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Life-cycle phenology of some aquatic insects: implications for pond conservation

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ABSTRACT

1. Life-cycles and growth patterns were determined for 21 dominant aquatic insect species in small permanent ponds in an arid, karstic region (SW France, site fr7300909 of the Natura 2000 conservation network). The species studied are widely distributed throughout Europe, but some life-cycle patterns are reported here for the first time.

2. The life-history patterns of the 21 species can be divided into five main types: (i) a semivoltine cycle spreading over 2 years; (ii) slow univoltine cycles; (iii) fast univoltine cycles; (iv) multivoltine life-cycles with a long winter generation and two or three summer generations per year; and (v) bivoltine life-cycles with two fast generations per year. Growth was either exponential over the whole developmental period for a given cohort, or divided into two or three successive periods during each of which the growth rate was fairly constant.

3. Biodiversity estimates strongly depend on the temporal and spatial scale over which observations are made. Ponds thus provide useful models to show how life-history patterns enable many temporally segregated populations to utilize small ecosystems. Conservation frameworks should therefore carefully consider the time-frame needed to survey ponds, as many species with fast cycles could be overlooked. The spatial scale needed to manage threatened habitats and thus preserve pond networks must be broadened, rather than attempting to target individual water bodies for particular management actions.

KEY WORDS: aquatic insects; wetlands; ponds; life-history; growth; temporal niche segregation; temperature; conservation

INTRODUCTION

The diversity of habitat types within wetlands allows them to be colonized by a wide range of specialist and generalist species (Masing *et al*., 2000). Wetlands are thus often considered as 'hot spots' of biodiversity within a region or a landscape (Gopal *et al*., 2001; Williams *et al*., 2004). However, wetlands and the biodiversity they support are threatened by human activity (e.g. agriculture, industry, urban development),

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though these ecosystems have significant ecological functions (Dugan, 1990) and recognized social and economic uses (Chapman *et al*., 2001). During the 20th century, wetland losses reached 40–90% in a number of north-western European countries (Hull, 1997), and in the United States more than 50% of these ecosystems have been destroyed by man (Tiner, 1984; Williams, 1990). Due to such large-scale habitat loss, many species are also endangered. This threat has prompted specific studies aimed at understanding the dynamics of wetland populations. Such an understanding is expected to help in planning conservation efforts such as the creation or restoration of ecosystems (Biggs *et al*., 1994). Although ponds have only recently started receiving some attention (Oertli, 1995; Hull, 1997; Angélibert *et al*., 2004), it is now well established that their management and conservation is closely linked to an understanding of the biodiversity and ecology of the biota they host (Gee *et al*., 1997; Gaston *et al*., 2005).

Many of the models used to predict the consequences of future conservation strategies require life-history data (Rustigian *et al*., 2003). Therefore, information on the life-cycles of aquatic species is of fundamental importance for virtually all aspects of wetland conservation, including the conservation of ponds. Aquatic insects constitute an important part of animal production within wetlands (Oertli, 1993), and are tightly integrated into the structure and functioning of their habitats (e.g. organic matter processing, nutrient retention, food resources for vertebrates such as amphibians, fish, or birds). In a given area, the spatial and temporal variability of habitat types are key factors influencing the biodiversity of insect communities (Minshall, 1984; Hanquet *et al*., 2004), and are reflected in the ecological strategies and adaptation exhibited by species (Townsend, 1989; Townsend *et al*., 1997). In contrast to the large volume of studies in river ecology, very little research has addressed the population dynamics of pond insects. Most attention has instead been paid to patterns of biodiversity such as spatial variations in species richness (Oertli, 1995), or species diversity *vs*. area relationships (Oertli *et al*., 2002). Information on the life-history of pond insects is generally sparse, and usually available for a few, separately studied, species (e.g., Di Giovanni *et al*., 2000). However, there have been no previous attempts to gather – in a single investigation – detailed life-cycle and growth data on a large number of pond insects that are likely to coexist. Such an investigation would provide an overview of life-history traits and would consequently have significant implications for planning management and/or conservation actions in a particular area.

In this investigation, the life-cycle phenologies, including growth patterns, of 21 aquatic insect species were determined in three small, permanent ponds in the arid, karstic region of the 'Causses du Quercy' (SW France). This area belongs to the Natura 2000 conservation network, and the results are discussed with reference to the implications for broader conservation strategies.

STUDY AREA

Located in south-western France, the 'Causses du Quercy' is a 2156 km^2 limestone plateau. This arid area is affected by Mediterranean, Atlantic, and Continental climates, and this is reflected in its distinctive weather conditions and vegetation cover. The dominant plant species found in the area are *Quercus pubescens* Willd. and *Acer monspessulanum* L., while the moorland vegetation is principally composed of *Juniperus communis* L. The area belongs to the Natura 2000 conservation network, and is identified as site fr7300909. The plateau has no natural surface fresh water; however, it has more than 300 artificial ponds (typically permanent, rectangular in shape, and shallow, with a density of less than one pond per square kilometre). These ponds, bored into the calcareous rock, were created to hold rain water and support agricultural activities, and it is a technique that has been practised since the 12th century. Abandoned during the 1960s, the ponds are progressively filling with sediment and aquatic vegetation. Although they are now at various stages of natural succession, they support an aquatic vegetation community classified for conservation by the European Fauna-Flora-Habitat guideline 92/43/CEE: '22.12X22.44, *oligo-mesotrophic calcareous waters with benthic vegetation of Characea*'. This study was conducted from November 2000 to November 2001 in three such permanent ponds with a rocky substrate (hereafter called 1, 2 and 3). These three ponds are at different stages of natural succession; their main characteristics are shown in Table 1. A thorough study of their physical and chemical features (together with a fauna and flora species list) can be found in Angélibert *et al.* (2004).

