LIFE CYCLES OF DONACIINAE (COLEOPTERA, CHRYSOMELIDAE)

A.O. BIEŃKOWSKI
Zelenograd 1121-107, 103460 Moscow K-460, Russia

Abstract

Donacia thalassina Germar, *D. clavipes* F. and *D. dentata* Hoppe each have 5 larval instars. The species studied have similar egg incubation periods and activity periods of larvae and adult insects. However the total development period from egg to egg requires 3 years for *D. thalassina* and *D. clavipes* and 2 years for *D. dentata*. This difference arises from the different periods of existence of larvae, pupae and adults within cocoons. Adults and sometimes pupae and full-grown larvae of *D. thalassina* and *D. clavipes* stay for a winter within the cocoons attached to the living roots of their host plants. In addition to these species a similar type of life cycle is typical of *D. vulgaris* Zschach, *D. obscura* Gyllenhal, *D. cinerea* Herbst, *D. semicuprea* Panzer and *D. crassipes* F. Adults of *D. dentata* do not hibernate within their cocoons and emerge in the same year. This type is also typical of *D. sparganii* Ahrens, *D. tomentosa* Ahrens and *D. versicolorea* Brahm.

Introduction

The habit of life and metamorphosis of Donaciinae has long attracted scientist's attention. There are many reports about the total longevity and duration of the separate immature stages. The earliest contribution on this subject is the article by Mulsant (1846). This author put *Sparganium* bushes and some imagines of *Donacia simplex* F. and *D. marginata* Hoppe in the cage with water and soil in spring. In autumn Mulsant found *Donacia* larvae between the basal parts of the leaves and supposed that these larvae developed from eggs laid by the captured beetles. At the same time he found the cocoons with the newly emerged beetles attached to the roots of *Sparganium* in nature. Therefore, he concluded that *Donacia* larvae develop from spring to autumn.

Perris (1848) was of a similar opinion. He found the pupae of *D. bicolor* Zschach in August and considered that they originated from beetles which oviposited in March and April of the same year, and larvae developed during 5 or 6 months.

Although Xambeu (1890) reported on the hibernation of *D. aquatica* L. larvae, the idea about the one-year life cycle of Donaciinae and development of larvae during one summer season was widespread in the nineteenth century and was even mentioned in the popular-scientific literature, such as Brehm (1895) and Lampert (1900).

MacGillivray (1903) was the first to notice that *D. palmata* Olivier larvae, collected simultaneously, are of considerably different sizes. He proposed the following explanation: the beetles do not emerge in definite broods and the development of larvae is rapid, so that all stages of the life cycle are present at any time during the summer and autumn.

Böving (1910) has carried out special research on the life cycle duration in Donaciinae. During 1902-1904 he collected the larvae of *D. semicuprea* in the same

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locality regularly every month all the year round and measured their length. From 12 to 63 specimens were measured each month. Larvae found from May to August represented 3 separate groups: 1-3, 5-8 and 10-11 mm in length, but those found from September to April varied gradually from 4 to 11 mm in length. Similar results were obtained with *D. marginata*. Therefore, Böving disproved the view that larval life lasts the one frostless season and maintained that the development goes on, at least, during the two summers with a stoppage of the growth in winter. Böving noted that he could not observe larval development during the second summer season, since male and female larvae, like the cocoons, were of different sizes. So he left unsettled the question, whether the larvae finished their development during the second summer, or a third summer is required.

In North America, Hoffman (1940) considered that Donaciinae have at least a two-year life cycle, because he found small and large larvae of some Donaciinae species before the period of oviposition.

Medvedev and Zaitzev (1980) discovered the young and mature larvae of *Neohaemonia voronovae* L. Medvedev at the beginning of August, when the flight period of this species is ending. These authors assumed that the larvae pupate in the spring, and the development requires two years.

Yang and Jing (1989) provided a developmental diagram of *D. provosti* Fairmaire, showing a one-year life cycle with the hibernation of full-grown larvae in the cocoons.

There is some information about the duration of eggs and pupae of Donaciinae in the literature. The eggs of *D. crassipes*, *D. versicolorea*, *D. marginata*, *D. semicuprea* and *Plateumaris braccata* Scopoli develop in 8-12 days (Boving, 1910); those of *D. malinowskyi* Ahrens in 10 days (Olsufjev, 1913). The duration of the pupal stage of *D. semicuprea* does not exceed 15-20 days (Xambeu, 1898), of *D. cinerea* and *Macroplea mutica* F. one month (Goecke, 1933 and Klefbeck, 1916, respectively). In the autumn there are well-chitinized beetles of many European and some North-American Donacia species including *D. proxima* Kirby, *D. cincticornis* Newman, *D. subtilis* Kunze, *D. cuprea* Kirby and *D. hirticollis* Kirby within the cocoons. The pupal stage of the other species, including *D. pubescens* LeConte, *D. pubicollis* Suffrian and *D. piscatrix* Lacordaire lasts until the following spring (Goecke, 1935, Hoffman, 1940).

Therefore, the two- or three-year life cycle is obviously typical of the majority of Palaearctic and Nearctic Donaciinae. Larval development continues during most of this period, and a few species develop during the one summer season. However nobody has especially investigated this subject since Böving (1910). The life cycles of the African Donaciinae are unknown.

Very little is known about the number of larval instars in the Donaciinae. However, Reid (1993) measured the head width and abdominal hook length of 36 larvae of *D. australasiae* Blackburn, collected simultaneously, and ascertained the presence of 4 size groups, corresponding to 4 instars.

Methods

This paper is based on the study of specimens of all developmental stages of *D. thalassina*, *D. clavipes* and *D. dentata*. I collected the material in the Moscow region in one locality for each species, and fixed it in 90 % ethanol. I was interested in the total life cycle longevity and in the duration of the separate stages, the number of larval instars, and also the relationship between the life cycle of *Donacia* species and the phenology of the host plant.

