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Life history adaptations of phyllopods in response to predators, vegetation, and habitat duration in north-eastern Natal

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Abstract

Phyllopod populations were monitored in three temporary pools differing in the amount of submerged, peripheral vegetation present, surface area and duration. The effects of these factors on the life history strategies employed by phyllopods were investigated. *Triops granarius*, various conchostracan species and the anostracan *Branchipodopsis* sp. inhabited the periphery of two pools where rooted, submerged vegetation was abundant while three *Streptocephalus* species dominated the central, unvegetated regions of the pools and the unvegetated pool. This distribution pattern appeared to be related to the animals' morphology and feeding habits. The peripheral regions of the pools were stressful habitats since they were colonized by large numbers of predators and competitors 30–40 days after inundation and they dried out sooner than the centre. The 'peripheral' species exhibited typical r-selected life history strategies; they grew rapidly, reproduced early and had short lifespans and in this way they overcame the threats presented by their habitat. The 'central' species took advantage of their predator-free, more stable habitat and exhibited life history patterns which tended towards the K-end of the r-K continuum. A degree of intraspecific variation in growth and reproduction was obvious and appeared to be related to differences in habitat duration of the three pools.

Introduction

The unpredictable nature of temporary pools and the need for their inhabitants to be adapted to survive under such conditions has been noted by many authors. In Williams' (1985) review of the biotic adaptations of animals living in temporary lentic waters of arid and semi-arid regions, he devoted a section to life history adaptations and predicted the importance of r-selection in highly ephemeral pools. Organisms in such habitats should display the following features: intense mortality in the early part of the life cycle, rapid development, high rates of maximal increase ($r_{\max}$), early reproduction, few periods of reproduction, short life cycles and density-independent mortality. However, Williams (1985) stressed, as had Pianka (1970) that 'no organism is entirely r-, K- or A-selected, for according to the risks involved, a balance will be struck which maximises the adaptive value of features drawn from each type of selection'. This may apply not only between species but intraspecifically too.

Wiggins *et al.* (1980) suggested that in temporary pools only limited amounts of nutrients are available to planktonic algae in the water column because these nutrients may be trapped in bottom sediments or adsorbed on organic particles and are consequently not returned to the dissolved form during the next wet phase. Such nutrients would, however, be available to the roots of vascular plants and in this way vegetation may serve to recycle sediment-bound nutrients. This system would only be efficient in pools exposed to the sun. Pools which are heavily shaded depend largely on leaf fall for nutrients, a system which appears to be less efficient in the nutrient budget than basins supporting heavy growth of rooted vascular plants. Wiggins *et al.* (1980) therefore considered resource levels (the type of vegetation) and habitat duration to be the most important factors determining the type of habitat and thus the community structure and faunal succession in temporary pools. They also suggested that these factors may affect the life history strategies of the fauna but noted that at a detailed level, little was known about the influences that habitat duration and resource levels have on individual species.

Literature comparing life history patterns of 'phyllopods' (used here in the sense of Fryer, 1987), from different types of temporary pools is scant. Although numerous studies have provided data on the biology of different species, features such as growth, reproduction and population densities have seldom included comparative information from habitats with different periods of inundation, degrees of predictability and types of vegetation.

Studies such as those of Belk (1977) and Hildrew (1985) showed that different reproductive and growth patterns, respectively, could be related to different habitat durations, predictability and in Belk's (1977) study, resource levels and predators as well. Takahashi (1976) however, suggested that temperature, population density and food sources were the causes of variation in growth and reproduction in *Triops granarius* (Lucas) populations in rice paddies. Laboratory studies of other species (Lake, 1968; Mitchell, 1987; Sluzhevskaya-Drobysheva, 1981) have provided similar results. In a study on the aquatic snail *Lymnea elodes* Say, Brown *et al.* concluded that although environmental factors had a greater influence on life history, genetic-based adaptations to a particular habitat (whether temporary or permanent) did cause measurable variation.

Physical and chemical factors undoubtedly influence growth, reproduction and longevity but the effect of the habitat on these aspects of life history has received little attention. The aim of this study was to monitor the phyllopod populations in habitats differing in duration, stability and the amount of vegetation present. Wiggins *et al.* (1980) and Williams' (1985) suggestions as to the importance of r-selected strategies to the inhabitants of ephemeral pools and the possibility of variation in these strategies being related to the habitat, where also examined.

Description of sites studied

Three pools in the Makathini area of north-eastern Natal, South Africa (Fig. 1) were selected. Pool 1 covered an area of about 15000 m^2 when full and consisted of one large deep (± 60 cm) basin, numerous smaller isolated or semi-isolated pools and shallow reed, sedge (*Cyperus distans* L.f., *Kyllinga erecta* Schumach. and *Cyperus fastigiatus* Rottb.) or grass-covered marshy areas. Pool 2 was approximately 2400 m^2 in area at maximum inundation. Initially this pool was vegetated only at the edges, mainly by sedges and reeds, but after about three weeks mats of floating *Ludwigia stolonifera* became established in the central part. Pool 3 was the smallest of the pools, attaining a maximum area of 600 m^2. Apart from being sparsely grassed around the perimeter, it remained devoid of any floating or submerged vegetation throughout the study.

