In situ grazing pressure and diel vertical migration of female *Calanus euxinus* in the Black Sea

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Key words: grazing pressure, vertical migration, copepod, Calanus, Black Sea

Abstract

Gut pigment and abundance of the female *Calanus euxinus* (Hulsemann) were measured from several water layers (defined by density values), with 3–5 h intervals during 30 h and 21 h at a station in the southwestern Black Sea in April and in September 1995, respectively. The female *C. euxinus* was observed to begin migration to the upper phytoplankton-rich layer approximately 3 or 4 hours before the sunset. Only a fraction of the female *Calanus* population (0.2% in April and 3.6% in September) did not migrate but remained at the depth of the oxygen minimum zone during the nighttime. The migrating population was determined to have spent 7.5 h in the euphotic zone in April and 10.5 h in September. The grazing rate of female *Calanus euxinus* was measured from the gut content data collected from the layers which contain the euphotic zone. The percentage of primary production grazed by the female *C. euxinus* was calculated as 14.5% in April and 9.5% in September.

Introduction

There is an intriguing relationship between diurnal migration and feeding activity in zooplankton. There may be several reasons for the vertical migration of zooplankton, but in any case this would interact with grazing. The herbivorous zooplankton grazing impact represents an essential part of phytoplankton and zooplankton interactions in the ecosystems. The gut fluorescence method has been increasingly applied to determine *in situ* algal grazing rates of planktonic copepods in recent years (e.g. Boyd et al., 1980; Dagg & Grill, 1980; Kiorboe & Tiselius, 1987; Dagg et al., 1989; Morales et al., 1993; Tsuda & Sugisaki, 1994).

In this paper, the diel vertical migration of female *Calanus euxinus* was described by means of time series sampling in the Black Sea. The *in situ* grazing pressure of these copepods was also determined. Since our aim was specifically to determine the share of female *Calanus* grazing as a percentage of primary production, we analysed the gut pigment content only for the copepods collected from the euphotic zone.

Physical and biological properties of the Black Sea

The Black Sea, with an average depth of ~ 1240 m, contains the world's largest anoxic water volume (4.6×10^5 km^3, $\sim 87\%$ of the sea volume) below a thin layer (about 150 m) of oxygenated surface waters (Oguz et al., 1992). A pycnocline (or halocline) separates the oxic and anoxic waters and there is a well defined oxygen minimum zone (OMZ; with less than 10μM O$_2$) between these waters. The depth of the OMZ varies both seasonally and from one part of the Black Sea to another depending on the circulation and the intensity of eddies. However, recent investigations have shown that the OMZ (as well as other chemical and physical characteristics of the water column) could be explained better by water density rather than depth (Tugrul et al., 1992; Saydam et al., 1993; Murray et al., 1993). If the OMZ (and the other characteristics) is explained as a function of water density then spatial and temporal variations disappear. For example, the lower boundary of the OMZ changes from 120 m to 175 m at different locations during the April and September 1995 cruises in the Black Sea when it is expressed in terms of length

units (e.g. meter), however it is always situated at the density of sigma-theta = 16.2 (Gokmen, 1996).

The distribution of the pelagic fauna is related to the boundaries of the OMZ (Vinogradov et al., 1992; Wishner et al., 1995). Vinogradov et al. (1992) has divided Black Sea pelagic ecosystem into two parts; the aerobiotic and the chemobiotic.

The aerobiotic waters of the Black Sea are biologically productive because of high run-off from rivers around the basin. The monthly primary production of water column for offshore areas from 1960 to 1991 was compiled by Vedernikov & Demidov (1993). In April the mean primary production was 520 mgC m^{-2} day^{-1} (range 50–990 mgC m^{-2} day^{-1}). In September the average value was 200 mgC m^{-2} day^{-1} (range 35–360 mgC m^{-2} day^{-1}). The euphotic zone depth (1% light depth of surface light) in the anticyclonic regions was around 35–40 m deep and in the cyclonic region around 30–35 m in May in the Black Sea (Vidal, 1995). However, the depth of the photosynthetic layer usually may extend down to 50–60 m with the optimum photosynthetic intensity being measured at a depth of 5–10 m (Bologa, 1985/1986). The seasonal primary production pattern in the Black Sea is bimodal. Diatoms predominantly bloom in spring, while *Emiliana huxleyi*, and to a lesser degree dinoflagellates, predominantly bloom in summer and fall (Hay & Honjo, 1989).

