Biomass and size structure of the scyphomedusa *Aurelia aurita* in the northwestern Black Sea during spring and summer

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**Abstract.** The abundance, biomass and size structure of the scyphomedusa, *Aurelia aurita*, was measured during two research cruises to the northwestern Black Sea (July–August 1995 and April–May 1997). Average biomass of *Aurelia* was relatively constant (132–179 g wwt m\(^{-2}\)) throughout the investigation period and similar to previous years. Abundance and biomass at individual stations appeared to be unrelated to temperature and salinity when the latter exceeded ~13. Biomass was low at coastal stations in the plume of the Danube where depth was <20 m and salinity dropped to <11. The spring cruise (April–May) coincided with, or just followed the peak of strobilation. The summer cruise (July–August) took place near the beginning of planulae larvae release. The population size structure was dominated by small individuals in spring, while large medusae prevailed mainly in late summer. *Aurelia* was, on average, larger at deep water stations during summer, suggesting that *per capita* food supply was higher further offshore. The individual body mass increased from spring through summer. Accordingly, the volume (wet wt) to length (bell diameter) relation changed significantly. If all medusae measured throughout the seasons were pooled, volume (V, in cm\(^3\)) was related to length (L, in cm) according to V = 0.08 L\(^{2.71}\), which is similar to measurements conducted in other coastal areas. In contrast to the common conjecture, we did not find inverse relations between biomasses of *Aurelia* and the combjelly *Mnemiopsis leidyi*. Preliminary feeding experiments indicate that *Aurelia* may feed upon small *Mnemiopsis*. The significance of indirect trophic relations and direct feeding interactions among the gelatinous zooplankton in the Black Sea has important consequences for the energy flow along the food web and, therefore, needs further study.

**Introduction**

The scyphomedusa *Aurelia aurita* L. (moon jellyfish) is a common zooplankton species in temperate coastal waters [e.g. (Möller, 1980; Bämstedt, 1990; Hamner *et al*., 1994; Omori *et al*., 1995)]. In the enclosed, brackish Black Sea its numbers and biomass underwent changes by several orders of magnitude in recent decades. From low levels reported for the 1940s and 1950s, the total biomass of *Aurelia* in the Black Sea increased during the period of its eutrophication and reached 1 million tons wet weight (wwt) in the early 1960s. Further accelerated anthropogenic stress, i.e. increasing nutrient load and pollution, boosted phytoplankton and zooplankton standing stocks. Planktivorous fish declined, and the population size of *Aurelia* exploded in the late 1970s, peaking at a total wwt of 300–500 million tons in 1980 (Gomoiu, 1980; Bronfman *et al*., 1991; Zaitsev, 1993); [(Mutlu *et al*., 1994) and references therein]. The peak biomass is equivalent to about 1.5 kg wwt of *Aurelia* m\(^{-2}\) (Shushkina and Vinogradov, 1991; Mutlu *et al*., 1994; Kovalev and Piontkovski, 1998). This corresponds to 1.5–4.5 g C m\(^{-2}\), depending on the carbon conversion factor used [e.g. (Schneider, 1988; Vinogradov *et al*., 1989)].
After the population bloom of the invading comb jelly, *Mnemiopsis leidyi*, in 1988/89 (Vinogradov *et al*., 1989; Shiganova, 1997), biomass of *Aurelia* was reduced to levels similar to those recorded in the 1960s. A slight increase was noted at the beginning of the 1990s when the biomass of *Mnemiopsis* declined from its peak value (Mutlu *et al*., 1994; Shiganova, 1997). Although these and other authors (Vinogradov *et al*., 1989; Shuskhina and Vinogradov, 1991; Kovalev and Piontkovski, 1998) inferred from the antagonistic interannual developments of *Mnemiopsis* and *Aurelia* that the ctenophore is the superior competitor for the same mesozooplankton food, experimental evidence supporting this conjecture is still lacking.

