Hydrobiologia **298**: 93–104, 1995.
D. Belk, H. J. Dumont & G. Maier (eds), Studies on Large Branchiopod Biology and Aquaculture II.

The description and preliminary prediction of the inundation pattern in a temporary habitat of Anostraca, Notostraca and Conchostraca in South Africa

M. T. Seaman, D. J. Kok & S. Meintjes
Department of Zoology and Entomology, University of the Orange Free State, Bloemfontein 9300, Republic of South Africa

Key words: temporary water, pans, southern Africa, model, branchiopod

Abstract

To explain the life-history strategies of temporary-water fauna, one must be able to describe the temporary habitat. It is necessary to know when it will be wet, how often this occurs, for what period each inundation lasts and what variability there is in this pattern. For logistic reasons one cannot follow each inundation in a pan for the ten years or more needed to establish a pattern. Based on the available inundation data for two seasons at Bain's Vlei Pan in a semi-arid part of South Africa, a model has been developed, using the rainfall pattern over ten years at nearby Bloemfontein, to predict inundation. Over a ten-year period predicted inundations ranged up to 87 days as a result of repeat-rain, with a mean period of 18.8 days, while a rain-episode of less than 20 mm was insufficient to inundate the pans. There was an average of 5.8 inundations per season. Single inundations do not exceed 20 days due to evaporation. When successive showers fall before periods of inundation are over, a specific extension of inundation is predictable. The precise implications of the inundation pattern on organisms requires much analysis. However, there are strong indications based on the growth, survival and pattern of egg-production among three species (Anostracan – *Branchipodopsis tridens*, Conchostracan – *Leptestheriella inermis*, and Notostracan – *Triops granarius*) from the pan and one species (Anostracan - *Streptocephalus macrourus*) from more permanent waters nearby, that the pattern of inundation is selective of the community held by the pan.

Introduction

Pans are most common in semi-arid conditions (Le Roux, 1978; Geldenhuys, 1982) where mean rainfall is low, evaporation rate is at least three times the mean rainfall, and a large degree of unpredictability of rainfall prevails. There is nevertheless a wide range of pan types (Le Roux, 1978; Goudie & Thomas, 1985), varying in size (area and maximum depth), salinity and chemical composition, and in inundation regime.

Due to the temporary nature of inundation, distance of pans from laboratories and apparent unpredictability of inundation very little precise information has been gathered on period and pattern of inundation. It is accepted that pans differ in their period of inundation (Geldenhuys, 1982) and that this should influence the biota. Geldenhuys, for instance found that vegetation cover was directly related to period of inundation. Sea-

Table 1. Rainfall (mm) per week over ten seasons at Bloemfontein. N is the number of weeks.

	N	Min	Max	Mean	St. Err.	St. Dev.
YEAR8182	52	0	110	12.2	3.5	25.4
YEAR8283	52	0	51	3.6	1.5	10.5
YEAR8384	52	0	80	6.3	2.4	17.2
YEAR8485	52	0	60	6.0	2.1	15.3
YEAR8586	52	0	93	5.9	2.6	19.1
YEAR8687	52	0	93	7.1	3.1	22.6
YEAR8788	52	0	437	24.2	9.3	67.4
YEAR8889	52	0	72	13.3	2.8	20.5
YEAR8990	52	0	59	8.5	2.4	17.5
YEAR9091	52	0	200	12.3	5.0	36.3

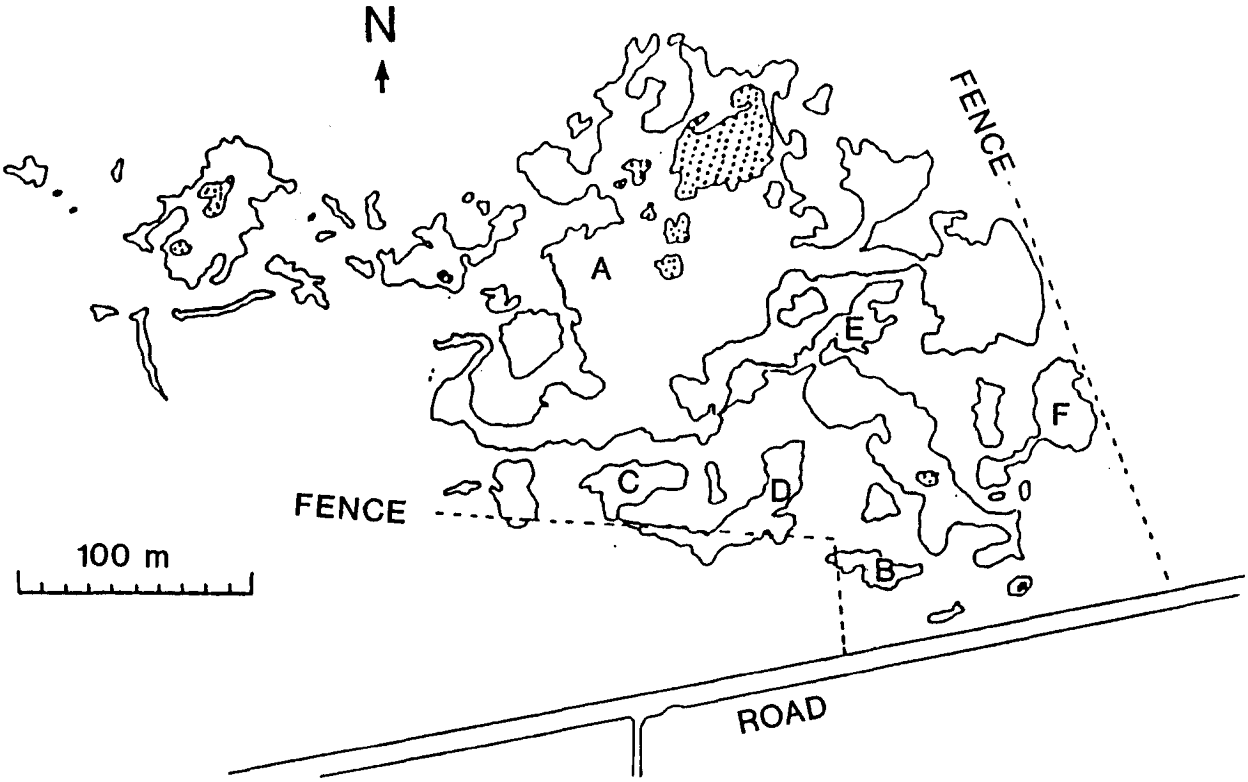


Fig. 1. Map of the Bain's Vlei nest of pans. Stipples indicate islands when the pans are inundated and the letters indicate the separate pan basins that were monitored.

Table 2. Rainfall (mm) per rainweek over ten seasons at Bloemfontein. N is the number of weeks.

