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Diel vertical distribution, and herbivory of copepods in the south-western part of the Black Sea

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Abstract

The abundance and population structure of copepods were studied in the southwestern part of the Black Sea in May 1994, April and September 1995, April, June and September 1996. Vertical distribution and diel vertical migration of copepods were studied in April and September 1995 and June 1996. In addition, the grazing rates of three size classes of copepods—300–500, 500–1000 and 1000–2000 μm—were estimated in September 1995. The total abundance of copepods was higher in June samples due to the large contribution of the warm water species, *Paracalanus parvus*. Vertical distribution appeared to be related to season, species, stages of species and the oxygen concentration in the water column. Female, copepodite V (CV) and copepodite IV (CIV) stages of *Calanus euxinus* and female *Pseudocalanus elongatus* showed strong diel vertical migration from the surface waters to the oxygen minimum zone (OMZ). Copepodite stage V of *C. euxinus* showed seasonal migration, and was observed in diapaused phase at the OMZ in June and in September samplings. The large (1000–2000 μm) and medium (500–1000 μm) fractions of copepods had maximum gut fluorescence at night. Total grazing represented 32% of daily total integrated primary production. Phytoplankton carbon ingested met all three fractions of the basic metabolic requirements of the copepod community in the Black Sea.

Keywords: Copepods; Vertical distribution; Grazing; Black Sea

1. Introduction

The Black Sea ecosystem presently faces dramatic changes in the last decades. Changes in the species composition and in phytoplankton blooms have taken place. These changes seem to be connected with the eutrophication and other types of contaminants from river, atmospheric and land based sources and new invader into the ecosystem *Mnemiopsis leidyi* (Zaitsev and Alexandrov, 1997; Mee, 1992; Kideys, 1994; Cociasu et al., 1996; Kovalev et al., 1998; Shiganova et al., 1998; Moncheva et al., 1998; Kideys et al., 2000; Petruanu et al., 1999). For the better understanding of the conditions, some scientific researches have been conducted at national, regional and international levels. One of these programs was NATO TU-Black Sea project and one of the major goals of this project was to contribute environmental and oceanographic data to the improvement of the health of the Black Sea through the application of interdisciplinary ecosystem models of the lower trophic levels of the biological community. Within this context, the aim of the present study is to report the

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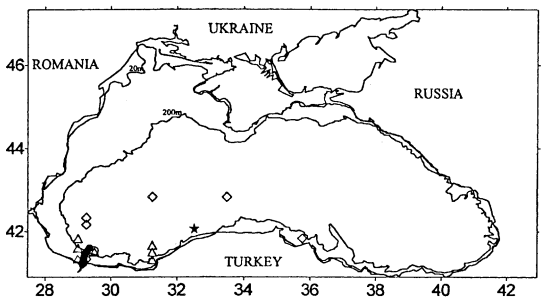

Fig. 1. Sampling stations of this study. ★ in May 1994, ○ in September 1995, △ in June 1996, ◇ in September 1996, ● in April 1995, 1996. Shown are the 20- and 200-m isobaths.

abundance, diel vertical distribution and grazing pressure of common copepods on the primary production in the southwestern part of the Black Sea.

1.1. Study area

Black Sea constitutes a unique marine environment. A strong halocline effectively inhibits vertical mixing. The oxygen supply to the deep waters is poor. As a result, permanent anoxia exists within 87% of the Black Sea's volume, making the Black Sea the largest anoxic basin of the entire world ocean. The halocline separates the oxic and anoxic waters and there is a well defined oxygen minimum zone (OMZ) between these waters (Murray et al., 1989; Tugrul et al., 1992; Saydam et al., 1993; Özsoy and Ünlüata, 1997).

The distribution of the pelagic fauna is related to the boundaries of the OMZ and divided Black Sea pelagic ecosystem into two parts: the aerobiotic and the chemobiotic (Vinogradov and Shushkina, 1992). The aerobiotic waters of the Black Sea are biologically productive because of high run-off from rivers around the basin. The chemobiotic environment includes the OMZ and the anaerobic layer. Only very few species can survive in the OMZ. *Calanus euxinus*, *Sagitta setosa* (Vinogradov et al., 1992a,b; Besiktepe et al., 1998; Besiktepe and Unsal, 2000) and *Pleurobrachia pileus* (Mutlu and Bingel, 1999) are observed in the OMZ.

