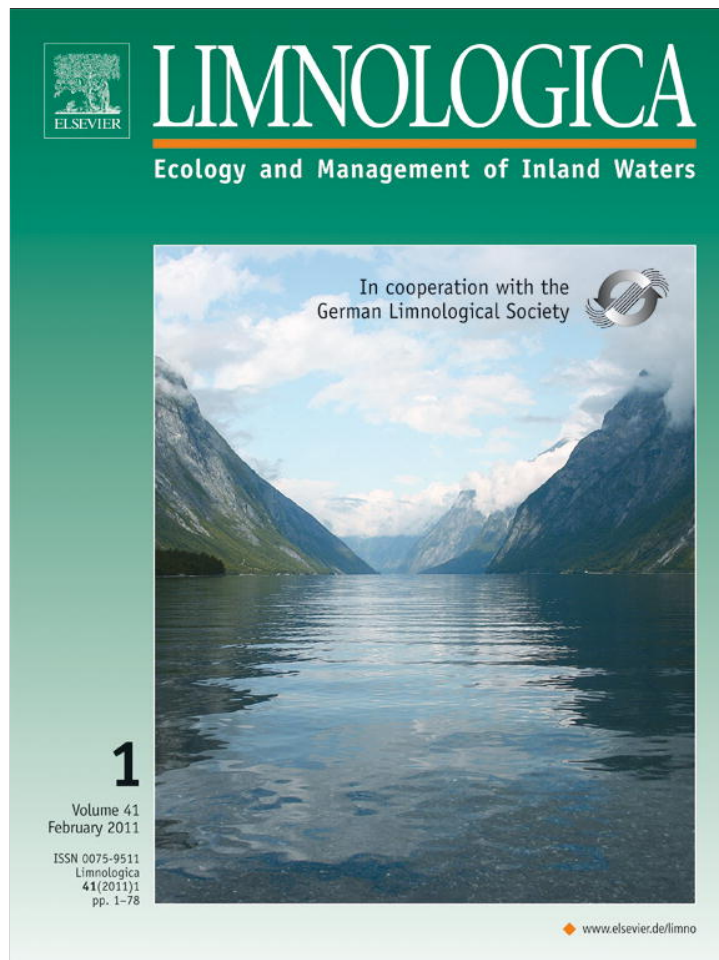


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Life history, seasonal variation and production of *Andesiops torrens* (Lugo-Ortiz and McCafferty) and *Andesiops peruvianus* (Ulmer) (Ephemeroptera: Baetidae) in a headwater Patagonian stream

Luis Beltrán Epele*, María Laura Miserendino, Pablo Pessacq

CONICET – Laboratorio de Investigaciones en Ecología y Sistemática Animal, UNPSJB, Esquel, Sarmiento 849, Argentina

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ABSTRACT

Life history descriptors of mayfly species are increasingly used in ecological assessment studies as indicator of environmental stress and also to evaluate the potential effects of climate change. We investigated the life history, annual production and competition of two congeneric mayflies: *Andesiops torrens* and *Andesiops peruvianus* in a Patagonian mountain headwater stream (La Hoya). From July 2004 to June 2005 a monthly sampling was conducted at riffle areas using a Surber net. Mean density of *A. torrens* ranged from 26 to 1080 ind m⁻² whereas that of *A. peruvianus* ranged from 7 to 629 ind m⁻². The annual production and P/B ratios of *A. torrens* (0.18 g m⁻², 3.90) and *A. peruvianus* (0.11 g m⁻², 3.35) at La Hoya stream were low, but within the expected values for cold water environments at high elevations. The two species had a similar larval life history with small larvae predominating in late summer and early autumn, middle size larvae being represented throughout winter, and mature larvae and emergence occurring in summer.

As a result *A. torrens* and *A. peruvianus* showed moderately synchronized univoltine life cycles. The temporal interspecific overlap on both density and biomass was very low. This suggests that these two species of grazers reduce the competition for resources by having a marked temporal segregation.

