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Myxococcal predation of the cyanobacterium *Phormidium luridum* in aqueous environments

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Abstract. Two strains of *Myxococcus xanthus*, and a strain of *Myxococcus fulvus* were compared with respect to their ability to entrap and lyse trichomes of the cyanobacterium *Phormidium luridum* var. *olivaceae*. All of these isolates form colonial aggregates and spherules in either axenic culture with a tryptone-salts medium or in a mixed culture with viable cyanobacterial cells as the sole source of nutrients. Light microscopy showed evidence of swarming activity on the surface of all three myxococci with the accompanying formation of fruiting structures. Extended incubation of mixed cultures showed the myxococci to be capable of long-term control of the cyanobacterial population with predator-prey population cycling occurring on average every 9 days. Serial transfer of mixed cultures into either fresh autotrophic medium or cyanobacterial cultures of 10^7 per ml showed the persistence of predatory activity. Myxococcal densities were shown to return repeatedly to initial virulent levels. Predator inoculum levels could be reduced to 50 cells per 100 ml in a cyanobacterial culture of 10^7 per ml. These *in vitro* data enhance the potential of the myxococcus predatory colony as a biological control agent for *in situ* cyanobacteria.

Key words: Biological control – Colony – Cyanobacteria – Entrapment – Lysis – *Myxococcus* – *Phormidium* – Predatory – Prey – Spherule

In our first paper describing the relationship between spherule-forming myxococci and cyanobacteria in aqueous mixed cultures, the early stages of this predatory interaction were emphasized (Burnham et al. 1981). Microscopy showed that the myxococci formed colonial spherules in which the peripherally-located myxococci were able to concentrate the cyanobacteria within the core of the spherules and cause their lysis. Because the interaction was carried out under autotrophic conditions, all nutrients for myxococcal growth and development must have originated from the prey cyanobacteria.

Although the myxococci were shown to be effective over nearly three weeks no experiments had been conducted to measure predatory ability under population levels similar to those that have been described in nature (Daft et al. 1975).

Long-term relationships between bacteria and cyanobacteria are not uncommon. These appear to be predominantly of the commensal or symbiotic type (Lange 1971; Echlin and Morris 1965) such as that illustrated in the micrographs by Pearl (1976) showing the surface colonization of nitrogen fixing heterocysts of *Anabaena* by bacteria. Such relationships have been reported for the myxococci. Nolte (1957) showed that when either of two species of *Anabaena* were present as sole nutrient sources in mixed cultures with any of three species of *Myxococcus*, including *M. fulvus*, the myxococci were able to grow and form fruiting structures without lysing the cyanobacteria. That antagonism does exist in nature between bacteria and cyanobacteria has been demonstrated by Fitzgerald (1969) by showing that bacteria-dominated sewage would permit the growth of the green alga, *Chlorella*, but not the cyanobacterium *Microcystis aeruginosa*. Gunnison and Alexander (1975) examined the degradation of algae by bacteria and pointed to the peptidoglycan component of the cyanobacterium's cell wall as their "weak link" against antagonistic bacteria. Fallon and Brock (1979) in describing the decomposition of cyanobacteria in a lake in Wisconsin showed that an antagonistic bacterial population of 10^3 cells per ml essentially depended upon the products of that degradation for their nutritional needs. Daft et al. showed that 44 lytic bacteria per ml effective against cyanobacteria could be isolated in Scottish waters. The significance of this relationship between these indigenous lytic cyanobacteria and the planktonic bacteria is questionable because of the finding by Daft et al. (1975) that 10^6/ml of one of these lystic strains were necessary to cause cyanobacterial lysis.

Although many details of cyanobacterial lysis by bacteria have been described particularly with reference to predatory strains (Shilo 1970; Daft and Stewart 1971; Stewart and Brown 1971; Stewart and Daft 1977) resembling *Lysobacter* sp. (Christensen and Cook 1978), none of these reports show the results of long term and serial transfer or low inocula experiments. This second paper describing the interaction between myxococcal strains and cyanobacteria in aqueous culture examines this long-term predatory and survival capability of the myxococci.

