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THE BENTHOS OF SOME SOUTHERN AFRICAN LAKES

Part IV: The recovery of the benthic fauna of St Lucia Lake following a period of excessively high salinity.

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Introduction: The fauna of the St Lucia Lake system as a whole has been reported upon by Day, Millard and Broekhuysen (1954) and Millard and Broekhuysen (1970). Both of these papers give qualitative accounts of the species diversity and attention was paid to the distribution of the fauna in respect of the various regions of the system. These authors suggested that the pattern of distribution of animals in the system was in response to the changing salinity regimes encountered in various areas at various times. Thus Day et al (1954) reported high salinities of 50.6^{o}/oo in False Bay during the winter of 1948, while the lowest salinities were recorded as 5.5^{o}/oo in False Bay in October/ November 1964 by Millard and Broekhuysen (1970).

Day et al (1954) considered the three areas in St Lucia, False Bay, North Lake and South Lake to be natural basins, pointing out that fairly sharp changes of salinity were experienced especially between North Lake and South Lake at Fanies Island (Fig. 1). The species diversity which they documented was shown to change with respect to the basins considered, and these authors attributed the poor fauna of False Bay as a result of high salinities.

Millard and Broekhuysen (1970) studied the area during a period of low salinity regime and came to the conclusion that low salinity could likewise affect the distribution of fauna along the length of the lake system.

Since the writing of these papers Wallace (1969) investigated the distribution of fish and their food organisms during a period of particularly high salinity during the early months of 1969. At this time the whole of the lake showed values in excess of 4^{o}/oo with a maximum of 89^{o}/oo in False Bay. By March the salinities had dropped considerably but even in South lake were still in excess of sea water

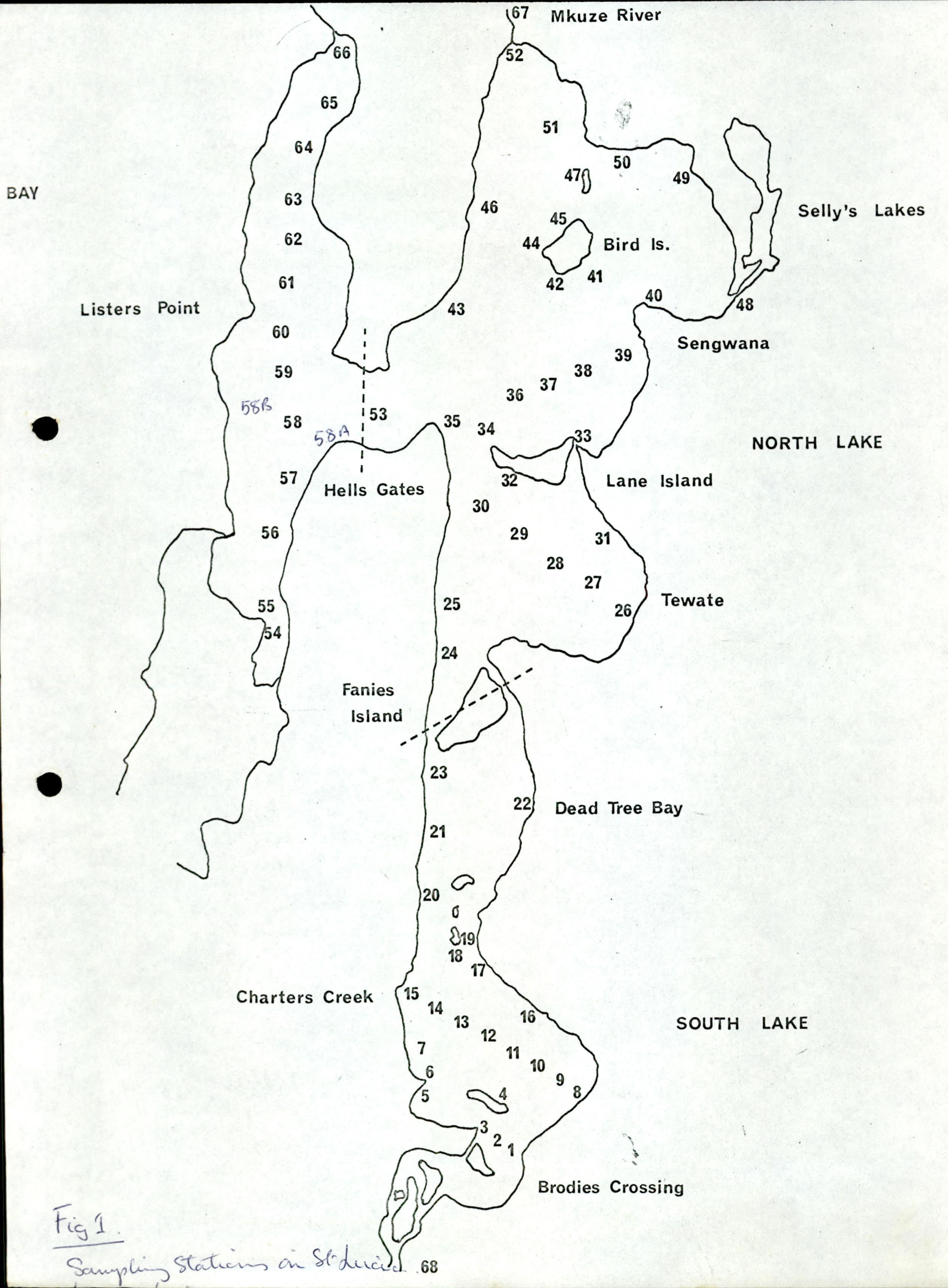

Fig 1.
Sampling stations on St Lucia

values. Grindley and Heydorn (1970) report that in July of 1969 South Lake salinities were between 34°/oo and 42°/oo and North Lake salinities were between 42°/oo and 48°/oo. However, by December the salinities had once again risen to greater than 70°/oo in False Bay.

The exceptionally high salinities are known to have resulted in some fish mortalities (Grindley and Heydorn 1970) and also of bivalve molluscs (Wallace 1969). Further detailed information on the effects of high salinity on the fauna was not collected during 1970.

High salinities continued to be experienced and in January 1972 all parts of the lakes had abnormally high salinities (Fig. 2). The present study was undertaken to further elucidate some of the effects of salinity changes on the distribution and diversity of the fauna of the lake. In this case the study was restricted to benthic animals as might be evaluated from a grab sampling programme. The system was sampled on three occasions, ~~February~~ January 1972, July 1972 and January 1973. At the start of the sampling period excessively high salinities were measured. During 1972 the salinities dropped sharply so that lower than sea water values were obtained in July with slight rises to about sea water values towards the end of the year. We could therefore compare the results between the various sampling periods so as to gain some sort of an idea of the response of the benthos both to absolute salinity concentrations and also to the rate of recovery after extreme concentrations had been experienced in some of the areas.

Methods

The benthos was sampled with a modified van Veen grab (Boltt 1969a) taking an area of 0.0225 m^2. Samples from sand and mud are markedly different, deeper samples with more volume being taken on softer substrates. This difference in sample volume is however not thought to be serious since the same area is sampled on both types of substrate and it has been shown that, for the majority of small fauna, a depth of grab sample of 4 cm is sufficient in sand (Wigley 1967).

This depth of grab sample in sand does not however adequately sample the larger bivalves although as the results show, juveniles are well sampled. Even in mud samples where the grab penetrates to 10 cm there is not adequate sampling of adult bivalves. However, there is evidence that the greatest part of the small forms of the fauna is to be found in the top 10 cm of muddy substrate. For example, Brinkhurst, Chua and Batoosingh (1969) have shown that 99% of the tubificid oligochaetes in the very soft sediments of Toronto harbour were within 6 cm of the surface.

The results from the grab sampling therefore must be interpreted with caution. Only small forms which live close to, or at the substrate surface, are being consistently sampled with this method.

The samples obtained with the grab were temporarily stored in plastic bags while in the boat, the time between taking a sample and its preservation never being more than 7 hours. The samples were subjectively categorised as sand, mud, muddy sand, or sandy mud. In sandy samples, the animals were removed by decanting the light material off the heavier sand using the method of Boltt (1969a). Special care was exercised when decanting off mollusc material from the sand. The decanted material was caught in a hand net with a mesh size of 0.28 mm, and preserved in formalin for later analysis in the laboratory. Muddy samples were stirred up and washed through the same net and preserved in the same way. Sandy mud samples were treated as mud samples, but muddy sand samples were treated as sand samples. The retained sand of the sandy mud samples was preserved with the sample as a whole and further reduction was undertaken in the laboratory. In a few samples fair amounts of large dead shell fragments were obtained. This was screened off with a 1.5 mm mesh sieve and the residue in the sieve was hand sorted for living animal material.

In the laboratory the samples were once again decanted so as to leave heavier mollusc material behind. The animals were picked from the sample with the aid of a scanning binocular microscope. The heavier fraction of sample was then digested with 10% nitric acid to remove the shells of the molluscs. The shell free mollusc material was then sorted away from other debris. The decalcified molluscan material remained perfectly identifiable, after experience had been gained from an examination of known decalcified molluscan material.

The animals were sorted to species and counted. In the majority of cases each species in each sample was separately dried to constant weight at 60°C on previously tared aluminium foil pans of 12 mm diameter weighing about 2 mg. Weighing was carried out on a Cahn Electrobalance to 0.002 mg. For the rest, samples with few individuals were lumped and after enumeration all the species dried and weighed together. In certain cases dried weight was estimated from the numbers of animals present, because of the inordinate time required to pick out all the individuals of, for example the nematodes and harpactecoid copepods. Large numbers were picked out and weighed and average weight of an individual was found. In the nematodes 6190 individuals gave a total weight of 16.972 mg giving an average weight of 0.0027 mg per individual. In the harpactecoids the average weight of 1133 animals was .0015 mg. In a few cases the weight of Assiminia was also estimated from their numbers. The average weight as calculated from the total weight of 48469 individuals was 0.0317 mg.

Some difficulty was experienced in counting the numbers of Assiminia in samples with greater than a thousand individuals. This was solved by syphoning the animals from a beaker which was vigorously stirred so as to keep the snails in suspension. The syphon tube was narrow enough to only let through a few animals at a time in a constant stream of water. The glass syphon tube was inspected through a binocular microscope and the animals counted with the aid of a hand tally counter as they passed the field of the microscope. The animals were then collected on a screen for the purposes of being transferred to the aluminium foil pans for drying and weighing. This technique was not applicable to the nematodes which had to be counted in the sample tray under the scanning microscope.

