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Dytiscid predators and culicid prey in two boreal snowmelt pools differing in temperature and duration

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Assemblages of dytiscid water beetles and immature mosquitoes were compared in two boreal snowmelt pools that differed chiefly in temperature, owing to differences in shading, and duration. The total abundance of dytiscids (incl. larvae) was similar in the two pools, whereas species richness was more than twice as high in the warmer, less ephemeral pool. Moreover, the latter had five dytiscid guilds, only two of which were represented in the former. Records from previous years indicate that there has been a greater degree of species turnover in the warmer, more exposed pool than in the colder, more shaded one. Large species were rare in both pools, whereas the abundance of the species in the smallest size-class varied widely. The different guilds were compared in terms of larval phenology. Three general patterns are suggested and tested on data from 40 pools studied previously: (1) as pool duration is increased, there is a corresponding increase in guild number, (2) as pool size increases there is a corresponding increase in the number of species within each guild, (3) as pool temperature increases there is a change in species composition, with the cold-adapted species being replaced by more warm-adapted ones. The mosquito faunas of both pools were strongly dominated by *Aedes communis*, whose development time was about five days shorter in the warmer pool. Initial numbers of *A. communis* were similar in the two pools, however, first-instar larvae suffered much higher mortality in the warmer pool.

1. Introduction

A major feature of local communities is that they include only restricted subsets of the regional species pools. This relationship has been a major focus of ecologists studying community structure. The local absence of regionally present species was termed "limited membership" by Roughgarden & Diamond (1986), who classified the causes as: (1) lack of adaptations to the physical environment, (2) limitations on dispersal, and (3) interactions among species.

Aquatic insects of boreal snowmelt pools are community components for which adaptations to

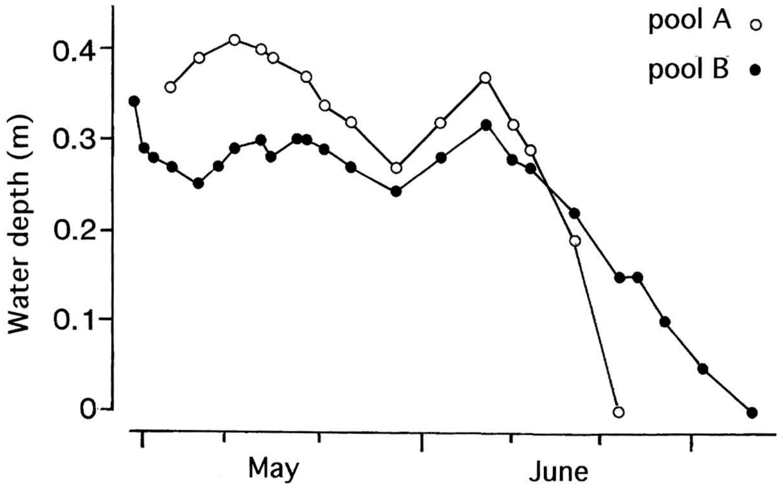

Fig. 1. Temporal variation in the maximum water depth of pools A and B during spring and early summer 1989.

local conditions have been given a high importance in determining species associations (Larson 1985, Nilsson 1986a, Nilsson & Söderström 1988, Nilsson & Svensson in press). Species in which the adults are active fliers should have little difficulty in dispersing. Furthermore, interspecific interactions are not expected to be important in relatively harsh environments with pulsing resources (Price 1984). Juliano & Lawton (1990a) found little evidence for widely or regularly spaced body forms in dytiscid assemblages in small acid waters in England. Moreover, field experiments with *Hydroporus* species in the same pools indicated that adults were not food limited (Juliano & Lawton 1990b). However, documented density-dependence of larval survival may regulate populations (Juliano & Lawton 1990b), although it is unknown whether such interactions may have any community-level effects. In larger, less temporary pools, predation by odonate larvae could be an important factor (Larson 1990).

Many species use temporary pools primarily for larval development (Wiggins et al. 1980), which generally must be completed before the pools dry out. In such species adaptations to the physical environment are chiefly a question of the ability to complete larval development, and to do it well to compensate for long periods with a negative r. The two most important abiotic factors in this context are pool duration and temperature (Nilsson & Söderström 1988, Pickup & Thompson 1990).

In this study we have compared the assemblages of dytiscid water beetles in two snowmelt pools that differ in duration and temperature. This approach was taken in order to relate differences in species and guild compositions to these two abiotic factors. The study also included immature mosquitoes, which made up an important part of the available food resources in the pools.