	N	Min	Max	Mean	St. Err.	St. Dev.
YEAR8182	13	21	110	48	7.9	28.5
YEAR8283	6	24	51	31	4.2	10.3
YEAR8384	7	24	80	47	6.7	17.3
YEAR8485	8	23	60	39	5.2	14.8
YEARB586	6	20	93	51	12.5	30.6
YEAR8687	5	56	93	74	7.3	16.4
YEAR8788	14	20	437	90	28.6	107.0
YEAR8889	18	20	72	39	3.6	15.4
YEAR8990	11	24	59	40	3.7	12.1
YEAR9091	8	20	200	80	20.7	58.6

$\bar{x}$ 9.6
s 4.25

Table 3. Details of seven successive inundations in Bain's Vlei Pans during 1985 and 1986.

Date of Inundation	Mean Inundation Period (days)	Maximum depth (cm)
15 October 1985	3.8	3.3
*29 October/ 10 November 1985	14.8	13.0
5 December 1985	8.5	8.5
19 January 1986	5.7	4.0
5 March 1986	18.0	8.7
16 April 1986	12.3	6.0
29 October 1986	17.7	11.9

* A follow-up inundation before drying

man & Kok (1987) related the animal community in pans to period of inundation. We can assume that the more temporary the water body the more likely is the biota to include such organisms as Notostraca, Anostraca and Conchostraca (Seaman & Kok, 1987). We can even make predictions that the shorter the inundation the more likely it will be, among related organisms (e.g. Anostracans), that those with shorter life cycles (e.g. *Branchipodopsis* spp. – own data) will prevail over those with longer life cycles (e.g. *Streptocephalus* spp. – own data, Mitchell, 1987, 1991; Anderson & Hsu, 1990; Brendonck, 1991), but we are not able to be specific in what we mean by long or short inundations or life-cycles. Seaman & Kok (1987) suggested that

Table 4. Predicted inundation periods (days) over ten seasons for Bain's Vlei pans from the rainfall/inundation model. N is the number of predicted inundations.

	N	Min	Max	Mean	St. Err.	St. Dev.
INUN8182	6	6	46	22.7	5.7	14.0
INUN8283	6	7	14	9.5	1.1	2.7
INUN8384	6	12	18	14.8	.9	2.2
INUN8485	5	7	38	18.0	5.8	12.9
INUN8586	6	3	24	13.0	3.1	7.5
INUN8687	4	15	28	18.8	3.1	6.2
INUN8788	7	3	80	22.9	10.6	28.1
INUN8889	8	3	87	22.1	9.5	27.0
INUN8990	5	7	52	25.4	7.8	17.4
INUN9091	5	3	48	20.2	7.8	17.5
INUN8190	58	3	87	18.8	2.2	16.6

waters that appeared to hold mean inundations of less than one month were dominated by temporary-water fauna, beyond which permanent-water fauna succeeded.

Inundation pattern in Bain's Vlei pans

As a certain amount of life-cycle data had been collected, and developed in our laboratory, by students and researchers (Mitchell, 1987, 1991; Seaman & Kok, 1987; Seaman *et al.*, 1991; Meintjes, unpublished data) over a number of seasons on organisms present in Bain's Vlei pans, a nest of temporary waters 10 km west of Bloemfontein, it became necessary to relate these to something more precise than the sometimes inaccurate information from single inundations. The inundations in Bain's Vlei pans seldom exceed a month, so it is a short-inundation pan.

This is a summer-rainfall area, so a year will run from July of one calendar year to June of the next for purposes of this study. We were fortunate to have accurate information on all the inundations in a continuous period of more than one year (1985/1986), which we used to calibrate a model against the rainfall of that season. The model was verified against inundation-data available from a subsequent year (Meintjes, unpublished).

Materials and methods

Bain's Vlei pans lie 10 km west of Bloemfontein (29 °03′S, 26 °06′E) and consist of a number of potentially interlinked basins each less than one ha (Fig. 1), with a maximum depth less than 30 cm. Six of these pans have been monitored at various times.

The model was prepared as follows. The average inundation period of the six pans was taken to represent Inundation Period. Rainfall was measured in Bloemfontein over ten years (July 1981 to June 1991) and was split up into Rainfall Per Week and could also be expressed as Rainfall Per Rain-Week.

Inundation Period was plotted against Rainfall Per Week in order to establish the basic relationship, taking into consideration the minimum rainfall needed to cause an inundation, the maximum rainfall necessary to fill the pans, beyond which the pans would simply overflow resulting in a finite period of inundation related to evaporation, unless repeat-inundation occurred which was also taken into account. The duration of multiple inundations was calculated by adding the inferred 'new' inundation from the calibration graph to that expected for the 'old' inundation, bearing in mind that the 'new' could only fill the pans to the extent that they were less than full. For example, if an inundation of 15 days was predicted for the 'old' inundation the pan would have an 'unused capacity' of a further 5 days. If this were to be followed by sufficient rain a week later to result in a 20-day inundation, one would allow that seven days of evaporation added to the original 5 days of 'unused capacity' would result in a revised 'unused capacity' of 12 days. Therefore the 'new' inundation would add only 12 days to the 'old', the remaining 8 days being lost due to the pans overflowing.

Inundation pattern was predicted for the ten years (July 1981 to June 1991) and specific parts of it (during the 1989/1990 rain season) were verified against actual measurements. No compensation was made for differing evaporation rate due to temperature differences.

Life-cycle data was deduced from Seaman *et al.* (1991), Mitchell (1991) and unpublished data of Van Niekerk, Seaman, Kok & Botha.

