

**A FIVE YEAR STUDY OF THE LARVAL LIFE HISTORY  
OF *COENAGRION HASTULATUM* (CHARPENTIER)  
AND *C. ARMATUM* (CHARPENTIER) IN NORTHERN SWEDEN  
(ZYGOPTERA: COENAGRIONIDAE)**

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*Received March 29, 1994 / Revised and accepted August 3, 1994*

The life cycles of the 2 spp. were studied in a productive pond during 5 yr. In both spp. a 2-yr life cycle was most common. Emergence of both spp. was fairly synchronous and peaked mainly in early June, often starting in late May. *C. armatum* seemed to be slightly earlier than *C. hastulatum*. Eggs probably hatched in July-Aug. Most larvae first overwintered in rather early instars, and a second and last time in the final instar. However, a small but variable part of the populations (best documented for *C. hastulatum*) showed a 1-yr life-cycle with the winter spent in large pre-final instars. This unexpectedly rapid development is probably explained by favourable local conditions. In both spp. a low recruitment of larvae in 1987 is explained by severe weather conditions in that year. It is discussed how detailed information about development and cohort splitting can emerge from limited material of this type.

## INTRODUCTION

Life history characters such as phenology, synchrony of development, voltinism, and survival rates are important in the understanding of population dynamics of dragonfly larvae (CROWLEY et al., 1987). Studies on the life history of dragonflies from higher northern latitudes are rare, in particular long term studies. Northern freshwaters are often cooler and also less productive than more southern ones. Thus, the population dynamics of dragonfly larvae in northern areas can be expected to differ from those in the south.

The purpose of this study is to present life history and population density data for the two damselflies *Coenagrion hastulatum* (Charp.) and *C. armatum* (Charp.) from northern Sweden. It also demonstrates how a careful analysis of a limited

amount of material, together with knowledge of some principles of dragonfly life-histories, can produce otherwise concealed information.

*C. hastulatum* is one of the most common damselflies in the north European part of the boreal region (JOHANSSON, 1993). The larvae inhabit small to medium sized lentic habitats. The geographical range and habitat preference in the north is similar in *C. armatum*, although that species is less common than *C. hastulatum*.

#### STUDY SITE

The study was conducted in northern Sweden in a man-made pond (Sofiehemsdammen), located in the outskirts of the city of Umeå, 63°50'N, 20°15'E. The pond is 2.25 ha, has a maximum depth of about 2.0 m, and is strikingly productive for these latitudes. Ice cover usually lasts from the beginning of November until the beginning of May. In May water temperature varies a lot (Tab. I), reflecting the duration of ice cover. Mean air temperature is highest in July (Tab. II), which is also reflected in the water temperature (Tab. I).

The adjacent vegetation is primarily made up of *Salix* spp. bushes. The littoral zone (0-0.5 m depth) is dominated by *Carex* spp. and to a lesser

extent also by *Equisetum fluviatile* L. with patches of *Drepanocladus* spp. mosses. In the deeper parts *Potamogeton natans* L. is very common. During the five year study, fish (perch, *Perca fluviatilis* L.; roach, *Rutilus rutilus* (L.); and pike *Esox lucius* L.) were abundant in the pond. The dragonfly assemblage comprises 13 species, of which *C. hastulatum* is the most abundant.

#### METHODS

We studied larval dragonfly populations in a shallow littoral area (15 × 5 m) from May through October in 1987-1991. The predominant vegetation in the sampling area was *Carex rostrata* Stokes and *Equisetum fluviatile* L. Larvae were sampled with a cylinder sampler (diameter 30 cm) plunged randomly into the bottom at a depth of 15-35 cm. The larvae within the cylinder were collected with a hand net (mesh size 1 mm) swept three consecutive times three in the cylinder (i.e. totally 9 sweeps). We took five cylinder samples and water temperature data on one of the first days each month during the ice-free season (Figs 1a-e, 2a-e). Dragonfly larvae were handsorted in the field in

Table I

The five year mean water temperature (°C) during sampling date each month. Mean min. and mean max. temperatures are shown in brackets

May	Jun.	Jul.	Aug.	Sep.	Oct.
5	14	19	19	14	7
(1-9)	(11-20)	(16-21)	(16-22)	(11-16)	(6-8)

Table II

Mean monthly air temperature from May through October. — [Data from Umeå airport which is situated 1 km WNW of the pond (SMHI, 1987-1991)]

Year/Month	May	Jun.	Jul.	Aug.	Sep.	Oct.
1987	5.7	10.6	14.5	10.3	7.5	6.4
1988	7.8	14.4	17.7	12.9	10.0	2.6
1989	9.0	13.7	16.0	14.3	10.1	3.1
1990	9.0	13.3	15.3	14.6	8.6	5.1
1991	6.1	10.7	16.3	15.5	7.6	3.8

a plastic tray filled with water, preserved in 70% ethanol, and later identified to species and measured in the laboratory.

