

13. A synopsis of ecological information on the saline lake rotifer *Brachionus plicatilis* Müller 1786

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Introduction

The rotifer *Brachionus plicatilis* Müller, shown in Fig. 13.1, is a cosmopolitan inhabitant of inland saline and coastal brackish waters. It tolerates a remarkable range of environmental conditions and, especially in alkaline (soda) lakes, may attain very high population densities. Like the familiar brine-shrimp *Artemia*, and the green alga *Dunaliella*, *B. plicatilis* is used widely as a basic food in the intensive culture of certain marine crustaceans and fishes. Indeed, most ecological knowledge of the species stems from its significance in mariculture (e.g. Solangi & Ogle, 1977).

Aside from commercial applications, studies of cosmopolitan forms like *B. plicatilis* are valuable in other ways. They may lead to useful insights into the ecology of saline lakes of the world generally, particularly insights that distinguish local or geographic influences and those of universal significance. They may strengthen the basis for comparison and perhaps classification of salt lake communities. And there may be rewards in promoting complementary investigations by ecologists interested in salt lakes in other countries.

B. plicatilis, in particular, is a potential focus for study of communities at lower salinities than those favoured by *Artemia* and *Dunaliella*, each already the subject of considerable study (e.g. Geddes, Borowitzka; this volume). It is interesting to consider generally the ecological attributes of *B. plicatilis* that suit it well, evidently, for life in saline water. Accordingly, this paper offers a brief resumé of present knowledge of the species, and indicates some options for further study.

Systematics

Brachionus plicatilis is a member of the Brachionidae, largest of the ploimate families among the monogonont Rotifera. There is some debate about the composition of the Brachionidae (e.g. see Pejler 1977a), but not over inclusion of *Brachionus*. The genus is defined by similarities in the structures of the lorica and foot, and species are discriminated by patterns of the pectoral and occipital lorica margins, by lorica shape, and by structure of the foot and position of the foot-opening (Sudzuki 1977; Sudzuki & Timms 1977). The genus has not been reviewed since 1940 (Ahlstrom 1940), despite several later additions (e.g. see Koste 1978) that suggest a total complement of about 34 species.

Strictly, the classical concept of a biological species cannot apply to Rotifera because their life cycles involve alternation of sexual and asexual generations. For rotifer taxonomy, Ruttner-Kolisko (1974) favours Simpson's concept of an evolutionary species – an ancestral-descendant lineage of populations with its own distinct evolutionary tendencies. Hence most recent taxonomic works (e.g. Ruttner-Kolisko 1974; Koste 1978; cf. however Kutikova 1970) are guarded in use of the term 'species', and represent forms like *B. plicatilis* as ecophenotypes within Formenkreise. Pejler (1977b) provides a useful general discussion of problems in rotifer systematics.

Koste (1978) regards *B. plicatilis*, with *B. baylyi* Sudzuki & Timms, as a member of the *plicatilis* species-group, within the *urceolaris* Formenkreis. Other members of the Formenkreis include the typically freshwater *B. urceolaris* Ehrenberg, *B.*

