The benthos of South Lake, St Lucia following a period of stable salinities

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The invertebrate benthos of South Lake, St Lucia was monitored monthly from August 1981 to July 1982 following a period of stable salinities of approximately 35°/₀₀. The overall mean biomass for the year (dry mass) was 2,63 g m^{-2} with mean values for muddy and sandy substrata of 4,19 g m^{-2} and 1,07 g m^{-2} respectively. The major contributors to standing stock were the bivalve *Solen cylindraceus* and the polychaete *Marphysa macintoshi*. A total of 37 taxa were recorded compared with 23 in a previous survey in 1972 – 73. Present results are compared with those of 1972 – 73 and the differences discussed. The main changes were a decline in *Assiminea, Nassarius* and *Prionospio* and an increase in abundance of long-lived bivalves together with larger polychaetes. Species diversity at the sampling sites is analysed and discussed in terms of equitability of distribution.

S. Afr. J. Zool. 1983, 18: 311 – 319

Die ongewerwelde bodemfauna van die Suidmeer, St Lucia, is maandeliks geanaliseer vanaf Augustus 1981 tot Julie 1982, net na 'n tydperk van stabiele soutgehalte van om en by 35°/₀₀. Die gemiddelde biomassa, uitgedruk as droë massa, oor die hele meer vir die jaar was 2,63 g m^{-2}, waarvan die gemiddelde waardes vir modder- en sandbodems onderskeidelik 4,19 g m^{-2} en 1,07 g m^{-2} was. Hierdie staande biomassa was hoofsaaklik saamgestel uit *Solen cylindraceus* (Mollusca, Bivalvia) en *Marphysa macintoshi* (Annelida, Polychaeta). 'n Totaal van 37 diersoorte is in hierdie opname gevind, teenoor 23 in 'n vorige opname in 1972 – 73. Die huidige resultate is met dié van 1972 – 73 vergelyk, en die verskille word bespreek. Die vernaamste veranderings was 'n afname in getalle van *Assiminea, Nassarius* en *Prionospio*, en 'n toename in die langlewende Bivalvia en die groter Polychaeta-soorte. Spesiesverskeidenheid by die monsterpunte is geanaliseer en word bespreek in terme van die egaligheid van verspreiding.

S.-Afr. Tydskr. Dierk. 1983, 18: 311 – 319

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Received 11 February 1983; accepted 12 March 1983

A number of surveys of the benthos of St Lucia, the largest estuarine area in southern Africa, have been undertaken. The first was carried out by the Zoology Department of the University of Cape Town between 1948 and 1951 (Day, Millard & Broekhuysen 1954) when average salinities were between 30,5 and 41,2°/₀₀. This was followed up in 1964 and 1965 by Millard & Broekhuysen (1970) during a low salinity (7 – 19°/₀₀) period and from 1972 to 1973 by Boltt (1975) during and immediately subsequent to salinities in excess of 55°/₀₀ in South Lake. Despite these variations the South Lake compartment of St Lucia has more stable salinities than the rest of the system where salinities in excess of 100°/₀₀ have been recorded (Natal Parks Board records).

The importance of understanding the seasonal benthic cycles in St Lucia and their relationships with physical conditions cannot be overstated in view of the large-scale salinity fluctuations and cycles which take place. A large array of fish, bird and reptile predators is dependent on the biomass and variety of benthic invertebrates.

The present survey was conducted in conjunction with, and as a necessary part of, a study of the feeding ecology of benthic fish species. The study was restricted to the South Lake compartment (Figure 1) and covered the period August 1981 to July 1982. Sampling was intensive and regular but restricted to four sites (Figure 1) where fish could also be collected. Despite the limitations of the programme the volume of data generated on the benthos was large and provides valuable comparisons with previous studies under different conditions. This is especially true since this survey was conducted over a period when the salinity was relatively stable, ranging from 31,0 to 44,5°/₀₀ (Figure 2) and following several years when the salt content was below 35°/₀₀. It was therefore decided that this separate paper was necessary in order to document changes and facilitate future studies at all trophic levels.

Materials and Methods

Samples were collected monthly from August 1981 to July 1982 at a depth of about 1 m at four sites (Figure 1) in South Lake, St Lucia. The two sites on the east side (Nkazana and Game Guard Camp) were in sandy substrata while those on the west (Gilly's Point and Makatatana) were in mud (Whitfield & Blaber 1978). A Zabolocki-type Ekman grab was used and sampled a surface area of 0,0236 m^2 to a depth of 4,5 cm. Four grabs were taken for each sample. After collection larger organisms were separated by washing the sample through a 1-mm sieve. A solution of 10% formalin was added to the remainder, the sample stirred into suspension and decanted through a 0,5-mm sieve. This procedure was repeated five times

