Habitat preference and life history of the mayflies *Metamonius anceps* Eaton (Nesameletidae) and *Meridialaris chiloeensis* Demoulin (Leptophlebiidae) in a Patagonian mountain stream

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The habitat preferences, temporal dynamics in density and the life history of two species of mayflies, *Metamonius anceps* and *Meridialaris chiloeensis*, were investigated in a Patagonian mountain stream over a period of one year. Benthic samples were taken in a low order *Nothofagus* forested stream. *M. anceps* was univoltine with small nymphs predominating in winter and emergence occurring in summer. *M. chiloeensis* showed a bivoltine life cycle with a winter and summer generation, and emergence period in spring and summer. Both species were significantly more abundant in the low water period than in the high discharge season. Gravels supported significantly more individuals of *M. chiloeensis* than sand in pools and leaf packs. Temporal overlap of abundance between species was low. The existence of different life history strategies and the temporal shift of main generations and density peaks were critical to allow species coexistence.

Keywords: insects, Ephemeroptera, life cycle, ecology, river, habitat preference

Introduction

Ephemeroptera nymphs are a conspicuous component of the macroinvertebrate fauna in mountain streams (Edmunds & Waltz 1996). In running waters of Argentina mayflies are represented by twelve families (Domínguez et al. 2001). In Patagonia, the family Leptophlebiidae is very diverse and widely distributed (Domínguez et al. 1994), among leptophlebiids genus *Meridialaris* shows a broad distribution range (26º to 55º S). *M. laminata* (Ulmer), *M. diguillina* (Demoulin) and *M. chiloeense* (Demoulin) are very abundant in the region. On the other hand, Nesameletidae (= Siphlonuridae), of amphinotic distribution, is represented only by *Metamonius* which is distributed from 33º to 55 º S including the coastal range in Chile and headwaters in the Cordillera (Chile and Argentina) (Mercado & Elliot 2004). In the last decade, the knowledge of Ephemeroptera in the area has gained attention. The altitudinal distribution of mayfly species and their environmental relationships has been described in rivers of the Cordillera and the Plateau (Miserendino & Pizzolón 2000, 2001). Mayfly communities have also been utilized to assess organic pollution and to evaluate the land use effects in some watersheds (Miserendino 2001). However, despite the common occurrence of mayflies in streams and rivers in Patagonia there have been few studies on their life histories (Gonser & Spies 1997).

Some Northern hemisphere studies on aquatic insects suggest that life histories are tuned to the seasonal availability of food, and that related species are temporally segregated (Vannote et al. 1980). In contrast 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-seasonal patterns of development and extended flight periods (Winterbourn et al. 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 shows 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 discharge and one might expect the life cycles of

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stream insects to demonstrate a greater degree of synchrony in growth (Miserendino & Pizzolón 2003).

In previous studies carried out in the Esquel-Percy River drainage system, *Metamonius anceps* and *Meridialaris chiloeense* were abundant and frequently recorded at headwaters (Miserendino & Pizzolón 2000, 2001). Information about their feeding habits is available; *M. chiloeensis* feeds on periphyton (Díaz Villanueva et al. 2004) and *M. anceps* shows gut contents dominated by fine detritus and diatoms (Hollmann & Miserendino 2004), both species being categorized as grazers. Finally, an important environmental database from La Hoya stream exists from earlier investigations. For these reasons we planned to achieve our research with these two species. Because the knowledge of life cycles greatly contributes to understand benthic community dynamics in rivers (Ward 1992), we propose 1) to describe the life cycle and to analyze synchrony in growth of two mayflies species *M. chiloeensis* and *M. anceps*, and 2) to assess their habitat preferences in a headwater stream in Patagonia.

Study area and methods

La Hoya stream is a 2nd order watercourse in the Esquel-Percy river drainage system in the Northwest of the Chubut Province. 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* (lenga), the native shrubs *Fuchsia magellanica*, *Ribes magellanicum*, *Mulinum spinosum* and the herbaceous *Stipa* sp. (León et al. 1998).

