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Ecology of Yellowstone Thermal Effluent Systems: Intersects of blue-green Algae, Grazing Flies (*Paracoenia*, Ephydridae) and Water Mites (*Partnuniella*, Hydrachnellae)

by

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INTRODUCTION

Despite the growing interest in systems ecology, a complete study of the species interactions determining the structure and process of a natural ecosystem does not exist. Thus, a desirable objective of ecological research at present is the complete analysis of the structure and interactions in an ecological system comprising autotrophy, herbivory, predation, parasitism and saprophagy. Such a study should produce useful testable hypotheses about the general structure, processes and interactions of ecosystems.

The algal-bacterial-arthropod ecosystems characteristic of thermal outflows provide an ideal opportunity for such research because:

1. They are isolated, natural ecosystems that have evolved considerable trophic diversity, yet the same families, genera and even species are found in thermal springs throughout the world. Despite this trophic diversity, these ecosystems contain few species.
2. They are not so large as to make a study of the entire system difficult, but they are large enough to permit adequate study and sampling without perturbing the system.
3. Analogous thermal ecosystems exist at many sites throughout the world and are available for corroboration of general conclusions by other investigators.

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4. The springs are easy to manipulate so that field experiments can be used to test model simulations.

Despite these advantages, thermal springs have seldom been studied from the standpoint of the total ecosystem. Tuxen (1944) studied the ecology of thermal springs in Iceland and collected some data on the natural history of the resident organisms. A more comprehensive study was made by Stockner (1967, 1968) but both the water chemistry of the Mount Rainier springs and the organisms were different from those of the thermal ecosystems reported here. A recent review (Brock, 1970) reveals the scarcity of ecological data for thermal systems cool enough for animals to be present.

The Hot Springs

Most of the alkaline hot spring effluent communities in the Lower Geyser Basin of Yellowstone National Park contain three major biotic elements:

1. an algal mat comprising several species of filamentous blue-green algae, 2. a primary biophage, the brine fly *Paracoenia turbida* Cresson, which feeds on the algal mat as both larva and adult; and 3) a red water mite, *Partnuniella thermalis* Viets, whose larvae are parasitic on adult *Paracoenia.* Additional animals are found in this simple community; some other genera of brine fly *(Ephydra, Lamproscatella)*, a parasitic wasp *(Pteromalidae, Urolepis)*, and lycosid spiders are present throughout their life cycle. Other species are important components of the system (i.e. the predaceous dolicopodid flies), but they spend only part of their life cycle in or on the mat.

In this paper we use studies of succession, population dynamics and species intersects to define the three basic elements in the biological interactions of these ecosystems. The term intersect is used to refer to the overlap in time and space of two species. These data will provide part of the framework for later, more detailed analytical models of the thermal spring ecosystem.

The biotic components and intersects

The Algal Mat

A discrete layered mat consisting of blue-green algae and bacteria grows profusely in most of the effluents from the alkaline springs in the Lower Geyser Basin of Yellowstone National Park. Two distinct types are found. 1) Mucilaginous mats that grow as firm, layered sheets with a slippery mucilagionus feel. 2) Encrusting mats that often form erect columnar growths accompanied and supported by extensive deposits of colloidal silica. Both kinds of mats grow in streams and pools; the more massive mats comprising a variety of filamentous blue-green algae are found growing at temperatures of 40 to 60°C. From 60 to 70—72°C the mats are thin because the algae are almost entirely unicellular forms, *Synechococcus*, (BROCK, 1967) and are subject to washout. Below 40°C the mat-forming filamentous blue-green algae are replaced by green algae and diatoms.

The mucilaginous mat is the habitat of *Paracoenia* and will be the only kind of mat considered here. The extensive layered mucilaginous mat develops under a variety of flow conditions and studies of the species composition, productivity and standing crop in controlled flows in wooden troughs have been compared (by WIEGERT & FRALEIGH, 1972) with other measurements of thermal spring productivity (BROCK, 1967; BROCK & BROCK, 1967; STOCKNER, 1968). Species composition is primarily determined by temperature and secondarily by water nutrient quality, whereas productivity is responsive to nutrient quality. If phosphate is high and the available nitrogen adequate (or N_2 fixation occurring) then temperature, flow and the level of free CO_2 will be the major factors determining species composition and rate of production.

The steady-state standing crop, on the other hand, is determined by the physical strength and geometry of mat growth. Filamentous algae intertwine with the bacterial filaments to form a firm resistant mat. The flow rates and gradient configuration of a spring determine the standing crop of mat. The rapid growth of mat exposed to water at 40—60°C builds up thick layers that restrict the channel until the current is either so swift as to tear away sheets of algae or the flow is blocked and diverted into new channels. When hot water flows over a broad flat surface, the flow pattern shifts frequently and unpredictably because growth of the mat in hotter areas keeps diverting the hot water to new areas. Shifting flow patterns are common to a majority of the hot springs. Some, represented by the pool-terrace system, commonly exhibit large scale changes in flow pattern. In contrast, the algal growth in the wide shallow channeled flows of the experimental systems devised by WIEGERT & FRALEIGH (1972) produce narrow patches of cool mat interspersed among braided flows of hot water such as seen in Figs. 1 and 2.

The Fly

Both the larvae and adults feed on the blue-green algae and the filamentous bacteria of the mucilaginous mat (BROCK, WIEGERT & BROCK, 1969). Adults can feed only from the surface of mat not covered with flowing water. The larvae, however, feed from all levels of the mat. Both the larvae and adult females are voracious feeders; the former because of their rapid growth potential (pupation within a week of hatching), the latter because of their large egg production.

