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Notes on the life cycles of Norwegian *Dixella* species (Diptera, Nematocera, Dixidae)

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The life cycle of 5 Norwegian species of the genus *Dixella* Dyar & Shannon, 1924, was investigated, some of them by a sampling programme in one or two localities, and one from samples taken in different places in southern Norway. Some of the species, possibly all, have two generations each year. Two of the species, *D. amphibia* (De Geer, 1776), and *D. nigra* (Stæger, 1840) spend the winter in the 3rd or 4th larval stage, the others (*D. aestivalis* (Meigen, 1818), *D. hyperborea* (Bergroth, 1889) and *D. dyari* (Garrett, 1924) probably in the egg stage.

Key words: Life cycle, Diptera, Dixidae, *Dixella*, Norway.

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Introduction

The larvae of Norwegian Dixidae are very similar in their way of nourishment and size, at least within the two genera found in Norway. The *Dixa* Meigen, 1818 species are found mostly in running waters, the *Dixella* Dyar & Shannon, 1924 species usually in standing waters. Often several species are found on the same locality. When several congeneric species coexist in a small pond or a stream, there is a great probability of differences in life-cycle patterns to avoid competition and to be reproductively isolated from each other (Illies 1952).

Very few studies have been done on the life cycle of the different species of Dixidae. Hubert (1952) studied *Dixella californica* (Johannsen, 1923) and found that the larval stage would take 43 to 63 days. Adding a few days for the egg stage (5 days are reported by Hubert 1952 and Peach & Fowler 1986) and the pupal stage (3–5 days as reported by Nowell (1951), Nicholson (1978, 1979)), the life cycle would take 2–3 months in California. D. Forsyth (1968), in an appendix to the treatise of John Belkin on the Culicidae of New Zealand, reported on the culturation of Paradixa neozelandica Tonnoir, 1924, having a lifecycle of only 20 days under optimal conditions in the laboratory. Vaillant (1969) says that *Dixella aestivalis* (Meigen, 1818) and *D. autumnalis* (Meigen, 1818) have two generations per year, one in the spring and one in the autumn, that the winter is spent in the larval stage and that the summer generation has a prolonged egg diapause, but gives no data to support these claims. He also says that most of the species have two generations a year, but that *Dixella verna* (Vaillant, 1969) has only one. Peach & Fowler (1986) studied the development of *Dixella autumnalis* in the laboratory, probably close to natural conditions, saying that it took 172 days from one generation to the next. Goldie-Smith (1989) investigated the eggs and larvae of two species of British Dixidae, *D. autumnalis* and *D. amphibia* (De Geer, 1776), but give no information on the duration of the larval stages. In the Handbook to the aquatic insects of North Europe, Wagner (1997) says that the Dixidae probably have only one generation each year.

My own study (Håland 1996) on the Norwegian Dixidae, and the study of Olsen (2008) have shown that at least 17 species occur in this country. At the same time as the studies on the life cycles was done, a study of the morphology of the larvae and pupae was also performed to secure accurate identification of these stages for the species not covered by Disney (1999). This will hopefully be published later.

Material and methods

For most of the species material of larvae and adults has been collected with a box dipped close to vegetation or emerging objects in the water throughout the warm parts of the year. A few larvae or pupae were reared to adults to confirm the identity of the larvae. Other adults were caught with a sweep net near the shore, but the focus has all the time been on larvae. The specimens were preserved in 70% alcohol in the field. Body length and head width of the larvae were measured using an eye-piece micrometer to the nearest 1/16 or 1/40 of an mm respectively. The body length has been measured from the front of the mouth-brushes (it is difficult to see where the head itself ends) to the end of the caudal appendage, and head width at the broadest part of the head. Since the head of the dead larvae is bent almost under the body, an ordinary pin or two was used to keep the body straight during the measuring. The results of these measurements are given in Figures 1–5 and in Table 1.