The significance of gelatinous zooplankton in the current food web of the northwestern Black Sea has been studied by various western and eastern laboratories within the joint European River Ocean Systems (EROS) study. An overall goal of the joint study was to assess whether the pelagic system has reached a new stable state in the mid-1990s, where both *Mnemiopsis* and *Aurelia* coexist at relatively high biomasses [see also (Shuskhina and Vinogradov, 1991)]. Details of the size structure and population dynamics of *M. leidyi*, which still dominates the zooplankton, have been reported elsewhere (Shiganova, 1997; Weisse *et al*., 2000). The goal of this study was to assess biomass and age structure of *Aurelia* in the northwestern Black Sea in space and time, and to analyse the potential reasons for the observed patterns. In particular, we compared the population structure of *Aurelia* measured at low *Mnemiopsis* biomass in spring with high *Mnemiopsis* biomass in the summer to detect any adverse effects of the comb jelly on *Aurelia*. We have sized a large number of *Aurelia* individuals during both seasons, and give volume to length power equations which varied significantly between the two periods studied. Finally, we report results of a feeding experiment indicating that *Aurelia* may feed upon small *Mnemiopsis* and discuss the implications arising from internal feeding loops among the gelatinous zooplankton in the Black Sea.

**Method**

*Aurelia aurita* was sampled in the northwestern Black Sea during two research cruises aboard the RV ‘Professor Vodyanitsky’, from 18 July to 28 August 1995 and from 9 April to 25 May 1997. The research cruises were each split into two legs. During summer 1995, the majority of sampling stations were located on the continental shelf (Figure 1); four stations (I-2, I-3, II-2 and II-27) served as deep-water reference stations. Roman numbers refer to the four cruise legs. Four stations (I-24, II-3, II-26 and II-28) were situated at the continental slope. The northernmost area close to the mouth of the River Dniepr was sampled only in August. The first leg of the spring cruise focused on coastal and shelf stations in the vicinity of the mouth of the Danube. The second leg of the spring cruise covered a similar station grid as the second leg of the summer cruise (Weisse *et al*., 2000). Station co-ordinates and sampling parameters were given in the original cruise reports (Lancelot and Egorov, 1995, 1997).

Prior to the zooplankton net hauls, water temperature and *in situ* fluorescence...
Biomass of *Aurelia aurita* in the Black Sea

Fig. 1. The investigation area in the northwestern Black Sea. Station numbers refer to the first leg of the summer cruise (July 1995).
were recorded by a CTD rosette equipped with calibrated sensors. Salinity was measured using the Practical Salinity Scale and is thus reported without dimensions or units. *Aurelia* was collected by vertical net hauls from bottom to surface or from 100 m to surface at deep water stations, respectively. This depth was chosen because the occurrence of *Aurelia* is mainly restricted to the layer above and around the thermocline (Vinogradov et al., 1989; Mutlu et al., 1994), and to enable comparisons with recent estimates from the same area (Mutlu et al., 1994; Shiganova, 1997). A WP-2 net (57 cm inner opening diameter, 200 μm mesh gauze; Hydrobios, Kiel) was used during the first leg, and a conical net of 1.13 m opening diameter, 300 μm mesh gauze, was used during the second leg of the summer cruise. The latter net was made by M-TG at GeoEcoMar and is referred to as MTG net. During the spring cruise, samples were obtained by a WP-2 net with 300 μm mesh gauze. Results reported are conservative estimates of *Aurelia* abundance and biomass because we assumed 100% filtering efficiency of the nets.

*Aurelia* were processed aboard ship immediately after sampling. Each animal larger than 1 cm was measured individually for total length in a Petri dish. A ruler or a fine grid attached to the bottom of the Petri dish allowed for a relatively precise length measurement to the nearest mm. Organism displacement volume was measured in a graduated cylinder of either 10 or 100 ml volume. Larvae <1 cm were counted without sizing, and their volumes were estimated from volume to length equations given below. During the second leg of the summer cruise, the animals were counted in size classes of 1 cm width, and the volume was measured individually as described above. Measured displacement volume was converted to wwt assuming a specific weight of 1.0 g cm⁻³ for *Aurelia*, and carbon biomass was then calculated by multiplying wwt by 0.001, i.e. 1 mg C = 1 g wwt (Schneider, 1988).

