Functional Analysis of a Thermal Spring Ecosystem, with an Evaluation of the Role of Consumers

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FUNCTIONAL ANALYSIS OF A THERMAL SPRING ECOSYSTEM, WITH AN EVALUATION OF THE ROLE OF CONSUMERS[1]

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Abstract. Low temperature ($< 40°C$) alkaline thermal spring effluents in Yellowstone National Park support a benthic algal-bacterial mat fed upon by a single herbivorous brine fly (Diptera: Ephydridae), which in turn is consumed by a number of arthropod predators (water mites, spiders, and a predaceous fly). A census of an entire spring ecosystem provided a framework upon which to integrate present knowledge of this system.

Growth of the algal-bacterial mat appears to be nutrient limited; measures of free CO_2 concentrations are good predictors of the differences in productivity within and among springs. *Paracoenia turbida*, the herbivore, saturates all suitable oviposition sites, and its larvae destroy all algae available below them. The larvae apparently suffer substantial density-dependent mortality late in their development, when they consume algal dams protecting them from hot water flows. Thus, they compete for limited space of suitable temperature. Algal-bacterial biomass persists because, at any one time, most of the mat is too hot for larvae, or is covered by flowing water and consequently unsuitable for oviposition. The brine fly eggs which constitute the prey for most predators are also largely unavailable because the flies insert them into the algal-bacterial mat, where they are difficult to remove and feed upon. The demand-availability ratio for fly eggs is high; therefore reproduction of the major predatory water mite, *Partnuniella thermalis* (Hydrachnellae) is probably limited by the supply of available eggs.

Despite the abundance of their prey species, then, both primary and secondary consumers seem to be resource limited because most of their prey are unavailable. The important role of refuges in defining the biomass structure of this ecosystem prompted us to define four conditions which tend to limit consumer influence on prey density: (1) evolutionary specialization by consumers, which narrows the spectrum of potential food; (2) poor food quality which does not allow population growth; (3) evolved defenses of the prey; (4) the degree of uncertainty in resource distribution in space or time. Restrictions of type (4) are difficult to document and may often go unappreciated, but an example from the thermal spring system shows the uncertainty in resource distribution may be evolutionarily insoluble, and it may be a powerful constraint on consumer impact. There is little reason to believe that these conditions are any less powerful in complex than in simple systems. By analogy then, the ability of consumers to influence prey density in complex terrestrial and aquatic systems may also be severely limited. The importance of refuges in complex systems might be inferred from measurements of community responses to low-level enrichment or harvesting.

Even though their direct influence on prey densities is limited, consumers in the thermal spring ecosystem increase the net primary production of the system and increase the efficiency of energy transfer between the first and second trophic levels. Thus, they affect processes, not prey densities, in this system.

Key words: Acarina; blue-green algae; community structure; consumers; Diptera; Ephydridae; population regulation; productivity; refuge; Wyoming.

INTRODUCTION

Hot springs are distinctly bounded natural systems that operate largely independent of their surroundings. Their hot water effluents maintain year-round temperatures above the summer maxima for adjacent systems, and lay down mineral substrates quite unlike adjacent rocks and soil. The biota of these springs consists of a few thermophilic species of algae, bacteria, and arthropods which are also distinct from those of surrounding communities. Effluents between 30°C and 45°C support metazoan herbivores, predators, and parasites, as well as microorganisms, and may be regarded as easily studied analogues of larger and more complex systems.

Descriptions of the biology of the components of such low temperature alkaline thermal effluents in Yellowstone National Park have been published
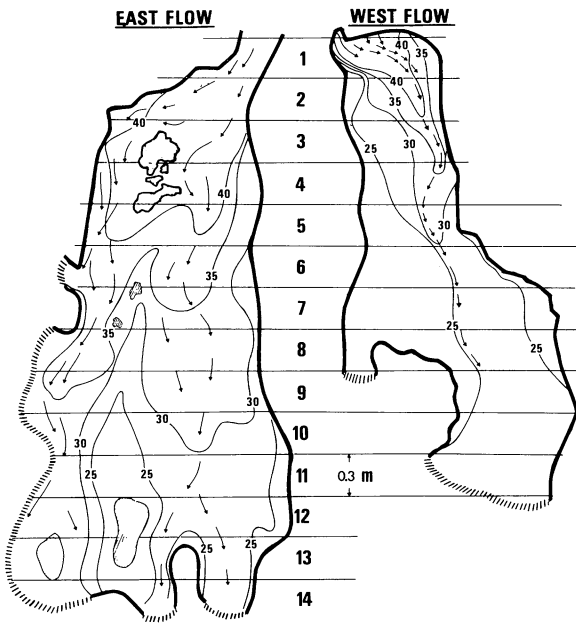
FIG. 1. Flow patterns and isotherms in Nez Perce Spring just before the census. Stippled and hatched areas are islands. Horizontal lines divide the sampling locations graphed in Fig. 3.
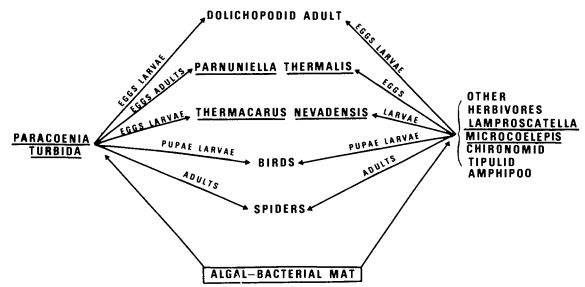

FIG. 2. The biophage food web of high productivity alkaline thermal springs in Yellowstone National Park.

vested and far enough removed from other springs to make significant immigration unlikely during the courses of our census. The spring lies in Yellowstone National Park, Wyoming, USA. 2.38 km east of US Highway 20, on a trail head road paralleling Nez Perce Creek. Two outflows from a single 43°C-source run over a convex creekbank (Fig. 1). Each outflow stream runs independently for $\approx$ 2.5 m over a hard siliceous precipitate (sinter), then percolates into loose substrate at the creek edge.

