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Benthic turfs vs floating mats of algae in river food webs

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In the Eel River of northern California, as in many other sunlit rivers worldwide, large growths of filamentous green algae accumulate during summer low flow periods. Algae initially grow as turfs, attached to the river bed, but over time detach to form floating mats. Floating mats differ from attached turfs as habitats for invertebrates in a number of respects. In paired trials, larval chironomids were 15–16 times more likely to be consumed by fishes when exposed in algal turfs on the river bed than when exposed in floating algal mats on the river surface. On average, 2.7 and 6.1 times more adult insects emerged from floating mats than from benthic algal turfs in shallow (< 30 cm deep) and deep (30–60 cm deep) habitats, respectively. Differences between algal mats and turfs as cover and habitat for resident insects lead to the hypothesis that the timing, abundance, and duration of floating mat habitats strongly influences the routing of insect production in river food webs, to aquatic consumers or to the land.

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Introduction

Aquatic vegetation, by providing cover, can strongly influence trophic interactions in freshwater communities. Both density (Vince et al. 1976, Cooper and Crowder 1979, Crowder and Cooper 1982, Savino and Stein 1982, Anderson 1984, Collins et al. 1988) and taxon-specific architecture (Rosine 1955, Pieczynski 1973, Dionne and Folt unpubl., Collins and Resh, in press) can affect the quality of aquatic vegetation as a habitat and refuge. Position of the vegetation in the habitat is a third critical variable. Many macrophytes and filamentous algae that initially grow attached to the bed later detach and float on the water surface. Although made up of the same assemblages of flora, floating mats and attached turfs differ markedly as habitats. Here I address four questions about attached turfs and floating mats of filamentous green algae that bloom in Northern Californian rivers during the summer low-flow period:

1. How extensive and persistent are algal turfs and mats during periods of low flow?

2. What are the densities of various organisms in turfs and mats, and how do these change over time?

3. What processes determine these densities? In particular, how do rates of colonization, predation, and emergence differ in the two types of habitats?

4. How do algal turfs and algal mats influence river food webs?

Results from this study and others suggest that position of algae can affect the availability of resident biota to aquatic consumers. As a result, the timing, extent, and persistence of blooms of algae in attached turf versus floating mat positions may strongly influence the routing of insect production in river food webs, to aquatic consumers or to the land.

Study system and sites

In northern California, and in many other parts of the world, blooms of algae often occur in clear, rock-bedded, sunlit rivers during periods of low flow. These growths are commonly dominated by the filamentous green alga, Cladophora glomerata (Blum 1956, Whitton 1970, Moore 1976, LeSage and Harrison 1980, Niiyama 1986, Freeman 1986). Initially, Cladophora grows attached to substrates (Bellis and McLarty 1967, Herbst 1969). Subsequently, if blooms are massive, large

amounts of algae detach and accumulate in mats on the water surface (Herbst 1969, Hillebrand 1983). In rivers, long algal turfs that develop in flowing regions detach and accumulate as floating mats in quiet pools and the slack water along channel margins (Fig. 1).

Here, I present field data from two northern California rivers that document the development and persistence of algal turfs and mats during three low flow seasons (May through September). Algae were monitored in the Rice Fork of the Eel River near Lake Pillsbury (39°25′N, 122°40′W) in 1986, and in the South Fork of the Eel River near Branscomb (39°44′N, 123°39′W) in 1987–88. The South Fork Eel drains sparsely-settled forest and pastureland before entering the northern California Coast Range Preserve. Here it is surrounded by a mature forest of coastal redwood (*Sequoia sempervirens*), Douglas fir (*Pseudotsuga menziesii*), and oak (*Quercus* spp.). Alder (*Alnus rhombifolia*), sedges (*Carex nudata*), and an introduced legume (*Melilotus alba*) line the river's active, boulder-filled channel. The Rice Fork Eel flows through open oak (*Quercus* spp.), manzanita (*Arctostaphylos* spp.), and chamise (*Adenostoma fasciculatum*) chaparral in the Mendocino National Forest. Willow (*Salix* sp.) and alder line its banks.

The Rice Fork Eel has a wide, open channel, and is sunlit for its entire length. The South Fork Eel, with a gradient of 0.5–0.6% over the reach studied, is bordered by canyon walls and gravel-rich river terraces. Its active channel is sufficiently wide (28–30 m) so that during low flow, when the water-filled area ranges from 3–15 m wide, much of the river is sunlit. Precipitation in coastal California falls mainly between October and April. After the winter floods, discharge drops steadily and water temperature rises (Fig. 2). During the low flow period, pool depths range from 0.5–1.0 m in the Rice Fork, and from 0.5–4.0 m in the South Fork. During this sunny, warm period, the river beds stabilize, the water clears, and filamentous algae proliferate.

Methods

Algae and physical conditions were monitored in the Rice Fork during 1987, and in the South Fork in 1987 and 1988. During the low flow season, densities and emergence of resident biota in algal turfs and mats were quantified in the South Fork Eel in 1988 and 1989. In addition, rates of accrual of organisms, and intensities of fish predation were compared in clumps of algae experimentally deployed in turf and mat positions.

Seasonal surveys of algae

Algae and physical conditions were monitored over the low flow season on 300–400 sites distributed over 40 cross-stream transects distributed along ca. 1.5 km of the Rice Fork, and on 40 sites along 4 permanent cross-stream transects distributed along 3 km of the South

Fork Eel. Once or twice each month, physical conditions and biota were monitored at pre-determined sites beneath meter-tapes strung across these transects (see Power and Stewart 1987 for details of this method). Proportions of sites with filamentous green algal turfs or floating mats were noted. Modal lengths of algal strands in these turfs and maximum diameters of floating mats were measured.

Monitoring of biota in naturally occurring turfs and mats

From May through August 1988, at monthly intervals, I collected mat and turf samples from the South Fork Eel for censuses of their resident biota. Underwater turfs were sampled with a 9 cm diameter, open-ended cylinder, fitted at the top end with a nylon stocking that was pulled up over the operator's forearm. To sample turfs on the river bed, the sampler was pressed against the substrate and most of the attached algae within the circumscribed 63.6 cm^2 was scraped loose. Then a lid was slid on the sampler's bottom side, and the sample was lifted to the surface. Water drained through the stocking sleeve, while the sample was retained. A ziplock bag was fitted snugly around the sampler's bottom, and the sample was backflushed into it. To sample floating mats, I used a 7 cm × 10 cm aquarium net (0.3 mm mesh). Portions of floating mats were collected by gently sliding the net under them, lifting, and turning the net contents into ziplock bags. All turf and mat samples were preserved in 70% ethanol, and their biota was counted in the laboratory under 10× magnification.

