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Life history and production of the burrowing mayfly *Ephoron virgo* (Olivier, 1791) (Ephemeroptera: Polymitarcyidae) in the lower Ebro river: a comparison after 18 years

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The life history of the burrowing mayfly *Ephoron virgo* (Olivier, 1791) (Ephemeroptera: Polymitarcyidae) was studied during spring and summer 2005 in the lower Ebro river (Catalonia) and compared to a previous study performed in 1987 (Ibáñez, Escosa, Muñoz and Prat 1991). The results showed an advancement of *Ephoron virgo* life cycle and an increase of production estimates. In 2005 larval development reached the maximum size one month earlier than in 1987, and adult emergence peak began three weeks earlier. Comparing adult sex ratios (F:M), there was a major presence of females in 2005 (1:4), while the opposite was observed in 1987 (2:1). Secondary production was higher in 2005 than in 1987, obtaining 950 mg dry weight/m^2/year with the increment summation method and 1080 mg dry weight/m^2/year using the removal summation method. Higher water temperatures were measured for the entire 2005 larval growth period, which were related to higher air temperatures. Therefore, that temperature increment was likely the main cause of changes observed in the *Ephoron virgo* life cycle.

Keywords: *Ephoron virgo*; life history; secondary production; temperature; Ebro river

Introduction

Ephoron virgo (Olivier, 1791) (Ephemeroptera: Polymitarcyidae) is a burrowing mayfly that inhabits many European and North African rivers, producing massive swarms in some of them. The filter-feeding larvae of this species construct U-shaped cavities in the riverbed in order to feed on suspended particles from the water currents produced by the movement of the tracheal gills. Its life cycle has been described earlier (Ibañez et al. 1991; Kureck and Fontes 1996). It is characterised by a diapause egg stage persisting during autumn and winter which is broken in mid-April when the larvae hatch. The growing period begins at this time and lasts until August, when male subimagines and females emerge. During a very short time males and females mate, and females oviposite. *Ephoron virgo* has been absent for decades in most of the polluted rivers in central Europe like the Rhine. Its return in the 1990s due to an improvement of water quality makes this species a good bioindicator of ecological quality (Kureck and Fontes 1996) of rivers. In the lower Ebro river *Ephoron virgo* usually inhabits areas of running water (Escosa, Ibàñez, Muñoz

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and Prat 1989) with substrates made up of gravel, cobbles with sand and fine sediments in the interstices, a habitat similar to those was observed in the Ardèche river (Mérigoux and Dolédec 2004). The species is not present in estuarine areas of the Ebro river with high salinity affected by the salt wedge (Muñoz and Prat 1993). At ecosystem level *E. virgo* is an important prey for fish and birds and a key species in organic matter processing (Van der Geest, Greve, Kroon, Kuijl and Kraak 2000). It enhances aerobic microbial activity by oxygenating river sediment in the microhabitat created in the burrows (Stief, Altmann, de Beer, Bieg and Kureck 2004).

The study of secondary production gives information about alterations in river function, reflecting changes in organism activities (Benke 1993), and is an estimation of the ecological yield of the studied population. Some secondary production studies are based on spatial and temporal variation of the species or communities (Benke, Van Arsdall, Gillespie and Parrish 1984; Snyder, Willis and Hendricks 1991; Buffagni and Comin 2000; González, Basaguren and Pozo 2003a); others have compared production in regulated rivers before and after a reservoir (Rader and Ward 1989) or the effect of floods in unstable rivers (Scrimgeour 1991). How competition influences production rates on species in the same trophic level (González et al. 2003b) or how predators could decrease production (Iversen and Thorup 1987; Lugthgart and Wallace 1992) was also described. But most of the studies are performed in small streams and only a few are known from large rivers. Therefore, our study is a contribution to the understanding and estimation of *E. virgo* secondary production in lowland rivers.

During the last years *E. virgo* adult mass emergences seemed to be less abundant in the lower Ebro than in the 1980s and the adults were not present in areas far from the river (up to 40 km) where they used to fly in the past. This suggested that larval densities along the river could have declined, and consequently a lower production should be expected. As global warming has likely caused the air temperature to increase during the last three decades in the studied area, and significant effects on phenology of terrestrial species of birds, insects and plants have been reported (Gordo and Sanz 2005), changes in *E. virgo* phenology may be attributed to climatic changes. Effectively, water temperatures, lower discharges (Prats, Val, Armengol and Dolz 2007) and the presence of reservoirs and a nuclear power station (Prats et al. 2004). Thus, knowing that *E. virgo* egg hatching is dependent on temperature, changes in its life cycle may be expected.

The main objective of this study was to compare results of the life history and secondary production in 2005 with those found 18 years ago (Ibáñez et al. 1991). We studied (1) larval densities, (2) developmental patterns, (3) life cycle period and (4) adult emergences in order to estimate *E. virgo* population dynamics and secondary production in the present ecological context.

Materials and methods

Study site

The Ebro river is one of the four most important rivers discharging to the Mediterranean sea. It is located in NE Spain and has a drainage basin of 85,550 km^2 with a length of 928 km. The lower part of the river (100 km from the river mouth) is regulated by two main hydropower dams (Mequinença and Riba-Roja) constructed in the late 1960s. A nuclear power plant was built in 1984 in Ascó, 15 km downstream of the dams. The sampling zone was located 40 km from river mouth (Figure 1), upstream the city of Tortosa, the same site studied in 1987 (Ibañez et al. 1991) and not influenced by the salt wedge. The riverbed substrate consisted of sand, gravel and cobbles. In this area the river

is 200 m wide with a low water flow. Its maximum depth is about 2.5 m. Due to the deep main channel it was not possible to sample across the width of the river as was done in 1987, but numerous areas with suitable depth and substrate were available. Mean daily discharge and temperature from the hydrological year 2004–2005 are shown in Figure 2. During the sampling period, monthly mean discharge were 332.46, 217.21, 184.55, 145.44 and 108.18 m^3/s for April, May, June, July and August, respectively, while the annual mean discharge in Tortosa is 396 m^3/s (1960–2005, Data from the Water Authority: Confederación Hidrográfica del Ebro, C.H.E.).

