Seasonal dynamics of the mysid *Neomysis integer* and its predation on the copepod *Eurytemora affinis* in a shallow hypertrophic brackish lake

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ABSTRACT· The study included field sampling, field experiments in enclosures and laboratory predation experiments. *Neomysis integer*, which underwent 2 generations during the study year (1992), occurred in high density, the maximum being 0.8 ind. l^{-1} or 1250 ind. m^{-2}. Estimated production was 2.2 g DW (dry wt) $m^{-2} yr^{-1}$ and peaked in August at 25 mg DW $m^{-2} d^{-1}$ The laboratory predation experiments revealed a high predation potential on *Eurytemora affinis*, the maximum predation rates on nauplii and copepodites + adults being 52 and 8 ind. $mysid^{-1} h^{-1}$, respectively. Stepwise multiple regressions on the data obtained from enclosure experiments conducted at various densities of *N. integer* and three-spined sticklebacks *Gasterosteus aculeatus* revealed that the number of nauplii and the total number of *E. affinis* were significantly negatively related to the densities of both *N. integer* and fish, albeit positively to the interaction between fish density and *N. integer* density. In addition, the density of the advanced stages was significantly negatively related to that of fish, while the chlorophyll *a* concentration was weakly negatively related to *E. affinis* biomass and highly positively related to that of *N. integer*. The results provide further evidence that *N. integer* enhances eutrophication in nutrient-rich brackish lakes, i.e. *N. integer* predation on zooplankton reduces grazing pressure on the phytoplankton. Moreover, the results indicate that mysids also stimulate phytoplankton growth more directly.

KEY WORDS: *Neomysis integer* · *Eurytemora affinis* · Mysid · Copepod · Predation · Brackish · Hypertrophic · Lake

INTRODUCTION

Invertebrate predation may have an important structuring impact on the zooplankton community in brackish as well as freshwater lakes (Hanazato 1990, Branstrator & Lehman 1991), in particular when the abundance of vertebrate predators is low (Gliwicz & Pijanowska 1989). Most mysids belong to the group of invertebrate predators, and prey on all sizes of rotifers, cladocerans and copepods (Arndt & Jansen 1986, Hanazato 1990). Mysids are occasionally found in freshwater lakes, sometimes being artificially introduced to improve conditions for commercial fishing. In brackish lakes, in contrast, they are very common, and

often even abundant (e.g. Beattie & de Kruijf 1978, Arndt & Jansen 1986, Moss 1994, Jeppesen et al. 1994).

It is well known from freshwater lakes that the presence of mysids in high density may affect zooplankton composition and abundance (Goldman et al. 1979, Bowers & Vanderploeg 1982, Fulton 1983, Langeland 1988, Hanazato 1990, Meijer et al. 1994), and recent research suggests that this may also be the case in brackish coastal areas (Rudstam et al. 1986, Hansson et al. 1990) and brackish lakes (Moss & Leah 1982, Jeppesen et al. 1994). Jeppesen et al. (1994) found an inverse relationship between the density of fish and that of the mysid *Neomysis integer* (Leach). It was argued that the predation pressure by *N. integer* on zooplankton is particularly high in hypertrophic brackish lakes because fish biomass is low and dominated by sticklebacks, which are inefficient predators on *N. integer*. A

further argument was that the availability of alternative food sources favoured this omnivorous species, thus keeping their density high even during periods of low zooplankton abundance and thereby maintaining a potentially high predation pressure on zooplankton. In contrast to this view, however, studies of a shallow eutrophic lake in the UK suggested that despite being present in high numbers, *N. integer* was unable to control the population of the dominant macrozooplankton, the copepod *Eurytemora affinis* (Irvine et al. 1993).

To further elucidate the structuring impact of *Neomysis integer* on the population of the dominant macrozooplankton *Eurytemora affinis* in a shallow hypertrophic brackish lake, we conducted a number of laboratory and *in situ* enclosure predation experiments and followed the seasonal dynamics of mysids and zooplankton for a 1 yr period. In addition, we studied how the impact of *N. integer* on *E. affinis* was affected by the presence of three-spined sticklebacks *Gasterosteus aculeatus*.

MATERIALS AND METHODS

Study area. The study was undertaken in Lake Ferring, a shallow brackish (salinity 3 to 6‰) lake situated in western Jutland, Denmark (56° N, 8° E), about 100 to 200 m from the North Sea (Fig. 1). The lake area is 3.2 km^2, and the mean and maximum depths are 1.5 and 2.6 m, respectively. The lake is hypertrophic (500 µg total-P l^{-1}) with a high algal biomass and a low Secchi depth, i.e. less than 0.5 m throughout the year, the summer average being 0.25 m (M. Søndergaard unpubl. obs.). The phytoplankton was dominated by small-celled colonies of cyanobacteria, mainly *Aphanothece* spp. which comprised more than 90% of the total phytoplankton biomass. The mean summer phytoplankton biovolume was approximately 50 mm^3 l^{-1}. The fish community was dominated by three-spined sticklebacks *Gasterosteus aculeatus* which, in terms of fish number. accounted for more than 95% of

the total catch in a standardized test-fishing conducted in August with multiple mesh-size survey gill nets ranging from 6.25 to 75 mm (Søndergaard et al. unpubl. obs.).

Field sampling. Sampling was undertaken monthly between October and March 1992, and every 2 wk from April to September. Zooplankton were sampled with a 3.3 l Patalas sampler at a mid-lake station, samples from depths of 0.2 and 1 m being pooled.

