

# **Investigations on the feeding habits of the rocky-shore mite *Hyadesia fusca* (Acari: Astigmata : Hyadesiidae): diet range, food preference, food quality, and the implications for distribution patterns**

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**ABSTRACT:** Within the food web of estuarine and marine rocky shore ecosystems phytophagous mites of terrestrial and marine origin constitute an important part as grazers on algae and as a food source for certain arthropods, especially zoophagous mites. This investigation deals with the feeding biology of *Hyadesia fusca* taking as an example a population located on an artificial rocky shore of the middle Weser estuary in Northern Germany. The species is characterized by a broad diet range; in feeding experiments diatoms, lichens, detritus as well as blue, red and green algae were accepted. Even analyses of faecal pellets produced by field specimen suggest a non-specific feeding habit. However, the influence of certain diets on mortality, offspring number and rearing success showed that the food quality differs significantly. The most suitable food, the Ulvaceae *Blidingia*, was clearly preferred in a series of pairwise choice tests. These findings correlate with the vertical zonation of the field population i.e.: higher population densities in the vegetation zone dominated by *Blidingia*. It can be concluded that in addition to abiotic factors food supply could play an important role for distribution patterns of phytophagous mites.

## INTRODUCTION

Rocky shores are inhabited by a variety of microarthropods of marine as well as terrestrial origin. In the green algae belt of the upper intertidal zone and in the lower supralittoral zone covered with lichens mites often dominate the microfauna with regard to species diversity and abundance (Schuster, 1965; Bartsch, 1978; Bartsch, 1982). Species composition, zoogeography, and vertical distribution of this group are well known (e.g. Halbert, 1920; Otto, 1936; Schuster, 1979; Schulte, 1977; Pugh & King, 1985 b, c; Ernst et al., 1993), but the functional role of mites in this ecosystem is only poorly understood. Especially the integration of terrestrial microarthropods in the rocky shore food web and the influence of biotic factors such as food supply on distribution patterns needs further investigation.

The mite coenosis of rocky shores comprises a wide spectrum of feeding habits, e.g. zoophagous (e.g. most Gamasina, Rhagidiidae, Erythraeidae, Bdellidae, Halacarinae), phytophagous (e.g. most Oribatida, Nanorchestidae, Hyadesiidae, Rhombognathinae), and saprophagous (some Gamasina, Uropodina, and Oribatida) species (Schuster, 1979; Pugh & King, 1985a).

On artificial hardsubstrates of estuaries in northern Germany, especially the surface-inhabiting algivorous Rhombognathinae and the species *Hyadesia fusca* (Lohmann) can reach extremely high population densities (Siemer, 1996; Bücking, 1995). At the Baltic Sea *Hyadesia fusca* often made up over 70 % of the total fauna in brackish-water rock pools with a dense green algae vegetation (Ganning, 1971) and on artificial sea defences (Kronberg, 1983). The Hyadesiidae have a transoceanic distribution and can be found in the intertidal and lower supralittoral of almost every rocky shore. In Europe the distribution of the euryhaline-marine *H. fusca* extends from northern Norway (70°N) all the way down to the Brittany coast in Northwestern France (48°N) (Schulte, 1977; Schuster, 1988; Fain & Schuster, 1989). In all known cases they are viviparous; the postnatal development comprises larva, protonymph, tritonymph and the sexual dimorphic adult. Mites of this species can be found (1) epilithic and within the algae cover (Otto, 1936; Kronberg, 1983; Ernst et al., 1993), (2) mesolithic in the outer region or fringe of crevices (Schulte, 1977; Pugh, 1985b), (3) among barnacles (Bénard, 1961; Pugh 1985b) and (4) permanently submerged in the green algae vegetation of rock pools (Halbert, 1920; Ganning, 1970; Östmann & Rönnberg, 1991). Moreover Ganning (1970) described the inside of the tubular thalli of *Enteromorpha intestinalis* (L.) Link (Chlorophyta, Ulvaceae) as being a microhabitat of, particularly, the larvae. However, in the Weser estuary *H. fusca* lives only epilithic and within the thin layer of epilithic green algae. During resting phases or periods of desiccation *H. fusca* withdraws into small cavities or congregates at the fringes of crevices (Ernst et al., 1993).

*H. fusca* is thought to be a specialised inhabitant and feeder of *Enteromorpha* (Ganning, 1970; Schuster, 1979) but the filamentous green alga *Cladophora glomerata* Kützting (Ganning, 1971), Cyanophytes (Kronberg, 1983) and microphytes (Bénard, 1961) have also been found in their guts or faecal pellets. *H. fusca* itself is a frequent prey for zoophagous mites like *Abrolophus* cf. *rubipes* (Trouessart) and *Bdella septemtrionalis* Atyeo et Tux. (Witte, 1972; Alberti, 1973) and has been found in the gut of the omniphagous amphipod *Platorchestia platensis* (Krøyer) (Stueber, pers. comm.), the isopod *Ligia oceanica* (L.) (v. d. Heydt, pers. comm.) and of the rock pool-inhabiting fish *Gasterosteus aculeatus* L. (Ganning, 1970).

The vertical distribution of *H. fusca* in the Weser estuary ranges from just below the lower distribution limit of the orange lichen *Caloplaca marina* (Wedd.) Zahlbr. down to the middle intertidal (Bücking, in press; Ernst, 1996). Nevertheless, the population is concentrated on a narrow band along Mean High Water level (MHW), dominated by green algae of the genus *Blidingia*. In 1991 a yearly mean abundance of 21 ind./cm<sup>2</sup> and a maximum of 87 ind./cm<sup>2</sup> was counted in this littoral zone, while only few Hyadesiids have been found in the supralittoral fringe (dominated by Cyanophytes) or in the middle intertidal with its predominant coating with *Fucus vesiculosus* L. and *Enteromorpha intestinalis*. Furthermore, it was observed that, when comparing adjacent surfaces that were different in rock type and therefore algae cover (*Blidingia* on concrete and *Enteromorpha* on sandstone) but situated on the same tidal level, the population density of *H. fusca* was about ten times higher on the *Blidingia*-dominated area (Bücking, in press).

The object of this investigation was to answer the question concerning whether the diet range, different feeding preferences or different qualities of the predominant food sources may influence the vertical distribution and population density in certain littoral or vegetational zones.

