

Impact of *Aurelia aurita* medusae (Cnidaria, Scyphozoa) on the standing stock and community composition of mesozooplankton in the Kiel Bight (western Baltic Sea)

G. Behrends^{1,*}, G. Schneider²

¹Institut für Meereskunde, Düsterbrookweg 20, D-24105 Kiel, Germany

²Biologische Anstalt Helgoland, Hafenstraße 46, D-25989 List/Sylt, Germany

ABSTRACT: During 5 consecutive summer seasons (1990 to 1994) both *Aurelia aurita* medusa and mesozooplankton abundances were investigated at 2 stations in the Kiel Bight (western Baltic Sea). Stocks of medusae varied considerably between the years, with median abundance of 1 and 0.3 ind. 100 m⁻³ in 1990 and 1991, 3 and 4 ind. 100 m⁻³ in 1992 and 1994, but 9 ind. 100 m⁻³ in 1993. Significant differences in the mesozooplankton stock and community composition were observed in 1993 when compared with the year of rather low *Aurelia* abundance (1991). Total zooplankton and copepod numbers both exhibited an inverse relationship with the abundance of medusae and were thus considerably lower in 1993 than in 1991. However, not all copepod species were affected by *A. aurita*. *Pseudo-* and *Paracalanus* spp. and *Oithona similis* showed dramatically reduced stocks in the bloom year when compared with the medusa-poor situation, but no significant changes were found for *Centropages hamatus* and *Acartia* spp. Also other zooplankton groups with the exception of bivalve larvae were reduced by the medusae. The differential response of zooplankton to varying abundance of medusae led to a shift in the trophic structure of the zooplankton community. Fine-filter feeders and raptorial feeders were much more important in years when medusae occurred in low densities, whereas coarse-filter feeders dominated in the opposite situation.

KEY WORDS: *Aurelia aurita* · Mesozooplankton · Predation · Kiel Bight

INTRODUCTION

Numerous studies have focused on the predatory role of gelatinous organisms in marine plankton communities (e.g. Alldredge 1984, Purcell 1985 and references therein) and it is generally accepted that their population consumption can be high when these organisms occur in sufficient numbers. Since collapses of zooplankton populations at certain times and inverse relationships between jellyfish biomass or number and zooplankton standing stock were observed in various areas, these phenomena were consequently assumed to be due to control by gelatinous predators (e.g.

Huntley & Hobson 1978, Deason & Smayda 1982, Feigenbaum & Kelly 1984, Panayotidis et al. 1988, García 1990, Matsakis & Conover 1991, Purcell 1992).

This may also apply for the Kiel Bight (western Baltic Sea). In this area a pronounced annual cycle of zooplankton standing stock is described in many papers (Lohmann 1908, Hillebrandt 1972, Martens 1976, Schnack 1978, Smetacek 1980). During winter and early spring zooplankton standing stock is low, but a mass development of mesozooplankton usually occurs in May. This bloom is primarily due to copepods, of which 2 species dominate: *Pseudocalanus minutus elongatus* and *Oithona similis*. Additionally meroplanktic larvae increase significantly with bivalve offspring contributing more than two-thirds of all larvae.

*E-mail: gbehrends@ifm.uni-kiel.d400.de

This bloom, however, is terminated abruptly in June with a sharp drop in copepod abundance and, to a lesser extent, meroplanktic larvae. On the whole, zooplankton abundance remains low during June, July and early August but peaks again in autumn. However — and more important in the context of this paper — pronounced interannual variation was observed for summer zooplankton biomass with rather high standard deviations between years occurring in June and July (Hillebrandt 1972).

