SEASONAL REASSEMBLY OF A RIVER FOOD WEB: FLOODS, DROUGHTS, AND IMPACTS OF FISH

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Abstract. Eighteen years of field observations and five summer field experiments in a coastal California river suggest that hydrologic regimes influence algal blooms and the impacts of fish on algae, cyanobacteria, invertebrates, and small vertebrates. In this Mediterranean climate, rainy winters precede the biologically active summer low-flow season. *Cladophora glomerata*, the filamentous green alga that dominates primary producer biomass during summer, reaches peak biomass during late spring or early summer. *Cladophora* blooms are larger if floods during the preceding winter attained or exceeded "bankfull discharge" (sufficient to mobilize much of the river bed, estimated at 120 m³/s). In 9 out of 12 summers preceded by large bed-scouring floods, the average peak height of attached *Cladophora* turfs equaled or exceeded 50 cm. In five out of six years when flows remained below bankfull, *Cladophora* biomass peaked at lower levels. Flood effects on algae were partially mediated through impacts on consumers in food webs. In three experiments that followed scouring winter floods, juvenile steelhead (*Oncorhynchus mykiss*) and roach (*Lavinia* (*Hesperoleucas*) *symmetricus*) suppressed certain insects and young-of-the-year fish fry, affecting persistence or accrual of algae positively or negatively, depending on the predator-specific vulnerabilities of primary consumers capable of suppressing algae during a given year. During two post-flood years, these grazers were more vulnerable to small predators (odonates and fish fry, which stocked steelhead always suppressed) than to experimentally manipulated, larger fish, which had adverse effects on algae in those years. During one post-flood year, all enclosed grazers capable of suppressing algae were consumed by steelhead, which therefore had positive effects on algae. During drought years, when no bed-scouring winter flows occurred, large armored caddisflies (*Dicosmoecus gilvipes*) were more abundant during the subsequent summer. In drought-year experiments, stocked fish had little or no influence on algal standing crops, which increased only when *Dicosmoecus* were removed from enclosures. Flood scour, by suppressing invulnerable grazers, set the stage for fish mediated effects on algae in this river food web. Whether these effects were positive or negative depended on the predator-specific vulnerabilities of primary consumers that dominated during a given summer.

Key words: algal blooms; Cladophora glomerata; *context dependency; effect sizes; flood scour; food chain length; interaction strength;* Lavinia (Hesperoleucas) symmetricus; *long-term studies; Mediterranean hydrologic regimes;* Oncorhynchus mykiss; *predator impacts.*

INTRODUCTION

In the absence of the temporal context provided by long-term research, serious misjudgments can occur not only in our attempts to understand and predict change in the world around us, but also in our attempts to manage our environment.

—John J. Magnuson (1990:495)

Context dependency is a major source of ecological complexity. Species interactions can vary in strength and even qualitative outcome in different environmental settings. Species with strong (i.e., "dominant" or "keystone") impacts on ecosystems in certain settings

can be weak interactors in other settings, even across sites separated by relatively short spatial scales (Paine 1980, Menge et al. 1994, Power et al. 1996*b*), or over time in one location (Dayton 1971, Estes 1995, Suttle et al. 2007). If we are to forecast ecological response to environmental change, we need more comprehensive understanding of why species' impacts on communities or ecosystems differ in different contexts. Long-term studies are needed to reveal effects of rare events (including coincidences or sequential contingencies of more common events), as well as lagged responses by the ecosystem (Schindler 1987, Leavitt et al. 1989, Likens 1989, Magnuson 1990). Long-term investigations of species interactions are rare, however, particularly in rivers.

Rivers offer repeated opportunities to study species' impacts as food webs reassemble after disturbance by flood scour or dewatering (Fisher 1983, Power et al.

1985). In Mediterranean climates, the seasonal timing of hydrologic disturbance is somewhat predictable. Typically, a rainy winter season is followed by a summer drought with little or no rainfall. Variation occurs from year to year, however, in the magnitude and timing of floods and the severity of subsequent drought (Gasith and Resh 1999). Timing of hydrologic events relative to vulnerable life history windows of organisms will strongly influence their populations and subsequent ecological impacts (Power and Stewart 1987, Resh and Rosenberg 1989, Resh et al. 1997, Fausch et al. 2001).

In many temperate rivers around the world, the filamentous green macro-alga *Cladophora glomerata* dominates water column biomass during warm, biologically active periods of stable base flow (Whitton 1970, Dodds and Gudder 1992). Over time, *Cladophora* becomes thickly covered with epiphytic diatoms (Stevenson and Stoermer 1982) and cyanobacteria. We investigated the effects of hydrologic context on impacts by fish and aquatic invertebrates on *Cladopora* and its epiphytes in a northern California river under a Mediterranean climate regime. Earlier experiments in this system had suggested that fish could have strong, indirect ("keystone") effects on *Cladophora* biomass following scouring winter floods, but not during drought years (Power 1990*a*, Power et al. 1996*a*, Wootton et al. 1996). To probe whether year-to-year variation in food web-mediated impacts of fish was related to hydrologic factors, we analyzed an 18-year record of discharge and seasonal algal surveys, as well as results from experimental food web manipulations during five of these years.

SITE DESCRIPTION

The study reach of the South Fork of the Eel River in Mendocino County, California, USA (Fig. 1) began 0.25 km downstream from a retired U.S. Geological Survey gaging station (USGS 11475500, "South Fork Eel near Branscomb") and extended 7 km downstream. The mean gradient of the river in this reach is 0.005, with drainage areas ranging from 114 km² upstream to 153 km² downstream. The river bed of sandstone and mudstone–shale bedrock and boulders is thinly overlain with mobile gravels, pebbles, and cobbles. Detailed descriptions of the site can be found in Power (1990*a*, *b*), Seidl and Dietrich (1992), Finlay et al. (2002), and Power et al. (2004). Hydrologic data from gaging station USGS 11475500 since we reactivated it in 1990 are *available online*.[5]

Year-to-year variation in hydrologic regimes

Like other rivers of the California North Coast, the South Fork Eel receives its rainfall primarily between the months of October and April (Anderson et al. 1987). During the biologically active summer low-flow season, most river habitat is in large shallow pools < 2 m deep,

[5] ⟨http://angelo.berkeley.edu/sensors/met⟩

connected by short riffles (Power 1990*a*, Finlay et al. 2002). Over the study period (1988–2005), the hydrograph of the South Fork Eel exhibited the regular seasonal flood drought cycles expected under this Mediterranean hydrologic regime (Fig. 2), but several hydrologic factors of potential biological importance varied from year to year. In some years but not others, winter floods were of sufficient magnitude to mobilize most of the riverbed. Bed-scouring floods are the major source of ecological disturbance in mainstem rivers that do not dewater. In rivers with gravel and coarser substrates, bed mobilization is typically initiated by discharges that reach bankfull stage (Parker 1978). The South Fork Eel is a bedrock-constrained, canyon-bound river without a distinct floodplain, and bankfull stage is difficult to evaluate in the field (see Plate 1). Bankfull discharges have a typical recurrence interval of 1.5 years (Dunne and Leopold 1978), which would occur at discharges above 120 m³/s, as estimated by a flood frequency analysis of a 30-year record when the Branscomb gaging station was operated by the USGS (Appendix A). Partial scour of the riverbed and rock-bound biota could occur at lower discharges, however.

A second hydrologic factor that could affect food webs is whether or not unusually late spring spates occur. We use the term "spates" to refer to pulses of increased discharge that, while well below bankfull discharge, can potentially detach and export algae and susceptible benthic invertebrates. Spates can also introduce or mobilize fine suspended sediments, reducing light available to algae.

A third hydrologic factor, minimum summer discharge and the relative contribution to base flow of runoff vs. groundwater (Beschta et al. 1987), could affect food webs by restricting habitat and altering temperature and nutrient loading (Grimm and Fisher 1984, Gasith and Resh 1999). In the South Fork Eel, flow typically drops to <1 m³/s during the summer drought (Fig. 2), and temperatures can rise to levels stressful for salmonids (e.g., Nielsen et al. 1994) and other cold-water taxa.

Phenology of key algal, invertebrate, and fish taxa

Each spring, *Cladophora glomerata*, which dominates primary producer summer biomass, initiates growth vegetatively from basal cells that survived winter flood scour on stable boulder and bedrock substrates. Over the summer, *Cladophora* biomass peaks and then wanes due to grazing and senescence. *Cladophora* biomass is reduced to scant, short filaments and loose detritus by late summer and early autumn, well before the onset of the fall and winter rains.

Cladophora, other algae, and detritus in the South Fork Eel are consumed by invertebrates that differ markedly in their vulnerability to local predators. Mobile, unarmored taxa such as mayflies and free-living chironomids are vulnerable to predatory invertebrates and fish. Heavily armored caddisflies (e.g., *Dicosmoecus*
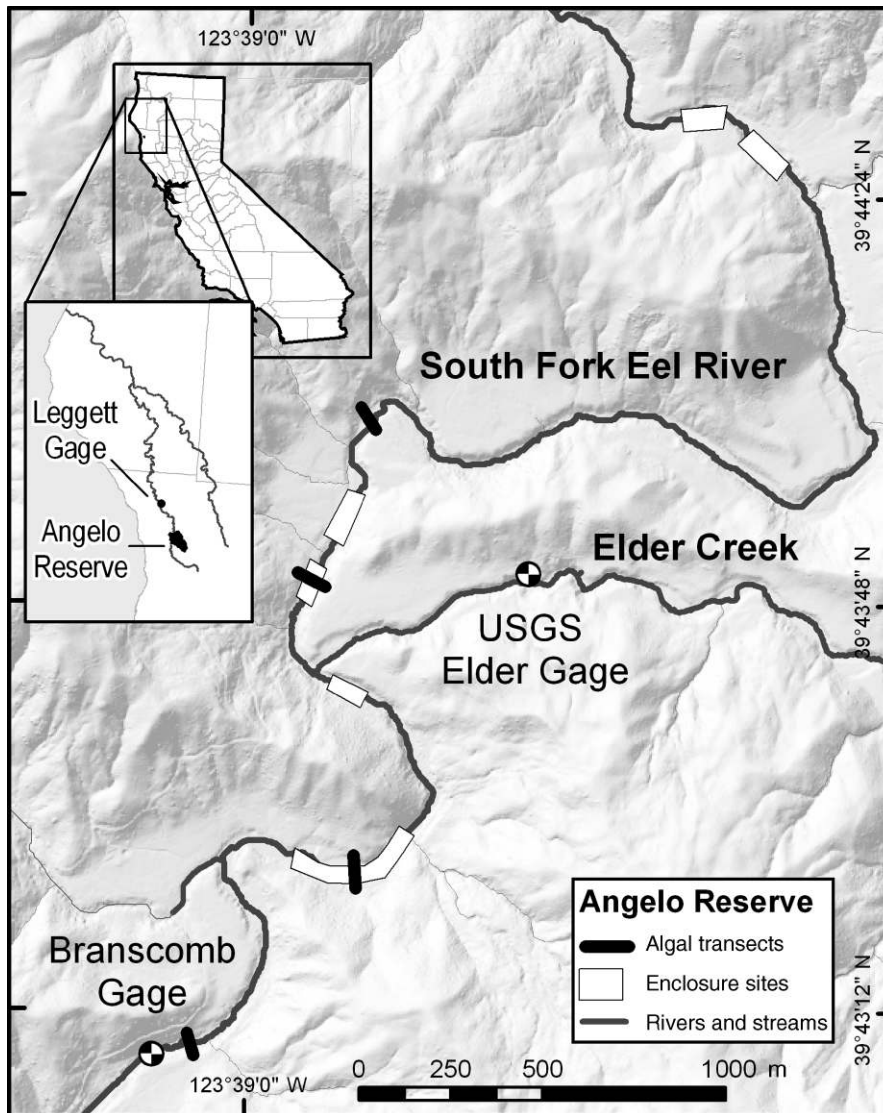
FIG. 1.   Study sites in the South Fork Eel River within the Angelo Coast Range Reserve, California, USA.

gilvipes, *Glossosoma* sp., *Neophylax* sp.), and sessile chironomids (*Pseudochironomus richardsoni*), caddisflies (*Tinodes* sp.), and aquatic moth larvae (*Petrophila* spp.) are relatively invulnerable (Hershey 1987, Johansson 1991). The dominant invulnerable grazer in the South Fork Eel is a large, univoltine caddisfly *Dicosmoecus gilvipes*. Overwintering as early instar (I–III) larvae, they build cases of leaf fragments and twigs, and abound along shallow river margins, where they can be exported or crushed (Parker et al. 2002) during high flows. In late spring and early summer, older instars (IV, V) of *Dicosmoecus* reconstruct heavier cases of gravel and move into deeper habitats. Over the summer, the abundance of invulnerable primary consumers relative to that of vulnerable taxa increases (Power 1992).