We conducted one experiment aboard ship to investigate if medium-sized *Aurelia* (3–5 cm bell diameter) feed upon small *M. leidyi* (1 cm). The latter were caught by the WP-2 net at station I-11 at 08.30 h on 26 July 1995 and poured into a 10 l bucket containing both the gelatinous zooplankton and the mesozooplankton from the net haul. Two hours after sampling and 2 h prior to the beginning of the experiment, ~20 *Aurelia* were transferred to a glass container filled with 0.45 μm filtered sea water of 15.6 salinity from the sampling location. To start the experiment, between five and 15 *Mnemiopsis* were transferred to 1 l glass beakers and three *Aurelia* were added to each container. A control without *Aurelia* received 10 *Mnemiopsis*. The number of *Mnemiopsis* was determined by visual inspection in each container at 2, 4, 6, 8, 10 and 20 h after the beginning of the experiment. To facilitate counting, the experimental containers were briefly illuminated from the side and gently stirred. At the end of the experiment, the water of each container was poured through a 100 μm sieve to ensure that no *Mnemiopsis* were missed during counting. The experiment was run in the dark at a temperature of 19.1 ± 0.9°C.

**Statistical analysis**

Volume (V) to length (L, = bell diameter) relationships were fitted to a power function of the form $Y = aX^b$. To test for significant differences ($P < 0.05$)
between V to L relations measured during the different seasons, raw data were log-transformed. The slopes and Y-intercepts of the resulting linear regressions were then analysed by an analysis of covariance (ANCOVA) using the general linear model of SPSS® for Windows, Version 7.5.2G. Datasets were homoscedastic (Levene’s test) and did not deviate significantly from the normal distribution (Kolmogorov–Smirnov test).

**Results**

**Environmental parameters**

The spring cruise started at the end of the winter period when surface water temperature was low (<7°C) and the upper part of the water column (<20 m) well mixed or only weakly stratified. With the onset of the seasonal thermocline, near-surface temperatures increased rapidly to >16°C in mid-May 1997. Water temperature varied less during the summer cruise, ranging from 19.6 to 25.3°C and generally exceeding 22°C at 5 m depth. Salinity showed some seasonal variation and was mainly affected by river run-off. Lowest salinity (10.1) was recorded in the plume of the Danube during the first leg of the summer cruise. At offshore stations where water depths exceeded 50 m, salinity generally ranged from 16–18.5 close to the surface. The Danube water was spread in a south-west direction during July. The impact of the Danube was less obvious 1 month later when the salinity distribution mainly reflected the general cyclonic circulation in the northwestern Black Sea. The pycnocline was at ~20 m depth and mainly driven by thermal stratification during summer 1995.

Phytoplankton, mesozooplankton, bacterial and protozoan biomass have been determined by our colleagues in parallel with the present study. While these studies have been, or will be reported in detail elsewhere (Bouvier et al., 1998; Becquevort et al., 2000; Alexandrov, submitted; Bouvier et al., submitted), the main results can be briefly summarized. Both phytoplankton and mesozooplankton biomass were higher in spring 1997 than in summer 1995. Bacterial and protozoan biomass showed the opposite trend. An inshore–offshore gradient was apparent in most biological biomass and production parameters, with peak values generally reached in the vicinity of the Danube.

**Catchability of the plankton nets used**

A comparison of the ‘catchability’ of the MTG net and the WP-2 (300 µm mesh gauze) net was made at eight stations during the second leg of the spring cruise. At five of these stations where the abundance of *Aurelia* exceeded 10 ind m⁻², neither numbers nor the average length of the *Aurelia* caught by the two nets were significantly different (student’s t-test; *P* < 0.05; Table I). We assumed that the smaller meshed WP-2 net used during the first leg of the summer cruise yielded similar results and did not correct for different net catchability.
Seasonal and spatial variation of the size distribution

The following analysis of the size distribution of *A. aurita* in the northwestern Black Sea does not consider ephyrae and planulae larvae (<1 cm) which could not be measured precisely. Length distribution (bell diameter) of the individuals >1 cm differed during the cruises. It was dominated by small juveniles in early spring and by larger individuals in the summer (Figure 2). The average bell diameter increased from 1.97 cm recorded in April to 2.58 cm measured in May, 1997, and was twice as large in July (4.04 cm) and August (5.43 cm), 1995.