2. Materials and methods

Copepod samples for abundance and population structure were collected in the southwestern part of the Black Sea in May 1994, April and September 1995, April and September 1996. Vertical distribution of copepods was analysed in April 1995, September 1995 and in June 1996. Grazing of copepod community was estimated from the samples collected in September 1995 (Fig. 1).

2.1. Hydrographic data

During all cruises, depth, and temperature of the water column were measured with a Seabird-SBE9

Table 1
Sampling depth layers used in this study and their characteristics

Sampling depth strata	Depth no.	Characteristics of depth strata
From the depth of the seasonal thermocline to the surface	1	mixed layer
From the depth of σ_θ = 14.6 to the depth of seasonal thermocline	2	σ_θ = 14.6 refers to the beginning of nitrification (Lipp and Kempe, 1993)
From the depth of σ_θ = 15.4 to the depth of σ_θ = 14.6	3	the majority of nitrification and remineralization of organic matter take place (Lipp and Kempe, 1993)
From the depth of σ_θ = 15.8 to the depth of σ_θ = 15.4	4	denitrification processes begin to occur at the depth of σ_θ = 15.4 (Baştürk et al., 1994)
From the depth of σ_θ = 16.2 to the depth of σ_θ = 15.8	5	σ_θ = 16.2 corresponds to the bottom of the OMZ. This is the daytime aggregation layer for late copepodite stages and the adults of *C. euxinus* (Vinogradov et al., 1992a,b).

OMZ = Oxygen Minimum Zone.

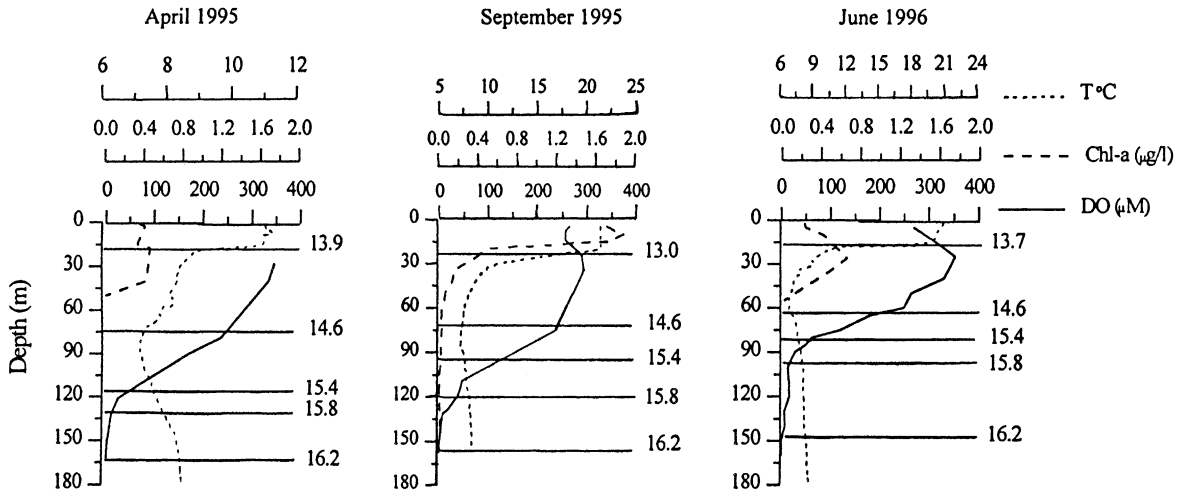

Fig. 2. Potential temperature, Chl-*a* and dissolved oxygen concentration are plotted against depth for 3 sampling months. Horizontal lines indicate the sampling depths and the corresponding sigma-theta values (for detailed explanation, see Table 1).

CTD profiler with fluorometer. Dissolved oxygen concentrations in the water column were determined by using modified conventional Winkler titration method (Konovalov et al., 1994). Chlorophyll-*a* (Chl-*a*) samples were collected from the discrete depths from the surface down to the depth of fluorescence minimum. Samples concentrated on GF/F filters were extracted with 90% acetone solution, and extracted according to Holm-Hansen and Riemann (1978). The fluorescence intensity of the samples was measured using a Hitachi F-3000 Model spectrofluorometer.

