Article

Life cycle, production and habitat selection of *Notoperla fasciata* and *N. magnaspina* (Plecoptera: Gripopterygidae) in a headwater Patagonian stream

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With 5 figures and 3 tables

Abstract: We examined the life history, annual production, diet, habitat preferences and competition of two species of stoneflies *Notoperla fasciata* and *N. magnaspina* in a Patagonian mountain headwater stream. Benthic samples and adult collections were taken monthly from July 2004 to June 2005. A habitat selection study was performed concurrently during high and low water periods in five substrate types. Although both species showed long life cycles (*N. fasciata*: 20 months and *N. magnaspina*: 3 years) their life histories and temporal dynamics were different. Growth was rapid during summer and early autumn as a result of warmer temperatures but *N. magnaspina* had a shorter emergence period (November to January) than *N. fasciata* (January to April). *N. fasciata* was the dominant *Notoperla* species with a mean annual density 6 times higher and secondary production 4.5 higher than that of *N. magnaspina.* While boulders in riffles and pools, and leaf-pack habitats supported significantly more individuals of *N. magnaspina* in the low water period (ANOVA, $p < 0.02$) habitat preferences were not observed in the studied species (ANOVA, $p > 0.26$). *N. fasciata* dominated in the high water period and *N. magnaspina* during the low water period. Analysis of gut contents revealed that both species were herbivorous grazers, and consumed the same food types. The interspecific overlap in density, biomass and annual production among habitat types was high in the low water period ($PS > 0.5$). However, *N. fasciata* were smaller than *N. magnaspina*. The existence of different life history strategies and the temporal shift of main generations and density peaks were critical to allow species coexistence and to reduce competition.

Key words: stonefly, secondary production, seasonal pattern, competition, semivoltine.

Introduction

Stonefly nymphs are a significant component of benthic communities in cold, clear headwaters where they are very diverse (Short & Ward 1980, Harper et al. 1991, Ward 1992, Stewart & Stark 2002). They constitute an important part of animal production within streams, and by possessing different functional feeding strategies are tightly integrated into the structure and functioning of their habitats (Stewart & Stark 2002).

According to Hynes & Hynes (1975) in most Plecopteran species growth takes ten to eleven months (univoltine), whereas others can require two to three years to complete their life cycle (semivoltine and merovoltine, respectively) (Huryn et al. 2008). Thus, there is a considerable variation in stonefly life cycle characteristics which reflects the species studied (Sánchez-Ortega & Alba-Tercedor 1991), and also the ecological conditions (particularly the climatic ones).

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Stonefly nymphs tend to have specific water temperature, substrate type, and stream size requirements that are reflected in their distribution and succession along the course of streams. In addition, a distinct microdistribution of species and size classes is frequently observed within a particular stream reach (Merritt et al. 2008). Stoneflies include species of all functional feeding groups; they are very efficient in the use of river resources. However, the existence of two or more species of the same guild in the same habitat could result in strong competition. Resource partitioning among species of the same guild has been linked to reducing competitive interactions (Sweeney & Vannote 1981, Teague et al. 1985). Therefore, the food ingested by nymphs may vary depending on species, developmental stage, or time of day (Stewart & Stark 1988, Stewart & Stark 2002).

In Patagonia, headwater assemblages are rich and dominated by a highly endemic biota; including stoneflies (Wais et al. 1987, Pessacq & Miserendino 2008). Research on ecological aspects of Plecoptera species in the region has increased notably with recent studies focussing on their altitudinal distribution (Albariño 1997, Miserendino 2000) and functional feeding behaviours (Albariño & Balseiro 1998). However, and 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, 2008), little is known about the life histories of aquatic insects in Patagonia (Gonser & Spies 1997, Suarez 2002, Hollmann & Miserendino 2006). A few studies have assessed the temporal and spatial overlap in the size and density of some species; including competition relationships (e.g. Hollmann & Miserendino 2008) but these studies did not consider analyses of secondary production. The knowledge of this parameter is of considerable ecological value because it integrates survival, growth and voltinism (Benke 1984). Moreover, when assessing habitat selection among related species the interspecific overlap using productivity measures can give an idea of population activity and success (González et al. 2003, Winterbourn et al. 2008).

Notoperla fasciata and *Notoperla magnaspina* (Gripopterygidae) are two large (body length 0.9–17 mm, 2–23 mm, respectively) Plecopteran species recently described (McLellan et al. 2006). They frequently cohabit very pristine, highly oxygenated Patagonian headwaters streams in the Sub-Antarctic Forest. These cold stenothermal species are presumably grazers and feed on periphyton (Díaz Villanueva &

Albariño 1999). The objectives of this study are: 1) to compare their life cycles and secondary production and 2) to assess habitat preference and intensity of competition between these two congeneric stoneflies in a headwater stream in Patagonia.

