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# Distribution and abundance of moon jellyfish (*Aurelia aurita*) and its zooplankton food in the Black Sea

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**Abstract** The distribution of moon jellyfish (*Aurelia aurita* Linnaeus, 1758) in the Black Sea was determined from plankton samples collected above the anoxic zone (maximum depth 200 m) in the summer, winter and spring during 1991–1995. Distribution was patchy. Average biomass ranged from 98 to 380 g $m^{-2}$, and abundance varied from 2 to 14 individuals $m^{-2}$. Biomass and abundance peaked in late spring and summer. The distribution was correlated with hydrographic features in the Black Sea, with higher concentrations occurring at the peripheries of anticyclonic eddies. Centers of the two main cyclonic gyres generally had a low biomass of *A. aurita*. From July 1992 to March 1995, the populations were largely concentrated in offshore regions. *A. aurita* were confined to the upper part of the mixed layer. Smaller *A. aurita* (≤1 cm) were present in early spring (March), and individuals reached maximum size in the summer. Release of the epyhrae occurred in spring on the northwestern shelf of the sea when the seawater temperature was 11–12 °C. Microscopic analysis of stomach contents showed that copepods and mollusks form their main diet.

## Introduction

The moon jellyfish *Aurelia aurita* is one of the most common macrogelatinous zooplankton species of the world's oceans. This group of zooplankton has received a great deal of interest from the scientific community due to its significant role in pelagic ecosystems (Möller 1980, 1984; Purcell 1985, 1990, 1991, 1997; Purcell and Nemazie 1992; Purcell et al. 1994; Schneider and Behrends 1994).

*A. aurita* is very common in the mixed layer down to the subthermocline region in the Black Sea. Small animals are mostly found above the thermocline, while larger individuals, up to 40 cm, are found just below it. The biomass of *A. aurita* fluctuates seasonally (Shushkina and Musayeva 1990a), being high in spring and autumn. The biomass has increased with increasing eutrophication of the Black Sea (Caddy and Griffiths 1990). From 1950 to 1962, Shushkina and Musayeva (1983) found a biomass on the order of 30 million tons wet weight. In 1978, a much larger biomass (400 million tons wet weight) for the whole of the Black Sea was calculated by Gomoiu (1981). In spring 1984 and autumn 1985 the wet weight of *A. aurita* was about 1 kg $m^{-2}$, averaged over the entire Black Sea (Flint et al. 1989).

The drastic changes in the ecosystem of the Black Sea after the introduction of *Mnemiopsis leidyi* in the early 1980s have stimulated numerous recent studies. Plankton studies in the Black Sea have mainly dealt with horizontal and vertical distributions, morphology, trophic relationships, predation, ecological roles and methods for controlling the *M. leidyi* population (Shushkina and Musayeva 1983; Vinogradov et al. 1989; Zaika and Sergeeva 1991; Harbison and Volovik 1993; Zaitsev 1993; Lebedeva and Shushkina 1994). Early efforts to study gelatinous zooplankton by the Commonwealth of Independent States (CIS) date back to the mid-1980s, with additional studies since the end of the 1980s. Vinogradov et al. (1985) first reported the extensive vertical distribution of *Pleurobrachia pileus* in the open water of the Black Sea. Following this, researchers from the CIS focused on various sectors of the Black Sea, especially the Novorosyisk, Odessa, Sevastopol and Crimean coasts, and the open Black Sea (Vinogradov et al. 1989, 1992; Shushkina and Musayeva 1990a, b; Vinogradov 1990; Shushkina and Vinogradov 1991a, b; Zaika and Sergeeva 1991; Volovik et al. 1993).

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There had been no studies in the Turkish region in the Black Sea until Mutlu et al. (1994) described the spatial distributions of gelatinous zooplankton in this area for June 1991, July 1992 and August 1993. In that study the authors found that the average biomasses of *M. leidyi*, *P. pileus* and *A. aurita* were approximately the same (200 g wet wt $m^{-2}$) in 1992 and 1993. *P. pileus* biomass doubled between 1990/1991 and 1993. Furthermore, Mutlu and Bingel (1999) and Mutlu (1999) studied the distribution and abundance of the ctenophores (*P. pileus* and *M. leidyi*, respectively) and their zooplankton food, in addition to morphometry and size distribution of these animals in the Black Sea. In the present study, the recent (1991–1995) distribution of *A. aurita* was studied with respect to the 1991–1993 data. The morphology, depth distribution, stomach contents of *A. aurita*, and relationships with other zooplankton groups were also examined.

## Materials and methods

Samples for studying the distribution of *Aurelia aurita* Linnaeus, 1758 in the Black Sea were collected in the winter (January 1992 and February 1994), spring (April 1993, May 1994, March 1995) and summer (June 1991, July 1992, August 1993). The areas investigated during the winter and summer surveys were restricted to the Turkish Exclusive Economic Zone (TEEZ; Fig. 1 in Mutlu and Bingel 1999), but spring cruises also included the Bulgarian and Romanian EEZs. Data from the summer cruises were published previously (Mutlu et al. 1994), but they are included here for comparison with data for the winter and spring.

The horizontal distribution (abundance and biomass) of *A. aurita* was studied by collecting the ctenophores with a Hensen net (0.7 m net diameter, 300 μm mesh). Samples were obtained by hauling the net at each station vertically from above the anoxic zone to the surface. The depth of the $H_2S$ layer (according to sigma theta, $\sigma_\theta = 16.2$; Tugrul et al. 1992) was determined with a SeaBird CTD. To estimate the diel vertical distribution of the organisms, a single Nansen opening–closing net (0.7 m net diameter, 200 μm mesh) was used. A series of discrete vertical hauls was made at a speed of 1 cm $s^{-1}$ from the top of the anoxic layer to the surface (0–150 m) at 15 m intervals in August 1993 and March 1995. In addition, more than ten dives were conducted at four stations in July 1992 and August 1993, using the BENTHOS, Mini-Rover (remotely operated vehicle) equipped with a PAL-color video camera. Further, live specimens of *A. aurita* were collected outside the harbor of the Aquatic Resources Research Institute in Yomra-Trabzon in September 1993 to establish biometric relationships for the species.

On board ship, gelatinous organisms were immediately separated from the other meso-zooplankton using a 2 mm mesh sieve. The total number of individuals and total wet weight of *A. aurita*, measured with a simple hand balance, were determined. Disc diameters of individuals were measured to the nearest millimeter, and individual displacement volumes (ml) were determined in finely graded cylinders. *A. aurita* were classified into two different size classes (≤10 mm and > 10 mm) to see numerical composition of the animal stages (epyhrae and medusae). Monthly length-frequency distributions were sorted into 3 cm length classes. In the laboratory, stomach contents of 862 individuals of *A. aurita* were examined in individuals preserved in 5% formalin buffered with borax.