Lake St Lucia was sampled on three occasions, ~~February~~ January 1972, July 1972, and January 1973. On each occasion the lake was sampled in a period of three or four days (Table 1).

Table 1

Sampling schedule for Lake St Lucia. The sampling sites are mapped on Fig. 1.

Date	Number of samples			
	South Lake	North Lake	False Bay	Total
~~Feb.~~ Jan 1972	17	18	10	45
July 1972	23	30	13	68
Jan. 1973	23	30	14	69

The sampling sites are mapped on Fig. 1. As nearly as possible the same sampling site was resampled on successive occasions. However, the accuracy of refinding ones position on the lake by dead reckoning is reasonably poor and therefore the duplication of sampling sites is very approximate.

RESULTS

i) The invasion of benthos into the northern reaches of the lake

The most striking result of the survey is the extended range of benthic forms in the lake shown between the first sampling in January 1972 to the second sampling in July 1972. In February 1972 only South Lake showed a long faunal list of 21 species, of which 10 were common (Table 2).

Table 2

The numbers of species recorded from van Veen grab samples from the different regions of Lake St Lucia. Both the total number of species and "common" species as judged from at least more than 10 individuals in any one sampe are enumerated.

Region	Number of species					
	~~January~~ ~~Feb.~~ Jan 1972		July 1972		January 1973	
	Total No.	N > 10	Total No.	N > 10	Total No.	N > 10
South Lake	21	10	23	13	22	12
North Lake	9	6	18	12	13	8
False Bay	1*	0	9	6	10	5

* *Polypedilum* sp. (Chironomidae)

North Lake was impoverished of species in January 1972 especially if the detailed distribution of the species is taken into account. Thus if the faunal list of the two samples STL 24 and STL 25 are removed from consideration in Table 2, a total of only 6 species were found of which only one was common. Except for the extreme south, North Lake was very nearly as barren as False Bay, where only one chironomid larva species was found in low numbers.

The sampling in July 1972 showed a dramatic change in the distribution of the benthic animals. Least change was recorded from South Lake (Table 2) where the total species list increased by two and the common forms by three.

Greater increases were shown in North Lake where both the total species list and the common species doubled in their diversity. When the southerly stations of North Lake (STL. 24 and STL. 25) are ignored, the increase was 3 times for all species and 12 times for the common forms. North Lake may be divided into three principle regions; between Fanies Island and Lane Island, (Stations 24 to 32, Fig. 2), between Lane Island and Bird Island (Stations 33 to 43) and north of Bird Island (Stations 44 to 52). The numbers of species recovered from these areas in July 1972 were respectively 17, 15 and 13, showing a decrease northward, indicating that certain species had not re-established themselves completely in the whole of North Lake by July 1972. Whereas the ~~February~~ Jan 1972 sampling of False Bay showed only chironomid larva of the genus <u>Polypedilum</u>, only 4 individuals being caught in ten samples, by July 1972, the species diversity had risen to 9, 6 of which were classed as common. Notably lacking from the species lists were the bivalves and small benthic crustacea.

The results of the sampling from January 1973 shows a decreased diversity when compared with the results of July 1972, although not nearly to the levels recorded for ~~February~~ Jan 1972. Least change was recorded for South Lake (Table 2). A slight increase of one species was noted in the total species list of False Bay although the common species was reduced by one by the complete lack of chironomid larvae. By contrast the greatest decrease was noted in North Lake where common species dropped by 4 and the total number by 5.

A more detailed examination of the lists shows that with respect to the total list, the important missing species were: the bivalves Theora lata, Eumarcia (Pitaria) kochi, the gastropod Littorina scabra, chironomid larvae and a small Platyhelminth. Indeed the chironomid larvae were absent in samples from the whole of the lake in January 1973. The differences noted for the common species were mainly due to the small numbers of the bivalves Solen corneis, Theora lata and Dossinia hepatica and the amphipod Grandidierella lignorum. The lack of bivalves may reflect growth with the result that the larger forms had dug themselves deeper into the sediment and become unavailable to the grab. Nevertheless it is considered that the distribution and weight of juvenile bivalves is well represented in the sampling programme.

No juvenile bivalves were recovered at all in False Bay during the period of study. In January 1972 only South Lake yielded Solen and none was recovered in North Lake. By July 1972, 8 samples showed the presence of juvenile Solen. However, the most northerly station was STL 39 indicating perhaps that the most northerly reaches of North Basin were still barren with respect to this bivalve. Not much further spread seems to have been made by January 1973, since the most northerly stations were STL 41 and STL 42, scarcely extending the distribution in the previous July.

An almost exactly similar situation was found in the Dossinia collected from Lake St Lucia. A single station in North Basin was found with Dossinia in it in the January sampling of 1972. This station (STL 24) is only just in the southernmost reaches of North Lake. By July 1972 specimens were found as far north as STL 40, but little extension of distribution was noted by January 1973.

ii) The effects of substrate on diversity

The substrates of St Lucia may be considered as essentially

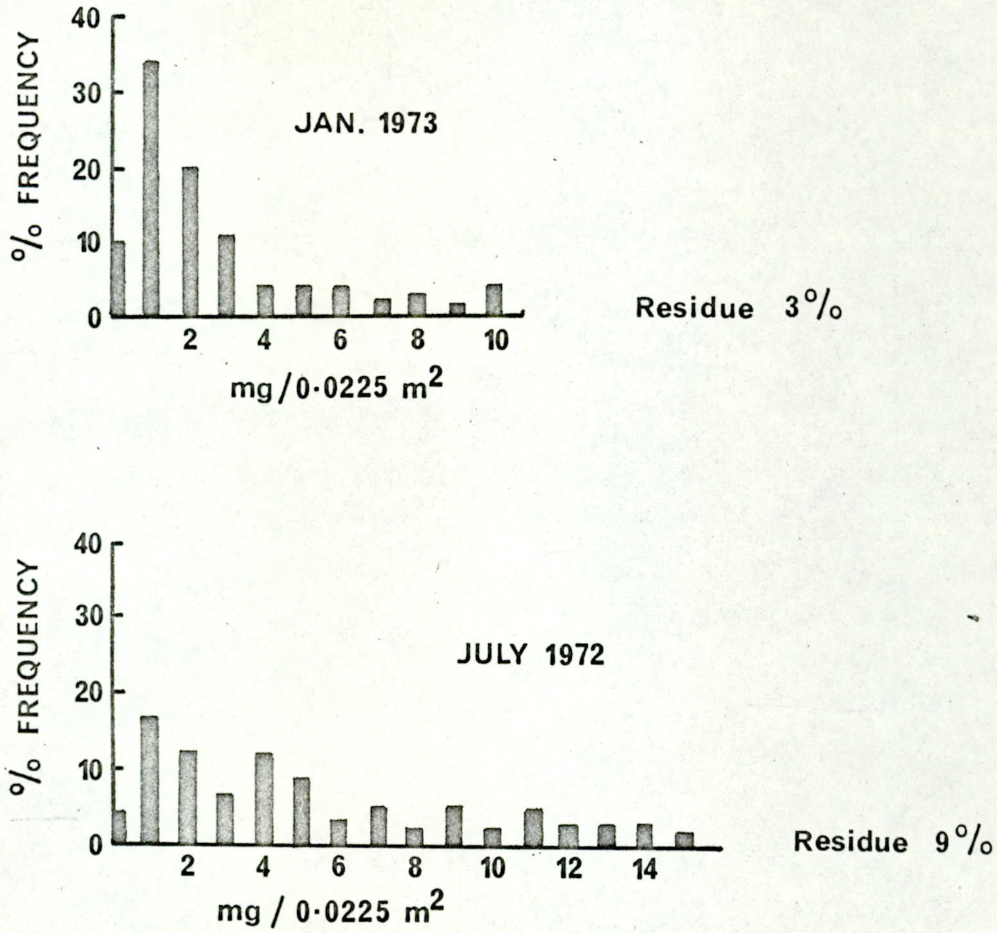

Fig 4. The frequency of samples of various weights from St Lucia. Assiminia and ~~other~~ large rare forms are not included. The residue refers to weights in excess of the axis shown.

either sandy or muddy. The total diversity of species represented in either of these substrates was very nearly similar. Thus a maximum of 14 different species was found in mud in any one sample in July 1972, only two greater than the maximum found in any sandy sample.

Table 3

The maximum diversity shown by any samples taken from either mud or sand at the various sampling dates.

Sampling date	Maximum No. of Species: Sand	Maximum No. of Species: Mud	Modal No. of Species: Sand	Modal No. of Species: Mud
~~Feb.~~ Jan 1972	10	9	5-7	5
July 1972	12	14	8	5
Jan. 1973	11	9	8	2-5

However, in general the modal value for the number of species found in sand was generally greater than that found in muddy samples (Table 3 and Fig. 3). Few animals were entirely restricted to one habitat. Principle among these were the small, numerically unimportant crustacea Grandidierella lignorum (sand), Apseudes digitalis (mud) and the Cumacea (sand).

iii) Numerical considerations

The numerically dominant forms taken by the van Veen grab were Assiminia bifasciata, Nematodes, Ostrocoda and harpactecoid copepods. These forms were not always dominant in all parts of the system at the various dates of sampling (Table 4).

Table 4

Numerically dominant forms from St Lucia in the various regions of the lake at the different sampling dates. + denotes the presence of samples with more than 100 individuals.

Sample date	Region	Assiminia bifasciata	Nematoda	Hapactecoid copepods	Ostracoda
~~Feb.~~ Jan 1972	South Lake	+	+	-	-
	North Lake	-	-	-	+
	False Bay	-	-	-	-
July 1972	South Lake	+	+	-	-
	North Lake	+	+	-	+
	False Bay	+	-	-	+
Jan. 1973	South Lake	+	+	+	-
	North Lake	+	+	+	-
	False Bay	+	+	+	+

The results in the main are reflections of increased distribution of the animals in the lake, particularly as between February 1972 and July 1972. However, the Ostracoda which were the one dominant form in North Lake in February 1972, shifted their emphasis from North Lake through to False Bay in July 1972, and were then barely dominant in False Bay with one sample with more than 100 individuals. Assiminia was the most important form in the substrate with respect to density, on one occasion reaching 11,000 individuals in 0.0225 m^2 (STL 44, July 1972), and many samples having greater than 1,000 animals. This animal was found on all types of substrates both mud and sand but in general greater numerical densities were experienced on sandy substrates (Table 5).

Table 5

The analysis of the density of Assiminia with respect to substrate type. N denotes the number of samples.

