Decomposing predation: Testing for parameters that correlate with predatory performance by a social bacterium

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Abstract

Predator-prey interactions presumably play major roles in shaping the composition and dynamics of microbial communities. However, little is understood about the population biology of such interactions or how predation-related parameters vary or correlate across prey environments. *Myxococcus xanthus* is a motile soil bacterium that feeds on a broad range of other soil microbes that vary greatly in the degree to which they support *M. xanthus* growth. In order to decompose predator-prey interactions at the population level, we quantified five predation-related parameters during *M. xanthus* growth on nine phylogenetically diverse bacterial prey species. The horizontal expansion rate of swarming predator colonies fueled by prey lawns served as our measure of overall predatory performance, as it incorporates both the searching (motility) and handling (killing and consumption of prey) components of predation. Four other parameters – predator population growth rate, maximum predator yield, maximum prey kill, and overall rate of prey death – were measured from homogeneously mixed predator-prey lawns from which predator populations were not allowed to expand horizontally by swarming motility. All prey species fueled predator population growth. For some prey, predator-specific prey death was detected contemporaneously with predator population growth, whereas killing of other prey species was detected only after cessation of predator growth. All four of the alternative parameters were found to correlate significantly with predator swarm expansion rate to varying degrees, suggesting causal inter-relationships among these diverse predation measures. More broadly, our results highlight the importance of examining multiple parameters for thoroughly understanding the population biology of microbial predation.

Introduction

Animal predators play major roles in regulating ecosystem dynamics [1, 2] both by directly affecting prey populations and by indirectly affecting non-prey species with which prey interact [3]. Because predatory phenotypes and their community-level effects are determined by multiple traits, characterization of those traits can provide important information about how specific features of predation influence community dynamics. Recent expansions of optimal foraging theory have modeled how foraging mode can impact the energetic flux [4] and structure [5] of whole communities. For example, the two spider species *Pisaurina mira* and *Phidippus rimator* hunt for *Melanopuls femurrubrum* grasshoppers by sit-and-wait vs. active searching modes, respectively, and these distinct hunting modes have been shown to differentially impact plant community composition in the grasslands these spiders inhabit [6]. Natural microbial communities also harbor numerous predators [7–9], but little is

currently known about their roles in determining the of structure, dynamics and functions of such microbial communities. However, classic experiments in simplified laboratory systems [10, 11], the broad phylogenetic distribution of microbial predators and their prey [12] and the pervasiveness of microbial predators throughout both terrestrial and aquatic habitats [13, 14] all strongly suggest that they play major roles in regulating the dynamics of microbial prey populations [11, 15].

Myxococcus xanthus is a globally distributed soil bacterium that can feed on other microbial cells both individually [16] and in swarming groups that have been likened to wolf packs [17]. Two major aspects of *M. xanthus* predatory behavior are roughly analogous to the traditional distinction between searching vs. handling components of animal predation [18, 19]. *M. xanthus* cells "search" for other microbes to prey upon by swarming through the soil matrix powered by two genetically distinct, yet complementary, mechanisms of gliding motility [20, 21]. Upon encounter, *M. xanthus* "handles" prey cells by secreting molecules that kill and degrade them [22–24] and then consuming their remains as a growth substrate. *M. xanthus* predation is thought to be a cooperative trait because secretion of predation-associated molecules (e.g. hydrolytic enzymes) might benefit not only secreting cells themselves but neighboring cells as well [17]. *M. xanthus* can utilize a wide variety of bacteria and fungi as prey, but these vary greatly in the degree to which they support *Myxococcus* population growth [25, 26] .

The expansion rate of *M. xanthus* colonies that simultaneously utilize prey as a growth substrate and increase their spatial territory by gliding motility [27] is commonly used as a metric of overall predatory performance on agar plates [28–30]. This performance measure incorporates both the searching and handling components of predation that are traditionally distinguished in foraging theory [31]. For example, Hillesland *et al.* allowed *M. xanthus* populations to swarm across plates containing spatially separate patches of prey bacteria and distinguished between the rate of searching for new patches vs. consumption (i.e. handling) of prey within patches [19]. Some studies have also quantified the dynamics or extent of prey death due to *M. xanthus* predation under conditions of colony expansion [26, 29]. However, it remains unclear which such alternative quantitative parameters are predictive of overall predatory performance.

