

Population dynamics and the trophic role of *Aurelia aurita* medusae in the Kiel Bight and western Baltic

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Schneider, G., and Behrends, G. 1994. Population dynamics and the trophic role of *Aurelia aurita* medusae in the Kiel Bight and western Baltic. – ICES J. mar. Sci., 51: 359–367.

The population dynamics and the trophic role of *Aurelia aurita* medusae in the Kiel Bight/western Baltic are described from nine years of investigation between 1978 and 1993. There is considerable yearly variation in standing stock with summer median abundance ranging from 0.2 to 16 ind. 100 m⁻³ and biomass from 0.2 to 4.4 g C 100 m⁻³. The lower variation is due to marked differences in size of adult medusae between years. In years of low abundance medusae exhibit an average disc diameter of about 30 cm and weigh about 1 kg. In bloom years, however, adult size is only about 20 cm and weight ranges between 200 and 400 g. Estimates of feeding are somewhat contradictory, but feeding rates of 40–80 mg C ind.⁻¹ day⁻¹ seem probable. It can be concluded that *Aurelia* medusae consume about 2/3 of daily secondary production in years of high abundance, and are thus responsible for a decline of mesozooplankton in these years.

Key words: *Aurelia aurita*, Kiel Bight, population dynamics, feeding rates.

Received 24 January 1994; accepted 13 May 1994.

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Introduction

During the last two decades, gelatinous predators in general and scyphomedusae in particular have attained growing scientific interest all over the world with respect to their role in food-web and population dynamics (e.g. Yasuda, 1971; Hernroth and Gröndahl, 1983, 1985a,b; van der Veer and Oorthuysen, 1985; Fancet and Jenkins, 1988; Malej, 1989; Hay *et al.*, 1990; Larson, 1991; Lebedeva and Shushkina, 1991; Kikinger, 1992; Purcell, 1992; Garcia and Durbin, 1993; Olesen *et al.*, 1994).

In the Kiel Bight (western Baltic Sea), populations of *Aurelia aurita* medusae are conspicuous members of the summer zooplankton. Although recruitment of this species takes place in winter and spring (Lohmann, 1908) biomass at that time is negligible due to poor growth (Möller, 1980; Schneider, 1989a). However, in late spring rapid growth occurs and the medusae reach adult size within a few weeks. During the summer, the biomass of *Aurelia aurita* equals that of all other zooplankton put together (Möller, 1978; Schneider, 1989a). It has thus been suggested that *Aurelia aurita* plays an important role in the plankton dynamics of the Kiel Bight.

Although general aspects of population dynamics of *Aurelia* have been known since the last century, no long-term ecological research has been carried out,

although a period of comparatively intensive research began in the late seventies. At that time population dynamics, standing stock, and their possible influence on herring larvae were studied in the Kiel Fjord by Möller (1978, 1980, 1984a,b). He also tried to estimate the predatory impact of *Aurelia* on mesozooplankton and concluded that the medusae consume almost all zooplankton available. However, later studies (e.g. Schneider, 1989a,b; Behrends and Schneider, unpubl.) revealed considerable interannual variations of abundance and biomass, so that Möller's conclusions cannot be extrapolated to every year. We now have data from nine years that allow us to re-examine previous conclusions. In the first part of this paper we summarize old and new data to elucidate the trophic role of *Aurelia aurita* in the Kiel Bight and to improve the estimates of population predation rates given in Möller (1980) and Schneider (1989b). In the discussion we identify the gaps in our knowledge in order to stimulate further research.

Standing stocks of *Aurelia aurita* medusae in the Kiel Bight

To estimate the abundance and biomass stocks of *Aurelia aurita* medusae various sampling programmes

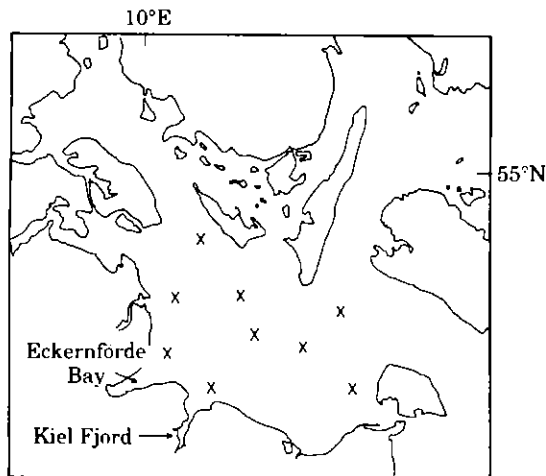


Figure 1. Map of the Kiel Bight with crosses denoting the stations examined by Behrends between 1990 and 1993.