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. 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 of deciduous *Nothofagus pumilio* (lenga), native shrubs *Fuchsia magellanica*, *Ribes magellanicum*, *Mulinum spinosum* and herbaceous *Stipa* sp. (León et al. 1998). Previous studies at la Hoya stream (McLellan et al. 2006) showed that *N. fasciata* and *N. magnaspina* cohabited at this reach. Inspection of density values showed that the site was also appropriate to carry out a life cycle study. *Dasyoma* sp., *Edwardsina* (*Edwardsina*) sp. Simuliidae, *Cura* sp. (Turbellaria), *Klapopteryx kuscheli* (Austroperlidae), *Senzilloides panguipulli* (Gripopterygidae), *Andesiops peruvianus*, *A. torrens* (Baetidae), *Meridialaris chiloeensis* (Leptophlebiidae), and *Metamonius anceps* (Nesameletidae) also occur in the benthic community (Miserendino & Pizzolón 2000).

Environmental features and sampling of Plecoptera

The study was carried out from July 2004 to June 2005. Air and water temperature, depth and stream width were measured monthly whereas current velocity and discharge were recorded bimonthly. Average depth was calculated from five measurements from one transversal profile across the channel with a calibrated stick. At the selected reach (50 m), substrate composition was estimated as percentage of each fraction: boulder, cobble, gravel, pebble and sand present in a 1 m² grid (Gordon et al. 1994).

In order to analyze seasonal variation in abundance and to describe life cycles, nymphs were collected monthly using a Surber net (0.09 m⁻²; 250 μm mesh size). On each occasion three replicates ($n = 3$) were taken in riffles. For life history descriptions nymphs from eight additional Surber samples were taken and pooled on each sampling date. Samples were fixed with 4 % formaldehyde solution. In the laboratory samples were sorted under 5 × magnification and then stored in 70 % ethyl alcohol.

Shoreline pitfall traps (Stanford 1975) were employed for the collection of teneral adults and emerging nymphs. At the sampling site, 5 plastic pots (1500 cm³), 12 cm diameter were embedded in the river bank and concealed by large flat rocks. The traps 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.

Functional feeding group assignment

Heads and mouthparts of *N. fasciata* and *N. magnaspina* were dissected and observed under $100\times$ microscope. Foregut contents of 20 large individuals (10 *N. fasciata* and 10 *N. magnaspina*) collected in different months were analysed following Palmer et al. (1993). The foregut content was homogenised over a slide in glycerine and 5 randomly selected fields were counted under a direct microscope at $400\times$ magnification. Five food categories were identified: 1) diatoms, 2) other algae, 3) detritus, 4) invertebrates and 5) minerals. Quantification of each item was based on the fraction of area covered in each field of the slide.

Life history analyses

To describe life histories of the species we measured total body length (L) as the distance between the anterior part of the head and the posterior part of the last abdominal segment, the interocular distance (IO), and the head capsule width (HCW) to the nearest 0.05 mm (Benke et al. 1999). Measurements were taken at $8–32\times$ magnification (depending on the size of the individual) 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: 803 nymphs and 435 adults of *N. fasciata* and 309 nymphs and 11 adults of *N. magnaspina*.

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 $DM = a\,Lb$, or after logarithmic transformation $\ln DM = \ln a + b \ln L$ (where: a, b = regression constants, DM = dry mass, and L = length parameters).

For dry mass determinations, each specimen was individually transferred to a piece of aluminum foil. Drying was performed at $105°$C for up to 4 h (Smock 1980). Animals were weighed on an electronic balance with 0.5 mg accuracy. In the procedure, 203 specimens (n = 110 *N. fasciata* and n = 93 *N. magnaspina*) were examined and measured.

Different regression models were evaluated to fit the data points to suitable regression equations. In general, linear regression models were appropriate.

Production method

Stonefly production was calculated using the size frequency method (Benke 1984) because specific nymphal cohorts could not be distinguished. Nymphs were assigned to 9 (*N. fasciata*) and 8 (*N. magnaspina*) body length groups for analysis. In the size frequency 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). Based on Fig. 1 length of nymphal life was assumed to be 20 months for *N. fasciata* and 36 months for *N. magnaspina* (CPI: 20 and 36, respectively), then "cohort production" was multiplied by 12/20 and 12/36 to estimate annual production (Benke 1993).

