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Carabid beetles as bio-indicators in Belgian coastal dunes: a long term monitoring project

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Summary

Since 1990, populations of carabid beetles are continuously monitored in different coastal dune habitats, situated along a transect from seaside marram dunes to inland moss dunes and dune grasslands. During the first four complete year cycles about 10.000 carabids belonging to 73 species have been obtained.
Less than 50% of these species seem to be continuously present: below certain observed threshold numbers, the turnover in ground beetle species is thus obvious. This level most probably indicates the limit between species with a resident population and those immigrating accidently or temporarily.
Carabid communities from the investigated dune habitats are well characterized: differences between years are relatively small due to a large number of species with a pronounced habitat or microhabitat preference, including some carabids, extremely rare in our country.
Important changes are observed in the population dynamics of many species from year to year, in most species however the dynamics are more or less similar in the different sampling stations. Time series patterns are nevertheless diverse and tentatively explained by means of climatological data. These results are illustrated and in this way also show details of the phenology of the life cycle for a number of hitherto poorly studied species.
Our results indicate the necessity of data on population level (e.g. dynamics, population structure or population genetics) when properly using terrestrial invertebrates as bio-indicators in conservation ecology.

Key-words: carabid beetles, long term monitoring, coastal dunes, biodiversity, population dynamics

Résumé

Depuis 1990, les populations de coléoptères carabiques sont suivies de manière continue dans différents habitats des dunes côtières. Ces habitats sont situés le long d'un transect allant du versant littoral de la dune à oyats jusqu'à une dune couverte de mousse située à l'intérieur des terres. Durant les quatre premièrs cycles annuaires, près de 10.000 carabides appartenant à 73 espèces ont été capturés.
Moins de 50% des espèces semblent être continuellement présents: le "turnover" dans les espèces de coléoptères carabiques est très marquant et indique que la population de ces coléoptères est composée d'espèces ayant une population résidente et d'autres qui immigrent accidentellement ou temporairement. Les communautés de carabides dans les habitats des dunes étudiés sont très bien caractérisées: des différences entre années sont relativement petites, dû à un grand nombre d'espèces ayant un choix d'habitat ou de microhabitat prononcé, incluant certains carabides extrêmement rares pour notre pays.
D'importants changement d'année en année dans la dynamique des populations de beaucoup d'espèces sont observés, tandis que les dynamiques de la plupart des espèces est plus au moins égales dans les différentes stations d'échantillonnages.
Les modèles observés de dynamique de populations sont très divers et sont tentativement expliqués à l'aide des données climatologiques. Les résultats sont illustrés ici et montrent des détail de phénologie pour un certain nombre d'espèces peu étudiées jusqu'à nos jours.
Nos résultats démontrent la nécessité de données au niveau des populations (p.e. dynamique, structure de populations, génétique de populations) si nous voulons utiliser les invertébrés en tant que bio-indicateurs pour la conservation de la nature.

Mots-clefs: Coléoptères Carabiques, monitoring à long termes, dunes côtières, biodiversité, dynamique de populations.

Introduction

Carabid beetles are increasingly used as taxonomic study group in biodiversity and as bio-indicators in monitoring or site assessment studies for nature conservation purposes (e.g. DESENDER et al., 1991, 1992; ERWIN, 1991; LOREAU, 1994; LUFF et al., 1989, 1992). The very high number of species, estimated some ten years ago at about 40.000 described species (NOONAN, 1985), as well as the well-studied pronounced habitat or even microhabitat preference of many of these (THIELE, 1977) are important reasons for the increasing interest they get. Furthermore, the majority of carabid beetles (at least in temperate or subarctic climates) are relatively easily collected in a more or less standardized way by means of pitfall trapping. Nevertheless much discussion remains on the necessary methodologies in sampling (details of techniques, intensity and duration of trapping) as well as in data analyses (multivariate analysis techniques for community and indicator analyses, see e.g. DUFRENE & LEGENDRE, in press) or in diversity assessment (cfr. SOUTHWOOD, 1978).

One problem related to the study of carabid diversity is to assess which part of the species caught at a certain site actually belongs to the local fauna and has reproducing populations. Related to this problem is the question of observed turnover in species richness from year to year on a given site. A short review of the literature shows that most authors either deny the problem (i.e. assume that all species caught on a site belong to the local fauna and/or that species caught in low numbers have a small local population) or use a more or less arbitrary limit between so-called local species and accidently caught species.

A second problem is the lack of knowledge on year to year variation in numbers for many carabid species, i.o.w. data on the magnitude of population dynamics in more or less natural situations. Such studies of course require a continuous long term sampling effort, which is probably the most obvious reason for their scarcity. If one does not take succession studies into account (which address different questions, e.g. GRUTTKE & WILLECKE (1993), MEIJER (1980)), there are indeed only a few studies where sampling has continued for over 4 years. As a result, until now relatively few authors have tried to document and explain these dynamics in carabids, and if and how these might be regulated (DEN BOER, 1990, 1991; DEN BOER et al., 1993; VAN DIJK, 1994; VAN DIJK & DEN BOER, 1992; LUFF, 1990; WEBER & KLENNER, 1987).

In the above context, a long term monitoring project was started in coastal dunes in Belgium. Since 1990, populations of carabid beetles and spiders are monitored in five coastal dune habitats, situated along a transect from seaside marram dunes to inland moss dunes and dune grasslands.
Besides fundamental research on population dynamics, phenology of the life cycle, habitat preference, dispersal power and the use of these invertebrates in biodiversity and conservation ecology, this study aims at defining, on a fine scale and during different years, the possibilities and constraints of ground beetle pitfall trap data for site assessment and bio-monitoring.

This first contribution reports on the data obtained for carabid beetles during the first four complete year cycles with more than 10.000 individuals belonging to 73 carabid species. The species inventory of the study site (this long term studied transect, along with surrounding habitats) has already been commented in a preliminary contribution (DESENDER & BAERT, 1992). No less than 15 species with special faunistic interest were mentioned, including several 'Red list' species (DESENDER et al., in press).
In this paper we will discuss (1) the yearly variation and turnover in species composition, (2) the observed carabid communities in different habitats and microhabitats and (3) the dynamics of relative abundance in the most numerous species, their possible causes, as well as their implications for bio-indicator projects. At the same time the last topic reveals extensive data on the phenology of the life cycle for a number of typical dune inhabiting carabid beetles, some of which are extremely rare in our country and have almost never been studied in detail before.

In earlier studies based on pitfall data collected in numerous other coastal dune ecosystems (DESENDER et al., 1991, 1992), we came to the conclusion that nearly all different dune habitats could be characterized by the presence of particular carabid species or assemblages. In this paper we will also try to answer a similar question, but in addition investigate if these communities differ from year to year.

Material and methods

The investigated dune habitats are located near the river IJzer estuary, where a field station of our Institute is located near the lighthouse. This area has by now mainly been studied for spiders (BAERT & DESENDER, 1993), carabid beetles as well as several Diptera families (cfr. POLLET & GROOTAERT, 1994, in press). A map shows the surroundings of the study area, with all other habitat types (Fig. 1). The field station is illustrated with its surrounding dunes on photographs (Fig. 2). Pitfall traps are continuously in operation, emptied at fort-nightly intervals and immediately sorted and their content identified. In addition, at regular intervals, microclimate as well as vegetation cover and structure are measured on the sampling sites. Along with soil characteristics and climatological data from a nearby station, these measurements are viewed as direct or indirect environmental variables in order to attempt to explain species distributions and population dynamics. Causal relationships (f.e. the influence of dynamics of prey species) are not studied. A summary of vegetation charateristics of the sampling sites is given in Table 1.

The continuously monitored transect starts from seaward marram dunes (station A, Fig. 2a,b,c), over the dune top (station B, Fig. 2d), followed by the landward side of the same marram dunes (station C, visible at the upper left of Fig. 2e). These three habitats are all dominated by marram grass. The remaining two sampling sites are situated more inland, one station close to the marram dunes (station D, Fig. 2e), one station further inland (station E). These sites are dominated by mosses, low herbs and lichens, which especially dominate in the fifth station (Fig. 2f).
These are dunes relatively undisturbed by tourism, which is extremely rare for Belgian standards. One of the most obvious results of this, besides possibilities for relatively 'undisturbed sampling', is the presence in a large part of the dune grasslands of the area of more or less continuous moss and lichen carpets. Such a vegetation type has become very rare in our coastal dunes because it is easily destroyed, especially during dry summers, by trampling. Sampling of these sites was started at the beginning of April 1990 by means of three pitfall traps on each site and