## MATERIALS AND METHODS

## Sampling and maintenance of the mites

The sampling of Hyadesiids assigned for laboratory experiments and field experiments was carried out at the location Langlütjen I. This is the ruin of a fortress, located in the mesohaline zone of the middle Weser estuary near Nordenham (km 69.5, 53°34' N. – 8° 31' E., salinity 9–19 PSU), extending as a peninsula into the Wadden Sea (Nationalpark Wattenmeer). The mean tidal rise is about 3.6 m; the bank reinforcement ranges from ca. mean sea level up to 2 m above the mean high water line with a slope of about 40°. The surface consists of weathered sandstone blocks which are stabilised by cast concrete. The vegetation shows a distinct zonation with *Enteromorpha* sp. and *Fucus vesiculosus* dominating in the middle intertidal zone, *Enteromorpha* sp. and *Blidingia* sp. in the upper intertidal zone, different Cyanophytes (but no black lichens) in the supralittoral fringe and lichens (*Caloplaca* spp., *Xanthoria* spp., *Lecanora* spp.) in the supralittoral zone (Ernst, 1995; Haase, 1995).

The Hyadesiids, obtained from *Blidingia* samples scraped off the rock surface, were separated into the ontogenetical instars, respectively sexes, and kept in cubic transparent polystyrol chambers (25 × 25 mm surface, 20 mm high) with lids. The bottom of the vessels was covered with plaster, enriched with a small amount of charcoal. The plaster was moistened with diluted artificial seawater (15 PSU, WIMEX®) and the vessels stored in a light thermostat at 20 ± 1°C with a 12 h/12 h light-dark cycle. Saturated air humidity was maintained by adding fresh water whenever necessary.

The algae and lichens assigned as food were sampled at different locations along the meso- and polyhaline zone of the Weser estuary, thoroughly cleaned in diluted seawater with the aid of a dissecting microscope and then distributed in a homogenous thin layer onto the plaster bottom. Surplus and even distribution of the food obviated the need for searching behaviour. The experiments were started by placing the mites into the feeding vessels.

## Recording of the diet range in the laboratory and in the field

After a period of at least 5 hours without food (complete defecation of food ingested before), adults (all tests) and also larvae, protonymphs, and tritonymphs (most tests) were transferred to prepared feeding vessels (one mite per vessel) and checked daily for at least one week. Feeding was attested, if new faecal pellets, clearly distinguishable from food fragments by their peritrophic membrane, were produced.

To examine the diet range in the field, adults from different littoral, or vegetation, zones were collected individually, rinsed in clean sea water, cleaned thoroughly under a field dissecting microscope and then transferred into small glass tubes filled with diluted artificial seawater. Their faecal pellets were analysed for food residues which were compared to preparations of detritus and plant samples collected at exactly the same places. For these analyses squeeze preparations were examined either in vivo or after staining with Toluidin Blue (1 %) or iodine-iodine-potassium (positive reaction with starch of pyrenoids) with the aid of a DIC microscope (stainings v. Gerlach, 1984). An epifluorescence microscope was used to check the food residues for primary fluorescence and as a test for Cyanophytes (phycocyan-mediated primary fluorescence with green light; see Kronberg,

1983). The identification of food components in faecal pellets produced by field specimens was facilitated by comparing them to faecal pellets of laboratory specimen fed with certain known diets.

### Experiments on food preference

Different plant species were offered to *Hyadesia fusca* in several tests with two food types each. The plaster bottom of the feeding vessels, similar to that described above but slightly smaller ( $18 \times 18$  mm surface, 15 mm high), was provided with food A and with food B, each kind covering a third of the total area (Fig. 1). The mites were placed along the midline between food A and B and their actual distribution was checked after 24 hours. A statistically significant difference in the number of test animals on the two food areas was interpreted as a preference for the food type concerned. By keeping the rela-

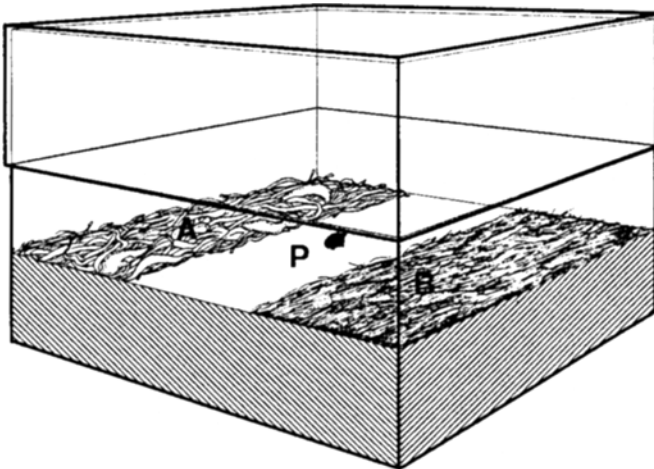


Fig. 1. Design of the polystyrol vessels used for the experiments on choice of food ( $18 \times 18 \times 15$  mm).  
A = Food A; B = Food B; P = Plaster of Paris-Charcoal Mixture

tive air humidity at 100 % and by diffuse illumination, humidity gradients and phototaxis were ruled out as factors influencing the choice behaviour.

The green algae *Blidingia minima* (Näg. ex Kütz.) Kylin, *Enteromorpha intestinalis* and *Rhizoclonium riparium* (Roth) Harv. as well as the lichen *Caloplaca marina* were compared, using 12 vessels per comparison each with 10 females. To take into account possible differences in the behaviour of instars and sexes, the distribution of females, males and tritonymphs (each  $3 \times 10$ ) after a period of 24 hours was compared in an additional pairwise-choice test with *Blidingia* and *Enteromorpha*. In order to study individual behaviour, 17 females were each placed in the centre of a vessel provided with *Blidingia minima* and *Enteromorpha intestinalis* and observed continuously for 6 hours. The intensity of feeding was checked by counting the faecal pellets per area after 24 hours.

### The effect of diets on mortality, reproductivity, and development

After sampling and storage for one day in the light thermostat without food, 20 females per diet were each placed in a feeding vessel of their own and checked every second or third day. New-born larvae were counted and removed at every control. Some of these larvae were transferred to feeding vessels with the same diet, and their further development was checked daily or every second day. Non-feeding mites and specimen that died owing to external factors (e.g. injury) were ignored for data evaluation.

The period of time between the first and last appearance of new-born larvae was defined as duration of reproduction. The mean birth rate for each female is the quotient of the duration of reproduction and the total number of larvae. In the case of females without offspring between start of investigation and death but who posthumously were found with fully developed embryos within their idiosoma (checked by squeezed preparations), the duration of reproduction and the birth rate was rated as zero.

Forage used for the food quality experiments was collected at different locations in the Weser estuary; the lichen *Caloplaca marina* from the supralittoral zone and the Chlorophytes *Prasiola stipitata* Suhr in Jessen from the supralittoral fringe, *Blidingia* and *Rhizoclonium riparium* from the upper intertidal and *Enteromorpha intestinalis* from the middle intertidal .

