratio was nearly 4:1 and at Kalpeni more than 2:1. Only near the eastern reef was the biomass of zooplankton low. Elsewhere in the surrounding seas, zooplankton was more abundant than in the lagoon (Table 3). Seaward traverses off Kalpeni showed that zooplankton was relatively abundant even five miles from the atoll (Appendix 2).

TABLE 3. *Nocturnal zooplankton biomass in the seas around Kavaratti and Kalpeni Atolls relative to that within the Lagoon*

Position	Kavaratti		Kalpeni
	Rising Tide	Falling Tide	
Lagoon	1.0	1.0	1.0
Sea:			
"Entrance"	1.2	2.1	1.2
Western	2.1	2.7	1.5
Eastern	0.4	1.1	0.5
NE Traverse	—	—	1.5
SW Traverse	—	—	1.7

TABLE 4. Taxonomic composition of ocean station 39 compared with that of lagoon station 35

Taxon	Density (No/m ³)		Percentage	
	Ocean	Lagoon	Ocean	Lagoon
Calanoid + Cyclopoid copepods	917	2	75	0.4
Pelagic Tunicates	48	0	4	0
Chaetognaths	28	0	2	0
Pelagic Polychaetes	7	0	0.6	0
Siphonophores	4	0	0.3	0
Harpacticoid copepods	2	366	0.1	65
Decapod larvae	3	53	0.3	9
Mysids	0	11	0	2
Gammarids	0	2	0	0.4
Ostracods	149	123	12	22
Miscellaneous	69	8	5.6	1.4
Total	1227	565	99.9	100.2

A conspicuous difference was obvious between samples from the lagoon and the surrounding sea, particularly at Kavaratti (Table 4). The lagoon "plankton" was characterized by epibenthic forms, such as mysids, harpacticoid copepods, and gammarid amphipods. Of the calanoid copepods, only *Calanopia* and *Pseudocyclops* were common in the lagoon. Such a fauna would be well adapted to maintaining itself within the lagoon in the face of the continuous apparently unidirectional, flushing which prevails at Kavaratti. The oceanic plankton was characterized by many species of calanoid copepods chaetognaths pelagic, tunicates and siphonophores. Very few of these entered the lagoon.

Table 1 shows that there was a significant difference, both at Kavaratti and Kalpeni, in the biomass of plankton outside the western reef and that inside the lagoon. Since it is clear that water enters the lagoon only on the western side at Kavaratti and mainly on the western side at Kalpeni, it is equally clear that plankton is being removed from the water flowing across the reef. In this way the biomass of zooplankton at Kavaratti was reduced by 61% and at Kalpeni by 23%. These are minimal values for the zooplankton contribution of the oceanic waters to the reef, since the composition of the zooplankton also changes in transit across the reef from an oceanic fauna to a fauna largely endemic to the lagoon. The actual zooplankton contribution of the ocean to the reef lies intermediate between the maximum represented by the sanding stock outside the reef and the minimum represented by the differences in standing stock on either side of the reef. Indeed if the "lagoon plankton" is endemic

to the lagoon and the result of local plankton production, then even when the biomass is *higher* than in the surrounding sea (Johnson 1954; Odum and Odum, 1955) the zooplankton contribution of the ocean to the reef could still be substantial.

It is now of interest to see how the abundance of plankton at Kavaratti and Kalpeni compares with the general level in the open ocean far from land and coral reefs (Table 5). For this comparison, data have been taken from curises made by the senior author in the Eastern Indian Ocean (CSIRO Aust, 1965, 1966). These data are considered to be comparable because the hauls were made at the surface, by night, with nets of similar gauze (mesh width 0.26 mm). The mean surface biomass by night in this region is of the order of 74 mg/m³. The average biomass of zooplankton in the sea surrounding Kalpeni atoll was twice as great as this, while at Kavaratti the average was five times as great. By this standard of comparison, the seas surrounding these atolls would appear to be relatively rich.

TABLE 5. *Nocturnal zooplankton biomass (surface) observed in the Laccadives, compared with similar observations from the N.S.W. continental shelf (Australia) and the eastern Indian Ocean*

Location	Zooplankton Mean	Biomass (mg/m ³) No. of observations
Ocean around Kavaratti	336	14
Ocean around Kalpeni	132	22
Eastern Indian Ocean	74	87
Lagoon, Kavaratti	189	6
Lagoon, Kalpeni	99	8
N.S.W. Continental shelf	136	12

It is also useful to compare the zooplankton abundance in the lagoons of Kavaratti and Kalpeni with values typical of the continental shelf (Table 5). Comparable values are available for the eastern coast of Australia (Tranter, 1962). Here the mean zooplankton biomass was observed to be 136 mg/m³. This mean lies intermediate between those observed in the lagoons of Kavaratti and Kalpeni.