An introduced minnow, the California roach (*Lavinia* (*Hesperoleucas*) *symmetricus*), dominates the fish fauna

in the upper South Fork Eel (Brown and Moyle 1996). Roach spawn continuously through the summer. Young-of-the-year fry (10–20 mm standard length (SL)) eat small crustacea, early instar chironomids (Moyle 2002), and diatoms (M. E. Power, *unpublished data*). Larger (45–60 mm SL) roach in mainstem rivers like the South Fork Eel have diets dominated by aquatic insects (Moyle 2002 and citations therein), although their guts sometimes contain algae. The only other common fish in the water column is the native three-spined stickleback (*Gasterosteus aculeatus*). Few stickleback adults survive scouring winter floods, but these repopulate the reach with numerous young-of-the-year stickleback (15–25 mm SL) by midsummer. Roach fry, stickleback fry, and odonate nymphs (lestid and coenagrionid damselflies, gomphid and aeshnid dragonflies) make up a small predator guild in shallow mainstem pools.
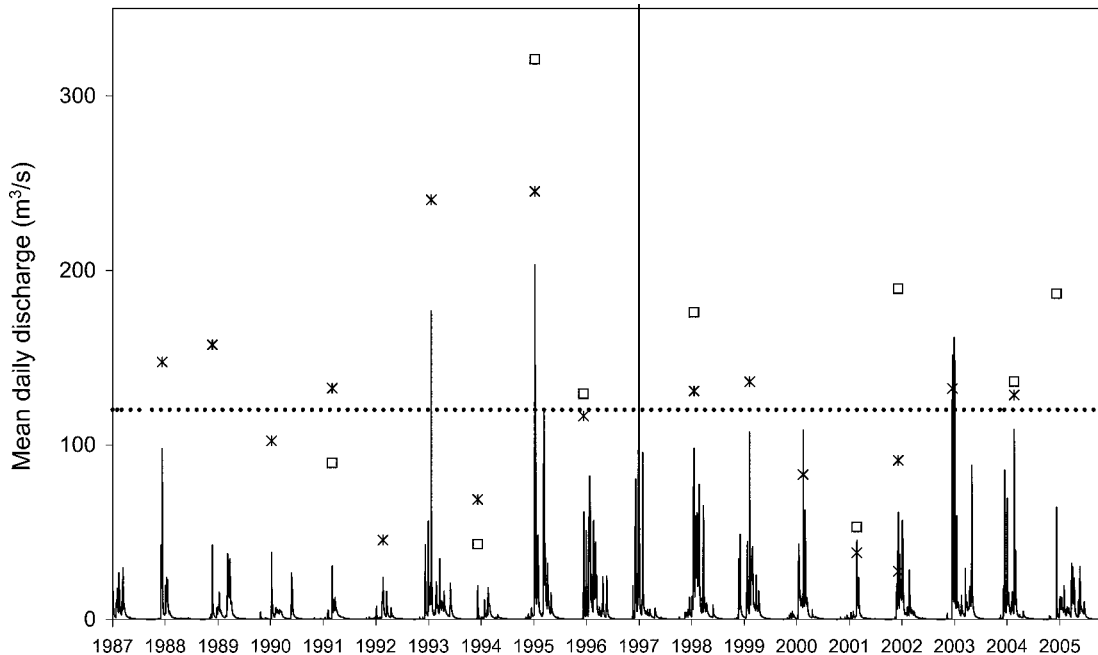
FIG. 2. Mean daily discharge (solid line) and estimated bankfull discharge of 120 m³/s (horizontal dotted line) of the South Fork Eel River at retired USGS Gage 11475500 (South Fork Eel River at Branscomb) from 1 January 1987 to 31 December 2005. The mean daily discharge record shown here is synthesized from regressions of Branscomb discharge with discharge monitored by the USGS at a nearby tributary, Elder Creek (USGS Elder Creek gaging station 11475560). The mean daily discharge for 12 December 1996 is off scale at 418.3 m³/s. Peak (hourly) discharges were measured on site (squares) or estimated from correlations with the South Fork Eel Leggett gage USGS 11475800 records of the USGS (crosses; see Appendix A and footnote 5 for Branscomb discharge data, which closely match data synthesized from Elder Creek discharge when both records are available).

Native winter steelhead or rainbow trout (*Oncorhynchus mykiss irideus*, referred to henceforth as steelhead) are also abundant in the study reach. Fry from winter spawning emerge at about 25 mm SL in March and April, and move downstream to rear in the South Fork Eel mainstem over the summer. By June and July, juvenile steelhead are abundant in shallow pool and riffle habitats. They are purely carnivorous, eating invertebrates and fish fry.

METHODS

We monitored hydrologic flow regimes (Appendix A) and algal phenology in the mainstem South Fork Eel River from 1988 to 2005. During five years, three following winter floods (designated here as "flood years") and two following drought winters without bed-scouring floods ("drought years"), we studied effects of fish on algae and invertebrates in large stream enclosures.

Algal surveys

We repeatedly surveyed four permanent cross-stream transects during summer from 1988 through 2005. Survey data from 1994 were collected from transects spatially offset from those monitored in all other years. These transects were located at roughly even intervals over a 4.5-km river reach (Fig. 1), and benchmarked at both ends with nails in trees or bedrock. We stretched a

meter tape between the nails, (nail to nail distance varied less than 1 cm over repeated surveys). At 0.5-m or 1.0-m intervals along each transect, we measured water depth, estimated surface current velocity, and visually assessed dominant and subdominant substrate particle sizes. Using a diving mask or Plexiglass view box, we noted the dominant and subdominant macroscopic algal taxa within an estimated area of 100 cm² around each sampling point. We recorded the modal height of attached filaments or the length from point of attachment of strands of algae floating over the site on the water surface, if these obscured view of the bed. We also characterized algal percent cover and condition, and noted conspicuous animals within the 100-cm² observation area (Power and Stewart 1987 and Power 1992 give further methodological details).

Experimental manipulations

During the summers of 1989, 1990, 1991, 1993, and 1997, 6-m² enclosures were installed in river pools around algal-covered boulders or bedrock (Appendix B). To begin each experiment, we electroshocked each enclosure to remove adult roach, juvenile steelhead, and potential predators on these fish, rough-skinned newts (*Taricha granulosa*) and aquatic garter snakes (*Thamnophis atratus*). We continued electroshocking until three consecutive passes in an enclosure yielded no fish >20 mm SL. After this procedure, we left some pens empty

TABLE 1.   Experimental design and sampling protocol for enclosure–exclosure experiments.

Year and treatments	No. replicates	Date fish stocked	Date cores sampled†	Enclosure transects
1989				
RS: 40 roach, 20 steelhead	6	5–7 Jun	5 Jun, 22 Jun, 16 Jul	5 Jun, 15 Jul
NF: no fish	6		5 Jun, 22 Jun, 16 Jul	5 Jun, 15 Jul
Open, near enclosures	3 or 6‡		5 Jun, 22 Jun, 16 Jul	5 Jun, 15 Jul
1990				
RS: 10 roach, 10 steelhead	6	22 Jul	26 Jul, 15 Sep	13 Jul, 28 Jul
NF: no fish	6		26 Jul, 15 Sep	13 Jul, 28 Jul
R: 20 roach	6	22 Jul	26 Jul, 15 Sep	13 Jul, 28 Jul
S: 20 steelhead	6	22 Jul	26 Jul, 15 Sep	13 Jul, 28 Jul
Open, near enclosures	6		26 Jul, 15 Sep	13 Jul, 28 Jul
1991				
RS: 10 roach, 10 steelhead	6	11 Jun	9 Jun, 27 Jun, 20 Jul	6 Jun, 12 Jul
NF: no fish	6		9 Jun, 27 Jun, 20 Jul	6 Jun, 12 Jul
R: 20 roach	6	11 Jun	9 Jun, 27 Jun, 20 Jul	6 Jun, 12 Jul
S: 20 steelhead	6	11 Jun	9 Jun, 27 Jun, 20 Jul	6 Jun, 12 Jul
Open, near enclosures	6		9 Jun, 27 Jun, 20 Jul	6 Jun, 12 Jul
1993				
R: 20 roach	5	7 Jul	5 Jul, 12 Aug	5–6 Jul, 12 Aug
S: 20 steelhead	5	7 Jul	5 Jul, 12 Aug	5–6 Jul, 12 Aug
NF: no fish	5		5 Jul, 12 Aug	5–6 Jul, 12 Aug
Open, near enclosures	5		5 Jul, 12 Aug	5–6 Jul, 12 Aug
1997				
RS: 10 roach, 10 steelhead	6	15–19 Jul	14 Jul, Aug 16	13 Jul, 16 Aug
NF: no fish	6		14 Jul, Aug 16	13 Jul, 16 Aug

† Cores were 9 cm in diameter on all dates except on 5 June 1989, when they were 5.6 cm in diameter, and on 14 July and 16 August 1997, when they were 8 cm in diameter.

‡ On 5 June and 16 July 1989, three core samples were collected from the open river bed within each of the four groups of enclosures installed at different river reaches; on 22 June 1989, six such core samples (two per site) were collected.

as "exclosures" and restocked enclosures with roach, steelhead, or both, collected from adjacent river habitat by seining, electroshocking, or minnow traps. Fish were size matched among enclosures, and ranged from 30 to 68 mm SL (steelhead) and 48 to 77 mm SL (roach).

Details of experimental design and procedures varied from year to year (Table 1), due in part to constraints imposed by the timing and spatial extent of algal blooms. The date of the peak bloom of *Cladophora* varied somewhat unpredictably among years, so the timing of installation of enclosures relative to this peak also differed. In 1989, enclosures were installed about 1.5 months before the July peak of the bloom; in 1990, enclosures were set out two months after the early *Cladophora* peak in May; in 1991, enclosures were installed 12 days after the *Cladophora* peak; in 1993, their installation coincided with the peak bloom; and in 1997, installation preceded the peak bloom by one month (Tables 1 and 2). The numbers of enclosures installed also varied from year to year. In 1989, 12 enclosures were installed in three locations distributed over a 3-km reach of river. Six cages (two per location) were left as fish-free exclosures; the other six were stocked with 40 roach and 20 steelhead (10 fish/m^2). In all subsequent experiments, 20 (3.3 individuals/m^2), rather than 60 fish were stocked. While densities of roach and steelhead can be as high as 40 fish/m^2 when they aggregate in favorable microhabitats, densities of 1–4 fish/m^2 are more representative of average condi-

tions experienced by fish over longer time scales. In 1990, 1991, and 1997, 24 cages were installed, with one replicate of each of four treatments (20 roach, 20 steelhead, 10 roach and 10 steelhead, or neither) in six locations (Table 1). In 1997, however, 12 downstream enclosures warmed to unsuitable temperatures for fish. These, and the two single species treatments, had to be dropped from the experiment.

