Macrophyte - Mollusc Relationship in Lake Kariba

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SUMMARY

Five species of submerged vegetation Lagarosiphon ilicifolius, Najas pectinata, Vallisneria aethiopica, Ceratophyllum demersum and Potamogeton octandrus; seven species of gastropods Melanoides tuberculata, Bellamya capillata, Biomphalaria pfeifferi, Bulinus tropicus, Cleopatra sp, and Lymnaea natalensis and four species of bivalves Corbicula africana, Caelatura mossambicensis, Mutela dubia and Aspatharia wahlbergii are correlated with environmental variables particularly slope and transparency, in Lake Kariba. Correlations were revealed through a multivariate direct gradient analysis technique - Detrended Canonical Correspondence Analysis.

2- A stepwise regression analysis further revealed interdependence between Cleopatra sp , B. pfeifferi, L. natalensis, B. capillata, and V. aethiopica as well as between C. mossambicensis and L. ilicifolius and N. pectinata..

3- The dependence of B. pfeifferi, L. natalensis, B. capillata, Cleopatra sp. on V. aethiopica and C. mossambicensis on L. ilicifolius and N. pectinata implies that a change in the biomass of the vegetation species may affect distribution and biomass of the faunal species.

INTRODUCTION

Macrophyte communities play a crucial role for animals and lower plants in aquatic ecosystems by providing habitat complexity, shelter, breeding area as well as being substrate for periphyton and sites of abundant food production for many aquatic animals

(Wetzel & Hough, 1973; Pelikan et al. 1978; Howard-Williams & Liptrot, 1980; Howard-Williams, 1981; Carpenter & Lodge, 1986). They therefore influence the diversity, abundance and population patterns of aquatic invertebrates and vertebrates (Williams, 1980; Wilzbach, 1985; Wilzbach & Cummins, 1986). For example Hall & Werner (1977) report that seasonal littoral fish movement in Lawrence Lake (Michigan, U. S. A.) is correlated with seasonally changing food levels and vegetation development.

In this paper, I report on the relationships between macrophytes and molluscs in Lake Kariba. Bivalves have a large standing crop in the lake (Kenmuir, 1980; Machena & Kautsky, 1988) and could play a crucial role in nutrient circulation (Kautsky, 1981). Bivalves are not predated on in the system, but because of their large biomass they could be exploited for human use. Gastropods, having although a smaller biomass (Machena & Kautsky, 1988) are predated by some fish species and are therefore important in the aquatic food chain.

The submerged vegetation of Lake Kariba consists of perennial macrophytes with a constant biomass and species distribution patterns determined by lake morphometry and transparency (Machena, 1987). This is likely to lead to a predictable community structure and production of secondary producers.

METHODS

Study area and field analysis

The study was carried out on the Zimbabwe side of Lake Kariba (16° 28' - 18° 06' S; 26° 40' - 29° 03' E.). The lake is big (5 250 km^2), man-made and is shared between Zambia and Zimbabwe. The study area and field methods have been described in Machena & Kautsky, (1988).

Submerged vascular plant cover, biomass and species co~~p~~mposition were determined using SCUBA diving in 0.5 x 0.5 m quadrats in stratified belts along 18 vertical transects that were spaced to cover variation in shore type and transparency. From diving along the transect the following were recorded: distance from the shore, depth, species composition, cover of vegetation by a visual estimation of bottom surface cover, and the approximate extent of each homogeneous belt.

Quadrats were placed at the bottom in a stratified manner and 2 to 3 samples were taken in each defined belt. Randomisation within the strata was achieved by swimming towards the surface and dropping the frame.

The vegetation including roots and surface sediment as well as mussels and snails was placed in 1 mm mesh samble bags. On the shore the plants and animals were separated into species. The plants were dried (in the laboratory) to constant weight at 105 °C . The length of mussels and snails were measured with vernier calipers in the field. Biomass (g dry weight including shells) was then calculated from lenght weight regression curves. For the bivalves *Aspatharia wahlbergii* Krauss, *Caelatura mossambicensis* von Mortens and *Mutela dubia* Gmelin the length-weight relationships given by Kenmuir (1980) were used. Along with the biological data, depth, transparency and degree of slope were also determined.

The plant data used in the correlation studies are cover values for each species and the environmental variables used are depth, transparency and degree of slope. The faunal data used are biomass values.

Data analsis

The objective of this study is to identify co-occurences of gastropods (7 species) and bivalves (4 species) with the submerged macrophytes (5 species), in relation with major environmental variables depth, transparency and degree of slope. This was done with detrended canonical correspondency analysis (DCCA) - a multivariate direct gradient analysis technique (Ter Braak, 1986; 1987a; 1987b). The vegetation species were entered as "active" species and the bivalves and gastropods were entered as "passive" species (Ter Braak, 1987b). In this ordination, the "passive" species scores are calculated after the ordination axes of the "active" species have already been extracted. The "passive" species scores are then placed in relation to the already extracted axes. In this procedure it is difficult to discriminate between the independent effects of the environmental variables and the pattern and structure of the vegetation, on the structure and distribution of the gastropods and bivalves.

Therefore two more ordinations by DCCA were performed; an ordination of the gastropods and bivalves with environmental factors as explanatory variables and an ordination of gastropods and bivalves with the macrophytes as explanatory variables. To substantiate the relationship elucidated in the latter case, I carried out a stepwise regression analysis of the bivalves and gastropods with macrophyte species they appeared to be related with, using the SAS/GRAPH package (SAS Institute Inc., 1981). In all cases the significance of the ordination was tested by the Monte Carlo permutation test (Ter Braak, 1987b).