DISCUSSION OF THE RESULTS

The observations at Kalpeni and more particularly at Kavaratti indicate that it is not correct to speak in general terms about coral reefs flourishing "in an empty ocean" (Sargent and Austin, 1954), or "in tropical waters of impoverished plankton content", (Odum and Odum, 1955). The results of this investigation support some previous observations that zooplankton is abundant near coral reefs, particularly at night (Russell, 1934; Emery, 1968). At Kavaratti the swarm of *Cypridina* seems to have swollen the zooplankton to a particularly high level.

The ocean provides a continuous potential source of energy to the reef in the form of zooplankton. At night the biomass of zooplankton available for use is not low by oceanic, or even by neritic, standards. The investigations at Kavaratti and Kalpeni show that much of this zooplankton biomass is lost in transit across the reef into the lagoon and is probably utilized by the reef community. It cannot be certain that the users are the coral polyps though in view of their special adaptive ability to prey on zooplankton organisms (Yonge, 1930) and their relative abundance on the reef, this seems to be the most likely possibility.

The next question is whether the zooplankton supply satisfies the total energy requirements of the reef. This question has been dealt with by Sargent and Austin (1954) and Odum and Odum (1955) and it is now re-examined in the light of the data from the present investigation. To place this problem in perspective, Table 6 has been prepared. The table shows the potential energy, in the form of zooplankton carbon, available, each night to a strip of reef, 1 cm wide, for various windward zooplankton concentrations and various rates of flow across the reef. A mean height of water above the reef of 1 metre is assumed. The range of zooplankton values (50-800 mg/m³, wet weight) and the range of current velocities (10-160 cm/sec) used in this Table include those obtaining at Kavaratti and other reef situations previously described (Sargent and Austin, 1949; Johnson, 1954; Odum and Odum, 1955; Kohn and Helfrich, 1957). In expressing zooplankton in terms of carbon equivalent, a conversion factor, 3 mg of carbon for each 100 mg wet weight, was used (Newell, 1966).

Because some data are available for surface currents in Kavaratti lagoon (Kannan, personal communication) along with zooplankton values, an order of magnitude can be indicated for the potential energy in the form of zooplankton carbon available each night to the reef at Kavaratti.

The surface currents in the lagoon increase from approximately 5 cm/sec in the southwestern corner (Fig. 2) to approximately 50 cm/sec where the water discharge through the gap in the reef ("entrance"). Because of the velocity gradient towards the constriction represented by the entrance, values at the southwestern corners give a better indication of the average velocity of flow across the reef. Allowing for an approximate value of 4:1 in the ratio of mean lagoon depth: mean depth of water over the reef, the mean rate of flow across the reef can be calculated to be of the order of 20 cm/sec.

The maximum standing stock of zooplankton available to the reef is no more than 500 mg/m³, wet weight (Table 1), and the net loss from ocean to lagoon is of the order of 300 mg/m³. If a mean contribution of 400 mg/m³ be taken and a mean rate of flow of 20 cm/sec. it may be seen from Table 6 that the energy available to the reef each night in the form of zooplankton carbon would be of the order of 0.96 gm C/cm strip/night.

TABLE 6. Potential energy available to the reef in the form of zooplankton Carbon

Current velocity (cm/sec)	Seaward Zooplankton Biomass (Mg/m ³ , wet weight)				
	50	100	200	400	800
	gm C/cm strip/night				
10	0.06	0.12	0.24	0.48	0.96
20	0.12	0.24	0.48	0.96*	1.92
40	0.24	0.48	0.96	1.92	3.84
80	0.48	0.96	1.92	3.84	7.68
100	0.96	1.92	3.84	7.68	15.36

* Value estimated for Kavaratti from the evidence available.

Assumptions: Mean height of water above Reef = 1 metre.

Conversion factor : 100 mg wet weight of zooplankton = 3 mg carbon (Newell, 1966).

The estimates of Kohn and Helfrich (1957) for the gross primary organic production of a Hawaiian coral reef are the order of 8 gm C/m²/day. These agree with values previously obtained by Sargent and Austin (1954), Odum and Odum (1955), and more recently by Qasim, Battathiri, and Reddy (in press) for Kavaratti Reef itself (4.9 gm C/m²/day). Since the reef at Kavaratti is about 300 m wide, the Kavaratti values for primary organic production are equivalent to 14.7 gm C/cm strip/day. This is an order of magnitude greater than the energy available to the reef in the form of zooplankton carbon (Table 6).