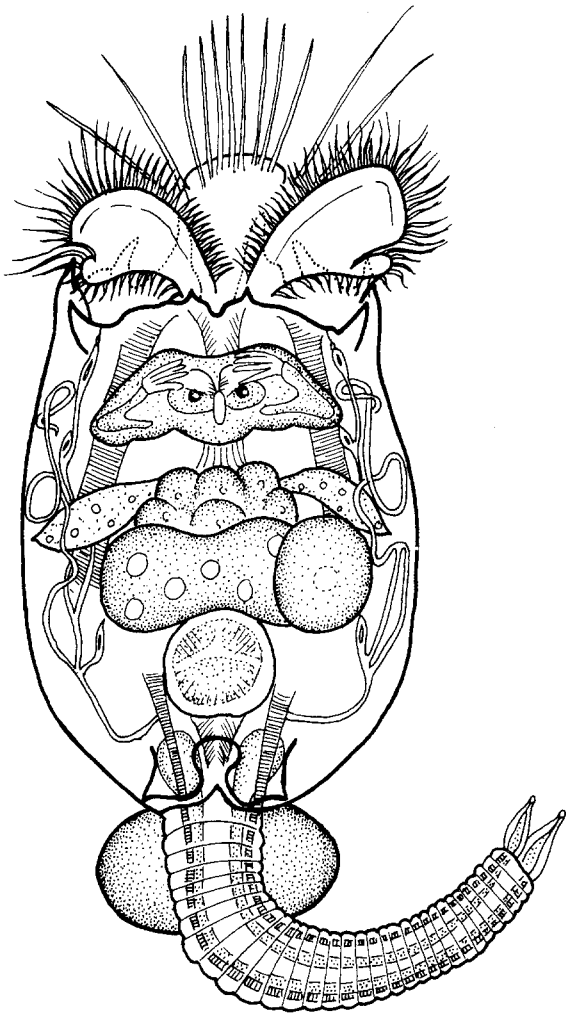


Fig. 13.1. *Brachionus plicatilis*. (Composite drawing by Ruth Hughes.)

variabilis Hempel and *B. rubens* Ehrenberg, and the saline water *B. pterodinoides* Rousselet and *B. novae-zelandiae* (Morris). Ruttner-Kolisko (1974) places *B. plicatilis* in a similar Formenkreis, apparently because the constituent forms may be crossed 'without difficulty' (loc. cit., p. 65), although earlier (p. 33) it is suggested that *B. plicatilis* and *B. urceolaris* will not interbreed (see, however, Ruttner-Kolisko 1969).

Taxonomic problems are exacerbated by the wide variations in size and shape displayed by forms among the Rotifera. *B. plicatilis* especially is variable (Koste 1980), as might be expected of an animal so tolerant of environmental variations and so widely distributed. For example, typical lorica

lengths recorded for *B. plicatilis* span 125–315 μm (Koste 1978), and a form approaching 440 μm recently was discovered in certain lakes of western Victoria, Australia (Koste & Shiel 1980a, b). In addition, Epp & Winston (1977) carried out physiological studies on cultured *B. plicatilis* averaging 400 μm 'body length'. It would be interesting to analyse the variation with regard for possible environmental correlations.

Environmental tolerances

B. plicatilis is recorded from all biogeographic Regions other than Antarctica (Pejler 1977a). Its distribution suggests an efficient means of dispersal, and seemingly its local occurrence depends mainly on the presence of a tolerable environment.

Dispersal undoubtedly is accomplished via the resting egg stage, through transport by wind, water and animals. However, whilst the factors initiating production of resting eggs are at least partly understood (see below), evidently little is known of the actual tolerances and longevity of the egg, or of the precise means and rate of dispersal.

The salinity tolerance of *B. plicatilis*, reported by Ito (1956, 1960), is from about 1 to 97 g/l. (Ruttner-Kolisko's (1972) suggested limit of 200 g/l is evidently a typographic error.) The species also has a wide tolerance of bicarbonate alkalinity, having been recorded from a range of 10 to 1 400 meq/l (Ruttner-Kolisko 1972). Highest population densities probably occur in waters of high bicarbonate concentration. For example, in Lake Werowrap, Australia, *B. plicatilis* has attained a peak density of 7 100 per litre, under conditions of 40.1 g/l salinity, 225 meq/l alkalinity, pH 9.8 and temperature 21 °C (Walker 1971, 1973). In such highly alkaline habitats, *B. plicatilis* typically is associated with another rotifer species, *Hexarthra jenkiniae* (de Beauchamp), but at lower pH the latter is replaced by *H. fennica* (Levander) (e.g. Ruttner-Kolisko 1974).

Epp & Winston (1977) showed *B. plicatilis* to be essentially an osmoconformer, its body fluid concentration changing (59 to 936 mOsm) with that of the environment (correspondingly, 32 to 957 mOsm). It does, however, maintain slight hyperosmoticity over most of the range tested (from c. 1 to 35 g/l). The imbalance evident at low concentrations (cf. environment 32, body fluid 59 mOsm)

points to intolerance of salinities below about 1 100 mg/l. Although *B. plicatilis* in culture can be maintained for some time at this salinity, given excess food and no competition, it is unlikely to occur in nature under these circumstances. Epp & Winston concluded that *B. plicatilis* is excluded from low salinities by its inability to tolerate a body fluid concentration of less than about 59 mOsm.