COMPONENTS OF THE ECOSYSTEM

The biophagous part of the food web of a typical alkaline thermal community in Yellowstone is illustrated in Fig. 2.

The blue-green algal-bacterial mat of Nez Perce Spring is the mucilaginous type described by Wiegert and Fraleigh (1972). Although the algae grow well only above 40°C, *Paracoenia turbida* Cresson (Diptera: Ephydridae), the fly which eats them, requires temperatures below 40°C, and grows best at 25–35°C. Consequently, the fly larvae are restricted to cool patches in the algal mat. Such patches occur along the edges of outflows or where hot water has been diverted around a patch by growth in thickness of the patch itself. Adults lay eggs in these locations, and larvae must grow to maturity, pupate, and emerge before shifts in water flows flood the areas again with hot water.

Several carnivores feed wholly or in part upon brine flies. *Partnuniella thermalis* Viets (Acarina: Protsiidae) is a water mite whose eggs hatch into parasitic larvae that station themselves on the mat and jump onto passing adults of *P. turbida*. The subsequent nymphal and adult stages of the mite feed on brine fly eggs and eggs of nonthermal insects that oviposit in thermal waters. *Thermacarus nevadensis* Marsh (Acarina: Hydrodromidae), the other thermophilic water mite, is known to feed on ephydrid eggs in the laboratory. The host for its parasitic phase is unknown. A nonthermophilic long-legged fly *Tachytrechus angustipennis* (Diptera: Dolichopodidae) is also an important predator (W. J. Kuenzel

(Wiegert and Fraleigh 1972; Wiegert and Mitchell 1973; Collins 1975a), and energy flow models of several of the components have been constructed (Wiegert 1973, 1975; Fraleigh and Wiegert 1975). Here we use the results of a complete census of a small spring community as a framework for integrating the published and unpublished data in order to evaluate and extend our understanding of the thermal ecosystem.

SELECTION OF A SPRING FOR THE CENSUS

A major criterion for selecting a particular spring was that it be at or near steady state, so we could assume stable age distributions and calculate survivorship curves for the metazoans censused. Wiegert and Mitchell (1973) suggested that shifts in the pathways of hot water flows (which kill large numbers of flies and water mites by lethal heating or cooling and drying) are largely to blame for fluctuations in the populations of Yellowstone's alkaline thermal springs. They showed that measures of habitat overlap between the mobile adults of the major herbivore, a brine fly, and its relatively sessile water mite parasite reflected the frequency of flow shifts, and could therefore be used as indices of constancy of the mite and fly populations in a spring. Such measures showed Nez Perce Spring was among the more stable system studied by Wiegert and Mitchell (1973, Table 2). We selected it for our census because it was also small enough (8.7 m²) to be completely har-

and R. G. Wiegert, *personal observations*). The adults run over the surface of the mat, feeding upon the eggs and young larvae of brine flies. The immature stages of the dolichopodid live in nonthermal areas.

The remainder of the fauna consists of herbivores that are common only at temperatures below 30°C. Chironomids (Diptera) and amphipods (Crustacea) are the most abundant. Small numbers of hydrophilid beetles, an elmid beetle (*Microcylloepus* sp.), a tipulid (Diptera), and a small ephydrid (*Lamproscatella dichaeta*) are also common. None of them is regularly collected in the primary habitats of the thermophilic fly and mite described above.

METHODS

On the nights of 11 and 12 July 1972, adult flies were aspirated from the algal-bacterial mat and the overhanging vegetation around the outflow. All *Thermacarus* adults and spiders active on the mat were also captured at this time. From 12 to 15 July all the algal-bacterial mat and the animals of the spring were carefully collected for counting and weighing. Strips of algae 0.3 m wide and perpendicular to the flow were searched for animals by picking the mat apart and lightly brushing *in situ*. After examining the area systematically a second time, the loose algal-bacterial mat was gathered and put in pans of water. The mat remaining on the substrate was scraped off, the surface of the substrate was scrubbed clean with a steel brush, and the scrubbings were collected. Animals were picked from the material and the algae and bacteria finally bagged. The contents of the bags were examined for fly larvae once more in the laboratory; then the mat samples were dried at 60°C, and the ash-free dry weight determined.

Completeness of the census

There were only 20–50 adult Diptera on the mat for 2 days following the nighttime collections; hence the 1,033 *P. turbida* and 129 *Tachytrechus* collected at night probably represent > 95% of the adult fly population at the spring. The completeness of our census of immature flies can be judged roughly by the yield from the second and third sortings. These procedures yielded only a 16% increase in numbers of third instar *P. turbida* larvae and a 3% increase in numbers of pupae. Therefore, we feel our counts of these stages are close to the real values. Second instar larvae were not effectively censused and are not considered in the analysis.

The water mites are secretive and were difficult to collect completely. Two weeks after the census, 124 adult *Thermacarus nevadensis* were taken on the regrowing mat. All these mites were fully sclerotized and pigmented and are not likely to have been recently transformed nymphs. They were probably

active at the time of the census and have been included in the census counts. After these collections only one *Thermacarus* was seen in the spring. The census of *Partnuniella thermalis* was difficult because the mite is small, secretive during the day, and easily conceals itself in the mat and the gravel along the edge of the spring. Of the total collection of 2,993 mites, 384 were taken in nighttime collections immediately after the main census. No more mites were seen subsequently, but substantial numbers probably went undetected in the sorting. The census count is therefore regarded as an underestimate.

RESULTS AND ANALYSIS

Figure 3 shows the changes in the densities of the mat-inhabiting organisms along the outflow channels of the two flows. The very low flow rate of the west flow (0.9 l/min) produced a relatively cool mat, and the thermophiles were most abundant in the strip of algae nearest the source (Fig. 3C). The flow on the east side (4.5 l/min) of the source, however, produced substantial areas at temperatures suitable only for the thermophiles. The less temperature-tolerant arthropods like the tipulid and the small brine fly *Lamproscatella* are restricted to the extreme downstream end of the mat (Fig. 3A). The biomass structure of the community is summarized in Table 1.

