SURVIVORSHIP CURVE AND ANNUAL FLUCTUATION IN THE SIZE OF EMERING POPULATION OF CORDULIA AENEAMURENSISTR SELYS (ODONATA: CORDULIIDAE)\(^1,2\)

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Synopsis


Population studies of Odonata have so far been carried out separately for either of the larval and the imaginal periods. The survivorship curve of Odonata from egg to reproductive adult is reported probably for the first time in the present paper, which deals with a population of Cordulia aenea amurensis SELYS at Hōrai-numa near Sapporo. The curve drawn from the averaged data of the 1966-1973 year-classes shows that the mortality rate is higher during the early stages of the aquatic period than during the later stages (Type III, Deevey, 1947), and that the rate is lower in winter than in the other seasons. About 99.8\% of the initial population (eggs laid) died during the aquatic period lasting five years, in which predation by Aeschna nigrofava M. Martin was regarded as a major cause of the deaths, based upon rearing experiments and miscellaneous observations. The number of mature adults arriving at the reproduction site was estimated at 0.07\% of the initial population. A considerable stability was confirmed in the size of emerging population: the maximum size was 2.2 times the minimum one among the six year-classes. It is likely that this stability is caused by the switching of prey selection by predators (cf. Murdoch, 1969) and/or the effect of refuge space from predators (cf. Macan, 1974) during the aquatic period.

Introduction

The population dynamics of Odonata have been studied mainly from the point of the survivorship curve (Macan, 1964; Lawton, 1970; Kurata, 1974 and Benke & Benke, 1975, for larval period; Corbet, 1952; Pajunen, 1962; Higashi, 1969, 1976; Parr, 1973, 1976 and Fujita et al., 1978 for imaginal period). However, up to the present, no comprehensive study on survivorship throughout the life history of one species has appeared, nevertheless such knowledge is indispensable to clarify the survivorship strategy of a given species. One purpose of the present paper is to fill this lack.

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1) Ecological studies of Cordulia aenea amurensis SELYS IV. Previous studies (UBUKATA, 1973, 1975 and 1980) are assigned to I-III of the series, respectively.

2) Partial fulfillment of Doctoral thesis (No. 1855), Hokkaido University.

As for the regulation of population size of Odonata, Moore (1953, 1957) inferred that density-dependent clashing among adult males prevents further increase in adults long before mortality factors have any effect on density, though he later eliminated the application of this theory to some species (Moore, 1964). Recently, Ito (1978) also stated that the territoriality of Odonata plays a certain role in stabilizing the size of its population, while Benke (1978) suggested that the predation by fishes and larger odonate larvae regulate an odonate population. The second purpose of the present paper is to show the degree of the population stability and to offer some conjectures on the stabilization mechanism during the aquatic period in a corduliid dragonfly, Cordulia aenea amurensis SELYS, leaving an examination of the hypotheses by Moore and Ito in a subsequent paper.

The outline of the life cycle of this subspecies in western Hokkaido is as follows: the eggs are laid during late June-early August and hatch 10 to 16
Japanese Ecological Society

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Most larvae (>80%) undergo an aquatic period of five years, while some individuals may require one more year to accomplish larval development. The latter type of life cycle is neglected in the present study, since the percentage of this type is considered to be low and not completely confirmed (cf. Ubukata, op. cit.). The emergence occurs during early June to the beginning of July, followed by the pre-reproductive period ca. 9 to 12 days (Ubukata, 1973). Territorial behavior, mating and oviposition are exhibited during the reproductive period from late June to early August (Ubukata, 1975).

Before going further, the author wishes to express his sincere gratitude to Prof. Shōichi F. Sakagami and Prof. Mayumi Yamada of Hokkaido University for their pertinent guidance during the present study. Cordial thanks are also due to Dr. Syoziro Asahina, National Institute of Health, Tokyo, for his encouragement. A part of the present study was supported by a grant (Biology, No. 23, 1975) from the Japan Society of the Promotion of Science.

Study Area

The field work, including population censuses, rearing experiments and behavioral observations, was carried out at a dystrophic pond (Hōrai-numa) surrounded by bog mats and forests near Sapporo, Hokkaido, Japan. The pond has a nearly circular contour (222 m) with a maximum diameter of about 80 m. The water level of the pond is stable throughout the year, fluctuating between ±10 cm above the average level. A more detailed description of the feature of the pond, vegetation, odonate fauna, and climatic factors were reported in previous papers (Ubukata, 1973, 1974, 1980).

The Potamogeton-zone fringing the pond surface was divided into five sectors (NE, NW, SE, etc.), each 40–55 m long along the shore (cf. Fig. 1 in Ubukata, 1975). The quantitative samplings of larvae were executed at NE (northeastern sector, 55 m long along the shore line). Sector NE was further divided into two subsectors, NEa (33 m long) and NEb (22 m long), each corresponding to a–e and e–g in Fig. 1 in Ubukata (1973, 1975).