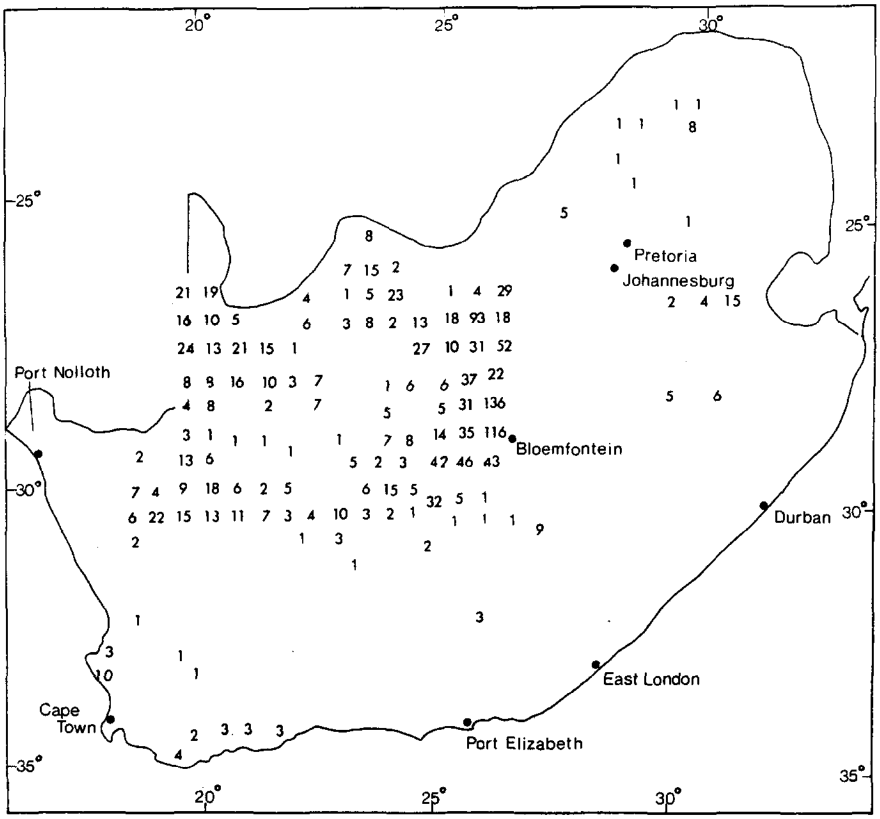


Fig. 2. The geographical distribution of pans in South Africa (after Goudie & Thomas, 1985). Numbers indicate the density of pans as calculated from 1:50000 maps.

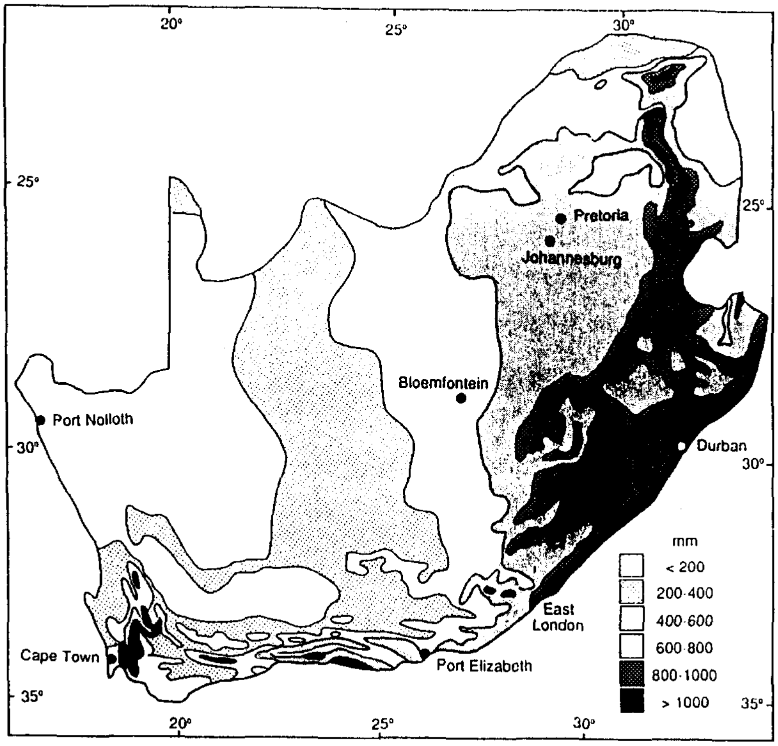


Fig. 3. Mean annual precipitation over South Africa (adapted from Department of Water Affairs, 1986).

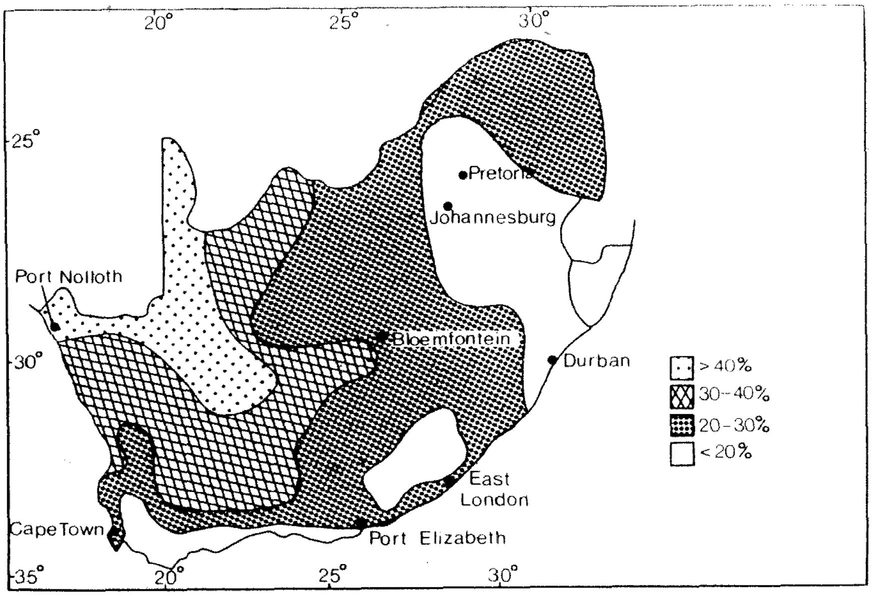
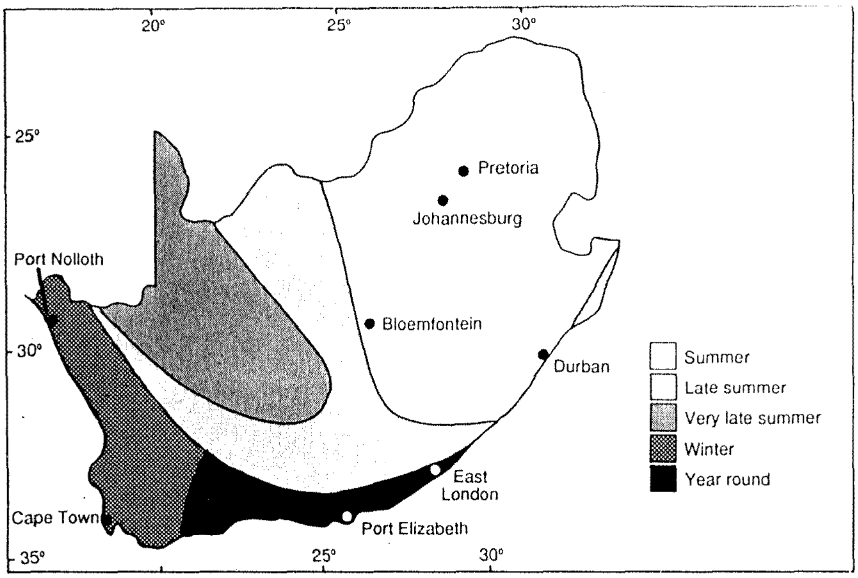


Fig. 4. Percentage deviation from mean annual rainfall over South Africa (adapted from Department of Water Affairs, 1986).



Results

Regional rainfall and evaporation characteristics in the region where pans are most common

Most South African pans (Fig. 2) lie in a region characterised by rainfall less than 600 mm per year (Fig. 3), an annual deviation greater than 25% (Fig. 4), predominant precipitation between summer and very late summer (Fig. 5) and evaporation greater than 1800 mm per year (Fig. 6).