In the analysis to follow we combine the census data with information from other studies to evaluate the mechanisms influencing production and standing crop of each trophic group. We simplify the system by ignoring the low temperature herbivores. Because a substantial portion of the *P. turbida* larval population has no contact with these potential competitors (Fig. 3A), and because data presented in another section show *P. turbida* is not strongly food limited, we feel this simplification is reasonable.

The algal-bacterial mat

The effect of erosion by water currents on mat density is illustrated by the relatively low densities in the upper three locations of the east flow, where the effluent channel was narrow and current velocity was high (Fig. 3B, Fig. 1). Otherwise, the two flows show consistent downstream decreases in mat density typical of the alkaline hot springs in the Yellowstone area. Comparison of the temperature-biomass relationships for the two flows (Fig. 3B) shows biomass is independent of absolute temperature values. These observations are consistent with those of Wiegert and Fraleigh (1972) for other Yellowstone springs.

The density and net productivity of algal-bacterial biomass in these hot springs is very high compared to those of most other natural lotic systems (Wiegert and Fraleigh 1972). Some of the conditions that allow very high productivity are high rates of nitrogen
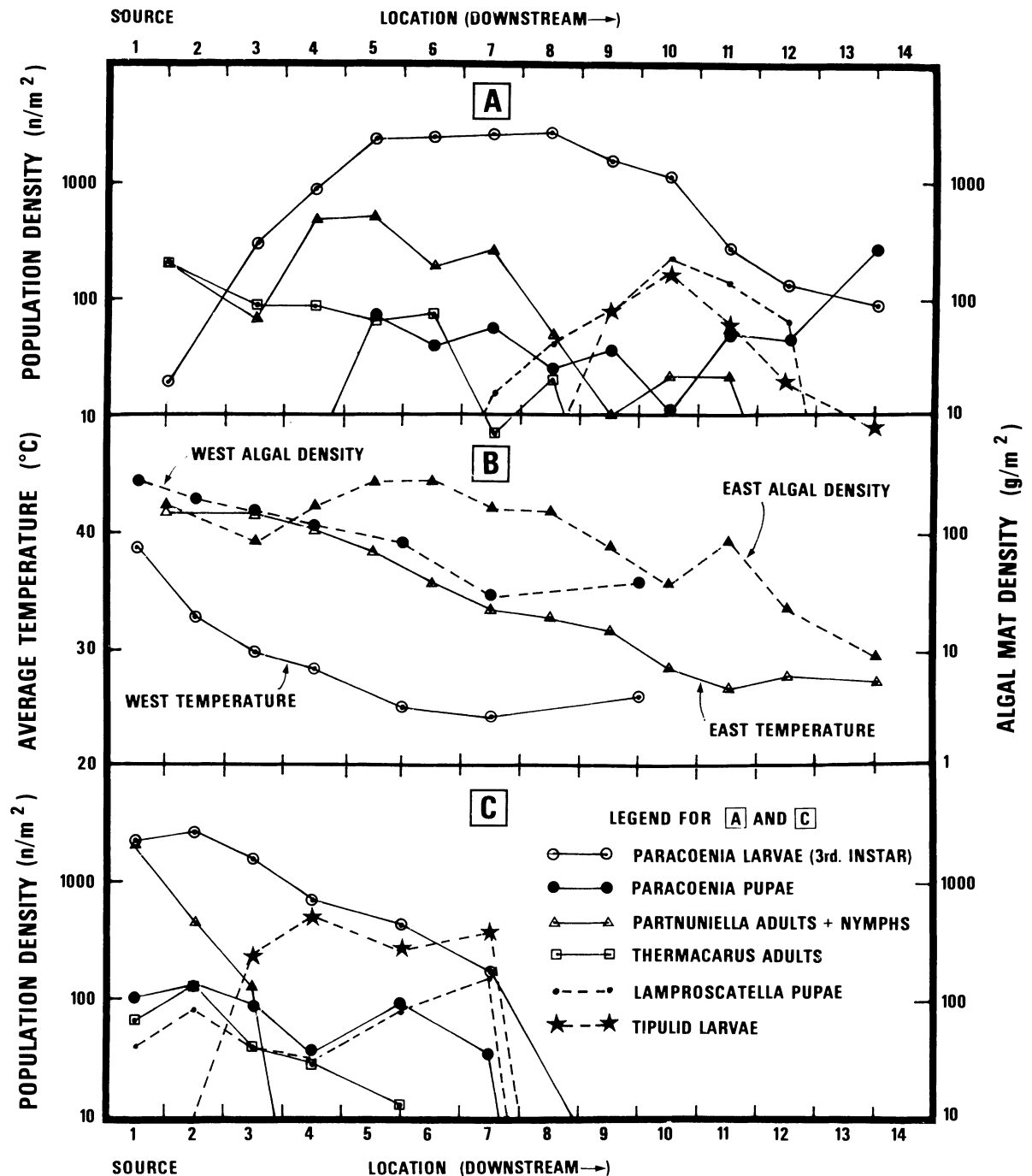
FIG. 3. The distribution of organisms with distance from the source of Nez Perce Spring. "Locations" are 0.3 m-wide strips of algae numbered from the source (Fig. 1). (A) Semilog plots of animal densities in the east flow, which carried 4.5 l/min of water. (B) Average temperature and density (log scale) of the algal-bacterial mat in both flows. (C) Semilog plot of animal densities in the west flow, which carried 0.94 l/min.

fixation, high concentrations of molybdate-reactive filterable phosphorus (.17 ppm) and supersaturated concentrations (45 ppm) of free CO_2 (Wiegert and Fraleigh 1972). Wiegert and Fraleigh observed that reactive phosphorus concentrations do not decrease

downstream from the source, whereas free CO_2 concentrations show sharp reductions due both to primary production and degassing to the atmosphere. Consequently, they hypothesized that the temperature-independent downstream decrease in mat density