The pools first filled after about 48 mm of rain fell in early August 1987. Pools 1 and 2 dried up after two weeks which resulted in the death of the initial phyllopod populations. Pool 3, however, held water until early January, i.e. for approximately 20 weeks. Heavy rains at the end of September refilled pools 1 and 2 and the main areas of these held water until January, by which time all phyllopod populations had disappeared. Only the small hoofprint-type pools and the peripheral, shallow areas of the larger habitats dried up during the study period, after the second inundation.

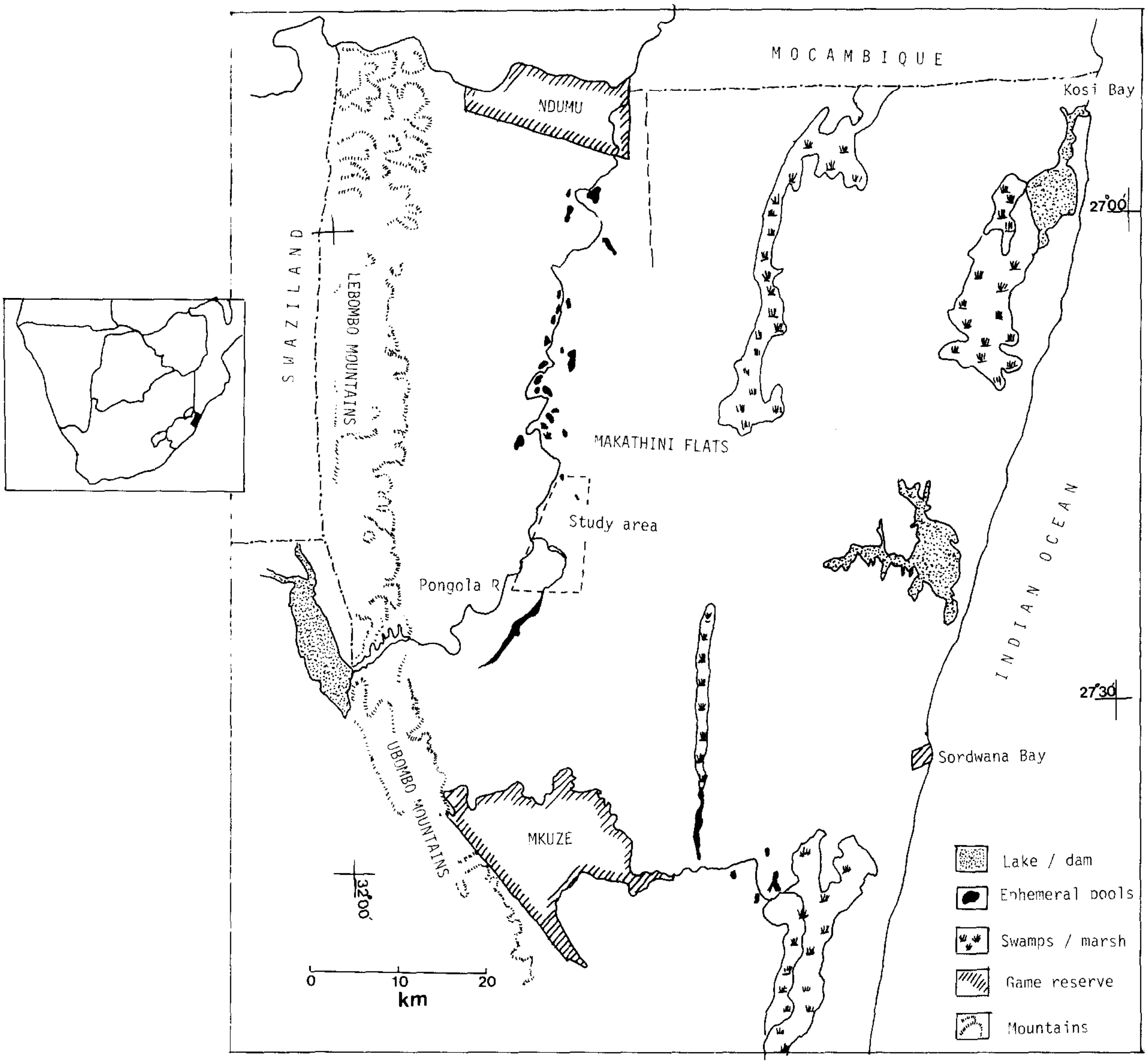

Fig. 1. Map of southern Africa showing the position of north-eastern Natal and the study area.

Materials and methods

Population abundance

A hand-held net with a mouth of 15 × 20 cm and a mesh size of 2 mm was used for taking quantitative samples. Transverse sweeps 80 cm in length were made and the depth to which the net had been submerged during the sweep was recorded. Trials in a clear pool showed that, provided disturbance of the water was kept to a minimum, and movement of the net during the sweep was swift, few animals appeared to escape. In shallow or heavily vegetated areas of the pans 80 cm sweeps were impossible and shorter 20 or 40 cm sweeps were made.