To ascertain the density of organisms per unit of algal biomass, I measured algal damp weight after most of the resident biota had been removed. The algae was spun for 50 revolutions in a salad spinner lined with 0.3 mm mesh netting, then weighed on an Ohaus Portogram balance to the nearest 0.1 g. Damp weight measured this way correlated closely with weight of *Cladophora* that had been dried to constant weight at 100°C (dry weight = 0.09 (damp weight) + 0.02, n = 44, r^2 = 0.98).

Colonization of virgin turfs and mats

To study colonization and accrual of biota on algal turfs and mats in the South Fork, I simultaneously placed clumps of pre-cleaned algae in mat and turf positions (at the water surface or underwater on the river bed, respectively), and harvested them at 5–6 d intervals. These colonization units were made from *Cladophora* of uniform appearance gathered from one location and brought indoors for cleaning. After washing small subsamples of algae several times in spring water, these subsamples were spread into 'monolayers' in white enamel pans, so that each filament could be inspected for associated biota. Organisms > 1 mm long were removed, with the exception of ceratopogonid larvae, whose diameter and color closely matched that of the

Fig. 1. Photograph taken within study reach of South Fork Eel during July, showing attached algal turf in the channel center, and floating mats accumulated along channel margins in slack-water areas.

Cladophora filaments. Clumps of algae (each 5 g (damp weight)) were tied with string as colonization units. Clumps deployed as turfs were anchored by their strings to the bed in depths of water ranging from 10–37 cm. Clumps deployed as mats were tied at the water surface. Each experimental mat was placed within 5 cm of being directly over an experimental turf to create a paired experimental design. Surface areas of mats and turfs when deployed in water were ca. 30–40 cm². On 13 July, 1988, four pairs were placed in each of ten locations distributed over two 25 m reaches of river. A total of 80 colonization units were deployed. Every 5–6 d, one pair was collected (using an 0.3 mm mesh net) from each of the ten river sites, and resident biota were counted under 10× in the laboratory.

Movements and fate of algal mats

Movements of floating algal mats were tracked within a 700 m reach of the South Fork, marked off at 25-m intervals along the right bank. Floating mats within this reach were tagged with cloth laundry tags (1 × 3 cm) which attached to mats with small metal clips. Tags, labelled with the date and original position of each mat, had no discernible effects on wind or current driven movements of mats. On three occasions over the next 21 d, positions of tagged mats were noted. If mats were permanently exported to emergent boulders in the channel or to the shore, their tags were collected.

Fish predation on biota in turfs vs mats

To examine rates of fish predation on fauna in turfs and mats, I tied 24 bundles of algae (damp weights ranged from 3.4–8.1 g) with string, and deployed them as turf-mat pairs, with turfs below associated mats. Each algal bundle contained five chironomid larvae (*Pseudochironomus richardsoni*) ca. 10 mm in length. To secure these larvae, I tied each with a thin cotton thread around its

middle, and drew the end of the thread into the algal clump until midges were partially concealed in the algae. In algal clumps deployed as floating mats, midges hung down, and in turfs, the midges were oriented upwards. Paired mats and turfs were exposed in the river from 46 to 60 min, from 1220 to 1700 hours on 6 August, 1988. During this time, observations were made on fishes. Roach and stickleback could be seen actively biting at the algal clumps on the river bed. After this exposure, clumps of algal mat and turfs were netted and examined in enamel pans. Tied midges were scored as present, or missing if the thread was empty or if only a small body section remained under the knot of the thread.

Insect emergence from mats vs turfs

On 17 and 18 August, 1989, 20 emergence traps were placed over natural mats or turfs in a reach of the river where algal growth was prolific. Traps were set into water ranging from 11 to 61 cm deep from 1630 to 1840 hours. Emerged insects in traps were collected after 24 h. Emergence traps were made from 25.4 cm diameter white PVC pipe, cut into 20, 40, and 60 cm lengths. Holes, 7.6 cm in diameter and covered with 0.3 mm mesh net, were placed at 4–8 cm intervals along four rows on each pipe for water exchange. Traps placed around floating algal mats were fitted with a diaphragm of 0.3 mm mesh, placed between the bed and the floating mat. This diaphragm prevented insects emerging from the bed from using floating mats as 'stepping stones' and being added to counts of insects emerging directly from floating mats.

A top, made of a separate 8 cm high section of pipe covered with 0.3 mm mesh net, was attached to each pipe base. Emerged insects aggregated in these tops. When tops were removed for sample collection, their lower openings were quickly covered with white plastic lids. Insects inside were sprayed through the screen with 70% ethanol. The immobilized adult insects were then collected with forceps and preserved in 70% ethanol for counting and identification in the laboratory. High contrast between insects and the white 0.3 mm mesh netting, the white lid walls, and the white plastic lid closing the bottom allowed even very small individuals, such as ceratopogonid adults, to be easily detected in the field.

Results
Seasonal proliferation and persistence of algal turfs and mats

In both rivers studied, long turfs of attached algae develop in late spring and early summer, and quantities subsequently detach to form floating mats. Timing of these events was similar over three years of observation. Algae in both turf and mat states were visually impressive during the peaks of the bloom (Fig. 1). *Cladophora* turfs attained lengths up to 6 m in the Rice Fork, and of
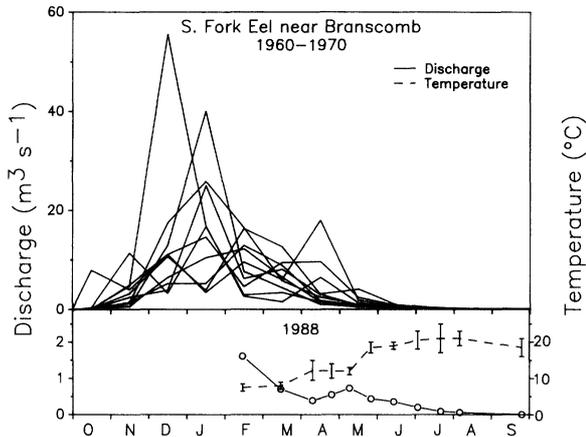
Fig. 2. Data from the U.S.G.S. gaging station, located within the study reach on the South Fork Eel, showing seasonal patterns of mean monthly discharge over a ten year period. The U.S.G.S. no longer monitors this station. Discharges measured over the same cross section in this study, and the ranges of daily temperatures measured in the main channel from February through September 1988, are shown in the lower part of the figure.

over 8 m in the South Fork. Floating mats in both rivers were commonly more than 1 m long. When turfs detached to form floating mats, these collected in quiet water along river margins (Fig. 1), or wrapped around emergent boulders in flowing regions. Because floating mats were concentrated into certain areas by wind and currents, they covered less area than did attached turfs. However, where mats accumulated, they provided dense, thick (20–50 cm) cover.