TABLE 1. Numbers and biomass of organisms from Nez Perce Spring. Numbers in parentheses are dry weights of individuals. Algal biomass is grams ash-free; all other weights include ash. Flow rates for east and west channels were 4.5 l/min and 0.9 l/min, respectively

| | Area (m²) | Algal-bacterial biomass (g ash-free) | Paracoenia | | | | Partnuniella adults (0.417 mg) | Thermacarus adults (2.671 mg) | Lamproscatella pupae (0.153 mg) | Tipulid larvae (1.322 mg) | Tipulid pupae (2.367 mg) |
			Second instar[a]	Third instar (0.677 mg)	Pupae (1.25 mg)	Adults (1.645 mg)					
East flow	5.603	638.1	---	6,466	437	---	2,248	321	299	187	12
West flow	3.104	258.4	---	1,906	146	---	745	68	152	486	37
Total numbers	8.707	---	---	8,372	583	1,033	2,993	386	451	673	49
Total biomass (g)	---	896.5	0.721	5.668	0.729	1.700	1.248	1.031	0.069	0.890	0.116

[a] Census of this and earlier developmental stages was relatively efficient compared to later stages.

TABLE 2. Fraction of total mat area in various temperature ranges, determined from Fig. 1

| | Range (°C) | | |
	25–35	30–40	35–40+
East flow	0.552	0.466	0.337
West flow	0.553	0.141	0.098

was caused by CO_2 limitation. Because molybdate-reactive filterable phosphorus is not necessarily a good measure of available phosphorus (Rigler 1968), this hypothesis may be questioned. However, a model of mat growth that incorporates the CO_2 limitation hypothesis mimics well the growth of mats in the field under a range of realistic CO_2 concentrations in the source water (Fraleigh and Wiegert 1975). In addition, a measure of CO_2 concentration allows separation of low productivity springs (which are characterized by terraced, encrusting, rather than mucilaginous, mat forms) from high productivity springs like the Nez Perce. Eight low productivity springs had source pH values of 7.60–8.77, while 11 high productivity springs ranged from 6.25 to 7.10. Low source pH results from high free CO_2 concentrations and the pH increases downstream as the CO_2 is degassed to the atmosphere. The success of Fraleigh and Wiegert's model and the latter observations do not prove that CO_2 limits productivity in Yellowstone's alkaline hot springs; at least, however, measures of CO_2 concentration are good predictors of production rates.

The herbivore Paracoenia turbida

Because *P. turbida* larvae do not grow well above 35°C, they can exploit only relatively cool patches of algal-bacterial mat. We suggest this seemingly restrictive temperature range can also be interpreted as an optimal one. Even if they had a higher temperature tolerance, larvae would seldom have an opportunity to feed above 40°C because most of the mat area exposed above the water surface and available for fly oviposition is relatively cool, not hot (Wiegert and Mitchell 1973). In addition, because cooling rates of effluent water decrease as the water approaches ambient temperature, lower temperature ranges encompass more mat area than higher ones of similar width. For example, the 25°–35°C temperature range in Nez Perce Spring takes in more of the mat area than any other 10°C-range closer to the optimal temperature of the algae (Table 2). For *P. turbida* to slide its larval temperature range upward would therefore tend to reduce both the area available for oviposition and the area for larval growth. Moving the temperature range downward to increase these areas would increase overlap with

TABLE 3. Calculation of survivorship values for *Paraoenia turbida* from census data for Nez Perce Spring. Duration of each immature stage was determined in laboratory cultures. Average adult lifespan was modified from age distributions given by Wiegert and Mitchell (1973) (see footnote below)

Stage (duration in days)	Census count	Daily flux	l_x	d_x
Egg (2)	----	23,920[a]	1.0000	0.912
Third instar larva (4)	8,372	2,093	.0875	0.954(0.71)[b]
Pupa (6)	583(3,636)[c]	97.2(606.1)[c]	.0041(.0253)[c]	(0.72–0.89)[c]
Adult (6–16)[d]	1,033	172.1–64.5	.0072–.0027	

[a] Calculated assuming the 598 ♀ ♀ censused each lay 40 eggs/day, as they do with excess food under a natural temperature and light regime in vials. No field fecundity measurements are available for *P. turbida*, but *Ephydra bruesi* ♀ ♀ are able to achieve their maximum fecundity in springs much less productive than Nez Perce, and at much higher adult densities. Therefore *P. turbida*'s fecundity is probably not limited under field conditions.

[b] Number in parentheses is an average d_x value calculated from the total number of third instar larvae and pupae counted in 16 sets of 30 samples from artificial substrates in the field over a 2-mo period in 1970. Sampling details were similar to those of Wiegert and Fraleigh (1972).

[c] These values were calculated using the long-term average d_x described under footnote b, instead of census counts of pupae.

[d] Wiegert and Mitchell's (1973) field age distribution implies an average adult lifespan of 7.5 days, but is based on somewhat arbitrary age classifications for older flies. Therefore, we felt the 6- to 16-day estimate was more appropriate than a single value.

herbivorous competitors (Fig. 3A). Simply widening the range to include temperatures above 40°C would increase the availability of algae, but this tactic may be precluded by the fly's mating scheme. Mitchell (1974), in a more detailed treatment of the evolution of thermophily, found wide thermal tolerance ranges associated only with nonrandom mating schemes which allowed development of clones, each one adapted to a narrow temperature range. The random mating of flies emerging from relatively cool and warm algal habitat would preclude clone development and restrict the width of the larval temperature range. In summary, consideration of patterns in resource availability as the flies perceive them suggests *P. turbida*'s relatively weak larval thermophily may make good adaptive sense.