The flies have been kept for several generations in the laboratory. Both blue-green algae and filamentous bacteria are suitable foods (Brock, Wiegert & Brock, 1969). All natural mat components were equally satisfactory food but laboratory cultured mat was not as good a food. Flies fed on laboratory cultured mat had a low fecundity and a reduction in the percent of eggs hatching (Wiegert & Collins, unpublished).

Although the adult flies can feed on algal mat at 50°C or higher, most of their activity in the field is restricted to the cooler mat (30—35°C) where the majority of egg-laying occurs (See Table IV and discussion below). Both laboratory and field observations show rapid development and maximal survival at 25—35°C; this we designate the optimum temperature range. Below that temperature range development is slower and above that range the percentage survival decreases. Eggs do not hatch and the first instar larvae die at temperatures above 40°C. The life cycle takes 14 days (egg to egg) at 35°C and the r_m is high, 0.25 flies per fly day (Wiegert & Collins, unpublished). Mature females can produce 100 or more eggs per day so large concentrations of larvae appear in new habitats in less than a week.

The Algal-Fly Intersect

Growth of the algal-bacterial mat does not occur below about 40—45°C, which is well above the optimum temperature for flies, hence, there is no intersect of the zone of algal growth with the habitat of the algal herbivore. This suggests two possible hypotheses: 1. Some inherent limit keeps the flies from being able to invade the temperature zones in which the algae grow best. 2. Factors other than the growth rate determine the availability of algal resources and the temperature preferences of the flies reflect adaptation to the most abundant long term supply of resources.

In deep-channeled swiftly flowing streams the algal mat has a reasonably constant standing crop because sheets of mat are torn loose and float away when the mat grows beyond some critical mass. However, the majority of the springs have shallow outflows more like those on the experimental boards and optimal fly habitats are produced by flow changes and the resulting temperature heterogeneity. Several different growth patterns can alter flow patterns so as to fly habitat.

Algal mat is often cooled when a major flow is diverted by mineral deposition at the lip of a pool overflow or blocking of channels by decomposing algae. If nearly all the flow is diverted, the algal mat will cool to ambient temperature and be "available" to the flies but such habitats are far from optimum because their temperatures, particularly at night, are low enough to retard fly development. Further, if blockage of the channel is complete, such areas will dry before flies can mature.

Small temporary "islands" of cool mat result from partial and temporary diversions of flow due to differential growth of the algal mat itself and these are more suitable as fly habitat because these islands are kept both moist and warm by flows on either side or by seepage flow. Such islands are quickly covered with eggs and the subsequent feeding by the numerous larvae perforates and then completely breaks up or "solubilizes" the filamentous structure of the mat, often providing new pathways for water flow and thus hastening the termination of the suitable temperature regime in the habitat.

Another type of fly habitat develops when the algal mat grows over the surface of the flow. The emergent algal surface is cooled by evaporation and the underside is heated by the hot water. The surface is an ideal habitat for fly larvae if the mat is so thick that temperatures of less than 40°C extend for a depth of a few millimeters.

Figs. 1 and 2 illustrate the effect of mat growth on the development of temperature heterogeneity and "islands" of larval habitat. Plywood troughs one meter wide provided a uniform substrate which had, before algal colonization, temperature isotherms at approximately right angles to the direction of flow (Fraleigh, 1971). There were minor irregularities in the plywood but the size, slope, water supply and flow rate were identical on the two Boards, so that the only major difference between the two Boards is the age of the mat. Temperatures in meters 1—3 taken on a 10 cm. grid at a depth of 5 mm 19 days (N. Board, Fig. 1) and 109 days (S. Board, Fig. 2) after colonization show the effects of algal development on flow and temperature heterogeneity. At 19 days the mat on the North Board had barely grown thick enough to divert flows, but not thick enough to be exposed. Flowing water covers most of the mat, only a few islands of suboptimum (35—40°C) larval habitat have been produced. Cooling of the unrestricted main channel is rapid and the 55°C isotherm reaches only as far as the second meter. In contrast the mature mat on the South Board constricts the hot water into a narrow channel and retards cooling so that the 55°C isotherm extends through the third meter. Consequently, this

