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Population dynamics of phytophagous mites inhabiting rocky shores – K-strategists in an extreme environment?

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Abstract: The population dynamics of six algophagous and one lichenophagous mite species found on littoral hardsubstrates of the Weser estuary were investigated (Hyadesiidae, Ameronothridae, Halacaridae, Nanorchestidae). Although living in an extreme environment, all these species showed typical K attributes such as long generation time and long reproductive periods. Generational synchrony differed among the investigated species. It ranged from univoltine life cycles with a rigid diapause control to non-synchronised populations with multiple overlapping generations. All species attained very high abundances in spring or summer, independent from time of offspring release (deposition of eggs or larviparity). The seasonal fluctuation of temperature and algal biomass as well as wave exposure are discussed as important factors influencing life cycle strategies.

Introduction

As a transition zone between sea and land, rocky shores are inhabited by a unique community of marine and terrestrial colonisers. The tidal submersion-emersion cycle causes high fluctuations of most abiotic factors including salinity, humidity, temperature, pH and mechanical impact (waves and water currents) (LEWIS 1964; STEPHENSON & STEPHENSON 1972; LITTLE & KITCHING 1996). The gradient between sub- and supralittoral of decreasing submersion time and mechanical stress and increasing fluctuations of most abiotic factors give rise to distinct zonation patterns of both flora and fauna. The limits of vertical distribution are modified by further physical factors like structure of hardsubstrate and biological factors such as interspecific competition (MATHIESON & NIENHUIS 1991; LITTLE & KITCHING 1996). Due to their impressive tolerance to these extreme conditions, microarthropods – especially mites of marine and terrestrial origin – constitute an important part of the rocky shore biocoenosis (SCHUSTER 1965, BARTSCH 1978). Species diversity, zonation patterns and ecophysiology of littoral mites have been the subject of several investigations (HALBERT 1920; OTTO 1936; SCHUSTER 1962, 1965, 1979; PUGH & KING 1985a, 1985b; LUXTON 1990; ERNST et al. 1993; ERNST 1996; SIEMER 1996a). And yet, only a few comparative studies on phenology and life cycle of littoral mites have been published (STRAARUP 1968; BARTSCH 1972; PUGH & KING 1986).

Along the north German coasts, natural rocky shores exist only at a few places (e.g. Helgoland in the North Sea or Rügen in the Baltic Sea). However, several hundred kilometres of man-made hardsubstrates can be found (e.g. bank reinforcements of estuaries, docks, embankments and breakwaters). Some of these little-investigated artificial rocky shores are more than 100 years old and inhabited by a complex biocoenoses comparable to natural hardsubstrates (ERNST et al. 1993). The results presented here are part of the PhD theses of the authors, which dealt with the mite community of artificial rocky shores of northern German estuaries. Estuaries are to be defined as an inlet of the sea reaching into a river valley as far as the upper limit of tidal rise (FAIRBRIDGE 1980) and are characterised by daily and seasonal high fluctuations of salinity, severe water currents and sediment transport, all due to the tidal inflow of sea water and the outflow of fresh water. Decreasing salinity and an increasing mud-sedimentation rate further upstream cause a diminution in diversity and abundance of most littoral mites (ERNST 1996; SIEMER 1996a).

The aim of the present paper is to contribute to our understanding of life cycle strategies of Acari in extreme habitats. For this purpose rocky shores are an ideal platform. On one hand this unique biotope was settled convergently by mites of nearly all orders (e.g. Mesostigmata, Astigmata, Oribatida, Prostigmata/Endeostigmata) of terrestrial or marine origin. On the other hand the rocky surface with its thin algae or lichen vegetation allows us to directly observe many species without destructive sampling techniques. Compared to the dynamic extraction in Berlese funnels used for soil microarthropods, the efficiency of the scraping technique described below is very high, especially for slow moving surface inhabitants like Hyadesiidae and Halacaridae. The advantage of artificial hardsubstrates for population studies is their homogenous surface structure and uniform vegetation, both leading to low variability in abundance within a given zone and clear zonation patterns.

The present investigation focuses on the phytophagous species, which attain extremely high abundance within the green algae zone of the upper eulittoral and the supralittoral liehen zone. Within the relatively simple food web of the rocky shore, they have a transient position between marine vegetation and predatory Acari of terrestrial origin (e.g. Erythraeidae, Bdellidae). Corresponding to their different taxonomic origin, they display a wide range of survival strategies regarding life cycle, reproductive modes and retreatment behaviour.

Data on phenology and abundance can be used in future investigations to estimate the influence of algophagous or lichenophagous mites on (I) the biomass and diversity of the marine vegetation caused by herbivory and spreading of sporelings and (II) the interdependencies with predatory mites.

Materials and methods

The sampling sites described below are located in the Weser estuary in northern Germany (Fig. 1a).

Brinkamahof II, the remains of a former fortress build in 1879, is located on the right side of the middle Weser estuary adjacent to the fairway near Weddewarden/Bremerhaven (Weddewarden, Fig. 1b). The part of the heterogeneous rocky shore used for sampling consists of weathered blocks of sandstone, extending from the level of mean low water up to 3 m above mean high water (MHW).

Langlütjen I, also the remains of a former fortress built in 1870, extends as a peninsula into the estuarine wadden sea near Nordenham. The circular rocky shore (Langlütjen-A, Fig. 1d), extending from mean sea level up to 2 m above MHW, is made of sandstone cubes fixed by cast concrete. The island is connected to the mainland by a small dam (Langlütjen-B), built of uniform concrete flags.

The salinity varies between 5-25 PSU (Practical Salinity Unit) at Weddewarden and 9-19 PSU at Langlütjen, both mesohaline localities with an annual mean of 13 PSU (ARGE Weser 1991-1994). Further sampling sites at the ferry landing places at Dedesdorf (oligo-/mesohaline, 2.0-7.4 PSU) and Sandstedt (oligohaline, 0.6 - 1.3 PSU) consist of basalt stones. From 1991 to 1994, the annual mean of tidal rise in the middle Weser estuary varied between 3.6 and 3.8 m with a MHW of 1.8 m and a MHWS (mean high water of spring tides) of 2.0 m above ordnance datum (Wasser- und Schiffahrtsamt Bremerhaven 1991-1994).

Sampling was carried out at following littoral levels (see Fig. 1b-d):

Mid eulittoral (*Fucus* zone): 1.6 m below MHW, submerged for approx. 5 h at mean high tide (MHT), with a predominating growth of *Fucus vesiculosus* L. and *Enteromorpha intestinalis* (L.) LINK. Samples were exclusively taken on areas covered with *Enteromorpha*. At Langlütjen, the *Fucus* growth varies during the seasons, often reduced to a sparse and patchy cover.

Upper eulittoral (*Enteromorpha* zone): 0.4 m below MHW, submerged for 2½ h at MHT, with a dense cover of *Enteromorpha* spp. and few filamentous green algae (e.g. *Ulothrix* sp.).

Uppermost eulittoral (*Blidingia* zone): at MHW with a thin cover of *Blidingia* spp. and few patches grown with cyanophytes. At Weddewarden *Blidingia* is accompanied by tufts of *Rhizoclonium riparium* (ROTH) HARV.

Littoral fringe (Black zone): 0.4 m above MHW, overgrown with a thin crust of different coccal and filamentous cyanophytes. At Sandstedt at this level, lichens and mosses already occur.

Supralittoral (Orange lichen zone): 0.8 m above MHW, grown with *Caloplaca* spp., *Xanthoria parietina* (L.) TH. FR., *Lecanora* spp. as well as other lichens.

The sample design was chosen with respect to the specific distribution pattern of the species concerned (ERNST et al. 1993). Within the eulittoral zone, *Ameronothrus marinus* (BANKS), *A. lineatus* (THORELL), *Hyadesia fusca* (LOHMANN) and Halacaridae were obtained by scraping off algal cover and uppermost sandstone layer (25 cm^2) by means of stencil and knife. The samples were transferred cooled to the laboratory, washed through a 63 µm test sieve and investigated for species composition and abundance. Percental instar distribution was determined for collected samples, or, in case of high abundance, by taking a random subsample (≥ 250 ind.). The two nymphal instars of *H. fusca* can not be macroscopically differentiated and are counted together. Dry weight of green algae was determined after thorough cleaning and dehydration at 60°C or 105°C.

Ameronothrids forming linear aggregations at the border of crevices in the littoral fringe (*A. marinus*, *A. lineatus*) were counted at each sample date along three marked crevice fringes, each 5 cm long. Instar distributions were determined from separate samples (n = 21-163 ind.), scraped off from adjacent crevices.

Considering the low sample size (n = 3-5 per height), mean population density is expressed as median with the interquartile range showing the variability. Instar density was calculated using median of abundance and percental instar distribution obtained from the pooled subsample.

In the supralittoral zone, population density of *A. maculatus* (MICHAEL) was directly observed on a single 25 cm^2 area. The instar distribution was determined from a separate sample (n = 26-82 ind.) scraped off in the vicinity of the observation area.

Nanorchestes amphibius TOPSENT & TROUESSART (Nanorchestidae, Pachygnathoidea) spend most of their life in crevices, but are temporarily active on moist surfaces.

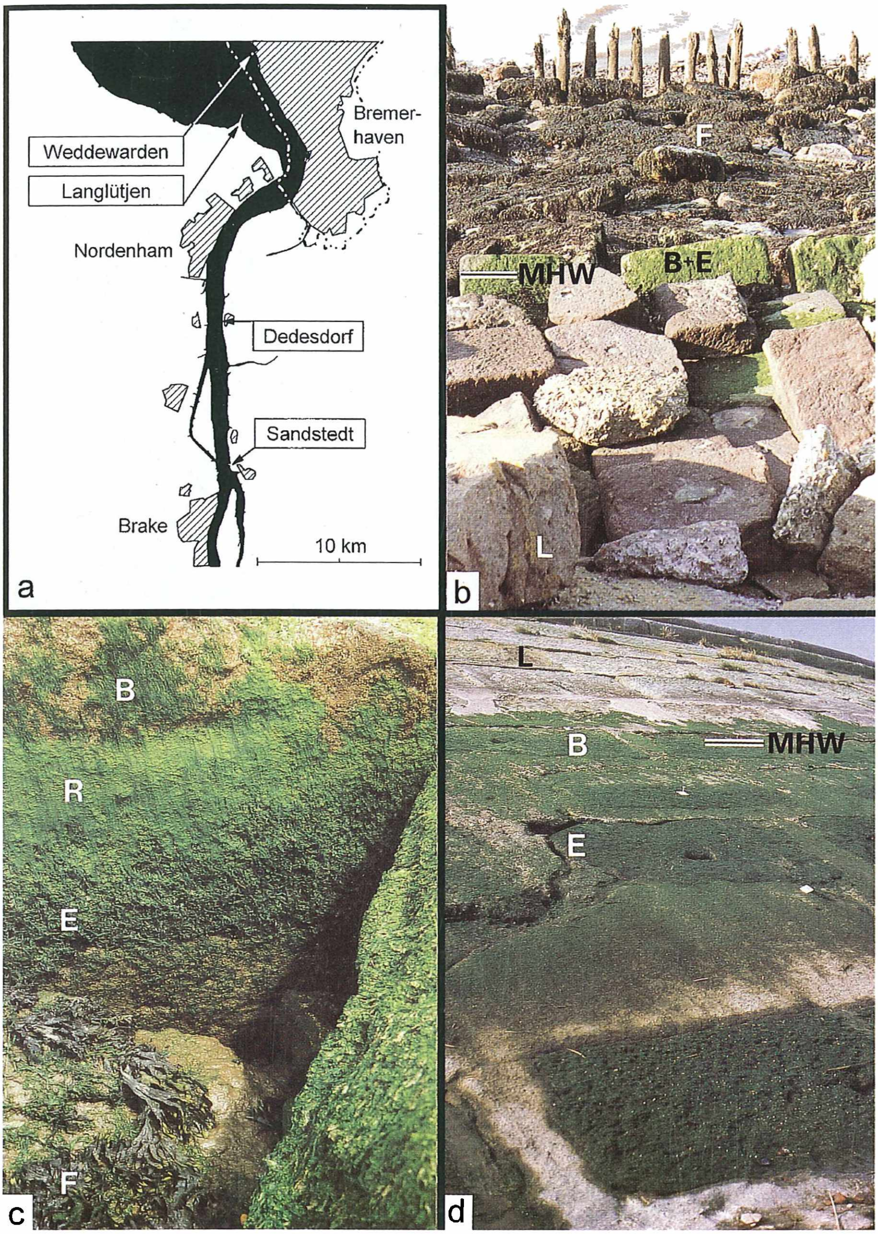

Fig. 1: Sample sites at the estuary of the Weser (northern Germany). a) Map, b) Littoral of the fortress Brinkamahof II (Weddewarden), c) Algae zonation on sandstone at Weddewarden, d) Bank reinforcement of Langlütjen I near Nordenham (Langlütjen-A) B = *Blidingia minima*, E = *Enteromorpha intestinalis*, F = *Fucus vesiculosus*, L = lichens, MHW = level of Mean High Water, R = *Rhizoclonium riparium*.

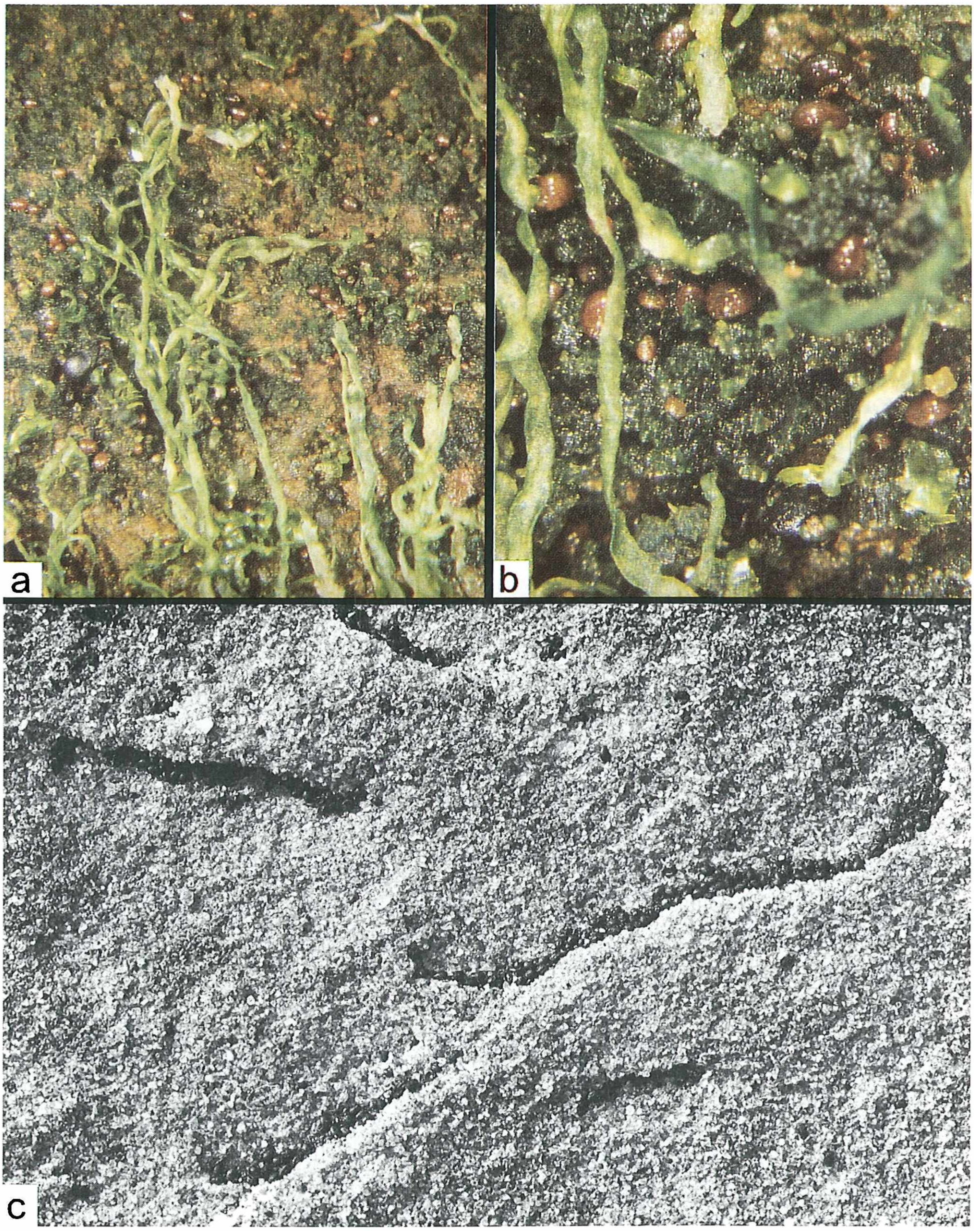

Fig. 2: Retreatment sites of littoral mites. a) Different instars of *Hyadesia fusca* on sandstone, surface covered with cyanophytes and *Blidingia minima*, b) Detail of a., c) Aggregation of *Ameronothrus marinus* along crevice fringes in the littoral fringe at Langlütjen-A.

