

Regulation of zooplankton by suspension-feeding bivalves and fish in estuarine enclosures*

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ABSTRACT: Enclosure experiments were conducted during April, June/July and September in the eutrophic estuary Roskilde Fjord, Denmark, to reveal the effects of inorganic nutrients, suspension-feeding bivalves *Mytilus edulis* and planktivorous fish (three-spined sticklebacks *Gasterosteus aculeatus*) on the zooplankton community > 45 µm. The addition of inorganic nutrients did not increase zooplankton biomass although it did increase the chlorophyll level, indicating that zooplankton production was not food limited. Filtration by *M. edulis* reduced the number of tintinnid ciliates and rotifers during all 3 experiments, but not the abundance of the larger zooplankton species. Additions of planktivorous fish reduced the densities of larger zooplankton species *Acartia tonsa* and *Pleopis polyphemoides* but not of smaller species. An immense increase in numbers of *A. tonsa* and *P. polyphemoides* was observed in enclosures without fish, indicating that the larger crustacean zooplankton is strongly predator controlled. Thus, the qualitative and quantitative development of the zooplankton community in the enclosures was controlled in 2 ways; from the top of the size spectrum by *G. aculeatus* and from the bottom of the size spectrum by *M. edulis*.

INTRODUCTION

Knowledge on the role of predation in regulating the composition of zooplankton communities in pelagic environments has increased markedly during the last 2 decades. Most evidence derives from lakes, and in particular from studies designed to predict effects of nutrient loadings and planktivorous fish on the qualitative and quantitative development of the zooplankton community (e.g. Andersson et al. 1978, Stenson et al. 1978, Henrikson et al. 1980, Goad 1984).

Eutrophication enhances phytoplankton primary production and biomass. Whether this increase is always channelled to higher trophic levels in marine environments is not clear (Nixon & Pilson 1983). Enclosure experiments have documented enhanced zoo-

plankton production in response to nutrient loading (Fulton 1984). However, in natural environments successional changes also occur among potential zooplankton predators. In lakes the abundance of cyprinid fishes increases in both absolute and relative terms when going from oligotrophic to mesotrophic conditions (Johansson & Persson 1986). This change in the fish population will increase predation on the zooplankton community (Henriksson et al. 1980).

The importance of small planktivorous fish in the food web of shallow marine ecosystems is well documented (e.g. Miller 1979, Zander & Hartwig 1982, Zander et al. 1984). Suspension-feeding bivalves may also play a central role in the energy flow of marine ecosystems (Dame 1980, Kautsky 1981, Cloern 1982), but the impact of suspension-feeding bivalves on natural zooplankton communities is not known.

Most studies of marine zooplankton have focused on meso-zooplankton (> 200 µm), but since microzooplankters (e.g. tintinnid ciliates and rotifers) are very abundant in estuarine environments and hence account for a large part of the community biomass and clearance (Andersen & Sørensen 1986, Jonsson 1986), we included species > 45 µm in the present study.

The aim of this study was to measure population

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growth of zooplankton > 45 μm when different combinations of nutrients, suspension-feeding bivalves and planktivorous fish were added to estuarine enclosures.

MATERIALS AND METHODS

Experiments were conducted in the eutrophic estuary Roskilde Fjord, Denmark, during spring (5 to 28 April), summer (17 June to 3 July) and autumn (8 to 25 September) 1986, at temperatures ranging from 0 to 22 °C. Sixteen transparent plastic enclosures (diameter 1.5 m, depth about 3.5 m) were filled with water from the fjord at the beginning of each experiment and fixed to a pontoon bridge (for further details see Riemann et al. 1988: companion paper). The enclosures were manipulated in duplicates by the addition of nutrients, suspension-feeding bivalves and planktivorous fish (Table 1).