RESULTS

Tables 1 and 2 show the distribution of mollusc and macrophyte biomass respectively. Figs. 1, 2 and 3 present the ordination results. In Fig. 1, the first axis represents vegetation zonation as related to water depth and transparency (Table 3) and explains 78.2% of the variation. The direction of the arrows shows that the trends run from left to right. Vallisneria aethiopica Frenzyl and Potamogeton octandrus L. are confined to shallow water of low transparency.

Najas pectnata (Parl) Magnus and Ceratophyllum demersum L. are found in deep water of increased transparency. Lagarosiphon ilicifolius Oberm is intermediate. The effects of both depth and transparency on axis I are significant at 1% level during the Monte Carlo permutation test. The second axis is related to slope with C. demersum as the more dependent species. An ecological interpretation is given in Machena (1987).

The positioning of both gastropods and bivalves on the vegetation ordination is of interest. The gastropods Cleopatra sp, Bellamya capillata Frauenfield, Biomphalaria pfeifferi Krauss are associated with V. aethiopica and P. octandrus in the shallow and low transparency water, but on steeper slopes. Lymnaea natalensis Krauss is associated with L.ilicifolius but only on very gentle slopes. Bulinus tropicus and Melanoides tuberculata Muller are associated with both L. ilicifolius and N. pectinata. The bivalves Corbicula africana Krauss and A. wahlbergii are associated with L. ilicifolius but are more tolerant of steep slopes. C. mossambicensis is intermediate in its slope relation and is closely associated with both L. ilicifolius and N. pectinata.

Fig. 2 shows the relationship between both gastropods and bivalves and the environmental variables. Both transparency and slope have a strong effect on the distribution of both gastropods and bivalves (Table 4). This effect is significnt (at 1% level) on axis I using the Monte Carlo permutation test. Except for C. massambicensis, all the bivalve and gastropod species prefer very gentle slopes and low transparency. C. mossambicensis is dominant in the analysis reflecting its dominance in abundance (Table 1). As Table 4 shows, the depth variable does not contribute significantly to the analysis.

In Fig. 3 a direct ordination of the gastropods and bivalves on the vegetation, axis I is related to P. octandrus and V. aethiopica (Table 5). Axis II is also related to P. octandrus. Axis I is significant (at 10% level) using the Monte Carlo permutation test, and this is a low level of significance. Although L. ilicifolius, C. demersum and N. pectinata are shown, they are not significant in the analysis (Table 5), and therefore cannot explain the the distribution of both gastropods and bivalves.

The regression analysis (Table 6) shows that one bivalve C. mossambicensis is strongly associated with both N. pectinata and L. ilicifolius, and four gastropods B. pfeifferi, L. natalensis B. capillata and Cleopatra sp. are strongly related with V. aethiopica. This information is similarly portrayed in Fig. 3.

DISCUSSION

The ordinations leading to Figs. 1 and 2 show that both the vegetation and fauna (gastropods and bivalves) are correlated with environmental variables, particularly slope and transparency. The fauna have a weak relationship with depth. Further, from the regressioon analysis, it is apparent that at least one bivalve and four gastropods are also related to macrophyte distribution. C. mossambicensis has a distribution related to that of both L. ilicifolius and N. pectinata. The gastropods B. pfeifferi, L. natalensis, B. capillata and Cleopatra sp. are related in distribution to V. aethiopica. One can not conclude a cause and effect relationship but the correlation between the fauna and the vegetation demonstrates a strong link. What physical and biological factors could be selectively attracting the fauna to respective macrophyes ?

Possible interactions between gastropods and specific plant species could be due to variation in compositioin of epiphytes on the vegetation, abundance and palatability of the vegetation and chemoattraction. Lodge (1985) found Planorbis vortex to be selectively attracted to a specific epiphyton composition, and the epiphyton composition between the macrophytes he looked at Glyceria maxima and Elodia canadensis differed significantly. In a comparison of biomass, production and composition of epiphytes growing on natural vegetation and artificial plants, Cattaneo & Kalff (1979) and Cattaneo (1983) concluded that epiphyte communities are not affected by the nature of their substrates. This view is not shared by S. Björk-Ramberg (pers. comm.) who found that in Lake Kariba V. aethiopica had a lower biomass of epiphytes dominated by diatoms and green algae when compared with L. ilicifolius and N. pectinata which had a higher biomass of epiphytic algae dominated by blue - greens. See also Ramberg et al (1987).

Carpenter & Lodge (1986) propose that grazers could be chemoattracted to macrophytes. Brönmark (1985) found Lymnaea peregra was attracted to chemicals excreted by Ceratophyllum demersum but not by the epiphyton itself. Brönmark, futher found that grazing on C. demersum in fact enhanced its growth rate. This is an indication of a mutual relationship between grazers and macrophytes. The gastropods either feed directly on the vegetation or graze on epihytes and detritus. *Lymnaea stagnalis* and *Physa gyrina* feed directly on *Potamogeton*; and *Littorea littorea* L. feeds directly on *Spartina alterniflora* (Carpenter & Lodge, 1986). In fact along the north eastern USA coast grazing by *L. littoria* reduces the growth of *S. alterniflora* stands considerably (Carpenter & Lodge, 1986). Some grazers prefer epiphytes over macrophytes because they do not have mouth parts capable of puncturing or tearing macrophyte tissue which may be unpalatable. In the seagrass (*Halodule wrightii*) meadows of south Texas (USA) with extremely productive epiphytic algae and extensive grazing by invertebrate fauna, Morgan & Kitting (1984) found little evidence of direct grazing on seagrass.