Sampling of larvae and laboratory methods

The sampling period began at the end of May 2005. Samples were collected every two weeks until August, when samples were taken every week. In order to obtain a quantitative estimate of larval densities we took eight random benthic samples in the studied area with a 0.25 m^2 Surber sampler (250 μm mesh net). The river bed was disturbed to a depth of

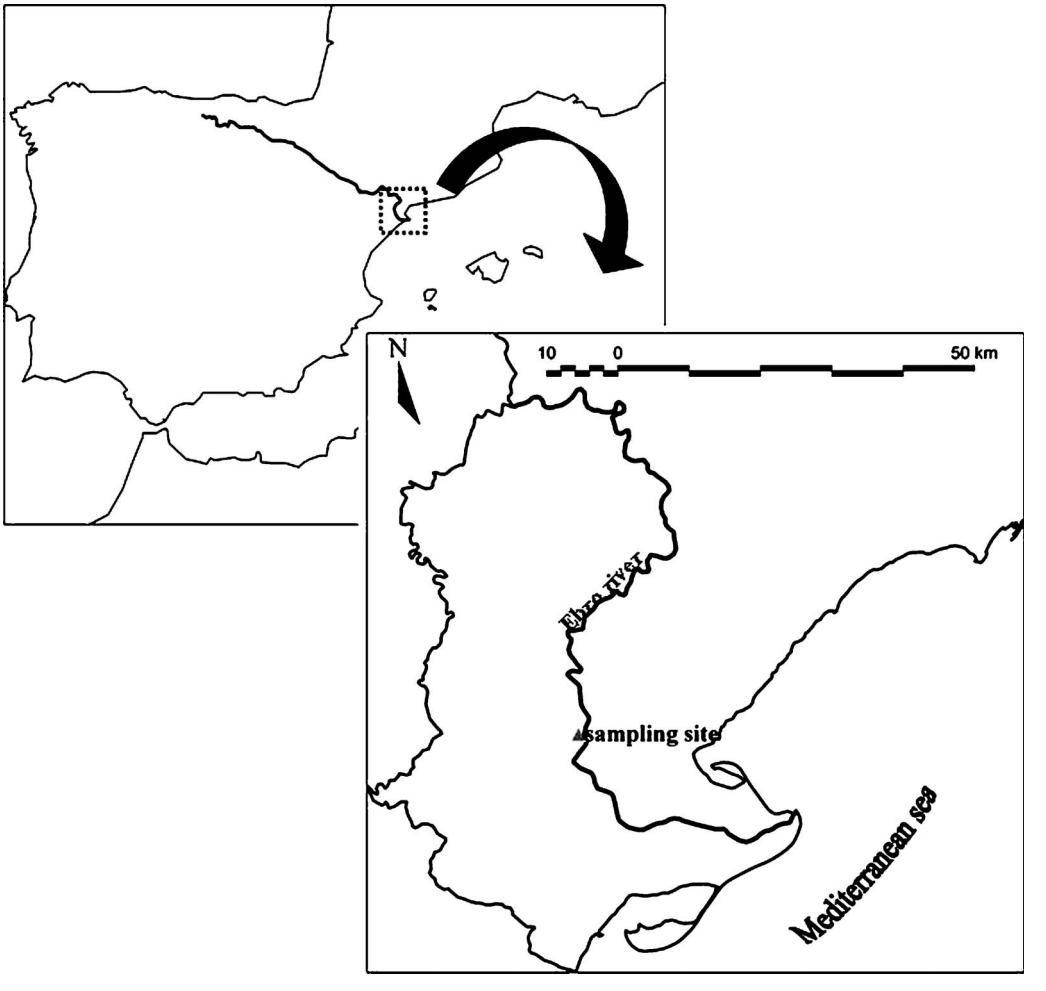

Figure 1. Study area in the lower Ebro river, located 40 km upstream of river mouth.

