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Citation	北海道大學理學部紀要, 19(3), 758-776
Issue Date	1974-10
Doc URL	http://hdl.handle.net/2115/27585
Type	bulletin (article)
File Information	19(3)_P758-776.pdf



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Relative Abundance and Phenology of Adult Dragonflies at a Dystrophic Pond in Usubetsu, near Sapporo¹⁾

By

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(With 4 Text-figures and 5 Tables)

Concerning the ecology and biology of the order Odonata, a good number of studies have so far been accumulated on the local fauna, life, history, ethology, etc. However the intensive studies at particular localities on the relative abundance and phenology have been hitherto relatively ignored except some precursory studies (Schmidt 1964, 1971, Miyakawa 1967 and Consiglio *et al.* 1972). Nevertheless, this approach is recommended to have basic data to apprehend community structure or interspecific relation of the Odonata.

Partly guided by this idea and partly forced by the necessity of having a sound background for the life history studies of particular odonate species, this survey was conducted periodically in 1971 at a mountainous dystrophic pond by counting the number of individuals.

Area studied

The survey was carried out at Hôrai-numa (Pond A, 530 m alt.), a mountainous dystrophic pond located at the foot of Mt. Muine (1,461 m alt.) near Sapporo. The pond is nearly circular and 222 m in shore contour, surrounded by bog mats covered mainly with *Phragmites* and *Sphagnum* and a deciduous broad-leaf forest with admixture of afforested conifers, isolated considerably (ca. 2 km) from any other stagnant waters. The aquatic vegetation consists mainly of *Menyanthes* and *Potamogeton*. The topography and vegetation are given in a previous paper (Ubukata 1973). The water is ca. 2 m deep including relatively poor aquatic fauna. The climatic conditions in Usubetsu (390 m alt.), 1 km apart from Hôrai-numa, given in Fig. 4 are Dbf (Köppen) or A''₃ (Kira) in climatic formula.

Methods

The seasonal trend of emergence of each species was surveyed from June 3 to August 14, 1971 by two different procedures, collection of exuviae and census of teneral individuals.

1) Studies on the biology of Japanese Corduliidae II.

J. Fac. Sci. Hokkaido Univ. Ser. VI, Zool. 19 (3), 1974.

Collection of exuviae: This procedure was executed for larger species of aeschnids, corduliids and libellulids. All exuviae found out were collected by examining the vegetation of the zone of 2 m wide along the water edge with a bamboo stick of one meter long almost every late afternoon and recorded as to sex and freshness. The number of exuviae collected during the survey must fairly reflect the real number of emerging population on a given day, since the emergence of Odonata mostly ends by mid afternoon.

Census of teneral individuals: This procedure was adopted for smaller species such as zygopteran and gomphid species which emerge often vastly and stay at the emergence sites for some intervals. The counting was made by walking every day along the water edge for ca. 30 min. at about noon. This method is not suitable for the interspecific comparison of emerging population, since daily rhythm of emergence and the duration of resting after emergence differ among species. However, the result can be utilized as a first approximation to the seasonal trend of emergence of each species.

Census of active individuals: In order to get a perspective on relative abundance and phenology during reproductive period, the census of *active individuals* or precisely *mature individuals within reproductive site* was executed every week around 13:00 of warm days from May 20 September 25, 1971. The hour of counting nearly coincides with the peak of daily activity of most species (12:00), except for *Sympetrum* spp. with the peak at about 10:00. The weather of census days was fine and not windy except June 6 (VI-1, cloudy), August 26 (VIII-4, cloudy) and September 25 (IX-5, cloudy). The census procedure was as follows: Walking slowly around the pond (ca. 15~30 min. for a turn around the shore), every mature individual was counted and recorded with regard to species, sex, and the performance of tandem or copula. Besides this periodical census, supplementary census and collecting were made between census days throughout the dragonfly season, May 20~October 25, which added some strayer species to the faunal list (Table 1).

Results and discussions

Results are divided into three parts, faunal composition, relative abundance and phenology. Some related discussions are given in each section.

1. Fauna of Hôrai-numa

The Odonata species collected or observed during the survey 1970~1973 are listed in Table 1 in the order of altitudinal preference of distribution, together with the distribution in Sapporo and the vicinity reported by Nagase and Hoshikawa (1968). Nine asterisked species out of 21 recorded ones belonging to eight families are residential in Hôrai-numa. Other 12 species are strayers, showing neither emergence nor stable oviposition activity. As for the species number, Libellulidae (8 spp.) occupies the 38.0%, followed by Agrionidae (3 spp.), Corduliidae (3 spp.), Lestidae (2 spp.) and Aeschnidae (2 spp.).

Faunal comparison with some other localities: Comparing the result given above with that in hilly and plain areas in Sapporo and the vicinity, 10 out of 21 species (47.6%) recorded at Hôrai-numa are common to the both. Six species are common only to the hilly area, and four species are so far known at Hôrai-numa alone. Three of these four species are typical high moor dwellers. On the other

Table 1. The species observed or collected at Hôrai-numa in 1970~1973, together with the record in Sapporo and the vicinity (Nagase and Hoshikawa 1968). Fam: Family name abbreviated with initial letters (Ag: Agrionidae. Le: Lestidae. Ca. Calopterygidae. Go: Gomphidae. Ae: Aeschnidae. Cg. Cordulegasteridae. Co: Corduliidae. Li: Libellulidae). D: Distribution type (after Asahina 1955; N₀: Holarctic. N: Palaearctic. N': North-Manchurian. S': South-Manchurian. S: Oriental. H_n and H_s: Endemic to Japanese Archipelago — Northern and Southern origin). H.P.: Habitat preference (after Asahina op. cit.; LR. Lowland running water. LS: Lowland stagnant water. MS: Mountain stagnant water. HM: High moor). Record: + Recorded, — Not recorded, * Residential.