Eight enclosures were fertilized by the addition of 0.67 g $\text{NO}_3\text{-N}$ and 0.10 g $\text{PO}_4\text{-P}$ per enclosure each time the enclosures were sampled. *Mytilus edulis* corresponding to 279 to 345 g wet weight made up by 333 to 569 individuals of 15 to 22 mm shell length were added to half of the enclosures. The filtration by the mussels added to each enclosure corresponded to filtration of the natural population in Roskilde Fjord (Riemann et al. 1988). The mussels were distributed in 3 Japanese pearl nets and suspended at depths of 1, 2 and 3 m. The role of planktivorous fish was studied by adding 10 g wet wt of three-spined sticklebacks *Gasterosteus aculeatus* (corresponding to 20 to 35 1-yr-old fish) to 8 enclosures. The biomass corresponded to the natural abundance of planktivorous species in Roskilde Fjord

Table 1. Enclosure manipulation. C: control; M, F, N: mussels, fish and nutrients, respectively. All treatments were duplicated

	– Nutrients		+ Nutrients	
	– Fish	+ Fish	– Fish	+ Fish
– Mussels	C	F	N	NF
+ Mussels	M	MF	MN	MNF

(Gislason 1980). At the end of each experiment water from the enclosures was filtered through a large 3.5 mm mesh net, to collect the added fish.

Mussels and fish were collected in Roskilde Fjord and the adjacent Isefjord and acclimated to ambient conditions in a well-box for 4 to 5 d prior to the experiments.

Sampling program. Salinity was measured at the beginning of each experiment, while temperature was measured on each sampling day. Zooplankton was sampled once at the beginning and once at the end of the April experiment, whereas triplicate samples were taken every second to fourth day during the June/July and September experiments. Water was sampled from 5 depths in the enclosures, using a 5 l plexiglass water sampler. Water samples from the different depths were mixed, and 25 and 10 l samples were filtered through 140 μm and 45 μm mesh nets, respectively. Samples were fixed in buffered formalin (2 % final concentration). Zooplankton was counted, identified and measured using a settling chamber and an inverted microscope.

Abundance data and length measurements (to the nearest 1 μm) were converted to biomass and clearance (assuming that zooplankton > 45 μm ingest particles within the same size range) according to data from the literature (Table 2) and assuming a Q_{10} of 2 and a conversion factor from dry weight to carbon of 50 %.

RESULTS

Temperature ranged from 0 to 22 °C during the 3 periods, while salinity was 11 to 13 ‰ (Table 3). Recapture of the added fish at the end of each period showed that 70 % of the fish survived the April experiment, 35 % the June/July experiment and 90 % the September experiment.

The number of tintinnid ciliates decreased in all enclosures during the 3 experiments, but the decrease was most pronounced in the enclosures with added mussels (Fig. 1). The mean length of ciliates *Tintinnopsis* spp. were 65, 95 and 80 μm during April, June/July and September, respectively. During June/July numbers decreased from more than 1000 l^{-1} to 20 l^{-1} in the

Table 2. Literature used in the conversion of abundance data to biomass and clearance

Taxon	Biomass	Clearance
<i>Tintinnopsis</i> spp.	Fenchel & Finlay (1983)	Fenchel (1986)
<i>Synchaeta</i> spp.	Hernroth (1985), Schinder & Noven (1971)	Starkweather (1980)
Polychaete larvae	K. Johansen (pers. comm.)	As bivalve larvae
Gastropod larvae	Pechenik (1980)	Pechenik (1980)
Bivalve larvae	Jespersen & Olsen (1982)	Jespersen & Olsen (1982)
<i>Pleopis polyphemoides</i>	Hernroth (1985)	
<i>Acartia tonsa</i>	Berggreen et al. (in press)	Berggreen et al. (in press)
<i>Balanus</i> spp. nauplii	Rodhouse & Roden (1987)	F. Møhlenberg (unpubl.)

Table 3. Temperature range and salinity during the 3 experimental periods

	Temperature range (°C)	Salinity (‰)
April	0–9	11
June/July	17–22	13
September	11–12	11

enclosures with added mussels, while the decrease in the enclosures without mussels was less pronounced (Fig. 1A). Lower numbers were recorded during the April and September experiments, and during April similar changes in the number of tintinnids were found in all enclosures.

