EMERGENCE CUES OF A MAYFLY IN A HIGH-ALTITUDE STREAM ECOSYSTEM: POTENTIAL RESPONSE TO CLIMATE CHANGE

MATTHEW P. HARPER[1,3] AND BARBARA L. PECKARSKY[1,2,4]

[1]*Departments of Entomology, Ecology and Evolutionary Biology, Cornell University, Ithaca, New York 14853 USA*
[2]*Rocky Mountain Biological Laboratory, Crested Butte, Colorado 14850 USA*

Abstract. To understand the consequences of human accelerated environmental change, it is important to document the effects on natural populations of an increasing frequency of extreme climatic events. In stream ecosystems, recent climate change has resulted in extreme variation in both thermal and hydrological regimes. From 2001 to 2004, a severe drought in western United States corresponded with earlier emergence of the adult stage of the high-altitude stream mayfly, *Baetis bicaudatus*. Using a long-term database from a western Colorado stream, the peak emergence date of this mayfly population was predicted by both the magnitude and date of peak stream flow, and by the mean daily water temperature, suggesting that *Baetis* may respond to declining stream flow or increasing water temperature as proximate cues for early metamorphosis. However, in a one-year survey of multiple streams from the same drainage basin, only water temperature predicted spatial variation in the onset of emergence of this mayfly. To decouple the effects of temperature and flow, we separately manipulated these factors in flow-through microcosms and measured the timing of *B. bicaudatus* metamorphosis to the adult stage. Mayflies emerged sooner in a warmed-water treatment than an ambient-water treatment; but reducing flow did not accelerate the onset of mayfly emergence. Nonetheless, using warming temperatures to cue metamorphosis enables mayflies to time their emergence during the descending limb of the hydrograph when oviposition sites (protruding rocks) are becoming available. We speculate that large-scale climate changes involving warming and stream drying could cause significant shifts in the timing of mayfly metamorphosis, thereby having negative effects on populations that play an important role in stream ecosystems.

Key words: Baetis bicaudatus; climate change; drought; emergence cues; mayflies; streams.

INTRODUCTION

Recent climate models predict unprecedented rates of global warming over the next century and beyond as a consequence of a buildup of greenhouse gasses in the atmosphere (Peters 1989, Houghton et al. 1990, Schneider 1993, Vitousek 1994). As air temperatures increase and precipitation patterns change, many studies have also predicted an increase in the intensity and frequency of extreme events in running waters, such as floods and droughts (Grimm 1993, Arnell et al. 1996, McKnight 2001, Humphries and Baldwin 2003). As these hydrological extremes become more common due to human influences on the environment, it is important to document their consequences on natural populations (Carpenter et al. 1992).

Sustained shifts in global climate patterns can have profound effects on the life histories and interactions among aquatic species (Firth and Fisher 1991). Since periodicity, phenology, and recruitment of keystone

species in streams are often tied to hydrology, changes in the components of the hydrologic cycle may have great ecological significance for aquatic populations and communities (Carpenter 1988, Grimm and Fisher 1991, Grimm 1993). For example, extended dry periods can alter the life histories of organisms in a way that either increases or decreases overall fitness (Hansen et al. 1986, 1987, Levine 1991, Sweeney et al. 1991). Warmer temperatures might produce faster growth rates with increases in metabolism and consequent increases in fecundity, or these drought periods could result in a greater frequency of lethal temperatures (Sweeney et al. 1991). Moreover, streams in the western mountains of the USA are highly susceptible to the effects of climate change, since they are strongly influenced by spring snowmelt (Poff 2002). Warming temperatures not only reduce the snowpack and associated water storage, but also cause early snowmelt and lower spring runoff (Barnett et al. 2004, Dettinger et al. 2004, Stewart et al. 2004).

A change in the thermal regime can have profound direct effects on stream organisms (Poff et al. 1992), because water temperature directly controls many vital life processes of ectotherms (Atkinson 1994). For example, temperature is not only an important cue for

the emergence of aquatic insects (Ward and Stanford 1979, Sweeney et al. 1991, Chadwick and Feminella 2001), but it also regulates their growth and development (Sweeney and Vannote 1978). If a population exists at a thermal optimum where their size and fecundity are maximized, stream warming would reduce the fitness of individuals in populations that develop in streams with suboptimal temperatures (Vannote and Sweeney 1980). Therefore, increases in water temperatures as a result of climate change have the potential to affect the reproductive success of stream insects by altering their phenology, size, and fecundity.

Previous studies of the mayfly *Baetis bicaudatus* (Baetidae) in high altitude streams of western Colorado, USA have shown that the amount of runoff from accumulated winter precipitation is correlated with the timing of metamorphosis to the adult stage, with mayflies emerging early in drought years and later in wetter years (Peckarsky et al. 2000). These patterns of emergence are consistent with the hypothesis that factors associated with water deficiency, either increasing water temperatures or declining stream flow rates, may affect the development of this mayfly thereby triggering early adult emergence during drought years. Furthermore, prior studies have shown that the size of mature *B. bicaudatus* determines their fecundity; and, in any one stream, in high water years females emerged later and were larger and more fecund than in low water years, when females emerged earlier (Peckarsky et al. 2001). Therefore, if the population exists at its thermal optimum, then human-accelerated climate change has the potential to significantly affect the fitness of this species, which is a key player in these high altitude ecosystems due to its relative abundance (Allan 1975, Peckarsky et al. 2001), its consumption of algae (McIntosh et al. 2004, Alvarez and Peckarsky 2005), and importance as a food source for invertebrate and vertebrate predators (Allan 1983, Peckarsky and Penton 1989).

Earlier studies of the effects of global climate change on stream invertebrates have tested either the effect of increasing temperature (Rempel and Carter 1986, Hogg and Williams 1996) or related changes in stream flow (Poff et al. 1992). The goal of this study was to investigate the responses of stream populations to both factors considered together. Using a long-term database during years with different hydrologic and thermal regimes in streams of a single high-altitude drainage basin in western Colorado, we established hypotheses regarding the proximate cues triggering emergence to the adult stage of the numerically dominant mayfly species, *B. bicaudatus*. We also compared the spatial variation in timing of emergence among populations in multiple streams of the drainage basin during two different years. Finally, we designed experiments to manipulate water temperature and stream flow independently, which enabled us to decouple the potential causal mechanisms explaining early emergence of this mayfly in low-flow years.