Species	Fam.	D.	H.P.	Hôrai-numa (Pond A)	Sapporo	
					low mountains	plains
<i>Sympetrum danae</i> (Sulzer)	Li	N ₀	HM	+	—	—
<i>Leucorrhinia dubia orientalis</i> Selys	Li	N	HM	++	—	—
<i>Cordulia aenea amurensis</i> Selys	Co	N	HM	++	—	—
<i>Trigomphus melampus</i> (Selys)	Go	H _s	LS	++	—	—
<i>Epiheca bimaculata sibirica</i> Selys	Co	N	MS	+	—	—
<i>Enallagma deserti yezoensis</i> Asahina	Ag	N	MS	+	+	—
<i>Aeschna nigroflava</i> Martin	Ae	H _n	MS	++	+	—
<i>Somatochlora uchidai</i> Foerster	Co	H _n	MS	++	+	—
<i>Mnais strigata</i> Selys	Ca	H _s	LR	+	+	—
<i>Anotogaster sieboldii</i> (Selys)	Cg	N'	LR	+	+	—
<i>Sympetrum baccha matutinum</i> Ris	Li	S'	LS	+	+	—
<i>Agrion lanceolatum</i> Selys	Ag	N'	MS	++	+	+
<i>A. terue</i> Asahina	Ag	H _n	MS	++	+	+
<i>Lestes sponsa</i> (Hansemann)	Le	N	LS	++	+	+
<i>Sympecma paedisca</i> (Brauer)	Le	N	LS	++	+	+
<i>Libellula quadrimaculata asahinai</i> Schmidt	Li	N ₀	MS	+	+	+
<i>Orthetrum albistylum speciosum</i> (Uhler)	Li	N	LS	+	+	+
<i>O. japonicum japonicum</i> (Uhler)	Li	S'	LR	+	+	+
<i>Sympetrum frequens</i> (Selys)	Li	H _n	LS	+	+	+
<i>S. infuscatum</i> (Selys)	Li	N'	LS	+	+	+
<i>Anax parthenope julius</i> Brauer	Ae	N	LS	+	—	+

hand, 18 species known in Sapporo are not distributed at Hôrai-numa. Among them, six are stream dwellers and 10 inhabitants of lowland ponds, leaving two species with preference for mountain stagnant waters, that is, *Aeschna juncea* (Linné) and *Somatochlora viridiaenea viridiaenea* Uhler.

Compared with other boreal moor habitats hitherto studied (Ozegahara, Central Honshu, Asahina 1954; Futatsu-yama, Kushiro marsh, Eastern Hokkaido, Iijima 1972), the number of species common to both is 20 (95.2% of species of Hôrai-numa), showing a clear similarity to other high or intermediate moor habitats in Northern Japan. However, the predominant species of Hôrainuma consists of pond dwellers such as *A. lanceolatum* and *L. sponsa*. In conclusion, the general feature of the Odonata fauna of Hôrai-numa can be regarded as a situation intermediate between eutrophic lake and oligotrophic moor, as is suggested by the

composition of aquatic vegetation, too, especially *Phragmitis*, *Potamogeton* and *Sphagnum*.

Ratio of northern and southern elements: Asahina (1955) analysed the Odonata fauna of Nagano Prefecture based on the distribution types of component species. As shown in Table 1, the fauna of Hôrai-numa is mainly composed of northern elements ($N_0 + N + N' + H_n$), which occupy 81.0% of the total species number. The ratio is comparable to that of Futatsuyama (83.1%), while higher than that of Sapporo (67.6%) and Ozegahara (62.9%). The difference from Sapporo and Ozegahara is apparently due to the avoidance of high moor habitat by southern elements and replacement of northern elements by southern ones in parallel with the latitude.

2. Relative abundance

2.1. Relative abundance in mature adults

A total of 2,147 mature adults belonging to 11 species were censused through the periodical survey in 1971 (cf. Appendix). Table 2 shows the result with the number of individuals and percentage ratios. From the table, *A. lanceolatum*, *L. sponsa* and *A. nigroflava* are regarded as dominant species in mature adults, occupying in combination 80.5% of the total individuals censused. Among other eight species, *S. paedisca*, *T. melampus* and *C. aenea* are relatively abundant. The real ratios of *Sympetrum* spp. must be higher than in the result, since their daily activity strongly decreased at the census time in afternoon.

Table 2. Relative abundance in mature adults censused through the periodical survey, 1971. ♂, ♀: Solitary and pairing individuals combined.

Species	Number of individuals censused				% (♂+♀) to total number	Sex ratio (% ♂ ♀)
	♂	♀	tandem + copula	♂ + ♀		
<i>A. lanceolatum</i>	509	208	204	717	33.4	71.0
<i>L. sponsa</i>	495	175	149	670	31.2	73.9
<i>A. nigroflava</i>	40	302	0	342	15.9	11.7
<i>S. paedisca</i>	131	35	35	166	7.7	78.9
<i>T. melampus</i>	111	9	7	120	5.6	92.5
<i>C. aenea</i>	87	1	0	88	4.1	98.9
<i>S. uchidai</i>	24	2	1	26	1.2	92.3
<i>L. dubia</i>	14	0	0	14	0.7	100.0
<i>S. frequens</i>	2	0	0	2	0.1	100.0
<i>S. infuscatum</i>	1	0	0	1	0.05	100.0
<i>S. danae</i>	1	0	0	1	0.05	100.0
Total	1,379	715	396	2,147	100.0	64.2

2.2. Relative abundance in emerged individuals

The density of active individuals depends on the mode of reproductive behavior characteristic of each species (2.3.2). Therefore the relative abundance obtained by the census of active individuals must be compared with that by emerged individuals, which gives a better approximation to the real abundance ratio of the inhabitant species.

The number of exuviae collected, teneralis counted or collected and final instar larvae collected immediately before the emergence period of each species are listed in Table 3 in the descending order of the size of emerging population. As to the collection of exuviae (1971) for larger species, the order is *A. nigroflava* (1,577) > *C. aenea* (255) > *S. uchidai* (33) > *L. dubia* (0, 1971; 2, 1970). The relative abundance in teneralis of spring species was estimated by collecting with nine emergence traps (1 m × 5 m) placed on the water edge at regular intervals in 1973. The order is as follows: *A. lanceolatum* (220) > *C. aenea* (185) > *T. melampus* (64). Unfortunately the trapping was not executed for the summer species.

Table 3. Relative abundance in emergence assemblage. -: not investigated.
(): collected in 1970.

