

**LIFE HISTORY PATTERNS OF
ONYCHOGOMPHUS UNCATUS (CHARPENTIER)
(ANISOPTERA: GOMPHIDAE)***

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Received March 5, 1997 / Revised and Accepted June 10, 1997

The results of a 4-yr study are reported. Data from Surber-samples of 3 running waters in southern France were compared with results from field enclosure experiments. Egg development lasted about one month under field conditions and two weeks at 25°C in the laboratory. *O. uncatus* has usually but not strictly 13 larval instars and a 3-yr life cycle. Each year emergence started in early June. The emergence curve was typical of a summer sp. Several aspects of seasonal regulation are discussed. The monitoring of population structure indicated a high mortality of final instar larvae (up to 99%) during winter. This mortality differed between the sample sites of one of the running waters. These differences depend on prey availability and on larval density. A field enclosure experiment revealed density dependence of larval size and growth.

INTRODUCTION

Studies on the life-cycle of dragonflies are numerous and the basic principles of larval development are well known (e.g. CORBET, 1962; 1980; NORLING, 1984a). CORBET (1954) divided the dragonflies of temperate regions in two groups, spring and summer species, according to their seasonal regulation. The main factors influencing seasonal regulation and larval growth are temperature and photoperiod (CORBET, 1955; 1956; 1958; LUTZ, 1974a; 1974b; INGRAM, 1975; NORLING, 1984a). Larval density and the availability and type of food also affect growth (HASSAN, 1976; LAWTON et al., 1980; PICKUP et al., 1984; BANKS & THOMPSON, 1987).

* Dedicated to the memory of the late Peter MILLER, who joined us at the Canal de Vergière for a while.

In this paper we want to present results of a four year study on the life cycle of *Onychogomphus uncatus*. In particular we want to focus on egg development, duration of the life cycle and the effects of density and food availability on larval growth and population structure. Life cycle studies have been carried out for several gomphid species. Most of these deal with egg and larval development (POPOWA, 1923; HAWKING & NEW, 1995), larval size frequency distribution in one habitat (HUGGINS & DUBOIS, 1982; FOLSOM & MANUEL, 1983; DUDGEON, 1989; HAWKING & NEW, 1996) or emergence patterns (e.g. TESTARD, 1975; MÜLLER, 1993a). As far as we know there are few long-term investigations combining these parameters (KURATA, 1971; AOKI, 1994; MÜLLER, 1995). In *O. uncatus* only data on seasonal regulation based on emergence studies have been published (FERRERAS-ROMERO, 1994; FERRERAS-ROMERO & CORBET, 1995; SUHLING, 1995).

Onychogomphus uncatus is a western Mediterranean dragonfly. According to SUHLING & MÜLLER (1996) its distribution stretches from northwestern Italy over the southern and western parts of France and the Iberian peninsula to North Africa. In central Europe an isolated population exists at the Rhine near Schaffhausen. *O. uncatus* is generally found in shady mountain streams in a typical community with *Boyeria irene* und *Cordulegaster boltonii* (JARRY & VIDAL, 1960; FERRERAS-ROMERO, 1984). In southern France it also lives in larger rivers and irrigation canals (SUHLING & MÜLLER, 1996). The larvae are able to burrow in different types of bottom substrata but prefer gravelly sand (SUHLING, 1996).

STUDY AREA

The study was carried out at three running waters in southern France: the Canal de Vergières (CdV), the Canal Centre Crau (CCC), and the Gaudre d'Aureille (GdA). The GdA is a small mountain stream in the Alpilles, a mountain range ca 15 km NE of the city of Arles (43°34' N, 4°50' E). The CdV and the CCC are situated in the stony steppe of the Crau, 25 km SE of Arles. The CdV borders the nature reserve "Peau de Meau" to the NW. The CCC is situated 2 km SE of the CdV.

The running waters differed in annual variation of temperature and water level (SUHLING, 1994). Whereas the CCC usually dries up numerous times for periods of 3 to 4 days in March and April the CdV does not. The water level of the GdA was usually between 10 and 30 cm but increased to 200 cm during floods in the rainy season. The bed of the canals consisted of a concrete like conglomerate partly covered by other sediments as mud, sand, gravel or boulder. The vegetation differed between the running waters. In the CdV the emergent vegetation consisted of several species of *Juncus* and *Scirpus*, *Mentha aquatica*, and *Berula erecta*, but in the CCC *Polygonum amphibium* was dominant. In both canals the stream channel was partly overgrown by submerged vegetation, particularly by Characeae and *Potamogeton coloratus* (CdV) and by *Groenlandia densa* and *Myriophyllum* sp. (CCC). The GdA was totally shaded and there were no aquatic plants. Whereas at our main study site, the CdV, as well as at the CCC the larvae could be found in high population densities, density was low in the GdA (SCHRIDDE & SUHLING, 1994; SUHLING, 1994). Detailed descriptions of all study sites are given in REHFELDT et al. (1991) and SUHLING, (1994).

