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Life cycle phenology, secondary production, and trophic guilds of caddisfly species in a lake-outlet stream of Patagonia

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ABSTRACT

Lake-outlets are transitional areas recognized as highly productive ecosystems in terms of density and biomass of aquatic insects. Life cycle, secondary production, trophic guilds and environmental constraints of caddisfly assemblages were investigated on a natural lake-outlet stream (Nant y Fall) in Patagonia, Argentina. We investigated the site monthly from May 2007 to April 2008 by recording environmental data and sampling caddis larvae using a Surber sampler at riffle areas ($n = 36$). *Mastigoptila longicornuta*, *Smicridea annulicornis*, *Smicridea frequens*, *Brachysetodes quadrifidus* and *Parasericostoma ovale* displayed well synchronized univoltine life cycles, while *Neoatopsyche brevispina*, *Neopsilochorema tricarinatum*, showed an asynchronous development pattern, although most of them had an extended recruitment, similar to those reported for non lake-outlet streams in the area. Annual secondary production per species varied from 8.22 (*B. quadrifidus*) to 3568.83 mg m^{-2} y^{-1} (*P. ovale*), with overall caddisfly production amounting to 4.8 g m^{-2} y^{-1}. Shredder/collector-filterer ratio was 3.3/1 suggesting that the system was detrital based. Redundancy analysis indicated that seasonally dynamic variables such as discharge, benthic particulate organic matter and temperature were the main predictors of seasonal caddisfly assemblage variation. We propose that the variety of food resources and the significant spatial heterogeneity at lake-outlet streams contribute to sustain a rich caddisfly community.

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Introduction

Life cycles of aquatic insects are generally driven by different environmental changes or events, mainly timing of floods or droughts, availability of food and seasonal temperature patterns (Sweeney et al. 1986; Richardson 2001; Jannot et al. 2007). As shown by several studies carried out in the Northern Hemisphere, the life history of numerous aquatic insects appears to be highly synchronized (Petersen and Cummins 1974; Richardson 2001). According to Lytle and Poff (2004) when the timing of floods and drought is sufficiently predictable among years, the life history strategy of organisms is generally synchronized with the long term dynamics of the flow regime. On the other hand, some insects in the Southern Hemisphere, such as those in New Zealand streams, have flexible and poorly synchronized life histories, without seasonal patterns of development and extended flight periods as a response to extremely unpredictable environments (Scarsbrook 2000). In any case, the timing of life cycle stages is the response to a complex series of selection pressures operating on all life stages (Richardson 2001). Voltinism and phenology of a life cycle may vary both spatially and temporally due to a number of abiotic (e.g. temperature, photoperiod, latitudinal clines) and biotic factors (e.g. resource limitation or availability, population density, competition or predators) (Resh and Rosenberg 1989; Mendez and Resh 2008). The knowledge of life histories traits has become useful when examining changes in the structure of communities with regard to seasonal variability, longitudinal zonation and biomonitoring (Statzner et al. 2001, 2005; Resh et al. 2005). In this sense, secondary production is related to the interaction between the population and its environment, and depends on several abiotic events with many components of the species life history, such as recruitment, growth and mortality (Butler 1984).

Lake-outlets differ significantly in terms of species composition and temporal sequencing of life history events from other fluvial habitats (Hauer and Stanford 1982; Stanford et al. 1982). The higher water temperature combined with large quantities of suspended particulate material (seston) can support high densities and biomass of filter feeders. Lakes act as traps of large particles including inorganic sediment; therefore outlet streams are not intensely scoured during spates. Flow in lake-outlets is more stable since the lake dampens fluctuations in discharge caused by rainfall, therefore reducing potential disturbance of flow stress (Giller and Malmqvist 1998). In many ways, lake-outlets are predictable and stable environments in which biomass may be maximized (Valett and Stanford 1987). For these reasons these transitional systems have been recognized as highly productive ecosystems

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(Oswood 1979; Richardson 1984; Eriksson 2001). At lake-outlets systems, Trichoptera communities seems to be dominated by net spinning caddisflies (Hydropsychidae) (Hauer and Stanford 1982; Vallania and Corigliano 2007) although other groups as Hydroptilidae and Leptoceridae can also be important (Miserendino and Pizzolón 2004; Miserendino and Brand 2007).

Trichopterans represent a major component of lotic patagonian environments, both in richness and abundance (Angrisano and Sganga 2009). As occurs with other aquatic invertebrate groups, patagonian Trichoptera exhibit a high degree of endemism (Angrisano and Sganga 2009), which makes them extremely vulnerable to environmental disturbances. Therefore, a better understanding of the ecology and functioning of freshwater communities is needed in order to face resource management and conservation purposes (Hering et al. 2009).

Only recently life history and secondary production topics came into focus of investigations in South American environments (Hollmann and Miserendino 2006, 2008; Epele et al. 2011; Epele and Miserendino 2011). Recently, Brand and Miserendino (2011b) analyzed the life history and production of five univoltine trichopteran species at a non lake-outlet, headwater stream in the Patagonian Mountains. This study revealed an extended recruitment in most species and relatively well synchronized life histories. Their levels of secondary production were low, and comparable to those reported for cold springs in temperate regions (Dobrin and Giberson 2003).

We investigated a lake outflow; the Nant y Fall stream, in a site located 1750 m downstream the Rosario Lake. Over a one year period, we analyzed the caddisfly community in order to answer the following questions: (1) how are the life history features in terms of voltinism, growth and phenology of caddisfly species in a lake-outlet stream? (2) What are the most important species in terms of secondary production? (3) Which are the main environmental factors influencing seasonal variation of caddisfly assemblages?

Methods

Study site

Samples were taken from the Nant y Fall stream (43°13′24″S, 71°25′17″W) located 1750 m downstream of Rosario lake in the Futaleufú-Yelcho basin of the Northwest of the Chubut Province in Patagonia (Argentina), at an altitude of 690 m a.s.l. Rosario lake has an area of 9.84 km²; it is a mesotrophic lake with a primary production reaching 2.48 g m⁻² in the warmer season (Izaguirre et al. 1993). A small part of the catchment is currently occupied by a Mapuche settlement. Land-use adjacent to the lake is mainly agricultural, with extensive livestock grazing. Both Rosario lake and Nant y Fall river are used for sport fishing since they are inhabited by the native pejerrey, *Odonthestes hatchery* (Eigenmann) and the exotic rainbow trout, *Oncorhynchus mykiss* (Walbaum). The indigenous small benthic catfish, *Hatcheria macraei* (Girard) is also present in the river (Di Prinzio et al. 2009).

