

Not to be cited without prior reference to the author

ICES STATUTORY MEETING 1993

C.M. 1993 / L:20
Sess. 8



DOES AURELIA AURITA REALLY DECIMATE ZOOPLANKTON IN KIEL BIGHT?

Gerald Schneider
Biologische Anstalt Helgoland
D - 25989 List / Sylt , Germany

ABSTRACT

The medusae of the scyphozoan *Aurelia aurita* are assumed to be voracious predators of mesozooplankton in the Kiel Bight (western Baltic) plankton system. This conclusion was drawn from the investigations in the Kiel Fjord in 1978 and 1979. Meanwhile, further work revealed conditions in Kiel Fjord to be untypical. Abundances, for example, are about one order of magnitude higher in Kiel Fjord than in Kiel Bight open waters. Therefore, extrapolations based on the Kiel Fjord data cannot be applied to the whole system. This paper tries to summarize the data now available and to compare estimated predation rates with zooplankton secondary production. The calculations reveal that medusae remove about two-thirds of secondary production in densely populated environments like the Kiel Fjord but only one-third of production in the Kiel Bight open waters. It is therefore concluded that predation by *Aurelia aurita* is important in near-shore areas and bays but play a much lower role in off-shore regions, representing most of the Kiel Bight water volume. Finally, the role of patchiness is addressed which may be an important factor on a smaller space scale.

Introduction

The medusae of the scyphozoan **Aurelia aurita** are a conspicuous member of the summer plankton in Kiel Bight. Although recruitment takes place in winter and spring (Thiel 1962), growth of individuals is small and, therefore, total biomass of ephyrae and young medusae is negligible (Möller 1980, Schneider 1989 a). However, with the onset of water warming and mesozooplankton development, medusae show heavy growth and reach their highest biomass in July and August, in which standing stocks of medusae are comparable to that of all other mesozooplankton organisms (Möller 1979, Schneider 1989 a). During this phase of maximal occurrence predation by medusae was assumed to reduce zooplankton stocks significantly (Möller 1980) leading to restrictions of zooplankton dynamics in the Kiel Bight during summer. However, the data base of these first evaluations appears comparatively poor for proper extrapolations to the whole Kiel Bight pelagic system. Meanwhile, more samplings were carried out covering eight years in different regions of the Kiel Bight. Monthly samplings at several stations in Kiel Bight open waters since 1990 (Behrends, unpubl.) enabled us to evaluate medusae stocks in off-shore waters which are more characteristic for the Kiel Bight proper than data from semi-enclosed bays and inlets. Therefore, it may be now possible to draw more subtly differentiated conclusions, also improving the first estimations of **Aurelia** population food demands given in Schneider (1989 b).

In this paper the author tries to summarize all data available and to estimate the predation impact of **Aurelia aurita** medusae as being dependent on abundance, medusae size and food requirements per individual.

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

To estimate the abundance and biomass stocks of **Aurelia aurita** medusae various sampling programmes were carried out. During 1978 and 1979 Möller (e. g. Möller 1980, 1984 a) investigated the narrow Kiel Fjord (Fig. 1), between 1982 and 1984 the author worked in Eckernförde Bay (e. g. Schneider 1989 a), and recently, monthly

samples are being taken by the fishery department of the Institut für Meereskunde, Kiel (Behrends, unpubl.). More details of the sampling methods are given with Fig. 1.

From these investigations abundances of medusae appear to be quite different between the various regions and also vary between years. Highest numbers were observed in Kiel Fjord in 1978 and 1979 and in Eckernförde Bay in 1982 (Fig. 2). Although there are strong fluctuations in the Kiel Fjord data, abundances exceeded 5 ind. / 100 m³ during most of the summer season, and in Eckernförde Bay up to more than 20 ind. / 100 m³ were encountered. In contrast, during 1983 and 1984 abundances were one order of magnitude lower in Eckernförde Bay and did not exceed 3 ind. / 100 m³. In Kiel Bight open waters numbers per 100 m³ were generally low in 1990 and 1991 but were comparable to the Eckernförde Bay data of 1983/84 in 1992. From these data it may be concluded that **Aurelia** population densities seem to be highest in the narrow (and polluted) Kiel Fjord but show generally lower abundances in the

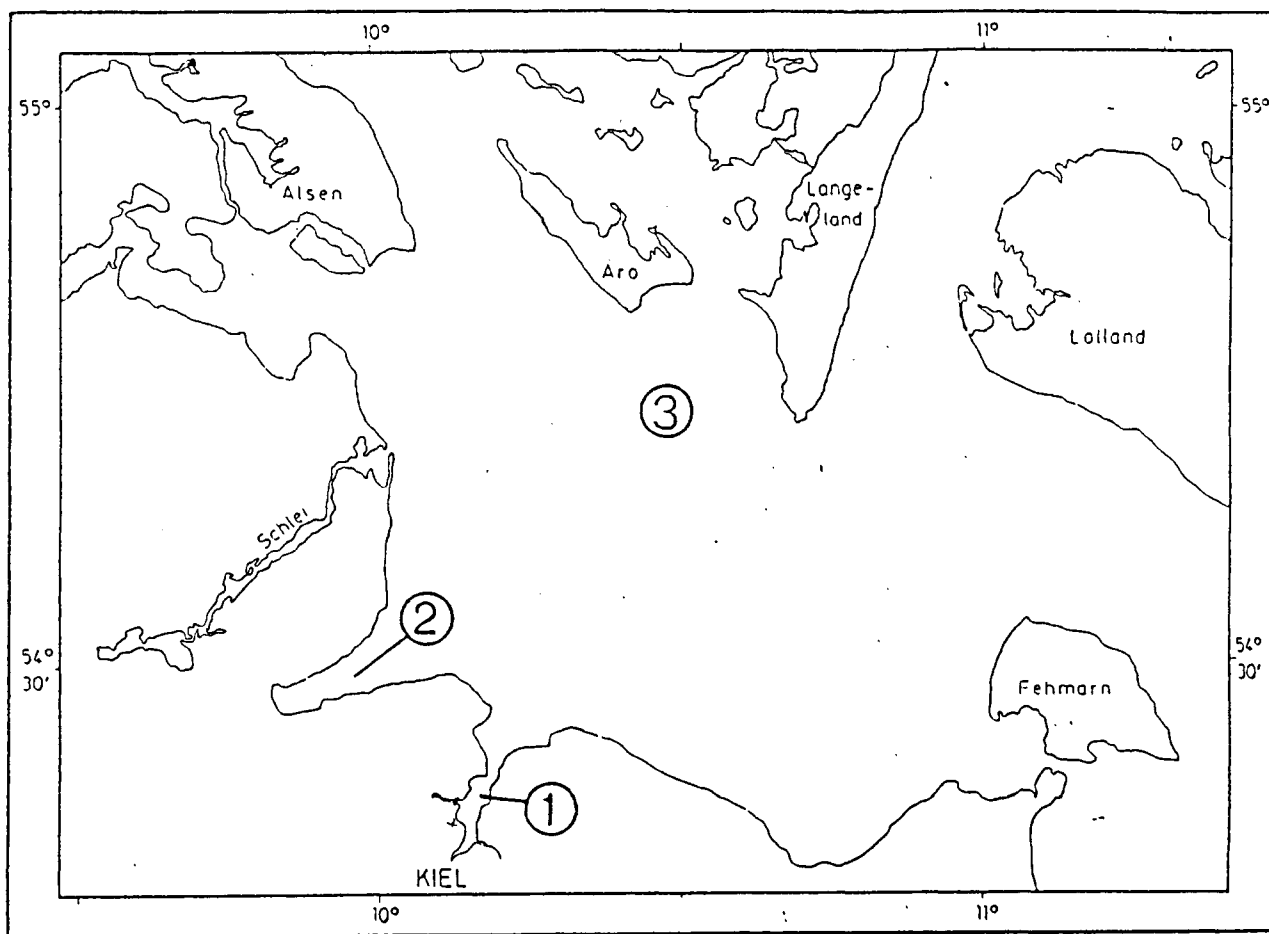


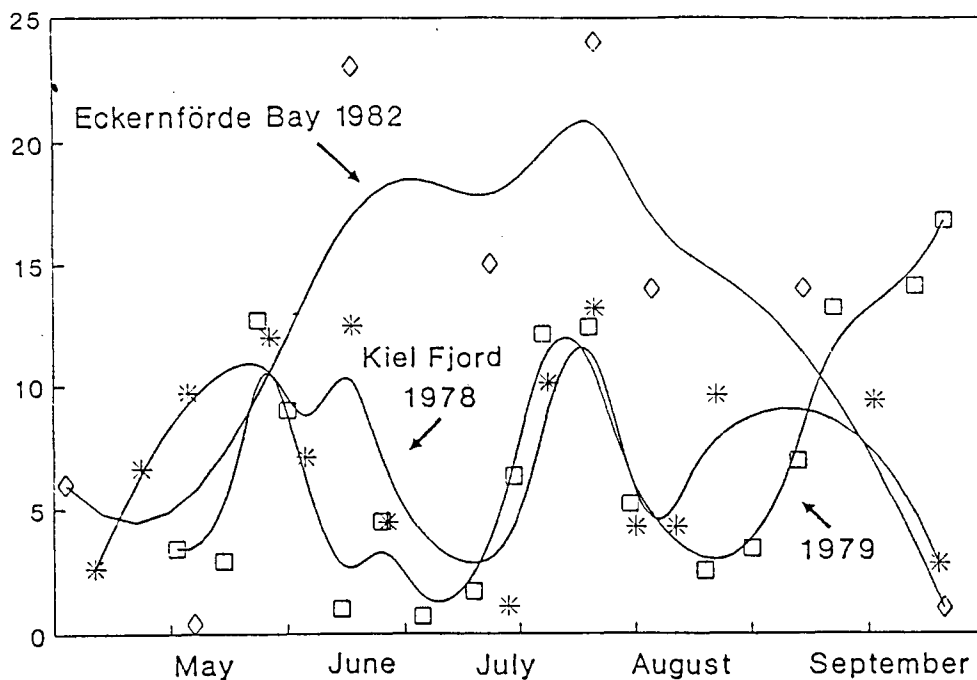
Fig. 1: Kiel Bight with investigation areas indicated by numbers

Area 1: Kiel Fjord. Investigation years: 1978, 1979. Principal investigator: H. Möller. Number of stations examined: 26. Sampling frequency: weekly. Gear: CalCOFi-net, 500 μ m.