Rainfall pattern at Bloemfontein

Over ten years the aggregate rainfall at Bloemfontein was greatest in late summer (Fig. 7) but was well spread-out. However, the annual rainfall pattern was highly variable between years (Fig. 8). The rainfall per week (Table 1) and per Rain-Week (*i.e.* a week in which rain was measured) (Table 2) reflect the variability in volume of rain. Rainfall per rainweek was always greater than 20 mm.

Seven successive inundations were followed in 1985 and 1986 (Table 3). During the second inundation there was reinundation before drying.

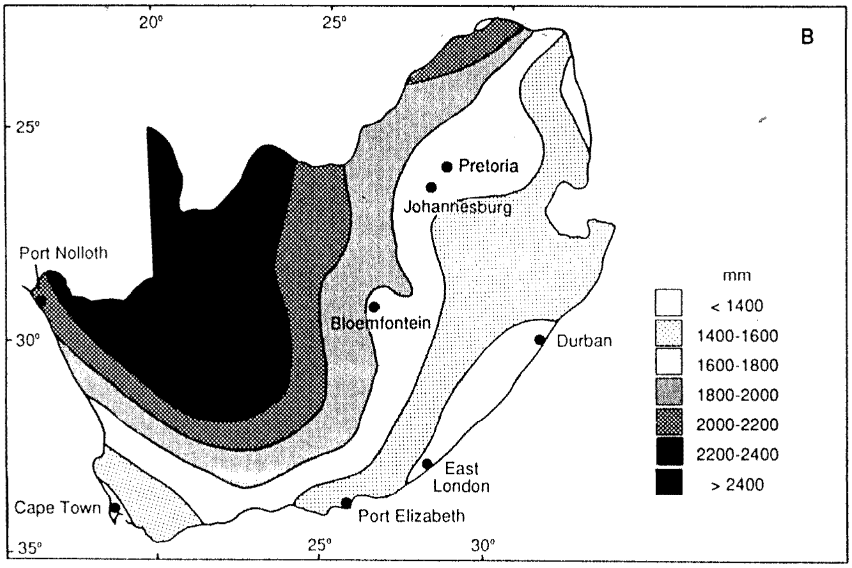


Fig. 6. Mean annual evaporation over South Africa (adapted from Department of Water Affairs, 1986).

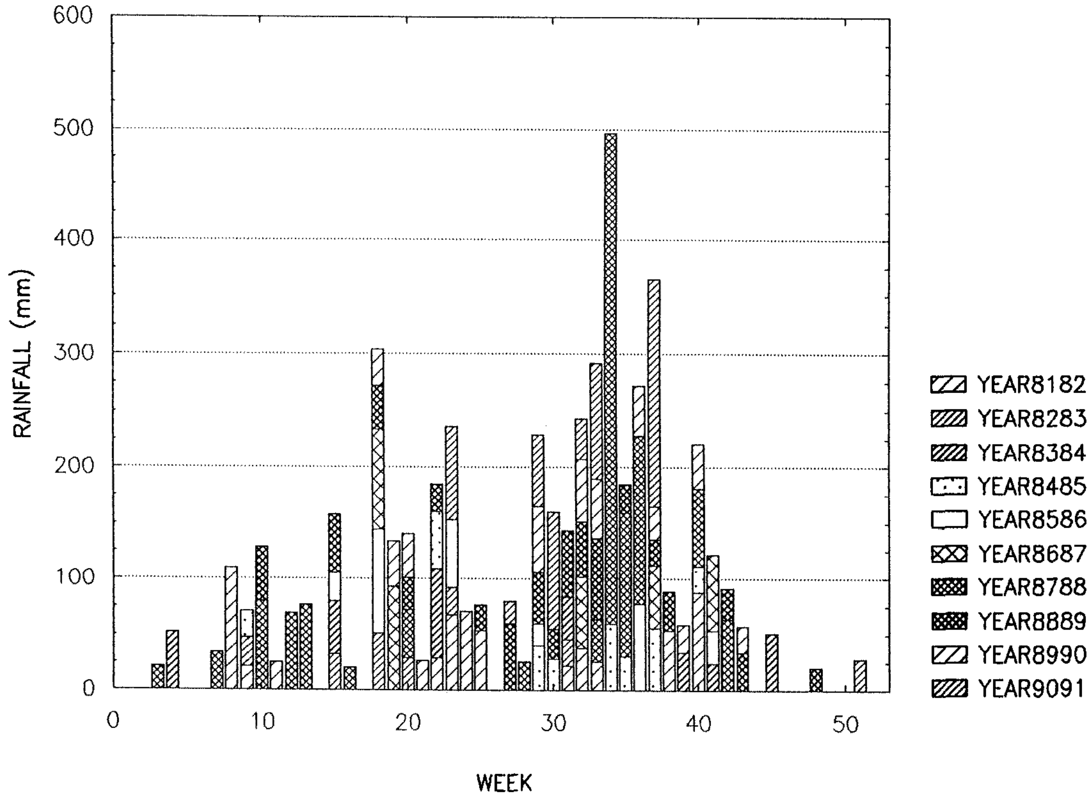


Fig. 7. Cumulative rainfall at Bloemfontein over ten seasons from 1981 to 1991.

Inundation versus rainfall in Bain's Vlei pans

Plotted against volume per rainfall episode, a curvilinear relationship resulted (Fig. 9). Below 20 mm of rain no inundation resulted because the water was soaked up by the dry earth and no surface flow was possible. Above about 80 mm of rain the pan was full and it overflowed resulting in the flattening of the graph, so inundation always lasted less than 20 days because