The stomach of each specimen was dissected under a stereoscopic binocular microscope by making an incision with a dissecting needle from the mouth through the cavity. Stomach contents were identified to the lowest possible taxonomic level, and individual food items were enumerated. The frequency of occurrence and numerical abundance (Holden and Raitt 1974) were calculated to provide estimates of the qualitative and quantitative importance of the prey.

The study area was divided into seven sub-regions in order to test for differences (using the non-parametric Kruskal–Wallis test) in abundance, biomass and size distribution: on-shelf or inshore areas (< 200 m depth), off-shelf or offshore (> 200 m), western Black Sea (west of 35°E), eastern Black Sea (east of 35°E) in the TEEZ (south of 43°N in the western Black Sea), and the EEZs of other riparian Black Sea countries (Bulgaria, Romania and the Ukraine) lying north of 43°N in the western Black Sea (Fig. 1 in Mutlu and Bingel 1999).

Abundances of the gelatinous species (*M. leidyi*, *P. pileus* and *A. aurita,* Mutlu 1999; Mutlu and Bingel 1999) and the abundances of copepods, ichthyoplankton, chaetognaths, phytoplankton, etc. (Niermann et al. 1998) were subjected to a non-parametric Spearman's rank correlation analysis (Sokal and Rohlf 1968).

## Results

### Biomass and abundance

#### *Horizontal distribution*

Spatial distribution of *Aurelia aurita* in the Black Sea was related to the general surface circulation. The locations of dense patches of *A. aurita* coincided well with coastal regions between local anticyclonic (Sakarya, Sinop, Kizilirmak, etc.) eddies (Fig. 1 in Mutlu and Bingel 1999). In June 1991, the central region of the Black Sea seemed to be virtually devoid of the moon jellyfish. Nevertheless, *A. aurita* exhibited a spreading to offshore areas between 1992 and 1995 (Figs. 1, 2). The mean wet weight of *A. aurita* at the study sites never exceeded 380 g $m^{-2}$, while the maximum wet weight (3224 g $m^{-2}$ off Eregli and Zonguldak, and 3120 g $m^{-2}$ off Constanza) was recorded for July 1992 and March 1995 (Table 1; Fig. 1). No significant difference in the mean biomass and abundance between the eastern and western Black Sea, and the TEEZ and the Bulgarian, Romanian and Ukrainian EEZs was observed throughout the sampling dates, except March 1995 (Table 2; Figs. 1, 2). A significant difference between inshore and offshore areas was found in some months, e.g. June 1991, January 1992 and March 1995.

#### *Vertical distribution*

*A. aurita* was confined to a narrow depth range in the upper parts of the mixed layer, at depths of 20–40 m during both day and night. No individuals were observed beneath the thermocline (Fig. 3). Toward midnight, *A. aurita* was found within the cold intermediate layer (CIL) at about 50 m, where the temperature was < 8 °C and the dissolved oxygen was relatively high (Fig. 3).

#### *Visual observations of vertical distribution*

In situ visual inspection using a Mini-Rover underwater video-camera in July 1992 and August 1993 showed that

