Demography of *Mesochra lilljeborgi* and *Amonardia normani* (Copepoda: Harpacticoida) reared on two diatom diets

Per Nilsson

Tjärnö Marine Biological Laboratory, Pl. 2781, S-452 00 Strömstad, Sweden

ABSTRACT: Life histories of 2 harpacticoids, *Amonardia normani* and *Mesochra lilljeborgi*, reared on 2 diatom diets, are compared. Both species showed differences in growth and survival between the 2 diets, but the effect was more pronounced in *M. lilljeborgi* which both reproduced and survived better when fed on *Navicula* sp. than on *Nitzschia frustulum*. Life tables were constructed for both species, and exponential rate of natural increase (r) was calculated to 0.163 d^{-1} (*Navicula* diet) and 0.134 d^{-1} (*Nitzschia* diet) for *A. normani*, and 0.113 d^{-1} (*Navicula* diet) and 0.074 d^{-1} (*Nitzschia* diet) for *M. lilljeborgi*. Results show that not only the quantity, but also the quality of the food is important for the growth of harpacticoid copepods.

INTRODUCTION

Harpacticoid copepods puzzle biologists with their highly oscillating populations and shifting sex ratios, and their population biology has been the object of many investigations (see Hicks & Coull 1983 for review). Food quality and quantity is often considered to be important in influencing the population development of harpacticoids. Several studies (e.g. Vanden Berghe & Bergmans 1981, Rieper 1982) have shown that some species of harpacticoids have selective feeding preferences. The small size of harpacticoids makes it difficult to follow individuals in the field, but the ease with which some species are cultivated, their short generation time and small size make them ideal for life-table analysis in the laboratory. A large number of life-table analyses on harpacticoid copepods have been made (Hicks & Coull 1983), but unfortunately many of these suffer from treating some life-history parameters in an inconsistent way, and especially confusing different measures of generation time (Bergmans 1984).

This study aims to: (1) describe the life histories of 2 harpacticoid copepods, *Mesochra lilljeborgi* and *Amonardia normani;* (2) examine if different diets may affect life-history parameters, and if so, at what stage in the life history these differences occur.

MATERIALS AND METHODS

Collection and cultivation. Gravid females of *Mesochra lilljeborgi* Boeck 1864 (Canthocamptidae) and *Amonardia normani* (Brady 1872) (Diosaccidae) were collected during September 1985 at a sheltered beach close to Tjärnö Marine Biological Laboratory on the west coast of Sweden. The females were cultivated in Petri dishes filled with GF/C filtered and autoclaved seawater (S = 28 ppt). The bottom of each dish was covered with a 3 to 4 mm layer of 1 % agar (Difco Bacto agar) which provided the copepods with a soft substrate and made it easy to observe and count specimens. The dishes were kept at 16 °C in a 12 : 12 h light-dark regime. The copepods were fed with a mixture of diatoms collected at the sampling locality. These were extracted by vigorous shaking of a sand sample, the supernatant then being poured into glass bottles containing f/2 medium (Guillard 1975) with silica added and kept at 14 °C in a cultivation room.

Experimental procedures. At the start of the experiment 10 gravid females of each species were individually isolated in Nunc multidishes, 35 × 17 mm (A/S Nunc, Denmark), containing agar and filtered seawater as described above. Five of the *Mesochra lilljeborgi* females were offered *Nitzschia frustulum* as food, while

the other 5 *M. lilljeborgi* females were given *Navicula* sp. The *Amonardia normani* females were treated in the same way. The *N. frustulum* culture was taken from laboratory collections, while *Navicula* sp. was isolated from the beach where the harpacticoids were collected. The monoalgal (but not axenic) cultures of *Nitzschia* and *Navicula* were grown using the same methods as described above for the algal mixtures. These 2 diatom species are of approximately similar naviculoid form and size. On 4 occasions samples were taken from the algal cultures, filtered on to a GF/C filter and analysed in a CHN-analyzer The C/N ratio of *Navicula* was 7.76 (SD = 0.20, n = 4) and the C/N ratio of *Nitzschia* was 7.43 (SD = 0.36, n = 4). The carbon content of the *Navicula* suspension was 40.7 µg C ml^{-1} (SD = 10.6, n = 4) and that of the *Nitzschia* suspension was 36.1 µg C ml^{-1} (SD = 6.5, n = 4).

In the following, I will use these abbreviations for different treatments: ANNA = *Amonardia normani* fed *Navicula* sp.; ANNI = *A. normani* fed *Nitzschia frustulum*; MLNA = *Mesochra lilljeborgi* fed *Navicula* sp.; MLNI = *M. lilljeborgi* fed *N. frustulum*.