The chemobiotic environment includes the OMZ and the anaerobic layer. Only very few species can survive in the OMZ. Of these the principal one is *Calanus euxinus* (Vinogradov et al., 1992), which achieves the maximum biomass amongst Black Sea copepods (Ergun, 1994). The late copepodite stages and the adults of *C. euxinus* undertake diel vertical migrations and they spend the daytime in the OMZ. They decrease their oxygen consumption rate in the OMZ (Vinogradov et al., 1992).

Methods

Diel vertical migration

Samples were collected from a 1250 m deep station chosen in a dynamically non-active region (Lat: 41.54 Long: 29.50) during 26–28 April and 27–28 September 1995 (Figure 1). Vertical distribution of copepods was determined by vertical hauls using a Nansen Closing Net of 70 cm mouth opening and 112 m mesh size. The water column was sampled over five depth strata (in terms of density levels; see Introduction) according

to major biogeochemical characteristics of the water column which may affect the distribution of mesozooplankton in the Black Sea (Figure 2). These depth strata are:

(1) from the depth of thermocline to the surface;
(2) from the depth of sigma-theta 14.6 to the thermocline; sigma-theta 14.6 roughly corresponds to lowest boundary of the euphotic zone (1% light level) (Oguz et al., 1996).
(3) the depth range between sigma-theta 15.4 and 14.6; at this stratum, the majority of nitrification and remineralization of organic matter take place (Lipp & Kempe, 1993).
(4) the depth range between sigma-theta 15.8 and 15.4; during the increase in the sinking of particulate organic matter, the upper boundary of the OMZ raises to the sigma-theta 15.4 (Basturk et al., 1994)
(5) and the depth range between sigma-theta 16.2 and 15.8; sigma-theta 16.2 corresponds to the bottom of the OMZ or the beginning of the anoxic water layer. According to Vinogradov et al. (1992), this is the daytime aggregation layer for late copepodite stages and adult of *Calanus*.

A series of vertical tows were taken in April and in September 1995 at 3–5 h intervals through a 30 h and 21 h cycle respectively. Samples were preserved in sodium-borate buffered 4% formalin-seawater solution, then subsampled with a Folsom splitter and identified by a stereomicroscope.

Determination of gut pigment content and grazing pressure

Following each vertical tow, female *Calanus euxinus* specimens were immediately separated on GF/F filters under the microscope for gut pigment content analysis, then frozen on dry-ice within 15 min after collection. Phytoplankton pigments in the guts of 10–15 freshly collected individuals of female *Calanus* (collected from the two uppermost layers in April and the uppermost layer in September encompassing the euphotic zone) were measured via whole animal fluorescence (Mackas & Bohrer, 1976; Boyd et al., 1980). For the background fluorescence of the female *Calanus*, a portion of the collected individuals were exposed to starvation in the GF/C filtered sea water during 24 h. Pigment analyses from each net tow were made in duplicate or triplicate depending on abundance of the organism.

For the gut evacuation rate experiment, copepods were collected at night from 50 m to the surface, where the maximum feeding is assumed to occur. After col-
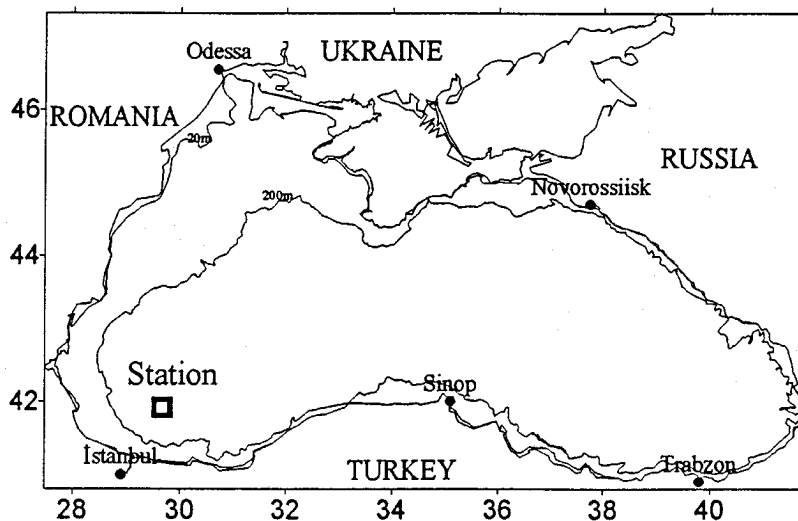
Figure 1. The sampling station in the Southwestern Black Sea.

lection, the cod end contents were rapidly retrieved and immediately sieved through a 2000 μm mesh to remove jelly organisms and sieved through 1000 μm mesh to remove smaller organisms. Some part of the filtrate was poured into soda/seawater solution (1:5, v/v) to anaesthetize the animals for initial gut fluorescence, whilst the rest was transferred into an aquarium filled with filtered seawater and kept in dark on deck. The decline rate of gut content was determined by periodically analyzing copepods at a time from aquarium over a 2 to 6 h period.