METHODS

Sampling

In each pond, samples were collected monthly from November 2000 to February 2001, then every 2 weeks from March to November 2001. Different techniques were used to obtain qualitative samples of aquatic insects within each pond. First, samples were randomly taken in each pond and at each sampling date by intensive sweeping of a hand net (mesh size = 250 μm) through the various habitats for 15–20 min. In order to maximize the number of available individuals on each sampling occasion, additional samples were specifically taken from the various substrate types (Table 1), each requiring a specific sampling technique (Oertli, 1993). Thin layers of mud (< 5 cm) deposited on the calcareous substrate and bryophytes were sampled using an air-lift sampler (Boulton, 1985) (sampling area 186 cm^2, mesh size of the net: 250 μm). Thick layers of mud (> 5 cm) were sampled using a plastic core sampler (sampling area: 28.2 cm^2). Specific cores (40 cm high and 4.4 cm in diameter) were used to sample the submerged section of *Typha* stems. The aerial part of the plant was cut at water level, and the remaining submerged part was quickly enclosed in the core and cut at approximately 35 cm under the surface of the water. *Chara* beds at mid-depth were sampled by rapidly enclosing plants in a plastic box (7.5 × 16 × 11.5 cm). The *Chara* plants were then cut with shears.

Table 1. Main characteristics of the three study ponds (min-max values observed from monthly samples, November 2000–November 2001), and distribution of additional sample units (substrate-specific samples, see text) in each pond (sampling method: A = air-lift sampler, P = plastic box, C = core, see text). After Angélibert *et al.* (2004)

	Pond 1	Pond 2	Pond 3
Elevation a.s.l. (m)	357	350	350
Area (m^2)	175	75	65
Maximum depth (m)	1.60	0.50	0.60
Water temperature (min-max, °C)	0.5–27.2	0.5–29	0.5–31.2
Suspended matter (min-max, mg L^{-1})	0.15–5.46	0.59–10.35	0.5–13.11
NO_2 (min-max, μg L^{-1})	0–27.5	0–108	0–110.67
NO_3 (min-max, μg L^{-1})	7.5–73	12.20–216.67	15–446.25
Total phosphorus (min-max, μg L^{-1})	3.12–30.21	13.55–48.65	31.10–125.77
SiO_2 (min-max, mg L^{-1})	0.24–3.31	0.25–1.9	0.54–6.13
Substrate composition (%):			
Mud	90–95	10–30	5–10
Bryophytes	5–10	—	—
Chara spp.	—	70–90	10–20
Typha latifolia	—	—	60–90
Number of additional sample units per month:			
Mud	4 (A)	3 (C)	2 (C)
Bryophytes	2 (A)	—	—
Chara spp.	—	3 (P)	2 (P)
Typha latifolia Linné	—	—	2 (C)

Invertebrates were preserved in the field in 5% formalin, identified in the laboratory and then preserved in 70% ethanol.

Life-history and growth

Twenty-one species were found in sufficient numbers throughout their developmental period to allow their life histories and growth patterns to be studied. All larvae were divided into size categories (0.1 mm) based either on head capsule width or tibia length of the third leg. Size–frequency plots for life-cycle determination were based on direct identification of larval instars (four species of Heteroptera, seven Coleoptera, five Diptera), or on head or tibia measurements when larval instars could not be easily identified (one species of Ephemeroptera, four Odonata).

Sets of larvae (at least 10 individuals) from different size categories were dried at 60°C for 24 h and then weighed. Larval mean individual dry weights (W, mg) were derived from linear regressions ($\ln W = a + bL$ with 95% C.L.) between the natural log of weight ($\ln W$) and tibia length or head capsule width. Mean individual dry weights of cohorts 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 (see, for example, Figure 8).

