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PRIMARY RESEARCH PAPER

Life history strategies and production of caddisflies in a perennial headwater stream in Patagonia

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Abstract Synchrony, one of the main traits of population life histories, refers to the degree to which individuals complete a certain stage of the life cycle at the same time. It can be governed by temperature, variations in temperature, photoperiodic cues, detritus inputs, or discharge regimes. We investigated life cycles and secondary production of five caddisfly species in a second order stream in the Patagonian Mountains. In addition, we analyzed what environmental variables were implied in the caddisfly assemblage variation. *Mastigoptila* sp. (Glossosomatidae) and *Eosericostoma aequispina* (Helicophidae), *Myotrichia murina* (Sericostomatidae), *Brachysetodes quadrifidus* (Leptoceridae), and *Neoatopsyche brevispina* (Hydrobiosidae) showed univoltine life cycles, with an extended recruitment with no overlapping cohorts and a relatively well-synchronized imaginal emergence taking place during spring summer seasons. However, *Myotrichia murina* (Sericostomatidae) displayed a complex life cycle with mixed populations taking 10–12 months to develop, and pupae being collected almost continuously. The annual secondary production per species varied from 11.06 (*E. aequispina*) to 310.5 mg m^{-2} $year^{-1}$ (*M. murina*), being overall caddisfly production (0.5 g m^{-2} $year^{-1}$) similar to that reported for cold springs in other regions. The highest growth rates (*K*) were observed during late winter and spring (mostly September) and ranged from 0.70 to 3.70% day^{-1} in *M. longicornuta* and *N. brevispina*, respectively. Redundancy analysis indicated that seasonally dynamic variables, water temperature, discharge, and detritus biomass were the main predictors of caddisfly assemblage variation; consequently at this cold stream (mean annual 5.9°C), with a regular availability of food supply, these parameters ruled Trichoptera life histories and secondary production. As documented for other mountainous temperate areas, synchrony would be a dominant trait on life histories of Trichoptera species inhabiting Patagonian streams.

Keywords Life cycles · Trichoptera · Biomass · Mountain rivers · Voltinism · Secondary production

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Introduction

The life history of an organism reflects a suite of interacting factors which includes genetic information, inter-specific relationships, and environmental characteristics (Butler, 1984). They are regulated mainly by river temperature (Komzák & Sedlák,

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2002; Dobrin & Giberson, 2003; Jin & Ward, 2007), food condition or its availability (Sweeney et al., 1986; Richardson, 2001), and respond to a series of selection pressures operating on all life stages encompassing both aquatic and terrestrial habitats (Richardson, 2001). Life history strategies (growth patterns, voltinism, and developmental time) are essential to understand species adaptation to the environment (Becker, 2005). One of the main traits of life history of populations is the synchrony; this refers to the degree to which individuals complete a given stage of the life cycle at the same time (Butler, 1984). This feature may be driven by different environmental factors such as temperature or variations in temperature, either alone or with photoperiodic cues, detritus input or discharge regimes (Sweeney & Vannote, 1981; Sweeney, 1984; Richardson, 2001).

Lytle & Poff (2004) argue that when the timing of floods and droughts is sufficiently predictable among years, the life history strategy of organisms is generally synchronized with the long-term dynamics of the flow regime. Life history adaptations include the timing of reproduction and growth, emergence into aerial stage and diapause. These strategies generally enable organisms to avoid mortality by escaping floods or droughts. When these events are little or not predictable, asynchrony in some life stages is frequently observed. For example, this is the case of some stream insects in the Southern Hemisphere, such as those in New Zealand, where flexible, poorly synchronized life histories with nonseasonal patterns of development and extended flight periods have been observed (Winterbourn et al., 1981). This apparent flexibility may be related to climatic constancy, unpredictability of discharge, and a greater continuity in supply of allochtonous inputs (Scarsbrook, 2000). In other studies carried out in Europe, Zwick (1996) reported that some stoneflies display an asynchronous hatching within egg clutches, possibly as a bet-hedging strategy in watercourses with irregular hydrological regime. Moreover, hatching asynchrony seems to be higher in populations subjected to a more variable flood regime, than those of the same species in more stable environments (Lytle & Poff, 2004). In extreme conditions as those experimented in desert streams, caddisflies can synchronize their metamorphosis (early imaginal emergence) with the average timing of flood season, to avoid flood mortality (Lytle, 2002).

Rivers draining the Patagonian Mountains are more predictable in terms of annual discharge patterns than those in the Patagonian steppe or the Plateau which are characterized by aridity. Discharge regime in the cordillera depends upon rainfall and snowmelt, showing relatively constant patterns over the years (Jobbágy et al., 1995; Beltrán, 1997; Paruelo et al., 1998). Therefore, one might expect life histories of stream insects to have a greater degree of synchrony in growth (Miserendino & Pizzolón, 2003), as indeed occurs with some species of stoneflies and mayflies (Hollmann & Miserendino, 2006, 2008).

Trichoptera larvae are a major component of lotic ecosystems (Ward, 1992), they significantly contribute to zoobenthic biomass, being an important link between primary production and consumers such as other macroinvertebrates and fish (Miserendino, 1999; Miserendino & Pizzolón, 2004; Wiggins, 2004; Angrisano & Sganga, 2009). Patagonian species are highly endemic, and are known to be sensitive to environmental disturbances (Miserendino & Brand, 2007; Brand & Miserendino, in press). Even though the taxonomical and ecological knowledge of the group in the area has improved in recent years (Miserendino, 1999; Angrisano & Sganga, 2009), at present there are no studies focused on population dynamics. An appropriate knowledge of life history strategies and production in an undisturbed low order stream is highly valuable for conservation purposes of aquatic resources.

Caddisfly species inhabiting streams in temperate areas tend to display univoltine life cycles (Richardson & Clifford, 1986; Marchant & Hehir, 1999; Mendez & Resh, 2008). Nevertheless, smaller and fast growing species show bivoltine or even trivoltine life cycles in warmer low order streams (Álvarez & Pardo, 2005; Jin & Ward, 2007). According to the River Continuum Concept (Vannote et al., 1980), the functioning of headwater systems rely on leaf litter input as the main source of energy. Many aspects of their community and population structure are governed and timed by this event. Particularly, the life cycle of macroinvertebrate species inhabiting Northern Hemisphere lotic environments appear to be synchronized with this phenomenon (Petersen & Cummins, 1974; Richardson, 2001).