Gut fluorescence samples were homogenized in 10 ml of 90% aqueous acetone and the fluorescence of the filtrate was measured before and after acidification with 10% HCl using Hitachi model F-3000 Fluorescence Spectrophotometer. The chlorophyll and phaeopigment content of each copepod was calculated using the equations of Strickland & Parsons, (1972, cf. Boyd et al., 1980).

The studies of gastric evacuation in copepods indicate that the evacuation rate of food from the gut is exponential (Mackas & Bohrer, 1976; Dagg & Grill, 1980). However our gut evacuation rate experiments were unsuccessful because values of gut pigment analysis did not decrease regularly but fluctuated greatly with time. Therefore, we instead used the equation of Dam & Peterson (1988) for the estimation of the evacuation rates which is based on the relationship between gut clearance time and temperature for a wide variety of copepods:

$$R = 0.0117 + 0.001794T,$$

where R = Instantaneous evacuation rate; T = temperature.

Gut evacuation rate can be used to convert each measure of gut contents to an ingestion rate. Ingestion rate is calculated from;

$$I = SR$$

where S = level of gut contents (ng pigment copepod^{-1}); R = instantaneous evacuation rate (min^{-1}). By extrapolation over 60 min this equation can be used to estimate hourly ingestion rates.

Since recent studies have revealed that ingested chlorophyll-a is converted to phaeopigments during passage through the copepod gut (Head & Harris, 1992), the gut content pigment was expressed as chlorophyll-a + phaeopigments in a chlorophyll-a equivalent weight.

Grazing pressure on primary production

The average abundance of female *Calanus* for the whole water column was calculated by combining the data from all performed tows. These were carried out at different hours (8 times in April and 6 in September) for the 5 different layers. Then the daily grazing pressure of the female *C. euxinus* was estimated by taking into account its average abundance with ingestion rate. Grazing pressure, which was calculated as total pigment, was converted to carbon (C) by using (Phytoplankton Carbon) PC:Chl-a ratio. The PC values were estimated from the cell volume measurements of phytoplankton using carbon-volume relationship of

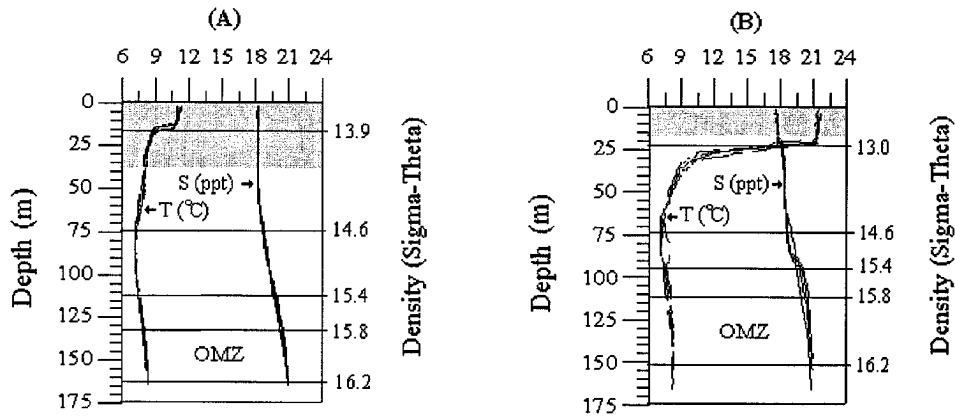## Temperature (°C) and Salinity (ppt)