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Introduction

Mayflies reside in an extremely wide variety of standing and running water habitats, though the greatest diversity occurs in rocky-bottomed, low order headwater streams (Waltz and Burian, 2008). In these environments, mayflies show high abundances and also constitute an important part of animal production. Mayfly larvae are mostly collectors, scrapers or grazers and feed on a wide range of detritus and algae, and some macrophyte and animal material (Domínguez et al., 2009). Ephemeroptera are also part of the diet of other organisms as invertebrates, fishes, amphibians or birds. For these reasons mayflies are considered one of the chief links within the riverine food webs (Cummins et al., 2008).

Knowledge of life cycles of aquatic species is of fundamental importance for virtually all aspects of stream conservation (Rustigian et al., 2003). From an applied point of view, changes in the life history descriptors (e.g. survival or mortality, growth rate, size and longevity) of mayfly species are increasingly used in ecological assessment studies as indicators of environmental

stress (Raddum and Fjellheim, 1993; Kluge, 2004–2008) and also to evaluate the potential effects of climate change (Winterbourn et al., 2008).

According to Pessacq (2009) there are 33 mayfly species within 20 genera in the Argentinean Patagonia. Moreover, larvae of Ephemeroptera constitute a conspicuous component of benthos communities in streams and, jointly with Diptera, may represent more than 50% of the relative abundance in non-impacted Cordilleran watercourses (Miserendino and Pizzolón, 2003, 2004). At present, information about systematic, biology and ecology of these taxa in most Patagonia is scarce (Pessacq and Miserendino, 2008). Knowledge of the life histories of Patagonian mayflies is poor compared to that of the of Northern Hemisphere species (e.g. Sweeney and Vannote, 1981; Alba-Tercedor, 1990; Giberson and Rosenberg, 1992; Richardson, 2001; Erba et al., 2003; González et al., 2003; Lee et al., 2008) and also to that of other countries in the Southern Hemisphere (e.g. Melo et al., 2002; Winterbourn, 2003; Winterbourn et al., 2008). Gonser and Spies (1997) analyzed the life cycle of Leptophlebiid species in Chile whereas Añón Suárez and Albariño (2001) described the life history and production of *Caenis* sp. (Caenidae) in the Escondido Lake (San Carlos de Bariloche, Argentina). Recently, Hollmann and Miserendino (2006) reported a univoltine life cycle for *Metamonius anceps* Eaton (Nesameletidae) and a bivoltine life

* Corresponding author. Tel.: +54 2945 451165; fax: +54 2945 452271.
E-mail address: luisbepele@hotmail.com (L.B. Epele).

cycle for *Meridialaris chiloeensis* Demoulin (Leptophlebiidae) at a headwater stream (La Hoya stream, same place of present paper). Concerning the members of Baetidae, there is only one study in a subtropical stream in Córdoba (Argentina) carried out by Corigliano et al. (2008) who documented multivoltinism for *Americabaetis* sp. and bivoltinism for *Camelobaetidius penai* (Traver and Edmunds). Nonetheless, these studies did not include analyses of secondary production. The estimation of this parameter is of considerable ecological value as it integrates density, biomass, growth and voltinism (Benke, 1984).

Andesiops peruvianus (Ulmer) and *A. torrens* (Lugo-Ortiz and McCafferty) are two Baetid species from South America that coexist on numerous watercourses in Patagonia, including headwater streams. Both species feed on periphyton and are categorized as grazers as stated by studies carried out in a low order Patagonian stream (Díaz Villanueva and Albariño, 2003; Díaz Villanueva et al., 2010). *A. peruvianus* is distributed at high altitudes (1000–4300 m.a.s.l.) between Colombia and Argentina along the Andean highlands, whereas *A. torrens* (600–2000 m.a.s.l.) is restricted to the Andean region with records in Chile and Argentina (Nieto, 2004).

We conducted this study at La Hoya, a headwater stream, relatively predictable in terms of discharge, and with an important environmental database resulting from earlier investigations. The main goals of this paper were to (1) analyze and compare the life history and secondary production of *A. peruvianus* and *A. torrens*, (2) identify the most significant length–mass relationships of the species in biomass calculation and (3) examine seasonal patterns of these two congeneric mayflies.