2.2. Sampling for abundance and population structure of copepods

Samples were collected by a Nansen Closing net of 200 μm mesh size in May 1994, and 112 μm mesh size in April and September 1995, April, June and September 1996 from the different depth layers beginning of anoxic layer to the surface in the

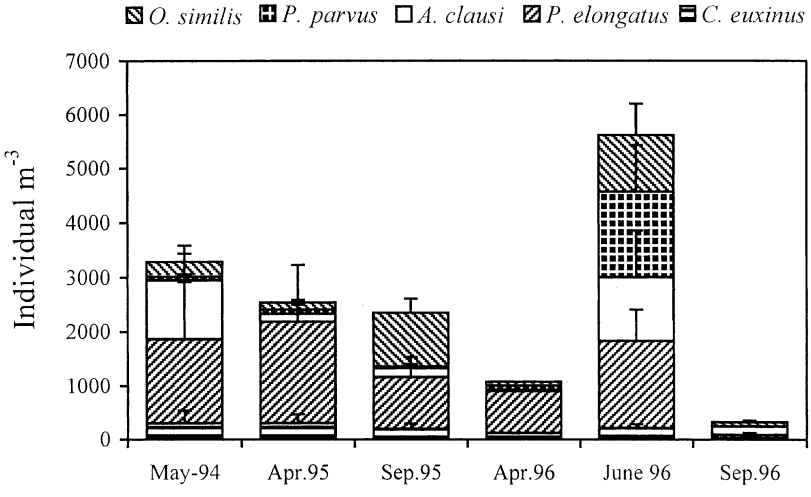

Fig. 3. Abundance (individuals m^{-3}) of copepods during the sampling periods.

southwestern part of the Black Sea. Collected samples were preserved with sodium borate buffered 4% formaldehyde-seawater solution until laboratory analyses. In laboratory, samples were subsampled with a Folsom Splitter and identified by a stereomicroscope. All copepods were enumerated, identified to species, staged (Boltovski, 1969) and their prosome lengths measured under a stereomicroscope.