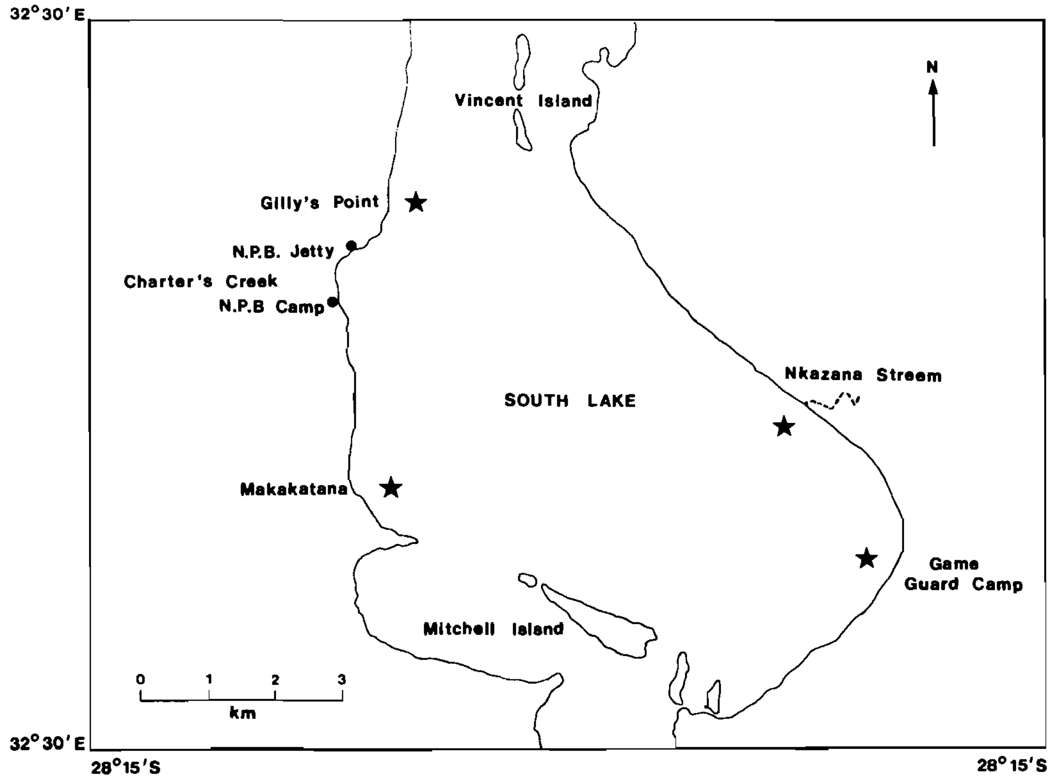

Figure 1 South Lake, St Lucia showing sampling sites (★).

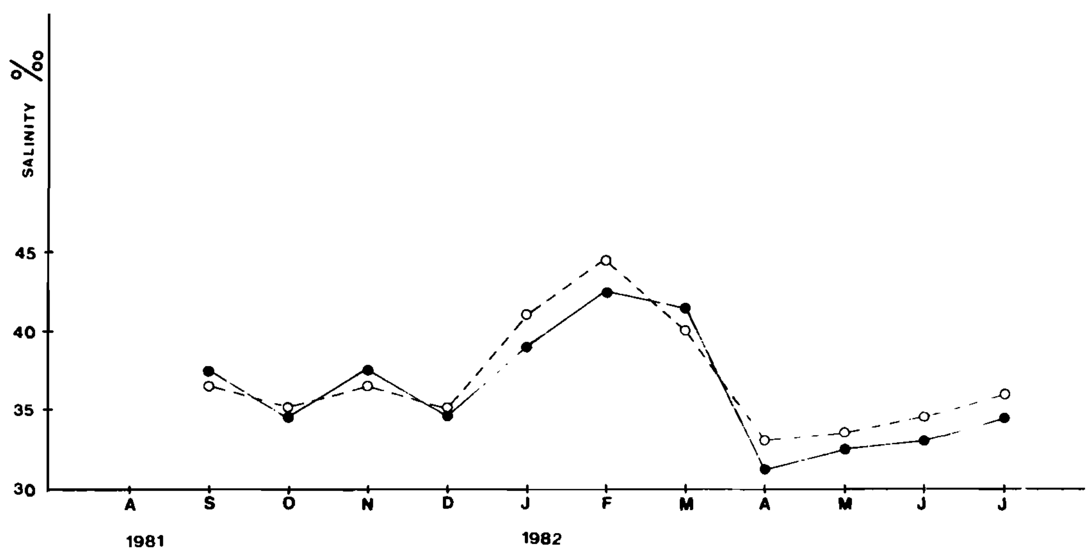

Figure 2 Salinities in South Lake, St Lucia from August 1981 to July 1982 (0---0 = western side, ●---● = eastern side).

to ensure the collection of all animals in the sample. The animals were preserved in 10% formalin and the vital dye Phloxin added to aid sorting and counting in the laboratory.

Samples were sorted to species as far as possible, counted and dried to constant weight at 60 °C and weighed to 0,01 mg on a Cahn 29 automatic electrobalance. Molluscs were weighed shell-free after dissolving the shells in a nitric acid solution.

Monthly salinities on the eastern and western shores were taken from Natal Parks Board records. Salinities varied little during the sampling period, ranging from 31 to 44,5°/oo (Figure 2), thus remaining close to that of seawater (35°/oo).

Results

The 37 taxa (identified as far as possible) which were collected at the four sites are listed in Table 1 according to whether they were (i) abundant (occurring in more than 75% of samples), (ii) common (40 – 74% of samples), (iii) present (less than 40% of samples) or (iv) rare (two or less individuals recorded). The species or taxa which occurred at all sites were the bivalves *Solen cylindraceus* and *Dosinia hepatica*; the opisthobranch *Haminea petersi*; the gastropod *Assiminea* sp.; the polychaetes *Marphysa macintoshi, Glycera tridactyla* and *Dendronereis arborifera*; oligochaetes; nemerteans; the crab *Hymenosoma orbiculare*; the tanaid *Apseudes digitalis*; the amphipod *Grandidierella lignorum*; cumaceans and the mysid *Mesopodopsis africana*. Of the remainder 14 were rare and contributed little to the overall biomass.

Three species were almost certainly underestimated owing to their mobility and hence grab avoidance: *Solen cylindraceus, Hymenosoma orbiculare* and *Mesopodopsis africana*. The last-named forms part of the zooplankton and its quantitative

Table 1 The relative abundance and mean numbers (m^{-2}) of benthic invertebrates at four sampling sites in South Lake, St Lucia during 1981 – 82. (A = abundant, C = common, P = present, R = rare, – = absent, $\bar{x}$ = mean, SE = standard error