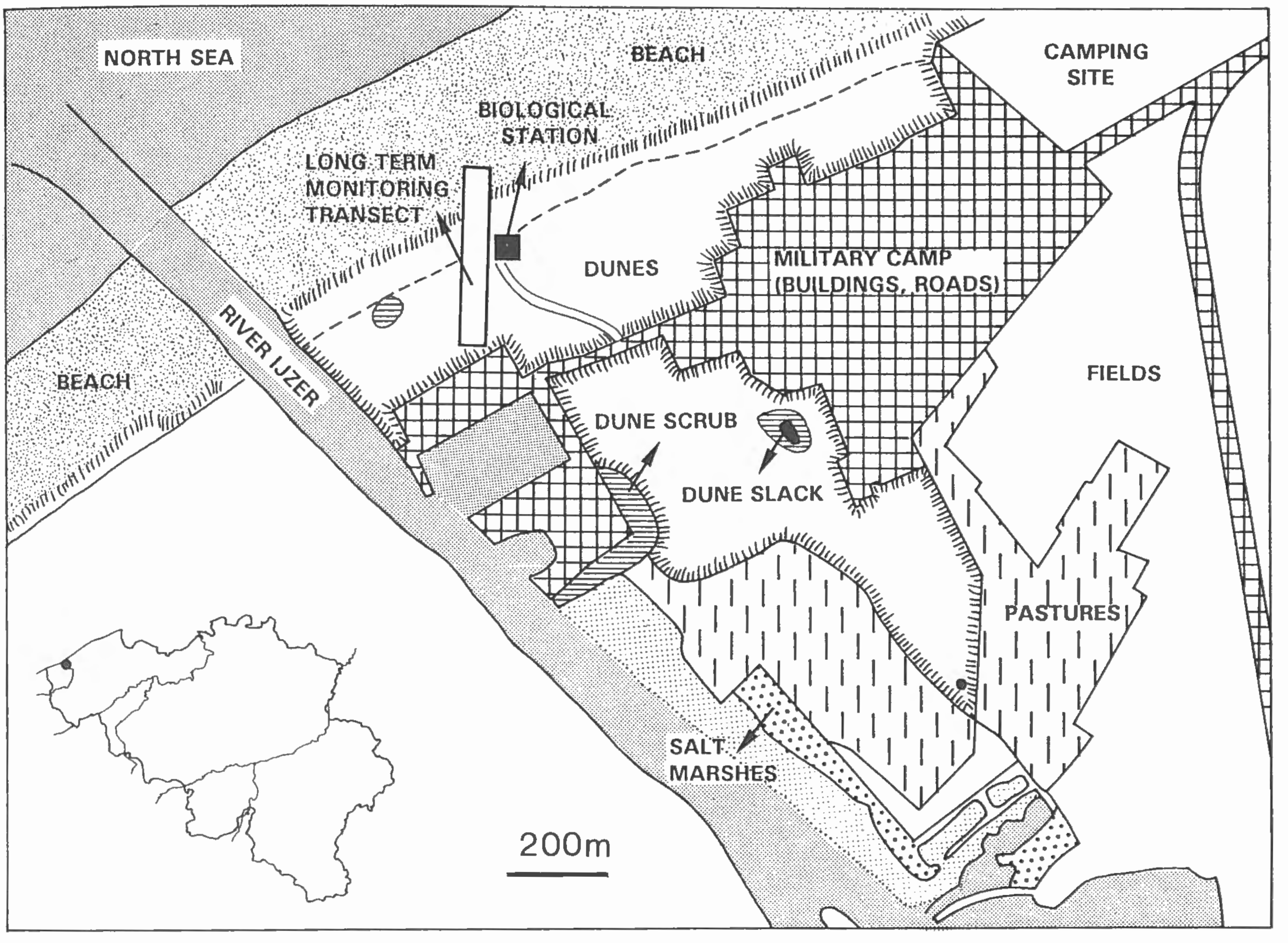

Fig. 1. – Map of the study area with the sampling sites.

has been continued without interruption ever since. The traps are glass jam jars with an aperture of 10 cm diameter and partially filled with a 10% formalin solution with detergent added.

In the autumn of 1993 our monitoring work was disturbed due to the unfortunate loss of the seaward marram dune station, which vanished during several heavy northwestern storms (compare Fig. 2a, b). The authorities have decided to protect this area with a concrete wall during 1994. Covered with sand (Fig. 2c), the site is now monitored again for its beetles and spiders.

During our first four years of monitoring we have experienced that an efficient long term pitfall trapping study requires a continuous inspection of the immediate surroundings of the traps in order to prevent these from getting deeper in the soil, resulting in possibly lower catches; in dune habitats, especially marram dunes, traps can occasionaly be covered by blowing sand, which has to be removed as soon as possible. Therefore the traps are emptied at most at fort-nights, if possible they are inspected even more regularly. Our results until now show no consistent decline over the years in certain traps or stations. We are therefore rather confident they reflect the real population dynamics within each species. In a forthcoming paper we will analyse dynamics over five years by means of coefficients of net reproduction (comparing subsequent year catches, cfr. DEN BOER & VAN DIJK, 1994): in general mean values of these show no consistent decline nor increase in the overall results for the abundant species.

In order to compare the species communities in the different stations and during different year cycles, the most numerous species of each year cycle were retained and their data transformed to relative abundance in the different traps (percentage distribution, equal weighing all retained species). Indirect (DCA) and direct gradient analyses (DCCA) were then performed by means of the CANOCO-software (TER BRAAK, 1988). Direct analyses included as environmental variables data on vegetation cover, microclimate and development of the litter layer.

Table 1. Vegetation characteristics (cover of most abundant plant species and mean total cover) of the sampling stations (vegetation mapping of 27/7/1990).

Vegetation (mean cover in %)		A	B	C	D	E
Ammophila arenaria		45	65	48	4	
Cirsium arvense		<1	5			
Solanum dulcamara		1				
Rubus sp.			1			
Carex arenaria			1	26	8	2
Euphorbia paralias				1		
Ononis repens					25	6
Senecio jacobaea					<1	<1
Erodium cicutarium dunense					2	2
Galium verum						2
Rumex acetosella						1
Festuca rubra						8
Hypochoeris radicata					1	2
Cochlearia danica						1
mosses					54	37
lichens					1	35
mean total cover:	herbs	47	72	75	41	25
	mosses & lichens	0	0	0	55	72
	litter	5	11	2	0	0
	bare sand	53	28	25	4	2

In the future such analyses will be elaborated even further by also including detailed soil characteristics (such as texture, humidity, chalk and humus content; DESENDER, in prep.).

Phenology data of the most abundant species were interpolated to values for each month and furthermore corrected for differences in number of days per month before graphical presentation. To investigate to what extent populations of different species fluctuate from year to year and what are possible causes of the observed populations dynamics, data were first summed for each year cycle. The possible concordance of fluctuations from year to year in different sampling stations (year cycle totals) were tested for the abundant species by means of Kendall's test of Concordance (SIEGEL, 1956). Such a test only makes sense for species occurring numerously in more than two sampling stations. For species, abundant in two stations only, the concordance was estimated by means of Spearman rank correlation values (SIEGEL, 1956).
Data on the population dynamics of the most numerous species were then analysed in an ordination (DCCA) based on total numbers per year cycle, in order to reduce and simplify the occurrence of patterns in these dynamics. Climatological data (obtained from the most nearby meteorology station Middelkerke, which is also situated close to the sea) were averaged first per month as well as per season. These data for temperature (minimum at soil surface level in grass), precipitation and wind speed were then z-transformed (substract the mean from each value and then divide by the standard deviation; in this way the overall mean = 0, the overall standard deviation = 1) in order to standardize them before analysis (direct gradient analysis) or before graphical presentation. Other climatological variables were also studied but did not increase the explanatory power in analyses or were even redundant (cfr. high inflation factors in DCCA-analyses). We will analyse these dynamics in more details, by incorporating also time-lags in the climatological variables, in a forthcoming paper (DESENDER, in prep.).
The nomenclature of the carabid beetles follows DESENDER (1995).

Fig. 2. – Study area:
2a: marram dune seaward sampling station in 1992;
2b: same view after heavy storm in the autumn of 1993;
2c: same view after protection with concrete wall during 1994;
2d: marram dune top;
2e: general view of the study area with the field station to the left of the lighthouse of Nieuwpoort; sampled moss dunes are visible in the front, whereas the landward marram dune sampling station is visible in the extreme upper left of the photograph;
2f: sampled moss dunes situated more inland of the marram dunes.

Table 2. Carabid beetle species inventory of a long term monitoring dune transect (1990-1994).

Agonum dorsale	*Bradycellus harpalinus*	*Harpalus vernalis*
Amara aenea	*Bradycellus verbasci*	*Leistus ferrugineus*
Amara anthobia	*Calathus ambiguus*	*Leistus fulvibarbis*
Amara apricaria	*Calathus cinctus*	*Licinus depressus*
Amara aulica	*Calathus erratus*	*Loricera pilicornis*
Amara bifrons	*Calathus fuscipes*	*Masoreus wetterhali*
Amara communis	*Calathus melanocephalus*	*Metabletus foveatus*
Amara curta	*Calathus mollis*	*Metabletus truncatellus*
Amara familiaris	*Clivina fossor*	*Microlestes maurus*
Amara fulva	*Demetrias atricapillus*	*Nebria brevicollis*
Amara lucida	*Demetrias monostigma*	*Nebria salina*
Amara ovata	*Dromius linearis*	*Notiophilus aquaticus*
Amara similata	*Dromius melanocephalus*	*Notiophilus biguttatus*
Amara spreta	*Dromius notatus*	*Notiophilus quadripunctatus*
Amara tibialis	*Dyschirius angustatus*	*Notiophilus substriatus*
Asaphidion stierlini	*Dyschirius luedersi*	*Panagaeus bipustulatus*
Badister bullatus	*Harpalus affinis*	*Pterostichus melanarius*
Bembidion femoratum	*Harpalus anxius*	*Pterostichus nigrita*
Bembidion iricolor	*Harpalus attenuatus*	*Pterostichus strenuus*
Bembidion lunulatum	*Harpalus latus*	*Stenolophus teutonus*
Bembidion mannerheimi	*Harpalus rubripes*	*Trechus micros*
Bembidion minimum	*Harpalus rufibarbis*	*Trechus obtusus*
Bembidion properans	*Harpalus rufipes*	*Trechus quadristriatus*
Bembidion quadrimaculatum	*Harpalus servus*	
Bradycellus distinctus	*Harpalus tardus*	

Results and discussion

1. *Species turnover*

From the 73 carabid species encountered in our complete data-set (a complete species list is given in Table 2), only half are continuously (each year) present (Fig. 3). The remaining 50% however occur only in very low numbers, and thus seem to be only temporarily or accidently immigrating. These presumably non-resident species, mostly are able to fly and are in many cases caught outside there natural reproductive period, thus further indicating they do not really belong to the local fauna. From year to year we keep observing newcomers as well as species disappearing from the stage again (Fig. 4). Furthermore there is a continously increasing cumulative number of species.

We are at the moment looking into more detail to the surrounding habitats of these dunes in order to try to reconstruct the origin of these presumably straggling beetles. Moreover, we are studying their wing and flight muscle development in relation to their reproductive state (DESENDER, in prep.). This should enable us to test more rigidly one of the two hypotheses whether such species are vagrants from other habitats or whether they belong to local populations passing through bottlenecks.