Material and methods

Study area

La Hoya stream is a 2nd order watercourse in the Esquel-Percy river drainage system in the Northwest of the Chubut Province (Patagonia, Argentina). The study site (42°50'27.8"S and 71°15'54.8"W) is located in the mountainous zone at 1237 m.a.s.l. The riparian forest is composed mainly by the deciduous *Nothofagus pumilio*, the native shrubs *Fuchsia magellanica*, *Ribes magellanicum*, *Mulinum spinosum* and the herbaceous *Stipa* sp. (León et al., 1998).

Environmental features and sampling design

The field study was carried out from July 2004 to June 2005. Air and water temperature, depth and stream width were measured in a monthly interval, whereas current velocity and discharge were recorded bimonthly. Surface current speed was obtained by timing a bobber (average of three releases) over a distance of 10 m (Gordon et al., 1994). Discharge was obtained by combining depth, wet width and current velocity as in Gordon et al. (1994). Monthly rainfall data were provided by the UNPSJB climatology department. Average depth was calculated from five measurements from one transversal profile across the channel with a calibrated stick. At the selected reach, substrate composition was estimated as percentage of each fraction: boulder, cobble, gravel, pebble and sand. The relative proportion of substrate was assessed using a grid (1 m²) as suggested in Gordon et al. (1994).

In order to analyze seasonal variation in abundance and to describe the life history, larvae were collected monthly using a Surber net (0.09 m²; 250 µm mesh size). At each occasion three replicates ($n=3$) were taken on riffles (boulders and cobbles). Adults were caught using a sweep net and a light trap combined

with a white fabric as suggested by Domínguez et al. (2009). Samples were fixed with 4% formaldehyde solution. At the laboratory samples were sorted out under 5× magnification and then stored in 70% ethyl alcohol. Larvae and adults were identified using regional keys (Nieto, 2004). In order to clarify any doubt on the specific identity of the larva of *A. peruvianus* (most larvae presented a few less denticles in the second row than in the first of tarsal claw row), several specimens were reared in laboratory and the adult stage was obtained. These specimens agree with the description of Lugo-Ortiz and McCafferty (1999) and Nieto (2004), and the variation observed in the larvae is considered within the intra-specific variation.

Life history analyses

To describe life history of the species we measured the length of the right foreleg femur (FL), the total length (TL) as the distance between the anterior part of the head and the posterior part of the last abdominal segment, and the head capsule width (HCW) of each specimen (Benke et al., 1999; Corigliano et al., 2008). Measurements were taken at 8–32 times magnification (depending on the size of the specimen) with a linear eyepiece micrometer inserted in a stereomicroscope (Snellen and Stewart, 1979; Short and Ward, 1980; Richardson, 2001). The number of specimens counted and measured for the life history descriptions were: 820 larvae of *A. torrens* and 680 larvae of *A. peruvianus*. Cumulative size frequency histograms were explored in order to define the size classes. Head capsule width classes of larvae were categorized in 0.15 mm intervals for *A. torrens*, and in 0.13 mm intervals for *A. peruvianus*. These data were employed to analyze larval development using monthly size frequency histograms. The presence of late instars (larvae with dark wingpads) of each species was documented in their respective months and indicated in histograms.

Length–mass relationships

To obtain biomass data we performed length–mass regression models for each species. Body mass relationships can be described by the general power equation $DM = aL^b$, or after logarithmic transformation $\ln DM = \ln a + b \ln L$ (where: a , b = regression constants, DM = dry mass and L = length parameter).

Head capsule width of the specimens was measured to the nearest 0.05 mm (stereomicroscope). For dry mass determinations, each specimen was individually transferred to a plastic vial (1.5 ml). Drying was carried out at 105 °C for up to 4 h (Smock, 1980). Specimens were weighed on an electronic scale with 0.1 mg accuracy. In the procedure, 198 specimens ($n=99$ *A. torrens* and $n=99$ *A. peruvianus*) were examined and measured. Different regression models (linear, exponential, etc.) were evaluated in order to obtain suitable equations. In general, linear regression models were appropriate.