A total of 12 samples was taken at three to four-day intervals from each pool starting a week after the initial filling and continuing until all phyllopod populations had died off. Six of these samples were 'edge' samples taken not more than 2 m from the perimeter of the pool, and six were 'centre' samples, taken from the central, deeper basin. Phyllopods caught in each sample were identified, sexed and measured (median carapace length for Notostraca, total body length excluding the caudal furcae for anostracans and the length of the conchostracan carapace). Reproductive condition was also noted before they were returned to the pool. Samples too large to analyse in the field were preserved in 70% ethanol and examined in the laboratory.

Analysis of samples

Abundance estimates were expressed as the number of animals m^{-3} of water. The mean of the six samples ± standard errors (SE) of shrimps per volume of water that passed through the net were calculated for the numerically dominant species in each pool. The χ^2 (variance to mean ratio) test for agreement with a Poisson series for small samples (Elliot, 1985) was used to determine the distribution of individuals in the population. This was necessary since it affected the analysis of the samples. The distribution of the phyllopods varied from day to day which made previously used equations such as Taylor's Power Law (Hildrew, 1985) and other transformations inapplicable to the data. The abundance data were therefore presented in a straightforward manner. The mean number of each species m^{-3} of water was plotted, together with 95% confidence limits for each sampling day. Edge and centre samples were compared using the non-parametric Man-Whitney-U test (Elliot, 1985), and where these did not differ significantly, (ie. *Streptocephalus macrourus* Daday and *Streptocephalus cafer* (Lovén) in pool 3) the two sets of data were combined.

The growth of the numerically dominant phyllopod species populations in the pans was monitored by measuring all individuals caught during sampling. The mean sizes for males and females, together with standard error were calculated using the equation for small sample sizes where the number of animals measured was less than 30 (Elliot, 1985).

Results

Population density and distribution

Considerable variation, both temporal and spatial was observed in phyllopod populations. Initially the *Streptocephalus* spp. immatures were aggregated but as populations declined, they became randomly distributed although on some days they were found to be regularly spaced. The conchostracan and *T. granarius* populations were either randomly or regularly distributed. Different species, however, appeared to prefer different regions of the pools. The vegetated, peripheral regions of pools 1 and 2 were inhabited by up to eight species which included the notostracan *T. granarius*, the conchostracans, *Eulimnadia africana* (Brauer), *Leptestheria rubidgei* (Baird), *Caenestheriella australis* (Loven) and two *Lynceus* spp. and the anostracan *Branchipodopsis* sp. The deeper central regions of the pools were dominated numerically by three anostracan species, *S. cafer*, *S. macrourus* and *Streptocephalus* sp.

Populations of the latter group showed similar density trends. Large numbers (100–2600 m^{-3}) were present initially but these decreased rapidly about two weeks after inundation of the pool, with a smaller population persisting for a further 30 to 40 days before disappearing (Fig. 2). In pool 3 small populations of *S. macrourus* and *S. cafer* were present for a total of 125 and 107 days respectively (Figs. 3, 4). The fluctuations shown in these figures are probably the result of sampling errors and changes in distribution, since it was clear that only a single cohort was present and that the population did not increase (Hamer, 1989).

The presence of anostracan populations at the edges of pools 1 and 2 appears somewhat contradictory to the separation made here of species into 'edge' and 'centre' groups and the placement of the *Streptocephalus* spp. in the latter group. However, these populations were usually more dense in the centre (Fig. 2) and peaks in the densities of populations at the edge usually coincided with decreases in their numbers in the centre. It is therefore possible that these fluctuations were