Only few other papers have evaluated which species of an inventory actually reproduce in a sampled habitat. LUFF (1990) also classified more than 50% of the carabid species in a long term study of a mosaic field/grassland site as presumed immigrants. EVERSHAM & TELFER (1994) concluded that about 50 % of the collected carabid fauna of a poor grassland road verge actually had bred there. In an earlier paper on an intensively grazed pasture (DESENDER & POLLET, 1988) we came to a similar conclusion. Increasing the number of traps beyond 3 to 6 pitfalls (which yields the locally reproducing species) did not lead to a plateau in the cumulative number of species obtained, but gave information of immigrating species from the surroundings.

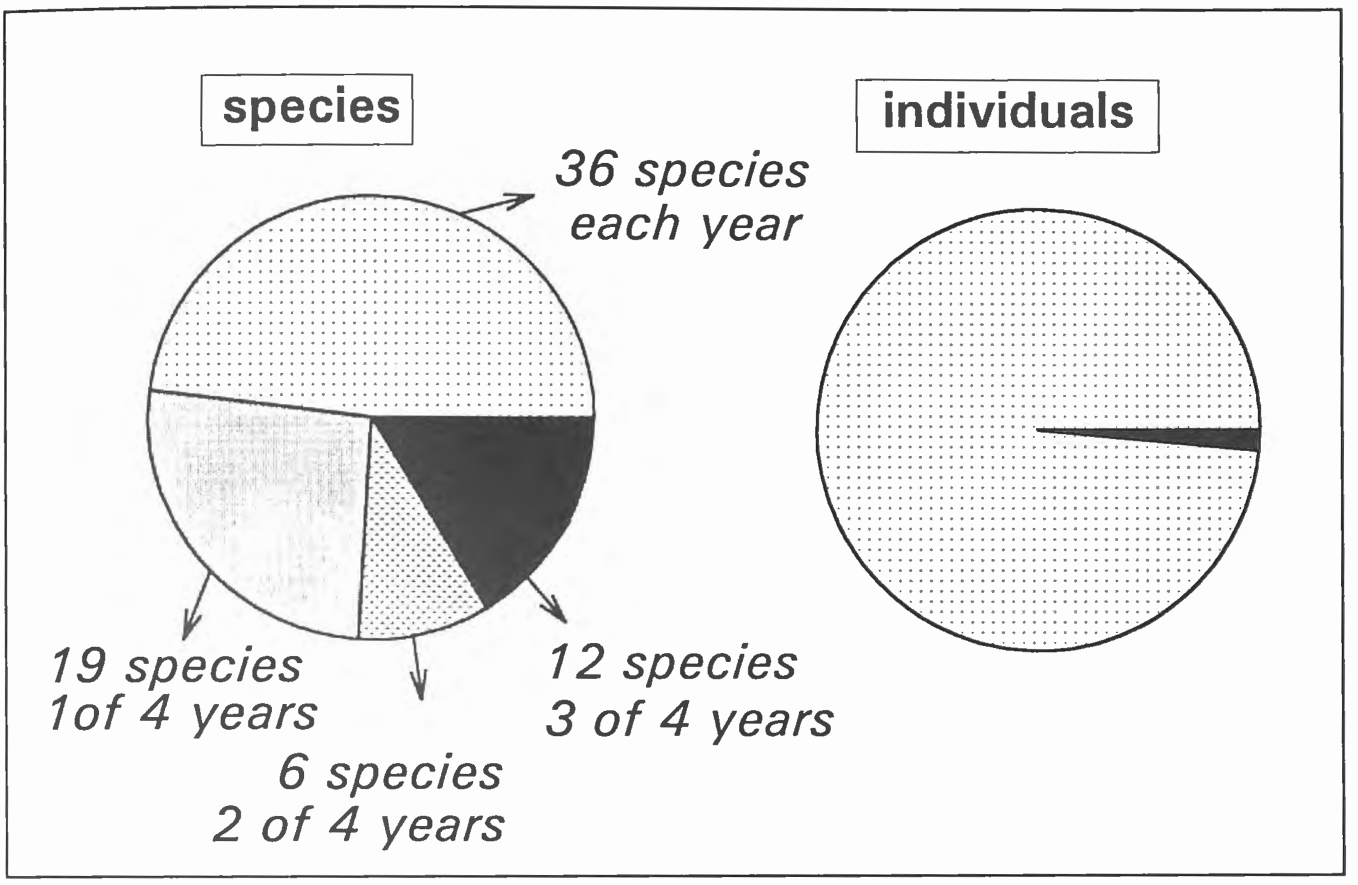

Fig. 3. – Proportion of carabid species (left figure) and individuals (right figure) caught during 1, 2, 3, or 4 year cycles in the investigated dune transect.

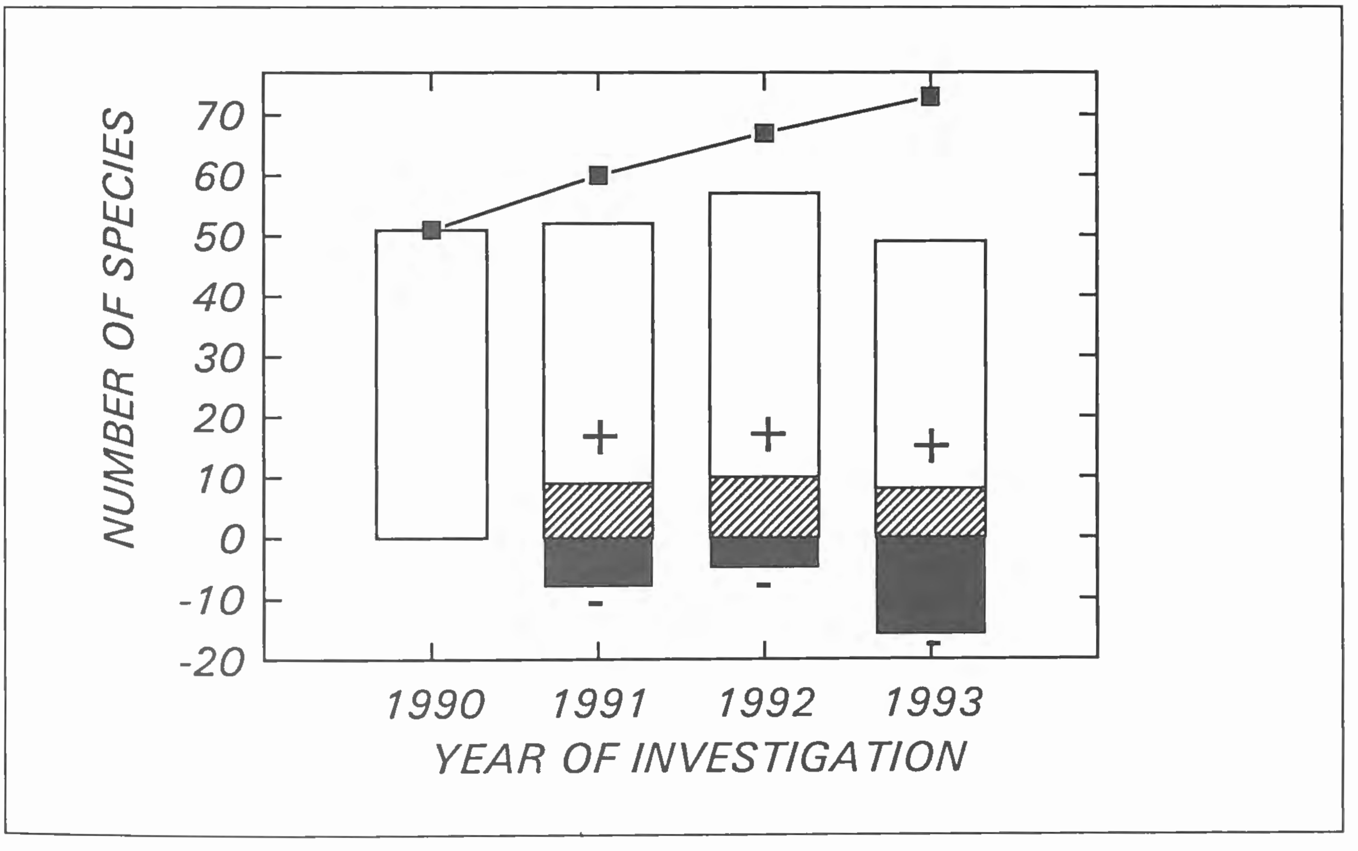

Fig. 4. – Turnover in species richness from year to year: each bar represents the number of species caught during a complete year cycle; hatched columns: species not present in the previous year; black columns: species lost as compared to previous year; line graph shows the cumulative total number of species.