Mysid density in the lake was estimated by means of day time vertical hauls undertaken with a 500 µm net (diameter 0.6 m) at 21 stations (replicates from each station) positioned so as to represent the whole lake area (Fig. 1). The nets were lowered to the bottom and allowed to rest for 1 min before undertaking the haul. Preliminary investigations showed that mysid density was independent of whether the nets were allowed to rest for 1, 2 or 5 min. The samples were fixed in 96% ethanol.

A diurnal investigation on mysid density was carried out in September, when vertical hauls were made at 7 stations and Perspex Breder traps (Breder 1960) were positioned on the sediment surface at 12 locations for 2 h (4 in each of the transects, Nos. 1 to 3, Fig. 1). Sampling was performed in the afternoon (15:00 h), at night (23:00 h) and in the morning after sunrise (08:00 h).

A qualitative investigation was made of the gut content of 20 mysids caught in net during the diurnal investigation, the food items being identified with the aid of a microscope at a magnification of 100 to 200×.

Production and growth rates. The length-frequency distribution of *Neomysis integer* on each sampling date was estimated from length measurements of 75 mysids selected randomly from a pooled sample of the vertical hauls. Microscope images of the mysids were digitized using a video frame grabber and their length (measured from the tip of their rostrum to the end of their telson) determined on the computer from the digitized image. Mysid growth rates were estimated by studying the change in the average length of *N. inte-*
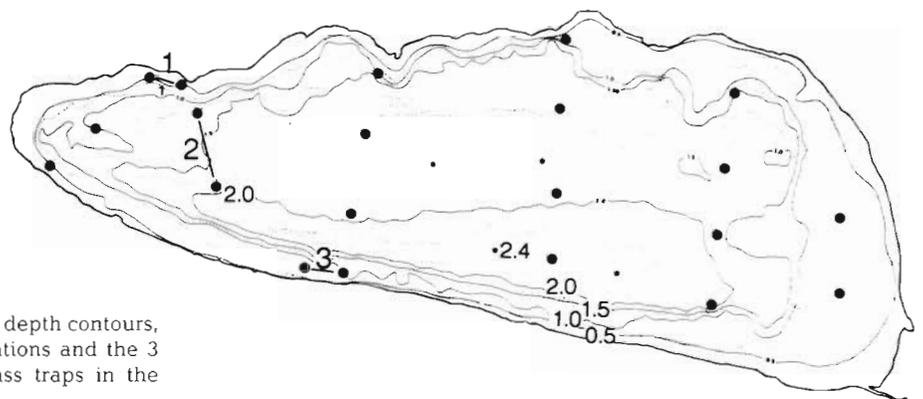

Fig. 1. Map of Lake Ferring showing depth contours, the locations of the 21 sampling stations and the 3 transects for incubation of plexiglass traps in the diurnal study (1 to 3)

ger between sampling dates on cohorts from January to May, from late May to mid-July, and from mid-July to late October. To calculate mysid biomass and production the length-dry weight relationship (24 h at 60°C) of mysids caught in January was used for the January to April samples, while that of mysids caught in August was used for August to December samples. In May and June, when both overwintering and summer generations were present simultaneously, the relationship for the combined data set was used. Mysid production (P, mg DW d^{-1}) (DW: dry wt) was then calculated according to Bremer and Vijverberg (1982) as:

$$P = \sum_{i=1}^{n} P_i,$$

where P is the daily population production, $P_i = \Delta W_i \times N_i$ and is the daily production by the ith size class, n is the number of size classes in the population, W_i is the daily weight increase by the ith size class, and N_i is the population density of the ith size class.

Eurytemora affinis biomass was calculated by applying a dry weight of 6.0 μg ind.$^{-1}$ for females, 5.0 μg ind.$^{-1}$ for males, 2.0 μg ind.$^{-1}$ for copepodites, and 0.5 μg ind.$^{-1}$ for nauplii (Bach et al. 1991). The somatic production (SP) for *E. affinis* was calculated according to Hirche (1992) as

$$SP = [\ln(W) - \ln(0.13)]/10^{(1.9686 - 0.04333 T)}$$

where W is the average dry weight of adult copepods (5.5 μg ind.$^{-1}$ assuming equal numbers of females and males) and T is the water temperature (°C).

Field enclosure experiments. Field experiments were carried out in 12 cylindrical enclosures made of tarpaulin sheets attached to a metal ring (diameter 1.5 m, depth 0.75 m). Each enclosure had a water volume of 1.3 m^3 and was open to the sandy sediment at the bottom. The enclosures were organized in 3 sets of 4 enclosures. Prior to initiation of the experiments mysids were removed from one set using 500 μm nets, and the density in the remaining 2 sets adjusted to approximately 0.5 and 1 ind. l^{-1}, respectively. The stickleback *Gasterosteus aculeatus* density was adjusted randomly to one of 3 levels: 0–1, 1–2, and 2–5 ind. m^{-2}. Because of loss due to mortality, mysids were added to the enclosures at each sampling date to maintain the required experimental density.

Enclosure mysid density was determined from vertical hauls as described above, while stickleback density was determined from the catches in Breder traps placed at the bottom for 1 h. We used the Zippin method to convert trap catches to enclosure density (Higgins 1985). In order to quantify zooplankton, 6.6 l of water was sampled in the centre of each enclosure at a depth of 0.2 m using a 3.3 l Patalas sampler. The water was filtered through a 80 μm filter and the specimens fixed in Lugols solution. Samples were taken twice weekly from July 22 to August 20. Backward stepwise multiple regression including date as a dummy variable was performed on all data from July 30 to August 20 (7 samples), thereby excluding the initial transitional phase, i.e. the first 8 d of the experiment. *Eurytemora affinis* was the only macrozooplankton recorded in the enclosures.