It is difficult to believe that zooplankton concentrations and rates of flow could be much higher than those used in this rough estimate. It is not known whether the October values of zooplankton biomass observed at Kavaratti would be greater or smaller than the annual average. During the transition period between the northeast and southwest monsoons, stable hydrographic conditions prevail in the general area of the Laccadives (Jayaraman *et al* 1960). Qasim (in press) believes that such conditions favour the blooming of *Trichodesmium* which ultimately enriches surface waters by fixing atmospheric nitrogen. This would probably be followed by further enrichment during the southwest monsoon as the stratification of the surface layer is broken down. The spectacular swarms of *Cypridina* seen throughout the Laccadive sea in October could well be the result of some such seasonal enrichment, in which case the biomass values recorded then could well represent a seasonal maximum.

It is equally difficult to conceive of velocities across the reef great enough to provide the energy requirements of the reef from the standing stock of plankton available. Similarly, although it is difficult to predict the nature of the flow around objects of such varied shape as coral colonies, it seems unlikely that this would tend to concentrate the plankton where it could be used by plankton feeding organisms.

The conclusion would seem to be inescapable — though zooplankton may be abundant and a significant source of energy to the reef, this is still not adequate to meet the total energy requirements of the reef community. The experiments of Muscatine (1967) would suggest that an alternative source of energy is provided by substances (glycerol etc.) formed photosynthetically by zooxanthellae living commensally with coral polyps, clams, and other members of the reef community. Johannes and Coles (1969) suggest that 'zooplankton are an essential source of nutrient elements both for the coral and its algal symbionts'. In tropical surface waters, nitrogen in particular is very low (Kirkwood, 1967; Qasim, in press), often below limits of detection. Although the carbon contribution of zooplankton to a coral reef may be small in comparison with that of photosynthesized by symbiotic zooxanthellae, the nitrogen contribution could well be critical in reef development.

ACKNOWLEDGEMENTS

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REFERENCES

- CSIRO AUST. 1965. Oceanographical Observations in the Indian Ocean in 1963. *Oceanographical Cruise Reports* No. 21, 23, 24, 25.
- CSIRO AUST. 1966. Oceanographical Observations in the Indian Ocean in 1962. *Oceanographical Cruise Reports* No. 17 and 18.
- EMERY, A. R. 1968. Preliminary Observations on coral reef plankton. *Limnol. Oceanogr.*, 13 (2): 293-303.
- GARDINER, J.S. (Ed.) 1903-6. *The Fauna and Geography of the Maldives and Laccadive Archipelagoes*. Cambridge: University Press. 2 Vols., 1-1079.
- HYDROGRAPHIC OFFICE 1961. *West coast of India Pilot*. 10th Edition, Admiralty, London.
- JAYARAMAN, R., RAMAMRITHAM, C. P., SUNDARARAMAN, K. V., AND ARAVINDAKSHAN NAIR, C. P. 1960. Hydrography of the Laccadives Offshore waters. *J. mar. biol. Ass. India*, 2 (1): 24-34.
- JEFFREY, S.W. 1968. Photosynthetic Pigments of the Phytoplankton of some Coral Reef water. *Limnol. Oceanogr.*, 13 (2): 350-355.
- JOHANNES, R.E. AND COLES, S.L. 1969. The role of zooplankton in the nutrition of Scleractinian corals. *Symposium on corals and coral reefs*, Mandapam Camp, 12-16 January 1969. (Abstract).
- JOHNSON, M.W. 1949. Zooplankton as an index of water exchange between Bikini lagoon and the open sea. *Trans. Am. geophys. Un.*, 30 (2): 238-244.