The number of the larval instars of insects can be determined by measuring strong, well-chitinized parts of the larval body, which increase immediately after the moult and do not grow up to the next moult. I measured the head width and the abdominal hook length (from the base of basal frame to the tip of the hook) of all larvae including larvae just hatched from eggs, larvae taken from cocoons as well as some larval exuviae taken from cocoons which contained pupae and imagines. In addition, I investigated the growth of the larvae during the summer season. I measured the length of the soft larval body, which increases gradually between moults. All measurements were made with an eyepiece micrometre using a binocular microscope. The conclusions on the total length of the life cycle and the duration of the different stages were made on the basis of the data on the larval instars, growth of larvae and dates of occurrence of eggs, cocoons and imagines.

I regard the period from the first appearance of the certain stage in the population to the appearance of the next stage as the longevity of the former stage, and the length of the largest previous larval instar and smallest following larval instar as the size limits of moulting larvae.

Captured larvae (except first instars) were determined by comparison with the larval exuviae from cocoons containing imagines, the method used suggested by Schmidt-Schwedt (1887) and Boving (1910)). The morphology of *D. thalassina*, *D. clavipes* and *D. dentata* larvae was previously studied by me (Bieńkowski, 1992).

The relatively small quota of earlier instar larvae in the collection was because these small specimens are more often lost when washing the soil clod containing the roots of the host plant.

First instar larvae are seldom found in nature owing to their very small size. Therefore, the majority of studied first instar larvae were reared from eggs taken from nature with the leaves, to which they were attached, and placed in the vessels with water. Larvae were fixed shortly after hatching. Eggs and first instar larvae collected on *Eleocharis palustris*, *Phragmites australis* and *Sagittaria sagittifolia* were attributed to *D. thalassina*, *D. clavipes* and *D. dentata* respectively, as in the locality, where the specimens were taken, only these species of Donaciinae occur on the host plants listed.

Results

Donacia thalassina Germar

1. Material

Material was collected at Zelenograd near the "Pump-house pond" in a small pond overgrown with various aquatic vegetation. Collections were made in August and September 1991 and from April to August 1992. Eggs were found only on 7 July 1994 on the inner side of lower, scale-shaped leaves of the host plant, *Eleocharis palustris*, under the water. Larvae and cocoons were found on roots, whereas beetles occured on stems and racemes of the host plant. A total of 251 larvae, 84 cocoons (including 22 with larvae, 43 with pupae and 19 with imagines) and 33 adults were collected. In addition 10 first instar larvae were reared from the collected eggs. In August 1992 the pond was very shallow because of drought, and all plants of *E. palustris* were left on the bank. Larvae of *D. thalassina* became very rare, and their collection was stopped.

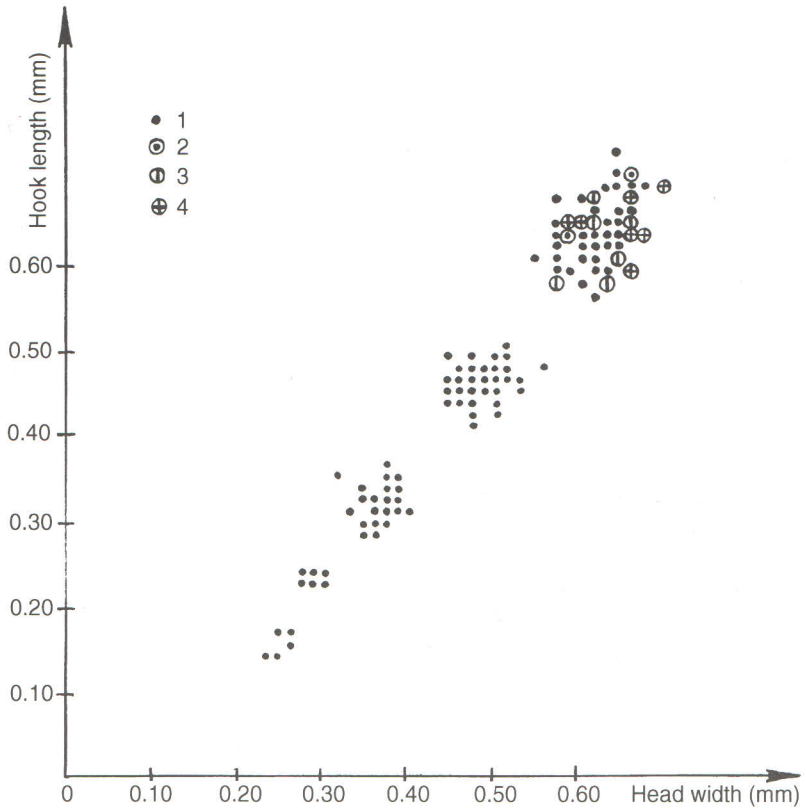

Fig. 1. Donacia thalassina larvae. Correlation of head width and abdominal hook length. 1 – larva, 2 – larva from cocoon, 3 – larval exuvium from cocoon with adult male, 4 – the same from cocoon with adult female. Specimens with the same measurements are marked one point.

2. Life cycle

The correlation of the head width and the length of abdominal hooks of all larvae without regard for the collection date is demonstrated in Fig.1. All specimens represent 5 well-defined groups corresponding to 5 larval instars. The last group on the left corresponds to the specimens reared from the eggs. The measurements of larval exuviae taken from the cocoons containing adult insects (6 males, 7 females) demonstrate the lack of sexual dimorphism of the final instar larvae. This fact allows the analysis of the results without regard for the sex of the larvae. The range and mean values of the head width and the abdominal hook length in the different larval instars are shown in Table 1.

