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HYDROLOGIC INFLUENCES, DISTURBANCE, AND INTRASPECIFIC COMPETITION IN A STREAM CADDISFLY POPULATION[1]

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Abstract. In an earlier study, exploitative intraspecific competition was demonstrated for middle instars of the caddisfly *Helicopsyche borealis* in Big Sulphur Creek, a stream in northern coastal California. This population is univoltine with early instars first appearing in June, growing into late instars the following spring, and emerging as adults in May. Competition occurs during the summer dry season (June–September), a period of low-flow conditions without storms or increases in stream discharge. Beginning in autumn, however, larval densities decline because of wet-season storms and high discharge. Using multiple regression, we found a strong relationship between spring (i.e., post wet season) density of late-instar *H. borealis* and various hydrologic parameters of the preceding wet season over a 4-yr period, 1985–1988. Of eight hydrologic parameters used as indices of disturbance, total wet-season rainfall and peak discharge together accounted for 42% ($P < .0001$) of the variation in *H. borealis* density. In contrast, densities of middle instars of the next generation in summer were unrelated either to the preceding wet-season hydrologic regime or late-instar densities of the previous generation.

Field experiments conducted in enclosures using larval densities of *H. borealis* that corresponded to harsh, moderate, and mild wet-season hydrologic regimes (low, intermediate, and high densities, respectively) indicated that: (1) increases in larval density had a strong negative effect on algal biomass (as chlorophyll *a*); (2) larval density was negatively correlated with the proportion of larvae that pupated, and with pupal size; and (3) the high density (mild hydrologic regime) treatment produced smaller adult males and females, and lower fecundities than intermediate and low densities (moderate and harsh regimes, respectively). In most years, storms and associated disturbance reduce late-instar *H. borealis* density below levels of larval competition; this counteracts earlier competition among middle instars that occurs during low-flow conditions. In drought years, however, densities may not be reduced as severely by wet-season storms and competition may continue until emergence. In this case, competition can reduce individual fitness, but because of high adult densities during these mild-disturbance conditions the reproductive capacity of the population is unaffected.

Key words: annual variability; aquatic insect; caddisfly; disturbance; Helicopsyche borealis; *hydrologic influences; intraspecific competition; stream.*

INTRODUCTION

The consequences of hydrologic disturbances to aquatic benthic communities have been well documented (see reviews by Fisher 1983, Sousa 1984, 1985, Resh et al. 1988). In marine systems, disruption of habitats during storms can occur directly from wave shock (Sousa 1979, Paine and Levin 1981, Dayton and Tegner 1984) and indirectly from battering by waterborne objects (Dayton 1971), in which organisms can be buried under sediments (Taylor and Littler 1982) or physically abraded from their substrata (Lubchenco 1986, Witman 1987). In freshwater stream systems, physical disturbance from storm-related flooding can

have similar negative effects on benthic communities. Scouring by high discharge disrupts benthic habitats (Allen 1951, Thorup 1970, Scullion and Stinton 1983, Gurtz et al. 1988), which can dislodge and kill stream organisms (Anderson and Lehmkuhl 1968, Sagar 1986). Catastrophic reductions in abundances of fishes (e.g., Hanson and Waters 1974, Erman et al. 1988), algae (e.g., Tett et al. 1978, Power and Stewart 1987), and invertebrates (e.g., Siegfried and Knight 1977, Fisher et al. 1982, Molles 1985, McElravy et al. 1989) as a result of storm-related disturbance in streams have been reported.

In addition to their catastrophic, short-term effects on abundances of benthic organisms, such disturbances can open previously occupied space for colonization and recruitment, and potentially can increase food availability by reducing densities of consumers. In situations where populations reach densities that deplete resources and form competitive hierarchies (e.g., Menge

1976, Hart 1985), disturbance can interrupt succession toward competitive monopoly (Lubchenco 1978, Sousa 1979, McAuliffe 1984*a*) and can promote coexistence both within and among populations (Paine 1966, 1979, Dayton 1971, Hemphill and Cooper 1983). Thus, when disturbances are intense or frequent, the influence of biotic interactions on natural communities can be reduced (Wiens 1977, Connell 1978, Reice 1985, Menge and Sutherland 1987).

In a recent study, Lamberti et al. (1987) documented strong intraspecific competition within a population of the algivorous caddisfly *Helicopsyche borealis.* Competition occurred among middle instars that reach high densities and deplete their periphyton food under low-flow conditions during summer through early autumn. Following this period, storms and floods occur during the wet season (October–March) and densities of late instars, present in the spring, can be greatly reduced (Resh et al. 1984). In this paper, we report the results of field observations and experiments conducted in Big Sulphur Creek over a 4-yr period that were designed to (1) examine the relationship between wet-season hydrologic disturbance and subsequent density of late-instar *H. borealis* and (2) assess the impact of competition on this population under different hydrologic disturbance regimes.

MATERIALS AND METHODS

Biology of Helicopsyche borealis

Helicopsyche borealis is a mobile, cased caddisfly (Trichoptera: Helicopsychidae) whose principal food is periphyton, which consists mostly of diatoms that occur on cobble and boulder surfaces in pools of moderate current velocity ($\approx$3–12 cm/s). Eggs are laid in May, and early instars first appear in June; these grow through the summer and autumn, and then overwinter as quiescent middle instars. Larvae resume feeding and grow to late instars in spring, and emerge as adults in May (Resh et al. 1984). Because middle instars overwinter in the stream they are potentially vulnerable to physical disturbance from floods associated with the wet season (October through March), when most (>90%) precipitation occurs and stream discharge is highest (Hill and Knight 1987, McElravy et al. 1989). Further details on the life history of this population are described in Resh et al. (1984) and Lamberti et al. (1987).