METHODS

REARING OF LARVAE FROM EGGS. – In order to study the development of *O. uncatatus* in the field, eggs were exposed in the CdV in cages. A total of 460 eggs were obtained by holding a plankton net in the water under an ovipositing female. No other common method for obtaining eggs from dragonflies, like “hand held oviposition” succeeded. The development of 215 of these eggs was observed in the CdV, with the remaining 245 reared in the laboratory.

For the examination of egg- and larval development in the field, we used plastic box frames (diameter: 11.6 cm, height: 6.7 cm) covered with gauze (0.5 mm mesh size). They were attached to the stream bottom with pieces of wire mesh fixed to both sides of the box and weighted down in the water with flat stones. 245 eggs were distributed evenly into each of three cages. Monitoring of egg development was started one week after oviposition. Eggs were examined using a binocular microscope at 50 X magnification and measured to an accuracy of 0.02 mm. For larvae bigger than 0.6 mm headwidth, a magnification of 20 X was used and measurements made to the nearest 0.05 mm. Measurements were taken of headwidth above the eyes and length of the abdomen from the first segment to the end of the anal pyramid. Larvae in the cages were not fed additionally. In several experiments it was confirmed that prey availability as well as current velocity, temperature, and oxygen content were within the natural range (SCHÜTTE, 1992).

DETERMINATION OF INSTAR NUMBER AND SIZE. – To determine larval instars we used headwidth frequency histograms of those larvae caught in the Canal de Vergière. For each instar a standard distribution of this measure around a mean headwidth should be expected. We separated the instars at those headwidths where the lowest number of larvae were found (cf. BENKE, 1970). For this we used only larvae from one sample site (2) because the headwidths differed between the sample sites (see below). For the early instars we used the results earned from rearing eggs and young larvae in the field at the same site. For those larvae caught in the field we used the terms for instars according to Lutz (1968a): F = ultimate instar, F-1 = penultimate instar, etc.

MONITORING OF POPULATION DEVELOPMENT IN THE FIELD. – In April, 1990, we established three sample sites in the CdV (sample sites 1, 2, 4). In April, 1991, two additional sites (3 and 5) were selected. The sample sites had a length of 25 m each and were distributed along a stretch of 2.6 km. The most downstream was site 1, followed by 2 and so on. Sites 2 and 4 which shall be dealt with in detail (see below) were 500 m apart. At these regular sample sites we caught dragonfly larvae and other aquatic macroinvertebrates using a modified SURBER-sampler (area: 0.325 x 0.325 m). For detailed information on the method see SCHRIDDE & SUHLING (1994). In 1990 the samples were taken in the first week of April, in the second week of July and the last week of October. In 1991 we started in April and from this date we took samples at least every three months until April 1993. All sample data are given in SUHLING (1994). The number of samples taken on each date is given in Figure 2. Using the number of larvae caught per sample we calculated the larval density per m². At the two other study sites, the CCC and the GdA, we did not sample regularly and used a hand net instead of a SURBER-sampler. Because of this we did not calculate larval density for these sites. On all larvae we took in situ measurements of headwidth, abdominal length, and in 1990 the length of the left hind femur. For measuring small larvae we used the method described above. Those larvae which were larger than 1 mm headwidth we measured to the nearest 0.01 mm using a dial calliper. After measuring, the larvae were released at the place they had been caught.

To obtain information about the availability of prey organisms we counted all macroinvertebrates and fish caught with the SURBER-sampler and calculated the accumulated density per m². Prey availability was calculated by dividing the mean density of *O. uncatatus* larvae by the mean density of prey organisms per sample site. In feeding experiments we found that larval *O. uncatatus* feed on nearly any prey they can handle: macroinvertebrates, planktonic species, and fry (SUHLING, 1994). Only some case-bearing caddis larvae (Trichoptera) were not considered as prey because *O. uncatatus* has a low ability to extract them from their cases.

MONITORING OF EMERGENCE. – Annual emergence was monitored in the years 1991 to 1993 beginning in the last decade of May and continued until no additional exuviae were found during two consecutive visits. Collections were made at sample sites 2 and 4 at the CdV. A standardized area of the banks and emergent structures in the stream channel were searched for exuviae between 16.00 and 17.00 CET. All exuviae found were collected, counted and sexed. The collection sites were inspected daily until the first exuviae were found. Later collections were made at intervals of 4 to 5 days. Because of the very light rainfall and no detectable changes in water level during the emergence period, we are sure that the number of exuviae that were dislodged before collection was negligible. For the 1992 emergence curve we collected only at site 2 and used additional data from KLEEMEYER (1994) who collected exuviae in two day intervals at site 4.