Area 2: Eckernförde Bay. Investigation years: 1982, 1983, 1984. Principal investigator: G. Schneider. Number of stations examined: 4. Sampling frequency: bi-weekly. Gear: CalCOFi-net, 500 μ m.

Area 3: Kiel Bight open waters. Investigation years: 1990, 1991, 1992 and on-going. Principal investigator: G. Behrends. Number of stations examined: 10. Sampling frequency: monthly. Gear: Bongo-net, 300 and 500 μ m.

n / 100 m³



n / 100 m³

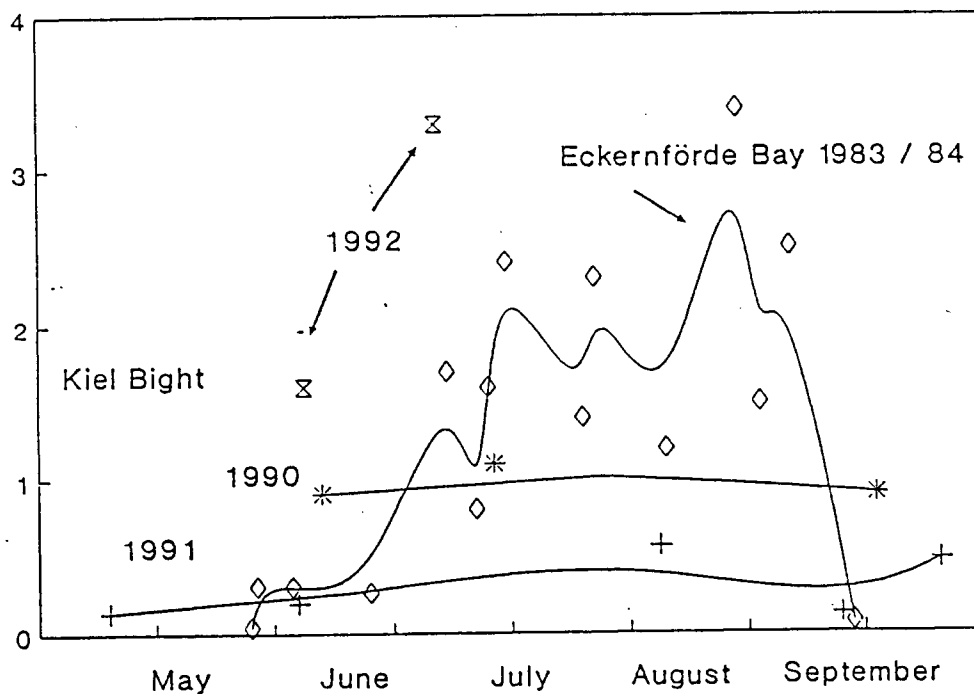


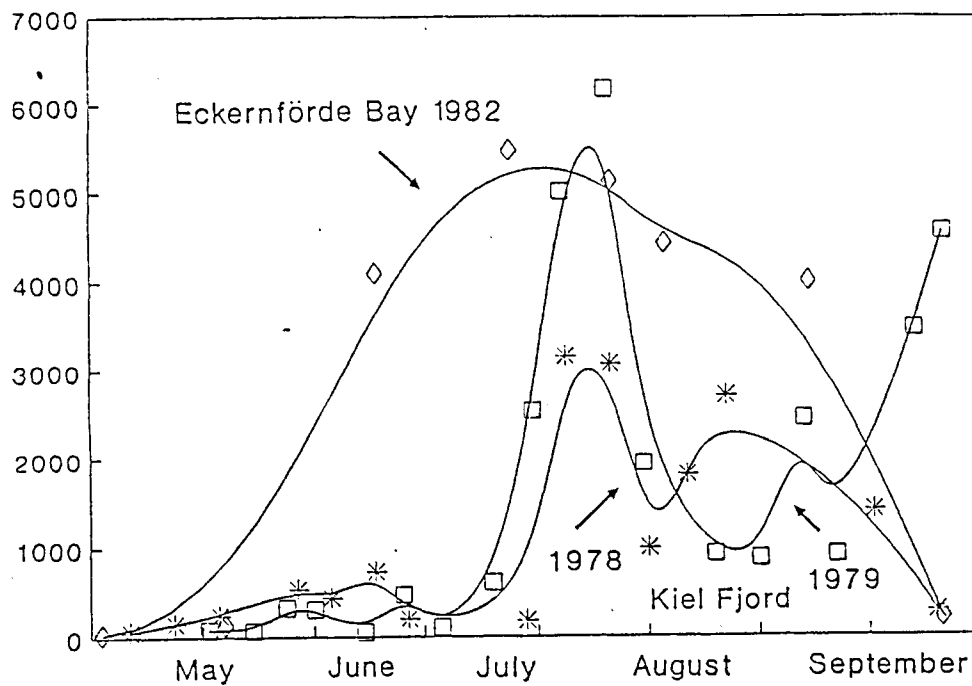
Fig. 2: Abundances of *Aurelia aurita* during summer.

Above: Regions of high abundance

Below: Regions of low abundance

Data: Möller (1984), Schneider (1989), Behrends (unpubl.).

mg C / 100 m³



mg C / 100 m³

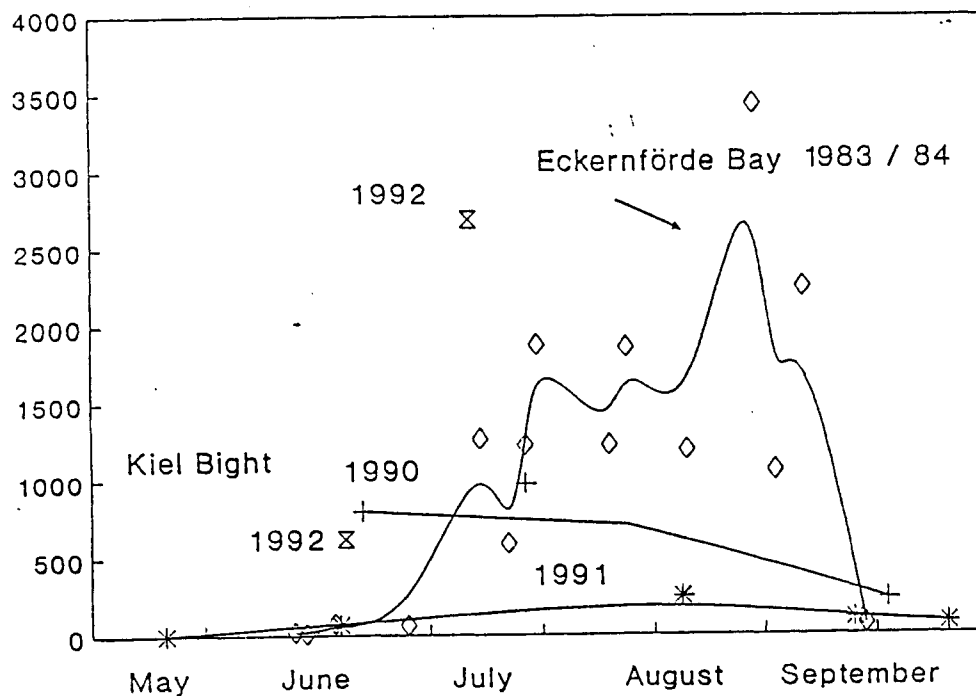


Fig. 3: Estimated carbon biomass of *Aurelia aurita* during summer. Conversions to carbon from wet weight or diameter values according to the relationships given in Tab. 1.

other regions of the Kiel Bight with approx. 3 medusae / 100 m³ as an upper limit. However, the 1982 data from Eckernförde Bay may indicate the occasional occurrence of bloom years. Assuming the strobilation centres to be in the near-shore regions and the bays, the low numbers in Kiel Bight open waters may be due to "dilution" of populations when invading into the open waters.

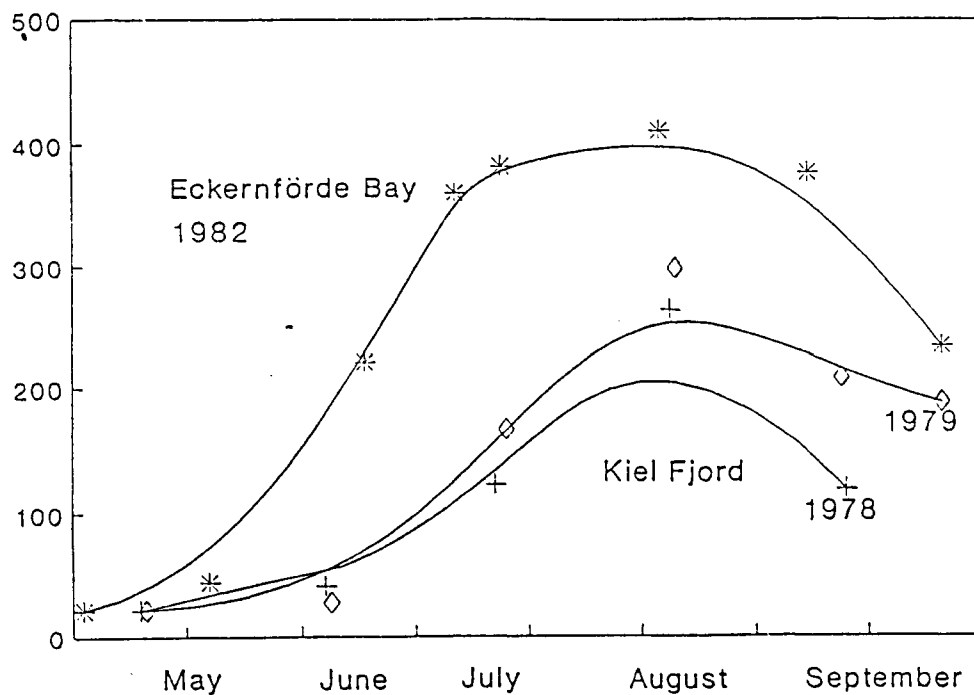
Carbon biomass values show the same tendencies as abundance (Fig. 3), however, the difference between regions and years appear to be not so pronounced. For example, during 1982 carbon biomass was about 5000 mg C / 100 m³ in Eckernförde Bay whereas during 1983 and 1984 approximately one-third this value (1500 mg C / 100 m³) was determined. This difference is much less than for abundance and the reason for this is difference in the final size of adult medusae as will be mentioned in the next section.