### Statistics

The statistical treatment of the preference experiment is based on the assumption that without any attraction or repulsion of the two food sources the individuals would be distributed homogeneously on the vessels bottom. For simplification, the few specimen found on the vessels walls were added to those on the uncovered plaster area. A chi-square test was carried out to compare the expected and observed frequencies of specimens cumulated for the three areas of the 12 vessels ( $H_0: E_{\text{Food A}} = E_{\text{Food B}} = E_{\text{Plaster/Walls}} = 1/3$ ,  $n = 120$ ,  $df = 2$ ,  $p < 0.01$ ). If this test indicated an inhomogeneous distribution, the "more attractive" food area was compared to the remaining area by a chi-square test for  $H_0: E_{\text{Food A}} = 1/3$ ,  $E_{\text{Food B + Plaster/Walls}} = 2/3$  ( $n = 120$ ,  $df = 1$ ,  $p < 0.01$ ).

The low sample size for the experiments on food quality implied that no reliable test on normal distribution could be carried out. Therefore, the effect of different diets on mortality, reproduction and development was compared using the two-tailed non parametric U-test after Mann & Whitney ( $p < 0.05$ ). A possible connection between long reproduction time and low birth rate was tested using the Spearman coefficient of rank correlation. ( $p$  for  $[H_1: R \neq 0] < 0.05$ ).

All statistical tests mentioned above were calculated according to Köhler et al. (1992).

## RESULTS

### Diet range

Table 1 shows the results of the feeding tests with marine and habitat-extraneous food.

Except for *Fucus vesiculosus* and *Ulva lactuca* L. (which have comparatively firm tissue), all other marine macroalgae, microalgae, lichens and detritus were accepted as

Table 1. Laboratory results of supply experiments with various kinds of food (+ accepted, - not accepted, \* only adults tested)

Food source	Sample site	Result
Marine plants (Weser estuary)		
<i>Xanthoria parietina</i> (L.) (Lichenophyta)	upper supralittoral	+
<i>Caloplaca marina</i> (Lichenophyta)	lower supralittoral	+
Different coccal and filamentous Cyanophyta	supralittoral fringe	+
<i>Prasiola stipitata</i> (Chlorophyta)	supralittoral fringe	+
<i>Blidingia minima</i> (Chlorophyta)	upper intertidal	+
<i>Rhizoclonium riparium</i> (Chlorophyta)	upper intertidal	+
Detritus floccules (inclusive different microphytes)	middle intertidal	+*
<i>Enteromorpha intestinalis</i> (Chlorophyta)	middle intertidal	+
<i>Rhodochorton</i> sp. (Rhodophyta) with epiphytic diatoms	lower intertidal	+
Epiphytic microalgae on <i>Fucus vesiculosus</i>	lower intertidal	+*
Young <i>Fucus vesiculosus</i> (without epiphytes) (Phaeophyta)	lower intertidal	-*
<i>Ulva lactuca</i> (Chlorophyta)	lower intertidal	-*
Fresh and decayed carrion (Weser estuary)		
<i>Anurida maritima</i> (Guerin) (Collembola)	upper intertidal	-*
<i>Ligia oceanica</i> (L.) (Isopoda)	upper intertidal	-*
Habitat-extraneous food		
<i>Ulothrix</i> sp. (Chlorophyta)	limnic sublittoral	+
<i>Pleurococcus</i> sp. (Chlorophyta)	tree bark	-*
<i>Myriophyllum spicatum</i> (L.) (Rosidae)	pond	-*
<i>Elodea canadensis</i> (Michx.) (Alismatidae)	pond	-*
<i>Sphagnum</i> sp. (Bryophyta)	peat-bog	-*
Birch leaves in various degrees of decomposition	edge of a forest	-*
<i>Laccaria laccata</i> (Skop. ex. Fr.) Berk ex Br. Mycelium (Fungi)	laboratory culture	-*

food. Fresh and decaying carcasses were never accepted, even when the specimen were exposed to longer periods of starvation. Habitat-extraneous food was not accepted, with one exception i.e. a limnic species of epilithic growing *Ulothrix* sp., a sublittoral filamentous green alga sampled at a bank reinforcement of the IJsselmeer (0.5 PSU, Netherlands). Many species of this genus are also present on marine and estuarine hardsubstrates.

The results of these laboratory tests were compared to results of analyses of faecal pellets obtained from mites sampled in the field (Table 2).

The food is obviously only partially digested by *Hyadesia*. With *Enteromorpha* as a food component, cell wall fragments, parts of chloroplasts, pyrenoids and, in few cases, also intact cells occurred in the faecal pellets. With *Blidingia* as food, additionally fragments of thalli consisting of up to 10 cells were found. Fine filamentous green algae were merely fragmented into smaller parts as a result of food processing (Fig. 2). Diatoms were detected either as intact individuals, empty shells or fragments of shells. Most of the Cyanophytes were found intact either as clusters of coccal species (e.g. *Chroococcus*) or as fragments of filamentous species (e.g. *Oscillatoria*). Many of the algae fragments found in the faecal pellets showed primary fluorescence comparable to that of living

Table 2. Food components in faecal pellets of *Hyadesia fusca* adults, sampled in various littoral and vegetational zones

Sample site	Food components (in order of decreasing estimated proportion)
Littoral fringe (sandstone), dominated by tetrasporal Cyanophytes ( <i>Chroococcus</i> sp.)	Cyanophytes, <i>Blidingia</i> sp., epiphytic diatoms, coccal Chlorophytes, fungal hyphae
Upper intertidal (concrete), dominated by <i>Blidingia</i> sp.	<i>Blidingia</i> sp., diatoms, different Cyanophytes, filamentous Chlorophytes
Upper intertidal (sandstone), in the upper part dominated by <i>Blidingia</i> sp., in the lower part dominated by <i>Enteromorpha</i> sp.	<i>Blidingia</i> sp., Cyanophytes, <i>Enteromorpha</i> sp., benthic diatoms, filamentous Chlorophytes, sediment particles
Middle intertidal (hardened sediment layer) with diatoms and few filamentous Rhodophyta	diatoms

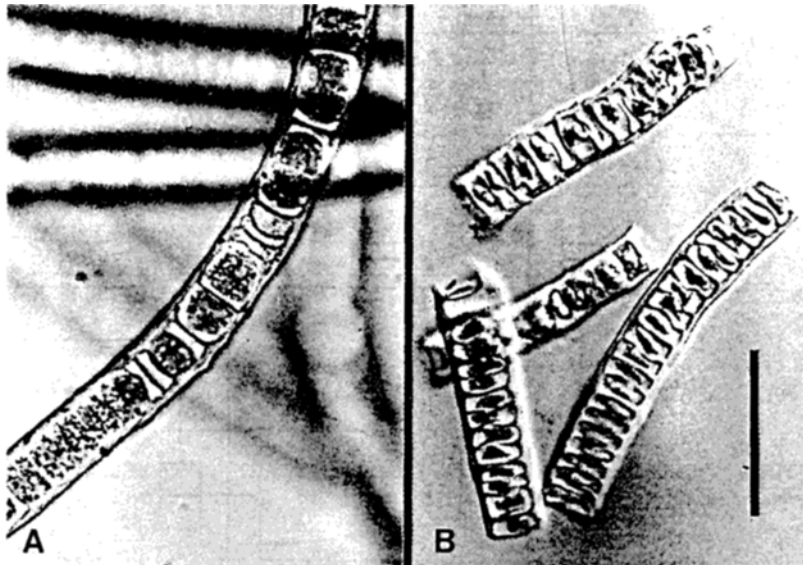


Fig. 2. A: Filamentous green alga, sampled at the ferry landing place Dedesdorf, Weser estuary; B: content of faecal pellets of an adult fed with this alga. Bar = 30  $\mu$ m

algae. Faecal pellets left on moist plaster for some days often gave rise to a growth of green algae germlings, which penetrated the peritrophic membrane.