Species	Number of exuviae collected, 1971	Number of teneralis collected by trap, 1973	Number of teneralis counted, 1971	Number of final instar larvae collected, 1973
<i>A. lanceolatum</i>	-	220	740	207
<i>L. sponsa</i>	-	-	173	-
<i>A. nigroflava</i>	1,577	-	0	27
<i>C. aenea</i>	255	185	0	6
<i>T. melampus</i>	-	64	17	3
<i>S. uchidai</i>	33	-	0	0
<i>L. dubia</i>	(2)	0	0	0
Total	1,865	469	930	243

A periodical larval sampling was made along the northern shore (a~g; Fig. 1B, Ubukata op. cit.) during May to October, 1973. The number of the final instar larvae collected soon before the emergence period (less than a half month) would have a correlation with the number of emerged individuals. In these final instar larvae (spring species, May 16~17; Summer species, June 30~July 3), the order was *A. lanceolatum* (207) > *A. nigroflava* (27) > *C. aenea* (6) > *T. melampus* (3) > *S. uchidai*, *L. sponsa* (0). The full grown larvae of lepid species were not represented in the collecting, partly due to the collecting method employed. Assuming the constancy of the abundance order between 1971 and 1973, the following order is obtained from three different procedures as the most reliable estimation for emerging assemblage: *A. lanceolatum* > *A. nigroflava*, *L. sponsa* > *C.*

aenea > *T. melampus* > *S. uchidai* > *L. dubia*. Ignoring the species such as *S. paedisca* and *L. sponsa*, whose exuviae, larvae or teneral were not collected quantitatively, the abundance order disregarding the difference in sexes generally coincides between two stages except for *C. aenea* and *T. melampus*.

2.3. Sex ratio

2.3.1. Sex ratio in emerging population: The ratio given by male percentage in emerging population was confirmed in the following four species: *T. melampus* (tenerals observed on June 12, the date of seasonal peak of emergence: 26 ♂, 30 ♀; 46.4%), *C. aenea* (exuviae collected throughout the season: 131 ♂, 117 ♀, 52.8%), *A. nigroflava* (ditto: 752 ♂, 819 ♀; 47.9%), *S. uchidai* (ditto: 15 ♂, 17 ♀; 46.9%). In each species the ratio did not significantly deviate from the ratio 1:1 in χ^2 test ($P > 0.05$), expected from the sex determination mechanism in the Odonata studied cytologically (Omura 1955, '57).

2.3.2. Sex ratio in mature stage: There are found some significant deviation from the ratio 1:1 ($P < 0.001$ in χ^2 test) in mature individuals at the pond (Table 2), ranging 70~80% in *A. lanceolatum*, *S. paedisca* and *L. sponsa* (all zygopterans), 90~100 in *T. melampus*, *C. aenea*, *S. uchidai* and *L. dubia* (exophytic anisopterans), while ca. 10 in *A. nigroflava* (an endophytic anisopteran). This disparity is evidently caused not by real sex ratio in the adult population but the difference in the pattern of the reproductive behavior. First, as to the type of oviposition, the endophytic oviposition of zygopteran and aeschnid species leads to a prolonged stay of the laying female at the pond, making superficially the female density higher than those adopting exophytic oviposition such as gomphids, corduliids and libellulids. Secondly, the prevalence of the territorial behavior delimits the male density at the breeding site (Moore 1953), shown by the low male density of *A. nigroflava* and *C. aenea* compared with that of zygopteran and gomphid species. Thirdly, the male pre-mating behavior affects the sex ratio. The species of cruising type, for instance, corduliids and aeschnids, tend to stay at the breeding site much shorter than the perching type species such as zygopterans, gomphids and libellulids. Furthermore, the shorter reproductive period of female in some species, especially *A. lanceolatum* and *L. sponsa*, results in the high male ratio.

3. Phenology

3.1. Phenology of emergence period

At Hôrai-numa the emergence of the Odonata begins in early June and continues till mid August (Fig. 1). The studied species can be divided into two seasonal types, spring and summer species (cf. Corbet 1954) except for *S. paedisca*. The former emerges from early June till late June with a considerable synchronization in early or mid June, while the latter from late June to early August with a

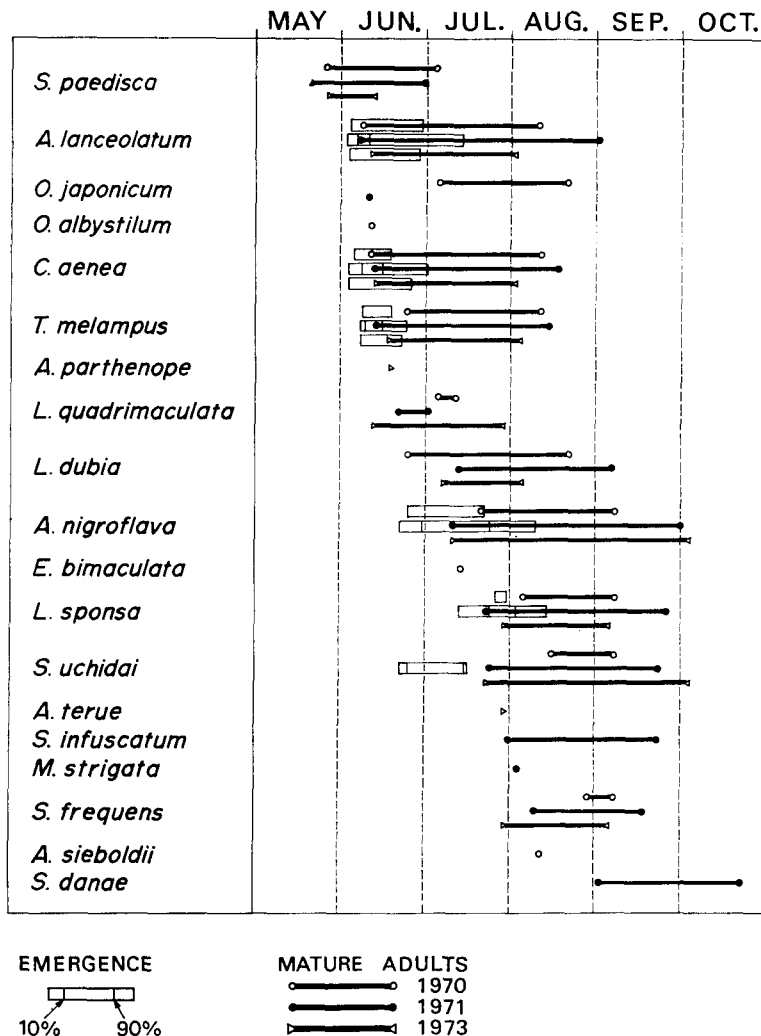


Fig. 1. Phenological sequence of odonate species at Hôrai-numa. The survey was less intensive in 1970 and 1973.

less pronounced synchronization (Fig. 2). *A. lanceolatum*, *C. aenea* and *T. melampus* are spring species, while *A. nigroflava*, *L. sponso* and *S. uchidai* summer ones. *S. paedisca* is a hibernating species, deviating from both types mentioned.

Emergence trend in each species is mentioned below. The emergence period means here the period during which the emergence continuously takes place,

excluding the exceptionally (more than five days) early or late emergence. The term, " EM_{10}^{90} ", used here means the interval in days between two dates by which respectively 10 and 90% of the annual population emerged (Fig. 2). The value of EM_{10}^{90} is inversely proportional to the degree of synchronization in emergence. The significance of the index is discussed in Concluding remarks.