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) (Gordon et al. 1994). Air and water temperature, depth and stream width were measured in a monthly basis whereas current velocity and discharge were recorded bimonthly. Average depth was calculated from five measurements from one transversal profile across the channel with a calibrate stick.

In order to analyze seasonal variation in abundance and to describe the life cycles, larvae were collected monthly from July 2004 to June 2005. Samples were collected with a Surber net (0.09 m⁻²; 250 µ mesh size), at each occasion three replicates were taken on riffles. In order to collect more larval instars for the life history description, eight additional Surber samples were taken and pooled on each sampling date. Samples were fixed with 4 % formaldehyde solution. At the laboratory samples were sorted out under 5x magnification and then stored in 70 % ethyl alcohol.

Life cycle analyses

To describe life cycles of the species, 2,969 larvae of *M. chiloeensis* and 329 larvae of *M. anceps* were measured. In the case of *M. chiloeensis* nymphs the body length was measured under a stereomicroscope (8X) (Huryn 1996, Buffagni & Gomba 1996, Gonser & Spies 1997). Abdomen length was used as a measure of the body size in *M. anceps*. It was measured with an 8X magnification from the first segment to the posterior tip of the abdomen, excluding cerci and telofilum (Winterbourn 2003). Adults were caught using a sweep net and a light trap combined with a white fabric as suggested by Domínguez et al. (2001). Larvae and adults were identified using regional keys (Domínguez et al. 1994, Mercado & Elliot 2004).

Habitat sampling

Another sampling was undertaken during high (September 2004) and low water periods (February 2005). In depositional areas (pools) two habitat types were sampled: sand and boulders. In run-riffle areas three different habitats were studied: boulders, gravel and leaf packs. Three Surber samples were taken from each habitat during the dry and wet seasons (*n*= 30). We chose this sampler because a previous survey in high gradient, low order streams in Patagonia, showed consistent results to distinguish benthos communities among different habitats (Velásquez & Miserendino 2003). To prevent small organisms escapes from debris, all material collected from leaf-packs was carefully washed and processed in the laboratory. Fixed-effects 2-factor ANOVA models were used to assess significant differences in total density between habitats (5), and dates (2). The interaction between habitat and season was also assessed. A posteriori comparisons among habitats were performed with Tukey's (HSD) test (p<0.05). The overlapping of the utilized habitat between both mayflies species during the low and the high water period was calculated with the proportional similarity index (PS) (Whittaker 1975). Values may range from 0 (no overlap) to 1 (total overlap).

Results

Environmental features

Temperature ranged from 1-12 ºC. Minimal water depth was 17 cm and maximum 30 cm. Stream width var-

ied from 2 to 5 m during the low and high water periods respectively. As in other head water streams with an important slope current velocity varied between 0.55 and 0.83 m.s^{-1}. Minimum discharge was 0.187 m^3.s^{-1} in February and maximum discharge was 1.245 m^3.s^{-1} in September (Table 1). Substratum was dominated by boulders (25 %) and cobbles (35 %), being pebbles (10 %), gravel (20 %), and sand (20 %) well represented.

Table 1. Range, mean and standard deviation of the main environmental features of la Hoya Stream during the study period.

Variables	Minimum-Maximum Mean (±SD)
Air Temperature (ºC)	-3 /16.5 (7.85±6.70)
Water Temperature (ºC)	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)

Life histories

M. chiloeensis: Maximum density of nymph was recorded in March (1300 ind. m^{-2}). In February larvae were absent in density samples; minimum densities were recorded in September (126 ind. m^{-2}) and May (170 ind. m^{-2}) (Fig. 1 a). *M. chiloeensis* had a bivoltine life cycle with a winter and a summer generation (Fig. 2). Overlapping generations were observed in January and February. Large collections of nymphs obtained in October and February were dominated by small individuals. Final-instar nymphs were collected in September, December, January and February. Subimagoes and adults were collected on sweep nets and traps in January and February.