Larvae in the three last instars (F indicates final, F-1 penultimate, etc.) were classified by means of their head-width, with wing-pad length as an additional help when necessary. The measurements were made with a Wild M5A microscope with an ocular grid. Only larvae with a head-width greater than 1 mm could be reliably identified and used in the graphs. Smaller larvae were, however, exceptional in the samples because of the methods. In late-instar larvae observations on intra-instar development were made by means of eye development (NORLING, 1971). In the F instar also wing-pad and prementum development were used for intra-instar development (for details see NORLING, 1984a).

To provide additional information on the emergence period and the flying season we counted the number of flying adults (single individuals and tandem pairs) on five occasions in 1992. This was done by walking a 100 m section once along the shore in the afternoon.

## RESULTS AND DISCUSSION

### *COENAGRION HASTULATUM*

#### Figure 1

EMERGENCE. — Changes in size composition and in intra-instar development in the three last instars are shown in Figure 1a-e. As no direct observations of emergence were made, observations on intra-instar development in the final instar (Fig. 1, upper parts of graphs) had to be the main source of information for that. The presence of larvae in the last of the seven developmental classes (phases) of this instar (prementum empty of tissue; see NORLING, 1984a) means that emergence is due within two days at summer temperatures. A peak in this phase, such as on the 1st of June 1988 and 1989, probably means that emergence has already started. Thus, in these two years, emergence most likely started during the last days of May. In 1990 it appears that most of the larvae that had overwintered in the final instar emerged in late May (Fig. 1d). On the other hand, during the cool spring of 1991, and probably also in 1987 (Tab. II), emergence may not have started until well into June (Fig. 1a, e). Thus, the early main peak of emergence is likely to take place normally in early June. The end of emergence is less well documented. Only in the cool summer of 1987 was a sampled specimen about to emerge found in early July (Fig. 1a). Emergence probably petered out at this time or in late June (cf. 1990, Fig. 1d). These conclusions are supported by the adult activity data for 1992, showing a maximum around mid June (Table III).

Table III

Number of single adults and number of pairs in tandem position at five visits to the Sofiehemsdammen (1992)

Date	<i>C. hastulatum</i>		<i>C. armatum</i>	
	Single	Tandem	Single	Tandem
2-VI	7	1	5	1
15-VI	16	6	4	-
30-VI	13	-	-	-
20-VII	3	-	-	-
31-VII	-	-	-	-

**LARVAL GROWTH.** — After rapid embryonic development, hatching probably starts in July, and by September all eggs appear to have hatched. The first larvae of the year appeared in the samples in August. Most overwintered at a relatively small size, head-width usually averaging 1.6 mm. A comparison with more detailed data from southern Sweden (NORLING, 1984a) suggests that this peak corresponds to the F-5 instar, and probably to the 8th instar if the prolarva is counted as the first one. For these larvae the life-cycle duration was unequivocally two years: during the next season they grew rather slowly and reached the F