Materials and methods

Isolation and identification

The myxococci used in this study were all isolated from grab samples obtained from roadside ditches draining agricultural fields in Northwest Ohio. Strains BG02 and BG03 were isolated in Bowling Green, Ohio while strain PC02 was isolated in Port Clinton, Ohio. Isolation was as described previously (Burnham et al. 1981) utilizing autotrophically grown lawns of the cyanobacterium *Phormidium luridum*. The characteristics of the PC02 strain, identified as a *Myxococcus*

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xanthus, have been described (Burnham et al. 1981). The BG02 and BG03 strains were identified using the criteria of Zahler and McCurdy (1974).

Organisms

The host cyanobacterium utilized in this study, *Phormidium luridum* var. *olivaceae* (No. 426) was obtained from the University of Texas Culture Collection of Algae and is maintained bacteria-free on Difco Algae Agar or in Difco Algae Broth (AB) as described earlier (Burnham et al. 1976). The myxococci were routinely maintained on ABT medium (Difco Algae Broth containing 0.2% Bacto Tryptone) or on *P. luridum* lawns on Difco Algae Agar (Burnham et al. 1981).

Mixed cultures. Routinely only the myxococci organized into colonial spherules were transferred directly from ABT cultures (1% v/v) and placed into 4- to 7-day-old autotrophically-grown *P. luridum* broth cultures. Various experiments were employed which necessitated the removal of all heterotrophic nutrients as well as cell quantitation. For these, the myxococcal spherules were removed by pipette from their ABT medium and washed twice with 5 volumes of algae broth. These spherules were then placed into a glass tissue grinder (Wheaton) and plunged over 50 times to disaggregate the vegetative cells comprising the spherule. These cell suspensions were diluted with AB medium to concentrations of approximately 10^6 bacteria per ml, as determined by microscope counting with a Petroff-Hausser chamber, and used for inoculations into aqueous *P. luridum* cultures. These inocula were immediately plated on ABT agar (Burnham et al. 1981) for subsequent more accurate quantitation.

For long-term experiments presented in this paper, the initial and subsequent inocula upon serial transfer was 5% (v/v). The flasks were maintained at 25° C and, unless otherwise specified, in 16 h light (3,200 lx) and 8 h dark. The 500 ml Erlenmeyer side arm flasks were rotary shaken at 100 RPM.

Microscopy. Light microscopy was carried out with a Zeiss Axiomat Microscope using quartz halogen illumination. For scanning electron microscopy (SEM), all cells and spherules were directly fixed in 4% glutaraldehyde in 0.1 M KH_2PO_4 at pH 7.2 for 12 h. Small spherules were filtered onto Nucleopore membranes prior to dehydration. All specimens were dehydrated and critical point dried as previously described (Burnham et al. 1981). Specimens were coated with gold palladium in a Polaron SEM Coating Unit E5100 and examined in a Cambridge 180 SEM.

Results

The three myxococcal strains utilized in this investigation of microbial predation all formed deliquescent to subspherical fruiting structures (Fig. 1) when grown on ABT agar.

When these myxococci are grown in liquid culture containing ABT they form colonial spherules (Fig. 2) as described for the PC02 strain by Burnham et al. 1981. The exact shape of these spherules depends upon the strain and its culture age. Figure 3 shows an immature colony of the BG03 strain to be almost totally comprised of swarming spikes of vegetative cells. Generally we have observed that older spherules have longer, more tufted fruiting structures. BG02 and PC02 strains form club-like semi-spherical fruiting structures on the colonial surface in liquid culture (Fig. 4). These are quite similar in organization to the fruiting structures seen in agar cultures (Fig. 1). Phase contrast microscopy of one of the small fruiting structures on an ABT plate (Fig. 5) reveals the curved rod appearance of older vegetative cells of the BG02 strain along with a cluster of myxospores. Although these strains will produce refractile myxospores as observed by phase contrast microscopy, they are more commonly seen as opaque structures (Fig. 5). Myxospores could be induced in all three strains using the glycerol technique of Dworkin and Gibson 1964.