It is possible that in Lake Kariba *V. aethiopica* and *P. octandrus* are more palatable than *L. ilicifolius* and *N. pectinata* and the wider leaves provide a better climbing surface (Lodge, 1975). Also according to Welch (1952) *Vallisneria americana* has a high protein and carbohydrate content. This could apply to *V. aethiopica* as well. *C. demersum*, *N. pectinata* and *L. ilicifolius* have highly dissected and tiny leaves which may not be suitable for snail climbing. Brown (1978) also reports that in Lake Malawi *Bulinus succinoides* has been found largely on *V. aethiopica*. The observations of S. Björk-Ramberg (pers. comm.) that in Lake Kariba, *V. aethiopica* had a lower biomass of epiphytes than *L. ilicifolius* and *N. pectinata* could be due to heavier grazing on *V. aethiopica*. Cattaneo & Kalff (1980) also found similarly shaped plastic *Myriophyllum* *spicatum* and *Elodea canadensis* (with highly dissected leaves) to have a higher biomass of epiphytic algae than plastic *Vallisneria americana* and *Potamogeton richardsonii*. Snails that are not associated with vegetation prefer other habitats e. g. *M. tuberculata* which settles on sediments.

C.mossambicensis is the dominant bivalve (Table 1) and is associated with *L. ilicifolius* and *N. pectinata*, the dominant vegetation species. Bivalves are filter feeders and phytoplankton, periphyton, detritus and associated microbial flora comprise their food. Bivalves do not feed directly on vegetation. Vegetation is important for reduced water flow and for food distribution and deposition of particulate matter (de March, 1978). The bivalve association with vegetation could be either indirect, through coinciding habitat requirements (both the bivalves and macrophytes are strongly correlated with environmental variables) or directly. In the former situation, bivalves prefer gentle ~~gentle~~ sloping areas as these are areas with reduced wave activity and a lower risk from covering by wave induced sediment material (Kenmuir, 1980). These are also the same areas with high biomass of vegetation (Machena, 1987). In the latter situation, vegetation stands could provide a suitably sheltered and nutrient rich environment. Organic carbon released by macrophytes is a major substrate for epiphytic bacteria. Association with *L. ilicifolius* offers a number of advantages. *L. ilicifolius* populations have a high turnover rate (2.5 x per year, Machena, Kautsky & Lindmark, in prep.), and this ensures a high turnover rate of detrital matter. There is little grazing of

L. ilicifolius in Lake Kariba and its high biomass is channeled predominantly through decomposition pathways.

In conclusion it is worth noting that the benthic faunal and floral composition and distribution in Lake Kariba are determined by the natural physical environment. Kautsky & Van der Maarel (1988) report that the phytobenthic and faunal zonation in the Northen Baltic sea is fairly constant and resilient (over many years). This zonation is also controlled by abiotic factors particularly depth and wave exposure. The Baltic Sea is a much larger system than Lake Kariba and the impression is that

physical environmental factors are important in determining the structure and composition of aquatic systems. Further, for Lake Kariba, the biomass and distribution of the gastropods B. pfeifferi, L. natalensis, B. capillata and Cleopatra sp. that are correlated with V.aethiopica and P. octandrus should be limited by the biomass and distribution of V. aethiopica and P. octandrus. Hence alteration of the biomass of V. aethiopica and P. octadrus e.g. through dredging and use of herbicides (management options) should in consequence alter the corresponding snail biomass. There are further implications in aspects of of the ecosystem food chain. For example, it is conceivable that the fish which feeds on snails in Lake Kariba Serranochromis codringtoni Boulenger, should also be limited by the distribution of the snails dependent on V. aethiopica. This may not be the case, however, as there are many snails that are not dependent on vegetation but some other factors and these may not be similarly limited.

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REFERENCES

Brönmark, C. 1985. Interactions between macrophytes, epiphytes and herbivores; an experimental approach. Oikos. 45: 26 - 30.

Brown, D. S. 1978. Freshwater molluscs. In: Biogeography and Ecology of Southern Africa. Vol. II. Dr. W. Junk. pp. 1155 - 1178.

Carpenter, S. R. & Lodge, D. M. 1986. Effects of submerged macrophytes on ecosystem processes. Aquatic Botany. 26:341 - 370.

Cattaneo, A. & Kalff, J. 1979. Primary production of algae growing on natural and artificial aquatic plants. A study of interactions between epiphytes and their substrates. Limnology and Oceanography. 24: 1031 - 1037.

Cattaneo, A. 1983 Grazing on epiphytes. Limnology and Oceanography. 28: 341 - 370.

Cattaneo, A. & Kalff, J. 1980. The relative contribution of aquatic macrophytes and their epiphytes to the production of macrophyte beds. Limnology and Oceanography. 25: 280 - 289.

de March, L. 1978. Permanent sedimentation of nitrogen, phosphorus and organic carbon in a high arctic lake. Journal of the Fisheries Research Board of Canada. 35: 1089 - 1094.