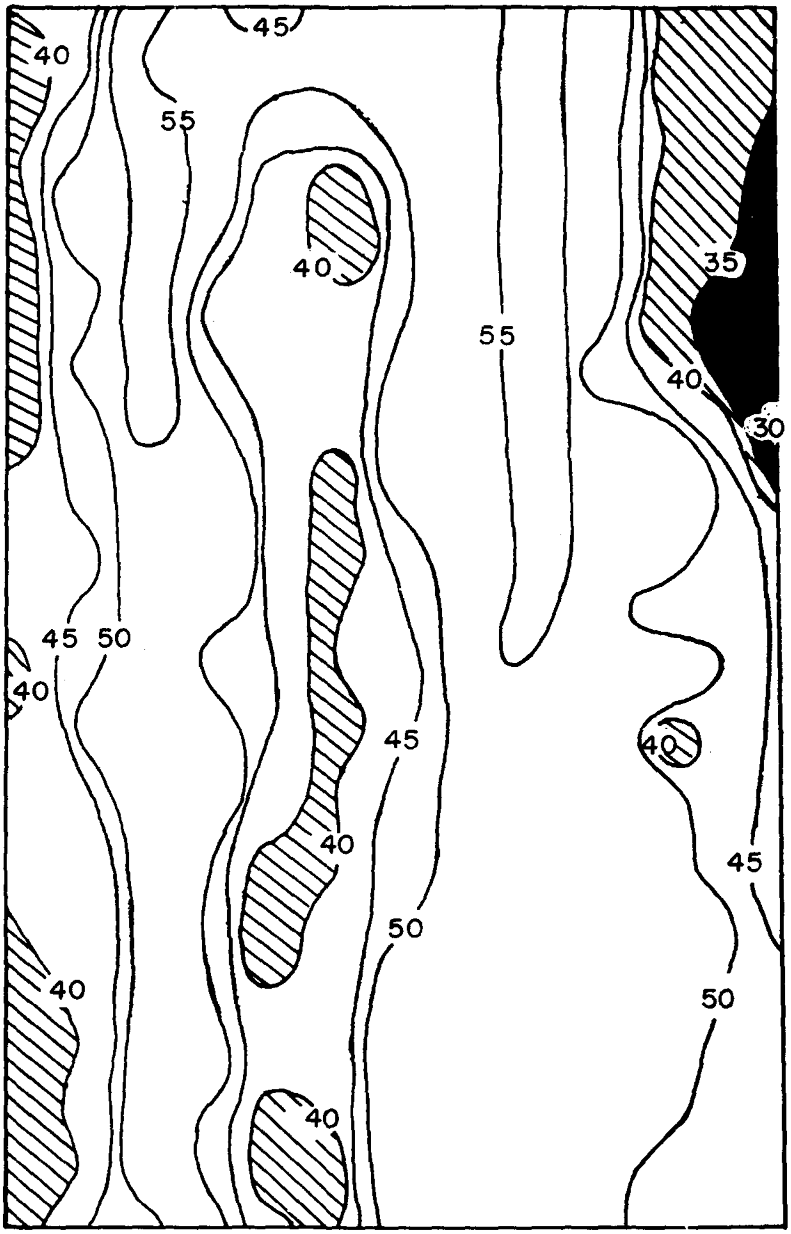
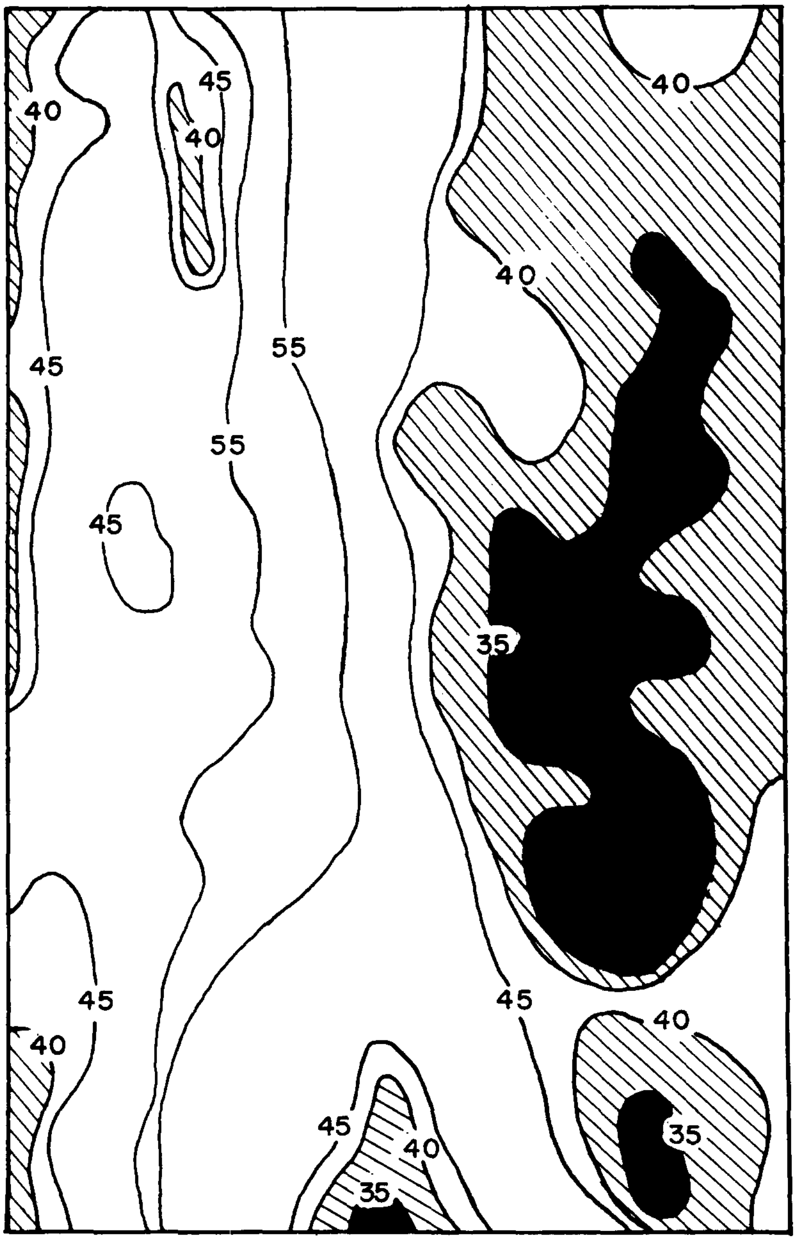


Fig. 1—2. Temperature heterogeneity in the mats developing in shallow wooden troughs. Growth of the algal mat diverts the flow of water and induces cooling and the formation of exposed, cool "islands" of optimum fly habitat. Fig. 1 19-day old mat, Fig. 2 109-day old mat.



channel of hot water warms large areas of mat lateral to the channel up to temperatures optimum for brine fly larvae.