The relative abundance at Langlütjen-A was estimated by single counts of active mites on marked surfaces (25 cm²) two, four and six hours after high tide at all littoral levels.

In order to proof further the hypothesis of spring migrations of *A. marinus*, a capture-recapture experiment was carried out. In the lower littoral fringe (20 cm above MHW) 900 individuals along one crevice fringe were labelled by painting the notogaster with red bee colour. Twenty-four and 48 h later, labelled mites were counted without removal at this crevice fringe, as well as below and above in steps of 7 cm broad bands (= 5 cm difference in altitude).

Determination was carried out according to SCHUBART (1971) for Ameronothridae, FAIN (1981) for Hyadesiidae, THOR & WILLMANN (1941) for Nanorchestidae and GREEN & MACQUITTY (1987) for Halacaridae.

Results

All studied phytophagous mites were active only on wet or moist surfaces and showed a distinct retreatment under dry conditions and, with the exception of Halacaridae, during submersion. The mesophytic Halacarids retreated to the base of the algae and into small cavities of the surface. *H. fusca* was also found in microcavities and at crevice fringes, forming small aggregations of up to 30 individuals, most of them with the anterior end directed downwards (Fig. 2a). In many cases, the larvae and young nymphs were found in the centres of such patches. *A. marinus* and *A. lineatus* aggregated at crevice fringes and other depressions of the surface (Fig. 2b), whereas *A. maculatus* was found hidden under lobes of foliose lichens. In all surface inhabiting species, preecdysial resting stages were also found hidden at the retreatment sites concerned. In few cases, ecdysial larvae and protonymphs of *H. fusca* occured within the hollow thalli of *Enteromorpha* sp. *N. amphibius* left the protecting crevices only for short periods after high tide. If disturbed, the mites were able to jump covering distances of up to 5 cm. Especially in the outer region of opened crevices, egg clutches and aggregations of all instars (mobile and in ecdysis) were found.

Hyadesia fusca (Astigmata, Hemisarcoptoidea, Hyadesiidae)

The seasonal development of abundance and instar distribution of *H. fusca* populations in the *Blidingia* zone at MHW were studied at three locations in the middle Weser estuary covering four sampling periods between 1991 and 1994 (Fig. 3-6).

During all sampling periods, the course of population growth between spring and autumn was correlated to the seasonal variation of algal biomass. Between 1991 and 1993 the increase in algal biomass of the uppermost eulittoral in spring was followed one month later by an increase in abundance of *H. fusca*; the decline of algal biomass in summer coincided with a subsequent stagnation (Fig. 3a) or depression (Fig. 4a, 5a) in abundance. A recovery of algal vegetation in August/September was followed by a second, either higher (Weddewarden) or lower (Langlütjen) peak in abundance. By contrast, at Langlütjen-B between July 1993 and August 1994 the course of algal biomass and abundance (Fig. 6a) was largely synchronous with only one annual peak (August 1993, June 1994).

During winter population density was low, although algal biomass rose again in November or December. Nevertheless, at Weddewarden the comparatively thick algal cover in winter 1991/92 coincided with the highest winter abundance of all sampling periods.

The seasonal variation of instar distribution and density (Fig. 3-6b, Tab. 1) revealed some interesting similarities and differences between sample periods and populations. At Weddewarden all instars were found throughout the year, while at Langlütjen no larvae were present at some of the sample dates between November and February. In all cases, the predominating hibernating instars were nymphs, most of them with a length between 360 and 420 µm – typical for tritonymphs. With rising temperatures in May the density of adults increased, followed by an increase in larvae and later in nymphs number (Tab. 1). Generally the first peak in population density was characterised by a high portion of larvae. At Weddewarden a second sequence of predomination in adults, larvae and nymphs occurred. In all other populations the instar distribution was less variable with a permanent high portion of nymphs. At Langlütjen (A and B) in 1992 the second lower peak in abundance was the result of a synchronous increase in density of all instars. Also in 1993 at Langlütjen-B all instars contributed to the increase in abundance in summer. In contrast to Weddewarden in 1991, the high adult density in August was not followed by a subsequent increase in larvae number (Tab. 1).

However, focusing on the percental instar distribution, in 1994 (Fig. 6b) the expected sequence of increases in the proportion of adults, larvae and nymphs was found.

Date	La	Ny	Ad	Date	La	Ny	Ad
Weddewarden				Langlütjen-A			
22.01.91	7	43	11	09.04.92	2	57	41
11.03.91	3	48	6	06.05.92	18	47	173
07.05.91	16	58	171	09.06.92	474	307	170
13.06.91	449	122	180	06.07.92	189	319	93
11.07.91	211	309	98	05.08.92	92	237	19
08.08.91	321	188	282	03.09.92	15	184	21
13.09.91	1267	618	282	08.10.92	64	344	74
20.10.91	31	215	28	09.11.92	4	108	38
18.12.91	66	444	52	02.12.92	0	23	2
07.02.92	17	211	23	13.01.93	1	24	2
				02.02.93	0	26	6
				03.03.93	1	17	4
				01.04.93	21	55	19
Langlütjen-B				Langlütjen-B			
09.04.92	14	95	202	12.07.93	54	155	41
06.05.92	31	12	327	11.08.93	280	339	252
09.06.92	275	208	253	05.09.93	45	93	185
06.07.92	140	1060	150	11.10.93	12	68	21
05.08.92	74	526	53	22.12.93	0	3	0
03.09.92	12	60	16	16.02.94	0	1	0
08.10.92	29	156	32	10.04.94	1	7	4
09.11.92	0	37	2	10.05.94	46	98	100
02.12.92	0	26	6	17.06.94	137	121	144
13.01.93	1	4	1	11.08.94	14	63	38
02.02.93	1	31	5				
03.03.93	2	15	15				

Table 1: *Hyadesia fusca*. Seasonal variation of instar density (ind./25cm^2) on *Blidingia* covered surfaces in the uppermost eulittoral. La = larvae, Ny = protonymphs + tritonymphs, Ad = adults.

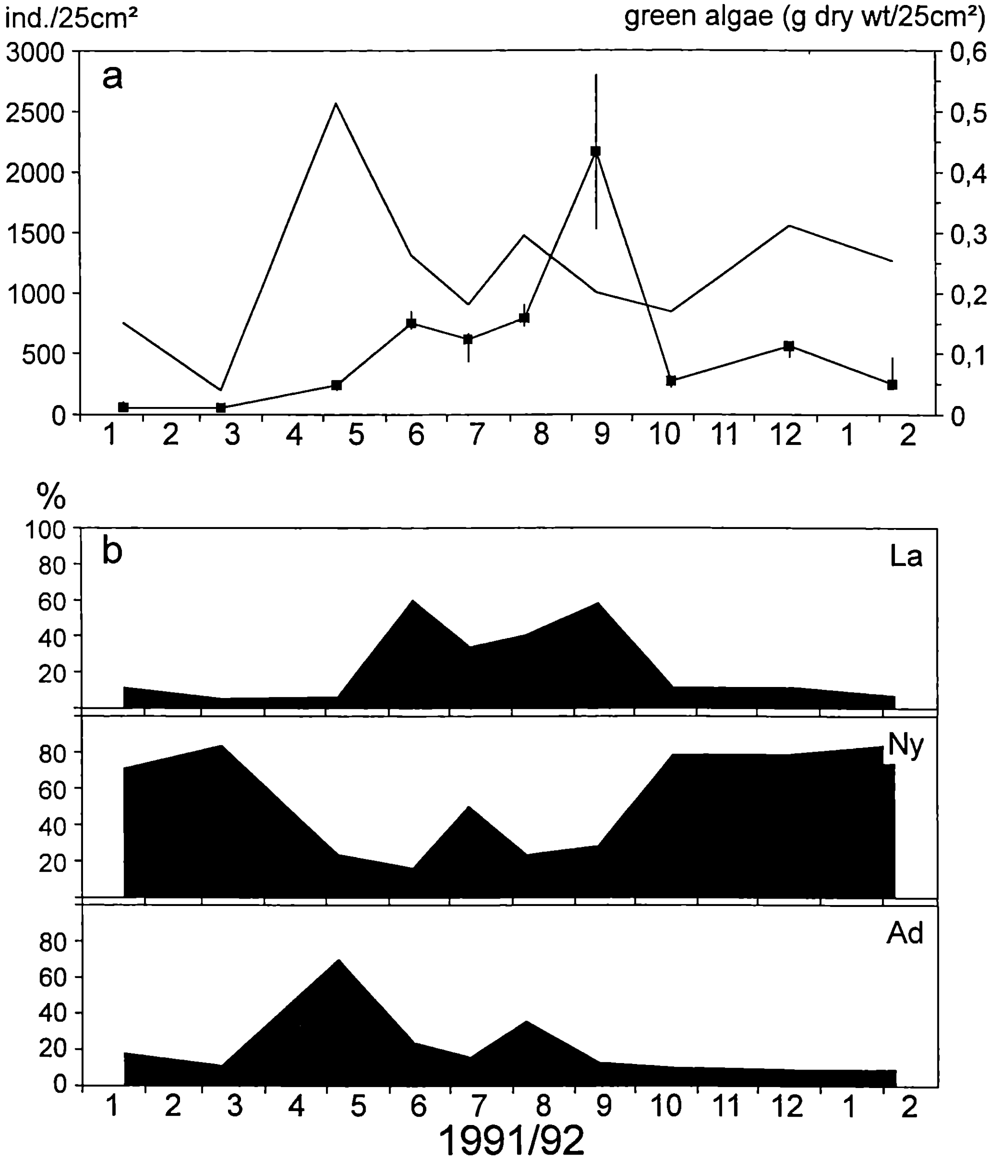

Fig 3: Population dynamics of *Hyadesia fusca* in the *Blidingia* zone at Weddewarden. a) Seasonal development of population density and algal biomass (median and interquartile range, n = 3), b) Development of percentage instar distribution.

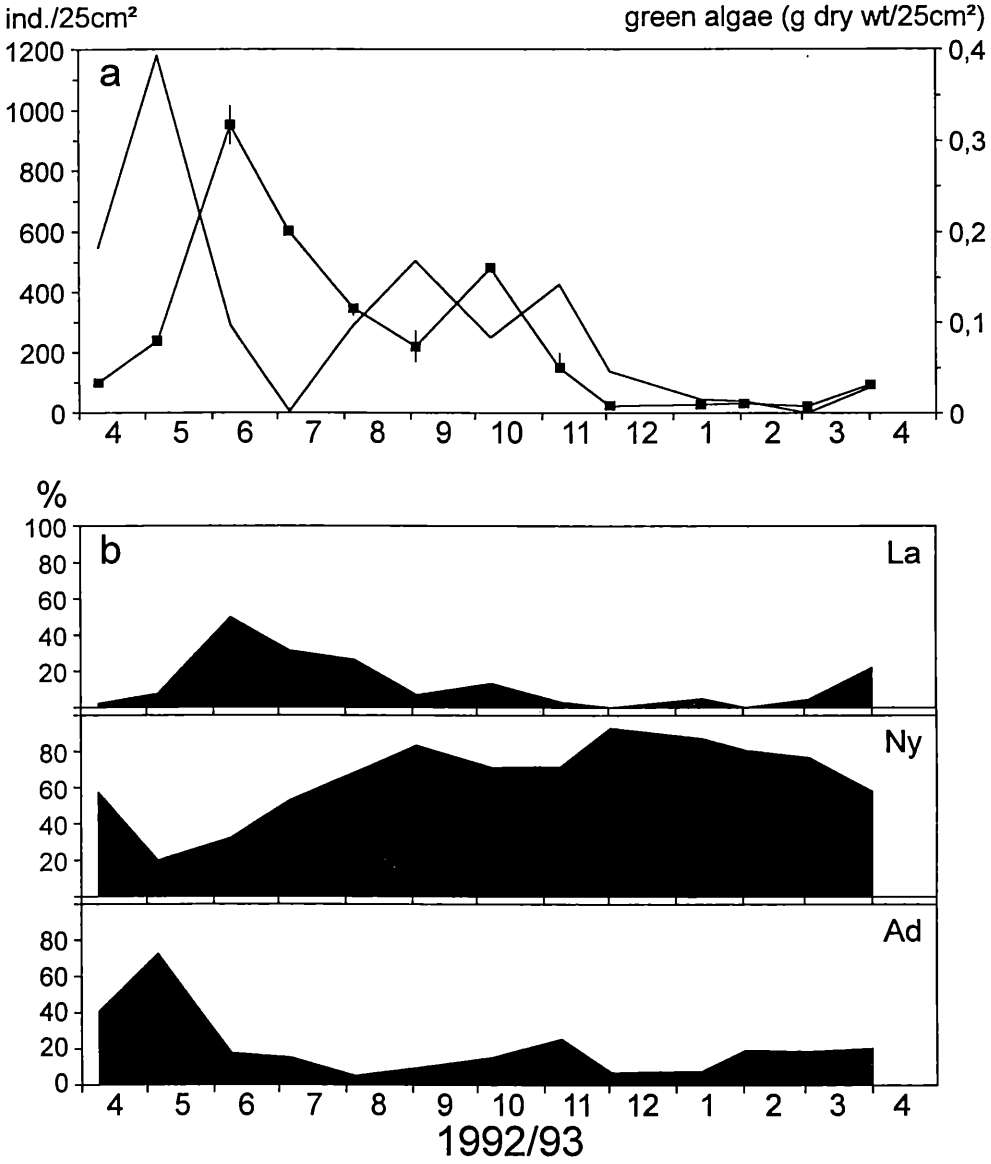

Fig 4: Population dynamics of *Hyadesia fusca* in the *Blidingia* zone at Langlütjen-A. a) Seasonal development of population density and algal biomass (median and interquartile range, n = 4), b) Development of percentage instar distribution.