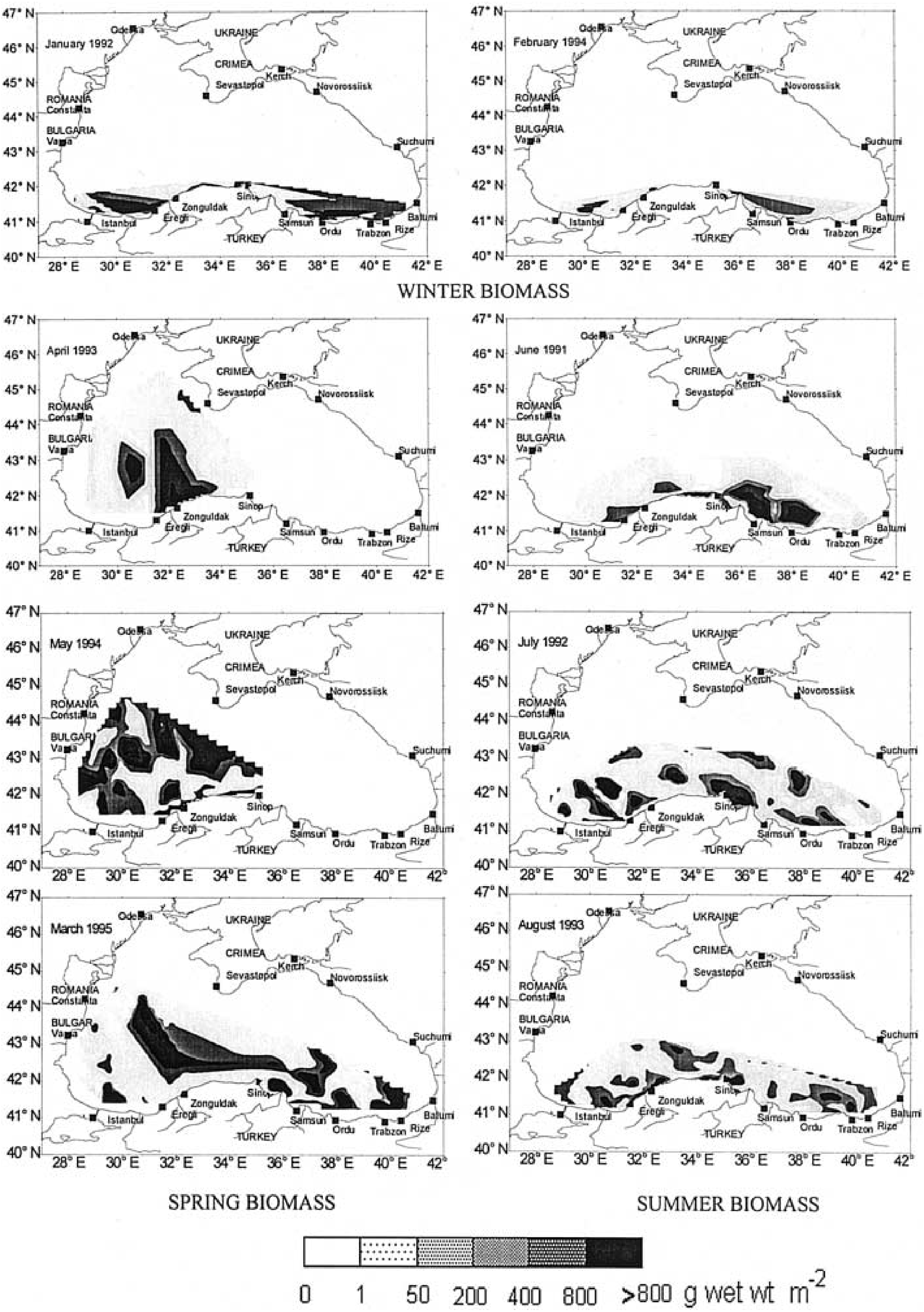
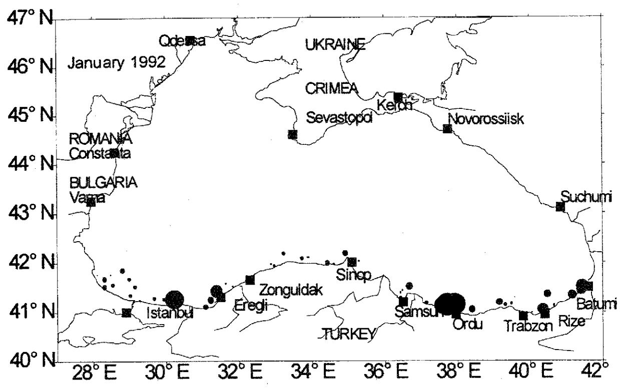
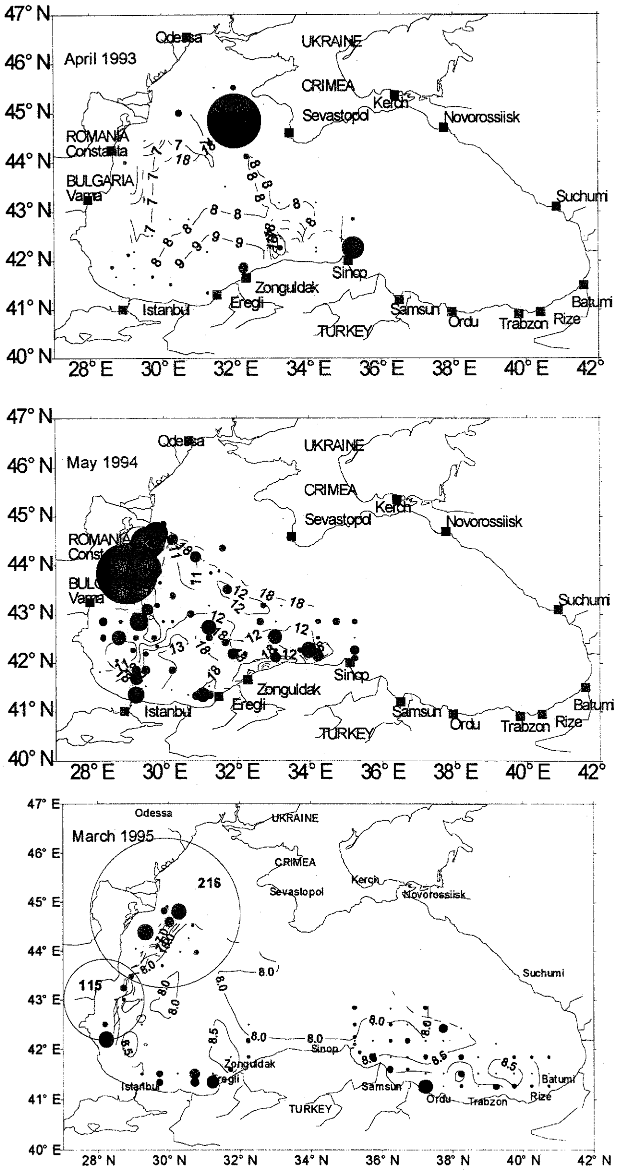
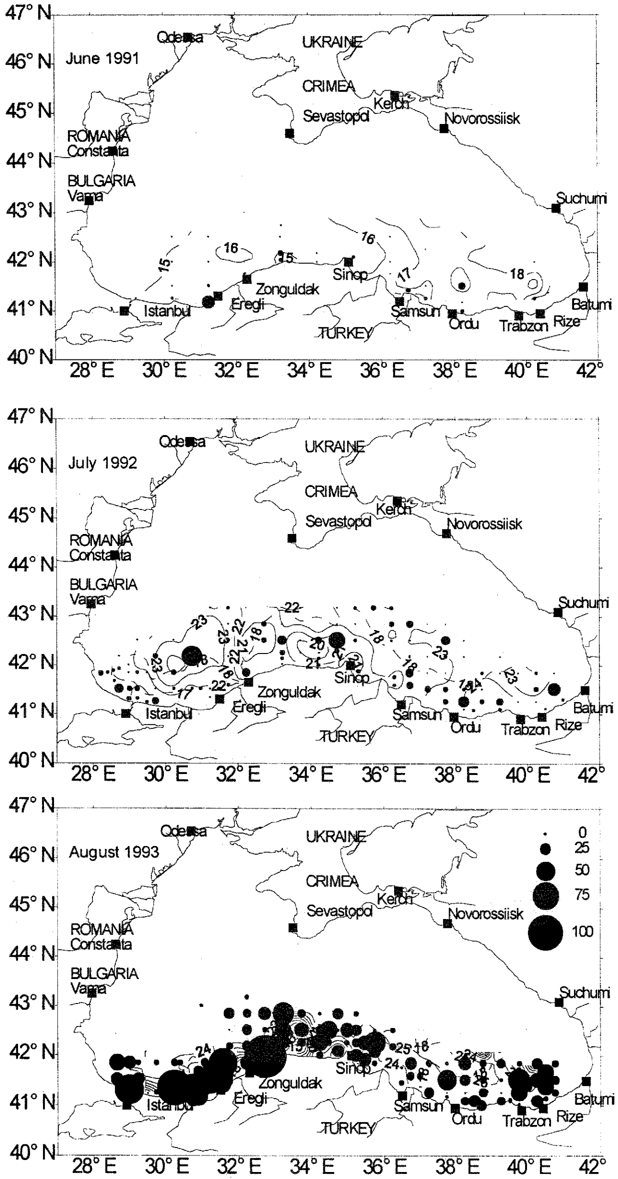


**Fig. 1** *Aurelia aurita*. Biomass distribution (g wet wt m$^{-2}$) from June 1991 to March 1995 (*no shading* within area studied represents 0–1 g wet wt m$^{-2}$)



WINTER ABUNDANCE





SPRING ABUNDANCE

SUMMER ABUNDANCE

◄

**Fig. 2** *Aurelia aurita*. Spatio-temporal abundance distribution (ind. m$^{-2}$) from June 1991 to March 1995 (*large open circle* equals 216 ind. m$^{-2}$; *small open circle* equals 115 ind. m$^{-2}$ in March 1995; *solid contour* is temperature at 5 m depth; *dashed line* represents salinity at 5 m)

individuals of *A. aurita* were distributed in the mixed layer. When the surface waters were warmer in August (25–26 °C; Fig. 5 in Mutlu and Bingel 1999), individuals of *A. aurita* were found at greater depths (down to 20–25 m) compared to depths measured in July 1992 (22 °C). No *A. aurita* was observed below the thermocline at 25–30 m (Fig. 5 in Mutlu and Bingel 1999).