The initial number of rotifers in April was about 400 l^{-1} , decreasing to 75 l^{-1} in enclosures with added mussels and 250 l^{-1} in enclosures without mussels (Fig. 1B). During June/July the number of rotifers decreased from about 150 l^{-1} to 10 and 35 l^{-1} in enclosures with and without mussels, respectively (Fig. 1B). In September only few *Synchaeta* were recorded at the start of the experiment. In enclosures without mussels their number peaked at more than 100 l^{-1} in the middle of the experiment, while the number was stable at about 5 l^{-1} in the mussel enclosures (Fig. 1B).

In contrast to the predation on *Tintinnopsis* spp. and *Synchaeta* spp., mussels had no effect on the abundance of the copepod *Acartia tonsa* (Fig. 2), although *M. edulis* can efficiently clear ambient water of *Artemia salina* nauplii (Jørgensen 1975).

The addition of fish *Gasterosteus aculeatus* influenced the abundance of *Acartia tonsa*. In April the initial number of *A. tonsa* was low, but the abundance of copepodites and adults increased during the experiment (Fig. 2). The increase in copepodites and adults was most pronounced in enclosures without fish. Numbers of nauplii were nearly constant during April in all enclosures. Larger effects of planktivorous fish were found in June/July. Numbers of copepodites and adults showed an 8-fold increase and nauplii more than a 40-fold increase in enclosures without fish, compared to reduced numbers of copepodites and adults and a nearly constant number of nauplii in enclosures with fish (Fig. 2). Only minor changes in numbers of the different developmental stages were seen in enclosures without fish during September, while decreasing numbers were measured in enclosures with fish (Fig. 2).

At the beginning of the June/July experiment 20 to 60 individuals m^{-3} of the raptorial cladoceran *Pleopis polyphemoides* were recorded (Fig. 3). Lower number of this species were found in enclosures with fish while a 5- to 250-fold increase was seen in enclosures without fish.