Figure 2. The potential temperature and salinity profiles plotted against both depth and water density at the station in April (A) and in September (B) 1995. Measurements were repeated several times during the stay at the station. The sampling layers are shown with horizontal solid lines corresponding to different sigma-theta values (see Methods for detailed explanation). The shaded area shows the euphotic zone. The water column between the surface and the depth of 15.8 density surface is oxic. The depth below 16.2 density surface is anoxic. OMZ = Oxygen Minimum Zone.
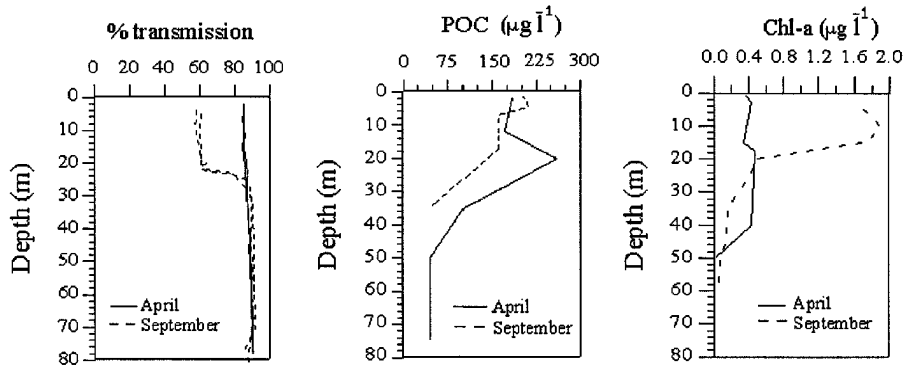

Figure 3. Vertical profiles of light tranmission, POC (Particulate Organic Carbon) and Chl-*a* (Chlorophyll-*a*) at the station in April and September 1995.

Strathmann (1967, Miss E. Eker unpublished data). The grazing pressure was obtained by dividing the calculated consumption of grazing rate by the integrated primary production of the water column (Yilmaz et al., 1996) .

Results

Hydrography and phytoplankton composition of the station

Salinity, potential temperature, Particulate Organic Carbon (POC), chlorophyll-*a*, and light transmission profiles obtained during the biological measurements are presented in Figures 2 and 3 to illustrate hydro-chemical properties of the water column (down to beginning of the anoxic water) of the region. In April the surface mixed layer is a relict feature of the winter time convective mixing and due to the spring time solar heating a new layer was formed in the first 10–15 meters of the water column (Figure 2). The depth of chlorophyll-a maximum was between 18–40 m (Figure 3). In September there was a sharp stratification at around 25 m depth due to the temperature. The Chl-*a* profiles showed maxima at 12–13 meters. Both in April and in September the light transmission measurements displayed minimum values near the surface indicating

the presence of higher amounts of suspended matter at this layer compared to lower depths, however the difference between the surface and deeper layers is much more pronounced in September. In September the transmission in the surface mixed layer was much lower than in April which was partly due to a higher abundance of both alive and broken gelatinous organisms observed visually in the former sampling period. In the top few meters, POC concentrations in September were also higher than that in April (Figure 3). The euphotic zone depth was 38m in April (corresponding to the two uppermost sampling layers) and 17 m in September (corresponding to the uppermost sampling layer).

In April there were 31 species of phytoplankton in the euphotic zone, and among these, the coccolithophorid *Emiliana huxleyi* was the most abundant species (Miss Elif Eker, unpublished data). *Heterocapsa triquetra* (synonym *Peridinium triquetrum*) and *Scrippsiella trochoidea* (synonym *P. trochoideum*) were the main species in Peridinea, and *Nitzschia delicatula* and *N. closterium* were the most dominant ones in Diatomea. Average phytoplankton concentration at the surface was 14×10^4 cells l^{-1} in April. This abundance was made up by 53% coccolithoporids, 19% dinoflagellates and 1.3% diatoms. In September both species number (56 species) and abundance (11×10^5 cells l^{-1}) were higher than those in April. Coccolithoporids represented almost entirely by *E. huxleyi* made up the bulk of phytoplankton abundance with 92%. The share of dinoflagellates and diatoms in phytoplankton was same with 2.8 and 2.9% respectively. *Exuviella cordata*, *E. compressa* and *Glenodinium paululum* among dinoflagellates and *Rhizosolenia calcar-avis* and *Nitzschia delicatula* among diatoms were the most abundant species (Miss Elif Eker, unpublished data).

During both sampling periods the oxygen minimum zone (OMZ) was observed between sigma-theta 15.8 and 16.2 (Figure 4).

