

The zoobenthic fauna of the Nhlabane coastal lake system, KwaZulu-Natal, South Africa, 20 years after construction of a barrage

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Abstract

The zoobenthos of the Nhlabane coastal lake system in northern KwaZulu-Natal was sampled quarterly during 1992 in order to study the zoobenthic fauna of the Nhlabane lake and estuary. The ecology of the system was changed in 1977 when a barrage was constructed across the upper end of the estuary. Physico-chemical parameters revealed that the previously estuarine southern basin of the lake had become completely fresh. The estuary remained closed during the study period due to a drought, the presence of the barrage and water abstraction from the lake. Benthic composition of the lake was typical of a shallow subtropical coastal lake, comprising a dominant estuarine associated crustacean component and a typical freshwater component characterised by oligochaetes, insect larvae and molluscs. Benthic densities varied with sediment type, with highest densities in detrital mud. The benthic composition of the estuary, dominated by estuarine amphipods and polychaetes, differed from that of the lake. There was a marked seasonal change in the benthic community in response to the low salinities in the estuary. Benthic species richness in the estuary was low relative to other estuaries, with a distinct dominance of a few numerically important taxa, indicating an unstable benthic community. Reduced freshwater discharge due to the barrage and the drought was the cause of the estuary mouth remaining closed throughout the study period.

Introduction

The Nhlabane coastal lake system is one of four freshwater coastal lakes in the vicinity of Richards Bay, KwaZulu-Natal. Studies to date on these lake systems focused mainly on water quality and utilisation of water resources (Hemens et al., 1981; Archibald et al., 1983; 1986; Turner, 1983; Fowles et al., 1986; Van Tonder et al., 1986; Walmsley and Grobler, 1986). Benthic data, except for a quantitative study on the benthos of Lake Cubhu (Cyrus and Martin, 1988), are at most limited to one-off biological surveys and unpublished reports (Fowles and Archibald, 1987; Reavell and Cyrus, 1989; Cyrus and Wepener, 1993; Wepener and Cyrus, 1994; Bolt, 1969a; Van der Elst and Chater, 1993). Historical data on the zoobenthic community of the Nhlabane system are totally lacking. Due to the paucity of biological data available and in view of the increasing industrial, mining and residential development in the catchments of these lakes, the need for obtaining basic ecological data was recognised.

The Nhlabane coastal lake system is situated north of Richards Bay in the dune mining lease area of Richards Bay Minerals (RBM). During 1977, a 3.8 m high concrete barrage was constructed across the outflow of the lake to increase the storage capacity for mining purposes (Fig. 1). In 1984, the barrage was raised a further 0.75 m to 4.55 m a.m.s.l. Prior to barrage construction, Lake Nhlabane consisted of two separate lakes, a northern freshwater and a southern estuarine lake, linked by a long, narrow channel. Estuarine conditions extending into the southern lake resulted in the presence of a salinity gradient and an associated estuarine fauna (Begg, 1978). After barrage construction, raising of the water level resulted in the merging of the two lakes into a single

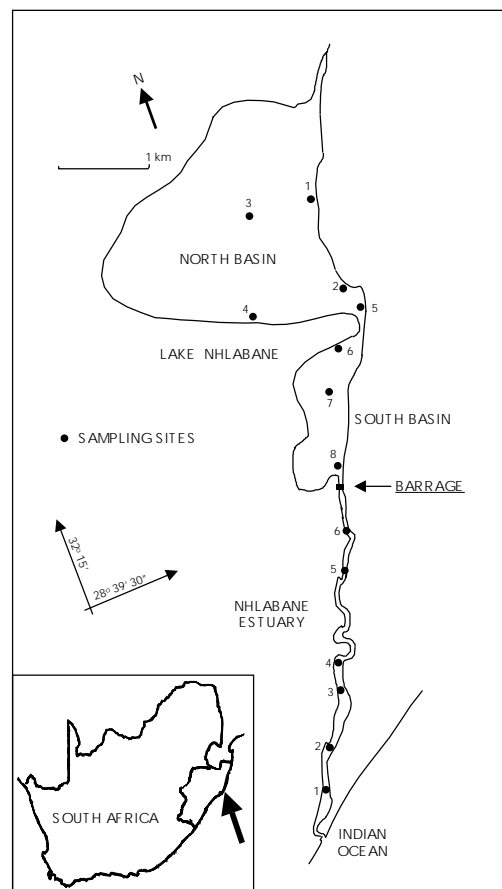


Figure 1

The Nhlabane Coastal lake system in northern KwaZulu-Natal. Sampling localities indicated with dots.

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bi-lobed freshwater lake with the two basins separated by a short channel (Fig. 1). The southern part of the lake then changed from estuarine to totally fresh. The barrage prevented the migration of estuarine associated fauna into the lake, and also caused many estuarine organisms to disappear from the lake (Begg, 1978). The question arose whether this transition from saline to freshwater caused the disappearance of all estuarine benthic fauna from the lake or whether a pattern similar to that observed in other freshwater coastal lakes would be found (Hill, 1968; 1975). The benthic fauna of lakes such as Lake Sibaya and Lake Cubhu are characterised by a dominant relict estuarine/marine associated crustacean component, and a freshwater component dominated by insect larvae, oligochaetes and molluscs (Boltt, 1969a; Cyrus and Martin, 1988; Cyrus and Wepener, 1993). This study was aimed at investigating the zoobenthic fauna of the Nhlabane coastal lake system during 1992, 15 years after completion of the barrage.

Study area

The Nhlabane coastal lake system (28°38'S, 32°16'E), is situated on the southern end of the Mozambique coastal plain (Fig. 1). The lake, with a surface area of 12.7 km² at full supply level, has a catchment of only 107 km². Runoff reaches the lake mainly through the Nhlabane River and two smaller streams draining into the northern basin. The mean annual precipitation in the catchment is 1 380 mm, most of which falls during summer. The marginal vegetation is dominated by the emergent macrophytes *Cladium mariscus*, *Cyperus papyrus* and *Phragmites australis*. Common submerged macrophytes include *Potamogeton pectinatus* and *P. schweinfurthii*.