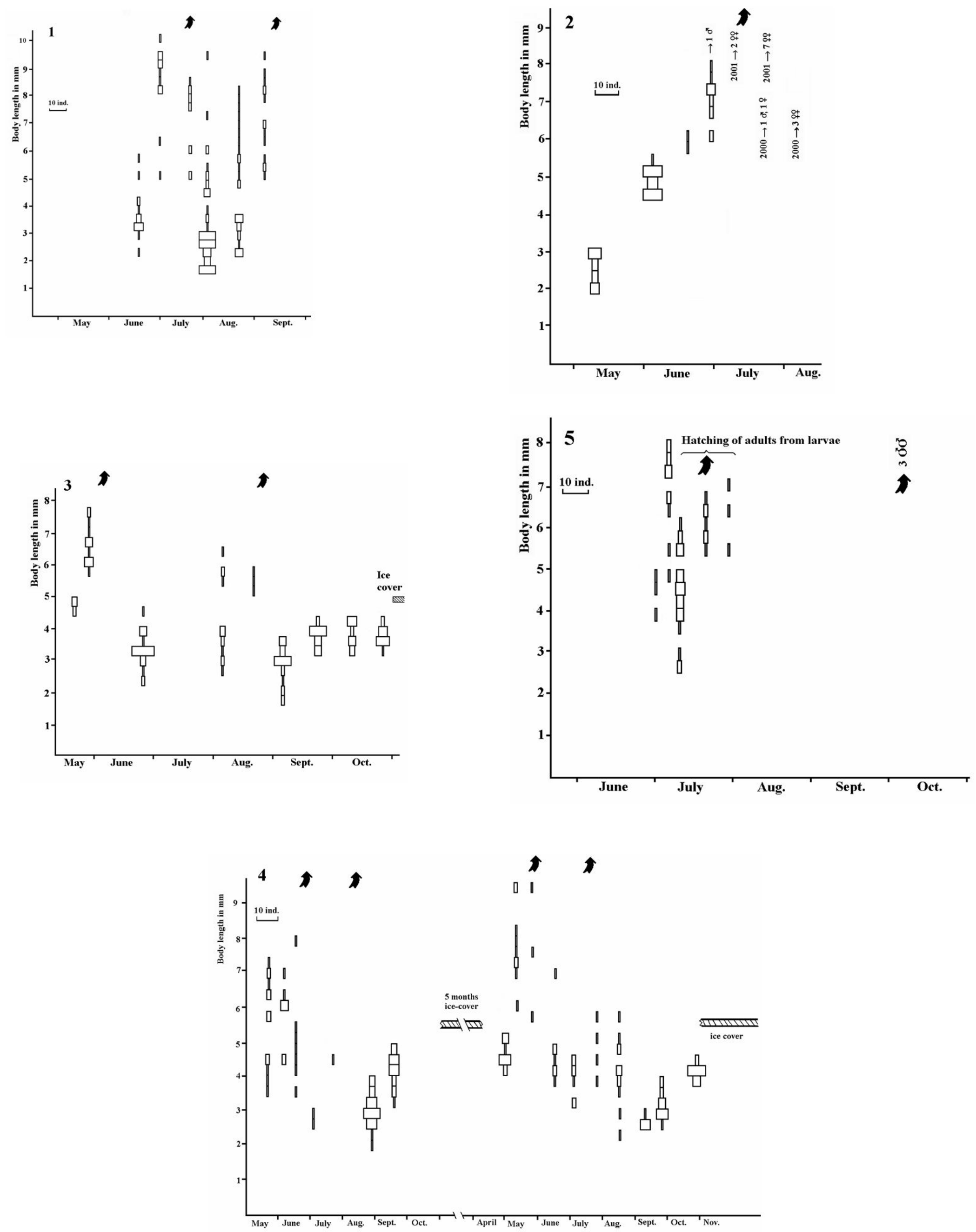
To distinguish the different instars the head width measurements were plotted against frequency (Figures 6–10), and this usually gave a clear picture of the head width of the different instars. In *D. hyperborea* (Bergroth, 1889) this picture was not so clear, for unknown reasons. By combining head width and body length, the picture usually becomes clear. . The body of the larvae sometimes showed tendencies to contraction, more or less, and that is why head width is a much more reliable measurement for the discernment of the different instars. However, to register the growth of the larvae, I decided to use body length, because a substantial growth can be registered even if no moulting into the next instar occurs. The body may contract more or less, sometimes very obviously, when killed, but since it is impossible to separate those with the smallest degree of contraction from the normal ones, all the larvae were used in the analysis often giving a greater span of body lengths than the living larvae would show.

The material is kept in the author's collection.
The UTM references are taken from the WGS84 datum, except those from Pålsbufjorden and Ossjøen.

The life-cycle of *D. aestivalis* was studied in the small lake of Vollsdammen, 767 m a.s.l. (UTM: 32VNP368231. EIS: 62) in Oppland county, Nord-Fron municipality, in 1997. Only this species of Dixidae was found here (except for 1 individual of *Dixa nebulosa* Meigen, 1830), so it was quite certain that also the smallest larvae belonged to aestivalis.