2. Material and methods

Field data were collected in two temporary pools (A and B) about 25 km NW of Vindeln (64°25′N, 19°30′E), ca. 200 m a.s.l., in northern Sweden. The area belongs to the "middle boreal" vegetation zone (Ahti et al. 1968) and consists mainly of coniferous forest in which *Picea abies* (L.) Karst. and *Pinus sylvestris* L. dominate. Snow covers the ground from about early November to late April.

Pool A is located 1 km NE of the village of Strycksele. The pool basin was formed during the construction of a forest road in the late sixties. The maximum size of the pool is 4.5 × 3.2 m. The pool bottom is covered by tussocks of *Polytrichum* moss, with forest litter and decaying leaves at its center. The vegetation during the dry phase includes *Equisetum sylvaticum* L. and *Calamagrostis* sp.

Pool B is located in a shallow depression on a clearing near a small road. The pool basin was

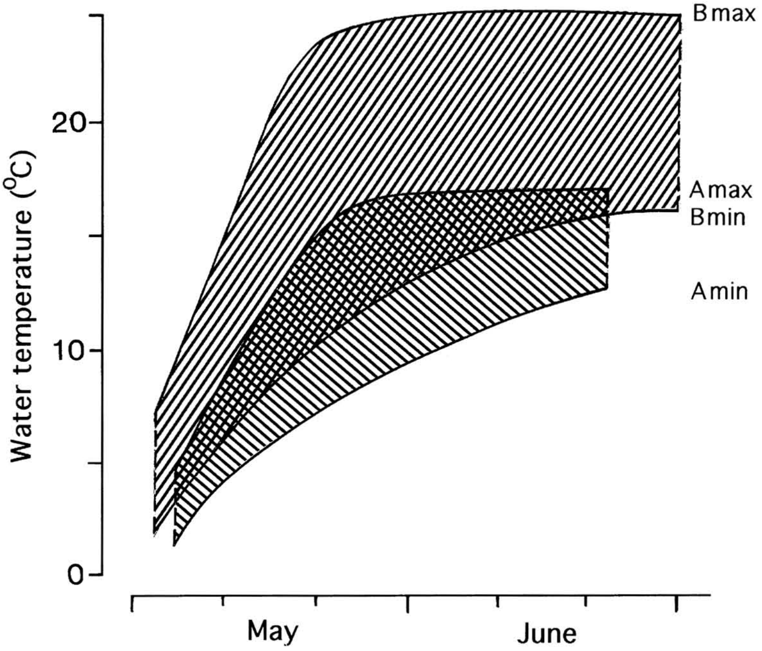

Fig. 2. Diurnal water temperature range for pools A and B during spring and early summer 1989. Minimum values refer to 0700–0900 hrs, and maximum values refer to 1500–1900 hrs during sunny days. Graphs were smoothed in order to show the seasonal pattern better.

probably formed when a nearby landing strip was constructed in 1965. The maximum size of the pool is about 8 × 4 m. The pool bottom consists of clay covered with *Drepanocladus* moss. The macrophytic vegetation is dominated by *Equisetum palustre* L. and *Alopecurus aequalis* Sobol.

Water depths remained at around maximum levels up until about 7 June (Fig. 1), after which levels rapidly decreased, with A and B drying out after about 2 and 4 weeks respectively. Data from other years indicate that B always lasts longer than A and, during wet summers, has a continuous wet phase until freezing occurs in late autumn.

Pool A is more shaded than B and received direct sunlight in its central part from 0820 to 1400 hrs (5 h 40 min) during a sunny day (10 June). The corresponding sunlit period for B was from 0430 to 1545 hrs (11 h 15 min). Pool B was always warmer than pool A (Fig. 2), with the temperature difference being about 2 or 3°C in the morning and 5–8°C in the afternoon. The highest temperatures recorded were 16.5°C in A and 24.3°C in B.

In 1989, the two pools were studied from the onset of thawing, in late April, until early November. The pools were visited at least every five days while they contained water and weekly, until early November, when dry. Pool A was also visited every ten days in 1986 to record the water depth and sample the dytiscid population. Samples for qualitative analysis were also taken occasionally in 1985 and 1986. Pool B was visited irregularly each year from 1982 to 1990. Although dytiscids were sampled occasionally, the intensity and method of sampling varied. Consequently, these data should chiefly be consulted for the presence of species during one or more years previous to 1989.