Habitat sampling

Because a previous study in high gradient Patagonian streams had shown benthic communities to be clearly differentiated between habitats (Velásquez & Miserendino 2003), we undertook additional sampling during high (September 2004) and low (February 2005) water periods. 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 on each occasion (n = 30). To prevent small individuals escaping from debris, all material collected from leaf-packs was carefully washed and processed in the laboratory. The number of specimens counted and measured for the habitat selection descriptions were: *N. fasciata* 346 larvae and *N. magnaspina* 60 larvae.

Statistical analysis

Prior to analysis data were checked for normality and homogeneity of variances using Kolmogorov-Smirnov and Levene's test, respectively, and transformed as $\log (x + 1)$ when appropriate (Gotelli & Ellison 2004). Fixed-effects 2-factor ANOVA models were used to assess significant differences in total density between habitats (5), and seasons (2). The interaction between habitat and season was also assessed. A posteriori comparisons among habitats were performed with Tukey's (HSD) test ($p < 0.05$). Overlap of habitats utilized by both stoneflies species during low and high water periods was calculated with the proportional similarity index (*PS*) (Whittaker 1975):

$$PS_{ab} = \sum_{i=1}^{n} \min\left(P_{ai}, P_{bi}\right)$$

where PS_{ab} is the proportional similarity between species "*a*" and "*b*" in density, biomass or production, n is the number of time intervals, P_{ai} is the fraction of density, biomass or production of species "*a*" that occurs during the time interval i, and P_{bi} is the fraction of the density, biomass or production of species "*b*" that occurs during the time interval i. *PS* values may range from 0 (no overlap) to 1 (total overlap). Based on the *PS* results and in order to explore patterns of competition for both species, we produced a figure combining size classes (based on total length) and number of nymph per habitat in a specific interval of time (low water period: February).

Results

Environmental features

Annual rainfall during the study period was 680 mm with a rainfall peak occurring in May (219 mm). Water temperature ranged from 1 (July) to 12 °C (February). 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. Water velocity varied between 0.55 and 0.83 m s^{-1} (mean current velocity 0.67 m s^{-1}). Minimum discharge (February) was 0.187 m^3 s^{-1} and maximum discharge (September) was 1.245 m^3 s^{-1}. The substratum was dominated by
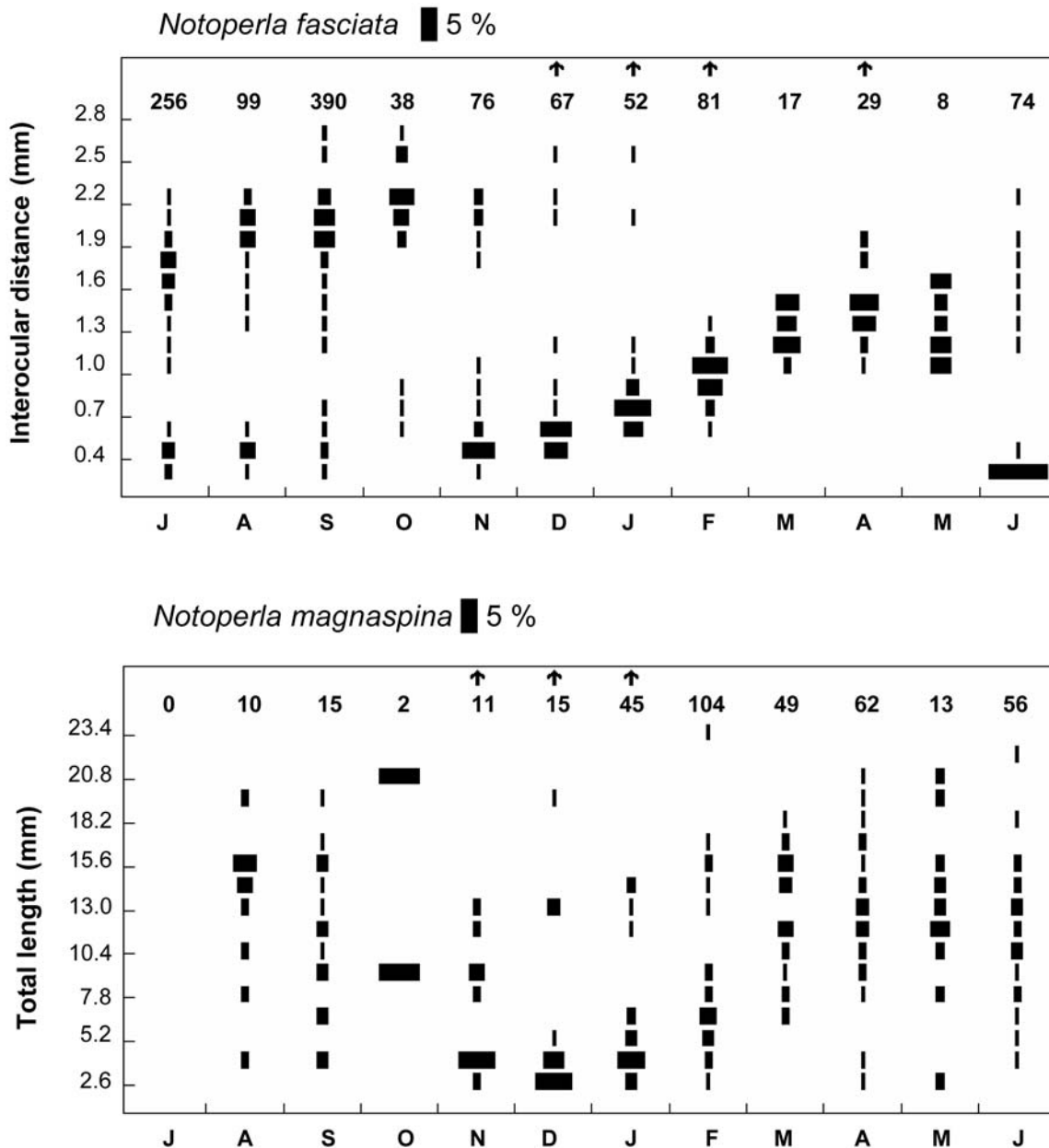
Fig. 1. Seasonal development patterns of *Notoperla fasciata* and *Notoperla magnaspina* in La Hoya stream, July 2004 – June 2005. Width of histograms represents proportion of sampled population in each size class (black bar units represent 5 %). Arrow indicates adult emergence period. Numerals above each column show numbers of larvae measured each month.