The temperature data used to construct Figs. 1 and 2 are summarized in Table I and indicate the relative mat area available to

Table 1. Tabulation of the relative areas of Figs. 1 and 2 that are suitable habitat for adult and larvae *Paracoenia turbida*. The Old Mat is 109 days old and the Young Mat is 19 days old.

	Old Mat		Young Mat	
	1-2 meters	2-3 meters	1-2 meters	2-3 meters
Percent flooded	38.5	53.1	58.0	74.1
Percent exposed and available to adult flies	61.5	46.9	42.0	25.9
Percent available to larvae (< 41°C)	47.6	30.1	25.2	14.0
Percent optimal for fly larvae (25-35°C)	11.2	13.3	10.5	2.1

flies. Adult flies walk and feed on the surface of any unflooded mat. The oldest mat (S. Board) had an average 46% of such surface available; 61.5% in meters 1—2 and 46.9% in meters 2—3. An average of thirty-nine percent of this mat was less than 40°C in the surface 5 mm and thus was available to fly larvae; slightly more than 12% of the mat was optimum habitat for fly larvae. In contrast, an average 66% of the young mat (N. Board) was covered by flowing water, and only 44% of meters 1—3 was available to adult flies. Less than 20% of this mat was cool enough to be available to larvae and only an average of 6.3% could be called optimal habitat.

These data show that heterogeneous mat temperature is the consequence of algal growth and the accidents of flow diversion. The brine fly *(Paracoenia)* can exploit this transient mosiac of available resource because of its short life cycle (14 days) and high r_m. Islands of favorable habitat will receive huge concentrations of eggs in a very short time and the rapidly growing larvae will decimate small areas of optimum habitat within days. Large areas of mat (several m^2) can be completely solubilized within weeks provided that the flow of hot water keeps the old mat within the 25—35°C range. Fig. 3 shows the decline in algal biomass and subsequent washout of solubilized material in a system where the temperature of an algal mat was suddenly changed from temperatures above 40°C to optimum habitat for flies. The Boards used in this experiment were described in detail by WIEGERT & FRALEIGH (1972). Briefly, the water of 43°C flows over a sequence of four separate troughs, each approximately 1 meter wide and 2 meters long. The water had been flowing over the boards at 30 liter/min for 2 months and standing crop of algal mat had reached a steady state. On July 28, 1969 the

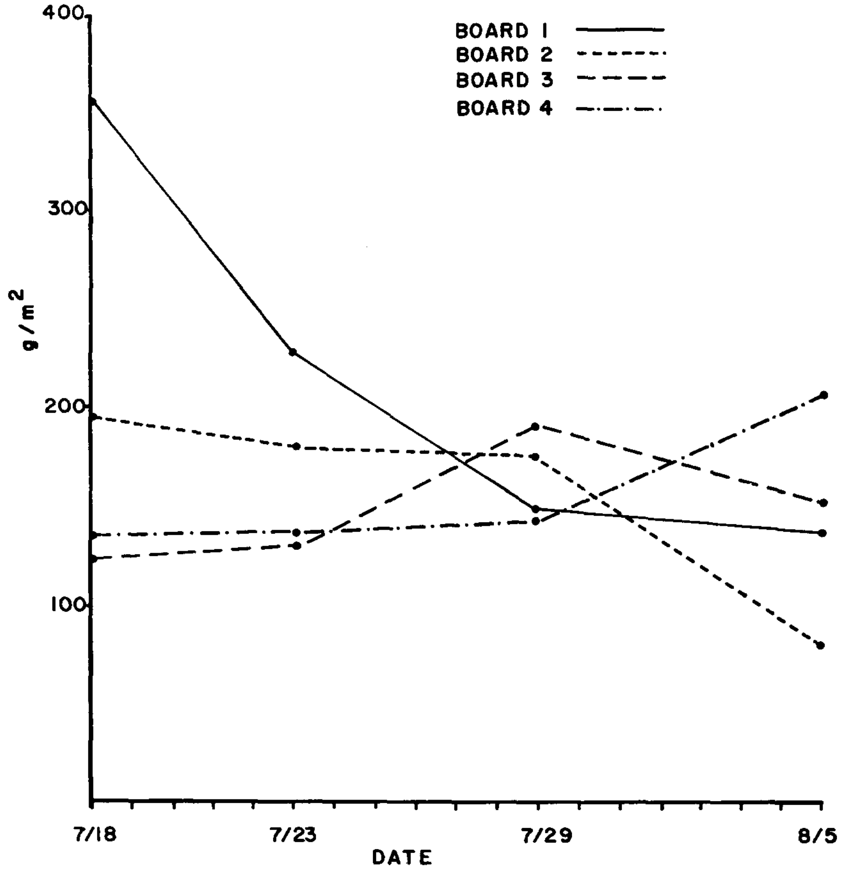


Fig. 3. Effects of cooling an algal mat to less than 40°C. Flow to the board troughs was decreased on July 18, 1969. The subsequent effects of fly grazing on the biomass (ash-free) of mat are shown as a function of time.

flow of water was reduced to approximately 1 liter/min of 43°C water and the temperature over most of the mat decreased to less than 40°C. The subsequent changes in the algal mat were strikingly different on each Board.