Growth and size of adult medusae

Growth means the increase in size and weight of an individual during its life. In this rigid sense no growth studies were carried out with Baltic *Aurelia* medusae. However, size-frequency-distributions for each sampling day were established and the mean values of the distributions were used to characterize growth (e. g. Möller 1980, Schneider 1989 a). For this compilation all weights are given in mg C / ind. which were calculated from diameters or wet weights according to the relationships given in Tab. 1 (after Fig. 5). Fig. 4 shows various growth curves obtained from the data available. As a general pattern growth is exponential in May and June and ceases in July and August. In these two months the medusae are adult and reproduce. In September a decrease of individual size can be observed in most years which is also termed "degrowth" (Hamner and Jenness 1974). Degrowth was observed to occur in starving medusae (e. g. Hamner and Jenness 1974) and it was proposed that the size decrease of our medusae is perhaps due to starvation in late summer. (e. g. Möller 1980). However, it can not be decided from field samplings whether the size reduction is due to true shrinkage of individuals or is only a statistical effect perhaps due to the death of the largest medusae. Interestingly, growth curves obtained with three North Sea *Aurelia* held in a "Planktonkreisell" with sufficient food (Fig. 5) also show a decrease after reaching the maximal diameter and the beginning of sperm release. Additionally, it is noteworthy that the medusae held in captivity lived slightly less than two years whereas in Kiel Bight most medusae die after 6 to 8 months in September or October.

However, the most important aspect is the variation of the size of the adults between environments or years of high and low abundances, respectively. As can be seen from Fig. 4 medusae appear to be smaller and lighter when abundant but are large and heavy when occurring in low densities (see also Fig. 6). Maximal carbon weights were about 200, 250 and 400 mg C / ind. in Kiel Fjord and Eckernförde Bay in 1982 whereas in Eckernförde Bay during 1983 and 1984 and in the Kiel Bight open waters weights ranged between 800 and 1100 mg C / ind. Therefore, at low population densities medusae can attain a larger size than at high abundances, perhaps indicating the limiting role of a resource (food ?) in case of the latter conditions.

mg C / ind.



mg C / ind.

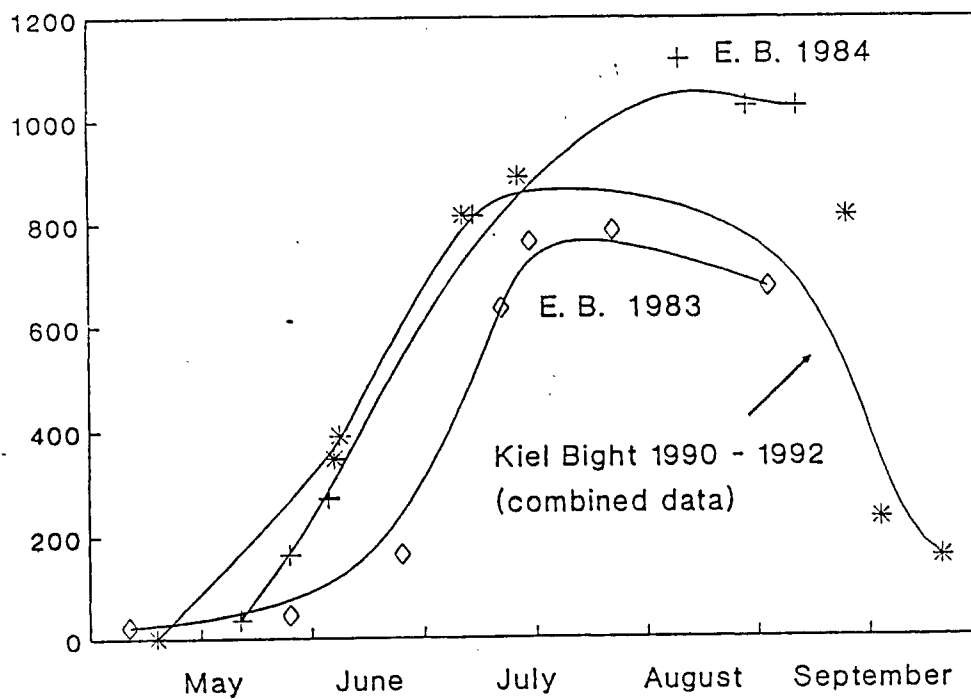


Fig. 4: Growth of *Aurelia aurita* when occurring in high (above) and low abundances (below).

Bell diameter (cm)

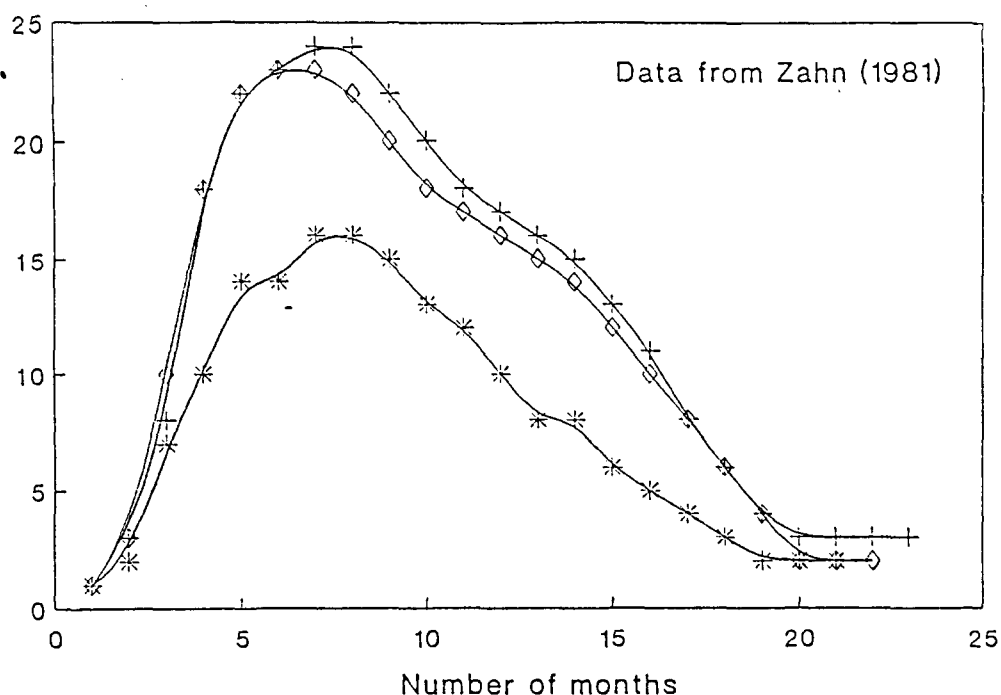


Fig. 5: Growth of three North Sea Aurelia held in a "Plankton-kreisel" for about two years.

Tab. 1: Some biometric and metabolism relationships of Aurelia aurita used for the calculations in this paper.

Conversion from cm diameter (DM) to g wet weight (WW)

$$WW = 0.088 \times DM^{2.75} \quad (\text{Schneider 1988})$$

Conversion from g wet weight (WW) to mg carbon weight (CW)

$$CW = 0.867 \times WW + 20.85 \quad (\text{Schneider 1988})$$

Respiration (R, ml O₂ / ind. / d) vs g wet weight (WW)

$$R = 0.103 \times WW^{0.94} \quad (\text{Schneider 1989 b})$$

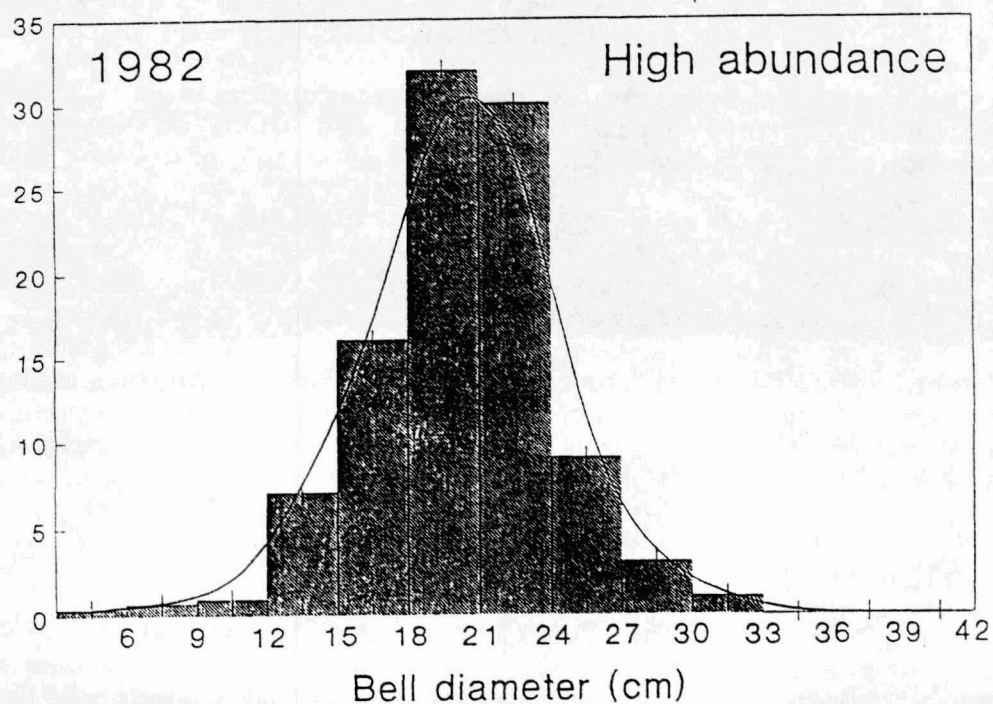
Ammonia excretion (NH₄, umol / ind. / h) vs g wet weight (WW)

$$NH_4 = 0.058 \times WW^{0.93} \quad (\text{Schneider 1989 a})$$

Phosphate excretion (PO₄, umol / ind. / h) vs g wet weight (WW)

$$PO_4 = 0.010 \times WW^{0.87} \quad (\text{Schneider 1989 a})$$

% of data (n = 552)