We expect that in Patagonian headwater streams, with a seasonal input of organic matter and a relatively predictable hydrological regime, the life cycle of caddisfly species would be highly synchronized, with no overlapping cohorts, and nonextended emergence period. We conducted this study in order (1) to assess the phenology and voltinism of five Trichoptera species, (2) to estimate their secondary production and *P/B* ratios, and (3) to analyze the seasonal variation of Trichoptera assemblages examining the main environmental constraints in a perennial low order stream in Patagonian Mountains.

Methods

Study site

The samples were taken from a second order stream (Chiquito stream, 71°30′22″W, 43°21′43″S) which belongs to the Frío Basin in the mountains of the Northwest of the Chubut Province in Patagonia (Argentina), at an altitude of 670 m.a.s.l. This permanent stream drains a small catchment of 11 km^2. The rainfall in the area, as estimated from Jobbágy et al. (1995), is 600 mm/year. The discharge pattern is bimodal, with a peak coincident with winter rainfalls, where 46% of annual precipitation occurs (Jobbágy et al., 1995; Paruelo et al., 1998), and a second one with snowmelt in spring. Riparian forest had a dense coverage, and provides shade during a long period of the year. It is composed by the deciduous tree Ñire (*Nothofagus antarctica*) with a dense shrub cover of native species (*Ribes cucullatum*, *Berberis buxifolia* and *B. heterophylla*, *Maytenus chubutensis*, and *Schinus patagonica*) (León et al., 1998). The input of litter fall in Patagonian mountainous environments is a well documented phenomenon (Miserendino & Pizzolón, 2004; Díaz Villanueva et al., 2010); in native deciduous *Nothofagus* leaf abscission takes place during autumn (mostly concentrated from April to July).

In a previous study at the sampling site, benthic samples included substantial amounts of leaves, fragmented organic matter, wood, macrophytes, and bryophytes (Masi & Miserendino, 2009). Autotrophic production seems to be considerable as revealed by analysis of chlorophyll *a* from periphyton communities in this river riffles (Miserendino & Masi, 2010).

Environmental characterization and sampling procedure

The site was sampled monthly from May 2007 to April 2008. Substrate size composition was estimated as percentage of boulders, cobbles, gravel, pebbles, and sand in the reach, using a 1 m^2 grid. Current speed (m s^{-1}) was measured, each date in mid-channel by timing a float (average of three trials) as it moved over a distance of 10 m (Gordon et al., 2004). Average depth (cm) was estimated from five measurements on three transects across the channel with a calibrated stick; wet width (m) of the channel was also measured. Discharge (m^3 s^{-1}) was obtained by combining depth, wet width, and current speed as in Gordon et al. (2004). On each sampling occasion, water temperature, pH, specific conductance (μS cm^{-1}), and dissolved oxygen (mg O_2 l^{-1}) were measured with a multi-parameter probe (Hach SensION 156). Water temperature was recorded continuously at 1 h intervals, averaged and stored every 24 h, using a thermograph (−20/+80°C, 0.1°C resolution) specially built for this project.

To analyze seasonal variation in abundance and to describe the life cycles, larvae were collected monthly on three riffles using a Surber net (0.09 m^{-2}; 250 μm mesh size). Additionally, one integrated sample was collected each month to obtain extra material. Samples were fixed in the field with formaldehyde solution (4%). Adult collection was performed every 2 weeks during the summer months, by sweeping the riparian vegetation for 15 min. Light traps were also placed at the site for a 45 min period at early night. Specimens were fixed and stored in 70% alcohol.

In the laboratory, larvae were sorted manually under 5× magnification, counted and preserved in 70% alcohol. All specimens were identified using available keys (Angrisano, 1998; Valverde & Albariño, 1999; Angrisano & Sganga, 2009).

Detritus occurring in the integrated samples of each month were divided into fine (250–1,000 μm) and coarse (>1,000 μm) particulate fractions (FPOM and CPOM, respectively). After that, coarse organic material (CPOM) was divided into wood, leaves (mainly entire leaves), and others (fragments of leaves, grass, seeds, roots, and buds, etc.). Additionally, we assessed the contribution of filamentous algae and bryophytes. All fractions were dried (60°C for 24 h) and weighed.

Life cycle analysis

From all Trichoptera-identified species those numerically dominant were selected to describe the life history. In the procedure at least two body measures from each specimen were taken and the most accurate (i.e. the one that allowed us to elucidate the size classes' structure) was used to produce histograms and determine size classes. Total length (TL) was measured from the anterior tip of the pronotum to the posterior margin of the IX segment of the abdomen, pronotum length (PL) was measured along the mid dorsal ecdysial line, and head capsule width (HCW) as the maximum width of the head capsule (Komzák & Sedlák, 2002; Becker, 2005). Measures were made under 8× and 32× magnifications (depending on the size of the species) with a binocular dissecting scope equipped with a linear eyepiece micrometer, to the nearest 0.025 mm (Richardson, 2001; Jin & Ward, 2007).

For each species, five size classes were deduced from the body measurements above described. The development of the cohorts was deduced from the population size structure at the various sampling periods (Tsuruishi, 2003; Álvarez & Pardo, 2005; Jin & Ward, 2007). The presence of late instars (pre-pupa and pupa) of each species was documented in their respective months and indicated in histograms, as well as the presence of adults.

Functional feeding group was assigned to each species according to available references (Miserendino & Masi, 2010; Brand & Miserendino, in press).

Length–mass relationships

Body mass relationship is usually described by the general power equation $DM = a\ L^b$, or after logarithmic transformation as $\log DM = \log a + b \log L$ (where: a, b = regression constants, DM = dry mass, and L = length parameters) (Miyasaka et al., 2008). To determine dry mass for each species, a representative number of each size class was selected. Each specimen was individually transferred to a plastic vial (1.5 ml). The pool of specimens was dried at 105°C for 4 h (Smock & Stoneburner, 1980). All individuals were weighed on an electronic balance with 0.1 mg accuracy. Different regression models were evaluated to fit the data points to suitable regression equations. In general, linear regression models were appropriate.

Secondary production, *P/B* ratio, and growth rates

Secondary production data combine information on individual growth and population survivorship, while it reflects the amount of energy available to higher trophic levels (Benke, 1984, 1996). Production was calculated using the size frequency method (Benke, 1993). Larvae were assigned to size groups for analysis. According to this technique, both annual production and annual *P/B* require a calibration based on the CPI (cohort production interval), which is the mean development time from hatching to final size (Benke, 1996).