## *Temporal fluctuations*

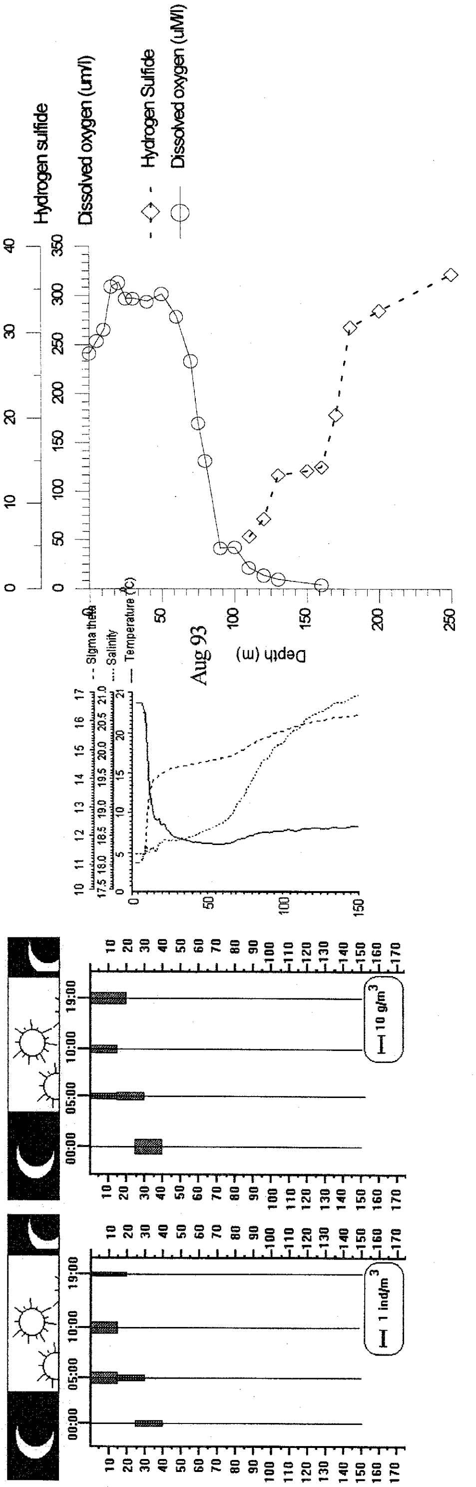
The mean abundance and biomass of *A. aurita* peaked in late spring (11 ind. m$^{-2}$ and 380 g m$^{-2}$) and in late summer (14 ind. m$^{-2}$ and 232 g m$^{-2}$). These values are two- and threefold higher than those obtained for winter (Fig. 6 in Mutlu and Bingel 1999). During the summer, the mean wet weight and abundance increased rapidly from June (136 g m$^{-2}$ and 2 ind. m$^{-2}$ in 1991) to August

**Table 1** *Aurelia aurita*. Maximum and mean (±SE) abundance (ind. m$^{-2}$) and biomass (g wetwt m$^{-2}$) in the Black Sea, 1991–1995

| | Jun 1991 | Jan 1992 | Jul 1992 | Apr 1993 | Aug 1993 | Jan/Feb 1994 | Apr/May 1994 | Mar/Apr 1995 |
|---|---|---|---|---|---|---|---|---|
| Max. abundance (m$^{-2}$) | 18 | 31 | 29 | 75 | 60 | 21 | 86 | 211 |
| Mean abundance (m$^{-2}$) | 2 ± 0 | 6 ± 1 | 4 ± 0 | 6 ± 2 | 14 ± 1 | 5 ± 1 | 11 ± 1 | 8 ± 2 |
| Max. biomass (g m$^{-2}$) | 2001 | 1429 | 3224 | 974 | 1326 | 961 | 2392 | 3120 |
| Mean biomass (g m$^{-2}$) | 136 ± 41 | 226 ± 32 | 201 ± 28 | 145 ± 34 | 232 ± 16 | 98 ± 21 | 380 ± 48 | 225 ± 41 |

**Table 2** *Aurelia aurita*. Abundance (ind. m$^{-2}$) and biomass (g wet wt m$^{-2}$) in western, eastern, inshore and offshore areas of the Black Sea during 1991–1995. *Bold numbers* indicate significant difference between inshore and offshore areas inside the specified areas of the Black Sea (non-parametric Kruskal–Wallis ANOVA, $P < 0.05$) (*n* number of stations sampled; *EEZ* exclusive economic zone)