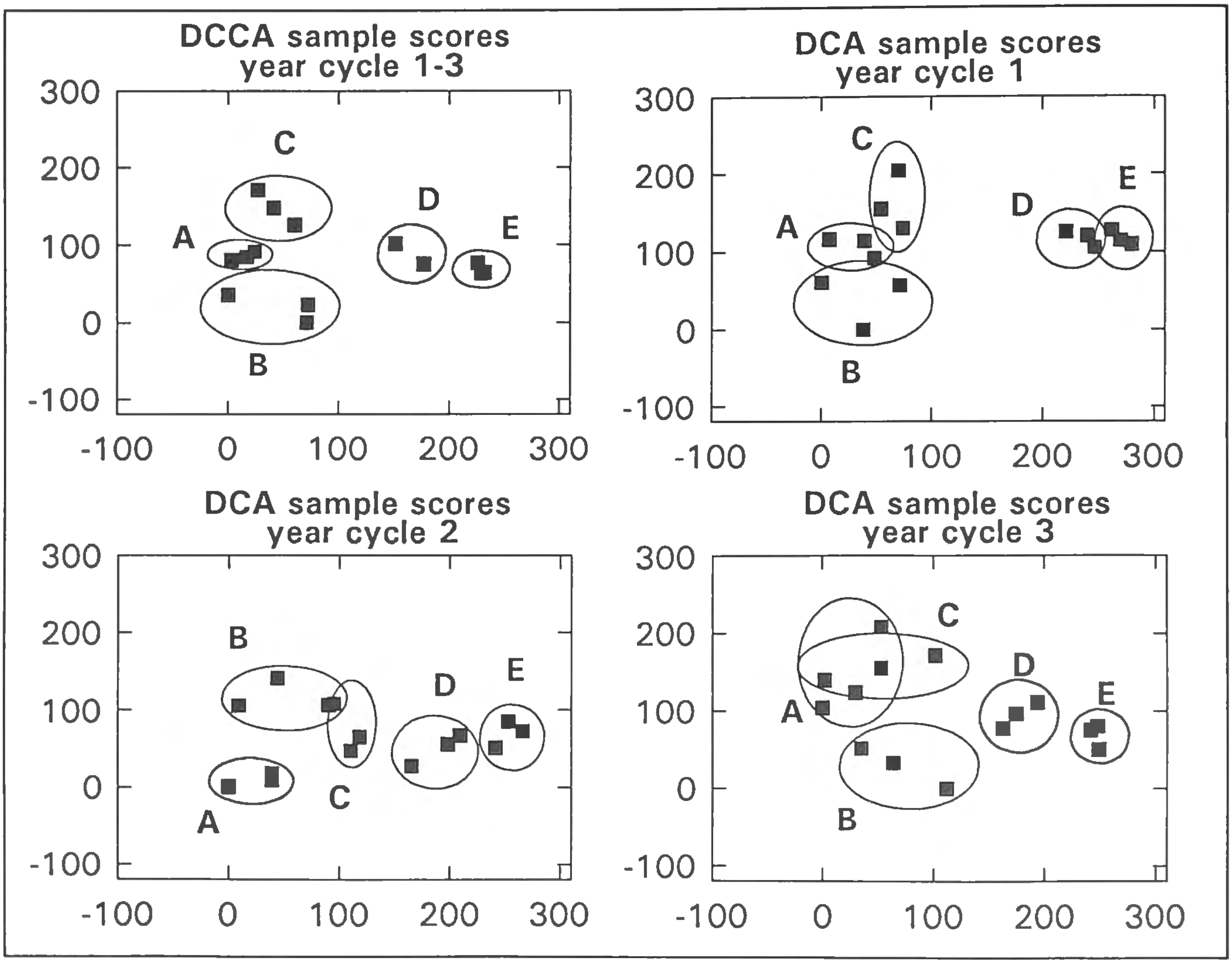

Fig. 5. – Ordination of individual pitfall trap data based on carabid beetle communities (traps from each sampling station are enclosed by ellipses): upper left graph: DCCA year cycle 1-3; other graphs represent DCA sample scores for respectively year cycle 1, 2 and 3.

2. *Carabid beetle communities*

A direct or indirect gradient analysis based on the 19 most numerous species from year cycle 1 to 3 (with the complete series for the 5 sampling stations) yield very comparable results. The results of the direct analysis (Fig. 5, upper left graph, sample scores), which is a detrended canonical correspondence analysis with a set of environmental data (after removal of redundant variables) related to the carabid species data (Fig. 6), show that all sampling stations are characterized by their species composition and relative abundance. A large amount of the total variation is explained by the first ordination axis, which is highly significantly related to a gradient of increasing light intensity and cover of mosses and lichens. Along this axis the separation between on the one hand the marram dunes (A to C) and on the other hand the dune grasslands dominated by mosses and lichens (D-E) is very obvious. The second axis explains only few more variation and seems inversely related to the presence of litter (highest values in the dune top, station B).

Typical species (cfr. Fig. 6: species scores and centroids of environmental variables) are on the one hand *Demetrias monostigma* (in A and C), on the other hand *Leistus ferrugineus* and *Bembidion lunulatum* (in B and A). The moss dunes are characterized by much more species, which are moreover much rarer in our country. Examples are *Harpalus anxius, Harpalus vernalis, Amara lucida, Calathus cinctus, Calathus ambiguus. Harpalus vernalis* and *Calathus ambiguus* are extremely rare and both threatened to such a degree that they have been included as 'endangered species' in a recently established 'Red list' for our flemish region (DESENDER et al., in press).

Ordination results for different year cycles are shown in Fig. 5. Detrended correspondence analyses show only minor differences from year to year, with a constant

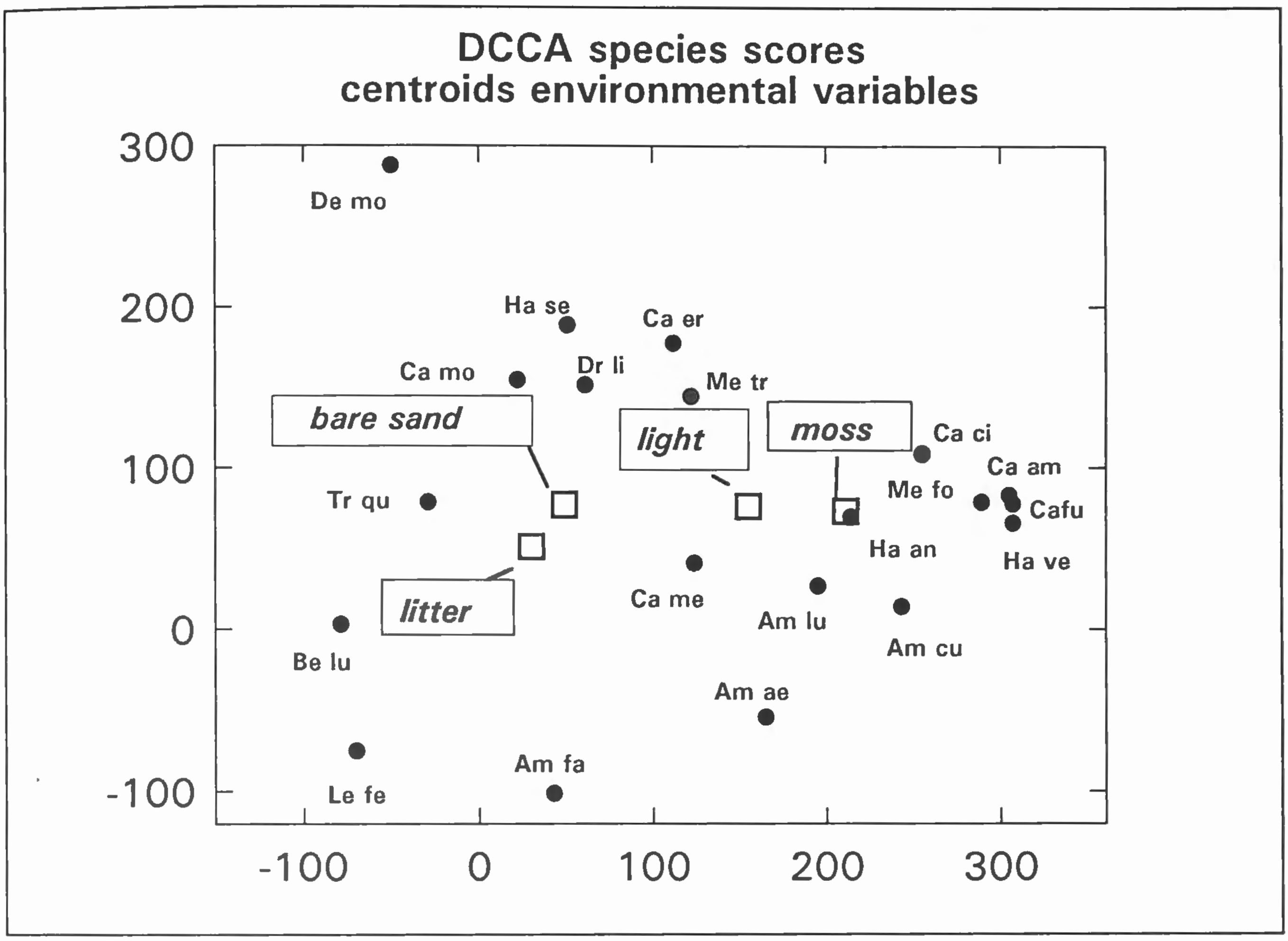

Fig. 6. – Species scores of the most abundant carabid species after DCCA on totals per trap (year cycle 1-3) along with centroids of environmental variables (see text for further explanation; only variables significantly related to ordination axes are added); abbreviations for each species composed by first two letters of genus and species names (cfr. Table 2).

regrouping of stations D and E, as well as station B versus A and C. This is a result of the continuous presence of many typical species with a pronounced habitat or even microhabitat preference, although many species show pronounced population fluctuations from one year to another (see further). In general there is always a clear separation between the carabid communities of marram dunes and moss dunes.

3. *Population dynamics and phenology of the life cycle*

3A. ***Testing for synchrony in population dynamics between sampling stations***

Kendall's test of Concordance (comparing year totals over the different sampling stations) yielded for the four most abundant species a significant value (*Calathus erratus*: S=52, $p<0.05$; *Calathus melanocephalus*: S=50, $p<0.05$; *Calathus mollis*: S=62, $p<0.01$; *Harpalus servus*: S=62, $p<0.01$). For seven more species, abundant in two stations only, a significant rank correlation value (Spearman r) was obtained between year values in both stations (*Amara aenea, Amara lucida, Calathus ambiguus, Calathus cinctus, Harpalus vernalis, Leistus ferrugineus*). The remaining species did not fluctuate similarly in different stations or were strongly dominant in one station only, thus not enabling to be tested properly for concordance in yearly fluctuations between stations.