% of data (n = 220)

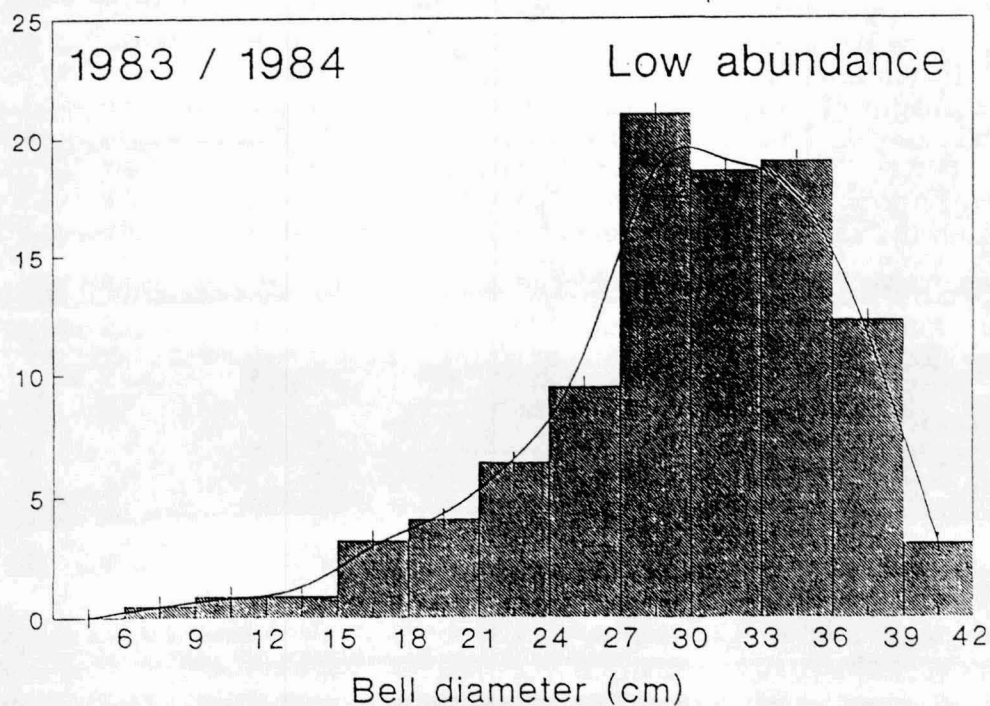


Fig. 6: Size-frequency-distributions in 1982 vs 1983/84 (August) in Eckernförde Bay. See also Fig. 1 for comparison of abundances.

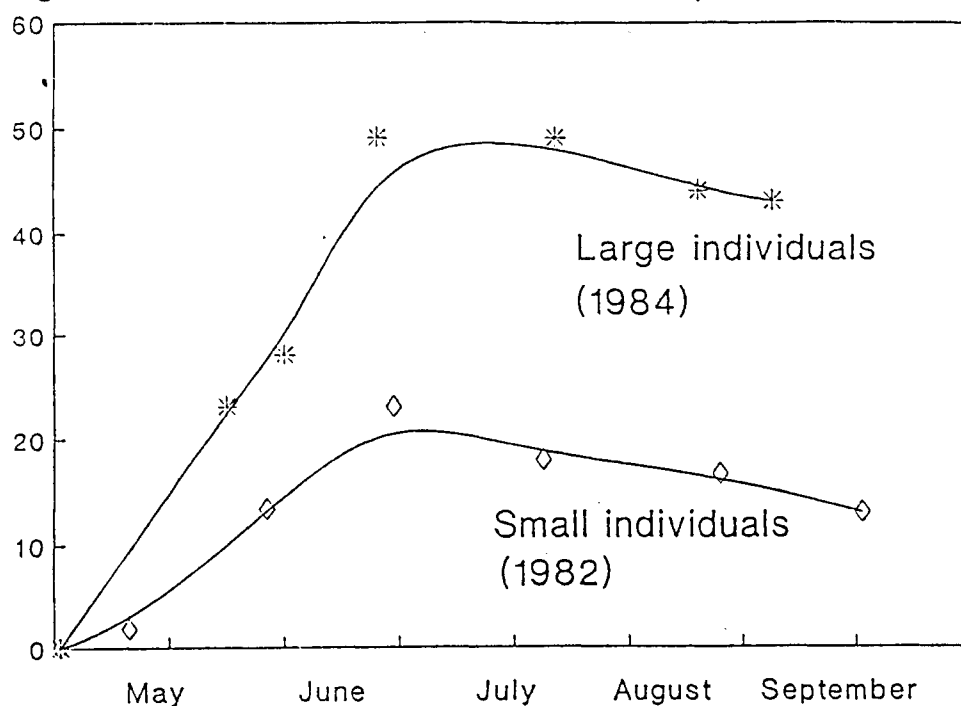
It should be noted that variations of water temperature seem to have only a small effect on adult size. This is indicated by the Eckernförde Bay data from 1983 and 1984 of which the first represents a warm year with surface temperatures up to 23° C whereas in 1984 only the typical 15° - 17° C were observed. Final sizes of medusae between these two years did not differ drastically. In contrast, final weight in the medusae-rich year 1982 was less than half the 1983 and 1984 values, but in 1982 a water temperature comparable to that in 1984 was determined. Nevertheless, the comparatively small differences in final weights between the 1983 and 1984 medusae may indeed be due to water temperature. Since there are no experimental studies it may be concluded with some caution that abundance is the major regulating factor of adult size and temperature may induce some minor variations.

Food and food demands

Since the investigations of Delap (1907), Orton (1922), Lebour (1922, 1923) and Southward (1955) it is known that **Aurelia aurita** has a very wide food spectrum ranging from protozoans to fish larvae and small or young fish. With respect to microzooplankton, Stoecker et al. (1987) were able to demonstrate that the medusae can use this food resource but select food items after capture. Non-loricata ciliates were preferred when compared with similar-sized algae, non-loricata ciliates were selected over tintinnids and large non-loricata ciliates over small ones. Bamstedt (1990) showed that the oligotrich ciliate **Strombidium aculeatum** was consumed by ephyrae and small medusae but phytoplankton at natural concentrations was not.

The food of Kiel Bight **Aurelia** was intensively studied by Kerstan (1977) via stomach analysis. Summarizing the results it can be concluded that the entire spectrum of plankton organisms occurring in Kiel Bight is used (no special attention was paid to non-loricata protists) including larvae of the chironomid **Clunio marina** and such curious things like arachnids and beetles probably blown from land. However, in terms of numbers mollusc larvae and copepods are most important (Fig. 7) and all other food items together contribute only 10 % of the total. Among the copepods **Centropages hamatus** is the prominent one making up 86 to 100 % of total copepods found in the gastral cavities. When assuming the individual carbon weights of copepods, "others" and mollusc larvae to be in the ratio 50 : 25 : 1 it can be estimated that copepods contribute 80 % of prey biomass, 15 % may be due to other organisms and mollusc larvae make up only 5 % of the total (Fig. 7). Therefore, predation on copepods appears to be most important for **Aurelia** nutrition. Additionally to plankton, in near-shore areas some benthic or hyper-benthic organisms will be taken also. Polychaetes, mysids, isopods and amphipods were found in the gastral cavities, however, the number of these prey decreases rapidly when studying medusae from more open waters. Fish larvae will be consumed only by medusae less than 8 cm in size due to the contemporary occurrence of young medusae and fish larvae in late spring. Nevertheless, predation on fish larvae appears to be significant, at least in Kiel Fjord (Kerstan 1977, Möller 1984 b, Heeger and Möller 1987).

mg C / ind. / d



mg C / ind. / d

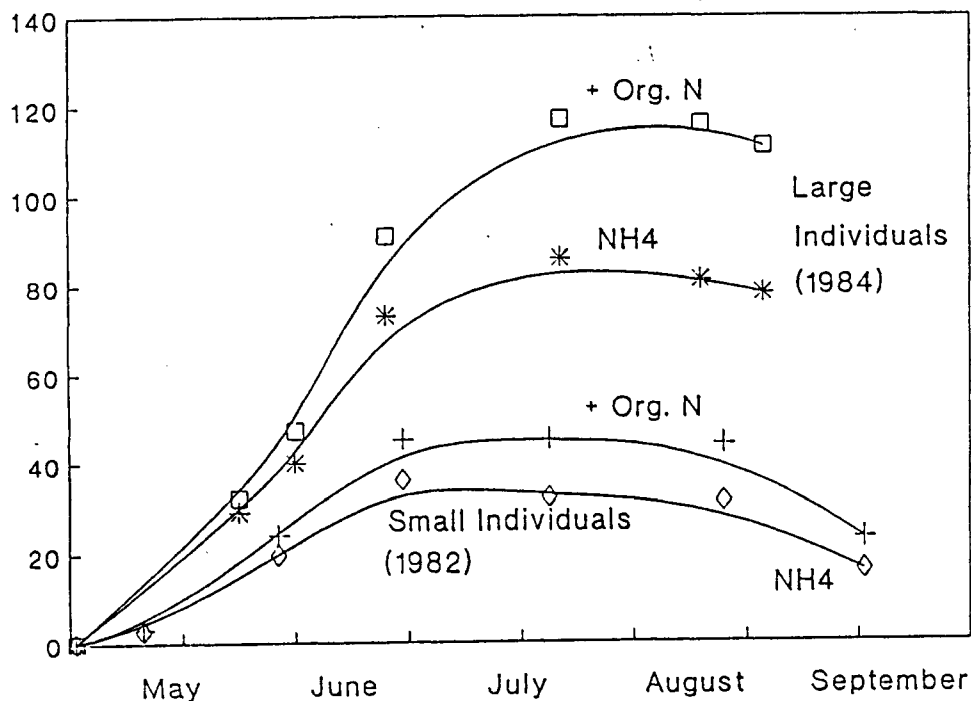


Fig. 10: Estimated food demands of *Aurelia aurita* according to field data as described in text.

