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Egg and larval development times for 35 species of tropical stream insects from Costa Rica

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Abstract. We examined total development times for 5 mayfly species, 2 stoneflies, 10 caddisflies, and 18 chironomid midges collected from three streams that flow through tropical evergreen forest in northwestern Costa Rica. Most eggs, larvae, and pupae were reared in the laboratory in a photoperiod of 12:12 LD and at 20°C, which simulated field conditions. Algae, algal detritus, and leaves were provided as food for all species; predators were also given various animal prey. All study species had total development times that were rapid relative to the univoltine life histories observed or assumed for many temperate species. Egg development times ranged from a few days to approximately a week for chironomids and from 10 to 38 days for mayflies, stoneflies, and caddisflies. Most chironomids had short larval/pupal development times: development was completed in 19–29 d by seven species, in 30–40 d by nine species, and in >50 d by two species. Relatively short development times (including the pupal stage when present) were also observed for the mayfly *Acerpenna* sp. (28 d) and the caddisflies *Wormaldia* sp. (45 d) and *Oecetis* nr. *prolongata* (52 d). Larval/pupal development times were longer for the other four mayflies (76–159 d), two stoneflies (83–167 d), and eight caddisflies (72–209 d). No evidence of egg or larval diapause was observed. The combination of rapid development and absence of diapause suggests that all these species have multivoltine life histories. This finding has important implications for temporal changes in the structure and function of the aquatic insect assemblage in these streams.

Key words: aquatic insect, tropical, development time, growth rate, life history, Ephemeroptera, Plecoptera, Trichoptera, Chironomidae, Costa Rica.

Total development time (i.e., the time between oviposition and adult emergence) reflects the rates at which eggs develop and hatch, larvae feed and grow, and larvae/pupae metamorphose to adults. The time it takes to complete development is a function of the combined influences of environmental conditions such as temperature, food availability, and photoperiod, and genetically determined physiological processes such as diapause and rates of growth and development (Sweeney 1984). Many temperate species have one-year life cycles (i.e., univoltine life cycles) with seasonal reproductive periods (e.g., Wiggins 1977, Clifford 1982, Stewart and Stark 1988, Newbold et al. 1994). In contrast, the general assumption has been that tropical aquatic insects develop quickly (i.e., have multivoltine life cycles) and reproduce throughout the year because of warmer water temperature and low seasonality in biotic and abiotic conditions (e.g., Oliver 1971, Bishop 1973, Clifford et al. 1973). This assumption is supported by evidence for a limited number of species from tropical locations (e.g., MacDonald 1956, Hynes and Williams 1962, Froehlich 1969, Hynes 1975, Statzner 1976, Marchant 1982) and from warm temperate locations (e.g., Gray 1981, Hauer and Benke 1991, Benke et al. 1992).

The presence of insect species with multivoltine life cycles rather than univoltine life cycles has important implications for the ecology of tropical stream insects, and in turn, the structure and function of tropical stream ecosystems. For example, with comparable densities and biomass, a multivoltine species should produce more individuals and have greater secondary production (Benke 1984), recover more rapidly from natural or anthropogenic disturbance, and track or exploit temporally variable resources more effectively compared with an univoltine species (Mackay 1992). While there is no reason to doubt that many tropical stream insects are multivoltine, three questions remain generally unanswered: (1) what are development times of tropical stream insects (e.g., 25, 50, or 150 d), (2) how much do development times of tropical stream insects vary among tropical environments (e.g., warm and wet ver-

TABLE 1. Location and time of collection of ovipositing females, and trophic relationships for larvae of Costa Rican stream insects. Absence of a collection record at a site does not mean that the species does not occur there. Trophic relationships were determined from observations of feeding in the laboratory.

Taxon	R. Tem-pis-quito	R. Tem-pis-quito Sur	Q. Mari lin	Collection time[a]	Trophic relationships[b]
EPHEMEROPTERA					
Acerpenna undescribed sp. Waltz	X			AM	G
Leptohyphes undescribed sp. 1 Funk	X			AM	G, SH
Leptohyphes undescribed sp. 4 Funk			X	AM	
Tricorythodes sp.	X		X	AM	G (SC)
Thraulodes undescribed sp. 1 Funk	X			PM	SC
PLECOPTERA					
Anacroneuria undescribed sp. CR13 Stark	X			AM	P
Anacroneuria undescribed sp. CR5V2 Stark	X				P
TRICHOPTERA					
Polyplectropus undescribed sp. 3 Holzenthal	X			PM	
Wormaldia sp.			X	PM	
Leptonema simulans simulans Mosely	X				F
Phylloicus elegans Hogue and Denning			X		SH, SC
Phylloicus ornatus (Banks)[c]	X		X		SH, SC
Phylloicus undescribed sp. nr. *ornatus* Holzenthal[d]	X			PM	SH, SC
Helicopsyche dampfi Ross	X	X		AM, PM	SC
Nectopsyche gemmoides Flint	X			PM	
Oecetis undescribed sp. nr. *prolongata* Holzenthal	X			AM	
Triplectides flintorum Holzenthal	X		X	AM, PM	SC, SH
CHIRONOMIDAE					
Tanypodinae					
Paramerina fasciata Sublette and Sasa	X	X	X	AM, PM	P
Orthocladiinae					
?*Cricotopus* undescribed sp. Cr-1 Epler	X				
Parametriocnemus undescribed sp. CR-1 Epler	X	X	X	PM	G, SH
Parametriocnemus undescribed sp. CR-2 Epler	X			PM	G, (SH)
Parametriocnemus undescribed sp. CR-3 Epler	X	X		PM	G, SH
Chironominae					
Chironomus anonymus Williston			X	AM, PM	G, SH, (SC)
Endotribelos grodhausi Sublette and Sasa	X		X	PM	G, SH
Endotribelos undescribed sp. CR-1 Epler	X		X	PM	G, SH
Polypedilum cf. *corniger* Sublette and Sasa			X	PM	G, SH
Polypedilum epomis Sublette and Sasa			X	PM	G, SH
Polypedilum microzoster Sublette and Sasa	X		X	PM	G, SH
Polypedilum obelos Sublette and Sasa		X	X	PM	G
Polypedilum undescribed sp. CR-1 Epler	X	X		PM	G, SH
Polypedilum undescribed sp. CR-3 Epler	X			PM	G, SH
Stenochironomus leptopus (Kieffer)			X	PM	
Stenochironomus cf. *quadrinotatus* Borkent	X			PM	
Stenochironomus undescribed sp. CR-1 Epler			X	PM	
Tanytarsus pandus Sublette and Sasa			X	AM	G

[a] AM = 0430–0630 h, PM = 1630–1830 h. Egg masses obtained from stream substrates were not given a collection time.

