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Age Structure, Phenology and Prey of Some Rheophilic Dytiscidae (Coleoptera)

by **K. Dettner, M. Hübner & R. Classen**

Abstract: Several species of water beetles (Dytiscidae; genera *Platambus, Agabus, Deronectes, Oreodytes)* from brooks of the Eifel region show distinct irregular patterns of distribution. Age classes were defined on the basis of internal genital organs. This together with larval data made possible the definition of two types of life cycles and interpretation of complicated phenological data. Protandry and the unique inhibition of sexual maturation in males of *Agabus paludosus* represent interesting phenomena which were discovered. Only minor differences with respect to age structure and phenology of the population were found between close allied species.
Smaller sized water beetles preferred larvae of Chironomidae as prey. Beetles of larger body size use a greater variety of food as well as ingesting larger larvae of Chironomidae. Within a water beetle species ingestion of prey organisms is positively correlated (qualitatively and quantitatively) with the presence and relative abundance of prey organisms present. No distinct nutritional niches were found among these several beetle species and moreover no age dependent nutritional variation was seen. The discontinuous distribution of the water beetle species probably may be traced back to the bionomics of the developmental stages.

Key words: Coleoptera Dytiscidae – age structure – population – phenology – nutrition biology – genital organ.

Introduction

Numerous brooks of the Eifel region and the pre-Eifel plain have been investigated by our group (Dettner, 1985a; Classen & Dettner, 1983; Meyer, 1980; Meyer & Dettner, 1981; Plymackers, 1980) in order to determine relative abundances of hydradephagan water beetles. The localities are situated in the vicinity of Aachen (Federal Republic of Germany) at the frontier between Belgium and Germany (Fig. 1; localities 1–7). As shown in Table 1 some physicochemical and structural characters of selected brooks have been shown to be quite similar (e.g. Inde: localities PS 1 and PS 2; Tiefenbach and Schlehbach). Nevertheless the presence and relative abundance of certain dytiscids varies considerably. Within the given localities it was only possible to positively correlate the occurrence of *Agabus paludosus* and *Ilybius fuliginosus* with the polluted, hard, warm and slowflowing water of the Saubach (Buck, 1971; Galewski, 1971). The patchy distribution of other rheophilic species is more problematic. At locality PS 2 (Inde) *Oreodytes rivalis*[1] for example represents 31% of the hydradephagan specimens collected and is absent from locality PS 1 which is situated closer to the Inde fountain, 3 km away from PS 2. In addition substantial quantitative differences in relative abundance of a given species at several localities are evident (e.g. *Deronectes lactus, Oreodytes rivalis, Platambus maculatus, Agabus guttatus;* see Tab. 1).

We supposed that the peculiar distribution of rheophilic hydradephagan species might be accidental or could be traced back to biotic parameters. In order to find biogenetic reasons for these unexpected distributional discontinuities, adults of several rheophilic species were regularly collected at two localities (PS 1 and PS 2) of the Inde brook in the vicinity of Aachen and their phenologies were established. At each locality the contents of the crops and the quantitative and seasonal varying availability of prey organisms were investigated in order to find whether or not several dytiscids show differences in niche within a given locality (e.g. as found by Seeger (1971) in haliplids). It is possible that absence of certain prey organisms could be responsible for the absence of certain dytiscid predators within different localities. In our studies of prey it was of interest to determine whether or not different age classes of adult beetles preferred different prey organisms. Another specific question that we addressed was the correlation between age of beetles and uptake of plant material. This was of interest because the glandular components of the hydradephagan beetles often show drastic seasonal quantitative variations (Classen & Dettner, 1983) and several components cannot be biosynthesized by the beetles themselves but must be manufactured from precursors from food (Dettner, 1985b). In order to perform a detailed age analysis of different water beetle species and to define age classes the internal genital structures were studied comparatively with respect to their structure and their age dependent variability. Some natural history data with respect to the rheophilic species mentioned have been given by Burmeister (1939).

Material and Methods

Quantitative records (Tab. 1) of water beetle fauna of brooks of the Eifel or pre-Eifel region (Fig. 1) were obtained from April to October

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[1] The proper name for this species actually seems to be *Oreodytes sanmakii* (Sahlberg, 1826).

1979 at the localities Gieschbach (3), Weser (4), Tiefenbach (5), Schlehbach (6) and Saubach (7). Within the localities PS 1 ("Probestelle" 1) and PS 2 of the Inde brook water beetles were quantitatively recorded from March to August 1980 following procedures described by DETTNER (1976) and MEYER & DETTNER (1981). In addition, adults of *Agabus paludosus* (Saubach, Fig. 1: number 7) and *A. bipustulatus* (pond situated in a heathy ground near Düren) were caught two times per month (phenological data were not recorded) between April 1979 to March 1980. The living beetles were transported to the laboratory and quickly frozen. Later the beetles were dissected under a stereo-microscope in order to isolate internal gonads and crops. Crops were opened and their contents preserved and stored in glycerine. Chitinous fragments were compared with co-occuring, intact arthropods of the sample locality. Squash preparations of testes, sperm ducts or receptaculi semini were examined for presence of sperm. 15 minutes after the frozen beetles were removed from the refrigerator, fresh weight and measurement of internal genital structures were done.

In the laboratory, hungry adults of some rheophilic water beetle species were kept in petri dishes (24 hours). Larvae of several insect orders were simultaneously offered to the beetles and their first choice was recorded. Several hungry specimens of *Platambus maculatus* were dissected at different times (30 min, 3 h, 20 h) after ingestion to assess the degree of digestion within the crop. Quantitative measurements of co-occuring invertebrates at the Inde localities PS 1 and PS 2 were performed together with the beetle samplings by using a stream bottom square foot sampler (mesh width: 1 mm; MERTENS, 1981).

Results and Discussion

Structure of internal genital organs and age dependent variation

Internal genital organs and their age dependent variations have been well-studied within carabids (e.g. KREHAN, 1970; THIELE, 1977). Only preliminary data for hydradephagan beetles are available (CLASSEN & DETTNER, 1983; DETTNER, 1979; SEEGER, 1971; SÜSELBECK, 1979).

Internal genital organs of females consist of a pair of ovaries (0) with numerous ovarioles, a median oviduct (OD) and a vagina (V; Figs 2,3). In accordance with BURMEISTER (1976) the receptaculum seminis (RS) of members of Agabini is saclike and connected with the oviduct but not with the bursa copulatrix (BC; Fig. 2: *Platambus maculatus*).

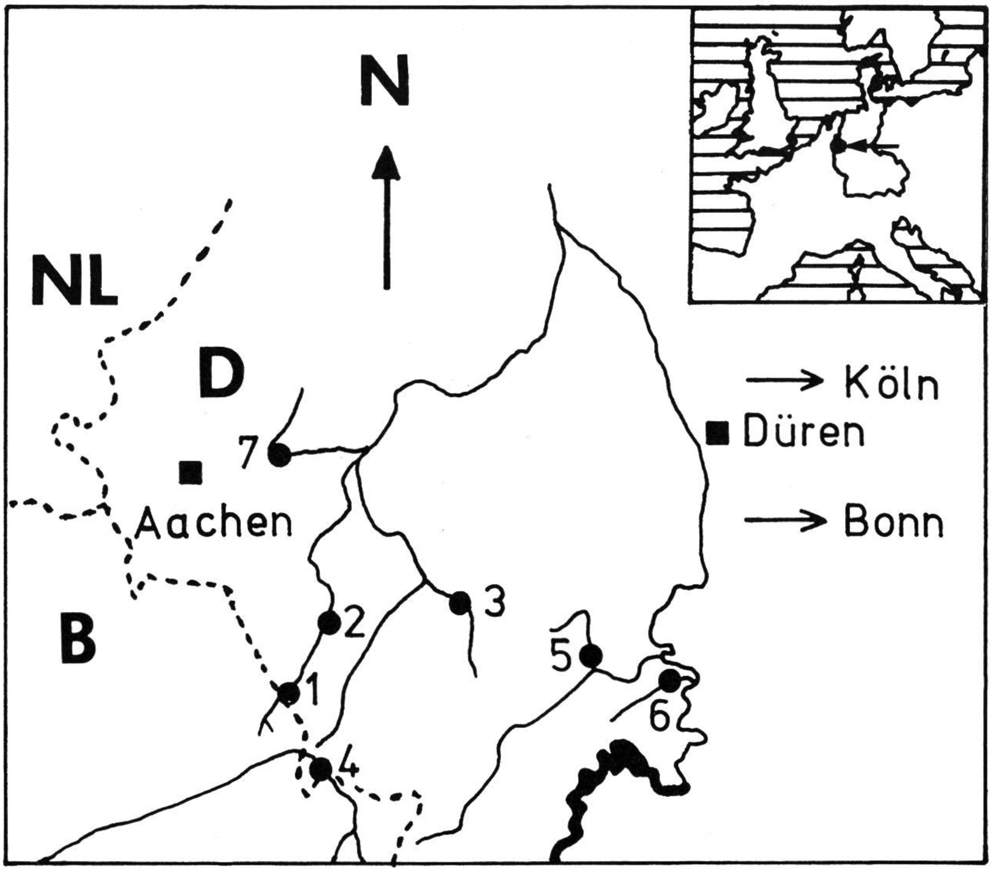

Fig. 1: Brooks in the vicinity of Aachen (western part of Rhineland) where water beetle samples have been taken (1: Inde, locality PS 1; 2: Inde, locality PS 2; 3: Gieschbach; 4: Weser; 5: Tiefenbach; 6: Schlehbach; 7: Saubach).

Within genera of the Hydroporinae, such as *Deronectes* (Fig. 2) or *Oreodytes* (Fig. 3), the receptaculum seminis originates close to the oviduct and is connected with the bursa copulatrix by means of a long ductus receptaculus. Among members of these hydroporine genera (Figs 2, 3) specific differences have been found in their internal genital organs. The receptaculum seminis of females of *Oreodytes rivalis* is soft and brightly coloured whereas females of both species of *Deronectes* have brown, chitinous capsules. Compared with those of *Deronectes latus* and *Oreodytes rivalis,* females of *Deronectes platynotus* are further characterized by a distinctly shortened ductus receptaculus.