The Nhlabane estuary, 3 km in length with a maximum width of 55 m in the lower reaches, assumes a meandering course through its floodplain (Fig. 1). It is dominated by extensive *Phragmites australis* beds and by submerged beds of *Potamogeton pectinatus* and *Ceratophyllum demersum*.

The Nhlabane estuary was closed throughout the study period as a result of reduced runoff from the catchment due to the drought, water abstraction for mining use from both the lake and the estuary and the presence of the barrage (Vivier et al., 1998). The estuary, which closed in early 1991, was artificially breached in August 1991, but only remained open for a few days. Salinities thereafter gradually decreased due to freshwater seepage both from a nearby mining pond and the lake. Infrequent overtopping of the sandbar at spring high tide during stormy weather was recorded, but due to the height of the sandbar across the estuary mouth, the inflow of sea water was restricted.

Materials and methods

Quarterly benthic samples were collected at the Nhlabane lake and estuary during 1992. Eight sites were sampled in the lake, five from the northern and three from the southern basin (Fig. 1). Six sites were sampled along the length of the estuary. A Zabalocki-type Eckman grab, which samples an area of 0.0236 m² to a minimum depth of 45 mm, was used to collect benthic samples. Five replicate grabs taken at each site were stirred and decanted five times through a 0.5 mm sieve in order to extract more than 95% of the animals from each sample (Cyrus and Martin, 1988). Samples were preserved in a 10% formalin solution, and stained with the vital dye Phloxine B to aid sorting in the laboratory. Samples were sorted in the laboratory and all animals were counted and identified to species level where possible.

Physico-chemical parameters of the water were measured at

each site. Oxygen and temperature measurements were taken using a WTW OXI Microprocessor. Turbidities were measured in Nephelometric Turbidity Units (NTU) using a Hellige Digital Direct Reading Turbidimeter. Salinities were measured using an American Optics temperature compensated refractometer, accurate to 0.5%.

Sediment samples were collected during summer 1992. The samples were preserved with 10% formalin to stop organic decomposition. Sediment grain size and median phi values were determined for each sample by measuring settling velocities (Lewis, 1984). The content of organic matter (%) of dried and weighed sediment samples was determined by incineration at 600°C for 6 h.

Multivariate data analysis was performed using the PRIMER statistical package (Clarke and Warwick, 1994). Hierarchical and agglomerative community classification methods were used on the benthic data. The log(x+1) transformed averaged benthic counts were used in determining the Bray Curtis coefficient, followed by hierarchical clustering, with group average linking, and ordination of the data through non-metric multidimensional scaling (MDS). In addition, the BIOENV function in PRIMER was used to relate the multivariate community structure to environmental variables to determine the variable causing the highest degree of variability in the benthic community. For this purpose the weighted Spearman Rank Correlation Coefficient (ρ_w) was calculated for permutations of abiotic variables. The coefficient lies in the range (-1,1) and values close to zero indicate the absence of a match between the community ordination and the abiotic variable.

Results

Lake Nhlabane is a clear water system with turbidities ranging between 2 and 20 NTU. Summer water temperatures, ranging between 28.3 and 29.9°C, reflected the subtropical nature of the lake. Water temperatures during winter ranged between 15.9°C and 16.4°C. The lake water was well oxygenated throughout the study period. The sediment of the lake was categorised as either muddy detrital or fine sand (Table 1). Muddy detrital areas were found in the deeper sections of the lake or adjacent to *Phragmites*

System	Site	Median phi value	% Organics	Status
Lake	1	4.3	24.7	Detrital mud
	2	2.1	1.1	Fine sand
	3	4.46	26.6	Detrital mud
	4	2.41	1.5	Fine sand
	5	4.5	48.8	Detrital mud
	6	2.41	1.1	Fine sand
	7	2.51	1.3	Fine sand
	8	2.7	29.2	Detrital mud
Estuary	1	1.73	1.1	Medium sand
	2	1.86	0.8	Fine sand
	3	1.13	0.9	Fine sand
	4	1.25	0.8	Fine sand
	5	1.1	0.5	Fine sand
	6	2.07	1.3	Fine sand

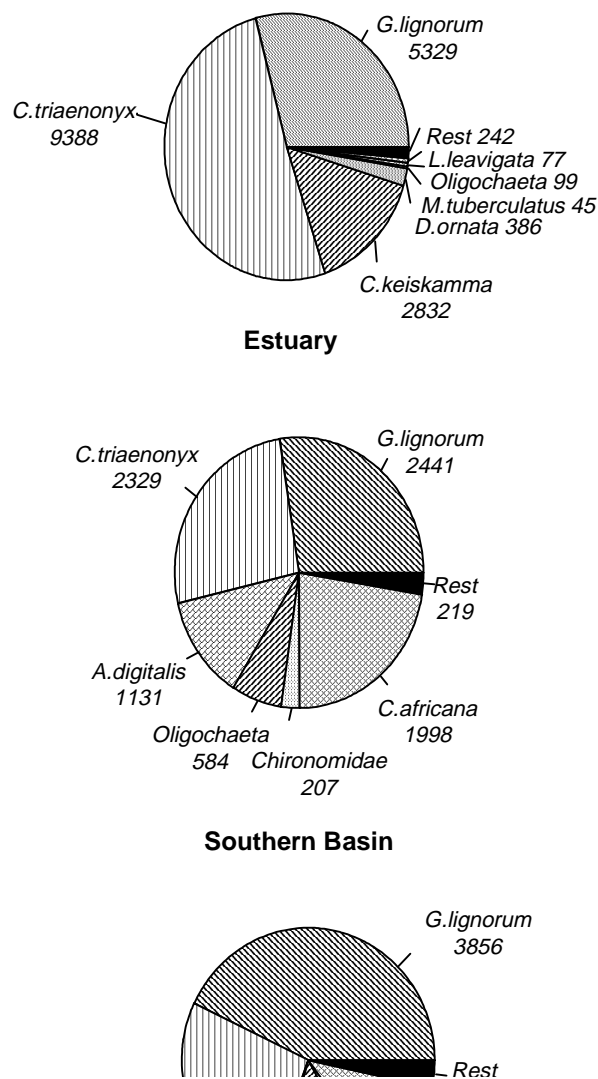


Figure 2

Pie graphs of the benthic composition of the northern and southern basin, Lake Nhlabane, and the Nhlabane estuary during 1992. Values given are mean densities (N.m⁻²) for all sampling sites and seasons.

and *Cyperus* beds along the shoreline, while fine sand was restricted to shallow open areas along the shoreline. Sites containing mud characteristically showed a high organic content (Sites 1, 3, 5 and 8), while areas with fine sand had a low organic content (Table 1). The water level of Lake Nhlabane decreased steadily during 1992 due to the drought and water abstraction, from 1m below overflow during January 1992 (summer) to 1.7 m below overflow in September 1992 (spring). A maximum depth of 3.7 m and 3.5 m were recorded in the northern basin and southern basin, respectively.