In this study, we measured both the rate at which *M. xanthus* populations expand while swarming across clonal lawns of diverse prey species and four additional parameters that were measured while predator populations were increasing in number but not expanding the size of their circumscribed territories. These other four parameters - predator population growth rate, maximum predator yield, rate of prey death, and maximum extent of prey death – are related to prey "handling" [18] because they emerge from direct interaction of predator and prey. These handling-related parameters were analyzed to assess the degree to which they correlate with a standard measure of overall predatory performance (rate of predator swarming expansion across prey lawns) and one another. These analyses allowed us to explore several previously unexamined aspects of microbial predation. For instance, it is unknown whether population growth rate during predation in the absence of group swarming is predictive of overall performance when predators are both increasing numerically and expanding their two-dimensional territory via gliding motility. Additionally, relationships between the dynamics and extent of predator growth and prey death remain obscure.

The rate of *M. xanthus* swarm expansion on prey lawns emerges from interaction between cell division rate and the dynamics of directional cell motility at a swarm's leading edge. Leading-edge cells migrate away from the high-density interior of the swarm, where the interior sub-population reaches stationary phase upon depletion of growth substrates

extracted from prey. One force that may affect this interaction is any predator Allee effect (i.e. benefit of high density [32, 33]) on prey handling efficiency that may occur at a swarm's leading edge. It has been hypothesized that *M. xanthus* predation may be more efficient (i.e. more effectively convert prey biomass into predator biomass) at high predator density than at low density [17]. If this occurs, then growth dynamics at a swarm's leading edge, where cells foray from high-density cell waves to interact with prey cells, may differ substantially from those in the non-swarming arenas in which we measured population growth rate, predatory yield, prey death rate and extent of prey death. In these arenas, predator and prey cells were dispersed randomly across the entire surface of an agar plate at a ratio of ~1:100,000. Thus, predator cells began growth as isolated individuals or in small cell clumps. Resulting predator microcolonies in this arena then grew together across the entire plate surface and subsequent population growth reflected increasing local density rather than expansion into new territory. Given the differences in the local growth environments of dividing cells in the swarming vs. non-swarming growth arenas examined here, any relationships between parameters across these environments are not obvious *a priori.*

Material and Methods

Species and culture conditions

Nine phylogenetically diverse species of bacteria used as prey in previous studies of *M. xanthus* predation [25] were examined here (Table 1), including several species thought to predominantly reside in soil habitats. Prey species were obtained from the Long Term Ecological Research (LTER) collection from Kellogg Biological Station, Hickory Corners, Michigan [34]; the Leibniz Institute German Collection of Microorganisms and Cell Cultures (DSMZ); the American Type Culture Collection (ATCC), and Richard Lenski [35] (Table 1). *M. xanthus* strain GJV2 was used as the predator and is a spontaneous rifampicin-resistant mutant of strain GJV1, a recent isolate [36] of the commonly studied reference strain DK1622 [37] and is highly proficient at development and motility [38].

To prepare prey suspensions, prey samples were inoculated from frozen stocks into eight ml of fresh R2 broth [39] and grown for 16 hours at 32 °C, 300 rpm. Cells were then centrifuged (4500 g, 15 min.) and resuspended to a standard biovolume concentration of ~10^9 μm^3/ml in liquid TPM buffer [40]. 100 μl of resuspended culture were spread across LB 1.5% agar plates (15 ml) prepared 24 hours prior to inoculation of prey and incubated at 32 °C, 90% rH for 48 h. Cells were then scraped into ten ml of TPM buffer, centrifuged and resuspended in fresh TPM to ~10^{10} μm^3/ml.

Cultures of *M. xanthus* were first grown on CTT 1.5% agar plates (4–5 days) and then inoculated from the colony edge into CTT broth [37] and grown overnight at 32 °C, 300 rpm. To initiate all assays, log-phase cultures of *M. xanthus* (~$2–3 \times 10^8$ cells/ml) were centrifuged (4500 g, 15 min.) and resuspended in liquid TPM buffer to ~5×10^9 cells/ml.

Estimates of *M. xanthus* growth and prey death

Eight ml aliquots of TPM or CTT 1.5% agar were allowed to solidify in 50 ml flasks two days prior to each experiment and were then kept covered at room temperature. Shortly before inoculation, 5–7 sterile glass beads (3 mm) were placed in the flasks to allow even spread of inocula. To inoculate TPM flasks with predator-prey mixes, 100 μl of a culture containing ~10^9 μm^3 prey cells and ~10^4 *M. xanthus* cells (diluted from the 5×10^9 cells/ml suspension) were spread across the agar surface. We used small and large initial predator and prey population sizes, respectively, to allow tracking of substantial predator population growth. As controls, prey-only inocula were spread onto TPM agar and predator-only

inocula were spread onto both TPM and CTT agar. Flasks were then left open in laminar flow hood for 15 min., covered and incubated at 32 °C, 90% rH.