| Area, Sampling date | Inshore | | | Offshore | | | Total | | |
|---|---|---|---|---|---|---|---|---|---|
| | Abund. | Biomass | (*n*) | Abund. | Biomass | (*n*) | Abund. | Biomass | (*n*) |
| Western Black Sea | | | | | | | | | |
| Jun 1991 | 6 | 256 | (6) | 2 | 62 | (24) | 3 | 101 | (29) |
| Jan 1992 | 5 | 214 | (30) | 6 | 217 | (7) | 5 | 215 | (37) |
| Jul 1992 | **6** | 166 | (14) | **4** | 209 | (67) | 4 | 201 | (81) |
| Aug 1993 | 15 | 281 | (19) | 16 | 235 | (75) | 15 | 244 | (94) |
| Jan/Feb 1994 | 6 | 136 | (25) | 3 | 155 | (10) | 5 | 112 | (35) |
| Mar/Apr 1995 | 18 | **62** | (28) | 5 | **228** | (23) | 12 | **137** | (51) |
| Eastern Black Sea | | | | | | | | | |
| Jun 1991 | 3 | 501 | (4) | 2 | 123 | (35) | 2 | 162 | (39) |
| Jan 1992 | **4** | **159** | (20) | **10** | **327** | (17) | 7 | 236 | (37) |
| Jul 1992 | 6 | **481** | (3) | 5 | **185** | (59) | 5 | 199 | (62) |
| Aug 1993 | 11 | 364 | (7) | 13 | 191 | (51) | 12 | 212 | (58) |
| Jan/Feb 1994 | 5 | 97 | (29) | 1 | 46 | (9) | 4 | 85 | (38) |
| Mar/Apr 1995 | 10 | 277 | (3) | 4 | 307 | (53) | 5 | **306** | (56) |
| Area studied (see Fig. 1 in Mutlu and Bingel 1999) | | | | | | | | | |
| Jun 1991 | **4** | **354** | (10) | **2** | **98** | (58) | 2 | 136 | (68) |
| Jan 1992 | **4** | **192** | (50) | **9** | **295** | (24) | 6 | 226 | (74) |
| Jul 1992 | **6** | 222 | (17) | **4** | 198 | (126) | 4 | 201 | (143) |
| Aug 1993 | 14 | 303 | (26) | 14 | 217 | (126) | 14 | 232 | (152) |
| Jan/Feb 1994 | 5 | 115 | (54) | 2 | 51 | (19) | 5 | 98 | (73) |
| Mar/Apr 1995 | 17 | **83** | (31) | 4 | **283** | (76) | 8 | 225 | (107) |
| Turkish EEZ | | | | | | | | | |
| Apr 1993 | **3** | **10** | (4) | **5** | **181** | (26) | 5 | 158 | (30) |
| Apr/May 1994 | 12 | 332 | (6) | 9 | 358 | (53) | 9 | 355 | (59) |
| Mar/Apr 1995 | 7 | **115** | (11) | 5 | **297** | (68) | 5 | **272** | (79) |
| Bulgarian, Romanian and Ukranian EEZ | | | | | | | | | |
| Apr 1993 | 5 | 107 | (10) | 10 | 145 | (10) | 7 | 126 | (20) |
| Apr/May 1994 | 24 | 316 | (12) | 7 | 540 | (14) | 15 | 437 | (26) |
| Mar/Apr 1995 | **22** | 66 | (20) | **2** | 166 | (8) | 16 | **94** | (28) |
| Area studied (see Fig. 1 in Mutlu and Bingel 1999) | | | | | | | | | |
| Apr 1993 | 4 | 79 | (14) | 6 | 171 | (36) | 6 | 145 | (50) |
| Apr/May 1994 | **20** | 321 | (18) | **8** | 396 | (67) | 11 | 380 | (85) |
| Mar/Apr 1995 | 17 | **83** | (31) | 4 | **283** | (76) | 8 | 225 | (107) |


Aug 93
Depth (m)
Hydrogen sulfide
Dissolved oxygen (um/l)
Hydrogen Sulfide
Dissolved oxygen (uM/l)
Sigma theta
Salinity
Temperature (°C)
00:00
05:00
10:00
19:00
1 ind/m³
10 g/m³

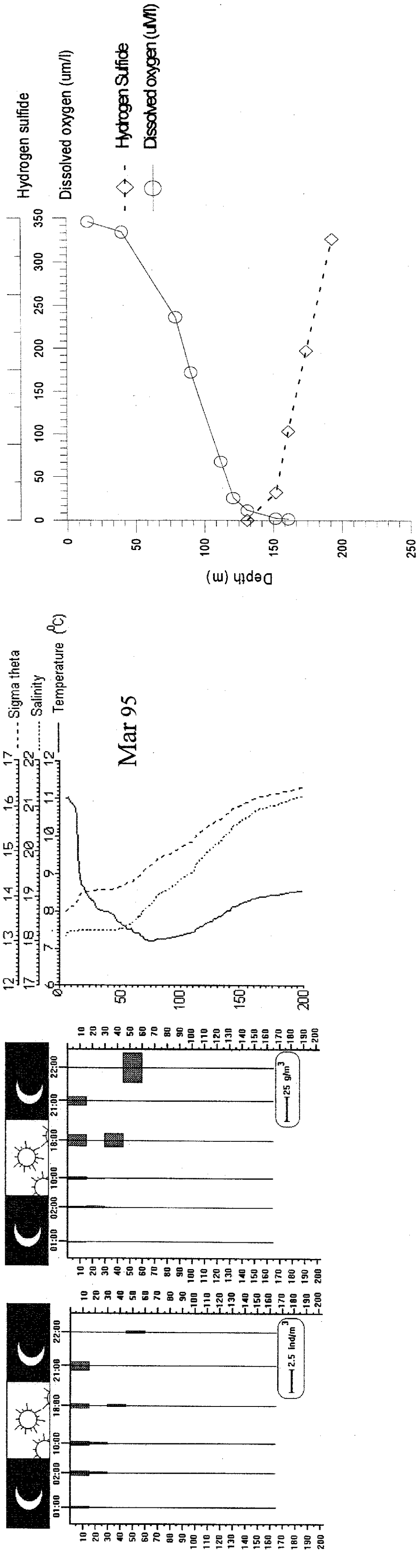

Mar 95
Depth (m)
Hydrogen sulfide
Dissolved oxygen (um/l)
Hydrogen Sulfide
Dissolved oxygen (uM/l)
Sigma theta
Salinity
Temperature (°C)
01:00
02:00
10:00
18:00
21:00
22:00
2.5 ind/m³
25 g/m³

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**Fig. 3** *Aurelia aurita*. Vertical distribution with respect to daily light conditions, temperature, salinity, density gradients, dissolved oxygen (μM), and hydrogen sulphide ($H_2S$ in μM), August 1993, station 41°30′N; 31°15′E, and March 1995, station 41°54′N; 29°51′E

(232 g $m^{-2}$ and 14 ind. $m^{-2}$) (Fig. 6 in Mutlu and Bingel 1999).

## Morphometric characters

Individual displacement volume and live weight were fitted to disc diameter by regression analysis. The relationship between the measurements was represented by a power function of the regression model (Table 3).

## Spatial and temporal size distribution

Using disc diameter as a measure of size, the size structure of *A. aurita* showed marked seasonal fluctuations (Fig. 4). The mean and median disc diameters of *A. aurita* increased from late winter (February) to midsummer (July) and decreased again in August. For the 1992–1995 period, the mean diameter generally did not exceed 10 cm. Disc diameter of the largest individual was 28 cm in January 1992, 21.4 cm in July 1992, 23 cm in August 1993, 17.7 cm in February 1994, 30.5 cm in May 1994, and 43 cm in March 1995 (Fig. 5). Specimens $>$ 10cm rarely exceeded 20% of the total population of *A. aurita* (Fig. 4). Young individuals called ephyrea ($<$ 10 mm body length) peaked with a value of 25% of the *A. aurita* population in March 1995, but accounted for only 5% in February 1994 and April/May 1994. The minimum (1%) was observed in August 1993 (Fig. 4). Release of ephyrea occurred in spring, and attained a maximum value in March, particularly on the northwestern shelf when the surface water temperature was about 11–12 °C. Thus, there appeared to be only one generation per year. Small specimens of *A. aurita* were widely distributed on the northwestern shelf. In spring (April/May 1994 and March/April 1995), the mean diameter was significantly higher in offshore and eastern regions than in inshore areas and the western Black Sea.