When nauplii were first released, the females were removed. The experimental cultures were then examined every second day. Each examination consisted of counting live and dead copepods, adding fresh water, and noting the presence of fouling bacteria and ciliates. At each occasion old food was removed and 2 ml of fresh algal suspension was added to each dish. I did not measure the carbon and nitrogen content of the food on each occasion, but food was always in excess, as plenty of food remained in the dishes after 2 d. When copepods in tandem formation began to appear, 10 such pairs from each experimental treatment were isolated and followed during the rest of their life cycle. At each examination I additionally checked the presence and colour of egg sacs. As soon as a new brood hatched, the adult couple were transferred to a new dish. The brood were then followed every fourth day until the 25th day. If any of the original 10 males died during the experiment, it was replaced by a new male. To count the number of eggs per egg sac, between 25 and 30 adult females of each treatment were placed in separate multidishes and checked daily. When a female produced an egg sac it was transferred to 4 % formalin, and thereafter to a drop of polyvinyl-lactophenol on a microscopic slide. The number of eggs per egg sac were then counted in an interference-contrast microscope (Olympus BH-A) at 250×. To estimate mortality and developmental time for the different juvenile stages, I followed approximately 100 nauplii from each treatment more carefully. These dishes were checked every day, the number of nauplii alive was counted and all dead individuals were removed. Since harpacticoids of both species tend to move quickly, the developmental

stage of nauplii and copepodites was difficult to determine. I therefore checked the development of copepodites by daily removing all cast exoskeletons and counting the number of segments on these. The cohorts of juveniles were followed up to the age of 25 d.

Calculations and statistical analysis. To analyse the time spent in different stages, I used the method of Nordby & Nordby (1976) as suggested by Bergmans (1981). They show that the duration of stage s equals

$$\int_{x=0}^{\infty} \phi_s(x)dx \qquad (1)$$

where $\phi_s(x)$ = probability of being in stage s at age x. I calculated this probability by graphical integration, using a planimeter.

Statistical treatment included calculating the arithmetic mean and standard deviation of the variables given in Tables 2 & 3. Statistical testing was made by Mann-Whitney U-test, with correction for ties where necessary (Siegel 1956). A binomial test was used for testing if the sex ratio of the broods differed from equality.

From the values of age-specific survival (l_x: the proportion of a cohort that still survives at age x) and fecundity (m_x: mean no. of offspring born per unit time to a parent aged x) values obtained as described above, I constructed life tables for all 4 treatments, based on 2 d age intervals. To calculate the different life-history parameters given in Table 4, I used the formulas given by Pielou (1977), but with discrete approximations. The exponential rate of increase, r, was calculated according to the Lotka equation

$$\Sigma l_x m_x e^{-rx} = 1 \qquad (2)$$

which was solved by iteration. The net reproductive rate R_0 equals

$$R_0 = \Sigma l_x m_x. \qquad (3)$$

Since the concept of generation time of iteroparous animals with overlapping generations is not intuitively clear (Pielou 1977, Ricklefs 1980), 3 different measures were calculated:

$$T = \ln R_0/r \qquad (4)$$

$$T_c = \Sigma x \, l_x m_x / \Sigma \, l_x m_x \qquad (5)$$

$$\bar{T} = \Sigma x \, l_x m_x e^{-rx} \qquad (6)$$

Also given in Table 4 is the capacity of increase, r_c, which is defined (Bergmans 1984) by