Density

Density of Assiminia per sample	July 1972 N	Mud	Sand	Jan. 1973 N	Mud	Sand
0 - 100	42	37	5	44	40	4
100 - 10,000 +	22	5	17	13	2	11

Combining the results of July 1972 and January 1973, 92% of all the mud samples taken had less than 100 individuals in them, whereas 76% of all sand samples had greater than 100 animals in them.

The rapidity of the recolonisation of the North Lake with high numbers of Assiminia is quite remarkable. In the February sampling of 1972 North Lake had only three stations with Assiminia. In all cases these stations were at the south end of the basin (Stations 24, 25 and 29) with the highest number of individuals at 91. By July 1972 all but 5 of the stations showed the presence of Assiminia with a maximum count of just over 11,000 individuals in one sample (STL 44). In the January 1973 samples showed 14 lacking Assiminia and the maximum count was just in excess of 6000 showing a generalised decrease.

The recolonization of False Bay by Assiminia was quite as rapid as for North Lake. By July 1972, 7 of the 13 samples had the snail present. However, in all cases the density of the animals was moderate to poor with a maximum recorded in one sample of 148 in July 1972 and only 22 in one sample from January 1973. This analysis is in one sense misleading since all the samples were from muddy substrates which we have shown to generally only hold moderate to poor densities. Indeed the great majority of the substrate in this part of the lake is undoubtedly muddy. However, small areas of sandy substrate are known in False Bay and an extra two samples were obtained from these areas in January 1973. These samples, which have not been included in the foregoing account, showed, in the case of the sandy sample (STL 58 A) 2685 Assiminia and the other sample of muddy sand with shell 158 Assiminia. These data would suggest that notwithstanding the paucity of numbers of the July sampling in the muddy substrates significant standing stocks may well have been present in False Bay even in the previous July sampling in the unsampled sandy areas. Moderate to high numbers of Nematodes were common in the benthic samples from St Lucia.

Table 6

Changes in the Nematode fauna over the study period in Lake St Lucia. N refers to the numbers of samples, and the percentages of each category are shown.

Density per sample	South Lake N	0	1-100	101+	Nprth Lake N	0	1-100	101+	False Bay N	0	1-100	100+
Sampling Date												
Jan. 1972	17	35%	35%	29%	18	83%	17%	-	10	100%	-	-
July 1972	23	4%	48%	48%	30	57%	10%	43%	12	85%	15%	-
Jan. 1973	23	12%	13%	70%	20	30%	23%	47%		8%	58%	33%

the same time as the spread of the Assiminia but the build up of animals appears to have been somewhat slower since peak values were only experienced in January 1973 (Table 6). Since we know so little of the biology of these animals it is difficult to assign any role they might play in the overall biology of the St Lucia system. In any event their weight is so small as to be of little importance to the biomass of the lake.

Three species were less dominant with respect to number, but with the exception of *Assiminia bifasciata* contributed on the average more to the total biomass of most samples. These were the polychaetes *Prionospio sexoculata* and *Glycinde capensis* and the juveniles of the bivalve *Dossiminia hepatica*. Once again with the exception of stations STL 24 and STL 25 in the south of North Lake all were confined to South Lake in February 1972.

Shifts in the pattern of population densities were noted, with respect to the polychaete *Prionospio sexoculata*. In South Lake in January 1972, relatively fewer samples lacked the polychaete than in July 1972 (65% and 82% respectively, Table 7). By January 1973 only 44% of the samples from South Lake were void of *P. sexoculata*.

Table 7.

The percentage of samples with various densities of *P. sexoculata* from the various areas of Lake St Lucia. The samples from each area are represented as 100%.

Region	Density per sample	Percentages pf samples Feb. 1972	July 1972	Jan. 1973
South Lake	0	65%	82%	44%
	1 - 9	29%	18%	34%
	10 - 100	6%	-	32%
	100 +	-	-	-
North Lake	0	94%	33%	43%
	1 - 9	6%	60%	43%
	10 - 99	-	7%	14%
	100+	-	-	-
False Bay	0	100%	23%	23%
	1 - 9	-	15%	38%
	10 - 100	-	54%	31%
	100 +	-	8%	8%

By contrast, an increase in void samples was noted in North Lake when July 1972 and January 1973 are compared (33% and 43% respectively, Table 6), but no change was experienced in False Bay.

The population of P. sexoculata was in general more dense in South Lake in January 1973, 32% of samples having more than 10 individuals, than in the previous July 1972. Similarly, the polychaetes in samples from North Lake were generally more dense in January 1973 than the previous July. In False Bay, however, whereas 62% of the samples had more than 10 individuals in July 1972, only 39% had these densities in January 1973.

Gravimetric analyses

The shell free dried weight of material recovered from the samples varied over a very wide range, typically from nothing to a maximum of 269.235 mg/0.0225 m^2 (11.954 g/m^2 STL 44 July 1972). STL 5 with 36 anemones gave 405.804 mg/0.0225 m^2 (18.017 g/m^2) but this result is atypical because of the particular requirements of the anemones living on *Zostra*, which itself is uncommon even in South Lake. Consideration of the numerical results shows that certain forms should be taken from consideration of the quantitative weight results as a whole for various reasons. Large forms such as the crab *Tylydoplax blepheriskios* add to the samples in which it is present, an excessive weight, which is biased because of the size of the animals. The distribution of the larger forms is probably not adequately sampled since their dispersion over the bottom is such that the grab is more likely to miss the animal than sample it. The experience of Boltt (1969) with the sampling of the relatively large snails *Melanoides tuberculata* and *Bellamya capillatus* in Lake Sibaya is a case in point. SCUBA diving showed these animals to be regularly distributed over the bottom of the lake although they were rarely encountered in the samples. The weight of such large forms as the crab (± 124 mg) has therefore been subtracted from samples containing the animals for the purposes of the analysis of the general characteristics of the quantitative weight of samples.

Furthermore, it has been shown that the small snail *Assiminia bifasciata*, which, although each individual only weighs on an average 0.0317 mg, is most abundant on sandy substrates and hardly so on muddy substrates (Table 5). While no great difference could be detected with respect to sandy and muddy substrates with regard to the other forms,

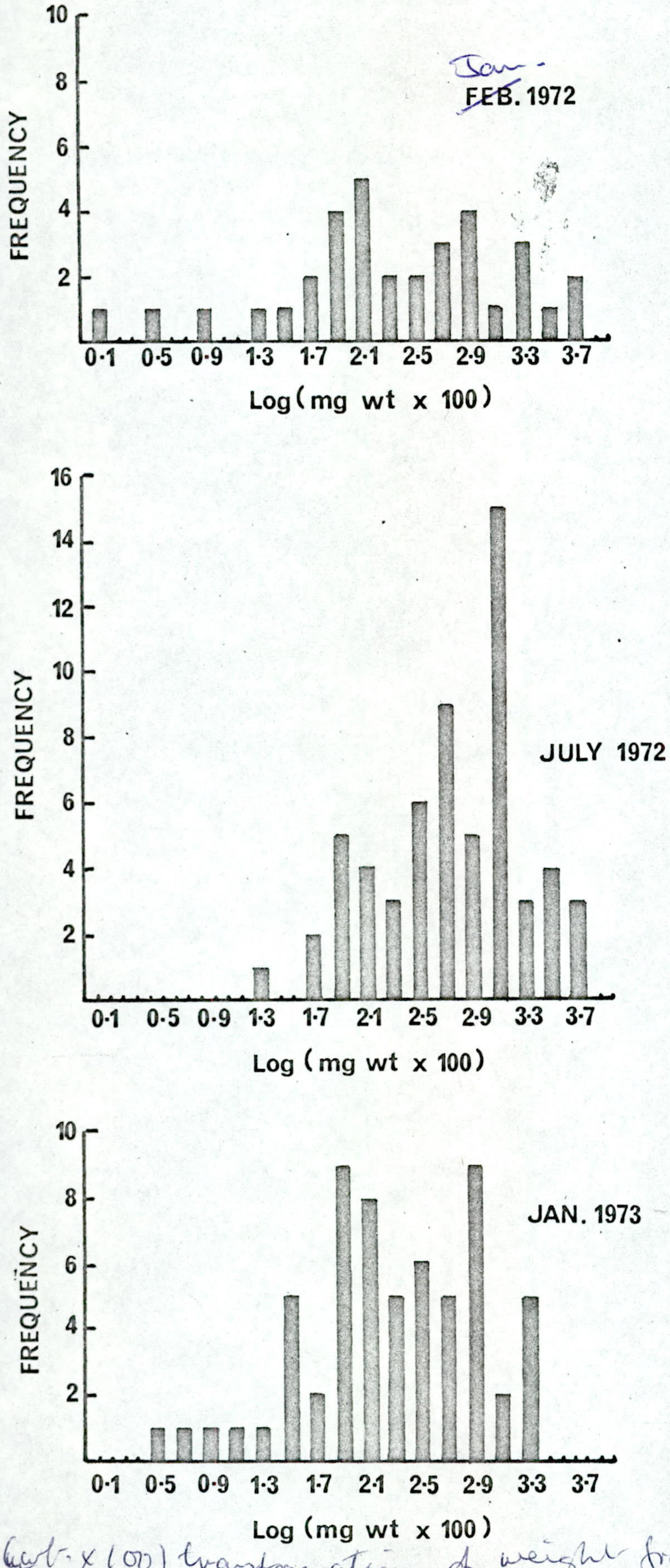

Fig 5. Log(wt. x 100) transformation of weight from samples plotted as a frequency. Assiminea and large heavy rare forms not included.