The population structure during the summer season is shown in Fig. 2. Larvae hatch at the beginning of July. The small number of first and second instar larvae collected does not permit the determination of the time when the first moult takes place. Obviously, this moult takes place in the same season since the smallest larvae captured before hibernation (8 August 1991 and 15 July 1992) and after winter (28 April 1992) belong to the second instar. Second instar larvae which hatched last year develop into third instars in April and May, and reach 3.2-3.4 mm in length. Consequently the number of third instar larvae increases in the population from the end of April to the

Table 1. Range and means of head width and abdominal hook length of *D. thalassina* larvae

instar	number of specimens n	width of head (mm) minimum	maximum	mean $\bar{X}$	length of hooks (mm) minimum	maximum	mean $\bar{X}$
1	10	0.24	0.27	0.26	0.15	0.18	0.16
2	13	0.29	0.32	0.30	0.24	0.26	0.25
3	53	0.33	0.42	0.39	0.30	0.39	0.34
4	88	0.47	0.59	0.51	0.44	0.54	0.49
5	113	0.57	0.74	0.65	0.60	0.78	0.69

end of May. Larvae which reached 4.3-5.9 mm in length moult into fourth instar. Fourth instar larvae are found from the end of April to the end of September. Almost all of them reaching 6.4-9.4 mm in length have time to develop to the fifth instar before hibernation (only one fourth instar larva was found in the third summer season). One fourth instar with a length of 4.4 mm collected on 1 August 1992, apparently delayed development owing to the drought. Fifth instar larvae appear in June and overwinter. Therefore, the development of larvae during the second summer season is very asynchronous. The larvae of two different instars similar in length and the same instar larvae gradually varying in length can occur simultaneously. All these facts indicate that larvae belong to the same generation. At the beginning of June of the third summer season, fifth instar larvae reaching 10.8-13.2 mm in length begin to construct cocoons. Fifth instar larvae collected in the middle of July 1992 were larger than those collected 2 weeks later, as in the beginning of August the former are in the cocoons, but the latter belong to the next, younger generation. Larvae in cocoons are found up to the beginning of August. They pupate from the middle of July up to August. The beetles emerge from the pupae in September. They do not leave the cocoons until the next spring. Some pupae also hibernate, and imagines appear from them in May of the following year. Their flight period extends from the end of May until the beginning of July.

D. thalassina has a three-year life cycle (Table 2). The incubation of eggs obviously does not exceed one month as adults appear at the end of May, but larvae hatch from eggs at the beginning of July. Larval development continues during 23 months and full-grown larvae spend one and a half months in cocoons before pupation. The pupal period either lasts about 1 month if not hibernating or 9 months if hibernating. In the first case the adults spend 9 months in the cocoons during the hibernation. The second instar larvae stay for the first winter, fifth instars for the second winter, pupae or adults in the cocoons for the third winter.

3. Relationship between the life cycle of *D. thalassina* and the phenology of its host plant

Oviposition, growth and development of the larvae occurs during the vegetative season of the host plant, *Eleocharis palustris* from spring to autumn. The flight period extends from the emergence of the young suckers above water-level almost until the end of flowering of *E. palustris*. Since beetles often sit on racemes and there is no damage to leaves and stems it is probable that the beetles feed on the pollen.

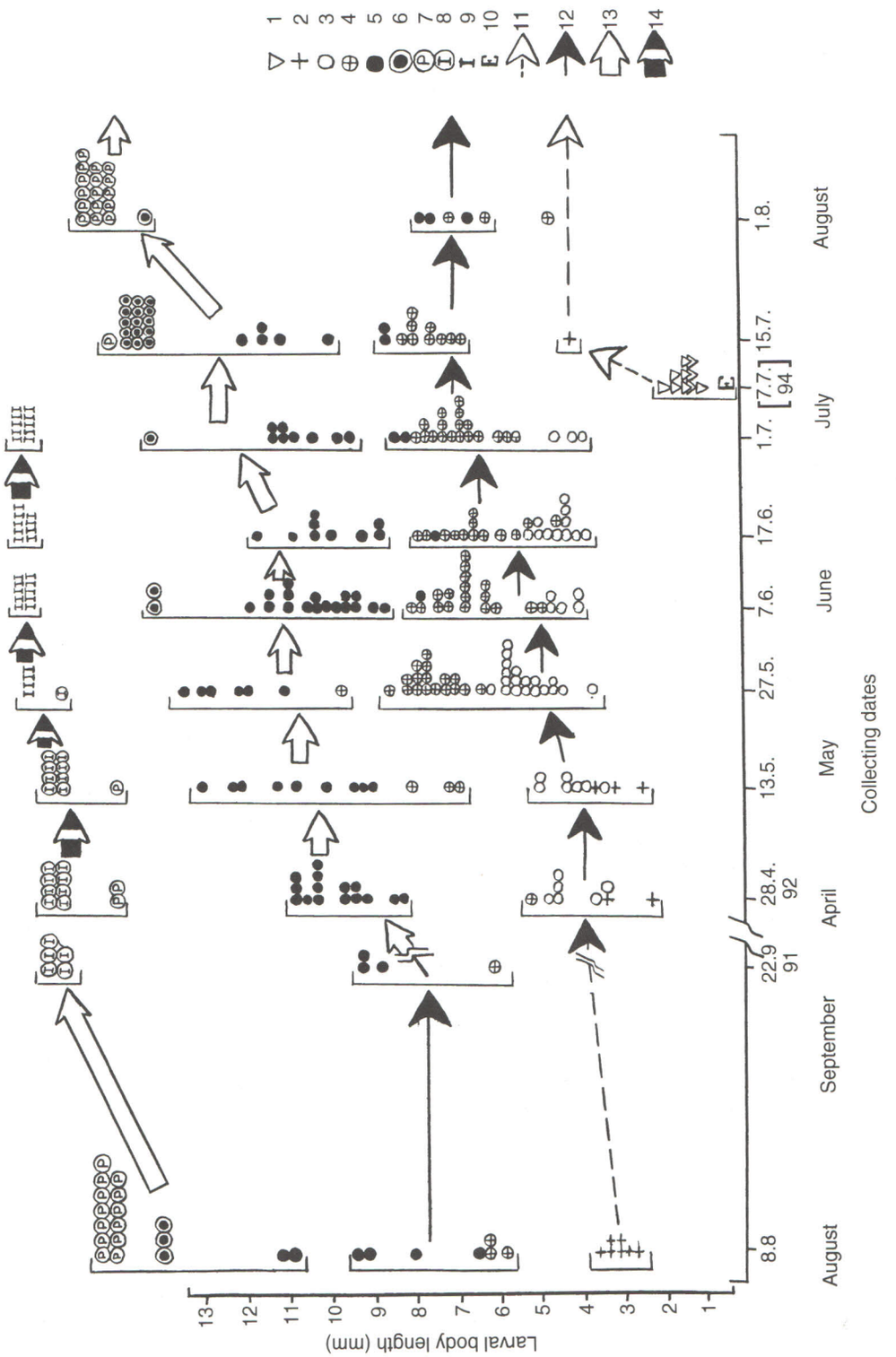
1 2 3 4 5 6 7 8 9 10 11 12 13 14
I E
Larval body length (mm)
13 12 11 10 9 8 7 6 5 4 3 2 1
8.8
August
22.9
91
September
28.4.
92
April
13.5.
May
27.5.
7.6.
June
17.6.
1.7.
[7.7.
94]
15.7.
July
1.8.
August
Collecting dates