Diel vertical migration

The vertical distributions of the female *Calanus euxinus* in April and in September are presented in Figures 5 and 6. The sun sets at 19:52h in April and at 17:43h in September. In both sampling periods the female *Calanus* began to migrate upward to the phytoplankton rich upper layers towards the evening. At night they concentrated in the first layer between the thermocline and the surface. After midnight the majority of copepods started to migrate downward. During
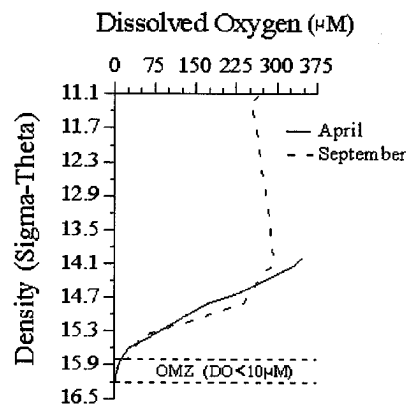

Figure 4. Vertical profiles of DO (Dissolved Oxygen) concentration at the station in April and in September 1995. OMZ = Oxygen Minimum Zone.

nighttime only a very small percentage of the female *Calanus* were present in the OMZ in both sampling periods: 3.6% in September and 0.2% in April. In the early morning (in April and in September the sun rises at 06:06h and 05:47h respectively) the bulk of the copepods was already in the OMZ. During daytime, female *C. euxinus* concentrated in the OMZ and this cycle was repeated throughout the sampling period. During the study, the abundance of the female *Calanus* in the water column showed some variations with different sampling time resulted most probably from physical dynamism as lateral intrusion of the water masses.

It was difficult to define accurately the extent of feeding period (in the sampling layers corresponding to the euphotic zone) due to the long (3–5 h) sampling interval; however, we can estimate roughly the duration that female *Calanus* spends at the euphotic zone from its vertical distribution figures (Figures 5 and 6). In April as some copepods are already in the upper layers at 17:00 and 18:00 hours, it could be assumed that they can begin to migrate around at 16:00h. The majority of the individuals must reach to the euphotic zone depth at around 21:00h. The lower boundary of the OMZ located at 162 m and thickness of the euphotic zone was 38 m so they should migrate at least 125 m to reach the euphotic zone. They spend 5 h to transit this 125 m resulting an upward speed of around 25 m h^{-1}. At 02:00h, just over the half of the copepods were still in the euphotic zone (Figure 5). According to the estimation of Hardy & Bainbridge (1954, cf. Marhall & Orr, 1972) the downward speed of *Calanus* is about 3 times higher than its upward speed over a long period experiment (i.e. 1 h). If this ratio is taken into account
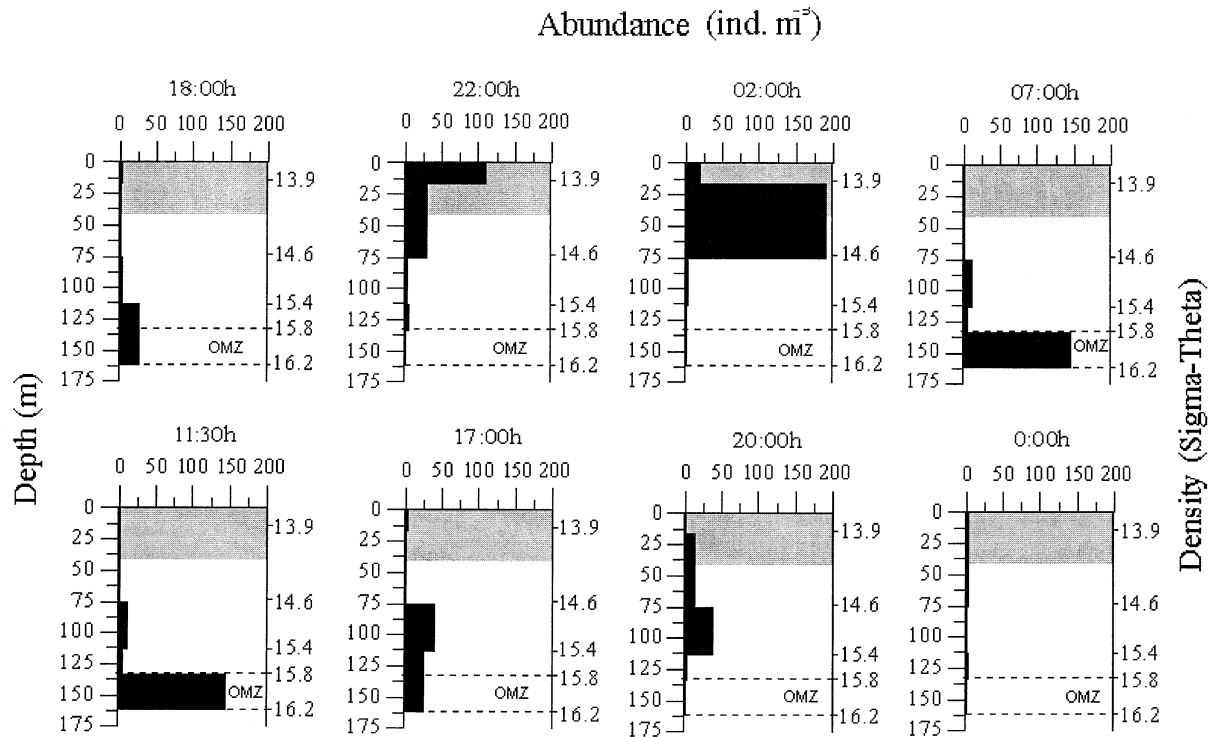
Abundance (ind. m⁻³)