[b] F = filterer, G = gatherer, P = predator, SC = scraper, SH = shredder (sensu Merritt and Cummins 1984).

sus cool and wet or seasonally warm and wet), and (3) are there mechanisms that induce or maintain seasonality in the life history in seasonal or "non-seasonal" tropical environments? Answers to these questions are necessary if we are to better understand the dynamics of tropical stream insects and their role in tropical stream ecosystems.

Several methods have been used to estimate development times for stream insects. The most common method requires sampling larvae (and often adults) at regular intervals during a year. Relative abundances of the various life stages are used to infer when oviposition, egg diapause, and egg hatching occur as well as temporal patterns of larval growth, pupation (if present), and adult emergence. This approach has been useful in north temperate regions where many species have univoltine life histories with distinct periods during which eggs, larvae, and adults are found. However, it is less informative with populations that are not tightly synchronized in their development or are multivoltine with overlapping cohorts. Several aquatic insects in temperate regions (e.g., many chironomids), and presumably most species in warmer regions of the world, exhibit such life histories. In these cases, two alternative approaches have been (1) to estimate larval development times from instantaneous growth rates (e.g., Benke and Jacobi 1986, Hauer and Benke 1991, Benke et al. 1992) or (2) to rear the insects from egg to adult in the field or in the laboratory under simulated field conditions (e.g., Dejoux 1971, Mackey 1977, Gray 1981, Sweeney and Vannote 1984). We used the latter approach to estimate egg and larval development times for 35 species of aquatic insects from three tropical mountain streams in Costa Rica. These data were compared with field or laboratory observations for related species from tropical and warm temperature locations, and for related species with summer generations at temperate locations.

Methods

Field collection sites

All species examined (Table 1) were collected from the Río Tempisquito (10°57′25″N, 85°29′42″W, 590 m a.s.l.), Río Tempisquito Sur (10°57′10″N, 85°29′25″W, 580 m a.s.l.), and/or Quebrada Marilin (10°57′04″N, 85°29′22″W, 600 m a.s.l.) near the Estación Biologica Maritza, Parque Nacionale Guanacaste, Costa Rica. These streams are tributaries of the Río Tempisque, which flows west-southwest from the Cordillera de Guanacaste to the Pacific Ocean. The R. Tempisquito and R. Tempisquito Sur are medium-sized streams (mean annual discharge = 0.30 and 0.42 m^3/s, respectively) with forest canopies that are partially open (mean stream width = 5.3 m for the R. Tempisquito, but is not available for the R. Tempisquito Sur). Quebrada Marilin is a small stream (mean annual discharge = 0.018 m^3/s) and has a closed canopy (mean stream width = 1.9 m). Upland vegetation adjacent to the collection sites is tropical evergreen forest that is the transition between lowland dry forest and higher elevation rain forest. Leaves fall into the streams throughout the year, with substantial increase during the dry season (January through May when only 0.3 m or 12% of annual rainfall occurs) relative to the wet season (June through December). Water temperature averaged 21.4°C (annual range = 20.0–23.0°C) in the R. Tempisquito, 21.3°C (annual range = 20.0–22.5°C) in the R. Tempisquito Sur, and 21.6°C (range = 20.0–23.0°C) in Q. Marilin. Daylength (sunrise to sunset) at this latitude ranges from 11.5 h in December to 12.75 h in June. More detailed descriptions of these three streams can be found in Newbold et al. (1995).

Rearing methods

Diel and seasonal variation in water temperature and light are not great at our study sites.

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Trophic relationships arranged in descending order of importance; classifications in parentheses are considered much less important than preceding classifications. Some species were not abundant enough to classify.

[c] Includes 359 adults reared from six egg masses collected at Quebrada Kathia, Estación Maritza, Parque Nationale Guanacaste, Costa Rica.

[d] Includes 181 adults reared from two egg masses collected at Río Orosi, Estación Patilla, Parque Nationale Guanacaste, Costa Rica.

In an effort to create conditions that were a relatively close simulation of natural light and temperature regimes, eggs and larvae were reared in constant temperature (usually 20°C) and light (photoperiod = 12:12 LD). This reduced the potential for differences between laboratory and field observations resulting from temperature or photoperiod.

Eggs.—Gravid females were collected by sweeping over the surface of the stream with a large insect net. Captured females were placed in a glass jar (3.0 cm deep; 2.5 cm diameter) filled with 10–20 mL of stream water. Females laid their eggs in the water or on the wall of the jar. Egg masses containing very young embryos were also scraped from rocks or boulders in or along the edge of the stream; development times for these eggs were potentially underestimated because oviposition dates were not known. Eggs were kept in constant (20 or 22 ± 1°C) temperature water baths. Date of first hatch, and in many cases median hatch, were noted. Egg data were summarized with arithmetic means and standard deviations when more than one egg mass was collected for a species. If larvae were needed for rearing, eggs were kept at 13 or 15°C to slow development and transported to the Stroud Water Research Center in Pennsylvania, USA.

Immatures.—All immatures were reared at the Stroud Center. Larvae of most mayfly, stonefly, and caddisfly species were transferred to polypropylene trays (23 × 45 cm, 22 cm deep) filled with water from White Clay Creek (Chester Co., Pennsylvania) and covered with mesh cloth. With the exception of a few preliminary rearings, offspring from only one female were placed in a tray. Individual trays were started as closed systems, with water temperature kept at 20 ± 1°C by a heat exchange coil in each tray that was connected to a large, temperature-regulated reservoir also filled with water from White Clay Creek. The bottom of each tray was covered with sand and gravel. Once immatures were large enough to be contained by a 500-μm screen, the coils were removed and water from the reservoir flowed through the trays (0.1–1.0 L/min). Additional current and aeration were supplied by an air stone. Light was provided by fluorescent lights (80 W Vita-lite; Duro Test Co.) suspended directly over trays.

In our early rearings, each tray was provided with two plexiglass plates (138 cm^2) that were well colonized by algae (predominantly diatoms; Sweeney and Vannote 1984) from White Clay Creek and/or leaves (primarily sugar maple [*Acer saccharum*], red maple [*Acer rubrum*], white oak [*Quercus alba*], and hickory [*Carya ovata, Carya ovalis*]) that had been soaked in stream water for at least a week. We soon discovered that survivorship was greater for some species when they were provided with more than one type of food (e.g., presumed collector-gatherers would also shred leaves; Table 1). Thereafter, we started trays with algal plates, a mixture of leaves, and algal detritus (algae scraped from plates and frozen to kill algae and colonizing invertebrates). Predaceous stoneflies were also provided prey in the form of chironomid and tipulid (*Limonia*) larvae, oligochaetes, Planariidae, and meiofauna (e.g., rotifers and ostracods) that colonize algae-covered plexiglass plates, while predaceous chironomids were given meiofauna and chironomids (*Limnophyes*). We attempted to provide a non-limiting supply of food.