Nant y Fall is a 2nd order stream (historical mean annual discharge, average of the last 39 year data: 2.47 m³ s⁻¹). Historical records showed a very small snowmelt peak close to the winter rainfall. The typical snowmelt peak of cordilleran streams is ameliorated by the lack of glaciers at headwaters in the catchment (Miserendino and Pizzolón 2004).

Aquatic vegetation covers one quarter of the studied reach and is represented mainly by the submerged *Isoetes savatieri* Franchet, *Myriophyllum quitense* Kunth, *Limosella australis* Brown, *Ranunculus flagelliformis* Sm. and *Callitriche lechleri* (Hegelm.) Fassett; the subemergent *Lilaeopsis macloviana* (Gand.) A.W. Hill and *Mimulus glabratus* Kunth; and the emergent macrophyte *Verónica anagallis-*aquatica L., *Eleocharis albibracteata* Nees et Meyen, *Juncus burkartii* Barros, *Juncus diemii* Barros and *Juncus microcephalus* Humb (Leon et al., 1998).

Environmental characterization and sampling procedure

The site was sampled monthly from May 2007 to April 2008. Substrate size composition was estimated as percentage of boulder, cobble, gravel, pebble, and sand in the reach, using a 1 m² grid. Air temperature and rainfall information was provided by INTA (Instituto Nacional de Tecnología Agropecuaria-Esquel Centro Regional Patagonia Sur). Current speed (m s⁻¹) was measured in mid-channel on three occasions 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 along a transect across the channel with a calibrated stick, wet width (m) of the channel was also determined. Discharge (m³ s⁻¹) was obtained by combining depth, wet width and current velocity as in Gordon et al. (2004). On each sampling occasion water temperature, pH, specific conductivity (μS_{20} cm⁻¹) and dissolved oxygen ($mg O_2 l^{-1}$) were measured with a multi-parameter probe (Hach Sens ION 156).

To assess organic matter composition, detritus from additional integrated samples taken with Surber sampler at each collecting date, were analyzed in the laboratory using a white tray (750 cm²) divided in cells (5 × 5 cm). Material was classified visually and sorted into four classes. Relative abundance of filamentous algae, bryophytes, macrophytes, leaves and wood material, and others (seeds, fruits, roots) was quantified monthly. After analyses leaves, wood material and others were combined as benthic particulate organic matter (BPOM).

In order to analyze seasonal variation in abundance, and to describe the life cycles, larvae were collected monthly on three riffles using a Surber sampler (0.09 m⁻²; 250 μm mesh size). Samples were fixed in the field with formaldehyde solution (4%). Adult collection was performed every two weeks during the summer months, by sweeping the riparian vegetation for 15 min. Additionally, light traps were placed at the site for a 45 min period at dusk. Adult specimens were fixed and stored in 70% alcohol and identified to the lowest possible level (Flint 1974; Holzenthal 1986a,b; Angrisano and Sganga 2009).

Larvae were sorted manually in the laboratory under 5× magnification, counted and preserved in 70% alcohol. All specimens were identified using available keys (Angrisano 1997, 1998; Valverde and Albariño 1999; Sganga and Angrisano 2005; Angrisano and Sganga 2009).

Life cycle analysis

From all the identified Trichoptera species we selected those numerically dominant to describe the life history. Two body measurements from each specimen were taken. Pronotum length (PL) was measured along the mid dorsal ecdysial line, and head capsule width (HCW) as the maximum width of the head capsule then the most accurate was used to produce the histograms and determine size classes (Komzák and Sedlák 2002; Becker 2005). Measures were made under 8× and 32× magnifications (depending on the size of the specimens) with a stereoscopic microscope equipped with a linear eyepiece micrometer, to the nearest 0.025 mm (Richardson 2001; Jin and Ward 2007).

The development of the cohorts was deduced from the population size structure at the various sampling periods (Céréghino et al. 1997; Tsuruishi 2003; Álvarez and Pardo 2005; Jin and Ward 2007; Yan and Li 2007). The abundance 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.

Length–mass relationships

Body mass relationship is usually described by the general power equation $DM = aL^b$, 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 all size classes were 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 and 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 and P/B ratio

Production was calculated using the size frequency method (Benke 1993). Larvae were assigned to size groups for analysis. *P/B* ratio was calculated as the ratio of production per unit time to mean biomass (Benke 1993). According to this method, 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).

Trophic guilds characterization

The diet of the seven species was analyzed by removing the foregut and midgut content through a ventral dissection of the thorax (Peckarsky 1996). The ingested items were described and identified under a microscope (100–1000×). The gut content of each specimen was mounted with glycerin on a microscope slide, six fields were selected and the proportion of each item in the field was estimated. Seven food items were identified: (1) diatoms; (2) other algae; (3) fine detritus (<50 μm); (4) leaf fragments; (5) prey invertebrates (mainly aquatic insects); (6) zooplankton; (7) inorganic detritus. This information was employed to the assignment of functional feeding groups as in Merritt et al. (2008).

Caddisfly community ordination

In order to identify the main environmental variables ruling caddisfly species seasonal variation we performed a multivariate analysis. 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 (ter Braak and Smilauer 1998). Ordinations were performed using the package CANOCO version 4.0 (ter Braak and Smilauer 1999). Biotic variables were $\log(x+1)$ transformed prior to statistical analysis to normalize and stabilize variance. Environmental variables presented in Table 1 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 and Smilauer 1998, 1999). A set of 5 independent variables was used to perform the definitive RDA analysis. In RDA biplots the first and the second axes represent the most important environmental gradients along which species and date samples are distributed. The significance of relationships on this pair of axis was tested using a Monte Carlo test (9999 permutations) (Jockel 1986).