Table 2. Life cycle of *D. thalassina*

years	months											
	1	2	3	4	5	6	7	8	9	10	11	12
1							E L1	L2	L2	L2	L2	L2
2	L2	L2	L2	L2 L3 L4	L2 L3 L4	L3 L4 L5	L3 L4 L5	L4 L5	L4 L5	L5	L5	L5
3	L5	L5	L5	L5	L5	L5 (L5)	L5 (L5) (P)	(L5) (P)	(P) (I)	(P) (I)	(P) (I)	(P) (I)
4	(P) (I)	(P) (I)	(P) (I)	(P) (I)	(P) (I) I	I	I					

E = egg; L1-L5 = 1st-5th instar larvae respectively; (L5), (P), (I) = larva, pupa, adult in cocoon respectively; I = emerged adult.

Donacia clavipes Fabricius

1. Material

Material was collected in Glubokoe lake, 23 km west of Zwenigorod. Collections were made from May to October 1993. Eggs were found attached to inner side of the lower leaves or to stem beneath the leaves of the host plant, *Phragmites australis*, under water. Larvae and cocoons were found on roots and basal parts of the stem, and beetles occured on leaves and in leaf axils. A total of 495 larvae, 173 cocoons (36 containing larvae , 48 with pupae and 89 with adults) and 8 adult insects were collected. In addition two first instar larvae were reared from the eggs.

2. Life cycle

The correlation of head width and the length of the abdominal hook of all larvae without regard for the collection dates is shown in Fig. 3. The specimens represent 5 groups corresponding to 5 larval instars. The last group on the left corresponds to the first instar larvae, two of which were reared from the eggs. The measurements taken from larval exuviae found in the cocoons containing adult males (n=10) are smaller than

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Fig. 2. Donacia thalassina. Population structure during the summer season. 1-5 – larvae of first-fifth instars respectively, 6-8 larva, pupa and adult in cocoon respectively, 9 – emerged adult, 10 eggs, 11-14 – generation development during the first-fourth summer season respectively.

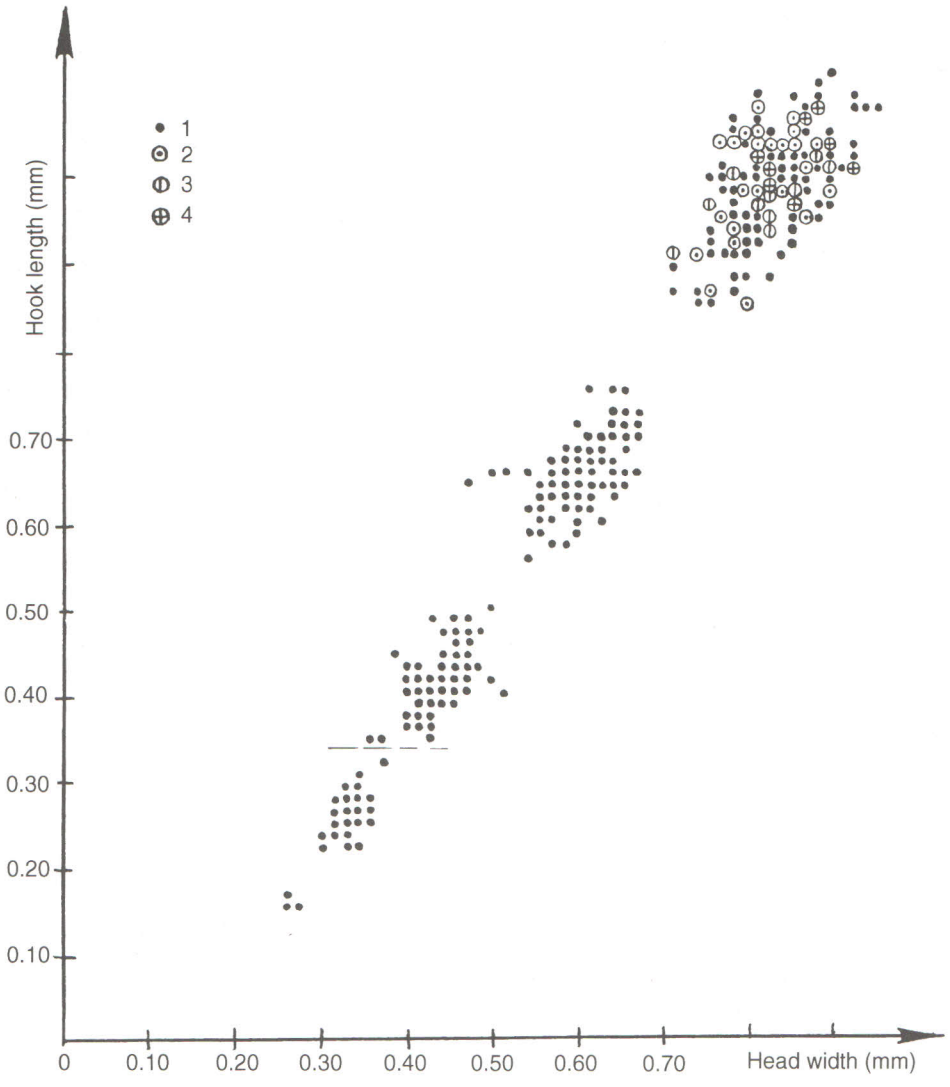

Fig. 3. *Donacia clavipes* larvae. Correlation of head width and abdominal hook length. 1 – larva, 2 – larva from cocoon, 3 – larval exuvium from cocoon with adult male, 4 – the same from cocoon with adult female. Specimens with the same measurements are marked one point.

measurements from the cocoons containing adult females (n=10). However male and female larvae of every instar do not form these separate groups. The range and means of the head width and the abdominal hook length in different larval instars are shown in Table 3.