![Size-frequency distribution of *Aurelia aurita* in the northwestern Black Sea during spring and summer.](https://academic.oup.com/plankt/article-abstract/22/2/223/1386252)

**Fig. 2.** Size-frequency distribution of *Aurelia aurita* in the northwestern Black Sea during spring and summer.
During late summer, when a large number of individuals \((n = 736)\) was measured, we also considered spatial differences. There was an obvious difference in the size structure of *Aurelia* at offshore and inshore stations (Figure 3). Individuals >6 cm prevailed at deep water stations, while the size distribution was shifted towards smaller sized animals at the inner shelf and coastal stations. The outer shelf stations do not seem to follow this trend, since the percentage of small juveniles in the 1–2 cm and 2–3 cm size classes was highest at the 50–100 m deep stations. This distribution was, however, strongly impacted by the neighbouring stations II-1 and II-12 where 38.7 and 45.7% respectively, of all *Aurelia* were smaller than 3 cm. At the other five outer shelf stations (II-4, II-5, II-14, II-25, II-33) the size distribution was more similar to the deep water stations, with the maximum percentage (25.7%) found in the 6–7 cm size category.

During spring 1997 we caught only a few *Aurelia* at deep water stations and no individuals at coastal stations. At the outer and inner shelf stations, the size distribution was almost identical with a mean bell diameter of 2.12 cm at the outer and 2.15 cm at the inner shelf stations.

The spring cruise apparently took place during or shortly after the peak of strobilation had occurred. This is because ephyrae larvae <1 cm (not shown in Figures 2 and 3) dominated numerically in spring, contributing 41.8 and 22.6% to the total *Aurelia* abundance during the first and second cruise leg, respectively. Their contribution to the population biomass of *Aurelia* was, however, very small, peaking in April with an average share of 1.7% of the total biomass. During the first leg of the summer cruise, some ephyrae and some more planulae larvae together accounted for 10.2% of the total number of *Aurelia*, but this may be an overestimate as it was, in some cases, difficult to discriminate between the small *Aurelia* larvae and other gelatinous zooplankton larvae when the latter were highly abundant. The contribution of larvae to total biomass was negligible during summer. The largest *Aurelia* (>10 cm) peaked in early spring when they reached one third (33.8%) of the total biomass of *Aurelia*.

<table>
<thead>
<tr>
<th>Station</th>
<th>Depth (m)</th>
<th>Abundance (n m⁻²) MTG</th>
<th>Abundance (n m⁻²) WP-2</th>
<th>Average length (mm) MTG</th>
<th>Average length (mm) WP-2</th>
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<tr>
<td>2</td>
<td>0–20</td>
<td>24.3</td>
<td>49.9</td>
<td>36.1</td>
<td>38.8</td>
</tr>
<tr>
<td>9</td>
<td>0–40/0–65*</td>
<td>154</td>
<td>162.7</td>
<td>29.4</td>
<td>28.0</td>
</tr>
<tr>
<td>10</td>
<td>0–20</td>
<td>97.5</td>
<td>105.7</td>
<td>18.8</td>
<td>22.8</td>
</tr>
<tr>
<td>12</td>
<td>0–20/0–24*</td>
<td>33</td>
<td>31.8</td>
<td>45.1</td>
<td>30.8</td>
</tr>
<tr>
<td>17</td>
<td>0–20/0–14*</td>
<td>61</td>
<td>134.4</td>
<td>10.0</td>
<td>12.2</td>
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<td>96.90</td>
<td>27.88</td>
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<tr>
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<td></td>
<td>53.1</td>
<td>55.36</td>
<td>13.9</td>
<td>9.88</td>
</tr>
</tbody>
</table>