Hall, D. J. & Werner, E. E. 1977. Seasonal distribution and abundance of fishes in the littoral zone of a Michigan lake. Transactions of the American Fisheries Society. 106: 545 - 555.

Howard-Williams, C. 1981. Studies on the ability of *Potamogeton pectinatus* to remove dissolved nitrogen and phosphorous compounds from lake water. Jour~~m~~nal of Applied Ecology. 18: 619 - 637.

Howard-Williams, C. & Liptrot, M. N. R. 1980. Submerged macrophyte communities in a brackish South African estuarine lake system. Aquatic Botany. 9: 101 - 116.

Kautsky, N. 1981. On the role of the blue mussel (*Mytilus edulis* L.) in a Baltic coastal ecosystem and the fate of the organic matter produced by the mussels. Kieler Meeresforschungen (Sonderheft). 5: 454 - 461.

Kautsky, H. & Van der Maarel, E. 1988. Multivariate approaches to the variation in benthic communities and environmental vectors in the Asko area, Northern Baltic proper. In: Hans Kautsky. Factors structuring phytobenthic communities in the Baltic Sea. PhD thesis. University of Stockholm.

Kenmuir, D. H. S. 1980. Aspects of the biology and population dynamics of freshwater mussels in Lake Kariba and Lake Mcllwaine. Lake Kariba Fisheries Research Institute Project Report No. 36.

Lodge, D. M. 1985. Macrophyte - gastropod associations: observations and experiments on macrophyte choice by gastropods. Freshwater Biology. 15: 695 - 708.

Machena, C. 1987. Zonation of submerged macrophyte vegetation in Lake Kariba, Zimbabwe and its ecological interpretation. Vegetatio. 73. 111 - 119.

Machena, C. & Kautsky, N. 1988. A quantitative diving survey of benthic vegetation and fauna in Lake Kariba, a tropical man-made lake. Freshwater Biology. 19: 1 - 14.

Morgan, M. D. & Kitting, C. L. 1984. Productivity and utilisation of the seagrass Halodule wrightii and its attached epiphytes. Limnology and Oceanography. 29: 1066 - 1076.

Pelikan, J., Hudec, K. & Šťastný, K 1978. Animal populations in fish pond littorals. In: Ecological Studies 28. Pond Littoral Ecosystems. Structure and Function. Springer-Verlag. Eds. D. D. Dykyjova & J. Květ. pp 74 - 79.

Ramberg, L., Björk-Ramberg, S., Kautsky, N. & Machena, C. 1987. Development and Biological Status of Lake Kariba - A man-made Tropical Lake. Ambio. 16: 314 - 321.

SAS Institute Inc. 1981. SAS/GRAPH User's Guide. SAS Institute Inc. Cary, NC 126 pp.

Ter Braak, C. J. F. 1986. Canonical correspondence analysis: A new eigen vector technique for mulivariate direct gradient analysis. Ecology. 67: 1167 - 1179.

Ter Braak, C. J. F. 1987a. The analysis of vegetation-environment relationships by canonical correspondence analysis. Vegetatio. 69; 69 - 77.

Ter Braak, C. J. F. 1987b. CANOCO - a Fortran program for canonical community ordination by (partial) (detrended) (canonical) correspondence analysis, principle components analysis and redundancy analysis (version 2.1). TNO Institute of Applied computer Science. Wageningen. The Netherlands.

Welch, P. S. 1952. Limnology. McGraw-Hill. Second Edition. pp 203.

Wetzel, R. G. & Hough, R. A. 1973. Productivity and role of aquatic macrophytes in lakes. An asseement. Polish Archives of Hydrobiology. 20: 9 - 19.

Williams, D. D. 1980. Some relationships between stream benthos and substrate heterogeneity. Limnology and Oceanography. 25: 161 - 172.

Wilzbach, M. A. 1985. Relative roles of food abundance and cover in determining the habitat distribution of stream-dwelling cutthroat trout (Salmo clarki. Canadian Journal of Fisheries and Aquatic Sciences. 42: 1668 - 1672.

Wilzbach, M. A. 1986. Influence of habitat manipulations on interactions between cutthroat trout and invertebrate drift. Ecology. 67: 898 - 911.

Table 1: Distribution of mollusc biomass in Lake Kariba (g m^{-2} dry weight including shells) (S.E. of means in parenthesis)
Total biomass for the lake obtained by multiplying average biomass values for each depth interval by 105.22 km^2*
Species names are given in the text.