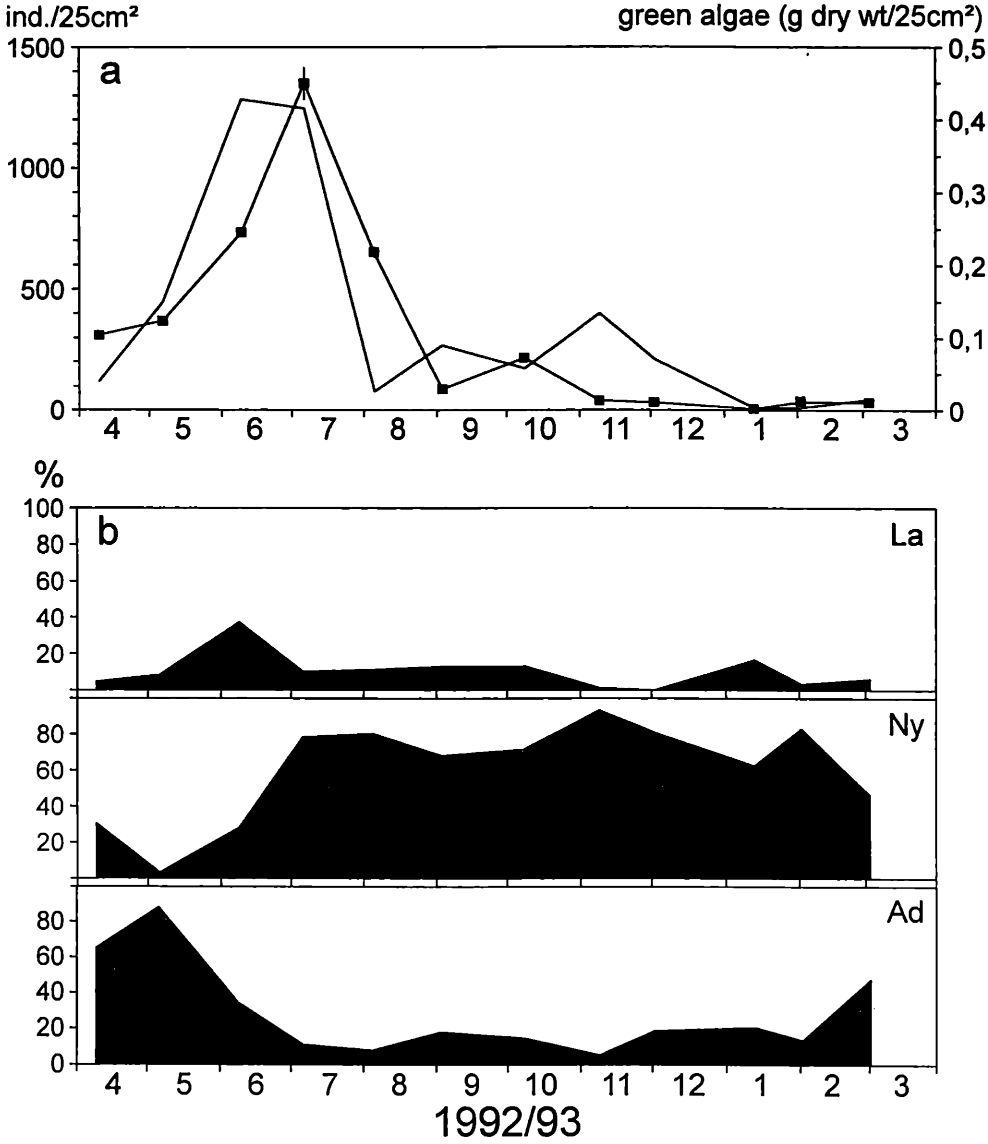

Fig 5: Population dynamics of *Hyadesia fusca* in the *Blidingia* zone at Langlütjen-B (1992/93). a) Seasonal development of population density and algal biomass (median and interquartile range, n = 4), b) Development of percentage instar distribution.

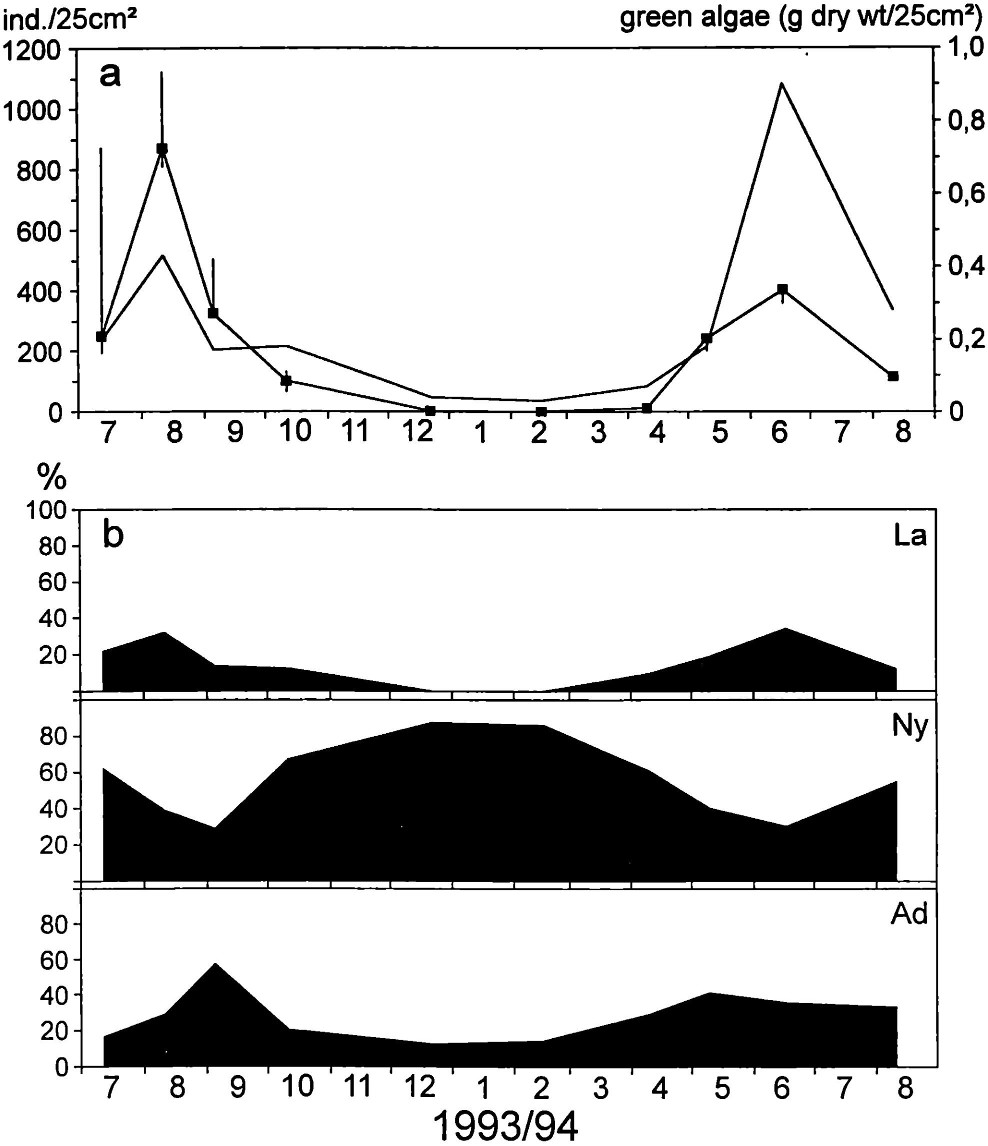

Fig 6: Population dynamics of *Hyadesia fusca* in the *Blidingia* zone at Langlütjen-B (1993/94). a) Seasonal development of population density and algal biomass (median and interquartile range, n = 5), b) Development of percentage instar distribution.

The comparison of the population dynamics in different littoral zones of Langlütjen-A revealed, that a retardation of population growth in lower zones occurred (Fig. 7). The increase in density in the *Blidingia*, *Enteromorpha* and *Fucus* zone started in May, June and July, with the maximum in June, July and August respectively. As described above, the abundance in the *Blidingia* zone decreased to September and recruited to October, but within the *Enteromorpha* zone it remained on the same high level from July to October. Similar to the *Blidingia* zone, the biomass of green algae in the *Enteromorpha* zone increased to May with a maximum of 0.45 g dry wt/25 cm². In contrast to the littoral zone above, no temporary decline of algal cover occurred. The dry weight very slowly decreased towards winter with a constant rate of approx. 0.4 g/month. In the *Fucus* zone, population density was extremely low with a maximum of only 44 ind./25 cm².

Despite the differences in population density, the seasonal development of instar distribution in the *Enteromorpha* and *Fucus* zone – with a peak of adults in May and one of larvae in June – reflected that described for the *Blidingia* zone.

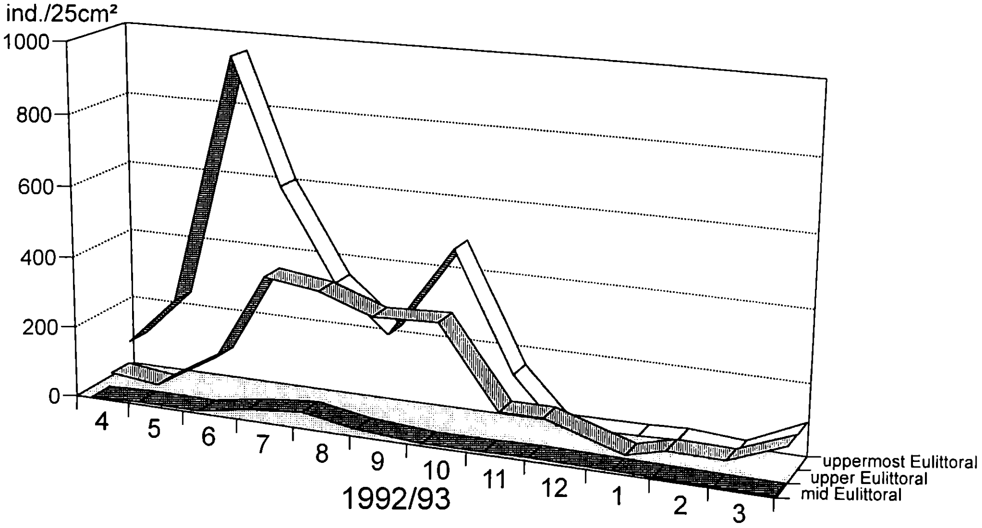

Fig. 7: Seasonal development of population density of *Hyadesia fusca* in different littoral zones at Langlütjen-A.

Ameronothrus marinus (Oribatida, Ameronothridae)

Comparing the abundance of *A. marinus* in the uppermost eulittoral (Fig. 8a) and the littoral fringe (Fig. 9a), a reciprocal pattern of seasonal variation can be seen. Population density within the *Blidingia* zone was high in summer and autumn and low in winter and spring. By contrast, only 40 cm above this level population density was high in winter and spring and low in summer and autumn. Similar to the *Hyadesia* population, abundance of *A. marinus* in the *Blidingia* zone decreased with the temporary decline in algal biomass in August and September (see Fig. 4a).

Focusing on the seasonal development of instar distribution in the *Blidingia* zone (Fig. 8b, Tab. 2) successive increases of the developmental stages, beginning and ending with adults, can be seen from April to October. From October onwards the number of tritonymphs and adults decreased rapidly in the *Blidingia* zone and their density at crevice fringes of the littoral fringe increased simultaneously. In contrast, no larvae and only few protonymphs were present in the littoral fringe.

	Uppermost eulittoral (ind./25cm²)					Littoral fringe (ind./5cm crevice)				
Date	La	Pny	Dny	Tny	Ad	La	Pny	Dny	Tny	Ad
09.04.92	1	1	0	10	47	0	0	0	21	100
06.05.92	8	1	0	2	96	0	0	0	0	61
09.06.92	203	43	1	0	185	0	0	0	0	22
06.07.92	163	90	20	0	120	0	0	0	0	9
05.08.92	115	61	108	0	56	0	3	11	0	1
03.09.92	16	40	49	62	33	0	0	5	13	11
08.10.92	0	3	42	154	160	0	0	15	15	7
09.11.92	1	1	12	45	66	0	1	6	23	50
02.12.92	0	0	3	4	3	0	0	7	65	144
13.01.93	0	1	6	9	5	0	0	24	112	125
02.02.93	1	4	10	18	16	0	0	15	127	132
03.03.93	0	0	6	25	27	0	0	2	42	111
01.04.93	2	4	2	26	47	0	0	1	24	103

Table 2: *Ameronothrus marinus*. Seasonal variation of instar density at Langlütjen-A on *Blidingia* covered surfaces of the uppermost eulittoral and along crevice fringes in the littoral fringe. La = larvae, Pny = protonymphs, Dny = deutonymphs, Tny = tritonymphs, Ad = adults.

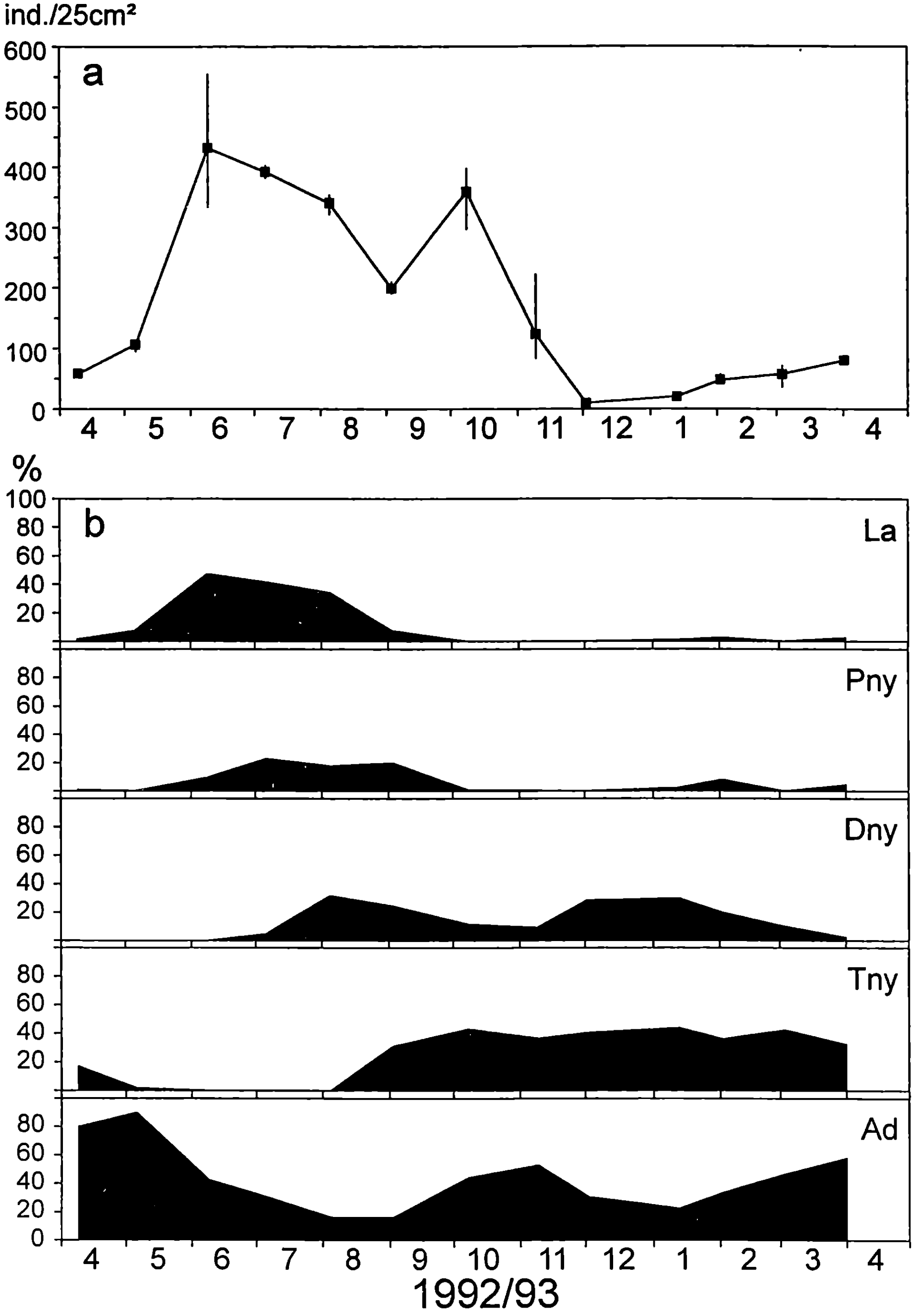

Fig. 8: Population dynamics of *Ameronothrus marinus* in the *Blidingia* zone at Langlütjen-A. a) Seasonal development of population density (median and interquartile range, n = 4), algal biomass see Fig. 4a, b) Development of percentage instar distribution.