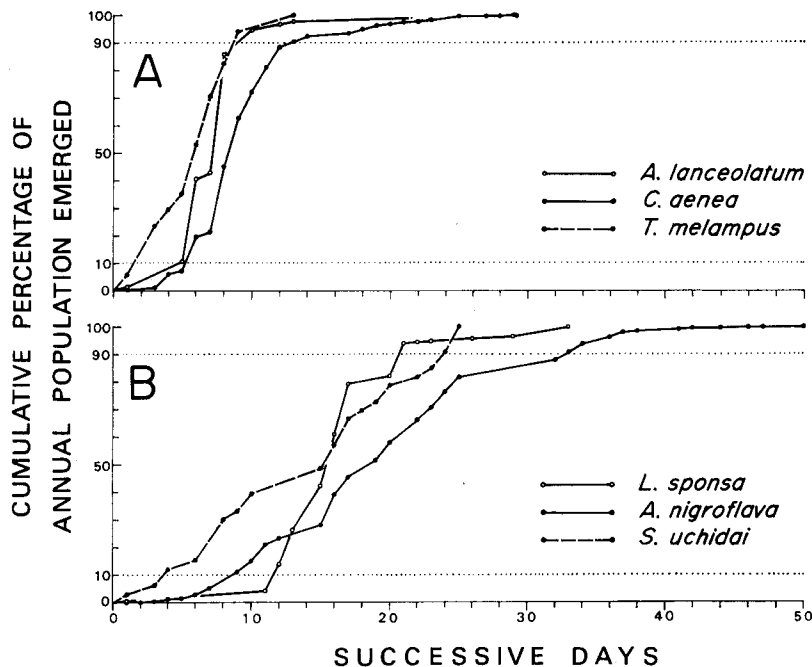


Fig. 2. Emergence curve of six dominant species: A, spring species. B, summer species.

Spring species

A. lanceolatum: Main emergence period from June 2 to 26, with clear synchronization around June 9, 90% emerging between June 5 and 11 ($EM_{10}^{90}=4$).

C. aenea: Continuous emergence from June 6 to 21 (♂) or 27 (♀) with peak on June 10 (♂) or 11 (♀). The value of EM_{10}^{90} was 7 in 1971 and 1972 as well (cf. Ubukata, op. cit.).

T. melampus: Teneral adults observed from June 7 to 19 with a prominent peak around June 12 ($EM_{10}^{90}=6$).

Summer species

A. nigroflava: Exuviae collected from June 23 (♂) or 26 (♀) to August 1 (♂) or 5 (♀). Synchronization weak ($EM_{10}^{90}=24$).

S. uchidai: Exuviae continuously collected from June 25 (♀) or 29 (♂) to July 7 (♀) or 15 (♂). Synchronization weak ($EM_{10}^{90}=20$).

L. sponsa: Teneral continuously seen from July 22 to August 13 with a relatively synchronized tendency ($EM_{10}^{90}=9$).

There is no essential difference in emergence period between 1970 and 1971 except for *L. sponsa* which delayed in the date of the first emergence by 13 days in 1970 than in 1971. However, the emergence of *L. sponsa* might be not so late in 1970, since the routine counting of teneral was not undertaken in this year and no survey was made during July 10~19, which must have decreased the chance of discovery. Among the species studied, only *A. nigroflava* exhibited a sexual lag in emergence period: Males appearing ca. six days earlier than females.

3.2. Phenology of adult stage

3.2.1. Seasonal change of species and individual numbers: The assemblage in May consisted of only one species, *S. paedisca*. Thereafter the number of species first increased in June, by the maturation of spring species (Figs. 3A and 4). About one month later the number increased again due to the maturation of the summer species. After the peak in early August (=7), the number decreased with two steps, by the disappearance of the spring species in mid August, and of the summer species in late September.

The total individual number fluctuates with four characteristic peaks throughout the dragonfly season, late May~late September (Fig. 3B). The first peak in late May is caused by the reproductive activity of *S. paedisca*. Thereafter the second, third and last peaks respectively correspond to the activity peaks of *A. lanceolatum* (end of June), *L. sponsa* (mid August) and *A. nigroflava* (early September).

3.2.2. Phenology of predominant species: Phenology of predominant species is described as to fluctuation of individual number, length of pre-reproductive (or maturation) period, of reproductive period and of maximum adult life span, based upon the data obtained in 1971 (Figs. 1 and 3C). The methods calculating these items are as follows (cf. Moore 1951 and Veron 1973). Length of pre-reproductive period: Interval between the dates of earliest emergence and of earliest appearance of mature individual at the pond. Maximum adult life span: Interval between the dates of last emergence and of last visit of mature individual at the pond. Reproductive period means the period of continuous existence of mature adults at the pond, that is, the first to last visit of *single* adult for cruisers (corduliids, male of aeschnids), or the last visit of *plural* adults for perchers (zygopterans, gomphids, libellulids and female of aeschnids) in order to exclude exceptionally early or late individuals.