Our knowledge of *P. turbida*'s biology was evaluated by calculating age-specific survivorship values for various life stages from census data, then comparing them to values predicted from our previous measurements of physical hazards, physiological mortality rates, reproductive rates, and the feeding rates of predators. We calculated survivorship curves by assuming a stable age distribution with no population growth. Then the number of individuals censused in each development stage represents an n-day accumulation of individuals where n is the length of that stage, and the number of individuals moving through the median age for that stage each day is the number censused per n. Survivorship values can be calculated by taking ratios of daily flux rates for successive stages.

The resulting life table for *P. turbida* (Table 3) showed high to impossibly high survivorship values (0.66–1.77) from the pupa to the adult stage. At the same time, the survival from third instar to the

pupal stage was much lower (.05) than a long-term average value of 0.29, calculated from a series of samples from another spring (see footnote b, Table 3). Both of these anomalies could result from abnormally low pupal numbers caused by several days' interruption of fly oviposition before the census, or by bird predation (Kuenzel and Wiegert 1973). Alternatively, the age distribution might be normal, but our expectations about survivorship and adult life span might be in error. We considered the latter possibility less likely than the former; therefore we used the long-term larva-pupa survivorship value specified above to calculate revised life table values involving pupae. The revised life table shows lower larva-pupa mortality and higher pupa-adult mortality than the one calculated directly from the census data (see $d(x)$ column in Table 3). These modifications have a conservative effect on our conclusions about the processes controlling *P. turbida*'s abundance. Using the unmodified life table in the analysis below would reinforce our interpretation.

To obtain survivorship figures from our previous knowledge of the flies for comparison with the observed figures, we separated mortality resulting from physiological causes, predators, and physical factors, then calculated the probability of surviving each type of mortality at each stage of the life cycle. We assume all three categories of mortality act independently; thus the product of the three survival probabilities equals the probability of surviving a period in the life table. The predicted and observed survival rates are presented in Table 4. Physiological mortality rates are derived from data on laboratory cultures; because it is impossible to separate physiological mortality from that occurring due to poor

TABLE 4. Calculated probabilities of surviving various sources of mortality for *P. turbida* in Nez Perce Spring, as compared to observed survivorship. Combined values are the products of the individual components

Period of life cycle	Physiology	Predators	Physical factors	Combined	Observed
Egg—Third instar	0.82	0.50–0.66	0.48	0.20–0.26	.087
Third instar—Pupa	0.65[a]	1.00	0.59[a]	0.38	0.29
Pupa—Adult	0.38–0.63[a]	0.28–0.59	0.73[a]	0.08–0.27	0.11–0.28

[a] Calculated from daily rates given by Wiegert (1975) from the middle of one stage to the middle of the next.

culture conditions, the values reported are regarded as high in the analysis. Derivations of predicted survivorship values for each part of the life cycle are discussed below.

The probability of surviving physiological mortality between oviposition and the middle of the third instar was conservatively estimated as 0.82, which was the proportion of 10 replicate cultures of 20 flies each that survived to pupation in a field experiment with excess food and no accumulation of wastes.

Predatory mortality on eggs and young fly larvae comes from two species of water mites and a dolichopodid fly (Fig. 2). The numbers of these predators censused were multiplied by independently determined daily feeding rates of individuals to determine prey intake (Table 5). By dividing the total potential prey intake by the daily egg output of the flies, we determined that the probability of an individual egg or larva being eaten was 0.34–0.50. This calculation assumes that predators do not interfere with one another, and that all predators censused take the opportunity to feed every day. We expect that both these assumptions are violated; therefore, we regard our estimate of predatory mortality as high. A conservative estimate of the probability of surviving predation is $1 - (0.34–0.50) = 0.50–0.66$.

We have measured two kinds of mortality from physical stresses. First, some larvae are killed in early instars because they encounter lethal subsurface temperatures as they hatch and burrow into the mat. The temperature grid for mapping isoclines (Fig. 1) included 70 points with surface temperatures suitable for oviposition (28°–38°C), six of which had lethal subsurface temperatures ($> 40°C$). Thus, the probability of surviving this source of mortality was estimated at $(70–6)/70 = 0.91$. Second, hot water flow shifts caused by changes in thickness of the growing algal mat destroy $\approx 10\%$ of the sites for larval development each day (Wiegert 1973). Assuming the value for survivorship from egg to third instar larva from the life table takes into account the period from oviposition through half the third instar (6 days), the probability of surviving such flow shifts would be $0.9^6 = 0.53$.

Combining survivorship values for physiological, predatory, and physical mortality yields a predicted

egg-third instar survivorship of 0.20–0.26. Because physiological and predatory losses were overestimated, the predicted survivorship is conservatively low. Even so, the observed value from the life table is much lower than the predicted one (Table 4). Since observed survivorship is much lower than can be accounted for by combining maximum estimates of various components of mortality, then some components must be missing from the calculations. Neither mortality from larval food limitation nor that caused by hot water influxes associated with larval feeding (feeding-induced flow shifts) was incorporated into the survivorship predictions in Table 4. Their contributions to larval mortality are evaluated below.

To evaluate the role of competition for food in lowering larval survivorship, we used pupa weight as an indicator of food stress. Weights of dipteran pupae and adults are reduced to 15%–20% of normal by severe food limitation (Sang 1949, Sokoloff 1955, Sullivan and Sokal 1963). We collected and

TABLE 5. Calculation of predator impact on survival of eggs and young larvae of *Paracoenia turbida* from Nez Perce Spring

Predator	N	Daily consumption Individual	Daily consumption Population
Partnuniella thermalis			
adults	2,993	1.5[b]	4,489
nymphs	1,185–2,997[a]	0.5[c]	592–1,498
Thermacarus nevadensis	386	1–2[d]	386–772
Tachytrechus angustipennis	129	20–40[e]	2,580–5,160
Total daily predation			8,047–11,919

[a] Calculated from data on larval and adult numbers. The first number assumes all larva-adult mortality occurs during the larva-nymph transition. The second assumes linear survivorship through the nymphal stage.

[b] From laboratory experiments using exposed eggs and freshly collected mites.

[c] Estimated from footnote b above.