Table 1
Physico-chemical parameters, annual mean standard deviation and total range values from Nant y Fall Stream (Patagonia, Argentina), during the study period (May 2007 to April 2008). SD: standard deviation.

Parameter	Mean ± SD	Range
Water temperature	11.6 ± 6	3.9–22.5
pH	7.6 ± 0.5	6.9–8.5
Conductivity (μS cm^{-1})	89.7 ± 15.2	72.3–119.4
Dissolved oxygen (mg l^{-1})	9.7 ± 1.7	7.06–13.2
Wet width (m)	17.1 ± 2.9	14.0–22.7
Depth (cm)	20.9 ± 3.9	2–70
Current speed (m s^{-1})	0.7 ± 0.2	0.5–1.16
% filamentous algae	7.5 ± 12.5	0–35
% bryophytes	1.2 ± 4.3	0–15
% macrophytes	58.7 ± 9.8	40–70
% BPOM	32.5 ± 12.3	15–55

Results

Environmental features

Substrate was dominated by gravel (30%), cobbles (25%), and boulders (20%). Water temperature ranged from 3.9 (July) to 22.5 °C (February) and the mean annual value was 11.6 °C. Discharge values ranged from 1.20 (July) to 7.21 m^3 s^{-1} (December) (Fig. 1). Wet width of the stream was between 14 and 22.7 m whereas depth ranged from 2 to 70 cm. Current speeds varied between 0.5 and 1.16 m s^{-1}, with maximum mean value recorded in summer. Physicochemical conditions indicated that waters were circum-neutral and well oxygenated. Conductivity was comprised between 72.3 and 119.4 μS cm^{-1} (Table 1).

Analysis of detrital fractions including autochthonous and allochthonous matter showed that macrophytes contributed with more than 53.3% in all seasons. Filamentous algae varied between 0 and 30%. Bryophytes were only present in summer benthic samples. Benthic particulate organic matter (leaves, wood and other fragments) also contributed with more than 26.7% in all seasons (Table 1).
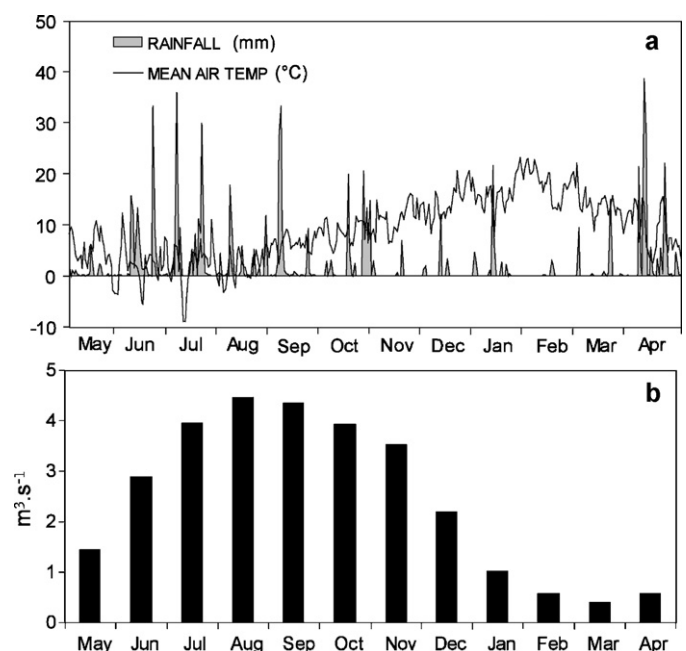
Fig. 1. (a) Daily rainfall (mm), mean air temperature (°C) and (b) discharge (m^3 s^{-1}) during the sampling period (May 2007 to April 2008), at Nant y Fall lake-outlet stream (Patagonia, Argentina).

Trichoptera assemblages and life history description

The Trichoptera community at Nant y Fall stream comprised 14 species, belonging to 7 families (Table 2). The overall highest density (8687 ind m^{-2}) was observed for *Parasericostoma ovale* (Sericostomatidae), followed by *Smicridea frequens* (Hydropsychidae) (3544 ind m^{-2}).

Seven Trichoptera species were the numerically dominant, therefore were selected for life history description: *Mastigoptila longicornuta* (Glossosomatidae), *Neoatopsyche brevispina*, *Neopsilochorema tricarinatum* (both Hydrobiosidae), *Smicridea annulicornis* and *S. frequens* (Hydropsychidae), *Brachysetodes quadrifidus* (Leptoceridae) and *P. ovale* (Sericostomatidae).

Mastigoptila longicornuta

The minimum density of *M. longicornuta* was 3.7 ind m^{-2} (July) and the maximum was 211.1 ind m^{-2} (November), biomass ranged from 0.06 to 79.6 mg m^{-2} in the same months (Fig. 2). A total of 163 individuals were measured and divided into five larval classes, based on the PL measurements. Larvae were absent in May, June and April. Recruitment was observed from July to September, after that, a fast growth period occurred. Prepupal stage was present in October, November and February. Pupae were found in samples taken in November, December and February. No adults were collected during the sampling period (Fig. 3). *M. longicornuta* had a clear univoltine life cycle, with an estimated cohort development time of eight months.

Neoatopsyche brevispina

The minimum density of *N. brevispina* was 22.2 ind m^{-2} (December and March), and the maximum was 162.8 ind m^{-2} (July). Biomass values were comprised between 3.8 (March) and 144 mg m^{-2} (October) (Fig. 2). A total of 169 individuals were measured and divided into five size frequencies. An extended recruitment period was observed from December to July. Prepupal stages were present from September to November, and in January, while pupae were observed in October, December, January and April (Fig. 3), which can suggest an extended flight period. A slow growth period was observed after egg hatching, during the summer and early autumn months (December to April), whereas a fast growing period occurred from August to December. The co-occurrence of many size classes from winter to early summer, suggests some degree of asynchrony. Therefore, *N. brevispina* life

cycle was difficult to define from this data, presumably with an average cohort development time of 12–13 months.

