Life History, Growth and Secondary Production of *Caenis luctuosa* and *Cloeon simile* (Ephemeroptera) in a Small Pond, S.W. France

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Abstract

We studied the population dynamics of the mayflies *Caenis luctuosa* (Burmeister) (Caenidae) and *Cloeon simile* Eaton (Baetidae) in a permanent pond in Southwestern France. Both species had a bivoltine life cycle. After slow and continuous winter growth, the rapid rise in water temperature in March resulted in increased growth rates until spring–summer emergence. The eggs laid by the adults of the winter generation yielded the individuals of a short summer generation in both species. The annual production values were the highest ever reported for species from both genera: 11.75 g dry weight m^{-2} year^{-1} in *C. luctuosa* and 2.05 g dry weight m^{-2} year^{-1} in *C. simile*, while P/B ratios (13 and 11.2 respectively) were similar to those reported for closely related species with bivoltine life cycles.

Keywords: Ephemeroptera, *Caenis luctuosa*, *Cloeon simile*, life history, growth, secondary production, temperature, ponds.

Introduction

Aquatic insects, such as Ephemeroptera, play an important ecological role within lotic and lentic communities, where they constitute a major part of macroinvertebrate biomass and production (Brittain, 1982). In small water bodies such as ponds, temperature is the major ecological factor affecting the seasonality, growth and development patterns of aquatic insects, when species find suitable habitat conditions (Learner & Potter, 1974; Oertli, 1995). The mayflies *Caenis luctuosa* (Burmeister, 1939) (Caenidae) and *Cloeon simile* Eaton 1870 (Baetidae) are widely distributed throughout Europe (Illies, 1978), in both running and standing waters (Elliott et al., 1988). They exhibit highly flexible life cycles depending on water temperature conditions (Landa, 1968; Brittain, 1974; Clifford, 1982). Some life history information is available (Macan, 1979; Grimeland, 1966; Landa, 1968; Brittain, 1974), but there

have been no detailed quantitative studies of their population dynamics in lakes or ponds. Perán et al. (1999) and González et al. (2001) recently studied the life history of *C. luctuosa* in Spanish streams, and provided the only available estimates of secondary production for this species. Therefore, the aim of this study was to provide quantitative data on the life cycle, growth and production of *C. luctuosa* and *C. simile* in a small permanent pond. The results are compared with quantitative data published for congeneric species.

Study Area

The Causse du Quercy is a 2156 km² limestone region in South-Western France. In this arid area deprived of any stream system, over 300 artificial ponds have been bored into the calcareous rock since the 12th century, in order to support agricultural activities. These small permanent ponds are actually the only aquatic ecosystems in the area (density less than one pond per km²). However, they are now abandoned, and progressively filling with mud and aquatic vegetation. The Sauvage pond is one such body (357 m a. s. l.) and oligotrophic (Angélibert et al., 2000). It is rectangular in shape, has an area of 175 m², and a maximum depth of 1.60 m. The bottom is constituted of thin layers of mud overlaying the calcareous rock (<1 cm, 80% of the bottom surface) and bryophytes (20% of the bottom surface). Water temperature varied from 0.5°C in winter to 27.2°C in summer (Fig. 1). Detailed descriptions of the fauna, flora, physical and chemical features of this pond were given in Angelibert et al. (1999, 2000).

Material and Methods

Six benthic samples were collected monthly from November 2000 to February 2001, then bimonthly from March to November 2001, using an air-lift sampler (Pearson et al., 1973; Boulton, 1985) (sampling area
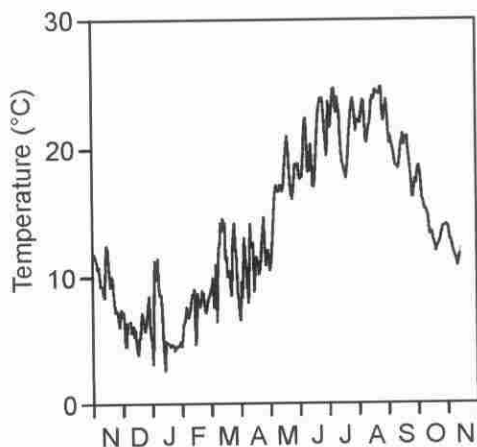

Figure 1. Mean daily temperature (°C, measurements at mid-depth) in the Sauvage Pond (November 2000–November 2001).