have been carried out in the Kiel Bight area (Table 1). During 1978 and 1979, Möller (e.g. Möller, 1980, 1984a) investigated the narrow Kiel Fjord (Fig. 1). Between 1982 and 1984 work was conducted in Eckernförde Bay (e.g. Schneider, 1989a), and, recently, monthly samples have been taken in the Kiel Bight (Behrends and Schneider, unpubl.). Generally, medusae were sampled with nets using several oblique hauls as close to the sea bed as possible (Table 1). The medusae were counted and the diameter measured to the millimetre or

centimetre. Conversions to biomass were carried out using the relationships given in Table 2, and are presented in carbon units. Over the nine years investigated, the abundance of medusae showed pronounced inter-annual variations (Fig. 2). The highest numbers were observed in the Kiel Fjord in 1978 and 1979, in the Eckernförde Bay in 1982, and in the open waters of the Kiel Bight in 1993. In contrast, abundances were very low in 1983, 1984, 1990, and 1991, but were moderately high in 1992.

Carbon biomass values show the same pattern as abundance (Fig. 2). However, the differences between years appear to be less pronounced (see e.g. the Eckernförde Bay data and the Kiel Bight data from 1992 and 1993). These comparatively small differences in biomass are due to the difference in the final size of adult medusae, as will be mentioned in the next section.

Growth and size of medusae

No growth experiments under controlled conditions were conducted with individual medusae in the earlier work. However, as shown in Figure 3, size-frequency distributions were established and the mean or median values of the distributions were used to characterize growth (e.g. Möller, 1980; Schneider, 1989a). Figure 4 shows various curves obtained from the data available after conversion of disc diameters and wet weights to carbon weights. In general, weight increase was exponential in May and June but ceased in July and August.

Table 1. Details of the *Aurelia aurita* sampling programmes carried out in Kiel Bight waters (see also Fig. 1).

	Investigation period		
	1978-1979	1982-1984	1990-1993
Region	Kiel Fjord	Eckernförde Bay	Kiel Bight
Numbers of stations	26	4	9
Location of stations shown in	Möller (1980)	Schneider (1989a)	This paper
Sampling frequency	Weekly	Bi-weekly	Monthly
Gear employed	CalCOFi-net	CalCOFi-net	Bongo net
Mouth diameter	1 m	1 m	0.6 m
Mesh size	500 µm	500 µm	300+500 µm
Principal investigator	H. Möller	G. Schneider	G. Behrends

Table 2. Biometric and metabolic relationships of *Aurelia aurita* used for calculations in this paper. Functions are either linear ($Y=a+bX$) or power functions ($Y=aX^b$). Abbreviations: D=disc diameter, WW=wet weight, C=carbon, N=nitrogen (from Schneider, 1988a, 1989a).

Relationship	Type of function	Y	X	a	b
Wet weight vs. disc diameter	Power function	g WW ind. ⁻¹	cm D ind. ⁻¹	0.09	2.75
Carbon weight vs. wet weight	Linear	mg C ind. ⁻¹	g WW ind. ⁻¹	20.85	0.87
Nitrogen weight vs. wet weight	Linear	mg N ind. ⁻¹	g WW ind. ⁻¹	5.56	0.23
NH ₄ excretion vs. wet weight	Power function	µmol ind. ⁻¹ h ⁻¹	g WW ind. ⁻¹	0.06	0.93