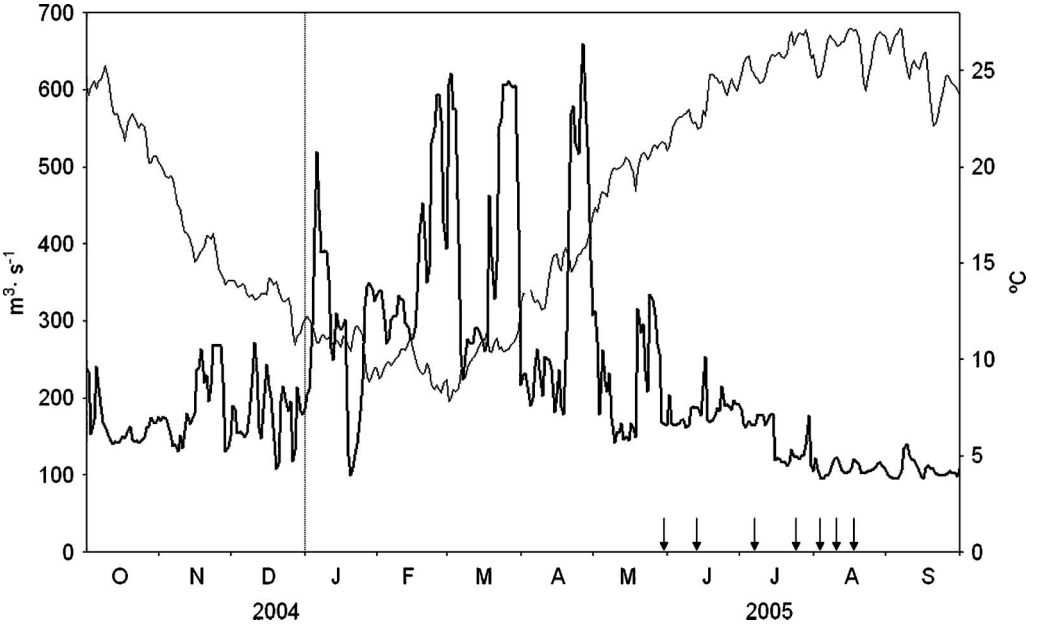

Figure 2. Mean daily discharge (thick lines) and mean daily temperature (light lines) during the hydrological year 2004–2005. Arrows show sampling dates of larvae.

10 cm and the contents were washed into the Surber net and deposited into a plate to identify and sort *E. virgo* larvae. Due to the difficulty of finding larvae in August, extra kick samples were taken to obtain more accurate body parameters during this period. Larvae were placed in 5 ml plastic vials and remained there for six months in 70% EtOH. Due to the small size of the larvae in the initial samplings, we sorted the benthic samples *in vivo* at the laboratory under a dissecting microscope to avoid field counting errors. Larvae were measured at the laboratory taking individual digital pictures with a Colorview Soft Imaging System camera attached to a Nikon SMZ800 stereoscopic microscope using the image analysis software Analysis SYS GMBH. We took three body measures to describe growth patterns: (a) body length (BL) (mm), distance between the end of the abdomen and the frontal process; (b) head width (HW) (mm), distance from eye to eye; and (c) wing pad length (WPL) (mm), length of the developing wing bud on the mesothorax (mm). The last body measure was not possible to be taken in all individuals caught before early July.

To determine the relationship between BL and dry weight (DW) all larvae were dried at 60°C for 24 h, placed into a desiccator for 1 h and weighed on an electronic balance BEL Ultramark 205 with a resolution of 0.00001 g. Larvae weighing was done in groups of individuals corresponding to each Surber sample. The individual mass was obtained from the individual mean weight of all Surber samples. In order to determine the effects of preservation on the biomass, living larvae were collected from the same site. Half of the larvae were measured and dried with the same method cited above but individually weighed with an electronic balance Sartorius BP211D with a resolution of 0.00001 g. The remaining larvae were stored for six months in ethanol 70% and also measured and dried individually. Effects of preservation with EtOH resulted in a weight loss of around 50%, depending on the size class (Figure 3). As studies in 1987 were performed with preserved

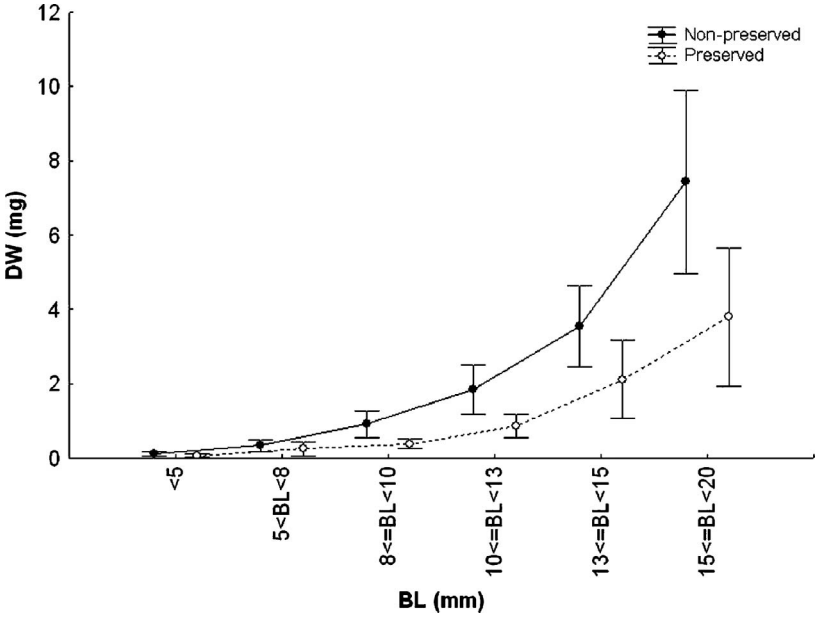

Figure 3. Relationship between body length (BL) and dry weight (DW) according to size classes from non-preserved and preserved larvae of *Ephoron virgo*.

larvae these data were used to correct data from that year. Therefore, we applied a correction factor for each size class to avoid an underestimation of biomass and secondary production calculations.

Secondary production calculation

The production was calculated for a period of 82 days (from 29 May to 19 August 2005) using two methods that may be applied to species with an unequivocal univoltine cycle: increment summation (IS) (Benke et al. 1984; Rigler and Downing 1984) and removal summation (RS) (Waters and Crawford 1973).

Temperatures and degree days

Degree days (DD) were calculated for each month during the hydrological year and for the whole larval period (April–August). Due to the lack of experimental data on the hatching temperature of *E. virgo* and knowing that egg hatching is in April, we assumed a threshold temperature of 14.5°C, corresponding to the mean monthly temperature of water in April 2005 and in April 1987. Only for 2005 were data available at 15 minute intervals for water temperatures (Xerta automatic station of the Water Authority: C.H.E.), so we could obtain an accurate daily mean record for that period. DD estimates were calculated using the following equation: $DD = \Sigma\ (T\text{-}To)$ (Southwood 1978) where T = daily mean temperature and To = threshold temperature for development.