As in Figure 3, the internal sexual organs of female water beetles provide a great deal of information with respect to the age structure of a population. Young females of *Oreodytes rivalis* of age class 1 are characterized by white, undifferentiated ovarioles, and their receptaculi semini are empty. Females of age class 2 have more differentiated

	Inde		Gieschbach	Weser	Tiefenbach	Schlehbach	Saubach
	PS 1	PS 2					
Altitude (m)	330	260	310	445	220	190	170
Width of Brook (m)	1–2	3	1.5–3.5	4.0–4.5	1.8–3.5	1.2–2.0	0.6–1.2
Shadow (%)	50	90	70	70	70	60	30
Current velocity (m/sec)	0.3–0.5	0.3–0.4	0.3–0.4	0.3	0.3–0.4	0.2–0.3	0.1
Water temperature (°C)	9	10.1	10.1	11.2	13	13.3	13.7
pH	6.1	7.1	5	4.9	7	7.2	7.7
Total hardness (°dH)	2	3.1	1.9	1.1	5.3	5.5	17.5
Deronectes platynotus (%)	5	6.36	–	11.23	–	–	–
Dereonectes latus (%)	33.48	12.84	0.98	39	0.23	–	–
Oreodytes rivalis (%)	–	30.98	–	–	33.51	0.63	–
Platambus maculatus (%)	37.96	26.65	23.34	2.8	3.07	5.2	0.35
Agabus guttatus (%)	1.2	0.12	9.76	11.6	–	–	1.91
Agabus paludosus (%)	0.22	–	–	–	1.65	–	15.98
Ilybius fuliginosus (%)	–	–	–	–	–	–	13.37
Gyrinus substriatus (%)	6.38	3.48	–	1.05	–	–	0.87

Tab. 1: Abiotic data of some brooks of the Eifel region and relative abundances of some selected rheophilic Dytiscidae and Gyrinidae

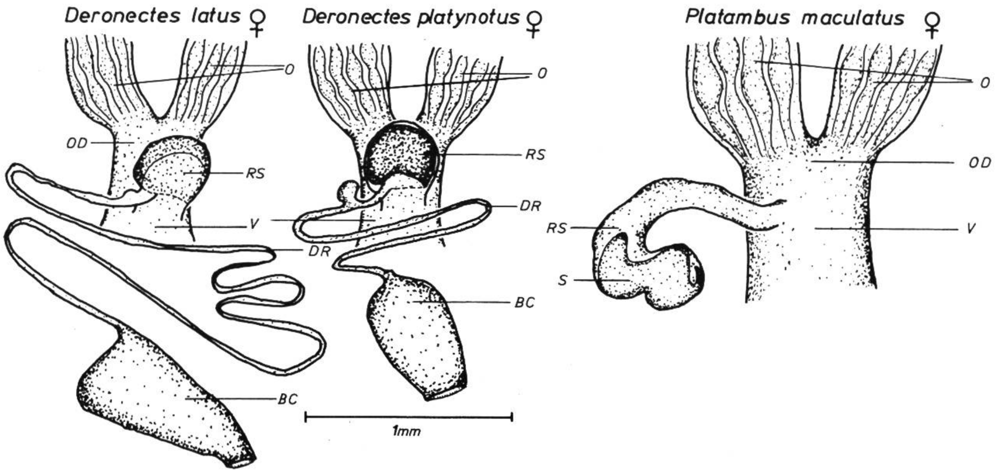

Fig. 2: Structure of internal genital structures of females of *Deronectes latus, D. platynotus* and *Platambus maculatus* (0: ovaries with ovarioles; OD: oviduct; V: vagina; RS: receptaculum seminis; BC: bursa copulathrix; DR: ductus receptaculus; S: sperms).

ovarioles and are mated as shown by seminal receptacles being completely filled with sperms. Later, within age class 3, ovarioles contain several mature eggs (3/1)[2] and presence of corpora lutea indicates the second part of stage 3 (3/2). When egg deposition is completed ovarioles contain only corpora lutea as seen in age class 3/3 of *O. rivalis* (Fig. 3).

It is amazing that there exist two theories with respect to the formation of corpora lutea. According to Gilbert (1956) and as supposed by this study, follicular cells degenerate after egg deposition to remain as corpora lutea which are correlated with the amounts of eggs deposited. On the other hand Joly (1945) surmises that the formation of corpora lutea may be due to egg resorption also. In the latter case no statement on completion of egg deposition would be possible.

It is possible to demonstrate quantitative, age dependent differences with respect to the length of the receptaculum seminis (RS), the male ectadenies (EK: accessory glands) or the fresh weights (W) of the beetles (Fig. 4). In females of *Agabus bipustulatus* the receptaculum seminis of age class 3/2 shows a maximum length (Fig. 4), in *Agabus paludosus* maximal values were recorded from female specimens of the age class 3/3. Furthermore average fresh weights of female *Agabus bipustulatus*

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[2] Within both ovaries of adult female beetles of age class 3/1 the following numbers of eggs have been observed: *Deronectes latus:* 1–8; *D. platynotus:* 1–7; *Oreodytes rivalis:* 1–12; *Platambus maculatus:* 2–50; *Agabus paludosus* and *A. bipustulatus: 8–20; Gyrinus substriatus:* 1–30.

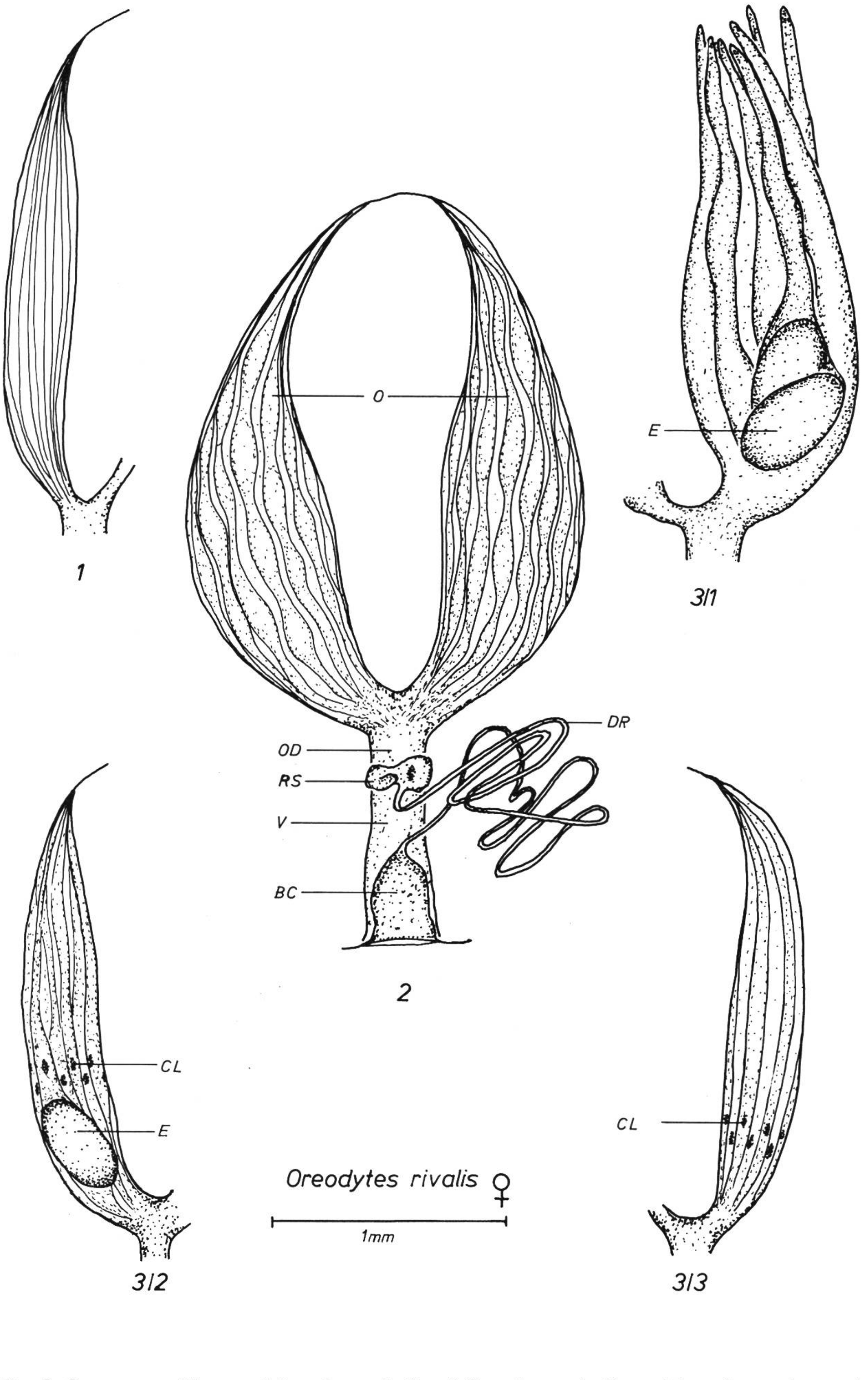

Fig. 3: Structure of internal female genitalia of *Oreodytes rivalis* and found age classes 1, 2, 3/1, 3/2, 3/3 (O: ovaries; OD: oviduct; V: vagina; RS: receptaculum seminis; BC: bursa copulathrix; DR: ductus receptaculus; E: mature eggs; CL: corpora lutea).