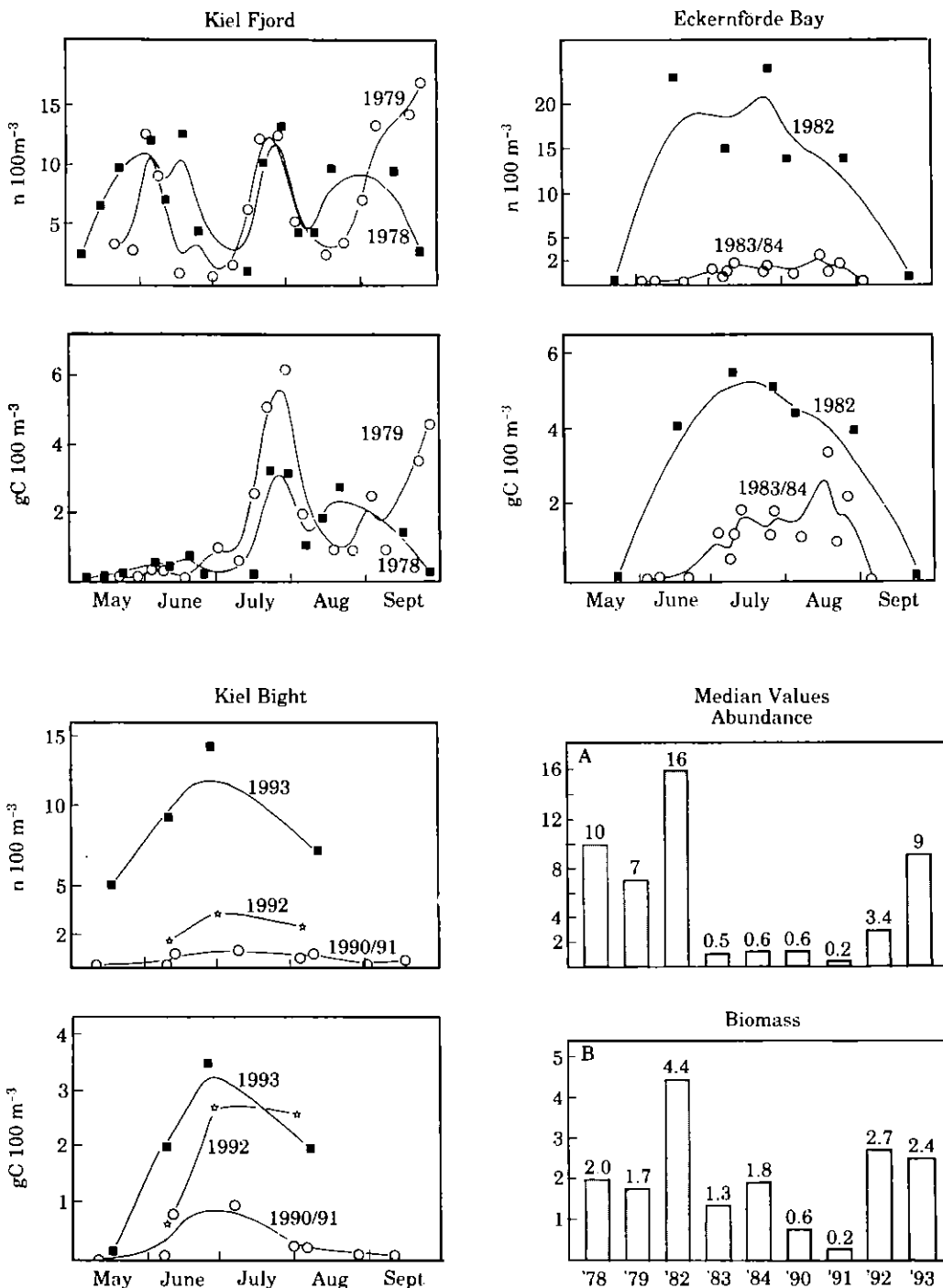


Figure 2. Variation of *Aurelia aurita* abundance and biomass in the various regions and years. Above left: Kiel Fjord. Above right: Eckernförde Bay. Below left: Kiel Bight. For clarity, data of very low medusa abundance (1983, 1984 and 1990, 1991) were pooled. Below right: median abundance (A, $n\ 100\ m^{-3}$) and biomass (B, $g\ C\ 100\ m^{-3}$) as calculated from all stations and dates between June and September.

Maximal weekly growth rates in the medusa-rich years 1978, 1979, and 1982 were 40–70 $g\ wet\ weight\ ind.^{-1}$, corresponding to 30–50 $mg\ C\ ind.^{-1}$. However, in 1983

and 1984 (low medusa abundance) maximal rates were 220 and 150 $g\ wet\ weight\ ind.^{-1}\ week^{-1}$ corresponding to 190 and 130 $mg\ C\ ind.^{-1}\ week^{-1}$, respectively.

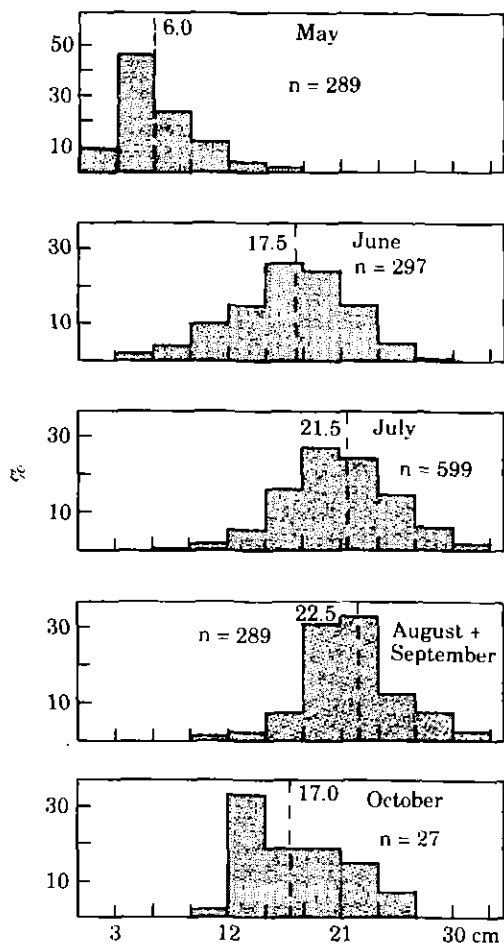


Figure 3. Size-frequency distributions of *Aurelia aurita* in summer 1982. Data for August and September are pooled because no differences were observed. Dashed line shows median (May, October) or mean values. n = number of medusae examined.