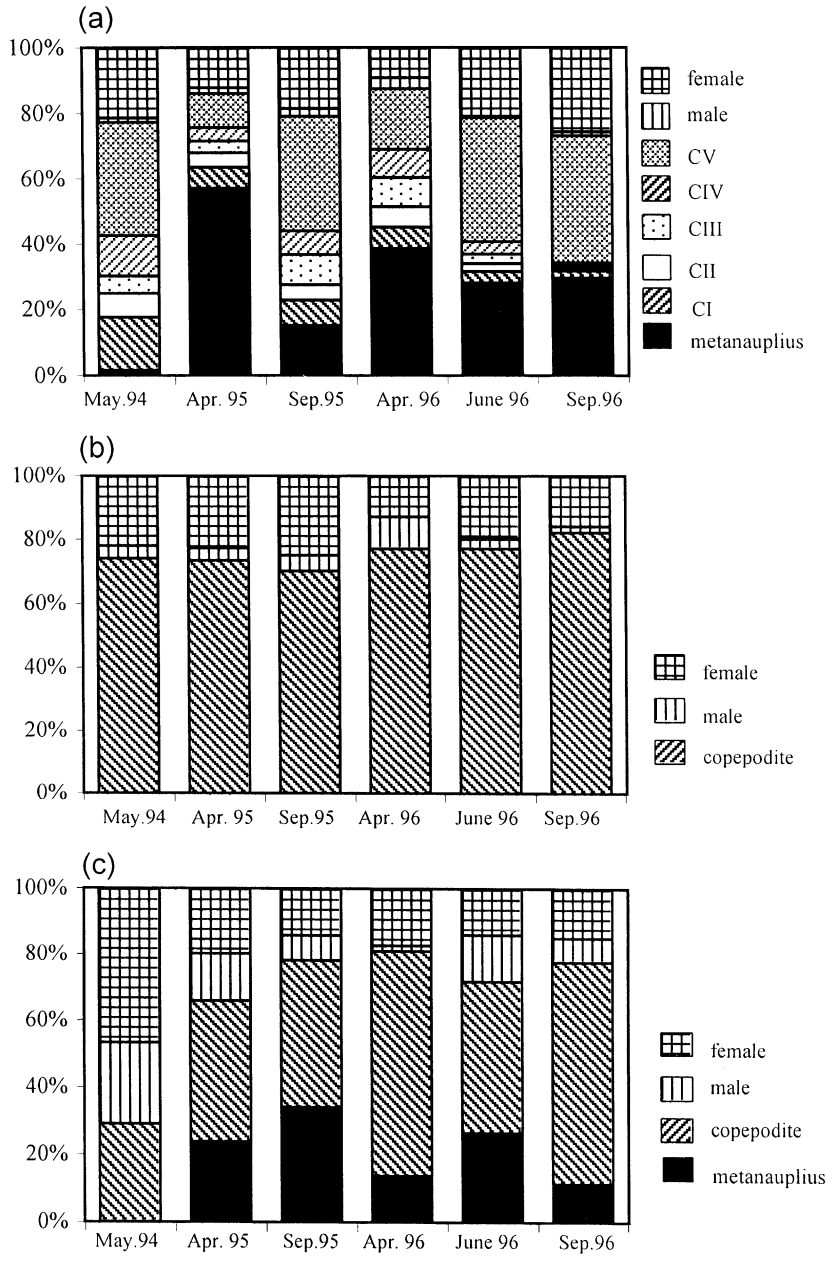

Fig. 4. Seasonal changes in frequency of stage composition of the copepods during the sampling periods. (a) *C. euxinus*, (b) *P. elongatus*, (c) *A. clausi*, (d) *P. parvus*, (e) *O. similis*.

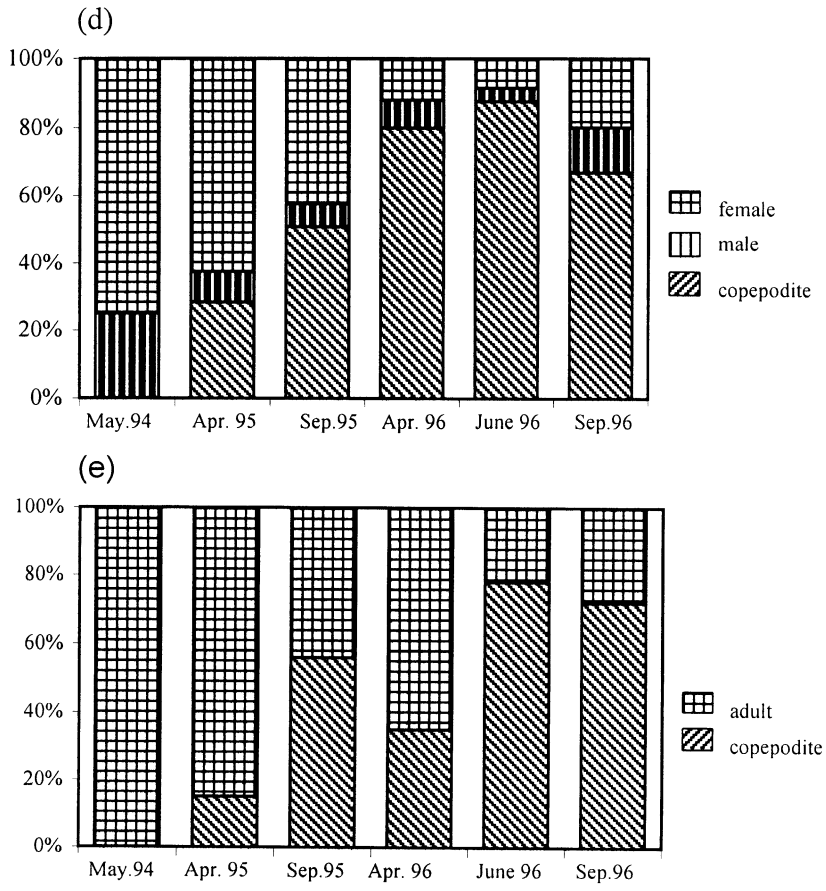

Fig. 4 (*continued*).

2.3. Sampling for diel vertical distribution of copepods

Zooplankton samples were collected from five different depth layers by a Nansen Closing Net of 112 μm mesh size in April and September 1995, and in June 1996. Samples were taken at 3–4 h intervals over a 30 h period in April 1995 and a 21-h period in September 1995 at a drifting station located in the southwestern part of the Black Sea (Fig. 1). Before each tow, the location of the station was fixed and before net tows, a CTD cast was done to identify depths of density layers. In June 1996, a 24-h period was completed from the different stations located in the southwestern Black Sea (Fig. 1). The density (Sigma-theta, σ_θ) was used to determine sampling depth intervals. Density was used because it is related to the major physical and biochemical characteristics of the water column that may affect the distribution of mesozooplankton in the Black Sea (Table 1).