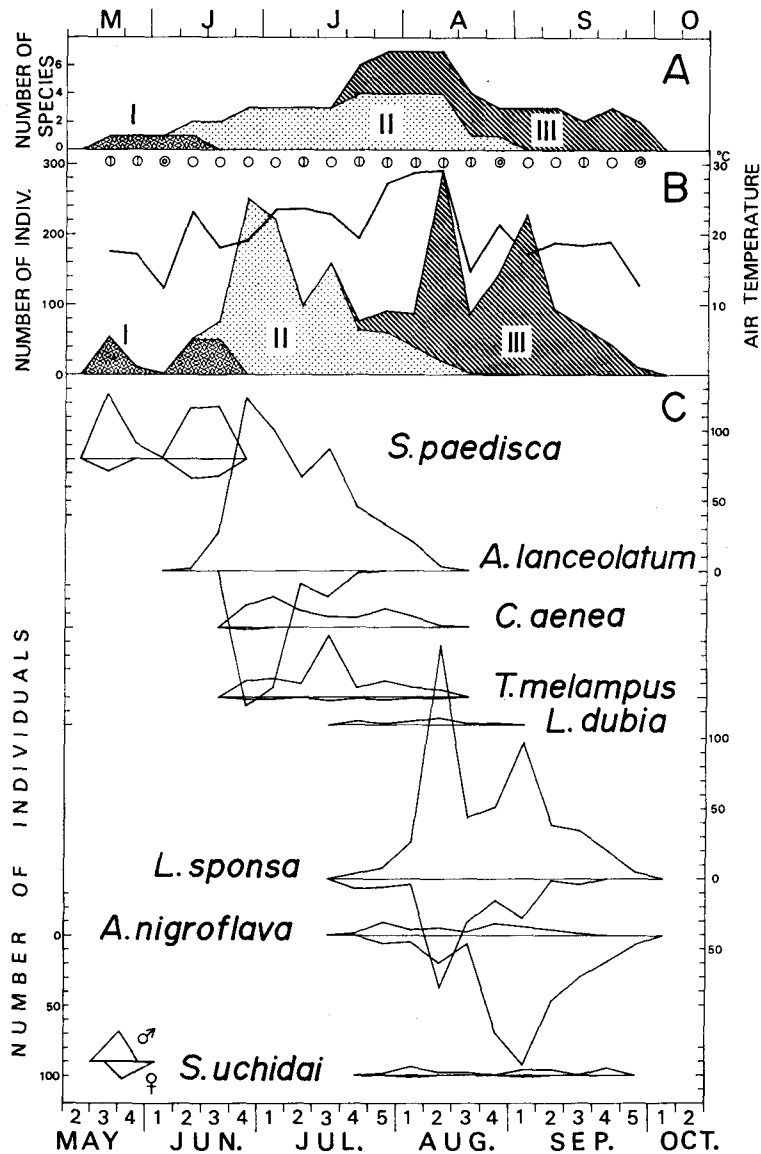


Fig. 3. Seasonal change of the number of species and individuals, together with the weather conditions at the census hour. Explanations are given as follows: A. species number of dragonflies censused: I, II and III, hibernating, spring and summer species. B. Total individual number with scale at left hand: I~III, ditto; Thick line, air temperature with scale at right hand; Symbols, amount of cloud: ○, 0~20%; ⊕, 20~80%; ⊙, 80~100%. C. Individual number of each species.

Hibernating species

S. paedisca: Posthibernating adults rapidly started the reproductive activity on May 20 and continued till June 16. A conspicuous fall of activity in early June was caused by the cloudy and cool weather of the census day. Both sexes were seasonally well synchronized. The adult life span must be 8~9 months or 2~3 excluding the hibernation. Emergence period is unknown but expected as August to September at Hōrai-numa. In 1970 the start of reproductive activity was explosive: No adult was observed in the afternoon, May 19, 22 and 23, nevertheless weather was fine enough, while more than 100 pairs were laying eggs in the afternoon, May 24.

Spring species

A. lanceolatum: Mature adults returned to the pond on June 7 (♂) or 15 (♀), that is 5 (♂) or 11 (♀) days after the emergence. The number of active adults reached the peak in late June and decreased thereafter till the disappearance on July 14 (♀) or August 14 (♂). From this sexual difference in decreasing trend, the average longevity of the female appears shorter than in the male. The maximum adult life span observed was 50 (♂) or 14 (♀) days.

C. aenea: The length of pre-reproductive period was 9 (♂) or 16 (♀) days. The reproductive period was from June 12 (♂) or 19 (♀) to August 17 (♂) or 6 (♀). As mentioned in 2.3.2, the male density is limited below 26 individuals caused by the territorial behavior (Ubukata, unpubl.) The maximum adult life span was 51 (♂) or 36 (♀) days.

T. melampus: Mature adults appeared on June 24 (♂) or 25 (♀), that is 6 (♀) or 12 (♀) days after emergence. The activity continued till July 7 (♀) or August 9 (♂) with a peak in mid June. The maximum adult life span was 56 days.

L. dubia: Mature males appeared from July 23 to August 7. In 1970 the males appeared ca. 20 days earlier than in 1971 (Fig. 1). This annual difference presumably owes to the small population size (highest number censused=5) of *L. dubia*, by which individual difference in emergence date affects directly the flight season of the population. Only one female was observed on August 5, 1971 throughout the survey. The emergence trend was undetermined so that pre-reproductive period and maximum adult life span remained unknown.

Summer species

L. sponsa: The length of pre-reproductive period was 10 days. The number of mature adults gradually increased from the first date, July 22, to early August and reached the peak in mid August. It dropped in late August for low temperature or cloudy weather and recovered in the beginning of September. Thereafter it decreased gradually until the disappearance on September 25 (♂) or 17 (♀). Females disappeared earlier than males, as is parallel to *A. lanceolatum*. The maximum adult life span was 43 (♂) or 35 (♀) days.

A. nigroflava: The length of pre-reproductive period was 19 (♂) or 27 (♀) days. The activity began on July 10 (♂) or 26 (♀) and ceased on September 16 (♂) or 25 (♀). Females, all in oviposition, exhibited a prominent peak in the beginning of September. The male density (highest number censused=10) is delimited by the territorial behavior. The considerable sexual lag in the reproductive period is due to partly the seasonal lag of the emergence in female and partly the difference of the length of pre-reproductive period. The maximum adult life span was 46 (♂) or 52 (♀) days.

S. uchidai: The length of pre-reproductive period was 36 (♂) or 32 (♀) days. Matures were seen from July 27 (♂) or 23 (♀) to September 22 (♂) or 2 (♀). No distinct peak was detected. The maximum adult life span was 69 (♂) or 49 (♀) days.

3.2.3. Comparison of phenology among dominant species: In this section the phenology of each species except *S. paedisca* and *L. dubia* is compared as to sex, species and seasonal types on the basis of the results given above.

Length of emergence period: There is no difference between sexes, except for *C. aenea* with longer emergence period in the female. But this difference may be superficial, since the number of emerged individuals in late June was very small. The order among the species is (numerals in brackets=length of continuous emergence period): *A. nigroflava* (40 ♂, 41 ♀) > *L. sponsa* (33) > *S. uchidai* (25) = *A. lanceolatum* (24) > *C. aenea* (15 ♂, 21 ♀) > *T. melampus* (13). The order simultaneously means that of summer species (25~41) < Spring species (13~24), corresponding to the degree of synchronization reflected in the order of EM₁₀⁹⁰: *A. nigroflava* (24) > *S. uchidai* (20) > *L. sponsa* (9) > *C. aenea* (7) = *T. melampus* (6) > *A. lanceolatum* (4). Thus, the emergence synchronization is more conspicuous in spring species than in summer ones (Fig. 2). The noticeable synchronization in *L. sponsa* comparable with that in spring species might be caused by the disturbance due to rainy and cool weather which continued during June 16~21, the 5~10th days of emergence. This difference in temporal pattern of emergence between two seasonal types supports the opinion by Corbet (1954, 1962) who classified temperate Odonata into two ecological types, *spring species* and *summer species*, the former emerging synchronously and earlier, presumably caused by the diapause in the final instar larvae as in *Anax imperator* Leach.

