

Population dynamics and life history of the oribatid mite *Ameronothrus lineatus* (Acari, Oribatida) on the high arctic archipelago of Svalbard

Guldborg Søvik^{1*}, Hans Petter Leinaas¹, Rolf Anker Ims² and Torstein Solhøy³

¹ Biological Institute, Department of Zoology, University of Oslo, P. O. Box 1050, Blindern, N-0316 Oslo, Norway

² Biological Institute, Department of Ecology, University of Tromsø, N-9037 Tromsø, Norway

³ Zoological Institute, Department of Ecology, University of Bergen, Realfagbygget, Allégt. 41, N-5007 Bergen, Norway

Submitted June 28, 2002 · Accepted October 1, 2002

Summary

Ameronothrus lineatus was studied in the northernmost part of its distribution range in the high Arctic. Survey sampling was carried out on two sites on West Spitsbergen: a *Carex* saltmarsh and a smooth layer of cyanobacteria, where the species was the only oribatid mite collected. On the latter substrate all mites were visible and could be sampled by hand, making it ideal for demographic studies. An experimental population was established in microcosms based on the mite-cyanobacteria system, and all three populations were sampled regularly during summer 1998. Our results suggested spatial variation in reproductive patterns between local populations. Influence of climatic variation on demography was illustrated by comparing reproduction in 1997 and 1998. Synchronous larviposition was observed in early summer, but recruitment also occurred throughout the season, and gravid females were found on all sampling dates. Both the saltmarsh and the cyanobacteria populations were female biased. A highly synchronous moulting involving at least 80% of the juveniles was observed in July, and it seems that juveniles moult once per season on average. The synchronous moult is suggested to be a phenological strategy to exploit the short arctic summer by timing moulting with the warmest part of the season. A generation time of 5 years was estimated. Juvenile stages of one year, continuous recruitment, and high adult longevity (2–3 years) give stable stage structures and stable population dynamics.

Key words: Phenology, demography, life cycle, moulting, sex ratio, reproductive biology

Introduction

The diversity of the arthropod fauna in arctic regions is fairly well known (Danks 1981; Coulson & Refseth, in press), and through the International Biological Programme (IBP) densities, biomass production, nutrient cycling and energy flow of tundra arthropod communities were investigated, with an emphasis on soil systems (Brown et al. 1980; Bliss et al. 1981). Information on population biology and life history strategies is,

however, fragmentary (Danks 1981, 1999). Detailed life histories and demography are known for only a few insect and collembolan species (Addison 1977; Danks 1981, 1999; Hertzberg et al. 1994, 2000; Birkenmoe & Leinaas 1999, 2000, 2001). Population studies have been carried out for a few collembolan species (Addison 1977; Hertzberg et al. 1994, 2000; Birkenmoe & Sømme 1998). In order to improve our understand-

*E-mail corresponding author: guldborg.sovik@bio.uio.no

ing of the functioning of arctic invertebrate systems, detailed knowledge on species level is a prerequisite (Hodkinson & Wookey 1999). Thus, life history, demography and trophic interactions are areas in which more studies are needed. Furthermore, other groups of terrestrial arthropods important in the Arctic, such as oribatid mites, should be studied.

Mites (Acari) inhabit some of the most barren and inhospitable areas of the earth. In arctic soils with organic matter the suborder Oribatida constitutes, together with collembolans, the dominant microarthropods (Danks 1981) and is an essential component of the soil ecosystem as secondary decomposers. Characterized by long life cycles, high adult survival and low fecundity (Norton 1994), oribatid mites differ in many aspects of life history from the general patterns seen in collembolans (Hopkin 1997). However, compared to the collembolans, our knowledge about the population biology and demography of arctic oribatid mites is scarce. Scattered papers describe stage structures (Hammer 1944; Seniczak & Plichta 1978), and seasonal variation in density (Hammer 1944; Webb et al. 1998), but no detailed studies exist. However, population dynamics, demography and life cycles of oribatid mites in cold regions have been studied in sub-alpine (Mitchell 1977; Kuriki 1995), alpine (Solhøy 1975; Schatz 1985; Tilrem 1994) and antarctic regions (West 1982; Convey 1994a, b; Block & Convey 1995; Marshall & Convey 1999). Most extensively studied is the antarctic species *Alaskozetes antarcticus* (Michael), which has a 5-year life cycle and low reproductive output (Block & Convey 1995; Convey 1998). Oribatid populations in alpine and polar regions have been suggested to have elongated life cycles because of low heat budgets compared with temperate populations, but to lack particular life history traits adapting them to the cold environment (Norton 1994; Behan-Pelletier 1999).

The present paper focuses on the population dynamics and life history of the oribatid mite *Ameronothrus lineatus* (Thorell 1871) in the high arctic archipelago of Svalbard. *A. lineatus* was chosen as study object because it was found in high densities in two quite different habitats: a *Carex* saltmarsh and a smooth layer of cyanobacteria, where it was the only oribatid mite living. In particular the cyanobacteria surface with the single oribatid species living and feeding on it, constituted a simple and unique system which proved to be excellent for population and life history studies of a microarthropod *in situ*. The two-dimensional surface allowed all mites in the population to be observed and sampled by hand, which is a great advantage compared with investigations of soil dwelling populations based on dynamic extraction methods with uncertain efficiency (Petersen 1978). Furthermore, dynamic sam-

pling methods fail to extract eggs and immobile pre-moult juveniles. Being able to sample all specimens in a population, we could estimate accurate stage-structure, timing of moulting, and length of life cycle, information usually not obtainable from field sampling. This study addresses the following aspects: What are the life history characteristics of an arctic population of *A. lineatus*? Are phenology and demography similar under different climatic conditions and in locally separated populations? Does the species show any adaptations to the polar climate? This is the first detailed description of the dynamics and life history of an arctic oribatid mite. The work is part of a more extensive study on the species, also including laboratory experiments, aiming at increasing our understanding of arthropod systems in cold regions.

Materials and Methods

Study organism

A. lineatus is a littoral species distributed in arctic and temperate regions of the Holarctic (Hammer 1944; Weigmann & Schulte 1975; Schulte et al. 1975; Danks 1981; Colloff 1984). The species becomes less tied to the marine tidal zone at higher latitudes (Schuster 1966), and on Svalbard we have found it underneath rocks 500 m from the shore, and 100–150 m above sea level (unpubl. data). Earlier works have described zonation in the littoral habitat (Schulte et al. 1975; Ernst et al. 1993) and diet (Schulte 1976), and Schubart (1975) made scattered observations on stage structure and sex ratio. But only one detailed study focusing on population dynamics and life cycle exists (Bücking et al. 1998).

A. lineatus follows the general life cycle of an oribatid mite with six distinct instars: prelarva, larva, proto-, deuto- and tritonymph and adult. There are few morphological differences between eggs and prelarvae in this species, and we therefore counted all as eggs. Contrary to most oribatid mites (Norton 1994), *A. lineatus* is larviparous. Juveniles go through a quiescent stage before moulting to the next instar.

Study sites

Fieldwork was carried out in the bay Colesbukta (78°5'N 14°57'E) and the valley Adventdalen (78°10'N 15°30'E) in the Isfjorden area, West Spitsbergen. Here the average air temperature is below 0°C from the beginning of September until the middle of May or beginning of June (Førland et al. 1997). Snow cover generally persists until the beginning of June (pers. obs.).

Table 1. Monthly precipitation (mm) and middle temperature (°C) with monthly normal precipitation and temperature from June to September in 1997 and 1998 at Longyearbyen Airport, Svalbard. Data obtained from the Norwegian Meteorological Institute

	Year	June	July	August	September
Precipitation	Normal	10.0	18.0	23.0	20.0
	1997	2.0	28.2	37.4	29.2
	1998	2.7	0.7	11.0	9.9
Temperature	Normal	2.0	5.9	4.7	0.3
	1997	2.6	5.3	4.7	0.6
	1998	2.7	8.3	6.9	0.3

Summer 1997 was wetter, while summer 1998 was warmer and drier than normal (Table 1). Surface soil temperature was recorded with Tinytalk dataloggers. In Colesbukta the logger stopped working properly early in the season, and we do not have temperature data from this site. In Adventdalen temperature was measured in the study site and within a microcosm. In July (11–31) the average temperature (with temperature range) was 10.8 (6.6–18.6)°C in both places, while in August it was 7.8 (4.0–14.3) and 8.0 (3.1–16.4)°C in the study site and microcosm respectively. Cumulative day degree totals (July 11–September 3) were 478 and 487 in the study site and microcosm respectively.

In Colesbukta sampling was carried out in the delta area formed by the rivers in Lailadalen and Colesbukta, at a distance of 400–500 m from the shore. The study site, about 10 × 10 m², consisted of water-logged mud flats covered with a smooth, thin (1 mm) layer of cyanobacteria with scattered *Puccinellia phryganodes* (Trin.) Scribn. & Merr. (Creeping saltmarsh grass). *A. lineatus* was the only arthropod found living on the cyanobacteria mats. In addition enchytraeids and nematodes burrowed into the substrate. The mites were patchily distributed, and were often observed in dense aggregations around the stems of *P. phryganodes*. There were no crevices in the surface where the animals could seek protection.