Two species (the mayfly *Thraulodes* sp. 1 and the caddisfly *Leptonema simulans*) were reared in miniature laboratory streams made from circular plexiglass chambers (14.5 cm in diameter; Mackay 1981). Each chamber contained gravel for substrate and water from White Clay Creek; water current was created by air bubbles. Chambers were placed in constant temperature (20 ± 1°C) water baths. Larvae were provided with algae (growing on the container walls and substrates) and daily additions of algal detritus. Larger *L. simulans* were also given deal tipulid (*Limonia*) larvae.

Chironomid larvae were reared in mesh-covered glass jars (2 L) containing sand and gravel for substrate and filled with 1.2 L of White Clay Creek water that was aerated slightly. Rearing jars were kept in constant temperature (20 ± 1°C) water baths. Larvae were provided with algae (growing on the container walls), algal and fine leaf detritus, and a piece (~15 cm^2) of leaf. Algal detritus and leaves were added periodically in some jars as larvae consumed the original food supply.

Rearing containers were checked daily for adults. When an adult was found, the container was examined carefully to obtain associated larval or pupal exuviae for taxonomic associations. Whole larvae (2–5 individuals) were also collected from each container for taxonomic references. Representative adults and associated larval/pupal material were sent to taxonomic

specialists for species identification or confirmation of the undescribed status of the species. Voucher specimens are currently being curated as part of the aquatic macroinvertebrate collection at the Stroud Water Research Center. Date of emergence and sex were recorded for each adult. Observations were pooled if adults were available from more than one egg mass. Emergence data were summarized as minimum, maximum, and median number of days from egg hatch to emergence. Adults of more abundant species were dried at 45°C for >48 h; mean male and female dry masses were averaged to calculate mean individual biomass for each species.

Egg and larval development times for the Costa Rican stream insects were compared with available field or laboratory observations for related species from tropical and temperate locations. Egg and larval development times were converted to degree days (DD = development time in days × average water temperature [°C] during development) for comparison of species living in different thermal environments. This approach assumes a low-temperature developmental threshold of 0°C for all species and therefore results in only rough estimates of degree-day requirements (Giberson and Rosenberg 1992). Inaccurate comparisons using this approach would result if temperature falls below developmental thresholds in some studies but not in others, or if developmental thresholds differed dramatically among species. Fortunately, errors in the degree-day comparisons presented here are presumably not great because temperature was warm in the examples cited and probably did not go below developmental thresholds. In addition, developmental thresholds for eggs of temperate species are often not more than a few degrees lower than those of tropical species (Sweeney, unpublished data). No data are currently available on developmental thresholds for larvae of tropical stream insects.

Results and Discussion

Ephemeroptera

Baetidae: *Acerpenna* sp.

Egg hatching for *Acerpenna* sp. began approximately 17 d after oviposition, with a median egg development time of 23 d (460 DD; Table 2). Larvae were successfully reared on an algal diet, completing larval development rapidly. Minimum larval development time was 26 d and median larval development time was 28 d (560 DD). *Acerpenna* sp. appears to be parthenogenic; all reared adults were female, females readily oviposited without mating, and 25.8–68.5% of the unfertilized eggs hatched.

Baetid mayflies often have more rapid development than other aquatic insects. For example, multivoltinism is not unusual for *Baetis* spp. in many temperate locations where other mayflies are univoltine (Clifford 1982). This life history results from rapid egg and larval development. Egg development for several baetid mayflies has been found to be much faster than the 23 d observed for *Acerpenna* sp. at 20°C. For example, egg development at 19–22°C was completed in 1–2 d (22–44 DD; Gray 1981) and 6 d (138 DD; Gray 1989, personal communication) for *Fallceon* (formerly *Baetis*) *quilleri*; 9 d (180 DD) for *Baetis rhodani* (Elliott 1972); 11 d (220 DD) for *Centroptilum* (formerly *Cloeon*) *triangulifer* (Sweeney and Vannote 1984); and 12 d (228 DD) for *Baetis soror* (Suter and Bishop 1990).

Larval development time for *Acerpenna* sp. was comparable to or shorter than that of most baetid species in warm environments; e.g., 18 d (495 DD) for *Baetis* spp. in a subtropical stream in Georgia, USA (Benke et al. 1992); 18 d (459 DD) for *Centroptilum* in Ghana (Hynes 1975); 28 d (840 DD) for *Cloeon fluviatile* in tropical Australia (Marchant 1982); 30 d for *Baetis* and *Centroptilum* in Uganda (Hynes and Williams 1962); 27 d (675 DD) for *C. triangulifer* from Pennsylvania reared at 25°C (Sweeney and Vannote 1984); and 45 d (900 DD) for *C. triangulifer* reared at 20°C (Sweeney and Vannote 1984). Development time for *Acerpenna* sp. was also similar to the 26-d (520 DD) development time predicted for *Baetis* spp. at 20°C using the temperature-dependent growth model derived by Benke et al. (1992) with a cohort P/B = 5 (Benke and Jacobi 1986). In contrast, larval development times for *Acerpenna* sp. and the other temperate or tropical baetid species listed above are longer than development times for *F. quilleri* from a Sonoran Desert stream (6–11 d, 132–242 DD; Gray 1981) and from a prairie stream in Kansas, USA (17 d, 391 DD at 23°C; Gray 1989, personal communication).

TABLE 2. Egg and larval development times for Ephemeroptera (mayflies), Plecoptera (stoneflies), Trichoptera (caddisflies) and Chironomidae (aquatic midges) collected from streams in Costa Rica and reared in the laboratory. Rearing temperature was 20°C except where indicated for eggs of Chironomidae. Development times were rounded to the nearest day.