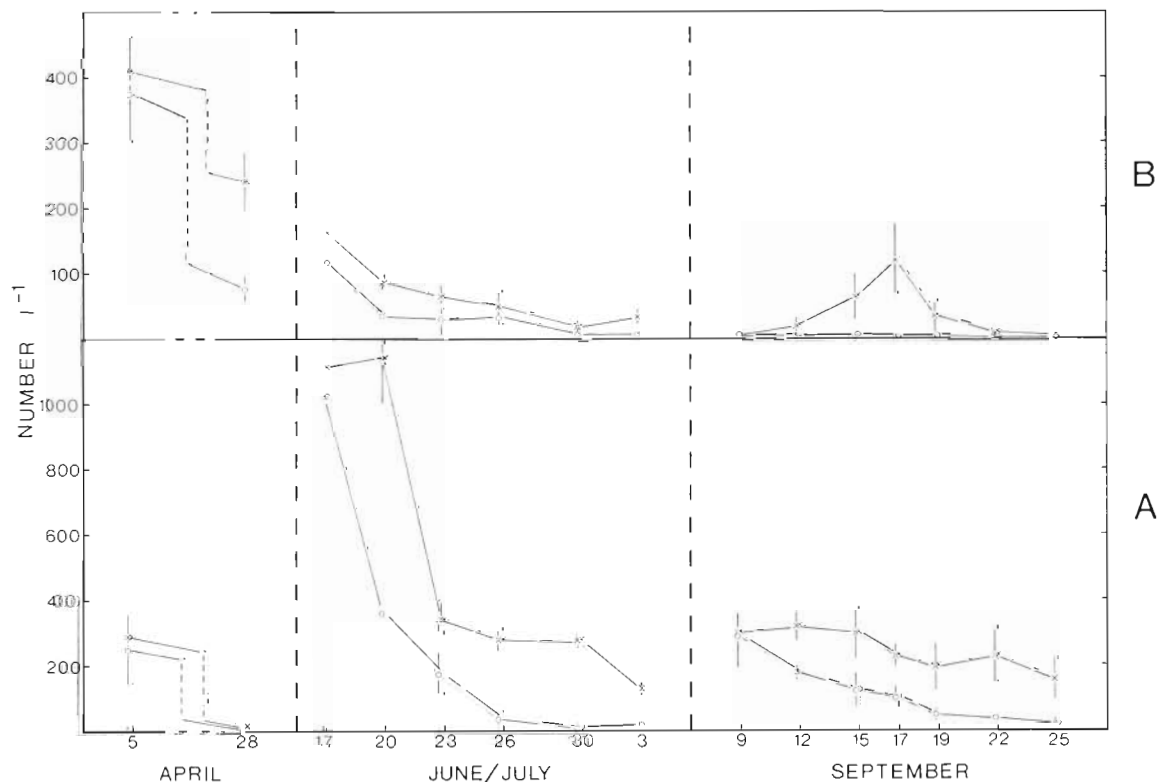


Fig. 1. Numbers of (A) tintinnid ciliates *Tintinnopsis* spp. and (B) rotifers *Synchaeta* spp. during the 3 experimental periods in enclosures with added mussels (○), and without mussels (×). Bars represent standard deviation ($n = 12$)

Addition of suspension-feeding bivalves and planktivorous fish had considerable effects on biomass (mg C m^{-3}) and calculated clearance ($1 \text{ m}^{-3} \text{ d}^{-1}$) of the zooplankton $> 45 \mu\text{m}$ (Fig. 4). During April, total biomass decreased in all enclosures, while total clearance increased in enclosures without fish and decreased in enclosures with added fish (Fig. 4). The increase in estimated total clearance in some enclosures, in spite of decreased biomass, was caused by enhanced clearance by the zooplankton as a result of higher temperatures. Biomass and clearance of *Tintinnopsis* spp. decreased in all enclosures to respectively 4 and 7 % of initial levels. *Synchaeta* spp. accounted for the major part of the biomass and clearance at the beginning of the experiment. In enclosures without mussels, *Synchaeta* spp. maintained a high biomass and clearance, while their importance decreased in enclosures with mussels. Biomass of *Acartia tonsa* increased during April in enclosures without fish, and their clearance increased likewise.

In June/July the total zooplankton biomass and especially the total clearance were higher than in April, and

additional species appeared in the samples (Fig. 4). Meroplanktonic species included larvae of polychaetes (*Nereis* spp. and *Polydora* sp.), gastropods (*Hydrobia* spp.), bivalves (mainly *Mytilus edulis*) and especially cirripedes (*Balanus* spp.); they accounted for 25 % of the biomass and 5 % of the clearance at the start of this experiment, but their importance decreased during the period. The cladoceran *Pleopis polyphemoides* appeared in all enclosures at the start, but with low biomass. During the experiment their biomass increased in enclosures without fish and decreased in enclosures with added fish. *Tintinnopsis* spp. accounted for more than one-third of the biomass, and about 90 % of the clearance at the start, decreasing in both relative and absolute importance during the period, especially in enclosures containing mussels. *Synchaeta* spp. showed the same tendencies as *Tintinnopsis* spp., although less pronounced, and clearance of these species constituted a smaller part of the zooplankton clearance. Biomass of *Acartia tonsa* was low at the beginning of the period, and clearance of the species accounted for a minor part of the total clear-