Cultures were harvested 2, 12, 24, 36, 48, 60, 84, 108, and 132 h after inoculation to estimate predator and prey population sizes. To harvest, five ml of TPM liquid were added to the flasks and the lawn of cells was separated from the agar surface by repeated pipetting of the TPM liquid. Cell suspensions were then transferred to a 50 ml Falcon tube containing 20–30 sterile glass beads (3 mm) and vortexed vigorously for 90 sec. Suspensions were diluted in TPM liquid and plated either into CTT 0.5% agar containing 10 μg/ml gentamycin sulfate for *M. xanthus* counts or onto LB 1.5% agar for prey counts. All prey used are sensitive to gentamycin and *M. xanthus* strain GJV2 is unable to grow on LB medium. Plates were incubated at 32 °C and were counted after two days for prey plates and six days for *M. xanthus* plates. Predator growth curves and prey death curves in the presence and absence of the predator were then generated from this data.

Swarming rate assays

Prey lawns for swarming assays were prepared by spreading 100 μl of prey suspension (~10^{10} μm^3/ml) onto TPM 1.5% agar plates (15 ml TPM, prepared 24 h prior to inoculation). After 30 min. at room temperature, 10 μl of the predator suspension (~5×10^9 cells/ml) were spotted on the plate center and allowed to dry for 60 min. Covered plates were then incubated at 32 °C, 90% rH. Swarm edges were outlined one and five days after inoculation and distances between time-point marks along two perpendicular diameters at random orientation were measured. Prey-specific swarming rates on prey lawns relative to prey-free controls were calculated as the average distance (mm) per day covered by the advancing swarm edge minus the *M. xanthus* swarming rate on starvation agar controls (Fig. 1). On prey-free TPM control plates, *M. xanthus* cells undergo starvation and fruiting body formation in the interior of the initially inoculated region, but cells at the perimeter do swarm outward to a limited degree.

Parameter estimation

Predator growth rate was calculated as the average slope of ln-transformed population size estimates over the 24–60 h. interval. This period was chosen to factor out any residual growth over the initial 24 h. period that might be due to nutrients acquired by cells during the pre-conditioning phase in CTT liquid or growth on nutrients present at very low concentrations in agar [25]. (*M. xanthus* populations increased on prey-free TPM plates over the initial 24 h. period and then ceased growing (Fig. 2)). In all prey environments except *Curtobacterium citreum* (CC) predator growth declined substantially or ceased after the 60 h. time point. To measure overall prey kill rate the average difference between the slopes of ln-transformed estimates of prey population size from 2 h. – 132 h. on TPM vs. TPM +predator plates was calculated. The maximum prey kill was estimated as the maximum difference observed across time points between ln-transformed prey counts in predator-free flasks and counts from flasks containing *M. xanthus,* standardized by the predator-free counts. Maximum predator yield was calculated as the largest population size reached by *M. xanthus* over the entire duration of the growth assays (132 hours).

Results

Trait variation across prey environments

Predator swarming—*Myxococcus* swarming rate on prey lawns served as our proxy for overall predatory performance and reflects the rate of population increase both while cells are dividing and while the colony is expanding via gliding motility. Prey-specific swarming rate varied greatly across prey species (Fig. 1, Table 2). Consistent with previous results

[25], swarming was fastest on *Escherichia coli*, which supported faster swarm expansion than did CTT agar plates containing 1% Casitone as the growth substrate (Fig. 1, Wilcoxon rank sum test, $p = 0.029$). At the opposite extreme, *M. xanthus* failed to swarm more on *C. citreum* lawns than on prey-free TPM starvation agar (Fig. 1). This result is consistent with an earlier finding that *C. citreum* appears to inhibit swarming by most *M. xanthus* natural isolates relative to starvation agar controls [25]. *Rhizobium vitris* (RV) and *Xanthomonas fragariae* (XF) supported only low degrees of prey-induced swarming, whereas *Bacillus bataviensis* (BB), Arthrobacter globiformis (AG), Pseudomonas fluorescens (PF), Cytophaga johnsonae (CJ) and *Micrococcus luteus* (ML) supported prey-specific swarming rates intermediate between those on *X. fragariae* and *E. coli* (EC) (in order slowest to fastest, Fig. 1).

Predator growth in the absence of swarm expansion—We also measured the rate of predator population growth on prey lawns when the perimeter of *Myxococcus* territory was held constant. This was accomplished by homogeneously spreading the mixture of the initial predator and prey populations across the entire surface of a prey lawn (or agar surface in the case of CTT and TPM controls), thus allowing no opportunity for subsequent horizontal swarm expansion beyond the area initially populated by predator cells. *M. xanthus* populations grew significantly on all prey species under these conditions (Fig. 2, Table 3), but growth rate varied substantially across prey types (ANOVA, $p < 0.001$; Fig. 2, 3a, Table 2).