2.4. Sampling for gut pigment content of copepods

Diel feeding of the copepod assemblages was investigated using the gut fluorescence method of Mackas and Bohrer (1976). Copepod samples were collected with a Nansen Closing Net (mouth opening 70 cm, mesh size 112 μm) via vertical hauls from 50 m, at which almost the base of the Chl-*a* (Fig. 2), up to the surface every 3–5 h in a daily station on 27–28 September 1995. After towing of the net, the cod end was taken immediately, sieved from 2000 μm mesh to remove jelly-like organisms, fraction-

ated into three size classes: 1000–2000, 500–1000 and 300–500 μm. Among phytoplankton species *Rhizosolenia* spp. was very abundant in 200–500 μm size fraction; in order to minimise the Chl-*a* contribution of this species to small size gut fluorescence, 300 μm was chosen for the lower size limit of small size fraction. Each size fraction was washed and rinsed with filtered seawater, then were filtered very gently on the GF/F filters; organisms other than copepods were removed under dim light before

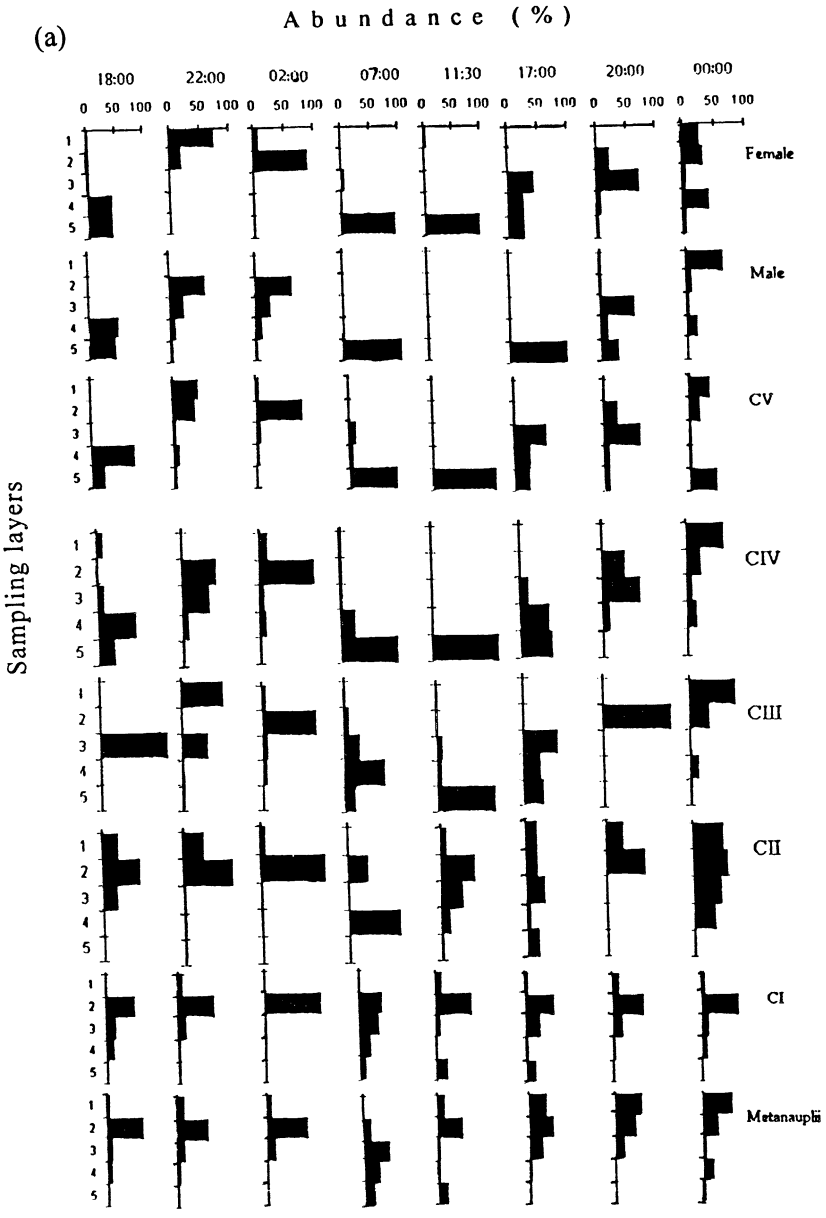