$186\,cm^2$, mesh size of the net: $250\,\mu m$). Samples were distributed in proportion to the relative abundance of the two substratum types: thin layers of mud deposed on the calcareous substrate (<1 cm) (four samples), and bryophytes (two samples). This provided the best qualitative (all substrata were sampled) and quantitative (replicate sample-units) estimates. However, due to the rather low number of monthly samples as well as mayfly seasonality, confidence limits of mean annual estimates are large. Therefore, we have indicated the lower and upper density and biomass observed during the sampling period. Invertebrates were preserved in the field in 5% formalin, identified in the laboratory and preserved in 70% ethanol. Water temperature was recorded hourly at mid-depth over the study period, using Tinytalk® temperature dataloggers.

Head capsule width, and wingpad length including mesonotum were measured using an ocular micrometer, then all larvae were divided into 0.1 mm size classes (based on head width) to construct size–frequency plots for life cycle determination. Differences in the mean annual frequency distribution of larval size (vegetation versus mud) for each species were compared using Kolmogorov–Smirnov two sample tests.

Sets of larvae (at least 10 individuals) of different size classes were dried at 60°C for 24 hours and weighed. Individual larval mean dry weights (W mg) were deduced from linear regressions ($LnW = a + b$HCW with 95% Confidence Limits) between the natural log of weight (LnW) and head capsule width (HCW). Mean individual dry weights from each site were natural log transformed to generate a series of subsegment linear regressions that represent a generation's seasonal growth patterns over the year. The relationship between the mean individual dry weight of the larvae of each generation and time was calculated as: $W_t = W_{t_0} \cdot e^{kT}$, where W_t = weight at instant t, W_{t_0} = weight at instant t_0, $T = t - t_0$ days, k ($mg\,mg^{-1}\,day^{-1}$) = instantaneous growth rate (Humpesch, 1979, 1981). Growth of individuals was expressed as specific growth rate, K, with $K = 100\,k$ (% dry weight per day ± 95% C.L.). The size–frequency method (Hynes & Coleman, 1968; Hamilton, 1969; Benke, 1979) was used to obtain estimates of species' annual production (g dry weight $m^{-2}\,year^{-1}$) from life history, density and biomass data. The turnover ratio (P/B = annual production / mean annual biomass) was also calculated.

Results and Discussion

The mean annual density of *C. luctuosa* was $1522\,ind\,m^{-2}$ (170–$5942\,ind\,m^{-2}$ depending on the considered period, see Fig. 2a). In our study pond, maximum density was recorded in November, with a secondary peak in January, whilst recent studies conducted in streams reported that the density of *C. luctuosa* peaked in August and October in northern Spain (Gonzáles et al., 2001), and in May and July in southeast Spain (Perán et al., 1999). We recorded a mean annual biomass of $7.04\,mg\,m^{-2}$ (0.43–$16.52\,mg\,m^{-2}$). Biomass was highest in November and June, whereas the above-mentioned authors observed peaks in May and August, and from February to July, respectively. Nymphs were found in both kinds of substrate, and the frequency distribution of size classes did not differ significantly ($p > 0.05$, Kolmogorov–Smirnov two-sample test) between mud and bryophytes (Fig. 2b).

To our knowledge, there have been no previous accounts of seasonal abundance patterns in *C. simile*. The mean annual density of *C. simile* was $456\,ind\,m^{-2}$ (22–$1745\,ind\,m^{-2}$), and the mean annual biomass was $1.46\,mg\,m^{-2}$ (0.02–$3.49\,mg\,m^{-2}$) (Fig. 2a). Peaks of density occurred in December and July. The seasonal pattern of biomass was quite similar to density variation, but the biomass also peaked in March. Although some individuals were found on muddy substrate, nymphs significantly preferred bryophytes, and there was a significant difference ($p < 0.05$) in the frequency distribution of size classes in *C. simile*. Larger nymphs (HCW ≥ 1 mm) were exclusively found on bryophytes (Fig. 2b).