Methods

The estimations of population density were made mainly for the 1970 and 1971 year-classes, i.e., the age groups that hatched, respectively, in 1970 and 1971 and emerged in 1975 and 1976. In drawing the survivorship curve, the estimates for other (1966–1973) year-classes were also used, since the population size was fairly stable among the year-classes. The causes of deaths were confirmed by the rearing experiments and miscellaneous observations.

Estimation of the number of eggs laid

As already reported (Fujisawa, 1957; Ubukata 1975), the oviposition of C. a. amurensis is performed by the rhythmical striking of the water surface by single females. The number of eggs laid at subsector NEa was estimated for the 1970 and 1971 year-classes from the number of oviposition flights and the average number of eggs laid per one oviposition flight. Since the number of oviposition flights was not quantitatively counted for subsector NEb, the total number of eggs laid at NE was estimated from the number of eggs laid at NEa divided by the ratio of the number of exuviae collected five years later at NEa to that of NE, in which equal mortality and no migration during larval period were assumed for the inhabitants of both subsectors. As this method involves many parameters, the validity of the estimated number of eggs laid will be tested later in Discussion.

Estimation of the number of larvae inhabiting NE

The number of larvae for each of the 1968–1973 year-classes was estimated from the data obtained by periodical larval samplings at NE during 1973 to 1974. At sector NE, about 93% of the larval population were distributed within a zone of 0–1 m from the shore (Ubukata, unpubl.). This zone of sector NE was divided into 11 quadrats, each 5 m long along the shore. Every quadrat was surveyed for 35 min. with a hand net (0.6 mm mesh with a mouth of 20 cm² and a handle of ca. 1 m length). All of the larvae discovered were sorted with tweezers and then measured for head width and body length within this time interval. After each unit sampling, all larvae sampled were returned alive into the same quadrat. This fixed-time sampling may result in biased estimations if much time is wasted on measuring and recording. However, the time estimated to be consumed by these tasks was only 6.6% to 17.3% in each periodical sampling, so that the difference in the time available for scooping and sorting between the maximum and minimum values was only 13% in terms of the latter. As the difference was not so large, no correction was made of the number of collected larvae.

Vol. 31, No. 4 Japan Ecological Society Dec., 1981

336
The sampled population of each month was separated into some year-classes by Cassie's method (Cassie, 1954) with the data of body length. More detailed accounts of the method were given previously by UBUKATA (1980).

**Difference in sampling efficiency according to larval size**

In order to compare the sampling efficiency among various sizes of the larvae a release-recollection experiment using models was executed. For the models of the larvae of *C. a. amurensis*, some seeds of potato were cut into 600 rectangular parallelepiped-shaped pieces of six different sizes corresponding to every other instar (Table 1). The potato was adopted because of its similarity to the larva in specific gravity (potato, 1.04; larva, 1.05). Next, one hundred model pieces for each size group were sunk as uniformly as possible into the water of a zone measuring 0.5 m wide and 5 m long along the shore at the central part of NE on October 14, 1975. Their re-collection was executed in the same manner as the routine monthly samplings through 140 scoops during two hours on the same day.

The number of re-collected model pieces is shown in Table 1. This result suggests a tendency that the sampling efficiency is lower in smaller larvae (size-groups A and B), which is consistent with the data of real larval sampling (cf. Fig. 4 in UBUKATA, 1980). This low efficiency was apparently caused by their small sizes, as they were mixed with and buried under mud and debris at the time of scooping by the hand net, which made their recovery difficult. On the other hand, there was no significant difference (*p* > 0.12, *χ*²-test) among the larger size-groups (C–F). Based upon this experiment, the number of larvae smaller than 4 mm were not estimated, and the equal sampling efficiency was assumed for larvae larger than 4 mm in the present study. Among 400 model-pieces of C–F, eight were re-collected during 35 min. (42 scoops) after the start of re-collection. From this result, the efficiency of the routine sampling applied for the model pieces is calculated to be 0.02.

**Efficiency of the periodical larval sampling**

The number of final instar larvae, which had been collected by periodical samplings from mid May to the beginning of June (just before the emergence period), was compared with the number of imagines which emerged at NE, which was estimated from the emergence traps in the same year. As shown in Table 2, on the average for 1973 and 1974, 5.75 larvae were collected and released by routine samplings from the 211 individuals which emerged immediately. From these values the

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**Table 1.** Size of the models used in the experiment on the sampling efficiency and the number of models re-collected. For each size group, 100 model pieces were scattered into the water before re-collection.