The upper salinity limit reported by Ito (1956, 1960; viz. 97 g/l, or 2 860 mOsm) is well beyond the range tested by Epp & Winston (1977). These authors were able to transfer animals directly to salinities up to 50‰ seawater concentration, but needed to acclimate cultures over several months to sustain transfer up to 100‰ seawater, and were unable to progress farther.

In later work, Epp & Winston (1978) demonstrated that whereas the activity and respiration of *B. plicatilis* decrease following rapid dilution of the medium, as is general among osmoconformers, changes of pH *per se* have no effect. Acclimation upwards from 10 to 50 and 100 mOsm (i.e. from c. 350 to 1 750 and 3 500 mg/l) invokes increased activity and oxygen consumption.

Complementary studies are reported by Worley (1928) and Ruttner-Kolisko (1972). Worley observed that *B. mülleri* Ehrenberg (syn. *B. plicatilis*) becomes temporarily sluggish on transfer from 45 to 32 g/l salinity. Ruttner-Kolisko's (1972) observations of activity and respiration of *B. plicatilis* spanned five dilutions of seawater (1–35 g/l salinity) and pure sodium-bicarbonate solutions of equivalent concentration (1–42 g/l NaHCO₃, or 12–500 meq/l alkalinity). In the pure bicarbonate solutions, the growth of clones diminishes with increased concentration. Oxygen consumption does not vary markedly (mean 55×10^{-4} µg/h; amictic ♀ with egg, at 20 °C), except for significant reductions at low salinity (1 g/l) and at higher bicarbonate concentrations (above 21 g/l NaHCO₃, or 250 meq/l alkalinity). Ruttner-Kolisko concluded that half-strength seawater is an optimal environment for *B. plicatilis*, with regard to the range tested (cf. Theilacker & McMaster 1971).

The number of eggs carried by female *B. plicatilis* apparently is correlated with salinity and/or alkalinity. Ruttner-Kolisko (1972) suggested that amictic females probably have a maximal production of 23–24 eggs per life-time, indicating that under optimal conditions females may carry up to

five eggs at one time (see further below). Recently, Lubzens *et al.* (1980) showed that rapid dilution of seawater cultures of *B. plicatilis* invokes a large increase in the number of females carrying multiple eggs. In Lake Werowrap, Walker (1973) reported that females typically carried one egg, except in the spring and summer periods of rapid population growth when two (very rarely three) eggs were carried. However, in nearby Red Rock Tarn, a pond of similar 'chlorocarbonate' composition but about half the salinity of Werowrap (i.e. about 15–20 g/l salinity and 100 meq/l alkalinity), female *B. plicatilis* generally carried 3–5 eggs. It seems plausible that the average number of eggs per female, relative to the maximum possible number, is indicative of whether optimal conditions prevail.

Most saline lake animals are derived from freshwater ancestors, a generalization that Beadle (1974, p. 264) suggested is valid for *B. plicatilis*. However, according to Epp & Winston (1977), the inability of *B. plicatilis* to regulate hypotonically in environments approaching seawater concentration may indicate a marine ancestry. This is an interesting problem that requires certain clarifications. In particular, it is necessary to clarify the upper limit of salt tolerance for the species, making allowance for the obviously important effects of acclimation. It would be useful then to have information about the osmotic behaviour of *B. plicatilis* at salinities beyond seawater, approaching the uppermost limit of tolerance, and some measure of its ability to withstand fluctuations in salinity, especially at high salinities. Further data are needed on activity and respiration and osmotic behaviour in highly alkaline waters of mixed chemical composition. The effect of increased pH on calcium availability may have implications for aging in *B. plicatilis* and other rotifer species (e.g. see King & Miracle 1980). A differential effect favouring *B. plicatilis* could help account for the development of dense populations of this species in alkaline waters.