	Nkazana (sand)			Game Guard Camp (sand)			Makakatana (mud)			Gilly's Point (mud)		
Taxon		$\bar{x}$	SE		$\bar{x}$	SE		$\bar{x}$	SE		$\bar{x}$	SE
Solen cylindraceus	C	148	88	A	151	60	C	49	11	A	498	150
Dosinia hepatica	P	14	5	P	21	6	P	19	10	P	53	49
Macoma retrorsa	R	2	2	–	–	–	P	5	3	–	–	–
Eumarcia paupercula	P	11	6	P	19	6	–	–	–	P	21	21
Theora lata	–	–	–	R	3	2	R	5	3	P	140	199
Siliqua sp.	–	–	–	–	–	–	–	–	–	R	2	0,5
Brachidontes virgiliae	–	–	–	–	–	–	R	6	3	P	15	4
Haminea petersi	R	1	0,8	P	8	3	P	8	4	R	1	0,8
Assiminea sp.	P	3	2	R	1	0,8	P	7	4	P	2	1
Marphysa macintoshi	A	3819	513	A	4236	1229	A	8885	1319	A	1536	412
Glycera tridactyla	P	272	15	C	201	73	C	127	47	C	646	303
Dendronereis arborifera	P	16	5	P	34	12	C	101	22	C	127	33
Sabellidae	P	8	5	P	112	68	P	40	22	–	–	–
Scolelepis sp.	–	–	–	–	–	–	R	2	1	R	3	3
Eunicidae	–	–	–	–	–	–	R	1	0,8	–	–	–
Ceratonereis sp.	–	–	–	R	1	0,8	R	2	1	R	21	18
Nereis sp.	–	–	–	R	1	0,8	–	–	–	–	–	–
Prionospio sexoculata	R	2	1	–	–	–	P	18	18	–	–	–
Phyllochaetopterus socialis	–	–	–	–	–	–	R	1	0,8	R	1	0,8
Lepidonotus durbanensis	–	–	–	–	–	–	R	1	0,8	R	1	0,8
Nephthys sp.	–	–	–	R	1	0,8	–	–	–	R	1	0,8
Sigalioninae	–	–	–	–	–	–	R	1	0,8	–	–	–
Oligochaeta	P	6	3	P	50	28	P	105	48	C	159	50
Nemertea	P	15	8	P	6	4	P	42	13	C	50	19
Nematoda	P	14	8	R	2	2	–	–	–	R	3	3
Sipunculida	R	1	0,8	R	3	4	P	111	54	C	286	104
Hymenosoma orbiculare	P	9	5	P	11	5	P	4	2	P	16	9
Apseudes digitalis			0,8	P	8	4	C	61	24	A	3336	1135
Grandidierella lignorum	P	152	112	C	85	30	C	1488	600	A	1165	254
Afrochiltonia capensis	R	1	0,8	–	–	–	–	–	–	–	–	–
Talorchestia sp.	R	1	0,8	–	–	–	–	–	–	–	–	–
Cumacea	A	3642	697	A	2478	563	C	320	88	A	604	131
Argulus sp.	R	1	0,8	–	–	–	–	–	–	R	1	0,8
Mesopodopsis africana	R	1	0,8	P	13	7	P	155	109	P	11	6
Alpheus sp.	–	–	–	–	–	–	R	1	0,8	–	–	–
Synidotea variegata	–	–	–	–	–	–	P	5	3	R	1	0,8
Hydrozoa	–	–	–	–	–	–	–	–	–	R	1	0,8
n = 37		23			21			28			28	

distribution in St Lucia has been described (Blaber 1979). The bivalve *Brachidontes virgiliae* occurs mainly in weed beds in South Lake and is hence underestimated in this survey.

The monthly total standing crops of benthos (g m^{-2}) at the sandy and muddy sites are compared in Table 2. No definite seasonal variations in biomass are evident but the mean crop of animals in the muddy sites (4,19 g m^{-2}) was four times greater than in the sandy sites (1,07 g m^{-2}). If all sites are considered together for the whole year the mean standing crop was 2,63 g m^{-2}.

Brief accounts of the seasonal fluctuations in numbers and distribution of the more common animals follow:

The bivalve *Solen cylindraceus* was the greatest contributor to biomass, particularly in muddy areas. A marked summer peak in standing crop occurred at the muddy Gilly's Point site but this was not reflected at other sites where late summer and autumn peaks were evident (Figure 3). Relatively low numbers were recorded throughout the year at the sandy Nkazana site.

Of the other bivalves, *Dosinia hepatica* and *Eumarcia paupercula* were widely distributed but numbers were too low to permit analyses of seasonal patterns, while *Macoma retrorsa, Theora lata, Siliqua* sp. and *Brachidontes virgiliae* occurred only in small numbers in the muddy sites.

Haminea petersi was widely distributed but numbers were insufficient to show any seasonal trends. *Assiminea* sp., a previously abundant gastropod (100 – 1 000 animals m^{-2} (Boltt 1975)), was recorded at all sites but in very low numbers (< 10 animals m^{-2}). Many empty shells were noted in virtually all samples.

Several polychaetes were recorded. *Marphysa macintoshi* (Figure 4) was abundant at all sites although the largest standing crops were at Makakatana (mud). There was seasonal variation in biomass with major peaks in autumn and winter and lows in summer. After *Solen* this species contributed most to overall biomass. *Glycera tridactyla* was relatively common at all sites but standing crops were low compared with *Marphysa*. Populations at all four sites showed three biomass peaks a year, from October to December, from February to April and from June to August. However, there were extreme oscillations in standing crops, particularly at Gilly's Point (mud) and Makakatana (mud) with reductions and increases of as much as 0,4 g m^{-2} within one month. *Dendronereis arborifera* (Figure 5) was common only at the muddy sites although present on the eastern shores. Peaks in standing crop occurred in summer and to a lesser extent in winter.

Table 2 Standing stocks of total benthos (g m^{-2} dry mass) in sand and mud in South Lake, St Lucia from August 1981 to July 1982

Month	Sand substrata	Mud substrata
August	1,15	3,12
September	0,67	4,32
October	0,96	3,74
November	0,63	4,20
December	1,06	5,03
January	0,84	3,95
February	1,30	8,55
March	0,87	2,47
April	0,56	5,50
May	3,23	2,85
June	0,85	5,52
July	0,72	1,07
$\bar{x}$	1,07	4,19
SE	0,20	0,55
Overall mean	2,63	

Another 10 polychaete species were identified in small numbers from South Lake (Table 1) but their contribution to standing crops was negligible. It is noteworthy that *Prionospio sexoculata*, which was abundant during 1972 – 3 (Boltt 1975), was uncommon during this survey.

If the monthly pooled standing crops of all the *Errantia* are compared with those of *Marphysa* it is evident that *Marphysa* is responsible for seasonal patterns since it is overwhelmingly dominant in terms of biomass. Overall polychaete numbers are thus highest in early summer and winter.

Small numbers of oligochaetes were present at all sites but they were more numerous in muddy areas. Their contribution in terms of biomass was negligible.

As with oligochaetes no attempt was made to identify Nemertea to species but they occurred at all sites and were common at Gilly's Point. No clear seasonal patterns were evident but numbers were generally greater in summer and winter. However, although they are one of the commoner faunal elements their biomass is low relative to that of polychaetes.