Chlorophyll a (chl a) in the enclosures was measured according to the method of Holm-Hansen & Riemann (1978) using water samples pooled from the same depths and at the same dates as described above.

The results from 3 of the 12 enclosures had to be excluded from the analysis, in 2 cases because the enclosure was damaged during a storm, and in the third case because the 'ecosystem' collapsed (the water became turbid, and all zooplankton and mysids disappeared within the first week).

Predation experiments. Laboratory experiments on *Neomysis integer* predation on *Eurytemora affinis* were carried out in 1 l glass bottles. The mysids and copepods used were collected using 500 and 80 μm nets, respectively. The mysids were allowed to acclimatize for 24 h in plastic holding tanks with approximately 10 l of aerated Lake Ferring water and on a mixed diet of *E. affinis* and trout feed in the form of pellets. About 1 h prior to the experiment, mysids in sets of 3 were transferred to bottles containing 1 l Lake Ferring water pre-filtered through a 50 μm filter to remove copepods. The experiments were initiated by transferring either 100, 200 or 400 nauplii and 100 copepodites + adults to the bottles. Three bottles served as controls. All experiments were conducted in aerated water in subdued light at 15°C and lasted 2 h.

Following incubation the water was filtered through a 50 μm filter and the mysids retained fixed in 96% ethanol and counted. The copepods were fixed in Lugol's solution and counted at a magnification of 25 to 50×. The predation rate (PR, number mysid^{-1} h^{-1}) was calculated as:

$$PR = (C_{start} - C_{end})/(number\ of\ mysids \times incubation\ time)$$

C_{start} and C_{end} being the number of nauplii and copepodites + adults in the bottles before and after incubation, respectively. Clearance rates (F, l mysid^{-1} h^{-1}) were calculated according to Gauld (1951) as:

$$F = [(\ln C_{start} - \ln C_{end}) \times litres]/ \\ (number\ of\ mysids\ l^{-1} \times incubation\ time)$$

and the preference value (S) was estimated according to Chesson (1978) as:

$$S = (R_i/Pt_i)/\sum_{i=1}^{n}(R_i/Pt_i)$$

where R_i is relative abundance of the ith prey type in the food, Pt_i relative abundance of the ith prey type in the environment, and n total number of prey types.

RESULTS

Field data

The average daytime catch of *Neomysis integer* in Lake Ferring increased in late May from a low winter level of approximately 100 ind. m^{-2} to a maximum level of 1250 m^{-2} (0.8 l^{-1}) in July followed by a decrease to a winter mean level of approximately 200 m^{-2} (Fig. 2). These values are conservative, however, as the diurnal investigation undertaken in September revealed that the number of mysids caught by vertical hauls was substantially and significantly ($p < 0.05$, Tukey's t-test) higher at night (1 ind. l^{-1}) than in the morning and afternoon (approximately 0.27 ind. l^{-1}) (Table 1). The higher catch during the night largely reflects migration from the bottom to the open water since the lake bottom Breder trap catch of mysids was significantly (2 to 3 times) greater during the day (average 360 ind. $trap^{-1}$) than during the night (Table 1).

The first juvenile mysids were observed in mid-May (Fig. 3). Recruitment continued until the end of October and was most intensive in mid-May, mid-July and mid-August. The mysids were approximately 2 to 3 mm when leaving the female marsupium, whereafter they grew to 17 mm. Three cohorts were identified. From the changes in the average length of the different *Neomysis integer* cohorts (Fig. 4) the following semi-log transformed linear relationship between mysid length (L, mm) and growth rate (GR, mm d^{-1}) was established: January to April cohort: GR = 0.024 ($p < 0.0001$, n = 5), May to July cohort: GR = 3.14×0.567^L ($r^2 = 0.82$, $p < 0.03$, n = 5), August to December cohort: GR = 2.41×0.538^L ($r^2 = 0.97$, $p < 0.001$, n = 7).

Differential log transformed linear relationships between dry weight (DW, mg) and length (L, mm) were found for the *Neomysis integer* caught in January (the winter generation): DW = $0.00347 L^{2.7046}$ ($r^2 = 0.98$, $p < 0.0001$, n = 50), and for mysids caught in August (the summer generation): DW = $0.00621 L^{2.4873}$ ($r^2 = 0.98$, $p < 0.0001$, n = 50). For the combined data set the relationship was DW = $0.00638 L^{2.433}$ ($r^2 = 0.98$, $p < 0.0001$, n = 100).

Table 1. Average catch of *Eurytemora affinis* (±SD) in Breder traps (n = 12) and vertical hauls (n = 7) in Lake Ferring at 3 different times on 25 and 26 September 1992