D. hyperborea (Bergroth, 1889) was studied in a small (about 15 x 5 m) temporary pool 760 m a.s.l. at Tverrbygda (UTM: 32VNP254249, EIS: 62), also in Nord-Fron in the summer of 1999. Here both *D. hyperborea* and *D. aestivalis* occurs together, the last one being quite rare, however, and probably only accidentally entering from a ditch some 50 m away. The pool is surrounded by Salix sp. and fir trees (Abies), and regularly dried out at the end of July and was dry for 3 – 4 weeks before showers filled it up in late August. Another biotope where *D. hyperborea* is frequent has also been sampled through many years, but only in the middle of the summer, around hatching time. This small pool, about 20 x 15 m, that also often dry out in the middle of the summer, is situated in Hol municipality in Buskerud county (UTM: MN-785004, EIS: 43) near the lake Pålsbufjorden also at about 760 m.a.s.l. It is surrounded by sparse fir trees (Abies) and some Salix sp.

D. nigra (Staeger, 1840) was studied first at Tjernlitjern near Brumunddal (UTM: 32VPN067493, EIS 46) in Hedmark county. This pond is situated at 132 m a.s.l. It is surrounded by common alder (*Alnus incana*), black alder (*Alnus*



Figures 1–5. The life cycle of *Dixella aestivalis* (Figure 1), *Dixella hyperborea* (Figure 2), *Dixella nigra* (Figure 3), *Dixella amphibia* (Figure 4), and *Dixella dyari* (Figure 5). The thick black arrows indicate the approximate time of main emergence. For the species spending the winter in the larval stage (nigra, amphibia), the approximate time of ice-cover is indicated.

Table 1. Number of specimens measured, mean size and standard deviation (in mm) of measured body length and head width of larvae of some species of *Dixella*. The measurements of *D. autumnalis** are taken from Peach & Fowler (1986).

			1. instar		**2. instar**		**3. instar**		**4. instar**
		n	**Mean ± SD**	**n**	**Mean ± SD**	**n**	**Mean ± SD**	**n**	**Mean ± SD**
D. aestivalis	body	11	1.67 ± 0.03	49	2.73 ± 0.41	27	4.17 ± 0.79	50	7.43 ± 1.40
	head	11	0.15 ± 0.01	49	0.26 ± 0.02	27	0.39 ± 0.02	50	0.55 ± 0.03
D. nigra	body	2	1.66	22	2.75 ± 0.35	94	3.82 ± 0.59	42	6.09 ± 1.09
	head	2	0.15	22	0.23 ± 0.01	94	0.33 ± 0.03	42	0.50 ± 0.04
D. amphibia	body	1	2.06	47	3.00 ± 0.34	85	4,21 ± 0.44	56	7.05 ± 1.18
	head	1	0.15	47	0.23 ± 0.01	85	0.32 ± 0.02	56	0.48 ± 0.04
D. hyperborea	body	7	2.21 ± 0.22	15	2.98 ± 0.43	27	4.95 ± 0.48	55	6.55 ± 0.94
	head	7	0.17 ± 0.01	15	0.28 ± 0.02	27	0.42 ± 0.02	55	0.51 ± 0.03
D. dyari	body			4	2.98 ± 0.32	38	4.09 ± 0.63	94	6.23 ± 0.91
	head			4	0.64 ± 0.01	38	0.37 ± 0.02	94	0.50 ± 0.02
*D. autumnalis**	body	35	1.17 ± 0.39	18	1.43 ± 0.05	7	2.25 ± 0.004	9	4.06 ± 0.32
	head	10	0.12 ± 0.006	27	0.17 ± 0.002	31	0.25 ± 0.028	13	0.41 ± 0.028