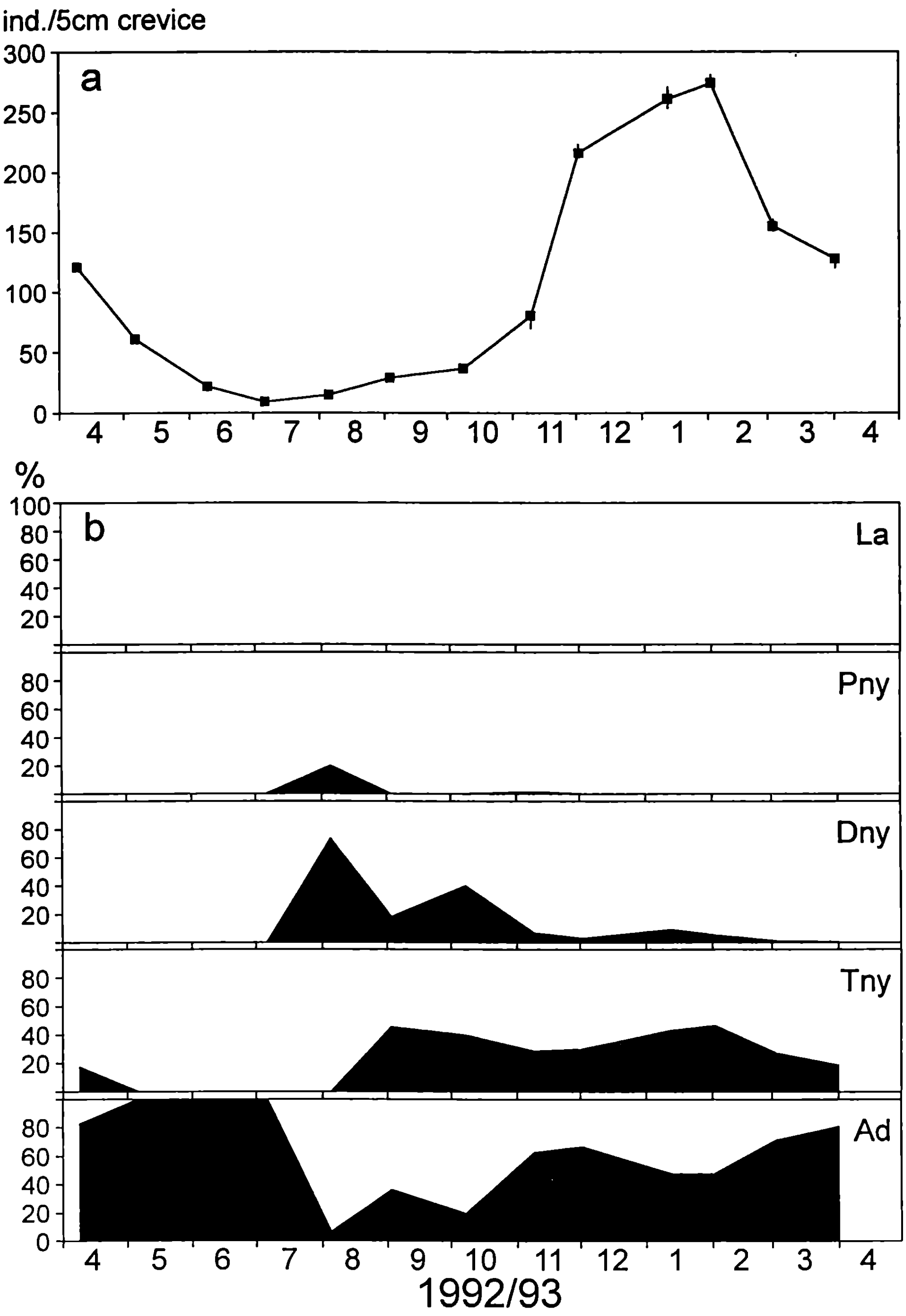

Fig. 9: Population dynamics of *Ameronothrus marinus* in the littoral fringe at Langlütjen-A. a) Seasonal development of population density (median and interquartile range, n = 4), b) Development of percentage instar distribution.

A successive increase of deutonymph, tritonymph and adult density was found here from spring to autumn, although in very low abundance (Fig. 9b). At both littoral levels, tritonymphs and adults constituted the predominant hibernating instars.

Population density below MHW was generally very low with a maximum of 68 ind./25 cm² (October) in the *Enteromorpha* zone and only 9 ind./25 cm² (August) in the *Fucus* zone (Fig. 10). Comparable to the *Hyadesia* population, there was no depression of abundance in summer but a similar development of instar distribution as in the *Blidingia* zone was found.

Fig. 11 shows the result of the labelling experiment. Along one crevice fringe in the lower littoral fringe – just above the *Blidingia* cover – 900 individuals of *A. marinus* were marked. After 48 hours, only 13 % of all marked mites found again were located above, 46 % still along and 41 % below the crevice between eulittoral green algae. 43 of the mites originally labelled were not found again. The covered distance was maximal 21 cm above and 63 cm below the crevice. Longer observation periods would have been desirable, but failed due to the progressive loss of paint. The trend of downward directed migrations in April coincided with the spring increase of abundance in the *Blidingia* zone (Fig. 8a).

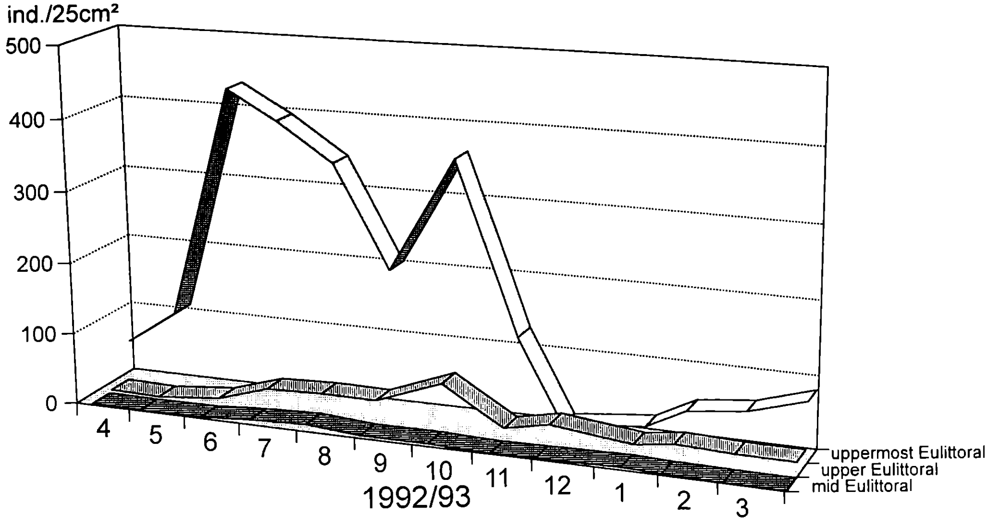

Fig. 10: Seasonal development of population density of *Ameronothrus marinus* in different littoral zones at Langlütjen-A.

Ameronothrus lineatus

The population density of *A. lineatus* in the *Blidingia* zone of Sandstedt was low from November to May, increased rapidly from June to July and remained high up to October, followed by a sudden decrease (Fig. 12a). Compared to *A. marinus*, the annual maximum of abundance was low with 59 ind./25 cm². The seasonal change of abundance in the littoral fringe was comparatively slow but also reciprocal to the *Blidingia* zone, oscillating between a maximum in winter and a minimum in summer (Fig. 13a).

From April to May the portion of tritonymphs in the littoral fringe declined as rapidly as the number of adults raised. Simultaneously with decreasing adult density from June to September, their number increased within the *Blidingia* zone (Tab. 3). During the period of high abundance in this zone, a sequence of increasing density of larvae (July), protonymphs (September) and deutonymphs (October) was found (Fig. 12b).

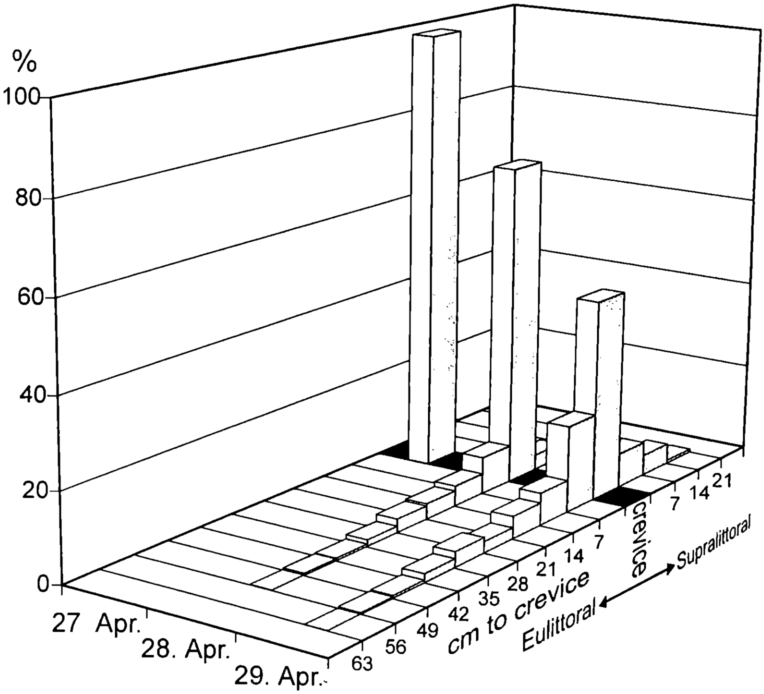

Fig. 11: Vertical distribution of *Ameronothrus marinus* nymphs and adults, initially located and labelled along one crevice fringe in the lower littoral fringe at Langlütjen-A (April 1993, n = 900).

	Uppermost eulittoral (ind./25cm²)					Littoral fringe (ind./5cm crevice)				
Date	La	Pny	Dny	Tny	Ad	La	Pny	Dny	Tny	Ad
07.04.92	0	0	0	0	1	0	0	0	89	40
05.05.92	0	0	0	0	1	0	0	0	4	103
02.06.92	0	0	0	0	2	0	0	0	0	120
09.07.92	24	2	0	0	33	0	2	4	0	64
17.08.92	17	2	2	0	28	3	2	1	0	20
09.09.92	18	22	0	0	16	2	10	48	2	0
01.10.92	3	21	16	0	19	0	9	46	3	3
01.11.92	0	0	0	4	3	4	4	21	71	0
15.12.92	0	0	1	2	2	0	3	24	105	18
04.01.93	0	2	2	0	0	3	6	24	106	41
03.02.93	0	3	3	3	0	6	17	68	193	17
19.03.93	0	0	0	1	1	7	3	14	91	16

Table 3: *Ameronothrus lineatus*. Seasonal variation of instar density at Sandstedt on *Blidingia* covered surfaces of the uppermost eulittoral and along crevice fringes in the littoral fringe. Abbreviations see Tab. 2.

In the littoral fringe the number of deutonymphs increased already in September, followed by tritonymphs in November (Fig. 13b). Only few new adults appeared as early as December, so that the population hibernated predominantly as tritonymphs. However, even in winter all instars were present.

Ameronothrus maculatus

The population density of *A. maculatus*, observed on a single area in the supralittoral zone, showed moderate fluctuations with low values from August to November (Fig. 14a).

The seasonal development of instar distribution (Fig. 14b) was characterised by a clear sequence of appearances and peaks of all instars. From April to June the number of tritonymphs decreased whereas the adult density rose. The larvae appeared first in June with a maximum proportion in August; proto- and deutonymphs followed in September with a peak in October and November respectively. The tritonymphs appeared first in November and constituted the dominant hibernating instar from December to March. In January/February the adults of 1992 disappeared, the population hibernated exclusively as deuto- and tritonymphs and first new adults were found in March 1993.

The seemingly low density from August to September coincided with the appearance of larvae and young nymphs. As these instars prefer hidden places below the lobes of foliose lichens and were therefore difficult to observe, abundance in summer was most probably underrated.

Metarhombognathus armatus (Prostigmata, Halacaridae)

The population growth of *Metarhombognathus armatus* (LOHMANN), investigated in the upper eulittoral of Weddewarden, was subject to high fluctuations with very low densities from November to March (60-114 ind./25 cm^2) followed by a steep increase to a maximum of 954 ind./25 cm^2 in May (Fig. 15a). In summer the population returned to a permanently low density of 187-322 ind./25 cm. The increase of population density was preceded by rise of algal biomass in spring, the subsequent decrease of abundance coincided with the decline of the algae.

As in *A. maculatus*, each of the successive instars occurred exclusively within a distinct period (Fig. 15b). The plateau of low abundance in winter and early spring coincided with a high proportion of adults (100% in January), the spring peak was characterised by subsequent increases in density of larvae and protonymphs and the second plateau in summer/autumn showed a predomination of deutonymphs (100% in August and September). The deutonymph was the sole aestivating instar, whereas the population hibernated exclusively as adults. Eggs and larvae were found as early as January, the last eggs in May and the last larvae in June.

Isobactrus uniscutatus (Prostigmata, Halacaridae)

At Dedesdorf the population of *Isobactrus uniscutatus* (VIETS) displayed a cycle of increasing and decreasing density. A single peak in summer (2604 ind./25 cm^2 in August) was followed by very low abundance in winter (73-124 ind./25 cm^2) (Fig. 16a). In contrast to this putative influence of the seasonal change in temperature, no clear correlation to the development of algal biomass could be seen. All instars were found throughout the year with only indistinct variations in percental distribution (Fig. 16b). However, the lowest density of larvae was found in winter, the highest in summer.