Taxon	Days to 1st egg hatch[a]	Days to median egg hatch[a]	Median days egg hatch to adult	Range days egg hatch to adult	Number of adults reared[b]	Individual biomass (mg, dry)
EPHEMEROPTERA						
Acerpenna sp.	17 ± 3 (7)	23 ± 1 (7)	28	26–34	86 (5)	0.47 (2)
Leptohyphes sp. 1	19 ± 5 (64)	19 ± 1 (5)	82	65–125	169 (12)	0.68 (41)
Leptohyphes sp. 4	29 ± 4 (2)	NA[c]	76	70–98	19 (4)	0.22 (4)
Tricorythodes sp.	19 ± 3 (16)	21 ± 1 (5)	86	58–109	97 (7)	0.35 (59)
Thraulodes sp. 1	18 ± 1 (3)	19 ± 1 (3)	159	131–165	6	2.73 (3)
PLECOPTERA						
Anacroneuria sp. CR13	38 ± 4 (2)	NA	83		1	NA
Anacroneuria sp. CR5V2	26[d]	NA	167	135–197	14 (2)	7.73 (11)
TRICHOPTERA						
Polyplectropus sp. 3	12	12	96	89–106	4	0.60 (3)
Wormaldia sp.	11	12	45		1	NA
Leptonema simulans	24[e]	NA	103	90–122	4 (3)	17.89 (4)
Phylloicus elegans	16 ± 0 (2)[d]	NA	72	66–87	47 (2)	5.32 (28)
Phylloicus ornatus	10 ± 0 (6)	11 ± 0 (5)	110	59–178	1404 (35)	4.26 (642)
Phylloicus nr. *ornatus*	10	NA	114	70–151	386 (5)	4.11 (190)
Helicopsyche dampfi	9 ± 2 (2)	9 ± 2 (2)	77	55–141	208 (10)	0.35 (81)
Nectopsyche gemmoides	23	NA	87	82–90	4	0.67 (3)
Oecetis nr. *prolongata*	10	10	52	50–54	3	0.51 (2)
Triplectides flintorum	13 ± 2 (3)	14 ± 1 (2)	209	151–261	87 (7)	6.46 (68)
CHIRONOMIDAE						
Tanypodinae						
Paramerina fasciata	4 ± 1 (3)[f]	4 ± 0 (2)[f]	40	26–86	25 (3)	0.02 (2)
Orthocladinae						
?*Cricotopus* sp. Cr-1	3[d]	3[d]	19	17–20	2	
Parametriocnemus sp. CR-1	4[f]	4[f]	30	21–57	258 (11)	0.05 (17)
Parametriocnemus sp. CR-2	9[g]	9[g]	24	22–33	32	0.05 (8)
Parametriocnemus sp. CR-3	4 ± 0 (4)[f]	4 ± 0 (4)[f]	36	21–73	551 (7)	0.04 (174)
Chironominae						
Chironomus anonymus	3 ± 1 (2)[f]	3 ± 1 (2)[f]	50	28–64	195 (2)	0.60 (60)
Endotribelos grodhausi	2 ± 1 (3)	3 ± 1 (3)	31	17–50	144 (3)	0.13 (48)
Endotribelos sp. CR-1	3[f]	4[f]	34	23–62	38 (3)	0.10 (16)
Polypedilum cf. *corniger*	5	5	26	20–37	70 (2)	0.07 (21)
Polypedilum epomis	4[f]	NA	22	18–33	90 (3)	0.08 (42)
Polypedilum microzoster	4[f]	4[f]	24	20–37	55 (2)	0.09 (17)
Polypedilum obelos	3	3	72	30–105	865 (3)	0.15 (287)
Polypedilum sp. CR-1	3 ± 1 (3)[f]	3 ± 1 (3)[f]	26	19–58	839 (10)	0.05 (265)
Polypedilum sp. CR-3	9[g]	9[g]	40	36–49	15	0.03 (3)
Stenochironomus leptopus	4[f]	4[f]	33		1	NA
Stenochironomus cf. *quadrinotatus*	9[g]	9[g]	23	22–23	2	NA
Stenochironomus sp. CR-1	3	3	30		1	NA
Tanytarsus pandus	2[f]	2[f]	33	25–41	58	0.05 (22)

[a] If more than one egg mass was examined, hatching data are summarized as $\bar{x}$ ± 1 SD and number in parentheses represents number of egg masses.

Leptohyphidae (formerly Tricorythidae): *Leptohyphes* sp. 1, *Leptohyphes* sp. 4, *Tricorythodes* sp.

Adults of *Leptohyphes* sp. 1. and 4 and *Tricorythodes* sp. were collected in morning swarms that formed 0.5–4.0 m above riffle/run areas (Table 1). Unlike some other leptohyphid mayflies (Jackson 1988), spatial or temporal segregation among species was not evident because males and females of all three species were collected simultaneously at one location. *Leptohyphes* sp. 1 was more common at the R. Tempisquito and *Leptohyphes* sp. 4 was more common at Q. Marilin.

Egg hatching for *Leptohyphes* sp. 1 began after 19 d (380 DD) and was synchronized (Table 2). Egg development took approximately 50% longer for *Leptohyphes* sp. 4 (29 d, 580 DD). Larvae of *Leptohyphes* sp. 1 were successfully reared in trays containing algae, algal detritus, and leaves that the larvae skeletonized rapidly. No adults were successfully reared from trays without leaves. Median larval development time was 82 d (1640 DD) for *Leptohyphes* sp. 1 (Table 2). Larval development for *Leptohyphes* sp. 4 took 76 d (1520 DD) when larvae were fed leaves, algae, and algal detritus. Larvae of *Leptohyphes* sp. 4 also appeared to consume leaves, but we have not determined if leaves are an essential part of the larval diet.

Egg and larval development times for *Tricorythodes* sp. were similar to those for *Leptohyphes* sp. 1. Median egg development of *Tricorythodes* sp. was 21 d (420 DD), and median larval development time was 86 d (1720 DD; Table 2). Unlike *Leptohyphes* sp. 1, larvae of *Tricorythodes* sp. were successfully reared on algae as well as algae supplemented with algal detritus and leaves.

Egg development has not been examined extensively for leptohyphid mayflies. Egg development times for the three Costa Rican leptohyphids in our study were approximately half as long as the development time observed for *Tricorythodes minutus* from a constant temperature stream in Idaho (40 d, 840 DD; Newell and Minshall 1978). In contrast, the Costa Rican leptohyphids had egg development times that were much longer than those reported for *Leptohyphes packeri* and *Tricorythodes dimorphus* from a Sonoran Desert stream (1–2 d, 22–44 DD; Gray 1981).

Leptohyphid mayflies in our study had larval development times that were 1.5–2× longer than larval development times reported for *T. minutus* (44 d in field and 48 d in laboratory, 836 and 960 DD, respectively; Newell 1976), for *Tricorythodes atratus* from the headwaters of the Mississippi River (50 d, 1025 DD at mean temperature = 20.5°C; Hall et al. 1980), and for *Tricorythodes* spp. from a subtropical river in Georgia, USA (31 d, 853 DD; Benke and Jacobi 1986). Moreover, the Costa Rican leptohyphids had larval development times that were 5–9 × longer than those reported for *L. packeri* and *T. dimorphus* (7–11 d, 176–242 DD; Gray 1981, Fisher and Gray 1983).