<table>
<thead>
<tr>
<th>Size group</th>
<th>Length (mm)</th>
<th>Width (mm)</th>
<th>Height (mm)</th>
<th>Instar of corresponding size</th>
<th>No. of models re-collected</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>1.5</td>
<td>0.5</td>
<td>0.4</td>
<td>F-10</td>
<td>0</td>
</tr>
<tr>
<td>B</td>
<td>2.4</td>
<td>0.8</td>
<td>0.7</td>
<td>F-8</td>
<td>0</td>
</tr>
<tr>
<td>C</td>
<td>4.1</td>
<td>1.4</td>
<td>1.1</td>
<td>F-6</td>
<td>3</td>
</tr>
<tr>
<td>D</td>
<td>6.8</td>
<td>2.2</td>
<td>1.8</td>
<td>F-4</td>
<td>3</td>
</tr>
<tr>
<td>E</td>
<td>11.0</td>
<td>3.6</td>
<td>3.0</td>
<td>F-2</td>
<td>8</td>
</tr>
<tr>
<td>F</td>
<td>19.0</td>
<td>6.0</td>
<td>5.0</td>
<td>F</td>
<td>4</td>
</tr>
</tbody>
</table>

**Table 2.** Efficiency of the fixed-time larval sampling estimated from the number of emerging individuals. Asterisk indicates average of two occasions of larval sampling; double asterisks indicate values equal to that value estimated for exuvial collection.

<table>
<thead>
<tr>
<th>Date of larval sampling</th>
<th>May 17–23, 1973</th>
<th>May 30–June 7, 1974</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of full-grown larvae sampled (<em>L</em>)</td>
<td>4.5*</td>
<td>7</td>
<td>11.5</td>
</tr>
<tr>
<td>No. of emerging imagines estimated from trap (<em>E_m</em>)</td>
<td>291</td>
<td>131**</td>
<td>422</td>
</tr>
<tr>
<td>Sampling efficiency (<em>L/E_m</em>)</td>
<td>0.015</td>
<td>0.053</td>
<td>0.027</td>
</tr>
</tbody>
</table>
sampling efficiency was estimated at 0.027, which is not significantly different \( (p>0.65; \chi^2\text{-test}) \) from that obtained in the experiment using models. In the present study, the reciprocal of this value was adopted as the conversion factor for estimating the number of larvae which exceeded 4 mm.

**Estimation of the number of emerging individuals**

The number of emerging individuals for each of the 1966–1971 year-classes from each sector of the pond was estimated from the number of exuviae collected or from the number of teneral imagines collected by the emergence traps.

1. Collection of exuviae: Routine collection of the exuviae was carried out at every shore of the pond daily (1971), every other day (1972, 1975) or irregularly (intervals of 1–5 days; 1974 and 1976) throughout June. At each of such routine samplings made during late afternoon, by which emergence of almost all individuals was finished, the leaves as well as the stalks of plants near the water edge \((\pm 2 \text{ m})\) were examined one by one with an approximately 1 m long stick. The sampling efficiency of this method was estimated at 0.74 \((n = 112)\) by executing exhaustive collections of the exuviae which were overlooked in the previous routine samplings (UBUKATA, 1973).

2. Trapping of emerging individuals: Eight traps \((1 \text{ m} \times 5 \text{ m})\) made of iron wire frames and vinyl-chloride sheets were set to collect emerging imagines at intervals of 20 m on the boggy shores in 1973 and 1974. In 1974, both exuvial sampling and trapping were simultaneously adopted. For that year, the number of emerging individuals at NE was estimated at 131 from the collection of exuviae. On the other hand, the average density of e-merging individuals was estimated at 1.73/m from three traps set up at NE. Multiplying this figure by the shore length of NE, the total number of emerging individuals was estimated at 95.3. Regarding the estimation by exuvial sampling as valid, the sampling efficiency of the emergence trap was calculated to be 0.73.

**Assessment of larval migration**

As the number of individuals in the aquatic stages was estimated only for sector NE, the amount and the direction of larval migration to or from the adjacent sectors must be assessed to obtain a more valid survivorship curve. However, as no direct evidence could be found in the present study, so the percentage of the exuviae collected from NE to those from the whole pond was compared with the percentage of oviposition flights at NE to those at the whole pond observed during circling censuses (cf. UBUKATA, 1975). The percentage of exuviae \((n = 1,628; 1971–1972, 1974–1976)\) and oviposition \((n = 29; 1971, 1973, 1974)\) were 33.8 and 37.9, respectively. Thus, as there was no significant change \((p>0.65; \chi^2\text{-test})\) in percentage between oviposition and emergence, the larval migration to and from the sector NE could be neglected.

**Rearing of larvae**

To control predation and starvation as causes of death during the larval period, some rearing experiments were executed both in the laboratory (Zoological Institute, Hokkaido Univ., Sapporo) and in the pond. In 1973, 13 larvae were collected from the pond on May 16–19 and reared in the laboratory till November 28. Each individual was kept separately in a wide-mouthed glass bottle \((50 \text{ mm} \times 100 \text{ mm high})\) and was fed *Tubifex*. Bottle water was exchanged with fresh water when necessary. In 1976, a rearing experiment with 14 larvae was carried out on the bottom of the pond from May 28 to November 25. The individuals were kept separately in bottles of the same size as mentioned above, which were covered with a piece of nylon net \((1.5 \text{ mm mesh})\). Beside *Tubifex*, some fragments of *Sphagnum* and a little mud were added to each bottle. A more detailed description of this method was shown in UBUKATA (1980).