Little more information is available on the environmental tolerances of *B. plicatilis*. Its distribution indicates a polythermal species likely to withstand extreme temperature ranges (e.g. 5 to 29 °C; Walker 1973). Epp & Lewis (1980) discussed the metabolic consequences of frequent radical temperature changes in a pond population of *B. plicatilis*. Its occurrence in high salinities shows an ability to tolerate relatively low oxygen concentra-

tions. Ito (1956) reported the concentrations of chlorinated lime, copper sulphate and calcium hydroxide needed to exterminate *B. plicatilis* from eel-culture ponds, and Ito & Iwai (1956a) described the phototactic and 'geotactic' responses of the species.

Food and feeding

B. plicatilis generally is regarded as a non-selective, polyphagous species among the filter-feeding planktonic Rotifera. Its diet may include various blue-green, brown, green and red algae, as well as bacteria and yeasts (e.g. Chotiyaputta & Hirayama 1978; Doohan 1973; Furakawa & Hidaka 1974; Hirata & Mori 1967; Hirayama & Watanabe 1973; Ito 1955a, 1957, 1960; Ito & Iwai 1957; Pourriot 1965, 1977; Ruttner-Kolisko 1972; Starkweather 1980; Walker 1973). Although Pejler (1977a) remarked that the diet may not include cryptomonads and chrysophytes, the latter should be included *fide* Theilacker & McMaster (1971) and perhaps Pozuelo (1977).

Laboratory studies by Ito & Iwai (1957) and Chotiyaputta & Hirayama (1978) have established that *B. plicatilis* selectively filters algae less than c. 12–15 μm in size, and that there may be some element of food quality selection. Chotiyaputta & Hirayama found that *B. plicatilis* selectively removes *Chlamydomonas* from a mixture with the larger *Olithodiscus*, and that filtering rates among senescent *Chlamydomonas* are less than among actively-growing cells.

Reported maximum filtering rates for (individual) *B. plicatilis* include 0.140 $\mu\text{l}/\text{min}$ among *Chlamydomonas*, 0.034 $\mu\text{l}/\text{min}$ among *Olithodiscus* (Chotiyaputta & Hirayama 1978), 0.100 $\mu\text{l}/\text{min}$ among *Chlorella* (Hirayama & Ogawa 1972), 0.050 $\mu\text{l}/\text{min}$ among *Rhodotorula* (Starkweather 1980) and 0.025 $\mu\text{l}/\text{min}$ among *Dunaliella* (Doohan 1973). Starkweather & Gilbert (1977) drew attention to the importance of allowing for rapid gut passage times in rotifer feeding determinations, and suggested that Doohan's estimates of ingestion could be too low. Starkweather (1980) demonstrated differences in the filtering rates of *B. plicatilis* in three different food suspensions (*Rhodotorula*, *Euglena* and bacteria), and found that rates decreased at high food concentrations.

Hirayama & Ogawa (1972) also found that filtering rates decrease in *Chlorella* densities greater than 2 million cells/ml, although the amount consumed may not change.

It is clear that *B. plicatilis* daily ingests a prodigious amount of food. From the data of Hirayama & Ogawa (1972), Dumont (1977) calculated that *B. plicatilis* may consume more than four times its dry weight of *Chlorella* each day. Doohan (1973) and Pourriot (1977) suggested that much of the ingested material is superfluous and passes through the gut undigested.

An analysis of the energy budget of *B. plicatilis* by Doohan (1973) indicated relatively low assimilation (19.4%). Of the assimilated energy, 56.7% was diverted to egg production and 40.9% to respiration. Dewey (1976, *fide* Edmondson 1977) found that for *B. plicatilis* maintained at three temperatures and fed variously on three diets, assimilation varied between 28.8 and 38.2%. Dewey also observed that the growth of clones varied with both quantity and quality of the food offered. A contrary conclusion was reached by Theilacker & McMaster (1971), who found no differences in the doubling times of *B. plicatilis* cultured with four algal species.

Life history

The life cycle of *B. plicatilis* follows the pattern typical of monogonont rotifers, involving both female parthenogenesis and sexual reproduction (e.g. Ruttner-Kolisko 1974; Gilbert 1977). Amictic female rotifers produce amictic (diploid) eggs that develop parthenogenetically into amictic females. This cycle may be interrupted by an environmental cue that induces production of mictic females, which produce mictic (haploid) eggs. Unfertilized mictic eggs develop parthenogenetically into haploid males. Fertilized mictic eggs form 'resting' eggs, containing encysted, dormant embryos; these ultimately hatch, again on an environmental cue, as amictic females.