$$r_c = \ln R_0/T_c. \qquad (7)$$

RESULTS

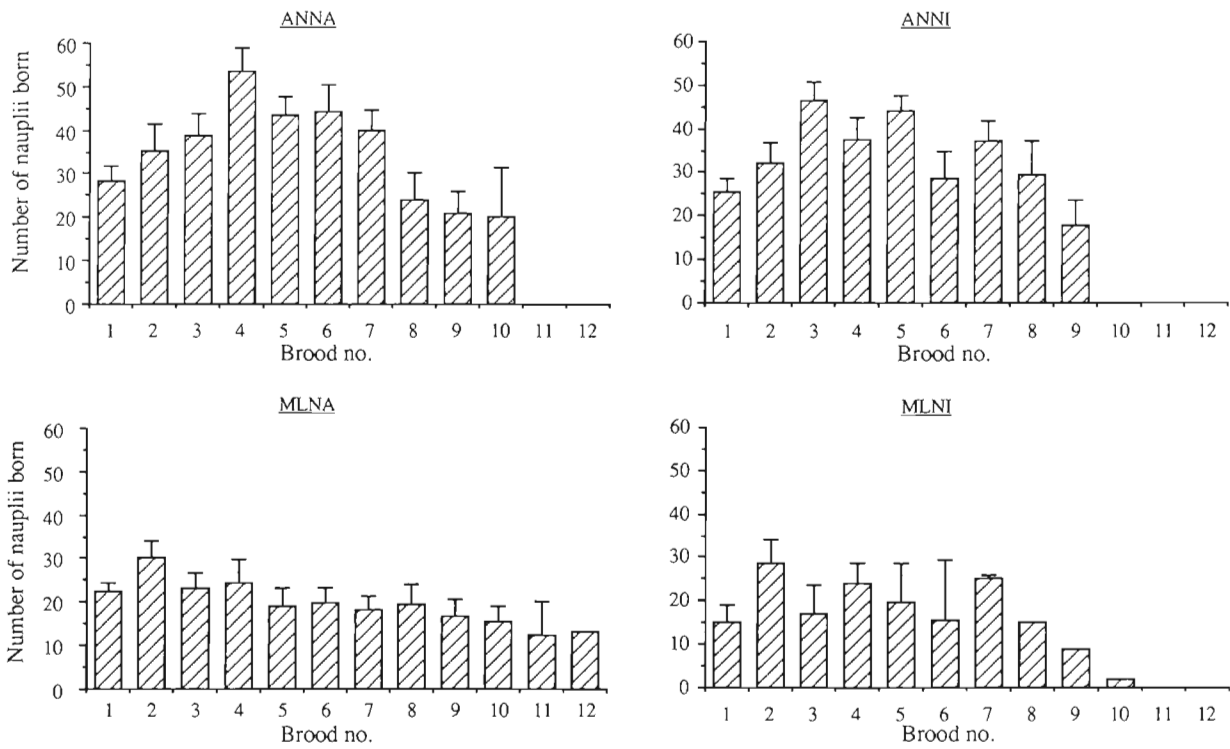The nauplii of both species always stayed on the bottom of the dishes, while copepodites and adults

Fig. 1. *Amonardia normani* and *Mesochra lilljeborgi*. Number of nauplii in successive broods in the life cycle of the females. Bars show arithmetic mean + SE. For explanation of abbreviations, see 'Materials and Methods'
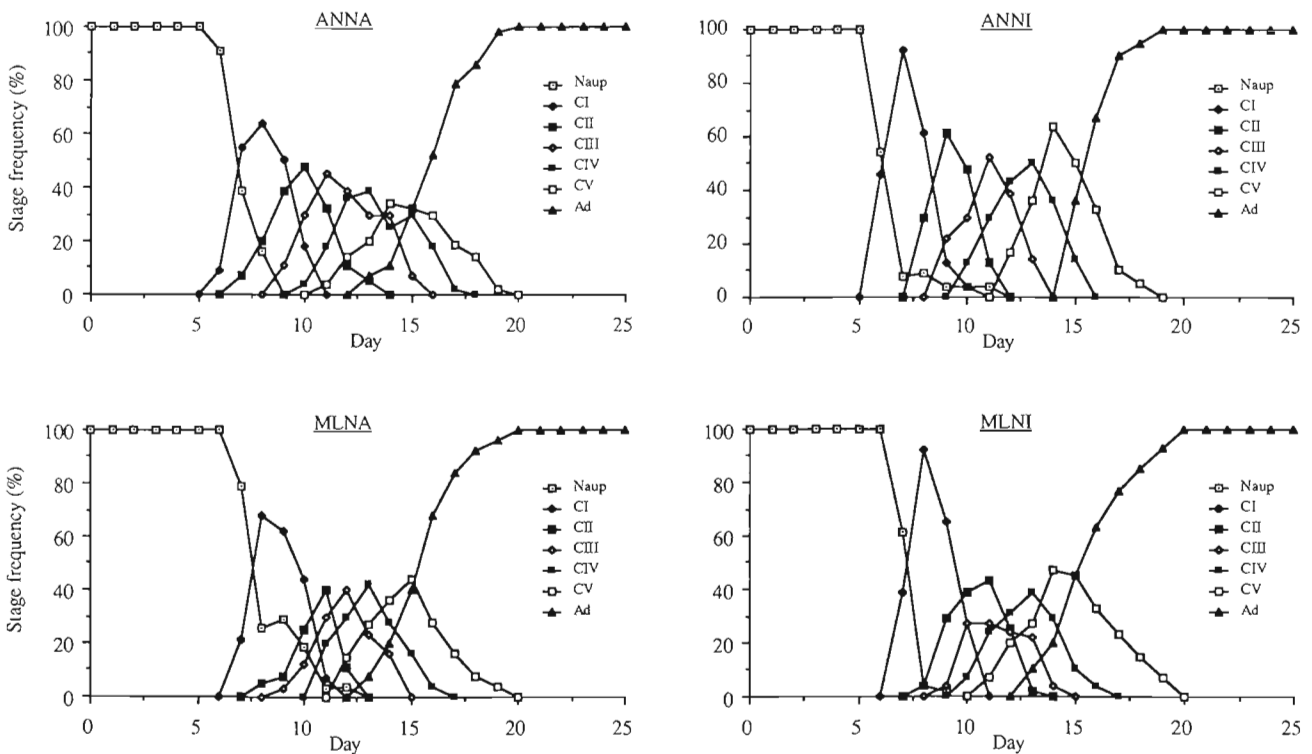