Study area

The study was conducted in a second-order segment of Big Sulphur Creek (38°47' N, 122°47' W, Sonoma County, USA), a permanent tributary of the Russian River in coastal northern California. Three pools (range: 30 m long, 4–5 m wide) containing a mixture of sand, gravel, and cobbles were used to estimate *H. borealis* density, and a single sunlit pool (20 m long, 4–5 m wide, 40% canopy cover, measured with a spherical

densiometer, Lemmon 1957), which had substrata that were similar to three survey pools, was used to conduct all in situ experiments. The stream is bordered by white alder (*Alnus rhombifolia* Nutt.), oaks (*Quercus* spp.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), California bay laurel (*Umbellaria californica* Nutt.), and sedge (*Carex* sp.). Further details of the study area are given by Lamberti and Resh (1983), Lamberti et al. (1987), and Resh et al. (1990).

Helicopsyche borealis *population census*

Multiyear censuses of *H. borealis* larval densities were made for (1) middle instars during the summer low-flow period from 1984 to 1988 and (2) late instars during spring following the wet season from 1985 to 1988. Densities were estimated in each pool by counting larvae on the stream bottom both on periphyton-covered natural substrata (cobble, boulder, or bedrock) and on unglazed red clay tiles (7.6 × 7.6 cm) that were conditioned with periphyton on the stream bottom for at least 2 wk. These tiles have been shown to accrue periphyton and invertebrate assemblages that are similar to those of natural stream substrata (Lamberti and Resh 1985). Census was made once each year for middle instars (during early-to-mid August 1984–1988) and for late instars (during late March to early April 1986–1988) except in 1985, when late instar counts were made twice, both before (23 March) and after (15 April) a late winter storm (25–27 March).

Hydrologic parameters

Eight physical parameters were chosen to represent hydrologic conditions in Big Sulphur Creek during the wet season. Hydrologic parameters were based on records from a United States Geological Survey (USGS) gauging station (for stream discharge) and a National Oceanographic and Atmospheric Administration (NOAA) station (for rainfall, using hourly precipitation data, and climatological data). Both stations were located at Big Sulphur Creek $\approx$3.2 km downstream from the study site.

Mean daily discharge data from USGS records were converted to peak daily discharges, a more precise indicator of disturbance of benthic habitats, by applying a correction factor of 2.4. This correction was based on empirically derived relationships between known USGS peak and mean daily discharges in Big Sulphur Creek during the wet season over a 3-yr period (1980–1983; E. McElravy, *personal communication*). Missing rainfall data were estimated using the normal-ratio method (Gilman 1964) from three nearby NOAA climatological stations that surround the Big Sulphur Creek site: Clearlake Highlands (15 km northeast), Cloverdale (22.6 km west), and Middletown (16.4 km east).

For the analysis of hydrologic influence on *H. borealis* density, we arbitrarily defined that a disturbance episode (hereafter referred to as a "storm") occurred when peak discharge at the study site exceeded 2.03

m³/s, ≈135 times that of summer baseflow levels (0.015 m³/s). This criterion was based on field observations in which a single storm (on 25–27 March 1985) of that magnitude reduced larval abundance by ≈50% (from 23.8 individuals/100 cm² on 23 March to 12.5/100 cm² on 15 April). Although it is possible that storms of lower intensity also may have significantly reduced larval density, our threshold should represent a conservative estimate of disturbance to this population. For example, this value was considerably less than the shear stress necessary to move the median stream particle in our study pools (e.g., 6.78 m³/s to move <2 mm particles), which was used previously as a threshold of hydrologic disturbance to benthic invertebrates in Big Sulphur Creek (McElravy et al. 1989).

Statistical analysis of field observations

The relationship between late-instar *H. borealis* density and hydrologic parameters was examined using two types of linear regression analyses. First, individual relationships between hydrologic parameters and $\log(X_i + 1)$-transformed *H. borealis* density was assessed using simple Pearson product–moment correlation (Zar 1974). Second, to assess the relative contribution of each hydrologic parameter to variation in *H. borealis* density, parameters that showed a significant relationship ($P < .01$) with density were analyzed together using stepwise multiple regression (PROC STEPWISE/MAXR program, SAS 1985). This method, unlike more conventional stepwise regression programs, identifies the "best" one-factor model, the "best" two-factor model, and so on, based on increases in r^2 (SAS 1985).

Field experiments

To examine the effects of the different post wet-season densities of late-instar *H. borealis,* we used in situ enclosures similar to those described in Lamberti et al. (1987) to confine larvae. Enclosures (area = 175 cm²) were modified polyethylene food containers that were screened (1-mm mesh) on two opposite sides to allow water exchange; enclosures were fitted with styrofoam collars, which were held in the stream by floating racks. Each enclosure contained a layer of fine sand that could be used by caddisfly larvae as case-building material, a tile conditioned with periphyton (i.e., tiles incubated in Big Sulphur Creek for 2 wk in the absence of grazers), and known densities of *H. borealis* larvae. When in place, the enclosure sides extended 3 cm above the water surface, which prevented the aquatic larvae from emigrating out of enclosures. Similar to methods described by Lamberti et al. (1987), we used both submersed plastic and tile surfaces (both of which accrued similar algal biomass) as the total grazeable area for *H. borealis* density calculations. Screens on each enclosure were brushed clean in place every 5–7 d to remove accumulated organic matter that would decrease water exchange.