METHODS

Field patterns

In summer 2003, we documented the emergence phenology of a *B. bicaudatus* population from one reach of the East River near the Rocky Mountain Biological Laboratory (RMBL), Gunnison County, Colorado, USA (see Plate 1). The study reach was ~250 m downstream from the one previously used to estimate emergence patterns of this mayfly (Peckarsky et al. 2000), but has subsequently been inundated by a beaver dam. Emergence phenology was determined by making quantitative collections of last instar larval exuvia (distinguishable by wing pad development). We deployed a block net (0.8-mm mesh) that trapped exuvia drifting from upstream for 5 min two times daily, at 1300 and 1600 hours once per week from 3 to 24 July. We corrected capture rate data for seasonal variation in flow using an efficiency curve developed by Peckarsky et al. (2000) after releasing known numbers of stained *Baetis* exuvia at 10-m intervals upstream of the block net over a range of stream discharges (0.30–2.00 m^3/s). The peak of mayfly emergence observed in summer 2003 was then compared to emergence peaks observed in the same stream during previous summers, including a drought year (1994), a high-water year (1995), and two average stream-flow years (1996, 1997).

We used a linear regression to determine if interannual variation in peak emergence of *B. bicaudatus* in the East River could be predicted from variation in stream flow or water temperature. Seasonal and annual patterns of stream flow for the five years in which we estimated emergence phenology were obtained from a USGS gauging station (ID = 09112500) located in the East River near Almont, Colorado. Each year, water temperatures were also monitored continuously in the study reach of the East River using Onset Stowaway data loggers (Onset Computer, Pocasset, Massachusetts, USA). However, data loggers malfunctioned in 1997; thus, four years of East River temperature data were used to predict timing of emergence. We used magnitude and date of annual peak discharge, as well as water temperature averaged over the duration of the development time of *Baetis* larvae as independent variables in the regressions to predict peak mayfly emergence.

In addition to this intensive field survey conducted in one stream over multiple years, an extensive survey of 10 streams from the Upper East River drainage basin was carried out in summer 1996. This enabled us to determine whether the onset of *B. bicaudatus* emergence could be predicted from spatial variation in stream flow and water temperatures among streams in any given year. We monitored water temperatures continuously with Onset data loggers, and estimated average stream discharge by measuring stream cross-sectional area and current velocity (Marsh-McBirney velocity meter Model 201; Marsh-McBirney, Frederick, Maryland, USA) at three transects on the same date in each stream. We used

PLATE 1.   *Baetis bicaudatus* male imago, Rocky Mountain Biological Laboratory. Photo credit: Angus R. McIntosh.

linear regression analysis to determine whether the spatial variation in the onset of mayfly emergence could be predicted from variation in average water temperature or average stream discharge. We ran all regression analyses using SAS (SAS Institute 1997).

Experiments

Since temperature and flow can covary in natural streams, we designed an experiment to examine their effects independently. To definitively decouple these two predictor variables (water temperature and stream flow) as potential proximate cues triggering *B. bicaudatus* metamorphosis, we conducted two simultaneous, but independent mechanistic experiments comparing the timing of mayfly emergence in two different flow environments (at ambient stream temperatures), and at warmed vs. ambient temperatures (with similar flows). Experiments were conducted in a system of 60 circular plexiglass flow-through chambers (microcosms) of 15 cm diameter (described and illustrated in Peckarsky and Cowan 1991) housed in a streamside greenhouse (Hansen Weatherport, Delta, Colorado, USA) receiving natural stream water by gravity. Each chamber contained a layer of washed gravel and four naturally algae-covered rocks (3–5 cm diameter) taken from the East River. To standardize the amount of algal resources available to *Baetis* larvae among treatments, the rocks used in the experiment were first scrubbed with brushes
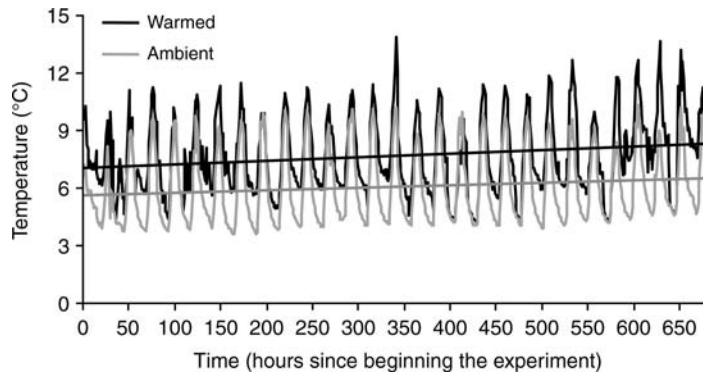
Fig. 1. Representative thermal regimes and their corresponding linear trends in warmed-water and ambient-water treatments that *Baetis bicaudatus* experienced throughout the course of the experiment. Data represent hourly measurements.

then incubated outdoors in plastic tubs inoculated with stream water for one week under ambient light conditions. To prevent resource depletion by *Baetis* during the experiment, rocks were replaced every two weeks with a new set of algae-covered rocks prepared in the same way. Previous microcosm experiments have shown that similar densities of *Baetis* did not deplete an ambient algal food source; and the levels of chlorophyll *a* on rocks remained relatively high due to continual recolonization of diatoms being transported through the water delivery system (Peckarsky et al. 1993, Alvarez and Peckarsky 2005). The two experiments were run simultaneously from 18 June to 23 July 2003, one including two levels of water temperature (warmed and ambient) and the other including two levels of stream flow (high and low).