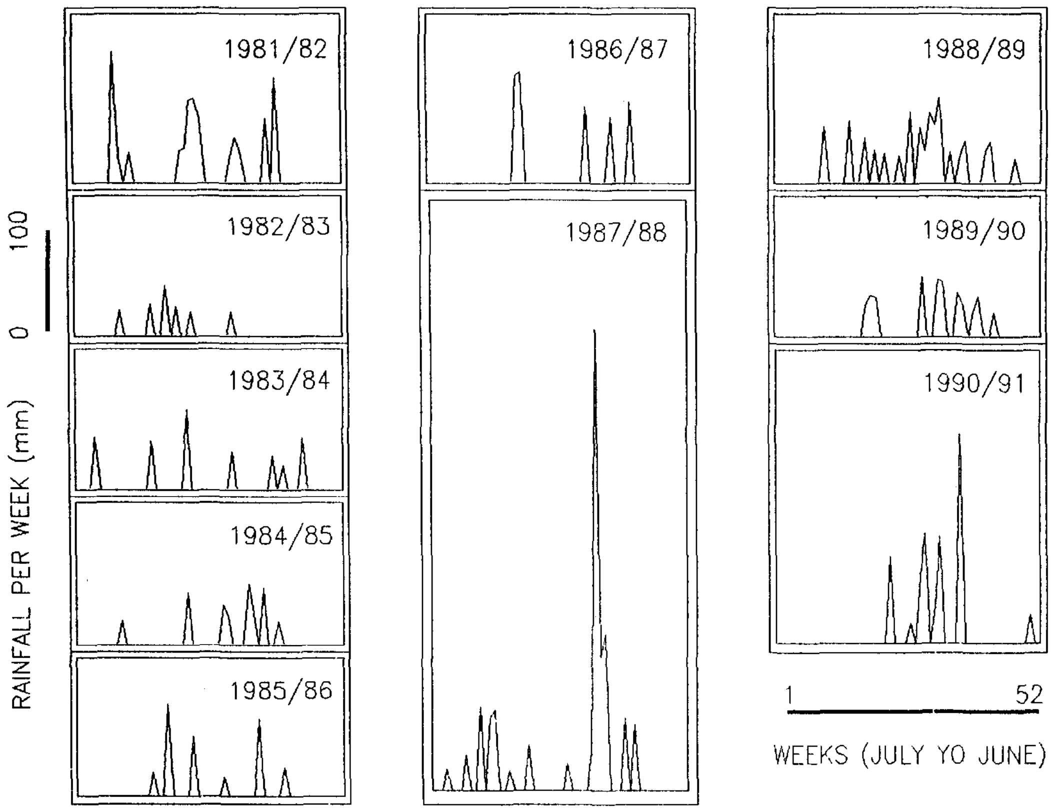


Fig. 8. Pattern of rainfall at Bloemfontein over ten seasons from 1981 to 1991.

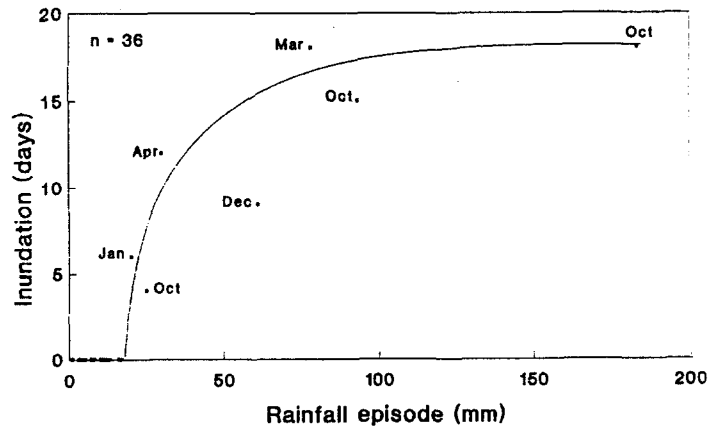


Fig. 9. The relationship between period of inundation resulting and rainfall episode during a continuous period in 1985 and 1986, marked by points and a line fitted by eye. The months label the positive inundations.

of evaporation, unless reinundation was sufficient to extend this period. The predicted inundation derived from this graph for the 1985/1986 rain year agreed satisfactorily with the actual inundation (Fig. 10) and was consequently used to calibrate the model for predicting inundation pattern in Bain's Vlei pan over ten rain seasons. Subsequent verification of this model, using incomplete data (*i.e.* from only some of the season's inundations) from the 1989/1990 rain season (Fig. 11), suggests that the model might underestimate period of inundation, but this was not sufficiently convincing evidence to necessitate modification of the model.

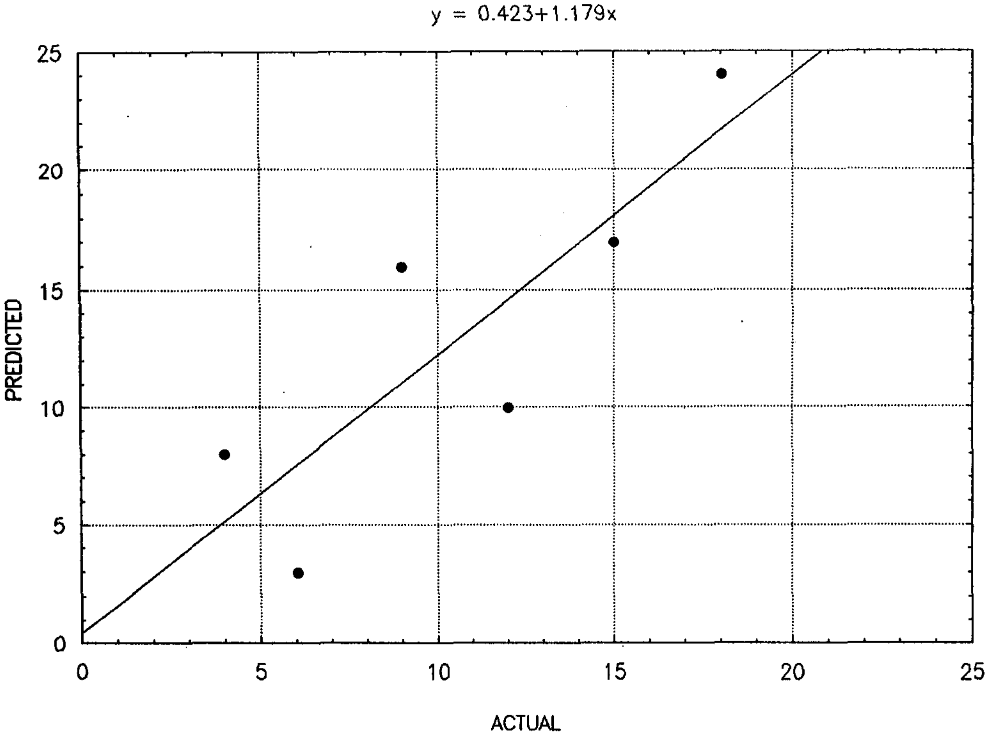


Fig. 10. The relationship between predicted and actual inundations as derived from Fig. 9.