Figure 5. Diel changes in the vertical distribution of female *C. euxinus* abundance (dark area) in April 1995. The shaded area indicates the euphotic zone. OMZ = Oxygen Minimum Zone.

the downward speed of *Calanus* will be 75 m h^{-1}, then it must take approximately 2 h to reach the OMZ. Since they were already in the suboxic layer at 07:00h, they must begin downward migration sometime between 02:00 and 05:00h. Consequently the duration of stay of female *Calanus euxinus* in the euphotic zone was 7.5 h in April. With a similar calculation, the duration of stay in the euphotic zone in September would be around 10.5 h, with an upward speed of around 34 m h^{-1} and downward speed of 102 m h^{-1}.

Gut pigment content

The background fluorescence for the starved individuals was estimated as 0.68 ± 0.39 ng pigment copepod^{-1}. After this value was accounted for, the overall average gut pigment concentration of female *Calanus* was calculated to be 10.1 ng pigment copepod^{-1} in April and 14.0 ng pigment copepod^{-1} in September (Table 1). Although gut content values were similar, the overall average ingestion rate varied due to the differences in the gut evacuation rate constant between the sampling periods. Using the equation of

Dam & Peterson (1988) the gut evacuation rate constant was 1.86 h^{-1} in April and 3.0 h^{-1} in September.

Grazing pressure on primary production

The ingestion rate of *Calanus* was calculated as 18.7 ng pigment copepod^{-1} h^{-1} in April and 42.0 ng pigment copepod^{-1} h^{-1} in September (Table 1). The average abundance of female *Calanus* in the whole water column was 3365 ind m^{-2} in April and 1343 ind m^{-2} in September (Table 2). These made up 11.4% of total copepod abundance (including copepodite stages) in April and 6.7% in September. Almost all female *Calanus* belonged to the migratory group. Only 3.6% in September and 0.2% in April were observed during the night time in the OMZ which could belong to a non-migrating population. By ommitting these non-migrating fractions, we assumed that each female *Calanus* in the water column migrate to the euphotic layer and spend 7.5 h day^{-1} in the euphotic zone in April and 10.5 h day^{-1} in September for feeding. Daily consumption by the female *Calanus* was estimated by taking into account the feeding duration, the number of individuals in the whole water column and

Table 1. Gut pigment content (S, ng pigment copepod^{-1}) and ingestion rate (ng pigment copepod^{-1} h^{-1}) of female *Calanus euxinus* in the layers encompassing the euphotic zone during April and September 1995. Gut evacuation rate constants (R) were 1.86 h^{-1} in April and 3 h^{-1} in September

Sampling hours	Gut Pigment Content in the Layers		Ingestion Rate $(I = SR)$
	from the thermocline to the surface	from sigma-theta 14.6 to the thermocline	
	April		
18:00	–	-	–
22:00	4.77	12.63	16.18
02:00	6.76	6.86	12.67
07:00	–	–	–
11:30	–	–	–
17:00	–	–	–
20:00	21.28	3.42	22.97
24:00	8.46	16.2	22.93
Overall Average =		10.1 ± 5.8	18.7 ± 4.4
	September		
19:00	8.7		26.2
23:30	8.7		26.1
03:30	18.8		56.3
07:30	–		–
12:00	–		–
16:00	19.9		59.6
Overall Average =	14.0 ± 5.3		42.0 ± 15.9

– there was not sufficient number of female copepods for the analysis.