It was not possible to strictly compare DD from 2005 and 1987 because in 1987 we only had one temperature measurement per month. However, the monthly mean from weekly measures in 2005 and the measures in 1987 (C.H.E.) were used to compare both

years. Applying the above equation but modifying the total number of DD for both years we obtained: DD = Σ (*T*m-*T*o)*d* where *T*m = monthly mean and *d* = number of days in the month. To support this approximation we used daily mean air temperatures (Ebro Observatory) to make correlation analyses with daily mean water temperatures (available from 1996 to 2005).

Adult collection

Adults were sampled twice a week in August 2005, with a total of eight different sampling days during the emergence period. The sampling time began at dusk, when the emergence occurs, and ended 50 minutes later. Due to its positive phototropism adults were trapped using car lights situated nearby the river. We placed two plates under the lights with some ethanol 70% and every 10 minutes we replaced the plates with empty ones. Adults were counted, separating males and females to obtain the sex ratio. When the quantity of adults was too much to be counted in 10 minutes we placed them into 250 ml plastic recipients with 70% ethanol and they were counted in the laboratory. The capture effort was always the same, using the same light intensity and the same light direction to the river.

Results

Larval density and life history

The high density obtained in late May decreased steeply in mid-June and when emergences began, from late July to the end of the sampling period, when the larval population was reduced to few individuals per m^2 (Figure 4). Survivorship curves in 2005 had the same pattern as in 1987 but shifted (see Ibañez et al. 1991).

Growth curves in 2005 showed a steady increase from May to early July and a marked increase to late July, when larvae reached a growth peak and attained the maximum

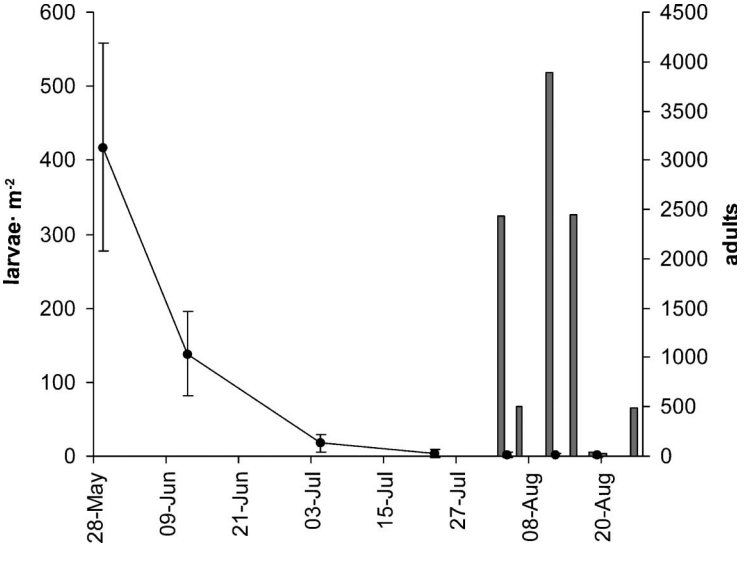

Figure 4. Mean larval densities and standard deviations, and number of adults (bars) captured during emergences in 2005.

average size. Individual size ranged from 4 to 8 mm in May, growing very fast until 18–20 mm in the peak of July (Figure 5). That is, growth was exponential until late July ($r^2 = 0.94$) and during August larvae had slightly lower body size and dry weight. As shown in Figure 6, wing pad length and head width also rose steeply in July, in close relationship with other growth parameters, indicating that the growth peak corresponded to the larvae about to emerge. When in late July larvae sex could be identified, we observed that females were bigger than males, being around 5 mm longer (Figure 7). At this time the sampled population was composed of 57% female and 43% males while on 4 August the larvae population was formed mainly of males (70%) and on 12 August females predominated (66.6%). The density of larvae during late July and August was very low and the collection of just a few specimens was even difficult.

Between-year differences in BL and DW were strongly marked for the same period. As can be seen in Figure 5, mean BL obtained in 2005 for early July was 10.9 $\pm$ 3.5 mm, while in 1987 BL did not reach 9.2 $\pm$ 3.7 mm until 30 July. The same pattern was observed for individual dry weight, in 1987 larvae reached an average of 3.02 mg on 7 August, while in 2005 the same values were obtained one month before on 4 July, so the maximum size and weight was attained earlier in 2005 than in 1987.

BL was positively correlated with head width (Spearman $r = 0.93$, $p = 0.00$) following a lineal relationship ($BL = 6.9\ HW + 0.3$) and a potential relationship ($DW = 0.0004\ BL^{3.6769}$) with DW (Spearman $r = 0.98$, $p = 0.00$).