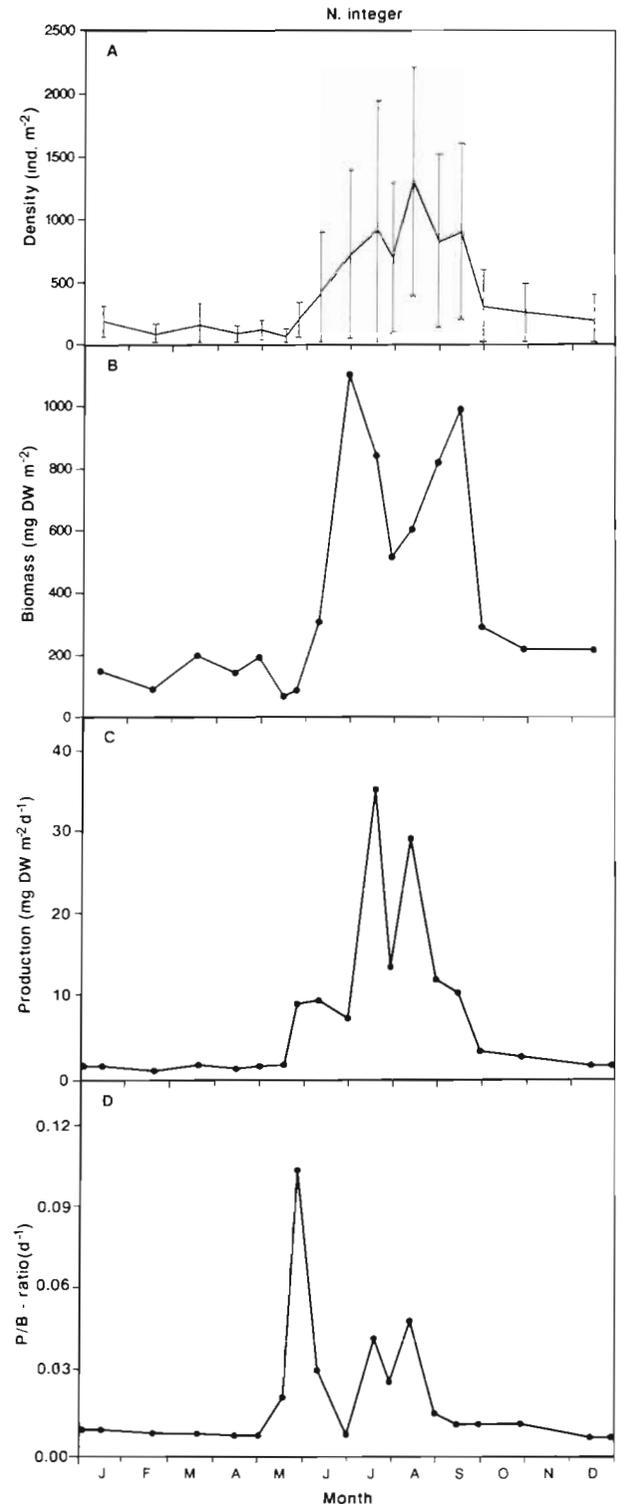| Time (h)	Breder traps (mysids trap^{-1})	Vertical hauls (mysids l^{-1})
15:00	360 ± 346	0.26 ± 0.23
23:00	132 ± 78	1.03 ± 0.68
08:00	268 ± 110	0.27 ± 0.19

Fig. 2. *Neomysis integer*. Seasonal variation in (A) population density (±SD, n = 21), (B) biomass, (C) calculated production and (D) P/B ratio in Lake Ferring in 1992

Mysid biomass increased from the end of May from low winter values of 100 to 200 mg DW m^{-2} to maximum values of 1000 to 1100 mg DW m^{-2} in the begin-
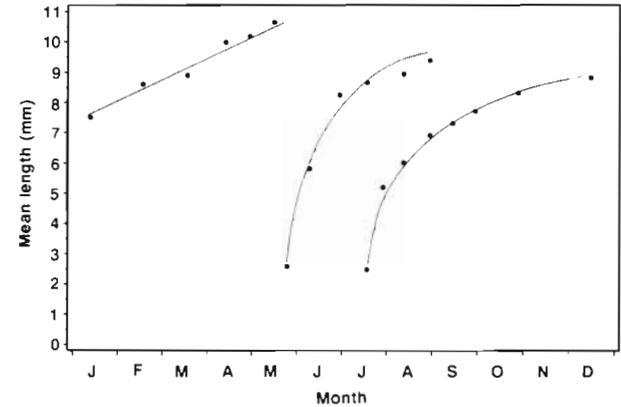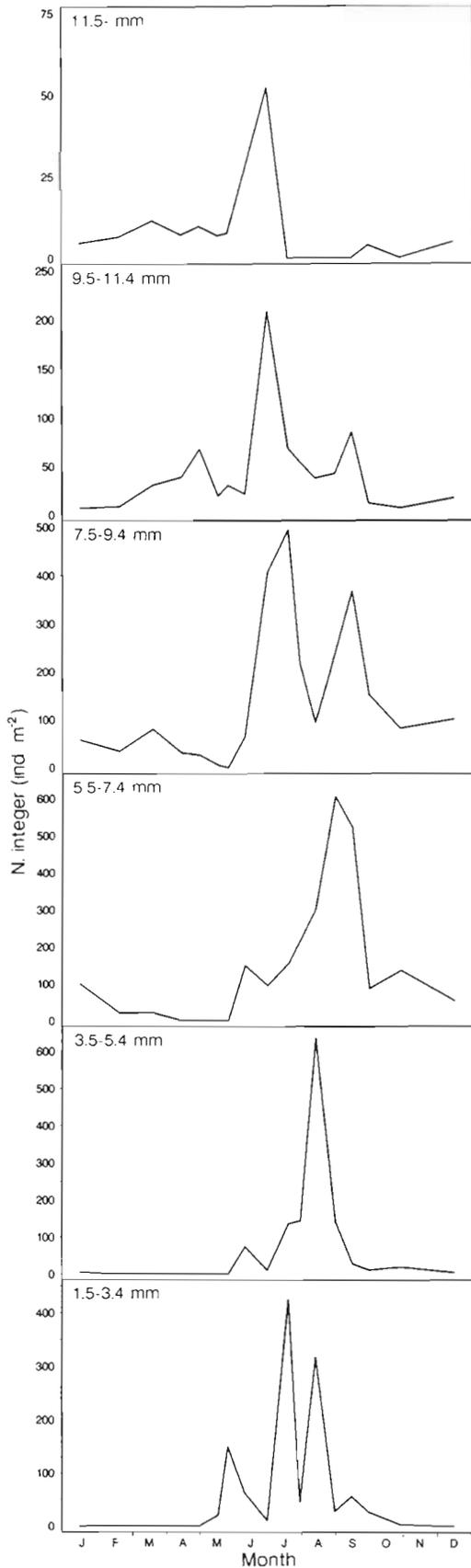
Fig. 4. *Neomysis integer.* Mean length of cohorts in Lake Ferring used for growth rate calculations