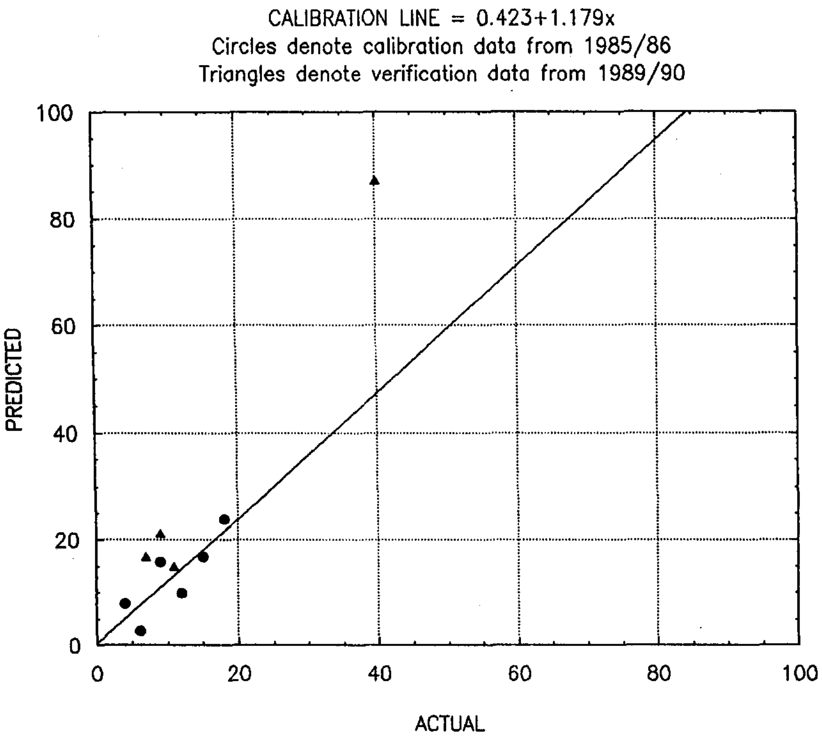


Fig. 11. Predicted inundation periods plotted against actual inundation periods (days). Circles denote the inundation data from 1985/1986 used to calibrate the model and the triangles denote inundation data from 1989/90 which has been used to verify the model.

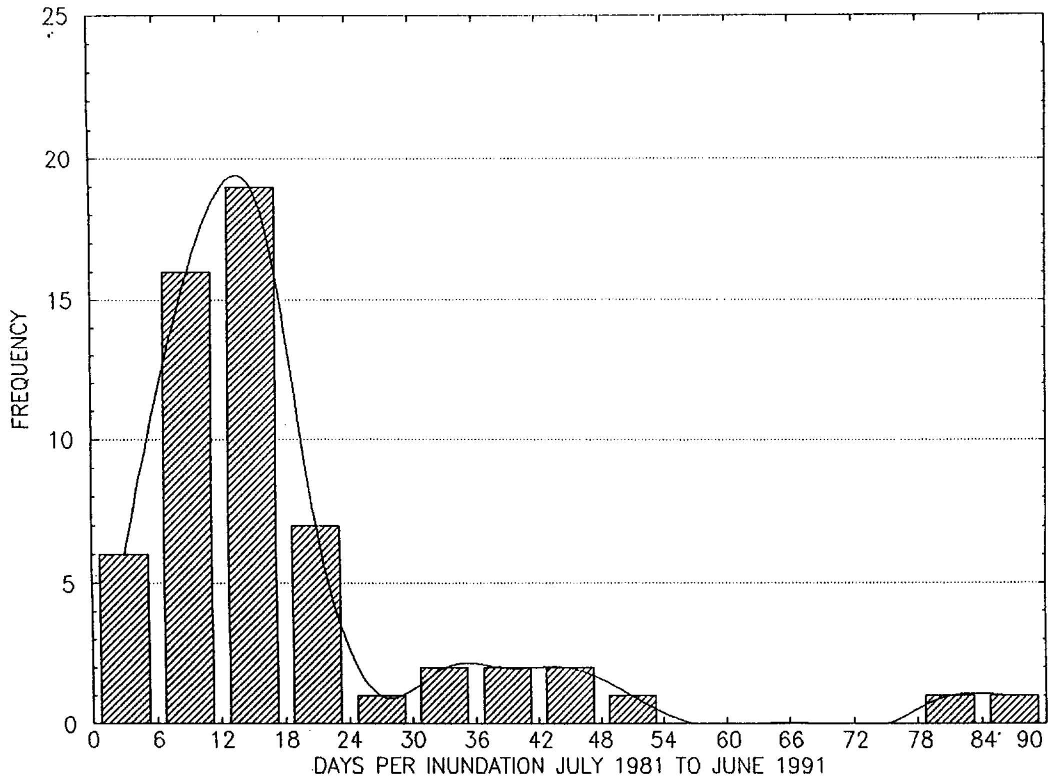


Fig. 12. Predicted frequency of inundations over the ten year period July 1981 to June 1991.

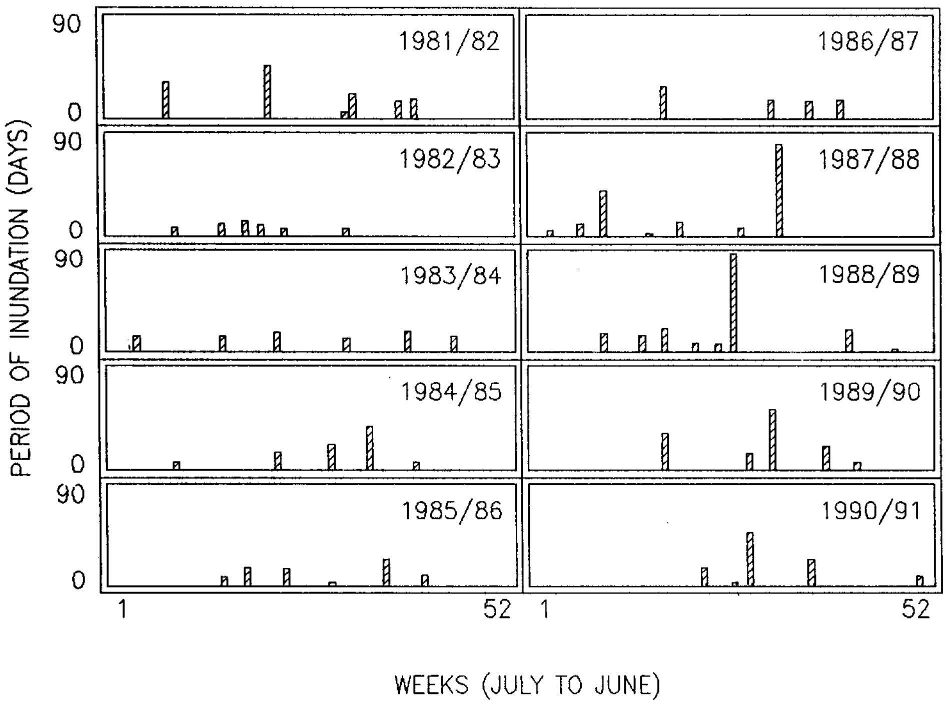


Fig. 13. Distribution and periods (days) of predicted inundations over ten rainfall seasons from July 1981 to June 1991.