The tanaid *Apseudes digitalis* (Figure 6) was only abundant at Gilly's Point (mud) where it showed a continuous increase in standing crop from February to June. It was least common on the sand of the eastern shores (Table 1). The amphipod *Grandidierella lignorum* (Figure 7) occurred at all sites but like *Apseudes* was only abundant in the mud of Gilly's Point. It was, however, more common than *Apseudes* in the sandy areas (Table 1). The main seasonal

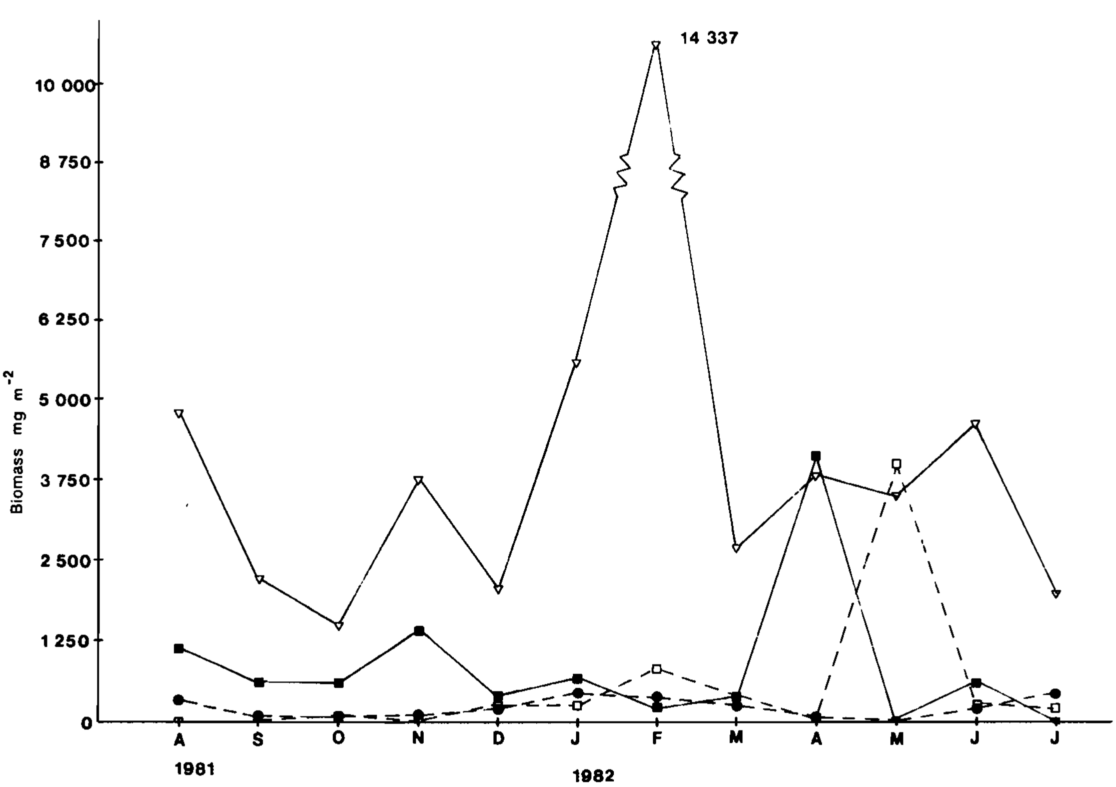

Figure 3 Standing stocks (mg m^{-2}) of *Solen cylindraceus* at four sites in South Lake, St Lucia (∇ — ∇ = Gilly's Point, ■—■ = Makakatana, ●---● = Nkazana, □---□ = Game Guard Camp).

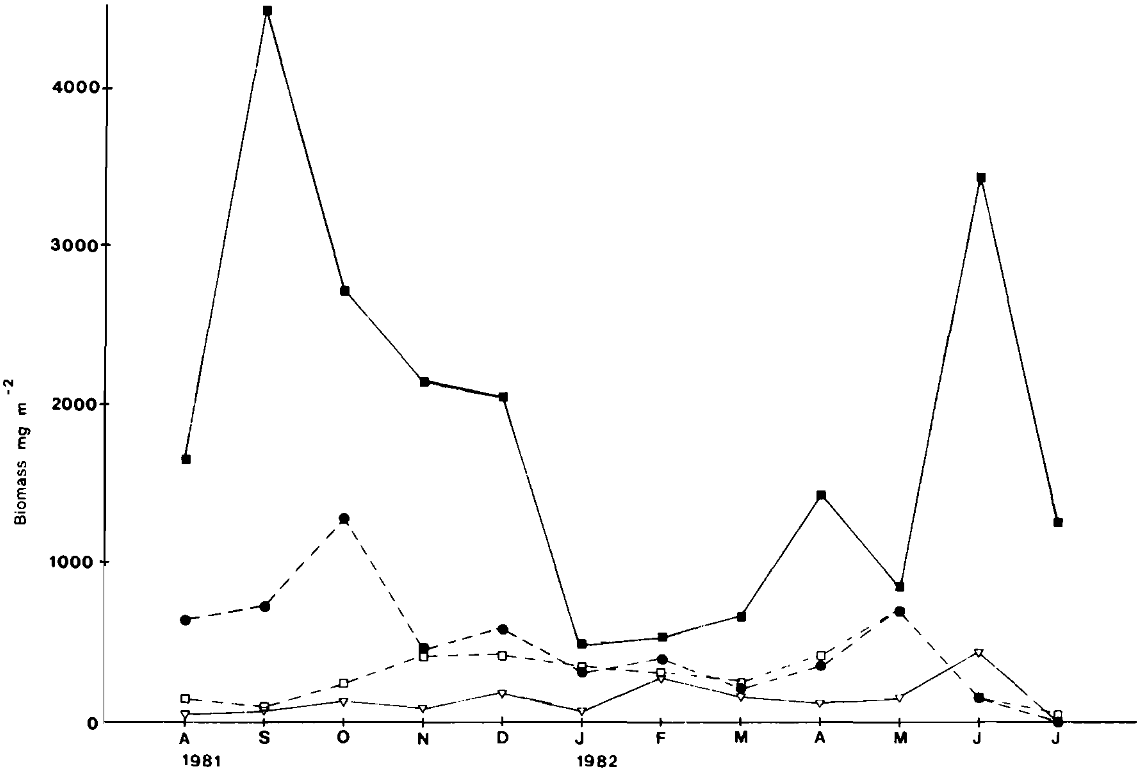

Figure 4 Standing stocks (mg m^{-2}) of *Marphysa macintoshi* at four sites in South Lake, St Lucia (▽ — ▽ = Gilly's Point, ■—■ = Makakatana, ●---● = Nkazana, □---□ = Game Guard Camp).