The analysis of samples taken from the natural habitat confirmed largely the results of the feeding tests. Quantity and frequency of the food components from adults of a distinct vegetation zone represented to some extent the respective food supply at the sample place. As an exception, the faecal pellets produced by mites sampled in the supralittoral fringe regularly contained *Blidingia* cells, though this alga occurred in this zone only as patches of few germlings. The occasional appearance of benthic diatoms and of sediment particles within the faecal pellets indicate that detritus is, albeit to a small extent, a part of the food ingested.

### Food preference

Figure 3 shows the results of the pairwise-choice test with 10 females per vessel. A significant inhomogenous distribution of the test population was recorded in all tests, except in the trial with *Rhizoclonium* - *Caloplaca*. The mites showed a strong preference for *Blidingia* ( $\chi^2 > 100$ ). Furthermore, they were more abundant on *Rhizoclonium* if compared with *Enteromorpha* + Plaster/Walls ( $\chi^2 = 11$ ), and on *Enteromorpha* if compared with

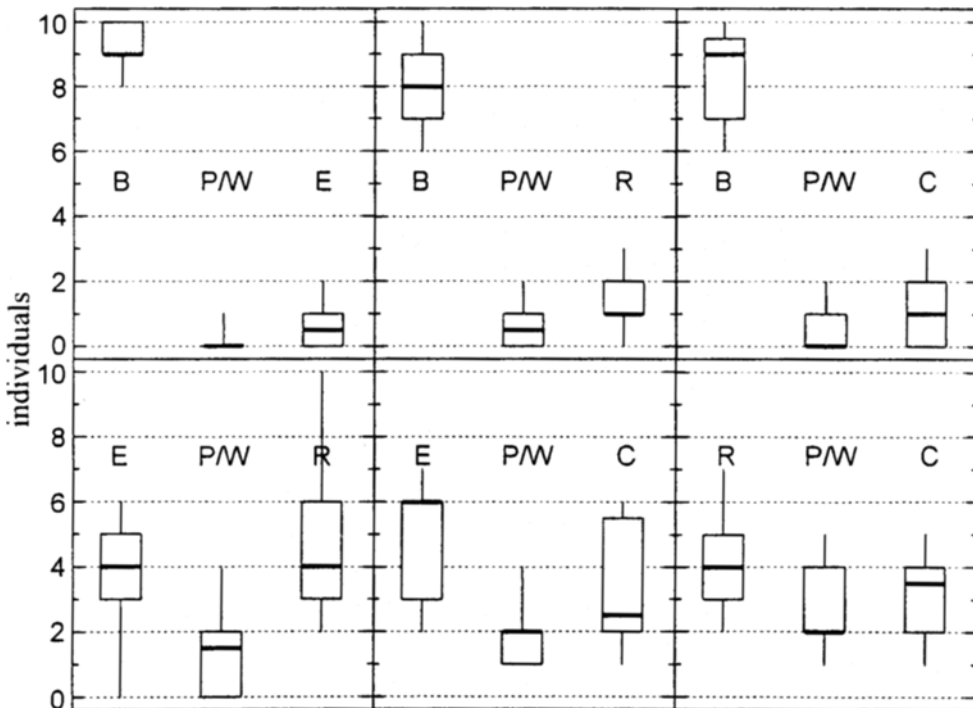


Fig. 3. Distribution of the test populations in the vessels in which a choice of food was offered. Box & Whisker Plot with median (bold line), interquartil range (boxes) and range (whiskers);  $n = 12$  with 10 individuals each. B = *Blidingia*, E = *Enteromorpha*, R = *Rhizoclonium*, C = *Caloplaca*, P/W = Plaster and Walls



*Caloplaca* + Plaster/Walls ( $\chi^2 = 14$ ). These two "preferences" have to be treated with caution regarding the relatively high variability (Fig. 3). With the exception of some trials with *Blidingia* supply, faecal pellets were found on both food areas of the vessels.

The distribution of the 30 females, males, and tritonymphs was 24, 27 and 26 individuals, respectively, on the *Blidingia* area (compared with *Enteromorpha*), thus significant differences in the choice behaviour of sexes or instars did not occur.

During 6 h of continuous observation, only 4 of 17 individually kept females moved to the *Enteromorpha* area, and only one of these fed on this alga, but within the first hour all migrated over to the *Blidingia* area. The mean number of faecal pellets per female and day was 18 (max. 36) on the *Blidingia* area, and 1 (max. 13) on the *Enteromorpha* area.

### Food quality

Differences in the nutritional quality of certain algae or lichens were tested regarding their dietary influence on survival time and reproduction of females and on the postnatal development of larvae (Table 3). It must be noted that the females originated from field samples, therefore individual age, number of previous births and the actual stock of

Table 3. Comparison of various food sources with regard to their effect on survival, larval births and development time. Arithmetic mean, standard deviation, range (in brackets) and sample size stated. Different characters in a column indicate significant differences (U-test after Mann & Whitney,  $p < 0.05$ )