Fig. 2. *Amonardia normani* and *Mesochra lilljeborgi*. Development of nauplial cohorts: stage frequency as a function of time. For explanation of abbreviations, see 'Materials and Methods'

frequently were seen swimming. In general, the copepods were feeding on the agar surface, but it was not uncommon to see them digging into the substrate. Adults and copepodites reacted negatively phototactic to strong light (i.e. the light of the dissecting micro-scope), while the nauplii seemed unaffected. Females were clasped at the caudal rami by adult males. Preco-cious coupling (males clasping immature females) was common. I saw adult males clasping 2nd stage and older female copepodites, and even clasping males. Feller (1980) reports that males of *Huntemannia jaden-sis* reclasped females immediately after the females had moulted exoskeleton. This was generally the case in the present study, but several times I saw males clasping moulted exoskeletons for many hours. The moulting process took about 15 min, and was often preceded by a long period of low activity of the harpac-ticoid. Females were never seen in the coupling posi-tion after they had produced a first brood.

The females carried the egg sacs (1 sac in *Mesochra lilljeborgi*, 2 sacs in *Amonardia normani*) for 4 to 5 d, often longer in the later part in their reproductive period. Sometimes the nauplii hatched from the egg sacs while these were still attached to the female, but more commonly the egg sacs were deposited on the agar gel, and the nauplii hatched there. Most of the

nauplii (80 to 90 %) from a brood hatched within 24 h after the egg sacs were deposited, but occasional nau-plii could hatch up to 4 or 5 d later. The last broods in the life cycle of the females were in general smaller than the earlier broods (Fig. 1). At the end of the repro-ductive period many females produced one or several egg sacs that were deposited on the agar, but never hatched. This was most common in *M. lilljeborgi* eating *Navicula*, where females on average produced 3.6 such unproductive egg sacs during their life cycle, but it occurred occasionally in *A. normani* and MLNI as well. These unproductive egg sacs are not included in Table 3.

The development of the 2 species was similar (Fig. 2). Developmental time varies between individuals within treatments, but these differences may be due to the uncertainty of the method of checking cast exoskele-tons. It could also be caused by the fact that the nauplii of a brood hatched during a time interval which could be more than 4 d in some broods. Fig. 2, however, is based on development of broods where all nauplii hatched within 2 d. The stage duration times calculated by graphical integration (Table 1) show that the development times were similar in both species, regardless of diet.

A much greater difference appeared at the age of first reproduction. Table 2 shows that the ANNA fema-les produced their first brood at a significantly earlier age than MLNI females, with the ANNI and MLNA females at intermediate levels. It is also apparent from Table 2 that MLNI differed from other treatments du-ring the rest of the life cycle: in reproductive period (though not statistically different from ANNA and ANNI), postreproductive period and average life span. The reproductive period and average life span of *Amonardia normani* were not significantly affected by different diets. Both treatments resulted in a short reproductive period followed by a long postreproduc-tive period. MLNA females had a longer reproductive period, but their shorter postreproductive period made

Table 1 *Amonardia normani* and *Mesochra lilljeborgi*. Dura-tion (d) of larval stages. Calculated by the method of graphical integration of cohort development (see text). See 'Materials and Methods' for explanation of abbreviations

Stage	ANNA	ANNI	MLNA	MLNI
Naup.	7.0	6.3	8.0	7.1
CI	1.9	2.2	2.0	2.2
CII	1.6	1.5	0.9	1.4
CIII	1.9	1.6	1.2	1.1
CIV	1.7	1.9	1.4	1.4
CV	1.7	2.2	1.8	2.2
Σ	15.8	15.7	15.1	15.4