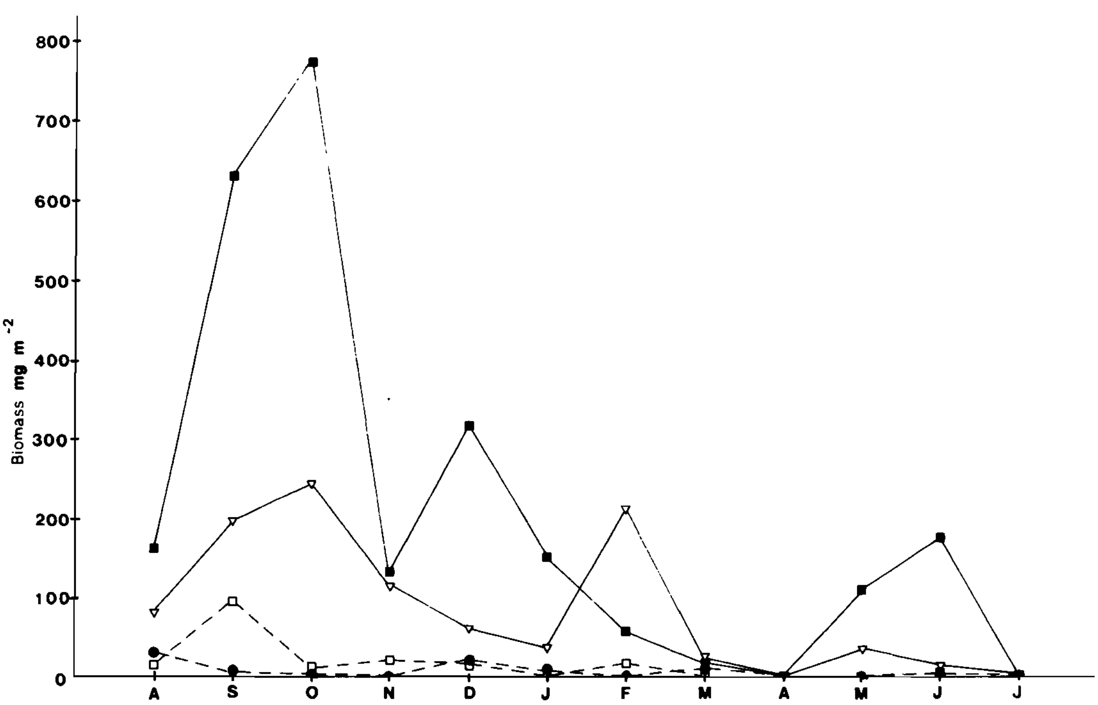

Figure 5 Standing stocks (mg m^{-2}) of *Dendronereis arborifera* at four sites in South Lake, St Lucia (▽ — ▽ = Gilly's Point, ■—■ = Makakatana, ●---● = Nkazana, □---□ = Game Guard Camp).

peaks at Gilly's Point were early summer and autumn. *Cumaceans* (Figure 8) were abundant at all sites except Makakatana where they were nevertheless common. They were particularly numerous on sandy substrata where summer and late autumn peaks in biomass were evident. This pattern closely follows that of the zooplankton (Blaber 1979).

Species diversity

The species diversities each month at the four sites are compared in Figure 9 using the Shannon-Wiener Index of Diversity,

$$H = \sum_{i=1}^{s} (p_i)(\log_2 p_i),$$

(Krebs 1972). For all months the species diversity index of the

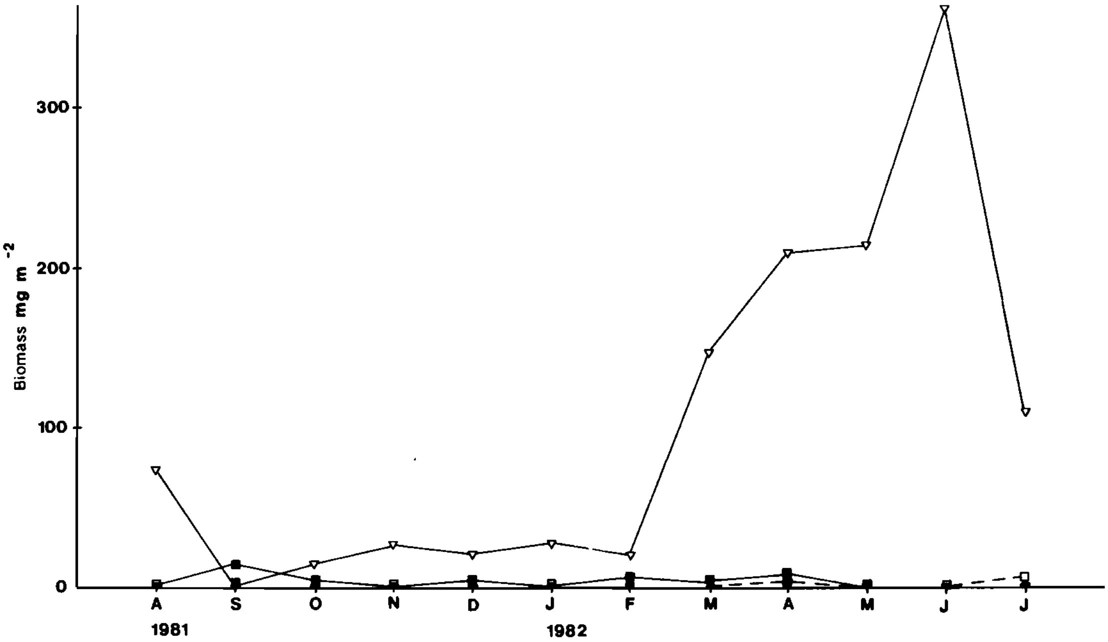

Figure 6 Standing stocks (mg m^{-2}) of *Apseudes digitalis* at four sites in South Lake, St Lucia (∇—∇ = Gilly's Point, ■—■ = Makakatana, ●---● = Nkazana, □---□ = Game Guard Camp).