Neopsilochorema tricarinatum

Density of *N. tricarinatum* ranged between 18.5 ind m^{-2} (December) and 81.48 ind m^{-2} (February) while biomass ranged between 5.92 (October) and 19.27 mg m^{-2} (June) (Fig. 2). A total of 87 specimens were measured and divided into five size classes. Smallest larvae were recorded at in six months. A fast growing period was observed from October to January. Prepupae and pupae were present during spring and early summer (Fig. 3). Life cycle of *N. tricarinatum* showed poor developmental synchronization, with an extended recruitment and co-occurrence of several size classes at most seasons, presumably with an average cohort development time of 12 months.

Smicridea annulicornis

Minimum density of *S. annulicornis* was 7.4 ind m^{-2} (June) and the maximum was 670 ind m^{-2} (April), biomass ranged from 8.67 to 361.8 mg m^{-2} in the same months (Fig. 2). A total of 426 individuals were measured and divided into five size classes. Larvae of size class I were present from February to October, indicating an extended recruitment. A slow growth in larval size occurred from February to March, while a fast growing period was observed from September to December. Pupal stage was present only in January, prepupal stage was not recorded. *S. annulicornis* had a clearly univoltine life cycle requiring 12 months to complete their development (Fig. 3).

Smicridea frequens

Density of *S. frequens* ranged between 40 and 3544 ind m^{-2} in December and July respectively. Biomass values were comprised between 18.4 (December) and 1074.1 mg m^{-2} (July) (Fig. 2). A total of 1907 individuals were measured and divided into five larval classes, based on the PL. Recruitment was observed in February, after that a stable slow growth period occurred until December. This period was characterized by the co-occurrence of classes III and IV. Pupae and prepupae were present in January whereas adults were collected in February (Fig. 3). *S. frequens* had a well synchronized univoltine life cycle with an estimated cohort development time of 12 months.

Brachysetodes quadrifidus

The minimum density of *B. quadrifidus* was 22.2 ind m^{-2} (April), and the maximum was 370 ind m^{-2} (December). Biomass was

Table 2
Minimum and maximum density (ind m^{-2}), mean annual density (ind m^{-2}) ± standard deviation of all Trichoptera species, found at Nant y Fall stream (Patagonia, Argentina), during the study period (May 2007 to April 2008). Species marked with an asterisk were selected for life cycle description and production estimation.

Family		Taxa	Min-max density (ind m^{-2})	Total density ± SD (ind m^{-2})
Glossosomatidae	*	*Mastigoptila longicornuta* (Schmid, 1958)	0–211.1	33.3 ± 59.7
Hydrobiosidae		*Cailloma pumida* (Ross, 1956)	0–7.4	0.9 ± 2.3
	*	*Neoatopsyche brevispina* (Schmid, 1957)	22.2–155.5	52.2 ± 38.6
		Neoatopsyche unispina (Flint, 1967)	0–55.5	20.3 ± 17.5
	*	*Neopsilochorema tricarinatum* (Schmid, 1955)	0–81.5	26.8 ± 20.8
		Rheochorema lobuliferum (Flint, 1967)	0–11.1	2.5 ± 3.9
Hydropsychidae	*	*Smicridea annulicornis* (Blanchard, 1851)	7.4–670.3	131.5 ± 192.2
	*	*Smicridea frequens* (Navás, 1930)	40.7–3544.4	1003.4 ± 1041.6
Hydroptilidae		*Oxyethira bidentata* (Mosely, 1934)	0–29.6	3.4 ± 8.8
Leptoceridae	*	*Brachysetodes quadrifidus* (Schmid, 1955)	22.2–370.4	134.2 ± 98.5
		Hudsonema flaminii (Navás, 1936)	0–7.4	2.1 ± 2.5
Limnephilidae		*Monocosmoecus* sp.	0–51.8	10.5 ± 19.6
		Verger sp.	0–66.6	5.8 ± 19.2
Sericostomatidae	*	*Parasericostoma ovale* (Schmid, 1955)	2508.6–8687.6	3977.8 ± 1841.7
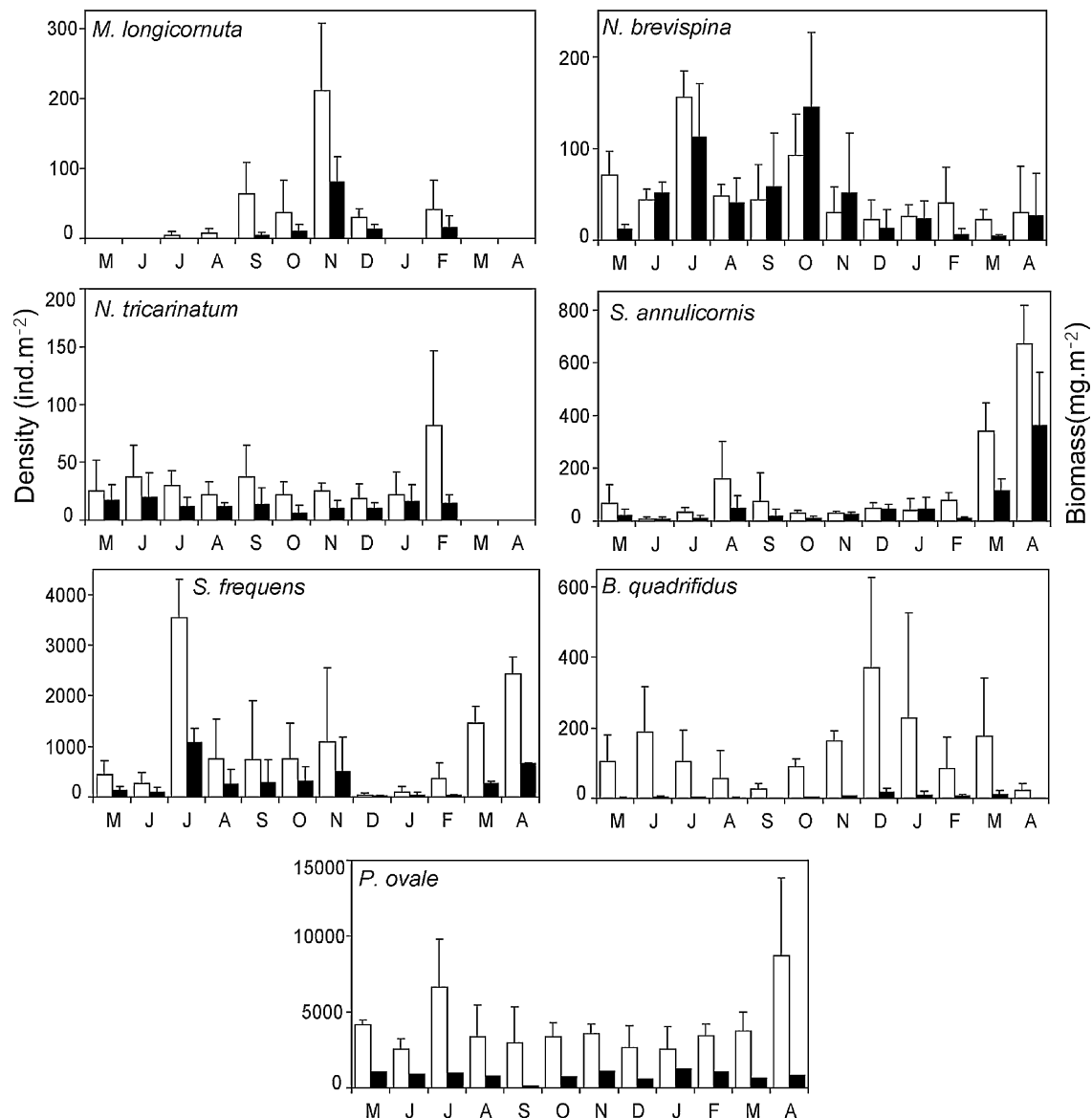
Fig. 2. Mean density (ind m^{-2}) (white bars) and mean biomass (mg m^{-2}) (black bars) of seven Trichoptera species, during the study period (May 2007 to April 2008), at Nant y Fall lake-outlet stream (Patagonia, Argentina).

