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Community structure in the Dytiscidae (Coleoptera) of a northern Swedish seasonal pond

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A community of Dytiscidae in a northern Swedish seasonal pond was studied. Altogether 33 species were recorded from the pond over a period of seven years. Two groups are recognized: (1) 10 core species that are abundant and reproduce in the pond every year, and (2) 23 satellite species that are less frequent occupants of the pond. The core species are the potentially most interactive ones, and if the community is structured by interspecific competition it should be most readily detected among these species. The use of food resources of the 10 core species is deduced from a comparison of larval phenology and seasonal distribution of prey organisms together with observations of larval diets made in culture. From these data the 10 core species are separated into two guilds. Guild I includes 5 *Hydroporus* species: (1) of small size, (2) with larval development in June, and (3) with larvae of the creeping type. Guild II includes 4 *Agabus* species: (1) of large size, (2) with larval development in May, and (3) with larvae of the creeping type. *A. labiatus* approaches guild I, but differs in the larger size, the creeping—swimming larvae, and in adult phenology. The most important larval prey animals are culicid larvae for guild II, and cladocerans and chironomid larvae for guild I. Species packing in guilds is studied in terms of adult and larval size differences. Size ratios show considerable variation, with means for each guild between 1.1 and 1.2. The coexistence of these species indicates either a lack of interspecific competition or the existence of other, yet unknown, relevant differences between species.

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1. Introduction

By tradition, most studies dealing with the species composition of water beetle communities have used an autecological approach (e.g. Meyer & Dettner 1981, Nilsson 1984). Furthermore, distributions of species or species-groups have been correlated mainly with abiotic factors (e.g. Cuppen 1983). The basic assumption made in this kind of work is that species interactions, chiefly competition, are nonexistent or at least secondary to autecological adaptation to abiotic features of the environment in determining community composition. A local community, in this view, includes the species preferring the actual kind of habitat and which have been able to colonize it, or put in the words of James & Boecklen (1984) "a collection of species that happen to exist together because of converging accidents of space, time, and environmental needs". The above outlined individualistic view of species in communities has been postulated as probable for most predatory insects (Strong 1983) as autecology, predation and the weather normally serve to maintain populations below densities that would deplete resources and cause situations of intense interspecific competition.

Lawton & Hassell (1984) briefly reviewed the field evidence of interspecific competition in predatory Coleoptera, and concluded that the few studies made provide at best weak and indirect evidence for competition. They also gave some negative results from field experiments with coexisting dytiscid species of similar body size, and stressed the lack of data on larval ecology.

The study of resource utilization in dytiscid water beetles is best related to differences in size, life cycles and larval morphobiotic types. From these parameters sets of functionally similar species, or guilds, can be recognized. If competitive exclusion is an important factor in determining the species composition of communities, then the size of guilds should be limited.

It is also necessary to obtain data on species abundance relations in order to separate the core and satellite species (Hanski 1982, see also Brown 1984 for a critique), i.e. to identify the species that are potentially most interactive and according to the theory should be more evenly spaced-out in the niche space. The number of rare species should be high as most dytiscids are good flyers and thus able to show up as accidental visitors, and in open systems they may enter a habitat directly from surrounding wetlands. In a given community the core species are the reproducing species of higher abundance. Reproduction per se is not a useful criterion, e.g. as single females of nonwintering spring migrants (Wiggins et al. 1980) can lay just a few eggs and then fly away to another site.

After the core species have been identified as such, and separated into guilds, the structure of the guilds can be analyzed in terms of size differences. In this study the dytiscid community of a seasonal pond is analyzed in the above terms.