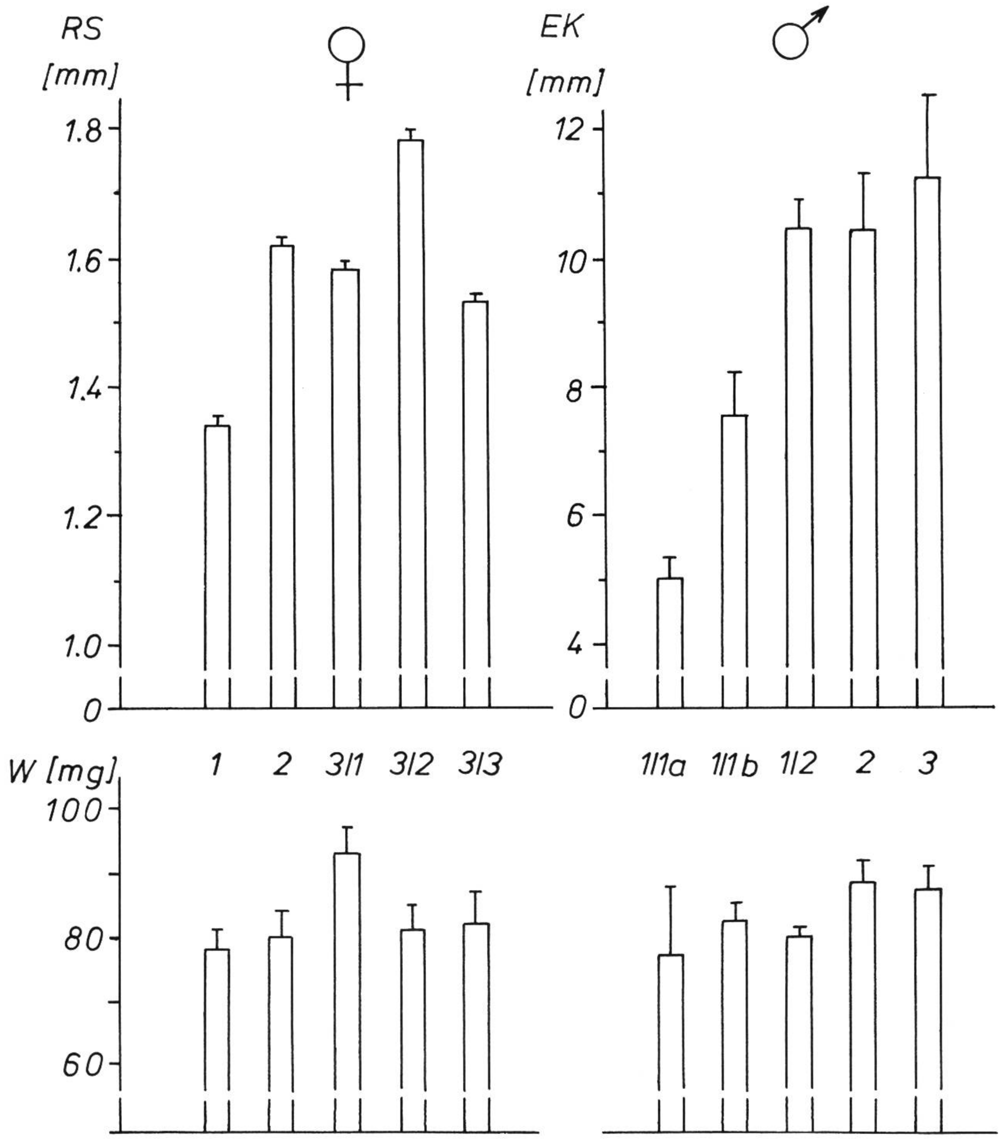

Fig. 4: Quantitative data (mean; S.D.) from male and female specimens of *Agabus bipustulatus* belonging to age classes 1, 1/1a, 1/1b, 1/2, 2, 3, 3/1, 3/2, 3/3 (X-axis). Above: length of receptaculum seminis (RS) and accessory glands (EK); below: fresh weights (W). Number of specimens investigated: ♀: stage **1**:5, **2**:6, **3/1**:6, **3/2**:32, **3/3**:51; ♂:**1/1a**:3, **1/1b**:4, **1/2**:6, **2**:21, **3**:50.

specimens containing mature eggs (3/1) are distinctly elevated; in *A. paludosus* females there was an increase of fresh weights from age class 1 to 3/2. Females which contain only corpora lutea (3/3) show distinctly reduced fresh weights (Fig. 4).

Internal genital organs of males consist of a pair of ectadenies (EK) which are fused to an ejaculatory duct (DE) (Fig. 5). From the basal part of each ectadeny, a sperm duct (NH: "Nebenhoden") originates and extends to the testes (H: "Hoden"). Within a given age class length and shape of ectadenies varies considerably within different species. The range of variation is from the shortened ovoid ectadenies of adults males of *Oreodytes rivalis* (Fig. 5) to the narrow and lengthened accessory glands in specimens of *Deronectes platynotus.* Yellow spots within the ectadenies (F, Figs 5, 6) are either localized basally *(Deronectes)* or apically *(Platambus).* Among members of Hydroporinae, sperm ducts and testes are rolled up and closely connected. Within the representatives of the Colymbetinae studied *(Agabus bipustulatus, A. paludosus, Platambus maculatus)* sperm ducts and testes are distinctly separate (Fig. 6).

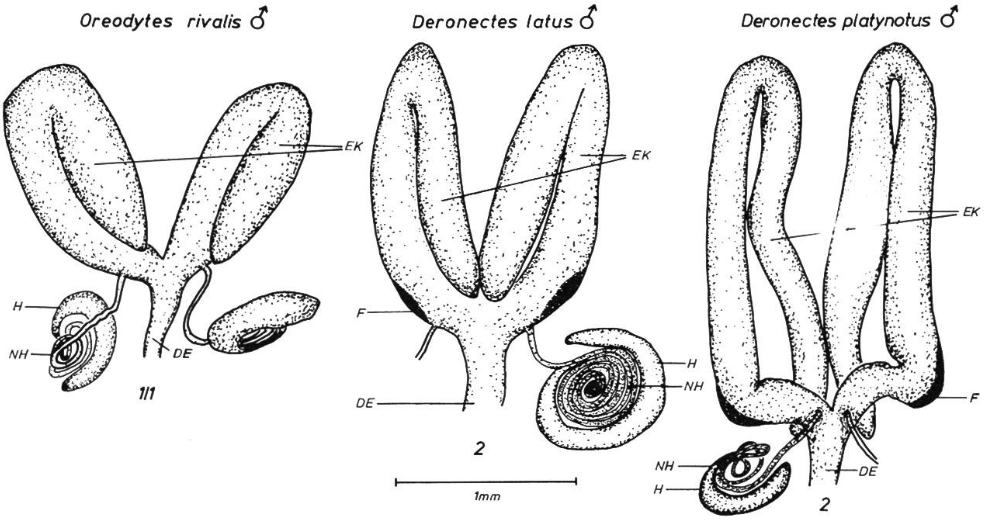

Fig. 5: Structure of internal male genitalia of *Oreodytes rivalis; Deronectes latus* and *D. platynotus* (EK: accessory glands; DE: ejaculatory duct; NH: spermatic duct ("Nebenhoden"); H: testes ("Hoden"); F: yellow spots).

Male hydradephagan beetles were grouped into following age classes: Within stage 1/1 no sperm could be recorded either from testes nor sperm ducts (Fig. 6). In this age class ectadenies are short and transparent (subgroup 1/1a) or lengthened and whitish (subgroup 1/1b). Male specimens of age class 1/2 are characterized by lengthened accessory glands, thickened seminal receptacles and testes filled with sperms. Mature males of age class 2 sequester masses of sperm in both testes and spermatic ducts. Age class 3 is defined by lengthened ectadenies, yellowish gonads and sperm bundles which are confined to the spermatic ducts. An intermediate stage, 2–3, between stages 2 and 3 could be separated in males of *Platambus maculatus* where testes are only incompletely filled with sperm (Fig. 6).

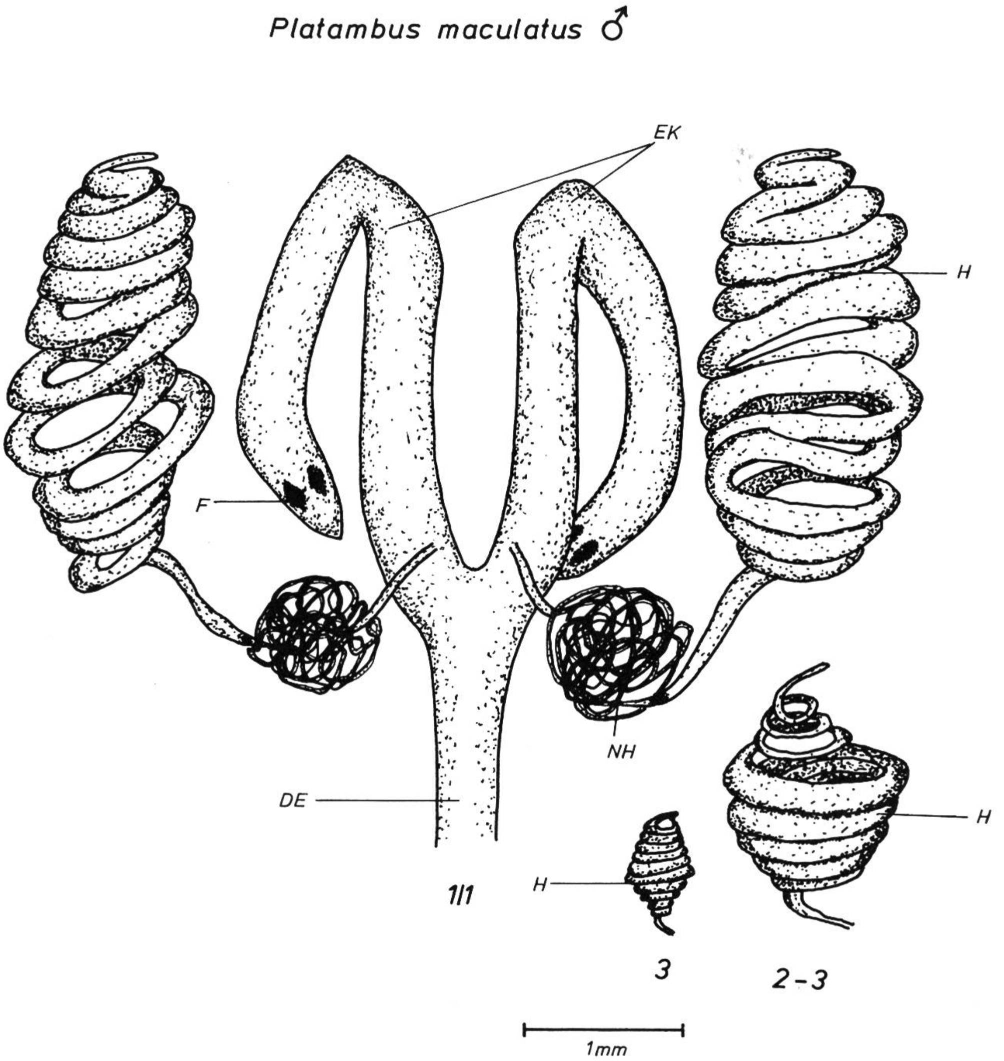

Fig. 6: Structure of internal male genitalia of *Platambus maculatus* and found age classes 1/1, 2–3 and 3. Within stages 2–3 and 3 only apical parts of the testes are figured (EK: accessory glands; DE: ejaculatory duct; NH: spermatic duct; H: testes; F: yellow spots).

Further qualitative age dependent changes were found with respect to the colour of sperm ducts. During stages 1/1 and 1/2 they are colourless but later they become white to silvery when filled with sperm bundles during stages 2 and 3.

Within different age classes of male specimens of *Agabus bipustulatus* the length of ectadenies distinctly increases from freshly pupated to older specimens (Fig. 4). In some cases the accessory glands are slightly shortened from stage 2 to stage 3 (males of *Deronectes latus, D. platynotus, Oreodytes rivalis*, and *Gyrinus substriatus*). The fresh weights of males of *Agabus bipustulatus* increase only slightly with age (Fig. 4).