Production measurement method

Mayfly production was calculated using the size frequency method (Benke, 1984) for comparison purposes, as this is the most used method in relevant literature (González et al., 2003; Lee et al., 2008; Winterbourn et al., 2008). Larvae were assigned to 7 head capsule width groups for analysis. According to this method, annual production estimation requires a calibration based on the CPI (cohort production interval), which is the mean development time from hatching to final size (Benke, 1979). Length of larval life was assumed to be 12 months for both

species, so “cohort production” has the same value as annual production (Benke, 1993).

Statistical analysis

The overlap in temporal distribution of density and biomass between both mayfly species (interspecific overlap) was calculated with the proportional similarity index (PS) (Whittaker, 1975; González et al., 2003). Values may range from 0 (no overlap) to 1 (total overlap). To assess possible associations between environmental variables (temperature and rainfall) and monthly mean density and biomass of each species a non-parametric test (Spearman rank correlation) was performed.

Results

Environmental features

The annual rainfall during the study period was 680 mm with a peak occurring in May (219 mm). Air temperature ranged from 1.1 °C (July) to 17.7 °C (February) (Fig. 1), whereas water temperature ranged from 1 to 12 °C in the same months. Minimal water depth was 17 cm and maximum 30 cm. Stream width varied from 2 to 5 m during the low and high water periods, respectively. As in other headwater streams with an important slope, water velocity varied between 0.55 and 0.83 m s⁻¹. Minimum discharge was 0.187 m³ s⁻¹ in February and maximum discharge was 1.245 m³ s⁻¹ in September (Table 1). Substratum was dominated by cobbles (35%) and boulders (25%), with gravel (20%), sand (20%) and pebbles (10%), also well represented.

Larval life history

Head capsule width resulted as the best measure to explain life history patterns (Fig. 2).

A. torrens had a univoltine life cycle with the first very small larvae being collected in February and with a density peak in April (class 1+2=142 larvae) (Fig. 2). Though early instars continued to be present throughout winter (June–September), final-instar larvae were not found in this season. Instead, a fast growth in larval size was observed from November to March. Large collections of larvae in March (n=291) were dominated by medium to large size individuals. Last instar larvae (class 7) were

recorded in late summer (February and March), larvae with dark wingpads (ready to hatch) were only recorded in March. *A. torrens* had a moderately synchronized, univoltine life cycle. Larvae needed at least 12 months to complete their development.

A. peruvianus also had a moderately synchronized, univoltine life cycle (Fig. 2). This species seems to have an extended recruitment starting in March where very small larvae appeared. Smallest size classes were present in early autumn, all winter and in early spring. Large collections of larvae were obtained in December (n=170) and January (n=115) being dominated by middle size individuals. Last instar larvae (class 7) were collected during December, January and February, and larvae with dark wingpads (ready to hatch) on February. Subimago and adults were collected on sweep nets in late November. As in *A. torrens*, larvae needed at least 12 months to complete their life cycle.

Larval density, biomass and secondary production

Biomass determination was performed using a mass–length equation based on head capsule width, which was chosen because this measurement showed the best adjustment in the regression models obtained (Table 2).

Mean monthly density of *A. torrens* ranged between 26 and 1080 ind m⁻², with a peak in March. *A. peruvianus* mean density was between 7 and 629 ind m⁻² and peaked in December (Fig. 1). In both species, the biomass showed the same pattern as density (Fig. 1). The annual production of *A. torrens* and *A. peruvianus* was 0.18 and 0.11 g m⁻², respectively (Table 3). P/B ratio of both species was similar, being 3.90 and 3.35 for *A. torrens* and *A. peruvianus*, respectively (Table 3). With exception of February and July the temporal interspecific overlap in density and biomass was low (Table 4). Thus, both species showed PS values lower than 0.5 at most months.