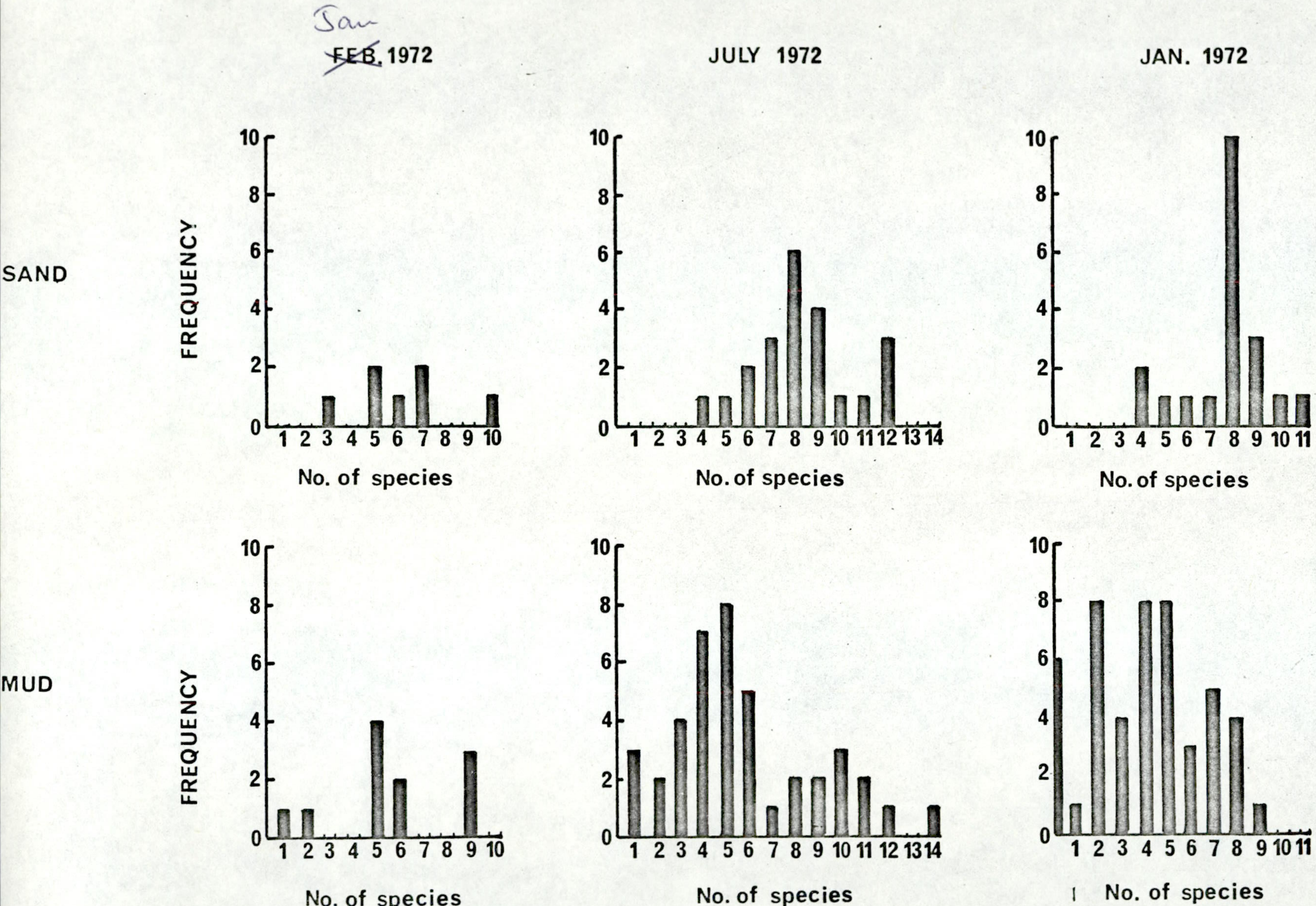

Fig 3. The frequency of samples with different numbers of species with respect to mud and sand from St Lucia.

this bias towards sandy substrates by Assiminia cannot be ignored. The weight of this animal has also therefore been taken away from the rest of the benthos and analysed separately.

In spite of these corrections the range of shell free dried weight of animals from the benthos still covered a very wide range of values (0.0 - 269.235 mg/0.0225 m^2) as can be judged from the frequency histograms shown for July 1972 and January 1973 in Figure 4. Furthermore it can be clearly seen that the distribution of weight is highly skewed towards the lighter samples. A log transformation of the results gives a more normal distribution, although it remains difficult to distinguish the main peak in some cases (Fig. 5). For the purposes of comparison, it is necessary to choose some standard, however crude. The results of the frequency histograms have therefore been plotted on probit paper as increments of log weight against the probit scale of percentage frequency. The 50% value less subjectively suggests the median and modal value of the sample weights (which now approximately coincide because of the transformation). The antilog of this 50% probit value is used as the modal value of the samples for the purposes of comparison.

Initially it is convenient to treat with the separate areas of the lake individually. It has already been shown that South Lake contained the greatest faunal diversity, and in January 1972 certainly contained the heaviest samples with respect to the other areas of the lake at that time (Table 8). In January 1972, South Lake showed a modal value of 4.8 mg/0.0255 m^2 (0.212 g/m^2) and in July 1972 the modal value was higher at about 7.6 mg/0.0225 m^2 (0.337 g/m^2). The shift of the mode towards greater weight was due to fewer very light samples, although the frequency distribution of samples with heavier values was similar. By January 1973 the modal value returned to about 4.8 mg/0.0225 m^2 indicating that possibly in summer smaller standing stocks are likely to be experienced.

Table 8.

The modal weights of benthos excluding large forms and the gastropod *Assiminia* from St Lucia Lake

Area	Date	wt. mg/0.0225 m^2	g/m^2.
South Lake	~~Feb.~~ Jan. 72	4.8	0.21
	July 72	7.6	0.34
	Jan. 73	4.8	0.21
North Lake	~~Feb.~~ Jan. 72	1.6	0.07
	July 72	3.6	0.16
	Jan. 73	2.2	0.10
False Bay	~~Feb.~~ Jan. 72	0.0	0.0
	July 72	7.9	0.35
	Jan. 72	1.3	0.06
Whole system	~~Feb.~~ Jan. 72	0.91	0.04
	July 72	5.8	0.26
	Jan. 73	1.9	0.08

North Lake samples had consistently smaller weights than South Lake, being 1.6 mg/0.0225 m^2 (0.07 g/m^2) in January 1972, 3.6 mg/0.0225 m^2 (0.161 g/m^2) in July 1972 and 1.5 mg/0.022 m^2 (0.067 g/m^2) in January 1973. Once again, however, a similar pattern is repeated with smaller samples experienced in the warmer months. A comparison of January 1972 and January 1973 is noteworthy since the weight was mainly due to ostrocods in January 1972 but due ~~mainly~~ to other groups in January 1973. This is reflected in a weight gain of about half again in January 1973 as compared to the January of the previous year.

In False Bay only 3 of 10 samples taken in February 1972 were recovered with any animals in them, and in each case only one or two chironomid larvae ~~(only)~~ were present. Even if all the samples had contained one chironomid larva each, the average weight would have been an insignificant 0.008 mg/0.0225 m^2 (0.00035 g/m^2). By July 1972 the modal value was

7.9 mg/0.0225 m^2 (0.35 g/m^2). Much of this material was made up of chironomid larvae which were lacking in the following January when the weights fell to 1.3 mg/0.0225 m^{-2} (0.058 g/m^2).

The weight of the bivalve material in the grab samples must be analysed with caution since only juvenile forms are properly sampled. Inspection of the raw data shows that juveniles of most species were found most commonly in July 1972 and only Dossinia juveniles were recovered in January 1973 to any extent. When these are substracted from the weight of the samples (together with Assiminia, etc.), values of 3.47 mg/0.0225 m^2 (0.154 g/m^2) were found in July 1972, while only 0.91 mg/0.0225 m^2 (0.041 g/m^2) were found in the following January. The removal of these forms from general consideration do not therefore conflict with the overall pattern of reduced standing stocks in summer.

In order to generate a rough estimate of the total weight of benthos in the various areas of St Lucia Lake the modes of the frequency distributions cannot be used since this will grossly underestimate the total standing stock. The mean weight of the samples can be used providing a number of assumptions are made. These are:

a) The distribution of the samples taken was truly representative of the various areas.

b) The number of samples taken was large enough to give a reasonable estimate of the total population mean per unit area.

Unfortunately the sample numbers were small for so large an area and statistical analysis does not solve the inadequacy. However, using these assumptions the average (as opposed to the modal) weight of the samples for the different areas are given in Table 9, from which a rough measure of the total standing stock may be obtained.

Table 9

Mean weights of samples from St Lucia from the three periods of sampling.

Date	Area	N.	mg/0.022 m^2	g/0.0225 m^2
Jan. 1972	South Lake	17	8.552	0.378
	North Lake	18	5.324	0.232
	False Bay	10	> 0.08	0.004
July 1972	South Lake	23	13.509	0.600
	North Lake	29	10.825	0.481
	False Bay	13	21.600	0.960
Jan. 1973	South Lake	24	11.925	0.530
	North Lake	30	2.703	0.120
	False Bay	14	1.767	0.078

By far the most important animal with respect to its biomass contribution is the small snail Assiminia bifasciata. The numerical analysis has already shown that these are more abundant on sandy substrates rather than muddy substrates (Table 4), and therefore more weight is contributed towards the total biomass on sandy samples than on muddy samples. Furthermore on sandy substrates the modal weight of Assiminia alone was two to three times that of the rest of the benthos. Thus in July 1972, the modal weight of Assiminia on sand was 25.7 mg/0.0225 m^2 (1.14 g/m^2) whilst that of the benthos as a whole less the Assiminia was 5.8 mg/0.0225 m^2 (0.26 g/m^2) and in January 1973 they were 9.4 mg/0.0225 m^2 (0.42 g/m^2) and 0.15 mg/0.0225 m^2 (0.007 g/m^2) respectively. It is interesting to note that the same pattern of reduced standing stock was noted in the summer of 1973 relative to the July of 1972.

On muddy substrates the number and hence biomass of Assiminia was low, having a maximum of 45 mg/0.0225 m^2 (2.00 g/m^2) whereas the maximum from sand was 263.076 mg/0.0225 (10.48 g/m^2). Many mud samples were void of any Assiminia at all, 38% in July 1972 and 73% in January 1973. However, the modal value of weight for samples containing

Assiminia in July 1972 was 0.794 mg/0.0225 m^2 (0.035 g/m^2) or about 25 animals of average size in most samples. In the following January 1972 the modal value of samples with Assiminia was 0.1514 mg/0.0225 m^2 (0.007 g/m^2) or just less than 5 animals per sample. These values add hardly at all to the benthic biomass of muddy samples particularly since many samples contained normal amounts of benthic material, but lacked Assiminia.

The mean weights of Assiminia make it possible to approximately assess the total standing stock of benthos in sand or in mud (Table 10).

Table 10

Standing stocks of Assiminia from Lake St Lucia as means from all samples of the lake from various times.