Length of pre-reproductive period: The order is: Male, *S. uchidai* (36) > *A. nigroflava* (17) = *T. melampus* (17) > *L. sponsa* (10) = *C. aenea* (9) > *A. lanceolatum* (5); Female, *S. uchidai* (32) = *A. nigroflava* (30) > *T. melampus* (19) > *C. aenea* (16) > *A. lanceolatum* (13) > *L. sponsa* (10). The period is generally longer in females than in males except *S. uchidai* and *L. sponsa*. This tendency is known also in other species, such as *Plathemis lydia* (Drury) (Jacobs 1955) and *Anax imperator* (Corbet 1957) and may be a tendency general to the Odonata, probably in connection with the ovarian development, if with some exceptions. The difference seen between Aniso- and Zygoptera seems not essential, since the long period in zygopteran (21~24, *Lestes rectangularis* Say, Gower and Kormondy 1963) and short period in anisopteran species (9, *A. imperator*, Corbet op. cit.) are also known.

Maximum adult life span: The order is: Male, *S. uchidai* > (69 days) > *C. aenea* (57) > *T. melampus* (51) = *A. lanceolatum* (49) > *A. nigroflava* (46) > *L. sponsa* (43). Female, *A. nigroflava* (51) = *S. uchidai* (49) > *C. aenea* (40) = *T. melampus* (38) > *L. sponsa* (35) > *A. lanceolatum* (18), in general, longer in male than in females except for *A. nigroflava*.

Maximum length of reproductive stage as to individual: Calculated as the maximum adult life span minus length of pre-reproductive period, the order is:

Male, *C. aenea* (51 days) > *A. lanceolatum* (44) > *T. melampus* (34) = *L. sponsa* (33) = *S. uchidai* (33) > *A. nigroflava* (29). Female, *C. aenea* (24) > *L. sponsa* (25) > *A. nigroflava* (21) > *T. melampus* (19) > *S. uchidai* (17) > *A. lanceolatum* (5). The period is longer in males in all species studied here especially in spring species.

Reproductive period at population level: The order is: Male, *A. nigroflava* (69 days) = *A. lanceolatum* (68) = *L. sponsa* (66) = *C. aenea* (65) > *S. uchidai* (58) > *T. melampus* (47). Female, *A. nigroflava* (62) > *L. sponsa* (58) > *C. aenea* (48) > *S. uchidai* (42) > *T. melampus* (32) > *A. lanceolatum* (29). In all species, reproductive period is longer in males than in females. This period is generally longer in summer species in females, whereas no difference exists in males between two seasonal types. In warmer region, for instance, Satsuma Pininsula, the reproductive period of summer species is generally longer than that of spring species irrespective of sexes (Naraoka 1972, cf. Fig. 4). This difference in length is probably caused by the prolonged emergence period in summer species. At Hôrai-numa, the maximum length of reproductive stage as to males of summer species is shorter than that of spring species, due to the longer pre-reproductive period (*A. nigroflava*, *S. uchidai*) or shorter adult life span (*L. sponsa*). By this reduction of reproductive stage in summer species, the reproductive period at population level does not differ between seasonal types. Such reduction of reproductive period in summer species in cool climate is probably due to the effect of severe climatic conditions upon emergence, feeding activity and survival.

Concluding remarks

Taketo (1960) introduced the term, EM_{50} , the time by which the half of annual emergence is reached, in order to indicate the degree of synchronization of emergence. Corbet (1962) also used this index to compare the temporal pattern of emergence between *Anax imperator* and *Aeschna cyanea* (Müller). However, this value is affected either by the sampling size or by the existence of exceptionally early emerged individuals, as already pointed out in a previous paper (Ubukata, op. cit.).

The interval between two dates by which respectively 10 and 90% of the annual population emerged, " EM_{10}^{90} ", was proposed in the present paper. The percentage, 90%, was chosen to cut off the "summer components" which are often included in spring species and emerge far later in emergence period (e.g. up to 10% of the annual population emerge ca. 25 days after the first peak in *A. imperator*, Corbet 1962). The stability of EM_{10}^{90} against EM_{50} is demonstrated in Table 4, by using the results on the same species obtained in separate years by Kurata and Morozumi (1966) and Lawton (1971). In both species, the value of EM_{10}^{90} does not much differ between the years, while that of EM_{50} is nearly twice higher in one year than in the other. Therefore EM_{10}^{90} seems more reliable to indicate the degree of synchronization, irrespective of sampling procedures and annual difference.

Table 4. Application of EM_{10}^{90} for two species.

Species	Locality	Year	Total individuals emerged	EM_{50}	EM_{10}^{90}	Author
<i>Ictinogomphus clavatus</i> Fabricius	Lake Suwa, Nagano Pref., Japan	1964	1,033	16	22	Kurata and Morozumi (1966)
		1965	4,916	33	16	
<i>Pyrrosoma nymphula</i> (Sulzer)	Durham, England	1967	147	8	15	Lawton (1971)
		1968	802	16	14	

Nextly, the phenology of odonate assemblage at Hôrai-numa is compared with that in other districts. First, the time of appearance of adult dragonflies of Hôrai-numa generally coincides with that in two other high or intermediate moor habitats, Kushiro marsh, Eastern Hokkaido (Iijima, op. cit.) and Shiga-kôgen, Central Honshu (Fujisawa 1957). These three localities lie under similar climate (annual mean air temperature= $5\sim 7^{\circ}\text{C}$) and involve similar Odonata fauna (cf. p. 760).

Compared with the phenology in Satsuma Peninsula, the southernmost area of the mainland of Japan (Naraoka, op. cit.), hibernating and spring species appear ca. 2 months later but the last summer species disappear ca. 1.5 months earlier at Hôrai-numa (Fig. 4). Therefore the dragonfly season of Hôrai-numa is 3.5 months shorter than that of Satsuma Peninsula. This reduction of dragonfly season is apparently due to the severe climatic conditions. As given in Fig. 4, the air temperature at Hôrai-numa is $6\sim 14^{\circ}\text{C}$ lower throughout the year than in Satsuma, which must retard the start of emergence of non-hibernating species and the flight activity of hibernating species while hastens the death of the last summer species. The temperature at which the dragonfly season starts is ca. 12°C in Satsuma Peninsula while 14°C at Hôrai-numa, being approximately similar for both as like the temperature of the last summer species being ca. 8°C (Satsuma) and 6°C (Hôrai). Thus, the mean daily temperature at the beginning and the end of dragonfly season nearly coincides between two areas, in spite of extreme difference in faunal make up (only 7 out of 21 species of Hôrai-numa are common to Satsuma Peninsula; 33.3%).