In summary, the majority of the abundant species showed distinct population dynamics fluctuating in synchrony in different sampling stations. This is not really surprising, in view of the relatively small distances between the sampling stations (at most about 250 m). At the same time these results suggest that more general (climatological) factors are responsible for the regulation of population dynamics on the different sampling sites (see further). Whether these populations have to be interpreted as 'subpopulations'

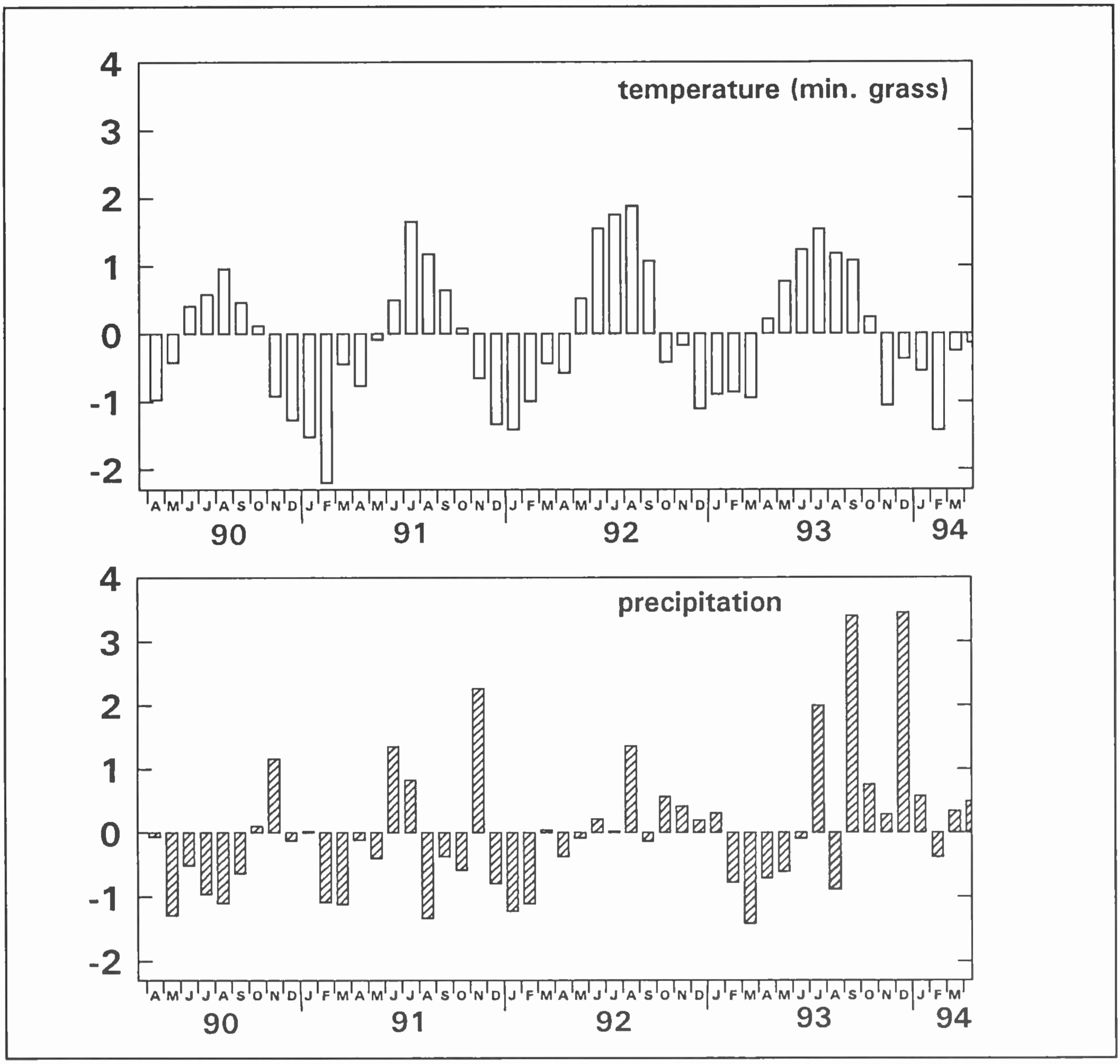

Fig. 7. – Detailed time series (z-standardized values) of mean monthly temperature (minimum on grass) and total monthly precipitation from the meteorology station at Middelkerke (source: K.M.I., Ukkel, Belgium).

from a larger 'deme' or 'metapopulation' is not yet clear, but will be investigated in more detail in the future by means of population genetic approaches.

3B. ***Patterns and tentative explanations of population dynamics in the most abundant carabid beetles***

The year totals of the most numerous species were subjected to an ordination (DCCA) in order to summarize the different patterns observed. As already mentioned, climatological variables were added as tentative explanatory variables in the analysis.
Mean monthly temperature and total monthly precipitation are plotted in Fig. 7 for the investigation period. The species scores along with the climatological variables, associated significantly to the two most important ordination axes, are shown in Fig. 8.: first of all these results show a large variability in the patterns of dynamics of different species. To illustrate this further, detailed time series are plotted for species in different regions of the ordination biplot (Figs 9-15). Where relevant, these figures illustrate data from different sampling stations (Figs 11, 12, 15).

At the upper right in Fig. 8, species are regrouped which appeared more numerous in the third and especially the

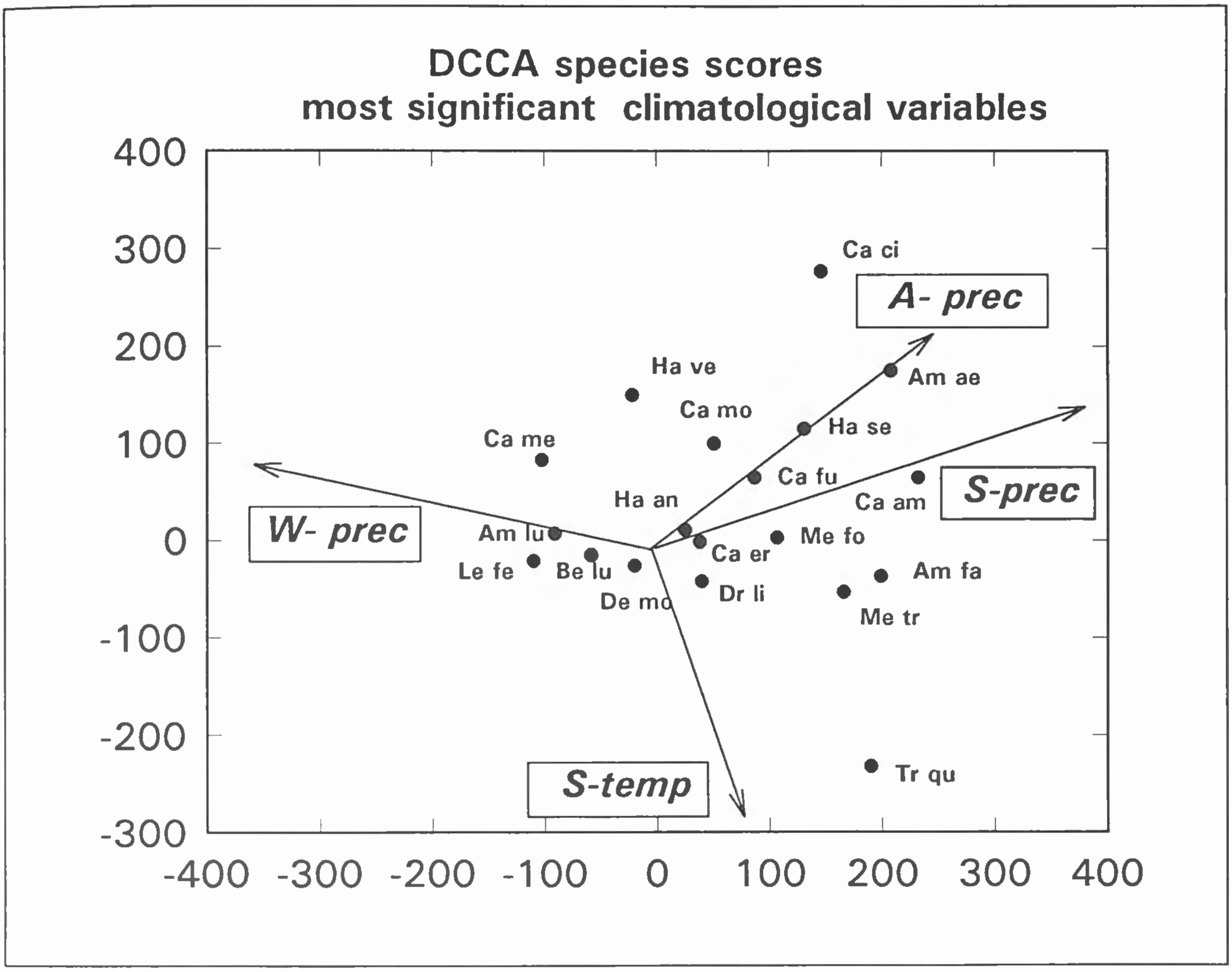

Fig. 8. – Species scores of the most abundant carabid species after DCCA on totals per year along with environmental biplot of climatological variables (see text for further explanation; only variables significantly related to ordination axes are added: A=autumn, S=summer, W=winter, prec=precipitation, temp=temperature); abbreviations for each species composed by first two letters of genus and species names (cfr. Table 2).

last year cycle. Examples are the spring breeder *Amara aenea* as well as the autumn breeders *Calathus ambiguus* and *Calathus cinctus* (Fig. 9). Their peak values coincide with high summer and autumn precipitation, periods in which these species possess larvae. Although very speculative, this could mean that in years with a low precipitation during summer and autumn, the larvae of these species, paradoxally known as xerophylous, severely suffer from dessication. Of course the influence could be indirect through for example the abundance of food or prey or there could be a time-lag in such effects. *Amara familiaris*, *Metabletus foveatus* and *Metabletus truncatellus* are spring breeders (Fig. 10), also conforming more or less to this pattern. In these cases, however, variation between years seems relatively lower whereas peak values have been noted especially during the third year cycle.

In the lower right of Fig. 8 *Trechus quadristriatus* is situated. This is a species with a preference for cultivated fields and ruderal sites, breeding during summer and autumn (THIELE, 1977). It was most numerous during the second and especially during the third year cycle (Fig. 11), although the pattern is not entirely concordant between stations A and B. Largest numbers coincide with the hottest summer in the series. Nevertheless, the species is more abundant in other habitats where much higher numbers are noted. During summer *Trechus quadristriatus* regularly exhibits a high dispersal activity and flies regularly, especially during warm and humid evenings (DESENDER, 1989).