RESULTS

Life-history patterns

The life-history patterns of the 21 study species (Figures 1–7) can be divided into five main types. (1) The semivoltine life-cycle of *Anax imperator* began in summer (June–September). It lasted 2 years and ended in late spring (June). There was a large range of larval sizes throughout the year, with two overlapping generations. (2) Five species showed slow cycles with one generation per year. The eggs began to hatch in the spring (*Coenagrion scitulum*, *Libellula depressa*, *Agabus nitidus*, *Haliplus lineatocollis*) or late summer (*Odontomyia ornata*), and growth occurred over a long period (9–12 months) before spring or early summer emergences. (3) Ten species exhibited fast univoltine cycles (one generation per year), with hatching periods in late winter (*Hygrotus inaequalis*, *Acilius sulcatus*), spring (*Chalcolestes viridis*, *Corixa punctata*, *Plea leachi*, *Hygrobia hermanni*, *Phaenobezzia* sp.), or early summer (*Haliplus mucronatus*, *Noterus clavicornis*, *Stratiomys potamida*) with a short growth period (2–4 months), and were adult by spring, summer, or autumn. (4) Three species were multivoltine (two or three generations per year) with a long winter generation (September to May) and one (*Culicoides* sp., *Dicrotendipes tritomus*) or two (*Cloeon dipterum*) short summer generations (from July to August). It should be noted that two additional mayflies, *Cloeon simile* and *Caenis luctuosa*, occurred in pond 1 (but not in ponds 2 and 3). Their life-cycle patterns were previously described in Cayrou and Céréghino (2003): both species had a long winter and a short summer generation. (5) Two species were clearly bivoltine, with two short generations per year, i.e., in spring and summer (*Naucoris maculatus*), or both in spring (*Notonecta maculata*).

Growth

A simple regression ($\ln W = a + bL$) provided the best means for measuring the relationship between dry weight (W) and head width or tibia length (L). Table 2 presents values for constants a and b ($\pm$ 95% CL) obtained for the 21 species studied. The 'r' values ranged from 0.82 to 0.99, and were significant for each species ($p < 0.05$ or $p < 0.01$).

Growth was exponential either over the whole developmental period for a given cohort, or over two or three successive periods during which the growth rate was fairly constant. During these periods, there was a

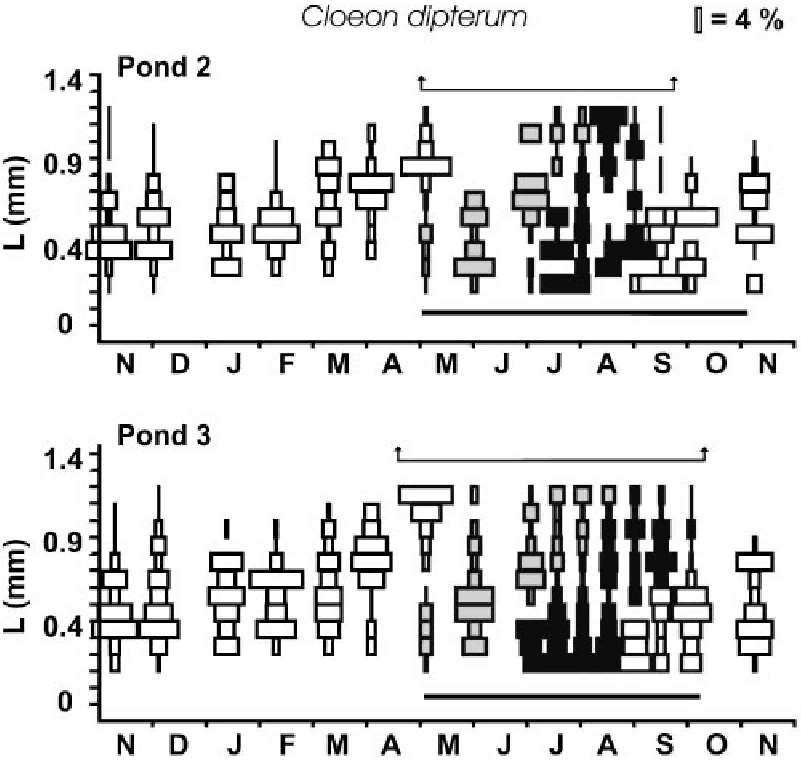

Figure 1. Life-history of *Cloeon dipterum* in ponds 2 and 3. Frequency distribution of head capsule width (*L*, mm) at each sampling date (November 2000–November 2001). The summer generations are represented in grey and black. The solid line at the bottom of the graphs represent the hatching period, arrows on the top of the graph indicate the emergence period.

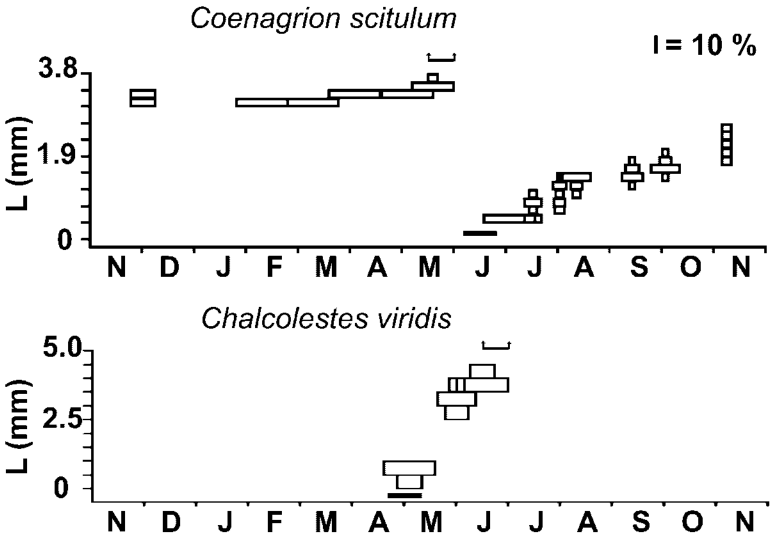

Figure 2. Life-history of *Coenagrion scitulum* and *Chalcolestes viridis* in pond 2. Frequency distribution of head capsule width (*L*, mm) at each sampling date (November 2000–November 2001). See caption to Figure 1.