In July and August the medusae were adult and reproduced. In most years a decrease of individual size could be observed in September.

The most important aspect was the density-dependent variation of the size of adults between years of high and low abundance. As can be seen from Figures 4 and 5, medusae appeared to be smaller and lighter when abundant but larger and heavier when they occurred in low densities. Maximal estimated carbon values ranged between 200 and 400 mg C ind.⁻¹ in years when medusae were abundant (1978, 1979, 1982, and 1993), whereas in the medusa-poor years weights ranged between 750 and 1050 mg C ind.⁻¹.

Food and estimated feeding rates

The food of *Aurelia* in the Kiel Fjord was intensively studied by Kerstan (1977) using stomach analysis. The

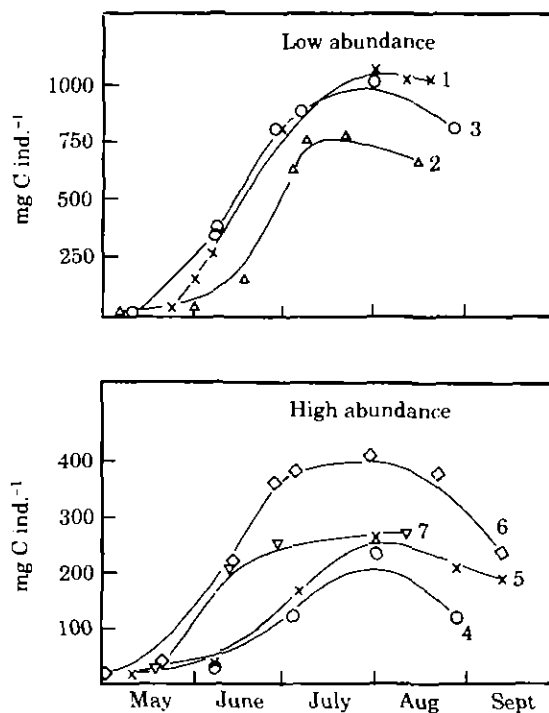


Figure 4. Development of *Aurelia aurita* body weight from spring to autumn in the different years of low and high abundance. Each point represents the median or mean weight calculated from size-frequency distributions. For clarity, standard deviations are not shown. Variation is high, averaging $\pm 30\%$. Numbers indicate years: years of low abundance: 1=1984, 2=1983, 3=1990-1992 (pooled because of low numbers of medusae examined). Years of high abundance: 4=1978, 5=1979, 6=1982, 7=1993.

results indicated that the entire spectrum of planktonic organisms occurring in the Kiel Bight was being used (no special attention being paid to non-loricate protists). In terms of numbers, however, mollusc larvae and copepods were most important (Fig. 6), all other food items together contributing only 10% of the total. Among the copepods *Centropages hamatus* was predominant, making up 86-100% of the total calanoid copepods found in the gastral cavities. Assuming that the individual carbon weights of copepods, "other organisms", and mollusc larvae were in the ratio of 50:25:1 (Hillebrandt, 1972; Martens, 1975), it can be estimated that copepods contributed about 80% of prey biomass, 15% being due to "other organisms", with mollusc larvae making up only 5% of the total. In addition to zooplankton, some benthic or hyperbenthic organisms will also be taken in near-shore areas. Polychaetes, mysids, isopods, and amphipods were found in the gastral cavities, but their numbers decreased in medusae from more open waters. Fish larvae were only taken by medusae less than 8 cm in diameter on account of the coincident occurrence of young medusae and fish larvae only in the late spring. Nevertheless, predation on