As is well known, seasonal segregation is one of the means by which the species occupying similar niches avoid competition for one another. The degree of seasonal segregation in adult stage within the odonate assemblage of Hôrai-numa is mentioned below, leaving the discussions on other isolating factors elsewhere. The species are divided conveniently into three life forms; *Zygoptera*, smaller *Anisoptera* and larger *Anisoptera* (Table 5).

Zygoptera: The three dominant species are fairly segregated from each other. Coexistence is seen only in spring. But, as *M. strigata* is a strayer from mountain stream, the other three agrionid species being similar in life mode and life history,

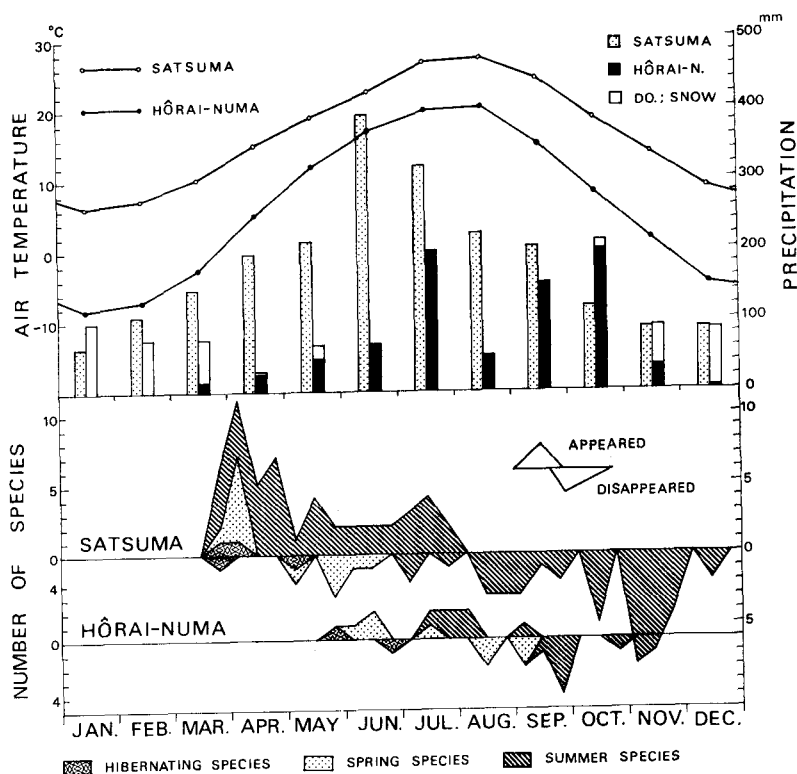


Fig. 4. Comparison of phenology and climatic conditions between Satsuma Peninsula (Naraoka 1972) and Hôrai-numa. Climatic conditions: Satsuma peninsula, record at Kago-shima Meteorological Observatory (1921~1950); Hôrai-numa, record at Usubetsu Pluviometric Station (390 m alt., 1 km apart from Hôrai-numa; 1971).

must be considered as to the interspecific competition.

Smaller Anisoptera: The spring and summer species are considerably segregated, while the overlap of dominant species occurs within both seasons: Namely, *T. melampus* — *C. aenea* in spring as *S. uchidai* — *S. frequens* in summer. In the latter case the two species are, to some degree, segregated spatially and diurnally (Ubukata, unpubl.). In the former case, there are considerable interferences between each other, in spite of the difference in flight pattern (*T. melampus*, percher; *C. aenea*, cruiser). Besides the dominant species, *L. quadrimaculata* and *L. dubia* in spring and *S. danae* in summer are far less abundant at Hôrai-numa, but their capacity in attaining higher population level is not excluded.

Larger Anisoptera: Except *A. nigroflava* flying in summer, there are no residential aeschnid species. *A. parthenope* and *A. sieboldii* do not prefer dystrophic lakes so that no competition is expected among Aeschnidae. *Aeschna juncea*

Table 5. Seasonal segregation of reproductive period in each life form at Hôrai-numa. Abundant species asterisked and species with habitat preference other than dystrophic lake parenthesized.

Season Life form	Early spring (late May~early June)	Spring (mid June~late July)	Summer (early August~ late September)
<i>Zygoptera</i>	<i>S. paedisca</i> *	<i>A. lanceolatum</i> * <i>A. terue</i> <i>E. deserti</i> (<i>M. strigata</i>)	<i>L. sponsa</i> *
<i>Smaller Anisoptera</i>		<i>T. melampus</i> * <i>C. aenea</i> * <i>L. dubia</i> <i>L. quadrimaculata</i> <i>E. bimaculata</i> (<i>O. japonicum</i>)	<i>S. frequens</i> * <i>S. uchidai</i> * <i>S. danae</i> (<i>S. infuscatum</i>) (<i>S. baccha</i>) (<i>O. albistylum</i>)
<i>Larger Anisoptera</i>		(<i>A. parthenope</i>)	<i>A. nigroflava</i> * (<i>A. sieboldii</i>)

often collected at lower lands in Sapporo was never found mixed with a similar species, *A. nigroflava*, at Hôrai-numa either in adults or exuviae, suggesting their vertical segregation in Sapporo districts.

Some cases of interference among different life forms, i.e. *Zygoptera* vs. *smaller Anisoptera* and *smaller Anisoptera* vs. *larger Anisoptera* were noted but less frequently than with the species of the same life form. No predation among different species has been directly confirmed. Summarizing, most dominant species are segregated for one another seasonally, but there are some cases exhibiting interspecific interference, necessitating closer study.

Finally, I wish to express my sincere gratitude to Dr. Shôichi F. Sakagami, for his pertinent guidance in the course of the present study, and to Prof. Mayumi Yamada for his kind reading through the manuscript and continuous encouragement. Cordial thanks are also due to Dr. Syoziro Asahina, National Institute of Health, Tokyo, for his kind advice and identification of some Odonata specimens.

Summary

The Odonata fauna of a dystrophic pond, Hôrai-numa (530 m alt.) near Sapporo, was weekly surveyed by collecting exuviae and censusing adults around 13:00 on fine days from late May to late September, 1971.