It has been suggested (e.g. Möller 1978/79, 1980), that this decline in zooplankton biomass during summer and especially the large interannual variation is due to predation by the scyphomedusa *Aurelia aurita*. This species, indeed, develops in May and reaches its peak population biomass in June or early July (Möller 1980, Schneider 1989a). However, considerably interannual variation was observed for this species, too (Schneider & Behrends 1994), so that bloom years and years with low population densities can be distinguished. Due to their carnivorous mode of feeding and the finding that in the Kiel Bight *A. aurita* medusae also accept all kinds of zooplankton as food (Kerstan 1977), the predation hypothesis (Paine 1966) appears to be the most likely explanation. Reduction of zooplankton, however, may lead to changes in lower trophic levels, so that *A. aurita* as a top-predator may perhaps induce trophic cascading (Carpenter et al. 1985), thus regulating the whole plankton system.

In this paper, we present data from a 5 year investigation (1990 to 1994), which compared zooplankton standing stock and *Aurelia aurita* occurrence with the ultimate goal of determining whether or not variations of medusae stocks are responsible for interannual variation of zooplankton abundance and species composition.

MATERIAL AND METHODS

Aurelia aurita samples were obtained monthly at 2 stations in the Kiel Bight (Fig. 1) during summer (June to September) 1990 to 1994. Oblique hauls as close to the sea-bed as possible were carried out at each station with a bongo-net fitted with a 300 and a 500 μm gauze. Generally, 100 to 200 m^3 of water was filtered. The medusae caught were counted and their diameter measured to the cm as described by Möller (1980). At the same stations and cruises, mesozooplankton was sampled by means of a WP-2 net with a 100 μm gauze in vertical hauls from 5 m above the sea-bed to the surface. The samples were preserved with 4% formalin buffered with borax and were counted later in the laboratory. Meroplankton was determined at group level (bivalve larvae, polychaete larve etc.), other zooplank-

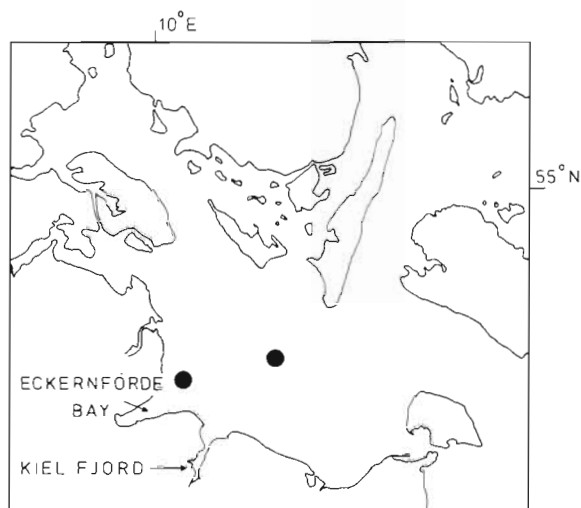


Fig. 1. Map of the Kiel Bight with dots indicating sampling stations

ton at species level. In the case of *Pseudocalanus minutus elongatus* and *Paracalanus parvus*, the young copepodite stages (C I to III) could not be separated. Therefore, in this paper the 2 species are treated together as *Pseudo-* and *Paracalanus* spp. The 4 *Acartia* species occurring in the Kiel Bight were also pooled because some of these species occasionally occurred in rather low numbers.

Prior to further statistical treatment, all data sets were tested for deviation from the normal distribution by means of the Kolmogorov-Smirnov test. Significant deviations were detected for the *Aurelia* data in 1990 and for the data of *Pseudo-* and *Paracalanus* spp. obtained in 1993 ($D_k = 0.455$ and 0.569 respectively). Thus, parameter-free methods were used for all calculations. The data sets are described either by the median, the range covering 50% of all data and the total range, or the median \pm median deviation. For comparison between years, the Kruskal-Wallis test for homogeneity was performed. In case of rejection of the H_0 hypothesis ($\mu_1 = \mu_2 = \mu_3 = \dots$), a Nemenyi test was carried out to determine the significant different data sets. All calculations were carried out with the aid of the STATEASY computer programme (Lozan 1993).