M. anceps: M. anceps nymphs peaked in January (55 ind. m^{-2}), they were absent in July and May (Fig. 1 b). *Metamonius anceps*, had a moderately synchronized, univoltine life cycle (Fig. 3). Very small nymphs were found in July. Medium-large sized nymphs predominated in September, October and from December to March; however a wide range of size classes was present
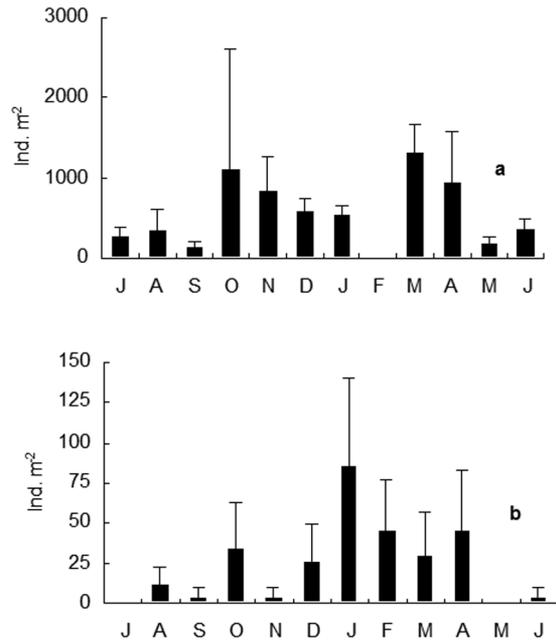

Fig. 1. Mean density per sample of a) *Meridialaris chiloeensis* and b) *Metamonius anceps* in La Hoya Stream during the study period. Data are mean values (±SD) and *n*=3.

at several months. Final instar nymphs were taken in monthly samples in September, October, February and April. We captured one adult in February.

Habitat selection

Gravel in riffle areas supported significantly more individuals of *M. chiloeensis* than leaf packs and sand in pools (Fig. 4) (ANOVA, P<0.002). Boulders in riffles had lower densities of *M. anceps* than the other habitats; however values were not significantly different among sampled habitats (ANOVA, P<0.06, Table 2). For both species, densities reported during the low water period were significantly higher than those of the high water period (season effect) (Fig. 4, Table 2). Excepting the sand habitat in pools, *M. chiloeensis* showed significantly higher densities in the low water period than at high water period in all habitat types (season and habitat interaction, Table 2).