Leptophlebiidae: *Thraulodes* sp. 1.

Egg hatching for *Thraulodes* sp. 1 began 18 d after oviposition, with a median egg development time of 19 d (380 DD; Table 2). In the laboratory streams, larvae were observed feeding on algae and algal detritus, completing larval development in 131–165 d (median larval development time = 159 d, 3180 DD). Like *Acerpenna* sp., *Thraulodes* sp. 1 appears to be parthenogenic; all adults from laboratory rearings and field collections were female and 74.2–95.2% of the unfertilized eggs hatched.

Development times from field or laboratory rearings are not available for other tropical leptophlebiids; however, Campbell (1994) used larval size distribution to estimate total development time (i.e., the combination of egg and larval times) for three leptophlebiid species (*Jappa edmundsi, Jappa serrata, Jappa* sp.) in a tropical Australian river system. Total development time for *Thraulodes* sp. 1 (178 d, 3560 DD) was

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[b] If adults were reared from more than one egg mass, number in parentheses represents number of egg masses.

[c] NA = data not available.

[d] Egg mass was collected from stream substrates; exact date of oviposition is not known.

[e] Data for an undetermined species of *Leptonema*.

[f] Eggs reared at 22°C.

[g] Eggs reared at 15°C.

similar to development time estimated for *J. serrata* (130 d, 3500 DD), and longer than for *J. edmundsi* (100 d, 2500 DD) and *Jappa* sp. (75–120 d, 2000–3000 DD).

Plecoptera

Perlidae: *Anacroneuria* sp. CR13, *Anacroneuria* sp. CR5V2

We have successfully reared two of the 11 species of *Anacroneuria* currently known to occur in these streams (unpublished data). Egg development time was 38 d (760 DD) for *Anacroneuria* sp. CR13 and at least 26 d (520 DD) for *Anacroneuria* sp. CR5V2 (Table 2). Larval development was completed in 83 d (1660 DD) for *Anacroneuria* sp. CR13 and 135–197 d (median larval development time = 167 d, 3340 DD) for *Anacroneuria* sp. CR5V2.

Most stoneflies have either univoltine or semivoltine life histories (Hynes 1976, Stewart and Stark 1988). The relatively rapid development time and absence of an egg or larval diapause is strong evidence that *Anacroneuria* sp. CR13 and *Anacroneuria* sp. CR5V2 are able to complete two or more generations per year. To our knowledge, our observations are the first clear documentation of multivoltinism for a stonefly. Bivoltinism has been considered for some stoneflies based on laboratory growth studies and/or the presence of overlapping cohorts in the field (e.g., Froehlich 1969, Hynes and Hynes 1975). For example, Froehlich (1969) estimated that larval development time for the detritivore *Paragripopteryx anga* (Griptopterygidae) from a Brazilian stream was 150 d (2175 DD), which is longer than for *Anacroneuria* sp. CR13 but shorter than for *Anacroneuria* sp. CR 5V2. Unfortunately, egg development was not observed for *P. anga*. Rapid larval development such as was observed for the stoneflies in our study is known to occur in other stoneflies (e.g., approximately 120 d for *Isoperla signata* [Ernst and Stewart 1985, see Stewart and Stark 1988 for further examples]); however, rapid larval development in these other species is preceded by a long egg diapause that results in a univoltine life history.

Trichoptera

Polycentropodidae: *Polyplectropus* sp. 3

Median egg development for *Polyplectropus* sp. 3 was 12 d (240 DD) and median larval/pupal development was 96 d (1920 DD; Table 2). Development times for *Polyplectropus* sp. 3 are shorter than those estimated for the polycentropodid *Neureclipsis crepuscularis* in the Savannah River, Georgia, USA (120 d, 2700 DD at 22.5°C for egg, larval, and pupal development combined; Cudney and Wallace 1980), but longer than those estimated for *Pseudoneureclipsis aculeata* in a mountain stream in Zaire (total development time as the combination of egg and larval/pupal times was ≈90 d, 1710 DD at 19°C; Statzner 1976, temperature from Böttger 1975), for *Polycentropus halidus* from a Sonoran Desert stream (6–28 d [132–616 DD] and 40 d [880 DD] for egg and larval/pupal development, respectively; Gray 1981), and for *Polycentropus flavomaculatus* from England (42 d, 588 DD at 14°C for larval development; Bass et al. 1982).

Philopotamidae: *Wormaldia* sp.

Median egg development for *Wormaldia* sp. was 12 d (240 DD) and larval/pupal development lasted 45 d (900 DD; Table 2). Total development time for *Wormaldia* sp. (57 d, 1140 DD) was much shorter than that estimated by Cudney and Wallace (1980) for a summer generation of the philopotamid *Chimarra mosleyi* (120 d, 2700 DD at 22.5°C) in the Savannah River, Georgia, USA.

Hydropsychidae: *Leptonema simulans simulans*

Eggs of *L. simulans* are found on large, partially submerged rocks in turbulent riffles. Females lay their eggs in contiguous rows forming flat patches (~1 cm in diameter) on rock surfaces that are above the water surface and continuously wetted by water splashed from the stream. Eggs from several females may be grouped together forming larger patches in some locations. In egg jars, females deposited their eggs on the glass walls above the water or on the plastic lid. Eggs began hatching 24 d (480 DD) after oviposition, and larval capture nets and gravel retreats were first visible after 30 d in laboratory streams. Larvae actively consumed algal detritus as well as animals that collected in the nets. Median larval/pupal development time was 103 d (2060 DD). The pupal stage lasted 21 d (range = 20–22 d, $n = 4$); thus, larval development was 82 d (1640 DD).

Egg and larval/pupal development times from field or laboratory rearings are not available for other tropical hydropsychids; however, Statzner (1976) estimated total development time for three hydropsychid species (*Cheumatopsyche boettgeri, Cheumatopsyche explicanda, Diplectronella medialis*) based on adult emergence from a mountain stream in Zaire. Total development time for *L. simulans* in our study (127 d, 2540 DD) was comparable to development times for *C. explicanda* and *D. medialis* (~120 d, 2280 DD at 19°C, temperature from Böttger 1975), but longer than for *C. boettgeri* (~60 d, 1140 DD). Similarly for temperate hydropsychids, total development time for *L. simulans* was comparable to development times for summer generations of *Hydropsyche incommoda, Hydropsyche rossi,* and *Cheumatopsyche passella* (120 d, 2700 DD at 22.5°C; Cudney and Wallace 1980), but longer than for *Cheumatopsyche arizonensis* from a Sonoran Desert stream (50 d, 1100 DD; Gray 1981) and *Cheumatopsyche campyla* from the Mississippi River (51 d, 1377 DD at 27°C; Fremling 1960).