FIELD EXPERIMENT ON DENSITY EFFECTS. – To get information about density effects on larval growth we carried out an enclosure experiment in the CdV. For this we used four cages of wooden frames with gauze (mesh size: 1.3 mm). These cages had different areas: 1.0, 0.25, 0.125 and 0.0625 m². Each cage was stocked with 30 F-2 larvae. The resulting larval densities were 30, 120, 240 and 480 specimens m². To monitor growth larval headwidth was measured at the beginning of the experiment in October 1992, and in January, April and June 1993.

RESULTS

EGG DEVELOPMENT AND HATCHING

The size of the eggs was 0.54 x 0.40 mm ± 0.01 mm (SD in both measures, n=25, measured 2h after oviposition). In the laboratory we observed that at 25°C, after one to several hours the jelly around the micropylar projection stuck tight to anything it touched. In the field eyes and limbs of the embryos could first be seen 24 days after oviposition. The first larva hatched after 27 days, the last one on the 33rd day. Out of 215 eggs we obtained only 50 larvae (23.3%), the other ones were not

Table I

Larval instars of *Onychogomphus uncatatus*: mean head width and abdominal length per instar and growth ratios between the instars based on measures from larvae reared in field enclosures and of those caught in the Canal de Vergière in 1992. – [For calculating growth ratio the headwidth was used]

Instar	(N)	Headwidth (mm) ±SD	Abdominal length (mm) ±SD	Growth ratio
I	(50)	0.39 ± 0.01	0.79 ± 0.04	
II	(69)	0.48 ± 0.01	1.00 ± 0.08	1.22
III	(36)	0.60 ± 0.02	1.37 ± 0.12	1.25
IV	(50)	0.72 ± 0.04	1.68 ± 0.12	1.20
V	(71)	0.87 ± 0.06	1.97 ± 0.21	1.21
VI	(164)	1.10 ± 0.07	2.48 ± 0.36	1.25
VII	(348)	1.35 ± 0.09	3.06 ± 0.36	1.23
VIII	(465)	1.71 ± 0.11	3.92 ± 0.42	1.26
IX	(415)	2.17 ± 0.14	5.04 ± 0.50	1.27
X	(303)	2.79 ± 0.19	6.41 ± 0.64	1.29
XI	(230)	3.53 ± 0.17	8.12 ± 0.64	1.27
XII	(149)	4.36 ± 0.16	10.15 ± 0.66	1.23
XIII	(91)	5.46 ± 0.12	12.29 ± 0.75	1.26

found again. Under laboratory conditions, 243 larvae hatched from 245 eggs (99.2%). On the 12th day eyes and limbs could be seen in all larvae. One day later the first hatch was recorded. On the 15th day after oviposition 99.9% of the larvae had hatched. The last hatched on the 16th day. Hatching itself was observed three times. The larva left the egg through a longitudinal slit. While the last abdominal segments were still caught in the slit, the first moult happened. The resulting skins were very thin and after being cast could not be recognized as exuviae. There was no free prolarva.

LARVAL INSTARS

A complete view of the instars of *O. uncatatus* in the CdV was obtained by combining the results of sampling and rearing experiments (Tab. I). As a rule there were 13 instars. Immediately after hatching the mean headwidth (HW) was 0.40. Headwidth increased stepwise at each moult so that all larvae could be assigned to a certain instar. In the CdV 78% of the larvae had reached the third instar 40 days after hatching, the others were already in the fourth instar (HW: 0.72 ± 0.03 mm, $n=7$). Due to small numbers the fourth instar was the last that could be distinguished by rearing of larvae, but larvae in this instar were also found by means of sampling. They had nearly the same mean size as the reared ones (0.73 mm \pm 0.04 mm, $n=43$).

Mean larval growth ratios between the instars ranged from 1.20 (instar 4) to 1.29 (instar 10). The overall growth ratio was 1.25. Measures taken before and after moults that could be observed revealed that there are also moults within the fixed instar limits and that instars can be omitted (Tab. II). So individual growth ratios ranged at least between 1.41 and 1.07.