Food source	Survival time (d)	Duration of reproduction (d)	Total number of larvae per female	Individual birth rate (larvae per female $\times$ d <sup>-1</sup> )	Development time (birth to adult) (d)
<i>Blidingia</i>	79 $\pm$ 39 a (21 - 136) 16	45 $\pm$ 17 a (7 - 69) 15	26 $\pm$ 10 a (5 - 38) 15	0.60 $\pm$ 0.14 a (0.38 - 0.90) 15	44 $\pm$ 7 a (33 - 58) 9
<i>Enterom.</i>	28 $\pm$ 20 b (6 - 101) 19	10 $\pm$ 6 b (3 - 26) 17	7 $\pm$ 3 b (3 - 14) 17	0.75 $\pm$ 0.38 a (0.29 - 1.75) 17	50 $\pm$ 10 a,b (39 - 60) 3
<i>Rhizocl.</i>	40 $\pm$ 25 b (10 - 91) 19	17 $\pm$ 15 b (4 - 46) 17	9 $\pm$ 7 b (3 - 30) 17	0.72 $\pm$ 0.35 a (0.17 - 1.50) 17	47 $\pm$ 8 a,b (36 - 56) 4
<i>Prasiola</i>	28 $\pm$ 22 b,c (10 - 87) 18	15 $\pm$ 23 b,c (0 - 67) 18	7 $\pm$ 8 b,c (0 - 25) 18	0.55 $\pm$ 0.43 a,b (0.00 - 1.50) 18	101 $\pm$ 37 b (52 - 140) 4
<i>Caloplaca</i>	34 $\pm$ 22 b,c (5 - 70) 16	19 $\pm$ 16 b (1 - 47) 14	6 $\pm$ 4 b,c (1 - 14) 14	0.43 $\pm$ 0.31 b (0.10 - 1.25) 14	73 $\pm$ 29 a,b (53 - 94) 2
Unfed	17 $\pm$ 6 c (10 - 37) 20	4 $\pm$ 3 c (0 - 9) 17	4 $\pm$ 3 c (0 - 12) 17	0.80 $\pm$ 0.68 a,b (0.00 - 2.25) 17	-

sperm within the receptaculum seminis were unknown. The values given below can be used to show relative differences in the effect of various diets, but do not fully represent the species-specific mean of lifetime, reproduction period or fecundity.

In the following text, differences of mean values as shown in Table 3 are pointed out in context with the development in time.

### Mortality

Compared to all other diets, a *Blidingia* diet ensured significantly longer survival.

No significant differences were ascertained in the other feeding tests. Compared to unfed individuals, only those fed on algae had a significantly higher mean survival time. Figure 4 shows the relative portion of survivors in the period after the observation began. Every dot in the figure represents a day on which the death of one or more mite(s) was ascertained.

Corresponding data on *Blidingia* and *Rhizoclonium* as a food source exist also for adults reared in the laboratory from larvae. The mean survival time was 100 days (SD = 51, range 29–235, n = 15) on *Blidingia* and 54 days (SD = 48, range 13–129, n = 6) if fed with *Rhizoclonium*. Even though these values tend to be higher than those for field adults of unknown age (differences not significant), they show the same relation of ca. 2 : 1.

### Reproduction

The duration of reproduction and the number of births of females fed with *Blidingia* was about twice as high compared to those of females fed with other diets. Both parameters are coupled with the individual survival time of the respective females. The birth rate obtained with the feeding of the various green algae ranged from 0.55 to 0.75 larvae per female/day (no significant differences, see Table 3). The birth rate of females fed with the lichen *Caloplaca* was significantly lower than that of females fed on other diets except for *Prasiola*. While the birth rate of the mites kept on *Blidingia* varied relatively little, the respective data of mites fed with other food had a high range. The unfed females differed from the fed ones in their very short reproduction period with frequent larvae births, which explains the unexpectedly high birth rate.

Looking at the development of the birth rate in the course of the experiment, it could be seen that with *Blidingia* as food larvae births occurred regularly during the entire reproductive period. With all other diets, except for the short-living females with *Enteromorpha* supply, at the very latest after three weeks of the diets longer periods of up to 29 days (*Rhizoclonium*) with no larvae production occurred. Figure 5 shows such interruptions of births comparing *Blidingia*, *Prasiola*, and *Caloplaca*.

A significant negative correlation between reproduction period and birth rate was found for the females fed with *Rhizoclonium*, *Prasiola*, and *Caloplaca* ( $R = -0.72$  to  $-0.78$ , n = 14–17).

### Development

Regarding the time period from birth to adult hatch (Table 3), development was retarded in females on a diet of *Prasiola* and of *Caloplaca*. Figure 6 shows the development of individuals for all diets tested (total lifetime of adults is not stated).