In the boreal region the frequent small nonpermanent waters often have species-rich dytiscid communities dominated by a few genera such as *Hydroporus, Agabus* and *Ilybius* (Nilsson 1982 and 1984, Larson 1985). In spite of their astatic character, these wetlands have a high durational stability and a high predictability (Southwood 1977), and several years of collecting indicate relatively stable community compositions. Assuming species interactions to be important, these communities should be studied from the viewpoint of niche theory (Schoener 1974) and searched for patterns, i.e. similarities or differences between the composition of specific communities. The community is here defined taxonomically. In spite of this the same resource pool is in most cases also used by other predatory aquatic insects, e.g. aquatic Heteroptera and larvae of Odonata and Trichoptera. Preferably, when investigating the structure in actual communities these groups should also be included. However, in the seasonal pond studied here they are of minor importance, being either absent or very rare. Semiquantitative data from one year are here matched with more random collections from six preceeding years.

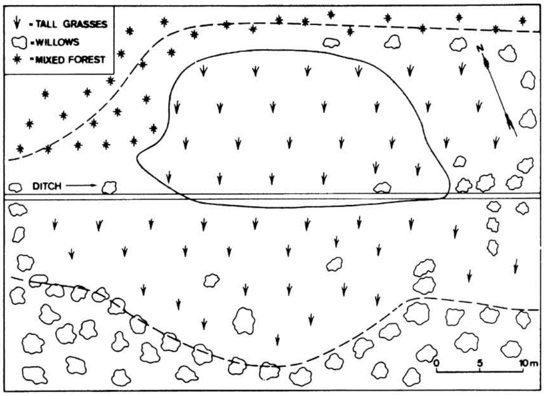

Fig. 1. Vegetation map of the seasonal pond studied. The solid line is the pond outline in early May, and the broken line shows approximately the extension of the river spring flood.

2. Study area

The seasonal pond studied (Stewart & Kantrud 1971) is situated in a small depression about 60 km from the Vindelälven river at Sirapsbacken, 25 km upstream from Vindeln (Fig. 1, see also Olsson & Söderström 1978: fig. 1). The area belongs to the "middle boreal" vegetation zone (Ahti et al. 1968), being covered mainly by coniferous forests of spruce (*Picea abies* (L.) Karst.) and pine (*Pinus sylvestris* L.). The total amplitude of the pond is about 1 − 2 m, largely depending on the river amplitude, which shows a marked interannual variation. In late April or early May melting snow forms a pond of about 500 m^2 (Fig. 1), delimited by a ditch and the surrounding forest, and with a mean depth of about 0.3 m. The pond bottom is covered with grasses of the genera *Calamagrostis* and *Deschampsia*, giving a very hummocky structure. The melt-water stage prevails for slightly less than a month, and during this time the water level shows a continuous decline. In late May the river flood water reaches the pond which now becomes the innermost part of an extensive river lagoon. As the river declines, the pond is formed again and, after a short period, is dry. This river-water stage exists for about one month, and differs from the preceeding stage in the warmer and markedly more coloured water. The water temperature is about 3 − 8°C during the melt-water stage and 10 − 15°C during the river-water stage (daily means).

The dry period is about 3 months, and in most years is followed by a wet period of varying length. During 1984 this rain-water stage was interrupted and the later continuous period lasted only for about 10 days before freezing.

The pond water-stage was continuously recorded during the period studied. The pond is an open system connected with a ditch to the river, and directly to the river during the spring flood. In the opposite direction, during wet periods, the ditch connects the pond with other ditches draining a mire.

Table 1. Yearly records of dytiscid species from the studied pond. Figures given are number of adults; presence is indicated by a +. Presence of larvae is indicated by *l*, and the species ranked as core species are marked *.