In 1993, much of the incipient bloom of *Cladophora* was exported by a late spring spate, and we were only able to find 15 suitable sites for enclosures where enough algae persisted. That year, only single-species enclosures (roach or steelhead) and exclosures were installed in groups of three in each of five locations. Taking all five experiments into account, the combined effects of roach and steelhead could be examined during two drought (1990, 1991) and two flood (1989, 1997) years, and the separate effects of roach or steelhead could be examined during two drought (1990, 1991) and one flood (1993) year.

At the onset and termination of experiments during all years, and at midpoints in 1989 and 1991, we estimated algal biomass and invertebrate density by collecting three algal cores from each enclosure, taken from boulder/bedrock substrates at upstream, middle, and downstream positions down the longitudinal center line. We also sampled algae and invertebrates from cores from comparable substrates on pool beds outside but within 1–2 m of enclosures, designated as "open"

TABLE 2. Hydrologic events and *Cladophora* and *Pseudochironomus* phenology, 1988–2005.

Summer year	Preceding peak discharge (m^3/s)	Date of peak discharge	Spring spate date†	Spate discharge (m^3/s)	Peak averaged modal height *Cladophora* (cm)	Date of peak bloom	Proportion sites with tufts‡
1988§	147.4	10 Dec 1987			24.1	20 Jul	0.57
1989§	157.3	22 Nov 1988	9 Mar	36.6	57.0	28 Jul	0.56
1990§	102.3	7 Jan 1990	27 May	81.2	33.6	13 May	0.25
1991	89.6	4 Mar 1991	4 Mar	89.6	24.8	30 May	0.30
1992§	45.3	19 Feb 1992			47.0	30 May	0.10
1993	240.4	20 Jan 1993	6 Jun	42.7	50.0	5 Jul	0.00
1994	43.07	8 Dec 1993	26 Apr	8.8	3.5¶	15 Jun	0.00
1995	320.9	9 Jan 1995	14 Mar	116.9	177.1	26 Jul	0.19
1996§	129.2	12 Dec 1995	22 May	24.3	17.3	20 Jul	0.00
1997	418.3	30 Dec 1996	23 Apr	6.3	127.0	7 Jul	0.00
1998	175.9	17 Jan 1998	23 Mar	65.8	265.0	6 Aug	0.10
1999§	136.2	7 Feb 1999	25 Mar	25.3	108.2	7 Jul	0.18
2000§	83.0	14 Feb 2000	11 Mar	12.4	298.0	28 Jun	0.37
2001	52.9	20 Feb 2001	3 Mar	24.0	11.5	2 Aug	0.13
2002	189.5	5 Dec 2001	10 Mar	5.5	142.9	13 Jun	0.16
2003	132.3	16 Dec 2002	28 Apr	76.65	111.0	4 Aug	0.01
2004	136.2	17 Feb 2004	21 Apr	15.2	49.3	12 Jul	0.03
2005	186.5	8 Dec 2004	18 May	71.8	52.5	20 Aug	0.00

† Spring spates are pulses of elevated discharge less than bankfull that occurred after 1 March.
‡ Proportion of sites with *Cladophora* at least 1 cm high where *Pseudochironomus* tufts could be constructed ($n > 10$).
§ Peak discharge estimated from record at the USGS Leggett gage, South Fork Eel River.
¶ The 1994 data were from different transects than in other years.

treatments. We also estimated initial and final algal biomass nondestructively by measuring its height along three transects per enclosures, and regressing height against dry mass. Appendix C gives details of these methods.

Toward the end of the experiments, we stood quietly by each enclosure for about 10–20 minutes between late morning and early afternoon on one to three days each year, and recorded the numbers of small predators observed in the water column and at the water surface. These taxa included surface dwelling water striders (*Gerris remigis*) and water-column dwelling young-of-the-year roach and stickleback fry (10–20 mm SL), which could pass through the mesh of enclosure walls. In 1993 and 1997, lestid damselfly (*Archilestes californica*) nymphs that perched in taller strands of *Cladophora* above the riverbed were also counted. Lestids were also taken in core samples. Counts of lestids from visual censuses and from cores were analyzed separately.

Statistical analyses

We analyzed results from individual experiments (within a year) with Wilcoxon rank sum tests for comparisons of two treatments, and with Kruskal Wallis one-way analysis by ranks for comparisons of more than two treatments. Analyses and computations were performed using JMP statistical software by SAS (Sall and Lehman 1996), and with a hand calculator. For an overall picture of how hydrologic context affected fish impacts, we measured effect sizes of fish (roach and steelhead together in 1989, 1990, 1991, and 1997, and roach or steelhead separately in 1990, 1991, 1993), on abundances of five benthic taxa (attached *Cladophora*, chironomids, mayflies, caddisflies, and small predators)

and four taxa inhabiting the water column or water surface (gerrid water striders, stickleback fry, roach fry, and lestid damselfly nymphs). Effect sizes were measured as response ratios (Hedges et al. 1999): $\ln(X_f/X_{nf})$ where X_f is the mean density of the taxon in the presence of fish (roach and steelhead together, or roach or steelhead separately), and X_{nf} is the mean density of the taxon in the absence of fish on the final sampling date for experimental enclosures during a given year. Confidence intervals (95%) were computed using Eq. 2 in Hedges et al. (1999), with $z_{\alpha/2} = 1.96$.

RESULTS

Hydrology and Cladophora phenology

Twelve of the 18 summers from 1988 to 2005 were preceded by a flood with instantaneous peak discharge greater than the estimated bankfull discharge (120 m^3/s; Table 2). In 10 of these summers, *Cladophora* peak blooms were large, defined a priori as attaining, on sites where growths occurred, average modal filament heights ≥ 50 cm (Table 2, Figs. 3 and 4). An algal bloom of this magnitude occurred only once (2000) in the six summers not preceded by bankfull discharge (Table 2, Fig. 4). Overall, large *Cladophora* blooms tended to follow winters with peak flows that equaled or exceeded estimated bankfull discharge ($P = 0.03$, Fisher's exact test). Across all 18 years, the proportion of surveyed sites with visible *Cladophora* on a given date (x) was positively correlated with the average modal height of *Cladophora* height on that date (y) by a power law relationship: $y = 0.22(x)^{0.14}$ ($r = 0.30$, $P = 0.002$, $n = 101$ observations).

The seasonal timing (Julian date [day of the year]) of peak *Cladophora* blooms, which occurred from 13 May
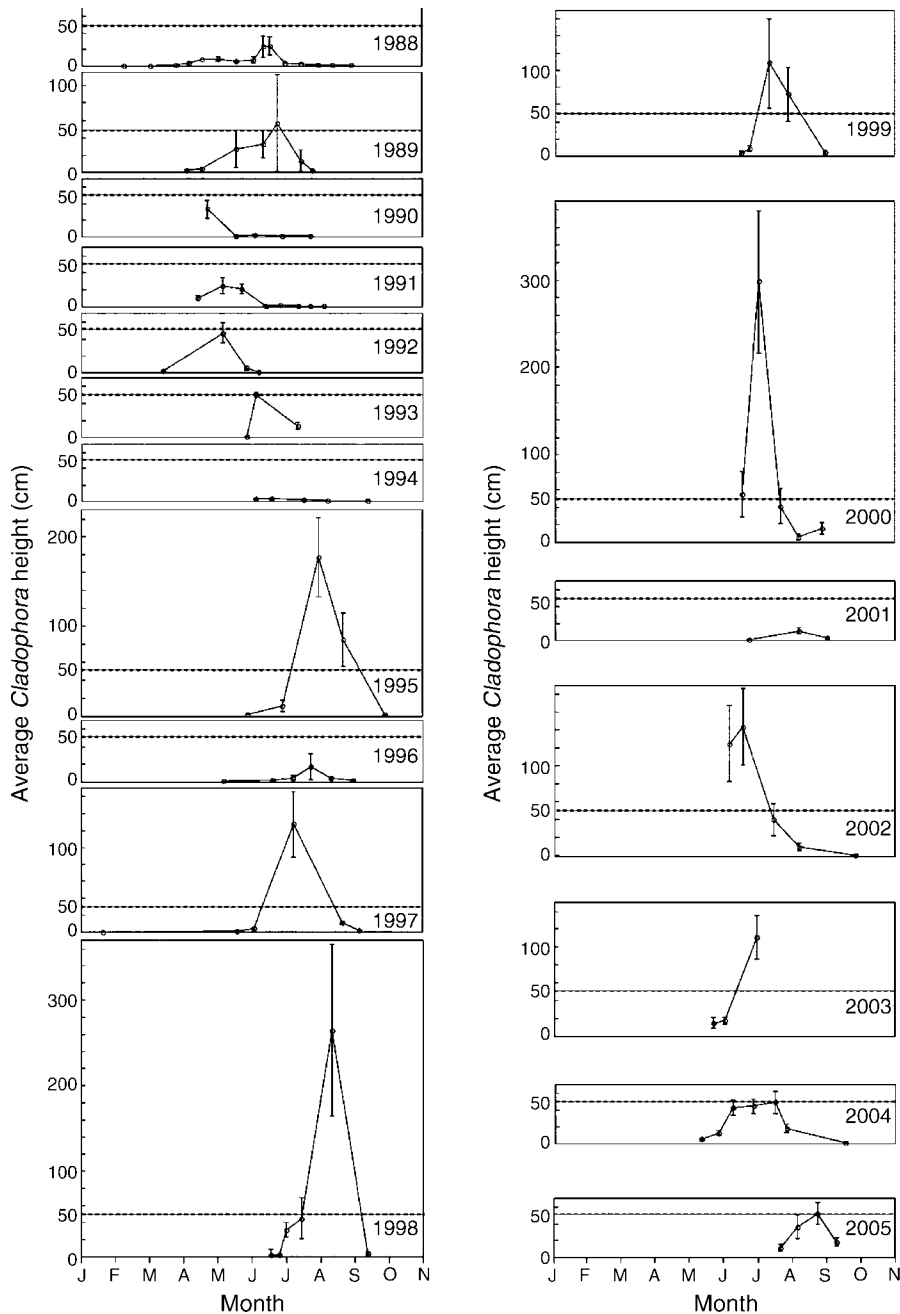
FIG. 3. Seasonal changes in averaged modal height of attached *Cladophora* (± 2 SE), on sites where it occurred during low flow seasons 1988–2005 from four repeatedly surveyed cross-stream transects (sites in Fig. 1). Attached *Cladophora* strands >1 m in height obscured view of the bed and were estimated from the length of continuous strands that covered a survey site, but they originated in part at locations upstream from the site. The height of 50 cm (dashed line) was designated a priori as a threshold for a large algal bloom. Data for 1994 were collected from three transects near, but not coincident with, transects monitored during the other 18 years.

to 20 August (Table 2) was not correlated with the magnitude of winter floods (peak preceding discharge) over the 18-year record ($r = 0.24$, $P > 0.20$, $n = 18$ years). A run of early blooms occurred at the onset of the 1990–1992 drought (Fig. 3), but blooms during subsequent drought years peaked later in the summer.