The mean individual weights of cohorts from each site were natural log transformed to generate a series of subsegment linear regressions that represent the cohort's growth patterns over the year. The relationship between the mean individual dry weight of the larvae of each cohort and time was calculated as $Wt = Wt_0 * e^{kT}$, where Wt = weight at instant t, Wt_0 = weight at instant t_0, $T = t - t_0$ days, k = instantaneous growth rate (mg mg^{-1} day^{-1}). Growth of individuals was expressed as specific growth rate, K, with $K = 100k$ (% dry weight day^{-1}) (Céréghino et al., 1997).

Caddisfly community ordination

To identify the main environmental variables ruling caddisfly assemblages along time at the study site, we performed a multivariate analysis using the entire caddisfly community. Redundancy analysis (RDA) was conducted to determine the linear combinations of environmental variables that best explained patterns in species abundances. RDA was chosen for ordinations because preliminary analysis showed that species abundance variation was better described by linear response modeling than by unimodal models (gradient length of axis one to four: 1.2; 0.5; 0.8; and 0.8, respectively) (ter Braak & Smilauer, 1998). Ordinations were performed using the package CANOCO version 4.0 (ter Braak & Smilauer, 1998). Biotic variables were log $(x + 1)$ transformed prior to statistical analysis to normalize and stabilize variance. Environmental variables (listed in Table 1)

Table 1 Physico-chemical parameters and biomass of filamentous algae, bryophytes, and detrital fractions

Parameter	Winter		Spring		Summer		Autumn		Mean annual values (±SD)
	Jun–Sep		Sep–Dec		Dec–Mar		Mar–Jun		
	Mean	Range	Mean	Range	Mean	Range	Mean	Range	
pH	7.06	6.94–7.21	6.99	6.85–7.18	7.64	7.4–8.01	7.51	6.9–8.01	7.30 ± 0.41
Air temperature (°C)	3.33	0–6	14	10.1–18	21.33	17–26	14.66	13–16	12.78 ± 8.64
Water temperature (°C)	3.53	2.4–5.3	7.23	5.1–9.1	11.2	8–13.1	8.83	7.8–10.5	7.7 ± 3.38
Conductivity (μS cm^{-1})	53.86	51.8–57.8	42.9	29.4–104.7	66.13	55.2–73–6	64.4	62.4–67.5	58.09 ± 11.91
Dissolved oxygen (mg l^{-1})	10.55	9.56–11.26	9.96	8.86–11.51	12.32	8.22–15.39	7.80	7.2–8.34	10.16 ± 2.43
Saturation percentage	80.2	76.8–85	84.53	77.6–93.6	114.46	80.1–131.8	69.33	64–73.6	87.13 ± 22.05
Wet width (m)	2	2	2.86	2.50–3.1	2.89	2.78–3	2.76	2.6–3	2.63 ± 0.42
Depth (cm)	10.88	9–13	15.48	14.53–20	11.27	9.13–14	12.71	10.13–16.6	12.59 ± 3.26
Current speed (m s^{-1})	0.66	0.4–1.18	0.89	0.69–1.07	0.73	0.52–0.86	0.60	0.5–0.66	0.72 ± 0.25
Discharge (m^3 s^{-1})	0.13	0.09–0.21	0.42	0.21–0.66	0.24	0.15–0.30	0.21	0.15–0.29	0.25 ± 0.16
Filamentous algae (g m^{-2})	0.048	0.008–0.11	0	0	0.18	0–0.55	0	0	0.06 ± 0.16
Bryophytes (g m^{-2})	2.45	1.3–4.62	5.71	0.9–8.36	1.82	0.54–2.86	2.03	0.54–3.9	3 ± 2.7
Leaves (g m^{-2})	2.04	0.83–3.36	0.76	0.3–1.24	1	0.22–1.43	3.03	1.34–6.04	1.7 ± 1.6
Wood (g m^{-2})	4.87	2.04–8	4.4	2.26–6.65	3.9	1.47–5.84	4.84	4.21–5.49	4.5 ± 1.9
Others (g m^{-2})	3.04	1.4–4.5	4	2.9–4.6	2.7	0.48–4.28	3.5	2.72–3.9	3.31 ± 1.28
CPOM (g m^{-2})	9.9	5.4–15.8	9.1	5.4–11.8	7.6	2.2–11.56	11.37	9.4–14.7	9.51 ± 3.88
FPOM (g m^{-2})	2.23	1.8–2.5	3.2	1.73–4.14	0.91	0.14–1.28	2.6	1.69–3.39	2.23 ± 1.25

Data are mean and range values by season (May 2007 to April 2008) from Chiquito Stream (Patagonia, Argentina)

SD standard deviation, *CPOM* and *FPOM* coarse and fine particulate organic matter, respectively

were considered to produce the ordination. To extract a reduced variable set, covariable environmental factors were excluded if the VIF (variable inflation factor) was >10 (ter Braak & Smilauer, 1998). A set of five independent variables were used to perform the definitive RDA analysis. The significance of the primary RDA axes was determined by the Monte Carlo permutation test (9999 permutations) of the eigenvalues (ter Braak & Smilauer, 1999).

Results

Environmental features

Substratum was dominated by cobbles (25%), pebbles (20%), and boulders (15%); the reach also presented patches of bryophytes. Water temperature ranged from 0.4 (May) to 15.9°C (February) and the mean annual value was 5.9°C. Cumulative degree days obtained from thermograph records were 2200 for all the study period and 1392 for the warmer months (December–April). Wet width was comprised between 2 and 3.10 m. Minimal water depth was 9 cm and maximum 20 cm. Current speed varied between 0.4 and 1.18 m s^{-1}, with maximum mean value recorded in spring. Discharge values ranged from 0.09 (June) to 0.66 m^3 s^{-1} (October), with an extreme value in October (spring) (Table 1). Physicochemical conditions indicated that waters were circum-neutral and well oxygenated. Conductivity varied between 29.4 and 104.7 μS cm^{-1} (Table 1).

Detrital analyses showed that bryophytes were present during all seasons, while leaf biomass showed the highest contribution in autumn (3.03 g m^{-2}). Filamentous algae were detected only in winter and summer benthic samples (Table 1).

Trichoptera assemblages and life history description

Caddisfly community at Chiquito stream was composed by 17 species belonging to 9 families (Table 2). *Neoatopsyche unispina* (1.23 ind m^{-2}) was the less abundant species at the site, whereas *Myotrichia murina* was the most abundant (334.5 ind m^{-2}). Five Trichoptera species were selected for the life history description: *Mastigoptila* sp. (Glossosomatidae), *Eosericostoma aequispina* (Helicophidae), *Myotrichia murina* (Sericostomatidae), *Brachysetodes quadrifidus* (Leptoceridae), and *Neoatopsyche brevispina* (Hydrobiosidae). *Mastigoptila* sp. still remains as a nondescribed species, but all individuals corresponded morphologically to the same species.