[d] *Thermacarus* can eat many more eggs than this, but is a generalized predator, feeding on eggs and young larvae of chironomids as well as ephydrids. This value is a very rough estimate of its impact.

[e] From personal observations of individual flies over several days by Wayne Kuenzel.

TABLE 6. Mean dry wt ± SE of pupae from the east flow of Nez Perce Spring while the fly population increased during the period of regrowth of the harvested mat. Average weight of 81 pupae from a culture exhibiting 82% survivorship from egg to pupa was 1.23 mg

Date	Pupal wt (mg)	Sample size
10 August	1.26 ± .06	11
18 August	1.16 ± .03	25
26 August	1.13 ± .03	19
4 September	1.16 ± .06	23
12 September	1.15 ± .06	22

weighed pupae from the first generation of flies produced on the regrowing mat after the census and continued this procedure for 5 wk until the fly population had reached apparently normal levels. Pupal weights did not decrease significantly as the fly density increased, and the weights are not significantly lower than weights of pupae from cultures suffering very mild food limitation with mortality not significantly above physiological levels (Table 6). We conclude that the discrepancy between observed and predicted survivorship of fly eggs and young larvae would not disappear if mortality from larval food limitation were included in the calculations.

To our knowledge the only larval mortality not yet considered occurs when larvae consume algal dams protecting them from neighboring hot water flows. The likelihood of such flow changes, hereinafter referred to as feeding-induced flow shifts, should increase with the larval density in a patch of algae. Given the evidence that larval food is not limiting, we suggest that feeding-induced flow shifts are responsible for the unexplained mortality during the egg-third instar transition. Mortality from this source should have a regulatory effect on fly population density.

Shifting our attention to the later immature stages, we find the observed survivorship from the middle of the third instar larval stage to the midpupal stage (0.29, Table 4) is lower than the predicted value (0.38). The latter value considers only mortality from physiological errors and that from flow shifts caused by algal growth. Other sources of mortality that might account for the discrepancy are larval washout and feeding-induced flow shifts during the last part of the larval stage. Collections of material washing out of Nez Perce Spring in 1975 included almost no P. turbida larvae or pupae, so washout is apparently unimportant. Feeding-induced flow shifts, on the oher hand, should be even more important in late larval stages than earlier, because such shifts become more likely as the algae in a patch of habitat are consumed, and as the larvae grow and increase their individual feeding rates. We conclude again,

by elimination of other sources of mortality, that feeding-induced flow shifts are important in reducing larval survivorship.

For the period between the midpupal stage and the average adult age, three components of mortality can be estimated. First, the values of physiological mortality of pupae and adults reported by Wiegert (1973) yield a probability of surviving of 0.38–0.63, depending on the adult lifespan used. Second, the probability of surviving passive flow shifts during the last half of the pupal period will be $0.9^3 = 0.73$. If larvae select cool sites for pupation (Fig. 3A), where lethal passive flow shifts are less likely, then this value may be low. Finally, the probability of capture by one of the 28 spiders collected at Nez Perce Spring can be estimated by assuming average consumption is half the maximum consumption of 4 flies per spider per day (John Moeur, *personal communication*). The probability of surviving predation is therefore 0.28–0.66, depending on the adult lifespan assumed. Combining these figures yields a predicted range of 0.8–0.27, which may be conservatively low if mortality from flow shifts is overestimated. The coincidence of the observed and calculated values in this case is very good (Table 4). Wiegert (1973) suggests storms could inflict another 10% mortality per day of adult life, but our calculations here suggest their effect must be substantially less than this. More precise measurements of mortality from predation, storms, and flow shifts caused by algal growth would improve our picture of this stage in the life cycle, but at least it seems we have identified enough sources of mortality to adequately account for observed losses.

The preceding integration of information from the census with independent data on the biology of the fly and its predators has allowed us to make quantitative statements about the importance of various sources of brine fly mortality. The figures indicate that the combined effects of physiological mortality, flow shifts caused by algal growth, and predation are not sufficient to prevent overexploitation of the larval habitat. Because pupal weights are not significantly reduced, we conclude that overexploitation does not result in intense competition for food. Rather, we suggest that larval feeding promotes influxes of hot water which sharply reduce larval survivorship in a density-dependent manner.

Despite P. turbida's limited access to the algal-bacterial mat, it may significantly increase the productivity of the system. The feeding fly larvae rapidly convert cool patches of algae that are no longer growing into highly productive patches flooded with hot, nutrient-rich water. Without the flies, senescent patches of algae would be removed only through erosion by water flows or disruption by rain or hail storms.

TABLE 7. Calculation of survivorship values of the water mite *Partnuniella thermalis* from census data for Nez Perce Spring

Stage (duration in days)	Census count	Daily change	l_x	d_x
Egg (13)	----	1,048[a]	1.0000	0.769–0.914
Parasitic larva (6–16)[b]	1,452	90.7–242	.0865–.2309	0.560–0.835
Adult (75)[c]	2,993	39.9	.0381	

[a] Calculated assuming each ♀ lays 0.7 eggs/day as they do in the laboratory. A sample of 350 adult mites had a sex ratio of unity, thus we estimate there were 1,497 ♀ ♀ in the population.

[b] Larvae remain attached to the host until it dies; thus the turnover time of the population of parasitic larvae will be equal to the average lifespan of hosts.

[c] Adults collected in the field often live 5 mo in the laboratory; mean adult lifespan was therefore roughly estimated as 75 days.

The parasitic water mite

Survivorship values for *Partnuniella thermalis* were calculated as those for *P. turbida*. Table 7 shows 76%–91% of the mites die before successfully attaching to a host. The eggs are laid in interstices of the mat and its sinter substrate, and they support no known predators. Therefore, we assume that hatching in the field is nearly complete, as it is in the laboratory. Survivorship during the transition from the egg to a larva attached to a fly, then, is probably primarily associated with avoiding hazards and successfully finding a host during the 2- to 5-day period after hatching and before larval energy reserves are depleted.