Table 2. *Mesochra lilljeborgi* and *Amonardia normani*. Time (d) of some important stages in the life cycle of females. Arithmetic mean ± SD. n: number of individuals used for the calculations. Lines join treatments whose medians are not statistically different at $p \leq 0.05$ (Mann-Whitney U-test)

Stage	ANNA	ANNI	MLNA	MLNI
Time spent as nauplius	7.0	6.3	8.0	7.1
Age at maturity	15.8	15.7	15.1	15.4
Age at first brood	22.4 ± 1.2 n = 30	24.2 ± 0.9 n = 22	24.6 ± 1.2 n = 18	27.6 ± 4.1 n = 16
Reproductive period	28.0 ± 6.5 n = 10	25.2 ± 10.3 n = 10	41.6 ± 18.4 n = 10	19.1 ± 13.3 n = 7
Postreproductive period	79.0 ± 15.1 n = 10	70.8 ± 30.2 n = 10	43.2 ± 33.6 n = 10	10.9 ± 5.1 n = 7
Life span (females)	130.2 ± 10.8 n = 10	121.0 ± 26.5 n = 10	109.8 ± 48.1 n = 10	55.0 ± 18.9 n = 10
Life span (males)	95.8 ± 30.2 n = 9	108.1 ± 23.1 n = 8	108.9 ± 42.4 n = 10	59.5 ± 31.6 n = 13

Table 3. *Amonardia normani* and *Mesochra lilljeborgi*. Reproductive capacity. Arithmetic mean ± SD. n*: number of females followed through life cycle; n: number of broods analysed. Lines join treatments whose medians are not statistically different at p ≤ 0.05 (Mann-Whitney U-test)

Parameter	ANNA	ANNI	MLNA	MLNI
Number of broods	8.5 ± 1.3 n* = 10	7.6 ± 1.9 n* = 9	11.1 ± 1.9 n* = 7	4.0 ± 2.8 n* = 8
No. of eggs/brood	56.3 ± 9.1 n = 23	58.2 ± 10.0 n = 20	34.9 ± 4.0 n = 30	32.4 ± 6.6 n = 30
No. of nauplii/brood	39.2 ± 19.4 n = 102	38.1 ± 15.4 n = 89	22.5 ± 9.8 n = 84	18.8 ± 11.6 n = 37
Sex ratio: % females	62.2 ± 19.6 n = 32	52.1 ± 19.7 n = 42	50.4 ± 17.0 n = 30	39.2 ± 13.6 n = 14

their average life span about equal to that of *A. normani*. The average life span of males was shorter than the life span of females in all treatments except MLNI (Table 2), but the differences between sexes was significant only in ANNA (Mann-Whitney U-test, p < 0.05).

In terms of fecundity, there was also a difference between the species (Table 3), with *Amonardia normani* laying fewer broods, but with a higher number of nauplii per brood than MLNA. MLNI produced fewer broods than other females, with fewer nauplii per brood. These differences are very clear in the age-specific fecundity curves of Fig. 3. The number of eggs per brood is much higher than the number of hatched nauplii per brood, and I frequently observed eggs that