		Sand		Mud	
		~~Mean wt.~~/ mg/0.0225 m^2 ~~mg~~	~~Mean wt.~~ g/m^2	mg/ mg/0.0225 m^2	g/m^2
Jan. 1972	(South Lake only)	36.58	1.62	5.297	0.235
July 1972	(whole lake)	73.345	3.26	1.426	0.063
Jan. 1973	(whole lake)	24.34	1.08	0.286	0.013

Discussion

The results show that there is a clear evidence of a rapid recolonization by benthic organisms in areas which had had intolerably high salt concentrations and where the salinity rapidly declined following a period of good rain in the catchment. Furthermore the numbers and weights of benthic organisms which were recovered at the second sampling were greater even than the samples which were taken in January 1973, indicating that certain forms had probably benn completely successful in re-establishing themselves. The principle animals of the samples from North Lake north of Bird Island and False Bay were the polychaetes, the small gastropod Assiminia bifasciata and the chironomid larva Polypedilum. The chironomid larvae ~~appear to be~~ are a special case with regard to their presence in these regions. These larvae appear to have been highly resistant to high salinity conditions and are also seasonal with respect to their presence or absence. Grindley and Heydorn (1970) report that during July 1969 a plague of adult midges appeared in the Lister point area of False Bay snf vhitonomif pupae were present in plankton samples from July through to early September 1969 in North Lake and False Bay. Salinities reached 70°/oo in parts of False Bay in December, suggesting that the midges had withstood high salinities earlier in that year. This experience was repeated in the present work when in January 1972 a few chironomid larvae were recovered from samples with 80°/oo salinity. The seasonal appearance of larvae is shown by their abundance in winter and their decline in summer samplings, both in this work and that of Grindley and Heydorn (1970) where the plankton samples in December were free of chironomid pupae. Of all the groups the midges therefore seem to have been able not only to inhabit the high salinity waters in the northern areas of the lake, but there is evidence (Grindley and Heydorn 1970) that abnormally high numbers were present in this otherwise vacant benthic niche during these periods.

It might be noted here that the midges collected by Grindley and Heydorn were identified as *Chironomus* (*Chironomus*)? *kaffrarius* by the Institute for Freshwater Studies of Rhodes University. Fish gut samples of larvae from St Lucia in 1969 submitted by Wallace were identified as a species of *Polypedilum* as were the chironomd larvae collected in the present case. It is possible that the most important form during the plague was a species of *Polypedilum*.

Between January and July 1972 populations of Polychaetes and *Assiminia* were re-established in False Bay and the northern reaches of North Lake which could only have come from far distant sources. There are two possibilities for such sources; either that small pockets of remnant populations may have been preserved in isolated areas of low salinity because of local dilution with freshwater from springs, or that these forms were driven back at least into the very south of North Lake, if not entirely into South Lake, and then migrated back into northern North Lake and False Bay.

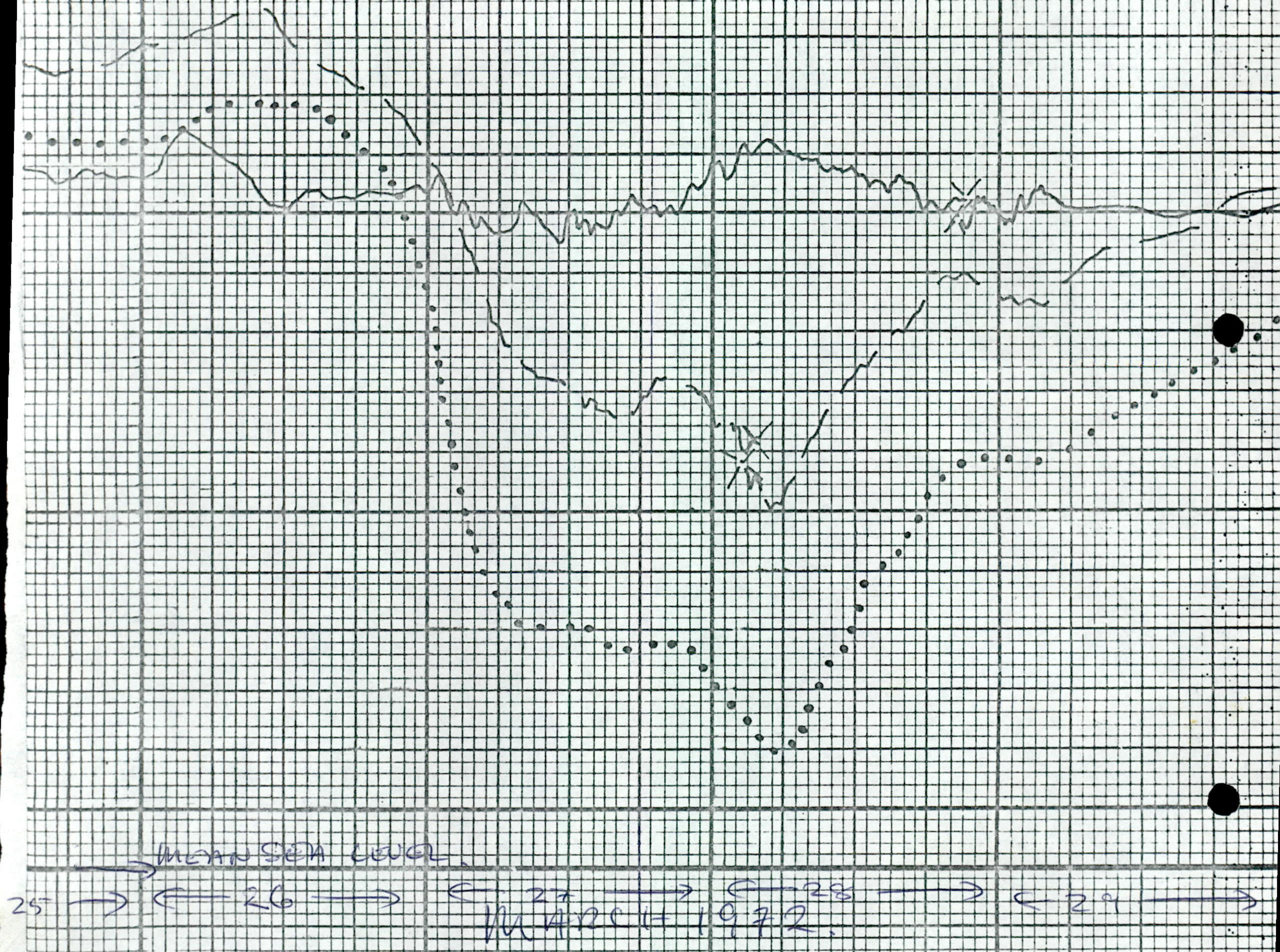

Fig 6. Each Cm of vertical axis equals 6 Cm in actual water level change. WATER LEVEL CHANGES from POTTERS CHANNEL .....
CHARTER CREEK — — —
LISTER POINT. ————

From Charts supplied by Natal Parks Board.

The first suggestion is not impossible since springs on the sides of St Lucia lake are known, particularly on the eastern shores of South Lake and North Lake. This suggestion does not seem probable for False Bay where high salinities were experienced even in the rivers. Furthermore, the springs of the eastern shore of St Lucia Lake may also have been seriously affected by the lack of rainfall. It would seem more probable that the benthic fauna had retreated to the south of the St Lucia lakes. How then were these forms able to migrate into False Bay in so short a time?

These forms probably have planktonic larvae which are produced in large quantities. Wind induced water level changes are commonly observed on the lake, an example of which is shown in Figure 6 for the period March 26th through to March 29th, 1972. The lowered lake level recorded for South Lake is compensated by increased depths in North Lake by water being shunted through the Narrows at Fanies Island. Similar changes in lake level are also experienced in False Bay with water being piled up at one and off the Basin from wind action. Large volumes of water are being at least transported to and fro across the bed of the lake depending on the wind strength and direction.

In how far transported water mixes with the water of the basin into which it has been transported is unclear. However, even if mixing is minimal, such that only plugs of water are transported back and forth, there is in this mechanism the required transport system for larval forms which last at least a few hours or some days in the plankton before settling. These settled larvae, on reaching sexual maturity would provide outposts for further distribution. The spread of the various species would then depend on the degree of water transport, the duration of a larva life in the plankton and the time taken to sexual maturity. It is particularly the small forms with planktonic larvae, high reproductive potentials by virtue of the production of large numbers of eggs per individual and short developmental periods to reproduction that have appeared in the north of North Lake and

False Bay. Although direct detailed information on the biology of most of these forms is lacking, they probably reproduce and grow to reproductive size in the short time of one to two months, as does G. lignorum. The results indicate that in spite of short developmental times to sexual maturity, some forms may be restricted in their rate of spread by limited egg laying capacities and short excursions into the plankton. The small crustacea Apseudes digitalis and Grandidierella lignorum are a case in point. Studies on G. lignorum have shown an average of only 6.5 eggs per egg laying female in a population comparable to that of St Lucia. A small percentage of the juveniles, which are produced throughout the year, enter the plankton at night and are therefore available for transportation. However, only limited though real extensions of distribution have been observed in this study. Confined to South Lake in January 1972, they were recovered from Station 47 in July 1972 and in Hell's Gates in January 1973. The populations were never large, even in South Lake, so that the densities of the amphipod which had dispersed from the original areas where they were preserved during the period of high salinity, must have initially been very low. Therefore, in spite of the short developmental time, their limited egg laying capacity and short planktonic life have restricted the rate of recolonization of more distant areas in the lake.

These quickly maturing forms are to be contrasted with the more slowly growing animals such as the bivalves Solen, Dossinia and Theora which though producing large numbers of larvae do so during a restricted season. The analysis of the data on the bivalves, particularly of Dossiminia shows that in spite of juveniles being present in the middle regions of North Lake already by July 1972 an insignificant extension of range was recorded in January 1973. McLachlan (1972) has found that most bivalves in Swartkops estuary near Port Elizabeth release their spat once a year in summer and/or spring. Only limited growth is experienced in one year, about 6 mm shell length for Dossiminia in one year, while the adults reach 20 mm in about 4 to 5 years (McLachlan 1972). Thus the spat reaching North Lake by July or earlier in 1972 would not have attained sufficient size to breed in summer or spring of 1972/73 and thus form an advanced outpost for further spread of the bivalves into False Bay and northern North Lake. In point of fact it is probable that only by being able to reproduce several times throughout the year that the small polychaetes and Assiminia were able to recolonize the whole system.

It is by virtue of a knowledge of the details of the biology of the various forms in the benthos that an understanding of the pattern of recolonization becomes available. However, in most cases, too little is known of the biology of the benthos to be able to confidently predict and interpret the results of the changing patterns of reinvasion of the benthos.

The standing stock of benthos in St Lucia taken as a whole is in general small compared to those of northern hemisphere temperate lakes (Table 11). The weights recovered from mud are particularly low as measured by the method employed. The contribution which might be made from larger bivalves is unfortunately not known quantitatively although the evidence of Wallace (1969) indicates that this may well be more important than the small forms sampled by the van Veen grab. The standing stock of the sandy areas is however more like the values experienced elsewhere. The fact that the greater part of this is made up of Assiminia is probably important in the food web of St Lucia since it is known that small snails make up the bulk of the diet of flamingoes ( ).