Mictic and amictic female *B. plicatilis* are morphologically indistinguishable. The mictic 'male egg', however, is smaller than the amictic egg, and the mictic resting egg is larger, with a thick, faintly granulated outer layer. The development time of the male egg is longer than that of the amictic egg (30 cf. 21 h at 20 °C), but the interval between laying

Table 13.1 Life history data for amictic females of *Brachionus plicatilis*.

| Temperature | Amictic egg development | Ave egg-interval | Maximum progeny | Ave juvenile period | Ave reproductive period | Ave senile period | Life-time |
|-------------|-------------------------|------------------|-----------------|---------------------|-------------------------|-------------------|-----------|
| °C | h | h | | h | h | h | h |
| 15 | 32 | 7.0 | 23 | 72 | 142 | 114 | 360 |
| 20 | 24 | 5.3 | 23 | 45 | 91 | 80 | 240 |
| 25 | 14 | 4.0 | 20 | 30 | 73 | 51 | 168 |

Source: Ruttner-Kolisko (1972).

is relatively short (3.5 cf. 5 h at 20 °C; Ruttner-Kolisko 1974). Little is known of the stimulus (or stimuli) responsible for the hatching of resting eggs; Ruttner-Kolisko's (1974, p. 35) observation that hatching in culture is irregular is perhaps some reason to expect that there is variation among resting eggs as an adaptation to uncertain environments.

A summary of Ruttner-Kolisko's (1972) data concerning amictic egg production by *B. plicatilis* is shown in Table 13.1. A notable feature is the relatively long period of senility: regardless of temperature, about one-third of the life-time of amictic females is occupied by the post-ovigerous, or 'senile' period. If this pattern applies also to natural populations, it seems remarkable that the senile individuals should remain, as they would be competing for food resources, contributing to crowding, and yet not contributing to reproduction. It is possible, however, that the egg-laying of females under culture conditions is more rapid than in nature, and that the natural period of senility is considerably shorter. In either case, the post-ovigerous phase of amictic females has interesting implications for rotifers in mass culture and in natural populations. For mictic females there is not a senile period, although the juvenile period is twice as long as that of amictic females (Ruttner-Kolisko 1974). This, too, has interesting implications for population structure.

Population dynamics and production

Factors in the production of mictic females were reviewed by Gilbert (1977). Most studies of *Brachionus* spp. implicate high population density, or crowding, as a factor in the induction of mixis, an

effect that Gilbert suggested may be mediated by a chemical substance released by the rotifers. The effect, however, is often not clear-cut. Miracle & Guiset (1977) observed mixis to develop in caged natural populations of *B. plicatilis*, possibly as a consequence of crowding; alternatively, an infestation of unidentified parasites, noted by these authors, may have been implicated. Theilacker & McMaster (1971) reported that mass cultures of *B. plicatilis* in densities up to 200 rotifers/ml showed no inhibition of reproduction, but did not indicate whether mixis occurred. Ito's (1960) study, involving long-term cultures of *B. plicatilis* without change of medium, indicated that large numbers of mictic females were produced when high population densities were first attained, but their numbers declined subsequently despite continuing high densities (cf. also Pozuelo 1977).

Ruttner-Kolisko (1974) implied that virtually any environmental change, as well as crowding, may induce mixis (see also Lubzens *et al.* 1980). However, Scott's (1977) data for *B. plicatilis* in long-term chemostat cultures suggest that in a stable environment, with a sustained excess of food, production of mictic and amictic females is continuous. The notion of a chemical intermediary was discounted because a proportional dilution effect could not be demonstrated; however, this assumes that there is not a simple threshold effect. Scott suggested that amictic females in culture may need to exceed a critical age before mixis can occur.

Reports by Ito & Iwai (e.g. Ito 1960; Ito & Iwai 1958), concerning the 'Mizukawari' (summer phytoplankton-kill) phenomenon in Japanese eel-culture ponds, contain much useful information on the ecology and population dynamics of *B. plicatilis*. In this situation, the summer population growth of rotifers is so rapid as to outstrip the

available food resources, leading to destruction of the rotifer population and adverse changes in water quality.

