LIFE CYCLE AND ANNUAL PRODUCTION OF *CAENIS* SP (EPHEMEROPTERA, CAENIDAE) IN LAKE ESCONDIDO (BARILOCHE, ARGENTINA)

D. A. Añón Suárez and R. J. Albariño

Centro Regional Universitario Bariloche
Universidad Nacional del Comahue
Unidad postal Universidad
(8400) Bariloche, Argentina

ABSTRACT

Life cycle and secondary production of *Caenis* sp nymphs were analysed during a year of study in Lake Escondido, in relation to depth, water temperature and vegetation distribution. Higher densities of nymphs were found in the upper littoral zone with *Schoenoplectus californicus* (2665 ind m^{-2}), compared to lower littoral covered with *Potamogeton linguatus* (29 ind m^{-2}) and the profundal (4 ind m^{-2}) zones. During the study this mayfly was univoltine with one emergence in summer. The highest production (0.67 g m^{-2} yr^{-1}) was observed in the *S. californicus* zone, and it was related to the highest values of organic matter content and water temperature in the shallower area of the lake.

INTRODUCTION

The knowledge about the different aspects of life cycle of aquatic insects contributes greatly to explain the benthic community dynamics in lakes. The estimates of secondary production have outstanding ecological importance because this parameter integrates density, biomass and voltinism in a single figure, also indicating the community success and functional importance in the ecosystem (Benke, 1984, 1993). Among the factors affecting the magnitude of the secondary production and life cycles of aquatic insects, most authors indicate the temperature and the photoperiod together with the quantity and quality of food as the most relevant ones (Vannote and Sweeney, 1980; Ward and Stanford, 1982; Sweeney, 1984).

Caenis sp nymphs are the most common Ephemeroptera in Lake Escondido, and together with the Chironomids (Diptera) are numerically the most important taxa of the benthic macroinvertebrates (Añón Suárez, 1991, 1997).

In Argentina, Domínguez, et al. (1992) and Domínguez, et al. (1994) have studied taxonomic aspects of ephemeropterans, and there have been also studies carried out on distribution, life cycles and production in patagonian lakes and reservoirs (Kaisin, 1989; Añón Suárez, 1991).

This is the first contribution about the life cycle and production of *Caenis* sp in an Andean lake, therefore, there are no previous data for direct comparison. The main goal of this study was to determine the annual production of *Caenis* sp and also to analyse the life cycle parameters (density, biomass, size-classes distribution and voltinism) in different zones of Lake Escondido. The population studied was identified as *Caenis* sp reissi group (E. Domínguez, pers. com.) and is currently under study for complete identification.

STUDY AREA

Lake Escondido is situated at 30 km west of San Carlos de Bariloche (41°2' S; 71°4' W, Argentina), at 764 m a.s.l., with an area of 8 ha., a maximum depth of 8 m and a mean depth of 5.5 m (Fig.1). An evergreen mixed forest of *Nothofagus dombeyii* (Mirb) Blumeand, *Austrocedrus chilensis* (D.DON), Florin et Boutleje and also the deciduous *Nothofagus antarctica* (G. Foster) Oesterd. composes the riparian vegetation.

The littoral area of the lake is occupied by two macrophytes *Schoenoplectus californicus* (Meyer) Soják (=*Scirpus californicus*) and *Potamogeton linguatus* Hangström. The central deepest area is partially colonised by the Characeae *Nitella* sp, although in a very low density.

The thermal regime of Lake Escondido is warm monomictic with periods of complete mixing during autumn and winter and direct thermal stratification during late spring and early summer (Balseiro and Modenutti, 1990). However, during hard winters its surface often freezes behaving as dimictic, like in this study period.

Dissolved oxygen concentration is high throughout the year, with values near 100% of saturation in spring (Balseiro and Modenutti, 1990). The Secchi disc is visible at the maximum depth (8 m) and conductivity oscillates between 80 $\mu S\ cm^{-1}$ (late summer) and 40 $\mu S\ cm^{-1}$ (winter) (Balseiro and Modenutti, 1990). The pH is 7.02 and the chlorophyll *a* concentration is low (0.5 mg m^{-3} and 1.8 mg m^{-3}: winter and summer 1988 respectively) (Díaz and Pedrozo, 1993). These characteristics indicate the oligotrophic condition of this lake (Balseiro and Modenutti, 1990; Díaz and Pedrozo, 1993).