In a more central position of Fig. 8, some species are regrouped with relatively few fluctuations from year to year: *Calathus erratus* however shows a somewhat different pattern according to the station (Fig. 12) with especially a more extended phenology period in the marram dune as compared to the dune grasslands. The extra seasonal activity in spring could be due to a higher sur-

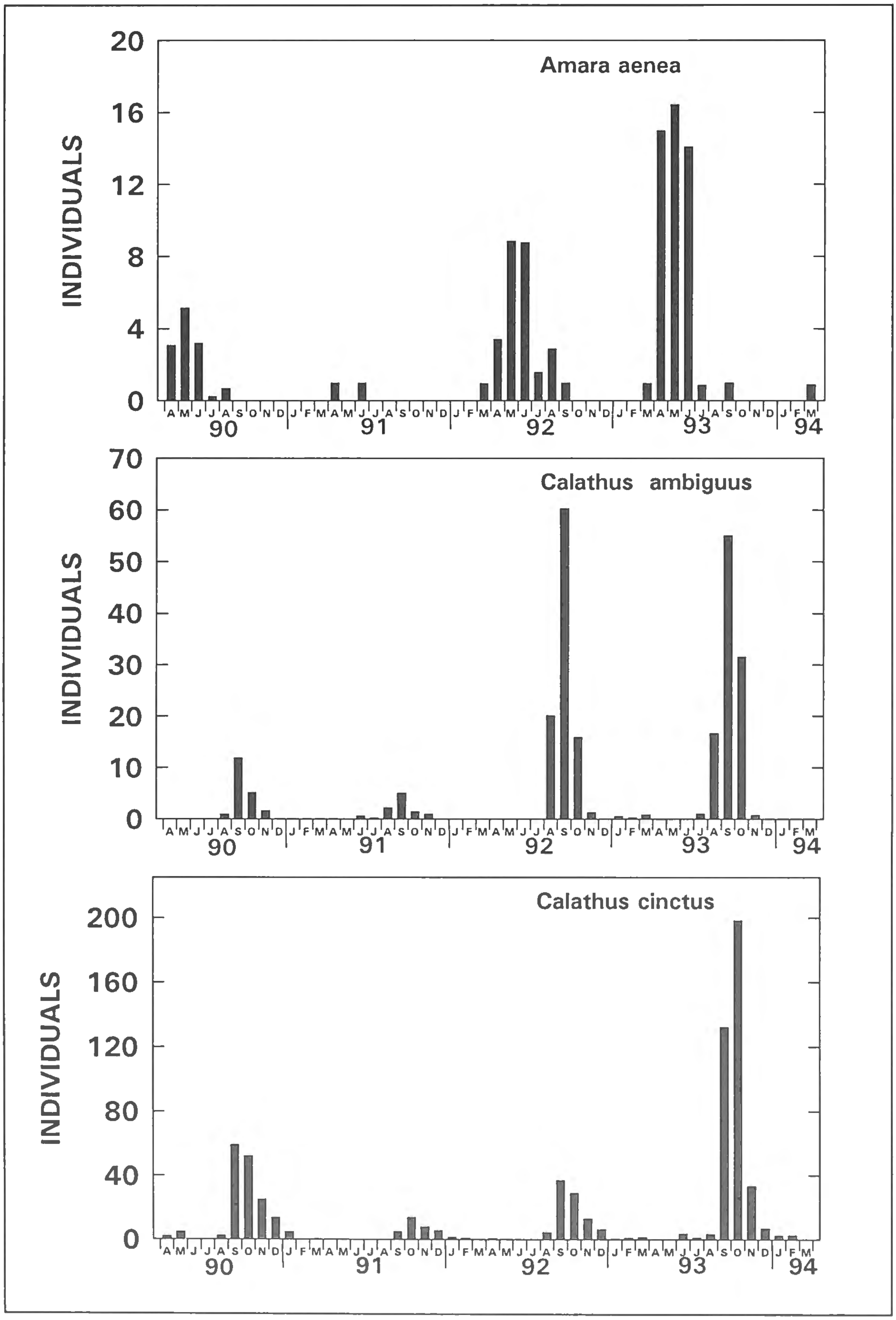

Fig. 9. – Detailed time series of monthly totals (males + females) of *Amara aenea, Calathus ambiguus* and *Calathus cinctus* from four complete year cycles in a dune transect.

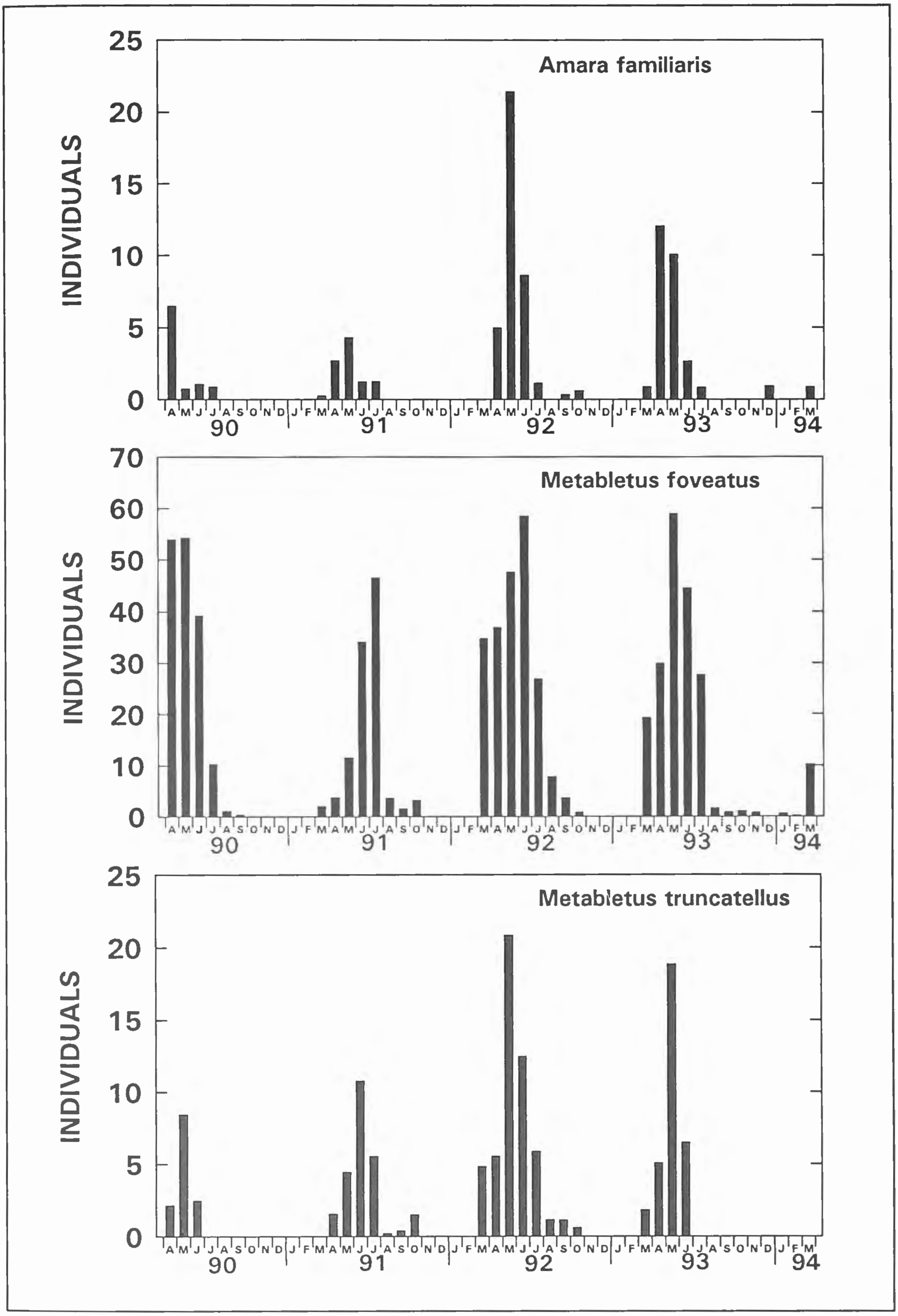

Fig. 10. – Detailed time series of monthly totals (males + females) of *Amara familiaris, Metabletus foveatus* and *Metabletus truncatellus* from four complete year cycles in a dune transect.