The greatest problem at this point in the life cycle is the highly clumped distribution of adult fly hosts for the mite larvae. Collins (1975a) presented evidence that most larvae hatch in areas devoid of flies, and the 9%–23% survivorship of larvae reflects successful attachment of the small fraction of the larval population that hatches in areas of high host density. Apparently, the locations of future fly activity are determined by chance, and adult mites cannot increase mite-host overlap by predicting and moving to the future locations of the flies. Collins suggested that larval adaptations, such as increased larval life span and mobility, which would increase the success of larvae hatching in areas devoid of hosts, have not evolved because they both involve making fewer and larger larvae. At their present size, > 50% of the larvae contacting flies are detected and removed before they can attach, and increased larval size would undoubtedly aggravate this problem. Thus, the 76%–91% mortality associated with *Partnuniella*'s parasitic stage may be an irreducible cost of exploiting an unpredictable and extremely clumped distribution of hosts, combined with host defenses which effectively filter out adaptations that could improve host-finding ability.

The life table for *Partnuniella thermalis* (Table 7) shows the environment of the nymphs and adults is much less hostile than that of the larvae. The $d(x)$ values indicate that similar proportions of individuals die in the egg-parasitic larva and the parasitic larva-adult transitions, but the mortality in the latter stage takes place over a 90-day period, compared to the 2- to 5-day preparasitic phase of the larvae. This contrast between larval and nymphal-adult mortality rates is interesting because adult and nymphal mites must cope with the same unpredictable and highly clumped distribution of resources (fly eggs) as the larvae (adult flies laying the eggs). However, these older stages are not constrained by the necessity of interacting physically with a host, and they have the option of solving the problems of resource distribution by searching for food over large areas and/or by having large storage capacity.

The adult mites do not range widely to locate food. They concentrate at fly oviposition sites, but there is no correlation between the number of eggs at or the age of an oviposition site (in a sampling area of tens of square meters), and the number of mites which concentrate there (Spearman rank correlations, $n = 47$, $p \gg .05$). This means the mites seek their food in a relatively small area, where they are subject to highly variable food intake. However, samples of mites collected haphazardly over a summer had feeding rates resembling well-fed rather than starved adult mites (Collins 1975a). Therefore, adults apparently have enough storage capacity to average successfully the oscillations in resource availability.

Density dependent regulation of the mite population probably involves the free-living rather than the parasitic stage. Fly hosts seldom average more than four larval mites per individual, and mites already attached to a fly may have a positive rather than a negative effect on the success of newly encountered mites, by forming an irregularity on the fly's body around which it is difficult for the fly to groom (Wiegert and Mitchell 1973). Thus, density-stabilizing competition for hosts does not occur. On the other hand, competition for fly eggs by adult and nymphal mites is probably intense. The census figures indicate mites and dolichopodid predators at natural

hunger levels could consume 34%–50% of the daily egg-output of the flies (Tables 3, 5). However, the great majority of the fly eggs (95.6% in a survey of 8,167 eggs) are inserted into the mat and are difficult for predators to attack. For example, 15 mites with access only to eggs inserted in the algae had a feeding rate of only 0.40 eggs/mite·day^{-1} (95% confidence interval = 0–0.81) compared to 2.34 (confidence interval = 1.07–3.61) for 10 adults with access to exposed eggs. With < 5% of the eggs exposed on the mat surface and a potential demand for 7–10× this fraction, adult and nymphal mites probably suffer a density-dependent restriction on their food intake. As noted above, adult mites in the field do not appear to be starved, but restrictions on their food intake may reduce reproductive output without greatly altering feeding behavior. Measurements of mite fecundity as a function of food intake are needed to test this hypothesis.

Because mite loads on flies are small, the effects of mite parasitism on adult flies is probably negligible. The average biomass of mites on a fly is only 0.3% of a fly's total egg production, and even the most heavily loaded fly with 37 mites carried a mite biomass equivalent to only 4.5% of her potential egg output. Accordingly, we have never been able to show differences in fecundity of female flies as a function of their mite loads.

On the other hand, the feeding of nymphal and adult mites (and dolichopodid flies) on P. turbida eggs may have an important ecological effect. Egg predation should tend to reduce the frequency of feeding-induced flow shifts by lowering the density of fly larvae developing around oviposition sites. In effect, fly mortality from feeding-induced flow shifts would be replaced by predatory mortality on eggs. Because feeding-induced flow shifts tend to kill larvae after they have consumed substantial amounts of algae, while egg predators kill before larval feeding has begun, replacement of the former kind of mortality by the latter reduces the consumption of algae by fly larvae that never mature. By reducing the amount of algal food thereby wasted, the egg predators increase the efficiency with which algal production is converted into flies. This change is equivalent to increasing the K-value of the flies at a given algal productivity. An increase in fly productivity would, in turn, increase the rate of food production for the mites. Therefore, the effects of the egg predators should be self-amplifying until available eggs become scarce.

It is also worth noting that egg predators attack a portion of the egg population which has a relatively low probability of maturing before flow shifts cause mortality. The first layer of eggs in an oviposition site is almost invariably inserted into the mat and relatively immune to predators. Eggs laid subsequently may be dropped on the mat surface because there is no room to insert them into the algae; alternatively, they may be inserted into the mat, only to be exposed by the feeding activities of larvae hatching from older eggs. Since the probability of feeding-induced flow shifts is expected to increase with the age of a site, these latecomers are more likely to be present when it occurs than are the first eggs laid there. Therefore, in feeding most heavily on exposed eggs, the mites reduce the flow of algal resources to those fly larvae least likely to mature if left alone.