RESULTS

The 5 summer seasons investigated represented different situations with respect to *Aurelia aurita* abundance. Both in 1990 and 1991 population stocks were rather low (Fig. 2), with abundance ranging between 0 and 4.4 medusae 100 m^{-3} and median values of 1.0 and 0.3 ind. 100 m^{-3} . In 1992, abundance was generally higher averaging 3.4 medusae 100 m^{-3} but maximum

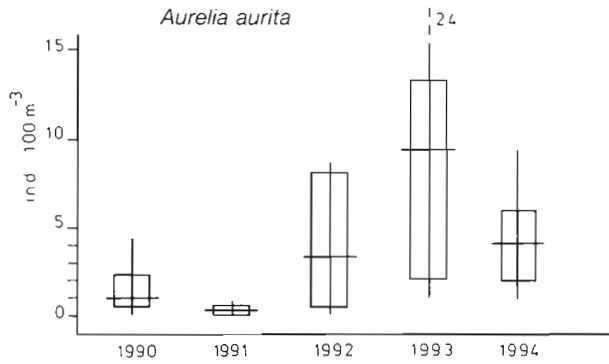


Fig. 2. Box-Whisker plots of *Aurelia aurita* abundance during summer 1990 to 1994. Vertical lines give total range, horizontal lines indicate the median value and boxes show the range of 50% of all data (between upper and lower quartiles). Number of data: 1990: n = 6; 1991: n = 6; 1992: n = 7; 1993: n = 7; 1994: n = 8

values were observed in 1993 with up to 24 medusae 100 m^{-3} and a median of $9 \text{ ind. } 100 \text{ m}^{-3}$. Finally, in 1994 the population density was similar to that in 1992 with a median value of $4.2 \text{ ind. } 100 \text{ m}^{-3}$. Thus, 1990 and 1991 represented years with low abundance, 1992 and 1994 were intermediate and 1993 was obviously a bloom year. Testing for significant differences (Table 1) revealed statistical significance between 1991 and 1993. The intermediate data of 1990, 1992 and 1994 did not differ significantly from those obtained during 1991 and 1993.

Total zooplankton numbers were inversely related to *Aurelia* abundance (Fig. 3A). In 1991 median abundance of total zooplankton was highest, but lowest in 1993, the bloom year of *Aurelia aurita*. Significance was achieved for these 2 years (Table 1). The results of 1990, 1992 and 1994 were intermediate between the significant end-points, thus indicating the trend of declining zooplankton abundance with increasing median abundance of medusae. The same result was obtained for the copepod fraction (Fig. 3B) but not for bivalve larvae (Fig. 3C), which showed no significant trend with increasing population density of the

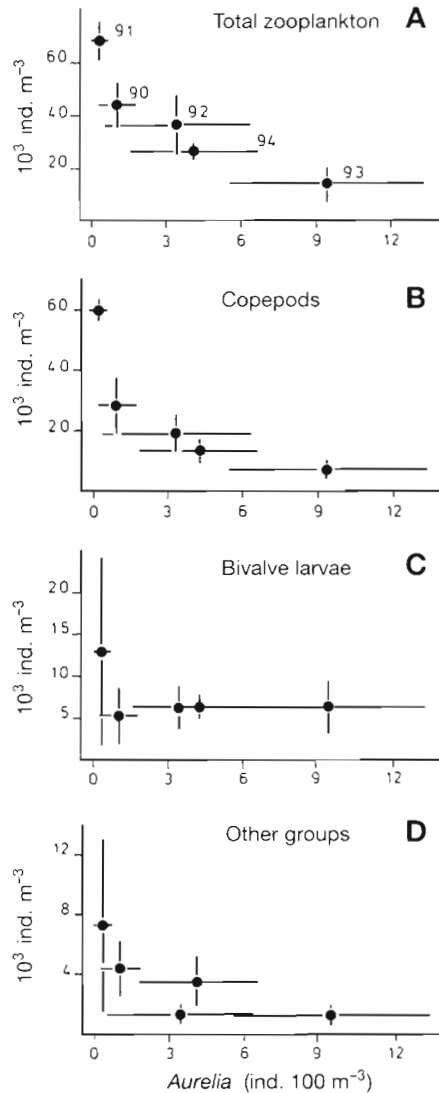


Fig. 3. Average abundance (median \pm median deviation) of (A) total zooplankton, (B) copepods, (C) bivalve larvae and (D) 'other groups' plotted against average abundance of *Aurelia aurita* medusae in the different summer seasons investigated. Numbers in (A) denote years