**Estimation of the survivorship during the pre-reproductive period**

In order to estimate the ratio of the survivors beyond the pre-reproductive period in terms of the number of emerging individuals, marking-rediscovery experiments were executed in 1971 and 1976. The newly emerged imagines collected on the shore of the pond were individually marked on the wings with a quick-drying ink or thinned lacquer paint and released. All of the individuals rediscovered at the pond were recorded during intensive behavioral observations in June and July. The total time spent for the observation was 103 hours (1971) or 118 hours (1976).

**Dissection of ovaries**

To confirm the number of eggs stored in the ovaries, a fresh female which had arrived at the pond and perched on a *Phragmites* leaf near the
water edge without performing oviposition at that time, was collected by a net on June 25, 1978. The insect was fixed with KAHLE's solution on the same day and dissected later on October 16, 1978.

Results

Number of eggs laid

1. The number of eggs laid per one oviposition flight: the average duration of undisturbed oviposition flights was 39.0 sec. (SD = 50.8, range 9–240 sec., n = 22), while it was 22.8 sec. (SD = 19.0, range 9–60 sec.) in five cases which were disturbed by males. The ratio of the disturbed oviposition was 34.3% in 1970 and 1971 (UBUTAKA, 1975). Therefore, the average duration of oviposition flights, including both cases, was calculated to be 33.4 sec.

The average frequency of water striking by which a lump of eggs was washed off was 0.56 times per second (SD = 0.08, range 0.50–0.67, n = 3; 1970, 1971). And the average number of eggs released per one water striking was estimated at 9.8 (SD = 11.1, range 1–30, n = 6) by counting the number of eggs released by females which were captured while laying at the pond and made to dip their abdomens in the bottle water (June–August, 1970, 1978, 1979). Multiplying these three parameters, the average number of eggs (e) laid per one oviposition flight was estimated at 183.

2. The number of oviposition flights per year at NEa: The number of females (f) laying at NEa observed from the adjacent shore per hour under favorable (fine or cloudy) weather is shown in Table 3 for each period of ten days during the reproductive period in 1970 and 1971. The oviposition activity occurred during 4:00–19:00 (UBUKATA, op. cit.), and it was almost independent of either air temperature or overcasting (Fig. 1), with no significant differences (p > 0.05, t-test) between low (5–15°C) and high (15–25°C) air temperatures and between fine and cloudy weather. From this activity pattern, a uniform rate of female arrival for oviposition during 14 hours from 4:30 to 18:30 was assumed for each period of ten days. The number of favorable days (D) when it was warm (air temperature ≥ 5°C) and not rainy is shown in Table 4 for each period of ten days in 1970 and 1971. The total number of oviposition flights (F) per year was calculated by the following formula:

\[ F = 14 \sum f_i D_i \]

where i was each period of ten days. The estimated

Table 3. Seasonal trend of female oviposition activity expressed by the average number of ovipositing females per hour at NEa. The length of time used as the denominator is the duration of observation, except the time of unfavorable weather (i.e., rainy weather) for the oviposition activity during the observation.

<table>
<thead>
<tr>
<th>Period</th>
<th>No. of observation days</th>
<th>Actual observation time (hour)</th>
<th>No. of ovipositing females observed</th>
<th>No. of ( \frac{f}{f} ) /hour</th>
</tr>
</thead>
<tbody>
<tr>
<td>June</td>
<td>11–20</td>
<td>8</td>
<td>5</td>
<td>26.6 15.0</td>
</tr>
<tr>
<td>June</td>
<td>21–30</td>
<td>5</td>
<td>8</td>
<td>14.1 49.5</td>
</tr>
<tr>
<td>July</td>
<td>1–10</td>
<td>8</td>
<td>6</td>
<td>35.1 10.2</td>
</tr>
<tr>
<td>July</td>
<td>11–20</td>
<td>3</td>
<td>3</td>
<td>8.0 14.1</td>
</tr>
<tr>
<td>July</td>
<td>21–31</td>
<td>9</td>
<td>5</td>
<td>19.6 5.7</td>
</tr>
<tr>
<td>August</td>
<td>1–10</td>
<td>3</td>
<td>7</td>
<td>5.3 7.3</td>
</tr>
<tr>
<td>August</td>
<td>11–20</td>
<td>4</td>
<td>4</td>
<td>5.4 1.3</td>
</tr>
</tbody>
</table>
Table 4. Number of days favorable for the oviposition of *C. a. amurensis* during each period of ten (or eleven) days. The day when the minimum air temperature was lower than 5 °C is counted as 0.5 day. The meteorological data were obtained from the records compiled by the Usubetsu Pluviometric Observatory (360 m alt. and 1 km from Hōrai-numa).