In 1989, dytiscid adults and larvae and culicid larvae and pupae were sampled at five-day intervals during the wet phase. Dytiscids were sampled with a small hand-net (frame diameter 150 mm, mesh size 0.6 mm). An area of about two ft^2 was sampled intensively for 30 s while stirring up the bottom material with one foot. On each sampling date, five samples were taken in each pool; from 9 May to 18 June in A (9 occasions) and from 30 April to 28 June in B (13 occasions). The samples were sorted fresh, and most individuals, except for *Hydroporus* larvae, were released after identification. Dytiscids in A were sampled every ten days in 1986 with a small hand-net. Three one-minute samples were taken on each occasion.

Culicid immatures were sampled with sieve-traps. Each trap consisted of a 50-mm-long orange plastic cylinder (cut drainpipe, inner diam. 102 mm) whose bottom end had been covered with fine netting (mesh-size 0.6 mm). The trap was attached to the end of a stick and placed on the bottom of the pond at a depth of 0.1–0.2 m. After 10 min the sieve was slowly lifted vertically out of the water, and the culicid immatures in the sieve transferred to alcohol. On each sampling date (10 occasions in A and 12 in B) five sieve-traps were used in each pool. The traps were placed at about equal distances from each other along the pool margins.

Numbers of culicid immatures and dytiscids in the two pools were analysed statistically with the Anova model (SYSTAT; Wilkinson 1990). Values were log-transformed in order to eliminate dependence of variance on means. Due to the later start of the mosquito development in pool A than in pool B, mosquito numbers were compared with a five-day phase shift.

The presence of other predators than dyt–iscids in both the net and sieve-trap samples were noted.

Some of the dytiscid beetles flying into the pools were trapped on the pool surfaces in transparent plastic boxes (referred to as "surface-traps"). These boxes (320 × 215 × 160 mm) were filled about 3/4 full with water (detergent added) and placed centrally in the pools. Their position could be manipulated by pulling on two strings attached to each box. Two traps were used in pool A from 4 May to 9 October, and three were used in B from 30 April to 9 October.

Pitfall traps were used near the pool margins, in order to study movements of adult and larval dytiscids outside the water. The traps, consisting of plastic cups (diam. 60 mm, height 40 mm), were sunk in the ground and provided with triangular wooden covers. Each trap was half-filled with 20% ethylene glycol (detergent added). Six traps were used near A from 4 May to 9 October, and 10 traps were used near B from 30 April to 9 October. The traps were spread out around the pools, initially about 0.2 m above the water margin. Traps in A were moved once in response to a decrease in water level.

Pitfall and surface traps were emptied every five days during the wet phase of the pools and weekly during the dry phase.

Water temperature was measured 5 cm below the surface at the pool center. Incoming solar radiation (W/m^2) was measured continuously at the pool center on 10 and 11 June.

Guild recognition in Dytiscidae chiefly followed the criteria used by Nilsson (1986a), i.e. body size, life-cycle type (Nilsson 1986b) and larval behaviour (Galewski 1971). Special emphasis was placed on characterizing larval prey types in terms of size, behaviour and phenology. Our guild designations are taxonomically delimited to Dytiscidae, i.e. other co-occurring predacious insects are excluded (cf. Simberloff & Dayan 1991).

All 15 *Hydroporus* species belong to guild 1 (Table 1). Larvae are of the creeping type, and the body is short, with the mean adult length ranging from 2.5 to 4.7 mm. The genus is univoltine, with summer larvae and overwintering adults (type I) except in *H. melanarius* Sturm, in which the timing of reproduction is apparently more flexible, and both larvae and adults overwinter (type V). Adults feed mainly on culicid and chironomid larvae, whereas larvae prey chiefly on cladocerans, copepods and smaller chironomid larvae.

Guild 2 is composed of five *Agabus* species and *Colymbetes paykulli* Er., ranging in mean adult body length from 7.2 to 18.4 mm (Table 1). Species in this guild are characterized by a larval diet that is more or less restricted to *Aedes* larvae and pupae. Adults probably have a wider food range, including chironomid larvae and items obtained by scavenging. The life cycle is of type I in *Colymbetes*, the adults of which probably do most of their feeding in permanent waters used for hibernation (Nilsson & Cuppen 1988). The *Agabus* species are semivoltine spring breeders that pass the first winter in the egg stage and the second winter as adults (type III). Larvae are of the creeping or creeping/swimming type.

Two *Agabus* species plus one species each of *Rhantus* and *Acilius* were assigned to guild 3 (Table 1). The life cycles are of type I, and the larvae are of the creeping or chiefly the swimming type. The larval diet is composed chiefly of cladocerans, chironomid larvae, and corixid larvae. Adult body lengths range from 6.3 to 15.4 mm. The comparatively large size together with the fact that most larvae are able to swim strongly suggests that the larval diet differs from that of guild 1, although a certain overlap should be expected.