Fifteen warm-water chambers were randomly allocated among 30 chambers located on the west side of the Weatherport, and the other 15 chambers were used as controls, receiving ambient stream water. To establish the temperature contrasts, natural stream water was gravity fed continuously from a nearby first order tributary of the East River to a tankless instantaneous propane water heater (Infinion C13LP; Low Energy Systems, Denver, Colorado, USA), and then to a large plastic bin (110 L), from which it was dripped from tygon tubing into the warmed chambers (average temperature = $37.50 \pm 2.54°C$; all errors reported are SE). Natural stream water was dripped to the control chambers ($8.0 \pm 1.76°C$). In both treatments, water dripped to the chambers at an average rate of 4.65 ± 0.95 mL/s, and was mixed with stream water at ambient temperatures (from the same tributary of the East River) that was delivered through two water jets on opposite sides of each chamber. Average velocity (measured with a Nixon micropropeller flow meter; Nixon Flowmeters Ltd., Cheltenham, Gloucestershire, UK) in the warmed chambers (12.44 ± 2.65 cm/s) did not differ significantly from that in the ambient temperature chambers (15.96 ± 6.46 cm/s; $t = 1.008$, df = 8, $P = 0.343$).

To record the water temperatures to which *Baetis* larvae were exposed over the course of the experiment, two Onset temperature loggers were placed at random in chambers of both warmed and ambient temperature treatments. The loggers were randomly moved weekly to other chambers of the same treatments. The average temperature over the run of the experiment in the warmed chambers (8.0°C, ranging from 6.2 to 12.2°C) was ~2°C warmer than in the chambers at ambient temperatures (6.2°C, with mean temperatures per day ranging from 5.1 to 7.2°C). Therefore, the small drip of warmed water successfully created a thermal regime distinctly different from that of chambers receiving an ambient temperature drip (Fig. 1). Furthermore, water temperatures fluctuated daily in both treatments, as occurs in natural streams; but both maximum and minimum temperatures were, on average, two to three degrees warmer in the heated chambers than the ambient-temperature chambers. The mean difference in daily temperature between both treatments was $2.29 \pm 0.30°C$, simulating increased temperatures experienced during drought years. Nonetheless, the thermal regimes in both temperature treatments were well within those observed in natural streams of this drainage basin (Peckarsky et al. 2001).

An additional 30 chambers on the east side of the Weatherport were used to manipulate flow rates while holding stream water temperatures at ambient conditions. Half of these chambers were randomly allocated to a high-flow treatment by keeping the gang valves delivering water to individual chambers completely open. The other chambers were maintained at low flow by keeping their gang valves partially open. The mean current velocity (measured with a Nixon flow meter at the surface of rocks midway between the two water jets) in the high-flow chambers (12.70 ± 2.15 cm/s) was over two times higher than in the low-flow chambers (5.31 ± 0.85 cm/s), and these differences were significant ($t = 11.098$, df = 28, SE = 1.156, $P < 0.0001$). Given that all chambers had the same dimensions, we can assume that high-velocity chambers also had >2× higher discharge than low-velocity chambers. While the small size of the experimental units maximized replication, it was not possible to simulate the range of flows observed in
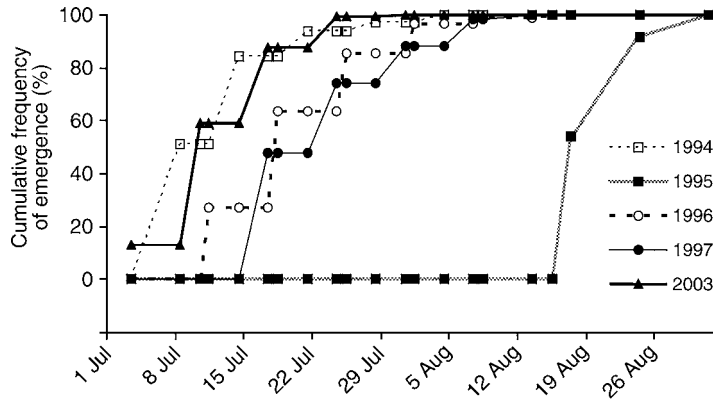
FIG. 2. Cumulative frequencies of emergence of *Baetis bicaudatus* over the summer in drought years (1994, 2003), average water years (1996, 1997), and a high-water year (1995) in the East River near RMBL (Rocky Mountain Biology Lab) in western Colorado, USA.

natural streams. Thus, failure to reject the null hypothesis could potentially be explained by relatively low flow in both treatments compared to levels reached in nature. Mean daily water temperatures were similar between high (5.9 ± 0.27°C) and low-flow treatments (6.37 ± 0.22°C; $t = -1.36$, df = 6, SE = 0.347, $P = 0.223$), and similar to those of the unheated chambers in the temperature experiment.

Dissolved oxygen measurements were taken with a YSI dissolved oxygen (DO) meter (YSI, Yellow Springs, Ohio, USA) in a random subsample of chambers from all treatments four times over a 24-h period during the experiment (0600, 1100, 1600, and 2000 hours). DO was near saturation in all treatments, and diel oxygen curves were similar among warmed and ambient temperature treatments and among high and low-flow treatments. Tukey's post hoc test of repeated measures showed that percentage of oxygen saturation did not differ significantly between warmed (65.29% ± 0.62%) and ambient temperature chambers (64.52% ± 0.69%) or between high (61.28% ± 0.64%) and low-flow chambers (60.18% ± 1.39%) ($F_{3,4} = 11.4$, $P > 0.05$).

We added 10 late stage II or early stage III larvae of *B. bicaudatus* to each chamber, and followed their development through the stage (III) when reproductive maturation occurs (Peckarsky et al. 2001). Emergence nets were placed over each chamber to capture the first winged stage (subimagoes) of emerging mayflies. The time of emergence of each subimago was recorded, as were numbers of larvae that died during the experiment in each chamber.