Table 1

Range, mean and standard deviation of the main environmental features of La Hoya Stream (Patagonia, Argentina) during the study period.

| Variables | Minimum–maximum mean (± SD) |
|---|-----------------------------|
| Water temperature (°C) | 1/12 (4.75 ± 3.55) |
| Depth (cm) | 17/30 (22 ± 11) |
| Width (m) | 2–5 (3.4 ± 0.85) |
| Current velocity (m s ⁻¹) | 0.55/0.83 (0.67 ± 0.10) |
| Discharge (m ³ s ⁻¹) | 0.187/1.245 (0.44 ± 0.22) |

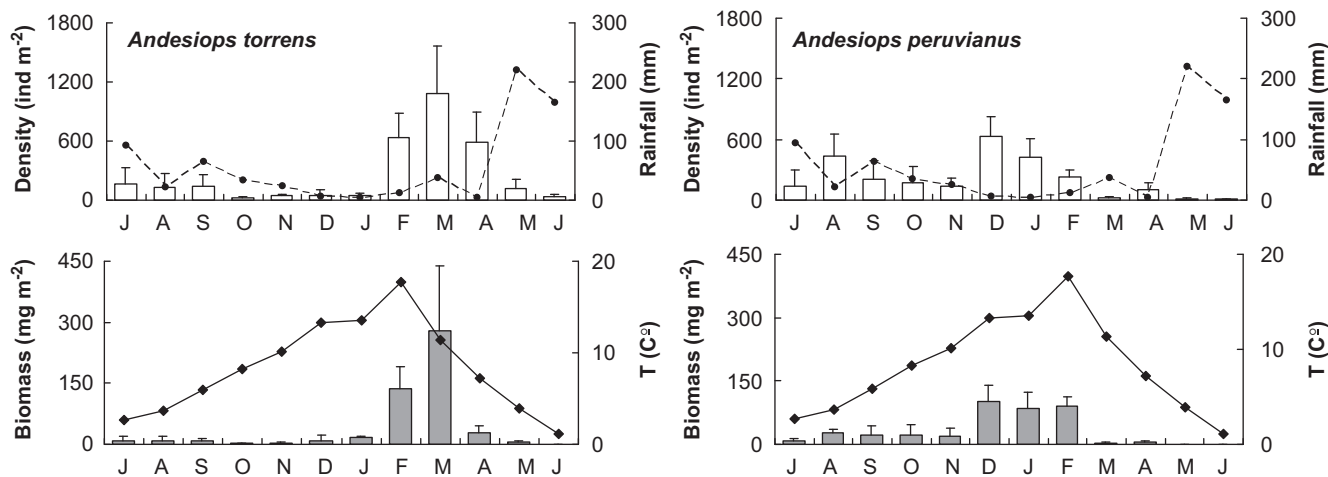


Fig. 1. Mean density (ind m⁻²) and mean biomass (mg m⁻²) of *Andesiops torrens* and *Andesiops peruvianus* in La Hoya Stream (Patagonia, Argentina) during the study period. Data are mean values (± SD) and n=3. Secondary Y-axis shows: mean air temperature (°C, solid lines) and rainfall (mm, dashed lines).