Moreover the standing stock as such may be a poor measure of the ability of the benthic community to supply food to higher trophic levels since it is the ability of the standing stock to replace its own weight of material and the rate at which this occurs which is important. Thus, for example, animals with short life cycles, such as presumably Assiminia and the polychaetes, may turn over at such a rate that although the equivalent weight of the standing stock is preyed upon by the birds and fish in a short time, the weight of animal material remaining in the benthos stays fairly constant or falls within reasonably narrow limits. Some indication of minimum production is given by the areas totally denuded, and re-occupied between January 1972 and July 1972.

With respect to <u>Assiminia</u> on sand, the minimum production over the lake as a whole during this period would be equivalent to the mean weight of the standing stock of the animals in July; 3.26 g/m^2. Certain areas appear to have been particularly productive. Thus station 44 gave a standing stock of 10.48 g/m^2 in July, a very high value indeed. These rough estimates indicate that this snail at least on sand provides an important source of food to higher trophic levels.

The minimal production of the other benthos in North Lake and False Bay were much more modest, being in the range of 0.1 g/m^2 to 0.2 g/m^2 as judged from the differences in standing stock between January and July 1972.

These estimates of production, however, are dubious since they take no account of predation ~~during the time~~. It is thought that more accurate measures would increase these figures considerably.

Comparison of the standing stock of July 1972 and January 1973 indicated that smaller values are experienced in summer than in winter. A similar phenomenon has been observed with respect to numbers of some forms in benthic samples from Lake Sibaya (Boltt 1969a) and also in plankton samples from the same lake (Allanson, unpublished). This phenomenon may be a reflection of differing rates of predation by higher trophic levels in the sense of Gerking (19) who showed that benthic invertebrates in North temperate lakes catch up on benthic ~~standing stocks~~ during periods of depressed feeding activity by fish ~~during~~ the winter and barely maintain themselves of "keep up" during the summer. It would be of interest to know if the modest temperature changes experienced by subtropical systems such as Lake St Lucia could affect the predation pressure on the benthos in the same way in which more marked temperature changes affect the predation pressure on benthos in Northern hemisphere lakes.

Not much further detailed understanding with regard to the details of changing salinities has been gained by the present study as compared with those of Day et al(1954) or those of Millard and Broekhuysen (1970). During the survey of Day et al in 1948 the salinities in False Bay reached a maximum of 52%o and the faunal list that is recorded from False bay, although impoverished relative to South Lake is nevertheless fairly long. At the commencement of the present program the salinities in False Bay were between 70°/oo an 80°/oo which appears to have excluded all benthic forms except the larvae of <u>Polypedilum</u>. North Lake salinities ranged between 60 °/oo and 70°/oo mainly in the upper half of the range. Except for the most southern limits of the area the benthos was particularly barren with only a few individuals of a limited range of species. The major exception of course being the Ostrocoda. At the actual time of sampling the salinity was 62°/oo possibly suggesting that the upper limmit for reinvasion was at about that level.

As far as South Lake is concerned it appears that the salinities were never in excess of 50°/oo and probably mainly in the low @40°/oo range. From the qualitative point of view with respect to species there was a slight reduction in the total species list and also in the common species as defined in this work. More instructive perhaps is the clear finding that the densities and the biomass of the area at that time were considerably lower that during either July 1972 or the following January 1973. There seems to have been a general depressive effect on the standing stocks of the system, but whether this effect is directly due to salinity or perhaps to an increased predation at that time is uncertain. The probability is that it is more likely to have been due to the former rather than the latter.

These observations lead to the clear indication for sampling at shorter intervals in order to more adequately answer these questions.

In an overall view it seems to be clear that the fauna of the lake benthos is of such a kind as to be opportunistic in character with respect to the reinvasion of denuded areas. The rapidity whith which the fauna recolonised both False Bay and North Lake was unnexpected. Nevertheless among the various species there was clear evidence of controls with respect to the rate of spread; the smaller quickly and constantly breeding forms spreading further than the larger forms with limited breeding periods only once a year.

With respect to the sedentary benthic forms it also seems clear that South Lake rather than the Channel forms the resevoir from which invasion further north takes place aftersevere salinity increases. It is possible that if the fauna had been driven into the channel leading from the lake the recolonisation of the Northern regions might have been severely curtailed because as the water levels of Figure 6 show during the period of dilution the general level of the lake was above sea level and there would have been a net flow towards the sea, tending to sweep the larvae

seawards rather than towards the lake. The limited ability for lateral transport of the planctonic larvae themselves is highlighted by work done by Grindley and his colleagues at the Port Elizabeth Museum (Grindley unpublished personal communication.). They have shown that with respect to Grandidierella lignorum and Copepods, that in Swartvlei zones of capture over populated bottom sediments as related to unpopulated bottoms were clear from synoptic plakton sampling.
with respect to St Lucia therefore benthic forms in the channel would not be able to avail themselves of the transport of water by the wind induced seiche of the various basins of the lake.

Acknowledgements.

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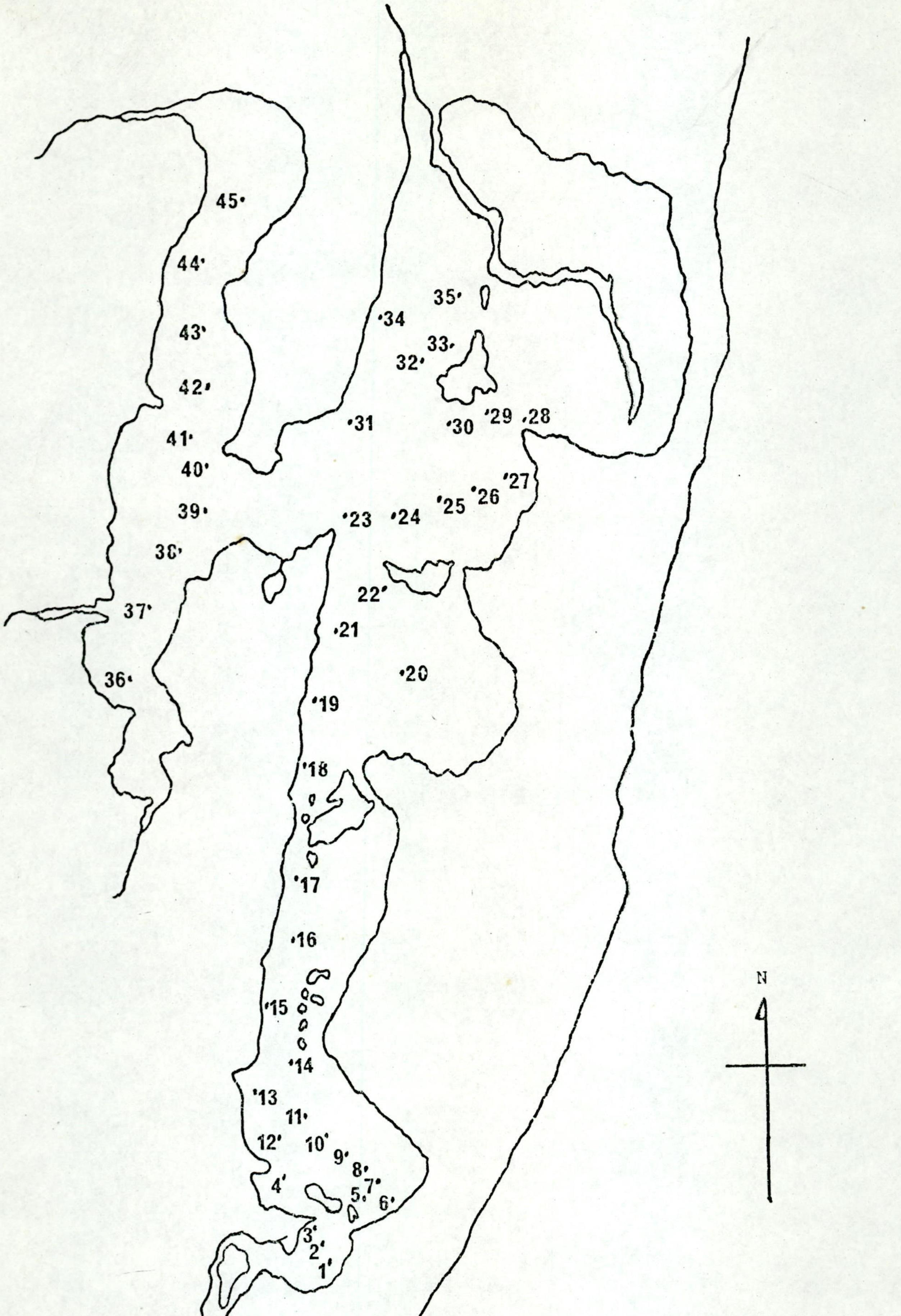

APPENDIX

Figure 1. Sketch map with positions and numbering of Stations in St Lucia, taken in January 1972. The data range given in Table 2 of appendix. The stations are equatable with figure one of main text.