STRUCTURE OF THE LARVAL POPULATION IN THE CdV

For the analysis of population development of *O. uncatatus* in the CdV we used a total of 5669 larvae from SURBER samples from all sites. Thus we wanted to avoid errors caused by local effects on larval development. During the investigation most larval instars were present at almost all sites. Those instars combined in category <F-6 in Figure 1 were found throughout the year and were especially abundant between September

Table II

Examples for atypical growth in single larvae of *Onychogomphus uncatatus*, indicating that instars were omitted (A) or moult within the typical limits (B, see Tab. I). Given are the headwidth before and immediately after the moult and the growth ratio

	Headwidth [mm]		Growth ratio
	before moult	after moult	
A	1.35	→ 1.90	1.41
B	1.40	→ 1.50	1.07
B	1.65	→ 1.85	1.12

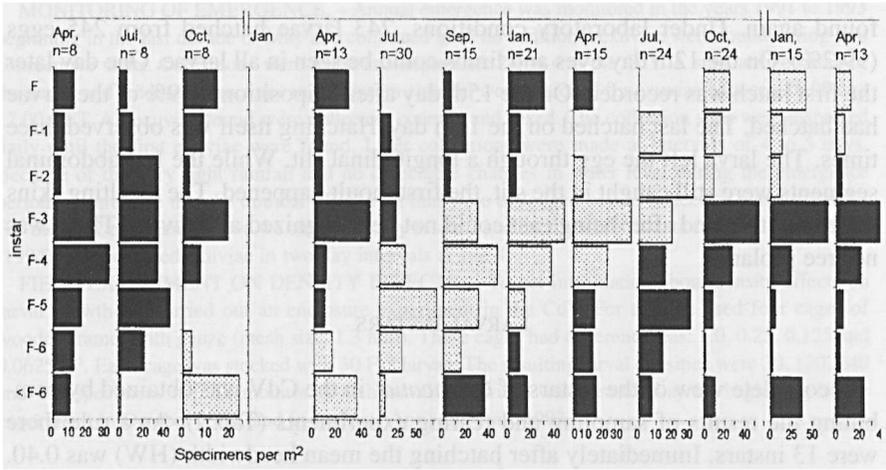


Fig. 1. Instar frequency diagram of *Onychogomphus uncatus* in the Canal de Vergière over a period of three years (density m^{-2} per instar and sample date). The young instar larvae were grouped (< instar F-6). The lightly shaded bars indicate the year class which emerged in 1993.

and early June. However, second instar larvae were only found in small numbers. First instars were not caught at all. Final instar larvae were less abundant during the emergence period from June to August than at any other time of the year.

Except for the summer months June to August we found three more or less clearly defined peaks in the size class distribution of *O. uncatus*. During the winter months we found mainly small larvae (< F-6) and instars F-3 and F. This distribution was found between October and April during the whole investigation with no major shift of the peaks. From May on there was a shift in community composition. In June the number of final instar larvae decreased and there were none left in July. As

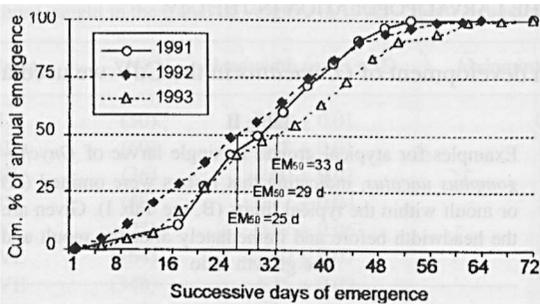


Fig. 2. Three year patterns of annual emergence in *Onychogomphus uncatus* based on counts of exuviae from two stretches of the Canal de Vergière in 1991, 1992, and 1993. Day 1 is the first day on which exuviae were found (1991): 3rd June; - (1992): 5th June; - (1993): 8th June. From this date exuviae were collected in intervals of four days.

a result the distribution curve shows only two peaks at that time.

EMERGENCE

The emergence curve was calculated from the accumulated exuviae of sites 2 and 4. In 1990, without monitoring the whole emergence period, we collected a total of 663 exuviae. In the following years the numbers were 1770 (1991), 1725 (1992), and 739

(1993), respectively. In these years emergence lasted between 64 and 72 days (Fig. 2). In all years emergence started in early June and ended between August 7th and 20th. It took between 25 and 33 days before 50% of the insects had emerged (EM_{50}). In all years the number of males was lower than that of the females. The percentage of males was 43.9 in 1991, 46.5 in 1992 and 42.6 in 1993, respectively.

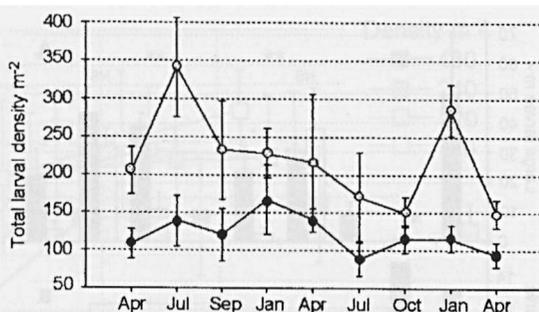


Fig. 3. Total larval density of *Onychogomphus uncatus* at sample site 2 (upper line) and 4 (lower line) in the Canal de Vergière from April 1991, to April 1993, measured in intervals of three months.