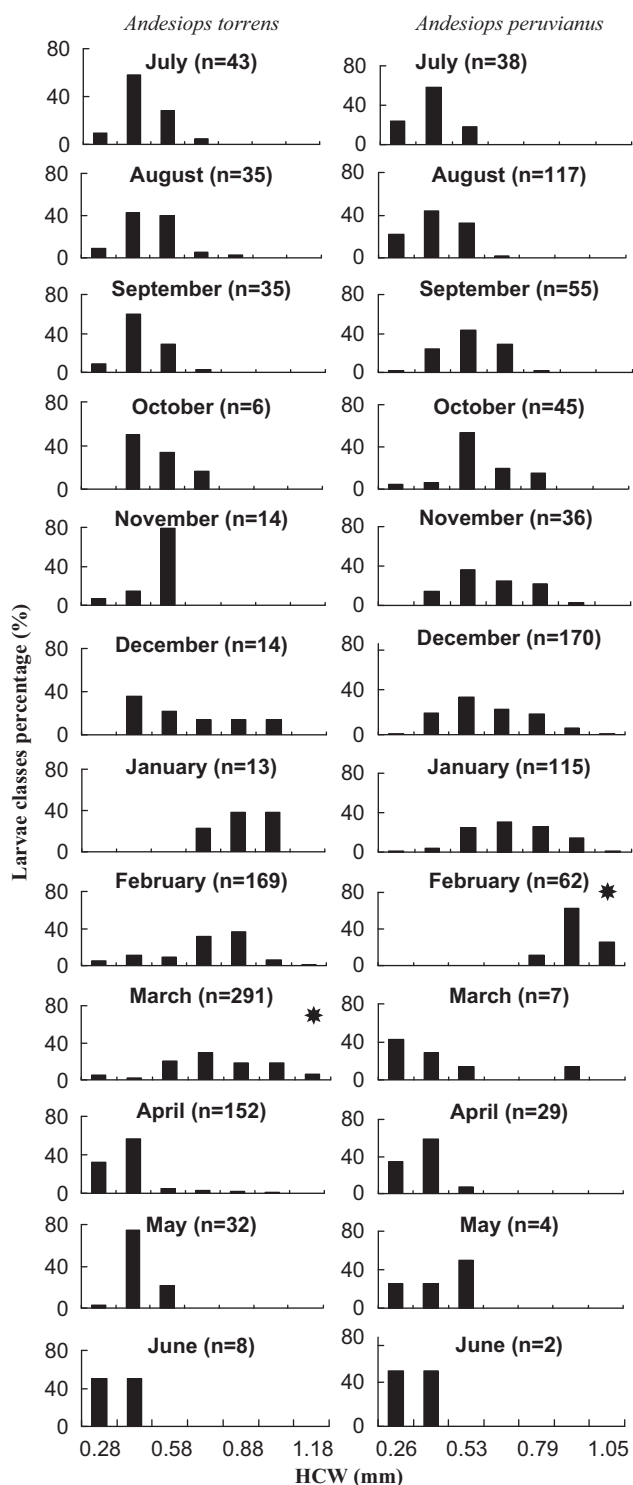


Fig. 2. Monthly larval size distribution (HCW=head capsule width) of *A. torrens* and *A. peruvianus* in La Hoya Stream (Patagonia, Argentina) from July 2004 to June 2005. Numbers above graphs show numbers of larvae measured in each month. (*) indicate presence of mature larvae (dark wingpads).

Exploratory analysis showed significant ($p < 0.05$) and positive correlations between species biomass and water temperature ($r=0.59$ and 0.66 for *A. torrens* and *A. peruvianus*, respectively). Moreover, significant and negative relationships were obtained between *A. peruvianus* and the monthly rainfall ($r=-0.68$ for biomass and $r=-0.62$ for density).

Table 2

Values for the constants a and b , obtained for dry weight and head capsule width (HCW, mm) for *Andesiops torrens* and *A. peruvianus*, (n) number of individuals used to calculate each regression. All correlation coefficients were significant ($p < 0.001$).

| | Regression constants | | r^2 | Range | n | |
|-----------------------------|----------------------|------------------|-----------------|-------|-----------|----|
| | a | b | | | | |
| <i>Andesiops torrens</i> | HCW | 0.472 ± 0.06 | 2.87 ± 0.1 | 0.89 | 0.24–1.18 | 99 |
| <i>Andesiops peruvianus</i> | HCW | 0.468 ± 0.09 | 2.33 ± 0.13 | 0.77 | 0.25–1.08 | 99 |

Discussion

According to our results *A. torrens* and *A. peruvianus* had univoltine synchronous life cycles, with hatching occurring in late summer and early autumn after a short incubation period, larval development in winter–spring seasons, and adults emergence restricted to summer months. Although a wide range of size classes were present in some months we did not detect overlapping generations as occur in other Patagonian mayfly species (Gonser and Spies, 1997). Other cohabiting mayflies at the same sites like the Nesameletidae *Metamonius anceps* (univoltine) and the Leptophlebiidae *Meridialaris chiloeensis* (bivoltine) showed asynchronous life cycles and in this latter case an extended recruitment (Hollmann and Miserendino, 2006). Similar results were documented for other mayflies of the Southern Hemisphere (Huryn, 1996; Campbell, 1986; Winterbourn, 2003). The size frequency histograms and the timing of mature larvae suggest that the flight period of *A. peruvianus* began earlier than that of *A. torrens*. Thus, the size of *A. peruvianus* larvae increased during spring, whereas *A. torrens* larvae did not start growing until early summer (December).