Calamoceratidae: *Phylloicus elegans, Phylloicus ornatus, Phylloicus* nr. *ornatus*

Eggs of *Phylloicus* spp. were encased in ball-shaped gelatinous matrices that were commonly found in pools attached to large rocks and exposed soils just below the water surface. Egg development was rapid for all three species (10–16 d, 200–320 DD, Table 2). Our laboratory and field observations confirm those by Wiggins (1977, 1984) that leaves are the primary case-building material for *Phylloicus* larvae, and an important part of the larval diet (along with algae). Leaf material incorporated into cases was also consumed as the larvae grew and removed the posterior ends of the cases (i.e., the older, smaller portions). Median larval/pupal development times were 72, 110, and 114 d (1440, 2200, and 2280 DD) for *P. elegans, P. ornatus,* and *P.* nr. *ornatus,* respectively (Table 2). The pupal stage lasted 14 d (range = 12–17 d, $n = 15$) for *P. ornatus* and 15 d (range = 14–16 d, $n = 4$) for *P* nr. *ornatus.* Using these estimates, larval development was 96 d for *P. ornatus* and 99 d for *P.* nr. *ornatus,* respectively.

Comparable data on egg and larval development are available for the tropical calamoceratid *Anisocentropus kirramus* from an Australian stream (Nolen and Pearson 1992). Egg development times for *Phylloicus* spp. were similar or slightly longer than that observed for *A. kirramus* (maximum of 10 d at 22–25°C), whereas larval development times for *Phylloicus* spp. were shorter than the several-month development suggested for *A. kirramus* from field collections (Nolen and Pearson 1992). Many other life history traits exhibited by *A. kirramus* (e.g., first-instar behaviors, feeding, case building, continuous emergence) are similar to those we have observed for *Phylloicus* spp. in Costa Rica.

Helicopsychidae: *Helicopsyche dampfi*

Eggs of *H. dampfi* are encased in a ball-shaped gelatinous matrix like those of *Phylloicus* spp. However, egg masses of *H. dampfi* were much smaller than those of *Phylloicus* spp. and generally are found singly or in small clusters below the water surface on cobbles (partially or completely submerged) in the shallow water along riffle edges. Egg hatching for *H. dampfi* began after 9 d (180 DD) and was synchronized (Table 2). Larvae successfully completed development on an algal diet, with adults emerging 55–141 d (median = 77 d, 1540 DD) after egg hatching (Table 2). The pupal stage lasted 16 d ($n = 3$); thus, larval development was 61 d (1220 DD). These development times are longer than those reported for *Helicopsyche mexicana* in a Sonoran Desert stream (6 d [132 DD], 33 d [726 DD], 11 d [242 DD] for egg, larval, and pupal stages, respectively; Gray 1981), but similar to those reported for *Helicopsyche borealis* in a stream in Oklahoma (16–17 d [320–340 DD] for egg stage, 63–84 d [1260–1680 DD] for larval stages; Vaughn 1985).

Leptoceridae: *Nectopsyche gemmoides, Oecetis* nr. *prolongata, Triplectides flintorum*

Development times differed greatly among the three leptocerid species that have been reared (Table 2). Egg development for *N. gemmoides* lasted 23 d (460 DD). Larval and pupal development of *N. gemmoides* were difficult to monitor because larvae burrowed in the gravel. Adults emerged 82–90 d (median = 87 d, 1740 DD) after egg hatching (Table 2). Development times for *O.* nr. *prolongata* were shorter than for *N. gemmoides*: egg development lasted 10 d (200 DD) and larval/pupal development lasted 52 d (1040 DD).

Egg masses of *T. flintorum* were collected from ovipositing females or from the damp undersides of logs lying across Q. Marilin, approximately 0.5 m above the water. Median egg development was 14 d (260 DD; Table 2). Larvae of *Triplectides* spp. are believed to be shredders (Flint 1991); however, larvae of *T. flintorum* also actively consume algae in the field and laboratory, and early instars appear to feed exclusively on algae in the laboratory. Late instars feed on leaves and algae. Larval/pupal development time for *T. flintorum* was the longest of the aquatic insect species examined in this study (range = 151–261 d, median = 209 d, 4180 DD; Table 2). The pupal stage lasted 21 d (n = 1); thus, larval development was approximately 188 d. The extended larval development may to some degree reflect time spent locating and preparing new cases as larvae grew; the other caddisflies in our study simply added to their old cases as they grew. When larvae of *T. flintorum* hollow out twigs for new cases, they select well conditioned twigs collected from a stream rather than twigs soaked briefly in water.

Diptera

Chironomidae: one species of Tanypodinae, four species of Orthocladiinae, 13 species of Chironominae

Egg development ranged from 2 to 9 d for the 18 chironomid species examined (Table 2). Longer egg development times (9 d, 135 DD) are for three species reared at 15°C whereas species reared at 20–22°C completed egg development in 2–5 d (44–100 DD). Egg development time generally decreases as temperature increases. For example, respective development times for *Chironomus anonymus* and *Polypedilum* sp. CR-1 were 6 and 7 d at 15°C (unpublished data) versus 3 d at 22°C. Thus, egg development times would presumably be 3–5 d at 20°C for those species examined only at 15°C.

Adult chironomids began to emerge 17–36 d after egg hatch (Table 2). Seven of the 18 species examined had median larval/pupal development times of <30 d (380–520 DD); nine species had development times between 30 and 40 d (600–800 DD); and two species had development times >50 d (1000 and 1440 DD). Longer development for *C. anonymus* to some degree must reflect the large size of the species (Table 2), but food limitation may have also contributed: it was difficult to keep food non-limiting in the first rearing (164 adults were obtained from a jar containing one egg mass). The large number of *Polypedilum obelos* adults reared (>280 adults from each of three egg masses) suggests the potential for food limitation contributing to longer development for *P. obelos*, although leaves and algal detritus were added frequently to these rearing jars. We were able to monitor the duration of the pupal stage for 12 species (*Paramerina fasciata* = 1 d, *Parametriocnemus* sp. CR-1 = 1 d, *Parametriocnemus* sp. CR-3 = 1 d, *C. anonymus* = 2 d, *Endotribelos* sp. CR-1 = 1 d, *Endotribelos grodhausi* = 2 d, *Polypedilum* cf. *corniger* = 2 d; *Polypedilum epomis* = 2 d, *Polypedilum microzoster* = 1 d, *P. obelos* = 1 d, *Polypedilum* sp. CR-1 = 2 d, *Polypedilum* sp. CR-3 = 2 d; n = 1–16 individuals for each species). Using these estimates and assuming 2 d in the pupal stage for the other chironomid species, median larval development time was 17–71 d (340–1420 DD).