Depth interval	0-1m n=40	1-2m n=27	2-3m n=14	3-4m n=16	4-5m n=3	5-6m n=3	6-7m n=4	7-8m n=3	9-10m n=2	Total for lake (tons)	% in group	total an
Corbicula	28.76(7.58)	13.64(3.90)	13.66(3.84)	13.79(3.84)	16.30(13.40)	7.50(7.50)	3.26(1.04)	1.11(1.11)	1.12(1.12)	10431.5	9.2	8.8%
Caelatura	163.20(31.80)	149.56(24.33)	188.91(50.48)	219.69(62.81)	98.73(55.50)	32.80(32.80)	1.92(1.92)	20.39(20.39)	0	92086.4	80.8	77.5
Mutela	26.61(3.82)	10.36(4.65)	0	15.21(7.05)	0	0	0	0	0	5490.4	4.8	4.6
Aspatharia	0	49.89(13.8)	6.4(6.48	0	0	0	0	0	0	5931.2	5.2	5.0
Total bivalve	218.57	223.43	209.05	248.69	115.03	40.30	5.18	21.50	1.12	113939.6	100	95.3
Melanoides	6.78(1.96)	5.80(1.42)	4.47(0.90)	5.44(1.39)	1.57(0.80)	5.80(2.10)	1.74(1.45)	4.3(4.34)	0.31(0.31)	3866.8	79.7	3.2
Bellamya	1.66(0.38)	0.24(0-12)	0.54(0.15)	0.15(0.15)	0	0	0	0	0	272.5	5.6	0.2
Cleopatra	2.45(0.58)	2.14(0.77)	0.31(0.13)	0.17(0-09)	0.50(0.50)	0.40(0.40)	0	0	0	628.2	13.0	0.5
Biomphalaria	0.11(0.03)	0.032(0.1)	0.04(0.03)	0.00(0.00)	0	0	0	0	0	20.0	0.4	0.02
Bulinus 1	0.04(0.02)	0.0033(0.00)	0	0.02(0.02)	0	0	0	0	0	10.5	0.2	0.01
Bulinus 2	0.06(0.01)	0.0148(0.0)	0.04(0.02)	0.11(0.05)	0.01(0.01)	0.24(0.24)	0	0	0	50.5	1.1	0.04
Lymnaea	0.02(0.01)	0.0244(0.01)	0	0	0	0	0	0	0	4.2	8.6	0.003
Total gastropods	11.12	8.25	5.40	5.90	2.08	6.44	1.74	4.3	0.81	4925.3	100	4.1
Others	0	0.22(0.05)	0.23(0.23)	0	0	0.	0	0	0	47.3	-	0.04
Total	229.69(32.2)	231.90(44.14)	214.7(65.10)	254.59(69.76)	117.11(47.01)	46.74(27.25)	6.92(2-20)	25.84(16.80)	1.93(1.30)	118839.7	-	100

* 105.22 km^2 is average bottom area per 1m depth interval between 0 and 15m depth (Machena & Kautsky, 1988)

Table 2: Distribution of macrophyte biomass in Lake Kariba (g m^{-2} dry weight ; S.E. of means in parenthesis). Total biomasses for the lake obtained by multiplying average biomass values for each depth interval by 105.22 km^2 *

Depth intervals	0 - 1m n = 33	1 - 2m n = 24	2 - 3m n = 21	3 - 4m n = 21	4 - 5m n = 18	5-6m n=2	Total for lake (tons) 0 - 6m	% Composition
Lagarosiphon ilicifolius	144.6 (32.0)	174.8 (59.3)	118.7 (42.7)	61.7 (44.0)	2.6 (1.4)	+	52 863	52
Najas pectinata	91.8 (38.0)	87.4 (36.4)	117.7 (59.0)	18.0 (9.8)	1.1 (0.8)	+	33 250	33
Vallisneria aethiopica	87.1 (24.0)	18.9 (12.5)	1.8 (1.2)	0.4 (0.4)	-	-	11 385	11
Potamogeton octandrus	4.8 (3.3)	-	-	-	-	-	505	0.5
Ceratophyllum demersum	0.9 (0.9)	3.6 (3.1)	19.1 (10.8)	4.3 (3.5)	-	+	2 935	3

* 105.22 km^2 is average bottom area per 1m depth interval between 0 and 15m depth. (Machena & Kautsky, 1988).

Table 3 : Kariba vegetation, gastropod and bivalve species data : T - values of regression coefficients for the first two ordination axes and the inter-set correlations of the enviromental data with the first two axes. Gastropod and bivalve species data has been entered as "passive", and that of vegetation as "active".

	Coefficients		Correlations	
AXIS	1	2	1	2
FR explained	0.78	0.18	FR extracted	
			0.226	0.044
Variables:				
Depth	7.37	0.95	0.56	0.12
Slope	-2.35	5.55	0.01	0.34
Transparency	8.26	-1.01	0.60	-0.02

FR = fraction of variance

Table 4 : Kariba gastropod and bivalve species data : T - value of regression coefficients for the first two ordination axes and inter-set correlations of the environmental data with the first two axes.

	Coefficients		Correlations	
AXIS	1	2	1	2
FR explained	0.71	0.27	FR extracted	
			0.084	0.042
Variables:				
Depth	0.27	-1.04	0.26	-0.10
Slope	3.0	2.79	0.45	0.28
Transparency	3.90	-1.13	0.36	-0.21

FR = fraction of variance.

Table 5 : Kariba vegetation, gastropod and bivalve species data : T - values of regression coefficients and inter-set correlation of environmental data with the first two axes. Macrophyte species have been entered as external variables.

	Coefficients		Correlations	
Axis	1	2	1	2
FR explained	0.59	0.30	FR extracted	
			0.063	0.035
Variable:				
Vallisneria	3.31	-1.52	0.38	-0.24
Potamogeton	3.47	2.90	0.31	0.28
Ceratophyllum	0.58	1.47	0.02	-0.15
Lagarosiphon	-1.03	0.78	-0.28	0.12
Najas	-0.31	-0.08	-0.09	-0.04

FR = fraction of variance

Table 6 : Regression showing relationship between plant cover and mollusc biomass (g dry wt m^{-2}) in samples from Lake Kariba. The regression analysis was carried out for only mollusc species that appeared to be related to particular macrophyte species in the mollusc ordination with macrophytes as the external factor (Fig. 3.).