		1977	78	79	81	82	83	84	Years
1.	*Hygrotus inaequalis*	1							1
2.	*Coelambus impressopunctatus*	1	1						2
*3.	*Hydroporus brevis*	29	10	+		+	+	300*l*	6
4.	*H. dorsalis*	1							1
5.	*H. erythrocephalus*							1	1
*6.	*H. fuscipennis*	25	4	+		+	+	16	6
7.	*H. incognitus*	5					+	14	3
8.	*H. levanderi*						+	1	2
9.	*H. melanarius*						+	1	2
10.	*H. neglectus*						+	1	2
*11.	*H. nigellus*	27	4	+		+	+	24*l*	6
12.	*H. palustris*							1	1
*13.	*H. rufifrons*	102	5	+		+	+	15*l*	6
*14.	*H. striola*	267	22	+		+	+	218*l*	6
15.	*H. tristis*					+	+	17	3
16.	*Agabus arcticus*	1						1	2
17.	*A. biguttulus*			+			+	1*l*	3
*18.	*A. confinis*	1		+	+	+*l*	+*l*	12*l*	6
*19.	*A. congener*	3		+*l*	+		+*l*	5*l*	5
*20.	*A. erichsoni*	3		+		+*l*	+*l*	10*l*	5
21.	*A. fuscipennis*					+*l*	+		2
*22.	*A. labiatus*	6	1	+			+	6*l*	5
23.	*A. sturmii*	1							1
*24.	*A. subtilis*	14			+		+*l*	4*l*	4
25.	*A. wasastjernae*	2		+				7*l*	3
26.	*Ilybius aenescens*	2							1
27.	*I. angustior*	2						1	2
28.	*Rhantus exsoletus*	4	1			+		2	4
29.	*R. suturellus*	2						2*l*	2
30.	*Colymbetes paykulli*	8						1*l*	2
31.	*C. striatus*	9						1	2
32.	*Acilius canaliculatus*	2			+*l*				2
33.	*Dytiscus marginalis*	2						1*l*	2

3. Methods and material

Semiquantitative samples of larvae and adults were taken every 10 days on eight occasions during the ice-free season, when water was present, 26.IV—11.X.1984. Upon each occasion five samples were taken with a water-net (mesh width 0.5 mm) used intensively for one minute over an area of two square-feet with a concommitant stirring up of the bottom material with the foot. The sampling points were distributed over the entire pond, though restricted to the shallower parts at periods of high water. The samples were immediately transferred to a flat bowl with some water, and the adults and larvae were subsequently extracted and transferred to 70% ethanol. The presence of other invertebrates was noted, using the 3-graded scale: low, medium, and high abundance. During this period additional qualitative samples were also taken upon 12 different occasions.

For the years 1977—79 and 1981—83, pooled data were used from irregular netting and trapping. In 1977 two traps (Nilsson 1978) were used for 24 hours each on 25—26.V and one on 2.VII, and net samples were taken on nine occasions on 17.V—17.VII (all collections for this year made by O. Söderström). In 1978 a net sample was taken by O. Söderström on 16.V. In 1979 a trap was in use over the period 9—17.V, and a net sample was taken on 12.V. In 1981 there is only a single net sample from 2.VII, and in 1982 two samples were taken on 15.V and 26.V. In 1983 net samples were taken on nine occasions from 29.IV to 22.X.

For the identification of *Hydroporus* larvae collected larvae were reared to the adult stage. The nomenclature mainly follows Silfverberg (1979).

4. Results

4.1. Core species

In Table 1, collection data from seven different years are listed together. The 1977 data was published by Nilsson (1978), in which *H. fuscipennis* was misidentified as *H. acutangulus* Th., and *H. submuticus* Th. and *Ilybius subaeneus* Er. were only found at another, nearby site. Altogether 33 species were re-

Table 2. Number of adults (ad) and larvae of different instars (L 1—3) of the core species of Dytiscidae in the studied pond during the ice-free season, 1984. Pooled data from five samples taken on each occasion.