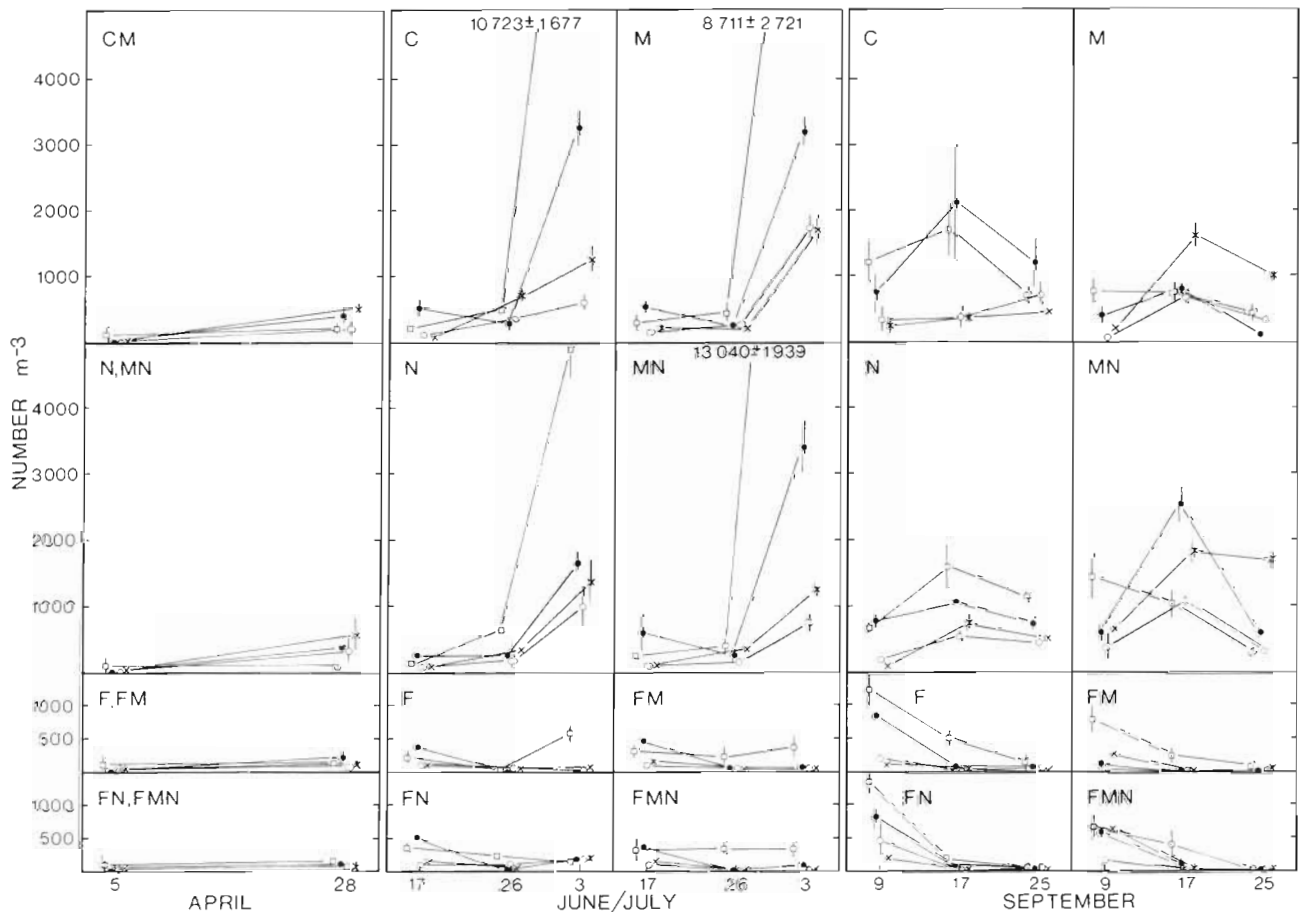


Fig. 2. Changes in numbers of the copepod *Acartia tonsa* during the 3 experiments. (\square) Nauplii $\times 10^{-1}$; (\bullet) copepodites I + II; (\circ) copepodites III + IV; (\times) copepodites V + adults. Bars represent standard deviation ($n = 6$)