The three *Ilybius* species, ranging in adult body length from 8.9 to 11.1 mm (Table 1), all belong to guild 4. The life cycle is of type IV, i.e. semivoltine summer breeders that pass the first winter as larvae and the second winter as adults. Larvae are of the creeping type. Larval development is confined to the period from late summer/autumn to early spring, and the chief prey is chironomid larvae. Adults, that overwinter out of water, have a broader diet, including culicid larvae, etc.

Dytiscus marginalis L. was placed in a guild by itself (guild 5). Placement of this species in a separate guild was motivated from its large size (mean adult body length 31 mm) and its divergent diet, i.e. the larvae prey chiefly on *Rana* larvae. During its development one larva has a mean consumption of 300 tadpoles (Blunck 1923). The life cycle is of type I, and larvae are of the swimming type. Adults take a broad spectrum of prey, and much of their feeding probably takes place in permanent waters used for hibernation.

In order to decrease the importance of accidental species, the species collected in the 1989 net samples were separated into breeding and non-breeding ones. Breeding species are those of

Table 1. List of species of Dytiscidae collected in pools A and B in net samples during 1989. Body length is presented as mean ± *SD*. Number of individuals refers to all samples and includes both larvae and adults. Numbers followed by asterisks indicate that one or more larvae were found (breeding species).

Species	Body length	Life cycle	Guild no.	No. of inds Pool A	No. of inds Pool B
Hydroporus neglectus	2.50 ± 0.07	I	1	0	2
H. acutangulus	2.99 ± 0.11	I	1	227*	1
H. nigrita	3.07 ± 0.11	I	1	1	0
H. fuscipennis	3.14 ± 0.06	I	1	0	2
H. puberulus	2.82 ± 0.13	I	1	0	6
H. obscurus	2.79 ± 0.09	I	1	0	4*
H. geniculatus	3.68 ± 0.13	I	1	6*	108*
H. rufifrons	4.66 ± 0.22	I	1	0	1
H. morio	3.39 ± 0.13	I	1	92*	0
H. erythrocephalus	3.73 ± 0.22	I	1	0	49*
H. melanarius	3.43 ± 0.13	V	1	2	0
H. memnonius	4.06 ± 0.11	I	1	1	0
H. tristis	3.01 ± 0.12	I	1	6	169*
H. incognitus	3.74 ± 0.12	I	1	3	20*
H. striola	3.21 ± 0.15	I	1	0	45*
Agabus congener	7.2 ± 0.2	III	2	0	161*
A. lapponicus	7.5 ± 0.3	III	2	24*	0
A. confinis	9.4 ± 0.2	III	2	0	2
A. opacus	8.0 ± 0.2	III	2	90*	0
A. erichsoni	10.4 ± 0.5	III	2	55*	3
A. labiatus	6.3 ± 0.2	I	3	0	81*
A. arcticus	7.6 ± 0.3	I	3	0	2*
Ilybius picipes	9.3 ± 0.2	IV	4	0	7*
I. crassus	11.1 ± 0.6	IV	4	0	2
I. aenescens	8.9 ± 0.2	IV	4	0	2
Colymbetes paykulli	18.4 ± 0.5	I	2	1*	14*
Rhantus suturellus	10.7 ± 0.3	I	3	0	22*
Dytiscus marginalis	30.9 ± 1.1	I	5	0	8*
Acilius canaliculatus	15.4 ± 0.8	I	3	0	9*

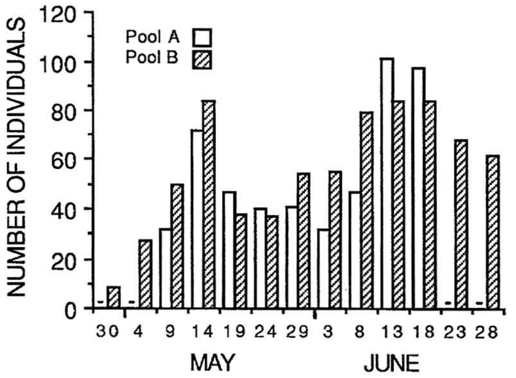

Fig. 3. Numbers of dytiscids (larvae plus adults) collected at 5-day intervals in net samples from pools A and B during spring and early summer 1989. Pooled values for five samples on each occasion.

which one or more larvae were found during 1989.