Table 2. Number of female *C. euxinus* in the oxic water column and grazing pressure on primary production in the euphotic zone during April and September 1995. Standard deviations are shown in paranthesis

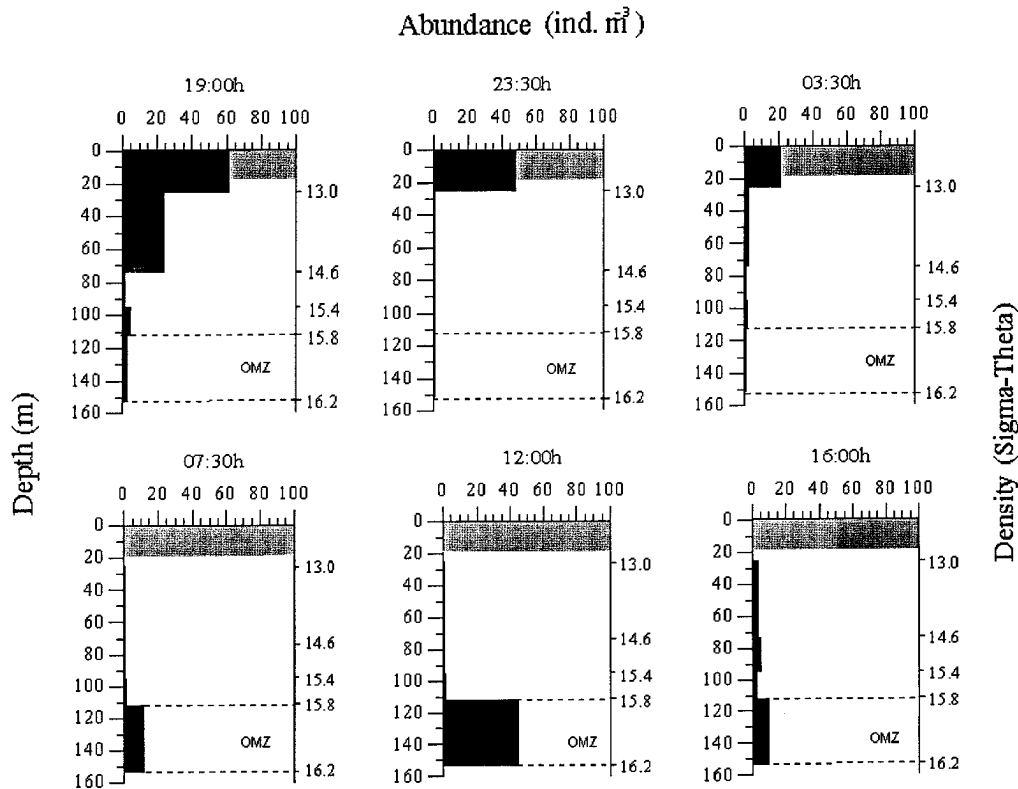|	April	September
No. of Ind. (m^{-2})	3365 (3340)	1343 (853)
POC (μg l^{-1})	178.9 (55.8)	188.6 (23.4)
PC (μg l^{-1})	25.8 (18.3)	85.0 (50.0)
Chl-*a* (μg l^{-1})	0.34 (0.05)	1.31 (0.51)
PC:Chl-*a*	76	65
Average Phytoplankton Conc. (cell l^{-1})	14×10^4 (2×10^4)	11×10^5 (54×10^5)
Consumption (as μg pigment m^{-2} day^{-1})	471.6 (112.1)	592.8 (224.8)
Consumption (as mgC m^{-2} day^{-1})	35.9 (8.5)	38.5 (14.6)
Primary Prod. (mgC m^{-2} day^{-1})	247.0	405.4
Grazing Pressure (%)	14.5 (3.5)	9.5 (3.6)

Abundance (ind. m^3)

Figure 6. Diel changes in the vertical distribution of female *C. euxinus* abundance (dark area) in September 1995. The shaded area indicates the euphotic zone. OMZ = Oxygen Minimum Zone.

gut pigment concentrations. In April 472 μg pigment m^{-2} day^{-1} and in September 593 μg pigment m^{-2} day^{-1}was found to be consumed in the euphotic zone by the female *Calanus* (Table 2). The PC:Chl-*a* ratios are 76 in April and 65 in September. These PC:Chl-*a* ratios were used to convert the consumed gut pigment to carbon. The estimated primary production values at this station were 247 mgC m^{-2} day^{-1} in April and 405 mgC m^{-2} day^{-1} in September (Yilmaz et al., 1996). So in April the consumption rate of female *C. euxinus* was calculated as 35.9 mgC m^{-2} day^{-1} representing 14.5% of the primary production, and in September the consumption was 38.5 mgC m^{-2} day^{-1}, equal to 9.5% of the primary production.