The one seasonal study of the dynamics of a natural, athalassic population of *B. plicatilis* appears to be that of Walker (1973), with regard to Lake Werowrap, a shallow (c. 1.4 m), saline (23–56 g/l) lake in western Victoria, Australia. *B. plicatilis* dominated the zooplankton of the lake throughout the period of study (1968–1970), although *Hexarthra jenkiniae* and two ciliate species occurred transiently. The pattern of rotifer population growth differed in each year, but there generally was a seasonal trend of peak growth in spring and summer, a decline in autumn, and low densities over winter. Until winter 1969, when the lake salinity had risen from about 25 to 45 g/l, the phytoplankton consisted of *Anabaena spiroides*.

Rotifer densities attained a relatively low summer peak of c. 2 000 per litre, and it appeared that *Anabaena* was not effectively utilized as a food. After winter 1969, the salinity rose beyond 45 g/l, and *Anabaena* was displaced by *Gymnodinium aeruginosum* and a species of *Chroococcus*, both within the effective size-range of filter-feeding by *B. plicatilis*. Increases in the algal populations during the following spring and summer were accompanied by a marked increase in rotifer densities, attaining a peak 7 100 per litre in late summer. Although algal production was sustained through autumn, both species declined in abundance, and *Gymnodinium* in particular changed physiologically and increased markedly in size. The *B. plicatilis* population declined sharply to sustain densities of c. 200 per litre through winter. Seasonal changes in egg numbers corresponded generally with changes in