A simple regression provided the best fit for the relationship between dry weight (W) and head width (HCW): $LnW = -5.82 \pm 0.365 + 4.9 \pm 0.407$ HCW in *C.*
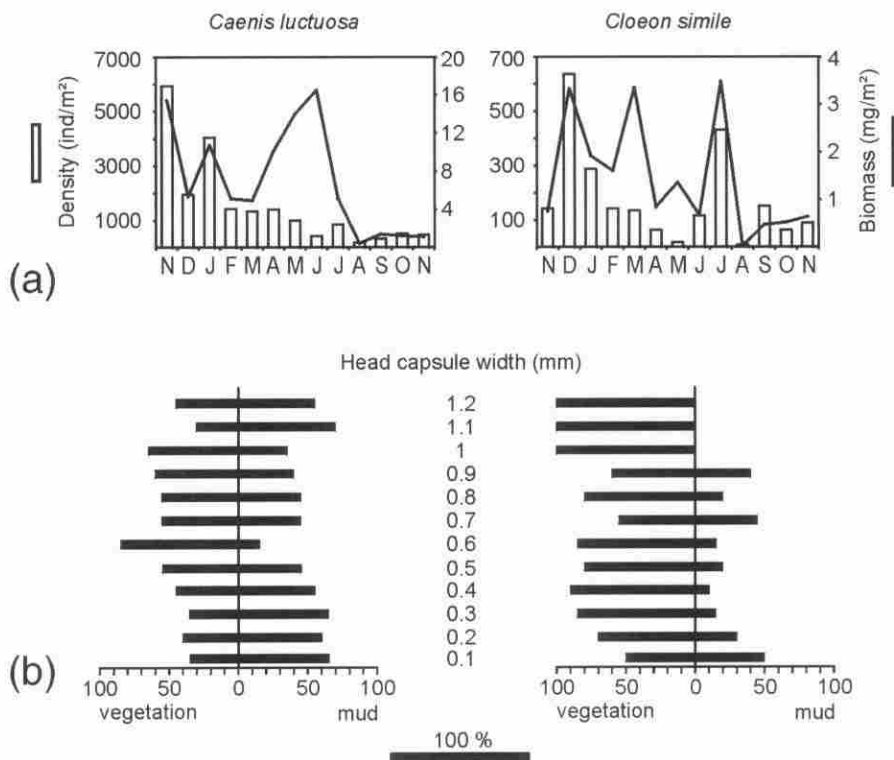
(a)

(b)

Figure 2.   (a) Larval density (ind/m²) and biomass (mg dry weight/m²) of *Caenis luctuosa* and *Cloeon simile* throughout the year. (b) Mean annual frequency distribution of size measurements in vegetation and on mud substrata.

luctuosa ($r^2 = 0.94$, $n = 54$, $p < 0.01$), and Ln$W = -12.04 \pm 0.17 + 4.6 \pm 0.22$ HCW in *C. simile* ($r^2 = 0.98$, $n = 83$, $p < 0.01$).