Board 1 had the largest initial standing crop of mat and the highest fly population (adults were distributed over the entire surface and larvae in isolated cool "islands"). Within 5 days the mat was covered with eggs. Newly hatched larvae were burrowing all through the mat and over 1/3 of the algal mat had already either been eaten or washed down to the lower Boards. By the end of the experiment on August 5, only 1/3 of the original standing crop remained. Board 2 gained washout material from Board 1 and had a lower initial adult fly population, presumably due to suboptimum temperatures (most of the mat on Board 2 was less than 25°C). After destruction of the mat on Board 1 water of warmer temperatures reached Board 2 and the flies began to destroy the mat. Both Boards 3 and 4 showed a net gain in total biomass as they accumulated washout from other boards. On both of these latter Boards the larval populations remained very low and temperatures were at ambient, commonly less than 10°C at night. Larval growth at these temperatures is very slow. In addition, much of the algal mat on these two Boards began to dry, further reducing its suitability for exploitation by *Paracoenia* larvae or adults.

The experiment summarized in Fig. 3 shows that: 1. *Paracoenia turbida* is able to exploit and quickly destroy optimum habitat (fresh, warm algal mat) by breaking down the "mat" structure and causing washout of the material not eaten and 2) mat that is outside the optimum or suboptimum range (too hot and under flowing water, or too cold and dry) is utilized slowly or not at all.

A small population of flies is always maintained in the narrow strips of insulated mat at the margins of an effluent stream and the few exposed "islands" of cool mat. This small population can quickly increase in density and can consume any mat that cools as a result of natural shifts in the spring flow. Thus, the fly seems to be adapted to an environment in which there are short term shifts in the availability of food resources. Variability of resource availability is determined by the geometry of the stream channel and modified by the patterns and rates of algal growth. The system in made even more unstable by the rapid destruction of the old mat by the fly.

It is not a disadvantage for the temperature tolerance of flies to lie well below the temperatures at which mat grows because there is more exposed mat in the cooler zones lateral to the flow than there is at higher temperatures near the growing face of the mat. Thus, the short-lived fly with a large daily egg production exploits the temperature zones in which the largest area of warm moist mat is found. The hypothesis that the temperature tolerance of the fly is fixed by some inherent physiological limit appears unnecessary, because food resources become less abundant at temperature zones above 40°C.

Life Cycle and Development of the Mite

Eggs are found scattered in the mat throughout the summer and there is no evidence of seasonality in oviposition. Female mites isolated in the laboratory deposit as many as 15 eggs in a day (1—4 eggs per day was most common). The eggs developed and hatched at temperatures from ambient to 36°C in 9 to 10 days. At temperatures of 36°C development was shortened by only a day. Higher temperatures adversely effect the survivorship of isolated adults. A set of 100 mites suffered 36% mortality during the initial five days of isolation at 36°C and produced 93 eggs. The remaining 64 mites were moved to room temperature (20—25°C) and produced 163 eggs with only 4% mortality in the next five days.

Engorged larvae do not detach from active flies. A series of 16 parasitized female flies were isolated and these flies deposited a total of 861 eggs. All the 31 mites on these flies remained on their host until after the host fly died. Mites also seem to remain on their host in the field, because old females have larger mean loads and a higher incidence of mites than young females (Table II). Seemingly mites ought to detach as flies oviposited because the flies generally oviposit in mat of the preferred temperature for mites (Table III). However, the fly oviposition sites are likely to change rapidly because fly larvae can destroy mat in less than ten days (Fig. 3). Detached mite larvae require 9—11 days for transformation at 20—25°C and are quiescent throughout this time, thus, fly oviposition sites may not be stable enough for the post-parasitic development of the mite.

Table 2. Percent of flies parasitized and average larval mite load on female flies. Each is the mean of 7 samples taken during the period 7/24 - 8/30, 1970. One standard deviation is given in parentheses.

	Percent parasitized	Mean number of mite larvae per fly.	
Spring	Young females	Young females	Old females
(Constant flow pattern)			
Nez Perce	65 (9)	1.74 (0.6)	4.91 (2.7)
Sinter	75 (8)	2.15 (0.9)	4.52 (1.8)
Vee-stream	69 (16)	1.58 (0.4)	4.62 (1.9)
(Variable flow pattern)			
Seeping	58 (17)	1.37 (0.8)	1.46 (0.8)
Quaking	52 (17)	0.95 (0.5)	2.28 (2.2)
Terrace	65 (15)	1.57 (0.6)	2.58 (1.5)

The mite requires a minimum of 23 days to go from the egg to the newly developed nymph and this accounts for only about 10% of the growth increment of *Partnuniella*. Adult mites are long-lived in the laboratory cultures, where 90 adult mites were kept for 2 months with only 31% mortality. The total life cycle of the mite must require several months. There is no pronounced seasonality in the parasitism of hosts so the mite population must consist of a set of overlapping generations.

The mite life cycle is several times longer than that of its fly host and the creeping aquatic nymphs of the mite cannot move from place to place as easily as the short-lived flies. This raised the question of whether the distribution of mite resembles the distribution of the host. Temperature and exposure define the fly habitat and the mite adults are found at temperatures that broadly overlap the optimum range for flies (Table III). These observations of field dispersion suggest that the fly and mite prefer the same temperature regime but they do not show whether mites succeed in moving from zone to zone as effectively as the flies. If the long lived slow moving nymphs and adults suffer greater mortality as flows change in a spring, then, survivorship of adults may limit the success of larvae. This can be measured with data on the parasitism of hosts by larvae in a variety of situations.

Table 3. Temperatures in the center of 20 *Paracoenia* egg masses compared with the temperatures at which 121 *Partnuniella* were observed on the mat and the temperatures at which 113 mites were taken from within the mat. Observations from all six springs described in the appendix were pooled.

