Life history and emergence patterns of stonefly species in mountain streams of the Futaleufú basin, Patagonia (Argentina)

M.E.T. Hollmann, M.L. Miserendino*


The temporal dynamics in density, life histories, and emergence patterns were described for the first time for five Plecoptera species in tributaries of the Futaleufú River in Patagonia, Argentina. Benthic samples and adult collections were made in five low order Nothofagus forested streams. Four species of Gripopterygidae; Aubertoperla illiesi, Notoperlopsis femina, Antarctoperla michaelensi and Senzilloides panguipulli had simple, highly synchronized univoltine life histories. The austroperlid Klapopteryx kuscheli takes more than two years to develop. Emergence periods of most of the species were concentrated in late spring and summer (October to February), which suggests seasonal and synchronized life histories. Most N. femina adults were collected in mid spring indicating this species emerged first, whereas S. panguipulli emerged last from January to April. Aubertoperla illiesi showed a slightly delayed emergence at the high elevation site (La Hoya Stream) when compared to a piedmont stream, suggesting that temperature was an important control. Although we were unable to describe the life history of Limnoperla jaffueli (Gripopterygidae) its adult emergence period was November to January. Life histories of Plecoptera species in the studied streams seem to have a high degree of seasonality at least at this latitude, and are possibly determined by predictable temperature patterns and discharge regimes. This first contribution on the life histories of Plecoptera species helps us to better understand the dynamics and functioning of pristine but fragile aquatic environments in Patagonia.

Keywords: aquatic insects; life history; Plecoptera; river; synchronicity; voltinism.

Introduction

Plecoptera nymphs are a conspicuous component of the macroinvertebrate fauna in pristine mountain streams worldwide (Short & Ward 1980). In Patagonian running waters (South America), stoneflies constitute a highly diversified and specialized group of aquatic insects (Wais et al. 1987). Only six of the 17 Plecoptera families (Eustheniidae, Diamphipnoidae, Austroperlidae, Gripopterygidae, Notonemouridae and Perlidae) are present in the region (Illies 1965) and as is usual with Plecoptera in the Southern Hemisphere the genera are endemic to their particular landmass (Mc Lellan 2001). This is a frequent characteristic of the stoneflies inhabiting Patagonian aquatic environments.

The ecological knowledge of stoneflies in the mountainous area of Patagonia has increased notably with recent studies. The altitudinal distributions of Plecoptera assemblages have been described by Albariño (1997) and Miserendino & Pizzolón (2000) and functional feeding behaviours of some abundant species have been the focus of other research (Albariño & Balseiro 1998, Hollmann & Miserendino 2004). Plecoptera communities have been used to assess organic pollution (Miserendino 2000) and to evaluate land use effects in watersheds affected by agriculture and cattle ranching (Miserendino & Pizolón 2004, Miserendino 2006). However, in contrast with the situation in the Northern Hemisphere (Harper et al.1991, Sheldon 1999, Tierno de Figueroa et al. 2001, Richardson 2001) and other countries of the Southern Hemisphere (Winterbourn et al. 1981, Bunn 1988), little is known about the life histories and emergence periods of aquatic insects in Patagonia (Hollmann & Miserendino 2006). In particular, no life history studies have been made on Plecoptera species in Patagonia.

Studies on aquatic insects in temperate regions suggest that life histories are tuned to the seasonal availability of food, and that related species are temporally segregated (Vannote et al. 1980, Richardson 1991). On the contrary, some stream insects in the Southern Hemisphere, such as those in New Zealand, have been characterized as having flexible, poorly synchronized life histories with non-see-
sonal patterns of development and extended flight periods (Winterbourn 1981). This apparent flexibility may be related to climatic stability, unpredictability of discharge, and a greater continuity in supply of allochthonous inputs (Winterbourn 1995, Scarsbrook 2000). The running water fauna of Patagonia show strong biogeographical affinities with that of New Zealand (Boothroyd 2000, Hitchings & Staniczek 2003). However, rivers in the Patagonian Mountains are more predictable in terms of annual discharge patterns and one might expect the life histories of stream insects to demonstrate a greater degree of synchrony in growth (Miserendino & Pizzolón 2003). Nevertheless, recent studies of life histories of common mayfly species in the Patagonian area show that synchrony of growth is lower than expected (Gonser & Spies 1997, Hollman & Miserendino 2006).