Several scientists, who have studied Baetidae life cycles, recorded bivoltine and multivoltine species in areas at similar latitudes as the present study (e.g. Alba-Tercedor, 1984; Erba et al., 2003). Moreover, Corigliano et al. (2008) studied mayflies life cycles in streams on hills in subtropical areas (Córdoba, Argentina) and again recorded multivoltine and bivoltine life cycles for *Americabaetis* sp. and *Camelobaetidius penai* (Baetidae), respectively. Similarly, Melo et al. (2002) reported a multivoltine life cycle for *Callibaetis willineri* Navás in a tropical stream. In fact, there are few reports of univoltine life cycles for Baetidae species in the literature, as for example that of *Baetis scambus* Eaton in headwater streams in the Sierra Nevada (Spain) (Alba-Tercedor, 1984) and of *Baetis melanonyx* (Pictet) at 830 m.a.s.l. in the Italian Alps (Erba et al., 2003).

According to Ward (1992), temperature is one of the most important environmental controls governing life histories of aquatic insects. Thus, mayflies in warmer, subtropical or tropical regions tend to be multivoltine, while those of temperate regions at higher latitude tend to be univoltine or semivoltine with seasonal traits (Clifford, 1982; Brittain, 1990) and similar patterns occur with altitude (Lee et al., 2008). As we mentioned, our study site is a typically cold headwater stream, therefore *A. torrens* and *A. peruvianus* display univoltine life cycles at this particular latitude and elevation in Patagonia. Nevertheless larval growth of a species could clearly differ between sites, or even from one year to another at the same site (Humpesch, 1979). For instance, the life history of *Baetis alpinus* (Pictet) (Baetidae) is quite plastic and largely dependent upon environmental conditions (temperature and elevation) (Alba-Tercedor, 1990; Kukula, 1997; López-Rodríguez et al., 2008), being multivoltine in Sierra Nevada streams at 640–760 m.a.s.l (Spain) (Alba-Tercedor, 1984), bivoltine at 615 m.a.s.l. (Austria) (Humpesch, 1979), univoltine at 1355 m.a.s.l. (Austria) (Humpesch, 1979) and semivoltine over

Table 3

Estimates of mean density, biomass (dry weight), annual production and *P/B* for *Andesiops torrens* and *A. peruvianus* in La Hoya stream (Patagonia, Argentina). Data were obtained by size frequency method using the material collected from July 2004 to June 2005. CPI=cohort production interval.

| Species | CPI | Mean annual density (ind m ⁻²) | Biomass (g m ⁻²) | Annual P (g m ⁻²) | <i>P/B</i> |
|-----------------------------|-----|--|------------------------------|-------------------------------|------------|
| <i>Andesiops torrens</i> | 12 | 255.25 | 0.04 | 0.18 | 3.90 |
| <i>Andesiops peruvianus</i> | 12 | 209.88 | 0.03 | 0.11 | 3.35 |

Table 4

Monthly interspecific overlap for *A. torrens* and *A. peruvianus* obtained from samples collected from July 2004 to June 2005 in La Hoya stream (Patagonia, Argentina). Values of proportional similarity index (PS) are presented (0=no overlap and 1=total overlap).

| | PS | |
|-----------|---------|---------|
| | Density | Biomass |
| January | 0.22 | 0.33 |
| February | 0.53 | 0.73 |
| March | 0.05 | 0.01 |
| April | 0.31 | 0.29 |
| May | 0.22 | 0.27 |
| June | 0.20 | 0.46 |
| July | 0.93 | 0.90 |
| August | 0.47 | 0.49 |
| September | 0.74 | 0.48 |
| October | 0.27 | 0.17 |
| November | 0.56 | 0.33 |
| December | 0.15 | 0.17 |

2190 m.a.s.l. in France (Lavandier, 1988). We expect life history patterns of both *A. torrens* and *A. peruvianus* to be different at other altitudinal ranges or latitude. In fact, emergence periods of *A. peruvianus* occur from December to April at the Grande, Nant y Fall and Corcovado rivers (350 m.a.s.l.) at the same latitude of the present study (Pessacq, pers. obs.).