The population structure during the summer season is shown in Fig. 4. Larvae hatch in the middle of July. Some of them moult and develop into second and third instars in the same season, since two small third instar larvae were collected in the middle of August. Second instar larvae are obviously present in this generation in August and September, but have not been collected owing to their small size. The majority the second instar larvae hibernates and occurs until the middle of July the following year. Larvae

Table 3. Range and means of head width and abdominal hook length of *D. clavipes* larvae

instar	number of specimens n	width of head (mm) minimum	maximum	mean $\bar{X}$	length of hooks (mm) minimum	maximum	mean $\bar{X}$
1	3	0.27	0.29	0.28	0.17	0.18	0.17
2	59	0.32	0.39	0.35	0.24	0.35	0.28
3	169	0.38	0.54	0.46	0.38	0.54	0.45
4	127	0.50	0.71	0.64	0.60	0.81	0.71
5	189	0.75	1.01	0.88	0.92	1.20	1.06

develop into the second instar reaching a minimum of 3.0 mm in length and into the third instar reaching 3.1-4.6 mm in length. Third instar larvae appear in the generation in August before the first hibernation and occur until August the following year. They develop into fourth instar larvae reaching 4.5-7.7 mm in length. Fourth instars appear in June, grow during the summer and overwinter. After the second hibernation fourth instar larvae occur in the generation until May and are absent in June. Larvae develop into fifth instars reaching 6.9-11.6 mm in length. Fifth instar larvae appear in the generation in August following the first hibernation and are present until the middle of August of the next year.

One fifth instar larva collected on 11 June was similar in length to fourth instars, which hatched the previous year, and this apparently belongs to the generation of the year before last, as fifth instar larvae of last year generation only appear in August. One fourth instar larva 11.2 mm in length collected on 18 July apparently was retarded in the development.

During the third summer season larvae begin to construct cocoons. This process goes on until September. Owing to the long duration of this period, it is impossible to ascertain the minimum length of larvae which constructed cocoons, but the largest one was 16.7 mm. In the middle of August the majority of specimens of the year before last generation already exist in the pupal or adult stage within cocoons. Before the third hibernation, 80% of cocoons contain adult insects, but some have larvae or pupae even after the winter. Larvae and pupae in cocoons are less resistant than adults to unfavourable conditions during the winter. Of specimens taken from cocoons collected on 12 May all adults were alive, but only half of the larvae and pupae had survived.

The flight period occurs in June. From body length measurements, the larvae of this and last years generations collected in September and October partly overlap. Among the specimens captured on 26 September the smaller third instars hatched this year, while larger ones together with the all fourth and fifth instar larvae last year. Among the specimens collected on 15-17 October second and third instar larvae hatched this year, but fourth and fifth instars last year. The relative number of larvae of different instars and body length before hibernation (15-17 October) corresponds to that after hibernation (12 May).

Two very large fifth instar larvae 17.2-17.3 mm in length found on 12 May probably fell out of their cocoons accidentally destroyed during their collection.

D. clavipes has a three-year life cycle as shown in Table 4. Egg incubation apparently does not exceed 1 month as adult insects occur in June, and larvae hatch from

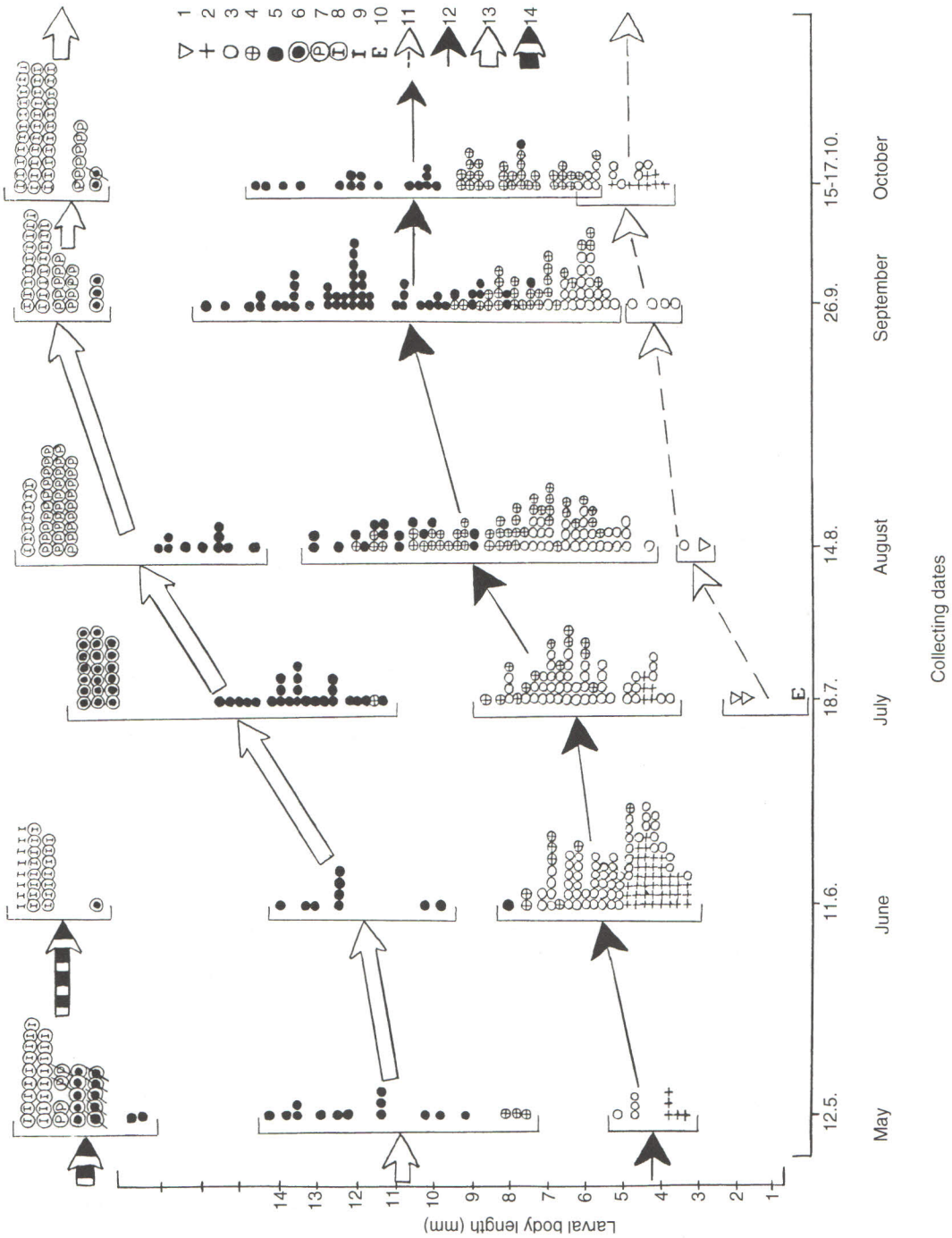
Larval body length (mm)
1 2 3 4 5 6 7 8 9 10 11 12 13 14
12.5.
11.6.
18.7.
14.8.
26.9.
15-17.10.
May
June
July
August
September
October
Collecting dates