Caenis luctuosa had a bivoltine life cycle with two distinct generations (Fig. 3a). There was a long winter generation, whose newly-hatched larvae appeared in September. Their growth continued during autumn ($K = 1.7 \pm 0.6\%$ day^{-1} from September to November), slowed in winter ($K = 0.29 \pm 0.4\%$ day^{-1} from November to March), and increased during spring ($K = 2.06 \pm 0.2\%$ day^{-1} from March to July). The eggs laid by the adults of the winter generation yielded the individuals of a short summer generation, which developed from July to September ($K = 3.07 \pm 0.7\%$ day^{-1}) (Fig. 3b). Final instar larvae of this summer generation were smaller than those of the winter generation (Fig. 3c). The emergence period (May–September) thus encompassed both generations. Clifford (1982) classified *Caenis* species as 'non-seasonal multivoltine', and the high flexibility of their life history patterns is known from previous studies (Table 1). Most authors have described uni- and bivoltine (with a short summer generation) life cycles for *C. luctuosa* (Landa, 1968; Brittain, 1974; Macan, 1979; González et al., 2001), and only Perán et al. (1999) reported four generations
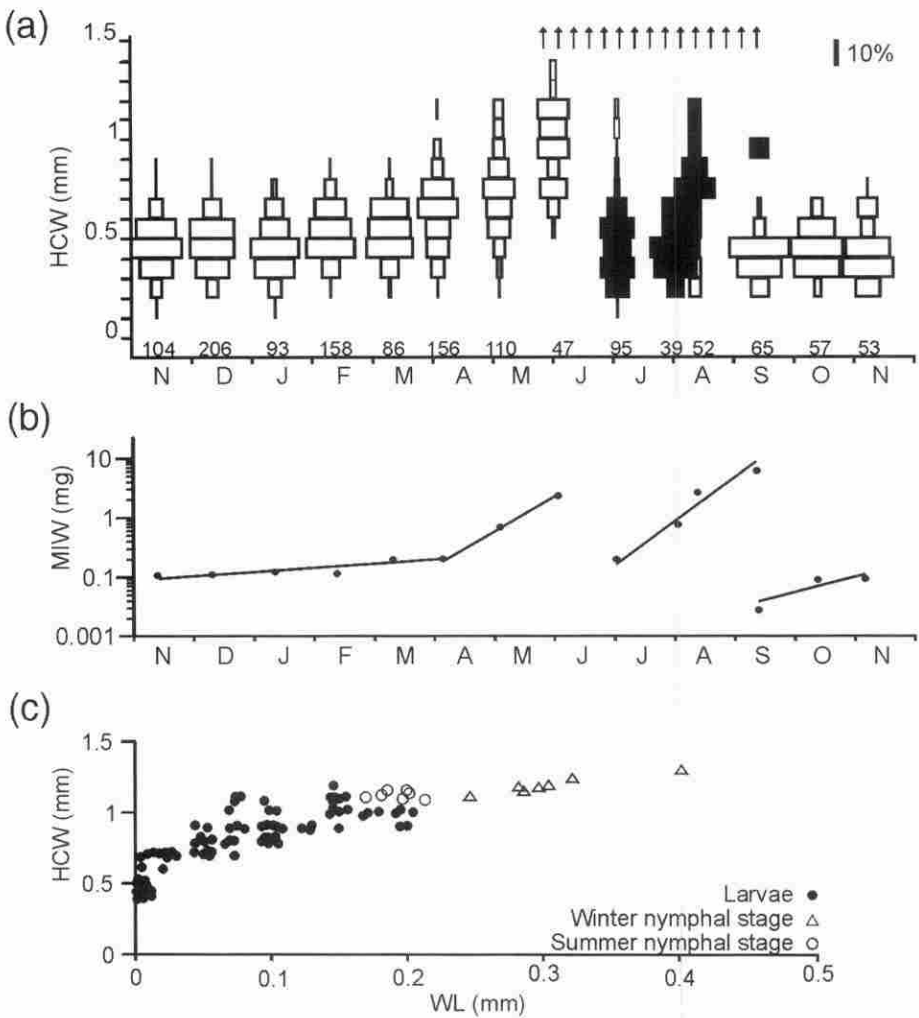
Figure 3. Life history and growth of *Caenis luctuosa*. (a) Frequency distribution of head capsule width (HCW, mm) at each sampling date. The summer generation is represented in black. Arrows on the top of the graph indicate the emergence period. Numbers on the abscissa indicate individuals measured. (b) Mean individual dry weight (MIW, mg) throughout the life cycle. (c) Relationship between head capsule width (HCW, mm) and wingpad length (WL, including mesonotum, mm).

per year in a semiarid stream (Table 1). The annual production of *C. luctuosa* in the Sauvage pond was estimated as $11.75\,g$ dry weight m^{-2} $year^{-1}$. This is the highest production estimate reported for *Caenis* species (Table 1). It represents about twice the value estimated by Perán et al. (1999) in S.E. Spain, and about 150 times the production estimated by González et al. (2001) in a small stream in northern Spain.

Table 1. Comparison of annual production and P/B ratio of several *Caenis* and *Cloeon* species. Conversion factors (Cummins & Wuycheck, 1971): 1 g dry mass = 20.7kJ; 1 g wet mass = 3.7kJ; 1kcal = 4.2kJ.