In the Rice Fork Eel in 1986, filamentous turfs or mats were not apparent on 21 May, 1986 (Fig. 3a), when most rocks on the bed were covered with adnate diatoms. By early June, turfs of filamentous green algae, primarily *Cladophora*, had developed. By the end of June, many of these had detached to form floating mats. Standing crops of both turfs and mats declined by the end of July, as did the proportion of monitored sites covered by mats, but not turfs (Fig. 3a). I began monitoring the South Fork Eel in June 1987, at the peak of turf development (Fig. 3b). As in the Rice Fork Eel, floating mats formed and peaked over the next three weeks. After August, mats were not present in the monitored areas. Attached turfs of algae persisted at low levels until the first floods, in October. In 1988, turf development again peaked in June in the South Fork Eel, and was followed by the peak release of mats over the next three weeks. (A single large floating mat was sighted under a transect station on the previous date (Fig. 3c)). In contrast to 1987, turfs and mats both persisted into the autumn. After 5 August, however, the only monitored sites with floating mats were in a large stranded side pool, and not in the main channel of the South Fork (stars in Fig. 3c). The first floods of the

season again occurred in late October, scouring most remaining algae out of the study reach.

Biota in algal turfs and mats

During the first part of the low flow period, the densities of insect larvae and other biota were generally low
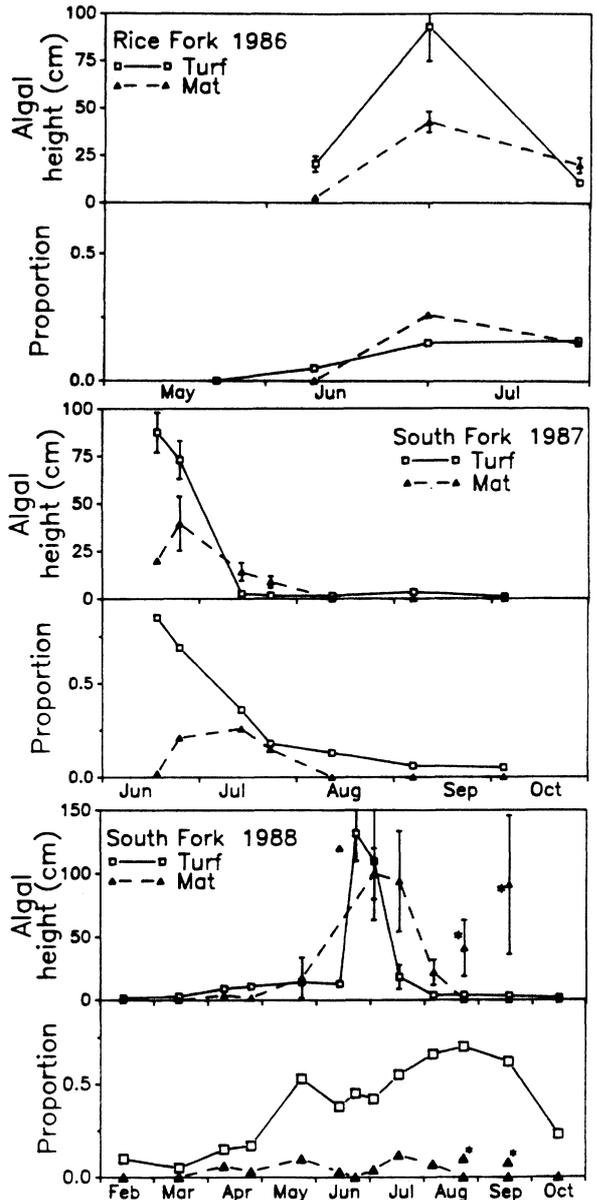
Fig. 3. Algal abundance in the low flow season in the Rice Fork Eel (3a), and the South Fork Eel (3b, c). Algal "height" refers to the modal length of filaments in attached turfs, or to the maximum diameter of floating mats. Both are presented as indices of standing crops. (Biomass and height or length of algal filaments measured in an Oklahoma stream were positively correlated (Power et al. 1985)). Means are plotted with 1 SE. Proportion of monitored sites with at least 50% cover of either turfs or mats are shown in the lower half of each figure.

70

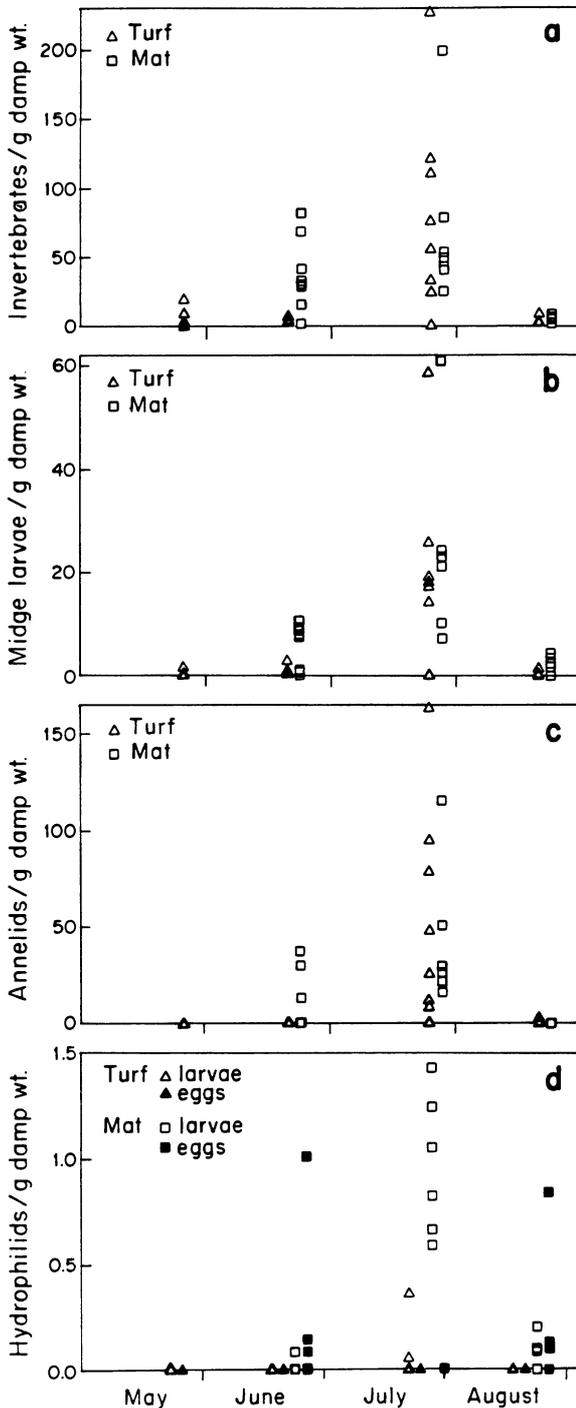Fig. 4. Densities (ind g^{-1} damp weight of algae) of total invertebrates (4a), midge larvae (4b), annelids (4c), and hydrophilid beetle larvae (4d), in naturally occurring turfs (triangles) and mats (squares) of algae. Each symbol represents an individual sample unit; heavily inked outlines indicate multiple sample units with similar densities. Monthly sample sizes of turfs and mats are given in Tab. 1.