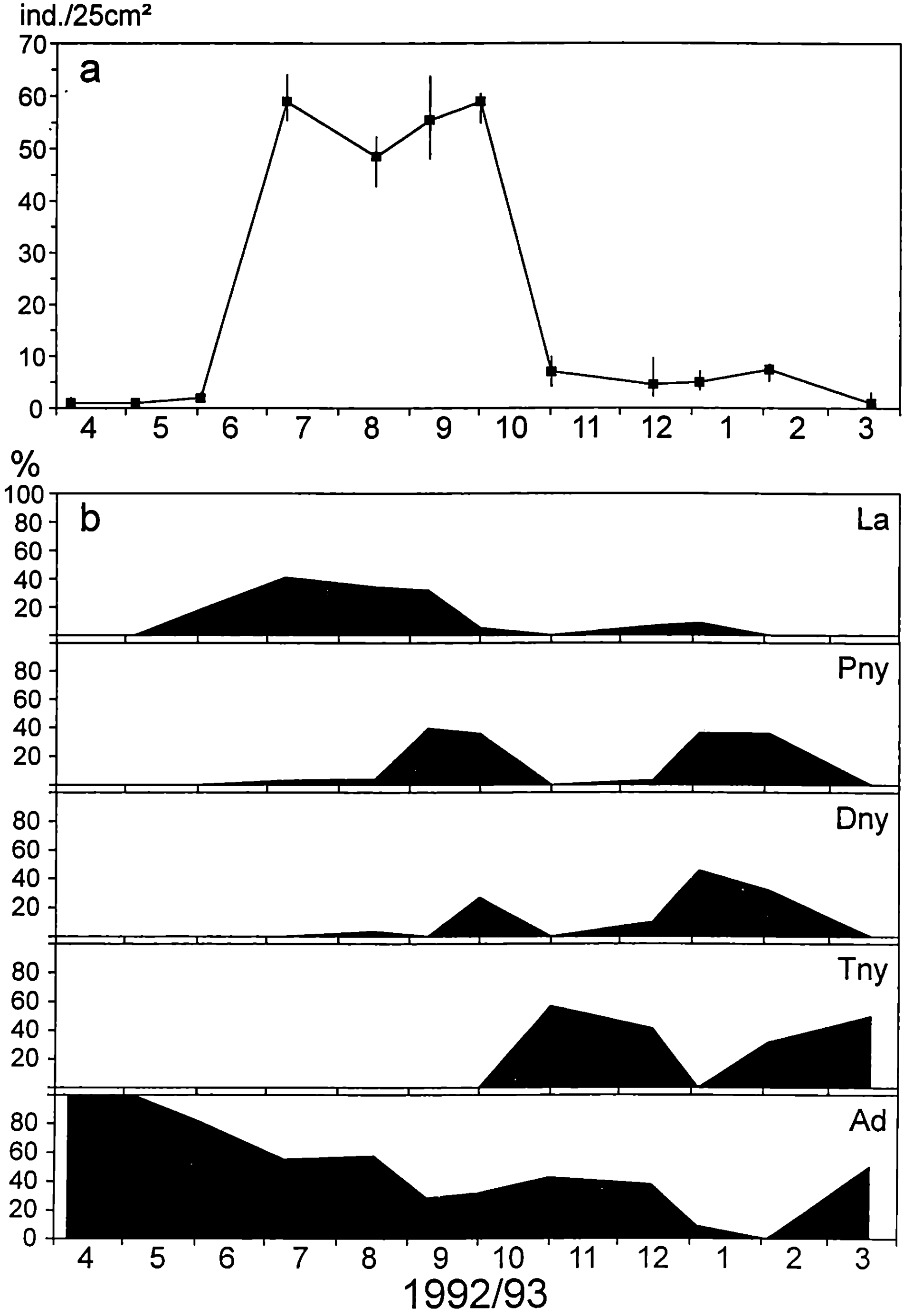

Fig. 12: Population dynamics of *Ameronothrus lineatus* in the *Blidingia* zone at Sandstedt. a) Seasonal development of population density (median and interquartile range, n = 4), b) Development of percentage instar distribution.

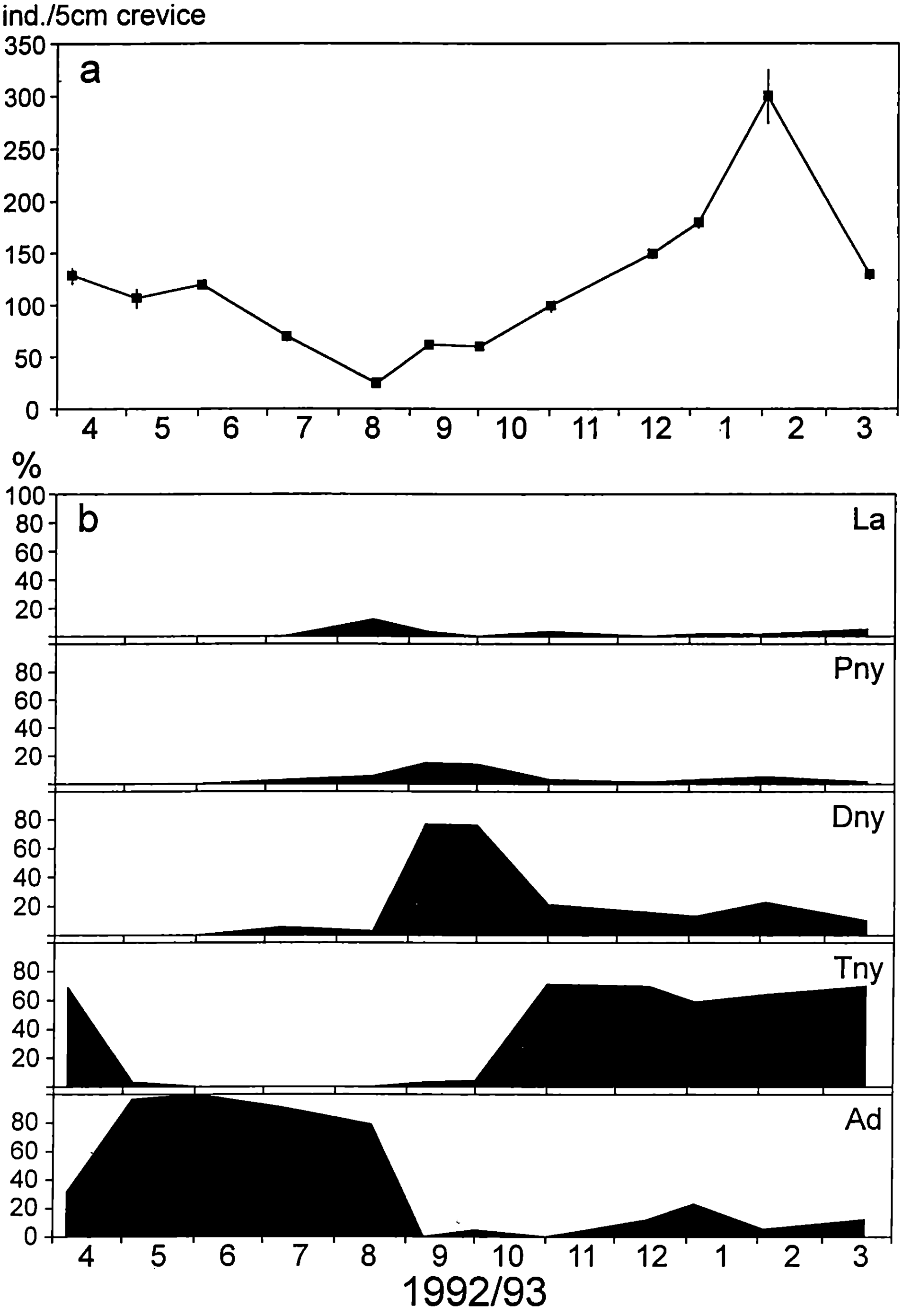

Fig. 13: Population dynamics of *Ameronothrus lineatus* in the littoral fringe at Sandstedt. a) Seasonal development of population density (median and interquartile range, n = 4), b) Development of percentage instar distribution.

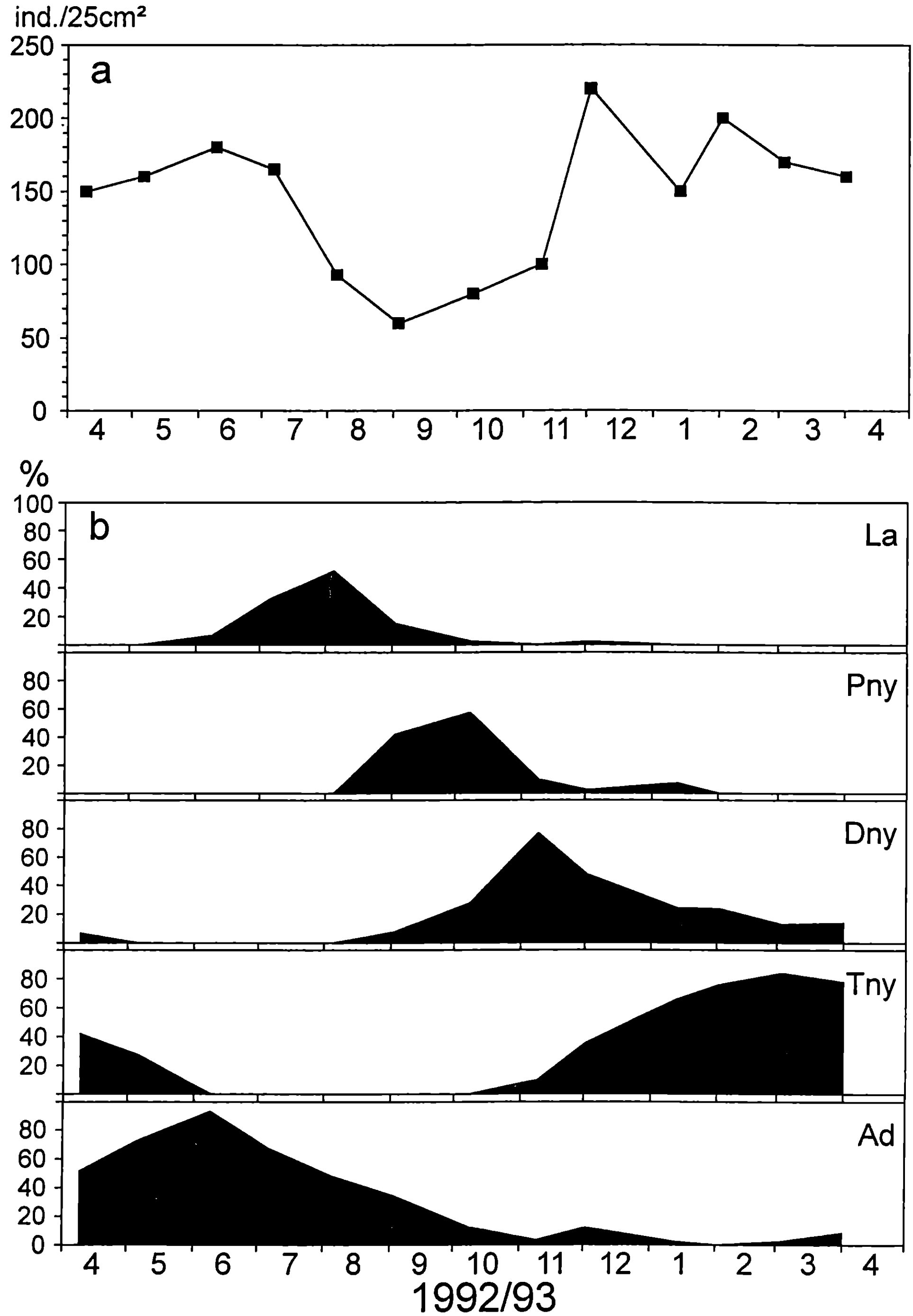

Fig. 14: Population dynamics of *Ameronothrus maculatus* in the supralittoral zone at Langlütjen-A. a) Seasonal development of population density (n = 1), b) Development of percentage instar distribution.

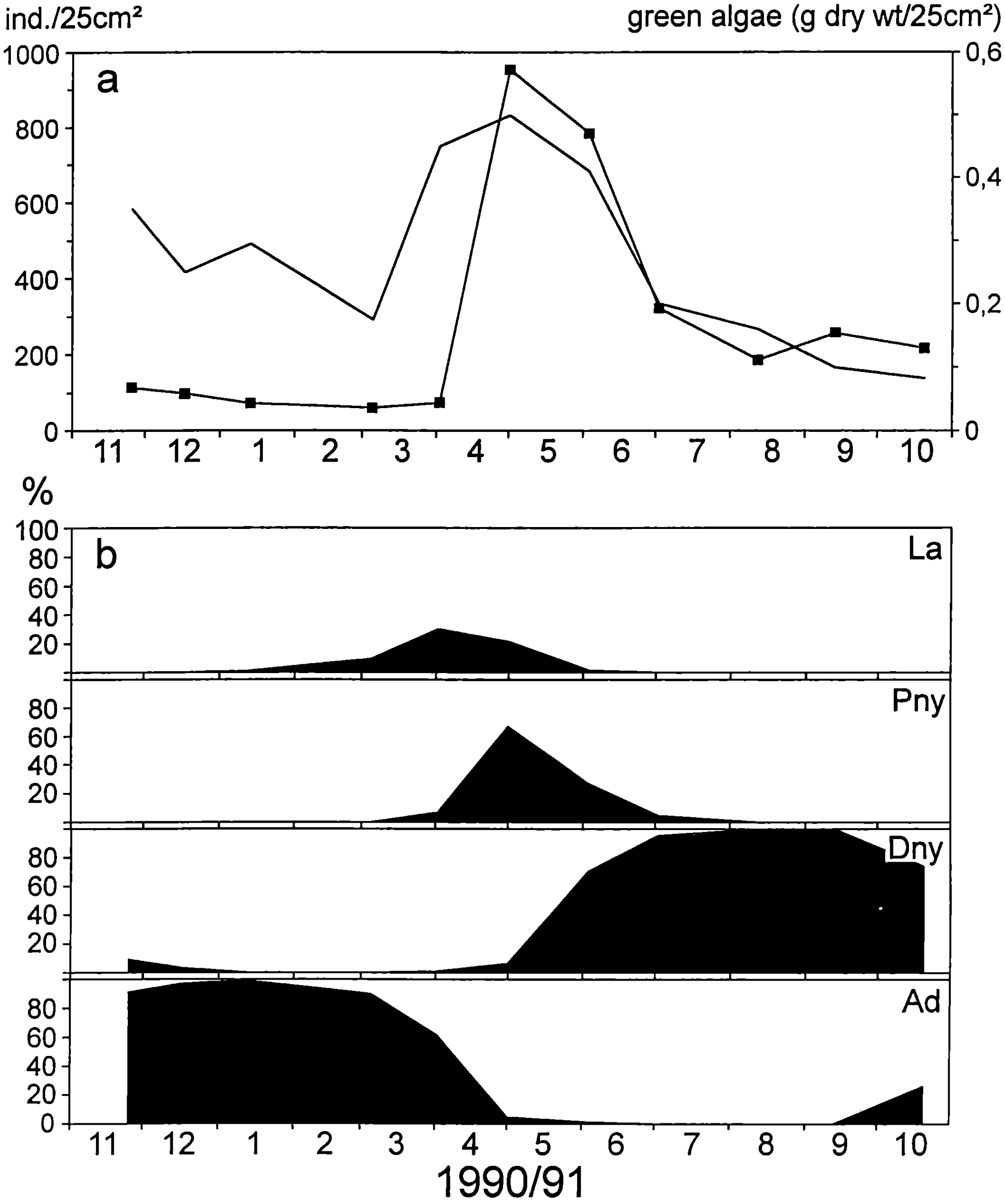

Fig. 15: Population dynamics of *Metarhombognathus armatus* in the *Blidingia* zone at Weddewarden. a) Seasonal development of population density (n = 1), b) Development of percentage instar distribution.