Interespecific overlap in density of species among habitat types was relatively low (PS values <0.3), maximum values of PS being observed in boulder in pools during the high water period, and in leaf-packs, boulder in pools and sand in pools during the low water period (Table 3).
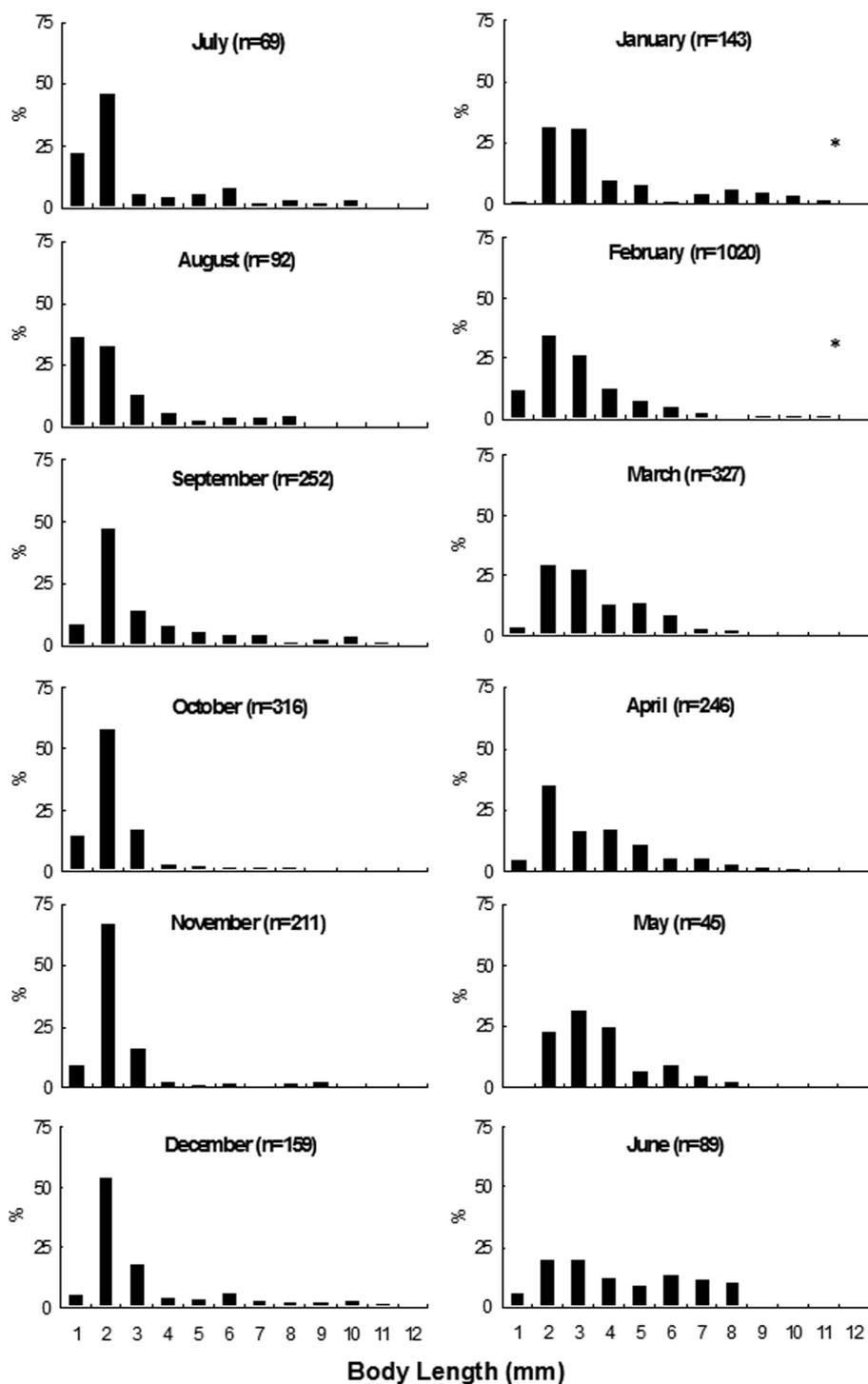
Fig. 2. Size-frequency distributions of *Meridialaris chiloeensis* larvae in La Hoya stream from July 2004 to June 2005, * indicate that adults were caught on the sampling date. *n* is indicated next to the months.