comprised between 0.26 (April) and 16.6 mg m^{-2} (December) (Fig. 2). A total of 433 individuals were measured and divided into five size classes based on the PL. *B. quadrifidus* presented a long recruitment period, with larvae of the size class I occurring from April to October. After that a fast growing period was recorded. Prepupae, pupae and adults were collected in February and March (Fig. 3). The development of the species was well synchronized, having a clearly univoltine life cycle with a maximum time required for development of 12 months.

Parasericostoma ovale

Density of *P. ovale* was comprised between 2509 ind m^{-2} and 8687 ind m^{-2} (January and April, respectively). Biomass minimum value was 142.5 (September) while the maximum was 1219.5 mg m^{-2} (January) (Fig. 2). A total of 3380 individuals were measured and divided into five size classes according to PL. Except in September, November and December, samples were dominated by size class IV larvae. Smallest larvae were present from April to September, indicating an extended recruitment period. Prepupae and pupae were present only in February, while adults were

collected both in February and March (Fig. 3). *P. ovale* had a synchronized, univoltine life cycle, with an estimated time for development of 11–12 months.

Secondary production and P/B ratio

Predictive equations for the conversion of length into dry mass were obtained for the seven taxa (Table 3), all regression models showed a good adjustment ($r^2 > 0.62$, $p < 0.001$). *P. ovale* showed the highest annual production (3568.83 mg m^{-2} y^{-1}) followed by *S. frequens* (836.20 mg m^{-2} y^{-1}) and *S. annulicornis* (239.56 mg m^{-2} y^{-1}) (Table 3). Annual *P/B* ratios were only slightly different from cohort *P/B* values, and were between 2.84 (*N. brevispina*) and 4.27 (*P. ovale*) (Table 3).

Functional organization of caddisflies

According to the gut content analysis, *M. longicornuta* was a generalist scraper, the two hydrobiosid species were clearly predators, and both *Smicridea* species were collector-filterers. Among
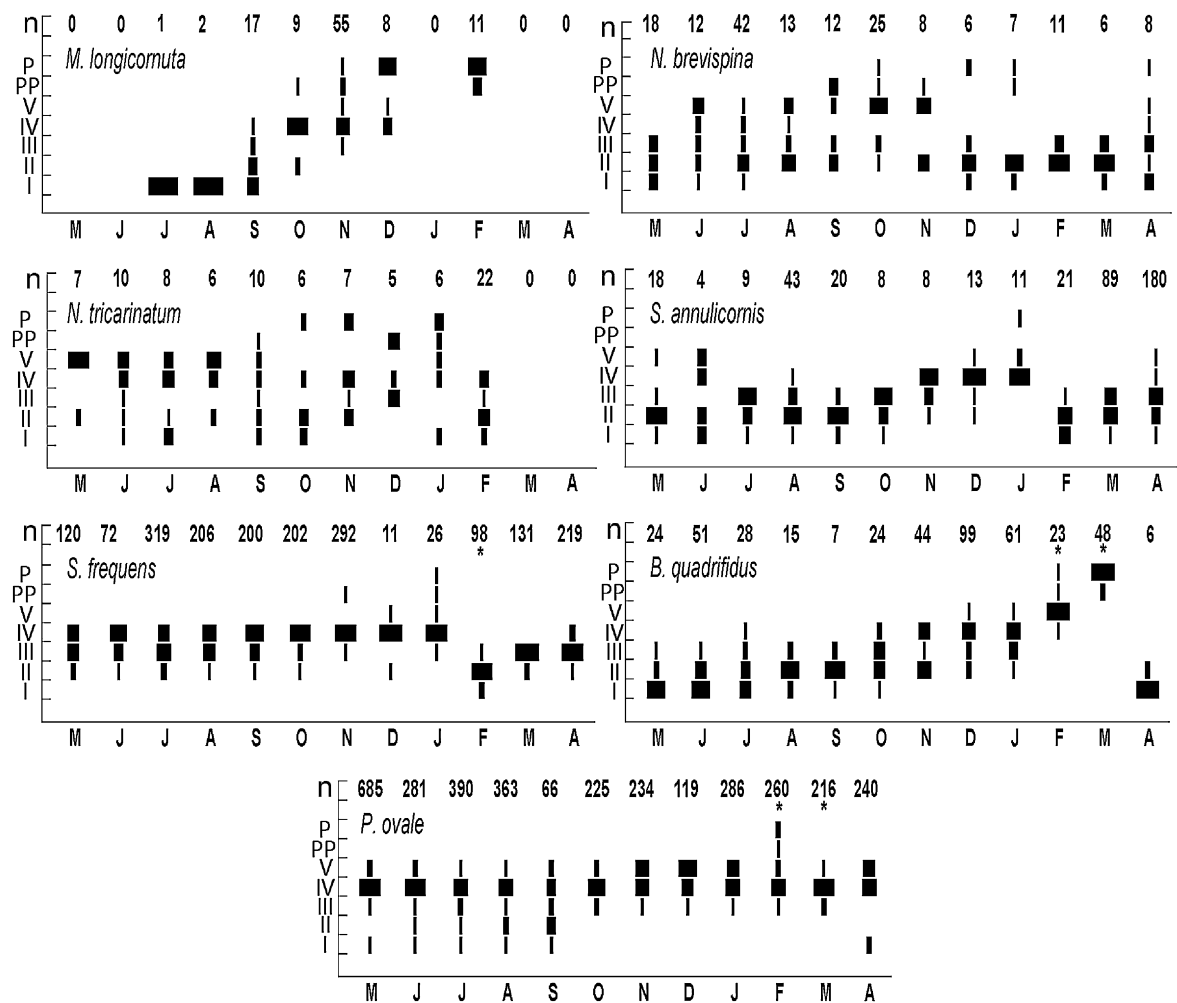
Fig. 3. Size frequency distribution of seven Trichoptera species, during the study period (May 2007 to April 2008), at Nant y Fall lake-outlet stream (Patagonia, Argentina). Width of the horizontal bars shows the proportional contribution of each life stage. The sum of all the bars represents 100%. *n* = number of specimens examined. Asterisks above number of specimens indicate the presence of adults.