<table>
<thead>
<tr>
<th>Period</th>
<th>No. of favorable days</th>
<th>Mean temperature (°C, 9:00)</th>
</tr>
</thead>
<tbody>
<tr>
<td>June 11-20</td>
<td>8</td>
<td>7.5</td>
</tr>
<tr>
<td>June 21-30</td>
<td>7</td>
<td>8.5</td>
</tr>
<tr>
<td>July 1-10</td>
<td>10</td>
<td>8.5</td>
</tr>
<tr>
<td>July 11-20</td>
<td>8</td>
<td>3.5</td>
</tr>
<tr>
<td>July 21-31</td>
<td>10</td>
<td>8.5</td>
</tr>
<tr>
<td>August 1-10</td>
<td>9.5</td>
<td>9</td>
</tr>
</tbody>
</table>

Table 5. Estimated number of individuals of *C. a. amurensis* at sector NE, Hōrai-numa.Italic type, 1970 year-class; bold type, 1971 year-class; Roman type, other year-classes, shown by subscripts: s, 1968; e, 1969; @, 1972; s, 1973.

<table>
<thead>
<tr>
<th>Stage</th>
<th>Age (year)</th>
<th>Month</th>
<th>Number of individuals estimated</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg</td>
<td>0</td>
<td>June-July</td>
<td>144000</td>
</tr>
<tr>
<td>Larva</td>
<td>1</td>
<td>Aug.</td>
<td>1074s</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sep.</td>
<td>704s</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Oct.</td>
<td>1185s</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>May</td>
<td>1333</td>
</tr>
<tr>
<td></td>
<td></td>
<td>June</td>
<td>1481s</td>
</tr>
<tr>
<td></td>
<td></td>
<td>July</td>
<td>1407s</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Aug.</td>
<td>741s</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sep.</td>
<td>185s</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Oct.</td>
<td>148s</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>May</td>
<td>222s</td>
</tr>
<tr>
<td></td>
<td></td>
<td>June</td>
<td>148s</td>
</tr>
<tr>
<td></td>
<td></td>
<td>July</td>
<td>481s</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Aug.</td>
<td>370s</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sep.</td>
<td>37s</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Oct.</td>
<td>37s</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>May</td>
<td>148s</td>
</tr>
<tr>
<td></td>
<td></td>
<td>June</td>
<td>74s</td>
</tr>
<tr>
<td></td>
<td></td>
<td>July</td>
<td>74s</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Aug.</td>
<td>74s</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sep.</td>
<td>148s</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Oct.</td>
<td>37s</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>May</td>
<td>222s</td>
</tr>
<tr>
<td></td>
<td></td>
<td>June</td>
<td>111s</td>
</tr>
<tr>
<td>Emergence</td>
<td>5</td>
<td>June-July</td>
<td>247</td>
</tr>
<tr>
<td>Mature adult</td>
<td>5</td>
<td>June-July</td>
<td>95</td>
</tr>
</tbody>
</table>

Values of *F* were 504 (1970) and 344 (1971).

3. The number of eggs laid per year at NE: Multiplying *e* and *F*, the total number of eggs laid per year at NEₐ was estimated at 9.22 × 10⁴ (1970) or 6.30 × 10⁴ (1971). The ratio of NEₐ to NE in the number of collected exuviae was calculated to be 0.64 from the data shown in Table 6 (for the 1970 year-class) or 0.75 (for the 1971 year-class). Accordingly, the number of eggs laid at NE was estimated at 14.4 × 10⁴ (1970), or 8.4 × 10⁴ (1971) (Table 5).

**Number of the larvae inhabiting NE**

A total of 280 larvae were collected on six occasions of monthly samplings from May to October, 1973, and 215 larvae on four occasions from June to September, 1974. In each population sampled monthly, 3–4 year-classes could be recognized (see Fig. 4 in UBUKATA, 1980), but the presence of an additional year class which was scarcely collected by this method was confirmed by UBUKATA (op. cit.) through rearing newly hatched larvae in the pond. The number of larvae inhabiting NE was estimated for each year-class from the data of the periodical sampling by multiplying the reciprocal of the sampling efficiency (0.027). The result of this calculation is shown in Table 5.

**Number of emerging individuals at NE**

The number of collected exuviae for each year and each sector is presented in Table 6. Multiplied by the reciprocal of the sampling efficiency (0.74), the number of emerging individuals at NE was estimated at 247 for the 1970 year-class (emergence, 1975) or 169 for the 1971 year-class (emergence, 1976) (Table 5).