Table 1. Results of the Kruskal-Wallis test for homogeneity ($H_0: \mu_{1990} = \mu_{1991} = \dots = \mu_{1994}$) and Nemenyi test if H_0 was rejected. a: accepted; r: rejected

Data set	H	p	H_0	Nemenyi	Difference
<i>Aurelia aurita</i>	13.598	0.0087	r	18.04	1991 vs 1993
Total zooplankton	11.065	0.0026	r	20.80	1991 vs 1993
Copepods	18.722	0.0009	r	20.46	1991 vs 1993
Bivalve larvae	1.932	0.7483	a		
Other groups	7.510	0.1113	a		
<i>Pseudo-</i> and <i>Paracalanus</i>	17.167	0.0018	r	18.43, 17.17	1991 vs 1993, 1991 vs 1994
<i>Oithona similis</i>	19.236	0.0007	r	13.49, 17.03	1991 vs 1993, 1991 vs 1994
<i>Centropages hamatus</i>	2.080	0.7210	a		
<i>Acartia</i> spp.	4.873	0.3006	a		

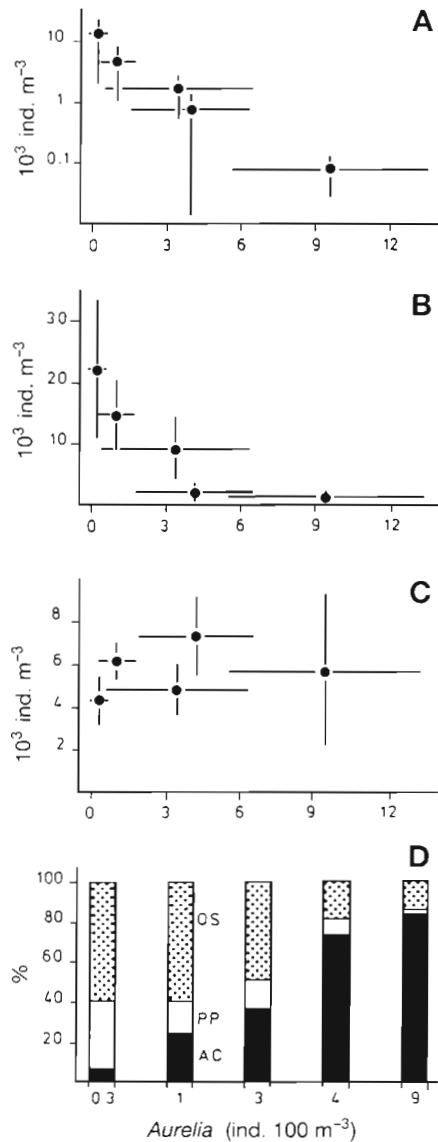


Fig. 4. Average abundance of (A) *Pseudo- and Paracalanus* spp., (B) *Oithona similis* and (C) *Centropages hamatus* + *Acartia* spp. plotted against average abundance of *Aurelia aurita* medusae. Note logarithmic scale of y-axis in (A). (D) Relative proportion (%) of the different copepods in relation to increasing abundance of medusae. OS: *O. similis*; PP: *Pseudo- and Paracalanus* spp.; AC: *Acartia* spp. + *C. hamatus*

medusae. The 'other groups' (representing cladocerans, chaetognaths, polychaete and gastropod larvae, appendicularians etc.) exhibited the same trend as observed for total zooplankton and the copepods (Fig. 3D) but without a significant result (Table 1).