In Adventdalen mites were sampled 1 km southeast of the town Longyearbyen, in a saltmarsh located about 50 m southwest of the Advent River and 400–500 m from the shore. The study site, approximately 10 × 10 m², consisted of wet mud flats covered by *Carex subspathacea* Wormsk. (Arctic saltmarsh sedge) and moss. At spring tide sea water sometimes reaches the area as is shown by the occurrence of driftwood. The organic soil layer was 2–3 cm thick, and the mites did not appear to be limited to the surface as in the Colesbukta area. *A. lineatus* was the only oribatid mite present. However, collembolans and Diptera larvae were also found here in addition to nematodes and

enchytraeids. In late June both sites were flooded by meltwater, and they remained wet throughout the summer.

Sampling design

The different populations required different sampling regimes and techniques. Thus, they were not comparable with respect to all parameters. Nevertheless their differences elucidated different aspects of the species' demography and life history.

In Colesbukta animals were sampled specifically from the high density patches in order to get a good representation of all life stages for detailed analyses of demography, life cycle and moulting patterns. On each sampling date (June 23, July 31, August 26, 1998) one disc (diameter 3.5 cm) of the cyanobacteria surface was sampled from ten haphazardly chosen patches of mites with a soil corer. The area is not easily accessible, which limited the number of sampling dates. On July 18 ten additional samples were taken haphazardly within the whole Colesbukta study site, independent of mite aggregates, by botanists visiting the area. These samples were also included in the Colesbukta data set. All mites were removed from the cyanobacteria discs with a soft brush under a stereomicroscope, and the presence of exuviae (cast-off skins) was noted.

To carry out more unbiased sampling and to control for possible migration in and out of the patches, as well as to get easier access to the study site, we established an experimental population based on the cyanobacteria-mite system. On June 23, 1998 a total of 50 discs from the high density patches were sampled by a soil corer (diameter 3.5 cm). Ten of these were sampled randomly to represent the sampling for June 23 (see above). The 40 additional discs were placed on mud from the site, in microcosms made of plastic boxes (diameter 4.2 cm, height 4.7 cm) with holes covered with plankton mesh for ventilation and drainage. The microcosms were placed in holes in the ground at the Adventdalen site, so that the inside surface was flush with

the tundra-surface. Because of their common origin, we defined this set of microcosms as one population, from which we collected a random subset of ten on July 15, August 5 and 25, and September 3, 1998. As the June 23 discs were sampled from this population, they were also used as the first data set for the microcosm series. This experimental population constituted the main focus of the population study, with the Colesbukta population as a natural reference living on the same substrate.

The microcosms were transferred to an environment with possibly somewhat different microclimatic conditions (temperature and humidity) than Colesbukta, which might affect the phenology and demography of the species. We therefore also studied the resident *A. lineatus* population in the soil outside the microcosms, thus enabling comparison with a natural population experiencing very similar abiotic conditions (see above). This also allowed us to study spatial differences in population dynamics and demography by comparing the cyanobacteria system with a saltmarsh population. On the Adventdalen site we haphazardly collected 13 soil cores (diameter 6.5 cm, height 3 cm) on each sampling date (July 8 and 15, August 5 and 25, and September 3, 1998). Preliminary sampling of the Adventdalen site in 1997 with a soil corer of diameter 3.5 cm had shown that a larger corer size was necessary in order to ensure a number of mites per sample high enough to analyse. We included the 1997 material in order to obtain reproduction data from a summer with more average weather (Table 1). Soil cores (diameter 3.5 cm, height 3 cm) were collected on June 29, July 21 and August 10 ($n = 10$), and on September 15 and 18, 1997 ($n = 40$). The soil dwelling animals from Adventdalen were extracted over 8 days using a high-gradient extractor (Macfadyen 1961). This method has its limitations as quiescent juveniles are not extracted, and the extraction efficiency of mobile juvenile *A. lineatus* is also considerably lower than that of adults (Søvik & Leinaas 2002).

Sample treatment

Mites were preserved in 70% alcohol. All specimens from the Colesbukta and microcosm populations were cleared in lactic acid and determined to instar and gender (adults). Larvae are easily recognized, having only three pairs of legs. Stage determination of nymphs was based on the number of genital papillae and genital setae. Adults are morphologically different from juveniles (Schubart 1975), and the sexes were distinguished by the presence of an ovipositor or a long penis. Presence of eggs and larvae in cleared, gravid females was recorded, where gravid

females are defined as females carrying eggs, prelarvae and/or larvae. Quiescent juveniles were easily recognized as turgid and completely motionless. Immobile specimens of normal appearance were considered dead. Body length of 120 specimens from all life stages and both sexes was measured to an accuracy of 0.0125 mm at $40 \times$ magnification under a stereomicroscope, using mites from the microcosms (August 5 and September 3 collections). Nymphs from Adventdalen in 1998 were not stage determined, but were pooled into one group. Adults were cleared and sexed, and progeny counted in females. Due to low numbers of immatures in the 1997 material, only adults were analysed.

Statistical analyses

All statistical analyses were carried out using the software S-Plus 2000. Number of specimens per sample was used as the unit in the comparison of densities between dates. Due to skewed distributions, data were analysed by non-parametric tests (Kruskal-Wallis). Population dynamics data from Colesbukta were not analysed due to non-random sampling of high density patches.

The July 18 data from Colesbukta were not included in any statistical analyses because of a different sampling regime. The proportion of quiescent juveniles was analysed by logistic regression models. A forward model selection procedure based on the deviance was used to determine which of the predictor variables (time and stage) should be included in the model. Rows containing zero animals were removed from the data set(s). If the residual variance of the models did not fit a binomial distribution (goodness-of-fit test), i.e., if data were overdispersed, the model was refitted using the quasi-likelihood method (link = logit, variance proportional to $\mu(1-\mu)$). Original and re-fitted models used respectively the deviance and F-statistic as test statistics. Multiple comparisons (simulation-based method) were used to obtain 95% confidence intervals (logit scale) for differences between stages, where intervals excluding zero showed significant differences between proportions.

The stage structure data were analysed by log-linear models (contingency table analysis). The predictor variables time and stage were found to be dependent in all populations (Pearson χ^2 -test). All full models were overdispersed and were refitted using the quasi-likelihood method (link = logit, variance proportional to μ^2). Contributions to the Pearson χ^2 from the different cells in the contingency tables determined which life stages contributed most to the observed dependency between time and stage.

The proportion of female mites, of gravid females, and females carrying larvae in the microcosms and Adventdalen in 1998 were analysed by logistic regression models as described above with time and site as variables. Adventdalen data from 1997 were analysed with time as variable. Data on eggs, larvae and total progeny per gravid female were analysed with log-linear models based on the poisson distribution, with time and site as variables.

Results

Population dynamics

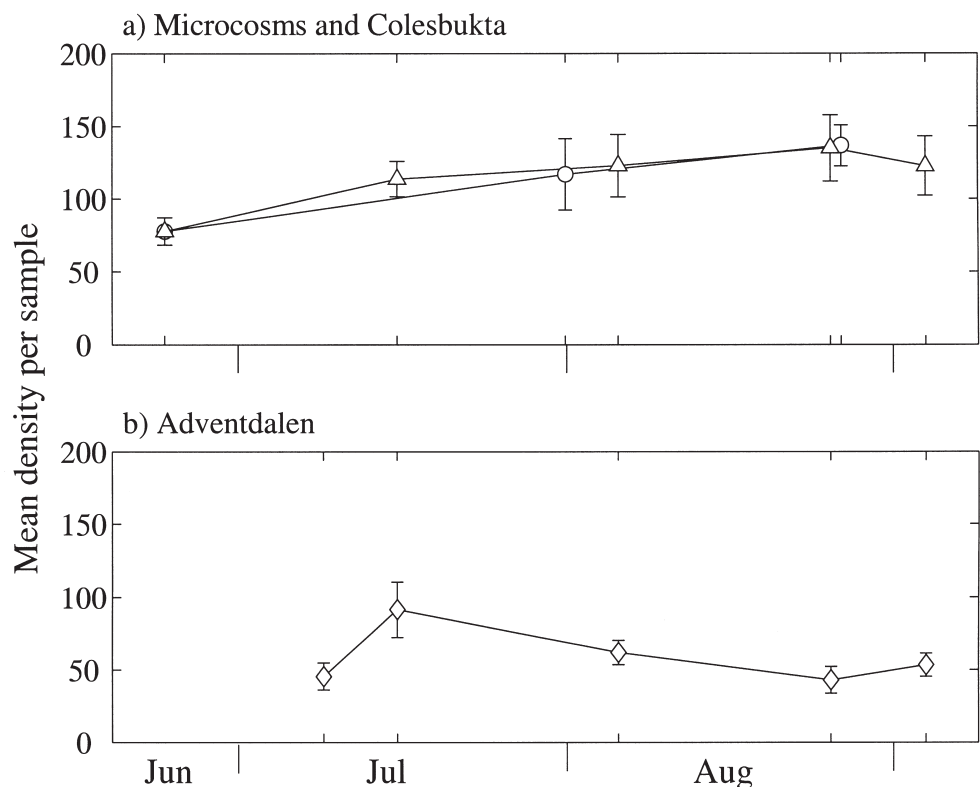
There was a close similarity in the late July and August densities of the microcosm and Colesbukta populations (Fig. 1a). No significant difference between sampling dates was found in the microcosm population (Kruskal-Wallis $\chi^2 = 5.64$, $df = 4$, $P = 0.227$). The Adventdalen population (Fig. 1b) showed a similar lack of significant variation during summer although the mean density doubled between July 8 and 15 (Kruskal-Wallis $\chi^2 = 8.67$, $df = 4$, $P = 0.070$). Difference in sampling design and extraction technique made comparison of density between the two former populations and the latter one of little relevance.