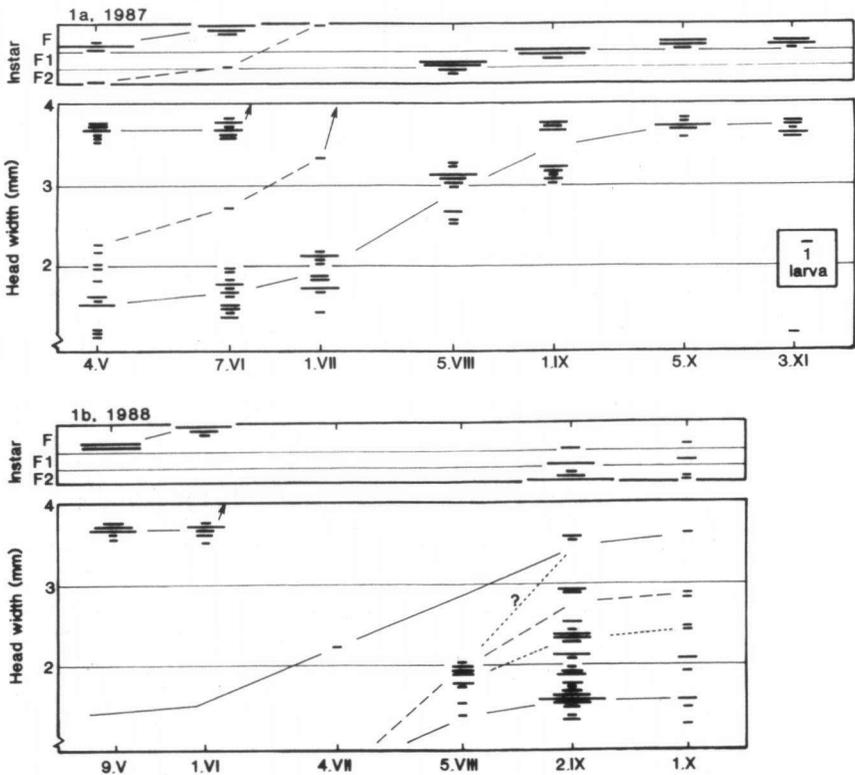


Fig. 1. Larval development of *Coenagrion hastulatum* larvae from May through November 1987-1991 (a-e). — [Lower parts are kite diagrams, showing head width distribution on the different sampling dates. The size classes are 0.05 mm. The inferred development is indicated with lines. Solid lines means 2-year development, broken lines 1-year development. The coarsely broken lines add a dimension of uncertainty. The upper parts are graphic presentations of the development in the last three instars (F denotes the final instar, F1 penultimate etc), showing the distribution of larvae among arbitrary instar subunits (see NORLING, 1984a). It can also serve as a guide to the instar composition in the lower part].