**Annual change in the size of emerging population**
The size of the emerging population from the whole pond was estimated by the collection of exuviae in every year from 1971 to 1976 (Table 6) except 1973, in which it was estimated at 647 by trapping. The largest population emerged in 1975, which was 2.2 times the smallest population emerged in 1972.

Survivorship during the pre-reproductive period

In 1971, 11 individuals (50%) out of 22 males marked at emergence were rediscovered at the pond during the reproductive period. The ratio 36.4% which was reported in a previous paper (UBUKATA, 1973), was corrected as above. In 1976, the ratio of rediscovered males was 38.4% \((n = 86)\). The emigration to other areas was conveniently regarded as death in the present study since there was no similar aquatic environment within 2 km from the pond. The ratio of females returning to the pond was not investigated because of the difficulty in discovering them. Using the ratio of 38.4%, 95 (1975) and 65 (1976) individuals which emerged at NE were considered to have returned to the pond. However, these ratios may be somewhat underestimated because some individuals might have been overlooked during the observation period.

Maximum longevity of imagines

The maximum longevity of imagines from emergence was confirmed by the last date of rediscovery after marking. The longest record was 50 days (males) or 45 days (females) among the 292 individuals (201 \(\varphi\), 91 \(\sigma\), \(\varphi\)) marked in 1976, while it was 39 days among the 22 males marked in 1971 (females, unknown). The interval between the date of the last observation of emergence (confirmed by exuvial collection) of male and the date of the last observation of adult males at the pond—regardless of whether they were marked or unmarked—was 51 days (males) or 42 days (females) at the maximum during 1971–1976 (cf. UBUKATA, 1975). These values support the estimates of the length of maximum longevity obtained from marking and rediscovery. No adult was observed anywhere around the pond after the date of the last visit of adults to the pond until the next emergence season, suggesting the virtual absence of the post-reproductive period.

Survivorship from egg to mature adult

The number of individuals estimated in the pre-
Mortality factors during the larval period

During the rearing experiment in the pond, out of ten individuals which were 4–13 mm in body length (estimated ages, 2–3 years; cf. UBUKATA, 1980) on May 28, 1976, six individuals had died by November 25, 1976 (Fig. 3, B). Predation and starvation were excluded as the causes of their deaths, because the bottles were covered by nets and sufficient food (*Tubifex*) was always present in their bottles. The lack of oxygen was also excluded, since the nets were washed almost semimonthly to facilitate the circulation of water.

In the laboratory, three out of ten individuals with body length (BL) 4–13 mm died during the rearing period from May 19 to November 28, 1973 (Fig. 3, A). The situation was quite similar to that of the rearing in the pond. In this case starvation was considered to be of slight importance among the mortality factors, since eight larvae with BL 15–21 mm survived without any food beyond three weeks in another experiment in the laboratory (October, 1973).

In the course of the larval collection at the pond, the following events were observed. A larva with BL 4.3 mm (estimated age, 1 year) was killed and consumed by a larva of the same species with BL 21.3 mm (estimated age, 5 years; final instar) soon after both were collected and released in a bucket (May 17, 1973). In another case, a larva with BL 11 mm (estimated age, 3 years) was killed by a full-grown larva (BL 37 mm) of *Aeschna nigro-

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**Fig. 2.** Survivorship curve of *C. a. amurensis* at Hōrai-numa. The data of all year-classes investigated were combined. Average values (●) and standard deviation (vertical bar) were calculated separately for the first half (May–July) and the latter half (August–October) of each year. Stages: E, egg; 1–F, larval instars; I, imago. Point of time: h, hatching; e, emergence. Months: J, June; D, December.

**Fig. 3.** Survivorship curves in the larvae of estimated ages 2–3 years, in terms of the number of those alive in late May–early June. A: That of ten larvae with body length 4–13 mm (ages, 2–3 years) reared in the laboratory. B: That of ten larvae of the same sizes reared in the netted bottles in the pond. C: That of natural population with body length 4–9 mm (age, 2 years). Vertical bar: 95% confidence limits in Poisson distribution.
flava MARTIN in the bucket (July 2, 1973). In addition, a dead larva (BL 8.2 mm; estimated age, 2 years) without any wound was collected on June 30, 1973, which shows the presence of mortality factor other than predation.

Mortality during emergence

The mortality during emergence was investigated in 1971 by intensive observations at the pond shore. In total, 4.2% of the emerging population (n = 265) died between the start of emergence and maiden flight due to the predation by jays, Garrulus glandarius pallidifrons KUBODA, (2.6%) and ants, Myrmica ruginodis NYLANDER, (0.4%) or to failure in emergence (0.8%) (UBUKATA, 1973). Another possible predators sometimes observed were wagtails, Motacilla cinerea LEACH.

Mortality factor during imaginal period

In the course of the field survey during 1970–1979, only one case was recorded as a cause of death for the imagines (excluding the emerging ones): the dead body of a mature male caught in a spider’s web was found in the marginal vegetation of the pond (July 21, 1979).