The age classes mentioned above are only useful if the activity of testes happens but once. If the testes are characterized by periodical activities, as shown for *Dytiscus* (BLUNCK, 1912), the sequence of age classes 2 and 3 would not be correct.

Age structure and life cycles

When age dependent variations in structure of internal genital organs are recorded by species and locality, significant information concerning life cycle and age structure of populations are available. In particular an interpretation of complex phenology diagrams seems possible when internal genital organs are measured at the same time. In addition to the rheophilic species from the Inde region, two further water beetle species from other localities were investigated (*Agabus paludosus:* Saubach; *Agabus bipustulatus:* Drover Heide) in order to analyze age structure during winter. Two distinct types of live cycles were found: beetles that breed in spring (1) are characterized by summer larvae and hibernate as adults (type 1 of NILSSON, 1985) and some species (2) which show flexible reproductive periods and hibernate both as larvae and as adults (type 5 of NILSSON, 1985).

The first type of life cycle was found among members of Hydroporinae such as *D. latus*, *D. platynotus* and *O. rivalis* and in *A. paludosus* (Colymbetinae). In *O. rivalis* (Fig. 7) the majority of specimens which were collected are females (approximately 7.4 females to 1 male). This situation is unusual among dytiscids. Therefore it is only possible to discuss the life cycle based on this sex alone. Within other species an age analysis of males was possible also. The sex ratios (♀/♂) varied from 0.7 *(P. maculatus),* 0.96 *(A. paludosus),* 1 *(D. latus),* 1.22 *(G. substriatus),* 1.33 platynotus) to 1.7 *(A. bipustulatus).* In *O. rivalis* (Fig. 7), egg deposition probably occurs two times during summer. The first is in early summer, indicated by occurrence of stage 3/1 females and the record of *Oreodytes* larvae during June/July (second period of oviposition: July). Near the end of July and early August immature adult beetles appear and are responsible for the third maximum in the phenology curve of this species. Only females of stage 1 and 2 hibernate and reappear during spring of the following year. Both *Deronectes platynotus* and *D. latus* (Fig. 8) show similar life cycles. However in the *Deronectes* species, egg deposition seems to be slightly later as seen in the somewhat later appearance of larvae and of the 3/1 stage females (Fig. 8).

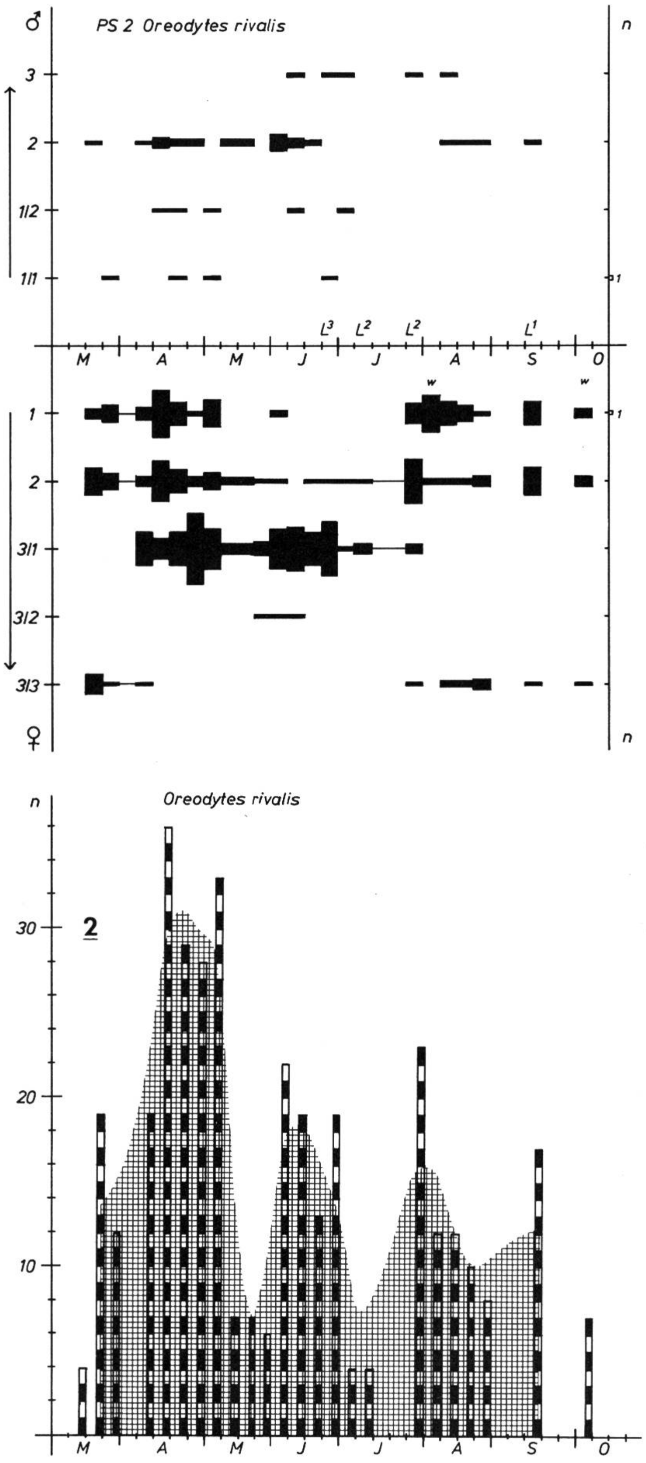

Fig. 7: Age structure (above) and phenology (below) of *Oreodytes rivalis* at locality PS 2 (Inde brook). The X-axis symbolizes months from March to October; in addition there was indicated when a first stage (L^1), second stage (L^2) or third stage (L^3) larva of *O. rivalis* was found at same locality. The width of horizontal bars (above) indicates different numbers of beetle specimens caught per class and per week.

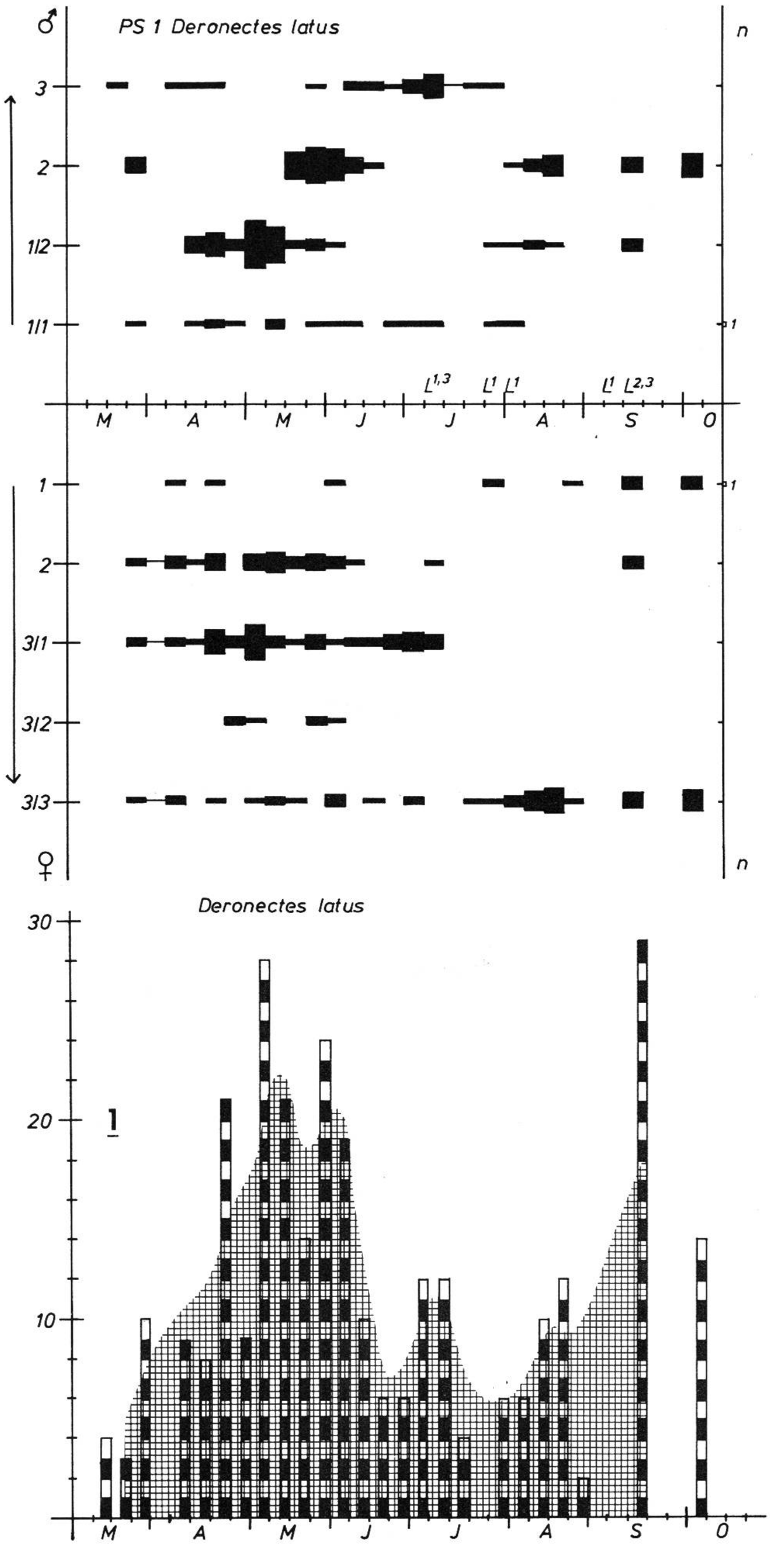

Fig. 8: Age structure (above) and phenology (below) of *Deronectes latus* at locality PS 1 (Inde brook). For further explanations see figure 7.

The age structure of *A. paludosus* (Fig. 9) from the Saubach differs distinctly from that of other water beetles investigated. It was nearly impossible to perform a population analysis for this species because young males were present during the whole investigation period. Among adult females, both the appearance of young specimens during August/September and the presence of 3/1 stage females during winter and spring to early summer indicate that the larval development of *Agabus paludosus* occurs during summer and the species shows a life cycle of Nilsson's type 1 mentioned above.