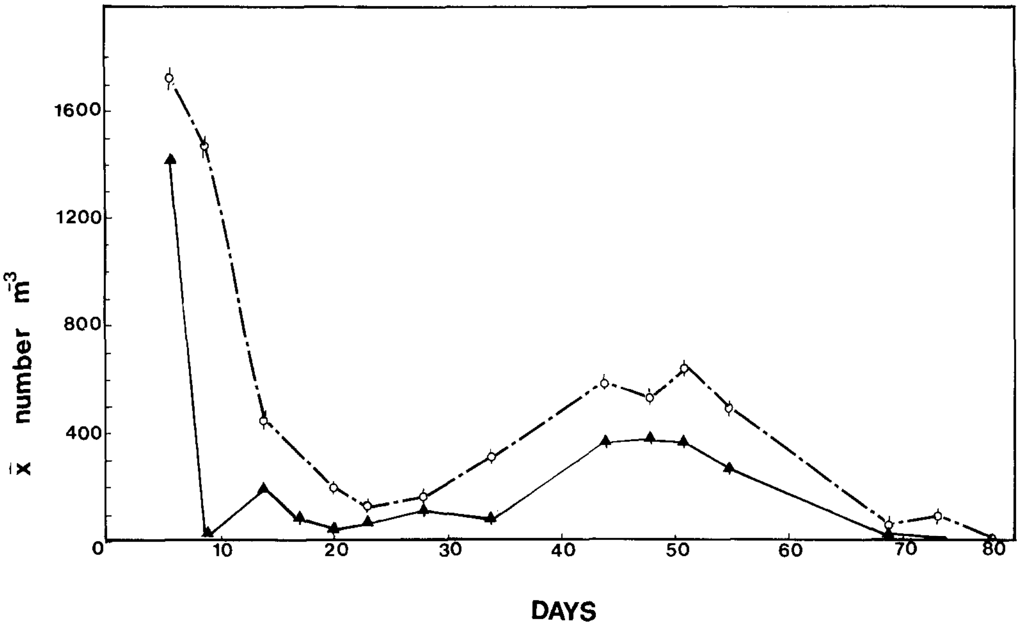

Fig. 2. Density of *Streptocephalus macrourus* in pool 2; mean number of animals m^{-3} water ±95% confidence limits ($p = 0.95$). Dotted line = centre; solid line = edge.

associated with changes in the distributions of the populations. *Streptocephalus cladophorus* Barnard was present in the peripheral regions of pool 1 but nearer the centre of the basin in pool 2. This species could, therefore, represent an intermediate between 'edge' and 'centre' species. Growth and reproduction data presented in Table 1 support this possibility.

The abundance of the other phyllopod species was difficult to represent graphically because

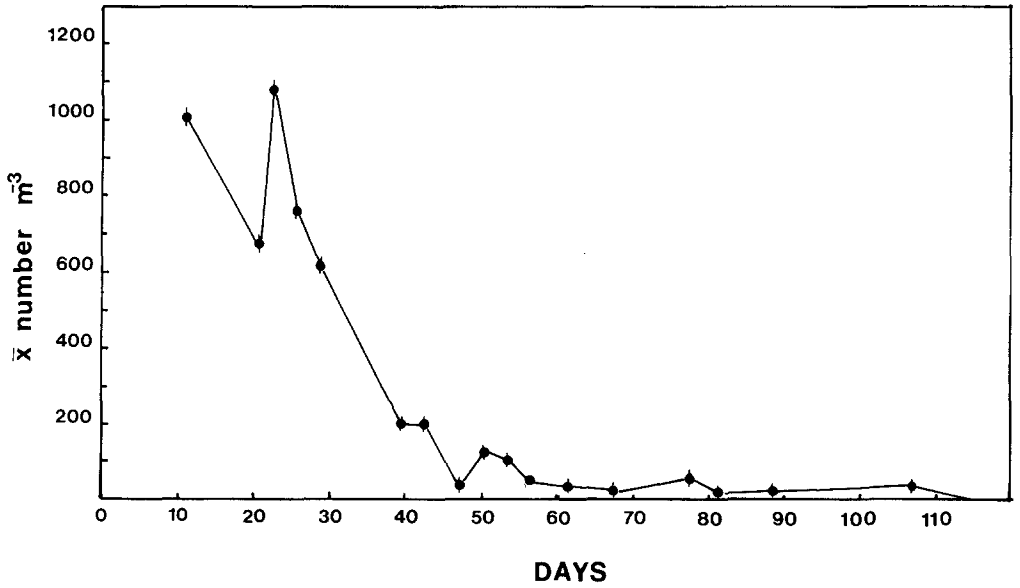

Fig. 3. Density of *Streptocephalus macrourus* in pool 3; mean number of animals m^{-3} water ±95% confidence limits ($p = 0.95$). Where confidence limits are not indicated, these were too small to illustrate clearly. Edge and centre samples were combined.