## Vertical size composition

Observations at station 41°30′N; 31°15′E in August 1993, and station 41°54′N; 29°51′E in March 1995 were conducted to determine the vertical size distribution in the Black Sea. In August 1993, all individuals of *A. aurita* were found in the mixed layer. Larger specimens (a mean disc diameter of 5.85 cm) of *A. aurita* were observed in the lower portion of the mixed layer (20–25 m) at 0500 hours. In March/April 1995, smaller individuals ($<$ 6 cm) were observed in the mixed layer, whereas larger individuals of 11–16 cm were at depths of 15–30 m.

## Stomach contents

Overall, the stomach contents of *A. aurita* individuals contained the following food components, in descending order of frequency: Copepoda (42%), Mollusca (35%), Cladocera (4%), fish eggs and larvae (3%) and others (16%). Of the five most important copepod species (*Acartia clausi*, *Calanus euxinus, Pseudocalanus elongatus*, *Paracalanus parvus* and *Oithona similis*), *A. clausi* was most frequently consumed (31%) by this jellyfish in the Black Sea. Following *A. clausi*, food consumed were *C. euxinus* (30%), *P. elongatus* (26%), *P. parvus* (8%) and *O. similis* (2%) in frequency of occurrence. In numerical occurrence, *C. euxinus* (37%) ranked first, and *A. clausi* amounted to 26% during the 1992–1995 study period. The greatest number of individual food items in the stomach of one *A. aurita* was 225 in March/April 1995 (Table 4). The individual food items were bivalve larvae (220 individuals), and five digested copepods (Table 4). The minimum percent of individuals fed was 10%, found in April 1993.

## Correlation with ambient zooplankton abundance

In July 1992, *A. aurita* abundance was positively correlated with *Mnemiopsis leidyi* ($P < 0.05$, $r = 0.3$, $n = 143$), but there was no correlation between *A. aurita* and *Pleurobrachia pileus* abundance. *M. leidyi* was more closely correlated with *P. pileus* ($P < 0.05$, $r = 0.6$, $n = 50$) in April 1993, as compared with previous years. In August 1993 and February 1994, the abundance of *A. aurita* was not significantly correlated with *P. pileus* and *M. leidyi* abundances. In contrast to the previous correlations in abundance from June 1991 to February 1994, *A. aurita* abundance was significantly negatively correlated with *M. leidyi* abundance ($P < 0.05$, $r = -0.25$, $n = 85$) and with *P. pileus* ($P < 0.05$, $r = -0.2$, $n = 85$) in May 1994. In March 1995, there

**Table 3** *Aurelia aurita*. Biometric relationships (*Y* dependent variable; *X* independent variable; *a* intercept; *b* slope; *r* correlation coefficient, significant at $P < 0.01$ level; *n* sample size)

| Relationship | Type of function | *Y* | *X* | *a* | *b* | *r* | *n* |
|---|---|---|---|---|---|---|---|
| Wet weight (W) vs. disc diameter (d) | Power | g W ind.$^{-1}$ | cm d ind.$^{-1}$ | 0.120 | 2.582 | 0.89 | 243 |
| Displacement volume (V) vs. disc diameter (d) | Power | ml V ind.$^{-1}$ | cm d ind.$^{-1}$ | 0.101 | 2.389 | 0.80 | 421 |

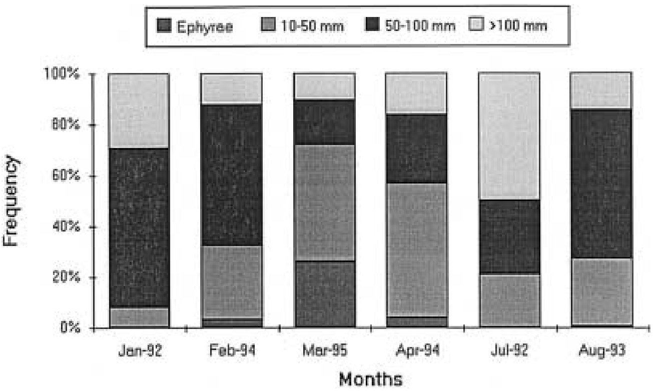

**Fig. 4** *Aurelia aurita*. Seasonal changes in frequency of four size classes and epyhrae and medusae from January 1992 to March 1995

were no significant correlations in abundance among these organisms. Comparison of the spatial distributions of abundance and biomass of *A. aurita* and *M. leidyi* reveals that in areas where *A. aurita* is in dense patches, the abundance and biomass of *M. leidyi* is reduced, and vice versa. Abundance of *A. aurita* was significantly positively correlated with *C. euxinus* abundance.

## Discussion and conclusions

Spatial patterns of *Aurelia aurita* abundance and biomass appear to be associated with surface circulation of the Black Sea, perhaps because most individuals occur in the upper mixed layer. Relatively higher biomasses were observed in patches in regions between the coastal anticyclonic eddies. Zhong (1988) previously suggested that currents, water temperature and salinity dictate the horizontal distribution of planktonic gelatinous organisms. High concentrations of *Mnemiopsis leidyi* were found in the eddies (Mutlu 1999). *A. aurita* and *M. leidyi* inhabit the same layer (Mutlu et al. 1994; Mutlu 1999) above and around the thermocline and compete for the same planktonic food. It is often suggested that *M. leidyi* depresses the population of *A. aurita,* pushing the latter to areas distinct from those of *M. leidyi. M. leidyi*, having a poor swimming ability, aggregated in the anticyclonic downwelling areas where non-motile zooplankton are concentrated. Since *A. aurita* was generally outcompeted by *M. leidyi* in such regions, its main biomass was found between the anticylonic eddies. Interactions of local, small-scale anticyclonic eddies in the region also affect distributions (Fig. 1). These complex interactions, along with currents, cause patchy distributions of organisms in offshore regions (Fig. 1). Purcell et al. (2000) suggested that aggregation of the jellies could potentially be advantageous for fertilization success. *A. aurita* was present mainly in the inshore area of the southern Black Sea in June 1991. After June 1991, *A. aurita* was distributed over a wider offshore area. The extreme population outburst of *M. leidyi* in the Black Sea took place in September 1989 (800 million tons for the entire sea, Vinogradov et al. 1992). This affected radically the entire pelagic fauna of the Black Sea, and *A. aurita* was forced offshore (Fig. 1). Significant differences in the biomasses and abundances were observed among regions only in June 1991, January 1992 and March 1995: higher accumulations were in the inshore areas compared with the offshore areas in June 1991 and March 1995. *A. aurita* was mainly distributed in inshore areas in June 1991, and the main reproduction period of *A. aurita* occurred in spring (March 1995).