Body length and moulting

The growth curve of *A. lineatus* is almost linear (Fig. 2). Females were considerably longer than males. The size increase from tritonymphs to males was the smallest one recorded between two successive stages. There was considerable overlap in length between the different life stages.

No pre-moult immatures or exuviae were found in the June 23 samples. In the microcosms about 80% of all juvenile mites were quiescent on July 15 (Fig. 3a), but no exuviae were found. Many were observed in dense clusters. By August 5 the proportion of quiescent juveniles had dropped considerably, and the microcosms were full of exuviae, suggesting a rather synchronous moulting. However, the interaction of time and stage was highly significant (logistic regression: $\text{time} \times \text{stage}$, $F_{12,180} = 3.83$, $P < 0.001$), showing that moulting was not completely synchronized in the four juvenile stages. On August 5 there were clear differences between stages, which were significant in 50% of the cases (tritonymph-larvae: 1.35–3.16; tritonymph-protonymph: 0.38–2.39; deutonymph-larvae: 0.30–2.49). Thus, older stages moulted later (Fig. 3a). Variation within stages was indicated by the approximately 20% non-quiescent immatures on July 15. These juveniles could have finished moulting, moulted later in the season, or moulting was possibly postponed until next summer.

Fig. 1. Population dynamics of a) the microcosm (Δ) ($n = 10$) and Colesbukta samples (\circ) ($n = 10$), and b) the Adventdalen samples (\diamond) ($n = 13$) during summer 1998, where population densities are given as mean number (all instars) per sample (\pm S.E.). The surface area of the samples from the cyanobacteria surface (microcosms and Colesbukta) and Adventdalen soil was 9.6 and 33.2 cm² respectively. The June 23 data are the same for the microcosm and Colesbukta series. Sampling dates (indicated by tick marks) are given in the text



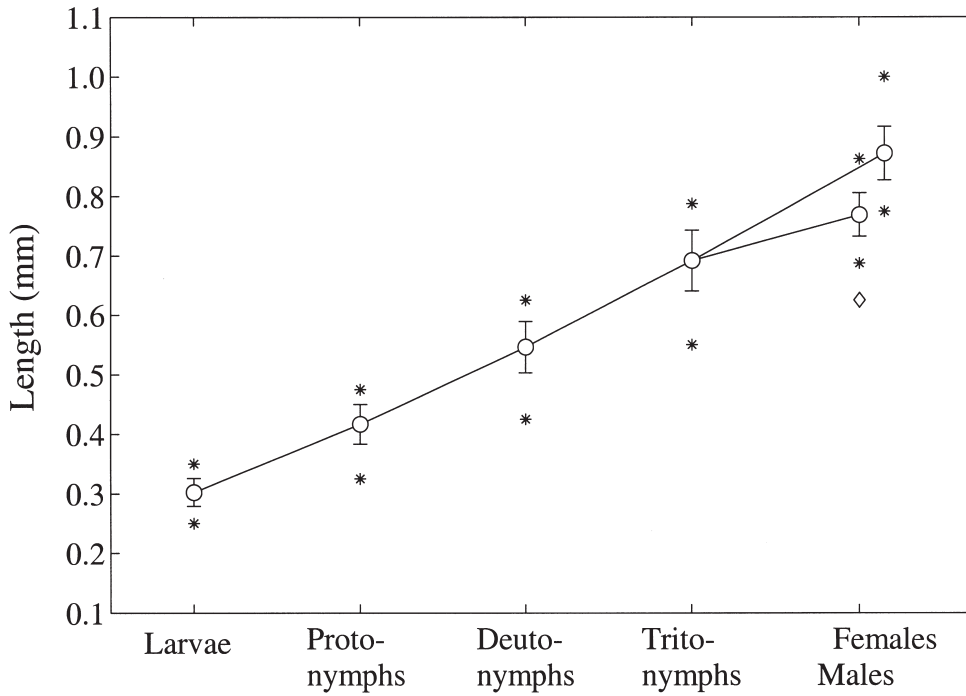


Fig. 2. Average body length (mm) of all life stages of *A. lineatus* (\pm S.D.) based on data from the microcosms ($n = 120$ for all stages and both sexes). Asterisks represent ranges (min-max). An outlier in the male sample is denoted by a diamond

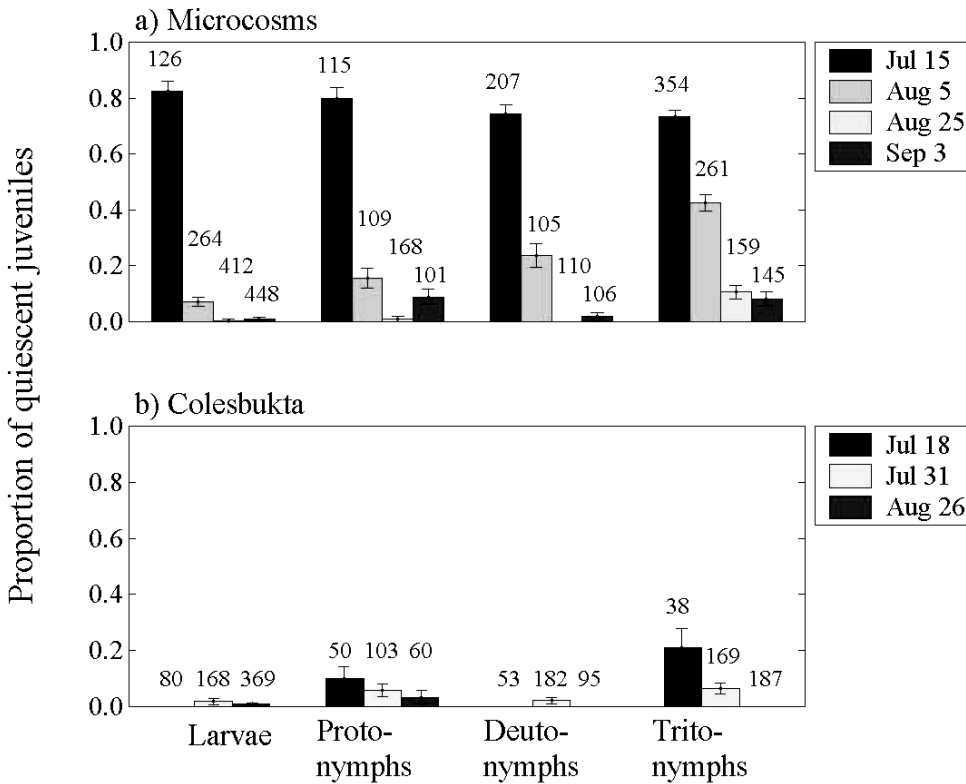
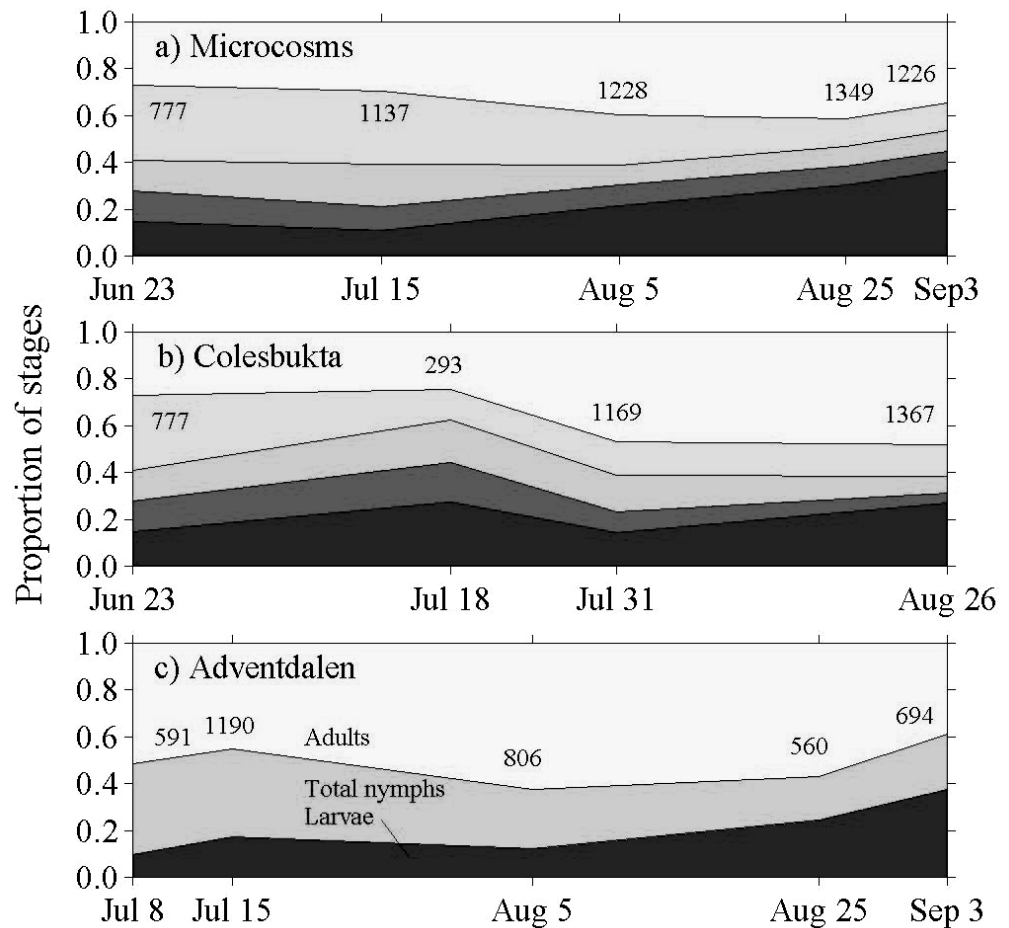