Chironomid egg development times are known for a limited number of species from tropical and temperate locations; most studies estimate egg hatching within a few days to a few weeks after oviposition, depending on the species and the temperature (e.g., Dejoux 1971, Nebeker 1973, Gray 1981, Menzie 1981, Ladle et al. 1985). Estimates for the 18 species examined in this study are comparable to the more rapid estimates in these studies as well as in unpublished data that we have for other Costa Rican chironomids (range = 3–24 d at 20°C) that were not successfully reared to the adult stage.

Our estimates of larval development time for Costa Rican chironomids are comparable to observations for other tropical chironomids (e.g., MacDonald 1956, Hynes and Williams 1962, Syrjämäki 1965, Dejoux 1971, Hynes 1975, MacLachlan and Cantrell 1980) as well as for temperate chironomids in warm conditions. For example, larval development times for summer/autumn generations for multivoltine species in temperate locations have ranged from several days (e.g., Mackey 1977, Gray 1981, Menzie 1981, Stites and Benke 1989) to a few to several weeks (e.g., Nebeker 1973, Mackey 1977, Gray 1981, Menzie 1981, Pinder 1983, Ladle et al. 1985, Rempel and Harrison 1987, Stites and Benke 1989, Berg and Hellenthal 1992). Two temperature-dependent growth models have been developed for chironomids at temperate

locations (Huryn and Wallace 1986, Hauer and Benke 1991). Using growth rates from these models and a cohort P/B = 5 (Benke and Jacobi 1986), the Huryn and Wallace model predicts a larval development time of 29 d at 20°C whereas the Hauer and Benke model predicts a larval development time of only 8 d. Several species in our study had larval development times that were similar to the Huryn and Wallace prediction, but none were comparable to the Hauer and Benke prediction. This difference between models presumably reflects physiological differences (e.g., different larval growth and development rates, final size) between species examined by Hauer and Benke (1991) and Huryn and Wallace (1986). Mackey (1977) observed the same degree of variation among several chironomid species from the River Thames. Because chironomid richness can be high at a single location on a Costa Rican stream (e.g., >150 species at our study reach in the R. Tempisquito, Coffman et al. 1992, W. P. Coffman, University of Pittsburg, personal communication), more data were obviously needed before generalizations can be made about development times for Costa Rican chironomids or the applicability of growth models derived for temperate species.

Factors affecting development rates in R. Tempisquito drainage

All aquatic insects reared from the R. Tempisquito, R. Tempisquito Sur, and Q. Marilin had development times that were fast relative to the univoltine life histories commonly observed or assumed for temperate species. Undoubtedly, rapid development reflects in part the warm average temperature and absence of thermal extremes that might limit growth (e.g., temperature below developmental thresholds). However, it also reflects the absence of egg or larval diapauses that can commonly prolong development and maintain univoltinism in temperate environments (Newbold et al. 1994). In fact, none of the 85+ aquatic insect species that we have examined have exhibited evidence of egg diapause (Sweeney, unpublished data). Our data support early suggestions that multivoltinism will be a predominant life history for insects in tropical streams (e.g., Oliver 1971, Bishop 1973, Clifford et al. 1973). The number of generations completed annually should vary among species, depending on their development times. Larval/pupal development times are partially a function of adult size: it generally takes more time to grow to a larger size (Fig. 1). Thus, small species such as *Polypedilum* sp. CR-1 (adult biomass = 0.05 mg; total development times = 29 d) should complete more generations per year than larger species such as *Phylloicus ornatus* (adult biomass = 4.3 mg; total development time = 121 d).

Unlike the 35 species examined here, there is evidence of longer life histories for some insects in these Costa Rican streams: the damselfly *Cora marina* (Polythoridae) appears to be univoltine (G. Pritchard, University of Calgary, personal communication) and the mayfly *Euthyplocia hecuba* (Polymitarcyidae) appears to be semivoltine (Sweeney et al. 1995). Univoltinism in *C. marina* may be the combined result of slow larval growth and seasonal reproductive success associated with wet-season spates. Three factors contributing significantly to semivoltinism in *E. hecuba* are: very long egg development (55 d), slow larval growth, and an extraordinarily large adult size (maximum = 35 mg for males and 135 mg for females). Seasonality in adult emergence of *E. hecuba* suggests that some environmental or physiological mechanisms (e.g., a biological clock) are also influencing development rate at some time during its life cycle. The role of factors such as environmental seasonality and physiological timing mechanisms on the developmental rates of the 35 insect species in our study remains to be examined.

Egg and larval development rates for many of the Costa Rican species we examined were comparable to or faster than temperate species living in warm environments. However, there were several cases where development times for the Costa Rican species were slower than those observed for their temperate relatives. The most dramatic difference was that none of the 35 species examined had extraordinarily rapid development times such as have been observed for some mayflies and chironomids living in the subtropical and desert regions of North America (Gray 1981, Benke and Jacobi 1986, Hauer and Benke 1991). For example, the egg development time for baetid and leptohyphid mayflies from Costa Rica was longer than the time it took related species from a Sonoran Desert stream to complete their entire life cycles

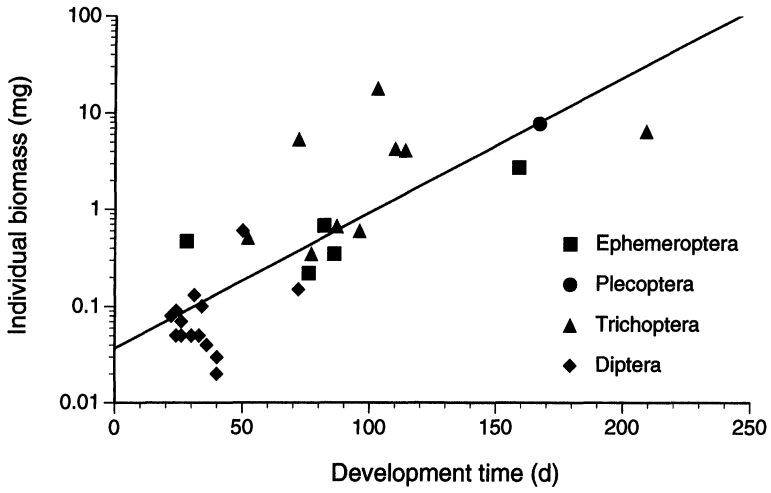

FIG. 1. Simple linear regression evaluating the relationship between median larval (and pupal, if present) development times and mean adult biomass (mg, dry) for Ephemeroptera, Plecoptera, Trichoptera, and Diptera from three Costa Rican streams ($r^2 = 0.65$, $p < 0.001$).