The nomenclature used follows Nilsson & Persson (1989). Only males of the cryptic species-pair *Agabus congener* (Thunberg) and *A. lapponicus* (Thomson) were identified to species. Based on previous taxonomic investigations (Nilsson 1987, Nilsson et al. 1988, pool A = VB2, pool B = VB5) all individuals from A were assigned to *A. lapponicus* and all from B to *A. congener*. Larvae of *Ilybius angustior* (Gyllenhal) or *I. picipes* (Kirby) from pool B could not be identified to species. Both species have been found in this pool, but since all adults collected during the 1989 net sampling were *I. picipes*, all larvae were assigned to this species.

Our observations indicated that most of the species caught in the net samples were capable of flight. Only *Hydroporus melanarius* appeared to be flightless (Eriksson 1972). Flight has never been observed in *H. neglectus* Schaum, *H. puberulus* LeConte or *H. obscurus* Sturm, but records from isolated pools of recent origin suggest that they are capable of flight (Nilsson unpublished work).

Taxonomic determinations of instar IV culicid larvae followed Utrio (1976). Instar I larvae and pupae were only determined to genus. Species determinations of the second and third larval instars were based on selected characters from Utrio (1976), assuming that only the species known from each pool were present.

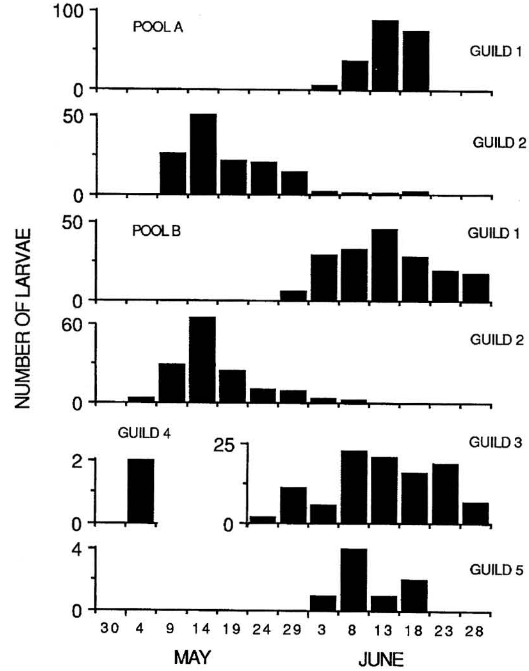

Fig. 4. Seasonal variation in the abundance of dytiscid larvae of guilds 1 and 2 in pool A, and of guilds 1–5 in Pool B. Pooled values from net samples from 1989.

3. Results

3.1. Dytiscid abundance and larval phenology

The difference in dytiscid numbers between the two pools generally remained low throughout the season (Fig. 3), and was not significant at any date when both pools were sampled (Anova, $F_{1,72} = 1.82$). Both pools displayed a bimodal distribution with coincident peaks. The first peak (14 May) was ascribed to recruitment of egg-overwintering *Agabus* larvae, while the second (13 June) was attributed to recruitment of *Hydroporus* larvae.

All five guilds were represented in B, whereas only guilds 1 and 2 occurred in A (Fig. 4). For guilds 1 and 2 larvae of the same guild had a similar phenology regardless of which of the two pools they inhabited; most guild-2 larvae were collected in mid-May, while most guild-1 larvae were collected in mid-June. Guild-4 larvae, which were very few in number, were all collected on 4 May in B. Larvae of the other two guilds in B occurred chiefly from late May until the pool dried out at the end of June.

In both pools, the large species were rare, whereas the abundance of the small *Hydroporus* species ranged from very low to very high.

3.2. Breeders and non-breeders

In A, three out of eight species in guild 1 and all four species in guild 2 were breeders (Table 1). All but two of the breeding species were present during all studied years (Table 2).

In B, 14 breeding and nine non-breeding species were found in the 1989 net-samples (Table 1). Six of the 11 species in guild 1, two of the four species in guild 2, one of the three species in guild 4, and all species in guilds 3 and 5 bred in 1989. A total of 32 species were collected in this pool from 1982 to 1989 (Table 3).

In total (over all years) 14 species were recorded in A and 32 in B. In 1989, 13 of these 14 species were recovered in net-samples from A, whereas the corresponding figure for B was 23 of 32.

Table 2. Annual records of species of Dytiscidae in pool A from 1985 to 1989. No data are available for 1988. Values for 1986 give pooled numbers of larvae plus adults from net samples. Abundance values for 1989 are shown in Table 1.