Emergence began in late July and ended in late August. Estimated dates of peak emergence were earlier in 2005. As shown in Figure 4, the most important number of adults were captured before 15 August (of a total 9.842 individuals captured, 9264 were from 3 to 15 August), while in 1987 the peak emergence period lasted until early September (Escosa et al. 1989). We observed that emergences were very low when the weather was adverse (windy or stormy nights). We obtained a sex ratio (M:F) of 1:4 in 2005, female biased, while in 1987 the adult population was male biased, with a sex ratio of

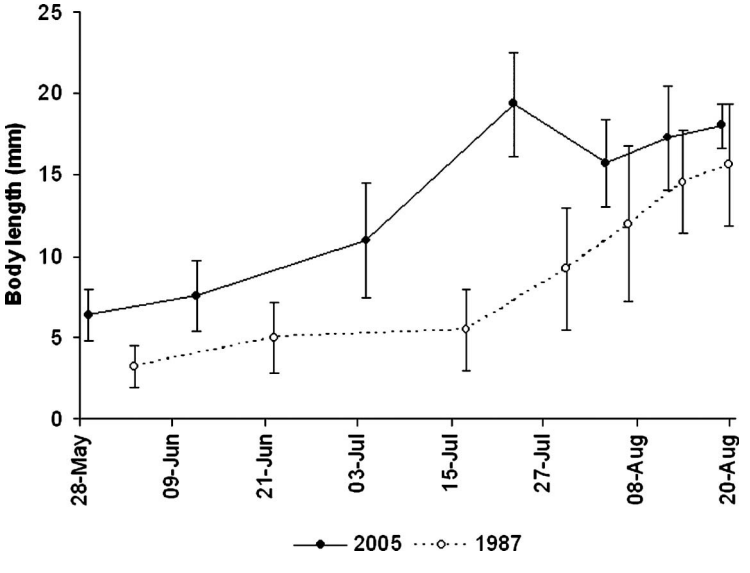

Figure 5. Mean body length (mm) and standard deviation of the larvae during 2005 and 1987.

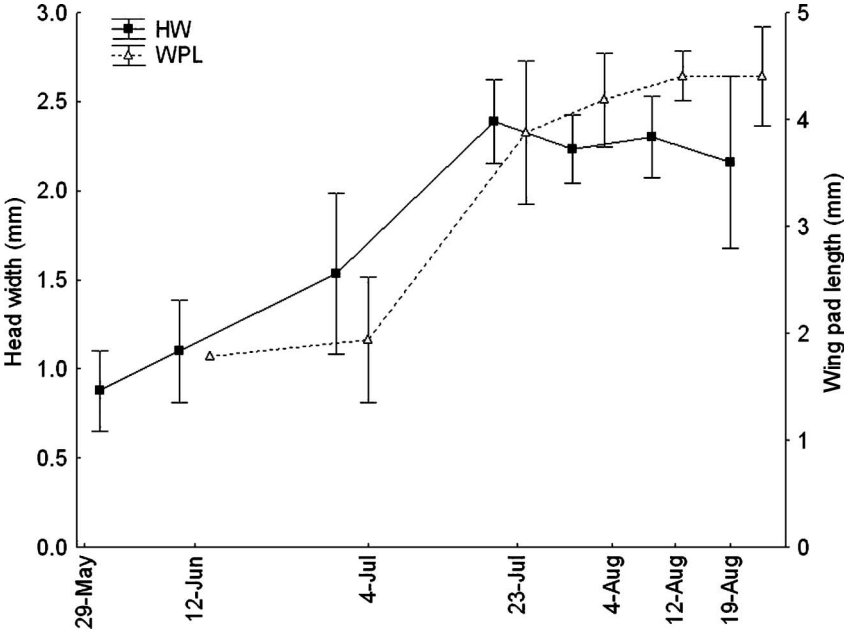

Figure 6. Mean and standard deviation of head width (HW) and wing pad length (WPL) during 2005.

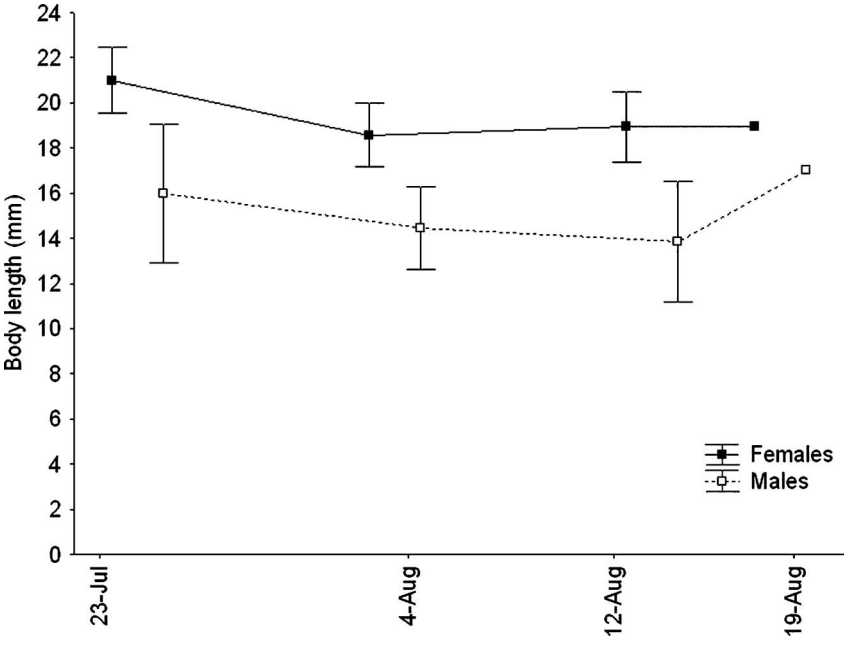

Figure 7. Mean body length (mm) and standard deviations of females and males during last stages of development in 2005.

2:1. The daily sex ratio varied depending on the sampling day but in 2005 was always female dominated (Figure 8). The emergence pattern was sex dependent; while males appeared during the first 10 min, females emerged 20 min later (Figure 9), except in mid-August when the number of captured adults was just a few individuals. During emergences the presence of insectivorous fishes, birds and bats feeding on *E. virgo* was constant.