shredders *B. quadrifidus* was categorized as strict shredder, while *P. ovale* would be a facultative shredder due to the presence of other items (diatoms and fine organic detritus) co-occurring with leaf fragments (Fig. 4). In terms of density and biomass, the dominant functional feeding groups were shredders followed by collector-filterers.

Caddisfly assemblages and environmental relationships

The first two RDA axes accounted for the 48% of the total variance in the species abundance data with its 2 first axes (Fig. 5). The species environment correlations were 0.95 and 0.89 for the first two axes respectively, and unrestricted Monte Carlo

Table 3
Relationships between head capsule width (HCW), pronotum length (PL) and dry weight of seven trichopteran species. 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 to obtain the regression ($p < 0.001$). Mean annual values of density (ind m^{-2}) and biomass (mg m^{-2}); annual production (mg m^{-2}), cohort and annual P/B ratio of seven trichopteran species at Nant y Fall stream (Patagonia, Argentina).

Taxon	Meas.	*n*	log *a*	*b*	r^2	Length (mm) range	Mean annual biomass (mg m^{-2})	Annual production (mg m^{-2})	Cohort P/B	Annual P/B
Glossosomatidae										
Mastigoptila longicornuta	PL	45	0.59 ± 0.165	2.88 ± 0.33	0.63	0.175–0.525	10.24	25.20	3.00	3.60
Hydrobiosidae										
Neoatopsyche brevispina	PL	125	0.24 ± 0.05	2.59 ± 0.10	0.84	0.15–0.9	33.47	85.87	2.84	2.84
Neopsilochorema tricarinatum	HCW	58	0.84 ± 0.09	4.45 ± 0.29	0.80	0.3–0.65	8.54	38.59	2.90	3.48
Hydropsychidae										
Smicridea annulicornis	PL	86	0.37 ± 0.04	2.17 ± 0.09	0.86	0.175–0.8	37.36	239.56	3.39	3.39
Smicridea frequens	PL	88	0.7 ± 0.06	2.63 ± 0.11	0.87	0.125–0.45	263.18	836.20	3.40	3.40
Leptoceridae										
Brachysetodes quadrifidus	HCW	144	−0.27 ± 0.09	1.78 ± 0.12	0.62	0.11–0.32	4.67	8.22	2.87	2.87
Sericostomatidae										
Parasericostoma ovale	PL	108	1.13 ± 0.09	4.00 ± 0.14	0.88	0.1–0.5	833.65	3568.83	4.27	4.27
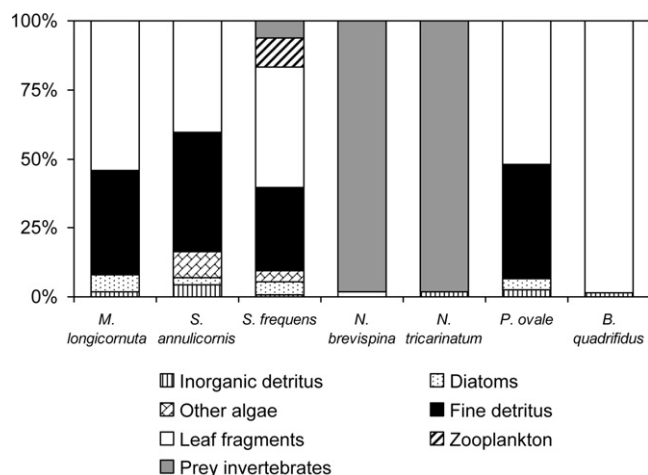
Fig. 4. Food item proportions in the gut contents of larval instars of seven caddisfly species at Nant y Fall lake outlet-stream, Patagonia, Argentina.

Table 4

Intraset correlations of environmental variables with the first two axes of RDA of Trichoptera species data at Nant y Fall stream (Patagonia, Argentina).

Variable	RDA 1	RDA 2
Eigenvalues	0.31	0.17
Species–environment correlation	0.95	0.89
% variance of species data explained	30.9	48
Correlation with axes		
Dissolved oxygen	0.08	0.17
Discharge	0.53	−0.73
Air temperature	0.46	0.20
Rain	−0.08	−0.24
BPOM	0.06	0.96

p-Values for Monte Carlo Permutation test. Axis 1: $F = 2.68$, $p < 0.01$. All canonical axes: $F = 2.08$, $p < 0.01$.