did not hatch. Table 3 indicates that on average 70 % (ANNA), 65 % (ANNI), 65 % (MLNA) and 58 % (MLNI) of the eggs hatched. This probably underestimates the hatching frequency of the eggs. Fig. 1 shows that the brood size changed during the life cycle. Unfortunately, I do not know the exact age of the females I used in the analysis of number of eggs per brood. However, they were at most 45 d old, that is at the age of maximum reproductive output, so if I had analysed some older females, the average number of eggs per egg sac would probably have been somewhat lower and consequently the true hatching frequency would be somewhat higher. Mortality is high in the larval stages for both species, as can be seen from Fig. 3. During adult life, the pattern differs between the
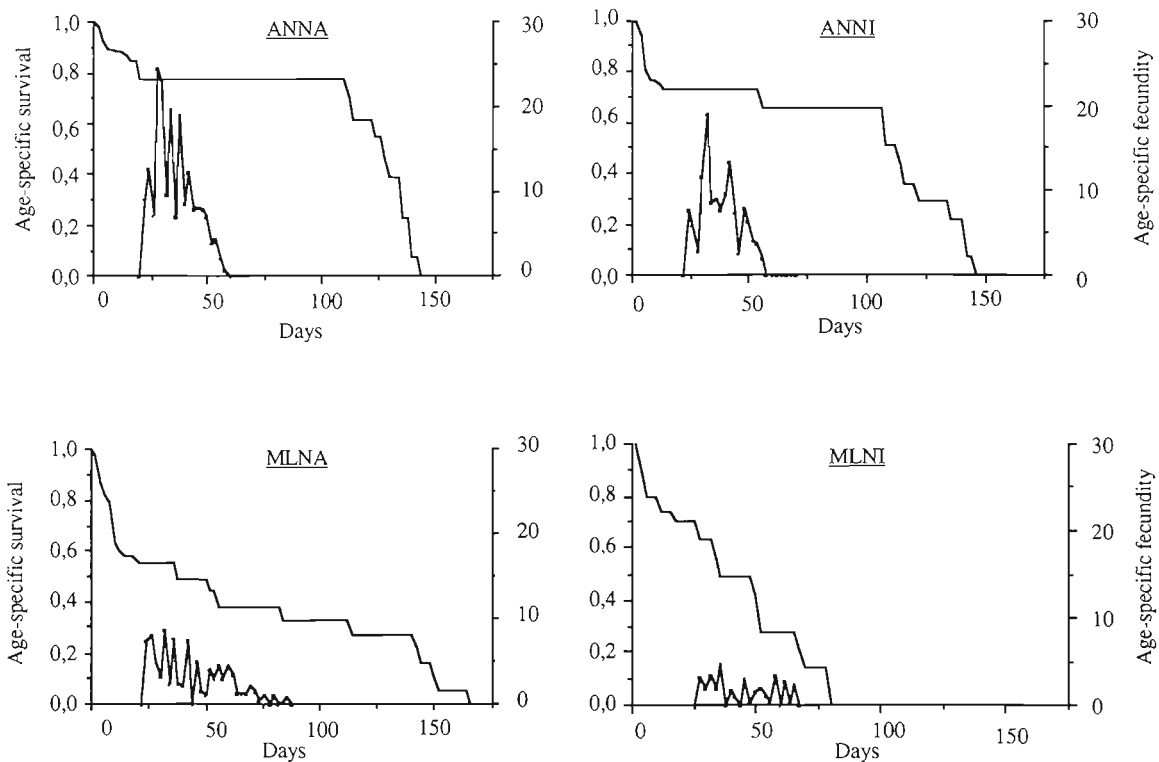

Fig. 3. *Amonardia normani* and *Mesochra lilljeborgi*. Age-specific survival and fecundity. Gross age-specific fecundity, m_x = number of female nauplii born per surviving female during each 2 d period. For explanation of abbreviations, see 'Materials and Methods'

2 species. *Mesochra lilljeborgi* has a constant mortality during the adult phase, a mortality that is higher in MLNI than in MLNA. *A. normani*, on the other hand, has a high survival until old age, when all individuals die within a short period.

The sex ratio also differed between species and treatments (Table 3). ANNA and ANNI had significantly more females than males (binomial test, ANNA: $p = 0.018$, ANNI: $p = 0.04$), MLNA had equal proportions of males and females (binomial test, ns), while MLNI had a significantly male-biased sex ratio (binomial test, $p = 0.012$). These differences in sex ratio contribute to the differences in age-specific fecundity (m_x), since these figures are based on number of females born per female (Fig. 3). Table 4 summarizes the life-history parameters that were calculated from the age-specific survival and fecundity schedules.

DISCUSSION

The aim of this investigation was 2-fold: first to describe the life histories of 2 harpacticoid species, taking care to avoid some of the most common computational faults, as advocated by Bergmans (1984); second, to examine if different diets can give differences in life-history parameters, and at what stage in the life history these differences occur. In the present study *Mesochra lilljeborgi* was more affected by differences in the diet than *Amonardia normani*. The experiments do not reveal if this is due to some difference in physiology, in food handling, or has some other cause. They do show that the diets affect the survival of adults and their ability to produce egg sacs (Table 3; Fig. 3). The developmental time of juvenile stages did not differ much between treatments (a statistical comparison is not possible due to the graphical integration method used, and the exclusion of cohorts with high development time variance), nor does the number of eggs per brood or the number of nauplii per brood. The reproductive period, postreproductive period, average life span and number of broods are statistically different between treatments in *M. lilljeborgi*. These differences

Table 4. *Amonardia normani* and *Mesochra lilljeborgi*. Summary of life history parameters. For details of calculations, see text

Parameter	ANNA	ANNI	MLNA	MLNI
r	0.163	0.134	0.113	0.074
R_0	152.7	94.3	46.2	15.7
r_c	0.141	0.120	0.091	0.067
T_c	35.6	37.8	41.9	41.8
T	30.9	33.9	33.9	37.2
$\overline{T}$	27.5	30.9	29.3	34.6

are not as pronounced in *A. normani*. Where there are differences between ANNA and ANNI, as for example in number of broods and average life span, these are not statistically different.