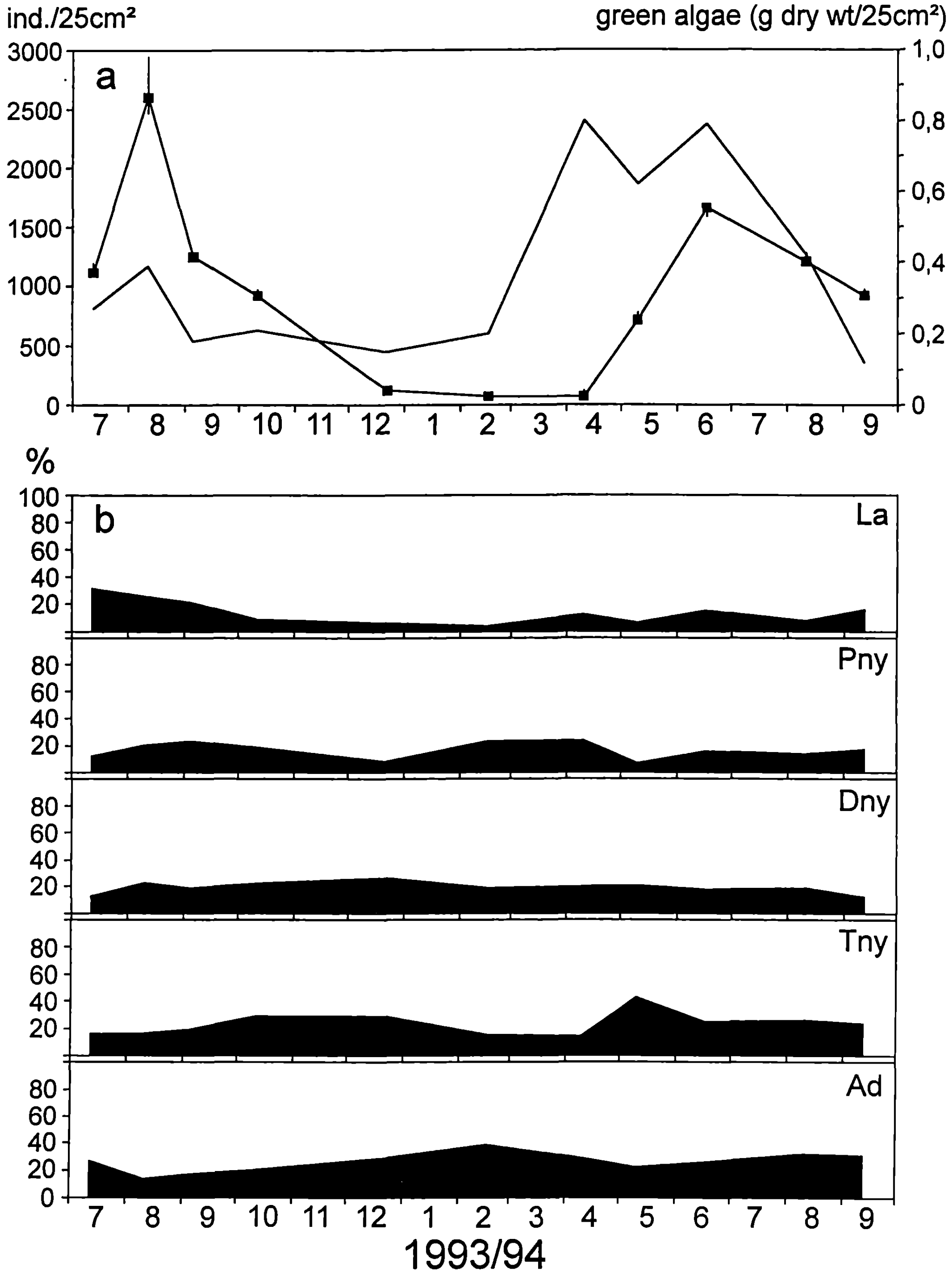

Fig. 16: Population dynamics of *Isobactrus uniscutatus* in the *Blidingia* zone at Dedesdorf. a) Seasonal development of population density (median and interquartile range, n = 3), b) Development of percentage instar distribution.

Nanorchestes amphibius (Endeostigmata, Nanorchestidae)

At each observation date, activity was highest approx. four hours after high tide on the surface located at MHW (Fig. 17). With approx. 100 ind./25 cm² the number of active mites was high from July to October, but showed high fluctuations at the other observation dates. From December to February no active *Nanorchestes* were found below MHW. All instars, even eggs, were present throughout the year, but with varying proportions. Since many individuals stayed within the crevices, we have no valid data on seasonal development of instar distribution. In addition, surface activity of *N. amphibius* is dependent on several parameters such as temperature and surface moisture. Therefore, the presented data should only be seen as a first trend regarding seasonal variation of abundance and zonation of this species.

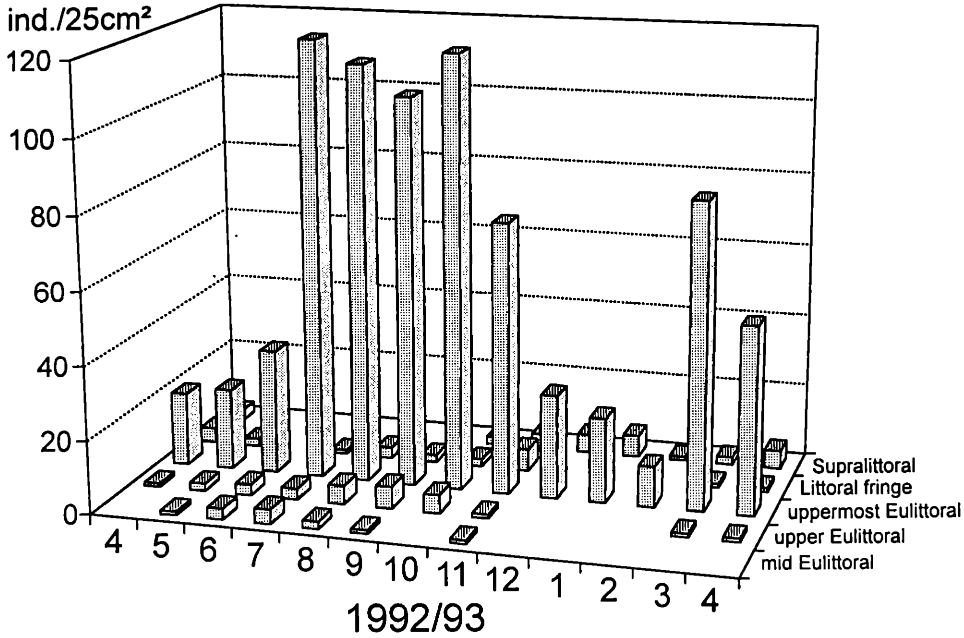

Fig. 17: Number of active individuals of *Nanorchestes amphibius* on marked surfaces in different littoral zones at Langlütjen-A.

Discussion

Influences on instar density and phenology

Appearance and density of instars are influenced by a multifactorial system of sources and sinks (Fig. 18). On one hand there are intrinsic but also environmentally influenced factors like sex ratio, reproductive rate, development time and adult longevity, on the other hand the population is exposed to several extrinsic and possibly instar-specific sources of mortality. Additionally, the population density within a given zone can be highly modified due to seasonal or daily migrations of one or more instars. In case of populations with low synchronisation of development, overlapping generations and long reproductive periods, the life cycle and generation time can not be recognised from phenology.

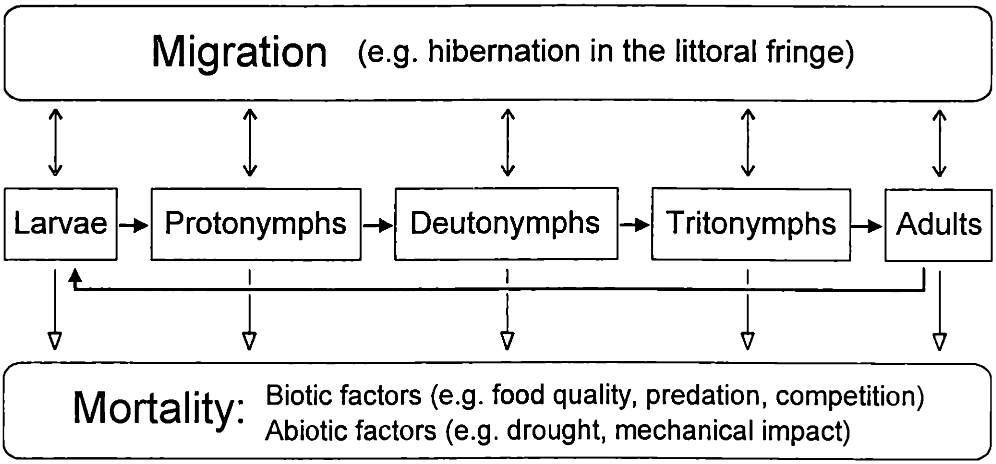

Fig. 18: Influences on instar distribution of a larviparous, littoral mite in the upper eulittoral. Closed arrows = development or reproduction, open arrows = mortality, double arrows = migration between zones.

Well known sources of mortality include drought, freezing and heat, osmotic stress and submersion (SCHULTE 1977; BARTSCH 1974; PUGH & KING 1985a; SØMME & BLOCK 1984). Furthermore, an important factor, especially for phytophagous littoral mites, is probably the loss of biomass of the algal vegetation. The algal cover is functioning as habitat, food source as well as protection against desiccation and dislodgment. During peak seasons of sporulation or severe drought, a high amount of the green algae thalli is torn-off due to waves and water currents (HAASE 1995), possibly together with a part of the epiphytic inhabitants. A retarded decrease in population density subsequent to the decrease in algal biomass (e.g. *H. fusca* and *A. marinus* at Langlütjen-A, June/July 1992) might be, amongst other factors, a result of the same abiotic stress, enhanced by the loss of the protecting algal cover. Thus a coincident decrease of mite abundance and algal biomass could correlate both directly and indirectly. It should be mentioned that in wave-exposed habitats many littoral mites are associated with balanids, which serve as refuge and obviously have the protective function discussed here for the algae (PUGH & KING 1985a).

For rocky shore communities, interspecific competition is often discussed as a further source of mortality or as a structuring force influencing zonation (examples in LITTLE & KITCHING 1996). At Weddewarden a maximum of 160 co-existing phytophagous mites/cm^2 was found in September 1991 (BÜCKING 1995). With regard to the retreatment behaviour described above, the availability of microcavities of the surface might be a limited resource, e.g. during peaks of larvae appearance. Especially in late summer, *H. fusca* and *A. marinus* were often found in dense patches together in the same cavity. However, the putative influence of interspecific competition on population density or zonation has to be shown by the experimental exclusion of one of the competitors.

BÜCKING (1995) assumes for the Weddewarden population of *H. fusca* in 1991 that, when comparing estimated consumption rate and algal biomass, food was unlikely to be a limited resource in the upper green algae zone. Especially in eutrophic estuaries, growth rate and production of the littoral algae vegetation is very high (HAASE 1995). However, the zonation pattern of *H. fusca* and *M. armatus* correlates to the food quality of the algae in the different zones (BÜCKING in press a, in press b; SIEMER in press). The seasonal changes in algal diversity, zonation and structure may have an influence on mortality, reproductive rate and development time, and therefore on population density in a given zone.

Hyadesia fusca

Free-living Astigmata are well known as important pests of stored food, but they are also very abundant in terrestrial habitats like steppe soils (GRIFFITH 1960; GHILAROV & CHERNOV 1975; cited in LUXTON 1981c). Most soil-inhabiting Astigmata are mycophagous, but some also feed on living plants (KRANTZ & LINDQUIST 1979; OCONNOR 1994).

The larviparous species *H. fusca* is a typical intertidal inhabitant of northern European rocky shores, distributed from northern Norway down south to the coast of Brittany (SCHULTE 1977; FAIN & SCHUSTER 1989). The species is euryhaline and can be found on open rock surfaces (KRONBERG 1983), within the algal cover (STRAARUP 1968), associated with balanids (BÉNARD 1961; PUGH & KING 1985a) and meso-/endophytic in permanent rock pools (GANNING 1970). *H. fusca* feeds on various macroalgae, microalgae, cyanophytes and, to a small extent, detritus (BÜCKING in press a).

There are few available literature data on the population dynamics of *H. fusca*. STRAARUP (1968) found large numbers of this species in the *Enteromorpha* belt of boulders located in the Skovshoved Harbour (Baltic Sea, Denmark). Population density, measured as ind. per 50ml algae sample, peaked first in July (1747 ind.) and again in September (2038 ind.). GANNING (1970, 1971) investigated populations living permanently submersed in the *Enteromorpha* tufts of brackish water rockpools near the Askö laboratory in Sweden (Baltic Sea). He described a single peak with 938 ind./0.1g algae dry weight in July 1965. At this time 98% of the population consisted of larvae. KRONBERG (1983) investigated the littoral fringe of artificial rocky shores in the Kieler Förde (Baltic Sea). She also found only one annual peak in summer with a maximum of 170 ind./10 cm^2. At some localities and sampling dates, *H. fusca* formed 70-75% of the living density (GANNING 1971; KRONBERG 1983).

LUXTON (1981c) reviewed data for numbers of all Astigmata per m^2 in the soils of various terrestrial ecosystems, ranging from 70 in arable soil to 50000 in steppe soil. Despite the very narrow horizon available to saxicolous mites, the annual monthly mean of abundance of the *H. fusca* populations here investigated is much higher with a range of 203 to 513 ind./25 cm^2 (= 81200 to 205200 per m^2). In contrast to *Hyadesia*, the population density of Astigmata in most soil habitats was highest in winter and lowest in summer (LUXTON 1981c). However, the Astigmata in littoral saltmarshes also peaked in summer (LUXTON 1967a).

Both GANNING (1970) and KRONBERG (1983) assume a single reproductive period of the Baltic Sea populations with hibernating adults and a first appearance of larvae in June or July. In contrast to that, BÉNARD (1961), who studied *H. fusca* (syn. *H. furcillipes* BÉNARD) at various rocky shores of the Normandy coast (France), found nymphs as sole hibernating instar. First adults and larvae appeared in June. STRAARUP (1968) has not segregated instars but mentioned that individuals of all sizes were present throughout the year. Obviously the population dynamics of *H. fusca* are highly dependent on local conditions. However, at least in the Weser estuary, *H. fusca* occured with all instars throughout the year. Except in March, larvigerous females were found at each sampling date (BÜCKING in press b). A similar year-round presence of all instars was reported for *H. kerguelensis* in the *Verrucaria* zone of the subantarctic Kerguelen islands (TRAVÉ 1988).

Generation time of *H. fusca* in the laboratory at 20°C, 100% RH, 12 h light/dark cycle and with *Blidingia* sp. as food was c. two months (BÜCKING 1995). However, at lower temperatures or other unfavourable conditions, development time may be prolonged, at higher temperatures it may probably be faster. Experiments with the low quality food *Prasiola stipitata* SUHR IN JESSEN revealed a maximum of 140 d from birth to adult hatch (20°C, 100% RH) (BÜCKING in press a). The long-term monthly mean of air temperature in Bremerhaven ranges from 0.9°C in January to 16.7°C in July and August (Amtsblatt des deutschen Wetterdienstes, monatlicher Witterungsbericht). However, continuous measurements of the effective microclimate on the shore, i.e. within the algal cover and during submersion (comp. SOUTHWARD 1958), as well as rearing experiments at lower temperatures are needed for better estimations of the effective generation time of field populations.

Combining the phenological data and the present results of laboratory rearing, the following life cycle and population cycle in the middle Weser estuary seems realistic:

The development of all *H. fusca* populations started with a high portion of tritonymphs in winter. Stimulated by rising temperatures in spring, the tritonymphs largely synchronously developed to adults. In most cases, the increase in adult density in the uppermost eulittoral exceeded the related decrease in nymph number, possibly due to vertical migration and concentration processes. High birth rate and low adult mortality, both supported by the thick protecting cover of algae, led to a first peak in larvae density, followed by a peak in nymph proportion.

At Weddewarden a further sequence of adults, larvae and nymphs peak was observed, indicating the occurrence of a second generation. Again, the adult peak coincided with a higher algal biomass. Measured from larvae peak to larvae peak (June to September), a generation time of approximately three months can be estimated. The assumption of at least two generations is supported by the observation, that each adult peak was accompanied by a temporary increase in the percentage of larvigerous females (BÜCKING in press b).