*WP-2 net. SD denotes one standard deviation.*

**Table I.** Comparison of catchability between the MTG (1.13 m opening diameter) and the WP-2 net (0.57 m opening diameter). Abundance and average length (bell diameter) of *Aurelia aurita* are given.
Biomass of Aurelia

Total average biomass of *A. aurita* in the northwestern Black Sea showed little variation between the sampling periods. It increased from 132 g wwt m$^{-2}$ recorded in July 1995 to 179 g wwt m$^{-2}$ measured 1 month later. The average *Aurelia* biomass was 133 g wwt m$^{-2}$ in April and 155 g wwt m$^{-2}$ in May 1997. Large spatial
and/or temporal differences produced large standard deviations; thus, seasonal differences between mean values were not significant (ANOVA, \( \alpha > 0.05 \)). The maximum *Aurelia* biomass recorded during this investigation was 750 g wwt m\(^{-2}\) at the outer shelf station III-16 during April 1997. A similarly high biomass (710 g wwt m\(^{-2}\)) was measured 1 month later at the deep water station IV-20. During spring, the biomass of *Aurelia* was generally higher offshore where water depth was >40 m. In summer 1995, total biomass of *Aurelia* peaked (300 g wwt m\(^{-2}\)) at the inner shelf stations I-21 and I-23 (Figure 1) off the Bulgarian coast. Relatively high biomasses (33–215 g wwt m\(^{-2}\)) were also measured at two shallow (<25 m) stations (II-6, II-7) in the northernmost part of the investigation area in the vicinity of the mouths of the rivers Dniepr and Dniestr. Salinity at these stations was >16. Low biomasses (<15 g wwt m\(^{-2}\)), in contrast, were recorded at shallow stations I-9 and I-11 in the plume of the Danube (Figure 1) where salinity was <11. We found no *Aurelia* at one of the two deep water stations (I-3, Figure 1).

Overall, small-scale differences between neighbouring stations were of similar magnitude to larger regional differences. When station III-13 off the mouth of the Danube was revisited 6 days later, the biomass of *Aurelia* had dropped from 743 to 10 g wwt m\(^{-2}\), although temperature and salinity had changed only little. Differences between subsequent hauls conducted at the same stations were much lower (Table I and own unpublished data). These pronounced differences point to a patchy distribution of *Aurelia* in the investigation area that may have blurred regional differences.

Except for low values at very low salinity (<11), we did not observe any relationship between the biomass of *Aurelia* and environmental parameters in the northwestern Black Sea. Both the abundance and biomass of *Aurelia* appeared uncorrelated to near-surface (5 m) water temperature and salinity. We could not, however, perform a rigorous statistical analysis on the distribution of *Aurelia* as abiotic parameters (temperature, salinity, nutrients) were all highly variable in the upper part of the water column where *Aurelia* occurred. Since we sampled the entire water column or, at deep water stations, from surface down to a depth well below the thermocline, the precise layer over which *Aurelia* was distributed and the respective environmental parameters remained unknown. Nonetheless, it is obvious that neither temperature, which was over 10°C higher in summer than in spring, nor salinity, which ranged from 14 to 20 in the upper 100 m at the shelf and deep water stations during both seasons, offer obvious explanations for the observed distribution of *Aurelia* in the northwestern Black Sea. Similarly, there was no marked effect of mesozooplankton biomass on the standing stock of *Aurelia* (data and analysis not shown). The average mesozooplankton biomass in the euphotic zone of the investigation area was 20 mg C m\(^{-3}\) in spring and 7 mg C m\(^{-3}\) in summer (B.G. Alexandrov, submitted).