The inability of *C. citreum* to stimulate greater swarming by GJV2 than occurs on starvation agar control plates suggested that *M. xanthus* might be unable to convert *C. citreum* cells (or products) into utilizable growth substrate. However, in contrast to this expectation, *M. xanthus* was in fact able to grow significantly on *C. citreum* in the absence of swarm expansion well beyond the minimal growth that occurs on prey-free starvation agar plates (Fig. 2, 3a, Table 3).

Growth rate in the absence of swarm expansion correlated significantly with prey-specific swarming rate across prey types (Pearson correlation $r = 0.41$, $p = 0.017$; Table 2). Nonetheless, despite this overall correlation relative performance ranks during swarming vs. growth without swarming are reversed in several instances (Table 3). For example, *M. xanthus* swarms faster across lawns of *A. globiformis*, *C. johnsonae* and *X. fragariae* than across *R. vitris* but nonetheless grows faster on *R. vitris* in the absence of swarm expansion than it does on those three species (Figs. 1–3). Also, although *E. coli* supported the fastest swarming by *M. xanthus* on any prey (Fig. 1), growth rate on *E. coli* in the absence of swarm expansion is similar to or even lower than growth rate on several other prey (BB, ML, PF and RV; Fig. 3a).

The maximum cell yield attained by *M. xanthus* during growth on prey in the absence of swarm expansion was greater than that on starvation agar and less than that on CTT agar for all prey types (Fig. 3b) but did not vary significantly across prey types (ANOVA, $p = 0.303$; Table 2). Despite the non-significance of variation, this parameter nonetheless correlated significantly with prey-specific swarming rate, our primary measure of predatory performance ($r = 0.46$, $p = 0.006$; Table 2), as well as with growth rate in the absence of swarm expansion ($r = 0.35$, $p = 0.039$; Table 2). Consistent with our other assays indicating that predatory performance is weakest on *C. citreum*, this species supported the lowest maximum predator yield (Fig. 3b, Table 3).

Predator-induced prey death—The rate at which *Myxococcus* killed prey cells varied across prey species (ANOVA, $p = 0.054$; Fig. 3c, Table 2), as did the maximum number of prey cells killed by *M. xanthus* (ANOVA, $p = 0.017$; Fig. 3d, Table 2). Prey kill rate

correlated significantly with overall prey-specific swarming rate ($r = 0.62$, $p < 0.001$; Table 2) but not with growth rate in the absence of swarm expansion ($r = 0.26$, $p = 0.128$; Table 2). Maximum kill correlated strongly with both prey-specific swarming rate ($r = 0.55$, $p = 0.002$; Table 2) and growth rate in the absence of swarm expansion ($r = 0.40$, $p = 0.025$; Table 2). The prey with highest *(E. coli)* and lowest *(C. citreum)* maximum kill values supported the fastest and slowest rates of *M. xanthus* swarming, respectively (Figs. 1, 3; Table 3).

Significant killing of prey by *M. xanthus* was detected for all prey species except *C. citreum* (Figs. 2, 3c, d; Table 3), which nonetheless supported *M. xanthus* growth (Figs. 2, 3a; Table 3). A likely reason why predator killing of *C. citreum* was not detected is that *M. xanthus* growth on *C. citreum* was slower than on any other prey (Table 3). The maximum population size achieved by *M. xanthus* on *C. citreum* by the end of our growth assays may have been too low to kill a detectable number of *C. citreum* cells (Fig. 2). In support of this hypothesis, significant predator-specific prey death for all other prey species was only detected after 60 hours, when *M. xanthus* had reached population sizes equal to or greater than the maximum size achieved on *C. citreum* at the final point of our growth assays. Detection of prey death lagged behind detection of *M. xanthus* growth for all prey, presumably because a minimum predator density had to be reached before prey death became detectable with our assay.

Intriguingly, *M. xanthus* colonies expand horizontally on *C. citreum* lawns no faster than on starvation agar (Fig. 1, Table 3, [25]). This poor performance at swarming on *C. citreum* is not attributable merely to a slow rate of cell division because on plates that did not allow swarm expansion, *M. xanthus* populations exhibited greater growth on *C. citreum* than on starvation agar (see later time points of CC graph in Fig. 2). Thus, *C. citreum* lawns appear to actually hinder the expansion of swarming *M. xanthus* colonies, possibly due to the secretion of an extracellular matrix that is physically difficult for *M. xanthus* cells to migrate through or that biochemically hinders motility functions.