MATERIALS AND METHODS

Samples were obtained during April 1988 - May 1989, approximately monthly (autumn - winter) and biweekly (spring 1988 - autumn 1989), with an Ekman grab (225 cm^2) in three different zones: Station A (upper littoral with *S. californicus*, 50 cm mean depth), Station B (lower littoral with *P. linguatus*, 4m mean depth) and Station C (profundal, 8 m maximum depth). Samples could not be taken during July because the littoral zone of the lake remained cover by an ice layer in most of its surface. Each sampling date, four replicate samples were taken in Stations A and B and seven in Station C. Samples were filtered in situ by using a conic net (212 µm mesh size) and the material retained was fixed with formalin 5%.

Temperature was obtained on each sampling date in Stations A, B and C by using a thermometer inside a Ruttner bottle (at nearest 0.5°C). Also total accumulated degrees/day for the three stations and the difference of the degrees/day accumulated between littoral stations (A and B) with respect to Station C (profundal zone) were calculated. The granulometric and organic matter contents analysis was performed in all three zones according to Jackson (1964).

In the laboratory the nymphs were separated from the sediment and stored in formalin 4%. Cephalic width (interocular distance) was used to determine the size-classes (Snyder et al., 1991; Pritchard and Zloty, 1994: Sweeney et al., 1995). The density (ind m^{-2}) of each size-class was determined to construct size-frequency histograms. Then, individuals of each class (total n = 119) were dried at 60°C during 24 hr (Sweeney and Vannote, 1986) and weighed at nearest 0.01 mg to estimate mean dry weight of each size-class. The mean biomass for each size-class and the secondary production of *Caenis* sp (g m^{-2} yr^{-1}) were calculated by three methods: "Size-Frequency", "Allen Curve" and "Instantaneous Growth" (Waters and Crawford,

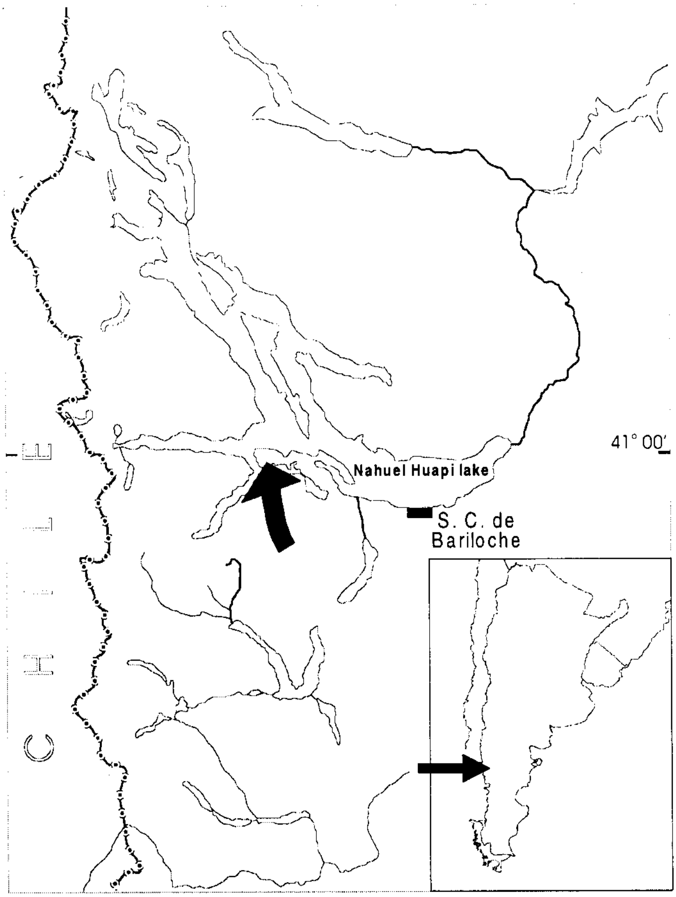

Fig. 1. Geographical position of Lake Escondido (grey arrow) and location of the study area (black arrow).