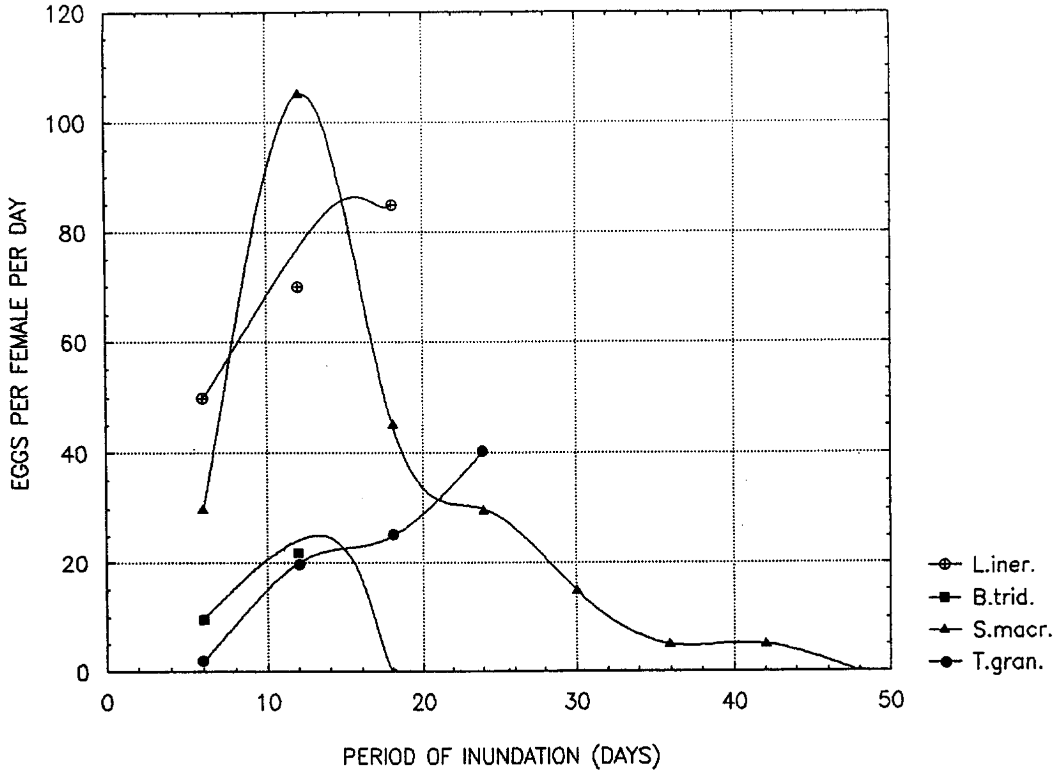


Fig. 14. Egg production per individual female of *Leptestheriella inermis*, *Branchipodopsis tridens*, *Streptocephalus macrourus* and *Triops granarius* over an unlimited period of inundation.

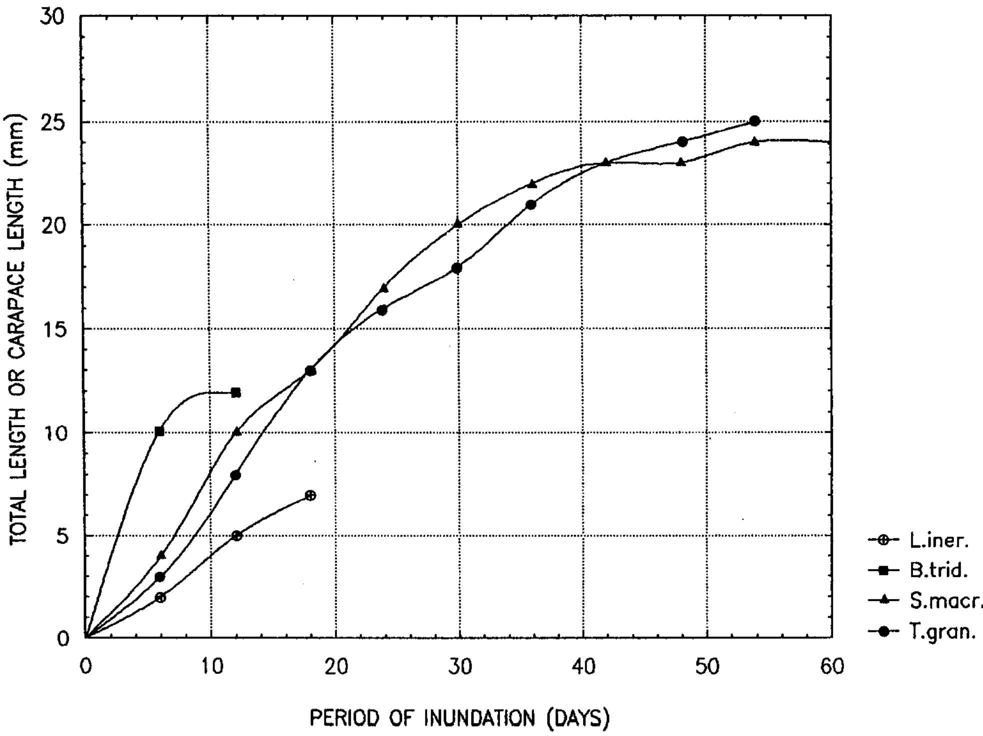


Fig. 15. Individual length (average of male and female) of *Leptestheriella inermis*, *Branchipodopsis tridens*, *Streptocephalus macrourus* and *Triops granarius* (carapace length only) over an unlimited period of inundation.

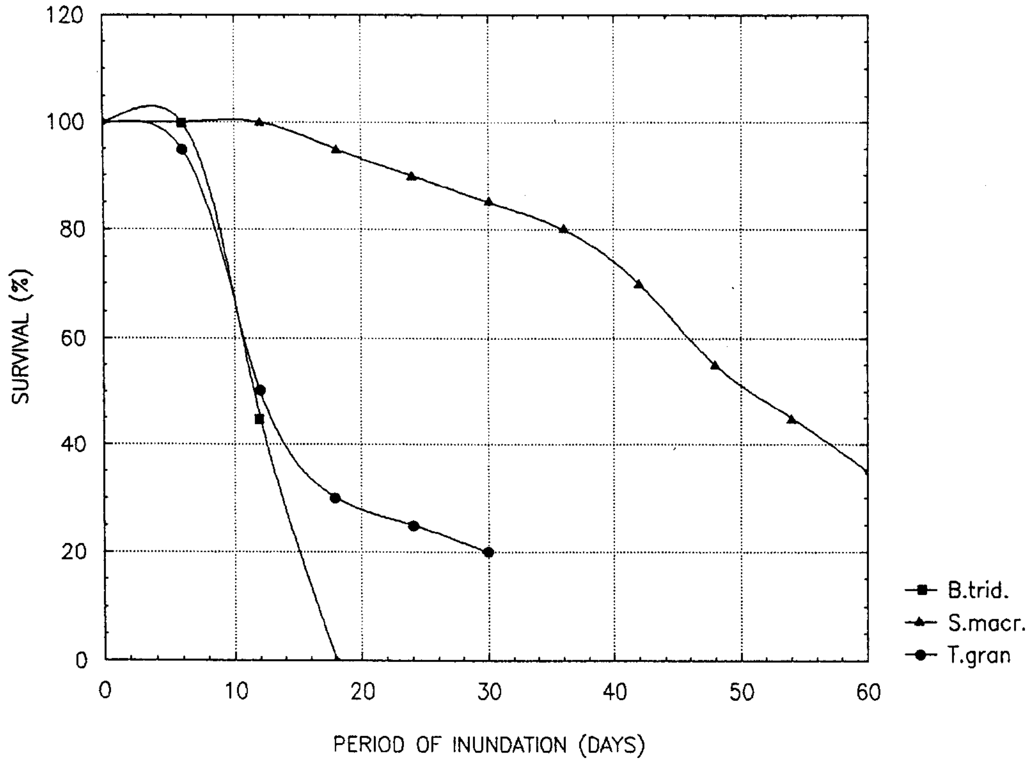


Fig. 16. Individual survival of *Branchipodopsis tridens*, *Streptocephalus macrourus* and *Triops granarius* over an unlimited period of inundation.