Consistently low salinities were recorded in the estuary. A maximum salinity of 4‰ was recorded in the upper reaches. A

reverse salinity gradient was present with slightly lower salinities at the mouth than in the upper reaches. This is believed to be partly due to freshwater seepage at the mouth from a dune mining pond in that area. Water temperature varied from 28 to 29°C in summer, to a minimum of 17°C in winter. Autumn and spring temperatures varied between 24 and 26°C. Highest oxygen concentrations (mg/l) were recorded during winter and spring, ranging from 6.8 to 9.2 mg/l. Summer and autumn oxygen levels were much lower, dropping as low as 4.1 mg/l at Sites 3, 4 and 6 during autumn. Turbidity levels were low except at Sites 1 and 2 during summer when turbidities of 48 and 30, respectively, were recorded. During the remainder of the study, turbidities never exceeded 10 NTU. The sediment of the estuary was fairly uniform at all sites and consisted of predominantly fine to medium grained sand (Table 1). The organic content of the sediment ranged from low to moderately low. The finest grain sediment and the highest organic content was predictably recorded in the upper reaches of the estuary.

The Nhlabane lake benthos, comprising 22 taxa, was characterised by a dominant relict estuarine component comprising the amphipods *Grandidierella lignorum* and *Corophium triaenonyx*, and the tanaid *Apseudes digitalis*, and by a freshwater component dominated by Oligochaeta, the mollusc *Corbicula africana* and Chironomid larvae (Table 2, Fig. 2). The relict estuarine component represented 71% of the total number of benthic organisms collected. *Grandidierella lignorum* was dominant throughout the lake, while *C. triaenonyx* showed high densities only in the detrital mud of the northern basin. *Apseudes digitalis* was abundant in the southern basin, while *C. africana* and oligochaeta were more abundant in the northern basin (Table 2). Of the 22 taxa, 19 were recorded in the northern basin and 18 in the southern basin. The two basins of the lake showed very similar benthic communities with all the numerically important taxa present in both areas (Table 2, Fig. 2). None of the taxa absent from one basin and present in the other contributed more than 0.1% to the total benthic density.

Hierarchical clustering and MDS ordination of the lake benthos (Fig. 3) showed little change in the community between different seasons. There was a gradient in the community across the sites of the northern basin, from Sites 3 and 4 at the one end through Site 2 to Sites 1 and 5 at the other end (Fig. 3). The community of Sites 6 and 7 from the southern basin grouped together slightly separate from the northern basin communities. Sites 1 and 5 of the northern basin showed much higher benthic densities, higher number of taxa and particularly more insect larvae taxa than Sites 3 and 4 (Table 2). *Corophium triaenonyx* and *C. africana* densities particular were much higher at Sites 1 and 5 than at the other sites of the northern basin. Highest overall densities were recorded in detritus rich sediment with both *G. lignorum* and *C. triaenonyx* being more abundant in such sediment than in sand. Mean densities of *G. lignorum* and *C. triaenonyx* were 15.9% and eleven times higher in mud than in sandy sediment, respectively. A similar trend was seen in the numbers of *C. africana*, oligochaetes and chironomid larvae.

Organic content of the sediment ($\rho_w=0.204$) and sediment grain size ($\rho_w=0.139$) were the environmental variables measured which best correlated with the distribution of the benthic community. The best overall correlation was produced by a combination of these two variables ($\rho_w=0.213$), thereby showing that these two variables were responsible for most of the variability observed in the benthic community. The correlation between the individual environmental variables and the distribution of the benthic community of the lake are plotted in Fig. 4. Temperature, turbidity, depth and oxygen had little effect on the distribution of the benthic community.

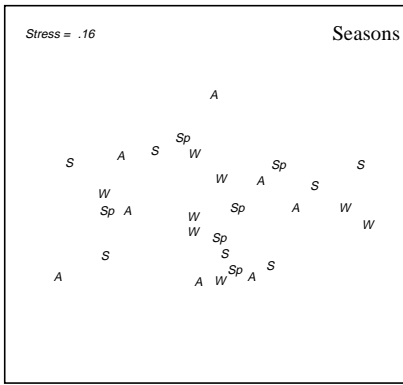
TABLE 2
BENTHIC TAXA RECORDED AT THE EIGHT SAMPLING STATIONS IN LAKE NHLABANE DURING 1992. MEAN SEASONAL DENSITIES (No·m⁻²) PER SITE, MEAN DENSITIES FOR ALL EIGHT STATIONS AND THE OVERALL PERCENTAGE CONTRIBUTION FOR EACH TAXUM ARE INDICATED. VALUES FOR THE FIVE DOMINANT TAXA ARE HIGHLIGHTED