To test for differences between the average date of emergence between treatments for each experiment (warm vs. ambient temperature and high vs. low flow), we used a *t* test with individual estimates of variance for each treatment rather than the pooled variance, because the number of chambers with individuals that emerged varied per treatment. The unpooled *t* test (Aspin-Welch-Satterthwaite-Student *t* test) results in fractional error degree of freedom. Mean emergence dates of *Baetis* per chamber were used as replicates. Cumulative relative frequencies of date of emergence of *Baetis* larvae were also compared among treatments using two-sample Kolmolgorov-Smirnov tests (Zar 1984). We
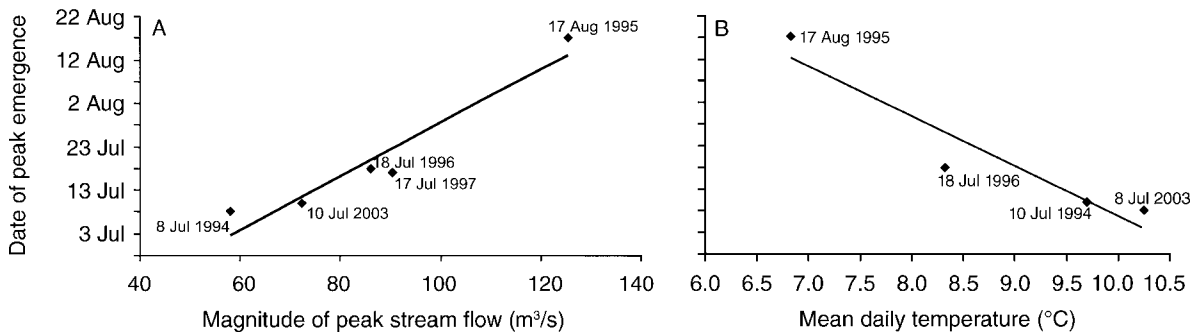

FIG. 3. (A) Relationship between the date of peak emergence of *Baetis bicaudatus* in the East River at RMBL and the magnitude of peak stream flow of the East River at Almont, Colorado over five years ($y = 0.616x + 147.98$, $r^2 = 0.923$, $P = 0.009$). (B) Relationship between the date of peak emergence of *Baetis bicaudatus* and mean daily temperature of stream water accumulated during the summer months of four years the East River near RMBL, Colorado ($y = -11.539x + 303.17$, $r^2 = 0.900$, $P = 0.052$). Due to a malfunctioned temperature logger, no temperature data were collected from the East River in 1997.
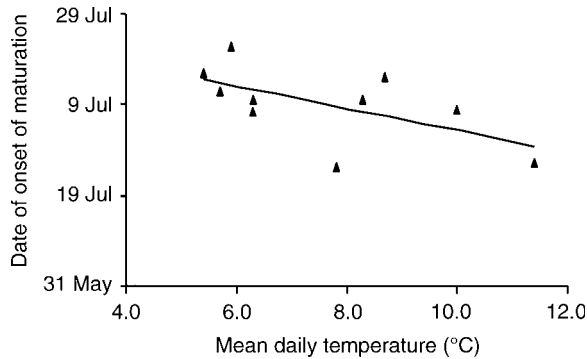
FIG. 4. Relationship between the date of onset of maturation of *Baetis bicaudatus* and the mean daily temperature of the stream water during the summer months in 10 different streams in 1996 ($y = -2.4678x + 208.91$, $r^2 = 0.353$, $P = 0.069$) in the upper East River Drainage Basin near RMBL in western Colorado. Mature larvae (stage IV) had black wing pads.

ran all statistical analyses using SAS (SAS Institute 1997).

RESULTS

Field patterns

In summer 2003, *B. bicaudatus* emergence in the East River, estimated from weekly collections of last instar exuvia, peaked during the week of 10 July, which was earlier than most years for which records exist, and consistent with the timing of emergence of this mayfly in a previous dry year (1994; Fig. 2). Both magnitude ($y = 0.616x + 147.98$, $r^2 = 0.92$, $P = 0.009$; Fig. 3A) and date of peak stream flow ($y = 2.062x - 121.74$, $r^2 = 0.92$, $P = 0.010$), as well as the mean daily temperature in the East River ($y = -11.54x + 303.17$, $r^2 = 0.90$, $P = 0.052$; Fig. 3B) were significant predictors of the variation in the peak date of *Baetis* emergence among years in this stream. However, stream flow and water temperature were negatively correlated in the East River (Spearman's $r = -0.987$, $P = 0.013$, $N = 4$), because in any one stream water temperature increases while stream flow decreases (Wetzel 1983), making it difficult to decouple the effects of these two potential causal factors.

In contrast, among 10 streams of the same drainage basin within the same year (1996), there was no correlation between stream flow and water temperature (Spearman's $r = -0.012$, $P = 0.97$, $N = 10$). Therefore we were able to decouple these two variables by comparing spatial variation in timing of emergence of *Baetis* across streams. This survey demonstrated that the onset of emergence could not be predicted from variation in stream discharge ($y = 0.636x + 190.01$, $r^2 = 0.0013$, $P = 0.922$). Cumulative degree days ranged from 41.9 to 200 in these 10 streams over the period of time when loggers were in the streams until the peak emergence date. Although there was a tendency for *B. bicaudatus* to emerge earlier in warmer streams, mean daily temperature did not significantly predict the variation in the onset of *Baetis* emergence among the 10 streams studied in 1996 ($y = -2.468x + 208.91$, $r^2 = 0.353$, $P = 0.069$; Fig. 4).

Experiments

Mean date of *B. bicaudatus* emergence did not differ significantly between the high (Julian date [day 1 = 1 January] = 197 ± 1.2 [mean ± SE]) and low (198 ± 1.6) flow chambers ($t = -0.180$, df = 23.41, $P = 0.859$). However, in the temperature manipulation, the mean date of emergence was four days earlier in the warmed chambers (Julian date = 195 ± 1.3) than in the ambient temperature chambers (199 ± 0.9; $t = 2.658$, df = 16.83, $P = 0.017$). Analysis of the frequency distributions of dates of emergence of individuals between treatments showed significant differences between warmed and ambient temperature treatments, but no significant differences between high and low-flow treatments (Fig. 5). In contrast to predictions from the East River data (Fig. 3A), individuals in the low-flow treatment did not emerge earlier than those in the high-flow chambers. Consistent with the patterns observed in the field (Figs. 3B and 4), *Baetis* emerged earlier from the warmed chambers than from the ambient temperature chambers (Fig. 5B).