Dependent variable	Independent variable	Error DF	r^2	significant
Aspatharia	Lagarosiphon	235	0.0093	ns
Caelatura	Lagarosiphon	235	0.0477	**
Caelatura	Najas	228	0.0358	**
Caelatura	Vallisneria	232	0.0006	ns
Mutela	Vallisneria	235	0.0057	ns
Aspatharia	Vallisneria	235	0.0038	ns
Corbicula	Vallisneria	205	0.0006	ns
Cleopatra	Vallisneria	235	0.1269	**
Biomphalaria	Vallisneria	235	0.0280	*
Lymnaea	Vallisneria	235	0.0896	**
Bellamya	Vallisneria	235	0.0896	**

* - P = .95

** - P = .99

ns - non significant.

Figure legends

Fig. 1. Ordination diagram based on canonical correspondence analysis of submerged vegetation, gastropods and bivalves with respect to three environmental variables. The macrophytes (□) were entered as "active" species, and the gastropods (●) and bivalves (○) were entered as "passive" species. The environmental variables (arrows) are: depth, slope and transparency. Abbreviation of species names are:
Lag ili = *Lagarosiphon ilicifolius*; Naj pect = *Najas pectinata*; Cer dem = *Ceratophyllum demersum*; Pot oct = *Potamogeton octandrus*; Val aet = *Vallisneria aethiopica*; Cor afr = *Corbicula africana*; Cae mos = *Caelatura mossambic~~us~~ensis*; Mut dub = *Mutela dubia*; Asp wah = *Aspatharia wahlbergi*; Mel tub = *Melanoides tuberculata*; Bel cap = *Bellamya capillata*; Cle sp = *Cleopatra sp*; Bio pfe = *Biomphalaria pfeifferi*; Bul tro = *Bulinus tropicus*; Bul sp = *Bulinus sp*; Lym nat = *Lymnaea Natalensis*.

Fig. 2. Ordination diagram based on canonical correspondence analysis of gastropods (●) and bivalves (○) with respect to three environmental variables - depth, slope and transparency (shown by arrows).
Abbreviations of species names are:
Cor afr = *Corbicula africana*; Cae mos = *Caelatura mossambicensis* Mut dub = *Mutela dubia*; Asp wah = *Aspatharia wahlbergi*; Mel tub = *Melanoides tuberculata*; Cle sp = *Cleopatra sp*; Bel cap = *Bellamya capillata*; Bio pfe = *Biomphalaria pfeifferi*; Bul tro = *Bulinus tropicus*; Bul sp = *Bulinus sp*; Lym nat = *Lymnaea natalensis*.

Fig. 3. Ordination diagram based on canonical correspondence analysis of gastropods (●) and bivalves (○) with respect to five environmental variables (vegetation species shown by arrows). Abbreviations of species names are:

Lag ili = *Lagarosiphon ilicifolius*; Naj pec = *Najas pectinata*; Cer dem = *Ceratophyllum demersum*; Pot oct = *Potamogeton octandrus*; Val aet = *Vallisneria aethiopica*; Cor afr = *Corbicula africana*; Cae mos = *Caelatura mossambicensis*; Mut dub = *Mutela dubia*; Asp wah = *Aspatharia wahlbergi*; Mel tub = *Melanoides tuberculata*; Bel cap = *Bellamya capillata*: Cle sp = *Cleopatra sp*; Bio pfe = *Biomphalaria pfeifferi*; Bul tro = *Bullinus tropicus*; Bul sp = *Bulinus sp*; Lym nat = *Lymnaea natalensis*.