Gram− vs. Gram+ differences—A previous study examining the predatory performance of many *M. xanthus* natural isolates across a large number of prey species found that, on average, *M. xanthus* isolates swarmed significantly faster on Gram− prey species than on Gram+ species [25]. We thus tested for any phylogenetically based differences in the average parameter values for these two prey categories (four Gram- and five Gram+ species). Gram− and Gram+ species were found to differ significantly only for maximum prey kill (Gram− mean = 0.106, Gram+ mean = 0.201, Wilcoxon rank sum test, $p = 0.008$).

Discussion

Much research has sought to characterize how the physical and behavioral traits of individuals contribute to animal predation [41–43]. For example, the two shrew species *Neomys fodiens* and *Neomys anomalus* co-exist in streams, but *N. fodiens* individuals are able to dive longer than *N. anomalus* and thus are able to reach and utilize a wider variety of prey [44, 45]. In contrast, fewer studies have sought to explore the relationships between the overall predatory success of a population and distinct population-level parameters that might be predictive of such success [19, 46–48].

Here we quantified several predatory parameters during growth of a motile bacterial predator on prey (growth rate in the absence of swarm expansion, maximum predatory yield, predator-induced prey death rate and maximum prey kill) and examined them both for variation across prey species and for their degree of correlation with a measure of overall

predatory performance, namely prey-specific swarming rate across a prey lawn. Variation in each of these four alternative parameters across prey was found to be significantly predictive of prey-specific swarming rate on prey lawns.

These observed correlations among our population parameters may have implications for how these parameters evolve, whether in response to selective pressure imposed on *M. xanthus* by prey or due to other forces. Specifically, our results suggest causal relationships among the parameters and that substantial evolutionary changes in one will tend to be associated with corresponding changes in others. Hypothetically, for instance, predator ineffectiveness at killing prey cells might cause not only a slow rate of prey death, but also slow predator population growth and might be mechanistically related to how much growth substrate predator cells can extract prey cells and thus also affect maximum predatory yield. Nonetheless, despite the overall parameter correlations there were several instances in which the relative ranks of prey species varied greatly across parameters (Table 3), thus indicating that these parameters can evolve independently to some degree.

One striking example of rank difference across parameters is the comparison of *M. xanthus* swarming vs. non-swarming growth on *E. coli.* Although predator growth on *E. coli* is slightly slower than on two other prey in the absence of swarm expansion (Fig. 3a, *P. fluorescens* and *B. bataviensis*), predator swarming on *E. coli* – which involves both numerical increase by cell divisions and territorial expansion – is much faster than on all other prey (Fig. 1). Thus, *E. coli* somehow uniquely promotes territorial expansion in a manner independent of exponential predator growth rate within a non-expanding territory. In principle, this effect might be due to individual *M. xanthus* cells at the leading edge of a swarm dividing at a faster rate when they are free to migrate into an open field of *E. coli* cells than in the presence of other prey. Alternatively, *E. coli* cells might biologically stimulate and/or physically allow faster predator motility than do other prey and thus promote enhanced territorial expansion specifically by effects on motility. Another exception to the general correlations found here is *C. johnsonae,* which supports one of the fastest prey-specific swarming rates but ranks low for all four of the other parameters (Figs. 1, 3, Table 3). Also, *M. xanthus* swarm expansion is slower on *R. vitris* lawns than any other prey species except *C. citreum* but *M. xanthus* nonetheless appears to have killed a larger fraction of *R. vitris* populations than those of any prey other than *E. coli* (Figs. 1, 3d, Table 3).

The extent of evolutionary co-variance among the predation parameters examined here could be tested either with laboratory evolution experiments or comparative studies of divergent natural isolates. For example, *M. xanthus* lineages selected for improved predatory performance in a laboratory prey environment evolved to swarm more efficiently across agar prey arenas [19]. Such evolved lineages could be examined for whether predation parameters underwent changes in a manner consistent with the correlations found here and analysis of accumulated mutations in such lineages could provide mechanistic insights not revealed by our correlation approach.

Two of the parameters examined here (prey kill rate and maximum prey kill) reflect predator effects on prey populations. Thus, the extent of co-variance among these and other parameters may have community-level implications. For example, evolutionary changes in predator cell division rate or maximum yield may be causally linked to prey kill rate and consequently affect how prey populations change over time. This possibility highlights the importance of investigating the nature of predator-prey interactions for understanding the composition and dynamics of microbial communities.