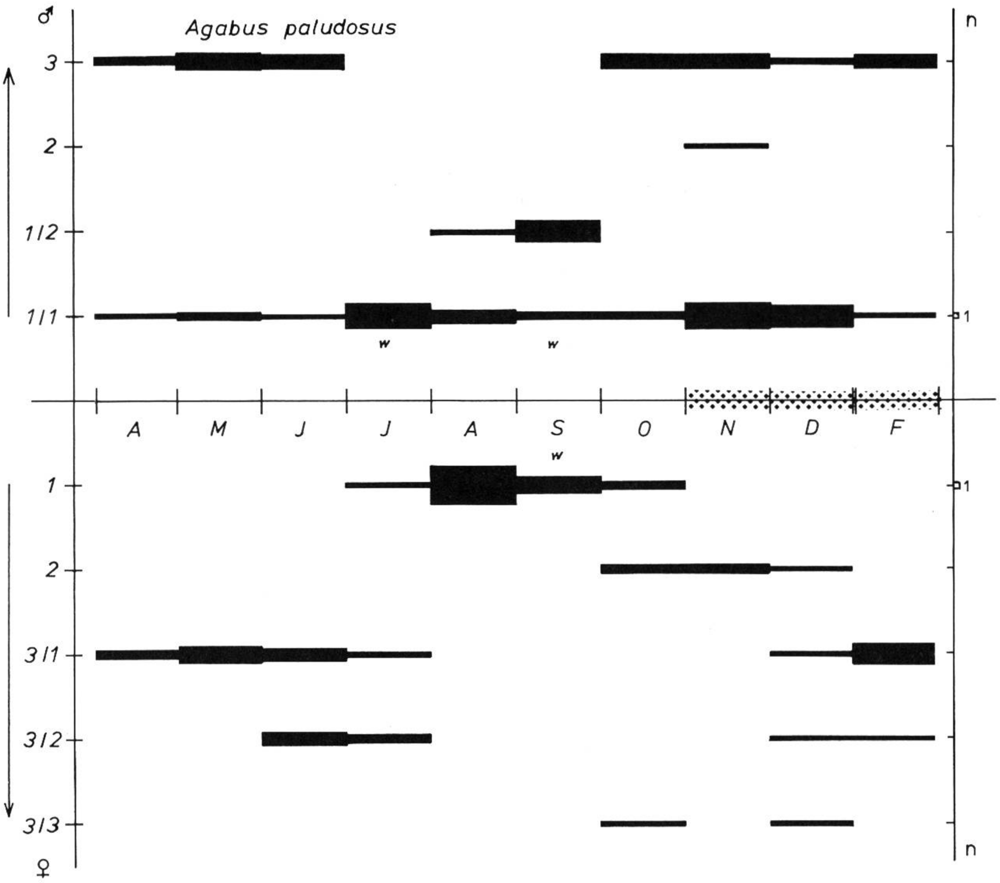

Fig. 9: Age structure of *Agabus paludosus* at locality 7 (Saubach). The width of horizontal bars indicates different numbers of beetle specimens caught per age class and per month. The presence of soft, immature adults is indicated by the sign "w" ("weich") which is placed above and underneath the horizontal bars. The winter months from November to the February are dotted. For further explanations see figure 7.

The high proportion of stage 1/1 males indicates that the sexual maturation is supressed or at least prolonged in males of *A. paludosus*.

This is the first report of this phenomenon from Adephaga as it was not in carabids (THIELE, 1977) and there is no reference to it in any other family in the suborder.

Early emergence of young 1/1 stage males as compared with the young females seems to be a tendency within insects and is known as protandry (WILLUND & FAGERSTRÖM, 1977). According to these authors, possible hypotheses to explain the functional significance of this phenomenon are: a) prevention of inbreeding, b) ensurance that only the "fittest" males survive long enough to mate with females, c) ensurance that females become fertilized immediately after eclosion to minimize pre-reproductive death of females and d) better chance to early emerging males to mate with more females than males emerging later.

The second type of life cycle (type 5 according to NILSSON, 1985) was found in *P. maculatus* (Figs 10, 11) and in *A. bipustulatus* (Fig. 12). Larvae appear during fall and hibernate together with 3/1 stage females (Fig. 10). The second suggestion is based on the fact that adult (3/3) females appear immediately in spring. In *P. maculatus*, life spans between both sexes obviously vary considerably. At both localities older stage 3 males die at the end of August or in September whereas older females hibernate. Although no anatomical proof of this was found, female hibernation might indicate that some females go through two reproductive periods. As seen in *A. paludosus*, *P. maculatus* shows a strong protandry which is quite evident in locality 1 (PS 1; Fig. 10). Within *A. bipustulatus* (Fig. 12) the appearance of older males (stage 3) and females (3/2; 3/3) is distinctly shifted toward the winter as compared with *P. maculatus*. In addition a considerable proportion of older *A. bipustulatus* males and females is found only during June, July; probably no suppression of the sexual maturation occurs.

No significant phenological and age structural differences were found between the localities PS 1 and PS 2 as compared to those of *P. maculatus*. In addition there is no evidence of temporal isolation between different species at the same locality.

Prey and other food

The phenology of species presented above demonstrates that rheophilic species show no temporal isolation at the same locality. All species occur in the same microhabitat and therefore a specialization in feeding among the different water beetle species seemed possible (see Introduction). To test this, comparative crop analyses of abundant water beetle species of the Inde brook were performed. Qualitative

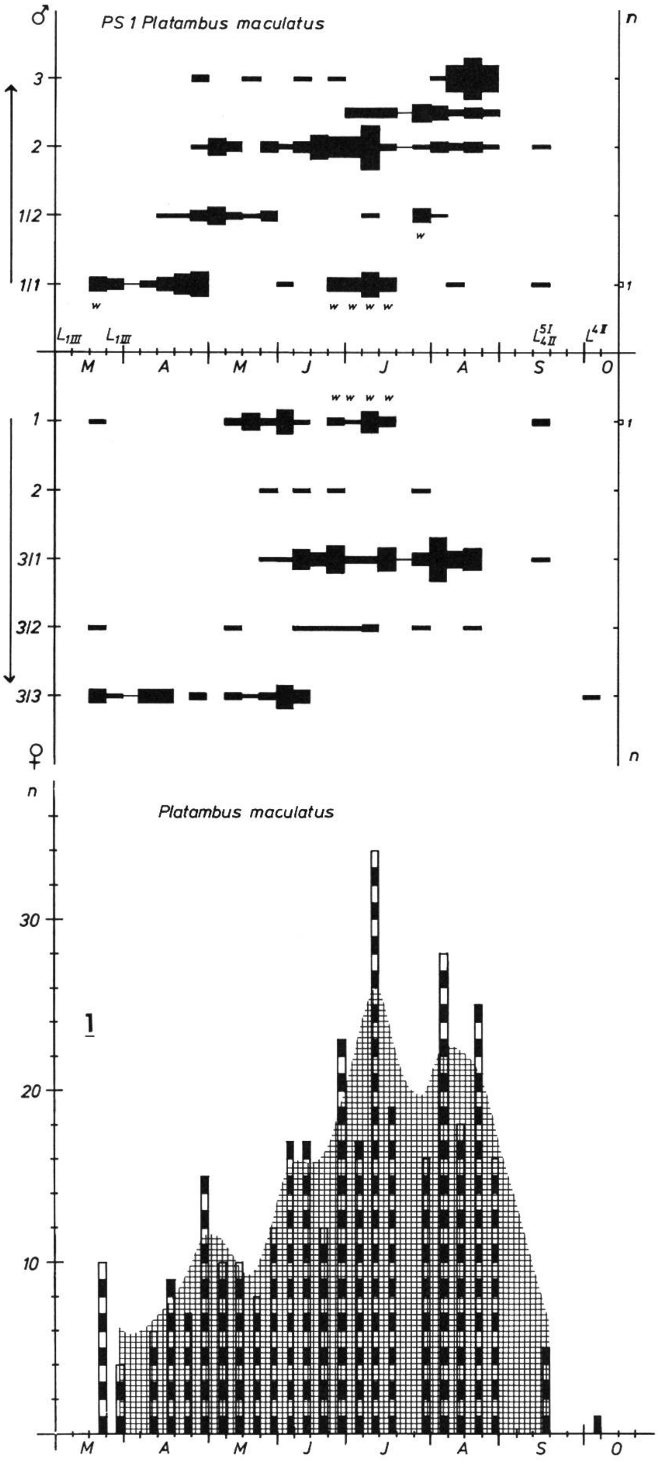

Fig. 10: Age structure (above) and phenology (below) of *Platambus maculatus* at locality PS 1 (Inde brook). The presence of soft, immature adults is indicated by the sign "w" which is placed above and underneath the horizontal bars. When four second stage larvae and five first stage larvae of *Platambus maculatus* were found at the same locality this was indicated by: $L_{4\,II}^{5\,I}$. Between male age classes 2 and 3 the intermediate stage 2–3 is figured by horizontal columns. For further explanations see figure 7.