Permutation test indicated that the first axis was significant ($F = 2.68$, $p < 0.01$), as was the sum of all the axes ($F = 2.08$, $p < 0.01$) (Table 4). This shows a strong relationship between the species abundances and measured environmental variables. All environmental variables selected in the ordination model were factors that changed seasonally. Consequently, the main environmental gradient (RDA 1) was determined by the discharge and air temperature variation, while the second axis highlighted a gradient associated mostly with BPOM and discharge (RDA 2). Species that peaked during the high discharge period and high BPOM (November, December), as for example the shredders *Verger* sp., *Hudsonema flaminii* and *B. quadrifidus* (Miserendino and Pizzolón 2004), were located in the right lower quadrant. Those species that peaked in the low water period as *S. annulicornis*, *S. frequens*, *N. brevispina*

and *P. ovale* were grouped in the left upper quadrant. Species that increased in abundance in the warmer months (*N. unispina*, *M. longicornuta* and *Monocosmoecus* sp.) were positioned in the upper right quadrant (Fig. 5). A group of species (*N. tricarinatum*, *R. lobuliferum*, *C. pumida* and *O. bidentata*) peaked in winter months characterized by lower temperatures and heavy rainfalls.

Discussion

The caddisfly species *M. longicornuta*, *S. annulicornis*, *S. frequens*, *B. quadrifidus* and *P. ovale*, displayed simple, univoltine life cycle with extended recruitment and flight period; this is in agreement with Brand and Miserendino (2011b), who found similar patterns for related species at a cold headwater stream in Patagonia. However, *N. brevispina* and *N. tricarinatum* described here had a complex non seasonal life cycle, with overlapping cohorts, differing with the univoltine pattern described in the aforementioned work for *N. brevispina*. At Nant y fall, both species showed an occurrence of many size classes in all seasons revealing some degree of plasticity in the life history pattern. Plasticity or flexibility in life cycle can be seen as an advantageous strategy in environments with climatic constancy, unpredictability of climatic extremes and a greater continuity in supply of allochtonous inputs, which reduces the need for faunal life cycles to be synchronized with seasonal energy pulses (Hart 1985). Bunn (1988) suggests that this phenomenon is a highly adaptive strategy for some Australian stream insects with slow life cycles. Poor developmental synchronization and generation overlapping has been documented in larval stages for mayfly species in Patagonia probably as a strategy to face intense seasonal discharges (Gonser and Spies 1997; Hollmann and Miserendino 2006).

According to our work, hatching was extended in five of the studied species, thus the recruitment period occurred from early summer to spring coincidently with the heavy rainfall period (from May 2007 to October 2007: 500 mm). This can be seen as a strategy to optimize survival of early instars. Extended recruitment is widely spread among aquatic insects (Elliot 1995; Lytle and Poff 2004), and may have an important role in the recolonization of streams after disturbances (Huryn and Wallace 2000), as for example spates after rainfall and snowmelt that can be particularly intense at Patagonian mountain streams. In agreement with described by Brand and Miserendino (2011b) synchrony in adult emergence was relatively high in most of the species reported here, with pupae and adults present only in spring-summer months. As stated by Butler (1984), this seems to be the most common point where synchrony is re-established within populations.

Glossosomatid species can display multivoltine life cycles in tropical regions (Jin and Ward 2007), however, as reported in European and North American rivers, those inhabiting cold temperate areas usually are univoltine (Ulfstrand 1968; Sangpradub et al.
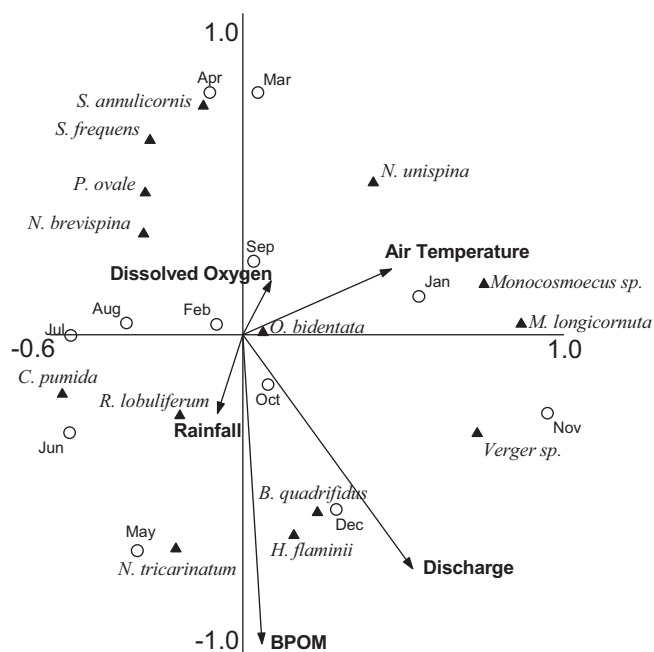
Fig. 5. Redundancy analysis triplot for species abundances (triangles), sampling dates (open circles) and environmental variables (arrows) at the Nant y Fall lake-outlet stream, during the sampling period (May 2007 to April 2008).

1999; Becker 2005). In our study, *M. longicornuta* was clearly univoltine which is consistent with documented for the congeneric *Mastigoptila* sp. at Chiquito stream (~2200 degree days) in the same year (Brand and Miserendino 2011b). Comparatively *M. longicornuta* grew faster than *Mastigoptila* sp. during spring season resulting in a shorter life cycle. Likely the supply of warmer waters from Rosario Lake epilimnion could account for these differences.

In agreement with Brand and Miserendino (2011b) the small sized *B. quadrifidus* (Leptoceridae) showed a univoltine and well synchronized life cycle. Similar patterns of development were found by Richardson and Clifford (1986) for the shredders *Ylodes frontalis* and *Triaenodes injusta* (Leptoceridae) in Canadian streams.