When grown in mixed culture with *Phormidium luridum* the BG02 strain will form knob like fruiting structures (arrow) on the surface of the entrapped cyanobacteria (Fig. 6). Figure 7 shows several vegetative cells and the ovoid morphology of the myxospores present on the surface of a lytic colony of the BG02 strain. Also evident in the micrograph is the presence of the extracellular extrusions which appear to hold the entire colony together (Burnham et al. 1981).

All three myxococcal strains appear to have a wide spectrum of predatory capability with most of the cyanobacteria tested being susceptible to entrapment and lysis (Table 1). Not all cyanobacterial species are equally susceptible to these myxococci. For example, the BG02 strain can lyse the *P. luridum* and *Nostoc muscorum* species much easier than it is able to lyse the *Anabaena cylindrica* species. This has been determined by comparing the number of myxococci needed per ml in mixed culture to successfully entrap and lyse the prey population. Predation of *N. muscorum* by the BG02 strain was found to be totally independent of whether this cyanobacterium was grown in a nitrogen-free medium or in the nitrate-containing algae broth. Table 1 also lists the eukaryotic green alga, *Chlorella vulgaris* which we have attempted to employ as a prey population. The myxococci are very efficient at entrapping them in large clumps; however, the *Chlorella* are not lysed and continue to survive in the mixed culture in large colonial aggregates held together by the myxococci.

All three myxococcal strains effectively lyse aqueous populations of *P. luridum*. Figure 8 illustrates that the BG02 strain is able to lyse a cyanobacterial population of 5×10^7 cells/ml more rapidly than either the PC02 or BG02 strains. All three strains, using a 1% inoculum, achieved maximum entrapment and lysis of the cyanobacteria within 3 days. The *P. luridum* when inoculated into AB under standard conditions grew normally.

Regrowth of the *P. luridum* following the initial predatory attack by the myxococci, i.e., culture cycling, commonly occurred and is illustrated by the turbidity curve for a BG03 mixed culture in Fig. 8 and a BG02 mixed culture in Fig. 9. In long-term experiments, such as that graphed in Fig. 9, this regrowth could occur repeatedly. Although in this particular experiment the *P. luridum* regrowth peaked at intervals of 11, 8 and 7 days, the mean cycle for all experiments was 8.9 days, with a standard deviation of 1.8 days. When regrowth of the prey population did occur their cell density never reached the initial levels.

A series of long-term serial transfer experiments were attempted utilizing *M. fulvus* BG02 and *P. luridum*. Figure 10 shows that, utilizing a serial 5% (v/v) inoculum into AB, the axenic *P. luridum* was able to grow back to original population levels in the 3–4 day intervals. When the myxococci