Species	P (mg DW/m^2)	P (kJ/m^2)	P/B	Generations per year	Habitat	Country	Reference
Caenis luctuosa (Burmeister, 1839)	11753.2	243.3	13	2	pond	France, Lot	This study
C. luctuosa (Burmeister, 1839)	6349.8	131.4	16	4	semiarid stream	Spain, Murcia	Perán et al., 1999
C. luctuosa (Burmeister, 1839)	76–93	1.57–1.92	7.9–7.1	1	stream	Spain, Northern	González et al., 2001
C. horaria (Linnaeus, 1758)	539	12.4	10.2	2	pond	Switzerland	Oertli, 1993
C. horaria (Linnaeus, 1758)*	191–939	3.8–18.8	13.5–7.1	1	shallow lake	England	Mason, 1977
C. macrura Stephens, 1835	236	4.9	13	2	stream	Czech republic	Zelinka, 1984
C. amica Hagen, 1861	430	8.9	13	2	pond	USA, Virginia	Christman & Voshell, 1992
C. amica Hagen, 1861	676	14	12.7	?	experimental stream	USA, Alabama	Rodgers, 1982
C. amica Hagen, 1861	4200	86.9	4.2	1	plain stream (cold)	USA, Minnesota	MacFarlane & Waters, 1982
Caenis spp.**	82.1	1.6	59.1	?	plain stream	USA, Georgia	Benke & Jacobi, 1994
Caenis sp.	589.5	12.2	5.8	1	reservoir	Argentina, Neuquén	Kaisin & Bosnia, 1987
Cloeon simile Eaton, 1870	2055.5	42.5	11.2	2	pond	France, Lot	This study
C. dipterum (Linnaeus, 1761)	298	6.8	8.7	2	pond	Switzerland	Oertli, 1993
C. dipterum (Linnaeus, 1761)	959	22	11.2	1	stream	Czech republic	Zelinka, 1984
C. dipterum (Linnaeus, 1761)*	14.5–7.2	0.3–0.15	0.9–8.2	1	shallow lake	England	Mason, 1977

*two years study.

**C. diminuta* Walker, 1853, *C. hilaris* (Say, 1839), *C. macafferti* Provonsha, 1990.

The production to mean annual biomass ratio (*P/B*) was 13, which agrees well with previous estimates for closely related species, and more generally for bivoltine species (Waters, 1977; Benke, 1984).

Cloeon simile also had a bivoltine life cycle with two generations (Fig. 4a). The winter generation extended from early September to May. Newly-hatched larvae grew continuously during autumn (*K* = 1.30 ± 0.6% day^{-1}, August–November), slowed down in winter (*K* = 0.43 ± 0.1% day^{-1}, November–February), and increased again during spring (*K* = 2.49 ± 0.5% day^{-1}, February–early May). The eggs laid by the adults of the winter generation gave rise to a short summer generation, which developed over two months (June and July, *K* = 8.70 ± 0.2% day^{-1}) (Fig. 4b). The emergence period extended from mid-April to the beginning of August, with adults from both generations. However, the final instar nymphs of the summer generation were
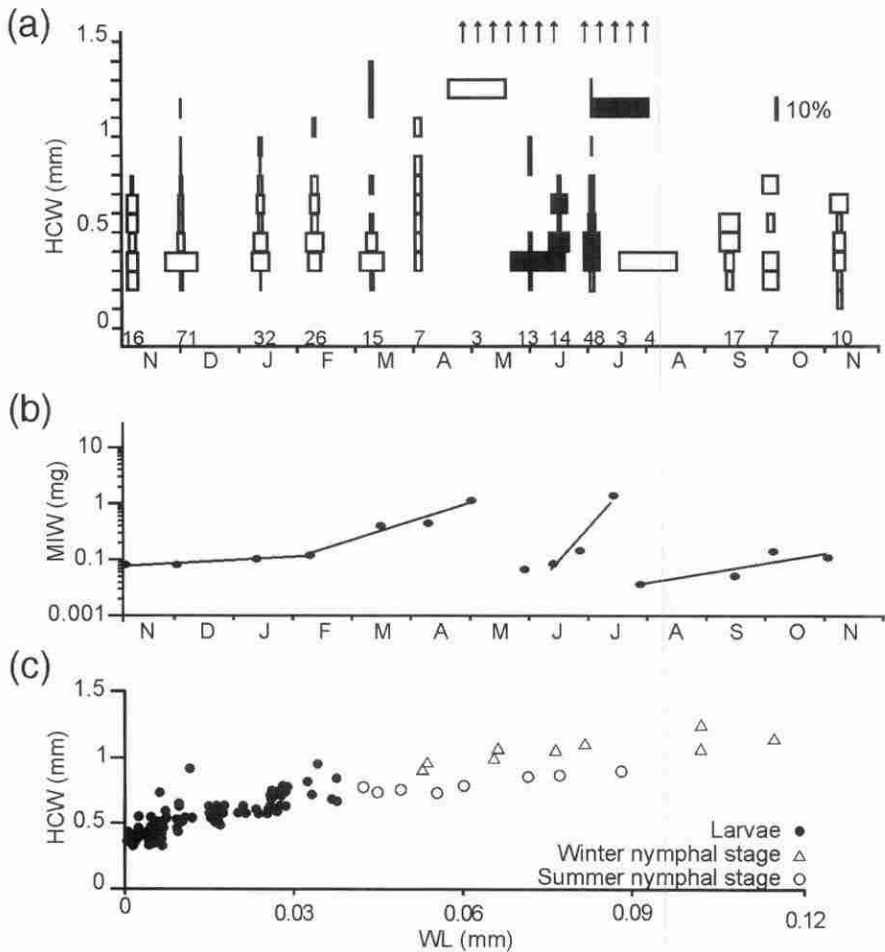