Knowledge of life histories and emergence periods of aquatic insects is crucial for understanding species biology and behaviour, and also for aquatic conservation purposes (Stazner & Resh 1993, Cayrou & Céréghino 2005). For example, life history studies and knowledge of the emergence periods of species in an area can help to improve the use and interpretation of biotic indices (Sheldon 1999). Most stonefly species are stenothermic; consequently, changes in thermal regime of watercourses can limit their distribution (Ward 1985, Quinn & Hickey 1990). In particular, the distributions and life histories of stoneflies can be strongly affected by river regulation (Perry et al. 1986, Brittain 1991, Miserendino & Stanford 2004).

In previous studies carried out in rivers of the Futaleufú Basin, Patagonia, larval Gripopterygidae and Austroperlidae were found to contribute strongly to benthic community density and production (Miserendino 2001, Miserendino & Pizzolón 2004). The species considered in the present study are abundant and frequently recorded in different rivers and streams in the Patagonian mountain ranges (Miserendino & Pizzolón 2000, 2003). In this paper we examine the life histories and emergence patterns of five stonefly species: Aubertoperla illiesi (Froehlich), Notoperlopsis femina (Illies), Antarctoperla michaelseni (Klapálak), Senzilloides panguipulli (Navás) and Klapopteryx kuscheli (Illies), inhabiting tributaries within the Futaleufú River basin, Patagonia.

**Study area and methods**

Life history studies were carried out at five sites in the Futaleufú Basin, Chubut Province (Fig. 1). La Hoya Stream is a 2nd order watercourse in the Esquel-Percy river drainage system. The study site is located in the mountainous zone at 1237 m.a.s.l (Fig. 1) and is surrounded by riparian forest composed mainly of deciduous Nothofagus pumilio, the shrubs Fuchsia magellanica, Ribes magallanicum, Mulinum spinosum and the herbaceous Stipa sp. (León et al. 1998). The Blanco, Baggilt, Rifleros, and Nant y Fall streams (lower Futaleufú Basin) are located along the strongly west-east decreasing rainfall gradient characteristic of the eastern side of the Andes, especially between 40 and 43° S (Paruelo et al. 1998). They are high gradient streams. Blanco and Baggilt headwaters include small glaciers, and headwater lakes are present in the Baggilt and Nant y Fall catchments. The Blanco and Baggilt catchments are covered by deciduous Nothofagus pumilio forest between 800 and 1300 m, and by the perennial Austrocedrus chilensis (Cupressaceae), which is also common...
in the high forest at the Rifleros stream (over 800 m). The downstream portions of the Rifleros and Nant y Fall basins are covered by N. antarctica forest. However, at these sites the riparian corridor has been completely invaded by the exotic Salix fragilis.

At each site the percentage of boulder, cobble, gravel, pebble and sand on the stream bed was assessed using a grid (1m²) (Gordon et al. 1994). Air and water temperature and stream width were measured monthly during a year (1991-1992 in Blanco, Baggilt, Rifleros and Nant y Fall streams, and 2004-2005 in La Hoya stream). Current velocity was measured during the high and low water period at all sites. Discharge was recorded bimonthly but was not available for Blanco and Rifleros. Specific conductance (at 20°C) was measured bimonthly with a Horiba U2-probe.

The data in this paper were assembled from a number of studies previously conducted in the area. Life histories of Antarcotoperla michaeliseni and Notoperlopsis femina were described from collections made at Baggilt and Rifleros rivers respectively. At these sites, larval samples were taken from September 1991 to July 1992. In addition to obtain adult specimens, monthly samples from October 2003 to April 2004 and from September 2004 to March 2005 were taken (Blanco, Baggilt, Rifleros and Nant y Fall). Life histories of Aubertoperla illiesi, Sensilloides panguipulli and Klapopteryx kuschelii were assessed from samples taken monthly from July 2004 to June 2005 at La Hoya Stream. In all cases benthic samples were collected from riffles with a Surber sampler (0.09 m²; 250 µm mesh). The sampling schedule for adults in La Hoya sites involved monthly visits from October 2004 to April 2005. Because larval collections come from separate research projects the procedures employed to obtain samples were different. Estimates of larval density were obtained from Baggilt and Rifleros streams from each of which eight samples were taken and pooled each month. At La Hoya Stream three samples were taken each month and analyzed, separately. In order to collect more larvae for the description of life histories eight additional Surber samples were taken from La Hoya Stream and pooled on each sampling date. Samples were fixed with 4% formaldehyde solution, sorted at 5x magnification and stored in 70% ethyl alcohol. Specimens were identified using available keys (Illies 1963, Mc Lellan 2001, Fernández & Domínguez 2001).