Taxa	Sampling stations									
	Northern basin					Southern basin			Mean	% Contribution
	1	2	3	4	5	6	7	8		
Platyhelminthes										
Tricladida sp	6				2			3	1	0.1
Nematoda										
Nematoda sp	34	2		11		15	9	30	13	0.2
Annelida										
Oligochaeta spp	970	2724	315	707	938	625	860	269	926	12.3
Hirudiniidae										
Hirudiniidae sp	15	6			12	2		2	5	0.1
Ostracoda										
Ostracoda sp	2				2			10	2	0.1
Mollusca										
<i>Melanoides tuberculatus</i>			2	21		4	13		5	0.1
<i>Corbicula africana</i>	1740	659	509	184	2205	198	243	157	737	9.8
Crustacea										
<i>Pseudodiaptomus hessei</i>	42	3	4	6	40	59	6	62	28	0.4
<i>Corophium triaenonyx</i>	9442	578	42	68	1719	53	366	279	1568	20.8
<i>Grandidierella lignorum</i>	6481	2322	2009	2788	5680	3137	3557	630	3325	44.2
<i>Boltsia minuta</i>						6	2	2	1	0.1
Cumacea sp	6								1	0.1
<i>Munna sheltoni</i>	29	2			11			16	7	0.1
<i>Mesopodopsis africanus</i>							6	2	1	0.1
<i>Apeudes digitalis</i>	182	11	25	21	203	1701	1150	549	480	6.4
<i>Caridina nilotica</i>	19	2			9				4	0.1
Brachyura sp	3						2		1	0.1
Insecta										
Tricoptera	286	84			100	2		97	71	0.9
Ceraptogonidae	180	4	9	9	83	28	57	58	54	0.7
Chironomidae	367	186	74	51	278	85	98	114	198	2.6
Ephemeroptera	288	17			415			55	97	1.3
Anisoptera						2			1	0.1
Total density	20092	6600	2989	3866	11697	5917	6369	2662	7524	
Number of taxa	18	14	9	10	15	14	13	17	22	

The benthos of the Nhlabane estuary, comprising 24 taxa, was characterised by an abundance of estuarine crustaceans, notably the two amphipods *G. lignorum* and *C. triaenonyx*, and the polychaetes *Ceratonereis keiskamma* and *Desdemona ornata* (Table 3, Fig. 2). These four species accounted for 96% of the benthos recorded. *Corophium triaenonyx* was the dominant species, representing more than 50% of the benthic organisms recorded. Benthic densities remained high throughout the study period, with highest total densities recorded during summer (21 375 m⁻²) and winter (20 381 m⁻²). Lowest densities were recorded during autumn (14 538 m⁻²). *Corophium triaenonyx* numbers were high during summer and autumn, but low during winter and spring, whereas *G. lignorum* numbers were high during winter and spring, but low during summer and autumn. *Ceratonereis keiskamma*

numbers remained stable, while *D. ornata* numbers were highest during autumn. Benthic densities were high at all sites along the estuary, with highest densities recorded in the upper reaches at Site 6 (21 834 m⁻²).

Multivariate analysis of the benthic community of the estuary showed a gradual but pronounced seasonal shift in the benthic community from summer through to spring at all sites (Fig. 5). Two major community groups were identified: the summer/autumn and winter/spring communities. During summer and autumn, there was a gradient in the community along the length of the estuary, with Sites 1 and 2, Sites 3 and 4 and Sites 5 and 6 clustering together. During these two seasons, the gradient in the community from lower to upper reaches was more pronounced than the difference between the seasons. The gradient started to break down during



S = SUMMER
 A = AUTUMN
 W = WINTER
 Sp = SPRING
 N = NORTH BASIN
 S = SOUTH BASIN

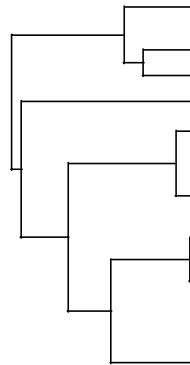


Figure 3 (left)
 Hierarchical clustering and multidimensional scaling plots of the Nhlabane lake benthic community during 1992. The MDS plots are overlaid by codes for seasons, sampling sites and basins, respectively.

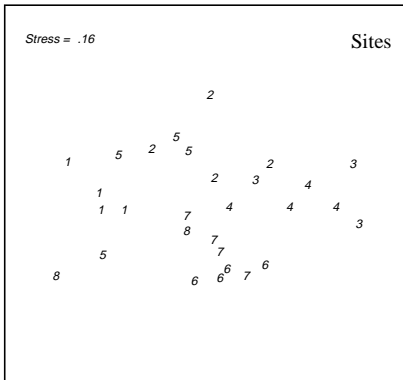
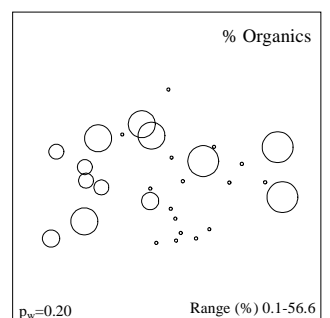
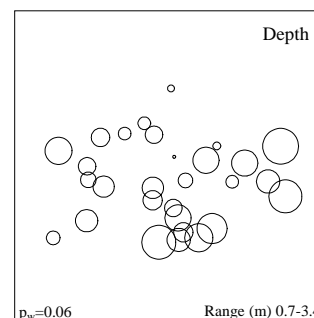
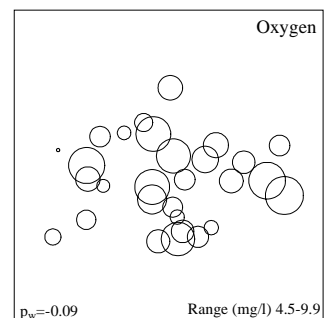
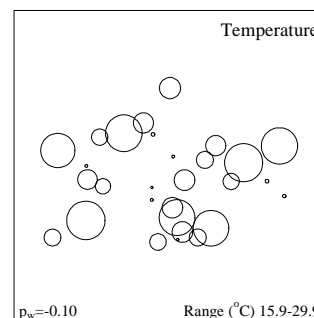
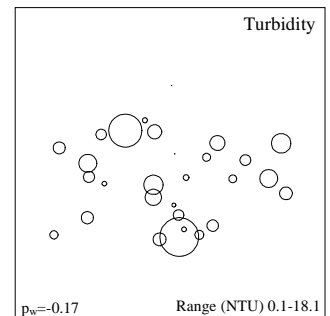
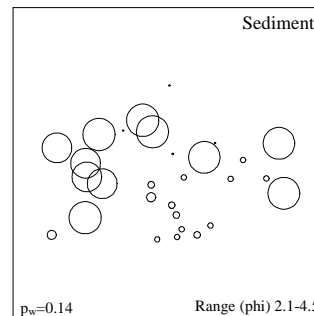
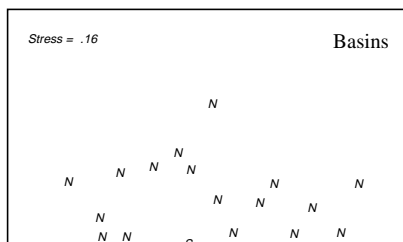


Figure 4 (bottom)
 Multidimensional scaling plots of the Nhlabane lake benthic community overlaid by selected abiotic variables measured during 1992. The correlation coefficient between each variable and the benthic community as well as the range are indicated on each plot.



winter and had disappeared by spring. The dendrogram showed that during spring, no evidence of a gradient could be observed, with Sites 1 and 3, Sites 2 and 6 and Sites 4 and 5 clustering together. The benthic communities of the different sites during winter and particularly spring were also spaced closer together on the MDS ordination plot than during summer and autumn, indicating a higher degree of similarity among sites during these seasons.