		26.IV	6.V	14.V	24.V	6.VI	15.VI	27.IX	11.X
Hydroporus brevis	ad	26	50	20	5	33	25	38	79
	L3	–	–	–	–	15	–	–	–
H. fuscipennis	ad	2	1	2	–	4	–	2	2
H. nigellus	ad	3	1	3	5	3	1	2	2
	L3	–	–	–	–	–	4	–	–
H. rufifrons	ad	1	8	2	1	2	–	–	1
	L1	–	–	–	–	5	–	–	–
	L2	–	–	–	–	2	–	–	–
	L3	–	–	–	–	–	2	–	–
H. striola	ad	16	29	25	4	12	34	19	51
	L1	–	–	–	–	2	–	–	–
	L2	–	–	–	–	2	3	–	–
	L3	–	–	–	–	2	14	–	–
Agabus confinis	ad	–	1	3	2	–	1	–	–
	L1	–	2	–	–	–	–	–	–
	L2	–	1	5	–	–	–	–	–
	L3	–	–	–	–	1	–	–	–
A. congener	ad	–	1	1	–	–	1	–	–
	L1	3	10	2	1	–	–	–	–
	L2	–	1	14	7	–	–	–	–
	L3	–	–	1	–	1	–	–	–
A. erichsoni	ad	–	1	–	–	–	2	–	–
	L1	4	1	–	–	–	–	–	1
	L2	–	8	18	–	–	–	–	–
	L3	–	–	2	2	–	–	–	–
A. labiatus	ad	–	1	1	–	–	–	–	–
A. subtilis	ad	–	–	–	–	–	1	–	–
	L1	5	12	1	–	–	–	–	–
	L2	–	8	9	1	–	–	–	–
	L3	–	–	2	2	–	–	–	–

corded from the studied pond. As collecting intensity and methods are highly different each year, no interannual comparison is possible. Figures can be given for only three of the years as the other years include data recording presence only. Larvae were not recorded at all in the first two years, and *Hydroporus* larvae only in 1984. This data set is used to designate the core species of this community. It is assumed that the community is stable during this period, i.e. that the core species are the same. This is very clear for the *Hydroporus* species, though seemingly less so for the other genera. As adults, the *Agabus* species stay hidden under the grass tussocks during the daytime and very few specimens are normally taken with the water net. They are also seemingly less attracted to the traps compared to the larger species like *Colymbetes*. The core species are considered as those recorded for five years or more. Also included is *A. subtilis*, as it was found in relatively high numbers in 1977 and larvae were present both in 1983 and 1984. To the core species of this community there belong five species each of the genera *Hydroporus* and *Agabus*.

In Table 2, the pooled data from the semi-quantitative sampling for 1984 is shown for the core species. Adults of all 10 species were found, as well as larvae of all except *H. fuscipennis* and *A. labiatus*. Larvae of *A. labiatus* occurred in the qualitative samples from 6—13.VI.1984, as did a single larva of *H. fuscipennis* on 13.VI. It can be seen that adult *Hydroporus* were found on all occasions, and the larvae only on 6.VI and 15.VI. Adult *Agabus* were found from 6.V to 15.VI, i.e. they over-winter outside the pond and are absent during the rain-water stage. The larvae of this genus occurred from 26.IV to 6.VI, except for those of *A. labiatus* found later in the qualitative samples. Further, a single 1st-instar larva of *A. erichsoni* was found in the autumn. Exceptionally, the diapausing eggs of this species

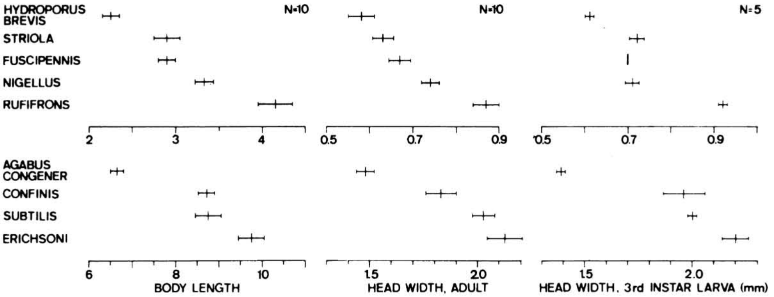

Fig. 2. Size distributions of species in guilds I and II. Adult body length measured medially from anterior margin of pronotum to tip of elytra. Head width of adults measured dorsally just anterior to eyes, that of larvae given as maximum width of head capsule in *Hydroporus* and width at ocelli in *Agabus*, both in dorsal view. All sizes given as mean±*SD* for five male and five female adults or five larvae (in *H. fuscipennis* only a single larva was available) from the studied pond.