Number of eggs stored in the ovaries

The number of mature eggs (light brown–dark brown) contained in the abdomen (ovary and oviduct) of the female dissected was 1,804, while the immature eggs (unpigmented) numbered less than 30. Several other females were also dissected, but the numbers of eggs stored were much less than the above, possibly due to the experiences of oviposition. In a female collected from the pond on July 31, 1979, there were counted 698 ovarioles in the paired ovaries.

Discussions

Survivorship

Curiously, the population studies of Odonata so far published have dealt with either the aquatic or the imaginal periods. A survivorship curve of Odonata from egg to mature adult has been obtained probably for the first time in the present study (Fig. 2). The curve of C. a. amurensis at Hôrai-numa bears a stepwise shape due to the low winter mortality rate3. The cause of the increase in survival rate during winter is surmised to be a reduction of feeding activity of predators due to the cooling of the pond water in winter (0–2°C; cf. Fig. 1 in UBUKATA, 1980). Similar falling of the mortality rate during winter can be also detected in the data of Pyrrhosoma nymphula SULZER and Epitheca spp. reported by LAWTON (1970) and BENKE & BENKE (1975), respectively. The survivorship curve of C. a. amurensis aloso suggests that the mortality rate during the early aquatic stages is higher than that during the later larval stages (Type III; DEEVEY, 1947), apart from the winter inactive period. Among the four authors who studied the survivorship of Odonata during the larval period, KURATA (1974) also showed data suggesting higher mortality during early instars than during later instars in Aeschna juncea (L.). Whereas MACAN (1964), LAWTON (op. cit.) and BENKE & BENKE (op. cit.) assumed uniform mortality rates throughout this period (Type II). The factors causing the higher mortality rate during the early larval stages of C. a. amurensis will be discussed later in the next section.

The present study suggests that about 0.07% (1970 year-class) or 0.08% (1971 year-class) of the initial population participated in reproduction five years after laying. The estimated numbers of eggs laid which must have the deepest influence on these rates were tested here. Multiplied by the sex ratios (♀ / ♀ + ♂) at emergence the percentage of surviving females to the total eggs laid was estimated at 0.04% (1970 year-class) or 0.05% (1971 year-class). The reciprocals of these values were 2,500 and 2,000, respectively, which were slightly larger than the number of eggs stored (1,800) in the ovaries of the dissected female, suggesting that the number of eggs laid was overestimated. It should be also considered that many females probably died before laying all the eggs stored. However, some of the other females might have continued to lay more eggs than 1,800 by subsequent oogenesis. Therefore, the difference between the estimated number and the actual number of eggs laid was not so large to such an extent that one was several times as large as the other. Unfortunately, the age specific fecundity could not be estimated in the present study. Estimation of this value is an urgent subject for researchers of odonate populations.

Stability of population size

A considerable stability was observed in the size

3) In the present paper, the term 'mortality rate' means the instantaneous mortality rate.
of emerging populations of *C. a. amurensis*: the maximum size was only 2.2 times the minimum one among the six year-classes surveyed. Similar stability in an emerging population of Odonata was also seen in two pond dwelling species, *P. nymphula* and *Enallagma cyathigerum* (Charpentier) (Macan, 1974). On the other hand, Kurata (1971) reported a case of instability in the number of emerging individuals of *Gomphus melanoeps* Selys at a stream: the maximum value was 13-fold of the minimum one among 11 successive year-classes. Kurata (op. cit.) pointed out that the change of the amount of flowing water probably have the greatest influence on the size of an emerging population, whereas the dwellers of permanent ponds, including *C. a. amurensis*, are free from such a catastrophic factor. In addition, the presence of a mechanism of population stabilization is expected for the population studied herein because of the narrowness in the range of population fluctuation. In the present paper, the possibility of population regulation by density-dependent mortality during larval and pre-reproductive periods is discussed in spite of the paucity of available data.

In a permanent pond such as Hōrai-numa, the mortality of odonate larvae is considered to be caused by either of disease, starvation or predation (cf. Benke, 1978). In the present study, the mortality rate was 89% for the five months around summer in the natural population (age, 2 years) of *C. a. amurensis* (Fig. 3, C; Table 5), while it was 60% for the six months around summer in the reared population (age 2–3 years) which was kept in netted bottles on the pond bottom. Higher mortality of the natural population was also suggested at age 3 years (83%, 1970 year-class; cf. Table 5). The difference in the rate between the netted and the natural populations would be much larger, because the deaths in the netted population occurred mostly during the first month of the rearing experiment (Fig. 3, B), which suggests the presence of individuals that could not adapt to the environments in the bottles. Excluding this first month, the mortality rate (per three months) from early July to early October was 20% in the netted population (n = 5), while it was 88% in the natural population (the number of collected larva = 34), which was significantly higher than the former (p <0.01; by Fisher’s direct probability method). Comparing these percentages, it is inferred that most of the mortality during the larval period was due to predation or starvation. The latter was unlikely to be a major mortality factor as was supported by the rearing experiment conducted in the laboratory, even if the growth was delayed (cf. Corbet, 1962; Lawton et al. 1980). On the other hand, predation is undoubtedly a major cause of the odonate mortality, judging from the direct observations (predation by *A. nigroflava* and by conspecifics) in the present study and from the reports of the gut content of predators (Pritchard, 1964; Benke, 1978; etc.). In the pond Hōrai-nama, *Notonecta reuteri* Hungerford and unidentified fishes were frequently observed, which were regarded as possible predators of *C. a. amurensis*. From these considerations, the higher mortality during the early larval stages is surmised to be caused by heavier predatory pressure during these stages.