1) The fauna of Hôrai-numa consists of nine residential and 12 straying species belonging to eight families, and characterized by the existence of high moor dwellers such as *Cordulia aenea amurensis* Selys, *Leucorrhinia dubia orientalis* Selys and *Sympetrum danae* Sulzer, and by a high ratio of northern elements (81%).

2) Out of 2,147 mature individuals censused in total, the most predominant species are *Agrion lanceolatum* Selys and *Lestes sponsa* (Hansemann) (both 65% of total individuals) followed by *Aeschna nigroflava* Martin. The order of relative abundance in reproductive period coincides in general with the abundance order in emerged adults.

3) The sex ratio is nearly 1:1 in emerging population in four species studied, while variable in mature individuals at the pond showing three types: 70~80% ♂♂ (*A. lanceolatum*, *L. sponsa* and *Sympecma paedisca* (Brauer)), 90~100% (*Trigomphus melampus* (Selys), *C. aenea*, *Somatochlora uchidai* Foerster and *L. dubia*), ca. 10% (*A. nigroflava*), probably due to the specific difference in territorial and/or oviposition behavior.

4) The phenology of dominant species can be divided into three types (E, emergence; R, reproductive period): Hibernating species (*S. paedisca*), E. perhaps in August~September, R, late May~early June; Spring species (*A. lanceolatum*, *T. melampus* and *C. aenea*), E, early~late June, R, late June~mid August; Summer species (*A. nigroflava*, *S. uchidai* and *L. sponsa*), E, late June~early August, R, late July~late September.

The seasonal segregation among dominant species is almost complete within three principal life forms, Zygoptera, Smaller and Larger Anisoptera, though competition is expected in few cases.

5) The comparison of phenology among six dominant species as to sex, species and seasonal type reveals the following tendencies: Length of emergence period, summer species (25~41 days) > Spring species (13~24), mainly due to the difference in the degree of synchronization reflected by the value of EM_{10}^{90} (interval in days between two dates by which respectively 10 and 90% of the annual population emerged), summer species (9~24) > spring species (4~7). Length of the pre-reproductive period, females > males. Length of maximum adult life span, males > females; Maximum length of reproductive stage as for individual, males > females. Spring species males (34~51 days) > summer species males (29~33). Length of reproductive period at population level, males > females.

6) Some effects of climatic conditions, especially of air temperature on odonate phenology were discussed, which revealed the reduction of reproductive period of summer species in cooler region by severe weather conditions affecting emergence, feeding and survival.

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Appendix

List of Odonata species censused in 1971 at Hôrai-numa.

1) The number of censused individuals is given after the scientific name, with a series of three figures: total ♂♂, total ♀♀, number of pairs given parenthetically.

2) The time of periodical census is given as follows: V-3 (May 20; 12:30~12:45), V-4 (May 29, 14:10~14:25), VI-1 (June 6, 13:06~13:25), VI-2 (June 10, 12:22~12:49), VI-3 (June 13, 13:08~13:48), VI-4 (June 24, 12:23~12:59), VII-1 (July 1, 12:21~12:42), VII-2 (July 10, 12:08~12:36), VII-3 (July 12, 13:42~14:06), VII-4 (July 23, 12:30~12:57), VII-5 (July 31, 13:30~14:10), VIII-1 (August 2, 12:47~13:22), VIII-2 (August 9, 14:08~14:37), VIII-3 (August 17, 14:08~14:45), VIII-4 (August 26, 14:25~14:50), IX-1 (September 2, 13:14~13:36), IX-2 (September 8, 13:55~14:10), IX-3 (September 14, 13:20~13:34), IX-4 (September 22, 13:10~13:28), IX-5 (September 25, 13:43~13:52).

1. *Agriion lanceolatum* Selys: VI-2 (2, 0, 0), VI-3 (27, 0, 0), VI-4 (123, 97, 95), VII-1 (101, 83, 81), VII-2 (67, 9, 9), VII-3 (87, 18, 18), VII-4 (45, 1, 1), VII-5 (33, 0, 0), VIII-1 (21, 0, 0), VIII-2 (3, 0, 0).

2. *Sympecma paedisca* (Brauer): V-3 (46, 9, 9), V-4 (11, 0, 0), VI-1 (1, 0, 0), VI-2 (36, 14, 14), VI-3 (37, 12, 12).

3. *Lestes sponsa* (Hansemann): VII-4 (4, 7, 0), VII-5 (8, 6, 0), VIII-1 (27, 4, 0), VIII-2 (167, 79, 78), VIII-3 (44, 31, 25), VIII-4 (51, 15, 13), IX-1 (97, 28, 28), IX-2 (38, 1, 1), IX-3 (34, 4, 4), IX-4 (20, 0, 0), IX-5 (5, 0, 0).

4. *Trigomphus melampus* (Selys): VI-4 (12, 1, 0), VII-1 (14, 1, 1), VII-2 (10, 0, 0), VII-3 (44, 2, 2), VII-4 (7, 1, 1), VII-5 (12, 2, 1), VIII-1 (7, 1, 1), VIII-2 (5, 1, 1).

5. *Aeschna nigroflava* Martin: VII-4 (1, 0, 0), VII-5 (9, 6, 0), VIII-1 (4, 5, 0), VIII-2 (5, 20, 0), VIII-3 (2, 6, 0), VIII-4 (8, 69, 0), IX-1 (6, 93, 0), IX-2 (4, 47, 0), IX-3 (1, 30, 0), IX-4 (0, 19, 0), IX-5 (0, 7, 0).

6. *Cordulia aenea amurensis* Selys: VI-4 (16, 1, 0), VII-1 (22, 0, 0), VII-2 (12, 0, 0), VII-3 (8, 0, 0), VII-4 (7, 0, 0), VII-5 (13, 0, 0), VIII-1 (8, 0, 0), VIII-2 (1, 0, 0).

7. *Somatochlora uchidai* Foerster: VII-5 (1, 0, 0), VIII-1 (6, 1, 0), VIII-2 (2, 0, 0), VIII-3 (2, 0, 0), IX-1 (4, 1, 1), IX-2 (4, 0, 0), IX-4 (5, 0, 0).

8. *Sympetrum frequens* (Selys): IX-1 (2, 0, 0).

9. *S. infuscatum* (Selys): IX-4 (1, 0, 0).

10. *S. danae* (Sulzer): IX-4 (1, 0, 0).

11. *Leucorrhinia dubia orientalis* Selys: VII-4 (3, 0, 0), VII-5 (1, 0, 0), VIII-1 (3, 0, 0), VIII-2 (5, 0, 0), VIII-3 (1, 0, 0), VIII-4 (1, 0, 0).