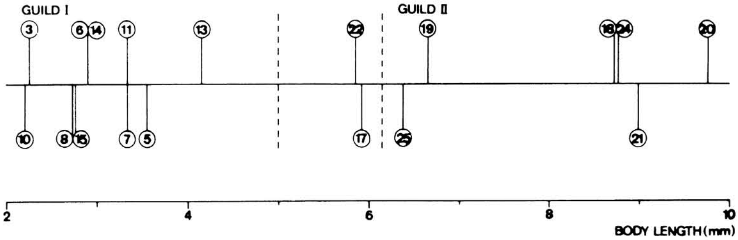

Fig. 3. Size distributions of core species (above) and the satellite species (below) belonging to the same guilds. Figures in circles refer to enumeration of species in Table 1. Mean values of adult body length measured as in Fig. 2.

already hatch in the autumn, and most probably the resulting larvae die during the winter (Nilsson 1986).

4.2. Guilds

Using size and life cycles the 10 core species are separated here into three groups. The five *Hydroporus* species (guild I) are of small size, the adults were found in the water during the whole wet phase; the larvae are of the creeping type (Galewski 1971) and their development was confined to June (life-cycle type 1, Nilsson 1986). The *Agabus* species, except for *A. labiatus* (guild II), are large, the adults were found from early May to late June (i.e. not during the autumnal rain-water stage), and their development was confined to May and early June (life-cycle type 3, Nilsson 1986).

The life cycle of *A. labiatus* belongs to the same type as that of guild I (Nilsson 1986). It differs, however, from the species of this guild in the larger size (mean body length without head 5.84 mm) and the larva is of the creeping—swimming type (Galewski 1971). Further, the adults were not found during the autumnal rain-water stage. As *A. labiatus* differs functionally from both guild I and II, it is treated separately.

Size distributions for guilds I and II, including body length and adult and larval head widths, are presented in Fig. 2. In guild I, *H. brevis* is the smallest species and *H. rufifrons* the largest. The three intermediate species *H. striola, H. fuscipennis* and *H. nigellus* partly overlap. *H. nigellus* is slightly larger as an adult, though very similar to *H. striola* in larval size. The single larva of *H. fuscipennis* studied indicates a smaller size than in the otherwise similar *H. striola.*

In guild II, *A. congener* is the smallest species. The other three species are more similar in size, and *A. confinis* and *A. subtilis* differ only in the larger adult head width in the latter species. In Table 3, size ratios between neighbouring species are given for both guilds as a measure of species packing in the niche space.

In Fig. 3, I have also given the body lengths of the rare species (occasional visitors excluded) that can be attributed to the recognized guilds. These species are all very similar in size to the corresponding core species, a fact that might provide a partial answer to their rareness in this community. Some of them are more abundant in adjacent habitats, i.e. a forest ditch or closer to the river.