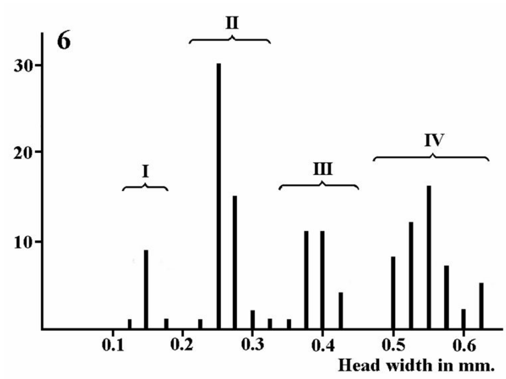
glutinosa), birch (*Betula*), fir (*Abies*), *Salix* sp., etc. and some *Sphagnum*-bog. It is some 130 x 100 m. Parts of the surroundings are quite marshy, with small pools containing *Dixella borealis* (Martini, 1929), *D. amphibia* and *D. hyperborea*, while *D. nigra* and *D. aestivalis* usually was found in the pond itself. The pond was visited irregularly during the summer 2007. Since this was an unusually wet summer, the water level in the pond was very high at the end of summer and autumn and it became very difficult to sample the population. It turned out that *D. nigra* was almost absent from the pond in 2007, only 7 individuals being found after 11 samples, having been much more numerous earlier years. So I decided to study the species also in another pond near Veslelien to the northwest of Brumunddal (UTM: 32VNN994573, EIS: 54) in the summer 2008. This is a pond about 70 meter in diameter, quite circular, created some 40 years ago to give water to the fields in the neighbourhood. Here *D. nigra* is much more numerous, occurring together with *D. aestivalis*, but usually in the more shadowy parts of the pond. For the measuring of head width and body length larvae from both these ponds were used.

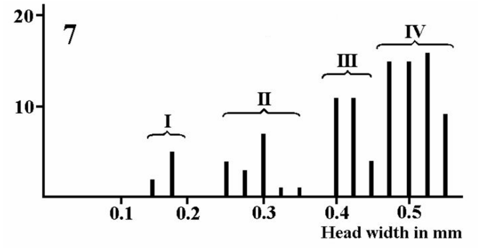
Dixella amphibia was also studied at Tjernlitjern in 2007 and 2008 since it occurred so frequently that it was possible to draw conclusions from the measured specimens.

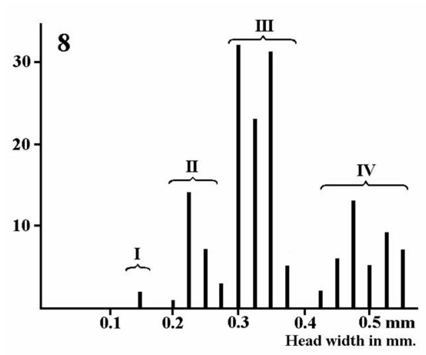
Dixella dyari (Garrett, 1924) has only been sampled in the middle of summer, and once in the autumn. It is quite frequent in several small dams (diameter 10–100 m.) at about 1100 m a.s.l near Vasstulan in Nore og Uvdal municipality (EIS: 34) in Buskerud county. Samples from different years and different small dams have been combined in the figure. These dams are usually surrounded by low bushes of Salix spp. No other species of Dixidae has been found at this height.

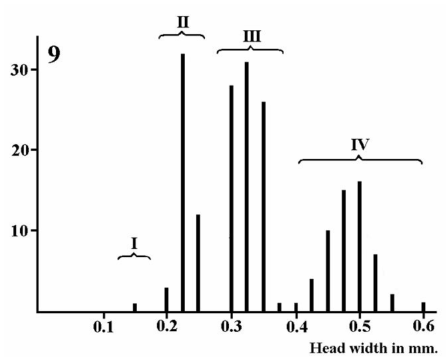
The life cycle of *D. aestivalis* in Vollsdammen is shown in Figure 1, and a diagram of head-width frequencies in Figure 6. From the distribution of the various larval stages it is fairly clear that the species has a bivoltine life cycle at Vollsdammen. There is possibly some overlapping of the generations. The great variation in body length in the 4th stage is probably a reflection of the big difference in body size of the sexes, and even in the head width, the females generally being clearly bigger than the males. This is also evident to some degree in all the other species.

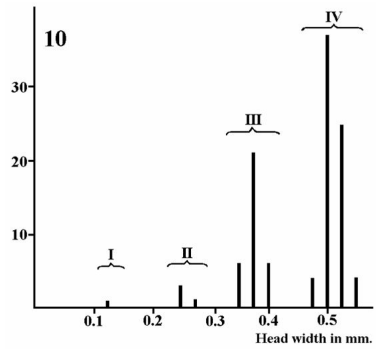
The life cycle of *D. hyperborea* from Tverrbygda is shown in Figure 2, and head widths in Figure 7. The early summer generation is completed before the pool dries up, the adults possibly survive in the bushes around the pool and they are probably laying their eggs in the pool after it refills in late August. At the small pooldam by Pålsbufjorden