Experiments were conducted in three successive years (1985–1987), with each experiment being designed to examine different density responses of *H. borealis* (Table 1). In the 1st yr experiment (1985, experiment 1: larval mortality), larvae were allowed to graze freely within enclosures (14 d) until the first sign of pupation, then larvae were removed, preserved in 5% formalin, and later examined to determine larval mortality.

Food abundance (as algal biomass) in experiment 1 was determined by measuring the chlorophyll *a* content of scraped periphyton samples taken from the tile surface of each replicate, condensed onto a Whatman GF/C filter (pore size 0.45 μm) using a Buechner funnel. Chlorophyll *a* was determined in the laboratory according to the methods described by Feminella (1990). Earlier studies in this stream (Lamberti et al. 1987, Feminella et al. 1989) have indicated that chlorophyll *a* is a reliable indicator of epilithic periphyton biomass, which constitutes the actual diet of most grazing invertebrates, including *H. borealis.*

The 2nd yr experiment (1986, experiment 2: pupal size and development) ended when adults were first observed (23 d); at this time all individuals, most of which were pupae, were preserved. Larvae were considered to have transformed to pupae after the larval cuticle had separated from the pupal epidermis (sensu Wiggins 1977). Pupae were extracted from their cases under a dissecting microscope, and measured by vacuum-drying (at 105°C for 24 h) and weighing batches of individuals. Mean individual pupal dry mass was then determined by dividing batch mass by the number of individuals in each replicate.

The 3rd yr experiment (1987, experiment 3: adult size and fecundity) ended after most larvae had pupated (12 d); at this time all individuals were transferred to the laboratory, and reared to adults in screened-topped polystyrene containers that were filled with aerated stream water (61 × 30 × 30 cm). Separate containers held all individuals of a given treatment density. Emerged adults were collected every 2–3 d, to ensure adequate time for mating and for females to oviposit their gelatinous egg masses. At this time, adult and egg masses were preserved in 5% formalin.

Body mass of adult females could vary by as much as 50% depending on whether or not they had released their egg mass, and thus would not be an accurate index of adult size. Instead, size estimates were made by measuring the length of the right forewing, from the jugal fold to the wingtip, using an ocular micrometer. The reliability of wing length as a predictor of adult mass was tested by regressing individual male wing length against male dry mass, which was measured with a Mettler microbalance. Fecundity was determined by counting eggs within each oviposited mass. To ensure that all eggs were recovered from females still withholding their eggs, the entire egg mass was removed under a dissecting microscope. Because this caddisfly is semelparous (J. W. Feminella and J. K. Jackson, *personal observations*), number of eggs per egg mass is

TABLE 1. Summary of experimental conditions used to examine the effect of density on late-instar *Helicopsyche borealis* in Big Sulphur Creek. N = number of enclosures.

Year	Experi- ment	Inclusive dates	Life stage examined	Treatment density (no./100 cm²)	Life history features examined
1985	1	15–29 Apr	Larvae	3, 11, 23, 46 (all N = 5)	Mortality
1986	2	14 Apr–7 May	Pupae	14, 26, 51 (all N = 5)	Rate of development, size
1987	3	24 Apr–30 May	Adults Eggs	14 (N = 6), 26 (N = 6), 51 (N = 5)	Adult size, fecundity

a reliable estimate of lifetime individual reproductive effort.

Densities of *H. borealis* used in all enclosure experiments (Table 1) were based on the range of natural larval densities estimated in Big Sulphur Creek after the wet season of 1985 (after 31 March). Treatment densities in enclosures were interspersed and apportioned to cells within racks either in a randomized block (experiment 1) or a completely randomized design (experiments 2 and 3). Larvae used in all experiments were collected from Big Sulphur Creek and then added to enclosures on the day each experiment began; approximately similar sized larvae were used across experiments (i.e., 0.83, 1.13, and 0.78 mg mean individual dry mass for experiments 1–3, respectively). Additional stream collections of pupae were made in 1986 and 1987, in which batches of pupae (N = 3, ranging from 16 to 43 pupae per batch) were dried and weighed, and were used as uncaged controls for comparison with pupal mass obtained from enclosure experiments.

Statistical analysis of field experiments

Response of the algal food source to grazing by *H. borealis* larvae in experiment 1 was analyzed by regressing algal biomass (as chlorophyll *a*) present at the end of the experiment against initial larval density. Responses of *H. borealis* larval mortality, pupal dry mass, and pupal development time in experiments 1 and 2 were analyzed by regressing these parameters against density of individuals present at the end of each

experiment. To stabilize variance and normalize data, dependent variables for experiments 1 and 2 were transformed using arcsine (i.e., for proportional larval mortality and pupal development data) or log(X_i + 1) (i.e., for arithmetic pupal dry mass data) before analyses were done. In experiment 3, because replicates of a given density level were pooled (cf. experiments 1 and 2), density was treated as a discrete, rather than a continuous, independent variable with three levels: low (14), intermediate (26), and high (51 larvae/100 cm²). Therefore, for this experiment, density effects on adult male and female size (as wing length) and female fecundity (as number of eggs per female) were analyzed with a nonparametric Kruskal-Wallis test on the ranked data and, if significant between-group differences were found, further analyzed with a Student-Newman-Keuls (SNK) a posteriori multiple-range test on ranks.

RESULTS

Wet-season hydrologic regimes and density of Helicopsyche borealis

During the study, hydrologic conditions showed substantial year-to-year variation (Table 2). Wet-season rainfall (25-yr mean ± SD: 145 ± 38.3 cm/yr) was moderate in all years except 1986, a year when storms were most numerous and intense, and mean discharge during storms, peak discharge, and total discharge were higher than all other years (Table 2).