Production estimates

As shown in Table 1 similar values were obtained for the annual production with the IS (950.42 mg/m^2/y) and RS (1079.78 mg/m^2/y) method. The annual turnover ratio (P/B) ranged from 10.11 to 11.49/y. The average population biomass during the entire sampling period was of 93.98 mg/m, being high in the initial stages due to abundant larvae densities and falling drastically when emergence began.

To be comparable to 2005, we applied the correction factor for the effects of preservation to the 1987 data of larval weight. In 1987 production was also similar using the two different methods but IS and RS values were less than half the production obtained in 2005 (Table 1).

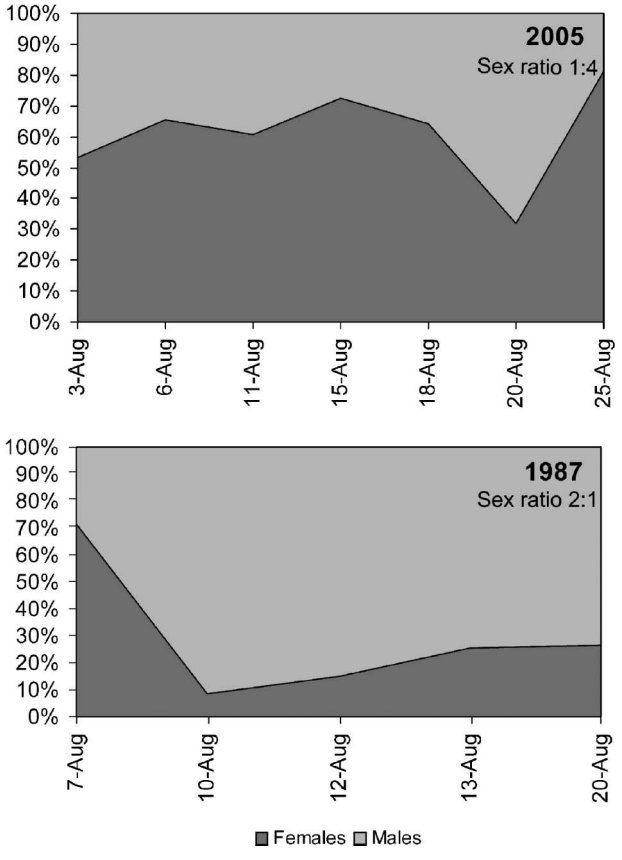

Figure 8. Percentage of adult males and females emerged in 2005 and 1987.

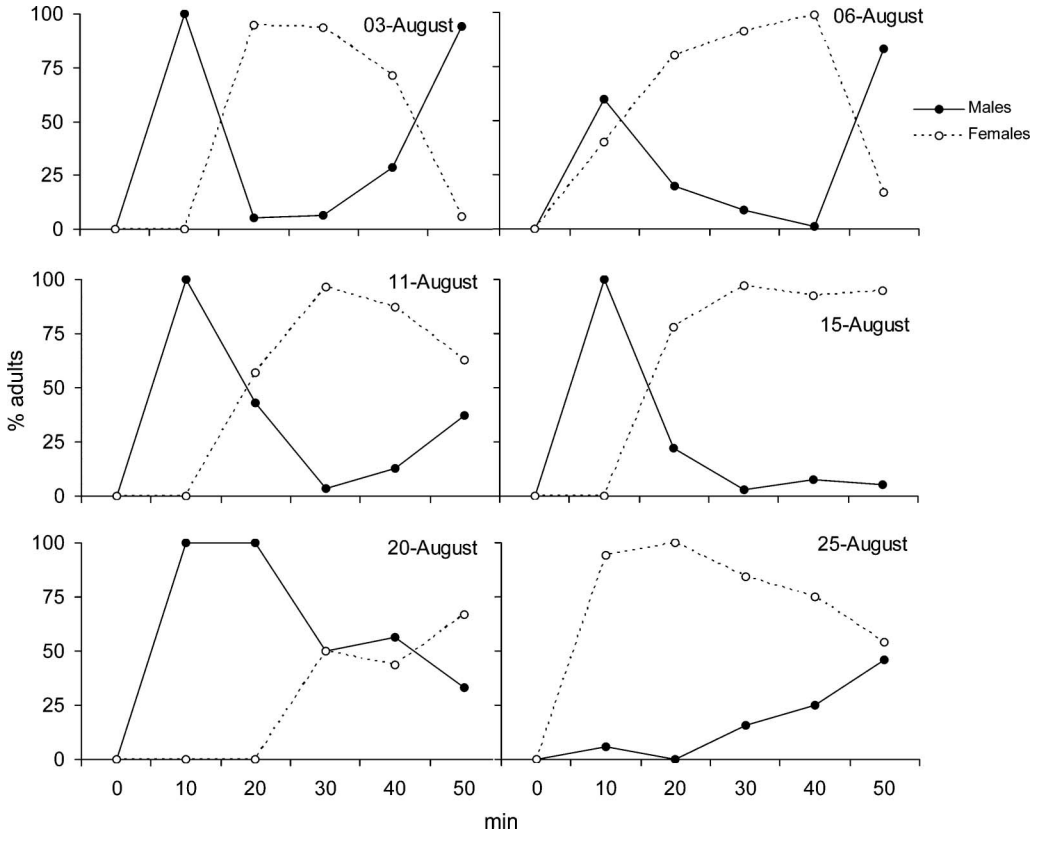

Figure 9. Percentage of adult males and females emerged in 2005 at 10 minute intervals.

Table 1. Average and total biomass (B), production (P) and P:B ratio using two methods for 2005 and 1987. All values were corrected for preservation procedures.