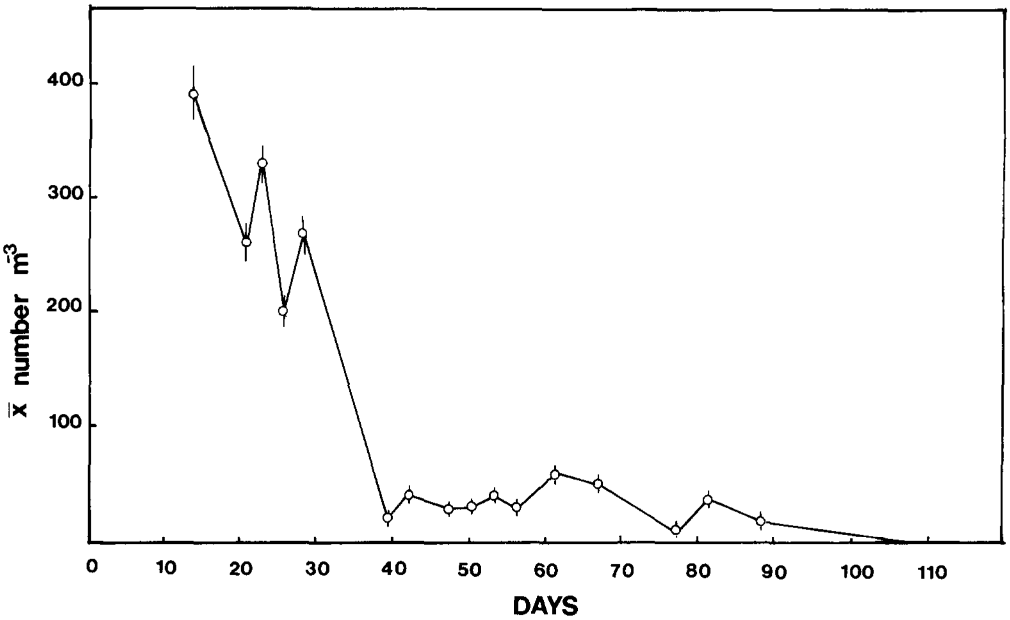

Fig. 4. Density of *Streptocephalus cafer* in pool 3; mean number of animals m^{-3} water ±95% confidence limits ($p = 0.95$). Edge and centre samples were combined.

most of these were present in the pools for only short periods and some occurred in small numbers (eg. the mean number of *Lynceus* spp. caught on any sampling day was 47.5 m^{-3} or 6 in a total of 12 subsamples). However, the population density trends of *E. africana* and *Branchipodopsis* sp. appeared to conform to a pattern shown by the other species occurring at the edges of the pools. These populations did not undergo the sudden early decrease in numbers that was exhibited by

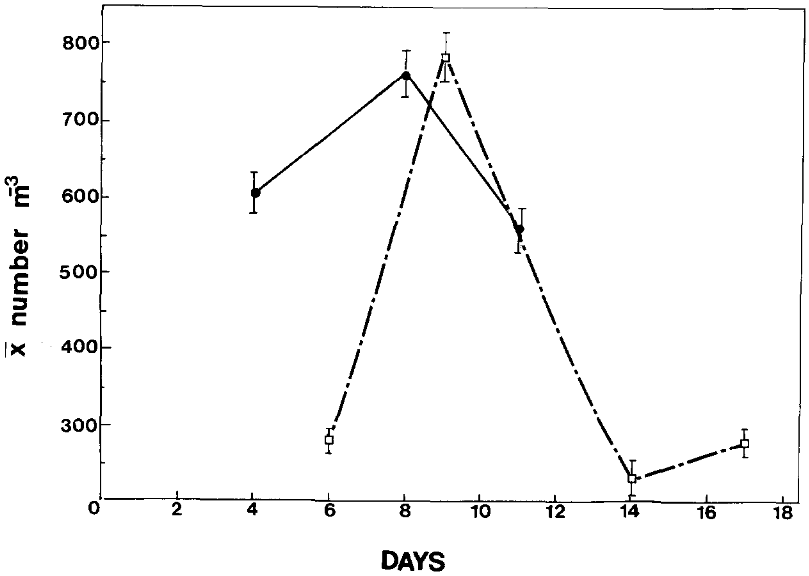

Fig. 5. Density of *Branchipodopsis* sp. in edge region of pool 1 (solid line) and of *Eulimnadia africana* (broken line) in the edge region of pool 2 (broken line). Mean number of animals m^{-3} water ±95% confidence limits ($p = 0.95$).

Table 1. Summary of growth and reproductive data for the dominant phyllopod species of the Makatini pools.

Species and locality	Average growth day^{-1} ± S.E. (mm)	% of maximum size increase day^{-1}	± age at 1st reproduction (days)	$\overline{X}$ ± S.E. size 1st reproduction	$\overline{X}$ ± S.E. maximum size (mm)	Maximum lifespan (days)	No. eggs/clutch (range)
Notostraca							
Triops granarius Pool 1	0.48 ± 0.18	3.81	7	5.65 ± 0.61	12.59 ± 0.95	26	4 – 26
Conchostraca							
Eulimnadia africana Pool 1	0.28 ± 0.17	5.21	10	4.64 ± 0.44	5.37 ± 0.73	19	225 – 296
Eulimnadia africana Pool 2	0.39 ± 0.17	5.50	8	6.48 ± 0.48	7.09 ± 0.74	18	–
Anostraca							
Branchipodopsis sp. Pool 1	0.77 ± 0.36	8.37	7	8.13 ± 1.00	9.20 ± 1.20	12	42 – 89
Streptocephalus cladophorus Pool 1	0.48 ± 0.22	5.00	10	7.28 ± 0.28	9.60 ± 0.98	20	38 – 66
Streptocephalus cladophorus Pool 2	0.50 ± 0.22	3.06	14	13.08 ± 1.62	16.35 ± 1.28	33	–
Streptocephalus cafer Pool 1	0.44 ± 0.23	2.83	10	13.00 ± 0.74	15.55 ± 1.39	35	64 – 252
Streptocephalus cafer Pool 3	0.28 ± 0.22	1.09	21	11.13 ± 0.96	25.77 ± 2.07	91	81 – 347
Streptocephalus macrourus Pool 1	0.25 ± 0.16	1.80	18	9.38 ± 0.41	13.68 ± 0.68	54	34 – 106
Streptocephalus macrourus Pool 2	0.21 ± 0.18	1.43	14	9.62 ± 0.33	14.70 ± 0.62	70	–
Streptocephalus macrourus Pool 3	0.22 ± 0.20	0.93	26	9.87 ± 0.94	23.73 ± 2.02	110	–
Streptocephalus sp. Pool 2	0.27 ± 0.18	1.54	16	10.90 ± 0.60	17.75 ± 1.82	65	18 – 68