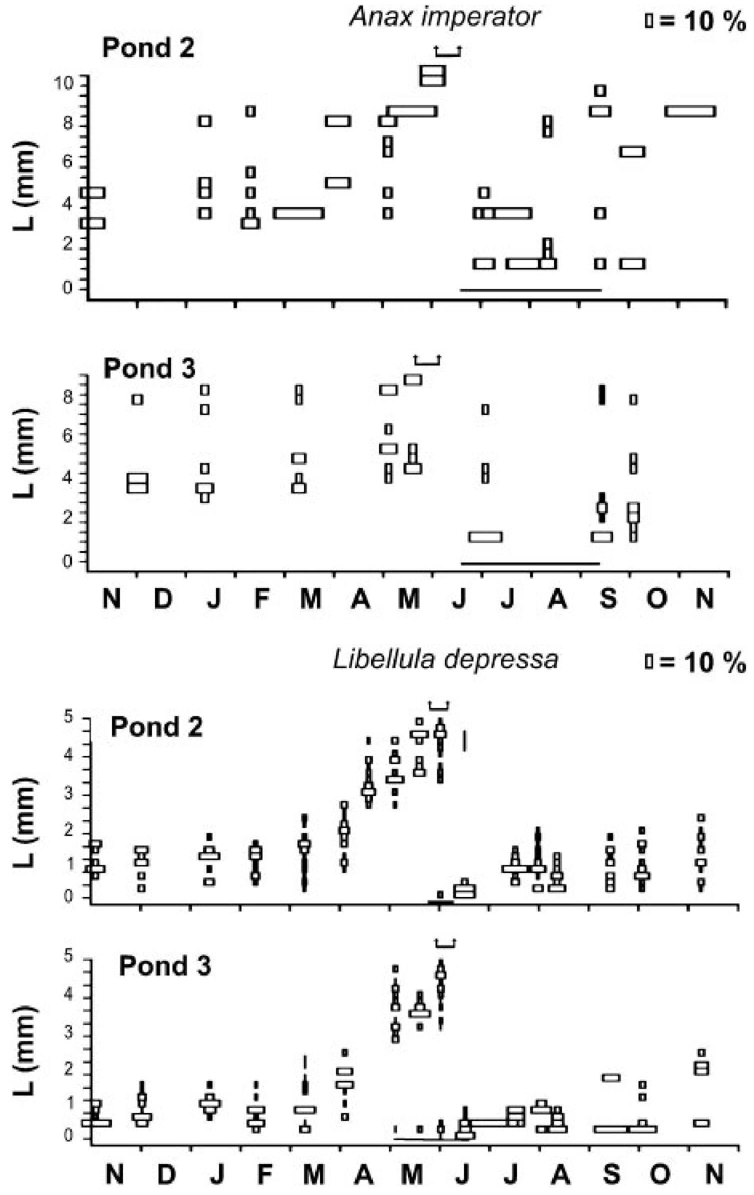

Figure 3. Life-history of *Anax imperator* and *Libellula depressa* in ponds 2 and 3. Frequency distribution of tibia length (*A. imperator*) or head capsule width (*L. depressa*) (*L*, mm) at each sampling date (November 2000–November 2001). See caption to Figure 1.

linear relationship between the logarithm of the mean individual dry weight of the larvae and time. Three cohort growth pattern types could be perceived (Figure 8): (I) growth occurred mainly in autumn and spring; it was low in winter; (II) growth was higher in summer and autumn than in winter and spring; and (III) all of the growth occurred continuously over 2–4 months in spring or summer.

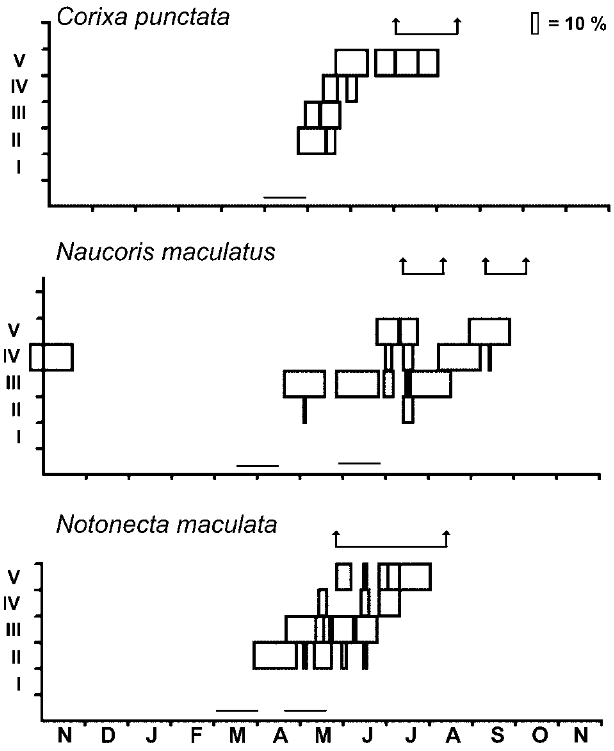

Figure 4. Life-history of *Corixa punctata*, *Naucoris maculatus*, and *Notonecta maculata* in pond 2. Frequency distribution of the various larval instars (I–III) at each sampling date (November 2000–November 2001). See caption to Figure 1.