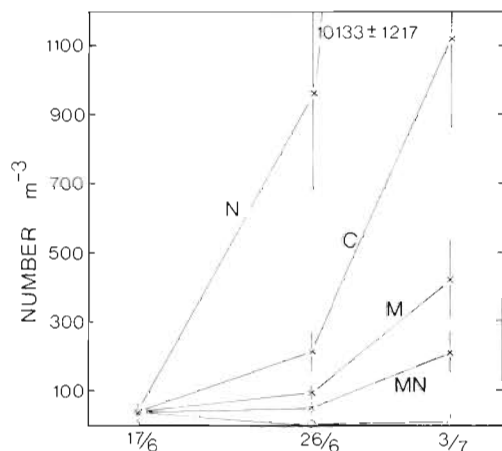


Fig. 3. Changes in numbers of the cladoceran *Pleopsis polyphemoides* during the June/July experiment in enclosures (○) with ($n = 12$) and (×) without fish ($n = 3$). Bars represent standard deviation

ance. Its biomass remained low in enclosures with added fish, while the species became dominant with respect to both biomass and clearance in enclosures without fish.

The development of biomass and the clearance of the zooplankton community during September followed the same trends as in June/July, but the initial biomass of the species was lower except for *A. tonsa* (Fig. 4), and together with a decreased clearance caused by lower temperatures, total clearance was also lower than in June/July.

DISCUSSION

Nutrient enrichment

During the present study effects of nutrient enrichment were not measurable on zooplankton biomass, although a pronounced increase in chlorophyll concentration was observed during the June/July and September experiments (Riemann et al. 1988). Other marine enclosure experiments have shown that nutrient enrichment increases chlorophyll levels and copepod (*Acartia tonsa*) production (Fulton 1984). Parsons et al. (1977) found that the addition of nutrients had little effect on the zooplankton community, and concluded that zooplankton composition was controlled by predation from ctenophores. The absence of an effect of nutrient addition suggests that zooplankton production was not food limited in our experiment, hence, the fertilized enclosures are treated together with the controls. The discussion accordingly focuses on the effect of suspension-feeding bivalves and planktivorous fish on zooplankton.

Predation by bivalves on microzooplankton

Suspension-feeding bivalves possess a large filtration capacity. In Roskilde Fjord the average biomass theoretically filters the water column twice a day (Riemann et al. 1988). Unfortunately the major part of the literature concerning filtration of *Mytilus edulis* focuses on the lower limit of the particle-retention spectrum. To our knowledge, there are no available data on the importance of small zooplankton species in the diet of suspension-feeding bivalves. Since particles from 2 to 200 μm are retained by *M. edulis* (Jørgensen & Goldberg 1953, Møhlenberg & Riisgård 1979), suspension-feeding bivalves may act as a major controlling element on small zooplankton species. Because protozooplankton and smaller zooplankton species constitute an important link in the flow of organic matter in marine environments (Azam et al. 1983), predation by suspension-feeding bivalves could be of major importance.

No effect of *Mytilus edulis* on the size of the *Tintinnopsis* population was found during the April experiment. The biomass decreased at the same rate in enclosures with and without mussels. In the major part of this experiment the low temperatures probably limited the clearance of the mussels (Schulte 1975). Filtration of mussels reduced the number of *Tintinnopsis* spp. during the June/July and September experiments (Fig. 1A). In both experiments the biomass of *Tintinnopsis* spp. stabilized at ca 300 individuals l^{-1} in enclosures without mussels, while their biomass in the mussel enclosures was considerable lower (Fig. 1A).

During April and June/July addition of mussels resulted in a faster reduction in the number of *Synchaeta* spp. than during September (Fig. 1B). In the September experiment the biomass of *Synchaeta* spp. was very low in the mussel enclosures. In contrast, the biomass increased and peaked during the middle of the experiment in the enclosures without mussels. In the enclosures with added mussels the mean length of rotifers was larger than in enclosures without mussels (180 and 115 μm respectively), suggesting that small rotifers were preferred by the mussels.

Predation on zooplankton

Addition of mussels did not influence the development of *Acartia tonsa* (Fig. 2) and the meroplankton (Fig. 4), although *Mytilus edulis* is reported to ingest particles up to about 200 μm (Jørgensen & Goldberg 1953). Presumably these zooplankters can perceive and escape the inhalant current of the mussels.