Fig. 3. Size-frequency distributions of *Metamonius anceps* larvae in La Hoya stream from July 2004 to June 2005, * indicate that adults were caught on the sampling date. *n* is indicated next to the months.
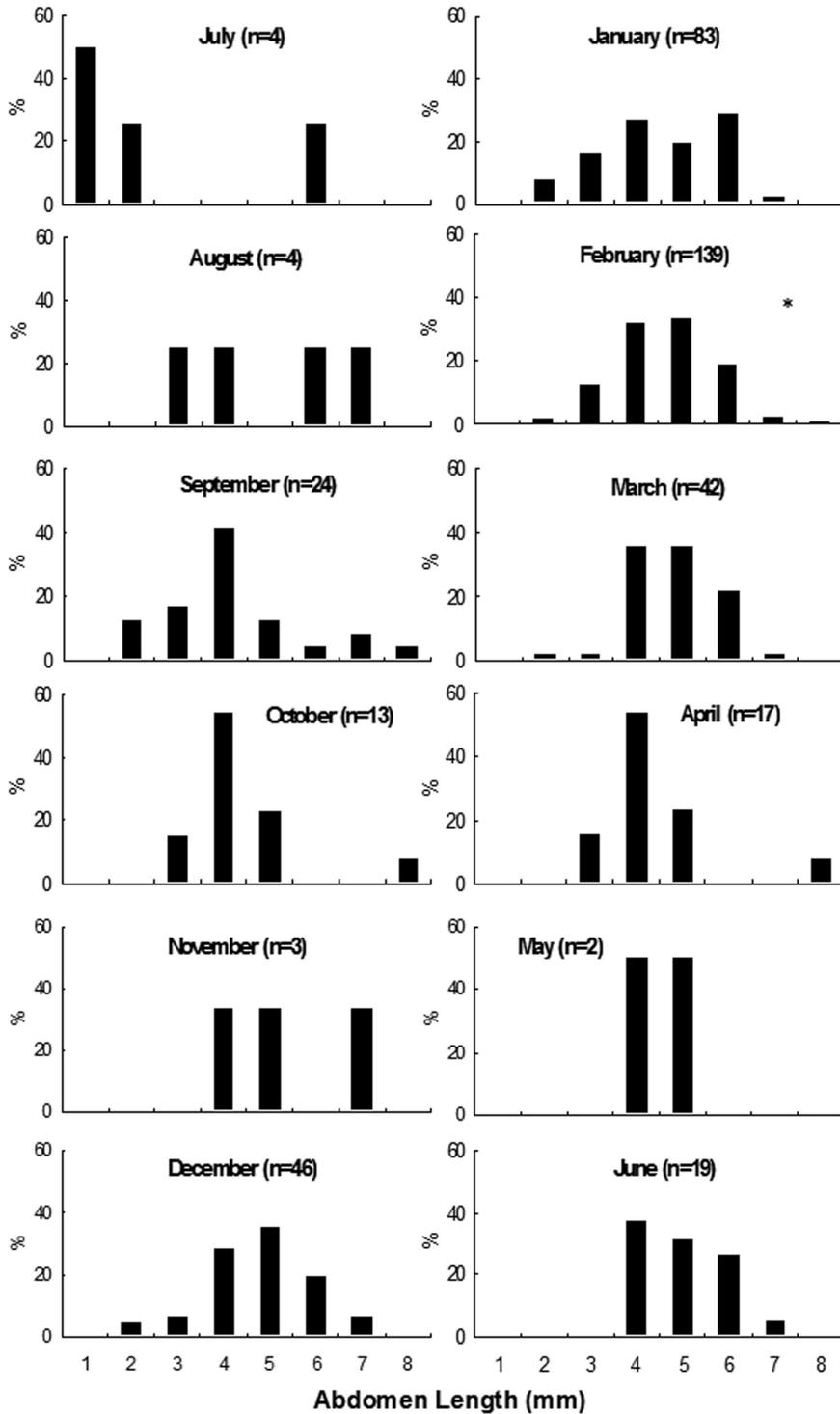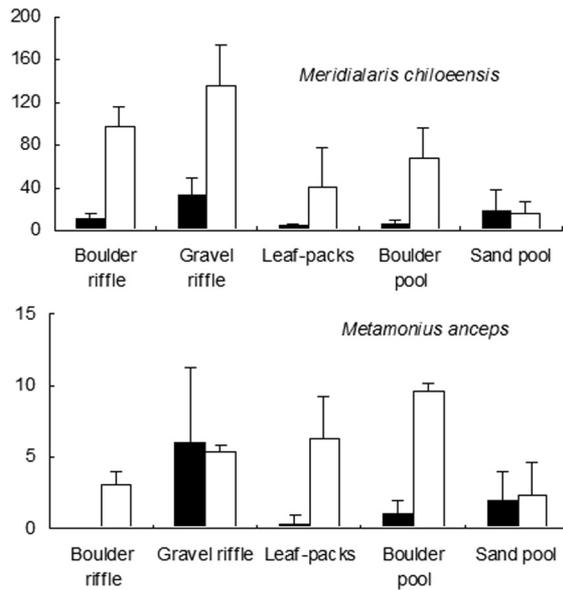
Fig. 4. Inter-habitat variation of *M. chiloeensis* and *M. anceps* (*n*=3) during the low water period (open bars) and high water period (black bars). Data are mean individuals per sample (±1 SE).