Acknowledgments

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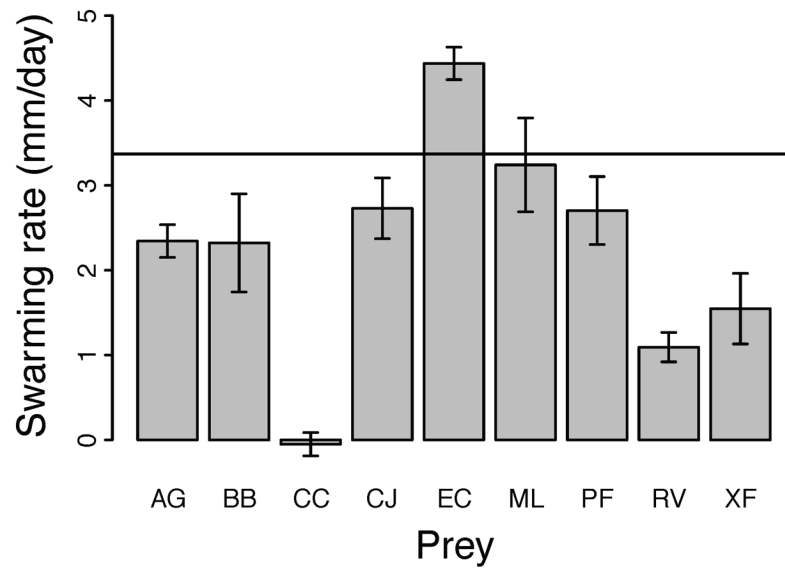
Figure 1.
Average *M. xanthus* swarming rate across prey lawns spread on starvation agar standardized by swarming rate on prey-free starvation plates (see Methods). A value of zero corresponds to equal swarming on prey vs. prey-free starvation agar plates. The solid line indicates the average *M. xanthus* swarming rate on nutrient rich CTT agar in the absence of prey. Error bars indicate the standard error of the mean.
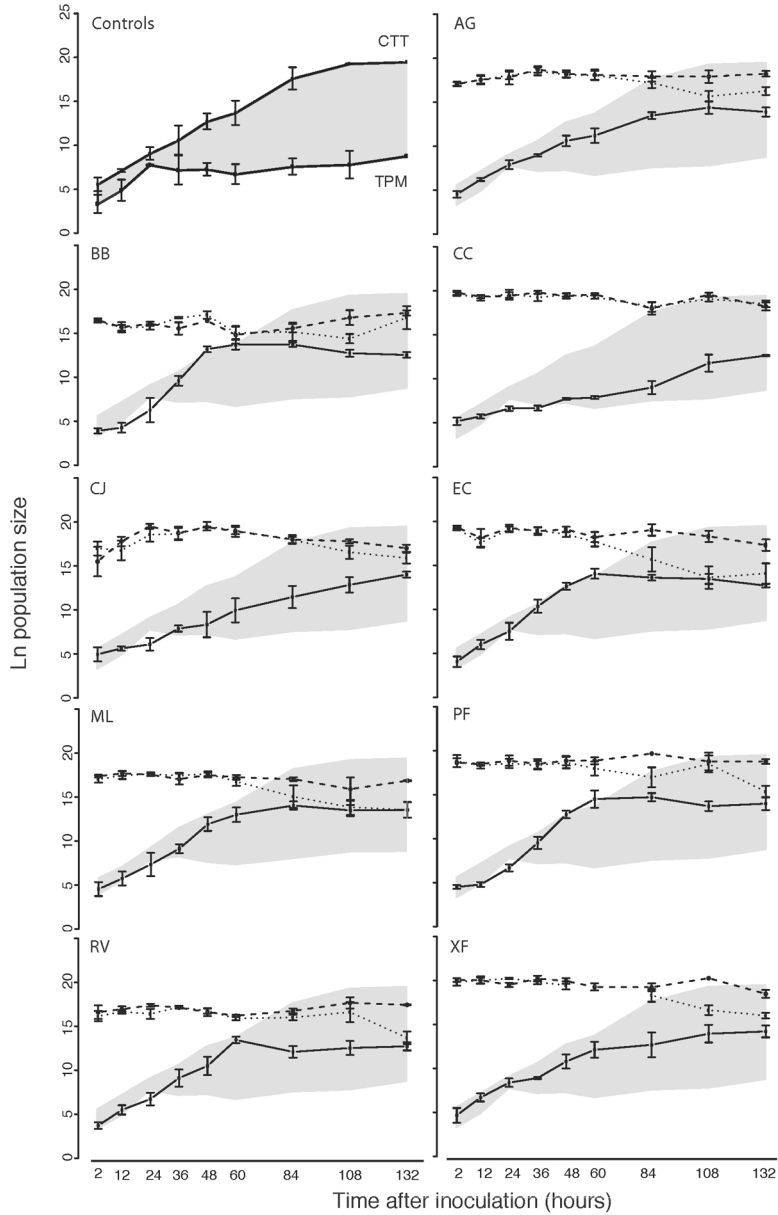
Figure 2.
Population dynamics. Controls (upper left): ln-transformed population size estimates of *M. xanthus* on starvation agar (bottom line) and nutrient rich CTT agar (top line). Growth on prey: ln-transformed population size estimates