Over the five weeks of the experiments, the percentage of mortality of *Baetis* larvae prior to emergence varied
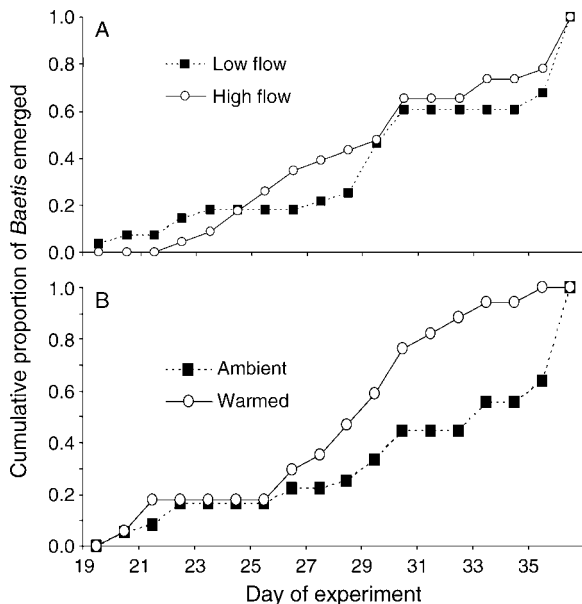

FIG. 5. (A) Difference in cumulative relative frequencies of *Baetis bicaudatus* emerging from the high-flow and low-flow treatments during the five-week microcosm experiment in June–July 2003 (K-S test; $D = 0.264$, $n = 18$, one-sided $P = 0.310$). (B) Difference in the cumulative relative frequencies of *Baetis bicaudatus* emerging from the warmed- and ambient-temperature treatments of the five-week microcosm experiment in June–July 2003 (K-S test; $D = 0.543$, $n = 17$, one-sided $P = 0.018$).

among treatments with the highest mortality occurring in the warmed-water chambers (89%). Mortality rates over the experiments were lower and similar in ambient temperature (63%), low-flow (57%), and high-flow (67%) chambers. Higher mortality rates in warmed water chambers reduced *Baetis* density over the course of the experiment compared to other treatments. However, Ode (2002) showed that larval density had no effect on emergence time of this species reared in similar chambers, suggesting that accelerated emergence in the warmed water treatments could not be attributed to lower densities.

DISCUSSION

The time series of field data reported in this study demonstrate that for the section of the East River near RMBL, interannual variation in both stream flow and stream water temperature at any one site can be used as reliable predictors of variation in the peak of emergence of *B. bicaudatus* to the adult stage. Furthermore, annual variability of these two factors may explain why the timing of emergence of this mayfly fluctuates so much from year to year at any one site (Peckarsky et al. 2000). These two variables were negatively correlated, because during periods of snowmelt, stream flows were high and water temperatures were low (Matthews 1998). However, throughout the summer, the influence of snowmelt declines, streams become shallower, more light is absorbed by the streambed, stream water is exposed to sunlight for longer periods, and as a consequence, water temperatures increase. Although both flow and water temperatures were good predictors of the peak of *B. bicaudatus* emergence, under natural conditions these two factors interact in complex ways to influence populations (Van-Winkle and Holcomb 1999); thus analysis of field patterns at one place over time did not resolve which factor was the proximate cue that triggered the metamorphosis of mayflies.

Investigation of field patterns among multiple streams within the same year in the East River drainage basin showed that temperature and flow regimes were highly variable among streams; and, more importantly, streams with higher discharge did not necessarily have lower temperature regimes (Peckarsky et al. 2001). This observation provided an opportunity to decouple the effects of flow and temperature on spatial variation in the timing of *Baetis* emergence among streams in any given year. Nonetheless, spatial variation in stream discharge did not predict the onset of *Baetis* emergence, and spatial variation in stream water temperatures only weakly predicted the onset of emergence, with individuals developing in warmer streams emerging earlier than those in colder streams. Thus, field patterns among multiple streams within the same year were consistent with the hypothesis that increasing water temperature, rather than receding stream flow was the proximate cue causing mayflies to emerge earlier in drought years.

The mechanistic experiments demonstrated more definitively that mayflies exposed to warmer water emerged earlier than those that developed at ambient stream water temperatures. Furthermore, we doubt that flow is a useful proximate cue explaining the interannual variation observed in the East River, despite the possibility that experimental constraints contributed to our failure to reject the null hypothesis that flow rates did not affect emergence. While mayflies do not have the sensory capability to detect variation in discharge (volume of water per unit time), they do have mechanoreceptors that can detect current velocities (Martinez 1987, Peckarsky 1979). Nonetheless, velocities are highly variable both vertically and horizontally within streams, and near bed velocities in the microhabitat of mayflies do not predict stream discharge (Statzner and Holm 1982, Peckarsky and Penton 1990, Lancaster and Hildrew 1993, Hart et al. 1996). Thus, under natural conditions it would be difficult for mayflies to use stream discharge or current velocity as reliable proximate cues to trigger emergence.

In contrast, the observation that mayflies exposed to warmed water emerged earlier than those that developed at ambient stream water temperatures is consistent with the hypothesis that these organisms used temperature as the proximate cue to metamorphose. Other mayfly populations have been shown to emerge sooner at increased temperatures than those developing in colder water (Wright et al. 1982, Sweeney et al. 1991, Watanabe et al. 1999). Hogg and Williams (1996) similarly observed earlier onset of emergence of aquatic insects in a warmed channel of an Ontario stream. It is especially important to note that the observed difference between treatments of four days in the timing of emergence is a significant amount of time for an adult mayfly. Previous studies have shown that the maximum lifespan of an adult male *B. bicaudatus* is four days (Peckarsky et al. 2002), and females may live for considerably shorter (Vance 1996). There are potential fitness costs of early emergence of stream insects in response to increasing environmental temperatures (Sweeney and Vannote 1978, Vannote and Sweeney 1980). In addition to the possible negative effects of warm water temperatures on mayfly mortality observed in the present study, Peckarsky et al. (2001) reported that mayflies emerging in dry years were smaller on average than in higher water years when emergence was delayed and feeding by larvae was extended. Thus, increasing water temperature could reduce mayfly fitness by accelerating emergence, thereby reducing size and fecundity of adult *B. bicaudatus* compared to populations that emerge later in high water years (Peckarsky et al. 2001). Given that trout are size-selective predators on larger *B. bicaudatus* (Allan 1978), and the potential for changes in algal biomass or community structure as a consequence of changes in grazer biomass (Steinman

1996), increasing stream temperature could have more far-reaching consequences on stream ecosystems.