	Temperature range in °C					
	20-24	25-29	30-34	35-39	40-44	45-49
Fly egg masses	0	5	10	4	1	0
Partnuniella on surface	10	53	27	28	3	0
Partnuniella on the mat	0	7	11	95	0	0

Host Exploitation

The mite larvae hatch from eggs laid in the water and then crawl to the surface, break through the surface film and then run about on the water surface and mat surface as well as on stones and the soil adjacent to the spring. The larval mites do not clump and are easy to see as they move about. Most mites that parasitize flies rest in groups on the host pupa (Corbet, 1967; Mitchell, 1957, 1964) and attack the fly as it emerges. That is not the case in *Partnuniella.* The larvae attach only to adult flies and are indifferent to pupae both in the field and in laboratory experiments.

In addition to running, the larvae jump up. Hosts are encountered either by larval mites running into a fly leg, the proboscis of a feeding fly, or else a mite larva may jump and land on a fly. Once on a host, the larvae move about in search of a membrane for attachment and the fly usually responds by grooming, often removing the mite larva.

An aging technique was necessary to determine whether mite larvae were more likely to attack young flies than old flies and wing wear was the best criterion. Flies with torn or broken wings were classed as old; flies with intact wings were called young. A set of 18 samples collected from six localities from 24 July to 5 August, 1970 included 9% (147/1624) flies with damaged wings. In a population of brine flies growing at the intrinsic rate of increase and having achieved a stable age distribution, flies 14 days or older will make up 10% of the adult fly population (WIEGERT & COLLINS, unpublished). The 9% of the flies with damaged wings were thus assumed to be two or more weeks old. Thirty eight percent (615/1624) of the flies carried engorged mite larvae. Since larvae become engorged by the third day after attachment, these flies were assumed to be older than three days. Thus the age distribution of the population, based on wing wear and the stage of larval mite engorgement was: 0—3 days 53%, 4—14 days 38%, 14 days 9%. The stable age distribution would be 0—3 days 46%, 4—14 days 44%, 14 days 10%. The two independently determined criteria for age estimates in field samples were accepted because of this close approximation of the stable age distribution.

Unengorged larvae represent the parasite load acquired by the host during the three days immediately preceding collection, and the proportions of engorged and unengorged larvae can be used to show differential rates of larval attachment. The numbers of engorged mites per fly increased with age because the larvae remain attached to the host. The proportion of unengorged alrvae on a host remains about constant (around 30%, Table IV), thus, older hosts must acquire young larvae more rapidly than young hosts.

Flies do groom when attacked by larvae and mites are found on membranes that the fly cannot groom very easily. The alary membranes at the base of the wing are difficult for the fly to clean because of their complex folds and the projecting wings and halteres. This was by far the most commonly attacked site on all hosts (Table V). The ventral membranes of the abdomen and thorax, especially those posterior to the third coxae, cannot be reached by the legs of the fly and are the secondary centers for mite attachment.

Older hosts aquire an excess of mites on the proboscis (Table V) and the increased accumulation of mites on older flies may result

Table 4. The numbers of mites carried by flies of different ages and sexes. Nineteen samples collected from 6 localities between 24 July and 5 August are pooled. A chi-square test based on the total numbers of engorged and unengorged mites was used to test the null hypothesis that loads are consistent in the four categories of flies. The chi-square value of 3.965 (d.f. = 3) P =0.265 is consistent with the null hypothesis.

	Young Flies (Wings Intact)		Old Flies (Wings Torn)	
	Female	Male	Female	Male
n of flies	736	741	74	70
no. of unengorged mites	288	79	209	55
no. of engorged mites	621	229	478	129
% of mites unengorged	32	30	26	30
mean load of mites per fly	1.23	0.93	4.16	2.63

Table 5. Data used for contingency tables to test for the consistency of load arrangements on hosts of different sexes and different ages.

Ho: Arrangement of mites on female hosts = arrangement on male hosts. Chi-square = 19.04 (4 d.f.) P =0.0008.

	Thorax	Alary	Wing	Abdomen	Proboscis
Females	175	570	57	210	205
Males	159	398	44	174	96

Ho: Arrangement of mites on young flies = arrangement on old flies. For females: Chi-square = 7.12 (4 d.f.) P = 0.13. For males: Chi-square = 16.34 (4 d.f.) P =0.0001.

	Thorax	Alary	Wing	Abdomen	Proboscis
Old female	130	436	48	146	149
Young female	45	134	9	64	56
Old male	122	319	34	124	88
Young male	37	79	10	50	8

from larval mites having a proportionally greater chance of permanently attaching to older flies than to younger flies. It may be an advantage for a larva to attach where there is already an attached larval mite because the attached mites would hinder efforts by the fly to scrape or brush off new arrivals.

There was a significant difference in the pattern of attachment on males vs. females (Table V) due to females carrying many more mites on the membranes of the proboscis. An excess of mites on the proboscis was the major contribution to the larger average loads on females (Table IV) and to the differences in attachment patterns among males and between males and females (Table V). The proboscis of female flies is more exposed to mites because female flies must feed extensively in order to sustain a daily egg production that often equals one-fourth of their body weight. Simple exposure rather than differences in mite behavior seems to adequately explain the larger loads on female flies.

The Fly-Mite Intersect

Fly populations oscillate in numbers because the flies exploit mat exposed by unpredictable changes in water flow and they can destroy these new resources in a few days. The size and location of fly populations can undergo drastic changes over time periods of one or two weeks.

The mites, with a life cycle longer than three months, require more stable situations because the creeping aquatic nymphs and adults of *Partnuniella* cannot follow shifting temperature zones as effectively as adult flies. The mites ought to achieve miximum success in springs of such small dimensions that larval mites can explore the entire spring but they should be less successful in the larger, more unstable springs where unpredictable fly hatches are spread over a large area.