Fig. 3. Proportions (\pm S.E.) of the different juvenile instars of *A. lineatus* found in the pre-molt quiescent stage at the different sampling dates summer 1998 for a) microcosms and b) Colesbukta. Proportions on June 23 were all equal to zero. For each locality, date and instar, all samples were pooled, and pooled mite numbers are given by figures

Fig. 4. Proportions of the different instars of *A. lineatus* summer 1998 for a) microcosms, b) Colesbukta, and c) Adventdalen. For each locality and date, all samples were pooled, and pooled mite numbers are given by figures. The five areas in a) and b) represent, from bottom to top: larvae, proto-, deuto-, tritonymphs, and adults respectively, while the three areas in c) denote larvae, total nymphs, and adults. Note different scales on the x-axes



In contrast to the microcosm population, there were no conspicuous peaks in the proportion of quiescent juveniles from Colesbukta (Fig. 3b). The largest proportion was found on July 18 together with exuviae, showing that some juveniles already had moulted by the middle of July. It is also possible that the random sampling on July 18 may have missed aggregates of quiescent juveniles. Only time was a significant variable (logistic regression: deviance = 37.26, df = 2, $P < 0.001$).

Stage structure

The stage structure of *A. lineatus* was quite stable in time (Fig. 4) and all stages were collected at all dates. Adults dominated in numbers, and the proportion of larvae and tritonymphs were high compared with the other juvenile instars. There was a highly significant interaction in the microcosm model (log-linear model: stage*time, $F_{16,225} = 4.52$, $P < 0.001$), reflecting that dominance shifted between stages during summer. Larvae on July 15 and September 3 constituted the cells in the contingency table contributing most to the

Pearson χ^2 . Tritonymphs also contributed substantially. Similarly, the interaction in the model of the Colesbukta population was significant (log-linear model: stage*time, $F_{8,135} = 4.02$, $P < 0.001$). Adults and tritonymphs on June 23 and larvae on August 26 made the highest contributions to the Pearson χ^2 . The Adventdalen data were analysed with nymphal stages combined. Adults constituted about 50% of the samples. The interaction was highly significant (log-linear model: stage*time, $F_{8,180} = 4.45$, $P < 0.001$). Larvae on September 3 made the largest contribution to the Pearson χ^2 , with larvae on July 8 and August 5, and nymphs on August 25 also contributing. Thus, changes in the structure of all three populations resulted mainly from an increasing number of larvae as summer progressed.

Sex ratio and reproduction

Large fluctuations in the sex ratio were observed in Colesbukta during a two-month period (Fig. 5a). However, it seems very unlikely that such large fluctuations reflected real changes in the population, as this would imply first a high female, and then a high male mortal-

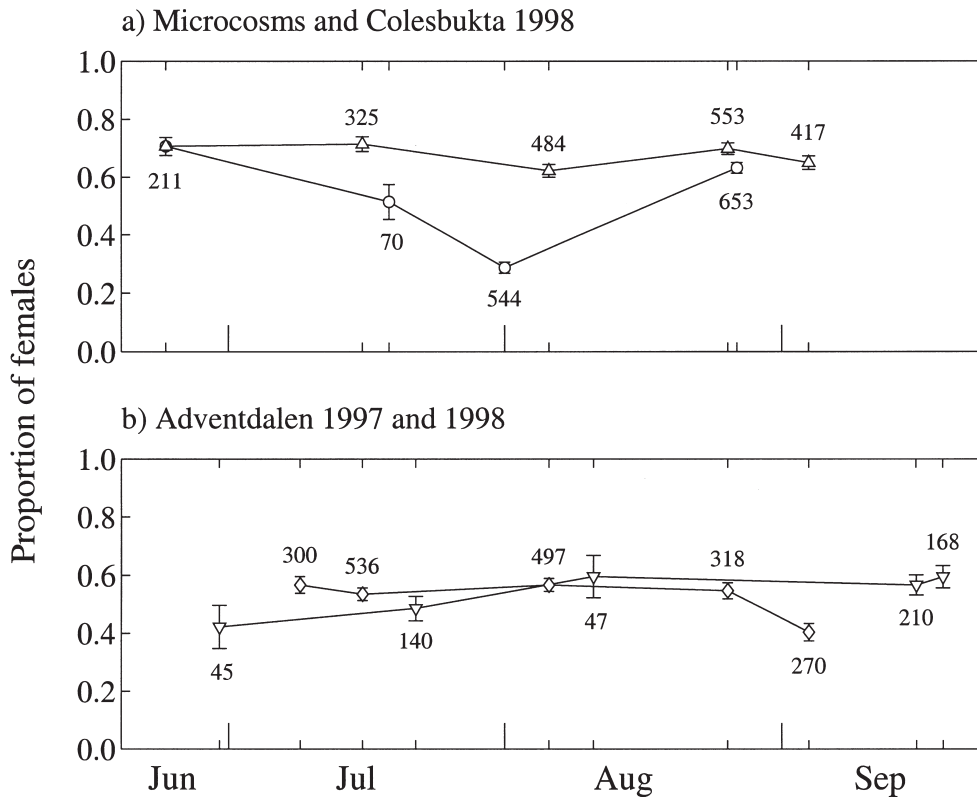


Fig. 5. Proportion of females (\pm S.E.) in *A. lineatus* in a) microcosms (Δ) and Colesbukta (\circ) in 1998 and b) Adventdalen in 1997 (∇) and 1998 (\diamond). Sample sizes (given by figures) are total adult populations for each locality and date. The data from June 23 are used in both the Colesbukta and microcosm series. Sampling dates (indicated by tick marks) are given in the text

ity. The fluctuations probably reflected a change in the spatial distribution of the sexes, made apparent by the non-random sampling of the cyanobacteria surface. In comparison the sex ratios in the microcosms and in Adventdalen seemed to vary little seasonally (Fig. 5a, b). A significant interaction between site and time (logistic regression: site*time: $F_{3,105} = 3.42$, $P = 0.020$) was caused mainly by a drop in the proportion of Adventdalen females in September. On removing these data, only site remained significant (logistic regression: $F_{1,100} = 35.26$, $P < 0.001$). Pooling samples from different dates, gave proportions of 0.67 (95% conf. int.: 0.65, 0.69; $n = 1990$) and 0.55 (95% conf. int.: 0.53, 0.58; $n = 1651$) from the microcosms and Adventdalen respectively. Thus, both populations deviated from a 1:1 sex ratio. In 1997 the slightly increasing trend through summer (Fig. 5b) was not significant (logistic regression: deviance = 7.30, $df = 4$, $P = 0.121$). All samples pooled gave a female proportion of 0.55 (95% conf. int.: 0.51, 0.59) ($n = 610$).

Gravid females were found on all sampling dates. The first sampling from Colesbukta (June 23) gave a very low proportion of pregnancy. In the microcosms this was followed by a peak of 93.5% in July, after which it decreased steadily through the summer (Fig. 6a). The proportion of gravid females in the Colesbukta population showed a similar temporal trend. As

the Colesbukta females may represent biased samples (see above), the reproductive data from this site were not analysed statistically. Also the Adventdalen population in 1998 showed reduction during summer, but on the first sampling date (July 8) on this site all females were gravid (Fig. 6b). This temporal difference was reflected in the highly significant interaction in the model of the Adventdalen and microcosm data (logistic regression: time*site, deviance = 28.08, $df = 3$, $P < 0.001$). Also in 1997 all females were gravid on the first sampling date (Fig. 6b). However, contrary to 1998, the proportion remained high, except for a drop in July, giving a highly significant effect of time (logistic regression: deviance = 58.97, $df = 4$, $P < 0.001$).