Spates of less than bankfull discharge (<120 m^3/s) might have affected summer food web reassembly if they disturbed grazers or producers during vulnerable life history stages. During 16 years, spates occurred in or after March, when early-instar *Dicosmoecus* caddisflies had litter cases, and were more buoyant than later
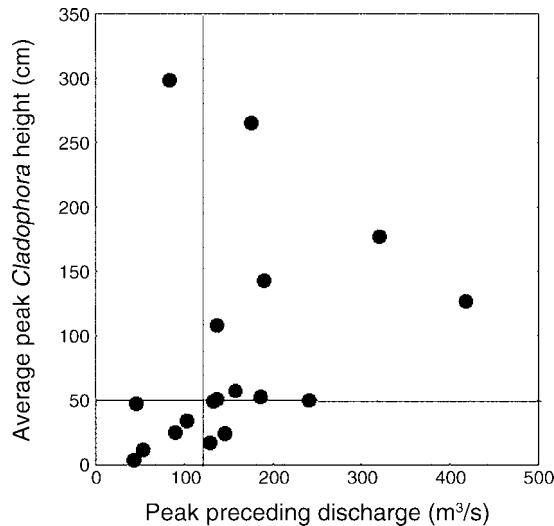
Fig. 4. Association from 1988 to 2005 of large peak *Cladophora* blooms with average algal heights ≥50 cm (the horizontal line indicates the 50-cm threshold for a large bloom) and peak discharges that exceeded estimated bankfull flow of 120 m³/s (vertical line) during the previous winter.

summer stone-cased instars. Despite the potential of these spates to export *Dicosmoecus* and reduce grazing, there was no significant association between the occurrences of late spates after 1 March and large algal blooms the following summer (Table 2, $P = 0.29$ for spates of more than 5 m³/s; $P = 0.13$ for spates of more than 50 m³/s, Fisher's exact test). Late spates during May or June of four years could have potentially exported *Cladophora* biomass during its early accrual phase, or reduced water clarity early in the growing season. Spates after 1 May, however, were also not associated with reduced algal bloom magnitude over the 18 years of study (Table 2, $P = 0.4$ for both spates of more than 5 m³/s and larger spates of more than 50 m³/s, Fisher's exact test).

Very late (post-May) spates had the potential to reduce recruitment of summer abundances of aquatic insects by exporting floating algal mats. These mats are important oviposition and rearing sites for a larval midge, *Pseudochironomus richardsoni*, which weaves "tuft" retreats in *Cladophora*. When abundant, *Pseudochironomus* infestations change *Cladophora*'s architecture and shorten its persistence (Power 1990b).

In 1993, the latest spate observed during this study (6 June, 42.7 m³/s) exported much of the incipient *Cladophora* bloom. *Cladophora* regrew to a peak bloom of 50 cm average height by July (Fig. 3), but, in contrast to other years (Power 1990a), did not detach and form floating mats. Tuft-weaving midges were extremely sparse during the summer of 1993 (Table 2). Their characteristic retreats allowed a semiquantitative comparison of midge recruitment among years. We designated potential *Cladophora* colonization sites for *Pseudochironomus* as occurring where turf lengths

equaled or exceeded 1 cm (woven midge retreats are typically 0.5–1.0 cm long). Low midge recruitment (<5% of suitable surveyed sites with filamentous algae occupied) was positively associated with years with late spring spates (Table 2, $P = 0.065$, Fisher's exact test, one tailed). The proportion of such sites along surveyed transects that were occupied by *Pseudochironomus* retreats peaked at >50% in the summers of 1988 and 1989, then dropped during the drought years, and dropped to lower levels during and after 1993, the year with the spring spate. There was modest apparent *Pseudochironomus* recovery from 1998 to 2002, but abundances were subsequently (2003–2005) low (Table 2).

Results of fish manipulations: comparisons among years

Effects of fish on algae.—During all years, *Cladophora* bloomed then senesced, inside and outside of experimental enclosures, from the onset of experiments in early or mid-summer until their termination 5–7 weeks later. Attached *Cladophora* had similar biomass among treatments at the onset of all five experiments (Fig. 5). During both drought summers (1990, 1991), algal biomass was low at the onset of experiments, and not significantly altered in fish treatments at the end of experiments (Figs. 5 and 6, $P = 0.24$ and $P = 0.09$ in 1990 and 1991, respectively, from Kruskal Wallis rank sums). During post-flood summers of 1989 and 1997, *Cladophora* declined more rapidly in enclosures with roach and steelhead, so that remnant biomass at the end of the experiments was significantly greater in fish-free exclosures (Fig. 5, $P = 0.017$ in 1989 and $P = 0.005$ in 1997, Wilcoxon rank sums). Average algal height of *Cladophora* turfs, and the average of the maximum heights measured in each enclosure were also greater in fish-free exclosures during both years (Fig. 7, $P = 0.004$ for 1989 average; $P = 0.009$ for 1989 maximum; $P = 0.008$ for 1997 average; $P = 0.008$ for 1997 maximum, Wilcoxon rank sums). During 1989, large floating mats dominated by the cyanobacteria *Nostoc* sp. formed in the absence of fish, while very little accumulated in their presence (Power 1990b, $P = 0.001$ from a Mann-Whitney U test). At the end of the experiment in 1997, floating mats of *Nostoc* and the loosely epiphytic diatom *Melosira* were observed in only one fish exclosure, and in none of the enclosures.

In 1993, following winter flood and a late spring spate, effects of roach and steelhead on *Cladophora* were evaluated separately. Effects of roach and steelhead were not statistically significant, but at the end of experiments the average height of *Cladophora* was greatest ($P = 0.018$) in the steelhead treatment (Fig. 7). The most dramatic response by algae in 1993 was the proliferation in steelhead treatments of white, cloud-like blooms of diatoms dominated by *Melosira* and *Cymbella*, initiated within residual *Cladophora* turfs. These diatom blooms expanded to fill much of the water column, attaining an average damp mass of 30.0 ± 11.6 g/m² (mean ± SE) in steelhead treatments. Sparser
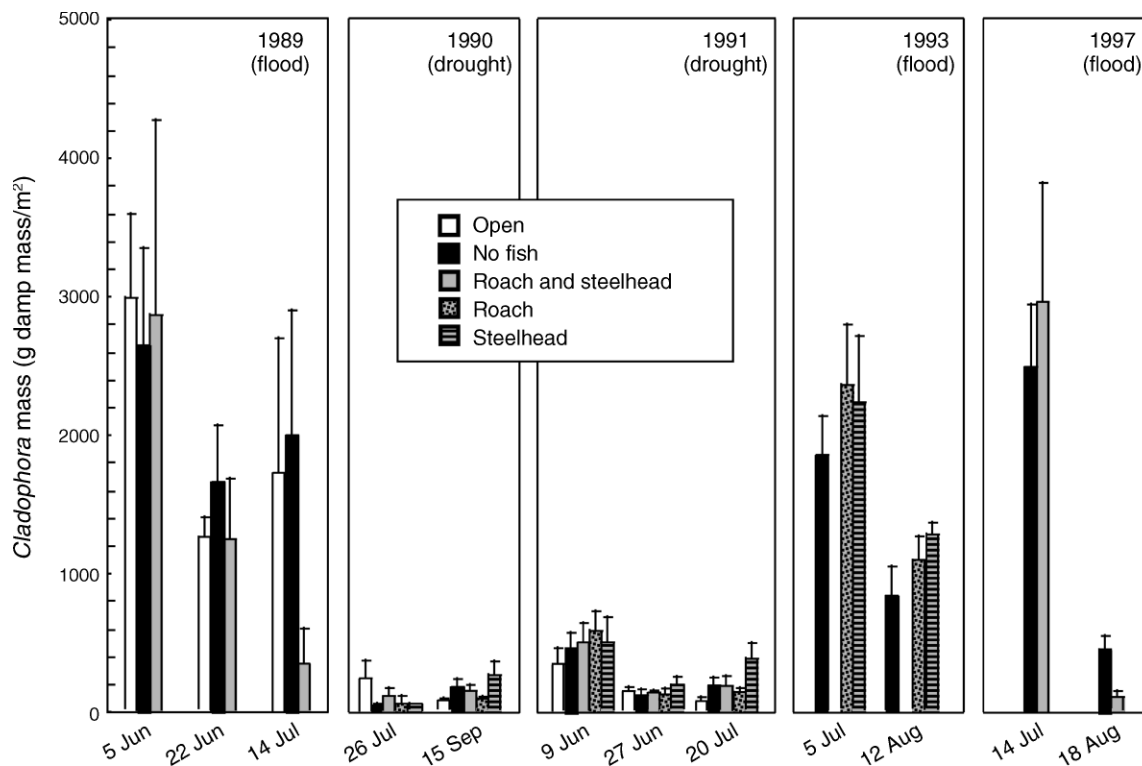
Fig. 5. Effect of fish treatments on the biomass of attached *Cladophora* and associated epiphytes over the five experiments. Damp masses of algae are means (+1 SE) across replicate enclosures of averages of three subsamples collected in each enclosure. Table 1 gives sample sizes for each year.

diatom blooms occurred in the fish exclosures (5.5 ± 1.7 g/m^2), but diatom blooms were completely absent in the adult roach treatment. The biomass of diatom mats was significantly different among treatments at the end of the experiment ($P = 0.016$, Kruskal-Wallis rank sums).

Effects of fish on primary consumers.—Effects of fish on benthic primary consumers also differed among years. Benthic primary consumers were rare, and not additionally reduced by fish treatments, during the two drought summers (1990, 1991). Mayflies, common in guts of both roach and steelhead (Power et al. 1992), were suppressed by fish in 1989 and 1997 ($P = 0.044$ and $P = 0.032$, respectively), but were apparently released by roach and steelhead separately in 1993 (Fig. 8). Fish effects on chironomids, most of which were primary consumers, were strongly positive in 1989 ($P = 0.02$, Wilcoxon rank sums), a year when *Pseudochironomus richardsoni* was extremely abundant, as evidenced by the tufted architecture of *Cladophora* inside and outside of enclosures (Power 1990b, Table 2). In other years when *Pseudochironomus* was not abundant, fish effects on other midges in enclosures were negative (in 1997) or not significant (1990, 1991, 1993; Fig. 9).

Cased caddisflies (*Dicosmoecus, Neophylax, Glossosoma,* and *Gumaga*) were not heavily consumed by adult roach and juvenile steelhead. During post-flood summers, however, most cased caddisflies counted in

enclosures were early instar limnephilids <5 mm in length. In 1989, small caddis appeared to be initially suppressed by fish ($P = 0.008$ at the midpoint of experiments on 22 June), but by the end of the experiments, caddisflies were sparse in all treatments (Fig. 10). Caddisflies were scarce in drought year 1990 and slightly more abundant in 1991, but in neither drought year did fish affect their abundance (Fig. 10). In 1993 and 1997, *Gumaga* recruited in higher numbers. Endpoint density differences were not significant in 1993. In 1997, apparently significant endpoint differences (Fig. 6) reflected large initial differences between enclosures and exclosures (Fig. 10), rather than treatment effects.