of *M. xanthus* (solid lines) and nine prey in the absence (dashed lines) and presence (dotted lines) of predator through time. The shaded area in each panel corresponds to the area bounded by *M. xanthus* population sizes on CTT and starvation agar controls. Error bars indicate the standard error of the mean.
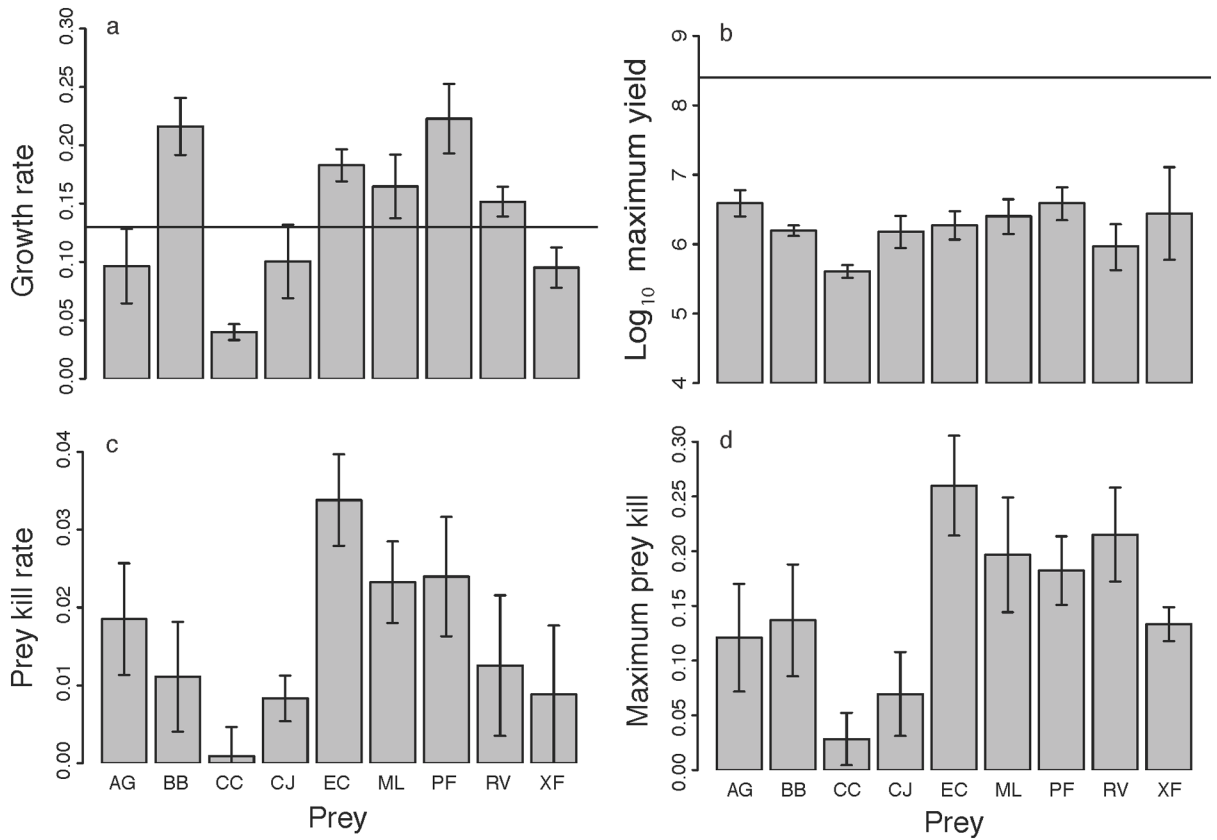
Figure 3.
Predator growth rate (a), maximum predator yield (b), prey kill rate (c) and maximum prey kill (d) for *M. xanthus* growth on nine prey species in the absence of swarm expansion. The solid lines in panels a and b represent the average value of each respective parameter measured on nutrient-rich CTT agar. The dashed line in panel b represents the average maximum yield on starvation agar. Error bars represent the standard error of the mean.