boulders (25 %) and cobbles (35 %); pebbles (10 %), gravel (20 %), and sand (20 %) were also well represented.

Life histories and emergence patterns:

A preliminary analysis (frequency tables and histograms) revealed that IO distance and L were the best measurements, for *N. fasciata* and *N. magnaspina*, respectively, to describe the life history pattern. Our data suggest that *N. fasciata* had a semivoltine life cy-

cle (Fig. 1) with adults emerging in December, January, February and April. Early instars began to appear between June and September with a peak in June. Growth was rapid in the warmer temperatures that occurred during summer and early autumn. *N. fasciata* larvae needed at least 20 months to complete their life cycle. On the other hand, *N. magnaspina* appeared to have a 3-year life history. Early instars appeared in November and were most abundant in December. Mature nymphs were collected during April, May, June

and October. As with *N. fasciata* growth was fast in summer and early autumn. Adults were collected between November and January (Fig. 1). All males of both species were brachypterous.

Gut-content and mouth parts analyses:

The microscope observations of mouth parts of *N. fasciata* and *N. magnaspina* showed well-developed and sclerotised mandibles and maxilae, with maxilae having lacineae and galeae of approximately equal size. The galeae (two-segmented) have an apical dense crown of bristles. In both species the lacineae showed apical rounded teeth and sharp ventral margins.

N. fasciata and *N. magnaspina* consumed the four food categories in similar proportions (Fig. 2). Detritus was the predominant item in both species (> 29 %). Other algae was the second most abundant item for *N. fasciata* (31 %), while minerals was the most abundant for *N. magnaspina* (24 %). Diatoms were important for both species (20 %). Only *N. magnaspina* (7 %) consumed invertebrates in our study. Both species are primarily herbivorous and could be assigned to the grazer functional feeding group.

Larval density, biomass and production

Body length (L) was selected to estimate monthly biomass because the regression models obtained showed the best fit for both species (Table 1). Density and biomass patterns were consistent for each species in the seasonal analysis (Fig. 3), with peaks in July for *N. fasciata* and in April for *N. magnaspina*. Mean monthly density of *N. fasciata* ranged between 11 to 950 ind m^{-2}, whereas for *N. magnaspina* varied between 7 to 107 ind m^{-2} (Fig. 3). *Notoperla fasciata* was the numerically dominant *Notoperla* species at the study site with a mean annual density 6 times higher and an annual biomass 2.5 times higher than that of *N. magnaspina* (Table 2). The annual production of *N. fasciata* was 2.37 g m^{-2} and was 4.5 times higher than that of *N. magnaspina* (0.52 g m^{-2}). However P/B ratio of *N. fasciata* was only 2 times bigger than P/B of *N. magnaspina* (2.58 and 1.37, respectively, Table 2).
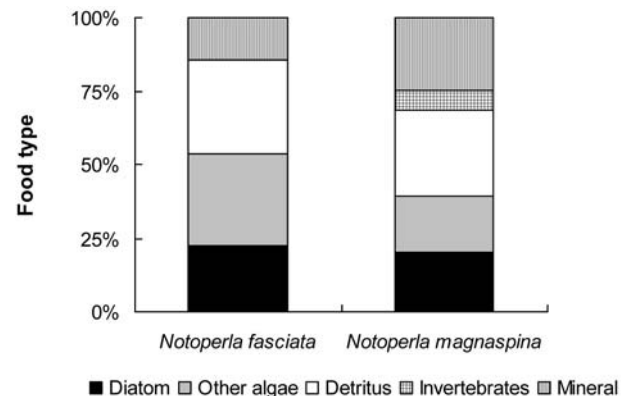