Only the most suitable measurement for separating size classes was employed and therefore displayed.

Mastigoptila sp. Larvae of *Mastigoptila* sp. were absent from benthic samples in February and March. The maximum density was found in November (588 ind m^{-2}) (Fig. 1a). Biomass of *Mastigoptila* sp. was comprised between 1.13 (April) and 64.4 mg m^{-2} (November) (Fig. 1a). A total of 762 individuals were measured and divided into five size classes based on HCW. Recruitment of this species occurred from April to October, although small larvae dominated April and May samples (Fig. 2). A slow growth in larval size was observed from June to August (Fig. 3a) (mean growth rate, $K = 0.25 \pm 0.19\%$ day^{-1}), whereas a fast growing period occurred from May to June (0.70% day^{-1}) (Fig. 3a). Prepupal stage was recorded from November to January, while pupal stage was observed in November and January. No adults were collected. *Mastigoptila* sp. had a clearly univoltine life cycle, with a maximum time of 10 months required for development.

Eosericostoma aequispina Density of *E. aequispina* ranged between 7 and 207 ind m^{-2} in April and August, respectively. Larvae were absent in March. Minimum biomass of the species was 0.22 mg m^{-2} (April) while the maximum was 9.05 mg m^{-2} (August) (Fig. 1b). A total of 186 individuals were measured and divided into five size classes based on HCW. The smallest larvae were present in May; samples from August to October were dominated by classes II and III (Fig. 2), and growth rates were the lowest, being mean K values from May to October of $0.56 \pm 0.24\%$ day^{-1}. A fast growth in larvae size occurred in the following months with $K = 2.97 \pm 2.32\%$ day^{-1} (Fig. 3b). Pre-pupal stage was not found, pupal stages were recorded in September, October, and February, and adults were collected in February (Fig. 2). *E. aequispina* had a univoltine life cycle, with an estimated cohort development time of 11 months.

Myotrichia murina The minimum density of *M. murina* was 22 ind m^{-2} (January) and the maximum was 858 ind m^{-2} (August), biomass ranged from 9.6 to 272.32 mg m^{-2} in the same months (Fig. 1c). A total of 1,057 larvae were measured and divided into five size classes based on the PL. *M. murina* life history was very complex. Groups of larval size class I occurred at different times including April–May, July, September, and November. Pre-pupal and pupal stages were present in eight different months (Fig. 2). No adults of *M. murina* were collected during the sampling period. From this data, we infer that those larvae that hatched in April–May, overwintered as class II and III, started to pupate in October and emergence occurring until the end of January. A second group hatched from July to November, grew rapidly through the summer, and overwintered as size class V, started to pupate in September and to emerge in November. The lowest growth rate was observed between July and September ($0.34 \pm 0.15\%$ day^{-1}), while the maximum from June to September ($1.5 \pm 0.34\%$ day^{-1}) (Fig. 3c). Life cycle of *M. murina* showed an extended recruitment, a long emergence period, and co-occurrence of many size classes in all seasons. Therefore, its generation time was difficult to define from this data, presumably with an average cohort development time of 10–12 months.

Brachysetodes quadrifidus Density of *B. quadrifidus* ranged between 18 and 314 ind m^{-2} (February and August, respectively). The minimum biomass values were 0.32 mg m^{-2} (March), while the maximum was 6.9 mg m^{-2} (August) (Fig. 1d). A total of 415 larvae were measured. Based on HCW, five size classes were distinguished. The smallest larvae were recorded at 7 months indicating an extended recruitment (Fig. 2). A slow growth in larval size was observed from March to September, after that a fast growing period occurred (Fig. 3d). Pupal and adult stages were recorded in February. Growth rate of this

Table 2 Functional feeding groups (FFG), minimum and maximum density (ind m^2), mean annual density (ind m^2) ± standard deviation of all Trichoptera species found at Chiquito stream (Patagonia, Argentina), during the study period (April 2007–May 2008)

Taxa	FFG	Min–max density (ind m^2)	Total density ± SD (ind m^2)
Glossosomatidae			
Mastigoptila sp.*	Scr	0–588.9	264.5 ± 211.6
Helicophidae			
Eosericostoma aequispina Schmid, 1955*	Scr	3.7–207.4	61.4 ± 64.4
Austrocentrus valgiformis Flint, 1997	Pred	0–44.4	18.5 ± 15.9
Hydrobiosidae			
Cailloma pumida Ross, 1956	Pred	0–33.3	6.1 ± 9.9
Neoatopsyche brevispina Schmid, 1957*	Pred	7.4–129.6	50.4 ± 42
Neoatopsyche unispina Flint, 1967	Pred	0–7.4	1.2 ± 2.4
Neopsilochorema tricarinatum Schmid, 1955	Pred	0–7.4	3.5 ± 3.4
Rheochorema robustum Schmid, 1955	Pred	0–11.1	2.8 ± 4.5
Rheochorema tenuispinum Schmid, 1955	Pred	0–18.5	8.6 ± 6.2
Hydropsychidae			
Smicridea annulicornis (Blanchard, 1851)	Col–fil	0–429.6	64.8 ± 132.5
Smicridea frequens (Navás, 1930)	Col–fil	0–18.5	6.2 ± 6.9
Hydroptilidae			
Metrichia neotropicalis Schmid, 1958	Scr	0–72.2	15.6 ± 24.7
Metrichia patagonica (Flint, 1983)	Scr	3.7–74	22.2 ± 23.2
Leptoceridae			
Brachysetodes quadrifidus Schmid, 1955*	Shred	18.5–314.8	142.6 ± 98.6
Sericostomatidae			
Myotrichia murina Schmid, 1955*	Shred	22.2–859.2	334.5 ± 292.2
Limnephilidae			
Monocosmoecus sp.	Shred	0–18.5	4.9 ± 6.9
Philorheithridae			
Psilopsyche molinai Navás, 1926	Pred	0–29.6	6 ± 6.9

Species marked with an asterisk were selected for life cycle description and production estimation

Scr scraper, *Pred* predator, *Col–fil* collector filterer, and *Shred* shredder

species ranged from 0.1 (June) to 0.81% day^{-1} (September) (Fig. 3d). *B. quadrifidus* exhibited a univoltine life cycle.