- JOHNSON, M.W. 1954. Plankton of northern Marshall Islands. *Prof. Pap; U. S. geol. Surv.* 260-F: 301-314.
- KIRKWOOD, L. F. 1967. Inorganic phosphate, organic phosphorus, and nitrate in Australian waters. *Division of Fisheries and Oceanography Tech. Pap.*, 25: 1-18 CSIRO Australia.
- KOHN, A.J. AND HELFRICH, P. 1957. Primary organic productivity of a Hawaiian Coral Reef. *Limnol. Oceanogr.*, 2: 241-51.
- MC EWEN, L.F. JOHNSON, M.W. AND FOLSOM, T.R. 1954. A Statistical analysis of the performance of the Folsom Plankton Sample Splitter, based upon test observations. *Arch. Met. Geophys. Klimatol.*, Ser. A, 7: 502-27.
- MOTODA, S. 1940. Comparison of the Condition of water in Bay, Lagoon, and open sea in Palao. *Palao trop. biol. Stn. Stud.*, 2: 41-48
- MUSCATINE, L. 1967. Glycerol excretion by symbiotic algae from corals and *Tridacna* and its control by the host. *Science*, 156: 516-19.
- NEWELL, B.S. 1966. Seasonal changes in the Hydrological and Biological environments off Port Hacking, Sydney. *Aust. J. Mar. Freshw. Res.*, 117 (1): 77-91.
- ODUM, H.T., AND ODUM, E.P. 1955. Trophic structure and productivity of a windward Coral Reef community of Eniwetok Atoll. *Ecol Monogr.*, 25: 291-320.
- QASIM, S.Z. (in Press)** 1970 Some characteristics of *Trichodesmium* blooms in the Laccadives?.
- QASIM, S.Z., BHATTATHIRI, P.M.A., AND REDDY, C.V.G. (in Press)* Primary production of an atoll in the Laccadives.
- RUSSELL, F.S. 1934. The zooplankton III. A comparison of the abundance of zooplankton in the barrier reef lagoon with that of some regions in northern European waters. *Scient. Rep. Gt. Barrier Reef. Exped.*, 2 (6): 159-201.
- SARGENT, M.C., AND AUSTIN, T.S. 1949. Organic productivity of an Atoll. *Trans. Am. geophys. Un.* 30: 245-9.
- SARGENT, M.C., AND AUSTIN, T.S. 1954. Biologic Economy of Coral Reefs. *Prof. Pap. U.S. geol. Surv.*, No. 260-E: 293-300.
- TRANter, D.J. 1962. Zooplankton Abundance in Australasian Waters. *Aust. J. Mar. Freshw. Res.*, 13 (2): 106-42.
- FRASER, J.H. (Ed). 1968. Zooplankton sampling. II Standardization of zooplankton sampling methods at sea. *Monographs on Oceanographic Methodology* 2: 147-174, (UNESCO Paris.)
- VANNUCCI, M. 1968. Loss of organisms through the meshes. *In Zooplankton sampling. Monographs on Oceanographic Methodology* 2: 77-86. (UNESCO Paris).
- VON ARX, W.S. 1948. The circulation systems of Bikini and Rongelap lagoons. *Trans. Am. geophys. Un.*, 29: 861-70
- YONGE, C.M. 1930. Studies on the physiology of corals. I. Feeding mechanisms and food. *Scient. Rep. Gt. Barrier Reef. Exped.*, 1 (2): 13-57
- YONGE, C.M. 1963. The biology of Coral Reefs. *Advances in Marine Biology*, 1: 209-260.

DISCUSSION

- JOHANNES : How long were your traverses across the reef?
- TRANter : The mean width of the four traverses will be 100 metres.
- JOHANNES : How were your samples collected?

** Since published *Deep-Sea Res.*, 17:655-660 (1970) (Eds.)

* Since published *Int. Revue ges. Hydrobiol.*, 57 (2): 227-246 (1972).

- TRANTER : We used a 0.2 mm mesh net fitted to a half-metre square frame towed at surface for about 100 m with filtering efficiency of 95% and sampled between 10 p.m. and 4 a.m. at Kavaratti Island.
- MUSCATINE : Could you give an idea of the quality of light penetration in the area?
- TRANTER : Dr. Qasim may be in a position to give this information.
- QASIM : The Secchi disk visibility is 27 m and the extinction coefficient is 0.017. The rate of production in the lagoon is 3.7 gms C/m²/day and outside the reef it is about 0.15 gms C/m²/day.
- BAKUS : The standing crop of zooplankton in the lagoon may be 3 to 5 times higher than outside. A large part of the plankton in the lagoon may be endemic.
- VANUCCI : There can be a large amount of nanoplankton which are not sampled by the net.
- QASIM : I don't think so.
- P.V.R. NAIR : In the light of the primary production figures which you gave earlier, it would appear that the contribution by nanoplankton could be very significant.
- QASIM : 3.7 gms c/m²/day mentioned is for the coral reef estimated by the Flow Method, and the value by 14 C is low.