Fig. 2. Food item proportions in the gut contents of larval instars of *N. fasciata* and *N. magnaspina*.

Table 1. Values for the constants ln *a* and *b*, obtained for dry weight (W, mg) and body length (L, mm), interocular distance (IO, mm) and head capsule width (HCW, mm) for *Notoperla fasciata* and *Notoperla magnaspina*, (n) number of individuals used to calculate each regression . All correlation coefficients are very highly significant ($p < 0.001$).

		Regression constants:		r^2	*range*	*n*
		Ln *a*	Ln *b*			
Notoperla fasciata	L	−3.65 ± 0.06	2.37 ± 0.03	0.98	1.05–15.2	110
	IO	1.46 ± 0.05	3.47 ± 0.07	0.96	0.21–1.4	110
	HCW	−0.15 ± 0.04	3.07 ± 0.06	0.96	0.32–2.35	110
Notoperla magnaspina	L	−3.79 ± 0.013	2.42 ± 0.06	0.95	1.60–23	93
	IO	1.12 ± 0.05	3.15 ± 0.11	0.90	0.65–2.2	93
	HCW	−0.40 ± 0.06	3.31 ± 0.09	0.94	0.97–3.37	93

Table 2. Secondary production information for *Notoperla fasciata* and *N. magnaspina*. Data were obtained by size frequency method using the material collected from July 2004 to June 2005. CPI = cohort production interval.