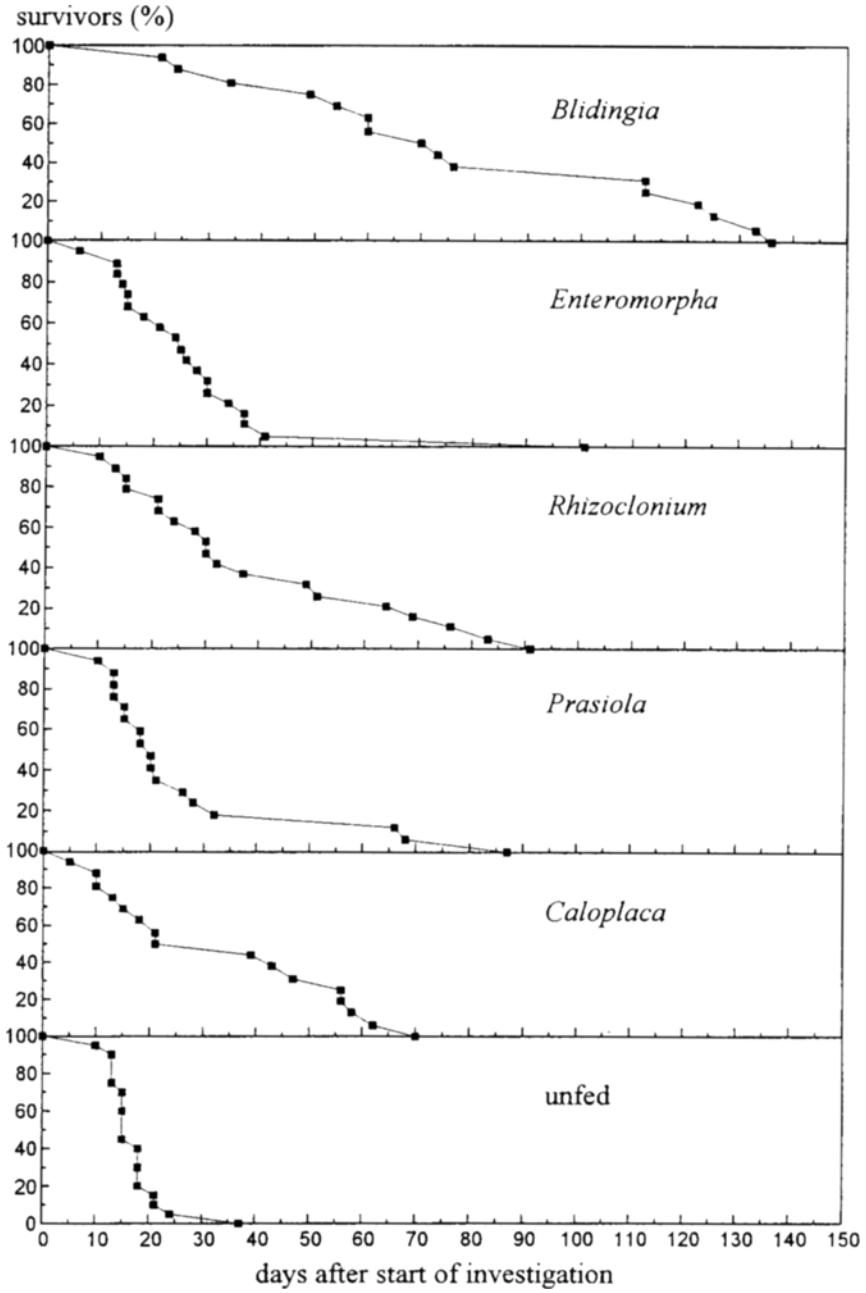


Fig. 4. Survival time of females fed with various diets

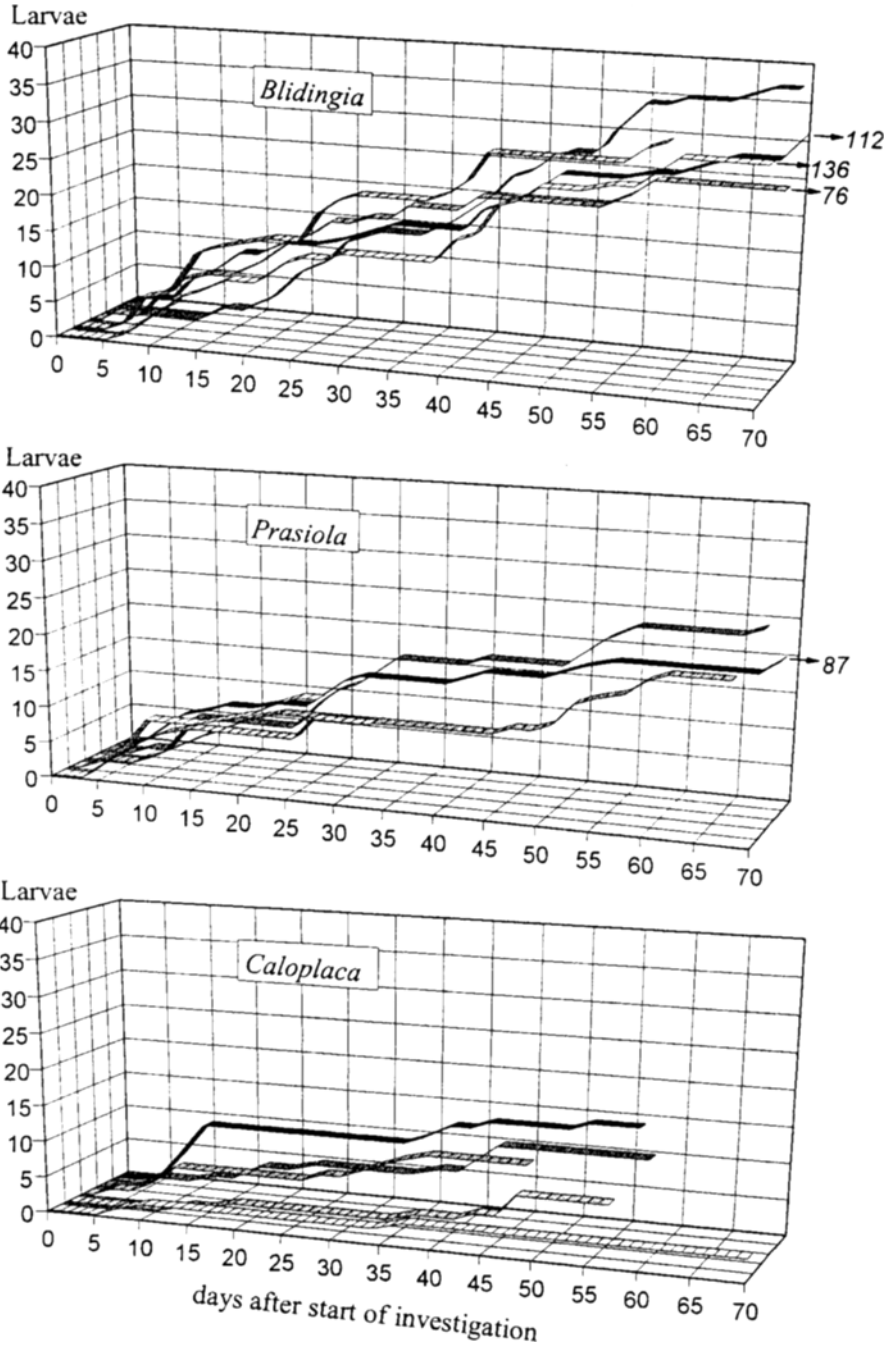


Fig. 5. Larvae births (cumulative) after start of observation of the respective five females with the longest duration of reproduction. The arrows point out the overall survival time of the female (without further larvae births)