	2005	1987	Unit
Average B	93.98	78.74	mg/m
Total B	657.89	551.18	mg/m
Annual P (IS)	950.42	440.76	$mg/m^2/y$
Annual P (RS)	1079.78	444.1	$mg/m^2/y$
Annual P/B ratio (IS)	10.11	5.60	y^{-1}
Annual P/B ratio (RS)	11.49	5.64	y^{-1}

Methods described are IS, increment summation; RS, removal summation.

Temperature

For the entire larval growth period (April–August) in 2005 we obtained a total of 1157 DD using the daily mean from 15 minute intervals. From mid-April (hatching) to the first emergence sampled in early August we estimated a total of 827.4 DD. To compare the water temperatures of 2005 with the ones of 1987 we could not use the 15 minute interval data and the comparison was made with the available records of mean monthly temperatures for both years multiplied by the number of days. With this method for 2005

we obtained similar DD (1152 DD) accumulated from April to August than if 15 minute data were used. For the larval period of 1987 we obtained a total of 1043 DD, a slightly lower value than in 2005. Month by month along the sampling period DD accumulation was always higher in 2005 (Figure 10). A significant correlation (Spearman's $r = 0.91$) between air and water temperatures in the period of 1996–2005 was found, therefore, air temperature may be used to estimate water values. From May to July 2005 mean daily air temperatures were almost 2°C higher than in 1987 (Figure 11). Thus, higher air and water temperatures during the larval period were obtained for 2005 compared with previous data from 1987.

Discussion

In species with a marked synchronisation such as in mayflies like *E. virgo*, different methods for production calculation should give similar values (Morin, Mousseau and Roff 1997). According to this, similar production estimates were obtained by using IS and RS methods (Table 1).

Secondary production in the Ebro river in 2005 was higher than in 1987, but not reaching the high values known from other *Ephoron* species such as *Ephoron leukon* (Williamson, 1802) and *Ephoron album* (Say, 1824) in North America (Table 2). In 1987 lower production values were obtained partly due to the higher male proportion with lower individual body mass. Population density during the first sampling collection in 1987 was underestimated because higher river discharge did not allow use of the Surber sampler, only the kick net. Therefore, low biomass and less production were obtained during the initial sampling period in 1987. Another factor that could explain the lower production in 1987 was a longer storage period. In 1987 larvae were stored for 30 months in 70% ethanol, while in 2005 storage was for six months, so the weight loss in larvae corresponding to 1987 could have been higher and this may be one of the reasons why lower production values were obtained.

Once emergences had begun, growth curves showed that larval body length and individual mass decreased, corresponding to larvae that were still ending the last instar development in August. This pattern of growth decline after first emergences has also been

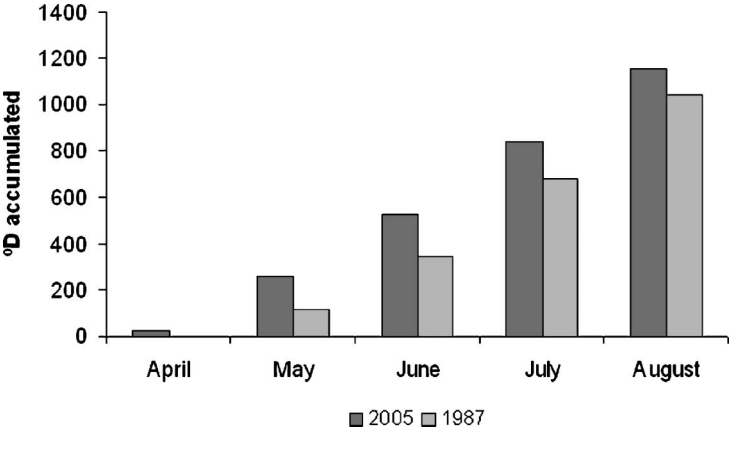

Figure 10. Degree days accumulated for 2005 and 1987 calculated from CHE (Confederación Hidrográfica del Ebro, Ebro Water Authority).

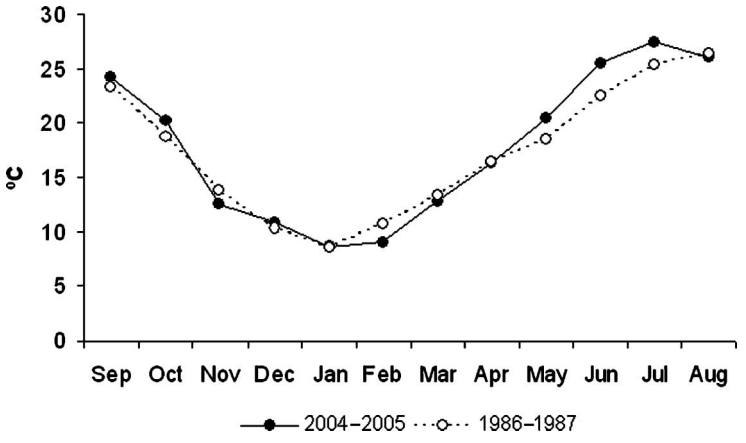

Figure 11. Average monthly air temperatures for 2005 (black dots and lines) and 1987 (white dots and discontinuous lines).

Table 2. Secondary production comparison of *Ephoron virgo* with other *Ephoron* species.