in benthic turfs (Fig. 4). In May, only attached turfs were present at collection sites. Total invertebrate densities (of organisms that would be retained by a 1 mm mesh) averaged 4.3 ind g^{-1} damp weight algae (Fig. 4a). Tab. 1 shows monthly invertebrate densities in turfs and mats, normalized to the damp weight of the algae, as well as the average algal biomass sampled per area (projected to the water surface) and the corresponding density of invertebrates per area. (Sampling was not adequate to extrapolate these densities to larger reaches of the South Fork Eel).

Of the invertebrates in algal turfs during May, most were trichopterans (mainly *Gumaga nigricula*), ephemeropterans, and mites. Chironomid and ceratopogonid larvae were uncommon in May, relative to their subsequent abundances (Fig. 5).

By 20 June, floating mats had detached, and contained higher densities of invertebrates per algal biomass than did benthic turfs harvested at the same time and place (Fig. 4a) (p < 0.04 from a 2-tailed Mann-Whitney U test). Invertebrates per area of river bed were also higher in floating mats (p < 0.04, Tab. 1). In late June, a guild of chironomid larvae dominated by *Pseudochironomus richardsoni* grew abundant, representing ca. 20% of all invertebrates counted in mats and in turfs (Fig. 5). These midge larvae lived in retreats of woven *Cladophora*, henceforth called tufts. They were slightly but not significantly more abundant in mats than in turfs (Fig. 4b, p < 0.10 from a two-tailed Mann-Whitney U test). Midge larvae eventually filled their tufts with fecal pellets. As fecal material accumulated, tufts were colonized by large numbers of small (2–8 mm) red oligochaetes (Fig. 4c). Predatory hydrophilid beetle larvae (*Enochrus* sp.) occurred almost exclusively in floating mats (Fig. 4d), hatching from white, bouyant egg masses that first appeared on floating mats in June.

Invertebrate densities peaked in July. At this time, there were no significant differences, per unit algal biomass or per unit area river bed, in invertebrate densities in algal turfs or mats, with the exception of hydrophilid eggs and larvae (p < 0.05 from a two-tailed Mann-Whitney U test). Oligochaetes in July were numerically dominant (Fig. 5), comprising more than 50% of the individual invertebrates in both turfs and mats. Chironomids (primarily tuft weavers) were second in importance, making up more than 30% of the individual invertebrates in both turfs and mats. Visually, mats appeared nearly saturated with tufts at this time – there was little unwoven algae. In July 1987, 80–95% by dry weight of the *Cladophora* in sampled floating mats was woven by midges.

By August, when algal biomass had sharply declined, densities of invertebrates in turfs and mats also decreased (Fig. 4, Tab. 1). At this time, densities (per algal biomass) of midge larvae and pupae were again significantly higher in algal mats than in algal turfs (p < 0.05 from a two-tailed Mann-Whitney U test), although

Tab. 1. Densities of invertebrates in attached turfs and floating mats of algae, and algal biomass per area, in the South Fork Eel, summer 1988.

	May *n(T) = 11, n(M) = 0	June n(T) = 8, n(M) = 9	July n(T) = 8, n(M) = 6	August n(T) = 5, n(M) = 5
inverts g^{-1*}				
turf	4.3 (0–20.0)	4.3 (2.6–7.7)	82.2 (0.5–228.6)	5.0 (2.8–9.8)
mat	no mats occurred	33.9 (1.7–82.1)	75.2 (41.6–200.3)	5.4 (4.7–7.8)
g algae cm^{-2}				
turf	0.1 (0–0.2)	0.3 (0.1–0.5)	0.3 (0.1–0.3)	0.1 (0–0.1)
mat	no mats occurred	0.2 (0.1–0.5)	0.2 (0.1–0.2)	0.2 (0.1–0.3)
inverts cm^{-2}				
turf	0.2 (0–1.0)	1.1 (0.2–2.5)	15.0 (0.2–33.0)	0.3 (0.1–0.4)
mat	no mats occurred	4.5 (0.5–8.3)	10.9 (3.3–14.4)	1.0 (0.4–2.6)

* n(T) and n(M) = sample sizes of turfs and mats, respectively g = g damp weight of *Cladophora:* numbers are means with ranges in parentheses.

densities of total invertebrates were not significantly different (p < 0.34). Oligochaetes dominated the turf fauna at this time, and chironomids the mat fauna.