In contrast to the Weddewarden population, at Langlütjen the high nymph density in summer was not followed by further peaks of the following instars. This observation might be the result of balanced in- and outflow of instar proportion and does not exclude the occurrence of further generations. In the laboratory the reproductive period of females fed with *Blidingia* lasted up to 69 d with a mean birth rate of 0.6 larvae/d. Dependent on feeding conditions, the development time of the two nymphal instars was prolonged up to 86 d (BÜCKING in press a). At least at Langlütjen, both factors – long reproductive period and variation of development time – probably led to a progressive overlapping of generations and accumulation of nymphs. This putative asynchrony of development in summer is reflected by the merely indistinct fluctuations of instar distribution. In autumn and winter, all populations displayed a high portion of tritonymphs, possibly due to a stop or retardation of development at this stage or lower mortality of nymphs.

It is interesting, that the spring/summer increase in population density started later in lower littoral zones. The seasonal development of instar distribution was more or less synchronous in all three zones, therefore a slow proceeding emigration from the uppermost eulittoral is unlikely. However, without further investigations, it can not be decided whether the lower zones are constantly settled or if repeated, wave-mediated dislocations of mites originating from the uppermost eulittoral occur.

Regarding different locations as well as different littoral zones, the population dynamics, e.g. the number of generations and abundance peaks per year, depend primarily on the local abiotic conditions, which are highly influenced by the structure and thickness of the algal cover. While a dense algal vegetation probably reduces desiccation stress and the risk of dislodgment caused by wave action, a breakdown of algal biomass, due to sporulation and wave mediated loss of thalli (HAASE 1995), might result in a dislodgment of epiphytic inhabitants. Consistently, most of the differences found between locations in the Weser estuary can be interpreted as the effect of different seasonal development of algal biomass. The unusually high second peak at Weddewarden may be explained by the fact that even in July/August 1991 a relatively thick algal cover and a high portion of larvigerous females were present, whereas at Langlütjen in summer in 1992 and in 1993 algal biomass and adult density were greatly reduced.

Ameronothridae

Oribatid mites are long known to be the most diverse and often dominant arthropods in soil habitats (PETERSEN & LUXTON 1982; WALLWORK 1983). Comparable to their soil relatives, the studied species of the genus *Ameronothrus* reached very high abundance of up to 432 ind./25 cm^2 (= 172800 ind./m^2). However, the littoral rocky shore is an apotypic habitat for Oribatids (NORTON 1994) and adaptations to the extreme environmental conditions should be expected.

In all known cases, species of the genus *Ameronothrus* appeared to be larviparous (SCHUBART 1971; SCHULTE 1977; TILREM 1994). SCHUBART (1971) suggest a univoltine life cycle for *A. marinus*, *A. lineatus* and *A. maculatus*. LUXTON (1967a) and WEIGMANN (1975) reported the seasonal variation of instar density of the hemiedaphic saltmash species *Ameronothrus schneideri* (OUDEMANN), suggesting an univoltine life cycle. Adults occurred the whole year round but with a single peak in percental proportion in June or July. The density of larvae peaked between June and August.

A. lapponicus DALENIUS was investigated at a high mountain habitat in Hardangervidda, Finse (South Norway) with extreme changes in temperature and long periods of severe drought (TILREM 1994). The species inhabits the top of erratic boulders covered with lichens (*Ramalina polymorpha* (ACH.) ACH.), which serve as microhabitat and food. All instars were found throughout the year but with a single summer peak in the proportion of gravid females. TILREM (1994) assumes that the extended and variable duration of instars results in overlapping generations and a duration of life cycles of four to six years. The elongation of life cycles is probably a function of heat budget and a common character of oribatids in cold environments (NORTON 1994).

Ameronothrus marinus

A. marinus inhabits the eulittoral zone of euryhaline as well as brackish to oligohaline rocky shores (SCHULTE et al. 1975). Tritonymphs and adults feed on macroalgae like *Enteromorpha* spp., whereas larvae, proto- and deutonymphs feed predominantly on microalgae. Feeding and defecation follow an endogenous tidal rhythm with three maxima of locomotion between high tides. In populations originating from a tideless littoral, feeding activity is synchronised with diurnal cycles (SCHULTE 1976a, 1976b).

The seasonal development of abundance and instar density found at Langlütjen-A indicate the following life cycle:

Adults and tritonymphs of *A. marinus* hibernated preferably at crevice fringes of the littoral fringe. In early spring, the tritonymphs hatched to adults and migrated with the adults of the former year into the growing *Blidingia* cover of the uppermost eulittoral. Here, the females gave birth to the larvae; the mean reproductive period lasted from May to September with a maximum natality in June. The majority of the offspring developed within four months to adults. During this period no larvae and only few nymphs were found above the *Blidingia* zone. In November most of the tritonymphs as well as the newly hatched adults migrated to the littoral fringe, where they hibernated. Only few individuals of all instars stayed within the algal cover.

SCHUBART (1971) reanalysed the data of SCHULTE (1970) for an *A. marinus* population from Weddewarden. He concluded that similar to all other ameronothrids analysed even *A. marinus* is univoltine with an adult peak in May/June and a maximum of births of larvae in July. Consistent with the Langlütjen population, the mean reproductive period lasted from May to September. Similar results were obtained by PUGH & KING (1986) in the Bracelett Bay (Gower, UK). In winter this population was composed predominantly of tritonymphs and adults.

It can be concluded that *A. marinus* is mainly univoltine with an incompletely synchronised life cycle and seasonal shifts of the hibernating tritonymphs and adults between upper eulittoral and littoral fringe. As in other ameronothrids, adult longevity is very high. In ecophysiological studies, unfed adults survived up to 265 d submersed in 32 PSU sea water at 15°C (SCHULTE 1977).

The described migration pattern, emphasised by the result of the capture-recapture experiment in the field, conflicts with findings of SCHULTE (1970, 1977). He concluded from the seasonal variation of population density at different littoral levels and of distribution limits of instars at Weddewarden, that *A. marinus* hibernated as adults predominantly in the mid eulittoral. In spring the adults are thought to return to the upper eulittoral where they start larvae deposition. Seasonal migrations of laboratory populations, kept in air conditioned plastic tubes with a moist plaster of Paris bottom and a slope of 45° (SCHULTE 1977), supported this view. However, SCHUBART (1971) assumes that the spring decrease of adult density in lower zones might be explained by male mortality, occuring earlier in lower zones than in upper zones.

SCHULTE (1976b, 1977) supposed that due to a lower tolerance of submersion and the dependence on microalgae as a food source, the larvae and young nymphs appear preferably in the uppermost eulittoral and littoral fringe. Older nymphs and adults, with a higher resistance to submersion and macroalgae as food, also inhabit lower zones. By contrast, we found no hints of such an instar specific zonation pattern. For example in July, the sample date with the highest population density in the *Fucus* zone of Langlütjen-A, six larvae, 12 protonymphs and only three adults were found on an area of 100 cm² (four pooled samples) 1.6 m below MHW. In winter, larvae and most protonymphs were not found above but below the majority of the remaining population.

Additionally to this seasonal patterns, in the laboratory adults, but not larvae and nymphs, showed an endogenous rhythm of vertical migrations between high tides, covering a difference in altitude of approx. 20 cm (SCHULTE 1973). Since our sampling was done on certain littoral levels but at different times after high tide, we can not exclude the possibility that the results are influenced by such tidal activity rhythms.

The advantage of the littoral fringe as preferred hibernation site at Langlütjen may be the low frequency of submersions and therefore a reduced risk of inoculative freezing. SØMME & BLOCK (1984) concluded from ecophysiological studies on the oribatid *Halozetes marinus* (LOHMANN) and the astigmatid *Hyadesia maxima* FAIN, SØMME & BLOCK that in the subantarctic inoculative freezing may be the main mortality factor during severe winters. In the *Blidingia* zone of Langlütjen waves and spray often formed a thick ice cover (e.g. in February 1993) (ERNST 1995).

Ameronothrus lineatus

A. lineatus can be found in terrestrial, limnic as well as marine habitats. In warmer climates, it tends to become stenotopic and can be found exclusively in marine habitats (SCHULTE et al. 1975). Within the rocky shore, it preferably inhabits the littoral fringe, where it feeds on epilithic algae and the phycobiont of lichens (SCHULTE 1976b). In contrast to all other studied mites, the population density of *A. lineatus* increases with diminishing salinities. The outer limit of distribution was found at localities with a mean of 5 PSU (ERNST 1996).

The seasonal development of population density and instar distribution at Sandstedt in 1992/93 is interpreted as follows:

The winter population, localised at the border of crevices in the littoral fringe, comprised all instars but was characterised by a predomination of tritonymphs. In April all juveniles resumed development so that in May/June the population consisted exclusively of adults. In July/August the adult population migrated into the *Blidingia* cover of the uppermost eulittoral, where the females gave birth to the larvae. Within two months the offspring developed to deutonymphs, which then migrated upwards into the littoral fringe. In November most of the deutonymphs developed to tritonymphs and in December some new adults also appeared.

A. lineatus is univoltine with only one reproductive period per year. However, dependent on date of birth and the following temperature conditions (quiescence in winter), the period from birth of larvae to adult hatch varied from five to nine months.

Ameronothrus maculatus

As *A. lineatus*, *A. maculatus* is holoeurytopic; it inhabits terrestrial, limnic, brackish and marine habitats. At rocky shores, it prefers the supralittoral lichen zone, where it feeds on the phycobiont of various lichens (SCHULTE et al. 1975).

Corresponding to the stability of the lichen vegetation in the supralittoral zone, the population density of *A. maculatus* was less variable than those of the intertidal species, which have to cope with rapid changes in algal biomass. At Langlütjen *A. maculatus* hibernated mainly as tritonymphs, accompanied by some deutonymphs. In spring all nymphs developed to adults and started reproduction in June. The natality was highest in July. Measured from peak to peak of instar density, development time in the field can be estimated as three, two, two and five months for larvae, protonymphs, deutonymphs and tritonymphs respectively.

SCHUBART (1971) also suggests an univoltine life cycle of *A. maculatus*, sampled on a wall in the city of Kiel (northern Germany, Baltic Sea). Adults were present the whole year round, but each of the successive instars appeared within a distinct period, beginning with first free larvae in May. Only adults and tritonymphs hibernated.

In summary, *A. maculatus* is univoltine but with a very long presence of adults and a long reproductive period (June to December at Langlütjen). The timing of the age class appearance – e.g. the composition of the winter population – depends on local conditions. However, it can be assumed that none of the larvae, which appeared in December reached the adult stage.

GJELSTRUP & SØCHTING (1984) have shown that the population density of *A. maculatus* in the rocky supralittoral of Bornholm (Denmark, Baltic Sea) depends on the structure of the saxicolous lichen community. The species was found in several lichens down to the littoral fringe, but was especially associated with *Lecanora atra* (HUDSON) ACH. 10 m above sea level. At Langlütjen, larvae and protonymphs were mostly found hidden under lobes of foliose lichens, whereas elder nymphs and adults can also be found on open surfaces. Distribution limits as well as the patchy distribution of *A. maculatus* are probably the result of the zonation and patchiness of the lichen community.

Halacaridae

It is long known that halacarids display two kinds of phenologies; species which appear with all instars the whole year round – e.g. *Isobactrus* spp. and *Rhombognathides spinipes* (VIETS) – and species with a sequential appearance of instars for distinct periods like *M. armatus*, *Halacarellus basteri* (JOHNSTON) and *H. balticus* (LOHMANN) (VIETS 1927; ANDRÉ 1946; STRAARUP 1968; BARTSCH 1972; PAHNKE 1974; MACQUITTY 1984; SIEMER 1996a, 1996b). The first type is thought to be characteristic of bi- or multivoltine species with overlapping generations, the second type of univoltinism (BARTSCH 1972; PUGH & KING 1986).

In the following, the phenology of the two investigated species will be discussed with regard to rearing data on development and generation time, life span and egg deposition.

Metarhombognathus armatus

M. armatus is a frequent inhabitant of rocky shores of the Atlantic (USA east coast, Canada, Greenland, France, Great Britain), the North Sea and the Baltic Sea (NEWELL 1947; BARTSCH 1972, 1979; STRAARUP 1968). It preferably inhabits the upper eulittoral zone, where it feeds on various green algae (SIEMER in press).

The development of the *M. armatus* population from Weddewarden was characterised by a clear sequence of stages. The adults hibernated and first larvae were found by January developing to new adults by October. STRAARUP (1968) and BARTSCH (1972) found a comparable phenology with hibernating adults, larvae in spring, deutonymphs in summer and new adults in October or November.

Reared females, kept at 5 °C (submersed, *Blidingia* diet), had a preoviposition period of one to two months. In the following a mean of 14 eggs were deposited continuously within 107 d (SIEMER 1996b). The egg-to-adult development needed two months. At 20 °C, development was significantly faster but stopped in the deutonymph stage. Development continued only after the newly hatched deutonymphs were transferred to 5°C. With such a temperature arrangement generation time, measured from egg-to-egg deposition, was 184 d (SIEMER 1996a). The need of the aestivating deutonymph for a chilling period in order to continue development can be interpreted as a diapause.

The following scenario of population dynamics at Weddewarden 1990/91 can be supposed:

The *M. armatus* population hibernated exclusively as adults. The first eggs were deposited by December and first larvae appeared in January. The peak in larvae hatch was reached in April. Within one up to two months these larvae developed to protonymphs. After a further two months (July/August), the population consisted mainly of deutonymphs. Due to the stop in development the proportion of deutonymphs accumulated to 100 % in August/September. Only after the ambient temperatures decreased below 10°C for longer periods in September/October, was the diapause terminated and first adults found.

The biological role of the synchronisation of the life cycle due to a diapause in *M. armatus* can be seen in context with the instar specific ecophysiology. Laboratory studies have shown that the aestivating deutonymphs resisted desiccation better than other instars, while hibernating adults had the highest survival rate after exposure to -5°C or -20°C (SIEMER 1996b). Probably more important, the timing of the life cycle leads to a coincidence of larvae peak and maximum algal density in spring. Larvae of *M. armatus* had the lowest survival rate compared to eggs, deutonymphs and adults when exposed to low air humidities. The protective features of the algal cover, as discussed above, seem also to be of value and benefit to this species.

Isobactrus uniscutatus

I. uniscutatus is known from the upper intertidal of rocky shores and salt march pools of the French and British Atlantic coast, the North Sea (UK, northern German estuaries), the Baltic Sea and the Mediterranean Sea (BARTSCH 1972, 1979; GREEN & MACQUITTY 1987; PUGH & KING 1985b). It feeds on green algae (SIEMER 1996b). KRONBERG (1983) found cyanophytes within the gut of an other species of the genus *Isobactrus*.

In view of the fact, that at Dedesdorf all instars were found throughout the year with merely indistinct fluctuations of instar density, no hints on the life cycle or number of generations per year are given by the field data. The population density peaked in August 1993, was very low in winter and peaked again in June/July in 1994.

BARTSCH (1972) also found a constant presence of all instars of *I. uniscutatus*. Using the percental distribution of instars, the author assumes that the species is able to complete its life cycle within a few weeks and that probably several overlapping generations per year occur. PUGH & KING (1986) studied the phenology of *I. ungulatus* BARTSCH in the South Wales area (UK) and suggest that this species has at least two generations per year. However, in view of the irregular pattern of appearance and disappearance of instars and of periods of maximum abundance shown by the authors, an estimation of life cycle data is rather difficult.