*A. aurita* were distributed over a narrow depth range both day and night, in and above the thermocline. Shushkina and Musayeva (1983) first observed a similar vertical distribution in late September 1987; this pattern has been repeatedly observed (Vinogradov et al. 1989; Shushkina and Vinogradov 1991a, b).

*A. aurita* displayed regular monthly variation in biomass and abundance from January to August, regardless of year. Starting in winter (January 1992), when the lowest values were observed, *A. aurita* showed an increase in biomass and abundance in early spring (March 1995), due to the contribution of a new spring generation; a sharp decrease in mid-summer (June 1991, July 1992), after high natural mortality (indicated by high compactness of jellyfish body and deterioration of their oral arms) of the winter generation; and a peak in late summer (August 1993), due to growth of the spring generation. This has been repeatedly observed by Vinogradov and Shushkina (1992). Shushkina and Musayeva (1983) showed a mass mortality of the winter generation and consequently a decrease in the biomass in mid-summer. Vinogradov et al. (1992) showed that mass reproduction of *A. aurita* and *M. leidyi* occurs in inshore waters, which warm up earlier than offshore waters. The northwestern shelf of the sea, being a very wide shallow area, presents suitable substrata for the reproductive sessile stage of jellyfish. Data based on size distribution showed that the jellyfish were involved in mass reproduction on the shelf in early spring (March 1995); offspring of that generation reached maximum size in late summer (August 1993). A subsequent increase in water temperature and the spring bloom of zooplankton caused growth of the population, resulting in a biomass peak in late spring (May 1994) to late summer (August 1993). Shiganova (1996) showed an increase in the biomass from April to August.

The median and mean values (Fig. 5) of *A. aurita* in the Black Sea were at minimum in winter (February 1994), increased rapidly from late spring (May 1994) to mid-summer (July 1992) and declined due to starvation in late summer (August 1993). Schneider and Behrends (1994) found the same trend in the Kiel Bight, Germany; however, the reduction occurred 2 months later than in the Black Sea. The time difference in the reduction could be due to spatial temperature differences between the Black Sea and the Kiel Bight. Möller (1980) found the

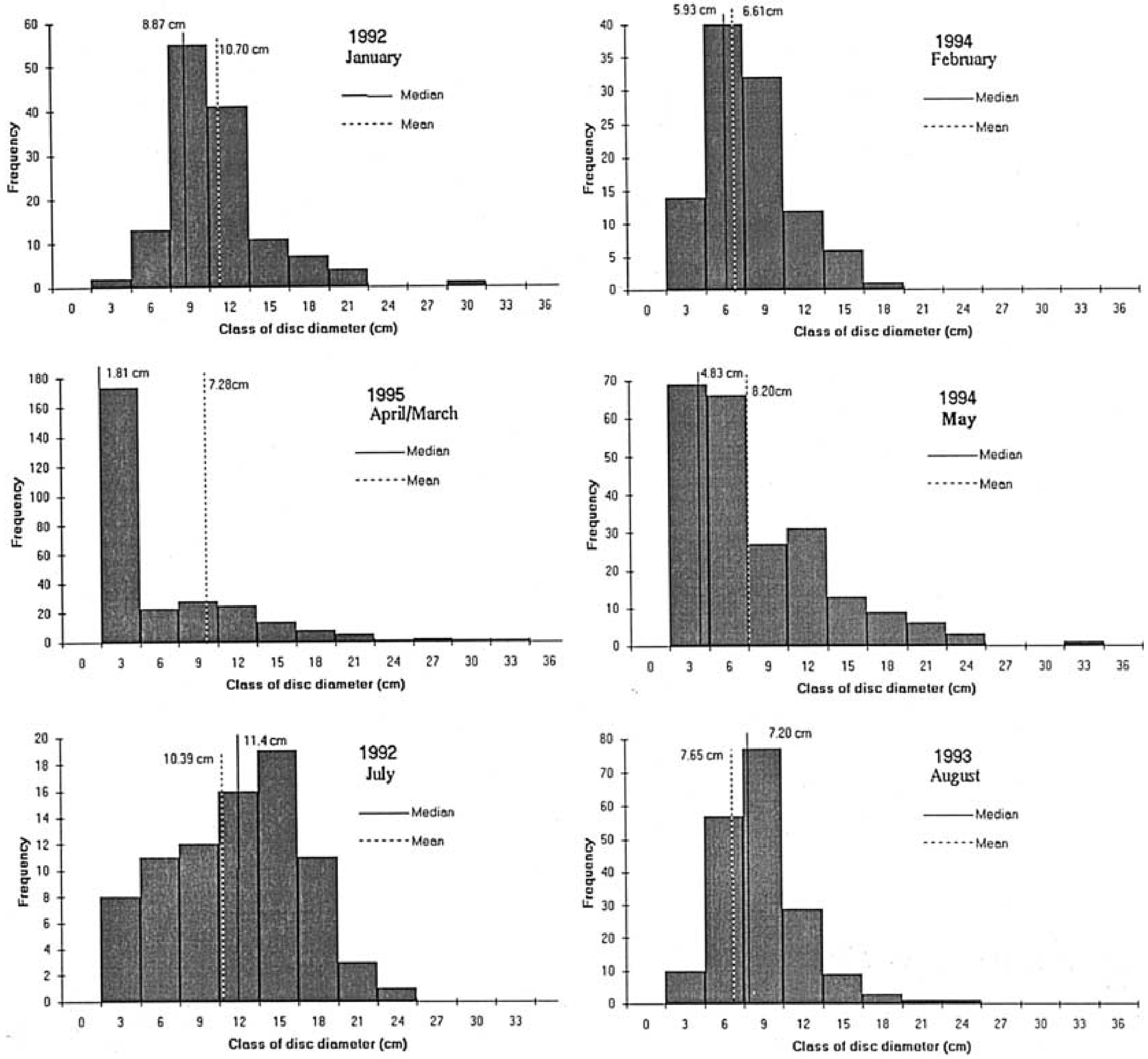

**Fig. 5** *Aurelia aurita*. Length-frequency distribution for six sampling dates from January 1992 to March 1995. Data from multiple stations are averaged to reflect winter, spring and summer conditions

largest medusae in August, and shrinkage in size in September due to starvation. Hamner and Jenssen (1974) found experimentally that medusae shrank an average of 39% after 34 days without food. The present study showed only one episode of reproduction in March/April 1995, when the investigated area covered the northwestern shelf of the Black Sea as well. The findings of Shushkina and Musayeva (1983) revealed the presence of two generations (winter and spring) occurring in the Black Sea. Möller (1979) determined that the start of *A. aurita* growth is related to the occurrence of large masses of copepods serving as the main food source for medusae (Möller 1980). The two generations were observed before *M. leidyi* devastated the ecosystem of the Black Sea. After the change in the ecosystem and return to the balanced phase, *A. aurita* displayed its peak release of ephyrea in March 1995, when *M. leidyi* contributed a minimum of young individuals to the Black Sea (Mutlu 1999).