The functional intersect of the mite habitat with the fly habitat will be the area in which the mites discover and attack flies. This can be estimated from the percent of flies parasitized (incidence) and the variability of the mite load in time and space. Estimates of the intersect of mites and flies were based on weekly collections from six different "natural" thermal algal mates in the Lower Geyser Basin and Gibbon River areas during July-August 1970. The locations and characteristics of these ecosystems are given in Appendix I. Most comparisons were based on young female flies because this is usually the largest age class and these flies presumably reflect the conditions of the three days prior to the sample.

A simple two-way ANOVA (Analysis of Variance) with no replication was performed on the sample averages from each date. All three measures (incidence on young females, mean larval loads on young females and mean loads on older females) gave similar results: There was no significant effect of sample date ($p > 0.1$) but locations differed significantly. However, for both incidence and mean loads on young females the F values were just barely significant at the 95% level ($0.0 < p > 0.05$) whereas the mean loads on old females showed a highly significant F ($p = 0.005$). When the data from all dates were combined, three locations, Nez Perce, Sinter and Vee-stream showed mean larval accumulations greater than 4.0 on old females and old female flies from the remaining three springs (Seeping, Quaking and Terrace) all carried mean loads of less than 3.0 mite larvae. The only physical factor corresponding to this division seemed to be the nature of the seasonal flow pattern. At all three of the latter springs (Seeping, Quaking and Terrace) there was clear evidence of shifting or inconstant flows in the form of drying mats, large areas of cool mat decimated by dense *Paracoenia* larval populations, and new mat in early successional stages. This was most obvious at Terrace, the largest of the sampled ecosystems and at Quaking, a spring in which the flow almost stopped in midsummer and then resumed.

The data were rearranged to separate variable flows springs (those in which mat growth and/or mineral deposition cause frequent and major shifts in flow pattern or where the flow of water is itself subject to change) from the so-called constant flow springs that had a well-defined stable channel during the summer of 1970. The rearranged data are summarized in Table II and another series of ANOVA using two locations, variable and constant and three replications of each gave the results summarized in Table VI.

Table 6. F values from ANOVA performed on: 1) Incidence on young females, 2) larvae per young female and 3) larvae per old female. The two flow patterns, constant and variable, each based on data from three springs. Time represents seven sampling dates in summer of 1970. Level of significance; * = P<.05, *** = P<.001.

Treatment	d.f.	Incidence	larvae/young ♀	larvae/old ♀
Flow pattern	1	7.10*	5.99*	23.29***
Sample date	6	1.70 N.S.	1.16 N.S.	1.75 N.S.
Interaction	6	0.35 N.S.	0.35 N.S.	1.51 N.S.

Again no seasonal differences were significant. But the variable flow group differed significantly from the constant flow groups in all three cases. The incidence of parasitism, mean larval load per young female and mean larval load per old female were all higher in the constant flow springs and the significance was increased over the simple 2-way ANOVA using location with no replications. Old females in particular, showed a uniformly high larval load in constant flow springs. Because of the limited dispersal ability of nymphal and adult mites compared to that of adult flies, the mite populations of variable flow springs would seldom be correlated with the short term oscillation of the fly in time and space. This would be expected to lead to the observed lower incidence of parasitism and mean larval load observed for variable flow springs.

Discussion and conclusions

The biomass of algal mat differs widely within and between thermal spring effluents. Above 60°C single celled blue-green algae, *Synechococcus*, are embedded in a mat formed by filamentous bacteria. The steady-state biomass, determined by the algal growth rate and the washout rate of algal cells, is lowest and most uniform in these mats. From 60° to 40°C the dominant filamentous blue-green algae form an interlocking mat that resists washout. Some of these mats are encrusting, others form a layered mucilaginous mat.

Mucilaginous mats erode when water currents are strong enough to loosen and tear off layers of mat, thus, the standing crop is lower and more stable through time in well channeled, swiftly flowing streams. Minerals deposited by most thermal waters tend to fill up channels and produce terraces. The shallow streams of water flowing slowly over terraces do not rapidly erode the algal mat. Growing mat can divert water by confining and/or damming the flow, consequently, there is an inverse relation between the current speed and the frequency with which the pattern of water flow changes. The biomass of algal mat is also inversely related to current because less mat is eroded as currents decline in speed.

Mucilaginous mat develops at 40° to 60°C but the ephydrid fly that eats the mat has a temperature optimum of 25° to 35°C. Furthermore, the adult fly doesn't feed below the surface of the water. The density of flies is therefore largest in less stable streams where shifting currents expose new areas of mat. These exposed patches of mat quickly cool and become covered with ephydrid eggs. The large numbers of larvae can destroy the structure of the mat, leading to washout, the entrance of hot water and mass mortality of larvae that have not pupated.

In older mats with a shifting flow pattern, the total area of mat within the optimum temperature range of the fly (25—30°C) is usually much greater than the amount of mat in any other 10°C range. Clearly the temperature tolerance of the fly is suited to exploiting the resources available to it. The short life cycle and high rate of egg production are also adaptations for exploiting short term oscillations in available resources that are common in such thermal effluents. Unless the fly could extend its maximum temperature tolerance and at the same time maintain its optimum development in the range 25—35°C, an adaptation to higher temperatures would result in a loss rather than a gain in available habitat.