Effects of planktivorous fish on the zooplankton were mainly seen as a decrease in the abundance of the

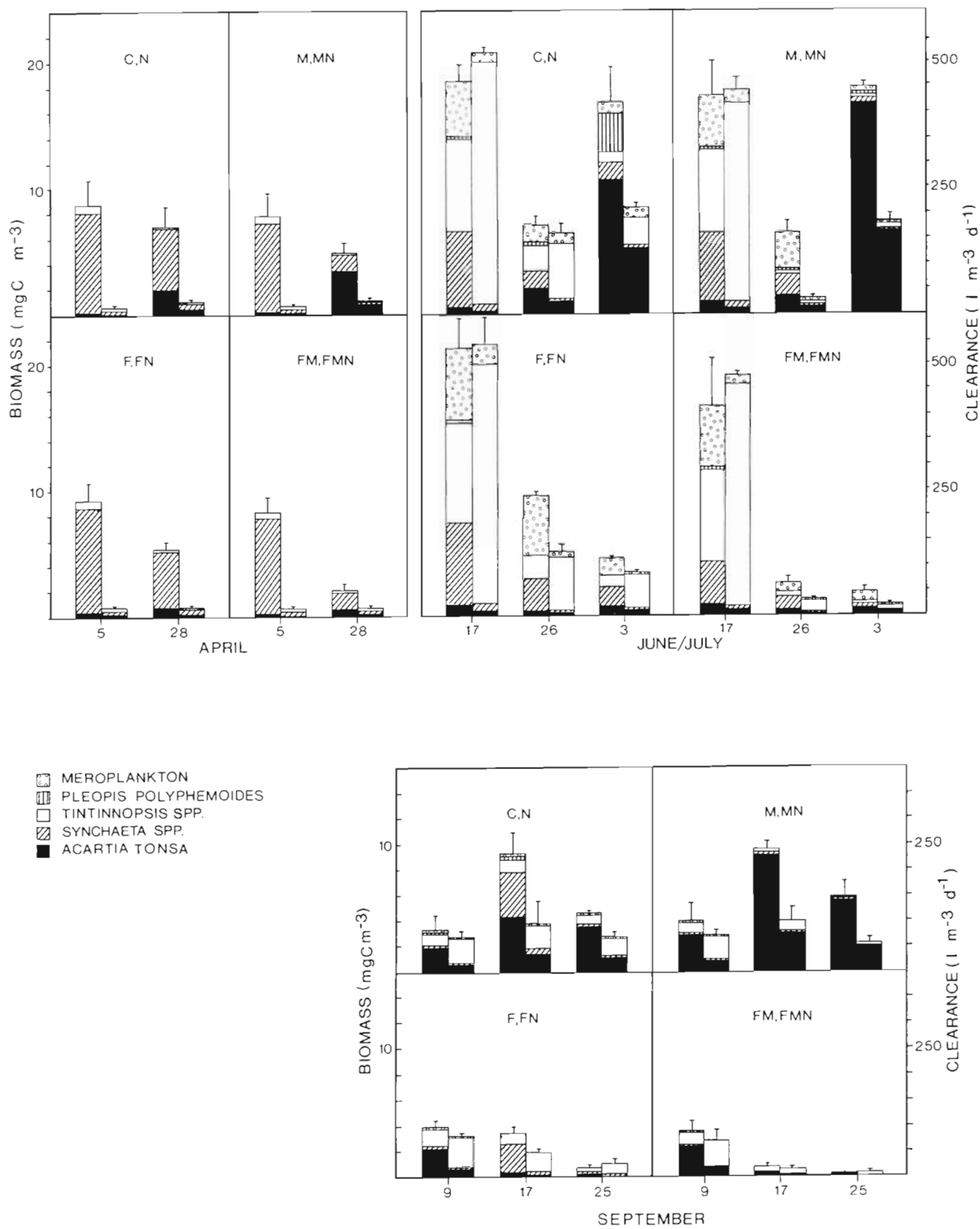


Fig. 4. Zooplankton biomass (left columns) and clearance (right columns) during April, June/July and September. Bars represent standard deviation ($n = 6$)