Figure 4.   Life history and growth of *Cloeon simile*. (a–c) See legend of Fig. 3.

smaller (Fig. 4c). The life cycle of *Cloeon simile* was similar to previous studies (Macan, 1979; Grimeland, 1966; Landa, 1968; Brittain, 1974). In addition, this study provided the first detailed quantitative accounts of its population dynamics. The annual production of *C. simile* was 2.05 g dry weight m^{-2} $year^{-1}$, and the *P/B* ratio was 11.21, i.e. the highest values reported for *Cloeon* species (Table 1).

Caenis luctuosa and *Cloeon simile* coexisted in the Sauvage pond. Both species were bivoltine with similar life histories, but slight temporal (summer generations) and spatial (*Cloeon* nymphs in bryophytes) segregation, and differences in the size of coexisting nymphs may have reduced any interspecific competition for food and habitat resources. Many *Caenis* and *Cloeon* species show large variations in life history patterns (Clifford, 1982; Elliott et al., 1988), from univoltine patterns in cold mountain or plains streams (MacFarlane & Waters, 1982; Zelinka, 1984; González et al., 2001) to bivoltine in warmer streams or ponds (Christman & Voshell, 1992; Oertli, 1993), and even multivoltine in semiarid areas (Perán et al., 1999). Such spatial differences are believed to be the consequence of differences in water temperature among aquatic ecosystems. Temperature is indeed the major ecological factor affecting the seasonality and development of mayflies (Vannote & Sweeney, 1980; Ward & Stanford, 1982; Sweeney et al., 1986; Newbold et al., 1994) and influences ephemeropteran densities through growth (Céréghino & Lavandier, 1998), adult size, and fecundity (Kondratieff & Voshell, 1981; Rader & Ward, 1990; Giberson & Rosenberg, 1992; Pritchard & Zloty, 1994). Although the growth patterns of a few mayflies were not significantly correlated with water temperature (e.g. *Rhithrogena hybrida* Eaton, see Breitenmoser-Würsten & Sartori, 1995), the growth of most Ephemeroptera species was reported to be temperature dependent (summarized in Brittain, 1990). In our study, we noticed that increased growth of the winter generations seemed to match with the rise in water temperature in spring (March, see fig. 1), and that the warmest period (summer) corresponded to the hatching and rapid development of a short summer generation in both species. Nevertheless, the relationship between growth rates (K) and mean water temperature (T) for each species was not statistically significant, although linear relationships were suggested by Fig. 5. Unfortunately, studies of population dynamics of these species are much too
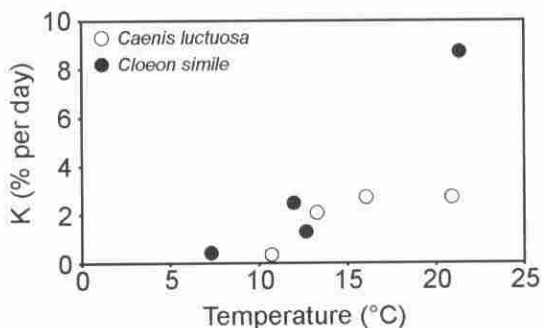

Figure 5. Relationship between growth rates (K) of the two species and mean water temperature.

scarce and/or limited to the description of the life cycle phenology, whereas some authors did not conduct continuous recording of water temperature at their study sites (González et al., 2001) — this lack of information thus prevents us from drawing conclusions on the relationships of growth rates to temperature in these species.

This study and similar work emphasise the need for further quantitative accounts of the population dynamics (including life cycle patterns, growth rates, production estimates and P/B ratio) of species with flexible life histories, with detailed reference to environmental conditions. Such information is valuable to ecologists particularly for secondary production studies.

Acknowledgements

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