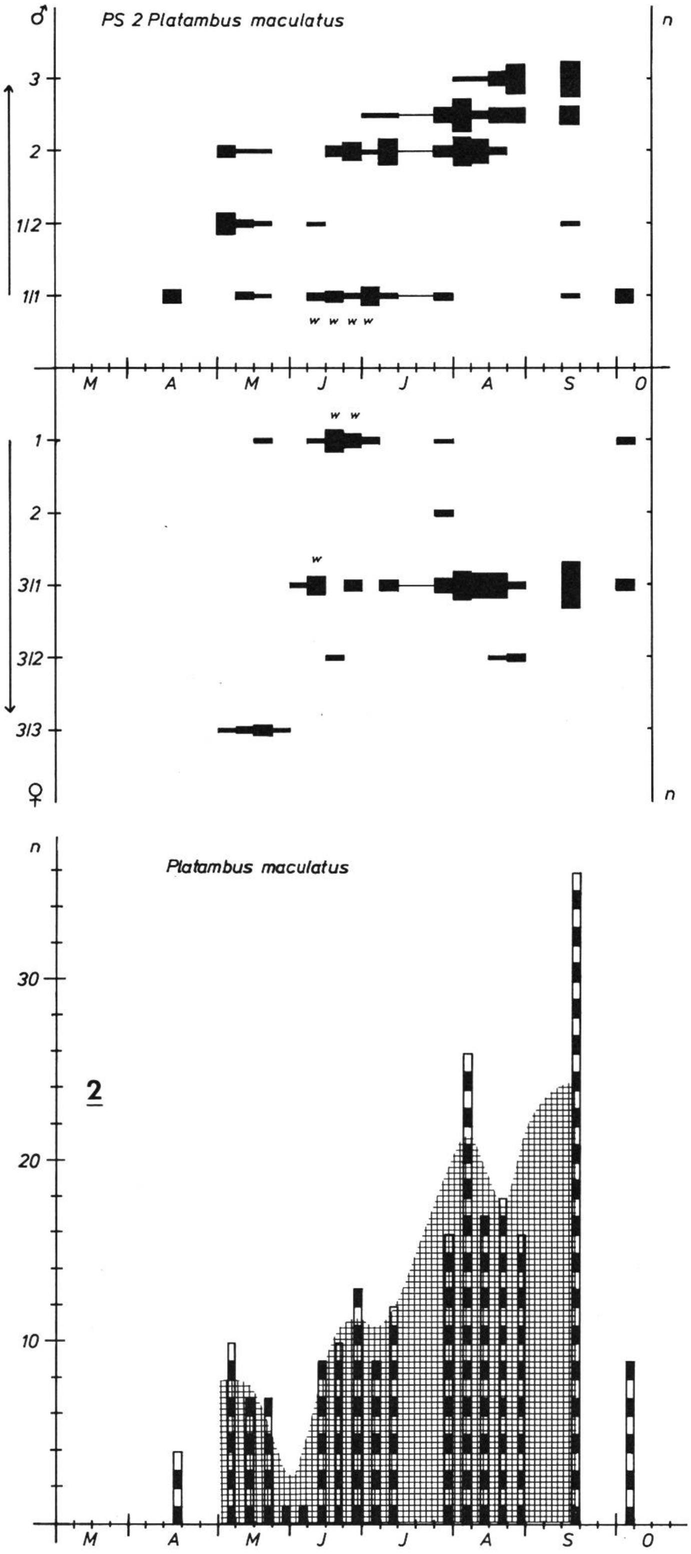

Fig. 11: Age structure (above) and phenology (below) of *Platambus maculatus* at locality PS 2 (Inde brook). For further explanations see figures 7 and 10.

comparisons as revealed by analyses of the contents in the digestive tracts have been performed within several species of Haliplidae (Seeger, 1971) and Dytiscidae (Süselbeck, 1979). A comparative analysis of length and shape of dytiscid mandibles and suggestions as to the feeding preferences of the water beetles is discussed by Galewski (1974). Other studies of feeding have emphasized individual taxa, for example, *Eretes sticticus* (Swamy & Rao, 1977) or of those Dytiscidae which are major predators of mosquito larvae (James, 1961, 1966). Detailed studies of feeding correlated to seasonal fluctuations of food (Seeger, 1971) or variations of suggested prey organisms dependent on age of the hydradephagan beetles have been done (Seeger, 1971; Süselbeck, 1979).

As in similar investigations dealing with crop contents of Carabidae (Thiele, 1976) high percentages of the crops didn't have any contents. In *P. maculatus* only 18.4% of the specimens investigated had no food within their crops whereas the corresponding amounts for *O. rivalis* is 60%, for *D. latus* 52.3%, for *D. platynotus 35.6% and for G. substriatus* 54%. It may be that different daily activity patterns and prey searching periods were responsible for these values which were obtained by collecting the beetles during the day time. This suggestion seems conceivable since nocturnal activity patterns have been found within Dytiscidae (Nilsson, 1978) and pieces of meat ingested by *Dytiscus circumcinctus* pass through the crop to enter the midgut only one hour after feeding (Deegener, 1910). Moreover many crops were filled with an undefinable fluid which may originate from nonsclerotized preys, from soft internal structures of sclerotized organisms or from digested sclerotized food material 10 or 20 hours after ingestion. By means of feeding experiments in the laboratory it became evident that the members of Hydroporinae studied often kill insect larvae in order to feed on soft larval structures alone, whereas *P. maculatus,* being larger, completely ingested the majority of it's prey. Specimens of *P. maculatus* were examined at different times after feeding on insect larvae. After 30 minutes a complete set of chitinous fragments were found within the crop. Three hours after feeding the crops of *Platambus* contained some brown fluid together with chitinous fragments which were distinctly macerated.

On the basis of the simultaneous collection of brook inhabiting invertebrates, using a square foot sampler (Mertens, 1981), it was possible to trace back the origin of some crop contents and to define categories as symbolized by different vertical columns in Figure 13.

For different water beetles at the localities PS 1 and PS 2 (Inde-brook) different food categories are indicated. The percentage of crops where a specific fragment category was found is symbolized by the height of the column. In species such as *P. maculatus* where different kinds of fragments could be recorded from one crop, the summation of the columns exceeds 100%.

From only a fraction of crop contents could the origin be determined. The most common of these were as follows: plecopteran larvae (cerci, antennae, legs), chironomid larvae (head capsules), chironomid adults (heads, antennae, pronota), plants or "further arthropods" (fragments from other insect groups or from Chelicerata). The categories "wings" and "compound eyes" based on fragments in the crop indicate the approximate fraction of adult insects eaten whereas the category "undefinable" symbolizes fluids or minute fragments of unknown origin.

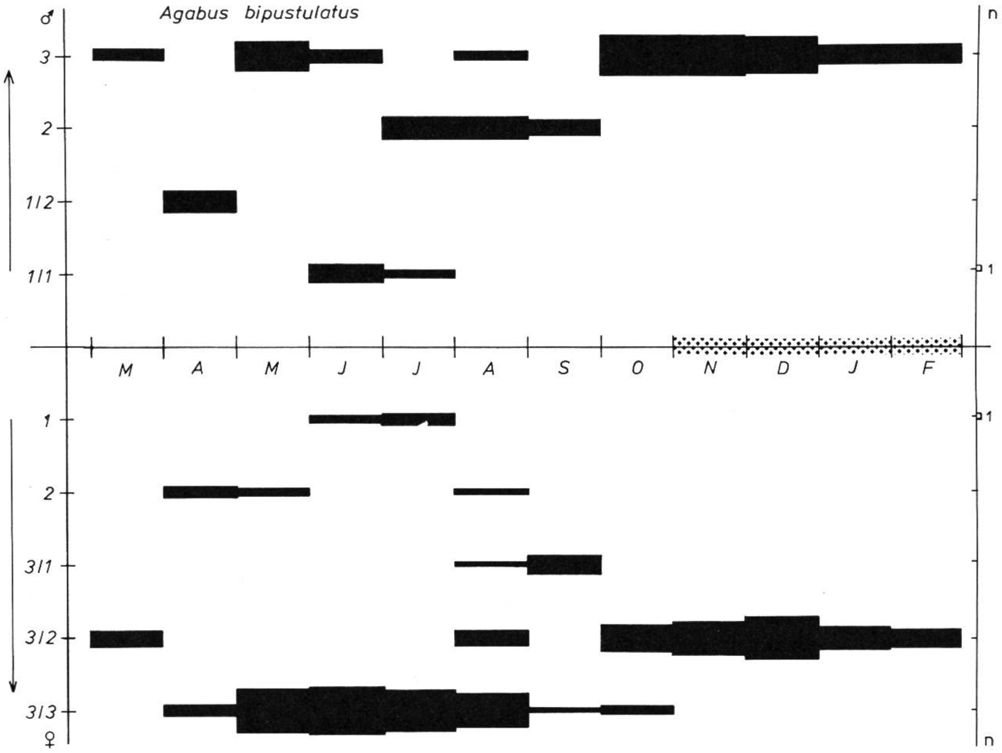

Fig. 12: Age structure of *Agabus bipustulatus* from a pond situated in a heath near Düren (Rhineland). For further explanations see figures 7 and 9.

If the crop contents within a given species are compared with the abundance of prey organisms at the localities PS 1 and PS 2 a positive correlation is evident. Stonefly fragments were commonly found in specimens from locality PS 1 (Fig. 13; PS 1: *D. latus, P. maculatus)* where the relative abundance of plecopteran larvae is 56.9%. On the other hand the relative abundance of chironomid larvae at PS 2 is more than six times as great as at PS 1 (3%) which is clearly reflected by the crop contents (Fig. 13). If the crop contents of the four dytiscid species are compared without considering the locality it is evident that the smaller sized specimens belonging to Hydroporinae *(Deronectes, Oreodytes)* feed mainly on chironomid larvae whereas the larger sized (colymbetine *P. maculatus)* prefers an additional wide range of prey organisms with a high percentage of adult insects (Fig. 13, categories wings, compound eyes). Therefore *Platambus* may leave the water or more likely ingests dead arthropods hanging at the water surface. From evidence in the categories "further arthropods" and "undefinable" it can be inferred that adults of *P. maculatus* feed on larvae and adults of Lepidoptera, trichopteran larvae, mites, spiders, eggs of unknown origins and larvae of *Deronectes* and *Platambus.* Characteristic of some *Platambus* specimens at locality PS 2 was the presence of ephemeropteran fragments within the crops. At this locality may-fly larvae had a relative abundance of 38.3%; may-flies were not found at locality PS 1. Crops of the few specimens of *Gyrinus substriatus* investigated were nearly completely filled with fragments of adult insects (categories: chironomid adults, wings, compound eyes) as would be expected from a beetle living and foraging on the water surface. From crop analyses it seems clear that chironomid larvae represent prey organisms which are prefered by smallsized rheophilic Dytiscids. If several larvae of different insect orders are offered simultaneously to hungry water beetles of the genera *Deronectes* and *Platambus* then specimens of species of *Deronectes* at first attack chironomid larvae whereas those of *Platambus* showed no preference to any larvae offered. Moreover the smaller (2.5–3 mm) *O. rivalis* prefered smaller chironomid larvae as compared with those of the larger (7–8.5 mm) *P. maculatus.* This is evident when the lengths of the Chironomidae head capsules ingested are measured for both predators (Fig. 14). The phenomenon that predators of different size ingest different sized food fragments must be expected according to WILSON (1975) or the detailed explanations given by SÜSELBECK (1979). Forthcoming studies should reveal if the diversity of head capsule lengths are due to a single or several chironomid species.