Oxygen concentration of the water ($\rho_w = 0.218$) was the abiotic factor measured which best correlated with changes in the benthic community, followed by water temperature ($\rho_w = 0.150$) (Fig. 6). A combination of oxygen concentration, temperature and water depth produced the best overall correlation ($\rho_w = 0.380$). Sediment grain size and organic content had a negligible effect on the shift in the benthic community. Although changes in salinity during 1992 were too small to produce any significant correlation with biotic changes, the generally low salinities in the system during this period probably still remained an important factor responsible for some of the changes in the estuarine community.

A comparison of Nhlabane lake and estuary benthic

TABLE 3
BENTHIC TAXA RECORDED AT THE SIX SAMPLING STATIONS IN THE NHLABANE ESTUARY DURING 1992. MEAN SEASONAL DENSITIES (No·m⁻²) PER SITE, MEAN DENSITIES FOR ALL SIX STATIONS AND THE OVERALL PERCENTAGE CONTRIBUTION FOR EACH TAXUM ARE INDICATED. VALUES FOR THE FOUR DOMINANT TAXA ARE HIGHLIGHTED.

Taxa	Sampling stations						Mean	% Contribution
	1	2	3	4	5	6		
Annelida								
Oligochaeta spp	40	81	235	95	68	76	99.2	0.5
<i>Ceratonereis keiskamma</i>	3775	4055	2103	2703	2627	1724	2831.2	15.3
<i>Desdemonia ornata</i>	1243	525	42	25	431	349	435.8	2.3
<i>Dendronereis arborifera</i>	2	4	114	42	34	38	39.0	0.2
Prionospio sp	4		6	8	9	4	5.2	0.1
Hirudiniidae								
Hirudiniidae	64	42	31	53	81	64	55.8	0.3
Ostracoda								
Ostracoda sp	13	4	68	13	38	13	24.8	0.1
Mollusca								
<i>Melanoides tuberculatus</i>	23	6	6	4	93	157	48.2	0.3
<i>Assiminea bifasciata</i>	6		6	11	30	28	13.5	0.1
<i>Pittaria kochii</i>	21	38	9	19	25	49	26.8	0.1
<i>Musculus virgiliae</i>	2	17	6	6		2	5.5	0.1
Bivalvia sp	6		6	11	30	28	13.5	0.1
Crustacea								
<i>Pseudodiaptomus hessei</i>	170	19	40	32	9	19	48.2	0.3
<i>Acartia natalensis</i>	2				10	2	2.3	0.1
<i>Corophium triaenonyx</i>	9099	9074	10290	9631	7904	10328	9387.7	50.6
<i>Grandidierella lignorum</i>	3862	4352	6004	4008	4843	8908	5329.5	28.7
<i>Melita zeylanica</i>			2	2			0.7	0.1
<i>Bolittsia minuta</i>	8			19		8	5.8	0.1
<i>Cyathura aestuaria</i>		31	174	14			36.5	0.2
<i>Lepthanthura laevigata</i>	206	163	70	19		6	77.3	0.4
<i>Munna sheltoni</i>	64	19	40	32	9	19	30.5	0.2
<i>Mesopodopsis africanus</i>	8	48	6	10	2		12.3	0.1
<i>Apseudes digitalis</i>	32		4	9	21	2	11.3	0.1
<i>Hymenosoma orbiculare</i>	68	42	2	17	23	6	24.3	0.1
Total density	18718	18520	19264	16783	16287	21830	18567	
	22	17	22	23	18	21	24	

communities showed that only 37% of the taxa present in the lake were also found in the estuary, while only 19% of the estuarine taxa also occurred in the lake. The mean density per site (No·m⁻²) in the estuary was more than double that recorded in the northern basin of the lake, and more than three times that recorded in the southern basin. Although the salinity in the Nhlabane estuary became very low during the study period, typical freshwater benthic taxa such as Chironomidae, Oligochaetes and other insect larvae remained absent from the estuary. Hierarchical clustering and MDS ordination of the lake and estuary benthic communities showed a complete separation of the lake and estuary benthos, being separated on the the Bray Curtis similarity axis at a similarity of 37% (Fig. 7).

Discussion

The benthic composition of Lake Nhlabane was representative of the typical relict estuarine coastal lakes found along the Zululand coast (Allanson et al., 1966; Bolt, 1969a) and along the Mozambique coastal plain, i.e. Lake Cubhu (Cyrus and Martin, 1988), Lake Sibaya (Bolt, 1969a, 1969b), Lake Nhlange (Bolt and Allanson, 1975), Lake Poelela (Bolt, 1975) and Lake Mzingazi (Cyrus and Wepener, 1993). All of these lakes contained a numerically important relict estuarine benthic component. It has been argued that the presence of estuarine fauna in such freshwater lakes is related to their geomorphological origin (Hill, 1968; Bolt, 1969a; Cyrus and Martin, 1988; Reavell and Cyrus, 1989). Sea level rise during the recent Flandrian transgression resulted in the formation of a number of estuarine linked coastal lakes along the Southern African coast. Some, such as Lake Sibaya, have become