Species	CPI	Density (ind m^{-2})	Biomass (g m^{-2})	Annual P (g m^{-2})	P/B
Notoperla fasciata	20	256.16	0.92	2.37	2.58
Notoperla magnaspina	36	41.98	0.38	0.52	1.37
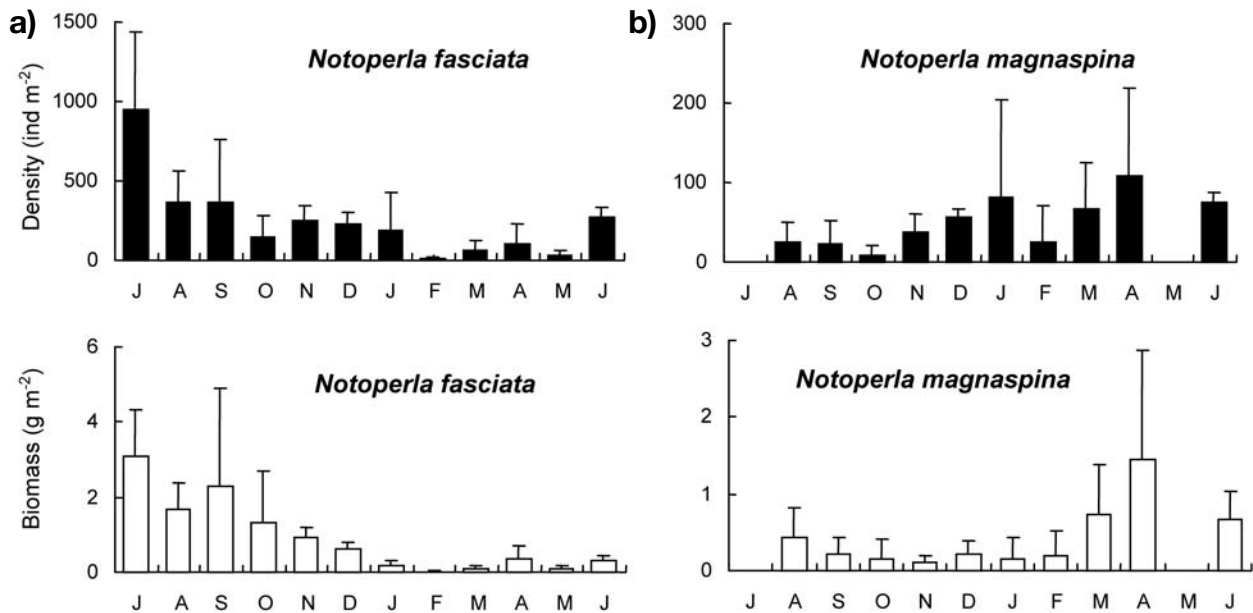
Fig. 3. Mean density (ind m^{-2}) and mean biomass (mg m^{-2}) of **a)** *Notoperla fasciata* and **b)** *Notoperla magnaspina* in La Hoya Stream during the study period. Data are mean values (± SD) and $n = 3$.
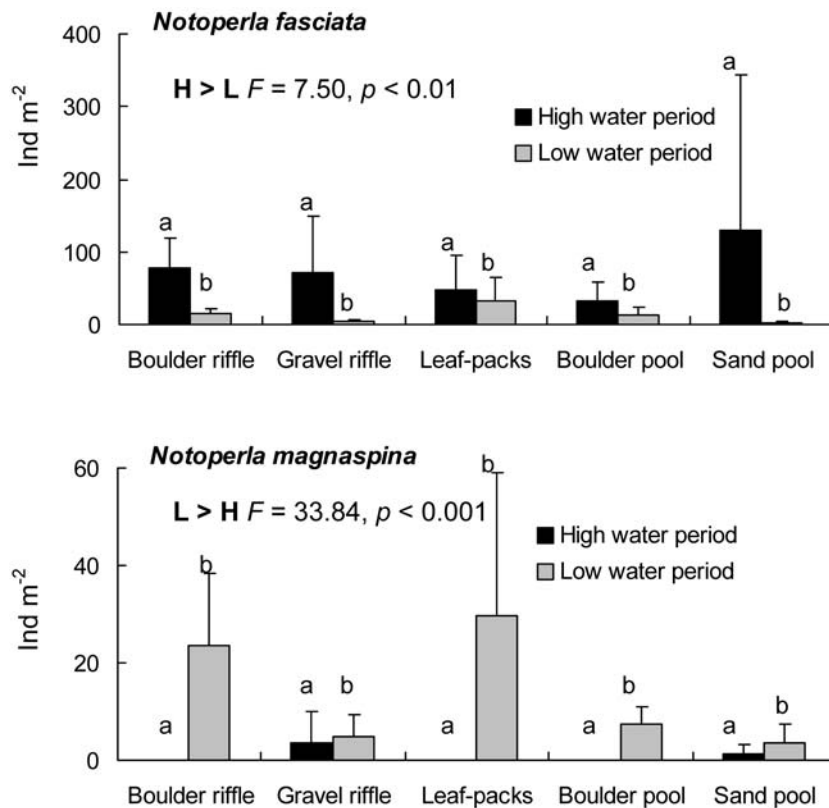
Fig. 4. Inter-habitat variation of *N. fasciata* and *N. magnaspina* ($n = 3$) during the low water period (grey bars) and high water period (black bars). Data are mean individual per sample (± 1 SE). Results of two-way ANOVAs examining the effects of habitat type and season on total density of *Notoperla* species are presented. H: high water period, L: low water period. Superscript letters show significant differences between seasons ($p < 0.05$).

Habitat selection and competition

N. fasciata and *N. magnaspina* densities were not significantly different among sampled habitats (ANOVA, $p > 0.26$). *N. magnaspina* densities during the low water period were significantly higher than those in the high water period (Fig. 4), whereas the opposite was true for *N. fasciata*. Post-hoc testing showed that boulders, and leaf-pack habitats, supported signifi-