According to Hicks & Coull (1983) harpacticoid copepods tend to increase stage duration during their development, so that the longest time is spent in the later juvenile stages. This was not the case in this study. Table 1 shows that in both species the time spent as nauplii is almost as long as the time in copepodite Stages I to V. Of the copepodite stages, Stages I and V were the longest. The method used here to identify different age stages is dependent on complete recovery of the exoskeletons. There is a risk of missing exoskeletons of small age stages, which would give too long durations of these stages. In order to avoid this, I always checked the dishes at least twice. Since the dishes were so small, I do not think that I missed many exoskeletons and the bias is probably not great.

For semelparous organisms, generation time is a concept that is easy to understand, but for iteroparous organisms where generations overlap (as in this study), the meaning is less obvious. Table 4 presents 3 measures of generation time: T (mean generation time), T_c (cohort generation time), and $\overline{T}$ (mean age of the mother of a newborn). The original concept T is defined by $T = \ln R_0/r$, and is the time it takes for the population to increase (or decrease) by a factor R_0. However, in a stationary population where $R_0 = 1$ and $r = 0$ this is indeterminate, and when generations overlap T does not represent a time span that can be measured directly. T_c (cohort generation time) is the mean age of mothers at the birth of their daughters. T_c equals T if the population is semelparous. If more than one generation exists in a growing population T_c is greater than T, and the more the generations tend to overlap the greater the difference between T and T_c (May 1976, Ayal & Safriel 1982). Leslie (1966) recommends the use of $\overline{T}$, the mean age of the mother of a newborn individual, which he considers to be the most meaningful definition of generation time. In summary: $\overline{T} = T_c$ when the population is iteroparous but stationary. In a growing iteroparous population $\overline{T} < T < T_c$, and in this case the differences depend on how much R_0 departs from 1 and on how much generations overlap (or the variance of the $l_x m_x$ curve: see May 1976).

The sex ratios in Table 3 are based on 5th stage copepodites and adults, and I cannot judge if this reflects the sex ratio at birth or if the skewed sex ratios are the result of differential juvenile mortality of the sexes. The mechanisms of sex determination in harpacticoids is still not completely known, although there seem to be both a genetical and an environmental component (see Hicks & Coull 1983 for discussion). I find it unlikely that different population density should

cause different phenotypic expression of sex in this study, since the reproductive adults were reared at a constant and low density (2 adults per dish), and there is no consistent relationship between brood size (which is the population density experienced by the offspring) and sex ratio (Fig. 4). Inbreeding cannot be the cause of the sex ratio variation either, since the females from MLNA, which produced 50 % females, and the females from MLNI, which produced only 39 % females, came from the same cultures and probably belong to the same generation. This is, however, of less importance in the present discussion, since both cases (skewed sex ratio at birth; different juvenile survival) yield the same r and R_0.

How do the values of Table 4 compare with other investigations? Hicks & Coull (1983) list some selected values of r from a number of laboratory and field studies of different species of harpacticoids. The values of r (0.074 to 0.163) and r_c (0.067 to 0.141) of the present investigation lie within the range of the laboratory r values in their review. Their list includes growth rates computed in different ways and can therefore only be

used as a rough comparison. The different investigations on *Tisbe*, as listed in Bergmans (1981), show that species of this genus generally have a very high r_m. The differences in r_m between *Tisbe* and *Amonardia normani* are mainly due to the shorter generation time of *Tisbe*, and not to the number of offspring (Table 4 of Bergmans 1981; Table 4 in the present work). Castel (1984) gives an r_m value of *Mesochra lilljeborgi* of 0.124 (15 °C, 20 ppt). This value of r is higher than the r and r_c values in the present investigation (Table 4), which is illogical considering that Castel measured a slower development of juveniles and fewer deposited egg sacs. Two factors contribute to this inconsistency. Firstly, as far as I can understand, what Castel calculates is a modification of $r_c = \ln R_0 / T_c$. However, his value of generation time (D in his Table 3) is probably an underestimation of the true T_c, which gives a high value of r. Secondly, Castel does not include any estimation of mortality. If a juvenile or adult mortality was included in the calculation this would give a lower value of R_0, and hence a lower r_c.