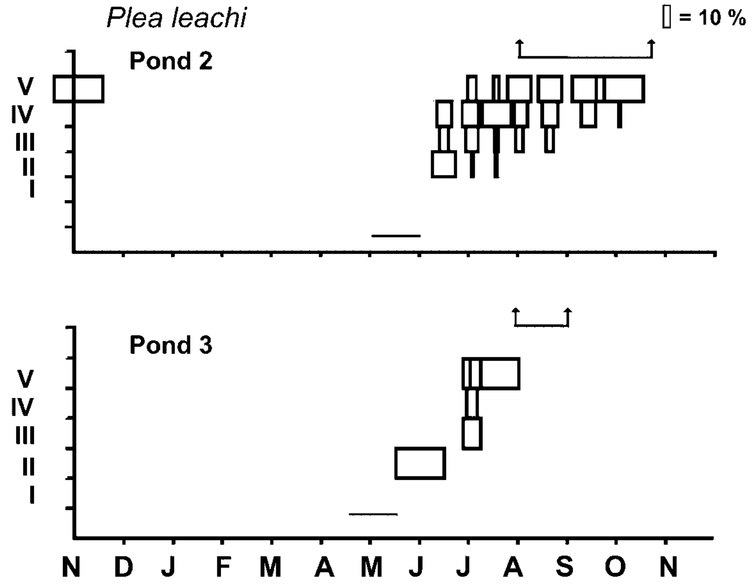

Figure 5. Life-history of *Plea leachi* in ponds 2 and 3. Frequency distribution of the various larval instars (I–V) at each sampling date (November 2000–November 2001). See caption to Figure 1.

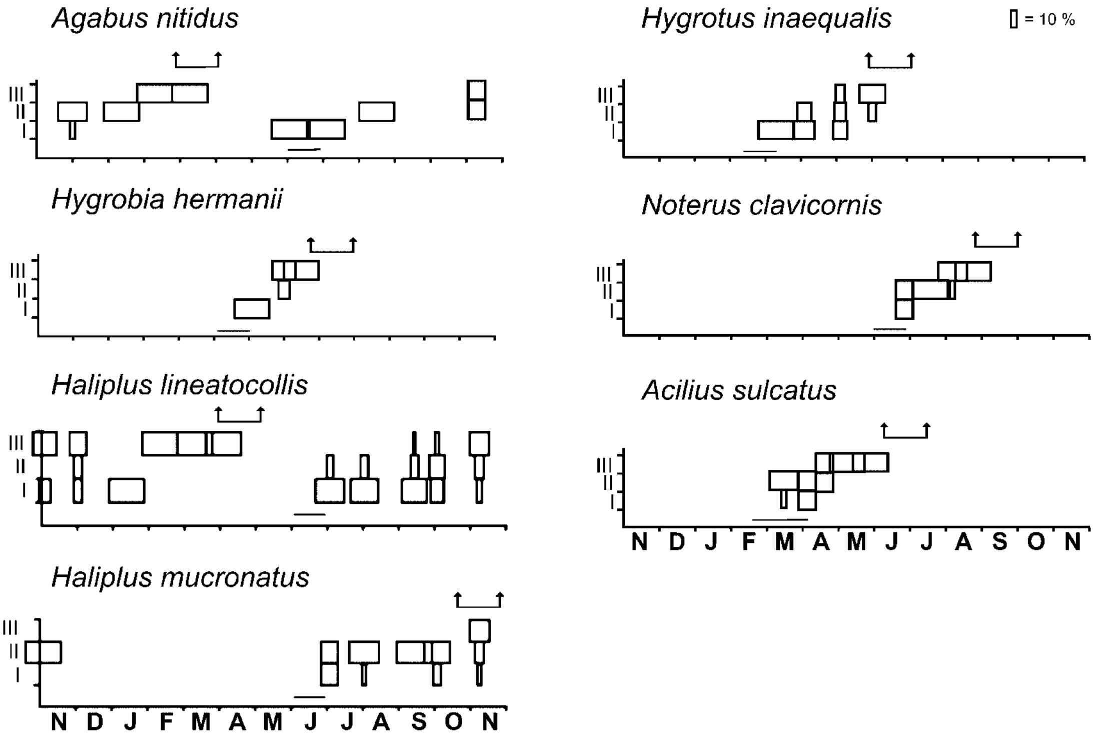

Figure 6. Life-history of Coleoptera species in pond 2. Frequency distribution of the various larval instars (I–III) at each sampling date (November 2000–November 2001). See caption to Figure 1.