	Year				No. of
Guild & species	85	86	87	89	years
Guild 1					
Hydroporus acutangulus	x	63	x	x	4
H. nigrita		2		x	2
H. geniculatus	x	11	x	3	
H. morio	x	23	x	x	4
H. melanarius				x	1
H. memnonius				x	1
H. tristis	x	7	x	x	4
H. incognitus	x	9		x	3
H. striola				x	1
Guild 2					
Agabus lapponicus	x	36	x	x	4
A. opacus	x	180	x	x	4
A. erichsoni	x	53	x	x	4
Colymbetes paykulli				x	1
Guild 3					
Agabus elongatus		2			1

3.3. Immigration

Few beetles were caught in the surface traps. The two traps in A caught four individuals of three species, all of which were breeders. Single specimens of *A. lapponicus* and *A. opacus* Aubé caught on 9 May probably reflect the spring migration from terrestrial overwintering sites to aquatic breeding sites. Single specimens of *H. acutangulus* and *A. lapponicus* entered the traps after the pool had dried out.

The three traps in B collected 12 individuals of six species, of which *H. geniculatus* Thoms., *H. tristis* (Payk.) and *A. congener* were breeders. The numbers collected before the pool dried up were equal to the numbers collected afterwards. *H. morio*, *H. nigrita* (F.) and *A. guttatus* (Payk.) were only represented by single specimens in 1989, and the two last-mentioned species had never been observed in B before. On 2 May 1990 at 1530, single flying specimens of *A. opacus* and *R. suturellus* (Harr.) were observed entering the pool.

3.4. Dispersal to and from pupation sites

Mature larvae of guild 1 were only found in the pitfall traps near B. Two larvae of *H. geniculatus* were trapped on 18 June and another two were captured on 25 June. Teneral adults of *H. geniculatus* and *H. tristis* were trapped on 9 and 16 July respectively.

Mature larvae of guild 2 were trapped from 11 to 25 June near A and from 4 to 18 June near B (12 *A. congener* larvae). At A, larvae of *A. opacus* and *A. lapponicus* left the water before those of *A. erichsoni* Gemm. & Har. Teneral adults of *A. congener* were trapped on 9 July at B, while tenerals of *A. lapponicus* and *A. opacus* were trapped on 2 and 20 August at A.

Of guild-3 members, single mature larvae of *A. labiatus* and *R. suturellus* were trapped on 2 July at B. A single larva of *A. bipustulatus* (L.) was trapped on 28 May at B, representing the only record of this species in 1989.

3.5. Mosquito development

The sieve-traps collected a total 1 900 and 1 117 mosquito larvae and pupae in pools A and B, respectively, i.e. there were significantly more mosquito immatures in A than in B (Anova, $F_{1,80} = 21.64$, $P < 0.001$). Besides the earlier start in spring, B had a drastic decrease in numbers from 4 to 9 May, not observed in A (Fig. 5). Significantly more larvae were collected in A than in B on sample occasions 3 and 4 (Anova, post-hoc tests, $F = 6.94$ and 10.57, $P < 0.01$ and 0.002, respectively).

Six and four *Aedes* species were represented in the sieve-trap material from pools A and B, respectively. *Ae. communis* (De Geer) dominated strongly in both pools (88 and 95% of all identified larvae, respectively). *Ae. diantaeus* H.D.K., *Ae. intrudens* Dyar, *Ae. punctor* (Kirby), and *Ae. excrucians* (Walk.) were found in both pools, in sieve-traps or net samples. *Ae. pionips* Dyar and

Table 3. Annual records of species of Dytiscidae in pool B from 1982 to 1989. Abundance values for 1989 are shown in Table 1.

Species	Year 82	83	84	85	86	87	88	89	No. of years
Guild 1									
Hydroporus neglectus			x					x	2
H. acutangulus								x	1
H. fuscipennis								x	1
H. puberulus								x	1
H. obscurus		x						x	2
H. geniculatus	x	x	x	x		x		x	6
H. rufifrons				x				x	2
H. morio		x	x						2
H. erythrocephalus	x	x	x	x		x		x	6
H. tristis	x	x	x			x		x	5
H. incognitus	x	x	x		x	x		x	6
H. striola	x	x	x	x		x		x	6
H. palustris		x							1
Graptodytes granularis		x							1
Guild 2									
Agabus congener	x	x	x	x	x	x	x	x	8
A. confinis								x	1
A. fuscipennis	x	x							2
A. erichsoni			x					x	2
Colymbetes striatus						x			1
C. paykulli		x				x		x	3
Guild 3									
Agabus sturmii		x	x	x					3
A. arcticus								x	1
A. labiatus		x	x	x		x		x	5
Rhantus suturellus	x	x	x	x		x		x	6
Acilius canaliculatus								x	1
Guild 4									
Agabus bipustulatus		x						x	2
Ilybius angustior				x					1
I. picipes								x	1
I. crassus								x	1
I. aenescens		x	x					x	3
I. fuliginosus			x					x	2
Guild 5									
Dytiscus marginalis					x			x	2