*A. aurita* showed no evidence of a layered size distribution in the water column. It was exclusively confined to areas above thermocline. Relatively larger specimens were found near the upper boundary of the CIL, whereas small individuals predominated the upper part of the mixed layer. Vinogradov et al. (1992) reported the same vertical size distribution.

While *A. aurita* was found to feed mainly on copepods (42%) and bivalve larvae (35%), it was also observed to be a predator on fish eggs and larvae (3%) in

**Table 4** *Aurelia aurita*. Frequency of occurrence (*FO*, as %) and numerical occurrence (*NO*, as %) of food items in the stomach of *A. aurita* in July 1992–March 1995 (0 indicates < 1%)

| Food items | Jul 1992 | | Apr 1993 | | Aug 1993 | | Feb 1994 | | May 1994 | | Mar 1995 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | FO | NO | FO | NO | FO | NO | FO | NO | FO | NO | FO | NO |
| Crustacea | | | | | | | | | | | | |
| Copepoda | | | | | | | | | | | | |
| *Pseudocalanus elongatus* | 5 | 3 | 11 | 4 | 8 | 5 | 11 | 3 | 8 | 2 | 11 | 2 |
| *Acartia clausi* | 14 | 8 | 0 | 0 | 15 | 8 | 7 | 1 | 16 | 5 | 12 | 0 |
| *Calanus euxinus* | 9 | 11 | 11 | 4 | 15 | 13 | 14 | 2 | 9 | 4 | 6 | 0 |
| *Oithana similis* | 0 | 0 | 0 | 0 | 2 | 2 | 5 | 2 | 2 | 0 | 1 | 0 |
| *Paracalanus parvus* | 0 | 0 | 11 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 |
| Unidentified copepods | 9 | 8 | 33 | 42 | 18 | 23 | 19 | 10 | 22 | 15 | 22 | 7 |
| Cladocera | 5 | 5 | 11 | 13 | 5 | 3 | 11 | 3 | 6 | 2 | 7 | 1 |
| Barnacle larvae | | | | | | | | | | | 3 | 11 |
| Ostracode | 9 | 22 | | | 2 | 6 | 1 | 0 | 2 | 0 | | |
| Cumacea | | | | | | | | | 2 | 0 | | |
| Amphipoda | 5 | 5 | | | | | | | | | | |
| Mollusca | | | | | | | | | | | | |
| Bivalve larvae | | | 11 | 25 | 5 | 12 | 18 | 73 | 27 | 70 | 28 | 74 |
| Gastropoda larvae | 9 | 5 | | | | | 1 | 0 | | | | |
| Appendicularia | | | | | 1 | 1 | | | | | | |
| Fish eggs and larvae | 19 | 13 | 0 | 0 | 3 | 4 | 4 | 0 | 0 | 0 | 0 | 0 |
| *Peachia hastata (Actinaria)* | 5 | 3 | | | 0 | 0 | | | | | | |
| *Pleurobrachia pileus* | | | | | 3 | 2 | 1 | 0 | | | 1 | 0 |
| Undefined food item | | | | | 16 | 15 | 7 | 1 | 5 | 1 | 3 | 0 |
| Polychaeta larvae | 9 | 5 | 11 | 4 | 2 | 1 | 1 | 0 | | | | |
| Total no. individuals examined | 47 | | 38 | | 348 | | 100 | | 120 | | 209 | |
| No. individuals with food items in gut | 11 | | 4 | | 113 | | 38 | | 32 | | 45 | |
| Max. no. of prey ind.$^{-1}$ | 14 | | 7 | | 16 | | 106 | | 32 | | 225 | |
| Total no. food items | 33 | | 24 | | 318 | | 511 | | 239 | | 821 | |

contrast with other gelatinous organisms, e.g. *P. pileus* (Mutlu and Bingel 1999) and *M. leidyi* (Mutlu 1999). Purcell (1985) identified many gelatinous zooplankters that could consume fish larvae, and fish larvae comprised 90–100% of the diets of cyctonect siphonophores, but only small percentages of the natural diets of other gelatinous predators. Shushkina and Musayeva (1983) highlighted the importance of *A. aurita* in the Black Sea as a predator on fish eggs and larvae and as a competitor for food with the planktivorous fish, as has also been suggested for other seas (Bailey and Batty 1983; Möller 1984). The primary prey of *A. aurita* were the small planktonic Crustacea (*C. euxinus, P. parvus*, *A. clausi*, *O. similis*, *P. elongatus* and Cladocera), the larvae of benthic invertebrates, Appendicularia and arrowworms. This finding is in agreement with that of Shushkina and Musaveya (1983). In the present study, *A. clausi* was found to be the species most frequently consumed by jellyfish. Purcell and Nemazie (1992) reported that the medusae of *Nemopsis bachei* primarily consumed copepodites of *A. tonsa* in Chesapeake Bay (USA), selecting against naupliar stages.

While *A. aurita* displayed correlation with other zooplankton, there was no correlation between *A. aurita* and *P. pileus*. They share the different layers of water column in the Black Sea, *P. pileus* occupying the deeper layer (Vinogradov et al. 1985; Mutlu and Bingel 1999). In general, there was a significant negative correlation between *A. aurita* and *M. leidyi*. The correlation could come from occupation of the same layer by the two organisms and high competition between them. A comparison of the spatial distribution of the two organisms showed that in areas where *M. leidyi* was predominantly present, *A. aurita* were rare, and vice versa (Mutlu 1999).

In conclusion, the spatial distribution of *A. aurita* was controlled by sea surface circulation and competition in the Black Sea during 1991–1995. High concentrations were found in areas between downwelling regions, while smaller concentrations occurred in the main cyclonic gyres. The biomass and abundance of *A. aurita* peaked in spring and summer. *A. aurita* extended over a narrow range of vertical depths, being confined to the upper part of the mixed layer by day and night. Smaller individuals (disc diameter ≤1 cm) dominated in spring, and maximum size was reached in summer. *A. aurita* reproduction peaked in the spring, the largest abundance occurring in March. Analysis of stomach contents of *A. aurita* showed that copepods and bivalve larvae form the main dietary components.

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