the 'central' species. Instead, in relation to their life-span, they either maintained a relatively stable number of animals (e.g. *Branchipodopsis* sp., Fig. 5) or numbers declined gradually over a two to three week period, after which the entire population disappeared within three days. This disappearance coincided with the invasion of the vegetated edge regions of the pools by a diverse community of insect, amphibian and arachnid predators and/or competitors for space and possibly also food.

Growth and reproduction

Growth was rapid in all cases and data for seven species from all three pans are summarized in Table 1. Two types of growth pattern were evident: one for the anostracans inhabiting the central areas of the pools (*S. macrourus*, *S. cafer*) another for species inhabiting the peripheral areas. In the 'central' species, initial growth was rapid and almost exponential. This was followed by a period of little or no growth and then by a

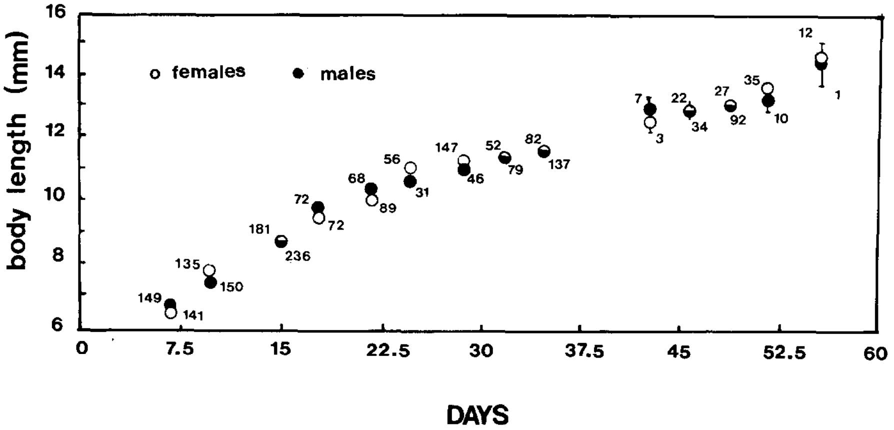

Fig. 6. Growth rate of *Streptocephalus macrourus* in pool 1. Mean total length, excluding the caudal furcae (edge and centre samples combined) ± S.E. Where S.E. are not represented, these were too small to illustrate. Numbers written above and below the symbols indicate the number of females and males measured (*n*) respectively.

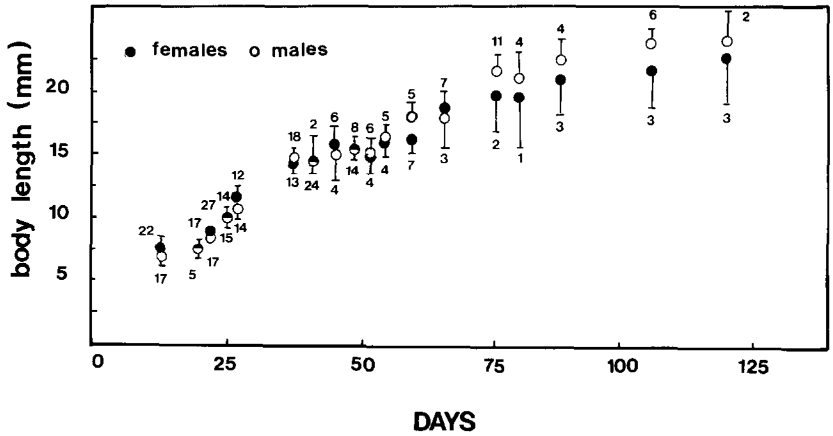

Fig. 7. Growth rate of *Streptocephalus macrourus* in pool 3. Mean total length, excluding the caudal furcae ± S.E. Numbers above and below the symbols indicate the number of males and females measured (*n*) respectively.