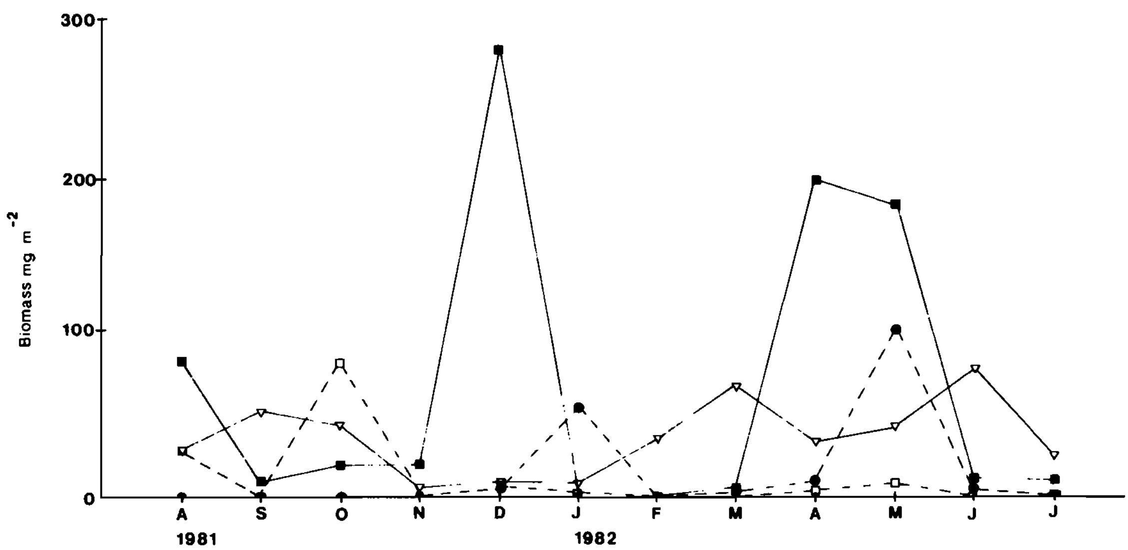

Figure 7 Standing stocks (mg m^{-2}) of *Grandidierella lignorum* at four sites in South Lake, St Lucia (∇—∇ = Gilly's Point, ■—■ = Makakatana, ●---● = Nkazana, □---□ = Game Guard Camp).

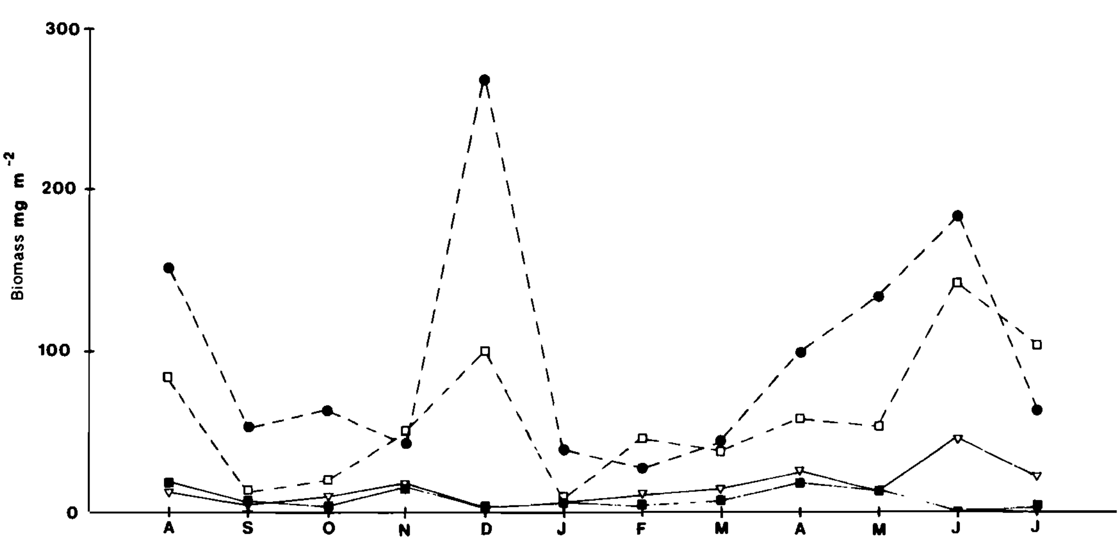

Figure 8 Standing stocks (mg m^{-2}) of Cumacea at four sites in South Lake, St Lucia (∇—∇ = Gilly's Point, ■—■ = Makakatana, ●---● = Nkazana, □---□ = Game Guard Camp).

mud at Gilly's Point was higher ($\bar{x}$ = 2,45) than other areas. The diversity indices of the eastern shores were similar ($\bar{x}$ = 1,34 and 1,46) but the lowest diversities were recorded from the mud of Makakatana ($\bar{x}$ = 1,11). It is important to note, however, that this index is not related only to the number of species present but to their equitability in terms of numbers of individuals. Heip's (1974) Index of Evenness,

$$E = \frac{e^H - 1}{N - 1},$$

shows that the equitability of distribution of species at the four sites (Figure 10) follows the pattern of species diversity (Figure 9). This strongly suggests that the evenness of allotment of individuals was largely responsible for differences in species diversity, rather than differences in numbers of species. In fact the two muddy sites, Makakatana and Gilly's Point, had the same overall species count (28) (Table 1) but the former had the lowest and the latter the highest diversity index. Thus Makakatana had a very uneven allotment of distribution of individuals among the species, whereas at Gilly's Point the total number of animals was more evenly divided between the species. The differences between the mud sites may be due to differences in substrata. Both were essentially muddy but Makakatana has numerous small rocks and some aquatic macrophytes while Gilly's Point is a uniform mud substratum.