Effects of fish on small predators.—Small benthic predators sampled in cores were generally an order of magnitude less dense than primary consumers. Taxa taken most commonly were coenagrionid and lestid damselfly and aeshnid and gomphid dragonfly nymphs. At the end of experiments, small predators were significantly depressed in fish treatments relative to controls during post-flood summers 1989 and 1997 ($P = 0.041$ and $P = 0.036$, Wilcoxon rank sums). Variation among exclosures precluded detection of a significant response ratio effect in 1997 and in 1993 (Fig. 6), when small benthic predators were twice as dense in fish-free exclosures as in steelhead treatments (Fig. 11). Small
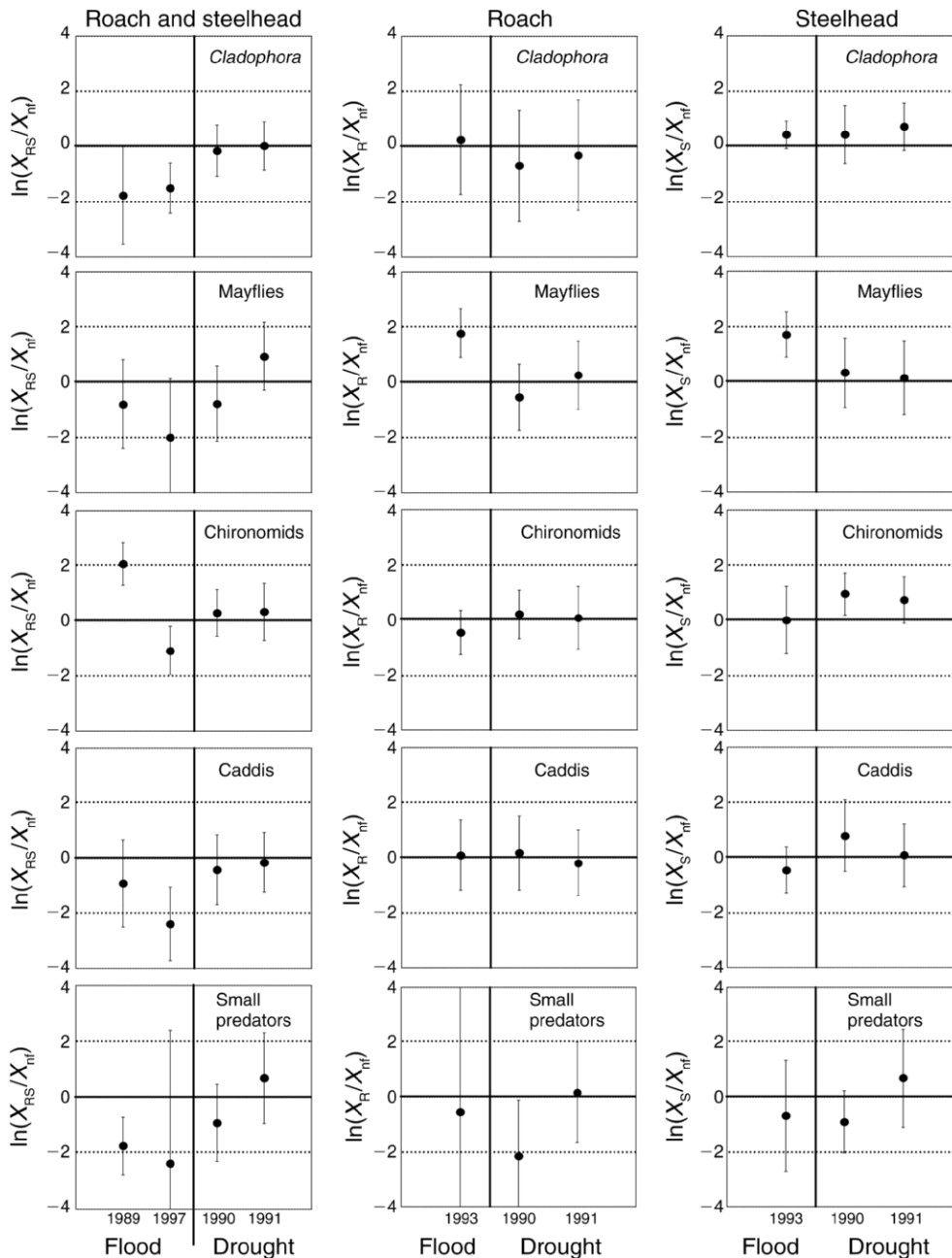
Fig. 6. Effect sizes of fish on benthic taxa on the final sampling date for experiments during flood years (1989, 1993, and 1997) and drought years (1990, 1991), with 95% confidence intervals. Effect sizes were measured as response ratios (Hedges et al. 1999), $\ln(X_f/X_{nf})$, where X_f is the mean density of the taxon in the presence of fish (roach and steelhead together [RS], or roach [R] or steelhead [S] separately), and X_{nf} is the mean density of the taxon in the absence of fish on the final sampling date for experimental enclosures during a given year. Interactions are considered strong if 95% confidence intervals do not cross zero.

benthic predators were rare during the two drought summers (1990, 1991) and were additionally reduced by fish only in 1990 (Fig. 6).

Small predator-consumers that patrolled the water column (young-of-the-year stickleback and roach fry) or the water surface (water striders, *Gerris remigis*) were suppressed or eliminated by steelhead during both flood and drought. Gerrids, stickleback, and roach fry were less affected by adult roach (Figs. 12 and 13), but lestid damselfly nymphs clinging to *Cladophora* turfs above the substrate (where they were not sampled in benthic cores) were suppressed or eliminated by both fish. Piscivorous impacts of steelhead, either alone or when stocked with roach, were more consistent than those of roach across years (Fig. 13), suggesting that impacts on fish fry when roach and steelhead were stocked together (1989, 1997)

were primarily due to steelhead. Steelhead impacts on stickleback (which have protective pectoral and dorsal spines) were not, however, as strong as their effects on soft, thin roach fry (Fig. 13).

Strong impacts of fish on benthic biota at lower trophic positions were more frequent in webs that assembled after floods than in drought years. Of the 20 post-flood benthic interactions depicted in Fig. 6, eight were significant in flood years (40% "strong"), while only two of 30 drought-year interactions were significant (7% "strong"). In contrast, in the water column, frequencies of strong fish impacts were similar in flood vs. drought years. Of the 15 post-flood water column interactions depicted in Fig. 13, 12 (80%) were significant in flood years, while 13 of 18 (72%) were significant in drought years. These results suggest that fish suppressed prey in the water column in all years, regardless of winter flood history, but that fish impacts on benthos were more likely when flood-mediated fish effects cascaded down to affect algal standing crop.

DISCUSSION

In the South Fork Eel River, large algal blooms tended to follow bed-scouring winter floods over 18 years of observation. This association could occur because of direct positive effects of large discharge or precipitation events on algae (e.g., inputs of nutrients), or because of indirect hydrologic effects on food web controls over algal accrual or persistence. The effects of flood scour on densities of a large, predator-resistant grazer lend support for the second hypothesis. *Dicosmoecus gilvipes* was one to two orders of magnitude less dense in the South Fork Eel after bed-scouring winter floods than during flood-free drought years (Wootton et al. 1996). In 1992, a drought year, Wootton et al. (1996) carried out an experiment that crossed *Dicosmoecus gilvipes* (30 individuals/m^2) with steelhead (0.75 individuals/m^2) treatments, and showed that the dominant controls on algae were exerted through the two-level food chain capped by *Dicosmoecus* as the "apex" (predator-resistant) grazer. Experimentally removing *Dicosmoecus* during this drought year released *Cladophora* and its epiphytes from near zero biomass in controls (with *Dicosmoecus*) to 60–90 g/m^2 dry mass (~600–900 g/m^2 damp mass) when *Dicosmoecus* was excluded (Fig. 1A in Wootton et al. 1996). In the absence of *Dicosmoecus*, *Cladophora* and its epiphytes (largely *Nostoc* and the diatom *Epithemia*) grew into conspicuous turfs and detached to form small floating algal mats. This month-long experiment measured algal biomass that grew on initially barren tiles or stream cobbles. Given these initial conditions, it is surprising that after just one month, algae in treatments without *Dicosmoecus* attained biomasses 20–33% as large as the peak biomasses observed at the start of flood year experiments in the present study, when algae had accrued over the spring without heavy grazing (Fig. 3). In the 1992 experiment, steelhead had a weak but
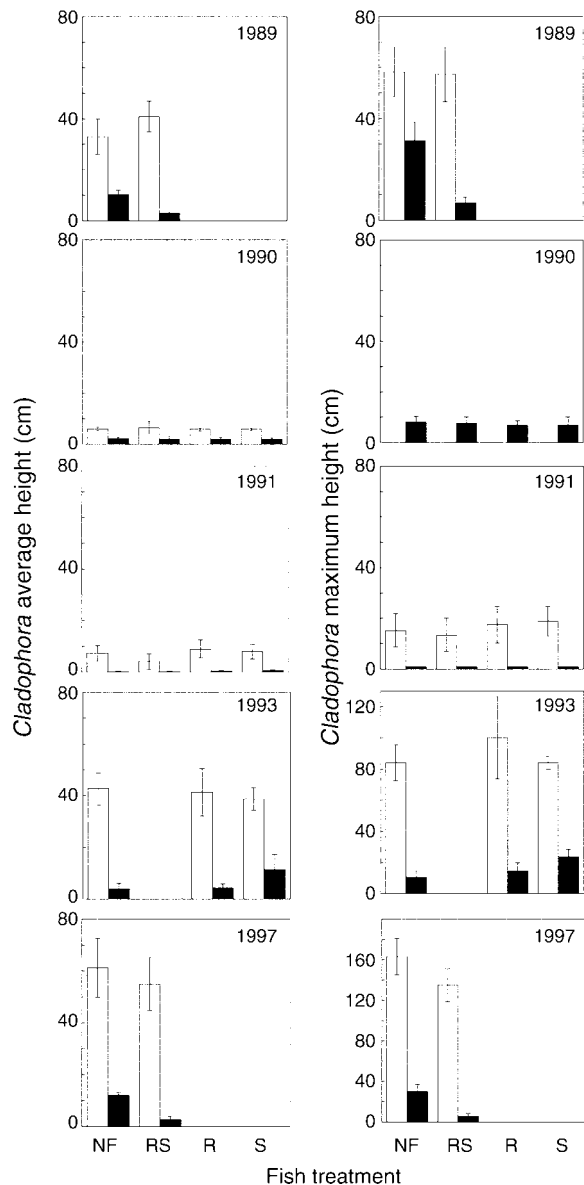

FIG. 7. Effect of fish treatments on the treatment means (±2 SE) of average height (left column) of attached *Cladophora* measured at 23–51 sites in each enclosure, and means of enclosure maximum heights of attached algae (right column), at the onset (open bars) and termination (solid bars) of experiments. There were no data on maximum algal heights in enclosures taken at the onset of the 1990 experiment. Treatments are: NF, no fish; RS, roach and steelhead; R, roach; S, steelhead.

statistically significant negative effect on algae, suggesting that again, as in 1989 and 1997, algae experienced steelhead impacts indirectly through two intermediate trophic levels.