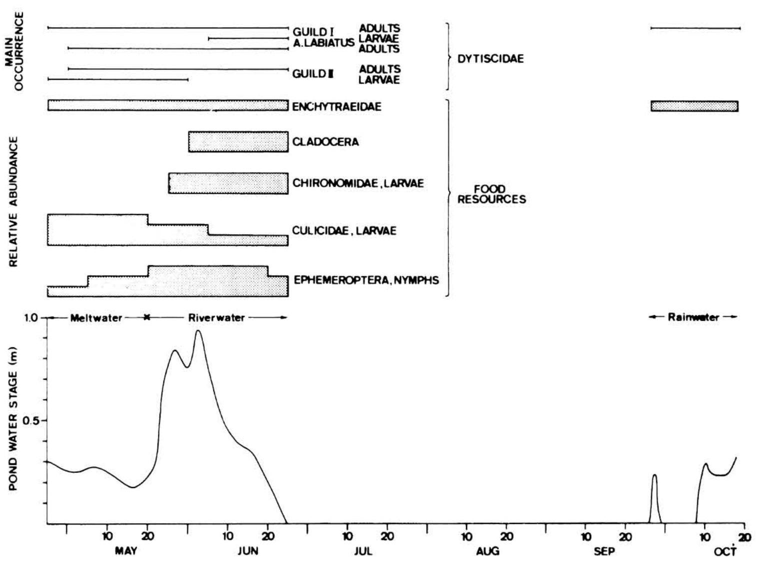

Fig. 4. Seasonal variation in pond water-stage, relative abundance of prey organisms, and main occurrence of adults and larvae of the dytiscid guilds in the studied seasonal pond 1984.

4.3. Resource distribution

Dytiscids are known as omnivorous predators (Balduf 1935), and in culture most species eat a wide range of items. Prey selection is seemingly much dependent on prey size and availability (Pajunen 1983). The most important food resources in the studied pond are cladocerans, larvae of Chironomidae and Culicidae, and nymphs of Ephemeroptera. There are also plenty of enchytraeid worms. The main features of the seasonal distribution of these groups are shown in Fig. 4 together with the water regime and the occurrence of larvae and adults of the recognized dytiscid guilds.

As a rule the adults occur in the water for a more extended period than the larvae, a fact that increases the potential overlap in resource utilization between the different guilds. Only in the autumn were the adults of guild I the only ones actively feeding. It seems, however, likely that the major part of the food harvesting occurs in the larval stage (Southwood 1981:47) and this period is clearly separated between the two guilds. The larval development of *A. labiatus* and the species in guild I coincide with the presence of cladocerans and chironomid larvae. The mayfly nymphs are at this time too large to form a suitable prey, at least for the *Hydroporus* species. The larval development of guild II chiefly follows that of the culicids, though mayfly nymphs are also preyed upon. A separation in time of the larval development of the guilds here results in the use of different prey.

5. Discussion

This study shows that Galewski's (1973) notion of a maximum of two species belonging to the same morphobiotic type in a water body, i.e. a maximum guild size of only two species in dytiscid communities, is not a general rule in nature. As the studied community is characterized by an extremely high number of species, the observed guild sizes of four and five species are probably near maximum. Guild size is, of course, dependent on how guilds are defined, and for example Ranta (1982) used the family Dytiscidae as a single guild. This could be meaningful given a very narrow resource pool, i.e. only one prey species, but otherwise, including the majority of natural habitats, differences in life cycles, size and hunting behaviour necessitate a further division. The assignment of species to guilds should be based on detailed data on resource use by all the species in the community (Connor & Simberloff 1984:319). In the present study resource use is deduced by comparing larval phenology and seasonal distribution of prey (Fig. 4) together with observations of larval diets made in culture.

Table 3. Size ratios (larger/smaller) between adjacent-sized species in guilds I and II, and the mean for each guild and measurement.

	Body length	Head width	
		adult	larva
Guild I (*Hydroporus*)			
rufifrons/nigellus	1.249	1.176	1.296
nigellus/fuscipennis	1.156	1.104	–
fuscipennis/striola	1.000	1.063	–
striola/brevis	1.274	1.086	1.180
Mean	1.170	1.107	–
Guild II (*Agabus*)			
erichsoni/subtilis	1.114	1.049	1.100
subtilis/confinis	1.005	1.109	1.021
confinis/congener	1.311	1.236	1.410
Mean	1.143	1.131	1.177

In a study of rock-pool communities (data from Lindberg 1944), Ranta (1982) recognized only three core species in the Dytiscidae. Of these, *Ilybius subaeneus* definitely belongs to another guild from the other two, viz. *Hydroporus melanocephalus* (Marsh.) and *Potamonectes griseostriatus*. Given the same treatment, rock-pool guilds thus consist of fewer species than those of the seasonal pond studied here. This could be expected mainly from the marked differences in habitat complexity and predictability. Ranta (1982) concluded that these data said little about whether there was competition or not, and emphasized the need for experimental tests.