When the crop contents of freshly pupated specimens of *O. rivalis* and *P. maculatus* were compared with appropriate older beetles, no significant differences were noticed with respect to the quality and quanti-

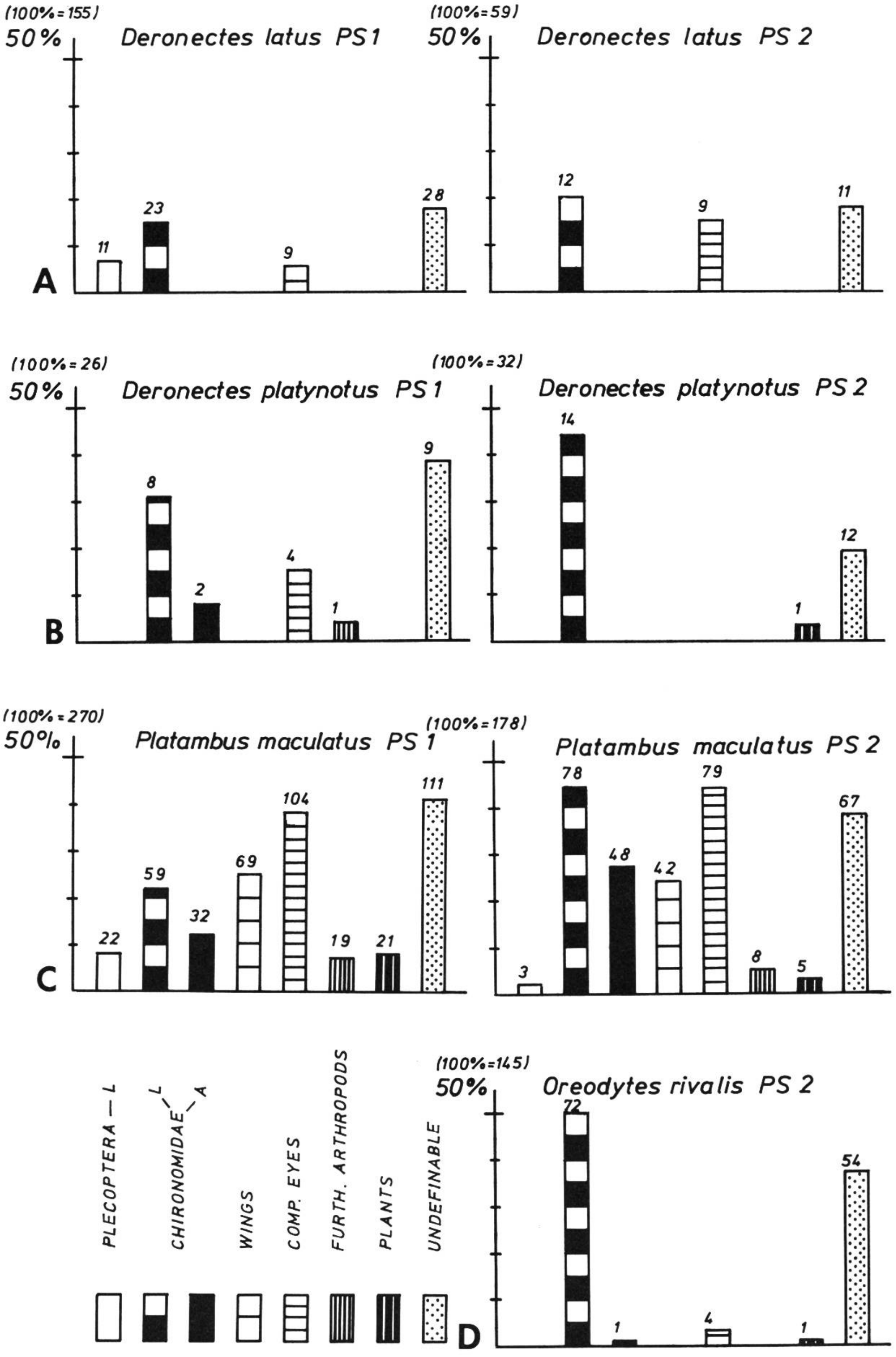

Fig. 13: Comparative analysis of the crop contents of *Deronectes latus*, *D. platynotus*, *Platambus maculatus*, *Oreodytes rivalis* at the localities PS 1 (left) and PS 2 (right) of Inde brook. The heights of the columns symbolize the percentage of crops where a specific fragment category (as indicated below) was found. In every case the total number of dissected beetles is indicated. (For further explanations see text.)

ty of ingested prey. This is not in accordance with results from Seeger (1971) and Süselbeck (1979) who found that the beetle menu differed with the age of the beetle.

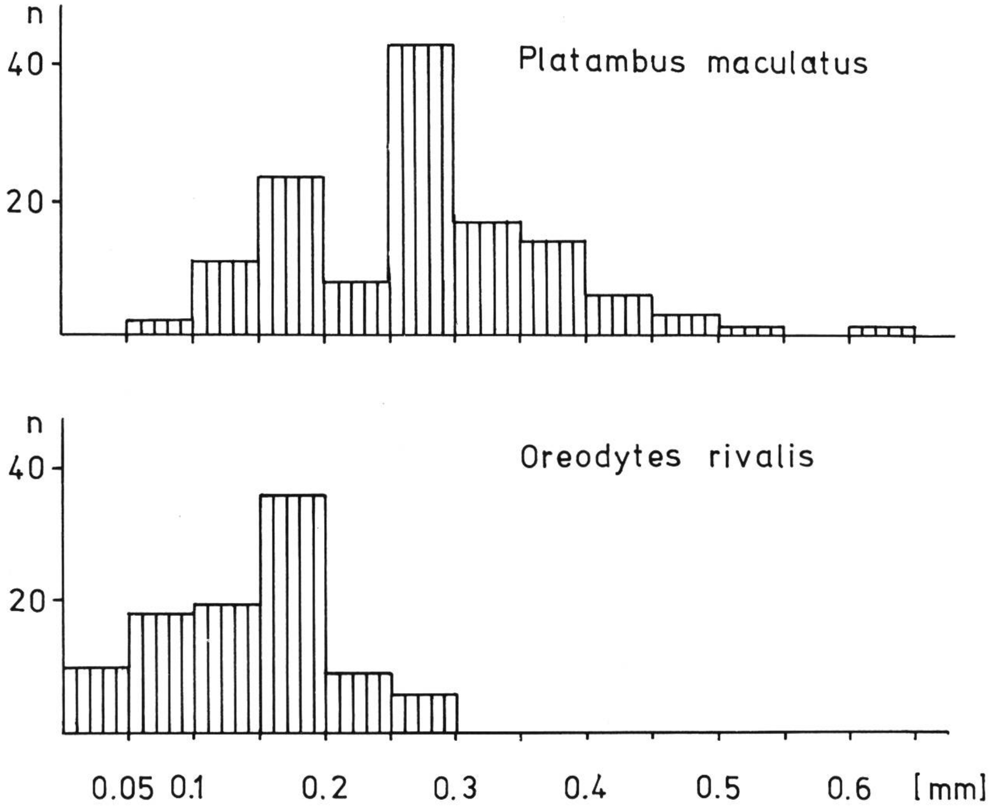

Fig. 14: Head length and number of ingested chironomid head capsules found in the crops of *Platambus maculatus* and *Oreodytes rivalis*. (For further explanations see text.)

If the seasonal fluctuations of the chironomid larvae at localities PS 1 and PS 2 are recorded by using a square foot sampler, the resulting phenology curves are seen in Figures 15–17 (columns). If these prey phenologies (Figs 15–17) are compared with the phenologies of their predators according to the localities (Figs 7, 10, 11) they agree only in part. It is evident that the number of ingested chironomid larvae (Figs 15–17; dotted line) and the number of crops containing chironomid head capsules are positively correlated. Predation is therefore density dependent (Figs 15–17; black line).

Furthermore it is interesting that the quantitative variation of ingestion of chironomid larvae per season is similar between different water beetles species such as *P. maculatus* (Fig. 15) and *O. rivalis* (Fig. 16) at the same locality. A few kilometers away however, at locality PS

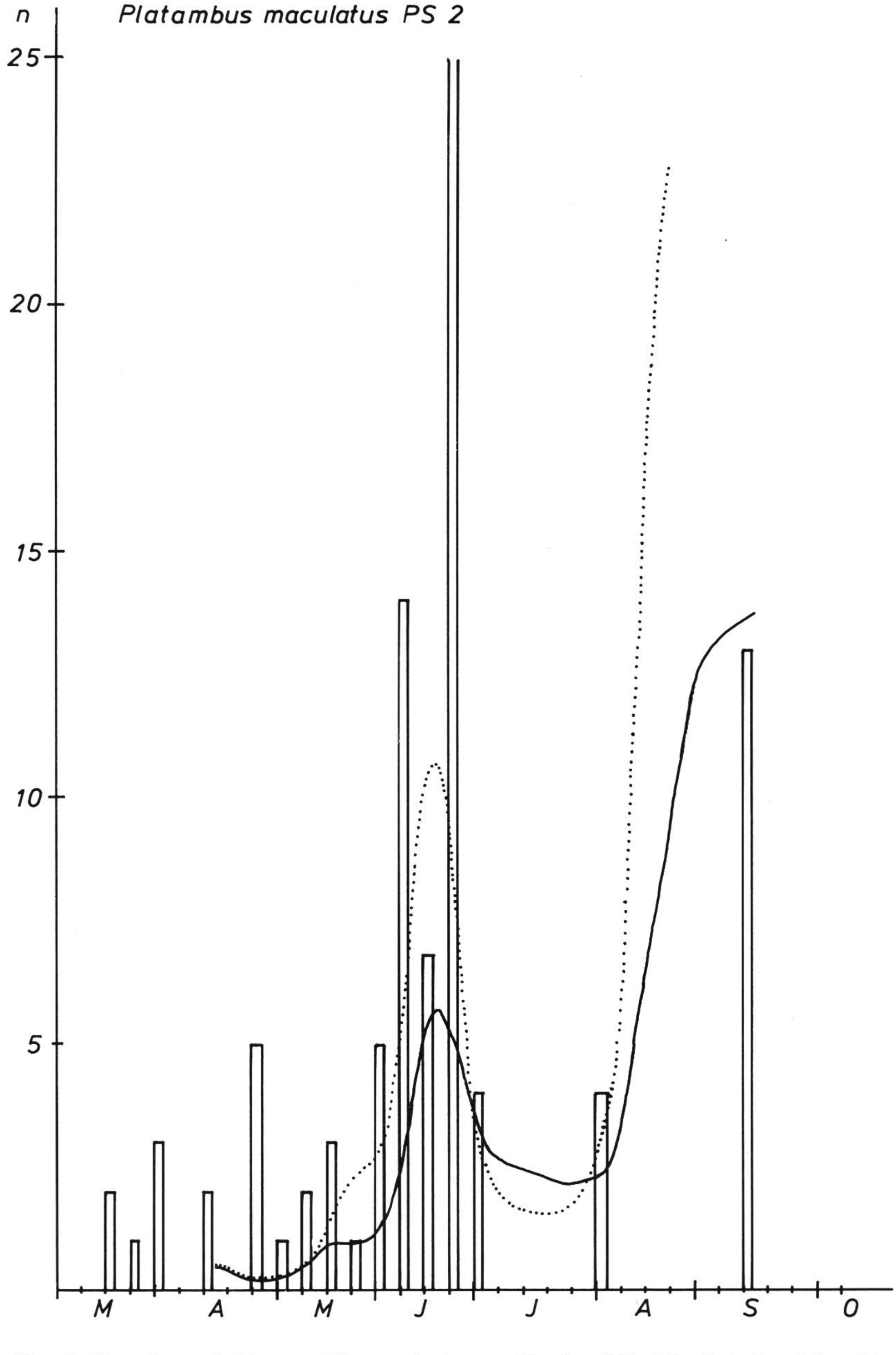

Fig. 15: Phenology of chironomid larvae (columns; Y-axis × 10) at the Inde brook locality PS 2 as compared with the seasonal varying number of ingested chironomid larvae (dotted line) or the number of *Platambus maculatus*-crops containing chironomid larvae (black line).