DISCUSSION

Compared with previous reports, some species seemed to exhibit flexible life histories. *Cloeon dipterum* occurs throughout much of Europe, and most authors have described univoltine and bivoltine (with a short summer generation) life-cycles (Clifford, 1982), whereas three generations per year were recorded in ponds 2 and 3 (see also Elliott *et al.*, 1988). *Libellula depressa* was clearly univoltine in ponds 2 and 3. However, Di Giovanni *et al.* (2000) noted that *Libellula depressa* had a 2-yr life-cycle, although some more rapidly growing individuals were able to emerge after 1 yr. The data in the present study suggested that *Anax imperator* had a 2-yr life-cycle. However, in colder regions (e.g. Germany, United Kingdom), *A. imperator* shows larval cycles extending either over 1 or 2 yr (Corbet, 1955; Sternberg and Buchwald, 2000), even at a given locality (which remains likely in our study area). *Corixa punctata* is mostly univoltine, but a second generation was observed by Papáček and Bohoněk (1989). According to Svensson *et al.* (2000), *Notonecta maculata* has one generation per year in Sweden, with adult emergence in August (compared with two generations per year and emergence from May to July in this study). *Acilius sulcatus* grew from February to June in pond 2 (this study), but from May to June in Wisconsin, USA (Hilsenhoff, 1993). Finally, previously undescribed life-cycle and growth patterns were detailed for the following species: *Naucoris maculatus*, *Haliplus lineatocollis*, *Haliplus mucronatus*, *Hygrotus inaequalis*, *Noterus clavicornis*, *Odontomyia ornata*, *Stratiomys potamida*, *Dicrotendipes tritomus* – thus contributing further to an understanding of the population dynamics of wetland insects.

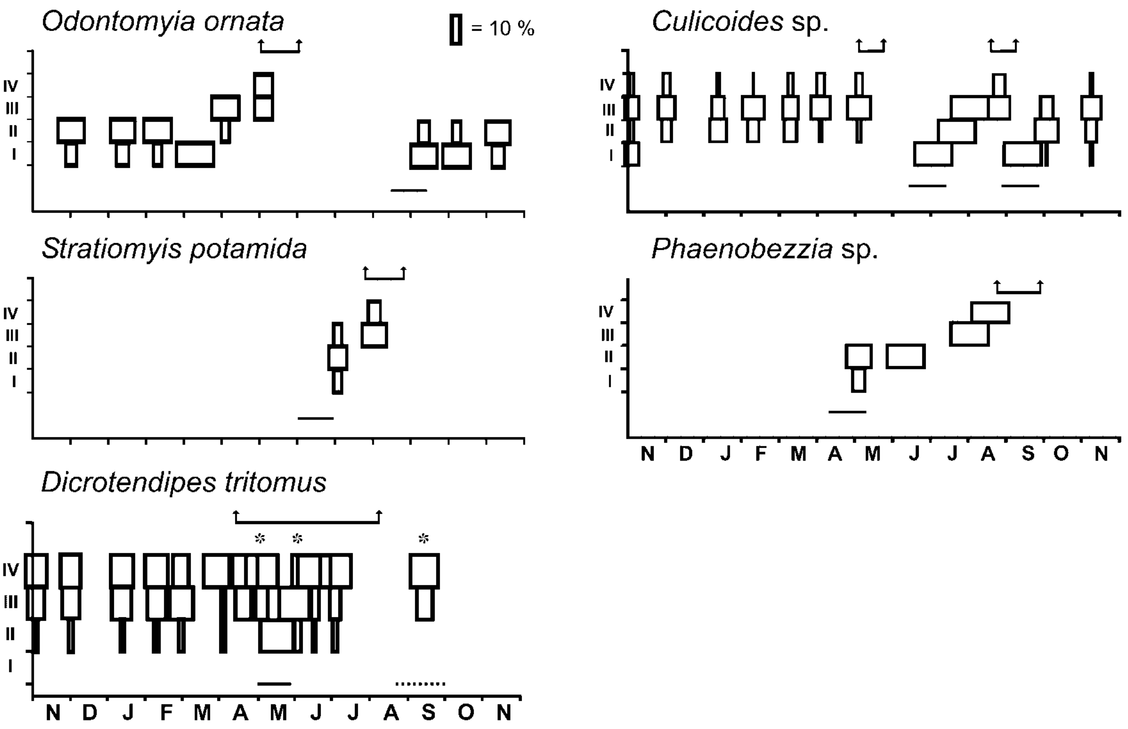

Figure 7. Life-history of Diptera species in pond 1 (*Dicrotendipes tritomus*) and 2 (other species). Frequency distribution of the various larval instars (I–IV) at each sampling date (November 2000–November 2001). See caption to Figure 1.