Though useful, the application of the core-satellite species concept is quite problematic. First, it should be limited to sets of species which may establish populations at the same local sites, i.e. habitat selection must be sufficiently similar (Hanski 1982). Even if the study is limited to a single site, this is not necessarily so, as the position of the actual habitat in the habitat spectrum of the encountered species could be different. The other problem is how to separate the core species, which by definition are locally abundant and regionally common (Hanski 1982). Some species, such as *Hydroporus brevis* in this study, are locally abundant but regionally rare. It might be noted that in guild I the two most abundant species, *H. brevis* and *H. striola* are very different in that *H. brevis* is regionally very rare but *H. striola* very common. It is also difficult to obtain abundance data that permit a satisfactory delimitation of core species. From Table 1 it is clear that the two above-mentioned species together with *H. rufifrons* are the three most abundant species of guild I. Selecting only these three as core species would result in higher and more even size ratios (adult body length ratios 1.444 and 1.274).

The size ratios of guilds I and II given in Table 3 are seemingly not consistent with the ideas of a minimum size ratio compatible with, and constant size ratios between, coexisting and ecologically similar species (Simberloff & Boecklen 1981). The coexistence of these species indicates either the lack of interspecific competition or the existence of other, yet unknown, relevant differences between species. Actual size distributions in the data presented by Ranta (1982) were not significantly different from random distributions, thus lending no support to the concept of communities structured by interspecific competition. In spite of these negative results, the search for pattern in dytiscid communities deserves further study, and here the core species and guild concepts are indeed very valuable. Results may be improved if patterns of species abundance were studied in terms of biomass rather than as numbers of individuals. As a rule the smaller species are more abundant, and this could be compensated for if populations were expressed in biomass. In this study this approach could render at least *Colymbetes paykulli* the status of core species, because a total sum of 13 larvae were found in the 1984 samples (but no adult). Functionally, this species approaches *A. labiatus*, but is much larger (body length without head 16 mm) and in the studied pond the larvae of *C. paykulli* mainly hunt mayfly nymphs.

The importance of interspecific competition for food resources in dytiscid communities is dependent on whether or not these are in limited supply. Data on how dytiscids influence their food resources are scarce. Arts et al. (1981) calculated from caging experiments that *Acilius* larvae may exert considerable influence on the numbers of *Daphnia* in ponds. Pajunen (1983) regarded the larvae of *Potamonectes griseostriatus* (DeG.) as inefficient predators that did not deplete chironomid populations in rock pools, mainly because chironomid larvae escaped predation in the bottom mud and were only available during migration. Several studies on mortality of immature Culicidae have concluded that predators, mainly dytiscids, are unimportant (e.g. Wiberg-Larsen 1978, Lumiaho & Itämies 1981) when compared to other factors such as dessication. On the other hand, Iversen (1971) concluded that predation by larvae of *Colymbetes fuscus* (L.) was the main cause of mortality (in total 87 % during the aquatic stages) in a population of *Aedes communis* (DeG.) in a temporary woodland pool. Further, Service (1976) concluded that in many situations predation will be the most important single factor determining population size, acting most heavily on the immature stages, though the actual evidence is weak.

It seems premature to make any general statements on this topic until more detailed studies are at hand. Nevertheless, a shortage of food resources in dytiscid communities cannot be rejected out of hand. It is here also necessary to discuss separately communities in which food resources are of the pulsing or ephemeral type (Price 1984), i.e. are available for a limited time and increase and decline rapidly. Under these conditions the probability of interspecific competition occurring is low (Price 1984, Larson 1985), and thus the coexistence of very similar species, as in the pond studied here, is made possible. On the other hand, the less diverse dytiscid fauna of environmentally more stable habitats, e.g. lakes and rivers, may reflect a situation with more intense competition. Future research in this field should include a comparative study of dytiscid community structure in habitats with different degrees of seasonality using the "core-satellite species" and guild concepts.

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