TABLE 1

Prey species.

Prey species (abbreviation)	Phylum and subdivision	Source [reference]	Strain Reference no.
Arthrobacter globiformis (AG)	Gram positive, High G+C subdivision	LTER [34]	LTER 27
Bacillus bataviensis (BB)	Gram positive, Low G+C subdivision	DSMZ	15601
Curtobacterium citreum (CC)	Gram positive, High G+C subdivision	LTER [34]	LTER 17
Cytophaga johnsonae (CJ)	Gram positive, Low G+C subdivision	ATCC	17061
Escherichia coli REL606 (EC)	Gram negative, Gamma subdivision	Richard Lenski [35]	N/A
Micrococcus luteus (ML)	Gram positive, Low G+C subdivision	ATCC	4698
Pseudomonas fluorescens (PF)	Gram negative, Gamma subdivision	LTER [34]	LTER 56
Rhizobium vitris (RV)	Gram negative, Alpha subdivision	DSMZ	6583
Xanthomonas fragariae (XF)	Gram negative, Gamma subdivision	DSMZ	3587

LTER: Long Term Ecological Research (LTER) site at Kellogg Biological Station, Hickory Corners, Michigan (http://lter.kbs.msu.edu); DSMZ (Leibniz Institute German Collection of Microorganisms and Cell Cultures (www.dsmz.de); ATCC: American Type Culture Collection (www.atcc.org).

TABLE 2

Variation within parameters and correlations between paired parameters.

	SR	GR	MCY	PKR	MPK
SR	AOV p < 0.001 KW p = 0.003	rho = 0.383 p = 0.025	rho = 0.517 p = 0.002	rho = 0.685 p < 0.001	rho = 0.541 p = 0.002
GR	r = 0.405 p = 0.017	AOV p < 0.001 KW p = 0.005	rho = 0.340 p = 0.040	rho = 0.268 p = 0.114	rho = 0.433 p = 0.016
MCY	r = 0.463 p = 0.006	r = 0.345 p = 0.039	AOV p = 0.303 KW p = 0.061	rho = 0.573 p < 0.001	rho = 0.780 p < 0.001
PKR	r = 0.621 p < 0.001	r = 0.258 p = 0.128	r = 0.565 p < 0.001	AOV p = 0.054 KW p = 0.049	rho = 0.507 p = 0.004
MPK	r = 0.545 p = 0.002	r = 0.401 p = 0.025	r = 0.823 p < 0.001	r = 0.481 p = 0.006	AOV p = 0.017 KW p = 0.079

SR: swarming rate; GR: growth rate of the predator; PKR: prey kill rate; MCY: log10 (maximum cell yield of the predator); MPK: maximum prey kill. Shaded cells show the significance levels of tests for parameter variation using two measures: Analysis of Variance (AOV) and Kruskal-Wallis Analysis of Variance (KW). The bottom left portion of the table shows Pearson product moment correlation statistics. The upper right corner of the table shows the Spearman's rank correlation statistics.

TABLE 3

Mean values and prey rank position for each parameter measured.

Prey	SR	GR	MCY	PKR	MPK
AG	***2.344 (5)	*0.093 (8)	***3.95×10^{06} (2)	*0.019 (4)	*0.122 (7)
BB	*2.323 (6)	**0.216 (2)	***1.64×10^{06} (6)	ns 0.011 (6)	*0.137 (5)
CC	ns −0.050 (9)	**0.039 (9)	***4.35×10^{05} (9)	ns 0.001 (9)	ns 0.028 (9)
CJ	**2.729 (3)	*0.100 (6)	**1.52×10^{06} (7)	*0.009 (8)	•0.069 (8)
EC	***4.438 (1)	***0.183 (3)	***1.90×10^{06} (5)	**0.034 (1)	**0.259 (1)
ML	**3.242 (2)	**0.165 (4)	**2.52×10^{06} (4)	*0.023 (3)	*0.197 (3)
PF	**2.703 (4)	**0.223 (1)	***4.23×10^{06} (1)	*0.024 (2)	*0.183 (4)
RV	**1.094 (8)	***0.152 (5)	**9.47×10^{05} (8)	ns 0.013 (5)	•0.215 (2)
XF	*1.547 (7)	**0.095 (7)	*2.75×10^{06} (3)	ns 0.009 (7)	**0.133 (6)

SR: Swarming rate; GR: Growth rate of the predator; MCY: Maximum cell yield attained by the predator; PKR: Prey kill rate; MPK: Maximum prey kill. Asterisks indicate significance levels for deviation from zero (SR, GR, PKR and MPK) or from the average yield of *M. xanthus* on nutrient-free TPM (MCY).

***
   $p < 0.001$,

**
   $0.001 < p < 0.01$,

*
   $0.01 < p < 0.05$,

•
   $0.05 < p < 0.1$;

ns $p > 0.1$.

The colors and numbers in parentheses both indicate ranks within a parameter (1 and green represent the highest rank, 9 and red represent lowest rank)