Shoreline pitfall traps (Stanford 1975, Miserendino & Stanford 2004) were employed for the collection of teneral adults and emerging nymphs. Pitfall traps were used at all sites (La Hoya, Blanco, Baggilt, Rifleros, Nant y Fall) plus two additional sites in La Hoya Stream. At each site, 5 plastic recipients (1500 cm³), 12 cm diameter were embedded in the river bank and concealed by large flat rocks. The cans were half filled with 10% formalin. A thin film of glycerine was applied to the surface of the fixative, to encumber teneral adults and emerging nymphs that fell into the pitfall traps. The pitfall traps were used continuously and emptied on each sampling trip. Additional adults were collected from each site by sweeping low riparian vegetation. Shrubs, small trees and high grasses on the shoreline were beaten with a sweep net for at least 10 minutes. All organic material, nymphs and adults were preserved in 70% ethanol. We tried to keep to a monthly schedule for sampling adults at most sites, however, some pitfall traps were vandalized or lost at Rifleros and Nant y Fall (September and November second year). To describe life histories of the species interocular distance was measured at 8-64 times magnification (depending on the size of the species) with a linear eyepiece micrometer inserted in a stereomicroscope (Snellen & Stewart 1979, Short & Ward 1980, Richardson 2001). The number of specimens counted and measured for the life history descriptions were: A. illiesi 1,422 larvae and 115 adults, S. panguipulli 163 larvae and 11 adults, A. michaeliseni 173 larvae and 29 adults, N. femina 241 larvae and 9 adults, and K. kuschelii 629 larva and 116 adults. Sex ratio analysis of the adults was performed per site using Chi-square test (p<0.05) (Sokal & Rohlf 1995).

**Results**

**Environmental features**

As it is a headwater environment La Hoya Stream was narrower and had lower air temperatures than the other sites considered in the study. However, most physicochemical characteristics were similar among sites (Table 1). Some climatic differences (air temperature, rainfall) related to the position of the tributaries in the basin are shown in Fig. 2. Temperature patterns were similar among sites despite the surveys being performed in different years. The discharge regime of running waters in the cordillera is related to rainfall (May-July) and snowmelt (September-October) which was higher in the lower Futaleufú Basin than at La Hoya stream. Most sites were cool and turbulent. The substrate was composed mainly of boulders and cobbles at most sites, however substrates were generally smaller at Rifleros and Nant y Fall (Table 1).

**Life histories and emergence patterns**

*A. illiesi*: Maximum density of nymphs in La Hoya Stream was recorded in July (1088 ind. m⁻²). Very low
densities of larvae were recorded in January (11 ind. m\(^{-2}\)) (Fig. 3). *A. illiesi* had a univoltine life history with recruitment of small larvae first seen in February (Fig. 4). Collections of nymphs obtained in March and April were dominated by small individuals. We observed slow growth in autumn followed by a rapid increase in larval size during spring and summer. Final-instar nymphs were collected in October and November. Adults were taken with sweep nets and traps from November to February (Table 2).

*S. panguipulli*: Nymphs peaked in abundance in La Hoya Stream in July (115 ind. m\(^{-2}\)), but were not found in October and few nymphs were recorded in September, November, December, February, March and June (Fig. 3). *S. panguipulli* had a well synchronized, univoltine life history (Fig. 4). Very small nymphs were found in February whereas medium-large nymphs predominated from May to September. Final instar nymphs were taken in monthly samples in December, January and February. The emergence period started in January and extended until mid-April (Table 2).

*A. michaelseni*: Nymphs peaked in abundance in Baggilt Stream in June (Fig. 3) but none were found in October, November and December. The life history was univoltine (Fig. 4) with adults emerging between October and February and peaking in December at most sites.
Early instar larvae began to appear during February and grew fast in the following two months. We found that sex ratio was male-biased in *A. michaelseni* at Baggilt, and this pattern was statistically significant (Table 2, $X^2=13.8$, $p<0.05$).

*N. femina*: *N. femina* had a univoltine life history with emergence starting in September before the other species (Table 2). Larvae appeared in February and were most abundant in April (Fig. 3). Mature nymphs were collected from July and September (Fig. 4). All the adult males captured were brachypterous.