These 1992 results indicated strong grazer limitation of algae during a drought year (Fig. 14), but do not rule out the possibility that nutrients may also have been limiting (e.g., Fisher et al. 1982, Grimm 1987). The
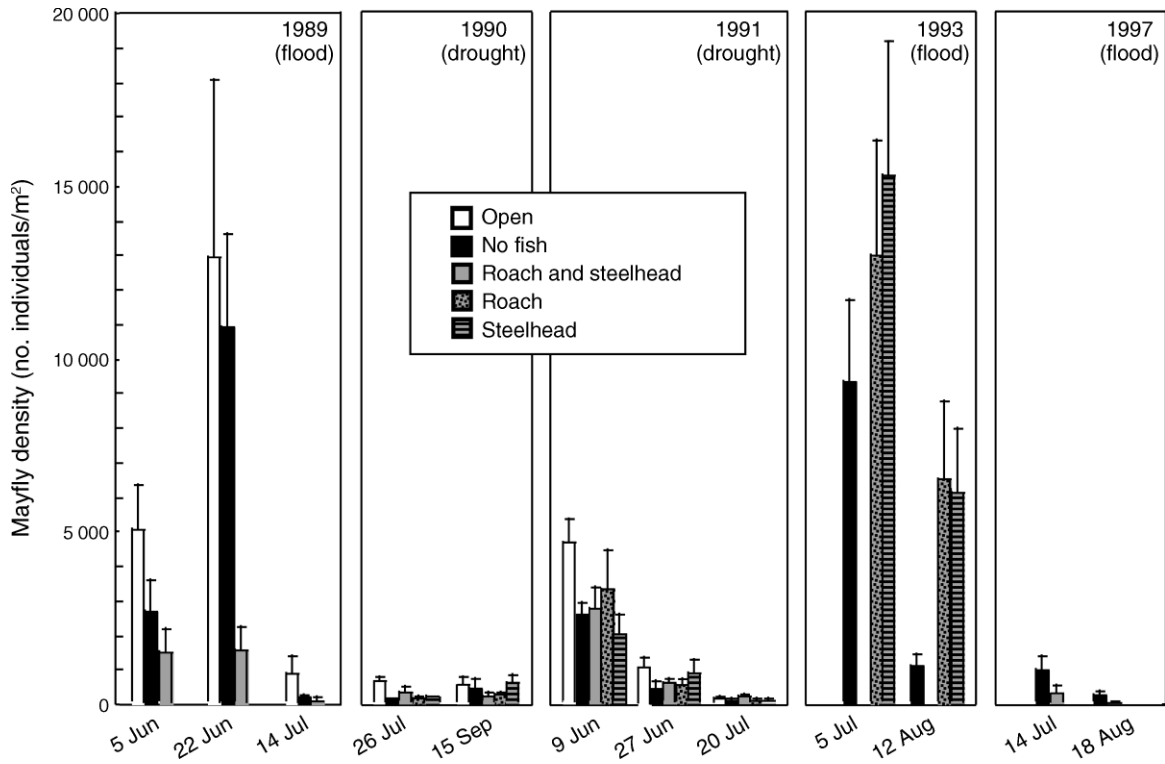
MARY E. POWER ET AL.

Fig. 8. Effect of fish treatments on the abundance of benthic mayflies (mean + 1 SE) over the five experiments from years 1989–1997.
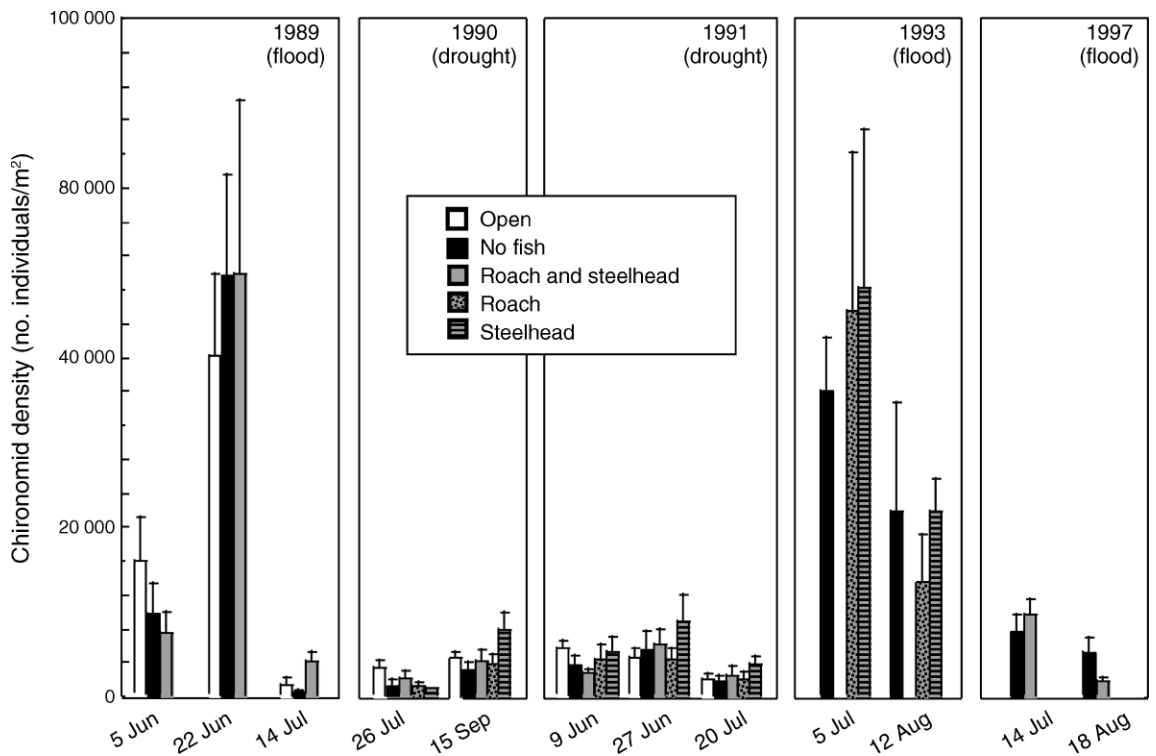

Fig. 9. Effect of fish treatments on the abundance of chironomids (mean + 1 SE) over the five experiments.
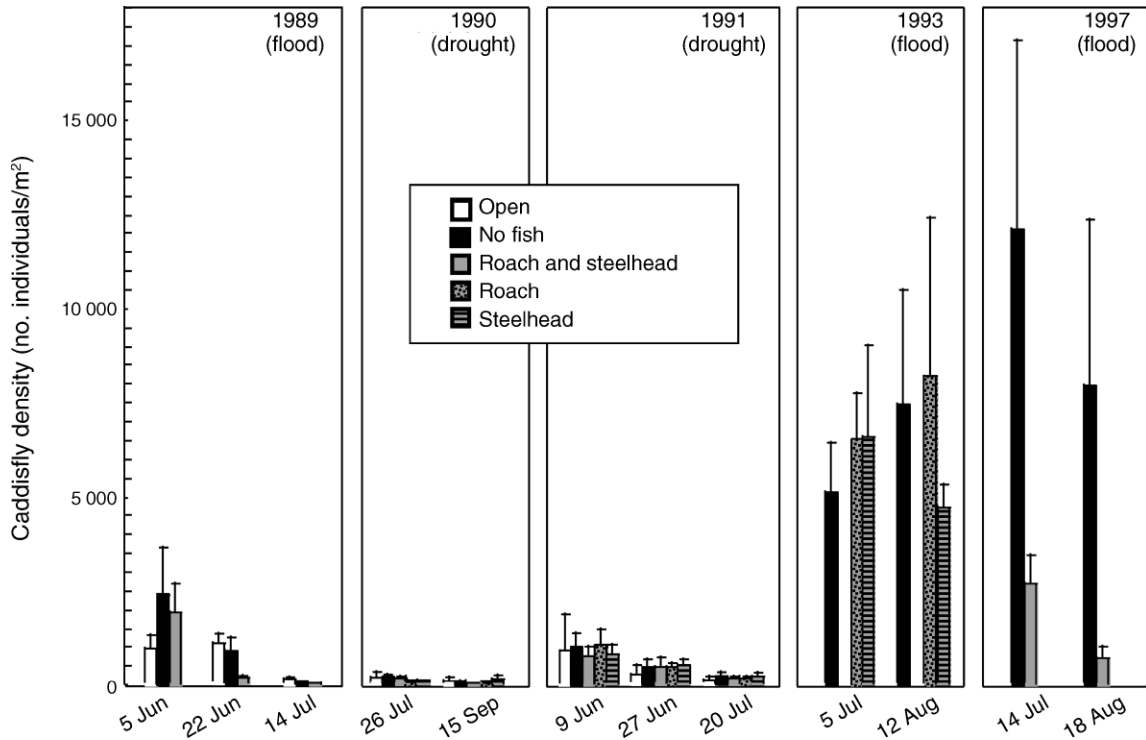
FIG. 10.   Effect of fish treatments on the abundance of caddisflies (mean + 1 SE) over the five experiments.
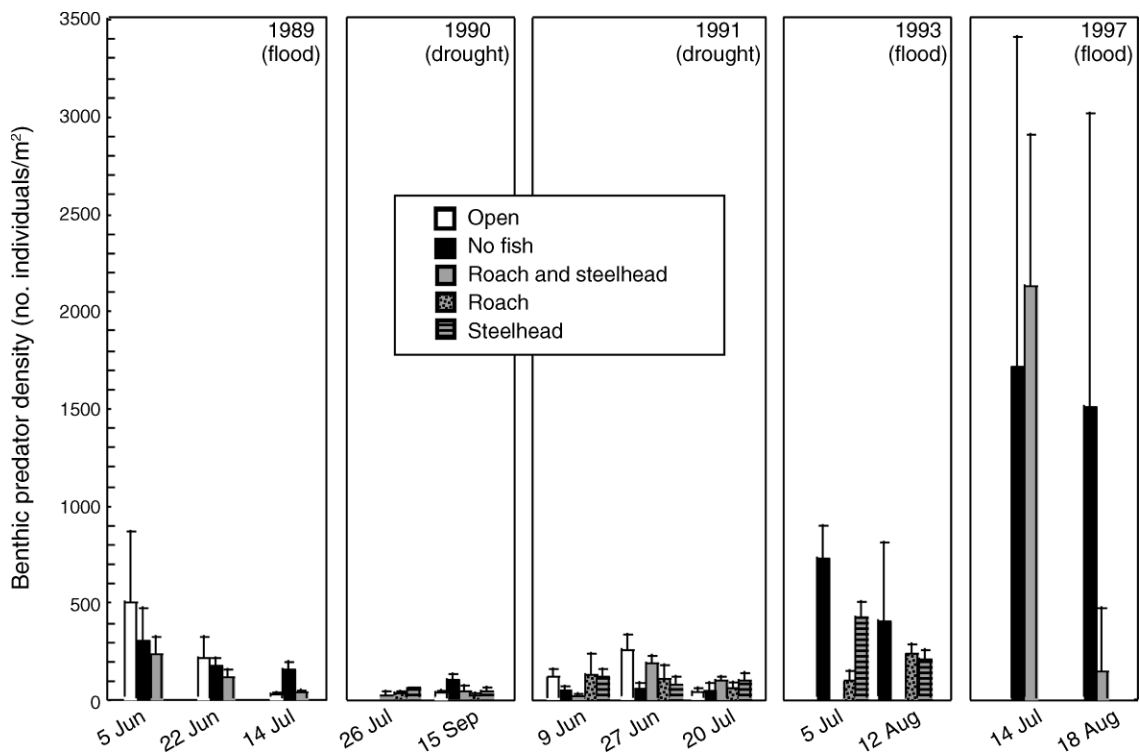