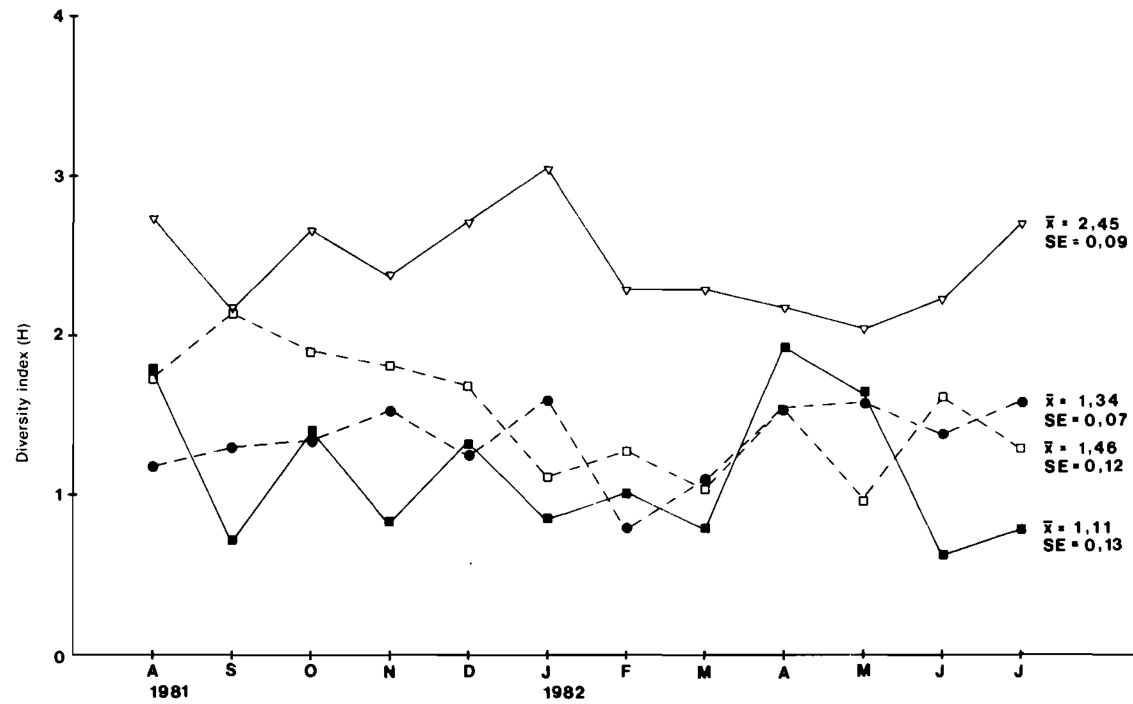

Figure 9 Shannon-Wiener diversity indices (H) for four sites in South Lake, St Lucia, 1981 – 82 (▽—▽ = Gilly's Point, ■—■ = Makakatana, ●---● = Nkazana, □---□ = Game Guard Camp).

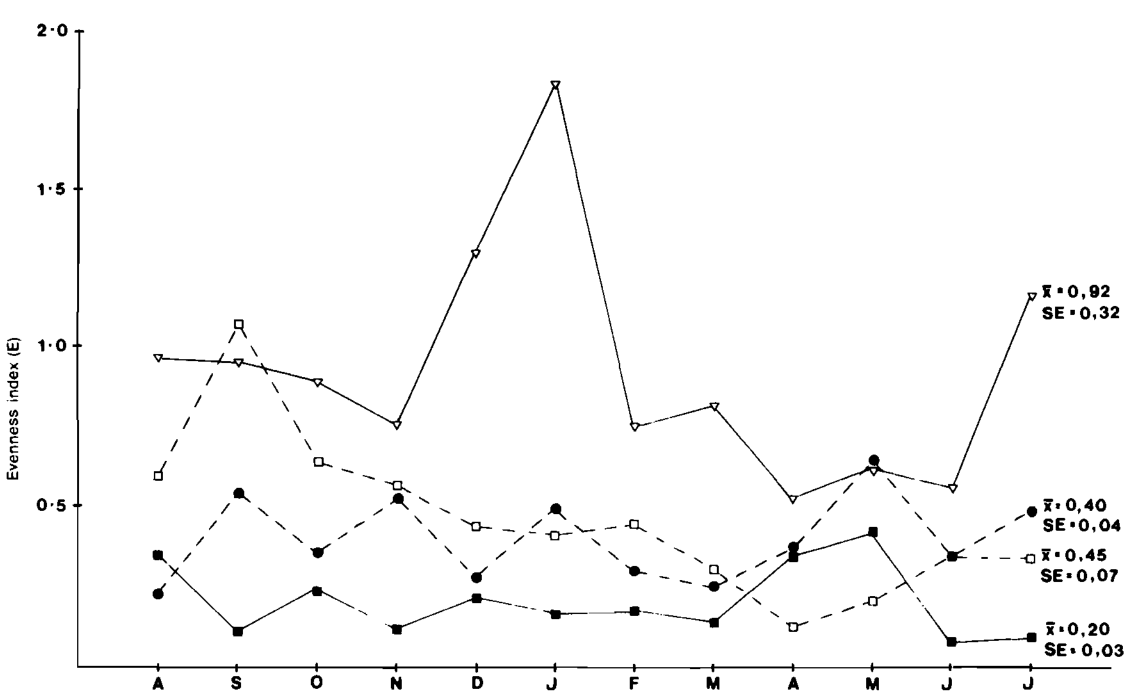

Figure 10 Heip's evenness indices (E) for four sites in South Lake, St Lucia, 1981 – 82 (▽—▽ = Gilly's Point, ■—■ = Makakatana, ●---● = Nkazana, □---□ = Game Gaurd Camp).

Discussion

The biomass of benthic invertebrates in South Lake during this survey was dominated by the bivalve *Solen cylindraceus* and the polychaete *Marphysa macintoshi*. Both species were present or common during the 1948 – 51 and 1964 – 65 surveys (Day *et al.* 1954; Millard & Broekhuysen 1970) but *Solen* was rare and *Marphysa* absent during 1972 and 1973 when salinities were high (Boltt 1975). Quantitative data are not available from the earlier surveys but the results from Boltt (1975) may be usefully compared with those from this study. The methods used were similar although Boltt (1975) used a Van Veen and not an Ekman grab.