1973; Waters 1979; Benke, 1984, 1993). The former is used when cohorts are recognisable or not and the latter are recommended when cohorts are discernible.

For the Size Frecuency method the equation is expressed as follows:

$$P = i\sum_{j=1}^{i} \sqrt{(W_{j+1} \cdot W_j)} \cdot (N_{j+1} - N_j)$$

where P is the annual production, $(N_{j+1} - N_j)$ is difference in mean annual density of each size-class, $\sqrt{(W_{j+1}.W_j)}$ is the geometric mean of its respective dry weight and i is the number of size-classes.

For the Instantaneous Growth method the equation is:

$$P = \sum G.B$$

where P is the annual production, $G = ln\ (W_t + W_{t+\Delta t})$ is the instantaneous biomass growth rate and B is the biomass at a given time.

For the Allen Curve method, annual production (P) is the area under the curve $\overline{N}$ vs $\overline{W}$, where is the mean number during Δ_t and W is the mean individual biomass.

RESULTS

Lake Temperature

Temperature values presented differences between the three Stations (Fig. 2.a). The maximum temperature values were 22°C in early January and mid February 1989 at Station A, and 20°C in mid February 1989 at Stations B and C (Fig. 2.a). Average temperatures were 14.3°C, 13.0°C and 12.4°C for stations A, B and C respectively. Heat accumulation were calculated for these sampling stations (Fig. 2.b.) with maximum values of 4920.9 (Station A), 4539.4 (Station B) and 4349.8 (Station C) degrees/day accumulated at the end of the sampling period. The differences between the accumulation of heat (degrees-day) in the littoral zone were also calculated in relation to the coldest zone (Station C) (Fig. 2.c). In Station B, this accumulation mainly took place between October 1988 and January 1989, reaching a maximum value of 190 degrees-day (Fig. 2.c). The heat accumulation in Station A was more important, reaching a difference with Station C of 571 degrees-day accumulated at the end of the annual cycle (Fig. 2.c).

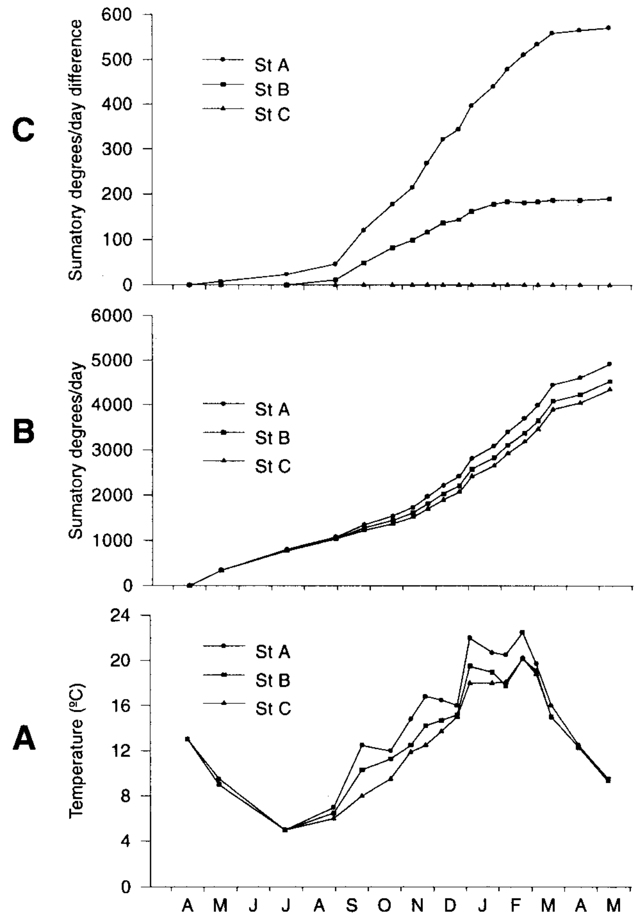

Fig. 2. (A) Monthly changes in temperature; (B) degrees/day accumulated and (C) Difference of degrees/day accumulated in Lake Escondido using Station C as reference, during April 1988 - May 1989.