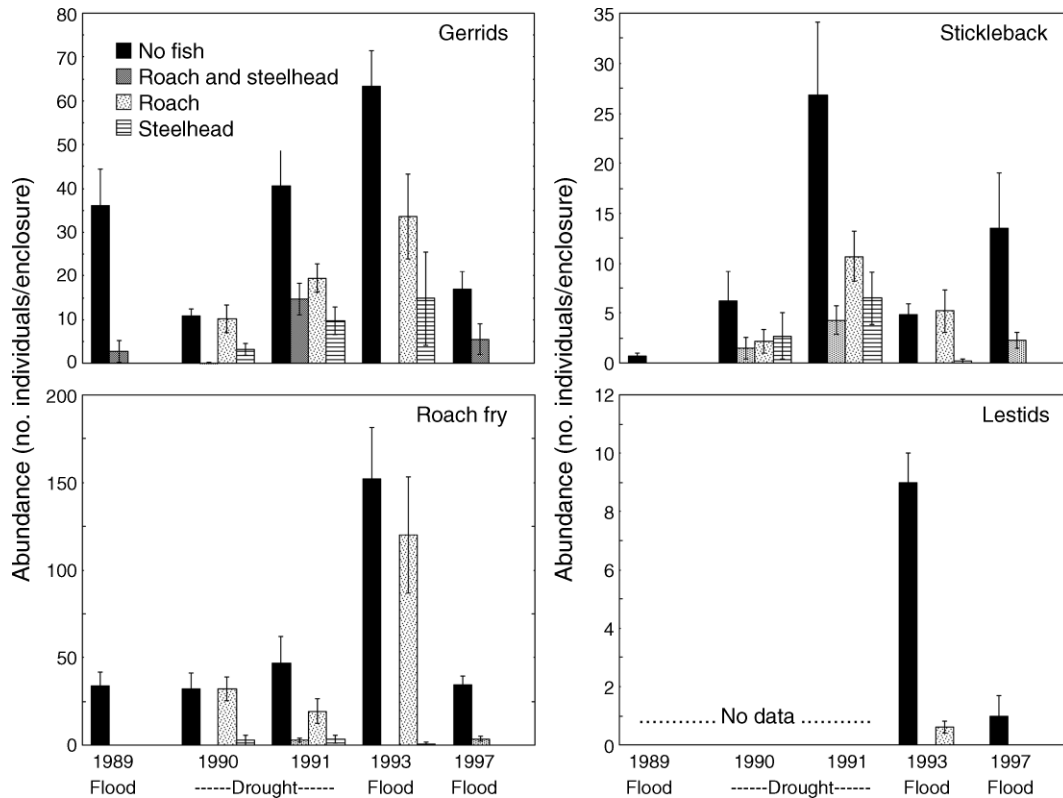FIG. 11.   Effect of fish on small predators sampled in benthic cores (mean + 1 SE) over the five experiments.

Fig. 12. Effect of fish treatments on the abundance of small water-column (roach and stickleback fry), surface-dwelling (gerrids), and turf-clinging (lestids) predators counted in situ at the end of five experiments (mean ± 2 SE). Lestids perched on *Cladophora* in the water column were only counted in 1993 and 1997. Otherwise, missing bars indicate that the taxon was absent.

relative importance of hydrologically mediated changes in nutrient vs. grazer control over algae remains to be quantitatively evaluated in the South Fork Eel River. Filamentous green algae and many diatoms tend to be nitrogen limited in this system (Hill and Knight 1988, Power 1991). In an experiment repeated during two drought years (1991, 1992) and one post-flood year (1993), however, Marks et al. (2000) found that nutrient enrichment consistently increased algal accrual by about the same amount. On unenriched control substrates, *Cladophora* biomass was not larger in 1993 than during the two drought years (Fig. 2 in Marks et al. 2000), as might have been expected if nutrients were less limiting during a post-flood summer.

In contrast to weak drought impacts, post-flood impacts of fish on lower benthic trophic levels were generally strong but variable, depending on the predator-specific vulnerabilities of the grazers capable of suppressing algae during a given year. The dominant algivore in the post-flood summer of 1989 was the tuft-weaving midge, *Pseudochironomus richardsoni*. In its retreat woven into *Cladophora*, this midge was not subject to roach or steelhead predation, but was vulnerable to small predators (odonate nymphs and young-of-the-year fish fry) that were in turn suppressed

by adult roach and juvenile steelhead (Power et al. 1992). Under these conditions, larger fish exerted a four-level, adverse effect on algae by removing the small predators capable of suppressing *Pseudochironomus* (Fig. 14, Power 1990b).

In 1993, steelhead appeared to exert a three-level positive effect, and large roach a two-level, direct negative effect, on diatom blooms in enclosures (Fig. 14). Cloud-like blooms of diatoms (dominated by *Melosira* and *Cymbella*) filled much of the water column in all five steelhead enclosures in 1993. Positive effects of steelhead on these diatoms may have been adverse for *Cladophora*, as dense epiphytes, shade, compete for nutrients, and possibly directly injure their host (Stevenson and Stoermer 1982, Dodds 1991).

A marked recruitment failure of *Pseudochironomus* in 1993 followed the latest spate to occur during the 18-year study, which exported floating algal mats important for *Pseudochironomus* oviposition and rearing (Power 1990a). The absence of *Pseudochironomus* (whose guts contain largely diatoms [Power 1991]) may have released epiphytic diatoms to bloom in 1993. The complete absence of visible blooms in the 1993 roach treatments strongly suggested that adult roach fed directly on these diatoms, which are higher in food quality than
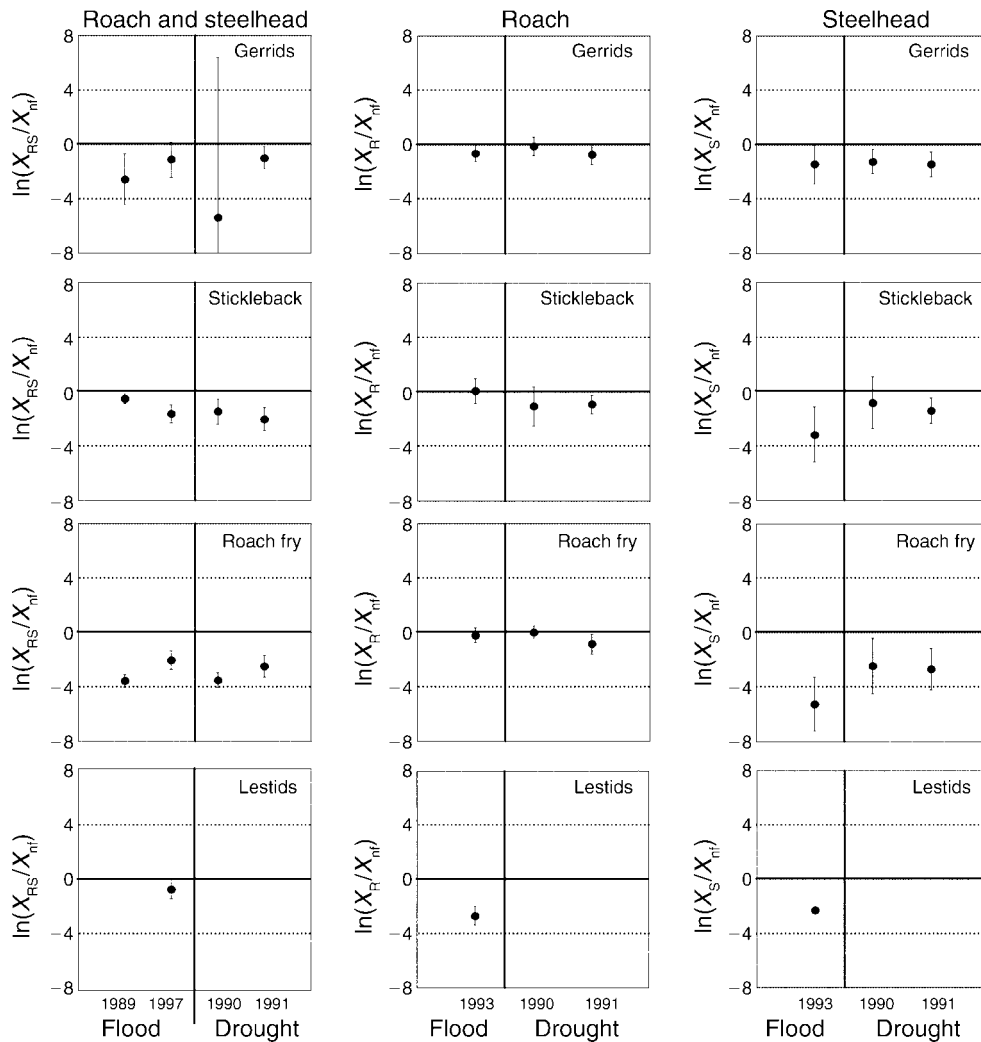
FIG. 13. Effect sizes (response ratios [Hedges et al. 1999]) of fish on taxa in the water column on the final sampling date for experiments during flood (1989, 1993, and 1997) and drought (1990, 1991) years, with 95% confidence intervals. Interactions are considered strong if confidence intervals do not cross zero.

Cladophora filaments (Boyd 1973, Dodds 1991, Kupferberg et al. 1994). Roach fry also consume some diatoms, and could swim through 3-mm mesh to colonize enclosures, but only persisted in the absence of steelhead. In exclosures without adult roach, roach fry may have reduced but did not eliminate diatom blooms.

The major invertebrate algivores in the 1993 summer food web were mayflies and free-living chironomids. Roach and steelhead had positive effects on mayflies (Fig. 6), despite feeding on them (Power et al. 1992). Positive effects of fish on mayflies may have been the indirect consequence of fish suppression of invertebrate predators, which were more abundant and probably more active (McPeek 1990) in the absence of the larger fish. In 1993, odonates were extremely dense in exclosures. Marks et al. (2000) observed high odonate densities elsewhere in the open river during this summer.

They hypothesized that odonate production was increased in 1993 by late June rains that maintained off river pools, where odonate nymphs have refuge from fish.