P. ovale had the highest secondary production ($3.57\,\mathrm{g\,m^{-2}\,y^{-1}}$) being this value three times higher than the one estimated by Iversen (1980) ($1\,\mathrm{g\,m^{-2}\,y^{-1}}$) for *Sericostoma personatum*, a semivoltine species from Denmark streams, and ten times higher than that reported for *Myotrichia murina* ($0.311\,\mathrm{g\,m^{-2}\,y^{-1}}$) (Brand and Miserendino 2011b), in a second order stream in Patagonia. *P. ovale* displayed a well synchronized univoltine life cycle at our study site; instead Brand and Miserendino (2011b) described an asynchronous and complex univoltine life cycle for the sericostomatid *M. murina*. Several members of this family are univoltine (Sangpradub et al. 1999), while others large sized sericostomatids require at least two years to complete their life cycles in temperate regions of the Northern Hemisphere (Huryn and Wallace 1988; Roeding and Smock 1989; Komzák and Sedlák 2002).

In lake-outflow streams, filter-feeder species may exhibit an increase in voltinism or a decrease in developmental time compared to those dwelling in non outlet fluvial systems (Parker and Voshell 1982; Richardson 1984). However, univoltine life cycles have been described for *Hydropsyche* species in cold temperate regions (Hauer and Stanford 1982; MacKay 1986; Willis and Hendricks 1992; Sangpradub et al. 1999; Merritt et al. 2008). Our results also demonstrated that the collector-filterers *S. annulicornis* and *S. frequens* were clearly univoltine, constituting the second group in importance both in density and biomass at the study system.

Lake-outlet streams are transitional areas that have been categorized as highly productive environments (Oswood 1979; Huryn and Wallace 2000) and our study is in line with those statements. Caddisflies were abundant in terms of density and biomass being overall annual production of assessed species ($4.8\,\mathrm{g\,m^{-2}}$) ten times higher than that found in a close headwater stream of the same region (Brand and Miserendino 2011b). A similar relationship was observed when comparing with macroinvertebrate community production in a previous study at Nant y Fall stream (Miserendino and Pizzolón 2004), which was carried out in a sampling point located 16 km downstream Rosario Lake, far enough from the lake influence. Two phenomena resulting from epilimnion water releases are considered important environmental factors driving benthos production at lake-outlets: the rich supply of suspended food items (Hoffsten 1999) and higher mean water temperature (Harding 1992). Although we did not measure the seston material deriving from the lake it is expectable that its values were high, even in location as distant from the lake as ours (Oswood 1979; Eriksson 2001). Moreover, the abundant particulate organic matter (POM) from the surrounding forest, and the autochthonous matter supplied by primary producers, contribute to the high caddisfly production. We observed dense mats of filamentous algae, bryophytes and allochtonous detritus at our study site coincidently with documented by Masi and Miserendino (2009). According to Valett and Stanford (1987), the lack of severe substratum disturbance at these particular environments, allows mats of benthic algae to grow, stabilizing the stream bottom.

As shown for other lake-outlet streams (Ward 1987; Harding 1992; Hoffsten 1999; Vuori et al. 1999) we expected a dominance of collector-filterers. Nevertheless, the facultative shredder *P. ovale* was in fact the dominant species, suggesting that the studied system was detrital based (Vannote et al. 1980; Allan and Castillo 2007). Miserendino and Pizzolón (2004) also found that the shredder *H. flaminii* (Merritt et al. 2008) followed by *P. ovale* dominated caddisfly community at Willimanco lake-outlet stream (Patagonia). However, filter-feeders were the second dominant group, particularly when adding density values of the co-occurring filterer *Simulium annulatum* (Diptera: Simuliidae) (Miserendino and Masi 2010). A contribution of 11% of the rotifer *Keratella thomassoni* in gut contents of *S. frequens* was found. This highlights the importance of seston material in their diet, since *K. thomassoni* is one of the main components of the zooplankton community in the Rosario Lake (Menu Marque and Marinone 1986).

A strong decrease in caddisfly richness has been shown at lake-outlet streams (Harding 1992). Giller and Malmqvist (1998) also agreed that typically there is a dominance of strong competitors such as net-spinners caddis larvae, which may negatively influence diversity in near-lake habitats. However, our site displayed substantially higher richness than that observed in other headwater streams of Patagonia (Miserendino 1999; Brand and Miserendino 2011a). Probably the variety of food resources and the significant spatial heterogeneity at our study site contributes to support a rich community as Collier et al. (2000) found in their study, represented with diverse functional feeding groups.

According to RDA analysis, BPOM, discharge, and temperature appeared as the most influential environmental variables in a seasonal scale. Same results were found for this and other regions (Statzner and Higler 1986; Scrimgeour and Winterbourn 1989; Miserendino 2001; Bonada et al. 2006; Hughes 2006; Brand and Miserendino 2011b). Likewise Miserendino and Brand (2007) report discharge and POM as important variables in determining caddisfly community composition. Our results also showed differences in the community structure in each season, with clear differences in autumn-winter and summer assemblages, this is in agreement with observations by Ruiz García et al. (2006) at headwater Mediterranean streams. However, only part of the seasonal variation in our data was explained by the RDA, other factors such as competition and predation could account for the unexplained variance in density data (Huryn and Wallace 2000; Allan and Castillo 2007). In a recent work Di Prinzio et al. (2009) documented that *O. mykiss* was the dominant species in the fish community at our study site. Exotic salmonids tend to affect benthic communities by decreasing the density of some epibenthic taxa (Molineri 2008) and reducing individuals body size (Buria et al. 2007).

The number of undisturbed lake-outlets is rapidly decreasing on a global scale. Freshwater modifications include damming for hydroelectric production, flood control, and irrigation using natural lakes or creating new ones (Giller and Malmqvist 1998). Patagonian aquatic environments are not exempt of these human interventions (Pascual et al. 1998; Miserendino et al. 2011). Our results suggest that lake-outlet streams in Patagonia can sustain unusual caddisfly diversity and are highly productive systems. We believe that this research not only contributes to the knowledge of the ecology and dynamics of caddisfly populations but also highlights the importance of these environments, in a scenario of increasing change.

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