LOCAL DIFFERENCES IN POPULATION STRUCTURE AND DENSITY

In the CdV there were considerable differences in community composition and larval density among the sample sites, particularly between sites 2 and 4. At site 2 total larval density was generally higher than it was at site 4 at any time. At the latter it never exceeded 160 larvae per m^2 (Fig. 3). In contrast, the proportion of large larvae was higher at site 4. Here it varied between 20 and 45% of the total population whereas at site 2 it reached a similar amount only in January (20%). Density of penultimate and final instar larvae together was significantly different at the two sites in September / October and April but more or less the same in January (Fig. 4). In January 1992, their density was even higher at 2 than at 4. The numbers of emerged individuals were also significantly higher at site 4 during the investigation (Tab. III).

LARVAL DENSITY AND FOOD AVAILABILITY

Table III
Annual emergence of *Onychogomphus uncatus* at two sample sites at the Canal de Vergière between 1990 and 1993

Year	No. of exuviae at sample site	
	2	4
1990	100	563
1991	350	1418
1992	59	1714
1993	86	653

The high density of *O. uncatus* at site 2 coincided with a low abundance of potential prey organisms. This resulted in a mean prey availability of less than one prey per larva throughout the investigation period. At site 4 prey availability was much higher, particularly in July 1991 when it was almost 40 times higher than at site 2. In 1992 the difference was lower but there was still 6 times as much prey per larva. Regarding all sites (cf. Methods) we found a correlation between the proportion of big lar-

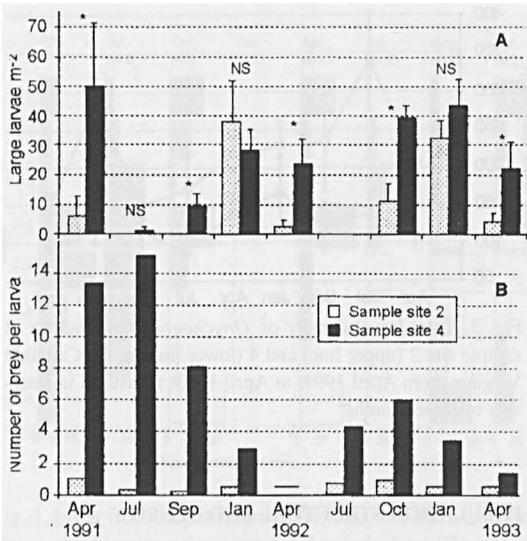


Fig. 4. (A) Abundance of ultimate and penultimate instar larvae of *Onychogomphus uncatatus* at the sample sites 2 and 4 in the Canal de Vergière at different times of the year in 1991, 1992, and 1993. The number of specimen per m² (+ SE), calculated from Surber samples is given. U-test: NS: not significant; * P < 0.05. (B) Prey availability per larva of *O. uncatatus* based on total density (see Fig 3) at the two sample sites. The data were calculated by dividing macroinvertebrate density by the density of *O. uncatatus* per sample site and month.

vae (last two instars) per site and both total larval density and prey availability. It decreased when total density increased (Spearman rank correlation, $r = - 0.825$) and increased with increasing prey availability ($r = 0.891$).

LARVAL SIZE

Between the sites there were also differences in the size of final instar larvae. This was true for the three running waters as well as for the sites within the CdV (Fig. 5). At site 2 mean headwidth was lowest and significantly higher at site 4 with a mean difference of 0.08 mm (t-test, $P < 0.01$). In the GdA and at CdV 1 headwidth was higher by almost 0.2 mm (t-test, $P < 0.01$).

DENSITY EFFECTS IN FIELD EXPERIMENTS

The effects of density on larval size (see above) were confirmed experimentally. In cages with different larval densities exposed in the CdV mean headwidth increased significantly from July to October 1993 (Fig. 6). Almost all surviving larvae had moulted at least once and had reached the F-1 and F instar. In the cage with the highest density only three larvae had reached the final instar whereas in the other cages their number was at least three times as high. During the winter months only larvae in the low density cage showed a slight increase

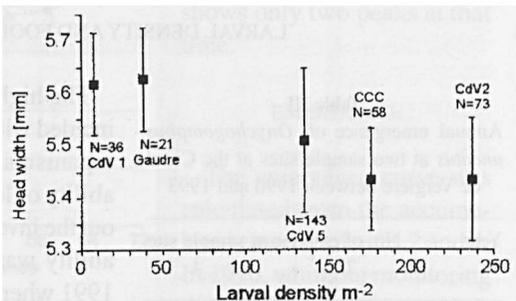


Fig. 5. Effect of larval density on the size of last instar larvae. The mean headwidths (\pm SD) of larvae caught in 1991 and 1992 at three sample sites in the Canal de Vergière, one in the Canal Centre Crau and one in the Gaudre d'Aureille are given.