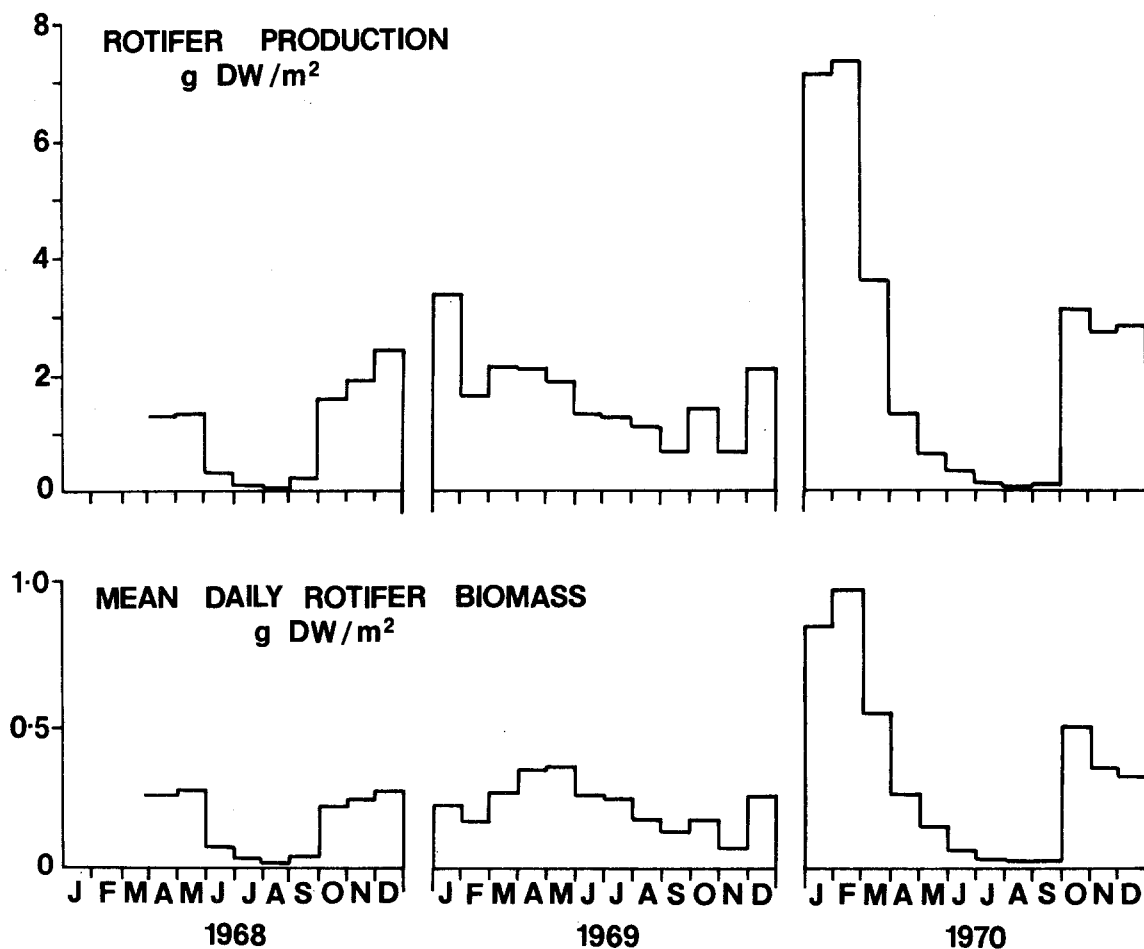


Fig. 13.2 *Brachionus plicatilis* in Lake Werowrap: Mean daily biomass and production on a monthly basis.

the rate of population growth, although as mentioned earlier the female rotifers rarely carried more than two eggs at one time. Male rotifers also were present in general accord with peak populations, and resting eggs were present in the lake sediments throughout the study. Additional information on natality and mortality is given by Walker (1973).

Unfortunately, life history data were not obtained for the Lake Werowrap population, and hence an accurate determination of the secondary production of *B. plicatilis* is not possible. However, a rough calculation is possible if Ruttner-Kolisko's data (Table 13.1) may be assumed to apply to the Werowrap population. To provide this estimate, numbers of amictic females (Walker 1973: Fig. 17) were used to calculate mean daily biomasses for each month, using the dry weight data of Doohan (1973: Table 4). Generation times at each mean monthly water temperature were estimated by linear interpolation and, where necessary, extrapolation of Ruttner-Kolisko's (1972) data. Finally, these were combined to compute estimates of monthly production by Galkovskaya's equation (e.g. Ruttner-Kolisko 1974, p. 30).

The monthly biomass and production estimates for *B. plicatilis* are shown in Fig. 13.2. By summation, estimated production over the latter nine months of 1968, and over 1969 and 1970, was 9.14, 19.09 and 28.92 g dry-weight/m². If calorific equivalents are calculated, using the values 5.034 kcal/g ash-free dry weight and 11.7% ash (Walker 1973), the respective estimates become 40.63, 84.86 and 128.55 kcal/m². For comparison, during 1970 the annual production of phytoplankton was c. 4 110 kcal/m² (Walker 1973), and annual production of the benthic chironomid *Tanytarsus barbitarsis* was c. 320 kcal/m² (Paterson & Walker 1974).

Doohan's (1973) analysis of the energy budget of *B. plicatilis* in culture included valuable information on production and efficiencies. Clearly, *B. plicatilis* is highly efficient at the conversion of assimilated energy into reproductive output. However, it is relatively inefficient at making energy available to predators, because of its small investment in body-growth.

Conclusion

Brachionus plicatilis is a consummate *r*-strategist,

as presumably are most inhabitants of athalassic saline lakes. It demonstrates clearly the principal correlates of *r*-selection (e.g. Pianka 1970): in a harsh, uncertain environment, the life cycle is short, competition generally is lax, and population densities are prone to marked changes, often with catastrophic mortality. Continued survival is ensured by dormant eggs that are easily dispersed and resistant to environmental adversity. Selection has favoured a high innate capacity for increase, and hence rapid population growth, providing for effective colonization of new habitats. The general outcome has been to favour productivity rather than efficiency.

Most information about *B. plicatilis* refers to populations in culture, and some care is needed in relating this to the ecology of saline lakes. However, it offers a strong basis for investigations of the dynamics of natural populations; the foregoing discussion points to several opportunities for particular study. There remains an intriguing path for future research: a series of fascinating problems in population ecology, and surely an important contribution to knowledge of salt lake communities.

Acknowledgement

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A small number of references, not mentioned in the text, have been added to provide a more complete bibliography.

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