Densities of middle-instar *H. borealis* during August low-flow conditions showed little variation from 1984

TABLE 2. Summary of hydrologic regimes in Big Sulphur Creek, 1985–1988.

Feature	Discharge year*				
	1985a	1985b	1986	1987	1988
Total precipitation (cm)	99	106	155	77	106
Number of storms†	3	4	6	5	4
Number of storm days‡	6	7	33	9	15
Storm average discharge (m³/s)	4.2	3.9	8.7	4.8	4.8
Peak wet-season discharge (m³/s)	23.2	23.2	72.3	25.0	23.5
Total wet-season discharge (10⁶ m³)	5.4	6.0	26.8	6.5	10.4
Average time between storms (d)	42.5	44	16	16.5	11
Maximum time between storms (d)	72	72	44	40	20

* Years refer to previous wet season (October–March). For example, the 1985 wet season includes October–December 1984 and January–March 1985. 1985a = 1985 wet season up to but not including a late-winter storm of 25–27 March; 1985b = 1985 period including the 25–27 March storm.
† Number of episodes in which stream discharge exceeded 2.03 m³/s.
‡ Number of days on which stream discharge exceeded 2.03 m³/s.

TABLE 3. Annual density estimates of *Helicopsyche borealis* in Big Sulphur Creek. Estimates were made in early- to mid-August of each year for middle instars and late-March to early-April for late instars; the 1984 densities of middle instars were taken from Lamberti et al. (1987).

A. Middle instars during summer low-flow conditions

	Year				
	1984	1985	1986	1987	1988
	Densities (no. individuals/100 cm²)				
Mean	88.3	76.6	74.3	81.4	70.7
SD	21.3	42.8	21.4	20.9	17.9
N	20	34	20	18	20

B. Late instars during spring

	Year*				
	1985a	1985b	1986	1987	1988
	Densities (no. individuals/100 cm²)				
Mean	23.8	12.5	12.4	34.1	15.0
SD	8.6	5.7	8.7	14.2	7.7
N	23	30	25	36	27

* 1985a = 1985 wet season up to but not including a late-winter storm of 25–27 March; 1985b = 1985 period including the 25–27 March storm.

to 1988 (Table 3A). Mean densities were not significantly different between years ($F = 1.59$, df = 4, 107, $P = .183$, log-transformation and ANOVA). Unlike middle instars, densities of late-instar *H. borealis* during spring (March–April) showed highly significant differences among years ($F = 34.8$, df = 3, 114, $P < .0001$, log-transformation and ANOVA; Table 3B). Between-year comparisons after the wet season of late instars indicated that densities were ≤15 individuals/100 cm² in all years except 1987, a dry year that had the lowest rainfall, and second lowest number of storm days and peak discharge (Table 2). There was no correlation between mean late-instar *H. borealis* density in spring and middle-instar densities of the next generation present the following summer ($r^2 = 0.02$, df = 90, $P = .203$, using log-transformed larval density).

Analysis of the relationship between density of late-instar *H. borealis* present in spring ($N = 141$ density estimates over the 4-yr study) and previous wet-season hydrologic parameters indicated strong negative ($P < .001$) relationships between density and all parameters except mean and maximum time between storms, and number of storms (Table 4). Inclusion of the five statistically significant parameters that related to density in a multiple regression analysis indicated that a highly significant amount of the variation in *H. borealis* density (47%) was explained ($F = 29.8$, df = 4,135, $P < .0001$). However, inclusion of just two of these factors (rainfall and peak discharge) accounted for 42% of the total variation (Table 5). The best three-factor model, including the number of storm days, mean discharge during storms, and peak discharge, increased r^2 to 0.469 (i.e., 47% of the total variation, Table 5). Stepwise inclusion of each factor into the regression model in both the two- and three-factor models significantly increased fit.

Densities used in enclosure experiments compared with field density estimates

Field census of late-instar *H. borealis* made over the 4-yr study indicated that the low-to-intermediate treatment densities (3–26 larvae/100 cm²) used in the enclosures, which were based on 1985 estimates, approximated the range of field densities in Big Sulphur Creek that occurred in years of differing hydrologic disturbance. Experimental densities corresponded to those field densities observed in years with slightly below-average and above-average rainfall and stream discharge (i.e., 1985, 1986, and 1988; Table 2).

During the study period, field densities of *H. borealis* late instars never reached levels used in the high-density treatments (46–51 larvae/100 cm²). However, projections of densities that would occur in extremely dry or drought years, based on the existing rainfall/density relationship from this study, indicate that densities may approach this level. For example, in an earlier 7-yr study (1977–1983) of benthic macroinvertebrates in Big Sulphur Creek, densities of *H. borealis* were >15 times as high in 1977, a drought year in which no significant storms occurred, as in each of the other 6 yr examined (E. P. McElravy et al. 1989, *personal communication*). By extrapolating to the rainfall levels of the 1977 wet season (i.e., 44.2 cm), we found that field densities (≈46 individuals/100 cm²) under these conditions would closely approximate those used in the high-density treatments (46–51 individuals/100 cm²).

TABLE 4. Results of simple linear regression of $\log(X_i + 1)$-transformed *Helicopsyche borealis* density against wet season hydrologic parameters in Big Sulphur Creek ($N = 141$ density estimates over the five time periods).