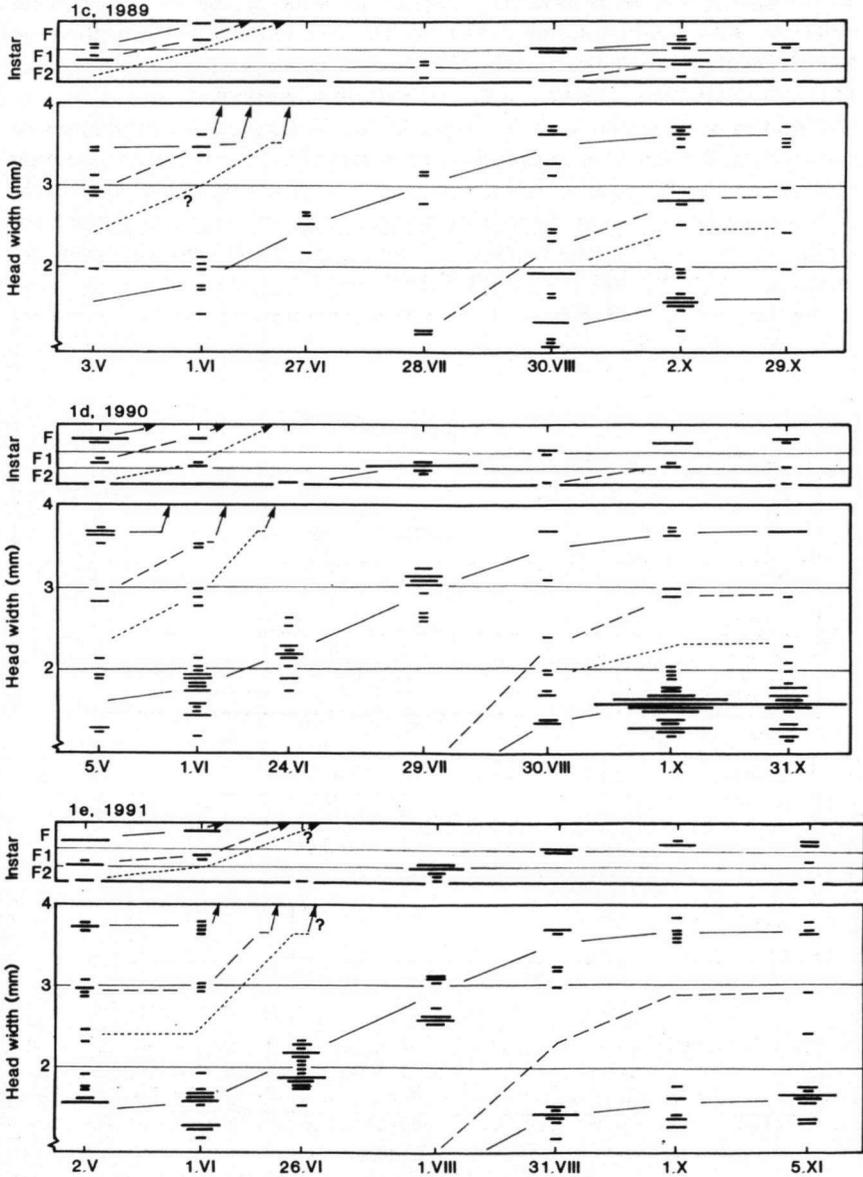


Fig. 1. Continued.

instar in August-September. After another overwintering, they emerged synchronously in late May or early June, depending on weather conditions.

**COHORT-SPLITTING.** — A small but variable part of the population was however univoltine. Such cohort-splitting is an ecologically important phenomenon (e.g. MARTIN et al., 1991). It is a rule rather than an exception in species with flexible life-cycles (NORLING, 1984b), and it is frequently overlooked.

Its detection in this study was facilitated by (1) accurate measurements of head-width and a high size resolution (0.05 mm) (Fig. 1), — (2) the estimation of intra-instar development in late instars, and — (3) the determination of instar number (in relation to emergence) by measurement of wing-pad length: for example, a larva with a head-width of 2.7 mm is F-1 if the hind wing-pads are 2 mm (cf. 7-VI-1987 and 1-VI-1990, Fig. 1), but F-2 when the wing-pads are 1.6 mm (cf. 28-VII-1989, Fig. 1). If the former (F-1) larva is about to moult and

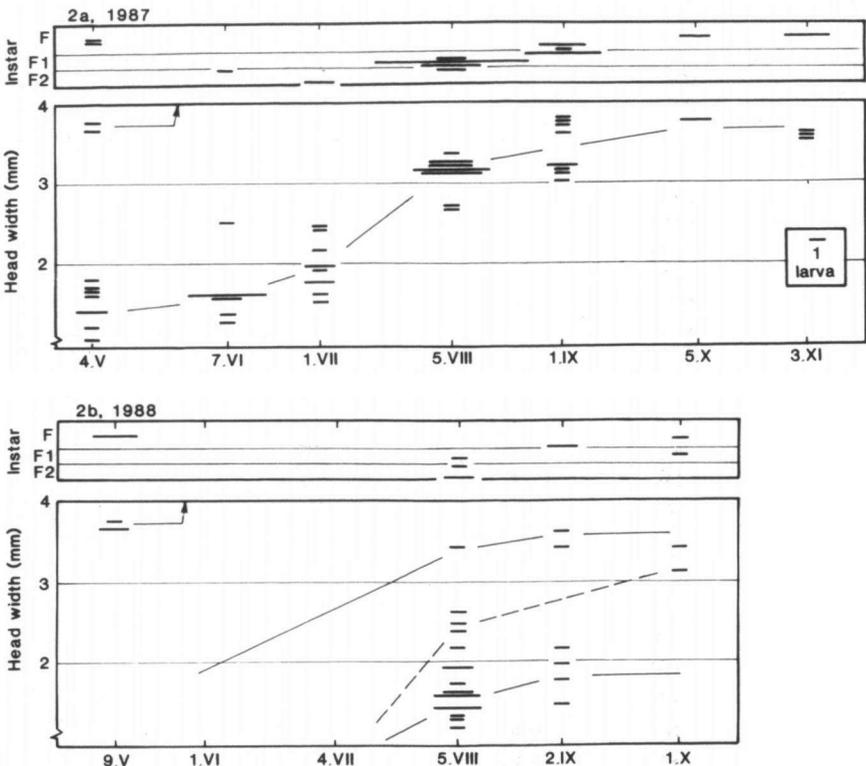


Fig. 2. Instar distribution of *Coenagrion armatum* larvae from May through October, 1987-1991 (a-e). — [See text in Figure 1 for further details].