In 1998 the proportion of the females carrying larvae increased in both the microcosms and Colesbukta from a very low level in June (Fig. 7a). In Adventdalen the proportion dropped from an initial high level of 56% to 21% within a week in early July and then increased sharply to a very high level of 95% (Fig. 7b). These differences are reflected in the significant interaction in the model describing the microcosm and Adventdalen populations (logistic regression: time*site, deviance = 180.43, $df = 3$, $P < 0.001$). In Adventdalen in 1997 there was a drop in the proportion of females with larvae in July, making time a significant variable (logistic regression: deviance = 11.68, $df = 4$, $P = 0.020$).

Fig. 6. Proportion of gravid females (\pm S.E.) of *A. lineatus* in a) microcosms (Δ) and Colesbukta (o) in 1998, and b) Adventdalen in 1997 (∇) and 1998 (\diamond). Sample sizes (given by figures) are total numbers of females for each locality and date. The data from June 23 are used in both the Colesbukta and microcosm series. Sampling dates (indicated by tick marks) are given in the text

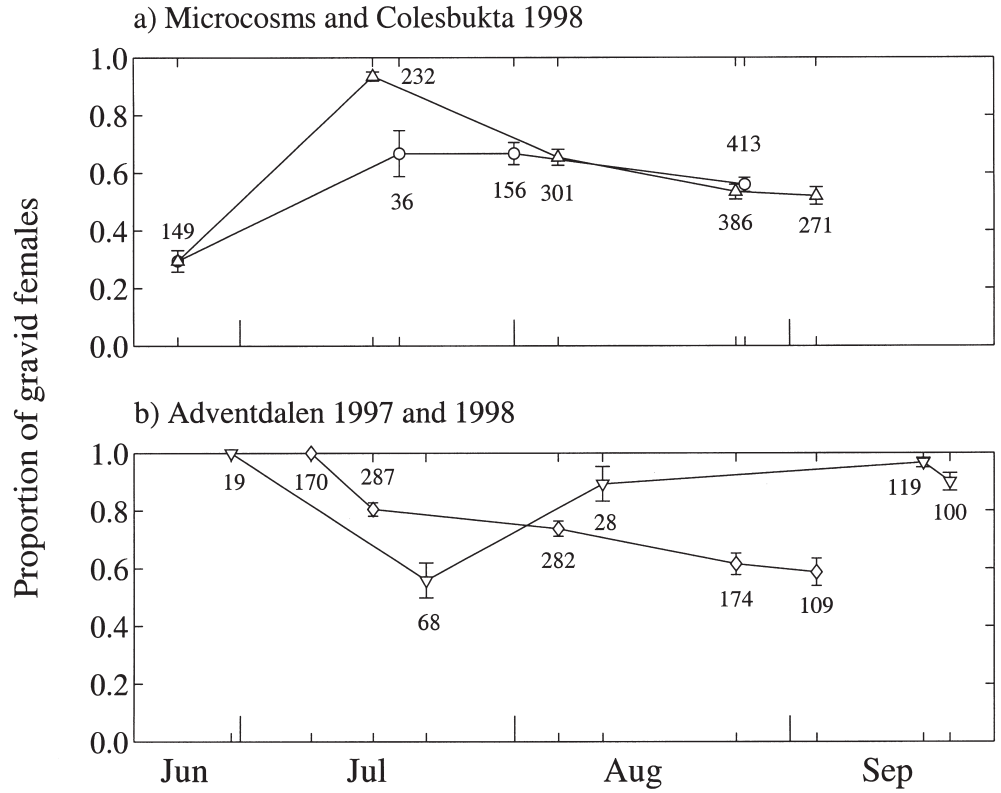
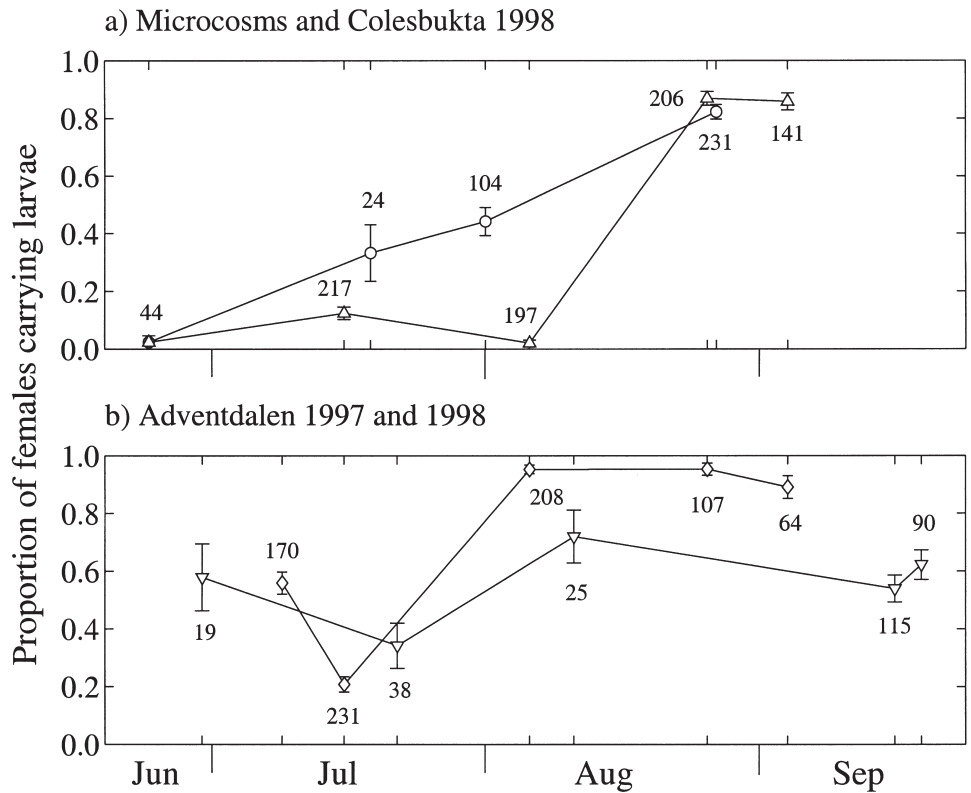


Fig. 7. Proportions of females carrying larvae (\pm S.E.) in *A. lineatus* in a) microcosms (Δ) and Colesbukta (o) in 1998 and b) Adventdalen in 1997 (∇) and 1998 (\diamond). Sample sizes (given by figures) are total numbers of gravid females for each locality and date. The data from June 23 are used in both the Colesbukta and microcosm series. Sampling dates (indicated by tick marks) are given in the text



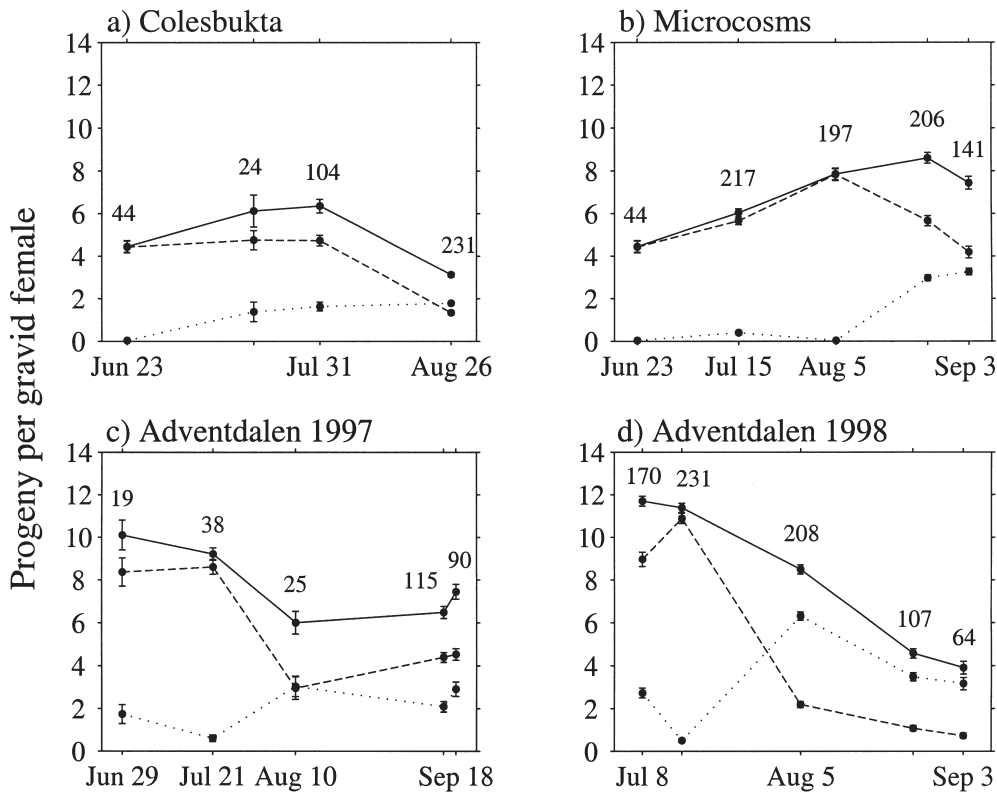


Fig. 8. Mean number of eggs (---), larvae (...) and total progeny (—) per gravid female of *A. lineatus* (\pm S.E.) in a) Colesbukta and b) microcosms in 1998, c) Adventdalen in 1997, and d) Adventdalen in 1998. Sample sizes (n) are given by figures. Note different scales on the x-axes