Table 2

Data collected by van Veen grab of $0.0225\ m^2$ from St Lucia - January 1972

	Station No.	Assiminea bifasciata	Solen corneus	Nassarius kraussiana	Tellina sp.	Pittaria kochii	Littorina scabra	Macoma sp.	Nemertine worms	Prionospio sp.	Glycinde capensis*	Capitella sp.	Apseudes digitalis	Grandidierella sp.	Harpactecoid copepoda	Cumacea	Ostracoda	Gomphid dragonfly nymph*	Chironomid larvae	Nematoda	Unidentified polychaetes (Juves)	~~Cleistosoma edwardsii*~~ Tylodiplax blephariskios	Total weight mg/C,0225 m^2
SOUTH LAKE	1	26	3	-	-	-	-	1	-	7	3	-	1	-	-	-	-	-	1	681	10	-	6,232
	2	37	1	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	1	18	1	-	3,716
	3	10	-	-	-	-	-	-	-	3	-	59	-	-	27	-	-	-	-	-	93	-	4,640
	4	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	31	3	1	2,625
	5	52	-	-	-	-	-	-	-	-	28	6	-	-	-	7	-	-	-	592	-	-	8,939
	6	1430	-	1	-	-	-	2	-	-	7	3	-	-	-	-	-	-	1	185	-	-	155,140
	7	-	2	1	1	-	-	-	1	-	3	4	45	-	56	-	-	1	-	-	-	-	42,823
	8	-	-	1	-	-	-	-	-	1	1	-	1	-	59	-	-	-	-	9	-	-	12,036
	9	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	2	-	-	0,010
	10	-	-	-	1	-	-	-	-	-	1	-	1	-	-	-	-	-	1	4	-	-	0,287
	11	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	0,034
	12	556	1	-	-	1	1	4	-	-	26	2	-	1	-	-	-	-	1	129	-	-	53,178
	13	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	2	-	-	-	-	0,287
	14	1560	-	-	-	-	-	-	1	1	10	1	-	-	-	-	-	1	-	139	-	-	63,028
	15	201	-	-	-	-	-	2	1	-	1	12	2	-	-	-	4	1	-	-	-	-	14,093
	16	1	-	-	-	-	-	-	-	3	-	-	-	-	-	-	13	-	1	8	-	-	1,062
	17	436	-	-	-	-	-	1	-	11	-	13	-	-	-	-	255	-	17	-	-	-	33,194
NORTH LAKE	18	31	-	-	-	-	-	4	-	25	2	20	-	-	-	-	241	-	7	9	-	-	18,171
	19	92	-	-	-	-	-	-	-	-	10	-	-	-	-	-	30	-	146	-	-	-	23,104
	20	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0,352
	21	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	41	-	-	-	-	-	0,845
	22	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	31	-	1	-	-	-	0,406
	23	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	21	-	1	1	-	-	C,178
	24	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	78	-	-	-	-	-	1,238
	25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	87	-	-	-	-	-	0,930
	26	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	813	-	-	-	-	-	4,426
	27	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	61	-	-	-	-	-	1,162
	28	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	435	-	-	-	-	-	1,810
	29	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	97	-	-	-	-	-	1,218
	30	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	64	-	-	-	-	-	0,682
	31	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	**
	32	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	224	-	3	1	-	-	2,761
	33	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	205	-	1	-	-	-	1,848
	34	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	14	-	-	-	-	-	0,587
	35	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	49	-	-	-	-	-	0,650
FALSE BAY	36	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
	37	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
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	42	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	43	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
	44	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	45	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	0,086

* Species not previously recorded from St Lucia.
** Specimen not adequately formalized for gravimetric analysis.

Table 12.

Detailed analyses of numbers of individuals from the various stations of St Lucia (see fig 1) and total weights from Van Veen Grab samples of 0.0225 m² area. Data from July 1972. Stations as Fig 1.

Area	Station	Assiminia bifasciata	Solen corneus	Nassarius kraussiana	Theora lata	Pittaria kochi	Littorina scabra	Dossinia hepatica	Cylichna africana	Nemertines	Prionospio sexoculata	Glycinde capensis	Glycera convoluta	Capitella capitata	Platyhelminths	Apseudes digitalis	Grandidierella lignorum	Harpacticoid copepods	Cyclopoid copepods	Cumacea	Ostracoda	Polypodium sp.	Nematoda	Polychaetes other	Tylodiplax blepheriskios	Eriopisa chilkaensis	Total wt. mg/0.0225 m^2	
SOUTH LAKE	St. 1	61	-	-	2	-	1	3	9	-	1	5	-	10	-	-	5	1	-	-	1	-	56	-	-	-	11.025	
	St. 2	30	1	-	-	-	-	4	5	-	-	7	1	51	-	-	4	24	7	-	48	-	448	2	-	-	20.493	
	St. 3	-	-	-	-	-	2	1	-	-	-	1	-	3	-	1	3	9	-	-	-	-	88	8	2	8	13.474	
	St. 4	2913	-	-	1	-	1	8	7	-	-	8	-	10	-	-	-	-	-	25	-	-	454	-	-	-	45.272	
	St. 5	7	-	8	-	-	-	5	-	-	-	1	2	13	-	-	10	-	-	1	-	-	121	2+1	-	-	63.892	
	St. 6	-	3	-	-	-	-	-	-	1	-	4	-	8	-	-	5	-	-	20	6	-	55	-	-	-	12.445	
	St. 7	-	-	-	-	-	-	-	-	-	-	1	-	5	-	-	4	2	8	-	-	-	16	-	-	-	164.412	
	St. 8	3092	1	-	1	-	2	-	6	-	2	9	1	4	-	-	-	23	-	2	-	-	440	-	-	-	0.636	
	St. 9	4158	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	162	-	1	-	133.956	
	St.10	-	-	-	3	-	-	2	-	-	-	3	1	6	2	105	-	9	2	-	-	-	42	-	2	-	72.030	
	St.11	-	-	-	-	-	-	-	-	-	1	-	-	-	-	6	2	-	-	-	-	-	61	-	2	-	153.419	
	St.12	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12.610	
	St.13	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	10	-	1	-	55.539	
	St.14	-	-	-	-	-	-	2	-	-	-	2	-	-	2	-	5	40	40	-	-	2	46	-	-	-	0.530	
	St.15	-	1	-	-	-	-	-	-	-	-	-	1	3	-	-	-	-	-	-	-	-	35	-	3	-	179.915	
	St.16	2299	-	-	-	-	3	4	-	-	-	20	1	-	-	1	-	-	-	9	-	-	499	-	-	-	89.907	
	St.17	2124	-	-	-	-	-	18	-	-	-	14	-	-	-	-	4	-	-	9	-	-	254	-	-	-	68.885	
	St.18	3074	2	-	-	-	-	1	-	1	-	7	-	-	-	-	-	-	-	2	-	-	+	-	-	-	85.687	
	St.19	2037	-	-	-	-	1	4	-	-	-	14	-	-	-	-	1	-	-	44	-	-	640	-	-	-	91.803	
	St.20	49	2	-	2	-	1	-	-	-	-	14	-	-	30	-	13	1	-	-	6	-	. 10	-	-	-	47.271	
	St.21	-	7	-	1	-	-	1	-	-	1	8	2	2	-	-	5	19	13	-	-	-	537	-	-	-	5.425	
	St.22	-	-	-	9	-	35	3	-	-	-	-	-	-	-	3	138	-	-	-	-	-	176	-	-	-	47.779	
	St.23	4367	-	-	4	-	-	38	2	-	-	16	-	1	2	-	5	9	21	-	-	-	303	2	-	-	39.063	
NORTH LAKE	St.24	1051	3	-	2	-	-	5	-	-	-	20	1	2	3	-	1	7	4	-	231	-	229	-	-	-	32.565	
	St.25	2492	5	-	-	3	-	-	-	-	5	26	2	-	-	-	-	-	23	-	-	-	206	-	-	-	113.736	
	St.26	536	3	-	-	-	-	5	-	-	2	7	-	-	-	-	-	-	-	-	-	3	113	-	-	-	27.877	
	St.27	-	-	-	3	-	-	1	3	-	3	4	-	-	-	-	-	-	-	-	-	-	20	-	-	-	10.550	
	St.28	-	2	-	3	-	-	2	-	-	1	7	-	-	2	-	3	-	5	-	27	-	109	-	-	-	43.022	
	St.29	4	-	-	2	-	-	-	5	-	2	3	1	-	-	-	-	4	1	-	15	-	-	-	-	-	11.196	
	St.30	6	-	-	-	-	-	-	-	-	2	3	-	-	-	-	-	-	-	-	26	-	-	-	-	-	0.758	
	St.31	7693	2	-	-	-	-	1	-	-	3	13	1	-	-	-	-	-	21	-	470	20	753	-	-	-	153.336	
	St.32	1039	20	-	-	-	1	-	6	-	7	17	-	-	20	-	3	96	12	-		-	929	-	-	-	38.134	
	St.33	563	13	-	42	-	-	1	2	-	8	18	-	4	-	-	29	27	3	-	1299	1	25	-	-	-	36.214	
	St.34	150	-	-	-	-	-	-	-	-	4	4	-	2	-	-	-	6	1	-	169	-	-	-	-	-	7.179	
	St.35	37	-	-	-	-	-	-	3	-	3	3	-	-	-	-	-	-	-	-	4	-	-	-	-	-	2.608	
	St.36	81	-	-	1	-	-	-	2	-	2	4	-	1	-	-	-	-	2	-	292	-	-	-	-	-	8.786	
	St.37	215	-	-	3	-	-	1	8	-	8	18	1	-	-	-	2	32	-	-	42	-	94	-	-	-	20.552	
	St.38	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
	St.39	447	9	-	-	-	-	-	6	-	-	31	-	5	-	-	18	-	-	-	443	1	942	-	-	-	12.819	
	St.40	7841	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	1328	-	-	-	-	-	109.292	
	St.41	1510	-	-	-	-	-	-	-	-	-	7	1	-	-	-	-	-	16	-	8	-	129	-	-	-	19.225	
	St.42	-	-	-	-	-	-	-	-	-	3	-	-	1	-	-	1	-	12	-	-	-	235	-	-	-	0.998	
	St.43	15	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	0.661	
	St.44	11185	-	-	-	-	-	-	-	-	2	7	-	-	31	-	1	-	10	-	24	-	934	-	-	-	269.235	
	St.45	52	-	-	-	-	-	-	2	-	13	2	-	-	-	-	-	-	-	-	37	-	-	-	-	-	6.273	
	St.46	61	-	-	-	-	-	-	4	-	-	3	-	-	-	-	-	-	-	-	161	-	-	-	-	-	5.511	
	St.47	181	-	-	1	-	-	-	3	-	10	6	-	-	-	-	1	-	-	-	-	-	-	-	-	-	8.133	
	St.48	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.038	
	St.49	105	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	2	-	-	-	-	-	-	-	-	6.852	
	St.50	44	-	-	-	-	-	-	-	-	8	10	-	-	-	-	-	-	-	-	42	-	-	-	-	-	6.282	
	St.51	40	-	-	-	-	-	1	2	-	-	11	-	-	-	-	-	-	-	-	31	-	-	-	-	-	7.218	
	St.52	69	-	-	-	-	-	-	-	-	2	9	-	-	-	-	-	-	-	-	64	7	-	-	-	-	5.711	
	St.53	13	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	12	-	-	-	-	-	1.269	
FALSE BAY	St.54	148	-	-	-	-	-	-	-	-	911	9	-	-	-	-	-	-	5	-	576	362	3	-	-	-	66.682	
	St.55	8	-	-	-	-	-	-	-	-	20	4	-	-	-	-	-	1	-	-	98	41	-	-	-	-	12.747	
	St.56	-	-	-	-	-	-	-	-	-	90	41	-	-	-	-	-	1	-	-	98	1	-	-	-	-	14.278	
	St.57	12	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	32	-	-	-	-	-	1.608	
	St.58	15	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.689	
	St.59	-	-	-	-	-	-	-	-	-	25	3	-	-	-	-	-	-	-	-	-	13	-	-	-	-	13.250	
	St.60	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Not sampled
	St.61	10	-	-	-	-	-	-	-	-	41	2	-	-	-	-	-	-	-	-	24	33	-	-	-	-	18.668	
	St.62	-	-	-	-	-	-	-	-	-	31	1	-	1	-	-	-	-	-	-	-	14	-	-	-	-	10.760	
	St.63	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	3.620	
	St.64	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Not sampled
	St.65	11	-	-	-	-	-	-	-	-	19	-	-	-	-	-	-	-	-	-	47	16	-	-	-	-	11.122	
	St.66	-	-	-	-	-	-	-	-	-	37	1	-	-	-	-	-	-	-	-	-	79	14	-	-	-	26.873	
Mkuze	St.67	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	21	-	-	-	-	16.093	
Channel	St.68	-	-	-	-	-	-	-	-	-	-	1	-	55	-	2	6	-	-	-	-	-	278	1	7	8	-	

Table 13.