Table 4. Life cycle of *D. clavipes*

years	months											
	1	2	3	4	5	6	7	8	9	10	11	12
1							E L1	L1 L2 L3	L2 L3	L2 L3	L2 L3	L2 L3
2	L2 L3	L2 L3	L2 L3	L2 L3	L2 L3 L4	L2 L3 L4 L5	L2 L3 L4 L5	L3 L4 L5	L3 L4 L5	L3 L4 L5	L4 L5	L4 L5
3	L4 L5	L4 L5	L4 L5	L4 L5	L4 L5	L4 L5	L4 L5 (L5)	L5 (L5) (P) (I)	(L5) (P) (I)	(L5) (P) (I)	(L5) (P) (I)	(L5) (P) (I)
4	(L5) (P) (I)	(L5) (P) (I)	(L5) (P) (I)	(L5) (P) (I)	(L5) (P) (I)	(L5) (P) (I) I						

E = egg; L1-L5 = 1st-5th instar larvae respectively; (L5), (P), (I) = larva, pupa, adult in cocoon respectively; I = emerged adult.

eggs in July. The duration of larval development is 24 months. The period from the beginning of cocoon construction to the emergence of beetles is eleven months. Second and third instar larvae stay for the first winter, fourth and fifth instars the second winter and adults, rarely larvae or pupae, in cocoons the third winter.

3. Relationship between the life cycle of *D. clavipes* and the phenology of its host plant

Oviposition, growth and development of larvae takes place during the vegetative season of the host plant, *Phragmites australis*, in the summer season. Beetles are active during the period of young stems and leaves growth and feed on leaves.

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Fig. 4. Donacia clavipes. Population structure during the summer season. Dead specimens are crossed out. 1-5 – larvae of first-fifth instars respectively, 6-8 – larva, pupa and adult in cocoon respectively, 9 – emerged adult, 10 – eggs, 11-14 – generation development during the first-fourth summer season respectively.

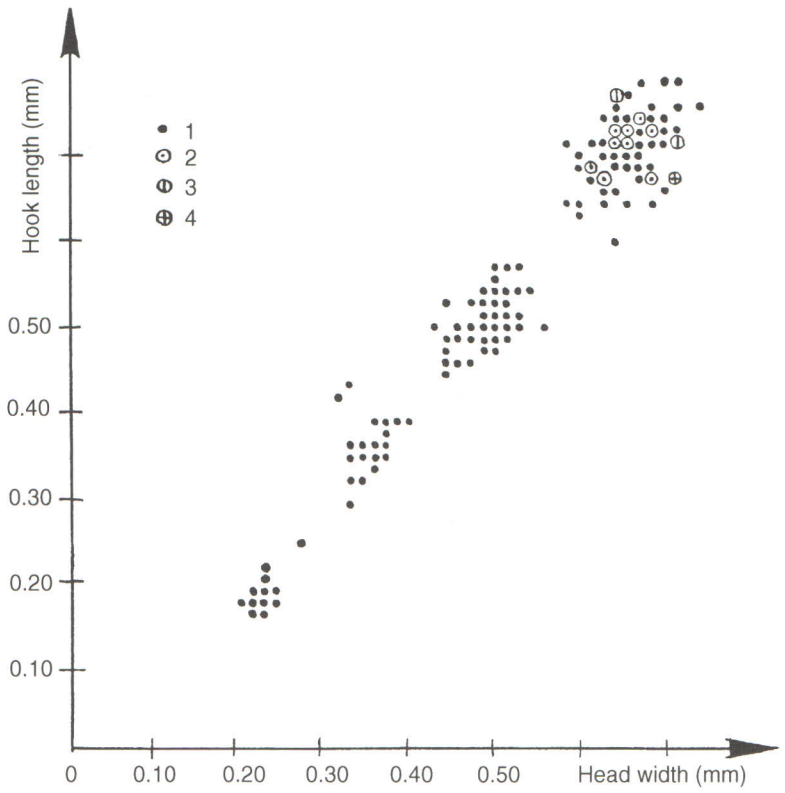


Fig. 5. Donacia dentata larvae. Correlation of head width and abdominal hook length. 1 – larva, 2 – larva from cocoon, 3 – larval exuvium from cocoon with adult male, 4 – the same from cocoon with adult female. Specimens with the same measurements are marked one point.

Donacia dentata Hoppe

1. Material

Material was collected in the same waterbody with *D. clavipes*. Collections were made from the beginning of June to the end of September 1993. Some eggs were collected on 31 July 1994. Eggs were found on the lower side near the edge of the floating leaves of the host plant, *Sagittaria sagittifolia*, and sometimes between 2 floating leaves partly overlaying each other. Larvae were found on roots and in leaf axils under the water, pupae in cocoons on roots of the host plant under water. At the beginning of summer the mature larvae and cocoons were also found on roots of *Carex* sp., growing near the *S. sagittifolia*. The reasons for this interesting phenomenon are considered below. Beetles were found on the leaves and flowers of the host plant. A total of 217 larvae, 36 cocoons (10 containing larvae, 23 with pupae and 3 with adults) and 16 adults were collected. In addition 20 first instar larvae were reared from the collected eggs.