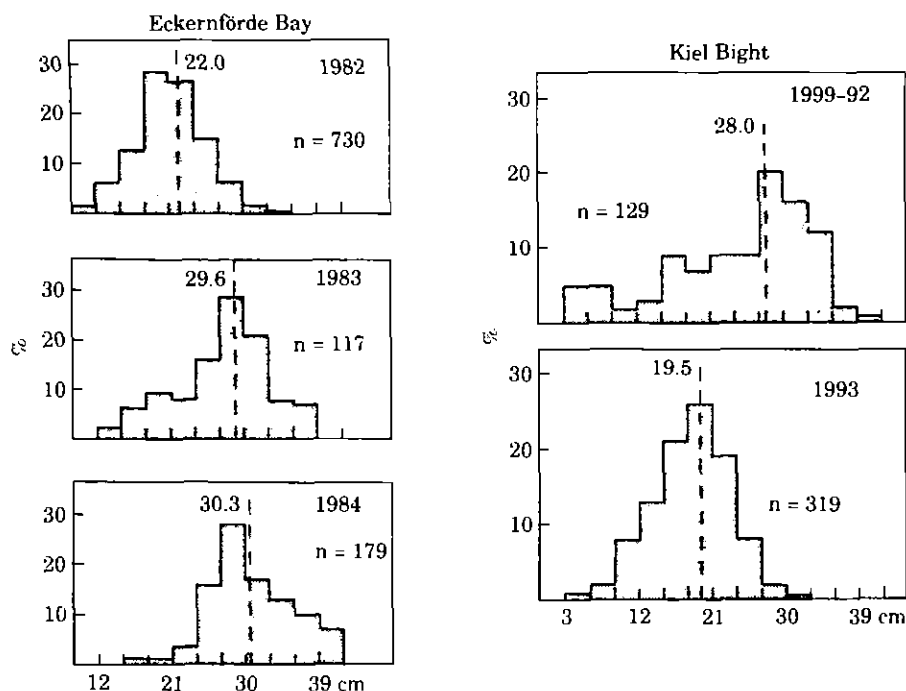


Figure 5. Size-frequency distributions obtained in July and August showing the differences in adult size in years of low (1983, 1984, 1990–1992) and high abundance (1982, 1993), respectively.

fish larvae appears to be important, at least in the Kiel Fjord (Kerstan, 1977; Möller, 1984b; Heeger and Möller, 1987).

Using data from Kerstan (1977) on numbers of food items in the stomach (Fig. 6) it is possible to calculate feeding rates (assuming constant feeding over 24 h) according to the equation:

$$F = N/D \times 24,$$

with F = feeding rate $\text{ind.}^{-1} \text{day}^{-1}$, N = number of food items in stomach, and D = digestion time (h). Assuming a digestion time of 4 h at all temperatures as measured by Kerstan (1977), between 2034 and 3858 prey items would have been consumed daily by *Aurelia* individuals with a diameter of 16–26 cm during June, July, and August 1976. Assuming an average carbon weight of 4 μg per food item (Martens, 1975), these values correspond to 8–15 $\text{mg C ind.}^{-1} \text{day}^{-1}$. In September and October feeding rates would have decreased to a minimum of 234 prey $\text{ind.}^{-1} \text{day}^{-1}$.

Kerstan also performed several feeding experiments with *Artemia* nauplii as food using 180-l aquaria. Incubation period was 6–8 h at a temperature of 16°C and food density ranged between 58 and 447 nauplii l^{-1} . Ingestion rates of similar-sized medusae (16–19 cm bell diameter) ranged between 17 000 and 120 000 nauplii $\text{ind.}^{-1} \text{day}^{-1}$ (median: 61 000 nauplii $\text{ind.}^{-1} \text{day}^{-1}$) corresponding to a median carbon ingestion rate of approximately 40 $\text{mg C ind.}^{-1} \text{day}^{-1}$.

An alternative approach is to calculate food requirements required to satisfy the demands for growth and metabolism (NH_4 release; Table 2) between two field samplings. Assuming the assimilation quotient to be 0.8 (Valiela, 1984), the average theoretical ingestion between t_1 and t_2 can be calculated as follows:

$$I_{(t_2 - t_1)} = \{ (W_{t_2} - W_{t_1}) / (t_2 - t_1) + (E_{t_1} + E_{t_2}) / 2 \} \times 0.8^{-1} \times 4.5$$

where: $I_{(t_2 - t_1)}$ = average ingestion rate between the two field samplings at t_1 and t_2 ($\text{mg C ind.}^{-1} \text{day}^{-1}$); W_{t_1} , W_{t_2} = average medusa weight at t_1 and t_2 (mg N ind.^{-1}); E_{t_1} , E_{t_2} = NH_4 excretion of a medusa at t_1 and t_2 ($\text{mg N ind.}^{-1} \text{day}^{-1}$); $t_2 - t_1$ = number of days between t_1 and t_2 ; 4.5 = average C:N ratio of Kiel Bight zooplankton by weight (Schneider, unpubl.).