Above: Calculated from growth and respiration

Below: Calculated from growth and NH_4 -release (" NH_4 ") and from growth + NH_4 -release + organic-N release (" + Org. N").

environments may indeed indicate the difficulty to sample enough food. Growth seems to be food limited in this case.

Tab. 2: Estimated feeding rates and food demands of *Aurelia aurita* individuals according to the different approaches.

Approach	mg C / ind. / d	Remark
Numbers of prey in stomach	23	a
Feeding experiments	73 ± 21	b
Growth + respiration	23 ; 50	c
Growth + NH ₄ - release	36 ; 85	c

- a Maximal rate, medusae size 16 - 26 cm, Data from Kerstan (1977).
b Mean ± SD, medusae size 16 - 21 cm, data from Kerstan (1977).
c Maximal rates for small and large medusae, respectively. Own Data (see also Schneider 1989 a).

Kiel Bight zooplankton secondary production and comparison with *Aurelia aurita* food demands.

Although Martens (1976) has estimated Kiel Bight annual secondary production to be about 34 g C / m² / a, he didn't give values for the various seasons. Therefore, for this compilation summer secondary production was estimated from primary production assuming a transfer efficiency of 15 % to the secondary producers, and alternatively, from zooplankton standing stock with a P / B ratio of 0.2 (Valiela 1984). The results are given in Fig. 11 and Tab. 3. Although there is high variability in the data, an average of about 100 mg C / m² / d (20 m water column) seems to be appropriate, so that about 0.5 g C / 100 m³ / d will be produced by the zooplankton during summer.

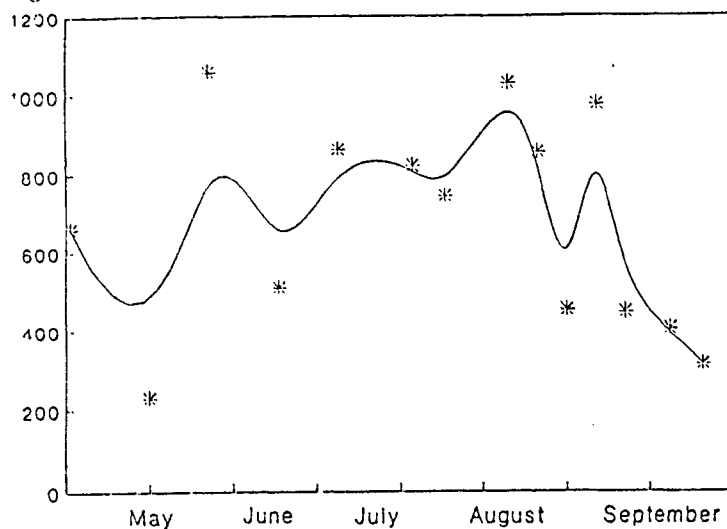
Tab. 3: Estimated daily secondary production (SP, mg C / m² / d) calculated via primary production (PP) and zooplankton biomass (ZPB).

	SP = PP x 0.15	SP = ZPB x 0.2
Total range	25 - 160	27 - 236
50 % range (Median ± 22 %)	68 - 128	50 - 137
Median	106	89
Mean ± SD	101 ± 42	97 ± 51
n	14	37
Integrated (153 d)	15 600*	14 700*

* approx. half the annual value given by Martens (1976)

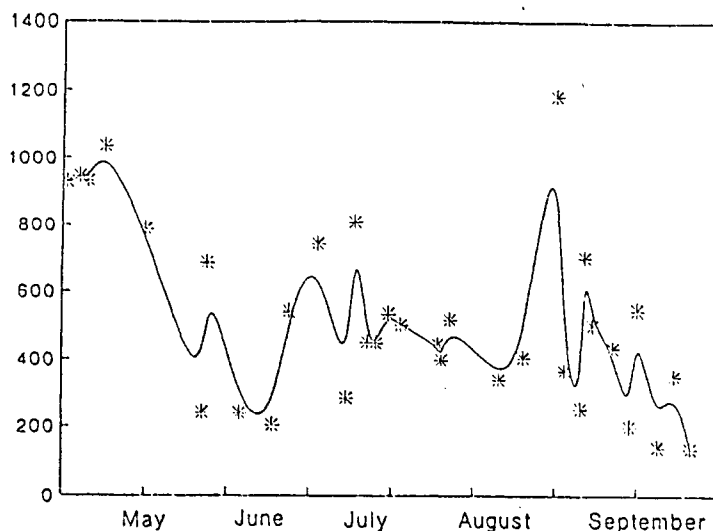
Kiel Bight primary production

mg C / m² / d



Kiel Bight zooplankton standing stock

mg C / m²



Estimated zooplankton secondary production

mg C / m² / d

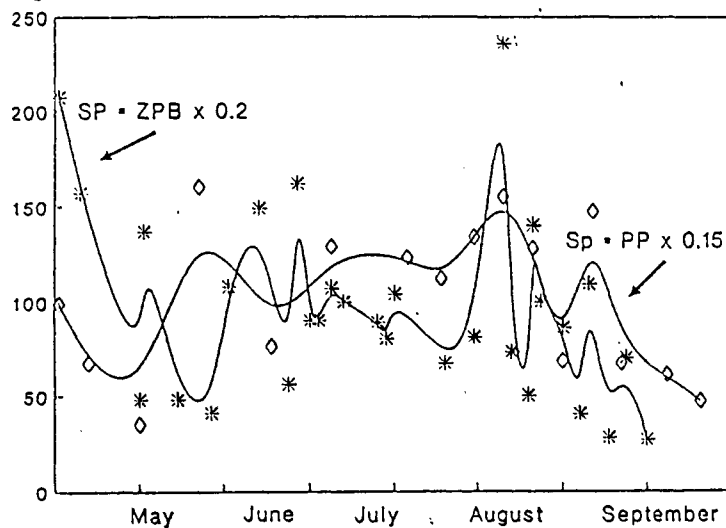
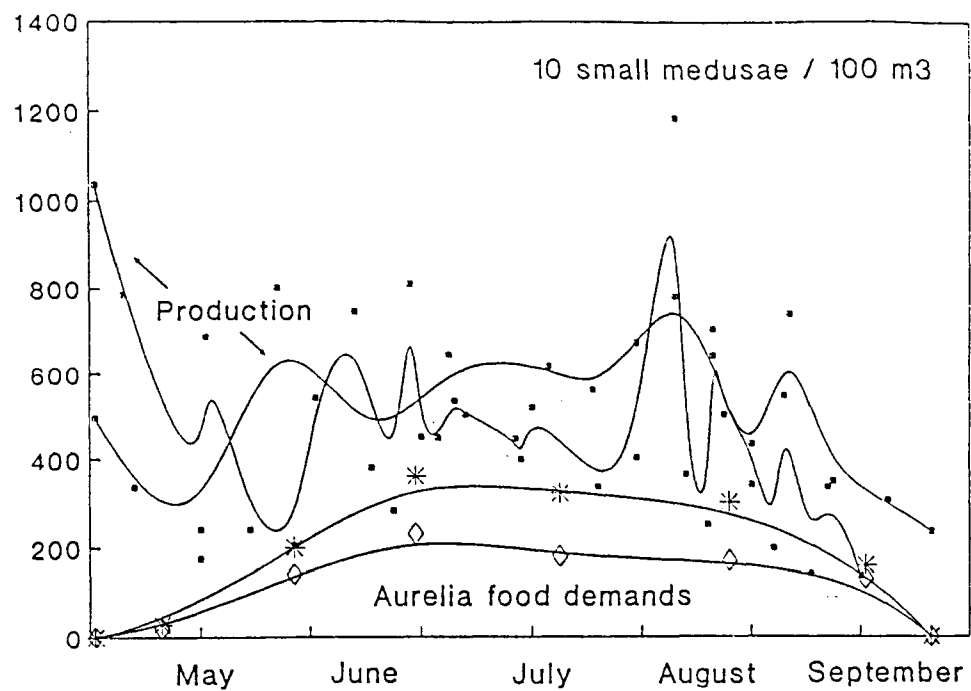