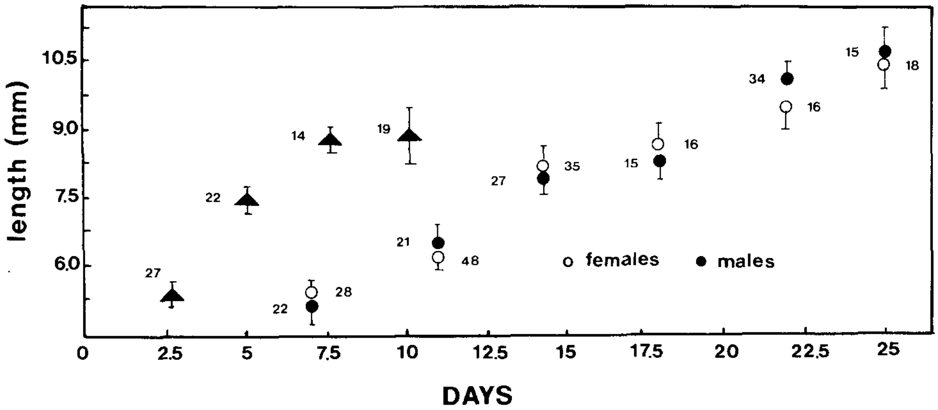

Fig. 8. Growth rate of *Triops granarius* in the edge region of pool 1 (open circles = females, shaded circles = males). Mean median carapace length ± S.E. Triangles represent the growth rate of *Branchipodopsis* sp. Mean total body length (excluding caudal furcae) ± S.E. (sexes do not separated). Numbers adjacent to symbols indicate the number of animals measured (*n*).

second period of growth until the population disappeared (Figs. 6, 7). Variation in the timing of these three growth phases, of the sizes reached and in size increases per day, was evident between species and intraspecifically in the different habitats (Table 1).

T. granarius and *Branchipodopsis* sp. in pool 1 provided examples of growth patterns typical of the species which inhabited the peripheral areas of pool 1 and the margins of pool 2. Although they experienced rapid initial growth, they then reached a period of slower growth with little subsequent increase in size (Fig. 8). These species disappeared from the habitat soon after this plateau had been reached and in both 'edge' and 'centre' species the decline in the growth phase appeared to follow closely the onset of egg production by the females (Table 1).

In addition to the different patterns of growth shown by 'edge' and 'centre' species, the former group had a greater size increase per day in terms of both length and in the maximum size reached (Table 1; columns 1 and 2). Reproductive trends, too, varied according to species and habitat. Those species living in the peripheral areas started reproducing sooner than the anostracans of the central regions (Table 1). However, because of the peripheral species' relatively brief lifespans, they had a shorter reproductive period than the late-reproducing, but longer-living 'central' species. Laboratory cultures of *S. macrourus*, *S. cafer* and *T. granarius* at 23 °C showed that egg broods are produced at two to three day intervals and that the number of eggs per brood increased with body size. Females of each of the 'central' species would, therefore, be expected to have a larger total egg-output than the females of the 'edge' species. This was true, particularly for species such as *T. granarius* and *Branchipodopsis* sp. which produced small clutches and had short lifespans (Table 1).

Discussion

This study has shown that the phyllopods of north-eastern Natal employ life history strategies typical of r-selection; they grow rapidly, reproduce early, have short life cycles with few periods of reproduction. However, there were distinct differences in their life history patterns, and also variation in the degree to which they were r-selected.

Distribution of the species within the pools appeared to be related to the presence of rooted submerged and emergent vegetation (and thus detritus) and water depth in the different regions of the habitats. Anostracans are generally filter-feeders, abstracting particles from suspension in the open water (Fryer, 1987) and they would thus have difficulty in feeding amongst the dense vegetation common in the shallow, peripheral regions of the pools. Relatively small species such as *Branchipodopsis* sp. ($\bar{x}$ body length = 7.5 mm) may, however, have been able to feed successfully in these areas at low densities. *T. granarius* and the conchostracans are omnivorous, feeding on detritus (Fryer, 1987) and these species were often seen swimming on the substratum and in the laboratory at least, only swam freely for short periods. Fryer (1988) also noted this behaviour in *Triops* and stated that the morphology of the Notostraca is not adapted to surface swimming but rather to a benthic habit. For species with such living and feeding habits the peripheral habitat, where rooted vegetation and thus detritus was abundant and the water shallow, would probably be more suitable than the deep and vegetation-scarce central regions. In addition to the lack of suitable food in the centre, the bottom waters of the central basin were usually oxygen-depleted relative to the surface and marginal waters (Hamer, 1989). Over a 24-hour period for instance, the range of dissolved oxygen concentrations was 6.3–3.3 mg l^{-1} while at the bottom of the central region it was 5.0–1.5 mg l^{-1}. Species which spend much time on the substratum would have to move closer to the surface when the availability of oxygen became stressful and for heavy-shelled animals such as the conchostracans and *T. granarius*, this would be energetically expensive.

However, the peripheral regions of the pools appeared to be stressful in other ways: they became colonized by a diverse non-phyllopod fauna many of which were predators and others possible competitors, and they dried up sooner than the central basin. The inability of phyllopods to avoid predators has been mentioned by a number of authors (Bishop, 1967; Hartland-Rowe, 1972; Wiggins *et al.*, 1980) and their lack of mobility means that they cannot leave a habitat which is drying up. The 'edge' species have therefore developed life history strategies which ensure their continued existence, while the 'central' species were able to take advantage of the relative stability (in terms of longer duration and an absence of predators) of this part of the habitat.