Parameter	r	Regression slope	P
Total precipitation	−0.546	-5.5×10^{-3}	.0001
Total wet-season discharge	−0.363	-1.5×10^{-5}	.0001
Number of storm days*	−0.351	-9.5×10^{-3}	.0001
Peak wet-season discharge	−0.306	-4.3×10^{-3}	.0002
Storm average discharge	−0.254	-1.7×10^{-2}	.0025
Maximum time between storms	−0.048	-6.1×10^{-4}	.583 NS
Average time between storms	−0.086	-1.6×10^{-3}	.310 NS
Number of storms†	0.073	2.0×10^{-2}	.391 NS

* Number of days on which stream discharge exceeded 2.03 m³/s.
† Number of episodes in which stream discharge exceeded 2.03 m³/s.

TABLE 5. Results of stepwise multiple regression between $\log(X_i + 1)$-transformed late-instar *Helicopsyche borealis* density and wet-season hydrologic factors. No further significant increase in r^2 was possible after three hydrologic factors were entered in the model; the full model ($k = 5$ independent variables) accounted for 47% of the variation in *H. borealis* density.

Hydrologic factor	Regression slope	P	Partial r^2	Cumulative r^2
Two-factor Model:				
Total precipitation	−0.011	.0001	0.298	0.298
Peak wet-season discharge	−0.127	.0001	0.121	0.419
Three-factor Model:				
Number of storm days*	−0.068	.0001	0.123	0.123
Storm average discharge	0.322	.0001	0.152	0.275
Peak wet-season discharge	−0.036	.0001	0.194	0.469

* Number of days on which stream discharge exceeded 2.03 m³/s.

Furthermore, in 1987, the driest year in the present study, the upper range of *H. borealis* field densities often was considerably >46 individuals/100 cm².

Effects of grazer density on algae

In experiment 1, algal biomass (as chlorophyll *a*) was inversely related to late-instar *H. borealis* density, with the highest standing crops occurring at the lowest larval densities (Fig. 1). The rate of decline in algal biomass was not linear across densities; a negative exponential regression model provided the best fit to the data. Filamentous green algae (mostly *Cladophora glomerata*) and sparse epilithic diatoms (*Achnanthes* sp., *Gomphonema* sp.) were present at intermediate and high larval densities; lush, diverse turfs of filamentous green algae and cyanobacteria, and epiphytic diatoms were present at low larval densities.

Effects of density on larvae and pupae

Larval mortality experiment. — Despite the short duration (2 wk) of experiment 1 (15–29 April), this interval marked the important prepupation growth period for late-instar *H. borealis*. Based on size estimates of individuals collected from Big Sulphur Creek, larvae more than doubled their size during this interval from 0.40 ± 0.02 mg (as mean individual dry mass) on 15 April to 0.83 ± 0.15 mg on 29 April ($\bar{X} \pm$ SD, $N = 3$
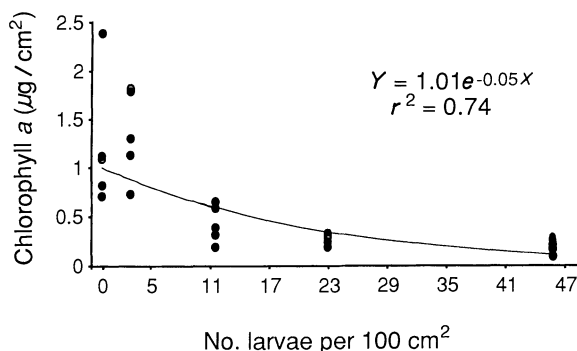

$$Y = 1.01e^{-0.05X}$$
$$r^2 = 0.74$$

FIG. 1. Relationship between algal biomass (as chlorophyll *a*) and density of larval *Helicopsyche borealis* in experiment 1. A negative exponential model provided the best least-squares fit to the data. The regression equation is based on $\log(X_i + 1)$-transformed chlorophyll *a* (*Y*-axis).

batches of 10–25 larvae per batch; see also Fig. 3A in Resh et al. 1984). Larval mortality in enclosures at the end of experiment 1 usually was low across all densities (mean mortality = 1.6% per enclosure), and in most (65%) enclosures all larvae survived the 2-wk experiment. There was no significant relationship between arcsine-transformed mortality and larval density (r = 0.36, $P > .05$).

Pupal development and size experiment. — Unlike larval mortality, development time for pupation and pupal size was strongly related to density of larval *H. borealis*. At the end of experiment 2, the proportion of larvae that pupated in enclosures was inversely related to density: proportions of individuals that had pupated were highest (average per replicate = 90%) for the low-density enclosures, lowest (65%) for those held at high densities, and intermediate (75%) for those at intermediate densities (Fig. 2A). Although we did not design our experiments to quantify the precise time to pupation or length of the final instar for each density, laboratory studies in 1987 indicated that numerous larvae (≈25%) persisted in high-density treatments for almost 3 wk after virtually all larvae had pupated in low- and intermediate-density treatments.

Size of pupae also was inversely correlated with density: the smallest pupae were always associated with highest treatment density (Fig. 2B). High within-treatment variation in pupal size at low and moderate densities may have resulted from uneven mixtures of male and female pupae in some replicates; this would cause the mean individual mass of some replicates to be lower than expected (i.e., those containing mostly males) while some others (i.e., those containing mostly females) would be higher. Mean individual pupal dry mass obtained for a given larval density in the enclosure experiment corresponded closely with pupal dry mass collected from the stream bottom during 1986 ($\bar{X} = 0.93$ mg), a wet year, and 1987 ($\bar{X} = 0.77$ mg), a dry year (Fig. 2B).