Table 1. Granulometric analysis and organic matter content in Stations A, B and C of Lake Escondido.

Stations	sand (%)	silt (%)	clay (%)	organic matter (%)
A	52.0	45.0	3.0	36.0
B	88.0	10.5	1.5	14.5
C	85.0	11.0	4.0	13.5

The maximum differences registered in the degrees-day accumulated between the sampling stations during late spring and summer were related to the thermal stratification observed in Lake Escondido during this period.

Granulometry and Organic Matter Content

In Station A the percentages of sand and silt were similar, and that of clay was very low with respect to those components. In Stations B and C, high percentages of sand were observed in relation to the fractions of silt and clay. The high percentage of organic matter registered in Station A (36%) might be due to the incoming of allochthonous material originating in the surrounding vegetation and the presence of rhizomes of the boggy *S. californicus*. Finally, there were no outstanding differences in the content of organic matter between Stations B and C (Table 1).

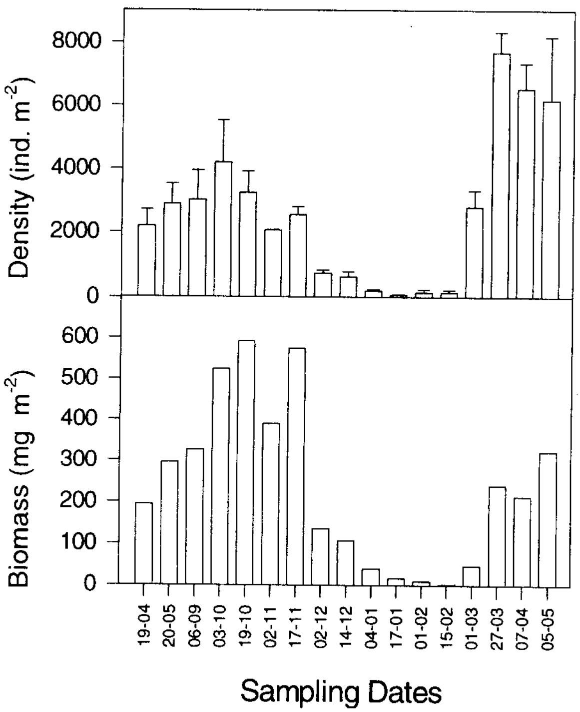

Fig. 3. Density and biomass variations of *Caenis* sp nymphs in Station A.

Life Cycle and Secondary Production

The density and mean biomass of *Caenis* sp showed evident differences between the area of *S. californicus* (Station A) and the deeper stations of the lake (B and C) (Table 2). In Station A the higher density values were observed from late March to early May 1989 (autumn) with a maximum of 7604 ind m^{-2} in early April (Fig. 3). The lowest densities were registered from December 1988 to mid February 1989 (summer) with a minimum of 67 ind m^{-2} in mid summer (Fig. 3).

The biomass presented the same pattern of density during this study (Fig. 3). Higher values were observed between October and November 1988, with a maximum of 591.90 mg m^{-2} in mid October (Fig. 3) and then, the biomass decreased with a minimum of 2.23 mg m^{-2} in mid February 1989 (Fig. 3).

The increment of body growth was evident during spring (Fig. 4). The greatest proportion of large size-classes was observed in mid January 1989; during February these classes showed a decreasing trend, and the individuals of the smallest ones, belonging to the new generation, began to increase (Fig. 4). The size-classes distribution, together with density and biomass variations (Fig. 3, 4), indicates that *Caenis* sp was univoltine, with one emergence period during summer.

Production estimates for Station A by the Allen Curve and Instantaneous Growth methods were similar while the Size Frequency method provided a higher estimate than the others (53 % and 83 % respectively) (Table2).

In Station A, the main habitat of *Caenis* sp population, secondary production and turnover ratio P/B were higher than Stations B and C (Table 2). In Stations B and C, the low number of organisms collected did not allow the calculation of the secondary production directly, so it was estimated multiplying the biomass of these stations by the turnover ratio of Station A (Waters, 1977,1979). By this way, secondary production in Station A was 2 to 3 orders in magnitude higher than that obtained in B and C (Table 2).