Neoatopsyche brevispina Density of this species ranged between 7 and 129 ind m^{-2} (January and May, respectively). Biomass of *N. brevispina* was comprised between 1.24 (January) and 36.85 mg m^{-2} (May) (Fig. 1e). A total of 162 larvae were measured and separated into five size classes according to PL. An extended recruitment period was observed from January to September (Fig. 2). All size classes were present in May and June. Few larvae were collected from October to December mostly belonging to classes III to V. *N. brevispina* growth rates ranged from 0.36% day^{-1} in May to 3.70% day^{-1} in September (Fig. 3e). Although no prepupae, pupae, or adults were found in the study, the absence of small larvae, dominance of large larval sizes from October to December, and the fast growing period occurring from August to December (Fig. 2) lead us to believe that *N. brevispina* had a univoltine life cycle; with an estimated developmental time of 12 months.

For all species, we observed a linear regression between time and the natural logarithm of individual mean weight, indicating that an exponential growth occurred during the life cycle (Fig. 3a–e). Moreover, when analyzing the litter fall pattern, we observed

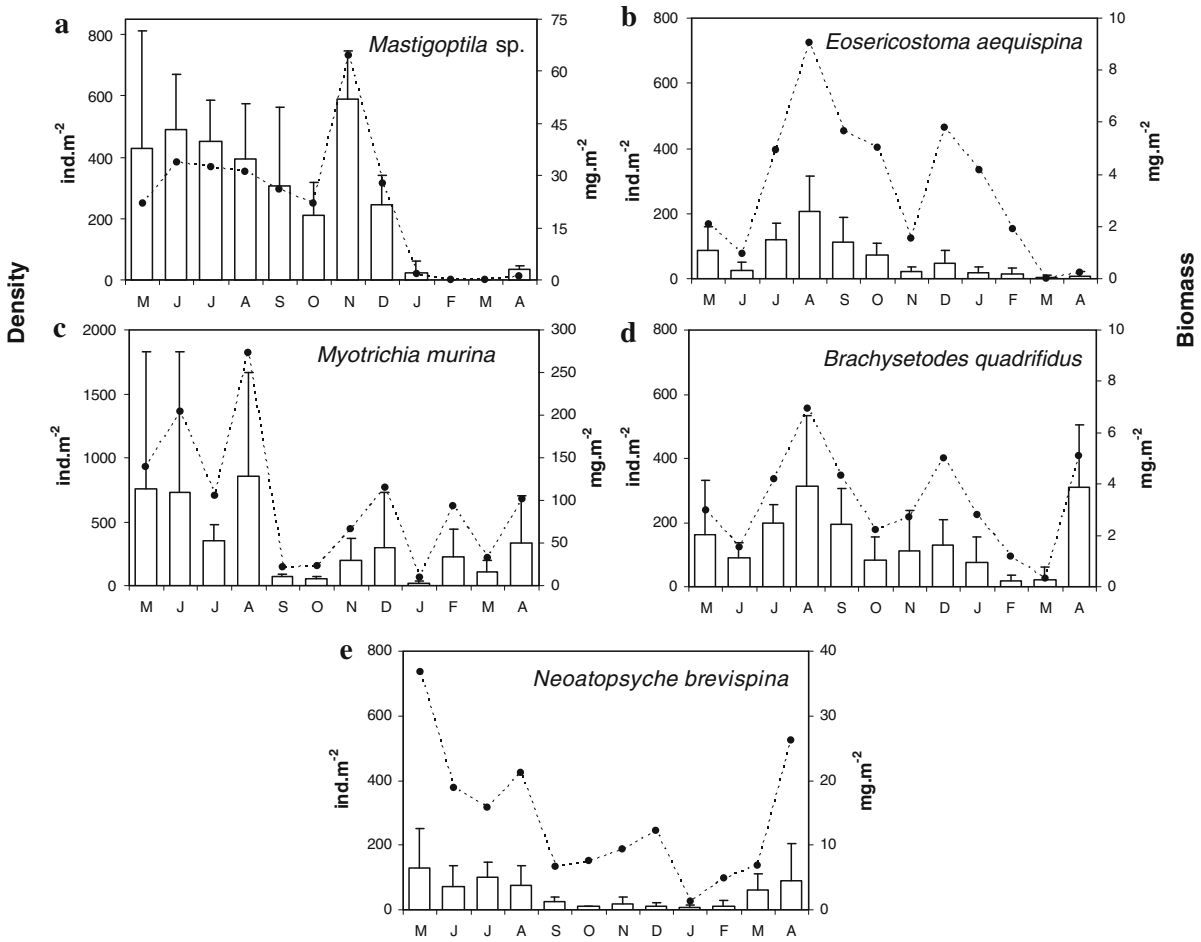

Fig. 1 Mean density (ind m^{-2}) (*bars*) and mean biomass (mg m^{-2}) (*lines*) of five Trichoptera species, during the study period (May 2007–April 2008), at Chiquito stream (Patagonia, Argentina)

that maximum density of the shredders *M. murina* and *B. quadrifidus*, was coincident with litter input in autumn (Fig. 3f).

Secondary production and *P/B* ratio and growth rate

Predictive equations for the conversion of length into dry mass were obtained for the five taxa (Table 3), all regression models showed a good adjustment ($r^2 > 0.61$, $P < 0.001$).

Myotrichia murina showed the highest annual production (310.5 mg m^{-2} $year^{-1}$) followed by *Mastigoptila* sp. (103.38 mg m^{-2} $year^{-1}$) and *N. brevispina* (62.13 mg m^{-2} $year^{-1}$) (Table 4). Annual *P/B* ratios were only slightly different from cohort *P/B* values, and were comprised between 2.78 (*M. murina*) and 5.46 (*E. aequispina*) (Table 4).

Caddisfly assemblages and environmental relationships

RDA of the species abundance accounted for the 56.0 of the total variance in the species abundance data with its first two axes (Fig. 4). The first axis (eigenvalue RDA1: 0.39) explained the temperature and FPOM effect on the species abundance and the second one (eigenvalue RDA2: 0.17) represented a gradient of discharge, dissolved oxygen and leaves biomass. The species–environment correlations were 0.94 and 0.85 for the first two axes, respectively, and unrestricted Monte Carlo Permutation test indicated that all axes were significant ($F = 2.507$, $P < 0.01$)