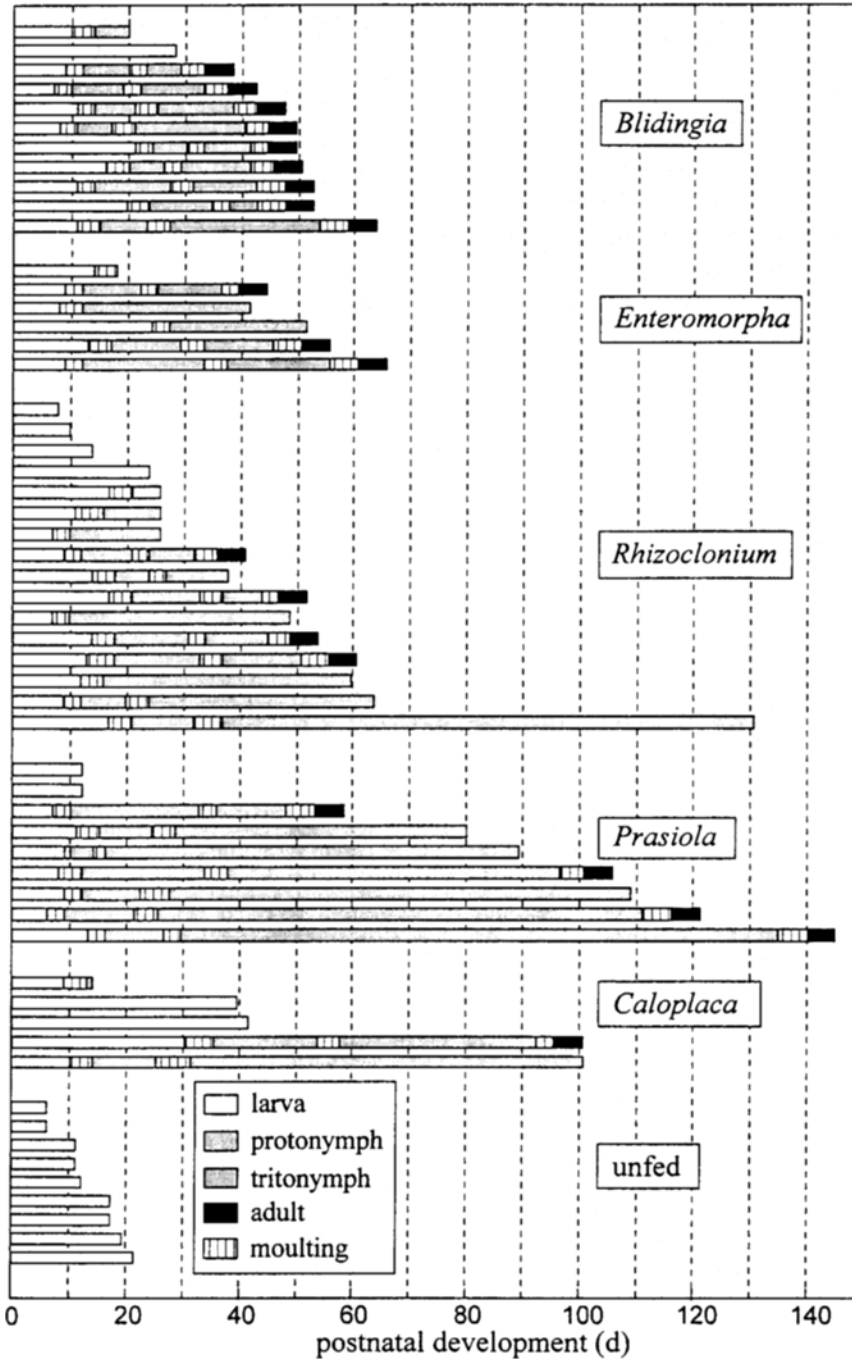


Fig. 6. Postnatal development from larva birth to adult hatch, comparing various diets at 20 °C with a 12 hour light/dark cycle (duration of the adult instar not given)

The various diets differed in their effect on the rearing success. About 80 % of the offspring reared on *Blidingia* finally hatched to adults; with other food supplies it was only 20 to 50 %. Unfed larvae showed no further development. The duration of development with different diets showed a high variability, both within groups and between groups. While one new-born larva reached adulthood in only 33 days (*Blidingia*), another took 140 days (*Prasiola*). The above mentioned retardation of development can obviously occur in all ontogenetical instars; conspicuous are the prolongation of the protonymphal instar if fed with *Enteromorpha* and the prolongation of the tritonymphal instar if fed with *Prasiola*. In some cases, development stopped though death occurred much later (up to three months). The frequency of such development retardations was low if reared on *Blidingia* and high with other food supply.

## DISCUSSION

### Feeding habits and food quality

This investigation shows that *Hyadesia fusca* has a substantially broader diet range than was formerly suspected. In Table 4 an overview of the updated results of gut content or faecal pellet analysis carried out in species of the family Hyadesiidae is given.

All Hyadesiids appear to be microphytophagous (in the sense of Schuster, 1956), but some also accept detritus as food. However, it can be assumed that the actual spectrum of food of the species listed in Table 4 is much broader.

The diet range of the observed population is probably more or less dependent on the accessibility of suitable food at the respective sample site. However, food ingestion does not automatically imply food utilisation. Judging by the observations that (1) *H. fusca* has a clear preference for a distinct green alga with high nutritional value and (2) green algae constitute a food component of nearly all investigated Hyadesiids, one may assume that this taxon is mainly algivorous. Nevertheless, the role played by the epiphytic microflora of macroalgae in the nutrition of Hyadesiids is still unknown. However, the bacteria-rich detritus constitutes only a small part of the food of *H. fusca*. A comparison of the nutritional quality of food samples from the field used in this investigation with that of axenic algae cultures could, perhaps, clarify the issue.

Higher plants and macroalgae with relatively firm tissues e.g. *Fucus* and *Ulva* were not accepted in the feeding tests. Tissue structure and therefore the ease with which the mites can manipulate and ingest their food is probably an important factor that influences the diet range of *H. fusca*. This assumption is further supported by the finding that *Enteromorpha intestinalis*, which is closely related to *Blidingia minima* but has greater cell lumina ( $12 \times 12$ – $20 \times 15 \mu\text{m}$  versus  $5$ – $7 \mu\text{m}$  diameter) and thicker cell walls (Bliding, 1963), is a low-quality food. Furthermore, in the course of the supply experiments the number of faecal pellets produced offering *Enteromorpha* as food was very low compared to that of *Blidingia*-fed test animals. Schulte (1976) assumed for certain algophagous mites of the genus *Ameronothrus* that the instar specific diet range correlates with the size of the chelicerae and depends mainly on tissue firmness and structure, but not on chemical composition of the algae. Larvae and protonymphs accepted only coccal algae and fungi, whereas deutonymphs, tritonymphs and adults fed also on macroalgae or lichens. Siemer (in press) found that the tiny larvae of the halacarid mite *Metarhom-*

Table 4. Gut content and/or faecal pellet analyses of certain species of Hyadesiidae

Species	Reference	Sample site	Gut/faecal pellet contents
<i>Hyadesia fusca</i> (Lohmann, 1894)	Ganning, 1970	supralittoral rock pools, North sea and Baltic sea	<i>Enteromorpha intestinalis</i> , possibly epiphytic bacteria
	Ganning, 1971	dito	<i>Cladophora glomerata</i> ,
	Bénard, 1961*	barnacles, Northwest- France (Cotentin, Bretagne)	mucous layer on barnacles with unicellular algae, bacteria and diatoms
	this investigation	estuarine intertidal and lower supralittoral of embankments (Northern Germany)	different macroalgae (Ulvales, Prasiolales, Cladophorales), microalgae (Cyanophytes, diatoms, unicellular green algae), detritus (incl. its microflora). In the labora- tory also Rhodophyta and lichens
<i>Hyadesia tumida</i> Bénard, 1961	Bénard, 1961	barnacles, Northwest- France (Cotentin, Bretagne)	mucous layer on barnacles with unicellular green algae, bacteria and diatoms
<i>Hyadesia sellai</i> Viets, 1937	Schuster, 1979	intertidal rocks and inside the cavity system of the <i>Lithophyllum-</i> <i>trottoir</i> , Italian adria	predominantly green algae, few Cyanophytes
<i>Amhyadesia</i> <i>costaricensis</i> Fain & Schuster, 1984	Fain & Schuster, 1984b	rocks of the upper intertidal (Costa Rica)	green algae (among others)
<i>Amhyadesia</i> <i>brasiliensis</i> Fain & Schuster, 1984	Fain & Schuster, 1984b	rocks of the upper intertidal with sessile fauna or epilithic algae turf (Brasil)	leftover of green algae thalli, Cyanophyta, seldom diatoms
<i>Amhyadesia</i> <i>heterophallus</i> Fain & Schuster, 1984	Fain & Schuster, 1984a	intertidal rocks, partly with calcareous algae (Maledives and Philippines)	presumably, green algae (green gut content)
<i>Hyadesia</i> <i>verrucosa</i> Fain & Schuster, 1985	Fain & Schuster, 1985	in depressions and crevices of intertidal rocks, covered with green algae ( <i>Istria</i> , former Yugoslavia)	presumably, green algae (green gut content and green faecal pellets)
<i>Hyadesia</i> <i>kerquelensis</i> Lohmann, 1907	Travé, 1988	in the <i>Verrucaria</i> -belt of the intertidal (Kerguelen islands)	<i>Verrucaria</i> sp. (lichens, only the phycobiont)
<i>Hyadesia zelandica</i> Luxton, 1989	Luxton, 1989	on rocks of the upper intertidal among barnacles, in fissures of encrustated oysters, on lichens and in other places (New Zealand)	detritus