DISCUSSION

The high density, biomass and production of *Caenis* sp observed in Station A (Lake Escondido) (Table 2) corresponded to higher values of degrees-day accumulated and organic matter percent (Table 1, Fig. 2). Stations B and C presented lower values for the parameters mentioned above (Table 2). It is widely known that the temperature together with the quantity

Table 2. Population parameters of *Caenis* sp in Stations A, B and C of Lake Escondido. D= density (ind. m^{-2}); B= biomass (g m^{-2}); P= secondary production (g m^{-2} yr^{-1}) and P/B= turnover rate, by three methods of secondary production estimation.

Method	Stations	Density	B	P	P/B
Size Frequency	A	2665	0.24	1.029	4.3
	B	29	0.003	0.011	-
	C	4	0.001	0.003	-
Allen curve	A	2665	0.24	0.671	2.8
	B	29	0.003	0.008	-
	C	4	0.001	0.003	-
Instantaneous growth	A	2665	0.24	0.562	2.3
	B	29	0.003	0.007	-
	C	4	0.001	0.002	-

and quality of the food available are the main factors that affect the life history of aquatic insects (Benke, 1984; Ward, 1992). In this respect the genus *Caenis* has been mentioned by Edmunds and Waltz (1996) as sprawler on vegetated fine sediments, with feeding habits as scraper of algae and fine organic matter collector (Palmer et al., 1993).

We used the results obtained by the Allen Curve method to compare other freshwater systems because this is considered to give better estimates than other ones (Lindegaard, 1989). Waters and Crawford (1973) stressed that Size Frequency method overestimate se-