Fig. 11: Summer primary production in Kiel Bight (above, left), zooplankton biomass (above, right) and estimated zooplankton secondary production (below). Data sources: von Bodungen (1977, prim. prod.), Hillebrand (1972), Martens (1975), Schneider (1989)

mg C / 100 m³ / d



mg C / 100 m³ / d

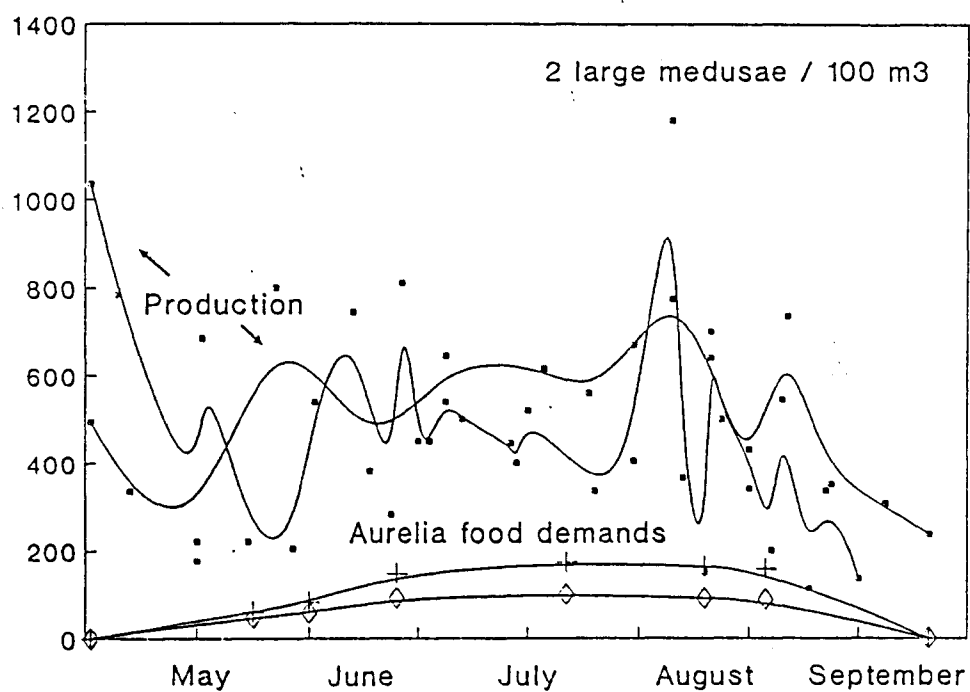


Fig. 12: Comparison of Aurelia food demands with estimated zoo-plankton secondary production.
Above: For 10 small medusae as being assumed to be representative for e. g. Kiel Fjord.
Below: For 2 large medusae as may be typical in Kiel Bight off-shore waters.

Comparing these figures with the estimated feeding rates given in Tab. 2 one large medusa per 100 m³ consumes about 20 % of daily secondary production whereas one small individual removes only about 8 % / d. However, for a more realistic estimate we have to take into account the different abundances of small and large medusae, respectively. As outlined above, small adult medusae occurred in dense numbers in Kiel Fjord and in Eckernförde Bay in 1982 whereas large ones were found in low numbers with 3 ind. / 100 m³ as an upper limit and an overall average of 2 ind. / 100 m³. Fig. 12 compares the food demands of 10 small and 2 large medusae with the estimated secondary production. According to the calculations via growth and ammonia release (which gives the higher figures) ten small medusae will probably consume about 330 mg C / 100 m³ / d corresponding to two-thirds of summer secondary production. It may be proposed that this situation will have a strong influence on zooplankton dynamics. On the other hand, feeding of two large medusae only accounts for about one-third of secondary production (160 mg C / 100 m³ / d). Therefore, it may be concluded that medusae predation is significant in situations represented by the Kiel Fjord and Eckernförde Bay data from 1982, but is less important in Kiel Bight open waters. More generally, the predation of *Aurelia aurita* seems to play a significant role in the various bays and inlets but not in the Kiel Bight proper. Therefore, the statement that *Aurelia* predation limits zooplankton dynamics in summer can only be applied to the marginal-zone but cannot be extrapolated to the whole system since abundance in the open waters is generally low.

The role of patchiness

The calculations and conclusions in the last section implicitly involves that *Aurelia* individuals are more or less evenly distributed in space. However, just that is not the case with medusae since patchiness is a well-known phenomenon among gelatinous zooplankton. Dense clusters of medusae were often observed in Kiel Bight from ships or by SCUBA-divers but were not studied systematically. Table 4 gives some data of patches sampled by chance during routine programmes. The ecological role of such patches clearly depends upon the number and size of medusae. Dealing only with the swarms no. 1, 2, 4, 5, 6, 7, and 10 biomass in patches range between 7.5 and 28 g C / 100 m³ which is about 3 to 11 times higher than the average zooplankton standing stock of about 0.5 g C / m² = 2.5 g C / 100 m³ (Hillebrandt 1972, Martens 1975, Schneider 1989 a). From the food demands it can be calculated that approx. 11 - 68 % of the zooplankton standing stock will be grazed upon per day and that predation is in the range of or even higher than secondary production. Ammonia excretion rates range between 7 and 28 mmol / 100 m³ / d fuelling 14 to 56 % of phytoplankton demands (Production: 0.8 g C / m² / d, von Bodungen 1975; see also Smetacek et al. 1987), and phosphate release is between 0.8 and 3.3 mmol / 100 m³ / d contributing 25 - 104 % of phytoplankton phosphorus demands. Therefore, the ecological impact of such patches may be conspicuous on a local scale, probably leading to a decrease of zooplankton stock and providing comparatively large amounts of regenerated nutrients. This may stimulate phytoplankton and microplankton production due to a reduction of the grazing

Tab. 4: Some characteristics of *Aurelia* patches sampled by chance in Kiel Bight.

No.	Abundance n/100 m ³	Average weight mg C / ind.	Total biomass mg C / 100 m ³	Food demands mg C/100 m ³ /d	NH ₄ -release m mol / 100 m ³ /d	PO ₄ -release
1	11	673	7 400	280 - 460	7.2	0.8
2	27	378	10 200	430 - 600	9.5	1.2
3	27	98	2 700	110 - 170	2.7	0.4
4	33	234	7 700	320 - 450	7.7	1.0
5	34	279	9 500	370 - 570	9.5	1.2
6	36	221	7 900	330 - 500	7.9	1.0
7	43	360	15 500	650 - 970	15.4	1.9
8	45	27	1 200	15 - 24	0.4	0.1
9	71	37	2 600	120 - 180	2.8	0.4
10	77	360	27 700	1160 - 1740	27.6	3.3

Data of abundance and medusae size from Möller 1984 a (no. 3, 4, 8), Behrends (unpubl., no. 9) and own unpublished data (no. 1, 2, 5, 6, 7, 10)

Calculations according to the relationships given in Tab. 1. Food demands determined via growth + respiration (left value) and growth + ammonia release (right value).

pressure exerted by mesozooplankton, which, in turn, may stimulate enhanced zooplankton production after disappearance of the medusae patch. It can be proposed that *Aurelia* patches may have a structuring effect in the Kiel Bight pelagic system, although this is not evaluated properly. Although expensive (de Wolf 1989), it is the author's conviction that studies on the role of patchiness are now more important than, for example, further physiological investigations including feeding experiments. Investigations dealing specially with the few questions given below may lead to further insight of the role of medusae and gelatinous zooplankton:

- What is the typical size of a patch and how many medusae can be found in it?
- Which is the more important process in patch formation: Hydrography or active crowding by medusae?
- How long does a patch exist? Is there a special behavior to avoid cluster break-up (see also Arai 1992 and Larson 1992)?
- Can we measure what we expect? Can we find lower zooplankton stocks and higher nutrients within a patch when compared with the surrounding waters outside the patch?

These questions and some related ones are worth to invest money and time in because the answers may perhaps be fascinating from a scientific point of view but may also be of some commercial interest.

Acknowledgements

I thank G. Behrends for the allowance to use her yet unpublished data from Kiel Bight open waters and S. S. Dengg for correcting the English.

Literature cited

- Arai, M. N., 1992.** Active and passive factors affecting aggregations of hydromedusae: A review. - *Sci. Mar.* 56 (2-3), 99 - 108.
- Bämstedt, U., 1990.** Trophodynamics of the scyphomedusae *Aurelia aurita*. Predation rate in relation to abundance, size and type of prey organism. - *J. Plankton Res.* 12, 215 - 229.
- Bodungen, B. von, 1975.** Der Jahresgang der Nährsalze und der Primärproduktion des Planktons in der Kieler Bucht unter Berücksichtigung der Hydrographie. - Ph. D. Dissertation, Kiel Univ., 116 pp.
- Delap, M. J., 1907.** Notes on the rearing, in an aquarium, of *Aurelia aurita* L., and *Pelagia perla* (Slabber). - *Fish. Ireland Sci. Investig.* 1905, 160 - 164.
- Hamner, W. M., Jenssen, R. M., 1974.** Growth, degrowth, and irreversible cell differentiation in *Aurelia aurita*. - *Am. Zool.* 14, 833 - 849.
- Heeger, T., Möller, H. 1987.** Ultrastructural observations on prey capture and digestion in the scyphomedusa *Aurelia aurita*. - *Mar. Biol.* 96, 391 - 400.
- Hillebrandt, M., 1972.** Untersuchungen über die qualitative und quantitative Zusammensetzung des Zooplanktons in der Kieler Bucht während der Jahre 1966 - 1968. - Ph. D. Dissertation, Kiel Univ. 138 pp.
- Kerstan, M., 1977.** Untersuchungen zur Nahrungsökologie von *Aurelia aurita* Lam. - Thesis, Kiel Univ., 95 pp.
- Larson, R. J., 1992.** Riding Langmuir circulations and swimming in circles: a novel form of clustering by the scyphomedusa *Linuche unguiculata*. - *Mar. Biol.* 112, 229 - 235.
- Lebour, M. V., 1922.** The food of plankton organisms I. - *J. mar. biol. Ass. U. K.* 12, 644 - 677.
- Lebour, M. V., 1923.** The food of plankton organisms II. - *J. mar. biol. Ass. U. K.* 13, 70 - 92.
- Martens, P., 1975.** Über die Qualität und Quantität der Sekundär- und Tertiärproduzenten in einem marinen Flachwasserökosystem der westlichen Ostsee. - Ph. D. Dissertation, Kiel Univ., 111 pp.
- Martens, P., 1976.** Die planktischen Sekundär- und Tertiärproduzenten im Flachwasserökosystem der westlichen Ostsee. - *Kieler Meeresforsch. Sonderh.* 3, 60 - 71.
- Möller, H., 1979.** Significance of coelenterates in relation to other plankton organisms. - *Meeresforsch.* 27, 1 - 18.
- Möller, H., 1980.** Population dynamics of *Aurelia aurita* medusae in Kiel Bight, Germany (FRG). - *Mar. Biol.* 60, 123 - 128.