DISCUSSION

Results of analyses of the individual components of the thermal spring community can now be integrated to describe the function of the entire community. Our investigations show that extrinsic factors govern whether the community will develop at all. The temperature and nutrient concentrations of the source interact to determine the primary productivity which occurs at temperatures suitable for flies. If the source is very hot and nutrients are depleted before parts of the effluent channel cool to below 40°C, the animals will not be included in the community. Fraleigh and Wiegert's (1975) analysis of primary production showed mat growth slows down as mat thickness increases, producing self-shading and preventing adequate nutrient diffusion to lower mat layers. There is strong correlative evidence that CO_2 is the major limiting nutrient, but direct experiments to show causality have not been done.

Paracoenia turbida females apparently saturate all suitable oviposition sites with eggs. The ability of egg predators to reduce the density of immature flies developing at these sites is severely limited because P. turbida inserts a large portion of its eggs into the algal mat, where they are not readily eaten by predators. In any cool patch of algae exploited by flies, the larvae will eventually consume the algal dams holding back hot water flows. When this occurs influxes of hot water kill larvae and pupae remaining in the patch. Our data suggests that larval densities are usually high enough to promote such feeding-induced flow shifts in a relatively short time after initial oviposition in a site, so that they often kill a large proportion of the immature flies. In other words, other sources of mortality are not sufficient to prevent overexploitation of the larval habitat. Algal-bacterial biomass persists because, at any one time, most of the mat is too hot for fly eggs and larvae, or it is covered by flowing water and therefore unavailable for oviposition.

Exploitation of the flies by the parasitic larval stage of Partnuniella thermalis is apparently limited by the unpredictable and highly clumped distribution

of hosts, coupled with host defenses that remove more than 50% of the mite larvae attempting to climb on. Consequently, the hosts remain under-utilized, making mite larval mortality density independent. Our calculation that *Partnuniella* and other egg predators could consume much more than the available portion of fly eggs suggests adults and nymphs are food limited. Measurements of hunger levels indicated this limitation was not serious enough to produce mortality, but it may help stabilize mite density by reducing fecundity.

The above summary suggests consumers in thermal springs have very little influence on the density of prey populations. Although both the primary and secondary consumers are apparently resource limited, high standing crops of algal food for the flies and dipteran food for the mites persist in the system. These high standing crops apparently represent refuge populations effectively immune from their consumers. Relatively unhindered by their predators, both the algal and fly populations achieve densities sufficient to cause strong density-dependent restrictions on their population growth. The fact that refuges apparently define the entire biomass structure of the spring ecosystem emphasizes the importance of understanding the kinds of mechanisms limiting the impact of consumers and defining refuges for prey. Using examples from this study and others, we can specify four mechanisms.

First, limits of consumer impact may be defined by evolutionary specialization of the consumer. A very obvious example is the way the inability of *P. turbida* adults to feed and oviposit through moving water films limits the area of algae exploited by the flies. Other limits in this category may be very subtly defined. For example, the seemingly restrictive temperature limits for *P. turbida* larval growth may have evolved as a compromise between competitive pressures reducing fitness at lower temperatures and decreasing resource availability reducing fitness at higher ones. The possibility of simply expanding the width of temperature tolerance may be precluded by the adult fly's mobility and mating scheme, which average the selective response to a variety of temperatures (Mitchell 1974).

Second, consumer impact may be limited by low food quality. Food may be abundant, but if it will not support substantial reproduction, much of it may go unexploited, as illustrated by Eisenberg (1970). There is no reason to believe that the low quality of the food results from evolutionary responses of the prey in these cases (Collins 1975*b*).

Third, consumer impact may be limited by the evolved defenses of the prey. The grooming behavior of *P. turbida* and its insertion of eggs into the algal-bacterial mat are examples of adaptations which re-

strict the impact of mite parasites and predators. The production of tanins in oak leaves (Feeny 1968) and the trichomes on certain plants (Gilbert 1971) are chemical and structural adaptations which appear to have the same kind of effect, and to have evolved for the same reason.

Finally, the impact of consumers may be limited by uncertainty in the distribution of resources in space or time. Boer (1968) thoroughly explored the implications of this mechanism from the point of view of the prey, and Andrewartha and Birch (1954) have done much to point out its importance through their discussions of relative food shortage (shortage relative to an organism's ability to disperse and search). In our thermal ecosystem the inability of female mites to predict the future locations of hosts for their larvae sets an upper limit to larval success. Evolutionary improvements in the larvae which would allow them to effectively find hosts may be precluded because they have undesirable secondary effects (Collins 1975*a*). Thus, the problem of randomness in host distribution may be evolutionarily insoluble. The distribution of every resource must involve some degree of temporal and/or spatial uncertainty which reduces the potential impact of its consumers. However, this kind of limitation is often subtle and difficult to document; its importance may often not be appreciated.

There is little reason to suppose that the above mechanisms should be less common or less developed in complex systems than in the thermal spring community. Indeed, their importance is obvious in Efford's (1969) description of energy flow in Marion Lake, British Columbia. By analogy, then, the biomass structure of many complex terrestrial and aquatic systems may largely reflect the sizes of refuges from consumers. Likewise, consumers in general may be resource limited much more frequently than one would conclude from a casual evaluation of resource abundance. This latter suggestion is important because resource-limited populations would respond to enrichment or harvesting in a very different way than populations operating well below carrying capacity. In fact, analyses of the effects of enrichment or harvest treatments on higher trophic levels would be one way of assessing the importance of refuges and resource limitation in complex ecosystems.

Despite powerful restrictions on their impact on prey density, consumers from the hot spring system have important effects on the community. The *P. turbida* population rapidly converts senescent patches of algae into highly productive ones, allowing greater productivity per square meter. Mattson and Addy (1975) have suggested a similar role for forest insects, and McNaughton (1976) has shown

African Wildebeest have the same effect on productivity in grasslands. In the thermal spring system consumers at the third trophic level have an analogous effect. Predation on eggs and larvae of the brine fly should reduce the level of density-dependent mortality in the late larval stages, thereby increasing the efficiency of converting algae into adult flies. These effects are consistent with the current idea that consumers affect processes, not prey densities, in ecosystems (Chew 1974, Mattson and Addy 1975, Lee and Inman 1975).

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