2. Life cycle

The correlation of head width and the length of the abdominal hooks of all larvae irrespective of collection dates is shown in Fig. 5. All specimens represent five groups cor-

Table 5. Range and means of head width and abdominal hook length of *D. dentata* larvae

instar	number of specimens n	width of head (mm) minimum	maximum	mean $\bar{X}$	length of hooks (mm) minimum	maximum	mean $\bar{X}$
1	21	0.21	0.26	0.24	0.17	0.23	0.19
2	1	_	_	0.29	_	_	0.26
3	39	0.33	0.42	0.37	0.30	0.45	0.38
4	81	0.45	0.59	0.51	0.47	0.60	0.52
5	107	0.62	0.78	0.68	0.63	0.83	0.74

responding to five larval instars. The last group on the left corresponds to the first instars, 20 of which were reared from the eggs. The next point to the right corresponds to second instar, of which only a single specimen larva was collected. It differs considerably from both first and third instar larvae in the head width and abdominal hook length. The second instars of this species are present in the population from the end of the vegetative season in Autumn until the beginning of the summer season next year. During this period, the larvae migrate or occur in the hibernacle, and it is difficult to find these small specimens. The measurements taken from larval exuviae found in cocoons containing adult insects (2 male and 1 female) differ slightly, but male and female larvae of every instar do not form these separate groups. The range and means of head width and abdominal hook length of all larval instars are shown in Table 5.

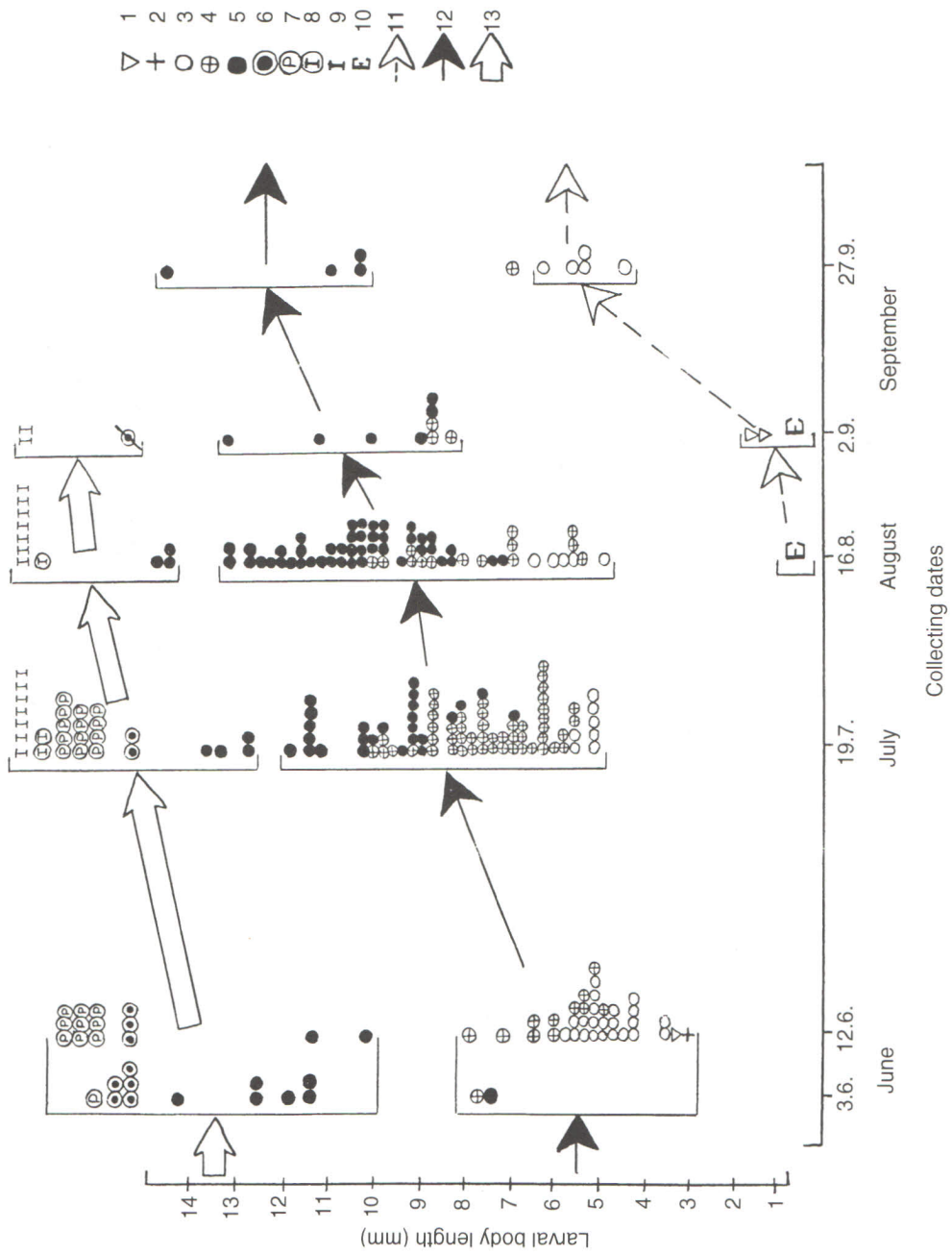
The population structure during the summer season is shown in Fig. 6. Larvae hatch from about the beginning of August to the beginning of September. Some larvae develop into second and third instars before the first hibernation, as some of the latter were found at the end of September. Other first and second instar larvae hibernate. Larvae moulting for the first time reach 2.8-3.1 mm in length, and for the second time – more than 3.3 mm in length.

One fourth instar larva found on 27 September apparently was retarded and belongs to last year generation.

Third instar larvae occur from August of the first year of development to the middle of August the following year. During the second summer their number decreases from the beginning of summer to August as they begin to develop into fourth instars in June, reaching 4.5-6.1 mm in length. Fourth instar larvae occur from June until the beginning of September. The number of fourth instar larvae reach a peak in the middle of summer but decreases in August and September when they develop into fifth instars, reaching 6.6-9.6 mm in length. Though one fifth instar larva was found at the beginning of June, this stage predominates from the middle of August. Larval development during the second summer is asynchronous, but all larvae develop into fifth instars by autumn. In June of the third summer, larvae reaching 14.3 mm in length begin to construct the cocoons. This process continues until the middle of August. However larvae constructing cocoons in August, have little chance of completing their development, as the roots of the host plant die off in September, and the cocoons attached to them are doomed to die. Pupation occurs from June until the middle of July. Apparently adult insects remain in cocoons for a short time.