larger holozooplanktonic species (*Acartia tonsa* and *Pleopis polyphemoides*: Figs. 2 to 4). No measurable effect was seen on the merozooplankton, probably because it was dominated by bivalve larvae with a diameter less than 150 μm and by nauplii of *Balanus* spp. Both disappeared from the pelagic system in the enclosures without fish because of settling. The decreased number of *A. tonsa* nauplii in the enclosures with added fish was probably caused by low recruitment, since the adults were eaten within a few days. Decreased biomasses of *A. tonsa* and *P. polyphemoides* could be expected to result in increased numbers of *Tintinnopsis* spp., since protozooplankton are an important food source for *A. tonsa* (Robertson 1983, Stoeckner & Sanders 1985) as well as for *P. polyphemoides* (Poggensee & Lenz 1981). This effect was, however, not observed during our experiments. Also no effect of *Gasterosteus aculeatus* on *Synchaeta* spp. was seen. The highly variable numbers of *P. polyphemoides* in enclosures without fish at the end of the June/July experiment are probably due to differences in initial numbers of individuals (Fig. 3), since parthenogenetic marine cladocerans have a high reproductive rate (Makrushin 1981, Poggensee & Lenz 1981), but food competition from *M. edulis* might also influence the development of *P. polyphemoides*, since the number of ciliates in enclosures with added mussels was lower than in the controls.

Our results demonstrate that *Gasterosteus aculeatus* prefers larger zooplankton species, which agrees with Gibson (1984), who found that *G. aculeatus* feeding on a mixed population of *Daphnia* preferentially exploited the larger prey. Moreover, Fulton (1984) found that predation by size-selective planktivorous fish prevented dominance by larger zooplankton species in estuaries. Fulton (1984) found in enclosures without fish that *Acartia tonsa* dominated compared to the smaller copepods (*Parvocalanus crassirostris* and *Oithona colvarva*), while addition of fish favoured the small zooplankton species. Investigations in freshwater have shown the same trends (e.g. Brooks & Dodson 1965). As a secondary effect of planktivorous fish, phytoplankton biomass may increase, as a result of the decreased grazing by herbivorous zooplankters (Anderson et al. 1978, Stenson et al. 1978, Henrikson et al. 1980, Goad 1984). This secondary effect was confirmed by our experiments, where a 20% increase in phytoplankton biomass was measured during June/July and September, compared to respective control enclosures (Riemann et al. 1988).

Pronounced effects of *Gasterosteus aculeatus* were found during June/July and September (Figs. 2 to 4), when temperatures were above 11 $^{\circ}\text{C}$ (Table 2), despite the fact that survival of the fish was only 35% during June/July compared to 70 and 90% during April and

September, respectively. The fish probably starved to death, since their calculated maintenance rations following Allan & Wootton (1982), exceeded available zooplankton during all 3 periods.

Zooplankton clearance rates

The calculated maximum clearance of the zooplankton community > 45 μm was about 3, 50 and 10% of the water column per day during April, June/July and September, respectively. This is of minor importance for the regulation of the phytoplankton biomass, compared to the clearance of *Mytilus edulis*, which was about 55, 220 and 120% of the water column per day respectively. This difference is probably not as pronounced in the fjord, where the bivalves are situated at the bottom, rather than suspended in nets in the water column.

In conclusion our results demonstrate that in Roskilde Fjord the holoplanktonic crustaceans are strongly predator controlled, especially during summer, since the increased phytoplankton biomass in the fertilized enclosures did not increase the abundance of *Acartia tonsa* and *Pleopis polyphemoides* while 'exclusion' of the fish resulted in an immense increase. The zooplankton community > 45 μm was controlled in 2 ways in the enclosures; larger zooplankton were preyed upon by *Gasterosteus aculeatus*, and microzooplankton by *Mytilus edulis*. Two important problems need further investigation: (1) the importance of small zooplankton species in the diet of suspension-feeding bivalves, and (2) the effect of this predation on cycling of organic matter in estuarine environments.

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