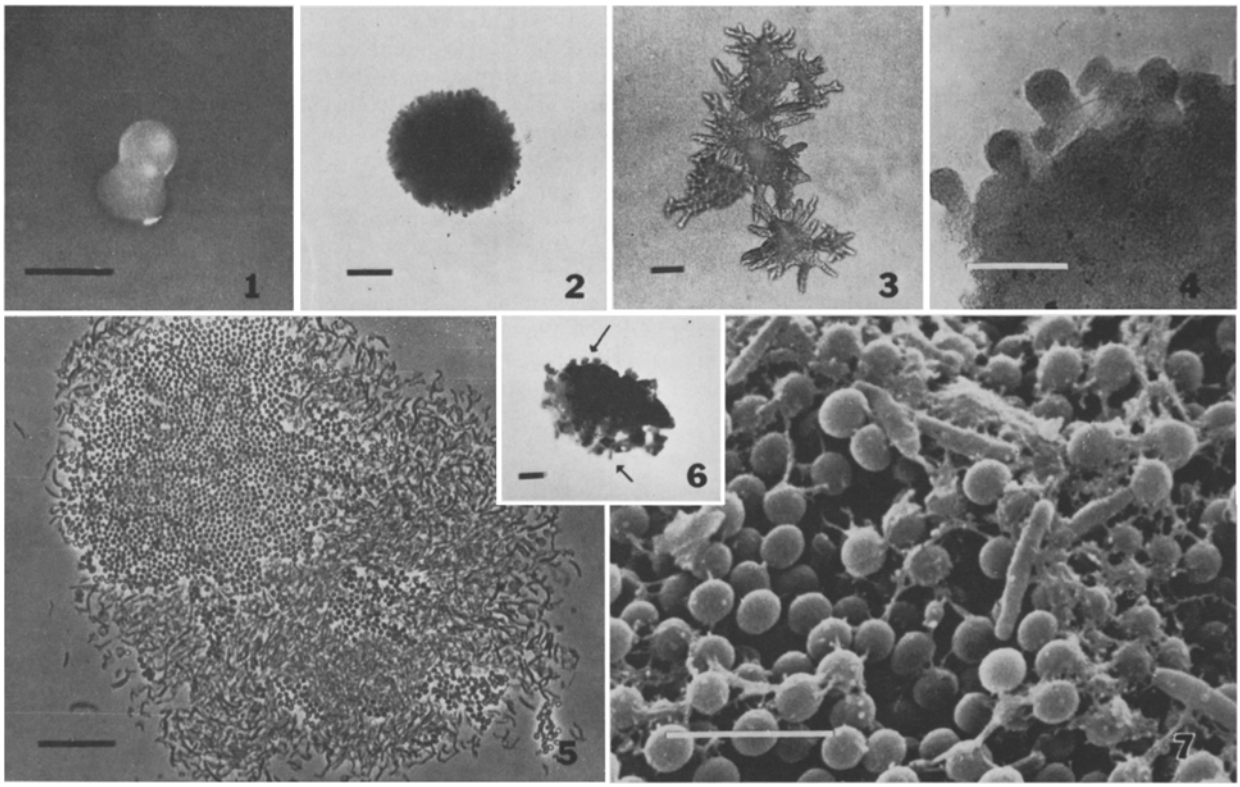

Fig. 1. *Myxococcus xanthus* BG03 fruiting structure after incubation for 7 days at 23° C on ABT agar. Bar equals 900 μm

Fig. 2. Light microscopy of a mature colony of *M. xanthus* BG03 grown for 8 days on ABT broth. Bar equals 400 μm

Fig. 3. Light microscopy of an immature colony of *M. xanthus* BG03 grown for 4 days on ABT broth. Bar equals 125 μm

Fig. 4. Light microscopy of the fruiting body structures on the surface of colonial spherule of *M. fulvus* BG02 for 7 days in ABT. Bar equals 100 μm

Fig. 5. Phase contrast micrograph of a segment of a fruiting body formed by *M. fulvus* G B02 after 7 days of growth on an ABT agar plate. Bar equals 20 μm

Fig. 6. Light microscopy of a predatory colony of *M. fulvus* BG02 after growth for 5 days in a culture of *Phormidium luridum* in AB medium. Note the presence of knob-like fruiting structures (arrows) on the colony surface. Bar equals 500 μm

Fig. 7. SEM of the myxospores and rod-shaped vegetative cells present on the surface of a fruiting structures, on a predatory colony. Bar equals 3 μm

were added at an initial concentration of 4×10^3/ml the *P. luridum* were clumped by the myxococci and inhibited from growing. The accumulative effect of this inhibition of cyanobacterial development is to cause the gradual loss of the *P. luridum* from the interactive culture. We were unable to detect any *P. luridum* after five transfers. By dilution alone and no multiplication the expected number of *P. luridum* after five transfers would be 6×10^3. In this experiment the myxococcal population increased to 1×10^5/ml and then repeatedly achieved a level of 3×10^4/ml through four transfers. After the fifth transfer the myxococci maintained a level of 5×10^2/ml in spite of the undetectable levels of *P. luridum*.