Concerning the 'regulation' of prey (host) density by predation (parasitism), many models have hitherto been presented (e.g., Lotka, 1925; Nicholson & Bailey, 1935; Holling, 1959; MacArthur & Connell, 1966). The density of a prey can be regulated by either or both of functional and numerical responses of the predator (Holling, 1959). The regulation of this cordulid population by numerical response seems to be improbable, because there was no indication of the presence of a monophagous or oligophagous predator which preys continuously on *C. a. amurensis*. The sigmoid functional response is a clear stabilization mechanism (Holling, 1961). Lawton et al. (1974) and Akre & Johnson (1979) revealed that a backswimmer, *Notonecta glauca* L. and a larval damselfly, *Anomalagrion hastatum* (Say), respectively, can show this type of response in the laboratory due to the switching of prey species (cf. Murdoch, 1969). Although the density ratio of *C. a. amurensis* in the prey community is relatively low (14% of the collected odonate larvae in 1973; Ubukata, unpub.), it is likely that the local density of this species is relatively high in microhabitats of certain types (e.g., underside of bog mats, on the fallen leaves of Carex, etc.). Therefore, the possibility that this regulation is accomplished by switching in general predators is not yet rejected. Another possible cause behind sigmoid functional response is the presence of refuge space in which the searching efficiency of predators is reduced (Murdoch, 1973). Macan (1974) suggested the significance of refuge space in the stabilization of an odonate population. In addition,
BENKE (1978) demonstrated that mutual predation among coexisting odonate species and cannibalism regulate the population density of each species under the presence of refuge space. As there are no additional data to test the existence of these mechanisms in C. a. amurensis, the following works should be done for the verification of these mechanisms: experimental removal and addition of prey, predator and aquatic vegetation (refuge) in an enclosed site in the pond, and descriptive studies such as behavior, microdistribution, population density and biomass of the species concerned, such as those executed partly by BENKE (1978).

On the other hand, in the present case, population regulation would have been probably in effective during the emergence and the pre-reproductive periods, because the predation pressure (mainly by birds) did not seem to be high during the emergence period, the emergence usually occurred on the underside of the leaves of Menyanthes trifoliata L., Phragmites communis Trinius, etc. (cf. UBUKATA, 1973), and all the imagines dispersed widely after maiden flight till the start of the reproductive period.

In conclusion, it is presumed that population regulation mechanisms operate in the larval stage during which a sigmoid functional response in predators is expected. The possibility that territoriality may play a role for the population regulation, as MOORE (1953, 1957) and Ito (1978) suggested, will be tested in a subsequent paper.

References


*in Japanese, **in Japanese with English summary, †not directly accessible.

**摘　要**
トンボ類の個体群動態の研究は、これまで、幼虫または成虫のいずれか一方のステージについてのみ行われ、全生活史を通じた生存率の調査結果は知られていない。本研究は1970年から1976年までにかけて、札幌市郊外の宝来沼において、カラカネトンボの個体群を材料として行われ、それにより、卵から成熟成虫までの生存曲線が得られた。

1. 1966年から1973年までの全級群を平均して推算された生存曲線は、冬期死亡率の低い階段状を呈し、夏期死亡率においては幼虫期前半において高い傾向（DEVEREY, 1947）を示した。

2. 産後5年間の水中生活期（卵・幼虫期）の間に、個体群の99.8％が死亡すると推定された。さらに、生存期まで生存する個体は約0.07％と推定された。

3. 他内で網かけ飼育をした実験個体群の死亡率は、自然個体群のそれより有意に低かった。本種幼虫が、オオリボシャシ等により捕食されるのが目撃され、飢餓は直接の死亡に結びつかない（飼育実験）ことから、幼虫期における主な死亡要因は被食であると推定された。

4. 6年間の調査で、各年度の羽化個体数の最大値は最小値の2.2倍にすぎなかった。この安定性の原因として、幼虫期における、①捕食者の食物選択におけるスイッチング、②避難場所による被食抑制、という二つの可能性が指摘された。