Author	Species	Study site	Annual P ($mg/m^2/y$)	Annual mean B (mg/m^2)	Annual P/B (y^{-1})	Method
Cid. et al. (present study)	*Ephoron virgo*	Lower Ebro river	950.42	93,98	10,11	IS
			1079.78		11,49	RS
Ibañez et al. (1991)	*Ephoron virgo*	Lower Ebro river	440.76	78,74	5,60	IS
			444.1		5,64	RS
Snyder et al. (1991)	*Ephoron leukon*	South river	398–2857	99–911	15.3–13.5	IS
Gibberson and Galloway (1985)	*Ephoron album*	Valley river	1430		22.8	RS
			1320		21.2	IG
			1320		21.2	AC
			1480		21.3	SF
Phillips et al. (1994)	*Ephoron album*	Ilinois river	5919	340	17.26	RS
			6698		19.52	IS
			6097		17.77	IG

Methods described are IS, increment summation; RS, removal summation; IG, instantaneous growth; SF, size frequency.

observed in other Ephemeroptera such as *Euthyplocia hecuba* (Hagen, 1861) (Sweeney, Jackson and Funk 1995) and *Ephoron shigae* (Takahashi, 1924) (Watanabe and Ohkita 2000) and seems to be temperature independent. Female larvae of *E. virgo* are bigger than male larvae with marked differences in body length and mass (Kureck and Fontes 1996), due to egg accumulation in the female abdomen, so a higher proportion of females in the sampled population could result in higher larval mean sizes. That is, the lower larval body sizes found on 4 August could be due to a male biased sex ratio.

Emergence and oviposition behaviour was the same as described for *E. virgo* populations in the Rhine river (Kureck and Fontes 1996) and similar to other *Ephoron* species such as *E. album* (Giberson and Galloway 1985), *E. leukon* (Snyder et al. 1991) or *E. shigae* (Watanabe, Mori and Yoshitaka 1999; Watanabe and Ohkita 2000).

According to Benke (1984) the most important factor limiting production in rivers where food is not a limiting factor is habitat characteristics, so production would be optimal when the functional habitat per unit area is high. Habitat available for *E. virgo* in the lower Ebro river has been reduced during the past five years due to the invasion of the macrophyte pondweed *Potamogeton pectinatus* L. As the macrophyte community is being established, they accumulate soft sediments in the habitat they occupy, changing river sediment and hydraulic conditions (Sand-Jensen 1998; Cotton et al. 2006; Wharton et al. 2006) so it is possible that areas *E. virgo* used to colonise nowadays are not a suitable habitat for the species. The decrease of dissolved phosphorous in all the drainage basin in the past 10 years is likely the cause of the observed phytoplankton reduction (Ibañez et al. 2008), affecting the food availability of *E. virgo*. The presence of the zebra mussel *Dreissena polymorpha* (Pallas, 1771) in the Riba-Roja dam, upstream of the sampling zone, could have also enhanced a decrease of total suspended materials by its filtering action. At the same time, populations of the Asian clam *Corbicula fluminea* (Müller, 1774) and the black fly *Simulium erytrocephalum* (De Geer, 1776) are well consolidated in the river, so they could compete with *E. virgo* for the same food resources. However, despite these possible competitors for food, higher production estimates were found in the studied area, giving the impression that food is not a limiting factor in this river. However, *E. virgo* production will probably decrease in the future due to habitat constraints (disappearance of gravel areas that will be covered by silt and organic matter debris accumulated below *Potamogeton pectinatus* stands).

Factors regulating growth and development in aquatic insects are mainly determined by water temperature, food quality and availability and competition (Sweeney and Vannote 1978; Vannote and Sweeney 1980; Ward and Stanford 1982; Rader and Ward 1989; Snyder et al. 1991; Atkinson 1994; Hogg and Williams 1996). These factors have a direct influence on larval size before emergence, on emergence timing, population densities and consequently on secondary production. Taking into account that density in the 1987 first sampling was underestimated due to methodological problems (small larvae not detected and the use of the kick net), we can conclude that larval densities followed the same pattern in 2005 but advanced some weeks. That is, the marked population decrease coinciding with the initial emergences occurred in mid-July in 2005 and in August in 1987, so the life cycle in 2005 was advanced three weeks. Since maturity and emergence depend on size and weight reached in a certain moment (Rowe and Ludwig 1991; Snyder et al. 1991), the early development of the larvae in 2005 agrees with the early emergences found. Several studies have shown changes in timing of life cycle events related with warming. Hogg and Williams (1996) observed that emergences of the stonefly *Nemoura trispinosa* (Claassen, 1923) and the caddisfly *Lepidostoma vernale* (Banks, 1897) were advanced two weeks with a water temperature increment of 2°C in spring and 3.5°C in summer, and also Langford (1975) noticed that in warm years with higher water temperatures first emergences of caddisflies and mayflies were advanced. The development of *E. virgo* studied in Morocco (Qninba 1986) started earlier than in the Ebro river in 1987 (Ibañez et al. 1991) due to warmer water temperatures and a different thermal regime. Moreover, an advanced emergence of terrestrial insects has also been reported in the lower Ebro, due to an increase of air temperature since the mid-1970s, especially in spring (Gordo and Sanz 2005). Since the larval growing period of *E. virgo* mostly takes place in spring, a similar response is

expected for this aquatic insect. Therefore, after 18 years higher water temperatures were likely the main cause of the shifted life cycle. Since both studies (1987 and 2005) were performed when the hydropower dams and the nuclear power station had already been built, and knowing that the study site is more than 50 km downstream, where no influence on temperature exists, we assume that water temperature increase is a result of warmer air temperatures. If the global trend of increasing temperatures is maintained we will find that life history parameters (timing of hatching and emergences) of this species may still change in the future. For this reason, experimental work to determine the effects of temperature increase on the species are required. Also data on the habitat preferences of *E. virgo* in the Ebro river and a more extended study of production along different parts of the river will be needed to determine how habitat influences the population dynamics of this species.

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