If kept submerged in artificial seawater (15 PSU) with *Blidingia* thalli as food and substrate, generation time of *I. uniscutatus* was seven, six and two months at 10°C, 15°C and 20°C respectively. At 5°C no development of eggs or larvae occurred (SIEMER 1996b).

Regarding the Dedesdorf population, no synchronisation of age class appearance can be seen except a high proportion of larvae in summer. Several generations occurred simultaneously. Given the temperature-dependent development time and the course of mean monthly air temperatures at Dedesdorf, some of the offspring could produce only one, others possibly two generations per year. Larvae which hatched in summer could have developed to adults in two to three months while larvae hatched in autumn hibernated as juveniles together with the adults of the former generation, and completed their life cycle at the earliest in spring.

Comparable to *I. uniscutatus*, the parthenogenetic species *I. setosus* (LOHMANN) had a generation time of 216 – 267 d at 9°C (MACQUITTY 1984). In view of the often higher air and surface water temperatures during summer, the author also assumes a maximum of two generations per year.

Nanorchestes amphibius

Littoral species of the genus Nanorchestes can be found worldwide (SCHUSTER 1988). Considering huge variations in body size, the taxon *N. amphibius* probably comprises several species, which have not been separated yet (THOR & WILLMANN 1941). They feed on coccal green algae (SCHUSTER & SCHUSTER 1977) and cyanophytes (BÜCKING unpublished). The antarctic species *N. antarcticus* (STRANDTMANN), which inhabits supralittoral rocks as well as terrestrial soil habitats, feeds on coccal green algae, cyanophytes, the green alga *Prasiola* sp. and fungi (FITZSIMMONS 1971).

At Langlütjen, *N. amphibius* preferably inhabited crevices and surface activity was restricted to short periods after high tide. Within crevices, huge clusters of eggs, moulting phases and active mites of all instars were found throughout the year. The species occurred from the mid-eulittoral up to the supralittoral, with a clear concentration around MHW. A similar vertical distribution was recorded for British rocky shores (PUGH & KING 1985a). SCHUSTER & SCHUSTER (1977) found that males of *N. amphibius* sampled on Helgoland (North Sea) started spermatophore deposition in the laboratory independent from sampling season, even in winter.

In summary, we have some hints on multivoltinism and a year-round reproduction, but this has to be supported by further studies on age class distribution and development time.

Conclusions on life cycle strategies

Voltinism and generational synchrony

The populations of the studied littoral mites differed mainly in the degree of synchrony of development. This ranged from the highly synchronised appearance of instars in *M. armatus* and *A. maculatus* to the less synchronised development of *H. fusca*, *A. marinus* and *A. lineatus* and finally the non-synchronised phenology of *I. uniscutatus*. The accumulation of at least one instar followed by a more or less synchronised continuation of development is most likely triggered by the seasonal change in temperature. In *M. armatus* the development of the deutonymph stopped until the decrease of temperature in autumn terminated the diapause. The accumulation of tritonymphs in autumn/winter, observed for *A. maculatus*, *A. lineatus* and *H. fusca* might be explained by an instar specific lower mortality or quiescence due to low temperatures and therefore low heat budget. WEIGMANN (1975) investigated the influence of temperature on the development time of the saltmarsh oribatid *Hermannia subglabra* BERLESE. At higher temperatures the development time of tritonymphs exceeded those of all other instars and stopped below ca. 12°C. The developmental threshold of eggs, larvae, protonymphs and deutonymphs was significantly lower (7-10°C). TRAVÉ (1988) described for *Hyadesia kerguelensis*, that the survival time of nymphs exceeded that of adults, if exposed to 4°C. Future investigations must show, if further evidence for this hypothesis can be obtained by rearing at different temperature arrangements. Furthermore the predomination of specific developmental stages in winter might be correlated to the instar specific ability to withstand freezing by supercooling (CANNON & BLOCK 1988). In *Ameronothrus lapponicus*, the absence of gut contents in winter, resulting in an enhanced supercooling ability, is thought to be an adaptation to extreme frost (TILREM 1994). However, this is probably more a physiological reaction than phylogenetic adaptation, caused by the extremely low heat budget and the frozen food, which is possibly unsuitable.

The continuous presence of gravid females, found for *H. fusca* (BÜCKING in press b), enables the population to react opportunistically when environmental conditions become favourable. In this respect, the coincidence of high adult density, increasing temperatures and dense algal cover in spring leads to a peak in natality and hence to further synchronisation of age class appearance.

The fluctuations of environmental parameters do not allow us to estimate the number of generations by dividing the laboratory generation time into 365 days. Several authors have shown the influence of physical or biological factors on development, e.g. a cold-induced quiescence in winter, a stimulating effect of fluctuating vs. constant temperatures, different food qualities and many more (summary in NORTON 1994). In species with long reproductive periods and a continual presence of adults (e.g. *H. fusca*, *A. marinus*, *A. lineatus*, *I. uniscutatus*) the generation time most likely depends on the specific season, in which an egg or larva is deposited. Therefore a single (*A. marinus*) or double (*H. fusca*) series of succeeding peaks of instar density per year does not exclude the occurrence of more or less generations per year, at least in parts of the population.

In summary, *M. armatus* and *A. maculatus* are strictly univoltine and the populations of the other Ameronothrids are univoltine at least in the main part of the populations. *I. uniscutatus* can be assumed to be uni- to bivoltine because of their relatively short generation time in the laboratory and the presented phenological data. *H. fusca* seems to be mainly bivoltine, but multivoltinism may occur in years with a substantial algal growth even in summer.

Parity

Regarding the offspring release of littoral mites, different oviposition modes as well as egg retention can be found. The Rhombognathinae glue a small group of eggs to the base or depressions of algal fronts by means of a viscous secretion (BARTSCH 1972, PAHNKE 1974). In contrast to this, *N. amphibius* deposits the eggs in clutches in protecting crevices. ERNST (1995) has shown that even crevices submersed at high tide are inhabited. However, within crevices the eggs are protected at least from larger predators, dislodgment by waves and probably desiccation.

Considering the high number of larviparous mite species in littoral environments, retained parity was discussed as adaptation to the extreme environmental conditions, in particular wave exposure (LUXTON 1967b; PUGH & KING 1986). In contrast to the vulnerable egg stage, the mobile larvae are able to avoid unfavourable conditions, such as desiccation or wave exposure, by their retreatment and aggregation behaviour. The observation, that larvae and protonymphs of *H. fusca* (this investigation) and the early developmental stages of intertidal *Ameronothrus* species (SCHULTE et al. 1975) were often found in the centres of such aggregations gives further evidence for mechanical stress as an important factor. At least for the genus *Ameronothrus*, egg retention has to be regarded as preadaptation. *A. lapponicus*, which is fully terrestrial and inhabits alpine hardsubstrates overgrown by lichens, is larviparous (TILREM 1994). This species probably belongs to the sister group of the species group more related to the littoral (SCHUBART 1971). It can be assumed that larviparity was already a character of the terrestrial stem species of the genus *Ameronothrus*. However, as described for the littoral, the exposed habitat of *A. lapponicus* is characterised by extreme changes in temperature and long periods of desiccation (TILREM 1994). Larviposition is frequent in Astigmata of different families inhabiting permanently water-filled treeholes. However, the environmental conditions within this habitat are rather stable (FASHING 1994).

r- vs. K-selection

The r-K selection theory predicts, that in populations dominated by density-independent mortality and subject to unpredictably fluctuating environmental conditions early maturity, high reproductive effort and large numbers of small offspring will be favoured. At the other extreme density-dependent mortality and high environmental predictability will favour delayed maturity, low reproductive effort and small numbers of (large, high quality) offspring. Hence, the position of species within the r/K continuum is often estimated by attributes like reproductive rate, semelparity vs. iteroparity, voltinism and adult longevity (see review in STEARNS 1977).

The relatively fast changing population density and distinct peaks of natality found for some of the species studied seem to be typical attributes of r-selected species, reacting to fast changes in environmental conditions such as algal biomass. Arguments against the rocky shore as an r-selective environment are (I) the stability of rock surface and crevices, which serve as retreatment sites, (II) the permanent availability of algae as food and (III) the predictability of seasonal and tidal fluctuations of abiotic factors. However, the often rapid loss of algal biomass in summer due to sporulation and drought as well as abrasion by ice-floes can be regarded as catastrophic events resulting in a remarkable decrease of population density.

Most astigmatid mites are specialised to exploit spatially or temporally restricted habitats and are regarded as typically r-selected (OCONNOR 1994). FASHING (1994) reviewed demographic data for various free-living Astigmata. Species considered as r-strategists deposited up to 47 eggs × female^{-1}d^{-1} for a period of only 12.5 days (*Sancassania rodriguezi*, 25°C, xenic diet). By contrast, *H. fusca* had a long larviposition period of 45 d with only 0.6 larvae per day (20°C, *Blidingia* diet) (BÜCKING in press a). Obviously offspring number is reduced for the benefit of reduced egg mortality. Other species like *Naidacarus arboricola* FASHING (Acaridae) or Pyroglyphidae with a generation time, birth rate and longevity comparable to *H. fusca* are discussed to be K-selected (HART & FAIN 1988; FASHING 1994; OCONNOR 1994).

The univoltinism of *M. armatus* and the ameronothrids contradict a rating as r-strategists. In view of the long generation time relative to many other mite groups, MITCHELL (1977) discussed oribatid mite populations to be unable to respond numerically to short-term changes in resource availability. The egg-adult developmental periods in oribatid mites, studied mostly between 20-30°C varied from three weeks in *Oppiella nova* (OUDEMANS) to more than one year in *Conoppia palmicincta* (review in NORTON 1994). However, most oribatid species in a Danish beech wood soil, even *Oppiella nova*, appeared to be univoltine or semivoltine (LUXTON 1981a, 1981b). The extended longevity of the adult ameronothrids is a typical character of Oribatida in general (NORTON 1994; LUXTON 1981a, 1981b). NORTON (loc. cit.) concluded that the shift from predation to particulate feeding (saprophagy and phytophagy) resulted in low metabolic rates, which finally caused slow development and low time-specific fertility. To maintain the population, a long adult life was required. These constrained “K attributes” are plesiotypic for oribatids and have often played a role as preadaptation of species invading extreme habitats.

The genus *Ameronothrus* seems to be preadapted in this respect, whereas the Hyadesiidae differ from most other free-living Astigmata in their relatively low reproductive rate and the loss of the facultative heteromorphic deutonymph (hypopus). The putative sister group of the Hyadesiidae are the remaining Hemisarcoptoidea (OCONNOR & MOSER 1985), the majority of whose taxa are closely related to wood-boring insects and still have a phoretic deutonymph. Hypopi are usually formed in reaction to abiotic stress and are specialised for passive dispersal by phoresy and for resisting adverse environmental conditions (OCONNOR 1982, 1994). In Hyadesiidae dispersal is probably guaranteed by hydrochory of all instars with dislodged algae. In particular larvae are often found inside the hollow thalli of *Enteromorpha* (GANNING 1970). The loss of the deutonymph in free-living astigmatid mites is often correlated to the adaptation to stable, widespread habitats (OCONNOR 1982).

The long generation time (bi- or univoltine), low egg number and long reproductive period of the Rhombognathinae (BARTSCH 1972, SIEMER 1996b) characterise this taxon to have typical K attributes. However, without knowledge on demographic data of the sister group and outgroups it can not be decided if these features are ancestral or have evolved in the course of adaptation to the littoral environment. KRANTZ (1978) places the Halacaroidea together with Tydeoidea, Eupodoidea and Bdelloidea within the cohort Eupodina. According to PAHNKE (1974) Bdellids and Halacarids share a specific ovipositor, which might be a synapomorphy of these two taxa. The low egg number and bi- or univoltinism of Bdellidae (ALBERTI 1973, 1974) support the view, that the K attributes of the Halacaridae are a plesiotypic trait.

In summary, all phytophagous mites tend to the K direction within the r/K continuum. According to STEARNS (1977), delayed maturity, low reproductive effort and long reproductive periods can be regarded as buffers against catastrophic population reductions, i.e. in environments with variable juvenile survivorship. Most, if not all, littoral mites are highly tolerant to abiotic stress and seem to invest into survival, not into high reproduction.

Summary

Littoral hardsubstrates along the Weser estuary are inhabited by a variety of phytophagous mites, feeding on algae, cyanophytes or lichens. These populations reach very high abundance in the upper eulittoral and lower supralittoral zone. This investigation dealt with the population dynamics of seven species of Astigmata, Oribatida, Prostigmata and Endeostigmata. Corresponding to their different taxonomic origin and convergent settlement of the littoral environment, they display a wide range of life cycle strategies.

The astigmatid species *Hyadesia fusca* was present with all instars throughout the year, but showed tremendous changes in population density and instar distribution. Dependent on local conditions, a single peak of natality and population density in spring or two peaks in spring and autumn occurred. The tritonymphs represented the main hibernating instar. The seasonal variation of age class distribution indicates the occurrence of at least two generations, but multivoltinism probably exists in parts of the population.

The studied species of Ameronothridae (Oribatida) are, at least in the main part of the population, univoltine but with different degrees of generational synchrony. All instars of the supralittoral species *Ameronothrus maculatus* appeared within distinct periods, whereas the adults of *A. marinus* and *A. lineatus* were found throughout the year. Natality of the three species peaked in summer; by winter most of the offspring developed to tritonymphs (*A. lineatus*, *A. maculatus*) or adults (*A. marinus*). Development and reproduction were continued in spring. The intertidal species *A. marinus* and *A. lineatus* showed spring migrations of the adults between their hibernation site, the littoral fringe and the site of larvae birth, the *Blidingia* cover at MHW. The next generation migrated back to the littoral fringe either as deutonymphs (*A. lineatus*) or as adults (*A. marinus*).

The two halacarid species represent the two extremes of generational synchrony. *Metarhombognathus armatus* is strictly univoltine and synchronised by a diapause of the deutonymph. Decreasing temperatures in autumn terminated the diapause, and the whole population developed to adults, which then hibernated. Most larvae hatched in spring and developed to deutonymphs

within three or four months. By contrast, *Isobactrus unicutatus* showed no synchronisation of age class appearance. Population density peaked in summer, but all instars were found throughout the year with only indistinct variations in proportion. With respect to rearing data, a maximum of two generations per annum can be assumed.

The endeostigmatid *Nanorchestes amphibius* was found with all instars throughout the year, but data on seasonal change of instar distribution and generation time are still lacking.

All intertidal species have to cope with the mechanical stress caused by waves and water currents. The eggs are protected from wave exposure by glueing them onto thalli of algae (Rhombognathinae), deposition within crevices (*Nanorchestes*) or retainment within the female's body (Hyadesiidae, *Ameronothrus* spp.). The mobile stages aggregate in cavities of the rocky surface, at crevice fringes or they retreat into crevices.

Common features of phytophagous mites in the littoral environment are long generation time, long reproductive periods and their ability to resist adverse environmental conditions. The latter includes high physiological tolerance, different types of retreatment behaviour and, in two species, seasonal migrations. Despite these typical "K attributes", the intertidal species undergo rapid changes in population density – that is tremendous high abundance in spring or summer, coincident with the peaks of offspring production, and low densities in winter, often characterised by the predomination of one hibernating instar. Most of these changes can be attributed to the seasonal fluctuation of environmental conditions, especially temperature and algal biomass. The timing of offspring release follows different strategies with two extremes: on one hand a coincidence of larvae hatch and algal growth controlled by a diapause (*Metarhombognathus armatus*), on the other hand a year-round presence of reproductive adults enabling the opportunistical reaction to seasonal changes of environmental conditions (*H. fusca*, *I. uniscutatus*, possibly *N. amphibius*).

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