Effects of density on adults and female reproductive effort

Adult size experiment. — In experiment 3, a total of 67 males and 55 females were reared to adults; ap-
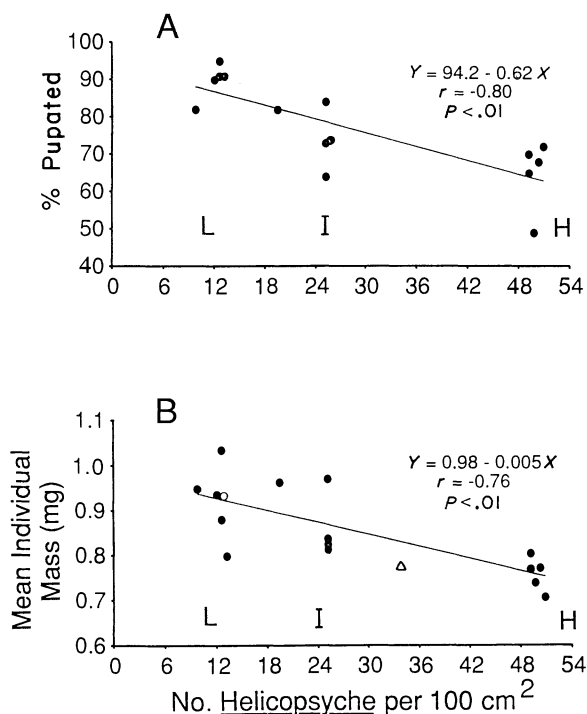
FIG. 2. Proportion of individuals that reached pupal stage (A) and size of pupae (B) as a function of *Helicopsyche borealis* larval density, in experiment 2. The correlation coefficients and P values for A are based on arcsine-transformed percent pupation data, and for B on $\log(X_i + 1)$-transformed mean individual pupal mass. Larval densities above the X-axis (L = low, I = intermediate, and H = high density) for both regressions were based on final densities of *H. borealis* in the enclosures at the end of the experiment. Mean individual dry mass of pupae from the stream bottom, used as uncaged controls, are plotted in graph B against larval densities estimated for 1986 (O), a wet year, and 1987 (△), a dry year.

proximately similar numbers of individuals of each sex emerged from each density treatment. For adult males of *H. borealis,* length of the forewing was found to be an effective predictor of dry mass. Linear regression analysis indicated a highly significant relationship between the two variables ($Y = 0.04X - 0.59$, $r = 0.88$, $P < .001$, $N = 35$).

Sizes of adult males and females, as indicated by wing length, both were influenced by larval density of *H. borealis* (males, $F = 24.4$, df $= 2, 64$; females, $F =$

53.2, df $= 2, 52$; $P < .0001$, one-way Kruskal-Wallis test). Males and females reared in the high-density enclosures were significantly smaller than those individuals reared in low and intermediate densities (males: $P < .01$, females: $P < .001$; SNK multiple-comparison test on ranks, Table 6).

Fecundity experiment. — A total of 36 egg masses were collected during experiment 3. Most (21) had been oviposited and were recovered from submersed objects in the rearing containers, whereas the remainder (15) were still partially attached to ovipositing females and were removed manually. Fecundity (as log-transformed numbers of eggs per egg mass) showed significant differences across the three density treatments ($F = 49.7$, df $= 2, 33$; $P < .0001$, one-way Kruskal-Wallis test). Numbers of eggs produced by females that were reared at the high-density treatment were significantly lower than those held at low and intermediate densities ($P < .001$; SNK multiple-comparison test on ranks, Table 6).

DISCUSSION

Disturbance effects on Helicopsyche borealis density

Middle instars. — Despite high annual variability both in the wet-season hydrologic regime and densities of late instars in spring, numbers of *H. borealis* in the subsequent generation reached uniformly high levels during the summer low-flow period over the 5 yr of this study. Because larvae at these high densities have been shown to be food limited (see Lamberti et al. 1987), intraspecific competition would appear to be a regular feature among the middle instars, regardless of previous hydrologic disturbance and its effect on densities of late instars.

Further evidence indicating high resilience of other stream organisms present during similar, low-flow periods has been found in Big Sulphur Creek (McElravy et al. 1989) and in other California streams with similar benign hydrologic conditions (Moyle and Vondracek 1985, Hemphill 1989). Streams in regions having distinct dry and wet seasons with relatively long, uninterrupted periods of low flow allow many populations sufficient time to recover fully to predisturbance levels. Alternatively, in streams in regions where precipitation

TABLE 6. Comparison of *Helicopsyche borealis* adult size, as indicated by length of forewing, and fecundity across three larval densities in experiment 3. Means with the same superscript letter are not significantly different at $P < .01$ (Student-Newman-Keuls multiple-range test on ranks). $N =$ numbers of adults examined.

| | Larval density of *H. borealis* (no./100 cm²) | | | | | |
| | Low (14) | | Intermediate (26) | | High (51) | |
Life history feature	$\bar{X} \pm 2$ SE	N	$\bar{X} \pm 2$ SE	N	$\bar{X} \pm 2$ SE	N
Size of males (mm)	2.44 ± 0.08[a]	22	2.39 ± 0.01[a]	28	2.23 ± 0.05[b]	17
Size of females (mm)	2.86 ± 0.09[a]	16	2.79 ± 0.05[a]	21	2.35 ± 0.07[b]	17
Fecundity (no. eggs/female)	317 ± 19.3[a]	18	288 ± 29.1[a]	16	171 ± 9.0[b]	17

patterns and hydrologic regimes are more variable over the year, population recovery may not be as frequent nor predictable (e.g., Grossman et al. 1982, Stout 1982, Diamond and Reice 1985, Reice 1985).