Mites were common in both habitats. Mites infested adult chironomids which emerged from mats, often appearing in rings of 10–12 individuals circling junctures in
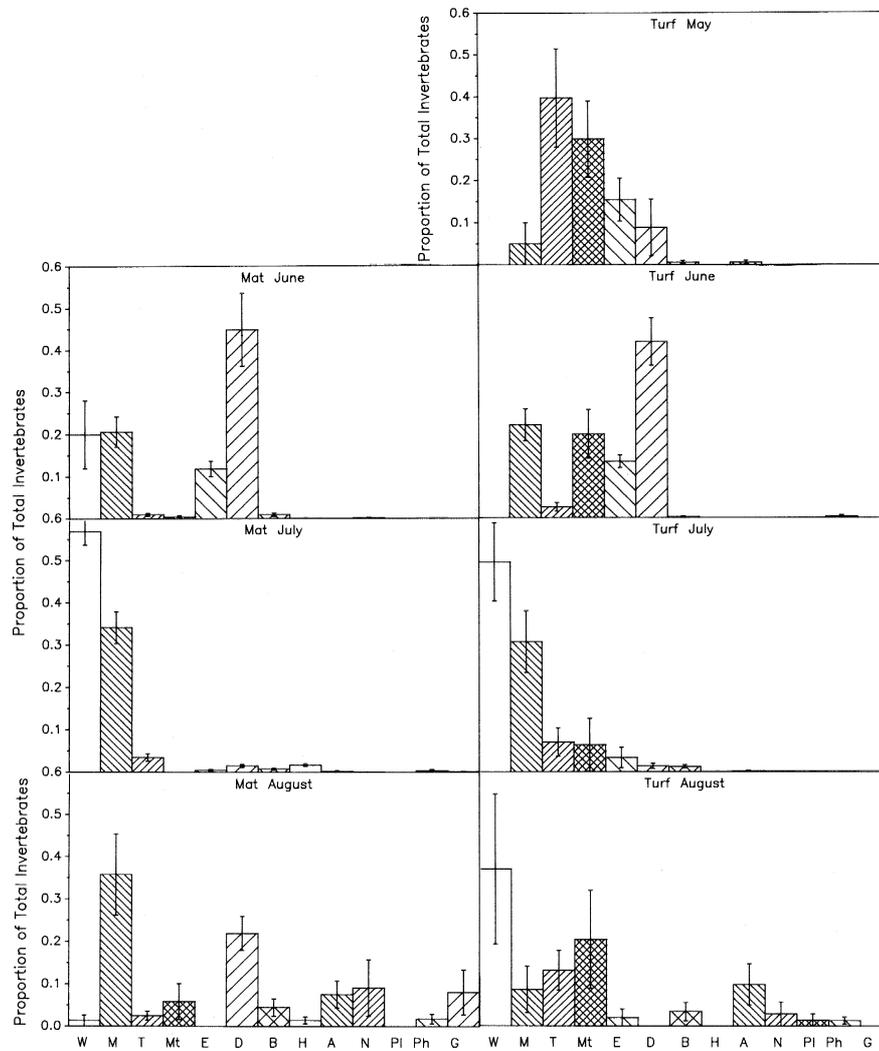
Fig. 5. Proportional composition of invertebrate fauna in naturally occurring algal turfs and mats over the low flow season. W = annelids, M = chironomid larvae and pupae, T = trichopteran larvae, Mt = mites, E = Ephemeroptera nymphs, D = dipteran larvae excluding chironomids (> 90% were ceratopogonid larvae), B = coleopteran larvae, excluding hydrophilids, H = hydrophilid larvae, A = amphipods, N = naucorids, Pl = planaria, Ph = Physa, G = gerrids and veliids.
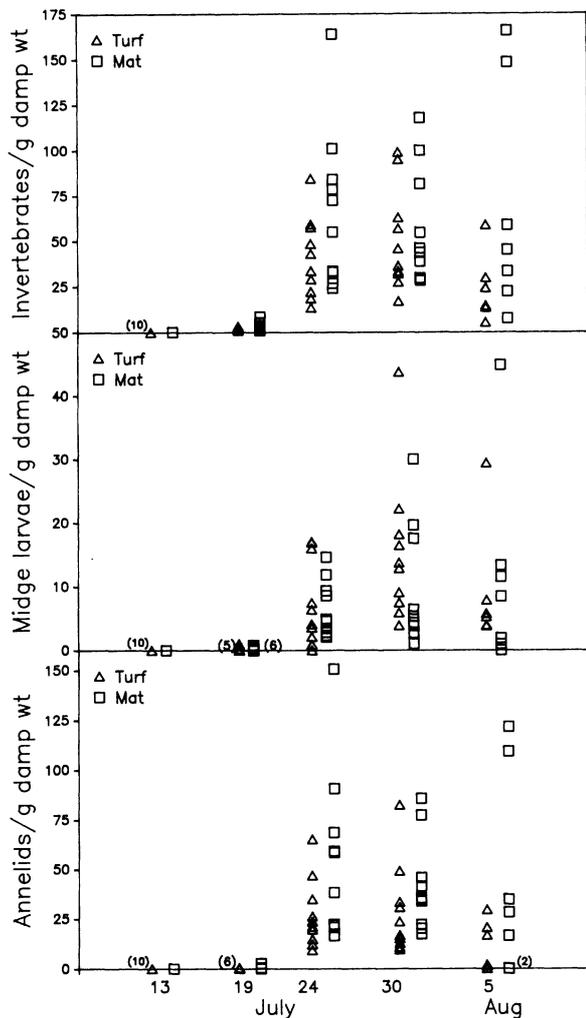
Fig. 6. Densities (ind g⁻¹ damp weight) of invertebrates colonizing pre-cleaned algal clumps, deployed as experimental turfs or mats. Symbols as in Fig. 4. Sample sizes (numbers of sample units retrieved) are: 19 July: 9 turfs, 9 mats; 24 July: 10 turfs, 10 mats; 30 July: 10 turfs, 10 mats; 5 August: 6 turfs, 7 mats.

the midge's cuticle between the head and thorax, and thorax and abdomen.

Colonization and accrual of biota in pre-cleaned algae

Differences in the biota of attached algal turfs and floating mats may have arisen because of differences related to their position, or because algae in mats had been available longer for colonization. To observe the differences that were due to position alone, I studied accrual of biota on pre-cleaned algae set out simultaneously in turf and mat positions.

Each clump initially weighed 5.0 g. Over the colonization period, all clumps lost biomass. Clumps set out as floating mats, when harvested after 11, 17, and 23 d,

averaged 2.11 g, 1.59 g, and 1.88 g, and clumps deployed as turfs averaged 2.68, 1.25, and 0.96 g. Densities of biota were normalized to the damp weight of each mat or turf unit when it was harvested.

After six days, experimentally deployed algal turfs and mats were both only sparsely colonized, with differences in the densities of total invertebrates slightly but not significantly higher in clumps deployed as floating mats (Fig. 6, $p < 0.12$ from a two-tailed Wilcoxon sign pairs matched rank test). A variety of taxa colonized both turfs and mats (Fig. 7). Throughout the experiment, chironomid larvae accrued at very similar rates on turfs and mats (Fig. 6b). After eleven days, large numbers of oligochaetes appeared, with higher densities on mats ($p < 0.02$ from a two-tailed Wilcoxon test). Subsequently, oligochaete densities increased in clumps in both positions, and differences between positions were no longer apparent (Fig. 6c).

After 17 and 23 d of colonization, faunas of both mats and turfs were dominated by chironomids and the oligochaetes that colonized their retreats (Fig. 7). Chironomid pupae developed in experimental algal clumps only after these had been in the river for 23 d, and on average, three times more pupae occurred in floating mats than in turfs.