A more vigorous test of the predatory capability of these myxococci was to serially transfer the mixed culture into early stationary growth phase cultures of *P. luridum* averaging 10^6 cells/ml. Figure 11 shows that the *M. fulvus* BG02 strain at 1% (v/v), inoculation levels) was repetitively able to reduce the absorbancy of the cyanobacteria. Entrapment and lysis did not occur immediately following inoculation but usually occurred after several days. Actual lysis of the *P. luridum* was confirmed microscopically as well as by processing the clumps in a glass tissue grinder, which then allowed a more accurate quantitation of the cyanobacterium. The *P. luridum* population was reduced on average of 2.7×10^3 cells/ml over 9 successive transfers. The myxococci were consistently able to multiply back to a population of about 2×10^7 cells/ml even though they were diluted 1/100 every 4 to 7 days. This experiment illustrated the stability of this predatory system, as myxococcal feeding on the *P. luridum* was independent of the number of transfers.

To investigate the minimum inoculum necessary to achieve predation of a 10^7/ml *P. luridum* population, a series of dilutions were carried out on a 48 h *M. fulvus* BG02 culture. These were inoculated into similar *P. luridum* cultures in AB. The results, shown in Fig. 12, indicate that 0.5 cells/ml can lyse a population of 3×10^7/ml cyanobacteria, a predator to prey ratio of $1:6 \times 10^7$. Figure 12 also illustrates that as the inoculum concentration of the myxococci is reduced the lag time prior to cyanobacterial lysis increases.

The low inoculum needed for predation (Fig. 12), as well as the ability of the myxococci to maintain a low but stable population in spite of few prey cells being present, suggests

Table 1. Comparative cyanobacterial susceptibility to aqueous myxococcal predation

Tested prey species	Myxococcal predator strain		
	PC02	BG02	BG03
Anabaena cylindrica[a] UTEX B629	+/−	+	−
Anabaena variabilis UTEX 377	+	−	−
Aphanizomenon flos-aquae[b]	ND	+	−
Lyngbya sp. UTEX 622	+/−	−	−
Microcystis aeruginosa[b]	ND	+	ND
Nostoc muscorum[c]	−	+	+
Oscillatoria sp. CBS 15-1865	−	−	−
Phormidium faveolaum UTEX 427	+	+	+
Phormidium luridum (UTEX 426)	+	+	+
Plectonema boryanum ATCC 18200	+	+	+
Symploca muscorum UTEX B617	−	−	−
Synechococcus sp. (Stanier 6908 strain) (previously ATCC 27146)	+	+	+
(*Chlorella vulgaris*) UTEX 260	−	−	−

[a] University of Texas Culture Collection of Algae
[b] Harvested directly from natural blooms (Balgavies Reservoir and Long Loch, Scotland)
[c] Department of Biological Sciences, U. Dundee, Dundee, Scotland
ND = Not done

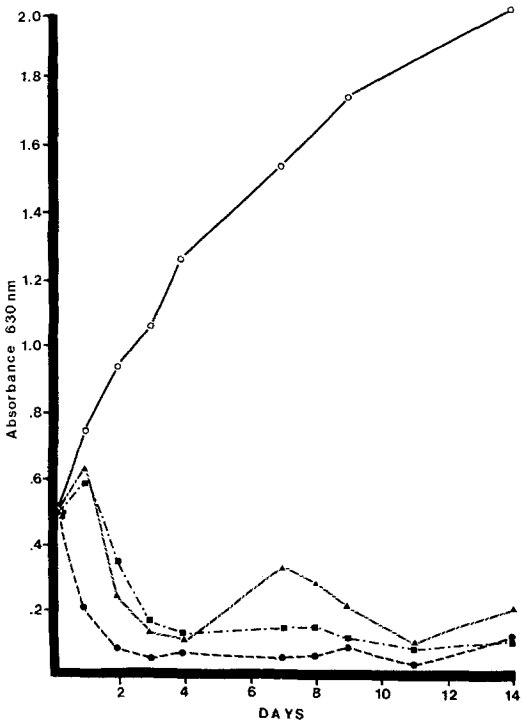

Fig. 8. Comparative clearing ability of the myxococci (10^6 cells/ml at 0 days) on a population of 10^7 *Phormidium luridum* cells/ml at 25° C. Myxococcal strains: BG02 (●); BG03 (▼); and PC02 (■). *P. luridum* control in AB (○)