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

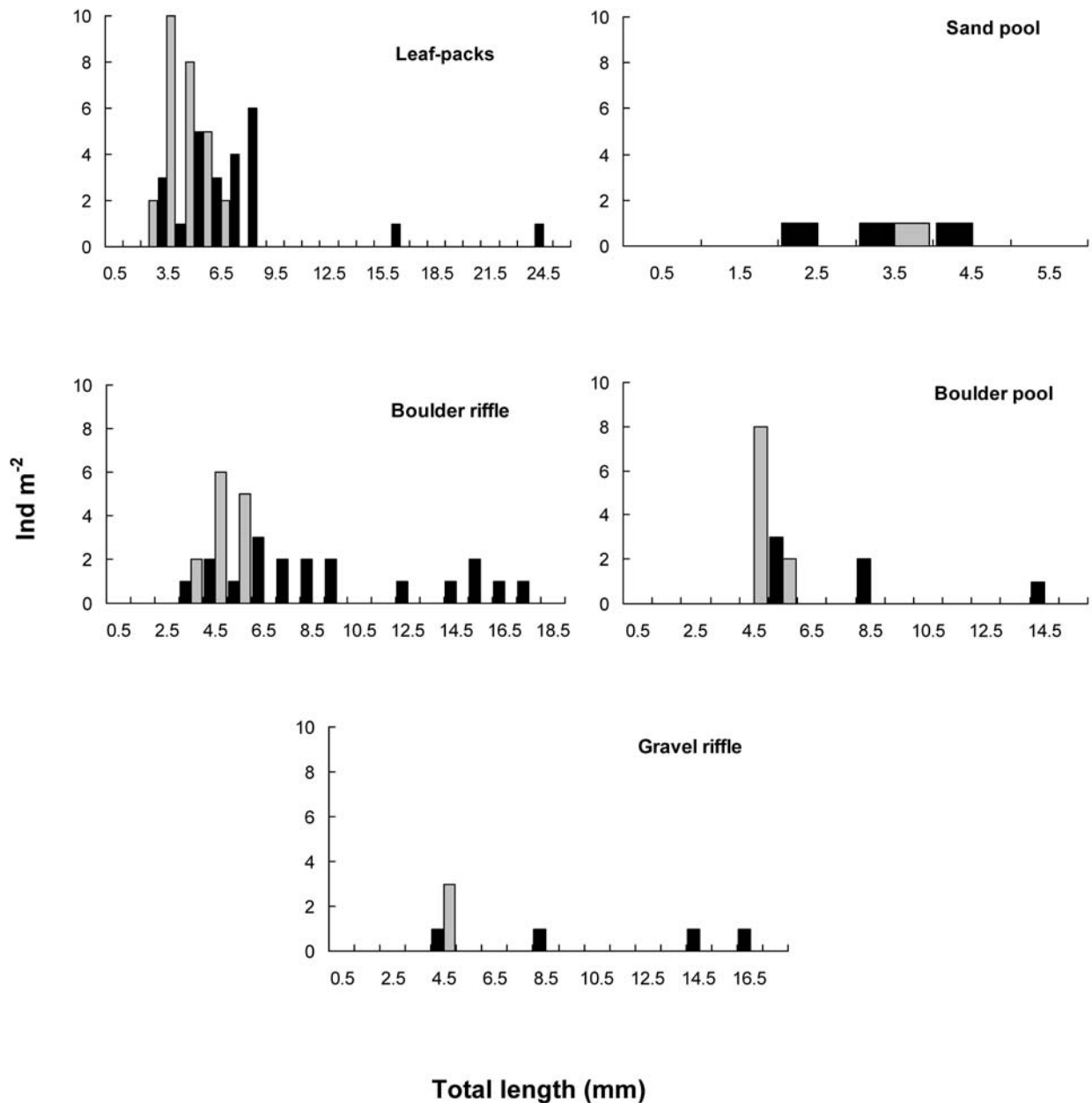|	High water period			Low water period		
	Density	Biomass	Annual production	Density	Biomass	Annual production
Boulder riffle	0	0	0	0.81	0.18	0.50
Gravel riffle	0.10	0.17	0.11	0.86	0.18	0.51
Leaf-packs	0	0	0	0.94	0.33	0.82
Boulder pool	0	0	0	0.62	0.65	0.73
Sand pool	0.02	0.002	0.006	0.5	0.33	0.53

cantly more individuals of *N. magnaspina* in the low water period than at the high water period (ANOVA, $p < 0.02$). The interspecific overlap in density, biomass and annual production among habitat types was very low during the high water period (*PS* values < 0.17, Table 3). However, at the low water period all *PS* values based on density and annual production were over 0.5 (Table 3). Inspection of size frequencies per habitat during the low water period (February) for both species showed that smaller nymphs of *N. fasciata* co-occurred with bigger ones of *N. magnaspina* (Fig. 5).

Discussion

This is only the second study of stonefly life histories in Patagonian streams and the first that includes secondary production. Our results indicate that these two large sized gripopterygid species had semivoltine (*N. fasciata*) and merovoltine (*N. magnaspina*) life histories in La Hoya stream. Similarly, many large sized Plecoptera species in the Northern Hemisphere have semivoltine life histories (Hassage & Stewart 1990, Yokum et al. 1995, Richardson 2001, Pretty et al. 2005) as do numerous Southern Hemisphere gripopterygids and austroperlids (Scarsbrook 2000, Hollmann & Miserendino 2008). As in other semivoltine stonefly species, the *N. fasciata* and *N. magnaspina* patterns (i.e. well synchronized and emergence periods restricted to a few months) fit with stable environmental conditions and predictable discharge patterns (Hollmann & Miserendino 2006). Thus, being a headwater channel, the environment of La Hoya stream has a marked seasonality with snowfall starting in May and a rainy period from May to September. Discharge is also predictable with most spates occurring during the spring snowmelt. This contrasts with patterns seen in temporary streams or unstable environments (Dieterich & Anderson 1995, Scarsbrook 2000). Other co-

habiting species such as the univoltine gripopterygids *Senzilloides panguipulli* and *Aubertoperla illiesi* also showed synchronised emergences at the same site (Hollmann & Miserendino 2008).