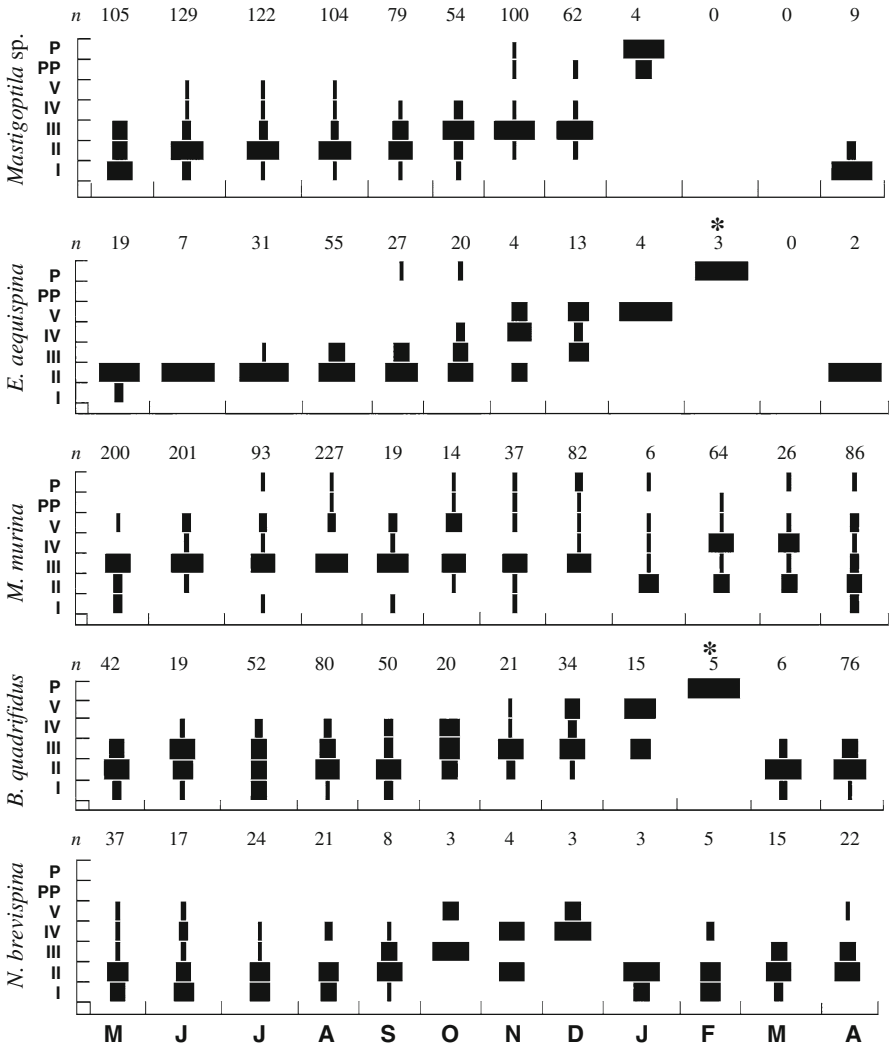

Fig. 2 Size frequency distribution of five Trichoptera species, during the study period (May 2007–April 2008), at Chiquito stream (Patagonia, Argentina). Width of the *horizontal bars* shows the proportional contribution of each life stage. The sum of all the bars represents 100%. *n* number of specimens examined. *Asterisks* above number of specimens indicate the presence of adults

(Table 5), showing a good relationship between species abundances and measured environmental variables. *M. neotropicalis* and *N. tricarinatum* peaked during the high discharge and high dissolved oxygen period which occurred in spring (October, November, and December). The opposite trend was observed for *P. molinai*, *N. brevispina*, and *N. unispina* which showed maximum densities at low water period. Leaves biomass was associated with low temperature, autumn months (May, June, July, and August); this is coincident with the litterfall period of *Nothofagus* forest. *M. murina*, *S. frequens*, and *N. brevispina* also peaked in these months. *Mastigoptila* sp., *E. aequispina*, and *B. quadrifidus* were associated with FPOM levels.

Discussion

Our results suggest that *Mastigoptila* sp., *E. aequispina*, *B. quadrifidus*, and *N. brevispina* had simple, univoltine, and synchronized life cycles; this is in agreement with what has been reported for caddisfly species of temperate areas (Richardson & Clifford, 1986; Dobrin & Giberson, 2003). Given that these are the first life history descriptions for South American caddisfly species, comparisons must be performed with studies in similar environments. A univoltine life cycle with no egg or adult diapause and larvae as the overwintering stage seems to be the main pattern for Trichoptera species living in cold headwater streams (Winterbourn, 1971; Wiggins, 2004) as in