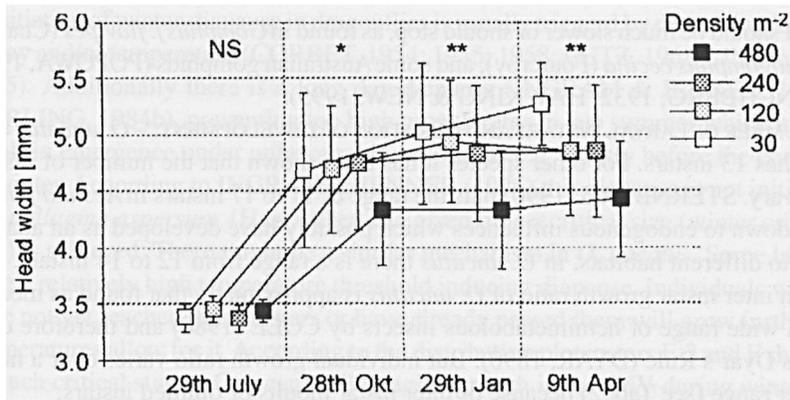


Fig. 6. Influence of larval density on the growth of *Onychogomphus uncatatus* in field enclosures. The development of the average headwidths (\pm SD) of the larvae ($N=30$ per cage) in each of four different sized cages from 29 July 1992, to 9 April 1993 are given.

in headwidth. However, density had no significant influence on the size of the final instar. Though individuals were bigger (HW 5.49 ± 0.09 mm SD) at the lowest density than were those at the other densities (5.38 ± 0.1 mm, 5.40 ± 0.16 mm, and 5.40 ± 0.05 mm) the difference was not significant (ANOVA, $P > 0.05$). Mortality decreased with decreasing initial density in the cage. Between October 1992 and January 1993 25.7% (= 7) of the larvae in the high density cage died and so did 13.8% (= 4), 12.0% (= 3), and 7.4% (= 2), respectively in the other cages (decreasing density).

DISCUSSION

EGG DEVELOPMENT. – The duration of egg development of gomphids has been studied in a number of species (see review in SUHLING & MÜLLER, 1996). The minimum duration previously recorded was in *Asiagomphus pryeri* (Sél.), which needed nine days from oviposition to hatch of the larvae (AOKI, 1994); the maximum duration was 56 days in *Gomphus pulchellus* Sél. (ROBERT, 1959). The rate of egg development increases with the ambient temperature (e.g. AOKI, 1994; HAWKING & NEW, 1995). In *O. uncatatus* the duration is between 13 and 16 days at 25°C in the laboratory. In order to estimate the duration of the whole life cycle it is useful to study the egg development in the natural habitat, as it has been done in *Sympetrum danae* (Sulz.) and *Cordulegaster boltonii immaculifrons* (Vander L.) (WARINGER, 1983; SCHÜTTE, 1997). In the Canal de Vergière *O. uncatatus* needs 27 to 33 days - twice as long as at 25°C. Because oviposition usually begins in mid June (see below) the first instar larvae can not be found before the middle of July. The latest oviposition was observed on September 20th when mean water temperatures in the CdV vary between 18°C and 14°C. At these temperatures egg develop-

ment should be much slower or should stop, as found in *Gomphus f. flavipes* (Charp.), *Ophiogomphus cecilia* (Fourcroy), and some Australian gomphids (POPOWA, 1923; MÜNCHBERG, 1932; HAWKING & NEW, 1995).

NUMBER OF LARVAL INSTARS AND DURATION OF DEVELOPMENT. – *O. uncatius* usually has 13 instars. For other species it has been shown that the number of instars can vary. STERNBERG (1990) puts the range of 11 to 17 instars in *Aeshna juncea* (L.) down to endogenous influences which possibly have developed as an adaptation to different habitats. In *O. uncatius* there is a range from 12 to 14 instars. The mean inter instar growth ratio of *O. uncatius* is approximately that found as median for a wide range of hemimetabolous insects by COLE (1980) and therefore confirms Dyar's Rule (DYAR, 1890). But individual growth ratio varies over a much wider range (see Tab. 2) because of inter instar moults or omitted instars.