Discussion

Besides the higher abundance of jelly substances, the high suspended matter (which is deduced from the light transmission profile in Figure 3) observed above thermocline (the mixed layer) in September is due to two other additional factors; the effect of Danube river and the phytoplankton. A higher input from Danube river to the sampling area is clear from the salinity profile (Figure 2) which is lower in this period than that in April (as was previously observed by Sur et al., 1994). Since rivers in general and Danube river in particular (Balkas et al., 1990) contribute a considerable amount of terrestrial material, a higher river input into the area would cause a decrease in light transmission observed in September. Perhaps as a result of this high river input, the phytoplankton abundance in this sampling period (11 × 10^5 cells l^{-1}) was also much higher than that in April (14 × 10^4 cells l^{-1}). As a result the high concentration of phytoplankton did not only contribute to a decrease in light transmission, but also to a higher content of chlorophyll-*a* in September compared to April (Figure 3).

In the Black Sea a great portion of copepods migrate daily from the OMZ containing little or no phytoplankton into surface waters where phytoplankton is abundant (Vinogradov et al., 1985 and 1992; Vinogradov & Nalbandov, 1990), and this was also observed for

the female *C. euxinus* in this study. In both sampling periods, excepting a very small percentage, almost all female *C. euxinus* were observed to undertake diel migration. This result is in a good agreement with that found by Vinogradov & Nalbandov (1990) and Vinogradov et al. (1992). Therefore we can conclude that despite the existence of a non-migrating population of copepodite V of *Calanus*, females of this copepods are migratory. We estimated the feeding duration of female *Calanus* at the euphotic zone to be about 7.5 h in April and 10.5 h in September. Morales et al. (1993) found that feeding lasted at least 6 to 8 h for large fraction (1000–2000 μm) of copepods. Our rough estimation of speed was 25 m h^{-1} upwards and 75 m h^{-1} downwards in April. In September, the speed values were 34 m h^{-1} upwards and 102 m h^{-1} downwards. These differences in speed between both sampling periods may come from several environmental conditions, most notably being the temperature. The values found here are in the range of experimental results of Hardy & Bainbridge (1954, cf. Marshall & Orr, 1972). They observed that *Calanus* migrated with a speed of 66 m h^{-1} upwards and 107 m h^{-1} downwards over a short experimental period (2 minutes) while the speeds were 15 m h^{-1} upwards and 47 m h^{-1} downwards over a longer experimental period (1 hour).

There may be several reasons for the higher grazing pressure value in April (14.5%) compared to that in September (9.5%). First of all, there is a higher abundance of copepods with lower primary productivity in April than that in September. Besides these, phytoplankton composition in April could suit better for *Calanus* feeding. Petipa (1964) observed that Peridinea was the dominant group and Diatomea was the second most abundant group in the gut of *Calanus*. Coccolithophorids were rarely observed as a food item. While in both seasons coccolithophorids are more important than the other groups of phytoplankton, in April the abundance percentage of Peridinea was 19% while that of Diatomea was 1.3% in phytoplankton. In September the percentages of these two groups of phytoplankton were equal (3%).

The values on grazing pressure of the present study are comparable with those in the literature. Morales et al. (1993) estimated copepod community grazing < 10% of the daily primary production in the northeast Atlantic. Tsuda & Sugisaki (1994) found that the grazing rate of the copepods was 1.4 to 2.0% of the measured primary production in the western subarctic North Pacific during spring. Their results indicate that the copepod community was unimportant as a primary consumer where nano and picoplankton had dominated over phytoplankton. For the grazing intensity, the size of phytoplankton is very important, nano and picophytoplankton being too small for grazing by copepods (Tsuda & Sugisaki, 1994). In contrast to many other regions, the contribution of picophytoplankton to the Black Sea phytoplankton is low (Stelmakh, 1988). Arinardi et al. (1990) estimated the grazing intensity of 27 species of female copepods to be between 5 and 26% of the primary production in the upwelling site in the Banda Sea, Indonesia.

According to Ergun (1994), in the Southern Black Sea the bulk of copepod abundance is made up of only five species; *Calanus euxinus, Acartia clausi, Pseudocalanus elongatus, Centropages kroyeri* and *Paracalanus parvus*. His results suggested that *C. euxinus* constituted the biggest proportion of the biomass in each sampling period; June 1991, January and July 1992. During these sampling periods the average percentage of *C. euxinus* was 85% as biomass and 22% as number among all 5 common copepods. Therefore the considerable grazing pressure by the female *C. euxinus* found in this study is not suprising. Finally it can be concluded that female *Calanus euxinus* has a major importance in the transfer of organic matter from primary producers to the higher taxa, including pelagic fish.

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