Comparisons were made using data from 1982, representing a year with highly abundant small medusae, and 1984, representing a year with large medusae at low densities. The results (Fig. 7) indicate that ingestion increase as the medusae grow, reaching maximum values when the medusae are adult. The maximum rates were about 35 $\text{mg C ind.}^{-1} \text{day}^{-1}$ for highly abundant small medusae in 1982, but were more than twice as high (80 $\text{mg C ind.}^{-1} \text{day}^{-1}$) for the less abundant large medusae in 1984. Assuming that ammonia release makes up only 70% of the total nitrogen (Raymont, 1983), release rates increased to 50 and 110 $\text{mg C ind.}^{-1} \text{day}^{-1}$. These latter rates are highly

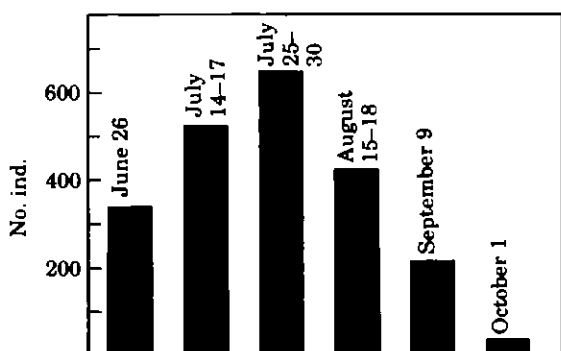
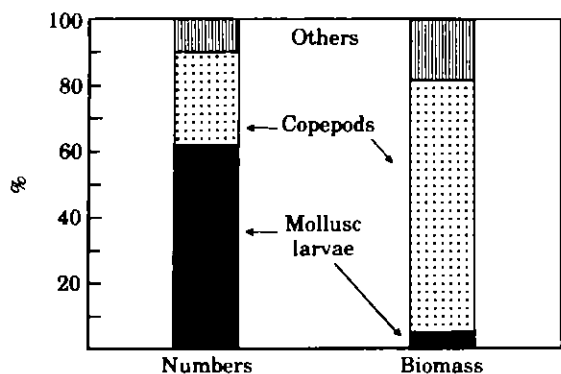


Figure 6. Above: main composition of food in gastral cavities of *Aurelia aurita* in terms of numbers (left) and estimated biomass (right). Below: number of food organisms found in gastral cavities during summer and early autumn 1976 (both drawings after Kerstan, 1977).

speculative since the amount of nitrogen output other than ammonia is unknown for *Aurelia aurita* and may be high and variable as in ctenophores (e.g. Kremer, 1977, 1982; Kremer *et al.*, 1986).

Reproduction is not considered here, however, but seems to be comparatively low in total energy budget (2% of growth + respiration + reproduction: Schneider, 1989b). Generally, these estimates are close to the results of Kerstan's experiments, at least for the small medusae. The critical point in our calculations, as well as in the results of the feeding experiments by Kerstan (1977), is that they reveal only potential feeding rates if enough food is available. The marked difference between these rates and the results deduced from Kerstan's stomach data, presented earlier in this section, may indicate food limitation due to the lack of prey when medusa stocks are high.

Impact on mesozooplankton

Due to their carnivorous mode of feeding it has been assumed that mass occurrences of *Aurelia aurita* lead to severe reductions of zooplankton standing stocks (e.g.

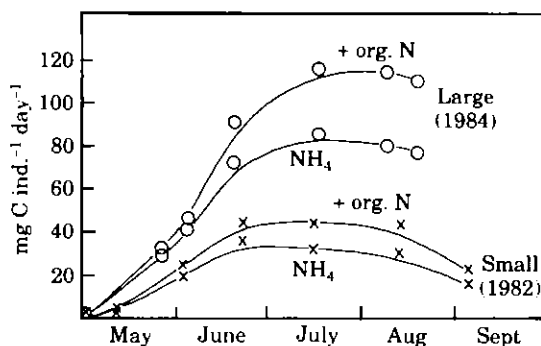


Figure 7. Estimated food requirements of a large (1982) and a small (1994) *Aurelia aurita* medusa to satisfy metabolism and somatic growth, as quantified by experiments and field samplings. "NH₄" = only ammonia excretion considered, "+ org. N" = nitrogenous compounds other than ammonia also taken into account.

Kerstan, 1977; Möller, 1980). Unfortunately, there are very few data to substantiate this. Nevertheless, negative correlations between herring larvae and displacement volume of medusa populations were found by Möller (1984b) in the Kiel Fjord when medusa volumes exceeded a certain threshold concentration. Recently, both mesozooplankton and medusae were sampled during the summer months of 1990–1993 at two stations in the open Kiel Bight (Behrends and Schneider, the results will be published elsewhere). From these data it appears that zooplankton abundance is low when *Aurelia* is abundant: median abundances of medusae were 0.6 ind. 100 m⁻³ in 1990/1991 (with no difference between these two years), 3.4 ind. 100 m⁻³ in 1992, and 9.4 ind. 100 m⁻³ in 1993. Median zooplankton numbers, however, were 53 000 ind. m⁻³ in 1990/1991, 36 000 and 14 000 ind. m⁻³ in 1992 and 1993, respectively.