Predicted long-term inundation pattern in Bain's Vlei pans

Approximately six inundations were predicted per year, with little variation in number (Table 4). Predicted duration was highly variable, ranging from three to 87 days, about a mean of almost 19 days, in a skewed distribution (Fig. 12). Pattern of inundation during each rain season was highly variable (Fig. 13).

Life-cycle data from some eubranchiopods in these waters

Figures 14 to 16 show that all four species examined (*Triops granarius*, *Streptocephalus macrourus*, *Branchipodopsis tridens* and *Leptestheriella inermis*) begin producing eggs well before maximum body length is reached. Egg production of *S. macrourus* tapers off sharply by 18 days and that of *B. tridens* ceases totally in that period. Those of *T. granarius* and *L. inermis* continue to increase beyond this period. While *B. tridens* grew rapidly (Fig. 15) and died off toward the end of the second week of inundation (Fig. 16), the other three species grew more slowly. *T. granarius* numbers decreased sharply by 18 days while *S. macrourus* had by far the greatest survival rate with about 30 per cent of the population being able to survive for two months in the laboratory.

Discussion

A useful model to predict the inundation of Bain's Vlei pans from rainfall data was developed and verified. It was based on the deductions that below 20 mm of rain there was insufficient surface flow to inundate the pans, between 20 mm and 80 mm there was a regression to predict period of inundation, above 80 mm the pans overflowed, and evaporation of the pans took 20 days, unless there was a follow-up rain which modified these values accordingly.

Although period of inundation must vary between pans, the pattern should be similar between pans in the same rainfall area. Therefore this model should have a wider predictive value. All that is necessary is a knowledge of the amount of rain needed in a single episode to result in surface runoff which in turn will result in an inundation (in this case it was 20 mm), of the further amount of rain needed to fill the pan to capacity or overflow (80 mm in this case), and the period of time for the water in the pan to evaporate (20 days in this case), assuming that the pan is not affected by groundwater movement.

The highly variable interannual and intraseasonal rainfall patterns in the region of pan abundance (Figs 4 and 8) belie the fact that one cannot develop a useful model of inundation. The inundation pattern derived from the model turned out to be remarkably stable between years. Over the ten years studied, the model predicted an average of 5.8 inundations per year, varying between four and eight in any one year, while the mean period of inundation of 18.8 days with a Standard Deviation of 16.6 days (Table 4) implies a degree of intraseasonal predictability that can be used as a base for a life history strategy.

Among the organisms from the pan (*Branchipodopsis tridens*, *Leptestheriella inermis* and *Triops granarius*) and the organism that was more common where inundations were longer (*Streptocephalus macrourus*) it was clear that all reached maturity within the first week of inundation and produced a store of eggs within the mean inundation period of about 19 days. All four species were iteroparous so, once egg production had begun, it continued until death of the organism, usually as a result of desiccation. *T. granarius* is a ubiquitous species in temporary waters of the Orange Free State (Seaman & Kok, 1987) and is therefore not solely from waters with inundations as short as 19 days, consequently it cannot be expected to show specialisations for such short inundations. While not enough is known of the pan habitat of *L. inermis* and while *S. macrourus* seems to be similar to *T. granarius*, it is clear that *B. tridens* is adapted to short inundations of maximum about two weeks (Figs 14 to 16). *B. tridens* grows rapidly to maximum length within eight days, most individuals are dead by two weeks and egg-production occurs within six and 14 days. Therefore the shorter the inundation the better for this species and the worse for the other anostracan *S. macrourus*.

The simplistic *r* and *K* life history strategy continuum (MacArthur & Wilson, 1967; Pianka, 1970) is not appropriate to these organisms. It is more appropriate to look at the combination of traits which make each population successful (Stearns, 1976, 1993), and the two most relevant ones are probably *time taken to maturity* and *iteroparity* which firstly allow the organism to reproduce while the aquatic habitat is available and secondly to keep putting eggs into the 'egg-bank' as long as the habitat allows.

Acknowledgments

The University of the Orange Free State is acknowledged for facilities and running costs. Marie Watson, Annetjie Botha, Sonja van Niekerk and Birgit Seaman are thanked for their technical contributions.

References

Anderson, G. & S-Y. Hsu, 1990. Growth and maturation of a North American fairy shrimp, *Streptocephalus seali* (Crustacea; Anostraca): a laboratory study. Freshwat. Biol. 24: 429–442.

Brendonck, L., 1991. Contributions to the study of the reproductive biology of *Streptocephalus proboscideus* (Anostraca, Streptocephalidae). Crustaceana 60: 145–162.

Geldenhuys, J. N., 1982. Classification of pans in the western Orange Free State according to vegetation structure, with reference to avifaunal communities. S. Afr. J. Wildl. Res. 12: 55–62.

Goudie, A. S. & D. S. G. Thomas, 1985. Pans in southern Africa with particular reference to South Africa and Zimbabwe. Z. Geomorph. N.F. 29: 1–19.

Le Roux, J. S., 1978. The origin and distribution of pans in the Orange Free State. S.A. Geogr. 6: 167–176.

MacArthur, R. H. & E. O. Wilson, 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, N.J.

Mitchell, S. A., 1991. The growth rate and growth efficiency of *Streptocephalus macrourus* (Crustacea, Anostraca) cultured on microalgae. Hydrobiologia 212 (Dev. Hydrobiol. 64): 1–10.

Pianka, E. R., 1970. On *r*- and *K*-selection. Am. Nat. 104: 592–597.

Seaman, M. T., D. J. Kok, B. J. von Schlichting & A. J. Kruger, 1991. Natural growth and reproduction in *Triops granarius* (Lucas) (Crustacea: Notostraca). Hydrobiologia 212: 87–94.

Seaman, M. T. & D. J. Kok, 1987. Ecological diversity in Orange Free State pans. In R. D. Walmsley & L. Botten (eds), Symposium on the ecology and diversity of wetlands in South Africa, Foundation for Research Development, CSIR, Pretoria, Occasional Report Series 28: 260–273.

Stearns, S. C., 1976. Life-history tactics: a review of the ideas. Q. rev. Biol. 51: 3–47.

Stearns, S. C., 1993. The Evolution of Life Histories. Oxford University Press, Oxford and New York, 249 pp.

Department of Water Affairs, 1986. Management of the Water Resources of the Republic of South Africa. Department of Water Affairs, Pretoria, South Africa.