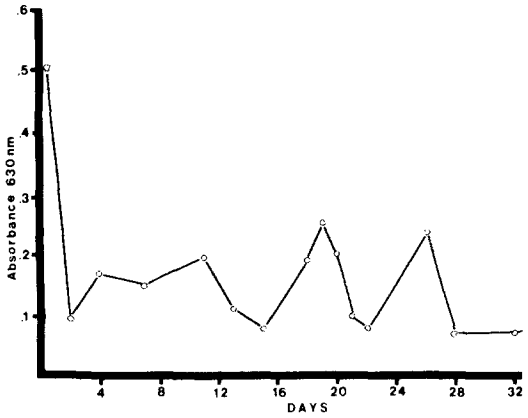

Fig. 9. Cyanobacterial density fluctuations observed when *Myxococcus fulvus* BG02 (10^5/ml at 0 days) is incubated with *P. luridum* (10^7/ml at 0 days) at 25° C

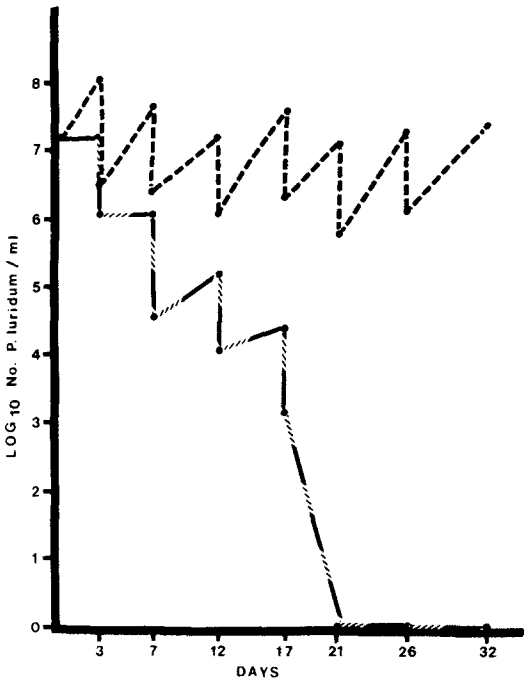

Fig. 10. Effect on *P. luridum* population levels of serial 5% transfers into fresh AB: Axenic *P. luridum* (–––); *P. luridum and M. fulvus* BG02 (10^5/ml at 0 days) (—////—). Vertical lines represent transfer points

that these myxococci might survive in environments containing extremely low nutrient levels.

The predatory ability of the myxococci was not affected by the number of days they were held in AB although morphologically a significant number of vegetative cells had converted to myxospores. Although lag times prior to lysis increased to nearly a week after 50 days in AB, entrapment and lysis stil occurred. Figure 13 illustrates the multiplicative ability of the BG02 strain once it was transferred from this AB holding culture to 10^7/ml *P. luridum* culture. When myxospores alone were inoculated (5×10^6/ml) into a *P. luridum* culture germination occurred followed by cyanobacterial lysis.

Discussion

This paper augments our previous description of myxococcal predation (Burnham et al. 1981) by showing that several myxococcal isolates are capable of controlling aqueous populations the cyanobacterium *Phormidium luridum* over extended periods of time. The predatory-prey cycling that is