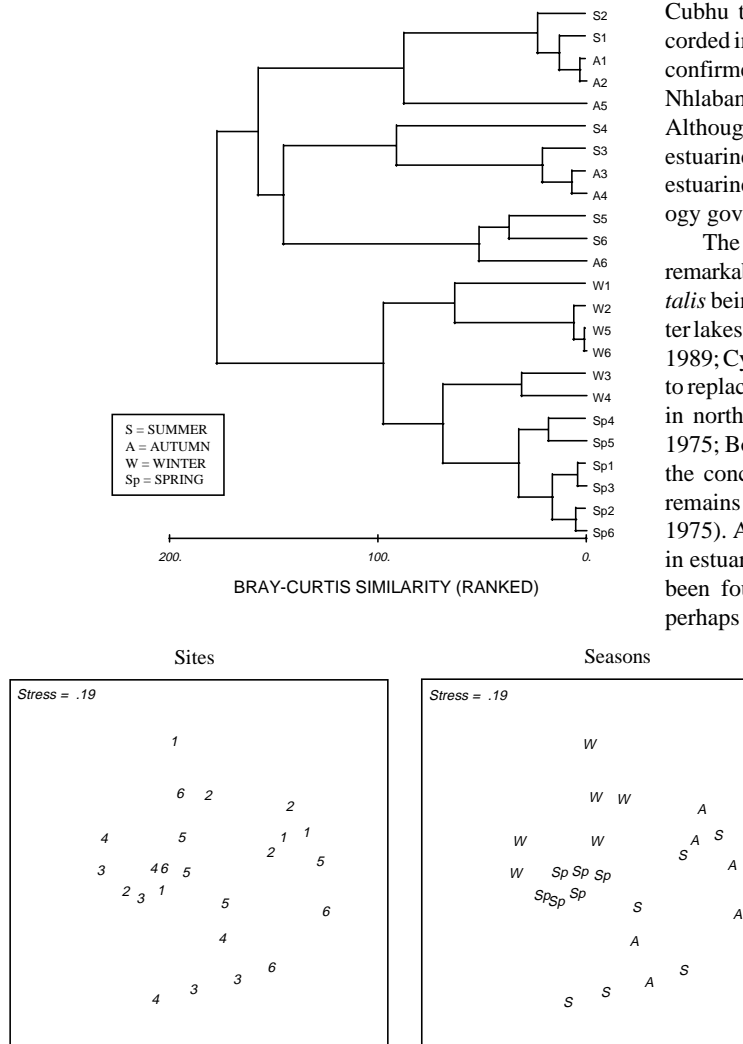


Figure 5
Hierarchical clustering and multidimensional scaling plots of the Nhlabane estuary benthic community during 1992. The MDS plots are overlaid by codes for seasons and sampling sites, respectively.

landlocked long ago. Others, such as Lakes Nhlabane, Mzingazi and Cubhu, have retained contact with the sea until recently and have become isolated from the sea through human intervention only during recent years. The benthic fauna of such coastal lakes include a component derived from the essentially marine environment of estuaries and another derived from the freshwater environment (Bolt, 1969b). The benthic composition of coastal lakes thus range from almost totally estuarine as seen in Lake St Lucia (Bolt 1969a; Blaber et al., 1984) to the condition observed in Lake Sibaya, where estuarine fauna only comprises about half of the benthic species (Bolt, 1969a). Lake Nhlabane has been isolated from the sea for seventeen years and although a typical freshwater benthic component has developed in the entire lake, the benthos was still dominated by relict estuarine fauna.

The ability of estuarine species to survive in impounded freshwater systems has been addressed before, but still remains unexplained (Bolt, 1969a; 1969b; 1975; Bolt and Allanson, 1975; Cyrus and Martin, 1988; Reavell and Cyrus, 1989). In Lake Sibaya, this phenomenon has been attributed to the high sodium concentrations in the water (Allanson and Van Wyk, 1969). Cyrus and Martin (1988), however, pointed out that marine crustaceans in Lake

Cubhu thrive under sodium concentrations similar to those recorded in natural freshwater systems (25 to 40 mg/l). This has been confirmed by similarly low sodium concentrations found in Lakes Nhlabane (Turner, 1983) and Mzingazi (Hemens et al., 1974). Although Bolt (1969a) showed that *G. lignorum* acclimated to estuarine conditions can only survive if the transformation from estuarine to freshwater conditions occurs very slowly, the physiology governing the process still needs further investigation.

The estuarine fauna which predominate in the coastal lakes are remarkably uniform, with *G. lignorum*, *C. triaenonyx* and *A. digitalis* being the major contributors in most of the Zululand freshwater lakes (Bolt, 1969a; Cyrus and Martin, 1988; Reavell and Cyrus, 1989; Cyrus and Wepener, 1993). *Grandidierella bonnieri* appears to replace *G. lignorum* in two brackish coastal lakes, Lake Nhlange in northern Zululand and Lake Poelela in Mozambique (Bolt, 1975; Bolt and Allanson, 1975). The presence of *G. bonnieri* and the concomitant absence of *G. lignorum* from these lakes still remains unexplained (Bolt, 1969a and 1975; Bolt and Allanson, 1975). As shown by the present study, *G. lignorum* abounds both in estuarine and freshwater conditions, but *G. bonnieri* has never been found in totally freshwater conditions in Zululand. It is perhaps noteworthy that *G. bonnieri* was found in the Umlalazi

Estuary south of Richards Bay (Hill, 1968), while it was conspicuously absent from the more frequently closed adjacent Siyaya Estuary, where *G. lignorum* dominated the benthos (Cyrus, 1993). Differences in sodium tolerance levels have often been suggested to determine the distribution of Gammarid species (Sutcliffe, 1968) and as such could perhaps explain the inability of *G. bonnieri* to become more widely distributed in Zululand coastal systems (Bolt, 1975; Bolt and Allanson, 1975).

Sediment type and sediment organic content are known to have a pronounced effect on the spatial distribution of benthic organisms (Wu and Richards, 1981; Cyrus and Martin, 1988). Benthic data from Zululand coastal lakes indicate that more benthic animals occur in sandy sediment than in mud (Bolt, 1969a; Bolt and Allanson, 1975; Cyrus and Martin, 1988). In Lake Nhlabane, higher benthic densities were recorded in mud

than in fine sand due to the high organic content of the mud. *Apeudes digitalis* occurred in far greater abundance in mud than in sand. *Corophium triaenonyx* occurred in numbers an order of magnitude higher in detrital mud than in sandy substrata, while *G. lignorum* densities were consistently higher in detrital mud. A completely different picture was recorded in Lake Cubhu, where both *G. lignorum* and *C. triaenonyx* occurred in numbers an order of magnitude higher in sand than in mud (Cyrus and Martin, 1988). *Grandidierella lignorum* is a benthic burrower which constructs tubes from sand grains and is expected to be more abundant in sandy areas (Cyrus and Martin, 1988). *Corophium triaenonyx* is not considered a true burrower but constructs tubes of fine sand or silt particles on the surface of solid objects on the substratum. The high *C. triaenonyx* numbers recorded in sand in Lake Cubhu substrata suggest that this species is, however, not limited to substrata containing predominantly silt or detritus, but also utilises sand containing little detritus. Cyrus and Martin (1988) suggested that *G. lignorum* is less adaptable to different sediment types, being more reliant on sandy substrata, while *C. triaenonyx* is able to exploit a greater variety of habitats. The data from Lake Nhlabane seem to dispute this and further investigation is needed to enable a