Table 2. Results of two-way ANOVAs examining the effects of habitat type and season on total density of *M. chiloeensis* (*n*=1297) and *M. anceps* (*n*=108) in La Hoya stream. Variables log (x+1) transformed, significant differences in boldface.

	df	Ms Effect	F	p
Meridialaris chiloeensis				
Season	1	3.16	36.11	**0.001**
Habitat	4	0.56	6.38	**0.002**
Season x Habitat	4	0.30	3.41	**0.03**
Metamonius anceps				
Season	1	1.58	23.3	**0.001**
Habitat	4	0.18	2.68	0.06
Season x Habitat	4	0.17	2.46	0.07

Discussion

The life cycle of *M. chiloeensis* was similar to that reported for the co-generic *M. diguillina* Ulmer by Gonser & Spies (1997) in the Estero Pirén stream at a lower latitude in Chile. The authors also observed poor developmental synchronization, and generation overlapping

Table 3. Interspecific habitat overlap for *M. chiloeensis* and *M. anceps* during high and low water period in La Hoya stream. Proportional similarity index values are presented (0= no overlap and 1= total overlap).

	High water period	Low water period
Boulder riffle	0	0.06
Gravel riffle	0.3	0.07
Leaf-packs	0.15	0.27
Boulder pool	0.25	0.25
Sand pool	0.19	0.26

occurring in January/February and April. A bivoltine life cycle with a winter-summer cycle was described for the leptophlebiid *Deleatidium* in two upland streams in Otago (New Zealand), albeit with a low degree of synchrony (Huryn 1996). This type of life cycle is characterized by an overwintering nymphal stage that completes its development in late spring, followed by a rapid summer generation. In La Hoya stream the relatively high number of larvae of *M. chiloeensis* about to emerge in January and February together with high numbers of small larvae in February suggest the occurrence of a winter generation that developed during autumn and winter with emergence taking place in September. A second more defined summer generation appeared in September-October with most individuals emerging from January to February. These results are also consistent with those observed by Scrimgeour (1991) for *Deleatidium lilli* in the Ashley River and by Huryn (1996) for the same species in the Sutton Stream (New Zealand). In *Deleatidium* the predominance of poorly synchronized life cycles and of cohorts with long flight periods would provide opportunities for intermediate growth and reproduction following spates (Scrimgeour 1991). It has been stated that the asynchronous development spreads life stages over time, thereby decreasing the risk of eradication by short term catastrophic events such as drought or spates. In a temporary stream in Oregon an extended hatching period in the leptophlebiid *Paraleptophlebia gregalis* resulted in the presence of early instar larvae during most part of the year, and was the key to asynchronous development and prolonged emergence periods (Dietercih & Anderson 1995). As we mentioned, as a headwater channel, La Hoya stream is an environment with a marked seasonality. Snowfall starts in May and the rainfall takes place from May to September. It is also predictable in terms of discharge with greater spates occurring mostly during the spring snowmelt. However, the observed pattern for *M. chiloeensse* would not fit with

stable environmental conditions of predictable discharge patterns as we expected. It is possible that a long period of high discharge (over six months) generates a physically harsh environment for this species. Our observations suggest that overlapping generations of *M. chiloeensis* took place in January but also in September, the month in which snowmelt was highest. Almost likely, an increase in temperature in September played a crucial role assuring adult emergence for the winter generation.