The presence of a wide range of different sized nymphs in most months was common for both *Notoperla* species. In *N. fasciata* and *N. magnaspina* nymphal growth was not constant during development; growth rate was faster in summer as a result of higher temperatures (Derka et al. 2004). As with other Plecoptera species from temperate environments (Hynes & Hynes 1975, Harper et al. 1991), the presence of small sized individuals of *N. fasciata* throughout winter and spring, and of *N. magnaspina* during summer and autumn indicated a long hatching period. There was no evidence of cohort splitting in our data for *N. fasciata* which had the clearest separation in size ranges of the two cohorts. Similar results have been reported for *Depaxia augusta* (Richardson 2001) and *Klapopteryx kuscheli* (Hollmann & Miserendino 2008) two semivoltine stonefly species. Size class variation resulted in three generations of *N. magnaspina* being present in most seasons. However, the presence of early instar nymphs in December and the wide variation of nymphal sizes in June suggest that *N. magnaspina* life cycle was more complex with a possible cohort splitting of 2 and 3 years. Size variation within cohorts could represent a form of plasticity in a species (Harper 1973, Dietrich & Anderson 1995) and Bunn (1988) suggested that this phenomenon is a highly adaptive strategy for some Australian stream insects with slow life cycles. The size-frequency histograms and the timing of mature nymphs suggest that the emergence period of *N. magnaspina* begins earlier than that of *N. fasciata*. Therefore, although both species coexisted throughout the year they had life histories with different phenology. Thus, nymphal recruitment as well as emergence periods were temporarily segregated in both species which likely reduced

Fig. 5. Size frequency distribution (based on body length) per habitat of *N. magnaspina* (black bars) and *N. fasciata* (grey bars) in the low water period (February), data are based on density values (ind. m^{-2}).

inter-specific competition (Ward 1992, González et al. 2003).

N. magnaspina (0.52 g DM m^{-2} y^{-1}) secondary production values were comparable to those reported for other semivoltine stonefly species from headwaters of the Northern hemisphere (Krzysztof & Stewart 1987, Griffith et al. 1994, Yokum et al. 1995). However, secondary production of *N. fasciata* (2.37 g DM m^{-2} y^{-1}) was remarkable and equivalent to that reported for *Acroneuria evoluta*, a univoltine perlid (Krzysztof

& Stewart 1987), and to *Leuctra nigra*, a semivoltine leuctrid (Thomsen & Friberg 2002). Nevertheless, secondary production of both *Notoperla* species falls into the expected ranges for temperate headwaters streams. Our *Notoperla* production estimation (2.9 g DM m^{-2} y^{-1}) suggests that the production of this genus probably represents a substantial contribution to the total energy budget of La Hoya stream.

We determined that *N. fasciata* and *N. magnaspina* are primarily herbivorous and belong to the scraper-

brusher feeding mode which agrees with that recently reported for the congeneric *N. archiplatae* (Díaz Villanueva & Albariño 1999, Albariño & Díaz Villanueva 2003). The analyses of the gut contents indicated a predominance of vegetable items (diatoms and other algae), followed by detritus. In addition to diatoms, other algae and detritus, the guts of many nymphs of both species contained substantial quantities of sand particles, probably swept into the mouth by the galea brushes during grazing or foraging (Winterbourn et al. 2008).

In contrast to studies on other stonefly species (Angradi 1996, Velásquez & Miserendino 2003) we did not find inter-habitat differences in density, biomass and production of *N. fasciata* and *N. magnaspina* and in-stream habitat selectivity seems unlikely for these species in la Hoya stream. Interestingly, there was a clear separation of the species in time with *N. fasciata* dominant during the high water period and *N. magnaspina* dominant in the low water period.

In conclusion these two gripopterygid species had a clear temporal segregation in density and biomass; they also showed some differences in life history attributes (nymphal recruitment, life cycle time and emergence periods). Size-frequency analysis suggested that competition between these two species was very low (Sweeney & Vannote 1981, Merritt et al. 2008). In this paper we integrated information of life histories, secondary production, feeding habits, habitat and competition that contributed to understand quantitative roles of the species in food webs and ecosystems (Huryn & Wallace 2000). This information is also crucial as a first step to conservation of Patagonian headwaters which are recognised as fragile and vulnerable environments (Carabelli & Scoz 2008, Miserendino & Masi 2010).

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