The microcosm females entered winter carrying almost twice as many embryos as the Adventdalen females (Fig. 8b, d). In contrast, in Adventdalen mean number of total progeny reached 11.7 in July, while an average above 9 was never recorded in the microcosms. There were also great temporal differences between the two populations in number of eggs and larvae per gravid female. In June, a single female was found carrying one larva in the microcosms, while the mean load of larvae in Adventdalen females in early July was 2.7. In autumn the mean number of larvae was almost the same (3.3 and 3.2 in the microcosms and Adventdalen respectively), but the number of eggs was much lower in Adventdalen (0.7 versus 4.2). Interactions were highly significant in all models (log-linear models: time*site, (eggs) deviance = 1608.30, df = 3, $P < 0.001$; (larvae) deviance = 1074.01, df = 3, $P < 0.001$; (total) deviance = 625.28, df = 3, $P < 0.001$). The maximum number of total progeny per female (23) was found on the Adventdalen site, as were maximum numbers of eggs (23) and larvae (13). In Colesbukta gravid females carried increasingly more larvae and a declining number of eggs as the summer progressed (Fig. 8a). In 1997 in Adventdalen the total number of progeny decreased in late July and then leveled out (Fig. 8c), giving a higher September average than one year later. Similar changes were seen in the

number of eggs. The number of larvae reached its maximum in the last part of the summer. Differences between dates were significant (log-linear models: (eggs) deviance = 153.21, df = 4, $P < 0.001$; (larvae) deviance = 90.42, df = 4, $P < 0.001$; (total) deviance = 53.22, df = 4, $P < 0.001$).

Discussion

Population dynamics

The similarity of mite densities from the high density patches in Colesbukta and the microcosms (Fig. 1) indicates that the microenvironment within the microcosms did not differ markedly in quality from that of the natural system from which they originated. Furthermore, it seems that the microcosm population never reached unnatural high or low densities within its confined space. Thus, the microcosms seem a realistic model system for the study of population dynamics and demography under natural conditions. The density of the Adventdalen and microcosm populations remained stable through the summer 1998. There was no increase in autumn, which might have been expected from the accumulation of larvae through summer. The early summer peak of larvae in Adventdalen (see be-

low) is, however, visible in Figure 1b. Hardly any studies on population dynamics of alpine or polar oribatid mites exist. The seasonal dynamics of oribatid populations on Greenland were either quite stable or characterized by a peak in July (Hammer 1944). Summer 1998 was exceptionally mild on West Spitsbergen (Table 1), probably offering good conditions for *A. lineatus* (see below). However, populations with long life cycles like *A. lineatus* (see below) do not readily respond to short-term temperature changes, as shown by the stable population dynamics in this study.

Life cycle

The synchronous moult in July may reflect a phenological strategy to time quiescence and moulting, which are vulnerable parts of development, with the warmest part of the arctic summer (Table 1; Førlund et al. 1997). Synchronous moulting in early summer has been reported in a few antarctic and sub-alpine oribatid mites (Convey 1994a; Kuriki 1995), and we suggest that the long winter in cold regions has a strong synchronizing effect on moulting. In laboratory cultures of *A. lineatus* juveniles, we have observed synchronous quiescence and moulting right after simulated winters, which supports our suggestion (Søvik & Leinaas, in prep.).

Moulting occurred earlier in Colesbukta than in the microcosms. The common origin of the two populations suggests that the observed difference in timing of moulting was due to differences in microclimate, which implies that a certain sum of degree days in early summer is required to initiate quiescence. Unfortunately no reliable temperature data from the Colesbukta site exist. Notwithstanding, moulting seems to be synchronized within, but not necessarily between, different local populations. However, within populations timing of moulting was positively correlated with ontogeny, with older stages moulting later. This could be due to deuto- and tritonymphs initiating quiescence later, or to a longer lasting quiescent stage in older instars. Earlier studies support the last hypothesis (Luxton 1981a).

The presence of all life cycle stages of *A. lineatus* at all sampling dates suggests that all stages overwinter. Similar seasonally stable stage structures have been observed in a number of polar and alpine oribatid mites (Solhøy 1975; Mitchell 1977; West 1982; Schatz 1985; Tilrem 1994; Kuriki 1995; Marshall & Convey 1999). In contrast in several temperate species cohorts can be followed through ontogeny (Luxton 1981b). This was observed also in a North German population of *A. lineatus* (Bücking et al. 1998). Because of its stability, the demography of *A. lineatus* was of little value in esti-

imating the duration of life stages. However, the synchronized moulting in the microcosms, together with low proportions of quiescent immatures at later sampling dates, suggests that each juvenile instar lasts approximately one year.

Given on average a one-year duration for each stage, *A. lineatus* will spend 4 years from larva to adult. Females start larviposition in their second summer as adults (see below), giving a generation time larva-to-larva of 5 years. As adults live for 2–3 years (see below), *A. lineatus* has a life span of 6–7 years. The few studies of alpine and polar oribatid mites suggest generation times of 2–4 (Schatz 1985), 3 (Mitchell 1977) or 5 years (Convey 1994a; Kuriki 1995). In contrast most temperate oribatid mites have generation times of 1–2 years (Luxton 1981a, b). The North German population of *A. lineatus* has a one-year life cycle with virtually all adults dying during their first winter (Bücking et al. 1998), implying that life cycle duration and adult longevity vary dramatically across latitudes. The prolonged life cycle of arctic *A. lineatus* may be explained by the suggested synchronized timing of moulting to the warmest part of the arctic summer, with each juvenile not being able to moult more than once per summer due to climatic constraints. Thus, each active stage will be prolonged in terms of degree days relative to temperate populations. The correspondingly larger time budget for growth per instar is consistent with the considerably larger size of arctic compared with temperate adults of *A. lineatus* as documented by Schubart (1975). For a population in southern England he obtained average sizes of 0.67 and 0.62 mm for females and males respectively, compared with 0.87 and 0.77 mm in the present study (Fig. 2).

Demography

Several factors, like variation in yearly recruitment or mortality and developmental patterns, may explain the observed proportions in the *A. lineatus* stage structures. Data from several years are required in order to determine the importance of each of them. The proportion of each stage remained fairly stable through the summer of 1998 (Fig. 4), which indicates low summer mortality in all juvenile instars. The increasing proportion of larvae during summer compared with older instars shows good recruitment in 1998. Similar high proportions of larvae were found by Tilrem (1994) in the alpine *Ameronothrus lapponicus* Dalenius and by West (1982) in sub-antarctic oribatid mites, and may indicate high mortality in the first active instar. Adults dominated in all three populations, reflecting high adult longevity. However, the high proportion of adults

in the Adventdalen population was partly due to the higher extraction efficiency of adults compared with immatures (Søvik & Leinaas 2002). The stage structures from Colesbukta and the microcosms (Fig. 4a, b) indicate an adult longevity of at least 2 years. A decreasing mortality risk with ontogeny and high adult survival seem to be characteristic of oribatid mites (Luxton 1981a; Norton 1994).

The stable sex ratio in the closed microcosms compared with the Colesbukta population suggests that the strongly varying sex ratio of the high density patches in Colesbukta was caused by a non-random distribution of adults on the cyanobacteria surface. One possibility is that males migrated into the high density patches attracted by virgin females recently moulted from tritonymphs. Another explanation, not necessarily excluding the first one, is reproductive migration to lower density areas. That fewer eggs were found in the Colesbukta females compared with those in the microcosms on July 31 supports this (Fig. 8a, b). Reproductive migration has been hypothesized for oribatid mites where adults and juveniles have been found in different soil horizons (Luxton 1982). However, the low proportion of females did not coincide completely with timing of larviposition, which took place the whole summer (see below).

In contrast to the seasonally quite stable sex ratios of both the Adventdalen and microcosm populations, temperate *A. lineatus* populations have been observed to have males dominating in spring (early male moulting) and females in late summer (high male mortality) (Schubart 1975; pers. obs.). Thus, on Svalbard males and females seem to moult simultaneously and to survive equally well. Our data suggest spatial differences in the sex ratio between local populations of *A. lineatus*. However, sex ratios from field samples can be misleading due to differential mortality and dispersal rates (Wrensch 1993), as illustrated by the Colesbukta population. Ratios diverging from 1:1 are not uncommon in oribatid mites (Luxton 1981a). Female biased sex ratios in other acarine sub-orders are often associated with haplodiploid genetic systems (Norton et al. 1993), however, genetic systems of oribatid mites are poorly known. As broods from different females will mix during the long development of *A. lineatus*, skewed sex ratio due to local mate competition (Fisher 1930) does not seem likely.