As wetland habitats, ponds have only recently started receiving some attention, and most of the current research still focuses on assessing the biodiversity they support (Briers and Biggs, 2003; Angélibert *et al.*, 2004) or are likely to host (Davies *et al.*, 2004; Gaston *et al.*, 2005). Among wetland inhabitants, aquatic insects have the potential to be relevant ecological indicators. Indeed, they are already widely used to reveal short- and long-term environmental changes in both running and still waters (Céréghino *et al.*, 2003; Verneaux *et al.*, 2004), most notably through the strong influence of human disturbance on the species richness of aquatic insects (Rosenberg and Resh, 1993). Such disturbances usually lead to losses of taxa (Compin and Céréghino, 2003). However, in a given area, biodiversity estimates (e.g. species richness, evenness, etc.) strongly depend on the spatial scale (type of habitat) and temporal scale (week, month, or season) over which observations are made. Water temperature is usually considered to be the major abiotic factor affecting the life-cycle phenology of aquatic invertebrates (Vannote and Sweeney, 1980; Sweeney *et al.*, 1986), influencing the seasonality and development patterns of aquatic insects through growth, adult size, and fecundity (Lavandier, 1988; Giberson and Rosenberg, 1992; Pritchard and Zloty, 1994). This study suggested that the increased growth of those species with long generations (e.g., *Cloeon dipterum*) seemed to correspond to the rise in water temperature in spring (March), and that the warmest period (spring–summer) favoured the hatching and rapid development of short summer generations in most species. Whatever the biotic and/or abiotic factors controlling the life-cycle phenologies, and, subsequently, the temporal patterns of aquatic insect communities within ponds, this study clearly emphasizes the temporal dimension of biodiversity in small bodies of water. The seasonality of wetland-dependent insects in particular may influence the biodiversity ponds may support. By overlapping the size–frequency plots of many coexisting species, it becomes clear that future management and/or conservation frameworks should

Table 2. Values for the constants a and b, with 95% confidence intervals, obtained from equation $\ln W = a + bL$ (see text). W= dry weight (mg), L= head width (*) or tibia length of the third leg (**) (mm). All correlation coefficients (r) were significant ($^{a}p<0.05$; $^{b}p<0.01$)

Species	a	b	r
Cloeon dipterum (Linnaeus)*	-5.37 ± 0.81	4.84 ± 0.45	0.97^{b}
Coenagrion scitulum (Rambur)*	-9.90 ± 1.34	1.44 ± 0.83	0.96^{b}
Chalcolestes viridis (Van der Linden)*	-8.51 ± 0.71	0.76 ± 0.29	0.96^{b}
Anax imperator Leach**	-8.11 ± 0.03	0.79 ± 0.38	0.93^{b}
Libellula depressa Linnaeus*	-9.20 ± 1.03	1.03 ± 0.11	0.97^{b}
Corixa punctata Geoffroy*	-6.66 ± 0.80	0.42 ± 0.06	0.82^{a}
Naucoris maculatus Fabricius*	-9.63 ± 0.40	0.43 ± 0.27	0.87^{a}
Notonecta maculata Fabricius*	-9.77 ± 0.17	1.24 ± 0.15	0.95^{b}
Plea leachi McGregor & Kirkaldi*	-6.66 ± 0.80	3.20 ± 0.74	0.92^{b}
Agabus nitidus (Fonscolombes)*	-13.12 ± 0.02	2.21 ± 0.37	0.95^{b}
Hygrobia hermanni (Fonscolombes)*	-12.70 ± 0.76	1.95 ± 0.64	0.97^{b}
Haliplus lineatocollis (Marsham)*	-12.39 ± 0.80	1.82 ± 0.47	0.92^{b}
Haliplus mucronatus Stephens*	-12.63 ± 0.62	2.10 ± 0.17	0.93^{b}
Hygrotus inaequalis (Foscolombes)*	-12.01 ± 0.92	1.97 ± 0.29	0.89^{a}
Noterus clavicornis (DeGeer)*	-16.21 ± 0.16	3.14 ± 0.44	0.90^{b}
Acilius sulcatus (Linnaeus)*	-15.88 ± 0.68	3.07 ± 0.80	0.96^{b}
Odontomyia ornata (Linnaeus)*	4.46 ± 0.16	0.80 ± 0.09	0.95^{b}
Stratiomys potamida (Meigen)*	4.30 ± 0.49	0.72 ± 0.43	0.93^{b}
Culicoides sp.*	-6.10 ± 0.23	0.41 ± 0.10	0.93^{b}
Phaenobezzia sp.*	-7.02 ± 0.05	0.38 ± 0.03	0.96^{b}
Dicrotendipes tritomus (Kieffer)*	-4.65 ± 0.63	0.53 ± 0.61	0.99^{b}

pay attention to the time-frame needed to survey ponds, as many species (chiefly those with short cycles and/or egg-diapause periods) could be overlooked. Similar recommendations are already part of protocols for sampling and assessment of both riverine and wetland habitats, e.g. RIVPACS sampling for rivers (Wright *et al*., 2000), and UK National Pond Survey methods (Pond Action, 1989).