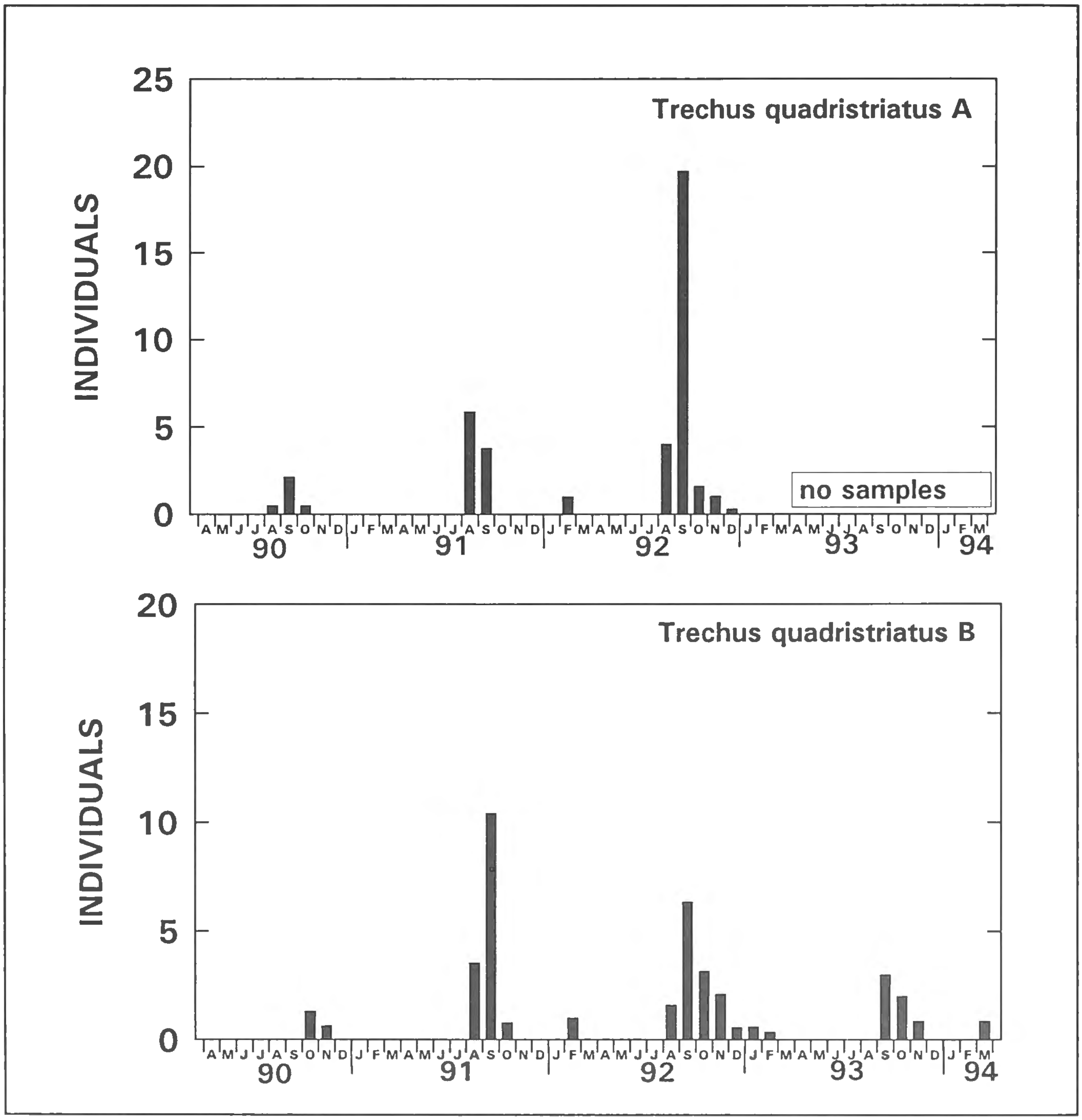

Fig. 11. – Detailed time series of monthly totals (males + females) of *Trechus quadristriatus* from four complete year cycles in two marram dune (A, B) sampling stations.

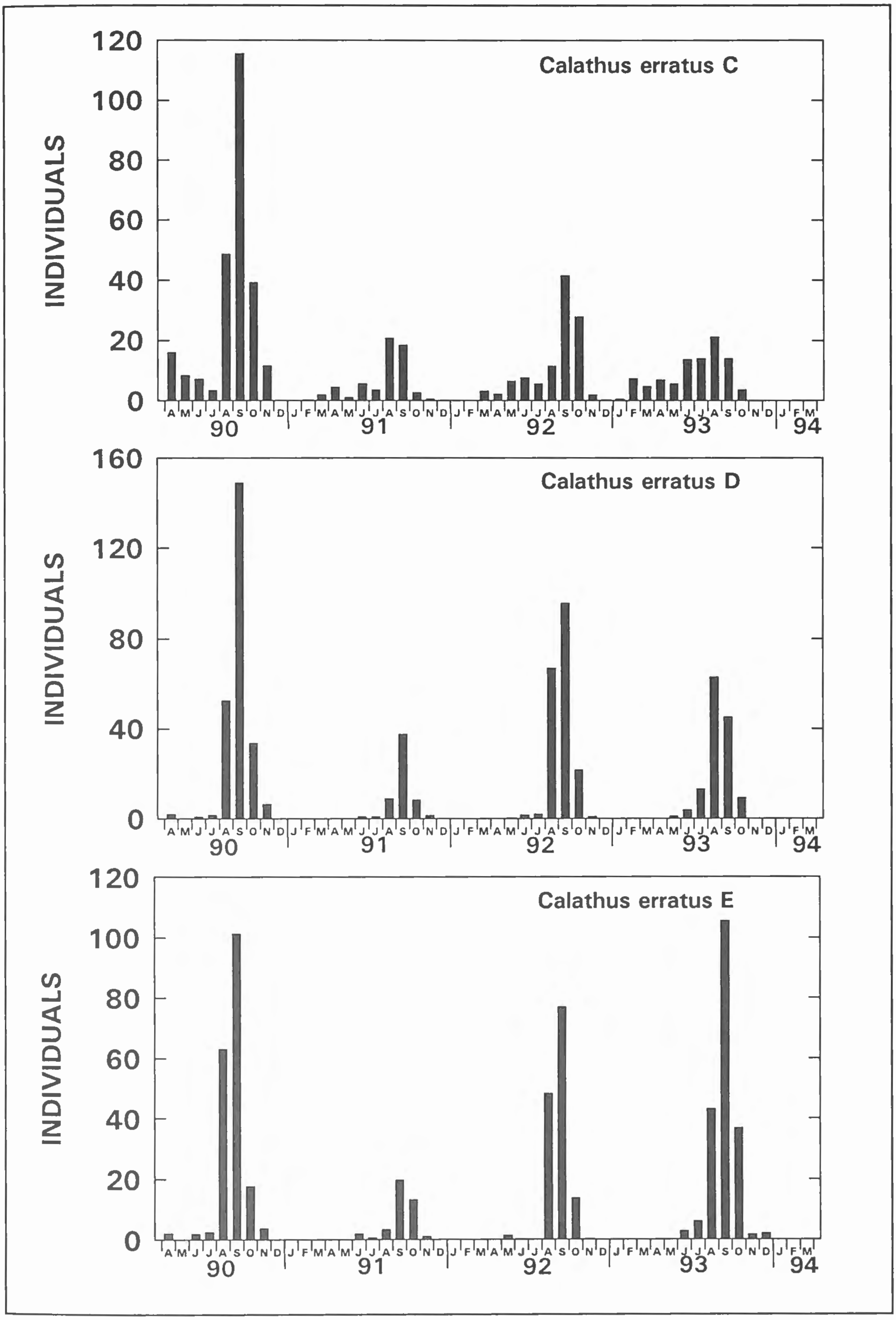

Fig. 12. – Detailed time series of monthly totals (males + females) of *Calathus erratus* from four complete year cycles in a marram dune (C) and two moss dune (D, E) sampling stations.

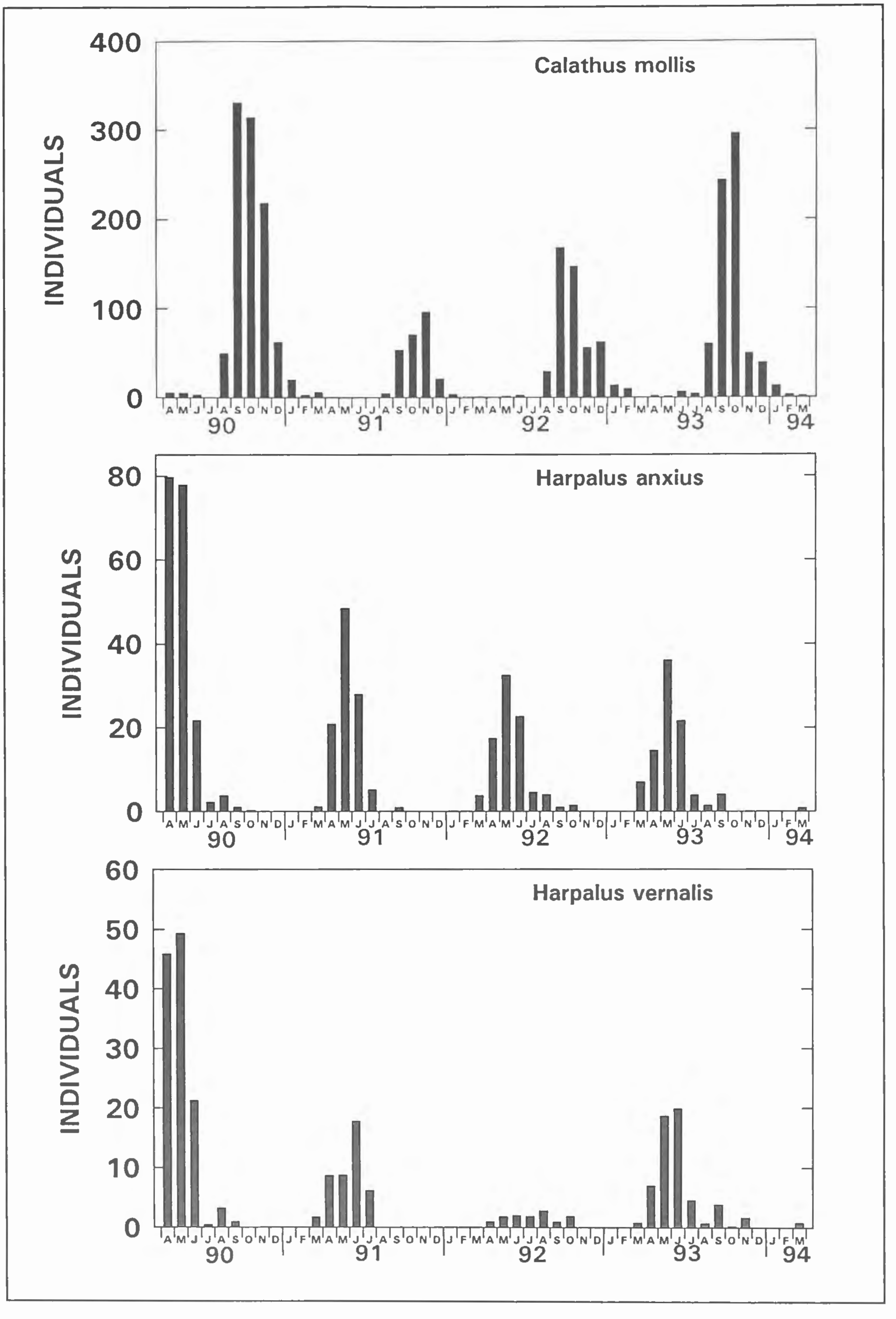

Fig. 13. – Detailed time series of monthly totals (males + females) of *Calathus mollis*, *Harpalus anxius* and *Harpalus vernalis* from four complete year cycles in a dune transect.