\* Bénard (1961) described this for *H. furcillipes* Bénard, 1961, which is according to Fain (1981) a synonym of *H. fusca* (Lohmann, 1894).

*bognathus armatus* (Lohmann) cannot proceed with their postembryonic development if kept on *Enteromorpha* as opposed to those kept on *Blidingia*. However, field adults had the same longevity on both algae.

The spectrum of accepted food at different localities may be influenced by the fact that the shape of thalli and thickness of cell wall of certain algae species may vary greatly under different abiotic conditions (e.g. Bliding, 1963). Young et al. (1987) have shown that *Enteromorpha intestinalis* from estuarine locations has thinner cell walls compared to the same alga from fully marine habitats. On the other hand, the low nutritional quality of certain filamentous or thin monostromatic algae, e.g. *Rhizoclonium* and *Prasiola* for *H. fusca* (this observation) or *Prasiola* for *M. armatus* (Siemer, in press), is evidence that a firm tissue cannot be the only reason for a low suitability.

Other possible factors influencing the suitability or acceptance of food could be (1) the energy and water content; (2) the carbohydrate and nutrient composition (e.g. starch, lipid, polyol, amino acids and vitamin content); (3) the relative proportion of indigestible components and (4) possible mechanisms of the algae that protect from being fed on. Levinson et al. (1992) reported the significant influence of various vitamins on lifetime, fecundity, and development in the flour mite *Acarus siro* L. (Astigmata: Acaridae). Bowman & Childs (1982) found amylase and chitinase in all of the six investigated Astigmatid mite species, and cellulase in two of them. However, the possible role of endosymbionts and their enzymes in the digestion of cell walls, well known in insects, is not fully understood in the case of mites.

One possible mechanism for algae to protect themselves from grazers is chemical defence (Paul, 1992), e.g. the production of toxic phenols and tannins as described for brown algae (Carefoot, 1977; Roussis et al., 1993; Winter & Estes, 1992). Many green algae, e.g. *Blidingia*, *Enteromorpha* and *Ulva*, produce a great amount of Dimethylsulfoniumpropionate (DMSP) (Reed, 1983), which is discussed to have protecting features, possibly due to the release of acrylic acid (Glombitzka, 1970; Keller et al., 1989). At least for *H. fusca* with its preference for *Blidingia* the DMSP seems not to be a deterrent.

The experiments on food preference revealed a searching behaviour favouring *Blidingia*, but the causality of this behaviour, e.g. different palatability, attractants of the preferred food, deterrents or repellents of the avoided food, mechanical stimuli (size and shape of thalli), remains unclear. However, the preference behaviour of *H. fusca* is obviously correlated to the suitability of the respective food. Contradicting this, Paine & Vadas (1969) concluded that availability of seaweeds, and not absolute food value, was a more decisive factor for the evolution of preferences of marine herbivores. For example, Carefoot (1973) has shown for the supralittoral isopod *Ligia pallasii* (Brandt) that feeding preference is not necessarily linked to the energy content of the food. On the other hand, in some cases food that was in short supply or totally absent in the natural habitat of certain marine herbivores was preferred in laboratory tests (Leighton & Booloatian, 1963; Carefoot, 1970, 1973).

#### The influence of feeding habits on distribution patterns

A migration to surfaces covered with *Blidingia* and a low mortality of juveniles and adults – accompanied by a higher fecundity – would lead to higher population densities. Evidence that preference behaviour and food quality could affect distribution patterns



and population density is given by the fact that a higher abundance of *Hyadesia fusca* was found on surfaces and in the littoral zone dominated by *Blidingia* (Bücking, in press). Food supply is of course only one of the many interacting factors influencing distribution limits and population dynamics. Carefoot (1977, pp. 46–47) remarked, that "The distribution of an organism represents the best compromise between its physiological and space requirements, and the conditions existing in the habitat". In particular the following must be taken into account: (1) alternating submersion and emersion; (2) high fluctuation of humidity, salinity and temperature – increasing with littoral height; (3) surface structure and composition – inclusive vegetation and sessile animals; (4) mechanical stress due to wave action, brushing action of algae and sediment-mediated abrasion and (5) interspecific competition (cf. Lewis, 1964; Little & Kitching, 1996). Nevertheless, in addition to the great risk of desiccation in the supralittoral zone, the abundance of low-quality food (lichens) would render impossible a build-up of a stable *H. fusca* population. Even the low nutritional quality of algae present in the middle and lower intertidal, e.g. *Enteromorpha* and red algae, may account for the low population density in this littoral region.

The low species diversity and abundance of mites of terrestrial origin in lower littoral zones are thought by many authors to be mainly the result of a restricted tolerance to submersion, a reduced time for foraging and – as previously mentioned – mechanical impact (Pugh & King, 1985b; Schulte, 1977; Schuster, 1979). In view of the fact that (1) *H. fusca* is a common inhabitant of Baltic rock pools (Ganning, 1970, 1971; Östman & Rönnberg, 1991) and that (2) specimens of the investigated intertidal population can live, feed and reproduce totally immersed for several months in the laboratory (Bücking, unpublished), foraging and inundation time can explain neither the absence of this species in the lower intertidal nor their low population density in the middle intertidal of the Weser estuary. The longer time of exposure to wave action and water currents in the lower intertidal zones might be an additional factor causing lower population densities. This view is supported by results of Östman & Rönnberg (1991) who observed significantly lower abundances of *H. fusca* in rock pools subject to regular wave action caused by ships compared to undisturbed reference pools. According to Pugh & King (1985b), the distribution of Hyadesiids on British rocky shores depends on the prevalence of barnacles which offer protection against wave action. However, both laboratory experiments on the ability of littoral mites to withstand mechanical stress and measurements of water pressure within the microhabitat of the mites, e.g. inside the dense algae cover or within cavities of the rock surface, have yet to be carried out.

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