In the post-flood summer of 1997, roach and steelhead together had significant negative effects on algae, as in 1989. Midges including *Pseudochironomus* did not recruit in large numbers to enclosures in 1997, and mayflies were also rare. Small benthic predators were extremely abundant at the onset of the 1997 experiments in both treatments (Fig. 11), which may have accounted for low initial mayfly and midge abundance. The grazer guild in 1997 was dominated by *Gumaga nigricula*. Because *Gumaga* recruits from distinctive egg cases lain and hatched during summer (Resh et al. 1997), late summer larval abundance is decoupled from the flood regime of the previous winter (C. McNeely, *personal*
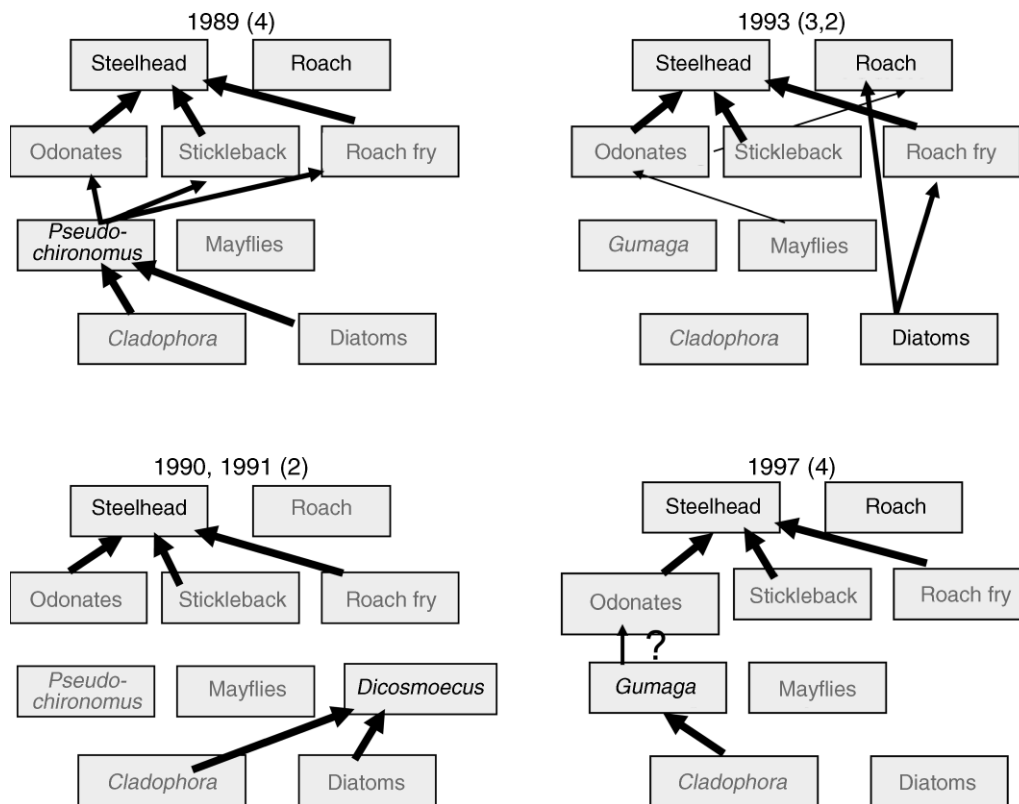
Fig. 14. Simplified diagrams representing inferences about food web interactions based on experimental results during three flood years (1989, 1993, 1997) and two drought years (1990, 1991). Numbers in parentheses refer to the number of strongly linked trophic levels connecting algal biomass to consumers in a given year. Web members that were strong interactors during a given year are shown in black type, with suppressed populations in gray type. Thick arrows depict strong interactions; thin arrows depict interactions that are weak in the presence of large roach and steelhead but become influential in their absence. In 1989, steelhead and roach suppressed a guild of smaller predators, releasing the algivorous midge *Pseudochironomus*, which suppressed both *Cladophora* and its epiphytic diatoms. In 1990 and 1991, large fish, particularly steelhead, suppressed water-column prey but had no effect on benthic fauna or flora. *Cladophora*, its epiphytes, and associated fauna were suppressed by grazing by the predator-resistant armored caddisfly, *Dicosmoecus*, which was abundant after winters lacking flood scour. In 1993, when the initial *Cladophora* bloom was exported by an unseasonably late (June) spate, steelhead and roach had no impact on *Cladophora*, but steelhead released and roach suppressed large blooms of diatoms initiated epiphytically on *Cladophora*. Roach fry were likely intermediaries mediating the three-level effect of steelhead on epiphytic diatoms this year. In 1997, steelhead and roach together had four-level adverse effects on *Cladophora* and its epiphytes, possibly mediated through a behavioral trophic cascade in which odonate predators suppressed the grazing caddisfly *Gumaga*.

communication). Fish had no significant impact on *Gumaga* densities. We hypothesize that adverse fish effects on *Cladophora* in 1997 may have been mediated by a behavioral trophic cascade (e.g., Beckerman et al. 1997). When disturbed by predators, *Gumaga* tend to withdraw into their cases and drop from grazing boulder and bedrock substrates on to the underlying gravel, where they often burrow under fine sediments (Bergey and Resh 1994; C. McNeely, *personal observations* in the South Fork Eel River). Such behavior would greatly reduce time spent grazing. On two occasions, however, we have seen *Gumaga* larvae being squeezed from their cases and consumed by burrowing (gomphid) dragonfly nymphs. If interference by invertebrate predators reduced *Gumaga* grazing rates, this nonlethal effect could account for the persistence of the higher algal biomass in fish exclosures, where invertebrate predators

were reduced (Fig. 14). Other hypotheses for fish effects on algae at the end of the 1997 experiments include suppression by small predators of an important algivore that we did not sample; or that in 1997, (unlike 1991, 1990, and 1993), roach grazing reduced attached *Cladophora*. We consider these hypotheses unlikely. A third possibility is that because a rainy spring kept flows turbid into late May 1997, *Cladophora* filaments were weakened by light starvation, and sloughed off rocks during incidental benthic feeding by roach and steelhead.

In summary, our observations and experiments support the view that year-to-year variation in the accrual and persistence of algae through the summer growing season are related to hydrologically-mediated food chain effects. Large algal blooms are more likely to follow winters with peak flows with recurrence intervals

PLATE 1.   (Left) Summer low flow in the South Fork Eel River in the Angelo Coast Range Reserve, California, USA, looking upstream to a typical shallow pool just upstream from a winter active cobble bar. This bar would be submersed under 1–2 m of water and mobilized during a scouring flood. A grove of riparian white alders (*Alnus rhombifolia*) line the channel bank just upstream and across from the cobble bar. (Right) View looking upstream during the early stage of a winter flood, which is still ~1 m below estimated bankfull depth. Debris from a previous flood caught in the leafless white alder tree in the center of the photograph is ~1.5 m above the present water surface. Photo credits: (left) Steve Glass, steve@glassphotography.com; (right) M. Power.

longer than 1.5 years, which reduce densities of predator-resistant grazers like the caddisfly *Dicosmoecus* or sessile taxa like the aquatic moth, *Petrophila* spp. Scouring floods provided algae with a window of time during which there was only one "functional" trophic level (producers) in the spring food web, before densities of consumers built up over the summer due to both recruitment and shrinking habitat. The threshold nature of this relationship (Fig. 4) suggests that bankfull discharge imposes mortality, rather than short distance transport, on *Dicosmoecus*. During smaller winter and early spring flow pulses, early instar *Dicosmoecus* (I–III) with buoyant litter cases could be lifted from tributaries and deposited alive downstream in the mainstem reach we studied. The ontogenetic transition from buoyant litter cases (which could serve as life jackets during spates) to heavy stone cases (useful as ballast while grazing epilithic algae under low stable flow) could be interpreted as an adaptation by these caddisflies to the predictable seasonality of Mediterranean river discharge.

Conclusions drawn from a relatively short, 18-year record must remain tentative, but are reinforced by comparable observations in other river drainages in the region (Power 1992, Wootton et al. 1996, Parker et al. 2002). During drought (or in rivers where artificial flow regulation [Power 1992] or sediment starvation [Parker et al. 2002] prevent scour), predator-resistant grazers suppress algae (Fig. 14). In rivers outside the biogeographic range of *Dicosmoecus*, defended sessile grazers (e.g., *Petrophila* spp.) abound in channels where flow-regulating dams or diversions prevent flood scour (Power 1992). Like *Dicosmoecus*, sessile grazers are severely limited by flood scour. If changes in management or climate in Northern California increase the frequency of river bed scour, large algal blooms should occur more frequently. In addition, more of this algal production should be channeled up food chains through edible grazers to support predators like juvenile salmonids. Conversely, land use or climate change that reduces the probability of flood scour during winter should weaken both energy flow through webs to fish, and fish impacts on lower trophic levels.

CONCLUSIONS

Colwell (1984) likened the idea that communities recovering from disturbance should re-assemble in a predictable fashion to the assumption that carefully following a recipe for curry will produce consistent results. He pointed out that even a curry in a cooking pot will vary from realization to realization depending on differences in the quality or quantity of the ingredients, the order in which they are added, and how well-mixed they are during simmering. Winter floods in Mediterranean rivers are more predictable than many other disturbances that reset natural communities. Nevertheless, the repeated realizations of food webs that reassembled during the subsequent summer low flow season differed in structure and function from year to year. "Differences in ingredients" (taxa dominating the algal grazing guild) account for the major differences between post-flood and post-drought food webs. In summers following flood-free winters, predator-resistant grazers survive in large numbers. In post-flood summers, early successional grazers that are vulnerable to predators dominate during the late spring, early summer period of peak algal accrual. Differences in the primary consumer "ingredients" among post-flood summers also appear to determine whether fish effects on algae are positive (if fish suppress all important algivores) or negative (if fish release algivores they do not control from small predators, which could otherwise limit these grazers). These three- vs. four-level food chain effects depend in part on traits (predator specific vulnerabilities) determined by morphology and behavior of algivores that dominate during a given realization of a

food web. Our inability to predict fish impacts on algae in during a given flood year is due in large part to our inability to forecast which taxa will dominate the invertebrate primary consumer guild.

Food webs in which dominant primary consumers are aquatic invertebrates may be more unpredictable than river food webs in which grazing fishes fill this role. Aquatic insects with complex life histories are subject to a wide range of potential limiting factors operating over the terrestrial or aerial habitat of adults, as well as in the aquatic habitats of larvae. Detecting brief events that may limit the annual recruitment of aquatic insects is extremely challenging. Not only are the populations in "the curry" not well-mixed, but some life stages are outside the cooking pot where we have focused our attention! Vertebrate grazers that spend their lives in river reaches of several km (e.g., armored catfish in Panama, or grazing minnows in Oklahoma) are more easily observed throughout their life histories than are insects with winged adults. Grazing fishes, because of their large body size, are also better able to average over periods of resource deprivation or unfavorable conditions. When their movements are unrestricted by predators, grazing fishes can track and dampen out the biomass consequences of spatial variation in primary productivity (Power 1983, 1984) that occurs over many scales in rivers and streams (Biggs 1995, Stevenson et al. 1996).

Impacts of vertebrate predators (fish, salamanders) may also be more consistent over variable contexts and therefore more predictable than impacts of invertebrate predators. Individual voracity of predatory fish can dampen density related variation in their impacts. In pools of a prairie margin stream, green algae were similarly protected from grazing by bass over a wide range of densities, because just one bass was sufficient to eliminate grazing minnows from pools (Power and Matthews 1983, Power et al. 1985). In the South Fork Eel experiments reported here, roach and steelhead together were stocked at 10 individuals/m² in 1989, but at 3.3 individuals/m² in all subsequent years. Few density-related effects were detected, despite this three-fold reduction in stocking density. One possible transient response to density was that in 1989, fish suppressed small caddisflies in the middle but not final sampling period of the experiment. This suppression was not detected with lower fish stocking densities in 1997. In general, we suggest that compensatory voracity of individual fish can damp out density-related variation in collective predator impacts on preferred prey, while density dependence may be more manifest when less preferred prey are consumed by fish in crowded, more food limited, conditions.

During the five field experiments, there was the potential to confound spatial heterogeneity with year-to-year variability. Algal accrual during a given summer was patchy, and varied with substrate stability as well as spatial heterogeneity in irradiation and nutrient loading.

As in other systems (Grimm and Fisher 1984, Stewart 1987), nutrient effects on algae are conspicuous where preferential hydrologic flow paths from the watershed enter the river channel as seeps or springs. We chose enclosure installation sites to block for this spatial heterogeneity, so that different treatments began the experiment with similar algal biomass. Initial spatial variability in key invertebrate taxa could not be detected, however, and seemed important for *Gumaga* in the 1997 experiments.

Despite these many challenges to predicting how temporal (hydrologic) context will modulate fish impacts on algae in the South Fork Eel River, our study supports some general ideas about how food chains should change over the course of succession. Life history tradeoffs tend to make early successional organisms (or life stages) more edible (Grime et al. 1968, Cates and Orians 1975, Elger et al. 2004). Therefore, in systems in which lower trophic levels are less mobile, hence less able to evade mortality due to local disturbance, disturbance can lengthen food chains by increasing the proportion of early successional edible prey (Power et al. 1996a, Wootton et al. 1996). Energy flow to predators should increase at intermediate stages of recovery from disturbance, as should predator impacts on primary producer biomass ("trophic cascades"). Whether predators will have positive or negative effects on producers depends on the lengths of the stronger "chains" in food webs. These path lengths depend on traits of dominant intermediate consumers during a given realization of community reassembly, and may remain difficult to anticipate.

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APPENDIX A

Hydrologic monitoring (*Ecological Archives* M078-009-A1).

APPENDIX B

Enclosure specifications (*Ecological Archives* M078-009-A2).

APPENDIX C

Methods for core sampling (*Ecological Archives* M078-009-A3).