Within the copepod fraction a different pattern was obtained for the species investigated. Both *Pseudo-/Paracalanus* spp. and *Oithona similis* appeared to be rather affected by increasing abundance of medusae

(Fig. 4A, B), whereas *Centropages hamatus* and *Acartia* spp. median abundances were more or less the same in the 5 summers studied (Fig. 4C, Table 1). Therefore, a shift in the relative copepod species composition was observed (Fig. 4D): more than 90% of all copepods in 1991 were formed by *Pseudo-/Paracalanus* and *Oithona* whereas in 1993 these 2 'species' made up only about 20%. Consequently, the share of *C. hamatus* + *Acartia* spp. has increased dramatically from approximately 10 to 80%.

Summarizing these findings, it can be concluded that the stocks of most zooplankton species will be negatively affected by medusae populations. However, this was not observed for bivalve larvae and the 2 copepods generally accepted to be typical summer species in the Kiel Bight.

DISCUSSION

The results have shown that zooplankton abundance in the Kiel Bight is significantly lower during years rich in medusae than in years with low medusa stocks. This seems to confirm the predation hypothesis mentioned above. Feeding experiments with *Aurelia aurita* medusae carried out by Kerstan (1977) revealed individual ingestion rates between 800 and 8000 *Artemia* nauplii h⁻¹, corresponding with 6 to 75 mg C medusa⁻¹ d⁻¹ when assuming a feeding period of 16 h d⁻¹ and a carbon content of 0.6 µg nauplius⁻¹ (Paffenhöfer 1967, Platt et al. 1969). The overall mean of 40 ± 17 mg C medusa⁻¹ d⁻¹ suggests a high predation potential when compared with the average carbon weight of 4 µg C ind.⁻¹ measured by Martens (1976) for copepods in the Kiel Bight (approx. 10 000 copepods medusa⁻¹ d⁻¹). Estimates of minimum carbon ingestion rates to satisfy at least metabolism and growth of the medusae revealed similar results (40 to 50 mg C medusa⁻¹ d⁻¹). It was concluded that in bloom years populations of medusae may consume about two-thirds of daily secondary production (Schneider 1989b, Schneider & Behrends 1994). These estimated rates are similar to those determined for other large scyphomedusae. Ingestion rates of *Stomolophus meleagris* ranged between 20 and 100 mg C medusa⁻¹ d⁻¹ (Larson 1991). Purcell (1992) measured a maximal copepod ingestion rate of 19 000 ind. medusa⁻¹ d⁻¹ in *Chrysaora quinquecirrha*. This probably corresponds to carbon values of about 70 to 80 mg C medusa⁻¹ d⁻¹. The predation potential of scyphomedusae is therefore high but its actual role in the field depends upon the abundance of the medusae.

Alternatively, variation of zooplankton abundance can also be caused by other factors, especially food limitation (e.g. Durbin et al. 1983, Kiørboe & Nielsen

Table 2. Average primary production and phytoplankton stocks (median \pm median deviation) during the summer seasons examined for medusa-zooplankton relationships. PP: primary production ($\text{mg C m}^{-2} \text{ h}^{-1}$); Chl *a*: chlorophyll *a* (mg m^{-3}); PPC: phytoplankton carbon (mg m^{-3}) determined via Utermöhl counting. Data from Horstmann & Hansen (unpubl.); $n = 8$ to 26

Year	PP	Chl <i>a</i>	PPC
1990	135 \pm 33	2.94 \pm 0.55	106 \pm 58
1991	82 \pm 12	2.40 \pm 0.17	204 \pm 128
1992	155 \pm 21	3.27 \pm 1.06	302 \pm 181
1993	119 \pm 38	3.61 \pm 0.94	229 \pm 164
1994	146 \pm 83	4.87 \pm 0.71	475 \pm 370