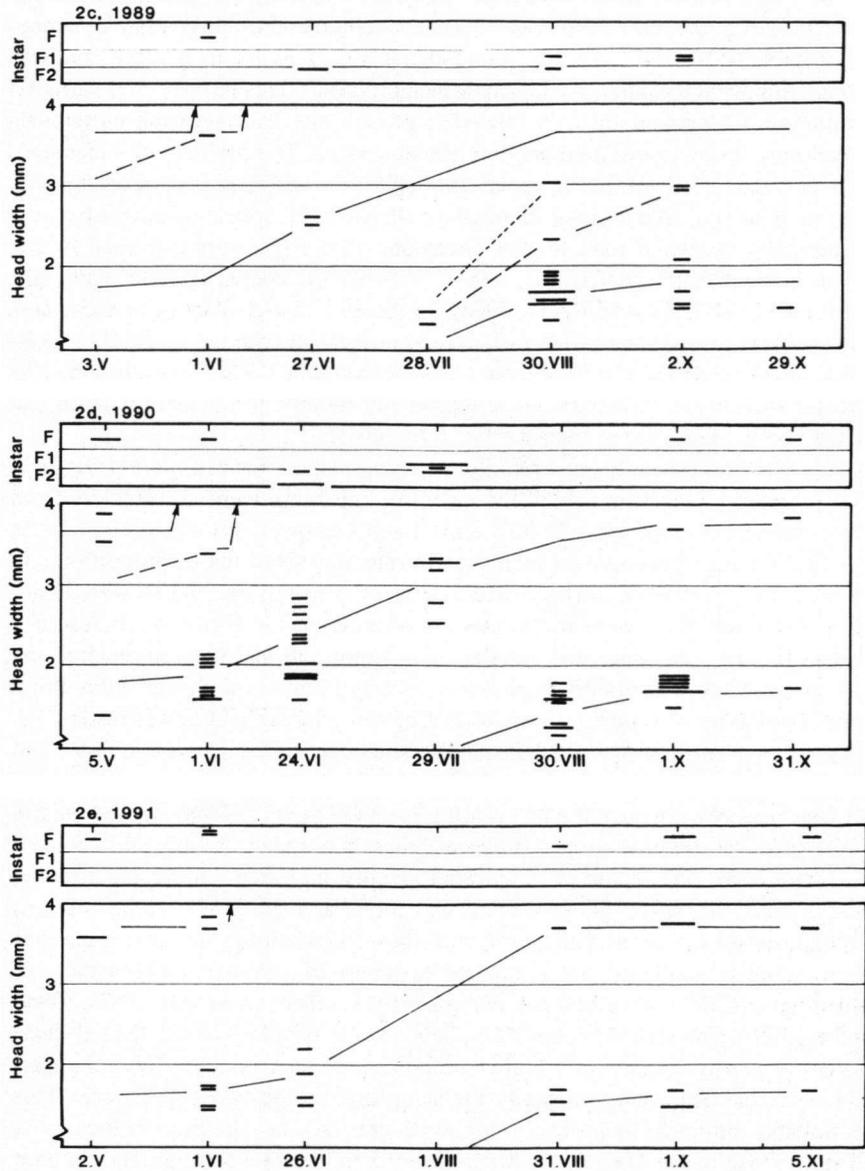


Fig. 2. Continued.

the latter one (F-2) has just done so, they are separated by a developmental gap of almost two moulting cycles despite being the same size.

Size differences within an instar (as defined above) are important for the detection of generation shifts. Odonates have a high and usually variable number of instars. NORLING (1984a) found that *C. hastulatum* in a more southern population went through 11-13 instars (incl. prolarva). This intraspecific variation in number of instars is usually related to growth rate. Fast-growing individuals develop with fewer instars than slow-growing ones. The problem of cause-and-effect is not resolved, but there are probably both intrinsic and environmental factors involved. In particular diapause or diapause-like phenomena, such as the hormonally regulated reduction of development rate probably exhibited by the semivoltine cohort (NORLING, 1984a, 1984b), are known to reduce the size increase per ecdysis (INGRAM, 1975). In the end, fast-growing specimens (i.e. univoltine) are smaller as final instars (and probably as adults; cf. SCHALLER, 1960) than more slow-growing ones (i.e. semivoltine). This size difference is greater still in earlier instars, but a reasonably reliable instar identification can hardly be made for more than the last three instars.

The univoltine cohort grew rapidly, and most larvae reached the F-1 instar in August-September. This cohort can easily be misinterpreted as stragglers from the semivoltine group (see 30-VIII and 2 and 1 respectively -X in 1989-1990, Fig. 1 c-d), partly because its high growth-rate may seem out of proportion and thus unlikely. However, the head-widths of the F-1 instars on 30-VIII were larger than 3 mm and they were in the process of entering the F instar, whereas F-1 instars in early October were smaller than 3 mm and had recently entered the F-1 instar. Such a size shift in an instar usually indicates a change from slow-growing larvae with many instars to fast-growing larvae with fewer instars, i.e. a generation shift. In the final instar the shift can be seen between 7-VI and 1-VII-1987, and between 5-V and 5-VI-1990 (Fig. 1 a, d).