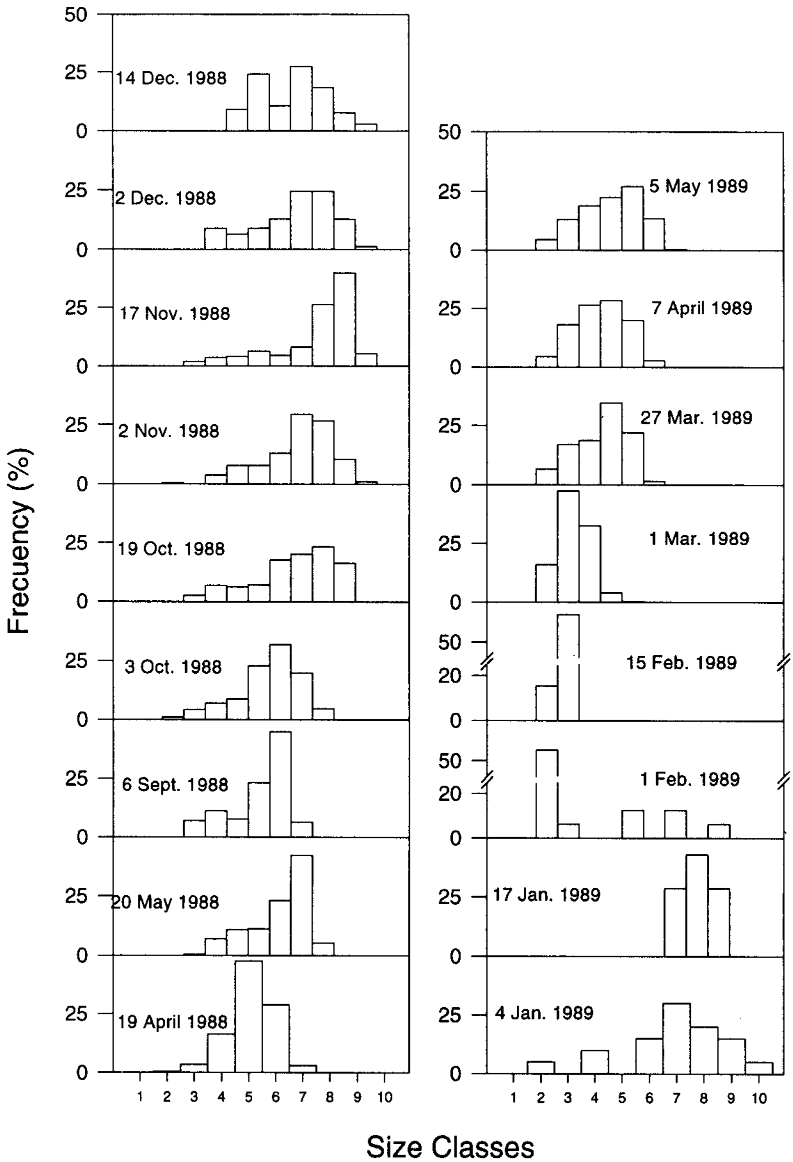

Fig. 4. Size-frequency histograms for *Caenis* sp nymphs in Station A of Lake Escondido during April 1988 - May 1989. X-axis (Size classes based on head-width, interocular distance, in mm): **1**= 0.14-0.21; **2**= 0.22-0.29; **3**= 0.30-0.37; **4**= 0.38-0.45; **5**= 0.46-0.53; **6**= 0.54-0.61; **7**= 0.62-0.69; **8**= 0.70-0.77; **9**= 0.78-0.85; **10**= 0.86-0.94.

condary production, because it is based on nymphal size it can wrongly consider more size classes due to different final sizes between male and female nymphs.

The early truncated survivorship curve in April-May 1988 (Fig. 4), may be due to missed small individuals or mortality related to biotic or abiotic factors. However, this loss would have a little effect in the estimation of secondary production.

Based on the Allen Curve method, the production in Station A is lower or similar compared with some waterbodies. For example, the maximum value obtained in Lake Escondido (0.67 g m^{-2} yr^{-1}) is lower than that estimated for *Caenis* sp in littoral zone of Ramos Mexía reservoir, North Patagonia (Argentina) (1.54 g m^{-2} yr^{-1}, Kaisin and Bosnia, 1987). A different situation was observed in the annual production of Chironomids of these two waterbodies. In this case, the values obtained in Lake Escondido for two genera common to both sites, were similar than those of the Ramos Mexía reservoir (Kaisin, 1989; Añón Suárez, 1997).

Other Caenids have showed higher or similar values than those obtained in Lake Escondido (Station A), for example *Caenis* sp (0.68 g m^{-2} yr^{-1}) (Rodgers, 1982) *Caenis macrura* (0.52 g m^{-2} yr^{-1}) (Zelinka, 1980) and *C. simulans* (0.75 g m^{-2} yr^{-1}) (Mac Farlane and Waters, 1982) in lotic systems, and *Brachycercus* sp (1.76 g m^{-2} yr^{-1}) in a small lake in Texas (Benson et al., 1980).

Production values for *Caenis* sp in Lake Escondido were also lower than was observed for species of other families. *Ephoron leucon* presented 2.860 g m^{-2} yr^{-1} (max.) (Snyder et al., 1991), *Ephemera spilosa* 0.037 g m^{-2} yr^{-1} (Dudgeon 1996a), and among five Heptagenid species the maximum production was 0.220 g m^{-2} yr^{-1} (Dudgeon, 1996b), as some examples of stream univoltine species. Waters and Crawford (1973) obtained higher values for the stream dweller *Ephemerella subvaria* (26.4 g m^{-2} yr^{-1}, larval wet weight; 4.4 g m^{-2} yr^{-1}, larval dry weight, see Waters, 1977).

On the other hand, the biomass turnover of *Caenis* sp in this study (P/B= 2.8) was lower than those included within the range indicated by Waters (1977) for univoltine species (P/B= 4 - 7). In Lake Escondido, this ratio was also lower than that obtained in the species above mentioned, as those show an average near 8.

It is difficult to explain the differences in the secondary production values from different waterbodies, because there are involved many factors interacting (food quantity and quality, temperature, salinity, habitat complexity and biologic interactions). However, in Lake Escondido, is clear that distribution of vegetation, high organic matter contents (that is food availability) and thermal pattern of the upper littoral zone (Station A), provide the most favourable conditions for the development of *Caenis* sp population.

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