Although essentially r-selected, the life history patterns of *S. macrourus*, *S. cafer* and *Streptocephalus* sp., when compared with those of the 'peripheral' species tended towards the K-end of the r-K continuum. Growth was, on average, slower (0.21–0.28 mm d^{-1}), the time and size at which egg production started varied (Table 1) but even though the females were still relatively small (9.38–13.0 mm), they were between 4 and 26 days older than gravid females of species occurring at the edge. As in K-selected organisms, they attained a large body size (particularly in pool 3), and outlived those species living at the edge. The long lifespan meant too, that numerous egg broods were produced per female. Population density and survivorship patterns of the 'central' species were, however, atypical of K-selected animals inasmuch as a high population density which declines rapidly early in the life history is a trait usually associated with r-selection. The reason for these early population decreases, which occurred in all the *Streptocephalus* spp. sampled, is uncertain but may be related to resource availability. Wiggins *et al.* (1980) suggested that only limited amounts of nutrients are available to planktonic organisms in the water column possibly because nutrients may be trapped in bottom sediments. The initial food available might have been insufficient to maintain a large anostracan populations, but no evidence was collected to support this hypothesis.

While the 'central' species avoided predation by inhabiting, predominantly, the predator-scarce unvegetated, deeper regions of the pool, the 'peripheral' species achieved this by completing their life cycle in less than 40 days, i.e. before predators became abundant in their part of the habitat. By compacting their life history into a short period, they maximised the chances of reaching maturity and reproducing before their unstable, short-duration habitat dried out. The life history strategies shown by the 'peripheral' species are, mainly, typical of r-selection. Growth was rapid (0.28–0.77 mm d^{-1}) and in most cases the leveling off shown by the *Streptocephalus* spp. inhabiting the centre, occurred while the animals were still small, and growth did not resume afterwards. Reproduction was early (7–10 days post-hatching) in all the 'peripheral' species, but since lifespans were only 12 to 33 days, probably only a few egg broods per female were produced. Population density was not typical of r-selected organisms; populations were relatively stable or declined gradually and the entire population disappeared as a result of a sudden crash. The disappearance of the 'peripheral' species occurred even if the habitat did not dry up, but whether this happened before the arrival of predators or as a result of them was not clear.

Since the life cycles of 'edge' species were short, and few broods of eggs per female were produced, there may have been some advantage in maintaining the initial population densities. the larger the population of egg-producing females, the greater the total egg output. The detritus available in these areas would probably have contained sufficient nutrients to support these populations. This scenario is in contrast to that documented for the 'central' species in which, although their populations rapidly became depleted, each surviving female produced many clutches of eggs. Since larger females produced more eggs, they achieved an even greater total egg output and this may account for their denser initial populations than those of the 'edge' species (Figs. 2, 3, 4).

Intraspecific variation in life history was also recorded in the three study pools. This was particularly noticeable in respect of growth, reproduction and lifespan of *S. macrourus* and *S. cafer* in pool 3 when compared with pools 1 and 2 and it would appear that this variation is correlated with habitat duration. Pool 3 did not dry up after the first inundation in August 1987, while the other two did, despite the fact that the former had a substratum with a higher sand and lower clay and organic matter content than the latter two (Hamer, 1989). The prolonged duration of pool 3 was probably a result of underground seepage and meant that the anostracan populations there were able to reach sizes at which many eggs per clutch per female could be produced (up to approximately 347), and since they lived for about 100 days, many clutches were produced. However, this and the other records of intraspecific variation observed may also have been related to food quality and availability.

Conclusions

The results of this study support the predictions of Wiggins *et al.* (1980) that vegetation (which influences the quantity and source of detritus) and habitat duration determine community structure, and that these factors determine the type of habitat and the life history strategies of its inhabitants. Williams' (1985) predictions that r-selected strategies are dominant in the life histories of ephemeral pool inhabitants as well as the presence of both inter- and intraspecific variation in this respect are relevant too. However, as has been shown by other studies (Lake, 1968; Mitchell, 1987; Takahashi, 1976), population density, food, temperature and water chemistry also influence growth, reproduction and longevity of phyllopods. Although Brown *et al*'s (1985) study of the snail *L. elodes* showed that food availability influenced growth and reproduction to a greater extent than the origin of the snails, those snails from temporary pools always grew more slowly, matured at a smaller shell size and had higher fecundities than individuals from permanent pools. This lends support to the possibility that adaptations to specific habitat types are genetically based. Belk's (1977) evidence for variation in the reproduction trends of an anostracan species being related to the predictability of the habitat gives further strength to this hypothesis. Hildrew's (1985) study showed that different growth and reproduction rates occurred within the same population in response to different inundation patterns.

Obviously further research is necessary to conclusively identify the effects of the various factors on life history strategies in temporary waterbodies. Translocation experiments, laboratory culture of animals from different habitat types, and reactions of phyllopods to food type and predators would provide interesting data on this subject.

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