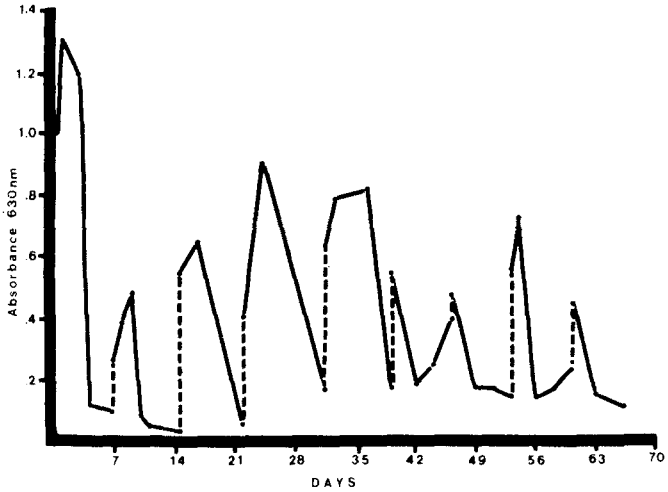

Fig. 11. Effect on *P. luridum* density of serial 1% transfers into mature *P. luridum* cultures (between $10^5 - 10^7$ cells/ml). The initial culture contained approximately 10^8 *P. luridum*/ml and 10^5 *M. fulvus*/ml. Vertical dashed lines represent transfer points

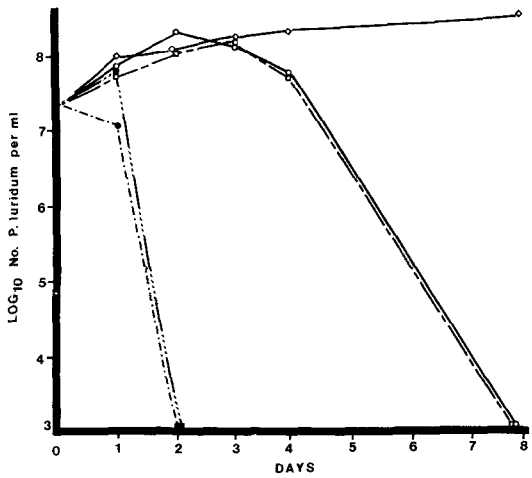

Fig. 12. The effect of different initial *M. fulvus* BG02 concentrations on the ability to equal constant (3×10^7/ml) populations of *P. luridum*. Myxococci/ml: 5×10^2 (●); 5×10^1 (■); 5×10^0 (□); 5×10^{-1} (○); 5×10^{-2} (◇)

consistently seen in long-term experiments indicates: a) that the predatory system is not 100% effective in eliminating the cyanobacteria; and b) that when sufficient prey populations develop in the presence of the myxococcal colonies, they are reduced to low levels by predatory action. The predatory system was experimentally stressed by (a) serial dilutions of the interactive culture with fresh medium (Fig. 10), and (b) serial dilution of the interactive culture with moderate density populations of the prey cyanobacterium (Fig. 11). In both cases, the myxococci responded to controlling the amount of cyanobacterial growth and reducing the overall population of cyanobacteria present.

Because the myxococcal population increased with each successive decrease in the cyanobacteria, in the complete absence of any heterotrophic nutrient, nutrient had to transfer from the cyanobacteria to the predator. Algal to bacterial nutrient exchange is not unusual in such interrelationships; however, these are usually symbiotic or

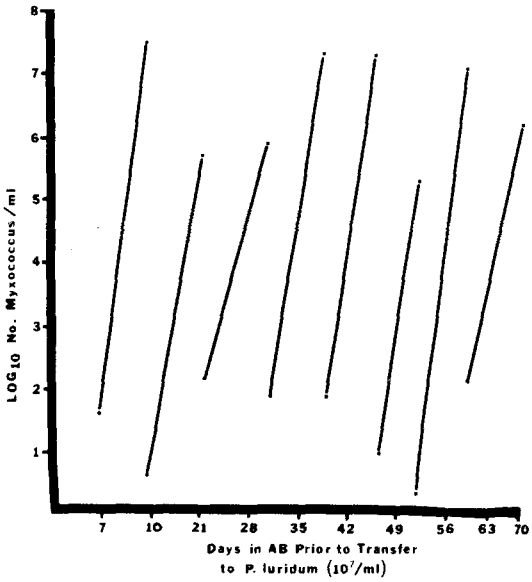

Fig. 13. Population changes of *M. fulvus* BG02 upon inoculation into constant populations of *P. luridum* (10^7 cells/ml). The myxococci were maintained in AB at 25° C for the number of days indicated by the lower point of each slope prior to being transferred to the cyanobacterial culture

commensal in that they occur without penalty to the algal or cyanobacterial partner (Ward and Moyer 1966; Lange 1971). The lytic or enzymatic nature of the myxococci (Sudo and Dworkin 1972) upsets this normal balance by damaging the cell integrity of the cyanobacterium.