During 1972 – 73, 23 taxa were recorded from South Lake whereas in 1981 – 82 the number was 37. This difference was probably due to the high salinities which preceded 1972 – 73 and the fauna may have been somewhat depauperate. The monthly and yearly mean standing stocks of benthos for 1981 – 82 are shown separately for mud and sand in Table 2. The results are in contrast with those of Boltt (1975) for 1972 – 73. In 1972 – 73 biomasses for sand varied between 1,08 and 3,26 g m^{-2} whereas in 1981 – 82 they were from 0,56 to 3,23 g m^{-2} with a mean of 1,07 g m^{-2}. On muddy substrata Boltt (1975) obtained values between 0,013 and 0,235 g m^{-2} while in this study they were markedly higher, from 1,07 to 8,55 g m^{-2} with a mean of 4,19 g m^{-2}. Boltt (1975) quotes a mean standing stock of 0,6 g m^{-2} for South Lake while this study produced a mean of 2,63 g m^{-2}.

The differences between 1972 – 73 and 1981 – 82 may largely be accounted for by changes in the faunal composition and particularly by changes to larger dominant species such as *Solen*. During 1972 – 73 sandy substrata were dominated by *Assiminea* sp. (> 1 000 animals m^{-2}) which were somewhat less common on mud (± 100 animals m^{-2}). In 1981 – 82 *Assiminea* was relatively uncommon (< 10 animals m^{-2}) and made a negligible contribution to total biomass although vast numbers of empty shells indicated its previous abundance. This almost total disappearance of *Assiminea* is curious and difficult to explain since salinity conditions were apparently favourable. It is paralleled, however, by the similar disappearance of another previously common gastropod, *Nassarius kraussianus*. Both are important in the food web. *Assiminea*, for example, is consumed by Mugilidae (Blaber 1976) and also by the crab *Scylla serrata* (Hill 1979) and probably benthic fish such as *Rhabdosargus sarba*.

Although a number of species are shown in Table 1 as abundant or common at both mud and sand sites, it is evident from Figures 3 to 8 that there are considerable differences between densities of the dominant taxa according to substratum. Cumacea (Figure 8) were more numerous on sandy substrata whereas *Apseudes* (Figure 6), Nemertea, *Solen* (Figure 3) and *Dendronereis* (Figure 5) densities were greater in mud. Boltt (1969) suggested that the amphipod *Grandidierella lignorum* will only build tubes in mud if sand is unavailable and that for this reason they are more common on sandy substrata in Lake Sibaya. From Figure 7 it is evident that in St Lucia this species is more common on mud than sand, perhaps being influenced by other factors such as greater availability of a detritus food source. In 1972 – 73 the tanaid *Apseudes* was found in greater densities in the muddy central basin of South Lake (Boltt 1975), an area which could not be sampled in the present survey. Nevertheless, present results also indicate higher densities in muddy areas (Figure 6).

It is worthwhile to compare the changes in abundance of certain species over a 10-year-period from 1972 and 1982 (Table 3). Although the sampling characteristics of the grabs were slightly different they could not account for the large differences between densities in 1972 and 1982 such as the decrease in *Assiminea* (from > 100 m^{-2} to < 10 m^{-2}) and increase in *Solen* (from < 10 m^{-2} to > 200 m^{-2}). Boltt (1975) states that the lake system in 1973 was recolonized by quickly maturing forms. The dominant bivalves in 1981 – 82 were relatively slow-growing forms such as *Solen* and *Dosinia* (Boltt 1975). It is likely that such forms gradually become dominant providing conditions remain suitable for sufficient time. Such was the case between 1973 and 1982. The virtual disappearance of the polychaete *Prionospio sexoculata* and of Nematoda is strange but may perhaps be due to interspecific interactions with larger forms such as Nemertea, *Marphysa* and *Glycera*. It is probable, therefore, that the situation in 1981 – 82 reflects the consequences of a stable period, populated initially by rapidly reproducing forms (Boltt 1975) but gradually becoming dominated by larger, slower growing species such as *Solen*. At the same time the species richness increased from 23 to 37 since very few species present in 1972 – 73 had entirely disappeared and more were added. According to diversity indices the species diversities at the four sampling sites were relatively consistent during 1981 – 82 despite the fluctuations in numbers of most species, a phenomenon which may have assisted in keeping the total standing stocks relatively stable.

Table 3 The changes in relative biomass of certain benthic invertebrates in South Lake, St Lucia between 1972 – 73 and 1981 – 82

Taxa which increased in biomasses	Taxa which decreased in biomasses	Taxa which maintained similar biomasses
Solen cylindraceus	*Assiminea* sp.	*Theora lata*
Eumarcia paupercula	*Prionospio sexoculata*	*Apseudes digitalis*
Dosinia hepatica	Nematoda	*Mesopodopsis africana*
Nemertea	Harpacticoida	
Marphysa macintoshi	*Nassarius kraussiana*	
Glycera convoluta		
Grandidierella lignorum		
Cumacea		

The reasons for the fluctuations shown by the species in Figures 3 to 8 cannot be adequately explained since little is known of their biology. One or two interesting points do however emerge: most species showed biomass peaks in summer and winter and, with the important exception of *Solen*, biomass lows in February 1982 when salinities peaked at 44,5°/oo. Whether the subsequent fall in salinity and increases in biomass are related is open to conjecture but it would seem unlikely that most populations either could or would respond as rapidly as within a month. Results from Mclachlan & Erasmus (1974) working in the eastern Cape showed that *Solen* and *Dosinia* are sensitive to salinity changes but unfortunately no data are available for salinities above 45°/oo. Both species can apparently tolerate salinities as high as about 45°/oo.

The relative importance of the various invertebrates in terms of the overall productivity of the benthos cannot be adequately described from this kind of survey since only standing stocks were measured and not production rates. In addition the biomass of larger, more mobile forms such as *Hymenosoma orbiculare* is certainly underestimated using only grab sampling (Forbes & Hill 1969). Nevertheless, until detailed knowledge of the biology of individual benthic invertebrates is available, the data presented in this paper provide the only indication of relative biomasses which can be utilized by higher trophic levels.

Acknowledgements

We are grateful to Dr R. Kilburn for identifying the molluscs and to the South African National Committee for Oceanographic Research, University of Natal and Natal Parks Board for financial support.

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