Late instars.—Comparisons among years indicated a strong association between the abundance of late instars and hydrologic disturbance, as indicated by statistically significant inverse relationships between density and wet-season rainfall, peak discharge, number of storm days, and mean discharge during storms. In addition, the 50% decline in *H. borealis* density shortly after the 25–27 March 1985 storm (Table 3B) provides within-year evidence that larval reductions can result directly from physical disturbance. Although other factors potentially could account for this sudden decrease (e.g., larval predation or movement to unsampled microhabitats to form pupal aggregations), we do not believe that these caused the observed decreases in *H. borealis* abundance. For example, just prior to pupation, late instars typically move from exposed, stream-facing rock surfaces (distributions typical of grazing larvae; see Lamberti and Resh 1983, Vaughn 1986) to aggregation sites on less exposed undersides or downstream surfaces of large substrata (Resh et al. 1984). It is unlikely, however, that this factor was responsible for the apparent reductions in abundance of *H. borealis* at the time density estimates were made because the sampling date (15 April) preceded pupation by ≈2 wk (29 April). Moreover, over the 10 yr this population has been studied in Big Sulphur Creek, predation has not been an important source of *H. borealis* larval mortality (see Lamberti et al. 1987).

In the context of stream benthic communities, Resh et al. (1988) characterized hydrologic disturbance as having a frequency (i.e., parameters with a discrete recurrence interval, such as number of floods) and an intensity component (i.e., parameters with a continuous magnitude, such as discharge). Short-term experimental studies that have examined the response of stream invertebrates to hydrologic disturbance usually have emphasized the importance of the frequency component (e.g., timing of disturbance events within a single year) as it affects the dynamics of species recolonization (McAuliffe 1984*a*, Reice 1985, Peckarsky 1986) and the competitive interactions among populations (Hemphill and Cooper 1983, McAuliffe 1984*a*).

Multivoltine invertebrate populations, whose abundances can rapidly return to predisturbance levels after flooding (Fisher et al. 1982, Hemphill and Cooper 1983, Sagar 1983, Molles 1985, Grimm and Fisher 1989) appear to be particularly influenced by disturbance frequency. Univoltine populations, however, have no immediate source of recruitment after a disturbance (Resh 1982), unless undisturbed refugia are present in terrestrial (e.g., refuge for adults) or hyporheic habitats (e.g., refuge for eggs, larvae, or pupae). For these populations, parameters reflecting disturbance frequency

may be expected to have less influence on density variation than those parameters that reflect disturbance intensity. This was the case for univoltine *H. borealis*: the multiple regression analysis indicated that several intensity parameters (e.g., rainfall, peak discharge, and mean discharge during storms) were prominently related to density. In contrast, only one parameter reflecting disturbance frequency (number of storm days) figured prominently in either the two- or three-factor regression models (Table 5). Furthermore, short-lived adults of *H. borealis* are not present during the time of year in which storms occur, and this population has no hyporheic component (Resh et al. 1984) that can repopulate denuded stream substrata.

The mode of action of hydrologic disturbances on stream communities may work by erosion (i.e., during storms) when habitats are scoured by floods, or by desiccation (i.e., during droughts) when aquatic habitats decrease gradually, and organisms become stranded above the water surface (Resh et al. 1988). In the present study, year-to-year differences in *H. borealis* densities appeared more influenced by erosive rather than desiccative forces. Unlike sessile invertebrates along stream margins whose densities may be severely reduced by declining water levels (McAuliffe 1984*a*), *H. borealis* larvae are highly mobile (Lamberti and Resh 1983, Vaughn 1985) and should easily be able to escape gradual water level decreases during the course of the spring. Furthermore, year-to-year differences in the amount of stream habitat probably had minimal influence on estimates of *H. borealis* abundance. At the time density estimates were made stream depths in pools were similar and discharge was uniformly low over the 4 yr of this study (range: 0.10–0.18 m³/s, mean daily discharge).

Food limitation and intraspecific competition among late instars

Results of experiment 1 indicated that late-instar *H. borealis* can reduce periphyton biomass in a density-dependent manner as do middle instars in Big Sulphur Creek (Lamberti et al. 1987), and other stream grazers (McAuliffe 1984*b*, Hart 1987, Hill and Knight 1987). In the present study, larvae at densities between 23 and 46 individuals/100 cm² produced uniformly low algal standing crops. This relationship, together with those of experiment 2 that show density-dependent effects on pupal maturation time and pupal size, suggests that larvae at or above this intermediate density are food limited and compete exploitatively for periphyton in the same manner as do middle instars (Lamberti et al. 1987). However, the results of experiment 3 indicated that larvae at intermediate densities metamorphosed to adults that were similar in size and had fecundities similar to low-density treatments. Thus, only those individuals above densities of 23 larvae/100 cm² appeared to have been severely food limited.

Although the treatment densities used in these experiments had no effect on larval mortality, the strong density-dependent effects on larval maturation time, pupal and adult sizes, and female fecundities all suggest that intraspecific competition can at times be intense for this population. Similar negative effects of increasing density on Trichoptera and other holometabolous insects in terrestrial as well as aquatic systems have been reported (e.g., delayed pupation: Diptera [Averill and Prokopy 1987]; reduced pupal size: Trichoptera [Hart 1987], Diptera [Quiring and McNeil 1984, Averill and Prokopy 1987], Coleoptera [Pearson and Knisley 1985]; reduced adult size: Coleoptera [Pearson and Knisley 1985], Diptera [Averill and Prokopy 1987]). In the present study, if periphyton was depleted initially, pupation and emergence by most H. borealis larvae may have increased food availability for those food-limited larvae remaining in the system. This may have occurred in intermediate- and high-density treatments where many individuals (25–35%, compared with 10% in low-density treatments) remained as larvae at the time the experiment was terminated. Under these more relaxed competitive conditions, larvae may continue to grow to sizes similar to those held at low densities, which would compensate for earlier food limitation. However, because the majority of larvae at high densities pupated and emerged at smaller sizes than those at lower densities, factors other than food (such as temperature or photoperiod [Anderson and Cummins 1979, Sweeney et al. 1986]) were more likely responsible for initiating metamorphosis for this population.