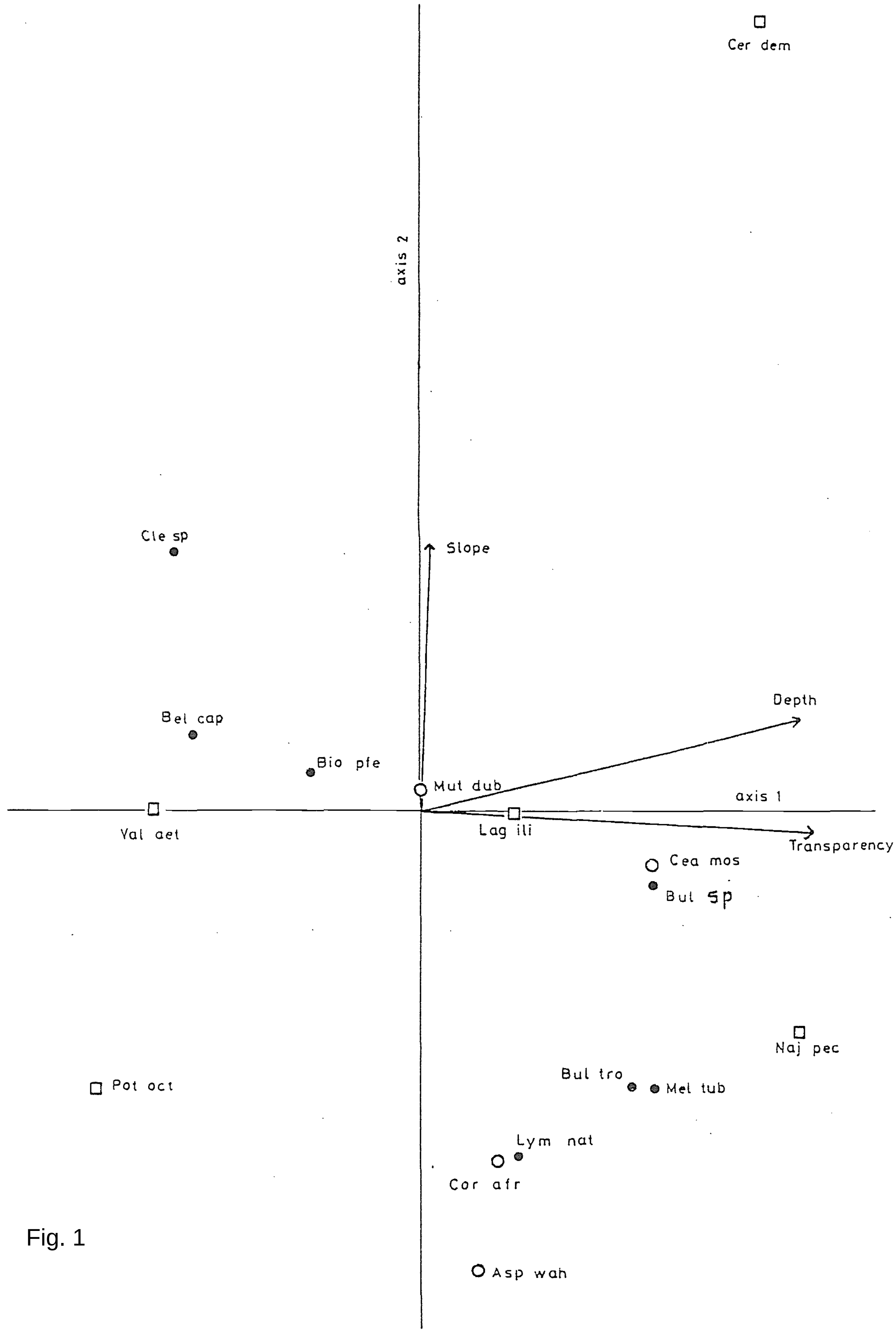
Cer dem
axis 2
Cle sp
Slope
Depth
Bel cap
Bio pfe
Mut dub
axis 1
Val aet
Lag ili
Transparency
Cea mos
Bul sp
Naj pec
Bul tro
Mel tub
Pot oct
Lym nat
Cor afr
Asp wah

Fig. 1

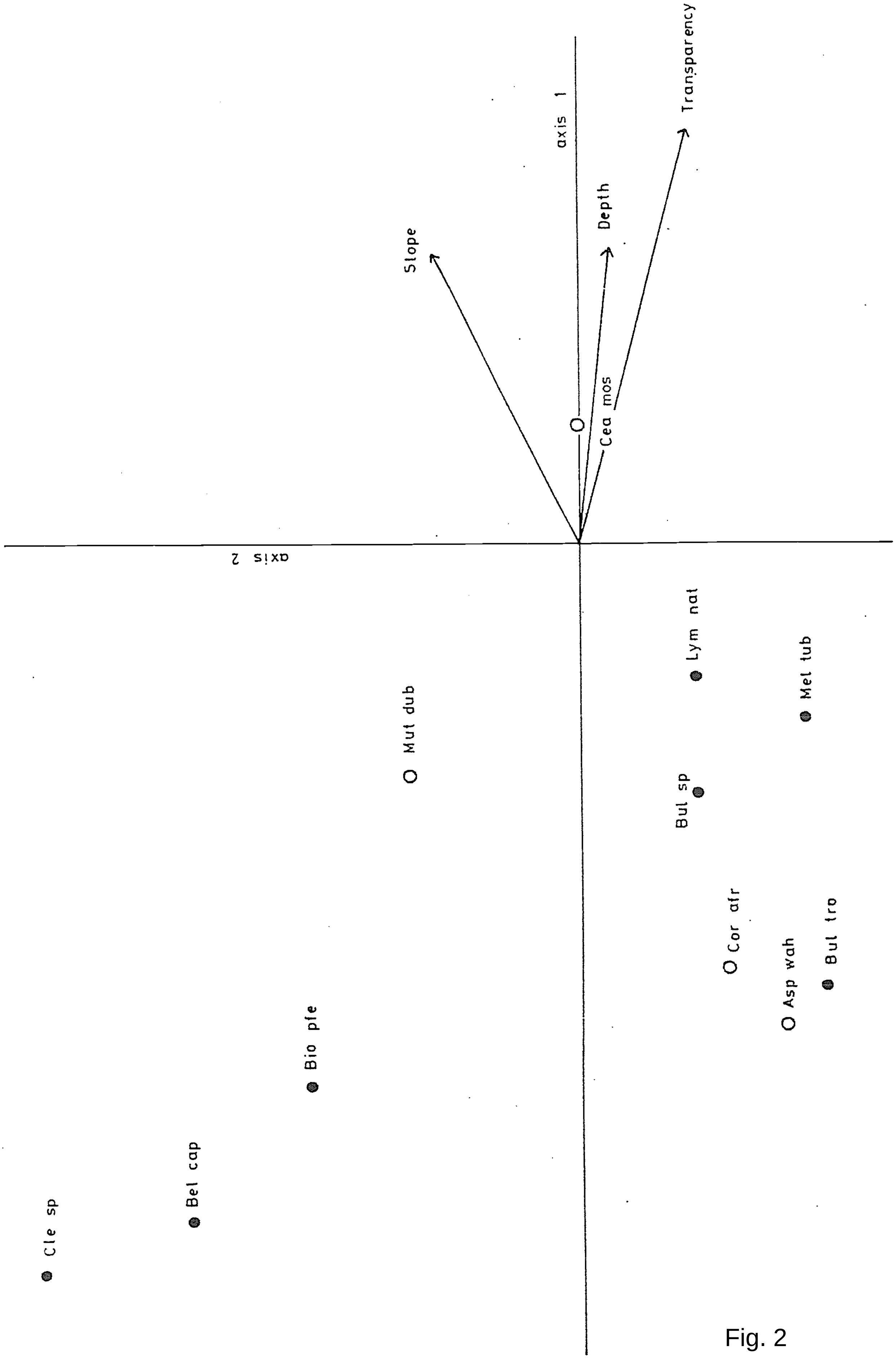
Transparency
axis 1
Depth
Slope
Cea mos
axis 2
Lym nat
Mel tub
Mut dub
Bul sp
Cor afr
Bul tro
Asp wah
Bio pfe
Bel cap
Cle sp