ning of July and mid-September (Fig. 2), after which it decreased again to winter levels. In late July and August biomass was 500 to 800 mg DW m^{-2}. Mysid production, based on vertical hauling, increased from winter and spring levels of 0 to 3 mg DW m^{-2} d^{-1} to maximum levels of 35 and 29 mg DW m^{-2} d^{-1} in mid-July and mid-August, (Fig. 2), thereafter decreasing gradually to winter levels. In comparison, calculated production of its potential prey, *Eurytemora affinis*, was less than 10 mg DW m^{-2} d^{-1} during most of the year apart from a short period in June, where it peaked at approximately 55 mg DW m^{-2} d^{-1} (Fig. 5). On an annual basis the total production was calculated to 2.2 g DW m^{-2} for *Neomysis integer* and 2.5 g DW m^{-2} for *E. affinis*.

The density of *Eurytemora affinis*, nauplii and advanced stages was almost equal throughout the year (Fig. 5), winter and spring (January to May) density being 5 to 30 ind. l^{-1} in both cases. A maximum of 72 nauplii l^{-1} and 60 copepodites + adults l^{-1} was reached in mid-June, density then decreasing to winter levels in July and August. In September to December the density was slightly higher than in July and August, the average density being approximately 25 ind. l^{-1} in both cases. As a consequence, copepod biomass was low in spring, the mean value being 60 mg DW m^{-2}. The maximum value of 300 mg DW m^{-2} was recorded in June, while the mean value was 135 mg DW m^{-2} in September to December (Fig. 5). The *Neomysis integer* P/B ratio ranged from 0.004 to 0.10 d^{-1} and the seasonal pattern was bimodal, the maxima being reached in late May and again in July and August (Fig. 2).

Fig. 3. *Neomysis integer.* Seasonal variations in the density of various size classes in Lake Ferring
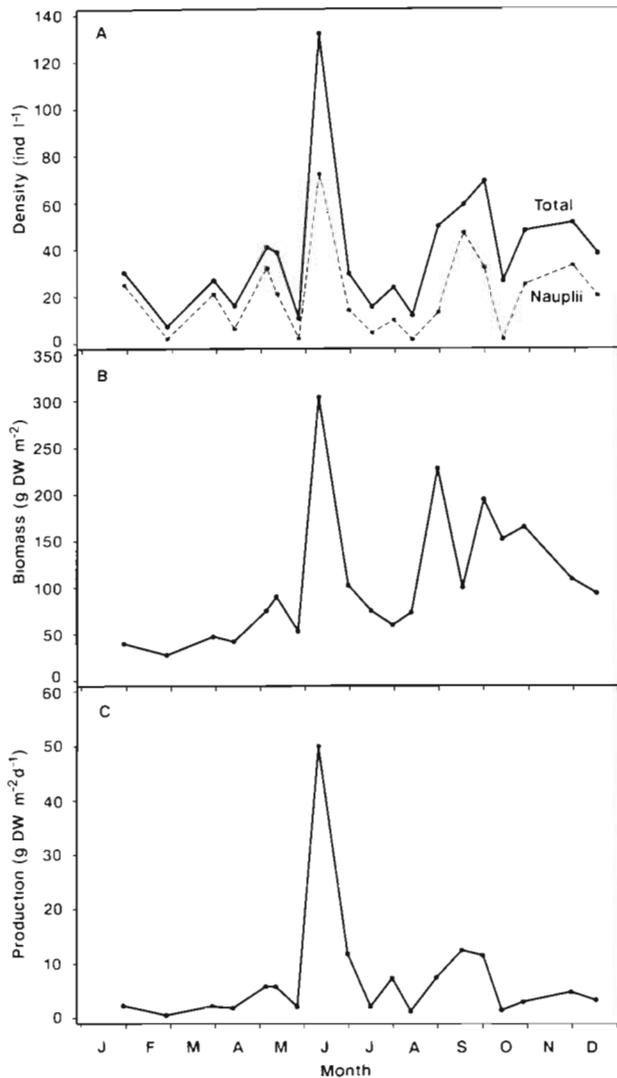
Fig. 5. *Eurytemora affinis*. Seasonal variation of (A) density (both total and naupliar), (B) biomass and (C) calculated production in Lake Ferring in 1992