**Volume to length (bell diameter) relationship**

The relationship between volume (V, in ml) and length (L, in cm, bell diameter) of *A. aurita* could be fitted to a power function of the form \( Y = a X^b \) (Figure 4). Note that although the curve fit was generally good, individual data points may
deviate from the curve by a factor of up to 2. The parameters of the equations obtained during spring and summer (July) were significantly different (ANCOVA of log-transformed data, $F = 258.03, P < 0.0001$). We did not include the dataset from the second leg of the summer cruise in this analysis because in August 1995, *Aurelia* was measured in size classes only. It is, however, obvious

![Graphs showing relation between displacement volume and bell diameter for different seasons.](image)

**Fig. 4.** The relation between displacement volume and bell diameter of *Aurelia aurita* during the different seasons. The data were fitted to the power functions given in each panel. Note that in August 1997 (bottom panel) the equation curve was fitted to the mean values of 11, 1 cm wide size classes. A total of 737 medusae was measured in these size classes.
from Figure 4 that the exponent b decreased while the coefficient a increased from spring through late summer. To illustrate the combined effect, we have calculated the average volume for three different size classes (2, 5 and 8 cm) of *Aurelia* medusae using the power functions given in Figure 4. Irrespective of the size, the average body mass (volume) was lowest in spring and highest in late summer. The relative increase was most pronounced (×8.9) in the smallest individuals. The body mass of an average 5 cm large medusa was twice as high in July 1995 (9.3 ml) compared with the spring 1997 (4.9 ml), and further increased until August 1997 (15.2 ml). The average volume of animals of 8 cm bell diameter was 1.9 times higher in late summer (35.2 ml) than during spring (19.4 ml).

When we pooled our measurements from spring and summer, the volume to length relationship became similar to values obtained in the Baltic Sea (Kerstan, 1977; Schneider, 1989) and in the North Atlantic (Stoecker *et al.*, 1987; Båmstedt *et al.*, 1994) (Table II).

The relation to Mnemiopsis

The total biomass (volume) of *Aurelia* and *Mnemiopsis* appeared unrelated at the sampling stations (Figure 5). This also holds true if the data were averaged over the respective season (data not shown).

We investigated the potential feeding impact of *Aurelia* on small (1 cm) *Mnemiopsis* with material taken from the inshore station I-5 where both species were abundant. The ctenophores decreased in each container where *Aurelia* was present (Figure 6, main panel). Assuming that this decline was caused by feeding of the jellyfish, we calculated a *per capita* ingestion rate of *Aurelia* which was

![Fig. 5. Population biomass of *Aurelia aurita* versus *Mnemiopsis leidyi* in the northwestern Black Sea.](https://academic.oup.com/plankt/article-abstract/22/2/223/1386252)
linearly related to the average *Mnemiopsis* concentration during the experiment (Figure 6, insert). The number of *Mnemiopsis* did not change in the control without *Aurelia* during the first 10 h of the experiment. The fact that 2 h and 4 h after the beginning of the experiment only nine small *Mnemiopsis* were found in the control indicates that some larvae may have escaped counting. At the end of the experiment, one larva had apparently disintegrated in the control. Without correcting for the potential counting error, each *Aurelia* would have ingested between 1.1 larvae day$^{-1}$ at the lowest and 2.7 larvae day$^{-1}$ at the highest *Mnemiopsis* concentration. Unfortunately, we could not repeat this experiment because the abundance of *Aurelia* at the other sampling stations was too low to obtain enough individuals of comparable size during the first leg of the summer cruise. During the second leg, the experimental facilities were unavailable aboard ship, and *Mnemiopsis* larvae did not occur during the spring cruise and at the beginning of the summer cruise.

**Discussion**

The abundance of *A. aurita* in the northwestern Black Sea measured during this study is similar to that found in other coastal areas [summarized by (Ishii and Båmstedt, 1998)] and comparable to recent estimates from the Black Sea. Mutlu *et al.* (Mutlu *et al.*, 1994) reported for June 1991, July 1992 and August 1993 a mean wwt of *Aurelia* ranging from 146 to 280 g m$^{-2}$ at inshore and 41 to 260 g m$^{-2}$.
at offshore stations in the western Black Sea. Kovalev and Piontkovski calculated *Aurelia* biomasses ranging from 69 to 1449 g m\(^{-2}\) for the central part of the Black Sea during 1990 to 1995 (Kovalev and Piontkovski, 1998). Our mean values of 132–179 g wwt m\(^{-2}\) fall into this range. Shiganova estimated somewhat higher values for the whole Black Sea for the period 1993 to 1996 (Shiganova, 1997). Considering that different nets were used, different areas have been sampled, and the distribution of gelatinous zooplankton is highly patchy, it seems impossible to draw any firm conclusions about recent changes in the biomass of *Aurelia* in the northwestern Black Sea. It is, however, safe to conclude that the current biomass of *Aurelia* is higher than during its minimum at the *Mnemiopsis* outburst, and several times lower than during the 1980s.