Movements of floating mats

Twenty-eight of the 53 floating mats tagged on 14 July, 1988 were re-located on 20 July, thirteen on 30 July, and twenty on 5 August. Over the first six days of observation, 14 tagged mats remained where they were marked, 11 had moved downstream (the maximum distance travelled by one was 96 m), and three had moved varying distances upstream, carried by upstream currents or wind in back eddies (Fig. 8a). After 21 d, most re-sighted mats stayed within 6 m of the site where they had originally been marked (Fig. 8b). From 20 July to 5 August, discharge in the South Fork dropped from 0.20 to 0.06 m³ s⁻¹ (Fig. 2b). As water level dropped, seven tagged mats were stranded on the shore, or on emergent boulders in the middle of the river. Here, they remained green and moist for weeks, wicking up water 6–8 cm above the river level. Dried mats along river margins were studded with tufts woven by midges. Many tufts were tipped with small holes, where midges had emerged.

Other mats which disappeared during the study may have decomposed and settled to the river bed, or drifted out of the observation reach. The first possiblity seems more likely, given the waning river flow over the study period.

Fish predation on turf vs mat fauna

The three fishes that are common in the study reach of the South Fork Eel are steelhead parr and fry (*Oncorhynchus mykiss* (*Salmo gairdneri* Richardson)), Cali-
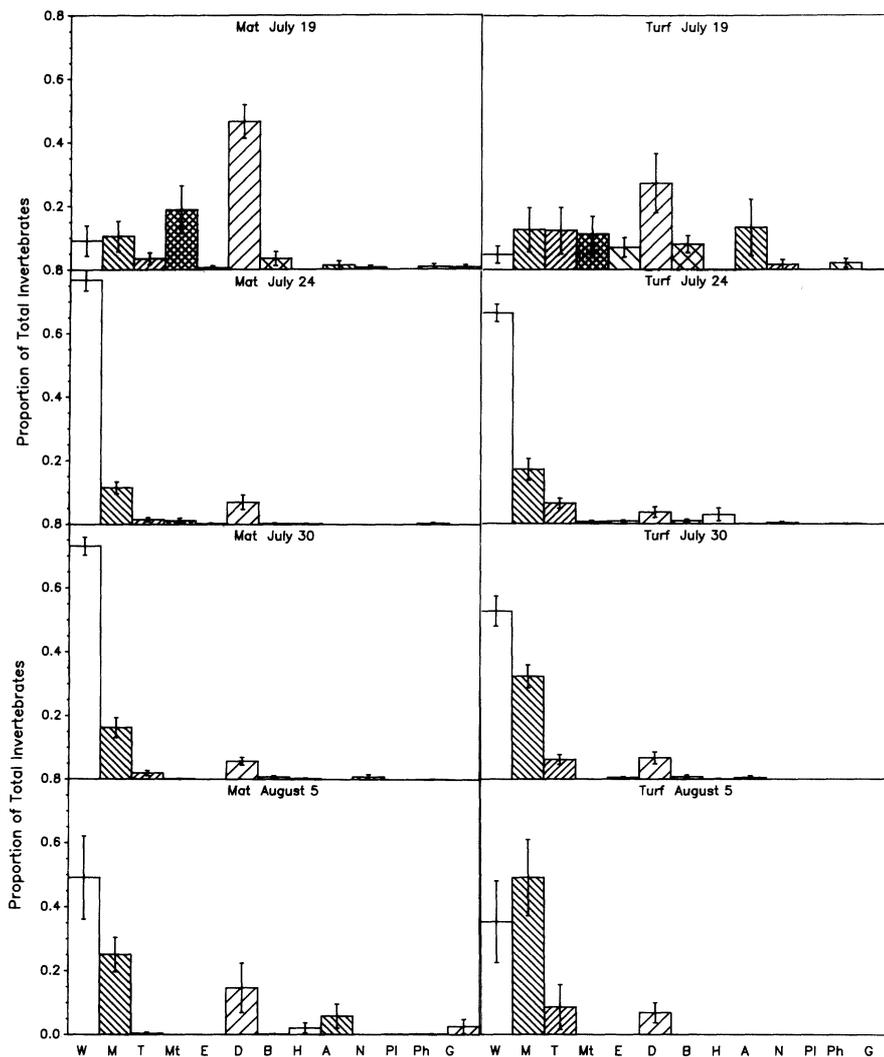
Fig. 7. Proportional composition of invertebrates colonizing experimentally deployed mats and turfs. Symbols as in Fig. 5.

fornia roach (*Hesperoleucas symmetricus* (Baird and Girard)) and three-spined stickleback (*Gasterosteus aculeatus* L.). Roach fed most commonly from the bed. Steelhead parr swam to the water surface to take drifting insects, but were never observed foraging within floating mats of algae. Small (2–3 cm SL) stickleback were sometimes recovered when large floating mats were netted, and the degree to which these fish forage within these habitats remains uncertain. However, ten stickleback observed for 49 min in shallow (10–40 cm) water took a total of 62 bites from the river bed, and none from the water surface, where natural algal mats floated. In northern Californian macrophyte beds, three-spined sticklebacks have been trapped at the bottom and mid-water column but not at the water surface (J. Collins, pers. comm.).

When midges 1.0 cm in length were tied into algal clumps and exposed to fish in the river in 'turf' or 'mat' positions, mats retained more midges than turfs over ca.

1 hour of exposure (Tab. 2). On average, 3.9 midges remained in the 12 mats, and 0.25 midges remained in the 12 turfs. Missing midges were usually completely gone except for a small (1 mm) segment behind the knot of the thread, indicating that individuals had not escaped, but had been eaten. Roach and stickleback (2–3 cm SL; Standard Length, Lagler 1956) quickly gathered at clumps deployed as turfs on the bed, and could be seen biting at midges. Steelhead parr (3–6 cm SL) sometimes assumed a station behind benthic turfs and defended the area against conspecifics, roach, and stickleback, but were not seen to feed on midges. No fish were observed feeding at algal clumps deployed as mats, although midges were missing from a few mats at the end of their trials (Tab. 2). For each pair deployed, however, more midges were missing from the turf on the streambed than from the floating mat (Tab. 2).
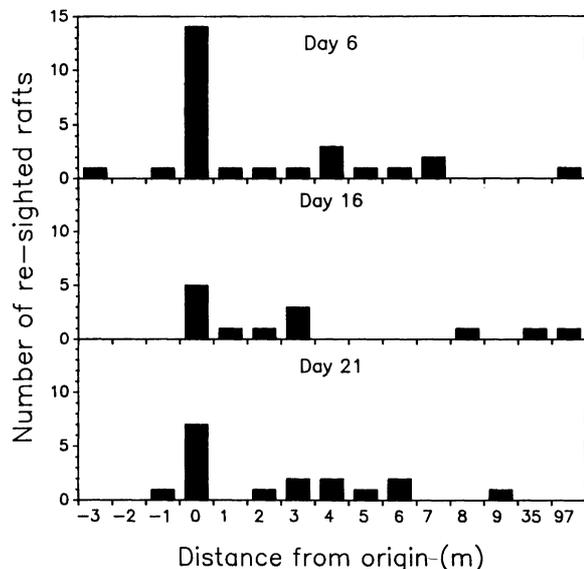
74

Fig. 8. Distance travelled by tagged mats after 6, 16 and 21 d from 14 July to 5 August, 1988. Negative distances indicate movements upstream from the original location.