Both species in this investigation had very long postreproductive periods. The difference between life span and reproductive period is illustrated in Fig. 3. Castel (1984) found a postreproductive period of female *Mesochra lilljeborgi* of 20 d, compared with the 42 d of MLNA. For *Amonardia normani*, Castel (1979) found a long postreproductive life span, ranging from 3 to 110 d after the last egg sac was deposited. This agrees with the time span I found (Table 2). Hicks & Coull (1983) give other examples of such long postreproductive periods. Why do the copepods remain unproductive during this period, and why do they lay unproductive egg sacs? The physical and biological regime (food supply, light, temperature etc.) did not change during the experiment, and there could be no crowding effect, since the female was always transferred to a new dish after depositing an egg sac. Since I never saw the females remating, it could be caused by a lack of sperm, even though there always was a male present. It could also be an effect of senescence. I do not know the life span of these copepods in nature, but they probably do not reach ages as high as in these experiments, or at least probably do not produce as many broods. This means that there would be little selection for successful reproduction at these ages in nature, and an accumulation of deleterious traits could result (Ricklefs 1980).

The use of agar as a bottom substrate, instead of sand or mud, can be criticised as it makes the habitat more artificial. However, counting and handling the copepods is so much easier and faster with an agar substrate that the disturbance to copepods is probably much lessened. Both species are easily cultivated when given a mixed diet, and there was no tendency for individuals to get trapped in food or agar. I do not think
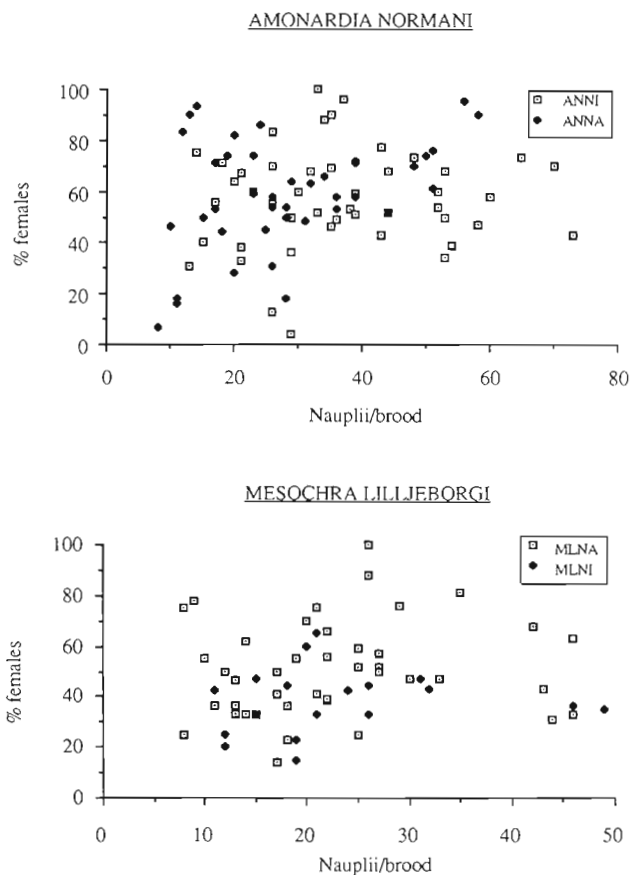

Fig. 4. *Amonardia normani* and *Mesochra lilljeborgi*. Sex ratio in broods as function of brood size. For explanation of abbreviations, see 'Materials and Methods'

that the agar causes any bias when comparing the 2 harpacticoid species.

Since this study aimed at investigating the food quality effects on life-history parameters, it is important to know if the diatoms are really assimilated, or if associated microbes form the main food source. Since the algal cultures were not axenic, bacteria were probably always present. However, microscopic inspection of fecal pellets showed that algal cells of both *Nitzschia* and *Navicula* are crushed, and do not simply pass through the gut undamaged. My future investigations will concern the ingestion and assimilation of bacteria and axenic diatoms by these 2 harpacticoid species.

Several investigators (Meyer-Reil & Faubel 1980, Hicks & Coull 1983, Montagna et al. 1983) have found that there is no straightforward relationship between total biomass of microorganisms and meiofauna. The results of the present work give one possible explanation. Differences in nutritional value of the food can give profound effects on the growth of harpacticoids, even if food is superabundant. Therefore it is vital to assess the quality as well as the quantity of resident microorganisms in order to understand how the food supply influences the behaviour of populations. An increased knowledge of how meioorganisms select their food *in situ* is necessary for future discussions about the population biology of meiofauna.

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