Enclosure experiments

In the enclosure experiments marked changes in *Eurytemora affinis* density were found that followed changes in the density of *Neomysis integer* and *Gasterosteus aculeatus*. Average copepod density during the 25-day experiment varied from 295 ind. l^{-1} when the density of the mysids and sticklebacks was low (0.04 ind. l^{-1} and 0.4 ind. m^{-2}, respectively), to less than 100 when mysid density was high (>0.25 ind. l^{-1}), in the latter case irrespective of stickleback density, which ranged from 0.25 to 4.2 ind. m^{-2} (Fig 6). Naupliar density decreased markedly at a mysid density of 0.1 ind. l^{-1}, nauplii accounting for approximately 50% of the *E. affinis* population at the lowest *N. integer*
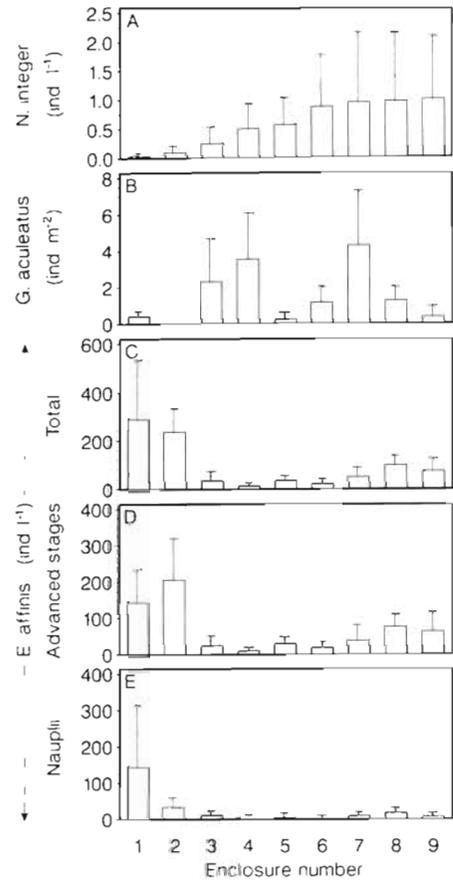

Fig. 6. Mean density (30 July to 20 August 1992) (±SD, n = 7) of (A) *Neomysis integer*, (B) *Gasterosteus aculeatus*, and (C) total *Eurytemora affinis*, (D) *E. affinis* copepodites + adults and (E) *E. affinis* nauplii in the 9 field enclosures ordered by increasing mean *N. integer* density

density, but only 10 to 25% at higher *N. integer* densities. In accordance with this, nauplii density was significantly negatively correlated to *N. integer* density [Table 2; log(n+1) transformed data] In contrast, no relationship was detected between the density of mysids and that of copepodites + adults, although both nauplii and advanced stages of *E. affinis* were negatively correlated to the density of *G. aculeatus*. Stepwise multiple linear regression on log(n+1) transformed data revealed a significant negative influence of *G. aculeatus* and *N. integer* on both *E. affinis* total density and the density of nauplii, while the contribution of fish × mysid was positive. In contrast, the density of the advanced stages of *E. affinis* was alone significantly negatively related to the density of *G. aculeatus* (Table 3).

Correlation analysis [log(n+1) transformed data] revealed a highly positive relationship between chl *a* and the *Neomysis integer* density, but only a moderately negative relationship to *Eurytemora affinis* and no re-

Table 2. Spearman correlation coefficients (with the statistical significance level in parentheses) based on log(n+1) transformed data collected on 7 sampling dates (30 July to 20 August) in 9 field enclosures. *, **, ***, **** represent the 0.05, 0.01, 0.001 and 0.0001 significance levels, respectively. ns: not significant

| | Three-spined sticklebacks | *Neomysis integer* | *Eurytemora affinis* number | | | *E. affinis* Total biomass |
			Nauplii	Copepodites + adults	Total	
N. integer	-0.002^{ns}					
E. affinis number						
Nauplii	-0.27^*	-0.46^{***}				
Copepodites + adults	-0.62^{****}	0.05^{ns}	0.49^{****}			
Total	-0.59^{****}	-0.06^{ns}	0.67^{****}	0.97^{****}		
E. affinis						
Total biomass	-0.62^{****}	0.04^{ns}	0.52^{****}	0.99^{****}	0.98^{****}	
Chl *a*	-0.03^{ns}	0.49^{****}	-0.32^*	-0.02^{ns}	-0.12^{ns}	-0.03^{ns}

lationship to *Gasterosteus aculeatus* density (Table 2). Stepwise multiple linear regression on log(n+1) transformed data revealed a highly significant relationship between chl *a* and *N. integer* density, and a slightly negative one to *E. affinis* density (Table 3).

Predation experiments

The predation experiments showed a positive relationship between naupliar density and the *Neomysis integer* specific predation rate (SPR) ($r^2 = 0.89$, p < 0.0001, Pearson's correlation) (Table 4). The SPR on nauplii at 15°C changed from an average of 15 ind. mysid^{-1} h^{-1} at a density of 100 nauplii l^{-1} to an average of 52 ind. mysid^{-1} h^{-1} at a density of 400 nauplii l^{-1}. SPR on the advanced stages of *Eurytemora affinis* was not influenced by changes in naupliar density, and

remained constant at an average of 6 ind. mysid^{-1} h^{-1} (p > 0.3, Kruskal-Wallis). Moreover, the clearance rates were not influenced by changes in naupliar density (p > 0.3, Kruskal-Wallis), probably indicating that the mysids catch the nauplii by 'filter feeding' (Gauld 1951). The average clearance rate was 0.34 l mysid^{-1} h^{-1} for nauplii and 0.08 l mysid^{-1} h^{-1} for copepodites + adults. The mysid preference value was 0.7 for nauplii and for advanced stages 0.3, the values being unaffected by naupliar density (p > 0.25, Kruskal-Wallis).