Our results show that *M. chiloeensis* preferred inorganic and stable substrates in run riffle areas, which is in agreement with the findings of Velázquez & Miserendino (2003). The study carried out in four rivers in the Cordillera suggested that *M. chiloeensis* seemed to be more habitat specific than *M. laminata* and *M. diguillina*, *M. chiloeensis* being strongly associated to the boulder-cobble-pebble habitats. Thus, *M. chiloeensis* was linked to more stable substrate in terms of persistence. On the other hand, *M. laminata* seemed to be very abundant in sand, macrophytes and gravel and *M. diguillina* more related to cobble and leaf-packs. At the river scale, a strong spatial segregation in the distribution of *Meridialaris* species seemed to occur, *M. chiloeensis* being restricted to the lower order sections and more diluted waters, and *M. laminata* clearly more abundant in the mean-high stream orders. *M. diguilina* appeared as eurizonal (Miserendino & Pizzolón 2000, 2001). Altitudinal zonation of Ephemeroptera species in temperate areas has been reported by Ward (1986). Domínguez & Ballesteros Valdez (1992) also observed a marked longitudinal replacement of leptophlebiid species in an Argentinean subtropical river. González et al. (2003) recorded temporal and spatial segregation reducing interspecific competition for two leptophlebiids in a Northern Spain stream at similar latitudes to those of the present study.

In this study the life cycle of *M. anceps* was consistent with those reported for two *Nesameletus* species in a mountain stream in New Zealand at similar latitudes (Winterbourn 2003). Both species were univoltine with small nymphs predominating in autumn-early winter and emergence taking place in spring and summer; moreover species showed a wide range of size classes present in winter months. Similarly, Campbell (1986) reported a life history poorly synchronized with adult emergence extending over five months for the Australian Nesameletidae *Ameletoides* sp. According to Mercado and Elliot (2004) the emergence period observed for adults of *M. anceps* seems to be shorter in the Chilean side, with the flight phase of the species happening in spring, mostly from November to January.

Interestingly we did not find evidence of habitat selection for *M. anceps* in our study. It is possible that larvae of *M. anceps* were difficult to sample quantitatively with benthic samplers because of their rapid swimming movements, this was noticed by McIntosh (2002) for other Nesameletidae species. Similarly, Winterbourn (2003) found that *Nesameletus* nymphs were very abundant in drift samples. *M. anceps* seems to be restricted to forested habitats and present over elevations of 1000 m.a.s.l. at least in this latitude (Miserendino & Pizzolón 2001). A recent review of the genera reported *Metamonius* in small mountain streams with cold, well-aerated waters, typically in the headwaters reaches of streams (Mercado & Elliot 2004). As other Nesameletidae species that occur in New Zealand streams (Hitchings & Staniczeck 2003) *Metamonius* would be associated to areas little perturbed by human activity.

The temporal density pattern observed in both *M. chiloeensis* and *M. anceps* was consistent with a previous research carried out at the same stream in 1991-1992 (Miserendino & Pizzolón, 2000) with maximum density reported in March for *M. chiloeensis* and in January for *M. anceps*. The decrease in density observed during the rainy season is a common feature in benthic communities of rivers and streams in the Cordillera (Miserendino & Pizzolón 2003, 2004). Reduced number of invertebrate densities following spates may not only represent mortality but also displacement of invertebrates. Invertebrate populations may redistribute themselves via behavioral drift and crawling from refuges occupied during floods (hyporheos, stream margins, instream debris, backwaters) (Scrimgeour 1991).

In conclusion, our study suggest that *M. chiloeensis* had a bivoltine life cycle while *M. anceps* was univoltine, nevertheless synchronization in growth was lower than we expected. *M. chiloeensis* showed some habitat preference while in *M. anceps* this was not observed. We found a low overlap of the utilized habitat types between species. As suggested by several authors (Sweeney & Vannote 1981, Brittain 1991) competition between related mayfly species may be reduced by temporal and spatial segregation. We think that the existence of different life history strategies in the studied species and a temporal shift of main generations and density peaks were crucial to allow species coexistence in la Hoya stream.

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