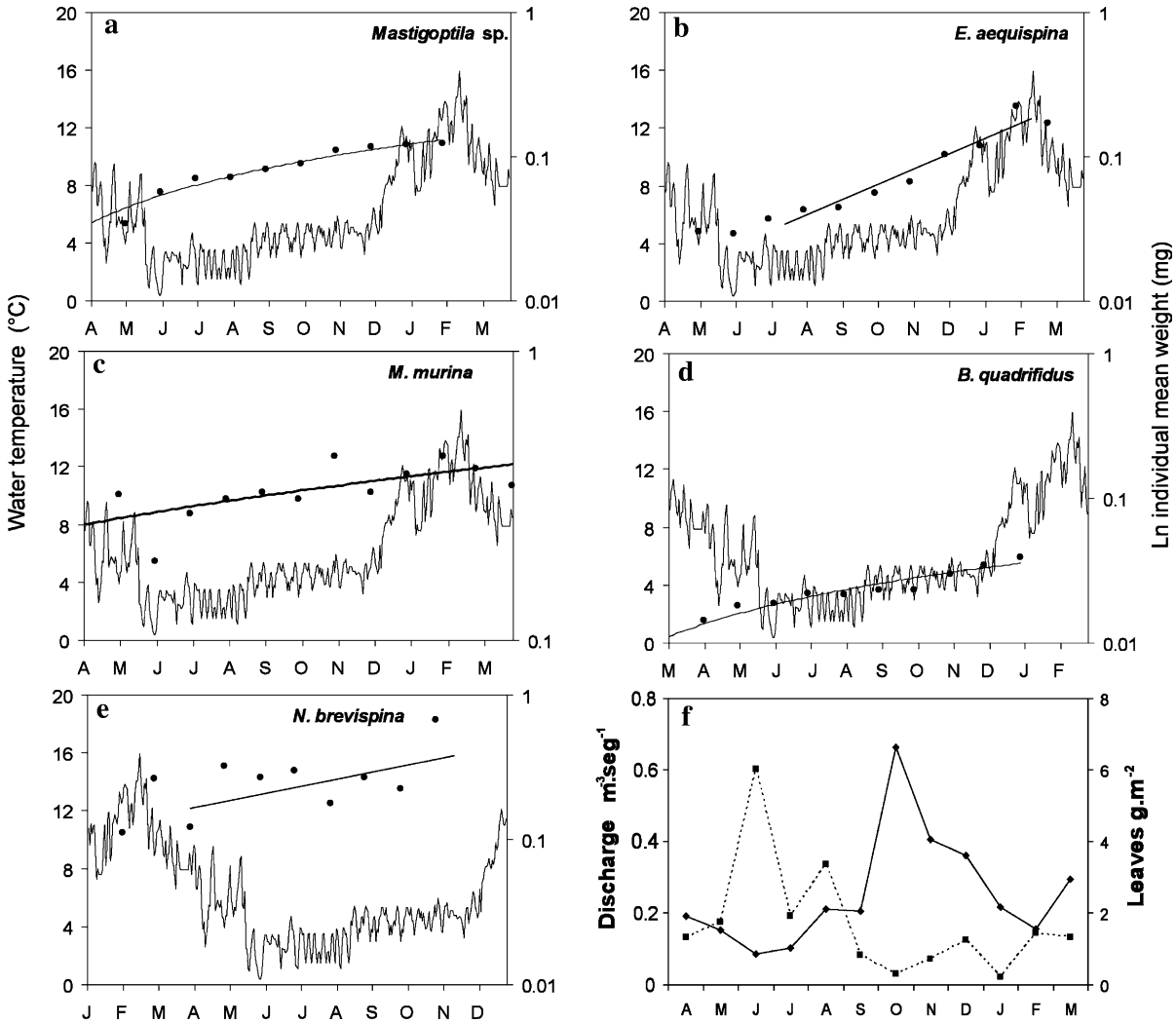

Fig. 3 **a**, **b**, **c**, **d**, **e** Mean daily water temperature during the study period (May 2007–April 2008) (*solid line*) and ln of individual mean weight (secondary Y-axis) for the five species. The regression line represents the growth rate for each species. Note that the month sequence was modified for some species to fit the life cycle. **f** Discharge (m^{-3} s^{-1}) (*solid line*) and leaves biomass (g m^{-2}) (*dashed line*, secondary Y-axis) of each sampling date during the study period (May 2007–April 2008)

Patagonia Mountains. However, *M. murina* displayed a complex size class arrangement with no clear cohort structure followed by a long flight period, thus emergence was poorly synchronized (Hynes, 1970). This has been documented for several New Zealand species (Winterbourn, 1966, 1978; Towns, 1981), possibly due to a lack of cues for synchronization of life stages (Scarsbrook, 2000).

In practically all species the hatching was extended, thus the recruitment period occurred from late summer to early spring. This feature is widely spread among aquatic insects (Moreira & Peckarsky, 1994; Elliott, 1995), and may have an important role in the recolonization of streams after disturbances (Huryn & Wallace, 2000), as for example spates after rainfall and snowmelt that can be particularly intense at Patagonian headwaters streams.

Moreover, all the studied species showed a slow growth rate encompassing the winter months. Lower temperatures and minor light levels can lead to a decrease in both, periphyton density and conditioning of leaf litter by bacteria which in turn can affect developmental rates in primary consumers and predators (Allan & Castillo, 2007). This might account

Table 3 Relationships between head capsule width (HCW), pronotum length (PL), and dry weight (DW) of five trichopteran species

Taxon	Meas.	n	log a	b	r^2	Length/width (mm)		Weight (mg)	
						Mean ± SD	Range	Mean ± SD	Range
Glossosomatidae									
Mastigoptila sp.	HCW	119	0.92 ± 0.12	3.04 ± 0.17	0.74	0.20 ± 0.05	0.12–0.3	0.08 ± 0.07	0.01–0.3
Helicophidae									
Eosericostoma aequispina	HCW	68	−0.28 ± 0.11	1.92 ± 0.18	0.61	0.25 ± 0.08	0.15–0.52	0.05 ± 0.05	0.01–0.3
Sericostomatidae									
Myotrichia murina	PL	133	0.38 ± 0.04	2.49 ± 0.07	0.89	0.37 ± 0.21	0.07–0.72	0.47 ± 0.69	0.007–2.7
Leptoceridae									
Brachysetodes quadrifidus	HCW	144	−0.27 ± 0.09	1.78 ± 0.12	0.62	0.19 ± 0.05	0.11–0.32	0.03 ± 0.02	0.01–0.13
Hydrobiosidae									
Neoatopsyche brevispina	PL	125	0.24 ± 0.05	2.59 ± 0.10	0.84	0.40 ± 0.22	0.15–0.9	0.37 ± 0.75	0.01–5.2

With a, b constants in $W = aL^b$, where W correspond to the DW, and L is the independent variable (HCW or PL measures)

Meas. measure, n number of specimens examined, *SD* standard deviation ($P < 0.001$)

Table 4 Mean annual values biomass (mg m^{-2}); annual production (mg m^{-2}) and cohort and annual *P/B* ratio of five trichopteran species at Chiquito stream (Patagonia, Argentina)

Taxon	Mean annual biomass (mg m^{-2})	Annual production (mg m^{-2})	Cohort *P/B*	Annual *P/B*
Glossosomatidae				
Mastigoptila sp.	23.68	103.38	3.28	4.36
Helicophidae				
Eosericostoma aequispina	2.23	11.06	4.55	5.46
Sericostomatidae				
Myotrichia murina	111.56	310.5	2.78	2.78
Leptoceridae				
Brachysetodes quadrifidus	3.71	11.39	3.07	3.07
Hydrobiosidae				
Neoatopsyche brevispina	15.25	62.13	4.07	4.07

for the observed patterns in growth for all our species, mostly herbivorous and predators. A winter slow growth period was observed by Richardson & Clifford (1986) for eight Trichoptera species including members of Leptoceridae, Helicopsychidae, and Molannidae from high latitudes (North America). Similarly, *Rhyacophila* species (Rhyacophilidae) also experience a developmental retardation, probably induced by declining water temperature, decreasing food supply, and shorter days (Elliott, 1969).

According to our results, the sericostomatid *M. murina* (TL range: 0.6–9.6 mm) would be univoltine, as its relative *Seriocostoma personatum* (Sangpradub et al., 1999). However, *Agarodes libalis* and *Fattigia pele* (large sized North American sericostomatids, maximum TL: 15 mm) require at least 2 years to complete their life cycles (Huryn & Wallace, 1988; Roeding & Smock, 1989).