1, *P. maculatus* shows other seasonal fluctuations with respect to predation on chironomid larvae. The seasonally varying supply of abundant prey organisms therefore seems to play a part in the amount of dipteran larvae eaten by the beetles. Supposed age specific differences of predators with respect to the quality of nutrition might therefore be traced often to a seasonally varying supply of different prey organisms and a distinct seasonal separation of the beetle age classes investigated.

During the phenological minima of chironomid prey the feeding pattern of the dytiscid predators is especially interesting. Two alternatives were found: (1) the beetle crops remain empty for several days (PS 2: *P. maculatus, O. rivalis)* when chironomids are reduced in number, and (2) as in *P. maculatus* (PS 1), there were several prey organisms in the *Platambus* crops which replaced the reduced number of chironomids. During mid-June remains of Geometridae larvae and water strider fragments could be isolated from the *Platambus* crops along with a few larvae of *Deronectes.*

As a whole it has been shown that some Dytiscidae from brooks show no obviously distinct food specialization as compared with certain other Hydradephaga. The patchy distribution of some rheophilic water beetle species within different localities therefore seems to be negatively correlated with the presence or absence of certain prey, at least if adult stages are studied. With respect to explaining the distribution of these species further work would be profitable by exactly determining oviposition and pupation sites and by defining habitats of both larvae and adults. According to MADSEN (1967) for example adults of *Oreodytes rivalis* prefer banks of gravelly brooks (deadwaters) and are especially found among *Alnus* roots whereas larvae habitats are mud and silty flats of low current. Furthermore the distribution of *O. rivalis* might be dependent from the availability of certain sized sand grains which are necessary for constructing pupal cells (MATHESON, 1914). Such detailed studies on water beetle bionomy (especially on their developmental stages) and on structural and chemical parameters of habitats seem necessary in order to verify if those distributional discontinuities are accidental or may be explained causally.

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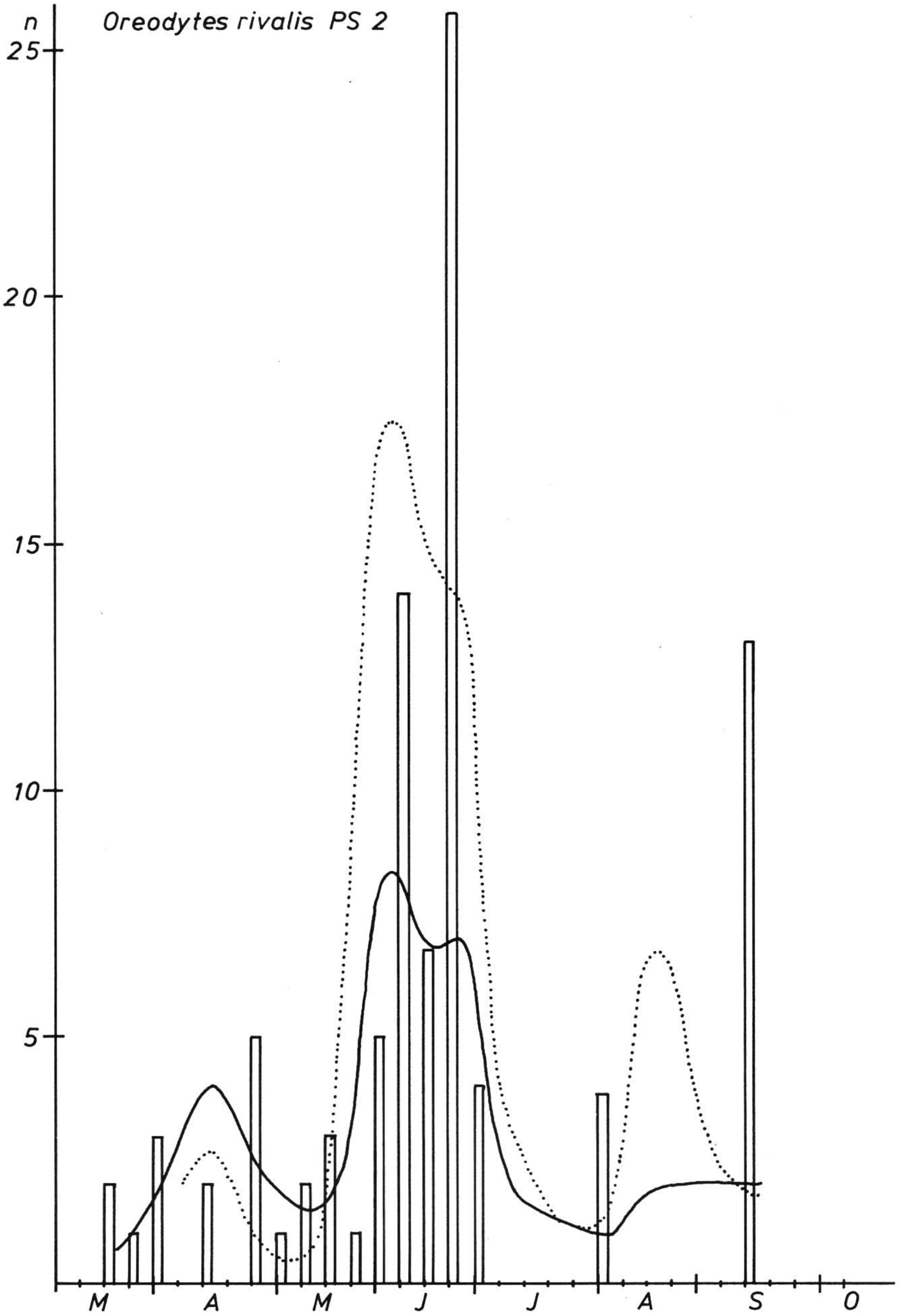

Fig. 16: Phenology of chironomid larvae (columns; Y-axis × 10) at the Inde brook locality PS 2 as compared with the seasonal varying number of ingested chironomid larvae (dotted line) or the number of *Oreodytes rivalis*-crops containing chironomid larvae (black line).

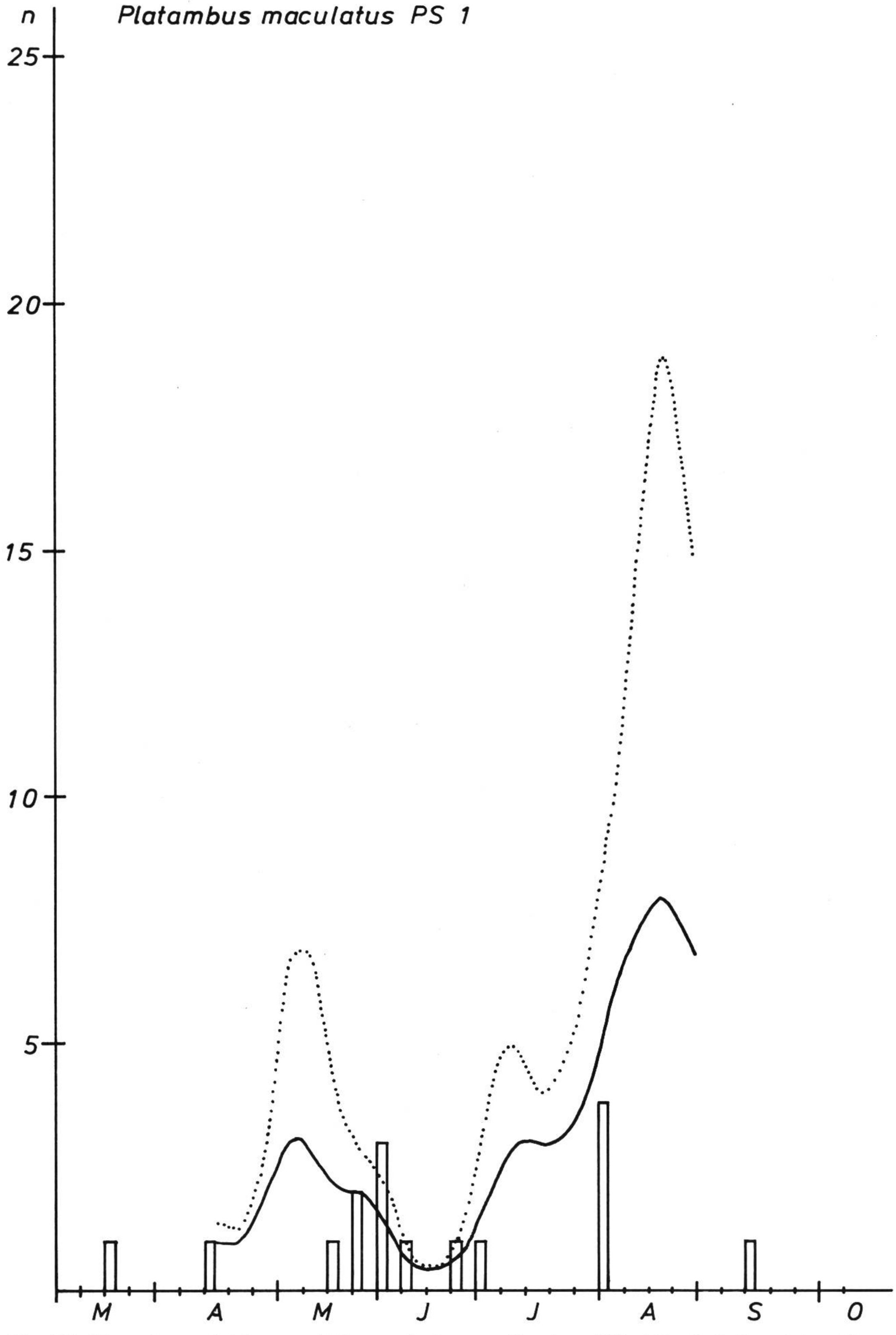

Fig. 17: Phenology of chironomid larvae (columns; Y-axis × 10) at the Inde brook locality PS 1 as compared with the seasonal varying number of ingested chironomid larvae (dotted line) or the number of *Platambus maculatus*-crops containing chironomid larvae (black line).

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