Normally, the life cycle of *O. uncatius* lasts three years in the CdV. This can be deduced from the fact that in every year there are always three generations at the same time, eggs and imagines included. For most of the year only larvae are present. The presence of different generations or age-groups is then reflected in the three-peaked frequency distribution of the instars. We can, however, not infer the age from the distribution as single larvae may take two or four years for their development (see below). From mid-June onwards when the first adults return to the CdV after the maturation period and start to oviposit we can find four age-groups: imago, eggs, and two age-groups of larvae. In our study this implies that most of those individuals that emerged in 1993 probably hatched in summer 1990 (see Fig. 1). Thus the life cycle is similar in duration with that of most other European gomphids (SUHLING & MÜLLER, 1996).

SEASONAL REGULATION AND EMERGENCE PATTERNS. – CORBET (1954) divided the dragonflies of temperate regions into spring and summer species according to their seasonal regulation. In spring species, such as *Anax imperator* Leach, the majority of the larvae spend the last winter before emergence as final instar larvae. As a consequence there is a high synchronisation in emergence. Most of the European *Gomphus*-species also belong to this category (SUHLING & MÜLLER, 1996). On the other hand, there is in general only low synchronisation in summer species as described by CORBET & CORBET (1958) for *Aeshna cyanea* (Müll.). *O. uncatius* in CdV has to be put into this category because of the distribution of larvae in January and the emergence observed over several years.

In *O. uncatius* growth occurs mainly between April and October when the mean daily maximum water temperatures exceed 15°C. During this period larvae moult between 4 and 7 times according to their age, as found in other gomphids by MÜLLER (1995). In the winter period development is greatly reduced. Two instar X larvae which had been marked in October 1992 were recaptured in April 1993 in the same instar (SUHLING, 1994). However, there are some individuals which also grow in winter. Thus there seems to be a facultative diapause as in *Anax imperator* (CORBET, 1957).

Initiation of winter-diapause in dragonflies is usually triggered by decreasing length of day and/or temperature (CORBET, 1954; 1955; 1958; LUTZ, 1968b; INGRAM, 1975). Additionally there is a long day-diapause (INGRAM & JENNER, 1976; NORLING, 1984b), preventing too high growth rates in late summer which might result in emergence under unfavourable conditions e.g. shortly before the coming of winter. According to INGRAM & JENNER (1976) this diapause is not initiated in *Enallagma aspersum* (Hag.) when at a given time a critical size (winter critical size) is achieved. There might be a similar mechanism in *O. uncatatus*. Some larvae have a relatively high temperature threshold inducing diapause. Individuals which have not yet reached these instars or have already passed them will grow further if temperatures allow for it. According to the distribution plot instars F-3 and F should be such critical stages. One can well imagine growth in the CdV during winter as the temperatures can exceed 15°C even in January. The lower temperature thresholds for dragonflies of the temperate zone lie between 8 and 12°C (PRITCHARD, 1982). In *O. uncatatus* (last instar) raised in the laboratory there was a significant increase in weight even at temperatures as low as 10°C (SUHLING & MÜLLER, 1996).

If seasonal regulation is mainly triggered by temperature we would expect a better synchronisation when there is a high yearly amplitude in temperature. In this case larvae could quickly grow up to critical instars at high temperatures in summer. On the other hand growth would come to a standstill at low temperatures in winter. In the CCC summer temperatures reach up to 33°C whereas in winter they range from 2-8°C. There *O. uncatatus* emerges two weeks earlier and the emergence curve is that of a typical spring species (SUHLING, 1995).

Cohort-splitting is rather frequent in dragonflies. This means that a part of a year-class emerges either before or after the majority of that year-class (CORBET, 1962). However, the individuals emerge markedly later in the year than do those of the previous generation. This results in a bimodal distribution of the emergence curve e.g. in *A. imperator* where 5-10% of the yearly emergence are made up by early emerging individuals of the following generation (CORBET, 1957). In *O. uncatatus* cohort splitting cannot be directly detected from emergence as it is a summer species. However one may assume that individuals emerging late in the year are the result of cohort-splitting. On the other hand there is a high probability for cohort-splitting in an early phase of larval development. Larvae of instars III to VII can still be found in May and June. These individuals are approximately two to three instars behind the majority of their year-class. If they do not catch up rapidly in growth in one of the following years it is rather likely that they will take four years to complete their life-cycles. As it takes approximately 80 days from egg deposition to instar IV (see above) one can easily deduce that larvae found in this instar in May must have hatched from eggs laid late in the previous year (e.g. in August) and have not grown during winter. There is also the possibility that these are larvae which have only grown slowly in summer (see below).

In *O. uncatius* reduced growth occurs due to high larval densities (Fig. 6). It may therefore be that larvae need an additional year to complete their life-cycles as has also been described for other species (MACAN, 1964; VAN BUSKIRK, 1993). Based on our findings from the field we assumed a three-year life-cycle for *O. uncatius*. Our data come from areas of high larval density and low prey availability. In *Lestes sponsa* (Hans.) the amount of prey significantly affects the growth rate of single instars (PICKUP & THOMPSON, 1984). We can therefore assume that larvae at low densities as found in the lower reaches of the CdV (see SUHLING, 1994), where growth is additionally accelerated by higher temperatures larvae may only need two years to complete their life-cycles.