The temporal density pattern observed in *A. torrens* was similar to that reported for other mayfly species in previous studies in the area (Hollmann and Miserendino, 2006), with maximum density and biomass in March. On the other hand, *A. peruvianus* decreased significantly in density during the rainy season (May–July) (high discharge period), which is a common response of benthic communities of rivers and streams in the Cordillera (Miserendino and Pizzolón, 2003, 2004). This pattern is opposite to what happens in subtropical environments. Where for example the mayfly *Camelobaetis penai* (Baetidae) seems to increase consistently in density at the rainy season (summer) in coincidence with warmer temperatures (Corigliano et al., 2008).

Temperature and discharge seem to be the environmental constraints in headwater Patagonian streams. La Hoya stream is an environment with a marked seasonality. It is also predictable in terms of discharge with greater spates occurring mostly during the spring snowmelt (Miserendino, 1995; Miserendino and Pizzolón, 2000). In summer the environment usually shows stable hydrological conditions with warmer temperature, and supports a variety of food resources (e.g. periphyton). Consequently, several species of aquatic insects including mayflies and stoneflies display a strong seasonal emergence pattern taking place in this period (Hollmann and Miserendino, 2006, 2008). Under these conditions the species almost certainly achieved the number of degree days needed to complete their development (Sweeney, 1984).

According to Winterbourn (2003) it is expectable that congeneric species having similar life cycles, larval growth patterns and functional feeding habits show high interspecific competition. Our observations of *Andesiops* species would indicate a low temporal overlap (as indicated by low PS values). They

coexisted in the same site, but, as other authors found (González et al., 2003), temporal segregation in resource use would have reduced interspecific competition. Thus, the larval recruitment and density peaks were temporarily segregated in both species (Ward, 1992; González et al., 2003).

A. torrens (0.18 g DM m⁻² y⁻¹) and *A. peruvianus* (0.11 g DM m⁻² y⁻¹) secondary production values were quite lower than estimated for other Baetidae species as for example *Baetis bicaudatus* Dodds (1.4 g DM m⁻² y⁻¹), *Baetis rhodani* (Pictet) (5.6 g DM m⁻² y⁻¹) and *Baetis vagans* McDunnough (1.80–2.5 g DM m⁻² y⁻¹) (Waters, 1966; Pearson and Kramer, 1972; Welton et al., 1982; Tokeshi, 1985). However, all the species investigated at the papers had multivoltine life cycles. As stated by Lee et al. (2008) estimated annual production of mayflies in temperate streams depends on species size and voltinism. In fact, *A. torrens* and *A. peruvianus* production values were comparable to those reported for mayflies from the Northern Hemisphere as the univoltine species *Ephemera spilosa* Navás (Dudgeon, 1996), *Habrophlebia lauta* (Eaton) and *Habroleptoides confusa* (Sartori and Jacob) (González et al., 2003), and the fast growing cohort of the multivoltine *E. orientalis* McLachlan (Lee et al., 2008).

The biomass turnover rate of *A. torrens* was slightly higher than that of *A. peruvianus* (*P/B*=3.9 and 3.35, respectively). Both values were close to those documented for *Caenis* sp. (*P/B*=4.3) in the Escondido Lake, Bariloche, Argentina (Añón Suárez and Albariño, 2001). According to Huryñ and Wallace (2000), the lowest estimations of community production are usually observed in cool-temperate and arctic streams and have been attributed to the constraints of low seasonal temperatures, nutrients and food limitation.

In addition to the analysis of life history patterns and interspecific competition, our research provided an estimation of annual secondary production and an overview of possible environmental constraints. Given the range of geographical distribution of these South American species we consider this paper valuable for further ecological research as for example their potential use in a scenario of climate change. It has been predicted a 3–4 °C increase in both summer and winter temperatures between 30° and 55°S in South America (Manabe and Wetherald, 1987) that would have significant effects in stream ecology of Patagonian running waters (turbidity, sediment deposition, runoff patterns). These changes will produce the loss of suitable habitats for cold-water specialists, which in turn can suffer reductions in their distributional range and local extinction. Hering et al. (2009) established five parameters to describe the species sensitivity to climate change impacts: endemism, preference for springs, preference for cold water temperatures, short emergence period, and restricted ecological niches in terms of feeding types. According to our results several of these characteristics would be present in *A. torrens* and *A. peruvianus*.

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