Fig. 2

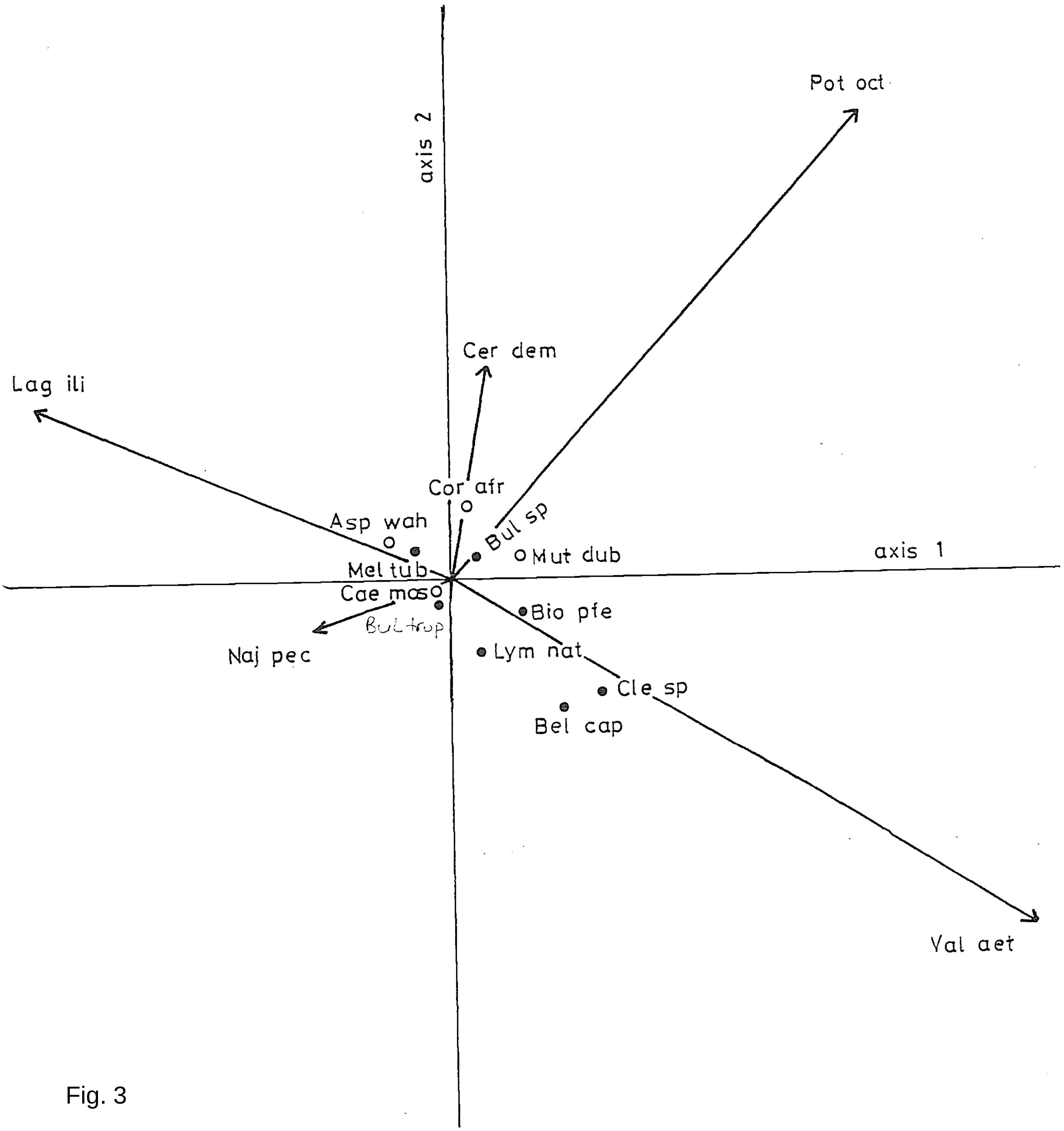
Pot oct
axis 2
Cer dem
Lag ili
Cor afr
Bul sp
Asp wah
Mut dub
axis 1
Mel tub
Cae mos
Bio pfe
Bul trop
Naj pec
Lym nat
Cle sp
Bel cap
Val aet

Fig. 3