Life-cycle attributes (e.g., reproduction, hatching and emergence periods) need to be carefully considered when restoring, managing and/or creating new ponds for conservation purposes (Ripley *et al*., 2004). Owing to the difficulty of pond creation in the study area (a limestone plateau), dredging the abandoned ponds is the only option for wetland restoration. Therefore, environmental managers should minimize the likelihood that dredging will eliminate populations (e.g., during the main growth or hatching periods). Theoretically, the acceptable period for dredging would be between adult emergence and egg-laying, i.e. during the flight and reproduction period. Given that most populations show a temporal sequence of species replacements (e.g. certain Coleoptera, Heteroptera), or have delayed life-cycle events (certain Odonata), defining an optimal period for dredging seems to be an impossible task. As an alternative, a plan of pond management should be envisaged over a large spatial scale to maintain the heterogeneity of pond networks in the area. Such a plan would imply promoting the conservation of all ponds, regardless of their successional stages. This is especially important when the density of ponds in the network is very sparse. Indeed, a recent study in the same area (Angélibert and Giani, 2003) on the dispersal capability of Odonata showed that dispersal phenomena were low because of the distance separating ponds. Thus, after dredging, species adapted to late succession ponds have little hope of finding suitable conditions in other ponds to ensure their development.

The insects studied are widely distributed throughout Europe (see the *Limnofauna Europaea* (Illies, 1978)) and are regarded as having a low conservation priority. However, they depend on wetlands and

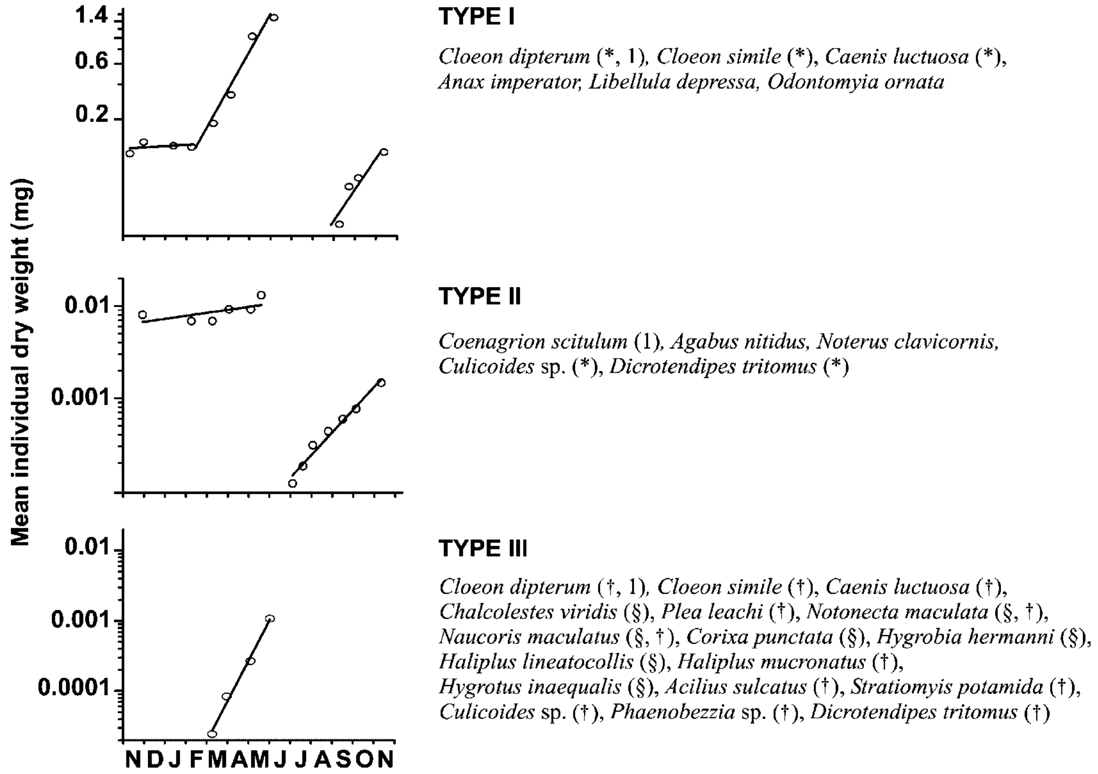

Figure 8. Cohort growth patterns (I–III, see text) for the study species. (*) = winter generation, (§) = spring generation, (†) = summer generation. 1 = example shown. *Cloeon simile* and *Caenis luctuosa* (pond 1): after Cayrou and Céréghino (2003).

ponds, habitats which are becoming increasingly threatened. Broader conservation strategies should therefore ensure that such currently common organisms do not become the endangered species of the future (Rustigian *et al.*, 2003). Ponds also provide useful models for studying how life-history patterns enable many populations to utilize small ecosystems, temporal segregation and/or differences in the size of coexisting nymphs certainly reducing interspecific competition for food and habitat resources (Svensson *et al.*, 2000; Cayrou and Céréghino, 2003). Subsequently, interesting ideas and/or alternative strategies can be derived for conservation planning. Because the growth of most species is markedly seasonal and many species are temporally segregated, the spatial scale needed to manage threatened habitats must be enlarged. Thus, when possible, pond networks should primarily be preserved rather than attempting to target some bodies of water for particular management actions.

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