(Gray 1981). Similarly, larval development time for baetid and leptohyphid mayflies was 2–9× longer for the Costa Rican species compared with species in a Sonoran Desert stream or subtropical stream in Georgia (Gray 1981, Fisher and Gray 1983, Benke and Jacobi 1986). In some cases, larval development times in our study were also longer than larval development times reported for north temperate relatives (e.g., *Tricorythodes* sp. 1 versus *Tricorythodes minutus* and *Tricorythodes atratus;* Newell 1976, Hall et al. 1980). Some differences may be the result of the variety of methods used, whereas others appear to reflect significant taxonomic differences that are presumably related to different evolutionary histories.

One explanation for the apparent discrepancies might be that laboratory conditions in our study in some way slowed development (e.g., because temperature was inappropriate or food inadequate). This view is actually the opposite of the commonly held belief that laboratory rearing conditions are so ideal (i.e., with optimal temperature and photoperiod and unlimited food resources) that development times observed in the laboratory may underestimate field development times (e.g., Mackey 1977, Ward and Cummins 1979). Because of the limited diel and seasonal variation characteristic of our Costa Rican study sites, we believe that temperature and photoperiod regimes in the laboratory had little or no effect on development time.

Food quality and quantity are known to affect larval development times; low food quantity or quality can increase development time and decrease adult size (Sweeney 1984). Obviously, the food we provided was of temperate origin, but a variety of unrelated temperate species have found it acceptable (e.g., Sweeney and Vannote 1984, Vannote and Sweeney 1985, Sweeney et al. 1986a, 1986b, Sweeney, unpublished data). In addition, it was readily consumed by the tropical species in our study, and laboratory-reared adults were similar in size to field-collected adults (personal observation). Other researchers have also observed the rapid consumption of temperate leaves by tropical microorganisms and macroinvertebrates (e.g., Stout 1989). We found in preliminary rearings that food preferences of some species differed from those expected from published accounts for related species. For example, leaves appeared to be very important in the diets of several species (e.g., *Leptohyphes* sp. 1, *Chironomus anonymus, Parametriocnemus* sp. CR-1, *Endotribelos grodhausi, Endotribelos* sp. CR-1) that we initially assumed to be primarily fine-detritus feeders. Conversely, species believed to be principally detritivorous shredders (e.g., *Triplectides flintorum, Phylloicus elegans, Phylloicus ornatus, Phylloicus* nr. *ornatus*) eagerly consumed algae when available. We attempted to ameliorate this influence in subsequent rearings (representing most of the adults reared) by providing an abundant and diverse supply of food that was

replenished frequently. Thus, with the possible exceptions of *Chironomus anonymus* and *Polypedilum obelos*, we do not believe that food increased the larval development times reported here. Assuming that food was not a factor, the extended larval development times such as were exhibited by baetid and leptohyphid mayflies from Costa Rica suggest that some species in our study have higher thermal thresholds for development (i.e., they accumulate degree days more slowly) or greater thermal requirements compared with some related species from more northern areas.

Implications for population dynamics and ecosystem function

Development times observed for the Costa Rican species have important implications for temporal and geographic variation in population dynamics and ecosystem function. First, development times should affect rates of change in the structure of the insect assemblages in these Costa Rican streams relative to temperate streams. For example, our study suggests that recovery rates following natural or anthropogenic disturbances (e.g., severe spates, stream drying, pollution spills) should be slower in these Costa Rican streams than in Sonoran Desert streams (Fisher et al. 1982, Jackson and Fisher 1986, Grimm and Fisher 1989, Bouton et al. 1992), but faster than in cooler temperate streams (e.g., Giller et al. 1991). Like the desert stream, the presence of mature, non-diapausing eggs in stream refugia and/or an "aerial reserve" of adults (cf., Gray and Fisher 1981) virtually insures that recovery of the insect assemblages in these Costa Rican streams will begin immediately following these disturbances; however, longer egg and larval development times should lengthen recovery time in the Costa Rican streams relative to Sonoran Desert streams. In contrast, recovery rates in the Costa Rican streams should be faster than in temperate streams because temperate insect assemblages are generally dominated by univoltine and bivoltine species that have delays inherent in their life histories (e.g., seasonal reproduction, egg or larval diapauses, temperature-limited growth rates).

Second, the several-fold difference in development times between chironomids and other insects in the Costa Rican streams suggests that chironomids might be more prominent in the early stages of recovery following disturbance. In addition, the structure of the insect assemblage may change following disturbance as other species are able to complete life cycles. One unknown factor that may affect his recovery process is the presence of eggs in refugia. If eggs from all species are abundant following a disturbance, then successional patterns may be minimal. Thus, successional patterns may be most evident in intermittent streams near R. Tempisquito because viable eggs are presumably rare when surface flow resumes at the beginning of the wet season.

Third, the combination of taxonomic variation in growth rates, temporal variation in the structure of the aquatic insect assemblage, and seasonal differences in leaf input and algal standing crop (J. D. Newbold, Stroud Water Research Center, unpublished data) should result in significant temporal variation in trophic structure in these Costa Rican streams.

Finally, because of geographic variation in development time and therefore growth rates, estimates of secondary production in these Costa Rican streams will differ from estimates from north temperate and warm temperate streams. Assuming comparable densities and biomass, aquatic insect secondary production should be greater than estimates for many north temperate streams (see review by Benke 1993), but less than the extremely high estimates from desert and subtropical regions of North America (Fisher and Gray 1983, Benke et al. 1984, Jackson and Fisher 1986). Preliminary observations suggest that aquatic insect densities and biomass are not exceptionally high in these Costa Rican streams, and therefore would not contribute to unusually high production.

The accuracy and general applicability of these predictions depends on how representative our results are to other tropical streams and how representative the limited studies of the desert and subtropical streams are to other warm temperate streams. The above discussion comparing available data for the individual species illustrates the obvious need for more data on stream insects from warm temperate as well as a variety of tropical locations (e.g., warm versus cool or wet versus dry) before these predictions can be assessed and possibly modified (Jackson and Sweeney 1995).

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