The flight period extends from the middle of July until the beginning of September.

D. dentata has a two-year life cycle as shown in Table 6. Egg incubation apparently


1 2 3 4 5 6 7 8 9 10 11 12 13
Larval body length (mm)
1 2 3 4 5 6 7 8 9 10 11 12 13 14
3.6. 12.6. 19.7. 16.8. 2.9. 27.9.
June July August September
Collecting dates

does not exceed one month, as eggs are laid in August, but the floating leaves turn yellow and die off at the beginning of September. The duration of larval development is 23-24 months. Both full-grown larvae and pupae spend one month in the cocoon. The first-third instar larvae stay for the first winter, fifth instars the second winter.

3. Relationship between the life cycle of *D. dentata* and the phenology of its host plant

In Glubokoe lake the vegetative period of the majority of aquatic plants including *Equisetum fluviatile*, *Nuphar lutea*, *Phragmites australis*, *Sparganium angustifolium*, *Typha latifolia* and *Carex* sp. starts in the middle of May, while the young rosettes of *S. sagittifolia* leaves only appear at the beginning of June. They are still attached to the tubers, which are the overwintering stage of this plant in this locality. I failed to find both larvae and cocoons on either short rootlets of young plants, or on tubers. However, on 3 June I collected 8 larvae including 6 fifth instars belonging to the generation of the year before last among the roots of *Carex* sp. growing near *S. sagittifolia*. In addition, 6 cocoons (5 containing larvae and one with a pupa) were found attached to the roots of *Carex* sp. On 12 June many larvae of all instars and cocoons were found on roots of *S. sagittifolia*, as well as one fifth instar larva and 9 cocoons (3 with larvae and 6 with pupae) on the young roots of *Carex* sp. grown in this summer. All cocoons collected on 19 July were attached to roots of *S. sagittifolia*. Apparently, some fifth instar larvae after hibernation do not need to feed on their specific host plant. Such larvae construct the cocoon attached to the root, fill it with air from the intercellular spaces of the root and pupate. For this purpose the roots of different plants for example *Carex* sp. growing in the locality may be used, especially at the beginning of June, when the roots of the host plant *S. sagittifolia* are not yet developed. However some fifth instar larvae require nutrition after hibernation and, of course, pupate on the roots of their host plant, which are already sufficiently grown and suitable for this purpose.

During the second part of summer, larvae also occur in the leaf axils. Beetles feed on leaves, gnawing out distinctive tracks.

In autumn the host plant dies off and only the tubers survive the winter, and *D. dentata* larvae leave the feeding places.

Comparison and general conclusion

The three *Donacia* species each have 5 larval instars. This is unusual in the Chrysomelidae, except for some representatives of the Cassidinae (Steinhausen, 1950).

The species studied have similar egg incubation periods and activity periods of larvae and adult insects. The main difference, which is striking, is in the total development period from egg to egg which requires 3 years for *D. thalassina* and *D. clavipes* and 2 years for *D. dentata*. This difference arises from the different periods of existence of full-grown larvae, pupae and adults within the cocoons. Adults and sometimes pupae and full-grown larvae of *D. thalassina* and *D. clavipes* stay for a winter within cocoons attached to the living roots of their host plants. The internal cavity of the cocoon is joined to the intercellular air spaces of the root. The host plant of *D. dentata*

←

Fig. 6. Donacia dentata. Population structure during the summer season. 1-5 – larvae of first-fifth instars respectively, 6-8 – larva, pupa and adult in cocoon respectively, 9 – emerged adult, 10 – eggs, 11-13 – generation development during the first-third summer season respectively.

Table 6. Life cycle of *D. dentata*

years	months											
	1	2	3	4	5	6	7	8	9	10	11	12
1							E	E L1	L1 L2 L3	L1 L2 L3	L1 L2 L3	L1 L2 L3
2	L1 L2 L3	L1 L2 L3	L1 L2 L3	L1 L2 L3	L1 L2 L3	L1 L2 L3 L4 L5	L3 L4 L5	L3 L4 L5	L4 L5	L5	L5	L5
3	L5	L5	L5	L5	L5	L5 (L5) (P)	L5 (L5) (P) (I) I	L5 (I) I	I			

E = egg; L1-L5 = 1st-5th instar larvae respectively; (L5), (P), (I) = larva, pupa, adult in cocoon respectively; I = emerged adult.

survives the winter only in form of tubers, all roots die off in autumn. Therefore, the hibernation of this insect within cocoons is impossible, and the formation of cocoons and emergence of adult insects happens during one summer season.

The flight period of *D. thalassina* coincides with the period of flowering of the host plant as the adults feed on pollen. This factor is of no importance for *D. clavipes* and *D. dentata* adults which feed on leaves.

As a result of my study of adult and immature stages of several other *Donacia* species collected from the different localities in the Moscow region from 1991 to 1994, I conclude that one of two above described types of life cycle is peculiar to a number of *Donacia* species.

The most notable characters of the first type of life cycle are: 1) flight period occurs in the spring and the first part of summer, 2) cocoons, containing mainly adults, hibernate. Besides *D. thalassina* and *D. clavipes* a similar type is typical of *D. vulgaris*, *D. obscura*, *D. semicuprea*, *D. crassipes* and *D. cinerea*.

The features of the second type are: 1) flight period occurs mostly during the second part of summer and autumn, 2) cocoons do not hibernate, and adults are found in cocoons only in the middle of summer. Besides *D. dentata* this type is typical of *D. sparganii*, *D. versicolorea* and *D. tomentosa*. The peculiarity of the latter species is that its cocoons are always attached to the inner side of leaves of the host plant, *Butomus umbellatus*, under the water and never occur on roots (personal observation, and Goecke,1933). The leaves of *B. umbellatus* die-off in autumn. Therefore, the hibernation of adults of *D. tomentosa* within cocoons is impossible in spite of roots of their host plant surviving the winter.

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