Stream grazers at some densities have been found to enhance biomass-specific productivity of periphyton (Gregory 1983, Lamberti and Resh 1983, Stewart 1987, Power 1990). Such grazer-induced increases in productivity may allow larvae at some densities to graze freely on low bimoass/high turnover periphyton assemblages without experiencing serious food shortages. This may apply to late-instar H. borealis, where larvae held at intermediate densities grew to adult sizes attained in low-density treatments (Table 6). Here, larvae may have been close to the carrying capacity of their renewable periphyton food, in which they produced uniformly low standing crops, but yet were not food limited.

The large reduction in egg production observed at high densities could have a strong negative effect on fitness of individual caddisflies. However, high larval densities did not reduce overall reproductive capacity of the whole population (i.e., the fecundity × average female density), because egg densities produced per density level were highest at the highest larval densities (Fig. 3). Over this range of larval densities the population reproductive potential will continue to increase (=undercompensated density-dependence, sensu Begon et al. 1986); only larval densities higher than those used in this study apparently would produce density-dependent mortality sufficient to depress population growth. However, it is unclear at this time whether carry-over effects of intense intraspecific competition of parents at such high densities contribute to reduced fitness or "quality" of offspring (see Anderbrant et al. 1985).

Conclusions

Disturbance in streams clearly can reduce densities of organisms, and in doing so can potentially affect the degree to which biotic factors, such as intraspecific competition, influence populations. Our results indicated that for H. borealis, the intensity of competition varied in relation to hydrologic disturbance, both over the course of the life cycle and annually. For middle instars during summer low flow, intraspecific competition is apparently a pervasive process because high larval densities can persist regularly for extended periods in the absence of storm-related disturbance. In sharp contrast, for late-instars during spring, competition appears to be restricted only to those extremely dry or drought years when high larval densities can persist under mild disturbance regimes.

To our knowledge, there have been no similar field studies that have examined relationships between intraspecific competition and physical disturbance. However, our results are supported by several studies of interspecific competition that also have indicated high spatial or temporal variation in competition across a range of disturbance. Competition is most prevalent when disturbance regimes are mild, and food (Zaret and Rand 1971, Smith 1981, Grant 1986) or space (Hemphill and Cooper 1983, Peckarsky 1983, McAuliffe 1984a, Lubchenco 1986) may become limited among sympatric species (but see Strong et al. 1984). In contrast, competition is least prevalent when disturbance regimes are harsh, preventing resource limitation primarily by reducing population densities. In natural communities, it is hardly surprising that the intensity of competition varies dramatically with disturbance, considering the high variability in physical harshness both on a seasonal and year-to-year basis, coupled with the high variability in recovery shown by populations after disturbance. Clearly, one of the major objectives of future studies should be to determine the frequency with which disturbance regimes regulate the prevalence of competition over terms longer than the studies themselves (Wiens 1977, Grant 1986), in order to assess the importance of competition both in terms of individual fitness and population growth potential.

Given natural variability, how frequently does the hydrologic regime allow competition to occur in late-instar H. borealis? Based on examination of 138-yr precipitation data for San Francisco (NOAA records), which show a high correlation with mean annual precipitation to a recording station near our study site
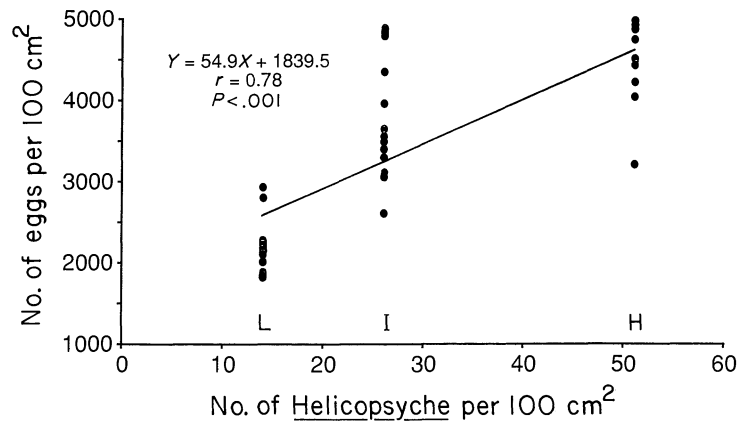
FIG. 3. Reproductive capacity (=fecundity × average female density) of the *Helicopsyche borealis* population plotted against mean larval densities (L = low, I = intermediate, and H = high) used in the enclosure experiments (*N* = 36 egg masses examined).

(Cloverdale, California: 1921–1988, $r = 0.77$, $P < .001$), such climatic extremes occur over the long term but are not common. For example, using the 1987 dry year as a benchmark, years with lower rainfall (hence those times when larval densities are high and the population is most likely to be food limited) occurred ≈10% of the time (14/138 yr); using rainfall levels similar to the 1977 drought as a benchmark yielded an even lower frequency of occurrence (5/138 yr or 4%). Thus, while such hydrologic regimes, through their effects on competition, can reduce individual fitness, these events are rare, but not nearly as rare as when the reproductive capacity of the entire population is reduced by disturbance in this stream.

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