COMPARISON WITH OTHER POPULATIONS. — NORLING (1984a) studied the life cycle of *C. hastulatum* in two different areas in Sweden. At one site, situated 5°8' (some 570 km) south of the present locality, he found a life-cycle duration of 1-2 years, whereas a 3-4 year cycle was found at a site 3°58' (some 440 km) to the north of our pond. Compared with these populations, the present one has a surprisingly "southern" life cycle, and its pattern of development seems almost indistinguishable from certain populations in the southern area (NORLING, 1984a and unpubl.). The southern population described in detail by NORLING (1984a) differs primarily by having a higher proportion of univoltinism. Even the start of emergence occurred at virtually the same time in the two populations! This remarkable similarity is probably due to several factors. The present locality is situated close to the Gulf of Bothnia, giving a milder late summer and autumn climate compared to inland habitats. The pond is also fairly shallow and productive. The more southern locality, an acid bog-pool, differs primarily by its ex-

tremely low productivity, which may explain the similarity. However, even in southernmost Sweden, a further 3° (330 km) south of Norling's southern pond, *C. hastulatum* has a 1-2 year development, but with only a small semivoltine group (Norling, unpubl.). On the other hand, the northernmost area is far inland, with a rather severe climate, probably close to the limit for the existence of dragonflies (NORLING, 1984a, 1984b).

POPULATION DENSITY. — Larval population density peaked in September or October and at maximum it reached 257 m<sup>-2</sup> in October 1990. These autumn density figures (34-257 m<sup>-2</sup>) are within the range of those found in other coenagrionids (MACAN, 1964; LAWTON, 1970; BANKS & THOMPSON, 1987; McPEEK, 1990). Prior to emergence (June), the densities of the last and the penultimate instar larvae ranged from 11-34 m<sup>-2</sup>. Also these figures are within the range of those found in other coenagrionids (MACAN, 1964; LAWTON, 1970; BANKS & THOMPSON, 1987).

DIFFERENCES BETWEEN YEARS. — In 1987 only one (3-XI) first-year class larva was found (Fig. 1). This summer was exceptionally cold and rainy (Tab. II) (see also JOHANSSON & NILSSON, 1991), and recruitment was probably very low. The 1987 cohort was small compared to the other four cohorts studied. In 1988 only one larva from this cohort could be clearly identified (4-VII). In spite of this, some final instar larvae appeared towards the winter (Fig. 1b). These should belong to the 1987 year-class, but it cannot perhaps be ruled out that they were younger: they were relatively small in size, and the fast growers in the 1988 year-class were exceptionally early (cf. below). Since the density of the 1987 year-class larvae was low, there might have been reduced competition. This might have resulted in higher survival rates of this year-class, but could also have increased the development rate of the following 1988 year-class, producing a higher rate of univoltinism than otherwise. With the help of a warm summer (Tab. II), this actually occurred (Fig. 1b).

#### COENAGRION ARMATUM

Figure 2

Despite the sparse and more erratic occurrence of *C. armatum* in the samples, a few results emerge. The general growth pattern and voltinism appear similar to that of *C. hastulatum* (Fig. 2 a-e). However, emergence probably started somewhat earlier as very few final instar larvae were present at the beginning of June. This is also supported by the number of adults present, which showed a peak in early June (Tab. III). These results are also in accordance with preliminary results from southernmost Sweden (Norling, unpubl.).

The dominant two-year life cycle is clearly seen in 1987 and 1990 (Fig. 2a, d). The occurrence of cohort-splitting and univoltinism is less conclusive, but appeared very likely in 1988 and 1989 (Fig. 2b-c), the very years when cohort-

-splitting was best documented for *C. hastulatum* (Fig. 1). Indeed, growth during 1988 appeared exceptionally rapid, as discussed for *C. hastulatum* above.

Throughout the five year study population densities were lower than in *C. hastulatum*, and peaked in August and September (max. 40 m<sup>-2</sup>). Also in *C. armatum* the cold summer in 1987 affected the recruitment, and no first-year class larvae, were collected this year.

#### ACKNOWLEDGEMENTS

We thank CHRISTIAN OTTO and JOHAN ELMBERG for valuable comments on earlier drafts on this article.

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