DISCUSSION

Neomysis integer had 2 generations in Lake Ferring during the study year. Recruitment started in May and June when the winter generation reproduced, and the resultant spring-born first generation constituted the

Table 3. Stepwise multiple regression showing the relationship between log(n+1) transformed values of chl *a*, the density of nauplii, copepodites + adults (Cop.+ adults) and all stages of *Eurytemora affinis* versus log(n+1) transformed values of *E. affinis* (only chl *a*), *Neomysis integer* and sticklebacks *Gasterosteus aculeatus* density, as well as date in the enclosure experiments in July and August. *, **, ***, **** represent the 0.05, 0.01, 0.001 and 0.0001 significance levels, respectively. ns: not significant

	Chl *a* (μg l^{-1})	F	*Eurytemora affinis* (ind. l^{-1}) Nauplii	F	Cop.+ adults	F	Total	F
Intercept	6.16	4544^{****}	3.29	60^{****}	4.46	561^{****}	5.18	426^{****}
E. affinis	-0.05	10^{**}	–		–		–	
Neomysis integer	0.21	19^{****}	-3.42	24^{****}	ns		-1.76	8^{**}
Sticklebacks	ns		-1.28	19^{****}	-1.25	41^{****}	-1.63	43^{****}
N. integer × fish	ns		2.49	9.5^{**}	ns		2.02	8^{**}
Dates		11^{****}		4.4^{**}	ns		ns	
1	0.06		-0.05					
2	-0.11		0.46					
3	0.08		-0.12					
4	0.19		1.63					
5	0.37		1.02					
6	0.25		-0.17					
Model r^2	0.67		0.60		0.40		0.46	
df	61		61		61		61	

Table 4. Mean (±SD) specific predation rates, clearance rates and selectivity coefficient of *Neomysis integer* feeding at 3 different densities of *Eurytemora affinis*. Water volume was 1 l, incubation time 2 h at 15°C in subdued light, and mysid density 3 l^{-1}. NC: density change in controls during the experiment

	Initial density (ind. l^{-1})	NC (ind. l^{-1})	Spec. predation rate (ind. mysid^{-1} h^{-1})	Clearance rate (l mysid^{-1} h^{-1})	Selectivity coefficient
Nauplii	100	2 ± 1	15 ± 2	0.38 ± 0.18	0.65 ± 0.09
Copepodites + adults (n = 3)	100	0 ± 2	8 ± 2	0.11 ± 0.05	0.36 ± 0.09
Nauplii	200	2 ± 3	26 ± 6	0.36 ± 0.22	0.75 ± 0.11
Copepodites + adults (n = 9)	100	2 ± 2	5 ± 4	0.08 ± 0.10	0.25 ± 0.11
Nauplii	400	3 ± 14	52 ± 11	0.30 ± 0.17	0.70 ± 0.12
Copepodites + adults (n = 6)	100	4 ± 4	6 ± 3	0.07 ± 0,04	0.30 ± 0.12

summer generation that together with surviving individuals of the winter generation reproduced in July and August, thus providing the new winter generation. Because of the protracted reproduction period, it was difficult to follow the individual cohorts; however, the seasonal variation in mysid size distribution was identical with that observed for *N. integer* in other brackish lakes, both in Denmark (Kaiser 1978) and elsewhere (Kinne 1955, Mauchline 1971, Borghouts 1978, Mauchline 1980, Bremer & Vijverberg 1982, Arndt & Jansen 1986, Irvine et al. 1993).

Mysid density and biomass in Lake Ferring was high (maximum 0.8 ind. l^{-1}, corresponding to 1250 ind. m^{-2}), the maximum biomass being 1100 mg DW m^{-2}. Similar mysid density was observed by Irvine et al. (1993), whereas much lower values were recorded by Bremer & Vijverberg (1982) and Arndt & Jansen (1986). Even though daytime mysid density in Lake Ferring was high, it was probably considerably underestimated. The diurnal study revealed substantial diel vertical migration of *N. integer*, the catches in Breder traps located at the lake bottom being 2- to 3-fold greater in daytime than at night, and the vertical hauls being conversely 4-fold less in daytime than at night. That mysids in shallow lakes undergo diurnal migration is well documented (Beattie & de Kruijf 1978, Bremer & Vijverberg 1982, Irvine et al. 1993), and the differences found between day and night hauls were comparable to those found in previous investigations (Grossnickle & Morgan 1979, Nero & Davies 1982, Irvine et al. 1993). Estimated mysid density (and hence potential mysid impact on zooplankton) may therefore be underestimated by a factor of 4, the true density probably therefore being nearer 3 ind. l^{-1} at maximum.

The high mysid density in Lake Ferring may reflect the hypertrophic character of the lake and the low predation pressure by fish; the fish biomass is extremely low and exclusively dominated by sticklebacks that

mainly prey on copepods and to a minor extent on juvenile *Neomysis integer* (M. Søndergaard & E. Jeppesen unpubl. obs.). High densities of *N. integer* (up to 13 ind. l^{-1}) have been found in other Danish hypertrophic brackish lakes in which fish biomass is low (Jeppesen et al. 1994). Moreover, the relationship between *N. integer* density and the biomass of fish caught in multiple mesh size gill nets is generally negative in Danish shallow brackish lakes (Jeppesen et al. 1994). The importance of fish is also evidenced by fish manipulation experiments undertaken in Lake Wolderwejd, The Netherlands, where removal of 75 % of the planktivorous fish biomass resulted in a major increase in *N. integer* density (Meijer et al. 1994).

The estimated growth rates of the various *Neomysis integer* size groups and the seasonal dynamics are similar to those found in previous investigations (Bremer & Vijverberg 1982, Asthorsson & Ralph 1984, Arndt & Jansen 1986). The validity of calculating mysid growth rates from field data was questioned by Asthorsson & Ralph (1984) on the grounds that it is periodically difficult to follow the cohorts. On the other hand, growth rates calculated from laboratory experiments may be influenced by the experimental conditions. In comparison with laboratory growth rates, Arndt & Jansen (1986) found higher rates in natural populations. Mysid production (not corrected for sampling error) was higher than 10 mg DW m^{-2} d^{-1} during most of the summer, reaching 35 mg DW m^{-2} d^{-1} in mid-July. Despite the much higher density in Lake Ferring, the level and seasonal variation in the *N. integer* P/B ratio was comparable to that reported in other studies on *N. integer* (Bremer & Vijverberg 1982, Arndt & Jansen 1986).