Emergence from algal turfs vs algal mats

No differences in emergence rates were detected between the two days of sampling (p (from a Mann-Whitney U test) = 0.12 and p = 0.15 for total insects and for chironomids, respectively), so data from 17–18 August and 18–19 August, 1989 were pooled in Tab. 3. Chironomids accounted for 74% and 78% of the total of 162 individuals sampled from turfs in deep (30–61 cm) and shallow (11–19 cm) water, respectively, and for 96% and 95% of the 579 individuals sampled from mats floating over deep and shallow water. Ceratopogonids and ephemeropterans comprised 6% and 3% of the total of 741 insects sampled from both habitats, with trichopterans and unidentified dipterans making up the rest (0.1% and 0.4%, respectively).

More chironomid adults emerged from floating algal mats than from algal turfs in both deep (p = 0.001, Mann-Whitney U test) and shallow (p = 0.017) water. In shallow water, 2.7 times as many chironomids emerged from mats as from turfs, and in deep water this ratio was 6.1 (Tab. 3). More chironomids emerged from turfs in shallow water than from turfs in deeper water (p = 0.014), while habitat depth did not affect the numbers of insects emerging from floating algal mats (p = 0.677). Emergence rates of less common taxa did not differ among habitats (Tab. 3).

Discussion

Floating mats and attached turfs of algae are seasonally prominent features of many freshwater communities. The effects of mats and turfs on communities will depend in large part on their relative quality as cover and

Tab. 2. Recovery of midge larvae *(Pseudochironomus richardsoni)* from algal clumps deployed as floating mats or on the bed as turfs.

Time	Water depth (cm)	Number recovered of five larvae exposed	
		Mat	Turf
1220–1326	35	5	0
1243–1344	30	2	0
1301–1405	21	5	0
1320–1420	15	5	0
1400–1500	24	4	0
1440–1538	15	3	1
1416–1513	20	5	0
1513–1618	21	1	0
1522–1620	30	5	0
1540–1626	15	3	0
1548–1648	24	5	0
1609–1709	27	4	2

$p \ll 0.005$, Wilcoxon matched pairs signed-rank test.

habitat for resident invertebrates. In this study, exposed chironomid larvae experienced lower rates of fish predation in floating algal mats than in benthic algal turfs. Because exposed *Pseudochironomus* are more vulnerable to fish than larvae inside their tuft retreats, these results cannot be used to estimate actual predation rates by fish on these chironomids under natural circumstances. The experiment does suggest that potential hazard from fish predation is higher for insects in benthic turf than in floating mat habitats. These findings are not surprising in light of the position of mats at the water surface. Lotic fishes after attaining lengths of 2–3

Tab. 3. Insect emergence (individuals/24 h) from algal mats and turfs.

			Benthic turf	Floating mat
Chironomids	depth (cm)			
	10–30	x̄	10.3	27.5
		SE	2.1	6.2
		n	9	10
	31–60	x̄	4.6	27.7
		SE	2.0	4.4
		n	7	10
Ceratopogonids	depth (cm)			
	10–30	x̄	1.9	0.9
		SE	0.5	0.5
		n*	9	10
	31–60	x̄	1.0	0.8
		SE	0.5	0.4
		n	7	10
Ephemeropterans				
	depth (cm)			
	10–30	x̄	1.0	0.7
		SE	0.3	0.4
		n	9	10
	31–60	x̄	0.4	0.3
		SE	0.3	0.3
		n	7	10

* n = number of trap samples; four lost when traps tipped over. Trap area = 506.7 cm².

cm often avoid lingering near the water surface due to risk from avian and mammalian predators (Power 1987, Schlosser 1988). Floating mats are, in addition, more dense and tangled than attached turfs, which waft open in the flow. Consequently, turfs are likely to be safer, and mechanically easier as foraging arenas for juvenile and adult fish. Foraging success and use of microhabitats by bass and sunfish decline with the density and complexity of cover provided by natural or simulated aquatic vegetation (Mittelbach 1981, 1984, Crowder and Cooper 1982, Savino and Stein 1982, Werner et al. 1983). In the South Fork Eel, steelhead and roach were observed to swim into algal turfs, and could be observed picking items from them (J. Nielsen and M. Power, pers. obs.).

Predation by invertebrates might be more intense in floating mats than in attached turfs, particularly if invertebrate predators such as hydrophilid beetle larvae are restricted to surface habitats (Landin 1976), or are excluded from deeper turf habitats by fish predation. Handling times of chironomid prey by hydrophilid larvae were relatively long, however (ca. 15–18 min, pers. obs.), and these beetle larvae generally consume only a few prey per day (J. Collins, pers. obs.). Hydrophilids in small enclosures had no noticeable impact on the density of larval chironomids (Power, unpubl. data). In some pelagic lake systems, effects of invertebrate predators are weaker than effects of fish predators, where fish, but not invertebrates, can drive zooplankton prey to extinction (Hall et al. 1976, Lynch 1979, O'Brien 1979, Vanni 1986, Stein et al. 1988).

The role of floating mats in the downstream dispersal of resident invertebrates appears minor. In the South Fork Eel, the hydrograph drops steadily as algal mats form in July. Most mats become beached on dry land or disintegrate near their point of origin. In other environments with different floating plant phenologies, insect phenologies, and hydrographs, floating mats of vegetation do contribute to dispersal. Sazima and Zamprogno (1985) observed young piranhas, which used floating macrophytes as cover from predators, dispersing with pieces of drifting mats. Drifting macrophytes also disperse invertebrate vectors of disease in tropical freshwaters (Holm et al. 1969). Aquatic insects have been observed rafting on dislodged algal mats (Crisp and Gladhill 1970, Gore 1979, Sheldon 1984).