In Adventdalen in late June 1997 100% of the females were gravid, and out of these about 60% carried larvae. A drop in the proportion of females carrying larvae in July, together with a drop in the number of larvae per female, implies that by July 21 many females had larviposited. A drop in the proportion of gravid females shows that tritonymphs had moulted to females as it is unlikely that in 40% of the overwinter-

ing females, which were all carrying eggs, all eggs had matured to larvae and were deposited within 3 weeks. On August 10, the proportion of gravid females had increased to nearly 90% and remained high the rest of the season, showing that the new females had started developing eggs, and that most females overwintered with progeny. A proportion of females with larvae at about 60% in the last part of the summer indicates that few new females had developed larvae. This suggests that females may live and reproduce for at least 3 summers, overwintering first with only eggs and then with eggs and larvae.

July 1998 data for the Adventdalen population again showed 100% pregnancy. The number of larvae per female was the same as in September 1997, while the number of eggs had doubled, which shows that all females started egg production in early summer. The sudden drop in the proportion of females with larvae, as well as in larvae per female, reveals that virtually all larvae from autumn 1997 were laid synchronously within one week in early July. Similar to 1997 the decreasing proportion of gravid females on July 15 must be due to tritonymphs moulting to females as 98% of the overwintering females on July 8 carried eggs. The proportion of females with larvae rose steeply from July to August, probably due to overwintering females maturing new larvae, or developing their first ones, depending on age. Considering that new females in 1997 started producing progeny during their first summer as adults, it is likely that this was the case also in the milder summer of 1998. Thus, it seems that the continual high proportion of females carrying larvae in the last part of summer 1998 also included new females, which suggests that embryonic developmental rate was higher in 1998 compared with 1997. However, experimental studies carried out in summer 1998 showed that none of the new females larviposited in 1998 (Søvik & Leinaas, in prep.). Contrary to 1997 the proportion of gravid females in Adventdalen in 1998 declined through summer. The number of progeny per female also decreased, which was in large part due to a very low number of eggs in September. Probably many overwintering females deposited all their progeny during the last part of summer. The drop in the proportion of females on September 3 suggests that many females then died. In an average year it is possible that some of these larvae would not have been deposited until the succeeding spring. Thus, as already noted, the rate of embryonic development was probably higher in 1998 compared with average summers like 1997. The data also indicate that the state of a population in early summer depends on its reproductive history the previous year.

In early summer the proportion of gravid females in the Colesbukta population was low, and a very low

proportion of these females carried larvae. Two explanations seem possible: there could have been a very early burst of larviposition before our first sampling, or the dynamics of the two populations were completely out of phase, with few females overwintering in Colesbukta with progeny because of a burst of larviposition the previous autumn. The high proportion of gravid females on July 15 shows that overwintering females had started producing new eggs. From July 15 to August 25 an increasing larval density in the microcosms shows a period of high recruitment. The fact that hardly any gravid females in the microcosms carried larvae on August 5, in contrast to the Colesbukta females, may indicate a synchronous larviposition shortly before that date. The seemingly marked difference between the microcosm and Colesbukta populations in proportion of females carrying larvae in early August may be due to difference in sampling dates relative to the assumed synchronous larviposition. During the rest of the recruitment period the number of larvae per female in the microcosms increased strongly, indicating a more gradual larviposition as larvae matured. The moulting of new females in the microcosms during August coincided with a decrease in the proportion of gravid females. As August and September data from the microcosms resembled the Adventdalen population in 1998 in the proportion of gravid females and females carrying larvae, it seems probable that also in the microcosms new females matured larvae, while many overwintering females deposited all their progeny in late summer. The observed variability in eggs and larvae per female in the microcosm and Adventdalen populations may be due to the timing of egg and larval development being out of phase, as suggested above.

Despite experiencing the same microclimatic conditions during summer 1998, the reproductive biology of the microcosm population differed markedly from that of the Adventdalen population. These results show that the demography of field populations depend on both the current microclimatic conditions, shown by comparisons between the summers of 1997 and 1998, as well as the previous demographic history of the population. Other factors may also be important, e.g., the substrate. This has implications for the interpretation of field data. Our results suggest that in most years newly moulted females immediately start developing eggs, which will be matured and deposited as larvae the following summer. Some alpine and antarctic species also start depositing eggs (or larvae) the second summer (Schatz 1985; Kuriki 1995; Convey 1994a). High adult survival leads to seasonal iteroparity, and since larvae and gravid females were found in all samples, reproduction is probably continuous. A burst of larviposition may occur in early summer.

However, embryonic development and timing of peak recruitment probably vary between sites and years, indicating a phenotypic flexibility responding to climatic conditions. Oviposition in other alpine and polar oribatid mites is either continuous through the summer or temporally circumscribed (Solhøy 1975; Mitchell 1977; Schatz 1985; Tilrem 1994; Convey 1994b; Kuriki 1995). The instantaneous clutch sizes in *A. lineatus* are higher than reported for most other oribatid mites (Luxton 1981a; Tilrem 1994; Kuriki 1995). For instance, females of the similar sized and confamilial *A. antarcticus* carry an average of only 4–6 eggs (Convey 1994b). However, information about turnover rates is necessary in order to make valid comparisons. With an adult longevity of 2–3 years, *A. lineatus* females might produce a total of 10–40 larvae.

Conclusion

The generation time of 5 years suggested for arctic populations of *A. lineatus* is longer than most described for oribatid mites, and is only comparable with oribatid life cycles from other extreme environments with short and cool summers. *A. lineatus* resembles the antarctic *A. antarcticus* in life history traits such as long life cycle and high adult longevity. These traits are to some extent also found in most temperate oribatid species, and Norton (1994) and Behan-Pelletier (1999) pointed out that oribatid mites seem to be simply pre-adapted to the polar environment. However, we suggest that the length of the life cycle of arctic *A. lineatus* is determined by a phenological strategy where adaptive timing of moulting with the warmest part of summer leads to approximately one instar per year.

The long life cycle may lead to higher juvenile mortality compared with temperate populations due to repeated winterings. However, traits like iteroparity, larger body size in females (possibly leading to higher fecundity), and female biased populations seem to counteract the effect of a higher mortality. Unfortunately, no detailed data exist on the reproductive biology of temperate populations of *A. lineatus*, which could have illuminated this suggestion. Furthermore, larviparity, a plesiotypic (ancestral) trait of *Ameronothrus* the genus, ensures a high survival of eggs and prelarvae. The timing of life cycle events such as moulting suggests distinct phenological strategies. On the other hand, the species also exhibits a flexible life history by overwintering in all stages. Furthermore, comparisons of the demography of two different populations, and between two years with different climatic patterns, demonstrate ability of *A. lineatus*

to respond to favourable conditions. Thus, the combination of flexible as well as programmed elements, plesiotypic as well as adaptive traits, of the life history of *A. lineatus*, makes the species well suited for a life in the harsh arctic environment.

Acknowledgements. Inger Alsos and Leidulf Lund were of great help with the field collections in Colesbukta, and Inger Alsos also identified the plant species in the study sites. Tore Brembu and Lars R. Hole kindly helped with the field and laboratory work summer 1998. Sigmund Spjelkavik lent us Tinytalks. Part of the laboratory work was carried out at the University Centre on Svalbard (UNIS), while the Norwegian Meteorological Institute provided the meteorological data. Valerie Behan-Pelletier, Steve Coulson and two anonymous referees gave valuable comments on previous versions of the manuscript. The study was financed by the Norwegian Research Council.