Figures 6–10. The frequency of different head-widths of the different larval instars (I–IV) of *Dixella aestivalis* (Figure 6), *D. hyperborea* (Figure 7), *D. nigra* (Figure 8), *D. amphibia* (Figure 9), and *D. dyari* (Figure 10).

the adults have been sampled between 3 July and 4 August, i.e. for more than a month, but in different years, probably dependent on the temperature and precipitation regime of the different years. There is a slight indication that the latest records have been when the dam did not dry out. I have however not been able to confirm this. There is one even later record from the pond Tjernlitjern by Brumunddal as late as 18 August. Here the species probably live in small depressions close to the pond, which do not dry out completely (very few larvae have been found, however), and it is possible that it has two generations here. The population around Tjernlitjern is so small that it has not been possible to get reliable data from this locality.

The life cycle of *Dixella nigra* in the Veslelien-pond is shown in Figure 3, and head widths in Figure 8. The larvae are quite big after the winter and the hatching of adults happens at the end of May and beginning of June. The next generation grows quickly and emerges in the middle of August, and new larvae appear in the beginning of September. The same pattern is also seen in the material from Tjernlitjern.

The life cycle of *Dixella amphibia* in Tjernlitjern is shown in Figure 4, and head widths in Figure 9, almost identical to the pattern shown by *D. nigra.* In the autumn the larvae are almost as big as those of *D. nigra*, having a second generation in July, a bit earlier than the second generation of *D. nigra*.

Dixella dyari has at least one generation at about 1100 m a.s.l. at Dagalifjellet (Buskerud, Nore og Uvdal) (Figure 5), the larvae growing very fast and the adults hatching in the middle of July. The head widths are shown in Figure 10. No sampling has been done earlier in the spring (May–June), and very little later on, so a second generation cannot be excluded. At a site 995 m.a.s.l. (BV, Buskerud: Hol, a pond near the eastern end of Ossjøen (UTM: 32VMM589944. EIS: 34) 3 males were found as late as 6 October 2001, and this might absolutely indicate two generations per year.

Table 1 gives the mean size of body length and head width of the 5 species studied and the corresponding figures given by Peach & Fowler (1986) for *Dixella autumnalis*. These figures are much smaller than those for the species I have studied. This is strange, because the size of the adults is almost equal.

Discussion

Most of the species of the genus *Dixella* investigated have definitely two generations each year.

The life cycle of *D. hyperborea* poses some questions, and further studies are necessary. Is it really true that only the females survive the dry period of the summer? Or can eggs be deposited before the dam dries out and survive these weeks in a kind of diapause, awaiting the first rain? Since the eggs of Dixidae have some resistance to drying (Hubert 1953), at least for a few days, it is nevertheless hardly conceivable that they can survive for several weeks at relatively high summer temperatures. This might imply an unusually long lifespan of the adult females with a corresponding need for water and nourishment. Usually adult dixids are reckoned only to take up water and sugar in fluid form (Nowell 1951, Peach & Fowler 1986). Nowell (1951) thought that adult dixids could only live for a week, but Nicholson (1978) kept them for two weeks in the laboratory. Probably they can live even longer under natural conditions.

D. nigra and *D. amphibia* obviously have two generations a year in Tjernlitjern, and probably most other places found in Norway. *D. nigra* so far in my material is always connected with ponds more or less surrounded by *Sphagnum* spp. (i.e., more or less dystrophic conditions), *D. amphibia* usually seems to prefer more eutrophic conditions, but they occur together in Tjernlitjern. One question here is why these species, that are the only species I have found in Norway living under dystrophic conditions also are the only species spending the winter in the larval stage, while all the others probably spend the winter in the egg stage. Do the larvae spend the winter months at the water surface under/in the ice, at the bottom of the pond, or in the moss at the edge of the pond, and if the last is the case, how far into the moss do they move? The life cycles of these two species are almost synchronous, and they sometimes but not always live in the same pond as they do in Tjernlitjern. There is certainly a possibility that they prefer different microhabitats in these ponds – this has not been investigated thoroughly.

It is a bit early to state whether the differences in life cycle pattern is the main way these species of *Dixella* avoid competition. Personal observations show that *D. dyari* has usually been the only species of Dixidae found in their habitats, above the tree limit at about 1000–1200 m a.s.l. Most of the other species often occur together with *D. aestivalis*, and sometimes together with other species, but the possibility remains that they use different microhabitats.

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