*K. kuscheli*: Maximum density of nymphs was recorded in La Hoya Stream in November (185 ind. m$^{-2}$) and minimum abundance was in June (7 ind. m$^{-2}$) (Fig. 3). We observed small nymphs from November to March (Fig. 5), which suggests that hatching occurred throughout spring and summer. Most mature nymphs were found from January to April. *K. kuscheli* appeared to have a 2-year life history based on this species large size and the cooler water temperatures of La Hoya stream. Numerous adults were collected in pitfall traps during late-spring and summer (November – January) (Table 2) and as in *N. femina* all males were brachypterous. However, in *K. kuscheli* at least 50% of the females were also short winged. We observed that sex ratios were male-biased in *K. kuscheli* at both sites, differences were statistically significant at Baggilt due to small sample size at La Hoya (Table 2, $X^2=56.5$, $p<0.05$).

We were unable to describe the life histories of several other species including *Limnoperla jaffuelii* because few nymphs were found in benthic samples. However, we captured 24 adults of *L. jaffuelii* in Nant y Fall, Blanco and Rifleros Streams between December and February (Table 2). Except for *S. panguipulli* we did not capture adults of stoneflies from April onwards at any of the sampled sites.
Discussion

This is the first study of stonefly life histories in Patagonian streams. Our results indicate that the small-medium sized (0.5-1.5 cm) Aubertoperla illiesi, Senzilloides panguipulli, Antarctoperla michaelseni and Notoperlopsis femina (Gripopterygidae) had univoltine life histories in the Futaleufú Basin. Similarly, many small-medium sized Plecoptera species in the Northern Hemisphere have univoltine life histories (Harper et al. 1991, Tierno de Figueroa et al. 2001, Richardson 2001) as do numerous Southern Hemisphere Gripopterygidae including Antarctoperlinae (Winterbourn 1966, 1978, Hynes & Hynes 1975, Bunn 1988, Death 1990).

In the present study N. femina had a fast winter growth cycle with well synchronized larval development and a short period of adult emergence. Notoperlopsis femina adults were collected in September, consistent with the report of McLellan et al. (2006) for this species in the Gualjain River (Precordillera and steppe transition at 500 m.a.s.l., 42°32’06”S, 70°25’44”W). As in our work all males they collected were short-winged. The life history of A. michaelseni was less well synchronized because of an extended hatching period during autumn, and an extended period of adult emergence (November to February in Baggilt Stream). Senzilloides panguipulli also had an extended hatching period during winter but adult emergence started in January and continued until April. In contrast, Aubertoperla illiesi had slow winter development in La Hoya Stream, rapid nymphal growth in spring, and emergence from October to February.

In the Futaleufú Basin, emergence of A. illiesi appeared to begin later at La Hoya Stream (1237 m a.s.l.) than at Nant y Fall Stream (415 m a.s.l.) and may reflect differences in temperature patterns, which in turn depend on elevation. Nevertheless, our results suggest that most of the gripopterygid species studied had well synchronized emergence patterns. This situation is consistent with the findings of Hynes & Hynes (1975) and Bunn (1988) who concluded that synchronized seasonal life histories appeared to be the rule rather than the exception for gripopterygid stoneflies in temperate southern Australia. In contrast, the relatively few New Zealand stoneflies studied have a mixture of well- and poorly synchronized life histories (Scarsbrook 2000).

Synchronized emergence is a widespread phenomenon among insects because it facilitates the finding of mates and reduces the exposure of adult individuals to predation (Stewart & Stark 1993, Dieterich & Anderson 1995). Richardson (2001) mentioned that there can be a degree of phylogenetic constraint in the timing of life histories, while environmental factors such as temperature...
Table 2. Numbers of adult female and male Plecoptera collected at five sites in the Futaleufú River basin in two consecutive years (La Hoya sites; 2004-2005; Blanco, Baggilt, Rifleros and Nant y Fall; 2003-2004). TF: total females, TM: total males. – no data * Significant differences (p<0.05, critical value $X^2_{(0.05,1)}=3.84$).