Interestingly, using increasing water temperatures to trigger emergence of this mayfly also results in emergence during the descending limb of the hydrograph, thus indirectly connecting its life history to changes in stream flow. Adult females of *B. bicaudatus* generally disperse upstream (Flecker and Allan 1988) and land on rocks protruding from the stream where they lay their eggs on the under side (Peckarsky et al. 2000; Encalada and Peckarsky, *in press*). Therefore, if females emerge when water levels are too high, protruding rocks may be limited in their natal streams and females may be forced to disperse to other streams to oviposit (Peckarsky et al. 2000). Conversely, if females emerge too late when water levels are low, risk of egg desiccation increases during the egg incubation period of this species (Encalada and Peckarsky, *in press*). Moreover, since mayfly adults are so short lived, both females and males need to emerge at the same time to mate successfully (Peckarsky et al. 2002). Thus, increasing temperatures could affect not only the timing of emergence and mating, but also successful oviposition and egg development in this species.

Phenotypic plasticity of timing of emergence of *B. bicaudatus* allows populations of this species to inhabit a wider range of thermal regimes and to persist through periods of altered temperatures, thus contributing to both temporal and spatial resilience of their populations. Having flexible behavioral or life history responses to a stressor such as drought can confer a fitness advantage over species with less flexible thermal requirements. For example, populations of many stream fish species persist periods of drought or increasing temperatures by seeking spatial refuges from unfavorable conditions (Sedell et al. 1990, Schlosser and Angermeier 1995, Magoulick and Kobza 2003). Nonetheless, warming temperatures have been shown to narrow the ranges of stream fishes worldwide (Erman 1986, Meisner 1990, Scott and Poynter 1991, Keleher and Rahel 1996, Rahel et al. 1996), which could constitute a negative consequence of human-accelerated global climate change.

Likewise, terrestrial organisms have shown variable life history responses to changes in temperature regimes. In a review of the effects of global climate change on insect herbivores, Bale et al. (2002) concluded that increasing temperature was the most important abiotic factor affecting populations of insect herbivores. Temperature can directly influence life history strategies, including development, growth, and phenology. In contrast to stream insects like *Baetis*, warmer temperatures may benefit terrestrial insect herbivores in temperate zones by extending the time available for growth and development.

Increasing temperatures can also affect insect herbivores and pollinators indirectly by influencing host plants (Bale et al. 2002, Dunne et al. 2003), especially if changing climate causes asynchrony between herbivores or pollinators and the availability of their host plants (Inouye and McGuire 1991, Dewer and Watt 1992). For example, experimental warming of a subalpine meadow near the Rocky Mountain Biological Laboratory has led to earlier onset and lengthening of the flowering period (Dunne et al. 2003). Furthermore, changes in early-season flowering phenologies (e.g., *Delphinium*) affect hymenopteran and hummingbird pollinators, which in turn affects the later flowering species (*Ipomopsis aggregate*) that depend on those pollinators (Inouye and McGuire 1991).

Generally, effects of increasing temperatures are more severe for species with narrow ranges of acceptable conditions, and can be compensated for by mobile or generalist herbivorous species (Hellmann 2002). For example, increasing air temperatures have been shown to increase the abundance or extend the ranges of nonindigenous insect pest species, which tolerate a wider range of abiotic conditions than their native counterparts (Cannon 1998). Furthermore, changes in temperature at lower or higher elevations can affect the migrations or timing of hibernation of populations of terrestrial animals, thereby altering their population dynamics (Inouye et al. 2000). If environmental changes are too fast, decreases in fitness associated with natural selection may overwhelm the ability of populations to adapt, thereby leading to extinctions (Lynch and Lande 1993).

We conclude that *B. bicaudatus* emerges early in dry years by using water temperature as the proximate cue for metamorphosis. Since life history events such as emergence and oviposition, which determine reproductive success of *B. bicaudatus*, are sensitive to changes in water temperature and flow regimes, the increase in the frequency of extreme hydrologic events in response to global climate change could have profound effects on populations of these abundant mayflies. Therefore, as a sensitive species that plays a key role in many stream ecosystems as a primary consumer and energy source for fish predators (Allan 1983, Taylor et al. 2002), *Baetis* mayflies could forecast the potential for damage to stream ecosystems as a result of global or regional increases in stream water temperatures.

Literature Cited

Allan, J. D. 1975. The distributional ecology and diversity of benthic insects in Cement Creek, Colorado. Ecology 56: 1040–1053.

Allan, J. D. 1978. Trout predation and the size composition of stream drift. Limnology and Oceanography 23:1231–1237.

Allan, J. D. 1983. Food consumption by trout and stoneflies in a Rocky Mountain stream, with comparison to prey standing crop. Pages 371–390 *in* T. D. Fontaine and S. M. Bartell, editors. Dynamics of lotic ecosystems. Ann Arbor Science, Ann Arbor, Michigan, USA.

Alvarez, M., and B. L. Peckarsky. 2005. How do grazers affect periphyton heterogeneity in streams? Oecologia 142:576–587.

Arnell, R., B. Bates, H. Land, J. J. Magnusson, and P. Mulholland. 1996. Hydrology and freshwater ecology. Pages 325–364 *in* R. T. Watson, M. T. Zinyowera, and R. H. Moss, editors. Climate change 1995: impacts, adaptations, and mitigation. scientific-technical analysis. Cambridge University Press, Cambridge, UK.

Atkinson, D. 1994. Temperature and organism size: a biological law for ectotherms? Advances in Ecological Research 25:1–58.

Bale, J. S. et al. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Global Change Biology 8:1–16.

Barnette, T., R. Malone, W. Pennell, D. Stammer, B. Semtner, and W. Washington. 2004. The effects of climate change on water resources in the west: introduction and overview. Climatic Change 62:1–11.

Cannon, R. J. C. 1998. The implications of predicted climate change for insects pests in the UK, with emphasis on non-indigenous species. Global Change Biology 4:785–796.

Carpenter, S. R. 1988. Complex interactions in lake communities. Springer-Verlag, New York, New York, USA.

Carpenter, S. R., S. G. Fisher, N. B. Grimm, and J. F. Kitchell. 1992. Global change and freshwater ecosystems. Annual Review of Ecology and Systematics 23:119–139.