Möller, H., 1984 a. Daten zur Biologie der Quallen und Jungfische in der Kieler Bucht. - Verlag Heino Möller, Kiel, 182 pp.

Möller, H., 1984 b. Reduction of larval hering population by jellyfish predation. - Science N. Y. 224, 621 - 622.

Orton, J. H., 1922. The mode of feeding in the jelly-fish *Aurelia aurita*, on smaller organisms in the plankton. - Nature (Lond.) 110, 178 - 179.

Paffenhöfer, G. A., 1967. Caloric content of larvae of the brine shrimp *Artemia salina*. - Helgoländer wiss. Meeresunters. 16, 130 - 135.

Schneider, G., 1988. Chemische Zusammensetzung und Biomasseparameter der Ohrenqualle *Aurelia aurita*. - Helgoländer Meeresunters. 42, 319 - 327.

Schneider, G., 1989 a. The common jellyfish *Aurelia aurita*: Standing stock, excretion and nutrient regeneration in the Kiel Bight, Western Baltic. - Mar. Biol. 100, 507 - 514.

Schneider, G., 1989 b. Estimation of food demands of *Aurelia aurita* populations in the Kiel Bight / Western Baltic. - *Ophelia* 31, 17 - 27.

Smetacek, V. et al. 1987. The pelagic system. in: Rumohr, J., Walger, E., Zeitzschel, B. (eds.). Seawater-Sediment interactions in coastal waters. Lecture notes on coastal and estuarine studies no. 13. Springer-Verlag, Berlin, 32 - 68.

Southward, A. J., 1955. Observations on the ciliary currents of the jelly-fish *Aurelia aurita* L. - J. mar. biol. Ass. U. K. 34, 201 - 216.

Stoecker, D. K., Michaelis, A. E., Davis, L. H., 1987. Grazing by the jellyfish, *Aurelia aurita*, on microzooplankton. - J. Plankton Res. 9, 901 - 915.

Thiel, H., 1962. Untersuchungen über die Strobilisation von *Aurelia aurita* Lam. an einer Population der Kieler Förde. - Kieler Meeresforsch. 13, 198 - 230.

Valiela, I., 1984. Marine ecological processes. Springer Verlag, New York, 546 pp.

Wolf, P. de, 1989. The price of patchiness. - Helgoländer Meeresunters. 43, 263 - 273.

Zahn, M., 1981. Wie alt können Scyphomedusen werden? - Zool. Beitr. 27, 491 - 495.

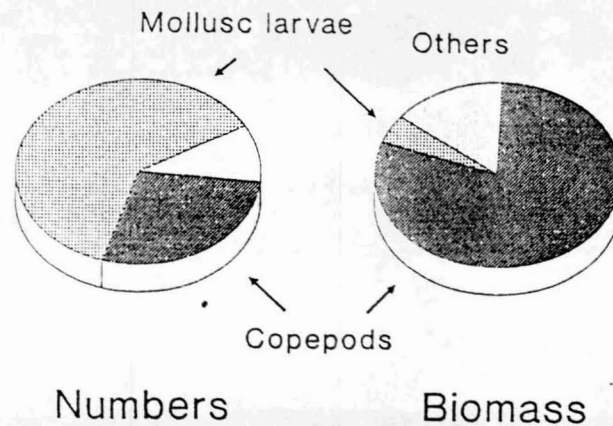


Fig. 7: Main composition of food found in gastral cavities of *Aurelia*. Left: Numbers of food items; Right: Estimated contribution of the different food to total biomass of prey (after Kerstan 1977).

Using the data of Kerstan (1977) on numbers of food items in the stomach it may be possible to calculate feeding rates according to

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

with F = feeding rate / ind. / d, N = number of food items in stomach, D = digestion time (h). Assuming a digestion time of 2 h, between 4 000 and 7 700 prey items will be consumed by *Aurelia* individuals 16 - 26 cm in diameter per day. In autumn feeding decreases to a minimum of 500 prey / ind. / d in October. Assuming an average carbon weight of 3 $\mu\text{g C}$ per food item these values correspond to rates between 1.5 and 23 $\text{mg C} / \text{ind.} / \text{d}$ (upper part of Fig. 8). Since the assumed digestion time of 2 h appears to be rather fast, rates are probably overestimated. Digestion of copepods takes about 4 h (Kerstan 1977) and Heeger and Möller (1987) found that herring larvae were digested within 8 h at 15°C. On the other hand, digestion time of smaller zooplankton is unknown but may be shorter than 4 h.

Kerstan also carried out several feeding experiments with *Artemia* nauplii offered as food. Fig 8. (lower part) shows the results of the experiments with medusae exceeding 16 cm in size (160 - 430 g wet weight). Between 1 073 and 7 700 nauplii were consumed per hour corresponding to daily rates between 25 000 and 185 000 nauplii per day. Since the caloric content of a nauplius is about 9 mcal / ind. (Paffenhöfer 1967) its carbon weight can be estimated to be about 0.6 $\mu\text{g C} / \text{ind.}$ Applying this value to the feeding rates given above, between 15 and 111 $\text{mg C} / \text{ind.} / \text{d}$ will be consumed by a large medusa with an average of $73 \pm 21 \text{ mg C} / \text{ind.} / \text{d}$ (neglecting the rather low result of experiment no. 9). These values are considerably higher than those calculated from the numbers of food items in the gastral cavities of similar sized medusae. The experiments carried out with smaller medusae (9 - 16 cm, 29 - 180 g wet weight) revealed predation rates between 15 000 and 116 000 nauplii per day corresponding to 9 - 70 $\text{mg C} / \text{ind.} / \text{d}$.