References

- Addison, J. A. (1977) Population dynamics and biology of *Collembola* on Truelove Lowland. In: Bliss, L. C. (ed) Truelove Lowland, Devon Island, Canada: A high arctic ecosystem. University of Alaska Press, Edmonton, pp. 363–382.
- Behan-Pelletier, V. (1999) Oribatid mite fauna of northern ecosystems: a product of evolutionary adaptations or physiological constraints? In: Needham, G. R., Mitchell, R., Horn, D. J., Welbourn, C. (eds) *Acarology IX: Vol. 2, Symposia*. Ohio Biological Survey, Columbus, Ohio, pp. 87–105.
- Birkemoe, T., Leinaas, H. P. (1999) Reproductive biology of the arctic collembolan *Hypogastrura tullbergi*. *Ecography* 22, 31–39.
- Birkemoe, T., Leinaas, H. P. (2000) Effects of temperature on the development of an arctic *Collembola* (*Hypogastrura tullbergi*). *Functional Ecology* 14, 693–700.
- Birkemoe, T., Leinaas, H. P. (2001) Growth and development in a high Arctic *Collembola*: adaptive variation in local populations living in contrasting thermal environments. *Ecological Entomology* 26, 100–105.
- Birkemoe, T., Sømme, L. (1998) Population dynamics of two collembolan species in an Arctic tundra. *Pedobiologia* 42, 131–145.
- Bliss, L. C., Heal, O. W., Moore, J. J. (1981) *Tundra ecosystems: a comparative analysis*. Cambridge University Press, Cambridge.
- Block, W., Convey, P. (1995) The biology, life cycle and ecophysiology of the Antarctic mite *Alaskozetes antarcticus*. *Journal of Zoology*, London 236, 431–449.
- Brown, J., Miller, P. C., Tieszen, L. L., Bunnell, F. L. (eds) (1980) *An arctic ecosystem: the coastal tundra at Barrow, Alaska*. Dowden, Hutchinson & Ross, Stroudsburg.
- Bücking, J., Ernst, H., Siemer, F. (1998) Population dynamics of phytophagous mites inhabiting rocky shores – K-strategists in an extreme environment? In: Ebermann, E. (ed) *Arthropod Biology: Contributions to Morphology, Ecology and Systematics*. Biosystematics and Ecology Series 14, Österr. Akad. Wiss., Vienna, pp. 93–143.
- Collof, M. J. (1984) Notes on two lichenophagous oribatid mites from Ailsa Craig (Acari: Cryptostigmata). *Glasgow Naturalist* 20, 451–457.
- Convey, P. (1994a) Growth and survival strategy of the Antarctic mite *Alaskozetes antarcticus*. *Ecography* 17, 97–107.
- Convey, P. (1994b) Sex ratio, oviposition and early development of the Antarctic oribatid mite *Alaskozetes antarcticus* (Acari: Cryptostigmata) with observations on other oribatids. *Pedobiologia* 38, 161–168.
- Convey, P. (1998) Latitudinal variation in allocation to reproduction by the Antarctic oribatid mite, *Alaskozetes antarcticus*. *Applied Soil Ecology* 9, 93–99.
- Coulson, S. J., Refseth, D. (in press) The terrestrial and freshwater invertebrate fauna of Svalbard (and Jan Mayen). In: Strøm, H., Goldman, H. V. (eds) *A catalogue of the terrestrial and marine animals of Svalbard: invertebrates, fishes, birds and mammals*. Skrifter 201. Norwegian Polar Institute, Tromsø.
- Danks, H. V. (1981) Arctic arthropods. A review of systematics and ecology with particular reference to the North American fauna. Biological Survey project. Entomological Society of Canada, Ottawa.
- Danks, H. V. (1999) Life cycles in polar arthropods – flexible or programmed? *European Journal of Entomology* 96, 83–102.
- Ernst, H., Siemer, F., Bücking, J., Witte, H. (1993) Die litorale Milbenzönose auf Uferbefestigungen des Weserästuars in Abhängigkeit von Substrat und Salzgehaltsgradient. Informationen zu Naturschutz und Landschaftspflege in Nordwestdeutschland 6, 401–416.
- Fisher, R. A. (1930) *The genetical theory of natural selection*. Clarendon Press, Oxford.
- Førland, E. J., Hanssen-Bauer, I., Nordli, P. Ø. (1997) Climate statistics and longterm series of temperature and precipitation at Svalbard and Jan Mayen. DNMI Rapport 21/97.
- Hammer, M. (1944) Studies on the oribatids and collembolans of Greenland. *Meddelelser om Grønland* 141, 4–210.
- Hertzberg, K., Leinaas, H. P., Ims, R. A. (1994) Patterns in abundance and demography in patchy habitats: *Collembola* in a habitat patch gradient. *Ecography* 17, 349–359.
- Hertzberg, K., Yoccoz, N. G., Ims, R. A., Leinaas, H. P. (2000) The effects of spatial habitat configuration on recruitment, growth and population structure in arctic *Collembola*. *Oecologia* 124, 381–390.
- Hodkinson, I. D., Wookey, P. A. (1999) Functional ecology of soil organisms in tundra ecosystems: towards the future. *Applied Soil Ecology* 11, 111–126.
- Hopkin, S. P. (1997) *Biology of the springtails (Insecta: Collembola)*. Oxford University Press, Oxford.
- Kuriki, G. (1995) Life cycle of *Trhypochthoniellus setosus* Willmann (Acari: Trhypochthoniidae) in a *Sphagnum* moor at Yachidaira, Northeast Japan. *Journal of the Acarological Society of Japan* 4, 113–122.

- Luxton, M. (1981a) Studies on the oribatid mites of a Danish beech wood soil. IV. Developmental biology. *Pedobiologia* 21, 312–340.
- Luxton, M. (1981b) Studies on the oribatid mites of a Danish beech wood soil. VI. Seasonal population changes. *Pedobiologia* 21, 387–409.
- Luxton, M. (1982) The biology of mites from beech woodland soil. *Pedobiologia* 23, 1–8.
- Macfadyen, A. (1961) Improved funnel-type extractors for soil arthropods. *Journal of Animal Ecology* 30, 171–184.
- Marshall, D. J., Convey, P. (1999) Compact aggregation and life-history strategy in a continental Antarctic mite. In: Bruin, J., van der Geest, L. P. S., Sabelis, M. W. (eds) *Ecology and evolution of the Acari*. Kluwer Academic Publishers, Dordrecht, pp. 557–567.
- Mitchell, M. J. (1977) Population dynamics of oribatid mites (Acari, Cryptostigmata) in an aspen woodland soil. *Pedobiologia* 17, 305–319.
- Norton, R. A. (1994) Evolutionary aspects of oribatid mite life histories and consequences for the origin of the Astigmata. In: Houck, M. A. (ed) *Mites. Ecological and evolutionary analyses of life-history patterns*. Chapman & Hall, New York, pp. 99–135.
- Norton, R. A., Kethley, J. B., Johnston, D. E., O'Connor, B. M. (1993) Phylogenetic perspectives on genetic systems and reproductive modes of mites. In: Wrensch, D., Ebbert, M. (eds) *Evolution and diversity of sex ratio in insects and mites*. Chapman & Hall, New York, pp. 8–99.
- Petersen, H. (1978) Some properties of two high-gradient extractors for soil microarthropods, and an attempt to evaluate their extraction efficiency. *Natura Jutlandica* 20, 55–122.
- Schatz, H. (1985) The life cycle of an alpine oribatid mite, *Oromurcia sudetica* Willmann. *Acarologia* 26, 95–100.
- Schubart, H. (1975) Morphologische Grundlagen für die Klärung der Verwandtschaftsbeziehungen innerhalb der Milbenfamilie Ameronothridae (Acari, Oribatei). *Zoologica* 123, 23–94.
- Schulte, G. (1976) Zur Nahrungsbiologie der terrestrischen und marinen Milbenfamilie Ameronothridae (Acari, Oribatei). *Pedobiologia* 16, 332–352.
- Schulte, G., Schuster, R., Schubart, H. (1975) Zur Verbreitung und Ökologie der Ameronothriden (Acari, Oribatei) in terrestrischen, limnischen und marinen Lebensräumen. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven, Sonderband 15*, 359–385.
- Schuster, R. (1966) Hornmilben (Oribatei) als Bewohner des marinen Litorals. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven, Sonderband II*, 319–327.
- Seniczak, S., Plichta, W. (1978) Structural dependence of moss mite populations (Acari, Oribatei) on patchiness of vegetation in moss-lichen tundra at the north coast of Hornsund, West Spitsbergen. *Pedobiologia* 18, 145–152.
- Solhøy, T. (1975) Dynamics of oribatei populations on Hardangervidda. In: Wielgolaski, F. E. (ed) *Ecological Studies 17. Fennoscandian tundra ecosystems Part 2. Animals and systems analysis*. Springer-Verlag, Berlin, pp. 60–65.
- Søvik, G., Leinaas, H. P. (2002) Variation in extraction efficiency between juvenile and adult oribatid mites: *Ameronothrus lineatus* (Oribatida, Acari) in a Macfadyen high-gradient canister extractor. *Pedobiologia* 46, 34–41.
- Tilrem, L. (1994) Life history traits in two oribatid mites (*Ameronothrus lapponicus* Dalenius and *Phauloppia* sp.) in an extreme high mountain habitat. *Cand. Scient. thesis*. University of Bergen, Norway.
- Webb, N. R., Coulson, S. J., Hodkinson, I. D., Block, W., Bale, J. S., Strathdee, A. T. (1998) The effects of experimental temperature elevation on populations of cryptostigmatic mites in high Arctic soils. *Pedobiologia* 42, 298–308.
- Weigmann, G., Schulte, G. (1975) *Ameronothrus schubarti* n. sp. aus dem marinen Litoral Kaliforniens. *Senckenbergiana Biologica* 56, 133–143.
- West, C. (1982) Life histories of three species of sub-antarctic oribatid mite. *Pedobiologia* 23, 59–67.
- Wrensch, D. L. (1993) Evolutionary flexibility through haploid males or how chance favors the prepared genome. In: Wrensch, D., Ebbert, M. (eds) *Evolution and diversity of sex ratio in insects and mites*. Chapman & Hall, New York, pp. 119–149.