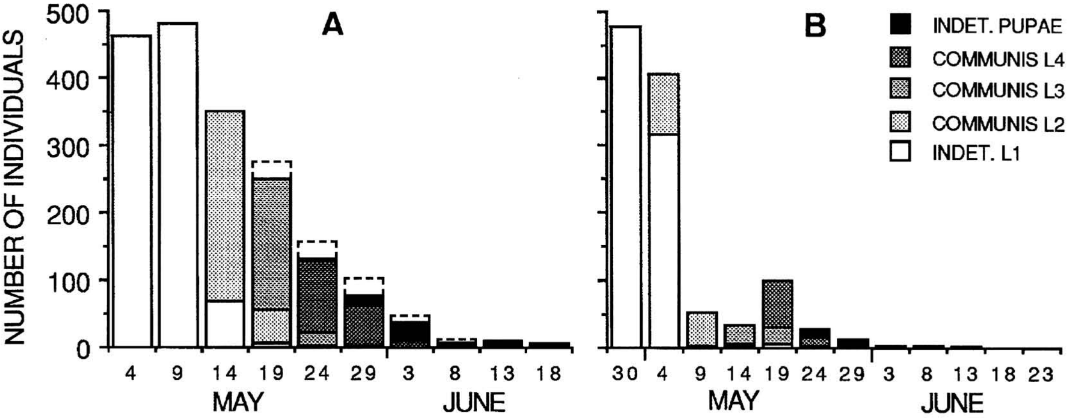

Fig. 5. Seasonal variation in the abundance of larval instars 1–4 and of *Aedes communis* pupae in pools A and B in 1989. Pooled values for five sieve-trap samples on each occasion. Hatched upper portion of bar gives total numbers of all species of Culicidae (larvae plus pupae).

Ae. punctodes Dyar were only found in A, and *Ae. cinereus* Meig. only in B.

Larvae of *Ae. communis* in B completed development about five days earlier than larvae in A (Fig. 5). The decrease in numbers between 4 and 9 May in B was due to high mortality of first-instar larvae (Fig. 5).

3.6. Other predators

Dytiscids were the only predators on mosquito larvae present in A. As *Mochlonyx* larvae started their development after that of the *Aedes* larvae, their relatively small size should make predation unexpected.

In B, corixid and gerrid bugs, and tanypodine larvae were abundant potential predators on mosquito larvae, besides the dytiscids. In this pool also a few odonate larvae (Johansson & Nilsson 1991) were found.

4. Discussion

All but one of the dytiscid species known from A were present in 1989, whereas in B only 2/3 of the total species number were found in this year. This difference, in combination with the higher species richness in B, suggest that the species turnover rate was higher in B than in A, probably because there was more immigration to pool B, owing to its more permanent nature and more exposed position (cf. Nilsson & Svensson, in press).

The fact that many species have been recorded from B throughout the years supports the view that immigration poses no difficulties for most species (Nilsson & Söderström 1988). Thus we suggest that "limited membership" (Roughgarden & Diamond 1986) is more a result of species-related differences in the range of habitats that can be tolerated (cf. Dunson & Travis 1991). The fact that *Agabus guttatus* was caught in the surface traps on B is especially interesting, since this is the first record of flight of this species (cf. Jackson 1956), which lives in smaller running waters (Nilsson & Persson 1989). A single female was caught between 25 and 28 June together with females of other strictly lotic species, such as the mayfly *Ephemerella ?ignita* (Poda) and the stoneflies *Amphinemura sulcicollis* (Steph.) and *Capnopsis schilleri* (Rost.).

Nilsson & Söderström (1988) suggested that pool duration was not an important factor affecting the local diversity of guild 2, because their larval food supply (immature culicids) would nevertheless decrease to zero once the adult mosquitoes emerge. This idea is corroborated by our data as the culicid abundance reached very low values before the pools got dry.

The mortality of instar I *Aedes* larvae was much greater in B than in A (Fig. 5). In B, the maximum number of instar II larvae collected on one occasion was only 18% of that of the first-instar larvae, whereas the corresponding value in A was 59%. We attribute this difference to the fact that the predator community was more diverse in B, including several other predacious insects besides the dytiscids.