LOCAL DIFFERENCES IN POPULATION STRUCTURE. – At sites 2 and 4 we consistently found differences in population composition. At site 2 there was a decrease in the abundance of late instar larvae from January to April in both 1992 and 1993. For the area of the collection site we calculated a larval density of 4,000 larvae of the three last instars in January. The numbers in April were only 4% and 11% of these, respectively for the two years. At the time of emergence only 1.5% and 2% were left (Tab. IV). This decrease may have been caused by either a high mortality during this period or by migration of the larvae.

In *Stylogomphus suzukii* Oguma distributional changes caused by drift seem to be part of the normal life-cycle (ARAI, 1994). In *O. uncatius* such changes which occur mainly in the last four instars take place mainly in April (SUHLING, 1994). However, the number of drifting larvae is too low to explain a decrease of 98% of the big larvae. Also upstream movements of the larvae could not be shown. Rather there is also a decrease in density upstream from site 2. We therefore consider the main proportion of the decrease to be caused by a high mortality of the final instar during the second half of winter. As the decrease in density varies between the sites we should expect localeffects to affect mortality, e.g. fish predation. But even large fishes do not feed extensively on last instar larvae (SUHLING, 1994). At site 2 total larval density is at least 1.5 times as high as it is at site 4. Competition due to

Table IV

Number of larvae of the last three instars at two sample sites at the Canal de Vergière estimated from larval density which was determined from Surber-samples compared with the number of emerged specimens. The percent proportion of emerged specimens in relation to larval abundance per site is given

	Sample site 2		Sample site 4	
	1992	1993	1992	1993
Estimated No. of large larvae in January	3950	4250	2857	5023
Emerged specimens	59	86	1714	653
% emerged	1.5	2.0	60.0	13.0

high density can directly induce increased mortality via competition for food (ANHOLT, 1990) or by cannibalism (VAN BUSKIRK, 1989).

INFLUENCE OF FOOD AVAILABILITY AND COMPETITION ON POPULATION STRUCTURE AND LARVAL SIZE. – In the CdV we found low densities of macroinvertebrates where the density of *O. uncatius* was

high. At site 2 the density of *O. uncatatus* alone was higher than that of all other macroinvertebrates together (SUHLING, 1994). Thus the high mortality could be a consequence of both, food shortage and increased cannibalism. Like *Ophiogomphus cecilia* (MÜLLER, 1993b) *O. uncatatus*, too, hunts from a hide in the sediment. However, experiments showed that after some days of starving larvae started hunting actively (SUHLING, 1994). This would result in higher frequency of encounters and might thus increase the rate of cannibalism. Larvae which found no prey in spite of searching then might become inactive again in order to spare the remaining energy reserves. During long periods of hunger such as winter we would therefore expect the effect of cannibalism to be reduced after some time. As encounters are also density dependent mortality in areas of low density are probably mainly induced by food shortage. Even short-term shortage induces an increase in activity and thus to an increase in cannibalism at high densities. Later, larvae also die directly from starvation. At site 2 we found both low food availability and a high abundance of *O. uncatatus*. It seems quite likely that high mortality at site 2 is caused by the high larval density in combination with reduced food availability.

MORTALITY. – Strikingly, mortality affected mainly fully grown larvae. One would expect them to feed on small larvae when food is scarce. It seems that preying on small larvae may not be enough to guarantee survivorship of the big ones. We may therefore think of an additional effect related with the high temperatures in the CdV. Daytime water temperatures may rise to 15°C even in January. Due to these conditions, larvae in the CdV have a facultative diapause and their metabolic rates are not sufficiently reduced. Consequently their need for food stays at a high level but cannot be met because of low prey densities. At site 4 the amount of prey is relatively high, even in winter, and mortality stays at a low level. In areas of low density like the lower reaches of the CdV this effect should be negligible.

INDIVIDUAL SIZE. – A further effect typical of high densities is a reduced size in the individuals (BANKS & THOMPSON, 1987; ANHOLT, 1990). But there was also a clear correlation with food availability as has been assumed by BANKS & THOMPSON (1987). In *O. uncatatus* we found smaller headwidths in areas of high density than in areas of low density. This may have consequences for reproductive success as found in *Pyrrhosoma nymphula* (HARVEY & CORBET, 1985).

ACKNOWLEDGEMENTS

We like to thank ANKE LANGENBACH and ANDREAS MARTENS for critical comments on the manuscript. Our study was supported by DFG and DAAD.

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