1994, Purcell et al. 1994). Assuming that most mesozooplankton in the Kiel Bight are to a large extent dependent on phytoplankton, we have compiled data of phytoplankton standing stock and primary production measured by colleagues at the same stations and cruises mentioned in this paper. The data given in Table 2 suggest that phytoplankton carbon, chlorophyll *a* and primary production vary somewhat between years but do not indicate food limitation in a certain year when compared with other years. Especially when comparing the 2 extreme years with respect to zooplankton abundance, 1991 and 1993, food limitation of zooplankton in 1993 appears unlikely. The role of microzooplankton and total particulate organic carbon can not be assessed due to lack of data. Abiotic conditions, i.e. temperature and salinity, did not show pronounced variation between the years 1990 and 1993, although temperature was unusually high during 1994 (up to 22°C). In view of these findings it is most likely that predation by medusae was the key factor regulating zooplankton standing stock between the years of investigation.

Not all kinds of zooplankton in the Kiel Bight were, however, reduced by the medusae. *Pseudo-* and *Paracalanus* spp., *Oithona similis* and probably 'other groups' appear to be more vulnerable to medusae predation than *Centropages hamatus*, *Acartia* spp. and bivalve larvae. Unfortunately, we were not able to carry out gut analyses for proof of food selection in medusae. Recently, Sullivan et al. (1994) demonstrated experimentally that *Aurelia aurita* took up comparatively more slow swimming prey (hydromedusae, barnacle larvae) than would be expected from their abundance in the plankton. *A. aurita* can easily consume prey with escape velocities smaller than marginal flow velocities whereas faster prey may escape more often (Costello & Colin 1994). These results cannot, however, explain the different response of the various species to *Aurelia* abundance in the Kiel Bight since escape velocities of the copepod

species are unknown. Kerstan (1977) found that bivalve larvae make up a rather substantial portion of *A. aurita* gut contents (up to 80% of total numbers). This may be due to their slow swimming speed. Consequently, a reduction of bivalve larvae abundance in bloom years of medusae could be expected, but was not observed. We assume, therefore, similar electivity for the different copepod species but suggest that those species were not reduced by predation of medusae which are able to compensate for the losses by reproduction. Both *C. hamatus* and *Acartia* spp. are known to be typical summer species (Lohmann 1908, Hillebrandt 1972, Martens 1976, Schnack 1978), reproducing during this period and attaining their annual population peak during midsummer. Nevertheless, reproduction of these species will, perhaps, be slightly affected by *Aurelia* predation insofar as predation seems to induce a time-lag of copepod peak occurrence compared to years with poor stocks of medusae. In 1991 highest abundance of these copepods was observed in July, whereas in 1993 peak abundance was found in August; however, no significant difference in absolute values was obtained for the whole summer season. By contrast *Pseudocalanus minutus elongatus* do not reproduce during the summer for unknown reasons (Otten 1913) but develop and reproduce in late spring. This period coincides with the main growth season of *A. aurita* in which food demand is larger than later in summer (Schneider 1989b). Consequently, the pronounced spring peak of this copepod is suppressed in bloom years of medusae: in May and June 1991 average peak abundance of *P. m. elongatus* (including the smallest copepodite stages) was 30 000 \pm 4000 ind. m^{-3} , but only 1000 \pm 700 ind. m^{-3} in 1993. The reproductive cycle of *O. similis* in the Kiel Bight is not fully understood but spawning appears to occur throughout the whole summer at a moderate level, increasing sharply in autumn (Lohmann 1908). Predation by abundantly occurring medusae on adults and developmental stages of this copepod can, therefore, hinder population build-up during the summer season. In case of bivalve larvae, for which positive electivity seems probable, release of newly liberated larvae by the benthic adults may compensate the losses due to consumption by medusae. However, it is also possible that the larvae survive gut passage as observed by Purcell et al. (1991).