The life cycle displayed by the shredder *B. quadrifidus* (TL range: 0.15–4.4 mm) was comparable to that found for small-sized leptocerids in low gradient boreal streams (Richardson & Clifford, 1986), and for New Zealand detritivorous species which showed univoltine and well-synchronized life histories (Scarsbrook, 2000). *Mastigoptila* sp. life cycle was similar to that described for other

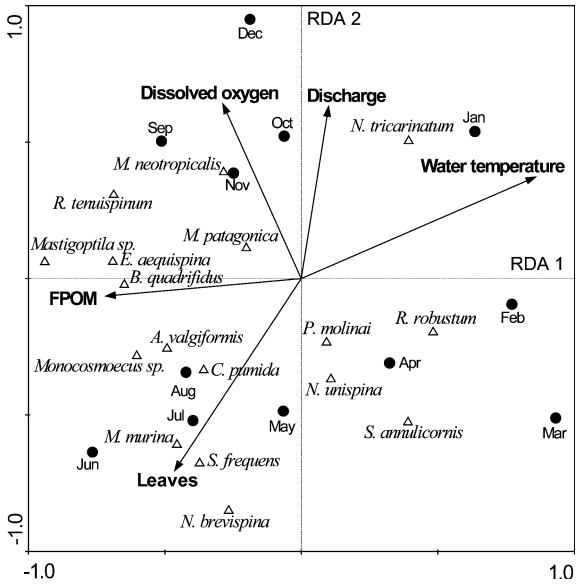

Fig. 4 Redundancy analysis triplot for species abundances (*open triangles*), sampling dates (*black circles*), and environmental variables (*arrows*) at the study site, during the sampling period (May 2007–April 2008)

Table 5 Intraset correlations of environmental variables with the first two axes of RDA of Trichoptera species data at Chiquito stream (Patagonia, Argentina)

Variable	RDA 1	RDA 2
Eigenvalues	0.39	0.17
Species–environment correlation	0.94	0.85
% Variance of species data explained	39.1	56.0
Correlation with axes		
Dissolved oxygen	−0.29	0.64
Discharge	0.01	0.63
Water temperature	0.86	0.37
Leaves	−0.46	−0.7
FPOM	−0.72	−0.06

P values for Monte-Carlo permutation test

Axis 1: $F = 3.845$, $P < 0.03$; all canonical axes: $F = 2.507$, $P < 0.01$

Glossosomatids at higher latitudes (Becker, 2005). However, in warmer regions with more suitable conditions, related species can develop multivoltine life cycles, with up to three generations per year (Álvarez & Pardo, 2005; Jin & Ward, 2007). Regarding *E. aequispina*, there is just one record of *Zelolessica cheira* (Helicophidae) from New Zealand displaying a univoltine seasonal life history (Michaelis, 1974). The univoltine life cycle described here for *Neoatopsyche brevispina* was similar to observed by Céréghino et al. (1997) for *Rhyacophila occidentalis* and *R. meridionalis*, and by Tsuruishi (2003) for *Hymalopsyche japonica* (Rhyacophilidae).

Concerning shredder's production, *M. murina* was by far the most relevant species (310.5 mg m^{-2} $year^{-1}$, 62% of caddisfly production). This value was substantially lower than that reported by Iversen (1980) (1 g m^{-2} $year^{-1}$) for *Sericostoma personatum*, a semivoltine species from Denmark streams. However, *P/B* ratio of *M. murina* (2.78) was comparable to that found for *S. personatum* (2.4–3.8), same study. In terms of density and production, scrapers were the second relevant group, being *Mastigoptila* sp. (103.4 mg m^{-2} $year^{-1}$) the species that contributed the most. Similar values were documented for univoltine *Glossosoma* species (60–260 mg m^{-2} $year^{-1}$) (Krueger & Waters, 1983). On the other hand, the estimated production value for the predator *N. brevispina* was lower than the one displayed by the semivoltine *Rhyacophila brunnea* (313 mg m^{-2} $year^{-1}$) in Canadian headwaters (Dobrin & Giberson, 2003).

Annual secondary production of the studied caddisfly species was 0.5 g m^{-2} $year^{-1}$. This was a low value but within the range observed in other studies at headwaters in cold areas; a similar value (0.41 g m^{-2} $year^{-1}$) was reported by Dobrin & Giberson (2003) in a spring-fed stream. Huryn & Wallace (2000) stated that the lowest levels of production documented for macroinvertebrate communities occur at cool temperate to arctic streams and appear to be attributable to a combination of seasonally low temperatures and nutrient or food limitation rather than to specific modes of feeding or life history attributes. According to our results, trophic basis at the studied stream seems to be dependent on litter input. Caddisfly assemblages were clearly dominated by shredders in terms of overall density, biomass, and production. However, scraper contribution was also important.

Resolving how environmental factors affect temporal patterns of lotic macroinvertebrate communities and the relative magnitude of these effects, is important for distinguishing environmental stress from the natural range of variation and for developing

generalized criteria to identify sites of high ecological integrity (Collier, 2008). According to our results (RDA analysis), seasonally dynamic variables such as water temperature, discharge, and detritus availability were the main predictors of caddisfly assemblage variation at our study site. These variables are commonly identified as determinants of temporal patterns of aquatic insects in perennial streams, draining deciduous forest (Miserendino & Pizzolón, 2003, 2004; Hughes, 2006; Ruiz García et al., 2006; Miserendino & Brand, 2007).

As stated by Lytle & Poff (2004) when the timing of floods and droughts is sufficiently predictable among years, the life history strategy of organisms is generally synchronized. This is in fact our stream scenario, a cold, undisturbed, hydrologically stable watercourse with substantial litter supply plus periphyton and bryophytes availability (Miserendino & Masi, 2010). Although synchrony can occur in any life cycle stage, Butler (1984) stated that adult emergence is the most common point where synchrony is reestablished within populations of aquatic insect. In our work, practically all the studied species displayed univoltine life cycles and synchronized emergence, as commonly reported for temperate perennial streams (Richardson & Clifford, 1986; Richardson, 2001; Jin &Ward, 2007), with temperature, discharge, and energy inputs potentially governing synchrony.

The results presented in this paper provide a better understanding of life history strategies and a quantification of Trichoptera secondary production in a typical, undisturbed, Patagonian low order stream. Headwater streams at Patagonia are being threatened by anthropogenic activities such as extensive cattle raising, logging, and forest management (Miserendino et al., 2008). There are also several dam projects for hydroelectrical power generation (Pascual et al., 1998; Vince, 2010) and there is a strong concern about these fragile and pristine environments (Carabelli & Scoz, 2008). All these human disturbances change not only water quality but also hydrological patterns and temperature regions, which can have significant effect on cold stenothermic caddisfly species that evolved in predictable discharge regimes. Therefore, the information provided in this paper constitutes a valuable tool for conservation and management purposes of these fragile and threatened environments.

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