Detailed analyses of numbers of individuals and total weights of animals from the Benthos of St Lucia as taken by Van Veen Grabs of area 0.0225 m². Data from January 1973, Stations as of Fig 1.

Region	Station	Assiminia bifasciata	Solen corneus	Nassarius kraussiana	Theora lata	Pittaria kochi	Littorina scabra	Dossinia hepatica	Cylichna africana	Nemertines	Prionospio sexoculata	Glycinde capensis	Glycera convoluta	Capitella capitata	Platyhelminths	Apseudes digitalis	Grandidierella lignorum	Harpacticoid copepods	Cyclopoid copepods	Cumacea	Ostracoda	Polypedilum sp.	Nematoda	Polychaetes other	Cleistosoma edwardsii	Tylodiplax blepheriskios	Eriopisa chilkaensis	Anemones	Total wt. mg/0.0225 m^2	g/m^2
	St. 1	-	-	-	-	-	-	-	-	-	19	2	-	24	-	-	-	-	-	2	-	-	985	1	-	-	-	-	10.70	0.483
	St. 2	-	-	-	1	-	-	-	-	-	1	1	-	14	-	-	-	-	-	-	-	-	-	-	-	-	14	-	21.212	0.942
	St. 3	-	-	-	-	-	-	-	-	-	-	3	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.096	0.137
	St. 4	115	-	-	-	-	-	2	-	-	2	1	-	2	-	-	-	-	-	-	-	-	-	1	-	-	-	-	12.477	0.554
	St. 5	-	3	-	-	-	-	-	-	-	-	3	-	17	-	-	6	849	-	1	-	-	2017	1	-	-	-	36	405.804	18.017
	St. 6	9	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	57	7	-	-	-	190	-	-	-	-	-	1.931	0.086
	St. 7	-	-	-	-	-	-	-	-	-	-	3	1	5	-	1	-	686	18	5	-	-	559	-	-	-	-	-	6.231	0.277
	St. 8	234	1	-	-	-	-	-	-	-	15	2	-	-	-	-	-	5	29	4	-	-	194	-	-	-	-	-	7.596	0.337
	St. 9	-	-	-	-	-	-	-	-	-	1	-	-	2	-	91	3	30	18	-	-	-	549	-	-	1	-	-	128.235	5.694
	St.10	-	-	-	-	-	-	-	-	-	-	-	1	-	-	406	1	59	-	-	-	-	413	-	-	-	-	-	23.986	1.065
	St.11	-	-	-	-	-	-	-	-	-	3	2	-	-	-	642	-	39	-	-	-	-	318	-	-	-	-	-	21.348	0.948
	St.12	-	-	-	-	-	-	2	-	-	-	-	-	-	-	312	-	101	-	-	-	-	296	-	-	-	-	-	22.778	1.011
	St.13	-	-	-	-	-	-	1	-	-	5	-	-	5	-	-	-	27	-	-	-	-	70	-	-	-	-	-	9.324	0.414
S[illegible] LAKE	St.14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	2	-	-	-	77	-	-	-	-	-	0.233	0.010
	St.15	-	-	-	-	-	-	-	-	-	1	-	1	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
	St.16	1506	-	-	-	-	-	1	-	-	33	-	-	-	11	-	-	10	16	6	-	-	192	-	-	-	-	-	35.287	1.567
	St.17	2839	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	17	2	-	-	178	-	-	-	-	-	56.828	2.523
	St.18	632	-	3	-	-	1	1	-	-	7	1	-	3	-	-	5	-	-	12	-	-	354	-	-	-	-	-	23.082	1.025
	St.19	498	-	-	-	-	-	2	-	-	17	2	-	1	9	-	-	-	13	7	-	-	632	-	-	-	-	-	20.382	0.904
	St.20	-	-	-	-	-	-	-	-	1	5	8	2	-	-	-	-	4	3	7	-	-	101	-	-	-	-	-	2.318	0.103
	St.21	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	121	10	-	-	-	38	-	-	-	-	-	1	-
	St.22	588	-	-	-	-	-	3	-	-	94	6	-	13	-	-	7	763	3	7	-	-	369	-	-	-	-	-	14.922	0.663
	St.23	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	27	1	-	-	-	274	-	-	-	-	-	0.842	0.037
	St.24	741	-	-	-	-	-	-	-	-	13	10	2	2	-	-	1	67	5	-	-	-	271	-	-	-	-	-	23.792	1.056
	St.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Not sampled	
	St.26	2563	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	14	-	-	-	-	357	-	-	-	-	-	82.127	3.646
	St.27	9	-	-	-	-	-	-	-	-	-	-	-	21	-	-	-	91	5	-	-	-	149	-	-	-	-	-	1.057	0.047
	St.28	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	25	1	-	-	-	192	-	-	-	-	-	0.714	0.032
	St.29	3531	-	-	-	-	-	2	-	-	3	-	1	-	-	-	-	3	-	-	-	-	202	-	-	-	-	-	100.544	4.465
	St.30	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	1	-	-	-	-	-	-	-	-	-	0.041	0.002
	St.31	6799	-	-	-	-	-	-	-	-	29	15	-	14	-	-	5	108	10	-	-	-	302	-	-	-	-	-	91.356	4.056
	St.32	639	-	-	-	-	-	-	-	-	1	11	-	8	-	-	-	449	-	-	-	-	512	-	-	-	-	-	23.040	1.023
	St.33	26	-	-	-	-	-	5	-	-	6	2	-	14	-	-	-	2616	3	-	-	-	253	-	-	-	-	-	8.607	0.382
	St.34	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	6	-	-	-	-	-	-	-	-	-
	St.35	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
	St.36	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Nil
	St.37	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		Nil
NORTH LAKE	St.38	1932	-	-	-	-	-	1	-	-	1	4	-	3	-	-	-	2	-	-	-	-	170	-	-	-	-	-	89.613	3.979
	St.39	9	-	-	-	-	-	-	-	-	7	2	-	1	-	-	1	531	7	-	-	-	661	-	-	-	-	-	2.951	0.131
	St.40	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Nil
	St.41	484	1	-	-	-	-	-	-	-	2	5	3	6	-	-	-	2	-	-	-	-	407	-	-	-	-	-	20.560	0.913
	St.42	1024	1	-	-	-	-	-	-	-	-	10	-	-	-	-	-	20	3	-	-	-	173	-	-	-	-	-	23.566	1.046
	St.43	75	-	-	-	-	-	-	-	-	3	1	-	6	-	-	-	46	2	-	78	-	27	-	-	-	-	-	2.136	0.095
	St.44	527	-	-	-	-	-	1	-	-	-	3	2	2	-	-	-	-	-	-	-	-	891	-	-	-	-	-	13.715	0.609
	St.45	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	-	-	-	-	159	-	-	-	-	-	0.446	0.020
	St.46	1	-	-	-	-	-	-	-	-	59	-	-	-	-	-	-	31	4	-	-	-	89	-	-	-	-	-	1.141	0.051
	St.47	-	-	-	-	-	-	-	-	-	1	-	-	2	-	-	-	2	11	-	-	-	16	-	-	-	-	-	0.366	0.016
	St.48	-	-	-	-	-	-	-	-	-	4	1	-	-	-	-	-	8	-	-	-	-	11	-	-	-	-	-	0.091	0.004
	St.49	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	-	-	-	-	93	-	-	-	-	-	0.266	0.012
	St.50	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	0.116	0.005
	St.51	74	-	-	-	-	-	-	-	-	33	1	-	-	-	-	-	1	-	-	3	-	20	-	-	-	-	-	1.183	0.053
	St.52	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Nil
	St.53	16	-	-	-	-	-	-	7	-	4	2	-	14	-	-	1	-	-	-	16	-	28	-	-	-	-	-	5.816	0.258
	St.54	1	-	-	-	-	-	-	-	-	207	2	-	-	-	-	-	151	3	-	136	-	25	-	-	-	-	-	9.946	0.441
	St.55	-	-	-	-	-	-	-	-	-	38	1	-	-	-	-	-	18	-	-	-	-	11	-	-	-	-	-	1.229	0.055
	St.56	5	-	-	-	-	-	-	3	-	22	2	-	-	-	-	-	15	-	-	-	-	18	-	-	-	-	-	1.907	0.085
	St.57	-	-	-	-	-	-	-	-	-	29	-	-	-	-	-	-	8	2	-	13	-	103	-	-	-	-	-	2.232	0.099
	St.58	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	56	-	-	-	-	80	-	-	-	-	-	0.374	0.017
	St.59	22	-	-	-	-	-	-	6	-	22	-	-	9	-	-	-	31	1	-	2	-	300	-	-	-	-	-	3.188	0.142
FALSE BAY	St.60	3	-	-	-	-	-	-	3	-	5	1	-	-	-	-	-	10	2	-	2	-	169	-	-	-	-	-	0.933	0.041
	St.61	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	8	-	-	-	-	4	-	-	-	-	-	0.032	0.001
	St.62	2	-	-	-	-	-	-	-	-	7	-	-	-	-	-	-	18	2	-	-	-	102	-	-	-	-	-	1.054	0.047
	St.63	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	St.64	3	-	-	-	-	-	-	-	-	4	-	-	3	-	-	-	94	1	-	13	-	30	-	-	-	-	-	0.695	0.031
	St.65	15	-	-	-	-	-	-	-	-	5	4	4	-	-	-	-	24	-	-	2	-	24	-	-	-	-	-	1.998	0.089
	St.66	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	No sample	
Mkuze	St.67	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Nil
Channel	St.68	-	-	-	-	-	-	-	-	-	-	-	-	13	-	-	-	-	-	-	-	-	-	-	-	-	5	8	36.539	1.622
																													2.602	0.116