If we accept our results as typical, mass occurrences of *Aurelia aurita* will have a significant influence on the zooplankton community composition which, in turn, may perhaps induce changes in the whole food web design as is suggested in Huntley & Hobson (1978), Deason & Smayda (1982) and Smayda (1993). The different species of copepods in the Kiel Bight represent 3 feeding types (Schnack 1982): *Pseudo-*

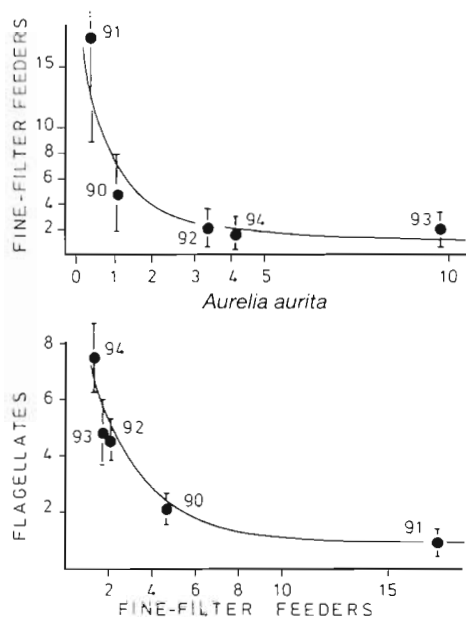


Fig. 5. Upper panel: median abundance (10^3 ind. m^{-3}) of fine-filter feeders (*Pseudo-* and *Paracalanus* spp. + *Oikopleura dioica*) in relation to median abundance (ind. $100\ m^{-3}$) of *Aurelia aurita* medusae. Lower panel: median abundance (10^6 ind. l^{-1}) of μ -flagellates ($<12\ \mu m$) in relation to median abundance of fine-filter feeders in the different summer seasons investigated. Data of μ -flagellates from Horstmann & Hansen (unpubl.); $n = 10$ to 26

calanus minutus elongatus and *Paracalanus parvus* are fine-filter feeders, the *Acartia* species and *Centropages hamatus* can be characterized as coarse-filter feeders or omnivores, whereas *Oithona similis* is a raptorial predator which, however, also needs plant material (Lampitt 1978, Lampitt & Gamble 1982). The rather low abundance of both *Pseudo-* and *Paracalanus* spp. and *O. similis* observed in the years of intermediate and high abundance of medusae led to a pronounced dominance of the coarse-filter feeders/omnivores and only a small share of fine-filter feeders compared to the situation found in 1990/91. Additionally, another fine-filter feeding species, the appendicularian *Oikopleura dioica*, was much more abundant in 1991/92 (median \pm median deviation: 3000 ± 1400 ind. m^{-3}) than in 1992 to 1994 (120 ± 120 ind. m^{-3}). Therefore, fine-filter feeders exhibited minimum values in the years of intermediate and high abundance of medusae. Consequently, it can be expected that the smallest plankton size classes experience a higher predation pressure when fine-filter feeders like *P. m. elongatus* and *O. dioica* are abundant. It is, indeed, encouraging that the so-called μ -flagellates ($<12\ \mu m$) were significantly less abundant in years with very low medusae abundance but high numbers of fine-filter feeding organisms when compared with

the opposite situation (Fig. 5). Although other mechanisms may also explain the interannual differences of the flagellates, and the role of larger protozoans especially cannot be evaluated here, it cannot be excluded that the observed inverse relationships reflect the reduced grazing pressure by *Pseudocalanus* and *Oikopleura* which, in turn, are controlled by medusae. This speculation points to more far-reaching consequences of abundant medusoid predators than the simple reduction of zooplankton prey alone. However, experimental work is badly needed to substantiate these latter speculations.

Acknowledgements. The sampling and the shipboard measurements of the medusae were done by R. Lütjhe and J. Kerstein. A. Burmeister and T. Freyer supported this investigation with their skilful technical assistance. Three anonymous reviewers contributed substantially to the final version of this paper and Y. Henschel kindly revised the English.

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This article was submitted to the editor

Manuscript first received: June 29, 1994

Revised version accepted: May 12, 1995