Reduction of zooplankton can only occur if predation by medusae takes up a substantial portion of secondary production. For this compilation summer secondary production was estimated from primary production (von Bodungen, 1975) assuming a transfer efficiency of 15% to the secondary producers, and, alternatively, from zooplankton standing stock values (Hillebrandt, 1972; Martens, 1975; Schneider, 1989a; Behrends and Schneider, unpubl.) with a P/B ratio of 0.2 (Valiela, 1984). Although there is high variability in the data, secondary production was about 100 mg C m⁻² day⁻¹ (20 m water column), so that about 0.5 g C 100 m⁻³ day⁻¹ would be produced by the zooplankton during the summer. Figure 8 gives a comparison between daily secondary production and estimated food demands to satisfy metabolism and growth of *Aurelia* populations. Assuming two large medusae 100 m⁻³ to be a maximum value for medusa-poor years, food demands are well below secondary production and the zooplankton standing stock will be little affected by *Aurelia*

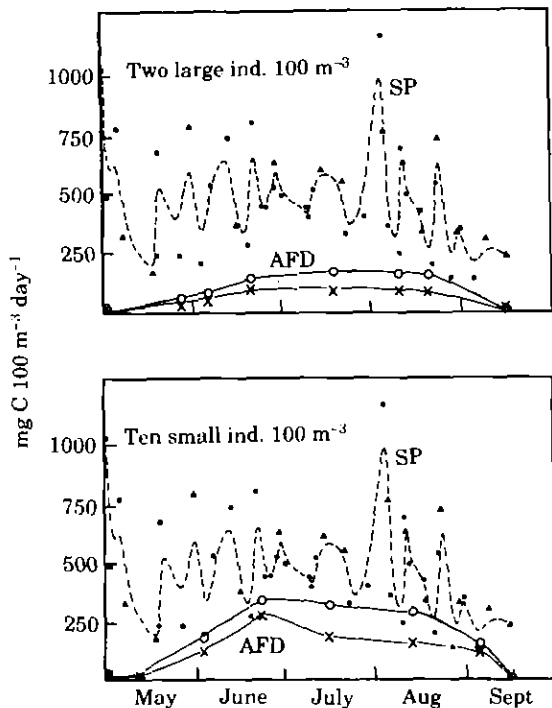


Figure 8. Comparison between average secondary production (dashed line) and *Aurelia* food demands (AFD) to satisfy metabolism and somatic growth in a medusa-poor year (above) and a bloom year (below). Calculations were carried out via ammonia excretion (crosses) and total nitrogen output (circles) according to the equation given in the text.

predation. In contrast, food requirements of 10 small medusae 100 m⁻³, a typical abundance in bloom years, are much higher and may lead to severe reductions in mesozooplankton standing stock. Although these calculations are based on the very simplistic approach given in the foregoing section, the results are in accord with the data from 1990–1993.

Discussion

Although we have good knowledge about the incidence, growth, and food requirements of *Aurelia aurita* populations in the Kiel Bight, some questions remain. The most important and still unresolved problem is the reason for the large interannual variations of abundance. This problem is intractable because there are so many life stages between generations of medusae, each of which can act as a population-limiting bottle neck. Limiting factors include the production and survival of the planulae larvae, asexual propagation of, and predation on, scyphistoma polyps, and variation of ephyrae released by the polyps. Schneider (1988b) demonstrated that different strategies of planula production occur between years. For example, female medusae of 500 g wet weight produced 120 000 planulae ind.⁻¹ in 1982,

260 000 in 1983, and 500 000 larvae ind.⁻¹ in 1984. The increase of planula numbers was accompanied by a decline in their organic content, which decreased from 0.68 µg C planula⁻¹ in 1982 to 0.28 µg C planula⁻¹ in 1984. It is clear that such variation will have some influence on the polyp stock arising from the surviving planulae.

Once a polyp stock is established, asexual budding of polyps may occur, thus increasing the population (e.g. Thiel, 1962). This will, however, be counteracted by predation on scyphistomae. According to the predation experiments of Hernroth and Gröndahl (1985) in the Gullmar Fjord of western Sweden the nudibranch gastropod *Coryphella verrucosa* (which also occurs in the Kiel Bight) appears to be a voracious predator on *Aurelia* polyps.

In the Kiel Bight, ephyrae release occurs throughout the year, with the main peak in winter and a smaller one in spring (Thiel, 1962). In the Gulmar Fjord strobilation was observed from autumn to spring, with the highest numbers of ephyrae released in autumn (Hernroth and Gröndahl, 1983a). The number of ephyrae released was found to be rather variable; in the Gullmar Fjord strobilae were polydisc (>five segments) in autumn, monodisc in winter, and intermediate in spring. In the Kiel Fjord, Thiel (1962) showed that polyps can strobilate several times per year, producing between 1 and 10 ephyrae per strobilation period, food playing an important role in the strobilation process. The growth pattern, and especially the differences in size of adult medusae in years of high and low abundances, is another aspect of population dynamics. During spring, ephyrae and young medusae show little or no growth (Möller, 1980; Schneider, 1989a). The exponential phase of growth coincides with the onset of warming and the first mesozooplankton peak in the Kiel Bight. It appears reasonable to explain the fast growth of medusae at that time with good food conditions and an elevated metabolism, leading to higher P/B ratios.