In early May, dytiscid abundance was slightly higher in B than in A (Fig. 3), probably because development began later in A. In both pools, the dominating dytiscids during this period were guild 1 adults and guild 2 larvae.

It has been suggested that mosquito larvae in temporary bodies of water are much less exposed to predators than those inhabiting permanent waters (Hinman 1934). This generalization appears to apply to our findings, i.e. the longer lasting pool B had a greater variety and abundance of predators, which, together, probably consumed more mosquito larvae than the dytiscids in A.

Pool size, temperature and duration are three important abiotic factors influencing the dytiscid species composition in boreal snowmelt pools (Nilsson & Svensson, in press). In this study we compared two pools of about the same size that differ in temperature and mean annual duration. The warmer and less ephemeral pool had a more diverse dytiscid fauna, in terms of species as well as guilds. How are these faunal differences related to the abiotic environment?

We suggest that this discussion should focus on larval development, since larvae are normally more vulnerable to dessication than adults and cannot migrate to other waters. Moreover, larvae must feed intensively, since they are forced to complete their development within a limited period of time. The duration and phenology of larval development varied among the five studied guilds, owing to differences in their size and life cycles. Because their eggs overwinter, guild 2 larvae can begin developing very early in the season and were also the first larvae to leave the water for pupation. Thus, by the time that larvae of guilds 1 and 3 begin developing, guild-2 larvae are about ready to leave the water. Since guild-1 species are smaller than guild-3 species, the former tend to develop faster than the latter. Guild-4 species require a wet period in late summer before larval development can begin. The timing of larval development among the species of guild 5 is probably related closely to the phenology of *Rana* tadpoles, i.e. they start developing slightly later than species in guilds 1 and 3.

This inter-guild variation is chiefly related to differences in pool duration. As pool duration increases, guilds should appear in the order 2, 1, 3, 5, and 4. Guild number per pool appeared to be positively related to pool duration. In our study, guilds 3–5 were excluded from A chiefly because of its short duration. A positive relationship between pool duration and number of guilds was also found in the 20 forest pools studied by Nilsson & Svensson (in press) ($r = 0.585$, $P < 0.01$), whereas the corresponding 20 clearing pools did not show this relationship.

Pool duration can also influence within-guild diversity. In our study, the number of guild-1 breeding species was higher in B than in A, probably owing to the presence of cladocerans in large numbers in B. The absence of this prey from pool A is probably due to its emphemeral nature, as cladocerans were not abundant until early June in B. On the other hand, the relatively higher number of guild-2 species in A could be related to the absence of the many other kinds of predators found in B. This absence should make more prey available for guild 2 in A than in B.

Within a given guild, what are the major factors determining the ecological distributions of member species? For guild 2, Nilsson & Söderström (1988) proposed that body size and thermal growth response are the two most important characters that species differ in. If species are adapted to different ambient temperatures, warm and cold pools should be occupied by different species. In fact, differences in thermal growth response could partly explain the differences found between the shared dytiscid guilds of pools A (cold) and B (warm) in the present study. In this view, temperature is a factor that chiefly replaces species. Such a replacement has been documented in a comparison between colder forest pools and warmer clearing pools in the same area (Nilsson & Svensson in press).

In boreal snowmelt pools, temperature is chiefly correlated with the degree of exposure to direct sunlight. We predict shaded and exposed pools will be found to differ in their dytiscid species composition, with the larger and more complex pools, which include both shady and exposed environments, being more diverse than the smaller ones.

Nilsson & Söderström (1988) suggested that guild-2 species differed in their lower thresholds for pool size, with larger species having higher tresholds. Since larger species normally exist at lower densities than smaller ones, larger species should be relatively more sensitive to pool size, i.e. in pools under a certain size, large species should be highly susceptible to local extinction, owing to their very small populations. The relationship between body size and abundance is supported by the present study.

Since mean body size differs between certain guilds, an increase in pool size might also be associated with an increase in guild number. However, the most pronounced association in this regard should be between pool size and the total number of individuals present. Besides larger populations, more individuals will also result in more species; thus we suggest that in boreal snowmelt pools the main trend associated with an increase in pool size is an increase in the number of species within guilds. This conclusion is corroborated from the data presented by Nilsson & Svensson (in press), both for forest and clearing pools (forest $r = 0.754$, clearing $r = 0.712$, $P < 0.001$, area log-transformed, guild 1 only).

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