*Aurelia* \(>1\) cm in size (bell diameter) reached 7.3 ind. m\(^{-3}\) recorded in near surface waters (0–14 m) at station IV-17 during the second leg of the spring cruise. With ephyrae larvae included, the maximum abundance was 13.9 ind. m\(^{-3}\). In a compilation of literature data, Ishii and Båmstedt recently showed that similar, and even higher abundances (up to 300 ind. m\(^{-3}\)) have been recorded from enclosed or semi-enclosed coastal areas of northern Europe (Ishii and Båmstedt, 1998). In the brackish Baltic Sea, where salinity is comparable to the northwestern Black Sea, peak abundance of *Aurelia* is an order of magnitude lower than it currently is in the Black Sea. Average and maximum summer biomasses are, however, comparable or even higher in the western Baltic than in the northwestern Black Sea. Schneider and Behrends reported a mean biomass of 2–44 mg C m\(^{-3}\) from 9 years of observation in the semi-enclosed Eckernförde Bay (Schneider and Behrends, 1994). The average carbon biomass of *Aurelia* calculated in the present study ranged from \(~3\) to 6 mg C m\(^{-3}\). This is a conservative estimate because we assumed a low wwt to carbon conversion factor of 0.001. Shushkina and Vinogradov (Shushkina and Vinogradov, 1991) and some later authors using the same data (Mutlu et al., 1994; Van Eeckhout and Lancelot, 1997) assumed that 1 g wwt is equivalent to 3 mg C for Black Sea *Aurelia*.

This seeming discrepancy between abundance and biomass in the two areas results from the different sizes of *Aurelia* in the western Baltic and the Black Sea. In the former, a maximum bell diameter of 42 cm has been found (Ishii and Båmstedt, 1998). During our investigation, the largest individual measured only 17 cm in bell diameter. Although low compared with the Baltic, this bell diameter is still higher than in the other coastal areas where the maximum abundance exceeded 5 ind. m\(^{-3}\) (Ishii and Båmstedt, 1998).

From their observation that adult medusae were much smaller in years when *Aurelia* was highly abundant and food, therefore, scarce, Schneider and Behrends suggested that food availability regulates adult size (Schneider and Behrends, 1994). Ishii and Båmstedt elaborated on the inverse relationship between abundance and size of *Aurelia* (Ishii and Båmstedt, 1998). According to their literature review, the bell diameter in open waters ranges from 20 to 30 cm, whereas the more abundant medusae from semi-enclosed/enclosed areas typically reach peak diameters of 4 to 10 cm. Ishii and Båmstedt also supported experimental evidence that food regulates growth and, thus, the average size of adult *Aurelia*. Medusae measured in the present investigation were, on average, larger further
offshore during summer. We conclude that the per capita food supply of *Aurelia* was higher offshore than on the continental shelf.

We have sampled in two different years and it seems likely that interannual variation contributed to the observed differences between spring and summer. Furthermore, the distribution of *Aurelia* was highly patchy during our investigation. In spite of these caveats, the seasonal variation of the average individual body mass is noteworthy. We covered the period of maximum growth of *Aurelia* after strobilation in early spring and the beginning mass release of planulae larvae in late summer. The higher volume at a given size measured in summer suggests that medusae were better fed later in the season, which is in accordance with the reduced mesozooplankton standing stock during summer. Inshore–offshore differences had little effect on this seasonal variation since individuals sampled at shelf stations dominated at all times. The varying nutritional conditions impacted the allometric relationship between volume and bell diameter (Figure 4). The seasonal variation of the volume to length power function is important if biomass is not measured directly as displacement volume (this study) but calculated indirectly from size measurements [e.g. (Kovalev and Piontkovski, 1998)]. If we had applied our ‘spring equation’ to the late summer situation, we would have grossly underestimated the true population biomass of *Aurelia*. Kovalev and Piontkovski assumed one constant allometric equation for all gelatinous zooplankton, $\text{wwt} = 0.0028 L^{2.19}$, to calculate the biomass of *Aurelia* in the Black Sea over 15 years (Kovalev and Piontkovski, 1998). From our study and the findings by others reported in Table II, it seems obvious that such an approach is problematic.