Chadwick, M. A., and J. W. Feminella. 2001. Influence of salinity and temperature on the growth and production of a freshwater mayfly in the Lower Mobile River, Alabama. Limnology and Oceanography 46:532–542.

Dettinger, M. D., D. R. Cayan, M. K. Meyer, and A. E. Jeton. 2004. Simulated hydrologic responses to climate variations and change in the Merced, Carson, and American River Basins, Sierra Nevada, California, 1900–2099. Climatic Change 62:283–317.

Dewer, R. C., and A. D. Watt. 1992. Predicted changes in the synchrony of larval emergence and budburst under climatic warming. Oecologia 89:557–559.

Dunne, J. A., J. Harte, and K. J. Taylor. 2003. Subalpine meadow flowering phenology responses to climate change: integrating experimental and gradient methods. Ecological Monographs 73:69–86.

Encalada, A. C., and B. L. Peckarsky. *In press*. Selective oviposition by the mayfly *Baetis bicaudatus*. Oecologia.

Erman, D. C. 1986. Long-term structure of fish populations in Sagehen Creek, California. Transactions of the American Fisheries Society 115:682–692.

Firth, P., and S. G. Fisher. 1991. Climate change and freshwater ecosystems. Springer-Verlag, New York, New York, USA.

Flecker, A. S., and J. D. Allan. 1988. Flight direction in some Rocky Mountain mayflies (Ephemeroptera), with observations of parasitism. Aquatic Insects 10:33–42.

Grimm, N. B. 1993. Implications of climate change for stream communities. Pages 293–314 *in* P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, editors. Biotic interactions and global change. Sinauer Associates, Sunderland, Massachusetts, USA.

Grimm, N. B., and S. G. Fisher. 1991. Responses of arid-land streams to changing climate. Pages 211–233 *in* P. Firth and S. G. Fisher, editors. Climate change and freshwater ecosystems. Springer-Verlag, New York, New York, USA.

Hansen, J., A. Lacis, D. Rind, G. Russell, I. Fung, P. Ashcraft, S. Lebedeff, R. Ruedy, and P. Stone. 1986. The greenhouse effect: projections of global climate change. Pages 199–218 *in* J. G. Titus, editor. Effects of changes in stratospheric ozone and global climate. Volume 1: Overview. U.S. Environmental Protection Agency, Washington, D.C., USA.

Hansen, J., A. Lacis, D. Rind, G. Russell, I. Fung, and S. Lebedeff. 1987. Evidence for future warming: how large and when? Pages 57–75 *in* W. E. Shands and J. S. Hoffman, editors. The greenhouse effect, climate change, and U.S. forests. Conservation Foundation, Washington, D.C., USA.

Hart, D. D., B. D. Clark, and A. Jasentuliyana. 1996. Fine-scale field measurements of benthic flow environments inhabited by stream invertebrates. Limnology and Oceanography 41:297–308.

Hellmann, J. J. 2002. The effect of an environmental change on mobile butterfly larvae and the nutritional quality of their hosts. Journal of Animal Ecology 71:925–936.

Hogg, I. D., and D. D. Williams. 1996. Response of stream invertebrates to a global-warming thermal regime: an ecosystem-level manipulation. Ecology 77:395–407.

Houghton, J. T., G. J. Jenkins, and J. J. Ephrams. 1990. Climate change: the IPCC scientific assessment. Cambridge University Press, Cambridge, UK.

Humphries, P., and D. S. Baldwin. 2003. Drought and aquatic ecosystems: an introduction. Freshwater Biology 48:1141–1146.

Inouye, D. W., B. Barr, K. B. Armitage, and B. D. Inouye. 2000. Climate change is affecting altitudinal migrants and hibernating species. Proceedings of the National Academy of Sciences (USA) 97:1630–1633.

Inouye, D. W., and A. D. McGuire. 1991. Effects of snowpack on timing and abundance of flowering in *Delphinium nelsonii* (*Ranunculaceae*): implications for climate change. American Journal of Botany 78:997–1001.

Keleher, C. J., and F. J. Rahel. 1996. Thermal limits to salmonid distributions in the Rocky Mountain region and potential habitat loss due to global warming: a geographic information system (GIS) approach. Transactions of the American Fisheries Society 125:1–13.

Lancaster, J., and A. G. Hildrew. 1993. Flow refugia and the microdistribution of lotic macroinvertebrates. Journal of the North American Benthological Society 12:385–393.

Levine, J. 1991. Global climate change. Pages 1–25 *in* P. Firth and S. G. Fisher, editors. Global climate change and freshwater ecosystems. Springer-Verlag, New York, New York, USA.

Lynch, M., and R. Lande. 1993. Evolution and extinction in response to environmental change. Pages 234–250 *in* P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, editors. Biotic interactions and global change. Sinauer Associates, Sunderland, Massachusetts, USA.

Magoulick, D. D., and R. M. Kobza. 2003. The role of refugia for fishes during drought: a review and synthesis. Freshwater Biology 48:1186–1198.

Martinez, L. A. 1987. Sensory mechanisms underlying the predator–prey interaction between perlodid stonefly nymphs and their mayfly nymph prey. Dissertation. Cornell University, Ithaca, New York, USA.

Matthews, W. J. 1998. Patterns in freshwater fish ecology. Chapman and Hall, New York, New York, USA.

McIntosh, A. R, B. L. Peckarsky, and B. W. Taylor. 2004. Predator-induced resource heterogeneity in a stream food web. Ecology 85:2279–2290.

McKnight, D. 2001. Freshwater ecosystems and climate change: recent assessments and recommendations. Limnology and Oceanography Bulletin 10:61–65.

Meisner, J. D. 1990. Potential loss of thermal habitat for brook trout, due to climatic warming, in two southern Ontario streams. Transactions of the American Fisheries Society 119:282–291.

Ode, P. R. 2002. The role of competition in the foraging ecology of two herbivorous stream mayflies. Dissertation. Cornell University, Ithaca, New York, USA.

Peckarsky, B. L. 1979. Experimental manipulations involving the determinants of the spatial distribution of benthic invertebrates within the substrate of stony streams. Dissertation. University of Wisconsin, Madison, Wisconsin, USA.