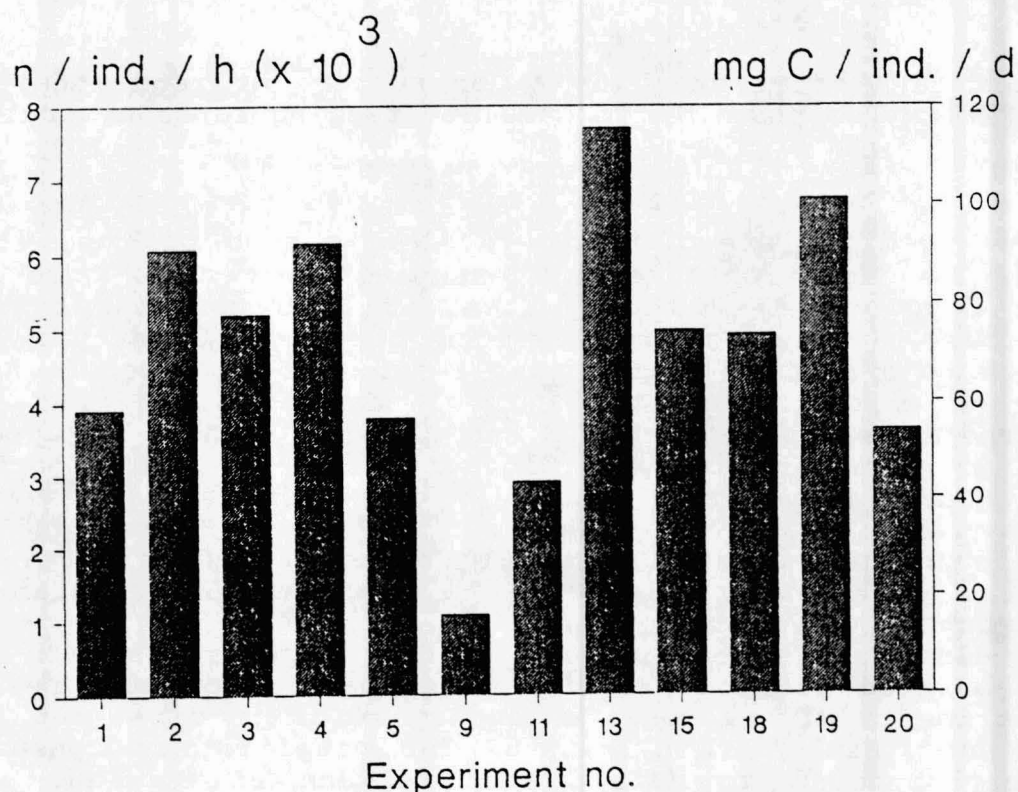
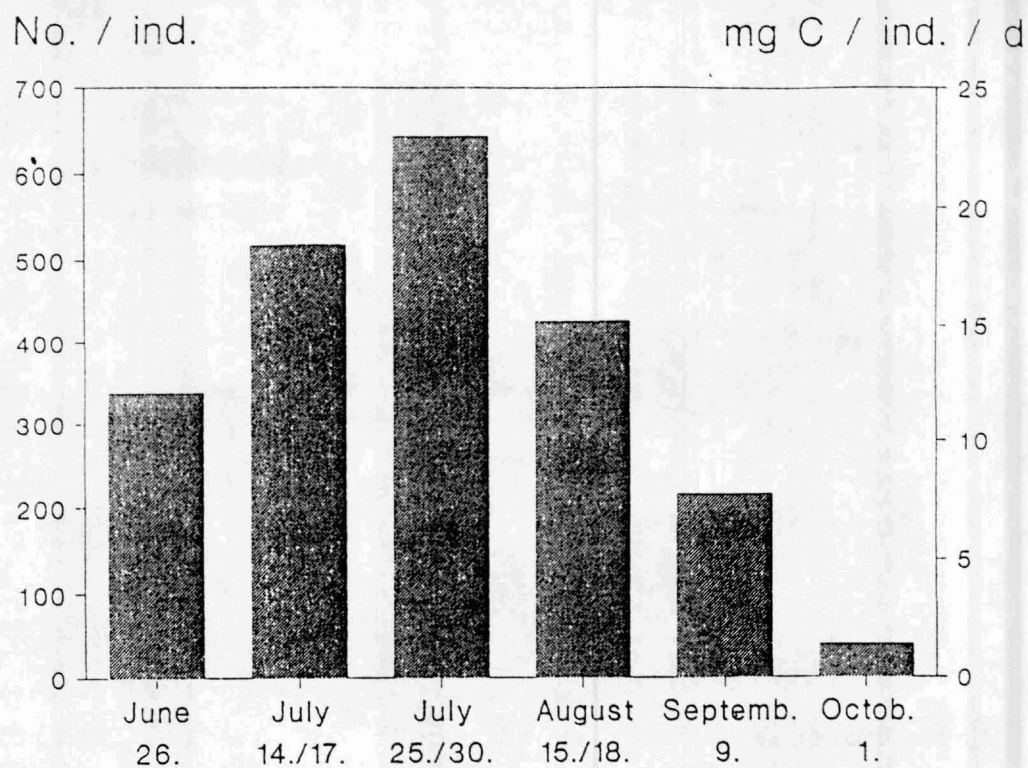
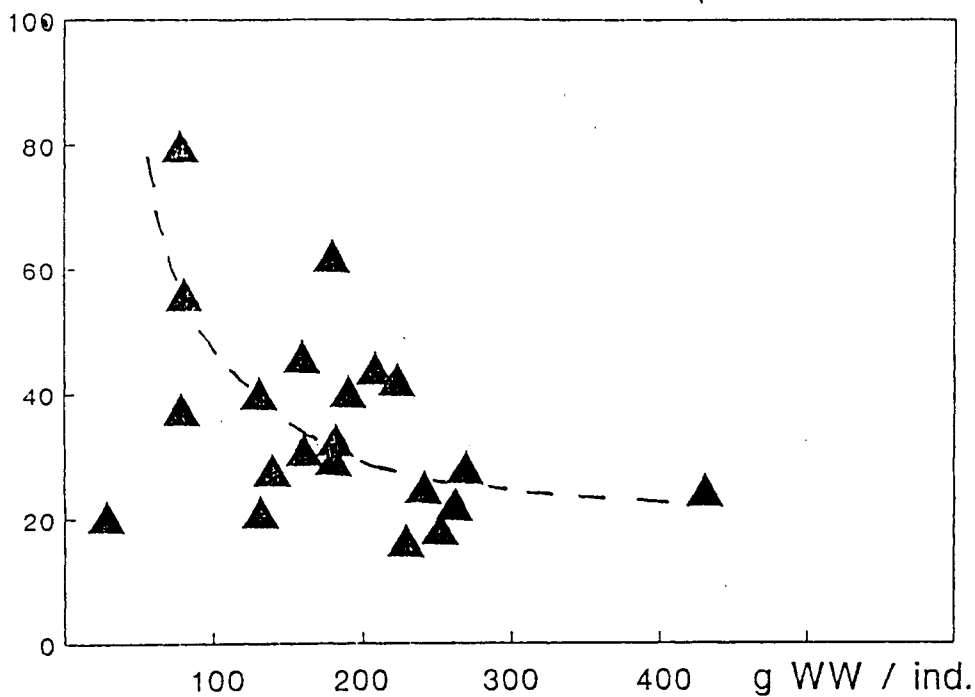


Fig. 8: Above: Number of food items found in gastral cavities of *Aurelia aurita* (No. / ind.) and calculated daily feeding rates (mg C / ind. / d). Original Data (No. / ind.) from Kerstan (1977).

Below: Feeding rates in numbers of *Artemia* nauplii / ind. / h and calculated carbon rates (mg C / ind. / d). Original data (n / ind. / h) from Kerstan (1977). Only the results of experiments with medusae exceeding 16 cm in size are shown here.

% Body - C / d



% Body - C / d

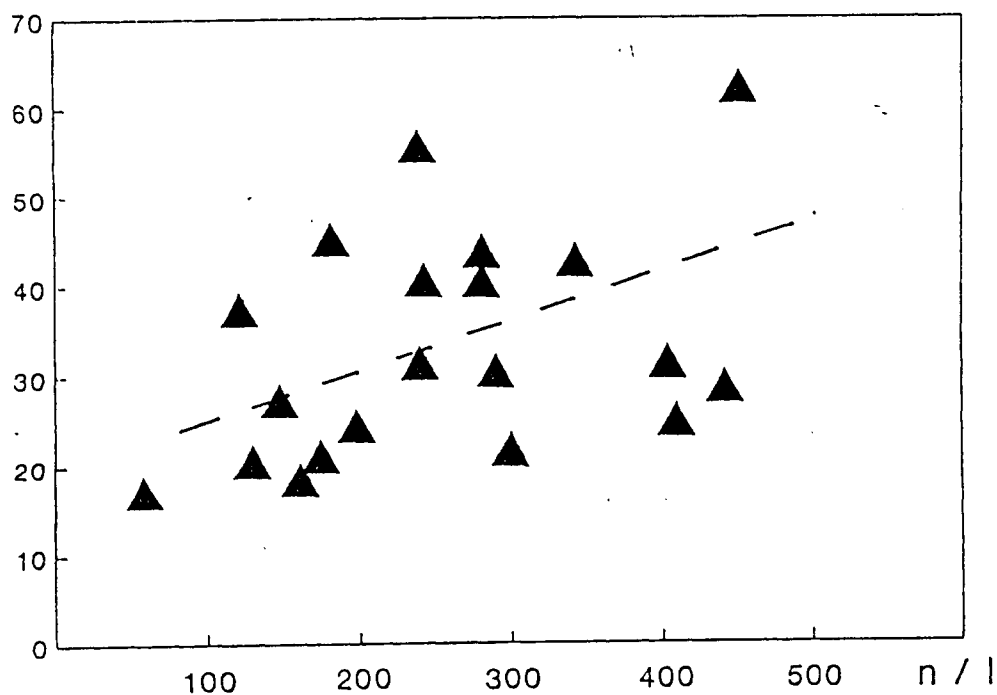


Fig. 9: Above: Calculated daily rations (in % of body-C / d) vs. medusae weight (g wet weight)
Below: Daily rations vs initial nauplii concentrations.
For these estimates all experimental values given in Kerstan (1977) were used.

Converting the original wet weight data of medusae to carbon weights, the daily rations in % of body carbon can be calculated. The results range between 18 and 80 % of body carbon per day. Arranging these data according to the wet weight of medusae examined (Fig. 9) it appears that the daily ration tend to decrease with increasing medusae weight. When arranging the daily rations according to the initial concentrations of nauplii in the experimental jar an increase of the ration with the amount of food offered seems to occur. Both findings are in general agreement with the results given in Bamstedt (1990). However, the daily rations calculated from Kerstan's original data are considerably higher than those reported by Bamstedt, who found maximum rates of 20 % based on ash-free dry weight. This discrepancy may be due to the high food concentrations in the experiments carried out by Kerstan, but may indicate the potential to heavy feeding when food is abundant.

Another approach to calculate the food demands of a medusa is to use field data and to calculate the average growth between two sampling cruises (in mg C / ind. / d), and to estimate the average respiration from the mean size of medusae according to the function in Tab. 1. Assuming the assimilation quotient to be 0.8, average food demands can be calculated as follows:

$$F(t_2 - t_1) = \left[(W_{t_2} - W_{t_1}) / (t_2 - t_1) + (R_{t_2} + R_{t_1}) / 2 \right] \times 1.25$$

- $F_{t_2 - t_1}$ = Average food demand between two samplings at t_2 and t_1 (mg C / ind. / d).
 W_{t_2}, W_{t_1} = Average weight of medusae at t_2 and t_1 (mg C / ind.).
 R_{t_2}, R_{t_1} = Respiration of a medusa at t_2 and t_1 with an assumed respiration quotient of 0.8 (mg C/ind/d).
 $t_2 - t_1$ = Number of days between two samplings.

These calculations were carried out with data from Eckernförde Bay in 1982 (small medusae, high abundance) and in 1984 (large medusae, low abundance). The results (Fig. 10) indicate that the food demands increase with growing medusae, reach a maximum value and decline somewhat after growth is completed. The maximum rates were about 20 mg C / ind. / d for highly abundant small medusae (in 1982) but was 2.5 times higher (50 mg C / ind. / d) for less abundant large medusae (in 1984).

The same calculations can be carried out with ammonia release as metabolic parameter (see Tab. 1) and nitrogen weight of medusae. To convert rates to the more common carbon units the Kiel Bight zooplankton C : N ratio of 4.5 : 1 by weight (Schneider, unpubl.) has to be taken into account. Assuming further that ammonia release makes up only 70 % of total medusae nitrogen output, the curves given in the lower part of Fig. 10 were generated. Dealing only with ammonia excretion, maximal food demands range between 35 and 85 mg C / ind. / d but increase to 45 - 120 mg C / ind. / d when other nitrogen components are also considered. However, the latter rates are highly speculative since the amount of nitrogen output other than ammonia is unknown for *Aurelia*. Summarizing the different results it may be concluded that predation rates between 50 and 80 mg C / ind. / d may be appropriate assumptions, at least when large medusae occur in small densities. The low rates and the low final weights observed in medusae in densely populated