The host susceptibility spectrum of this predatory mechanism appears very dependent upon the individual myxococcal strain. From the data presented in Table 1, the BG02 strain shows the broadest predatory ability, with 10 cyanobacterial species lysed. Many of the negative hosts are effectively entrapped by the myxococci but not significantly lysed. This same situation is seen with the green alga, *Chlorella vulgaris*. Daft et al. (1975) showed that cyanobacteria-lysing bacteria are very common in fresh water habitats and that these are capable of lysing many species of bloom-forming cyanobacteria. Four previous myxobacterial isolates, later identified as *Lysobacter* sp. (Christensen and Cook 1978), were studied in detail and, although they all showed broad lytic ability, each isolated possessed a slightly different spectrum of lytic capability, similar to that shown for the three myxococcal strains in this paper.

The myxococci were able to control the *P. luridium* populations with inocula as low as 50 cells/100 ml. This is in marked contrast to the requirements of the *Lysobacter* CP-1 studied by Daft et al. (1975) which needed inoculum levels of 10^6/ml for successful lysis the low population levels of the BG02 strain. The required level of *M. fulvus* BG02 however, was similar to the levels of myxobacteria found by Daft et al. (1975) to be present in natural surface waters, i.e., from 1 to more than 110/ml with a mean of 44/ml for seven different habitats. The development of predatory colonies from such low inocula could be explained by their use of cyanobacterial secretions as early nutrient sources (Daft et al. 1975). Ward and Moyer (1966) demonstrated such potential by showing that the growth of non-predatory bacteria in mixed culture in an autotrophic medium paralleled the growth of the algal partner.

In our initial description of the morphology of the predatory colony we suspected the processes of swarming and spore formation to be important mechanisms in the entrapment and lysis of the cyanobacterial cells (Burnham et al. 1981) by these lytic colonies. The slight differences that these three myxococcal strains show with respect to the formation in liquid medium of 1) lytic colonies, and 2) fruiting structures, appear to have no effect on their ability to entrap or lyse the *P. luridum*. The formation of aggregates of the myxobacterium CP-1, now *Lysobacter*, was reported by Daft and Stewart (1973). In addition, when they added high numbers of *Lysobacter* to blooms of cyanobacteria the viable counts of the lytic bacteria fell rapidly. Such as drop would be expected when the myxobacteria aggregate into colonial units if fragmentation techniques were not employed in the myxobacterial enumeration.

This aqueous colonial morphology of the myxococci suggests an interesting analogy with the predatory bacteria, the bdellovibrios. These predators penetrate the host bacterium's cell wall and enjoy the environmentally-protected periplasm in which to enzymatically liberate prey nutrients (Rittenberg and Thomashow 1979). This is very similar to the protected core created by the peripheral myxococcal vegetative cells in the colony. The massive encapsulating myxococcal population provides, through its collective swarming activity and fibrous adhesions (Burnham et al. 1981), an analogous mechanism to the Gram-negative wall of the infected bdellovibrio host. Huffaker et al. (1976) contend that predators need to possess several attributes to be successful control agents: adaptability to physical conditions; searching (or trapping) capacity; ability to multiply; power of prey consumption; and ability to survive in periods of low host density. The description presented earlier by us (Burnham et al. 1981) on the nature of the aqueous myxococcal predatory colonies, coupled with the structural and population data described in this report indicate that the myxococcal predatory system tested in vitro does possess such attributes. Such abilities should ensure and explain the survival of the myxococcal species in fresh water habitats.

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