To our knowledge, seasonal variation in the volume to length relationship of *Aurelia* has not been found in previous studies. Some regional and/or temporal shifts in the parameters of the power function have been reported by Båmstedt et al. from the coastal north-east Atlantic (Båmstedt et al., 1994). It is remarkable that in spite of its pronounced seasonal variation, the average (April–August) volume to length relation we calculated for the Black Sea *Aurelia* is in close agreement with results obtained in other coastal areas (Table II).

Direct feeding relationships among gelatinous zooplankton are known from several species [e.g. (Greve, 1970; Matsakis and Conover, 1991)]. In Scandinavian waters, another common scyphomedusan species, *Cyanea capillata*, has been shown to feed upon *A. aurita* (Båmstedt et al., 1994, 1997; Hansson, 1997). Direct predation on *Aurelia* by other gelatinous zooplankton has not yet been demonstrated in the Black Sea. However, several studies (Vinogradov et al., 1989; Mutlu et al., 1994; Shiganova, 1997; Kovalev and Piontkovski, 1998) have reported long-term antagonistic development between the moon jelly *A. aurita* and the comb-jelly *M. leidyi*. Most of these authors and their co-workers assume that the inverse effect of *Mnemiopsis* on *Aurelia* is indirect because the former species is the superior competitor for the same mesozooplankton food. In contrast to this conjecture, we did not find any indication for an inverse relation between the biomass of the dominating two gelatinous zooplankters (Figure 5). High *Aurelia* biomass of 300 g wwt m$^{-2}$ occurred over a wide range of *Mnemiopsis* biomass. Moreover, the individual body mass of *Aurelia* was higher in summer than during
spring in spite of an approximately threefold higher average biomass of adult (>1 cm) *Mnemiopsis* during summer (Weisse et al., 2000). Clearly, competition between *Aurelia* and *Mnemiopsis* for the same zooplankton food awaits experimental investigation.

Similarly, direct feeding between these two species needs to be studied in more detail. Our feeding experiment with medium-sized *Aurelia* and small *Mnemiopsis* provides preliminary evidence that mutual trophic relationships exist among the gelatinous zooplankton in the Black Sea. Our experiment needs to be verified with more and differently sized *Aurelia*. We report this first measurement of grazing to indicate the potential significance of an internal loop among the gelatinous zooplankton in the Black Sea. This conjecture is supported by laboratory experiments which demonstrated that ephyrae of the scyphomedusa *Chrysaora quinquecirrha* not only feed upon *Mnemiopsis* but prefer the ctenophore over ciliates, dinoflagellates, rotifers and copepod nauplii (Olesen et al., 1994). Another scyphomedusa, *Cyanea capillata*, did not grow on either *Artemia* nauplii or copepod-dominated mixed zooplankton, but grew well with the ctenophore *Bolinopsis infundibulum* as food (Båmstedt et al., 1997). From their experiments, Båmstedt et al. concluded that *A. aurita* may be a key prey for *C. capillata* (Båmstedt et al., 1994).

We have demonstrated that medium-sized *Aurelia* feed upon small *Mnemiopsis*. We assume that larger *Mnemiopsis* prey upon ephyrae and planulae larvae of *Aurelia* when they are abundant. If such mutual feeding relationships exist between *Aurelia* and *Mnemiopsis*, they may explain why current attempts to model the food web structure in the northwestern Black Sea (Van Eeckhout and Lancelot, 1997) fail to realistically describe the observed seasonal variation between *Aurelia* and *Mnemiopsis*.

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