Insect emergence from floating mats was ca. 3 times higher than from algal turfs in shallow water, and ca. 6 times higher in deeper water. Higher rates of emergence from mats may be due to both greater abundances and faster development for mat insects. As discussed above, warmer conditions in the algal mat could hasten the development and emergence of insect residents (Sweeney and Vannote 1978, Ward and Stanford 1982, Sweeney 1984). This factor may have accounted for the higher densities of midge pupae found in experimental algal mats than in turfs which had been available for colonization for the same 23-d period.

Preliminary observations indicate that temperature and food availability, which co-determine growth and development rates of aquatic insects (MacKey 1977, Sweeney and Vannote 1978, Anderson and Cummins 1979, Waters 1979, Pajunen 1986), differ in algal mats and turfs. At midday in July and August, floating mats are often 7–9°C warmer than nearby benthic turfs, and accrue visibly higher standing crops of epiphytic diatoms. Diatoms are dominant items in the guts of *Pseudochironomus* larvae studied here (Power, unpubl. data) and in chironomids in other studies (e.g. McLachlan et al. 1978). These chironomid larvae also ingest detrital particles. Such particles may be concentrated by floating algal mats acting as "extra-organismal filters". In laboratory trials, water cloudy with fine organic matter cleared within minutes after it was swirled in flasks containing algae confined in coarse mesh baskets (Power, pers. obs.). Similarly, floating mats of water hyacinth in the Rio Atibaia of southeast Brazil trap quantities of particulate foods in their dense, tangled roots, and support rich faunas of microcrustacea, immature insects, and nematodes, fed upon by young piranhas (Sazima and Zamprogno 1985).

Temperature and other physico-chemical conditions fluctuate more widely in algal mats than in turfs. At the surfaces of floating algal mats in The Netherlands, temperature, oxygen concentration, and pH showed diel variation of 16 to 30°C, 6 to 12 ppm, and 7.5 to 9.9 pH units, respectively (Hillebrand 1983). Midge larvae are known to tolerate environmental extremes (Butler 1984 and references therein). Most midge larvae we observed had hemoglobin in their body fluid, allowing them to tolerate periodic hypoxia (Walshe 1951). The hydrophilid beetle larvae breathe air through anal respiratory tubes. Midge larvae and hydrophilid larvae from algal mats survived repeated, abrupt transfers from 6 to 28–32°C in the laboratory (Power, pers. obs.). However, the range of physical conditions in floating mats may have exceeded tolerances of other lotic insects, such as immature stoneflies and mayflies, which were uncommon in mats (Figs 5, 7).

Although not measured in this study, insect recruitment via oviposition by aerial adults was probably high on floating mats. Many chironomids lay egg masses or ribbons that float or attach to surface objects (Miall 1895). As oviposition sites, floating mats can "short circuit" lotic food webs, allowing insects to colonize, develop, and emerge from rivers with minimal exposure to benthic or water column predators.

To explain the observed variation in invertebrate abundances in mats and turfs over the low flow season, more information is needed on rates and local synchrony in turfs and mats of oviposition, development, larval migration, invertebrate and vertebrate predation, and mortality from parasitism and physical stress. Rates of these gain and loss processes would change seasonally as temperatures warm, as resource and habitat availabilities grow then decline, and as animal pop-

ulations fluctuate. With the limited information available, I propose the following hypothesis to account for the seasonal patterns in densities of algal-dwelling invertebrates observed during low flow in the South Fork Eel:

Insects are sparse in May, with populations still recovering from the scouring floods of winter and spring. Algal turfs proliferate at this time, and detach to form floating mats. When algal mats first appear in June, they harbor higher densities of invertebrates than turfs, where fish predation may be more intense. Floating algal mats, by serving as refuges from fish, oviposition sites, or warm, food-rich incubators, produce a large pulse of insect recruitment, which saturates all algal habitats by late July. Once 'saturation' densities are reached, resident chironomids can prevent other larvae from settling, and larvae can force each other out of their retreats (McLachlan 1969a, b, Cantrell and McLachlan 1977, LeSage and Harrison 1980). Consequently, both mat and turf habitats are flooded with enough colonists to swamp fish predation in benthic turfs, and average densities in both turfs and mats become similar. Colonization experiments carried out during this putative 'saturated period' in late July and early August revealed similar rates of accrual by chironomids, which dominated the insect fauna, in experimental mats and turfs. Even during this time of extremely high recruitment to both habitats, however, some mats and some turfs have low invertebrate densities, producing the overall pattern of extreme spatial variability for which aquatic insects are notorious (Needham and Usinger 1956, Resh 1979). Potential sources of this spatial varation are differences in the age of algae (which can grow after, as well as before detachment); or in the time since algae detached to form floating mats. These differences could not account for spatial variation in the colonization units (Fig. 5), in which both sparse and high densities occurred in algal clumps available to colonists for the same time periods. Other potential sources of spatial heterogeneity in densities of algal-dwelling insects are variation in encounter rates of mats by ovipositing females; variation in predation and larval emigration and immigration; and variation among mats in local temperatures. Vannote and Sweeney (1980) have proposed that temperature can synchronize development in local subpopulations of aquatic insects. Sampling after synchronous emergence would reveal low-density patches.

After July, extensive mat habitats are no longer available, and fish predation may once again lower densities of insects in benthic turfs and overall recruitment. By late August, densities of insects are low in mats as well as in turfs, possibly because of failure of larvae or ovipositing adults to encounter the few disintegrating floating mats that remain.

According to this hypothesis, insect populations (dominated by chironomids) explode in mid-summer because of the algal mat refuge. Clearly, this hypothesis must be tested experimentally before it can displace alternative explanations. River temperature alone seems insufficient to account for insect fluctuations during the low flow season, as average water temperature remained around 20°C from May to September.

These results, though preliminary, suggest that the degree to which algae develop and persist as turfs versus floating mats can strongly influence food delivery to fish in river communities. If floating mats persist until insects can complete their life histories and emerge, they serve as life rafts and floating incubators. If floating mats break up before insects emerge, they may serve as time-release capsules of food for fish. Floating algal mats, while initially short-circuiting the flow of insect production to fish, eventually create a large food pulse when progeny of mat residents disperse to the bed or the water column after floating habitats have saturated, been exported, or have disintegrated.

The dramatic fluctuations in plant biomass and associated invertebrates observed in this study do not occur in rivers where algivorous fishes are the dominant herbivores (Power 1984). Even when primary productivity is high, large standing crops of algae do not accrue in these rivers, except in areas where these large, long-lived, mobile grazers are excluded by their own predators (Power et al. 1985). In contrast, in sunlit rivers which lack strong, persistent herbivory, algal phenology, in particular the timing and magnitude of mat proliferation and mat persistence, may have important effects on the routing of insect production, to aquatic consumers or to the land.

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