APPENDIX 1. *Kavaratti zooplankton survey*

Stations	Time	Volume of water Filtered (m ³)	Biomass (mg/m ³)	<i>Cypridina</i> (No/m ³)
<i>Series 1 : Oct. 20</i>				
<i>Sea:</i>				
LA 2/26/68	1740 — 1745	92.0	54	0
LA 2/27/68	1800 — 1805	93.0	251	155
LA 2/28/68	1827 — 1830	53.2	835	2076
LA 2/29/68	1847 — 1849	24.0	598	1750
LA 2/30/68	1917 — 1919	36.8	146	98
LA 2/31/68	1945 — 1947	25.5	53	55
LA 2/32/68	1955 — 1957	22.2	605	1604
<i>Lagoon</i>				
LA 2/33/68	2020 — 2022	26.2	167	840
LA 2/34/68	2100 — 2104	52.8	379	852
<i>Series 2: Oct. 21/22</i>				
<i>Lagoon</i>				
LA 2/35/68	2250 — 2252	29.2	114	281
LA 2/36/68	2302 — 2304	31.0	170	748
<i>Sea:</i>				
LA 2/37/68	2328 — 2330	29.0	463	1124
LA 2/38/68	2343 — 2345	27.5	303	495
LA 2/39/68	0020 — 0022	26.5	316	249
LA 2/40/68	0035 — 0037	32.0	588	1125
LA 2/41/68	0108 — 0110	27.5	161	335
LA 2/42/68	0140 — 0142	32.0	163	7
LA 2/43/68	0150 — 0152	26.8	165	30
<i>Lagoon:</i>				
LA 2/44/68	0213 — 0215	28.8	157	375
LA 2/45/68	0237 — 0239	27.5	148	472

APPENDIX 2. *Kalpeni zooplankton survey*

Stations	Time	Volume of water Filtered (m ³)	Biomass (mg/m ³)	Cypridina (No./m ³)
<i>Series 1 : Dec. 21</i>				
(Lagoon)				
LA 5/55/68	0010 — 0015	75.4	165	<1.0
LA 5/56/68	0051 — 0056	66.6	79	<1.0
LA 5/57/68	0121 — 0126	73.3	79	<1.0
LA 5/58/68	0135 — 0140	79.0	44	<1.0
LA 5/59/68	0209 — 0214	91.8	59	<1.0
LA 5/60/68	0235 — 0240	77.8	39	<1.0
LA 5/61/68	0254 — 0259	90.5	145	1.8
LA 5/62/68	0314 — 0319	77.8	178	2.6
<i>Series 2: Dec. 24</i>				
(Circum-Atoll)				
LA 5/66/68	0014 — 0016	37.3	91	<1.0
LA 5/67/68	0040 — 0042	89.6	52	<1.0
LA 5/68/68	0059 — 0101	45.3	44	<1.0
LA 5/69/68	0127 — 0132	79.0	42	<1.0
LA 5/70/68	0140 — 0145	84.9	74	<1.0
LA 5/71/68	0214 — 0219	86.1	146	<1.0
LA 5/72/68	0241 — 0246	89.0	141	<1.0
LA 5/73/68	0300 — 0305	88.6	128	<1.0
LA 5/74/68	0315 — 0320	87.5	175	<1.0
LA 5/75/68	0337 — 0342	90.3	145	<1.0
<i>Series 3 : (Dec. 27)</i>				
(Seaward Traverses)				
LA 5/77/68	0020 — 0025	73.1	151	<1.0
LA 5/78/68	0040 — 0045	73.3	182	<1.0
LA 5/79/68	0057 — 0103	74.6	179	<1.0
LA 5/80/68	0115 — 0120	104.2	127	<1.0
LA 5/81/68	0137 — 0142	84.1	132	<1.0
LA 5/82/68	0147 — 0152	57.5	89	1.0
LA 5/83/68	0430 — 0435	58.9	87	<1.0
LA 5/84/68	0445 — 0450	73.3	69	1.5
LA 5/85/68	0502 — 0507	83.9	155	1.0
LA 5/86/68	0522 — 0527	58.9	256	2.0
LA 5/87/68	0537 — 0542	56.8	214	<1.6
LA 5/88/78	0555 — 0600	55.6	233	<1.0

APPENDIX 3 *Tidal Data (Beypore) for the sampling periods of the Kavaratti and Kalpeni surveys*

Date	Time	Height(m)
October 20	0353	0.60
	0958	1.23
	1619	0.30
	2301	1.24
21	0434	0.62
	1026	1.25
	1649	0.16
	2343	1.35
22	0514	0.65
	1056	1.26
	1720	0.04
December 21	0100	1.68
	0635	0.93
	1127	1.27
	1802	0.12
24	0303	1.63
	0915	0.78
	1422	1.20
	2018	0.49
27	0450	1.47
	1158	0.60
	1859	1.18
	2310	1.00