<table>
<thead>
<tr>
<th></th>
<th>2003-04</th>
<th>2004-05</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Oct</td>
<td>Nov</td>
</tr>
<tr>
<td>La Hoya</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aubertoperla illiesi</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Klapopteryx kuscheli</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Senzilloides panguipulli</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Blanco</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Antarctoperla michaelseni</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Aubertoperla illiesi</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Baggilt</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Antarctoperla michaelseni</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Aubertoperla illiesi</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Klapopteryx kuscheli</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Nant y Fall</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Antarctoperla michaelseni</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Aubertoperla illiesi</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Linnoperla jaffueli</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Rifleros</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Antarctoperla michaelseni</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Linnoperla jaffueli</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Notoperlopsis femina</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

and day length can also constrain growth and emergence patterns (Sweeney 1984; Ward 1985, 1992). We suspect that some of the observed differences in emergence periods of our gripopterygid species such as $A. illiesi$ were related to differences in water temperature at the various sites. Thus, February was the warmest month at La Hoya Stream during the study period, whereas January was the warmest month in the lower Futaleufú River basin. How-
ever, this should be taken with care since only 4 adults of
A. illiesi were collected at Nant y Fall during October.

Long life histories are typical of many larger predatory and detritivorous stoneflies (Merrit & Cummins 1996) such as the New Zealand eustheniid Stenoperla prasina and the austroperlid Austroperla cyrene (Scarsbrook 2000). Consistent with this pattern we found that the large austroperlid Klapopteryx kuscheli (mature larval length > 3cm) that feeds mostly on Nothofagus pumilio leaves (Albariño & Balseiro 1998) took about two years to complete its life cycle. Semivoltine (2 year) life histories have also been reported for predator and detritivore stoneflies in north-temperate regions (e.g., predators: the chloroperlids Sweltsa onkos and S. fidelis, detritivores: the leuctrid Depaxia augusta) (Harper et al. 1991, Dietterich & Anderson 1995, Richardson 2001).

Extended larval recruitment, differential growth rates of males and females and cohort splitting (i.e., a separation into faster and slower-growing larval groups) are all found in some aquatic insects with long life cycles and extended emergence periods (Butler 1984, Townsend & Pritchard, 1998). Although K. kuscheli is one of the largest stoneflies inhabiting Patagonian running waters we found no evidence of cohort splitting and adults were seen only in late spring and summer. However, early instar larvae were present from November to May indicating extended recruitment. A study on the life cycle of the even larger Pteronarcyidae Pteronarcys californica in Alberta showed that it spent at least 4 years in the larval stage, had extended larval recruitment as in K. kuscheli, probable cohort splitting, and a high degree of synchrony in adult emergence.

Since emergence is a single event in a life history, the sex of emergents must influence the mating behavior and reproductive success (Stewart 1994). Differences in sex ratio have been observed for several species of stoneflies (Zwick 1990, Sheldon 1999, Petersen et al., 2006). Our study suggests that sex ratios of K. kuscheli and A. michaelseni were male-biased in Baggilt stream. Similar observation has been reported for the stonefly Calineuria in a cold stream in Montana (Sheldon, 1999). However, sex-specific differences can be related with adult behavior, longevity and habitat usage (Petersen et al., 2006). Then, it is possible that pit-fall traps effectively caught more males (all brachypterous) than females of K. kuscheli. Brachyptery is more common in permanent aquatic habitats (Harrison 1980) and frequently associated with an increase in altitude and latitude, particularly where insects are exposed to cool temperatures and high winds (McLellan 2001).

The life histories of many southern hemisphere stream invertebrates appear to be seasonally flexible in contrast to the more synchronous life cycles exhibited by numerous north-temperate species, and may be a consequence of selection driven by climatic unpredictability and equability (Winterbourn 1995, Lake 1995, Gonser & Spies 1997, Scarsbrook 2000). Flexible life cycles are found in the mayfly species Meridialaris chiloensis and Meta- monius anceps that inhabit La Hoya Stream (Hollmann & Miserendino 2006) but not in the Plectoptera species considered in this paper. Thus, in La Hoya, Baggilt and Rilferos streams, stonefly life histories were well synchronized and emergence periods were restricted to a few months. We recognize that latitude and altitude can have strong effects on emergence patterns resulting in synchrony (Füreder et al. 2005), and can account for at least some of the geographic variation in the timing of emergence (Richardson 2001). For this reason extrapolation of our findings to streams elsewhere in Patagonia need to be made with caution.
Acknowledgements:

Special thanks to G. Alday, C. Di Prinzio, P. Diaz, A. Humai, A. Gómez and R. Magallanes for valuable help during the sampling and to C. Brand for laboratory assistance. We are grateful to Dr. Miguel Archangelsky for helpful comments on the English version of the paper. We greatly appreciate the reviews of Dr. Mike Winterbourn for his thoughtful and constructive suggestions. Thanks to anonymous reviewers for valuable comments that greatly improved the manuscript. This is Scientific Contribution n° 23 from LIESA.

References