Oscillations as short as 10 to 14 days can be exploited by the fly, but the mite *Partnuniella*, with a life cycle of over three months, must move about when conditions change. The long-lived creeping aquatic stages of the mite are at a disadvantage in the most unstable systems when the flow is diverted from relatively large (several m^2) areas of mat. Such areas dry up, killing the adult and nymphal mites. Even in more stable systems, where the patches are smaller and movement of adult mites into newly-cooled mat areas is possible, the incidence of parasitism is low because the embryonic development of mite eggs takes as long as two weeks, longer than necessary for the destruction of a patch of mat by the fly larvae. Thus, host discovery in such systems depends on the ability of the mite larvae to move from one patch of mat to the next.

The intersect of mite larvae with the adult flies they parasitize is a sensitive measure of mat stability. If thermal habitats are independent of most external short term edaphic factors or perturbations from invasions of non-thermal species there should be no seasonal changes in the rate of parasitism. No significant seasonal changes in percent of flies parasitized were found in a set of six springs examined during the period July-August 1970.

The three springs with variable flow pattern and consequent mat instability showed greater variation in the incidence of parasitic mite larvae, but both the mean incidence of parasitism and the mean larval loads per female were significantly lower than in stable flow springs, as expected if the mite was unable to respond to short term shifts in available resources.

This analysis of the fly-mite intersects in a set of thermal springs supports our hypothesis that the abundance and relative densities of organisms in higher trophic levels can be predicted from knowledge of the growth and stability patterns of the filamentous blue-green algal mat in thermal spring effluents. The higher trophic level, in this case the parasite of an herbivore, is the most sensitive measure of community stability because all perturbations of the system affect the parasitic mite.

SUMMARY

As subjects for ecosystem studies, thermal spring effluents offer the advantages of trophic diversity with taxonomic simplicity, ease of sampling, replicability, world-wide distribution and manipulability. The dominant primary producers (filamentous blue-green algae) are grazed by ephydrid flies. These in turn harbor larvae of the water mite *Partnuniella*. The high instrinic rate of increase of the fly enables it to exploit temporary cool spots in the mat. The lower fecundity and longer life cycle of the mite restrict its ability to exploit temporarily suitable habitat. Thus the intersect of mites with flies is a sensitive measure of stability in the algal mat. Springs with a variable-flow pattern and consequent mat instability had both a lower mean incidence of parasitism and a lower mean larval load per fly. The data support our hypothesis that the abundance and relative densities of organisms in higher trophic levels can be predicted from knowledge of the growth and stability patterns of the filamentous blue-green algal mat in thermal spring effluents.

APPENDIX I

The following descriptions indicate the conditions of the six localities during the summer of 1970. Temperatures were all recorded on September 7, 1970 (Ambient temperature 10—12°C) and deviations of more than a degree from temperatures taken during early July (Ambient T = 20—24°C) are noted. These are all springs in which mat develops at temperatures below 70°C. All but Terrace Spring have no previously published name because they are either small or away from tourist areas. The substrate of all the springs is a silicaceous deposit commonly called sinter.

Nez Perce: A small unnamed spring on the bank of the Nez Perce River, lies adjacent to a sevice road at a point that is 1.4 miles east of U.S. Route 289. A 44°C outflow originates 8.3 meters south of the river and two flows diverge over a convex deposit of sinter. The east flow dries or seeps into the sinter before reaching the river, the west flow reaches the river. These streams generally flowed over attached mat and cooled to 24—37°C in 3 meters. Flows were constant in rate and location so the flies were limited to a rather constant crop of algal mat along the margins and a few small islands of cool mat. The total area of mat was about 8.5 m^2.

Quaking Mat: This mat is in Serendipity Meadow study area (WIEGERT and FRALEIGH, 1972). The stream from a 74°C spring is channeled into an area 1.8 by 1.2 meters at temperatures of 49.5 to 31°C at maximum flow. Around the end of July an abrupt flow reduction let the mat cool to less than 30°C and it was destroyed by flies. The flow began again around August 20 and reached the earlier flow rate by September 4. The floating mat provides a constant fly habitat at the margins and a variable area in large cool islands.

Sinter Mat: This is about 40 meters northwest of Quaking Mat and was produced in 1968 by clearing away sedges so that a stream at 59°C flowed over an old sinter deposit. A pool of water over 50°C supports a thick mat and the outflow is at 49.5°C. Only the margins and an occasional small cool island are cool enough for flies.

Seepage Spring: This is one of a series of small springs on the east bank of the Firehole River 11.1 miles south of Madison Junction to U.S. Route 289. A series of 5 small flows at 32—62°C formed a broad stream on July 27 but there was only one outflow at 39.5°C on September 7. The well-confined stream had several marginal areas of cool mat at any one time. These shifted upstream because the flow was decreasing and cooling through the sampling period.

Terrace Spring: This large mat lies 0.6 miles north of Madison Junction. A violently bubbling spring of 59.5°C fills a large pool west of the road and a stream at 49.5°C flows under the road. The water then diverges over three or four terraces and streams from the lowest terrace at temperatures of 34.5° to 45°C. The terrace area of about 35 by 40 meters provided large areas of unstable fly habitat and the main stream draining the terraces provided fly habitat for at least 100 meters downstream.

Vee-stream: This area lies on the east bank of the Firehole River about 60 meters south of the south bridge on Fountain Flats Drive. A 54° spring 2 meters from the river diverges into two streams that flow over the sinter and these have fairly large shallow marginal areas that provide perhaps 2—3 m^2 of good fly habitat at most times. The spring had a constant flow during our study.

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1. The water emerges from the ground at a pH of about 6 due to large amounts of dissolved CO_2. Equilibration with the atmosphere causes a rapid rise of pH to between 8 and 9.