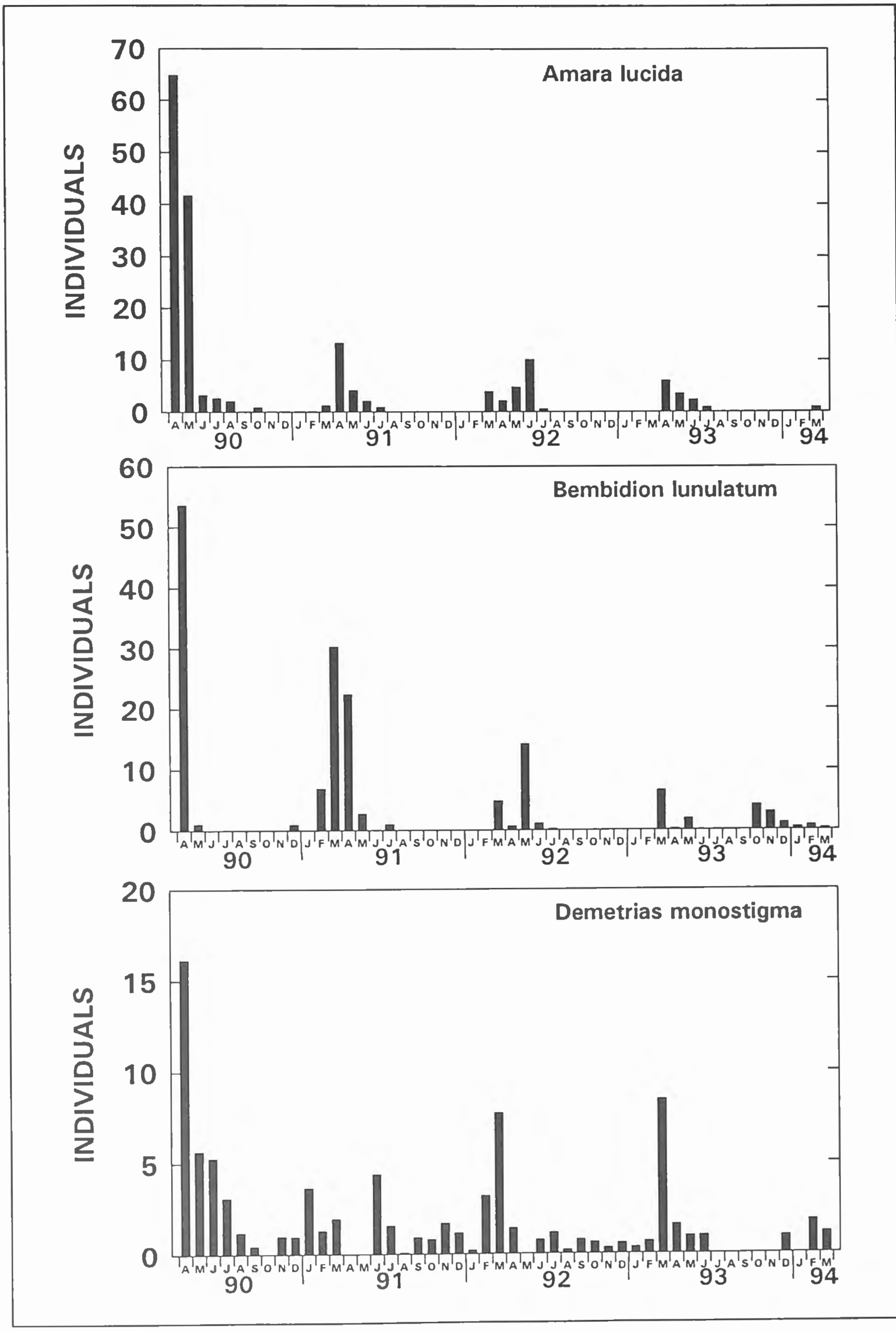

Fig. 14. – Detailed time series of monthly totals (males + females) of *Amara lucida, Bembidion lunulatum* and *Demetrias monostigma* from four complete year cycles in a dune transect.

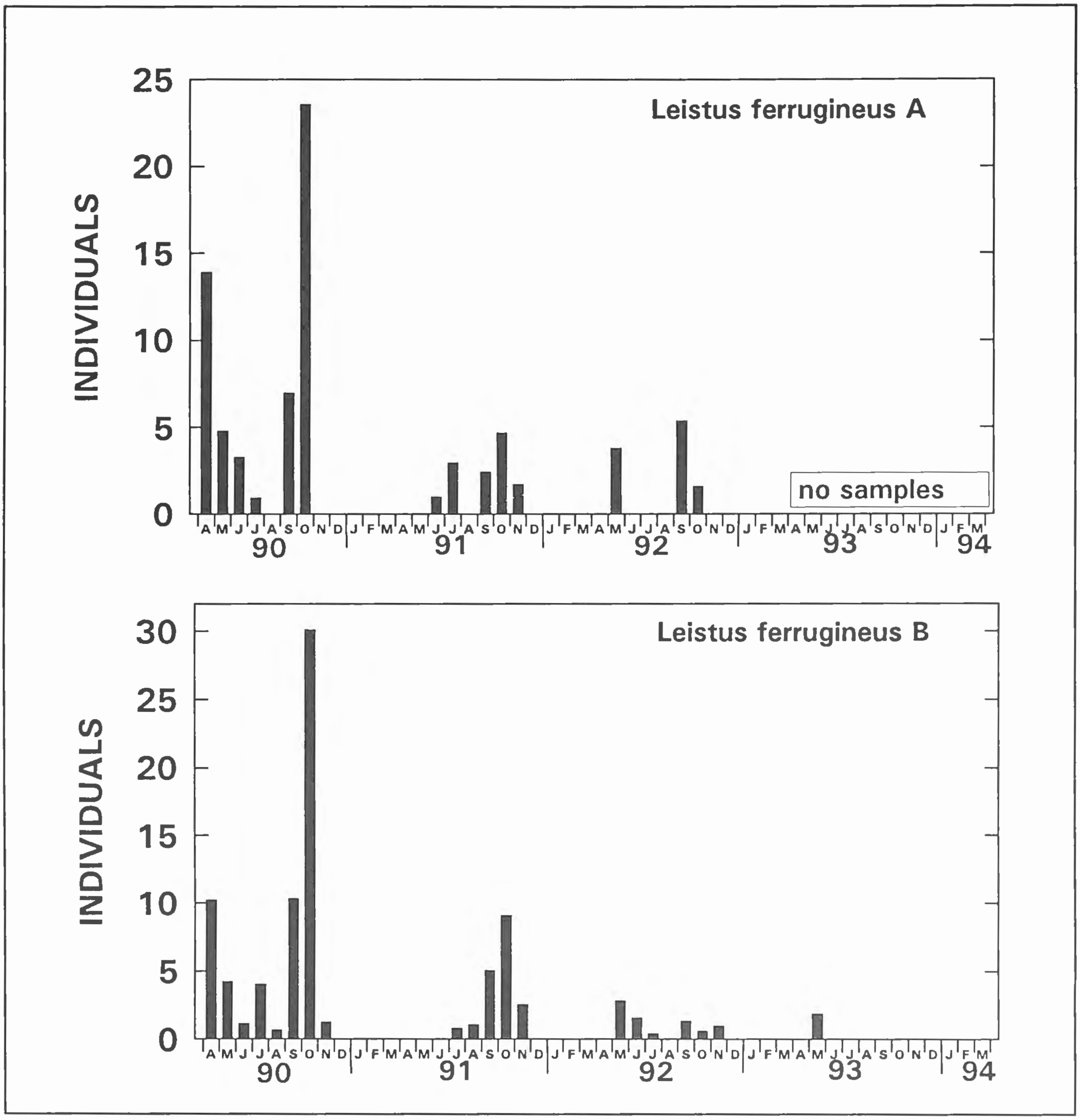

Fig. 15. – Detailed time series of monthly totals (males + females) of *Leistus ferrugineus* from four complete year cycles in two marram dune (A, B) sampling stations.

vival during winter in this habitat as compared to the possibly less protected moss dunes. Another possible explanation is an earlier start of the activity season of *Calathus erratus* in the south facing marram dune site (station C) as compared to the other sites. *Harpalus anxius*, *Calathus mollis* and, to a certain degree, also *Harpalus vernalis* show highest numbers in the first year (Fig. 8). *Calathus mollis* again is an autumn breeder, whereas both small-sized *Harpalus* species are probably spring breeders.

More to the left of the ordination biplot *Amara lucida*, *Bembidion lunulatum* and *Demetrias monostigma* (Fig. 14) are situated along with *Leistus ferrugineus* (Fig. 15): all these species show a continuously decreasing population, concordant between different stations (cfr. Fig. 15), and coinciding with higher precipitation values during winter. Interestingly, *Leistus ferrugineus* is a carabid species with larvae showing a relatively high soil surface activity during winter! The larvae as well as the adults are moreover known as specialized predators on springtails, which they hunt at night. A speculative hypothesis here could be an indirect relation to humidity, related to springtail activity and abundance. In that case, one would expect a time-lag between prey and predator density, but this was of course not investigated in our study. On the other hand *Leistus ferrugineus* is one of the few carabid species known to hold a summer diapause, which could explain why its dynamics seem *not* to be influenced by summer temperature nor precipitation. The phenology graphs of *Amara lucida*, *Bembidion lunulatum* and *Demetrias monostigma* (Fig. 14) moreover show that all these species invariably have their highest activity during early spring. Whether this is merely coincidence will be investigated in the future.

Conclusions

(1) We observe a high turnover in carabid species from year to year indicating that many species immigrate accidently or temporarily; simply for this reason already, species richness and diversity measures must be used with caution.
(2) Carabid communities from the investigated dune habitats are well characterized; differences between years are relatively small due to a large number of species with a pronounced habitat or microhabitat preference.
(3) Populations of many species fluctuate to a high extent from year to year, mostly, though not always, synchronously in different populations; climatological data at least partly seem to explain the observed population dynamics.
(4) Because of the constraints, mentioned above, data on population level (dynamics, structure, genetics,...) are recommended for a more straightforward use of terrestrial invertebrates as bio-indicators in conservation ecology.

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