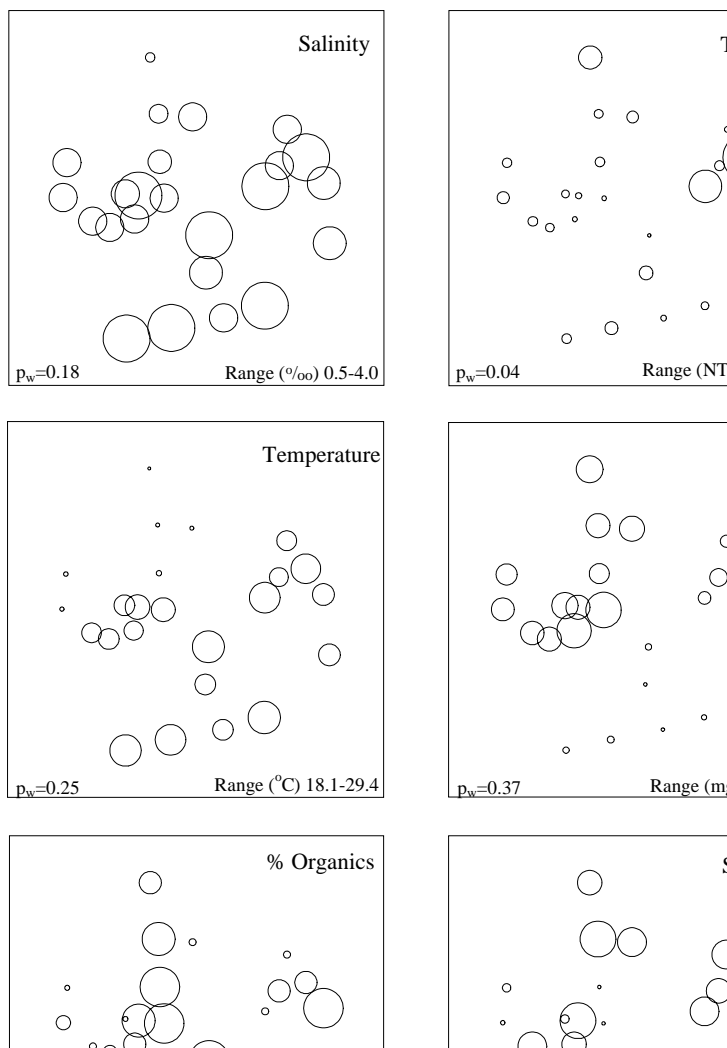


Figure 6
Multidimensional scaling plots of the Nhlabane estuary benthic community overlaid by selected abiotic variables measured during 1992. The correlation coefficient between each variable and the benthic community as well as the range are indicated on each plot.

better understanding of this seemingly controversial matter. Since this discrepancy in crustacean substrata preference can only partially be explained by the nature of their tube building activity, it must be assumed that other factors such as availability of organic detritus in the sediment are also important, as shown in the present study. It has also been suggested that food availability or water chemistry at the water/substratum interface might be responsible for such different patterns in these lakes. Anoxic conditions, caused by metabolic processes of substrata rich in organic matter, also affects the distribution of benthic organisms (Boltz and Allanson, 1975). Boltz (1969a) has also shown that *G. lignorum* is very sensitive to changing carbon dioxide levels in the water.

The benthic fauna of the Nhlabane estuary compared well with that of a number of other estuarine systems, such as the Siyaya,

Wilderness and the Bot River estuaries (Davies, 1984; De Dekker and Bally, 1985; Cyrus, 1993; Cyrus and Mackay, 1995). The Siyaya estuary has a benthic composition very similar to that of the Nhlabane estuary, also being dominated by *G. lignorum*, *C. triaenonyx*, and the polychaete *C. keiskamma*. Polychaetes and amphipods are generally regarded as dominant organisms in most estuaries and lagoons (Stoner and Acevedo, 1990).

The benthos of the estuary can be regarded as typical estuarine (Stoner and Acevedo, 1990), with no freshwater component recorded during the study period. In this respect the Nhlabane estuary differs from most other systems, in which some freshwater organisms, particularly chironomidae, are normally recorded under low salinity regimes (Blaber et al., 1984; Davies, 1984; De Decker and Bally, 1985).

The spatial distribution and abundance of estuarine and marine benthos are often related to salinity, organic content and silt-clay fractions of the sediment (Nichols, 1970; Wu and Richards, 1981). These factors were of limited importance in determining the spatial distribution of the benthos in the Nhlabane estuary, because there was little variation between sites in the organic content and sediment grain size and also because salinities were low at all sites during the study. Oxygen content and water temperature were the most important abiotic variables determining benthic distribution.

The highest salinity recorded throughout the estuary was 4‰. Estuarine systems with little freshwater inflow which remain closed for extended periods generally tend to become hypersaline in the middle and upper reaches (Whitfield and Bruton, 1989). This has not been the case in the Nhlabane estuary. The generally low salinities observed in the estuary, with highest salinities in the upper reaches, are suggested to be caused by continuous freshwater seepage from the lake and mining ponds adjacent to the estuary. Although infrequent overtopping of the sandbar separating the estuary from the sea had been recorded during spring tides, sea water input was insufficient to increase the salinity of the system.