Peckarsky, B. L., and C. A. Cowan. 1991. Consequences of larval intraspecific competition to stonefly growth and fecundity. Oecologia 88:277–288.

Peckarsky, B. L., C. A. Cowan, M. A. Penton, and C. Anderson. 1993. Sublethal consequences of stream-dwelling predatory stoneflies on mayfly growth and fecundity. Ecology 74:1836–1846.

Peckarsky, B. L., A. R. McIntosh, C. C. Caudill, and J. Dahl. 2002. Swarming and mating behavior of a mayfly Baetis bicaudatus suggest stabilizing selection for male body size. Behavioral Ecology and Sociobiology 51:530–537.

Peckarsky, B. L., and M. A. Penton. 1989. Mechanisms of prey selection by stream-dwelling stoneflies. Ecology 70:1203–1218.

Peckarsky, B. L., and M. A. Penton. 1990. Effects of enclosures on stream microhabitat and invertebrate community structure. Journal of the North American Benthological Society 9:249–261.

Peckarsky, B. L., B. W. Taylor, and C. C. Caudill. 2000. Hydrologic and behavioral constraints on oviposition of stream insects: implications for adult dispersal. Oecologia 125:186–200.

Peckarsky, B. L., B. W. Taylor, A. R. McIntosh, M. A. McPeek, and D. A. Lytle. 2001. Variation in mayfly size at metamorphosis as a developmental response to risk of predation. Ecology 82:740–757.

Peters, R. L. 1989. Effects of global warming on biological diversity. Pages 82–95 in D. E. Abrahamson, editor. The challenge of global warming. Island Press, Washington, D.C., USA.

Poff, N. L. 2002. Ecological response to and management of increased flooding caused by climate change. Philosophical Transactions of the Royal Society of London 360:1497–1510.

Poff, N. L., S. Tokar, and P. Johnson. 1992. Stream hydrological and ecological responses to climate change assessed with an artificial neural network. Limnology and Oceanography 41:857–863.

Rahel, F. J., C. J. Keleher, and J. L. Anderson. 1996. Potential habitat loss and population fragmentation for cold water fish in the North Platte River drainage of the Rocky Mountains: response to climate warming. Limnology and Oceanography 41:1116–1123.

Rempel, R. S., and J. C. H. Carter. 1986. An experimental study on the effect of elevated temperature on the heterotrophic and autotrophic food resources of aquatic insects in a forested stream. Canadian Journal of Zoology 64:2457–2466.

SAS Institute. 1997. JMP 3.2.2. SAS Institute, Inc., Cary, North Carolina, USA.

Schlosser, I. J., and P. L. Angermeier. 1995. Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and implications for conservation. American Fisheries Society Symposium 17:392–401.

Schneider, S. H. 1993. Scenarios of global warming. Pages 9–23 in P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, editors. Biotic interactions and global change. Sinauer Associates, Sunderland, Massachusetts, USA.

Scott, D., and M. Poynter. 1991. Upper temperature limits for trout in New Zealand and climate change. Hydrobiologia 222:147–151.

Sedell, J. R., G. H. Reeves, F. R. Hauer, J. A. Stanford, and C. P. Hawkins. 1990. Role of refugia in recovery from disturbances: modern fragmented and disconnected river systems. Environmental Management 14:711–724.

Statzner, B., and T. F. Holm. 1982. Morphological adaptations of benthic invertebrates to stream flow—an old question studied by means of a new technique (laser doppler anemometry). Oecologia 53:290–292.

Steinman, A. D. 1996. Effects of grazers on freshwater benthic algae. Pages 341–373 in R. J. Stevenson, M. L. Bothwell, and R. L. Lowe, editors. Algal ecology. Academic Press, San Diego, California, USA.

Stewart, I. T., D. R. Cayan, and M. D. Dettinger. 2004. Changes in snowmelt runoff timing in western North America under a "business as usual" climate change scenario. Climatic Change 62:217–232.

Sweeney, B. W., J. K. Jackson, J. D. Newbold, and D. H. Funk. 1991. Climate change and the life histories and biogeography of aquatic insects in eastern North America. Pages 143–176 in P. Firth and S. G. Fisher, editors. Global climate change and freshwater ecosystems. Springer-Verlag, New York, New York, USA.

Sweeney, B. W., and R. L. Vannote. 1978. Size variation and the distribution of hemimetabolous aquatic insects: two thermal equilibrium hypotheses. Science 200:444–446.

Taylor, B. W., A. R. McIntosh, and B. L. Peckarsky. 2002. Large-scale invertebrate manipulations in stream ecosystems: invertebrate removal, algal response, and opportunities for innovation. Limnology and Oceanography 47:893–899.

Vance, S. A. 1996. Morphological and behavioural sex reversal in mermithid-infected mayflies. Proceedings of the Royal Society of London B 263:907–912.

Vannote, R. L., and B. W. Sweeney. 1980. Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. American Naturalist 115:667–695.

Van-Winkle, W., and B. D. Holcomb. 1999. Would hydrologic climate changes influence trout persistence? Transactions of the American Fisheries Society 128:222–240.

Vitousek, P. M. 1994. Beyond global warming: ecology and global change. Ecology 75:1861–1876.

Ward, J. V., and J. A. Stanford. 1979. Ecological factors controlling stream zoobenthos with emphasis on thermal modification in regulated streams. Pages 35–55 in J. V. Ward and J. A. Stanford, editors. The ecology of regulated streams. Plenum Press, New York, New York, USA.

Watanabe, N. C., I. Mori, and I. Yoshitaka. 1999. Effect of water temperature on the mass emergence of the mayfly, Ephoron shigae, in a Japanese river (Ephemeroptera: Polymitarcyidae). Freshwater Biology 41:537–541.

Wetzel, R. 1983. Limnology. Second edition. Saunders, New York, New York, USA.

Wright, L. L., J. S. Mattice, and J. J. Beauchamp. 1982. Effect of temperature and sex on growth-patterns in nymphs of the mayfly Hexagenia bilineata in the laboratory. Freshwater Biology 12:535–545.

Zar, J. H. 1984. Biostatistical analysis. Second edition. Prentice Hall, Englewood Cliffs, New Jersey, USA.