As to whether a high density of *Neomysis integer* affects the population structure of its potential prey, *Eurytemora affinis*, the laboratory predation experiments showed that mysids had a selective preference for nauplii and that the predation potential was high, with

maximum predation rates on nauplii and copepodites + adults of 52 and 8 ind. mysid^{-1} h^{-1}, respectively. Converted to biomass, this amounts to a daily ration of approximately 360 % d^{-1} (3.6 g DW g^{-1} DW d^{-1}). These rates are similar to observations made in other laboratory studies on *N. integer* (Irvine et al. 1990, 1993). If the *in situ* predation rate was really so high, mysids in Lake Ferring would exterminate the nauplii and copepodite populations in a few days. This also applies to the field enclosures with the highest densities of *N. integer* (0.5 to 1 ind. l^{-1}). However, as the predator and prey species coexist in both the enclosures and the lake as a whole, the predation pressures found in the laboratory experiments must be overestimates. There are various possible explanations for this. Firstly, *E. affinis* may find it more difficult to escape predation in the experimental chambers than in the field. In the lake the *N. integer* seek refuge from fish predation by staying near the bottom during daytime, but at the same time thereby affording the pelagic *E. affinis* a higher chance of survival. Secondly, there are alternative food sources in the lake, *N. integer* being known to be omnivorous and also able to feed on detritus and algae (Mauchline 1971, Bremer & Vijverberg 1982, Arndt & Jansen 1986, Irvine et al. 1993). That this was the case in Lake Ferring was confirmed by qualitative analysis of *N. integer* gut contents; these consisted, apart from copepods, of cyanobacteria, chlorophytes and diatoms, as well as various zooplankton such as ciliates and rotifers. Fragments of vascular plants, pollen and detritus were also detected. Further evidence of omnivory is provided by the fact that *N. integer* would only be able to meet a maximum of 22 % and as little as 6 % when corrected for sampling error of its food energy requirements from *E. affinis*, if we assume a growth yield of approximately 20 % for *N. integer* (as the production of *E. affinis* and *N. integer* was calculated to 2.5 and 2.2 g DW m^{-2} yr^{-1}, respectively). That the predation rates found in the laboratory studies are overestimates is further emphasized by the fact that a daily ration of 360 % d^{-1} will result in a growth rate far exceeding that obtained from the lake data (Fig. 2), and considerably greater than that found in several other studies (Cooper & Goldman 1980, Chigby & Sibley 1994). As the mysids used in the laboratory studies were prefed with *E. affinis*, the possibility can be excluded that prestarvation could explain the high predation rates obtained.

The enclosure experiments showed that at natural lake densities, *Neomysis integer* had a significant negative effect on the abundance of nauplii as well as on the total number of *Eurytemora affinis*, but not on the number of copepodites + adults. In contrast, *Gasterosteus aculeatus* had a negative impact on all stages but particularly the advanced stages, as has been reported in many other studies (e.g. Worgan & FitzGerald 1981,

Castonguay & FitzGerald 1990, Pont et al. 1991). The contribution of sticklebacks × *N. integer* in the multiple regression was positive for the nauplii (Table 3), however, which may be explained by the fact that *N. integer* seeks refuge from fish predation near the bottom (Meijer et al. 1994), thereby reducing the predation pressure on the nauplii, which typically inhabit pelagic waters.

Since *Neomysis integer* and *Gasterosteus aculeatus* coexist in many hypertrophic brackish lakes, including Lake Ferring, it is therefore likely that the predation pressure on *Eurytemora affinis* in such lakes is particularly high, the *E. affinis* being preyed upon both from 'below' (*N. integer*) and from 'above' (*G. aculeatus*). The coexistence of *N. integer* and sticklebacks may explain why the zooplankton grazing pressure on the phytoplankton is generally lower in hypertrophic brackish lakes, including Lake Ferring, than in corresponding freshwater lakes, where planktivorous fish are the exclusively dominant macropredator (Jeppesen et al. 1994).

In the enclosure experiments a highly positive correlation was found between chl *a* and *Neomysis integer* density. This may in part be explained by predation on the phytoplankton-grazing copepods since chl *a* and nauplii density were negatively correlated (Table 2). However, the correlation to *N. integer* was much stronger than to copepods. Moreover, the stepwise multiple regression showed that *N. integer* contributed highly significantly to residual variation in chl *a* when copepods were included in the model, while sticklebacks did not (Table 3). Similar results were obtained in enclosure experiments in another Danish brackish lake (F. Nielsen & E. Jeppesen unpubl. obs.). These results suggested a more direct stimulation of phytoplankton growth by *N. integer*, perhaps because nutrients consumed when feeding on the sediment surface are subsequently excreted to the water above. In fact, the experiment by Nielsen & Jeppesen (unpubl. obs.) showed markedly higher phosphorus levels in enclosures with *N. integer*. As the density in the enclosures (0.5 to 1 mysid l^{-1}) in Lake Ferring was comparable to that in the lake (Figs. 4 & 5), it seems reasonable to suggest that mysids negatively influenced the environmental state of the lake in terms of higher algal biomass and consequently a lower Secchi depth. In support of this view multiple regression analysis of 3 years' data from the lake showed that besides being significantly negatively related to the total zooplankton biomass, chl *a* was positively related to the *N. integer* density (Nielsen & Jeppesen unpubl. obs.).

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