The observation that adult medusae are much smaller in years when *Aurelia* is abundant indicates a density-dependent mechanism regulating adult size. Bearing in mind the high population food requirements given in Figure 8 and the results of the zooplankton data from 1990–1993, it seems probable that the medusae more often experience food limitation in medusa-rich years than in medusa-poor years, so that competition for a limited resource leads to the observed differences in size of adults. Recently, Olesen *et al.* (1994) have shown that highly abundant *Aurelia* medusae (up to 300 ind. m⁻³) reach only a size of approx. 4–5 cm in a Danish Fjord, which is probably due to food limitation. Alternatively, it has been proposed (Möller, 1980) that temperature variations between years influence size of adult medusae for metabolic reasons. However, those variations of water temperature seem to have only a small effect. This

is indicated by the data from 1983 and 1984: 1983 was an unusually warm year with surface temperatures of 23°C; in 1984 15 to 17°C were observed, being more typical of this area. The final diameters of medusae were rather similar in the two years (Fig. 5). In contrast, the average size was much lower in 1982, a year with high medusa abundance, but temperatures comparable to those in 1984. Without experimental studies we can only suggest that abundance and competition for food are the main factors governing adult size of medusae, with temperature inducing some minor variations.

In late summer or early autumn a decline of medusa size was found in some studies (see Figs 3, 4). Since shrinkage was observed in starving medusae (e.g. Hamner and Jenssen, 1974), it is proposed that the size decrease of our medusae was due to starvation in late summer. However, it is impossible to decide from field samplings whether a size reduction is due to true shrinkage of individuals or is only a statistical effect caused by the death of the largest individuals or the advection of smaller medusae from the central Baltic Sea.

The longevity of *Aurelia aurita* may vary between different regions and in the laboratory. In the Kiel Bight, as well as in the North Sea, *Aurelia aurita* live for 8–10 months (Russell, 1970; van der Veer and Oorthuysen, 1985; this paper), and a somewhat shorter life span was reported from Tomales Bay in California (Hamner and Jenssen, 1974). In contrast, in Japanese waters, *Aurelia* lives between 1 and 2 years (Yasuda, 1971). In the laboratory three North Sea medusae lived for about 2 years (Zahn, 1981), evidently much longer than in the field.

Generally, at the end of their life *Aurelia* sampled in the field show a deterioration, with loss of gastric filaments, tentacles, and oral arms (Russell, 1970; Hamner and Jenssen, 1974; Kerstan, 1977), but this process takes longer in the laboratory (Spangenberg, 1965). Sampling problems exist in the field as deteriorating medusae sink to the sea bed, and, although still alive, are not collected by nets, indicating a comparatively fast death. Degeneration in the sea, however, may be accelerated by infestations with the parasitic amphipod *Hyperia galba* (e.g. Russell, 1970; Kerstan, 1977; Möller, 1984a).

Although some open questions in population dynamics remain, this contribution may have demonstrated that *Aurelia aurita* medusae in certain years play an important role in the Kiel Bight pelagic ecosystem due to their large predation pressure on the zooplankton community. The estimated ingestion rates given above cannot be compared with the results obtained in most of the other studies (e.g. Båmstedt, 1990; Fancett and Jenkins, 1988; Garcia and Durbin, 1993; Olesen *et al.*, 1994) for various reasons. However, ingestion rates measured for *Stomatolophus meleagris* ranged between 20 and 100 mg C medusa⁻¹ day⁻¹ (Larson, 1991), and maximal copepod

ingestion of *Chrysaora quinquecirrha* was 19 000 ind. medusa⁻¹ day⁻¹ (Purcell, 1992), probably corresponding to approx. 70–80 mg C medusa⁻¹ day⁻¹. These rates are similar to those of *Aurelia aurita*, and may indicate that all scyphomedusae can induce collapses of zooplankton populations when medusae occur in sufficient densities. Beyond this, new roles begin to emerge, such as possible top-down regulation of plankton community composition (see also Smayda, 1993). This will, however, be discussed in another paper together with the presentation of our 1990–1993 data.

Acknowledgements

We are highly indebted to P. Kremer and J. Purcell for discussion, and two unknown reviewers helped with their valuable comments to improve this paper. Mr R. Wilson kindly corrected the English.

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