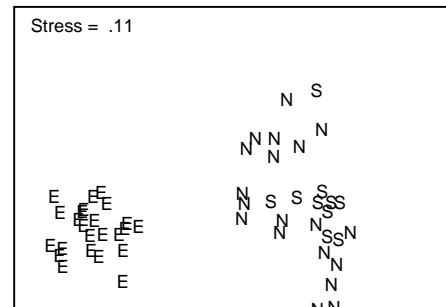
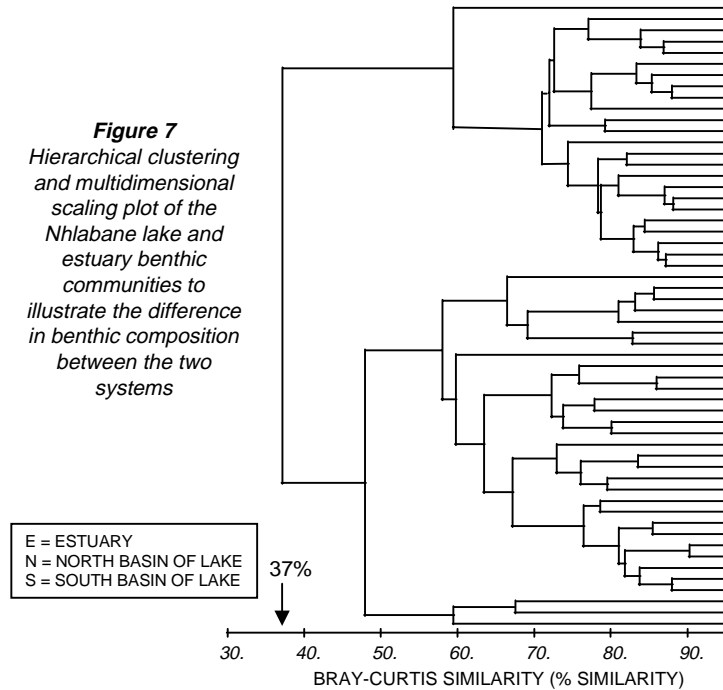
The Nhlabane estuary is considered a temporary open/closed estuary (Whitfield, 1992), which under normal climatic conditions, as with the Bot River and Siyaya estuaries, only occasionally opens to the sea. The study period coincided with a general drought in southern Africa which resulted in reduced freshwater input and the consequent closing of the estuary mouth during 1991. Freshwater discharge into the estuary was further affected by the barrage across the upper reaches of the estuary and by water abstraction from the lake. Whitfield and Bruton (1989) have shown that biotic diversity in small temporary open/closed estuaries decline during prolonged closed phases, while permanently open tidal estuaries in which normal salinity regimes are

maintained, such as the Knysna estuary with 319 species, normally have very high benthic diversities (De Decker and Bally, 1985). Wade (1972) and Warwick (1993) also showed that estuarine communities in unstable salinity environments have lower diversities and are characterised by the presence of a small number of dominant species. The benthic fauna of the Bot River estuary became impoverished during periods of mouth closure as a result of lack of contact with the marine environment (De Decker and Bally, 1985). The low species richness of the Nhlabane estuary during the present study (24 taxa) and the dominance of a few numerically important species are therefore indications of a stressed benthic community in response to the low salinity conditions throughout the estuary (Whitfield and Bruton, 1989). This is attributed to the closed estuary mouth.

The effects of impoundments in rivers on the downstream estuarine environment are well documented (Read, 1983; Reddering, 1988; Whitfield and Bruton, 1989; Reddering and Rust, 1990; Grange and Allanson, 1995; Ardisson and Bourget, 1997). Channel dimensions of estuaries are generally determined by the erosion capacity of river floods that discharge from the catchment basin. If a dam artificially reduces the discharge of a river or the time interval between river floods were lengthened, the estuary adjusts to the new environmental conditions by shrinking its channel dimensions (Reddering, 1988). The dynamic behaviour of an estuary is influenced significantly by the dimension and state of its tidal inlet, because the state of the inlet controls the exchange of water, food and organisms between the estuary and the marine environment. Reddering (1988) showed that reduced discharge from rivers result in estuary mouths closing more easily and for longer periods of time. It also reduces the efficiency of river floods to effectively scour estuarine channels to its normal dimensions. As an overall result, smaller estuary channels are established and estuaries close more frequently. In addition, reduced river discharge also adversely affects primary production in estuaries and consequently food resources for suspension-feeding communities (Grange and Allanson, 1995). In view of this, the barrage constructed across the tidal head of the Nhlabane estuary is expected to reduce river discharge into the estuary under normal climatic conditions and the frequency of river floods capable of scouring the tidal inlet. During the study, the drought and water abstraction from the lake further aggravated conditions and resulted in low lake levels. The estuary mouth closed during 1991 when the drought started and only opened when artificially breached in August 1995 (Vivier et al., 1998). Water abstraction from the estuary further reduced the chances of the mouth opening under these conditions. As stressed by Whitfield and Bruton (1989), the continued proper functioning of estuaries relies on the maintenance of the natural dynamism and the oscillating phases imposed on such systems by riverine and marine influences. The over-exploitation of water resources in river catchments has been shown to have far reaching consequences effecting the ability of estuarine systems to carry out their normal processes and functions.

Prior to barrage construction, tidal exchange extended into the southern basin of the lake. Begg (1978) found the southern basin to be brackish with a clear presence of estuarine fauna. Although no pre-barrage benthic community data are available, water quality data (Begg, 1978; Turner, 1983; Walmsley, 1993) and the limited biotic data available (Pike, 1965; Begg, 1978; Walmsley, 1993) indicate that estuarine conditions prevailed in the southern basin,

Figure 7
Hierarchical clustering and multidimensional scaling plot of the Nhlabane lake and estuary benthic communities to illustrate the difference in benthic composition between the two systems



suggesting that an estuarine dominated biota inhabited the area. Conductivities as high as 1 630 mS/m, sodium concentrations of 380 mg/l and chloride concentrations of 682 mg/l were recorded over the period 1976-1977 (Begg, 1978). During 1977, prior to barrage construction, eight species of estuarine fish were recorded in the southern basin (Walmsley, 1993). After barrage construction, the lake became fresh and most of the estuarine fauna disappeared (Wepener et al., 1995). The comparison between the benthic community of the estuary and the lake during this study reflects the changes that must have occurred in the southern basin after construction of the barrage. This involved the introduction of typical freshwater benthic species yet at the same time retaining the numerically important relict estuarine benthic component.

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