Fig. 5. Vertical distribution of different developmental stages of *C. euxinus*. Abundance is expressed as percentage of total population in the water column. Depth intervals are defined in Table 1. The sampling time is presented above the *x*-axis. (a) Samples collected during 26–28 April 1995; sunset = 19:52 h; sunrise = 06:06 h (local time). (b) Samples collected during 27–28 September 1995; sunrise = 17:43 h; sunset = 05:47 h (local time). (c) Samples collected during June 1996; sunset = 20:47 h; sunrise = 05:25 h (local time).

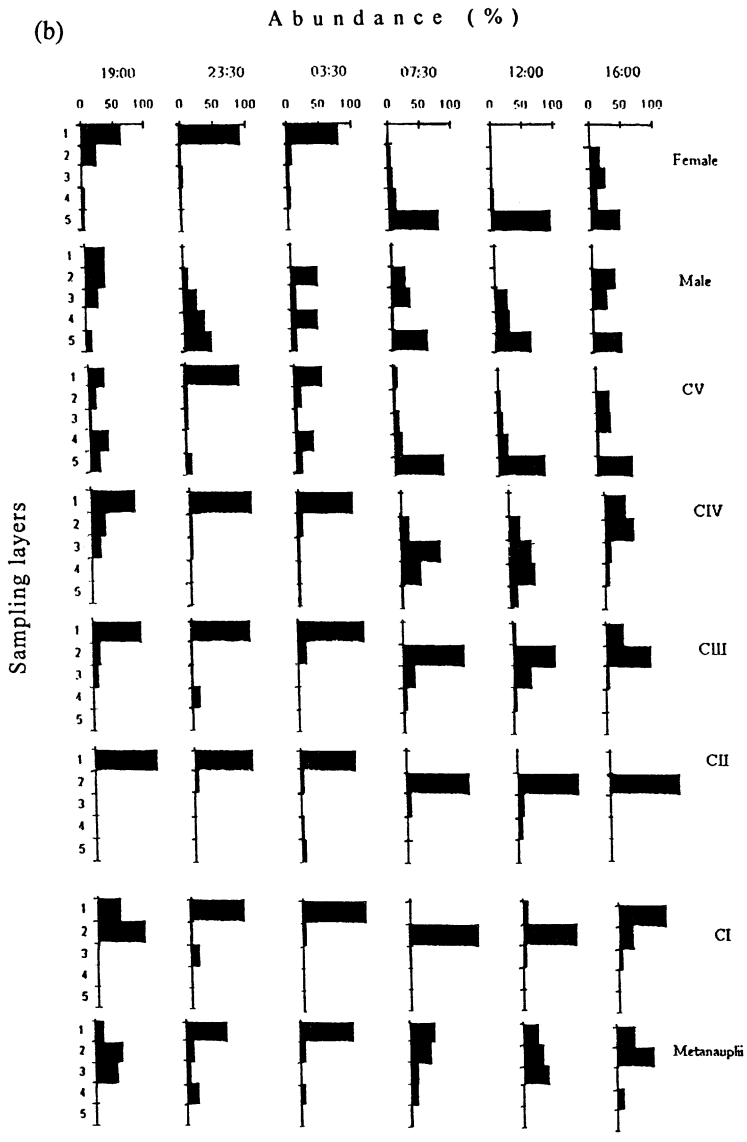

Fig. 5 (*continued*).

freezing at −20°C. Duplicate or triplicate samples were taken for each size class. The sampling process and fractionation took about 10–15 min. The numbers of organisms on the GF/F filters ranged from 8 to 28 for 1000–2000, 8 to 41 for 500–1000 and, 46 to 141 for 300–500 μm. Filters with copepod samples were homogenised in 10 ml of 90% acetone, and the fluorescence of the filtrate was measured before and after acidification with 10% HCl using Hitachi F-3000 model Spectrofluorometer. The gut content pigment was expressed as ng pigment (Chl-*a* + phaeopigment) per copepod individual for each size class. Copepod sample for enumeration and identification within 50 m was taken before every tow for gut pigment content.

2.5. Ingestion

Hourly ingestion rate is calculated from gut pigment content and calculated gut evacuation rate us-

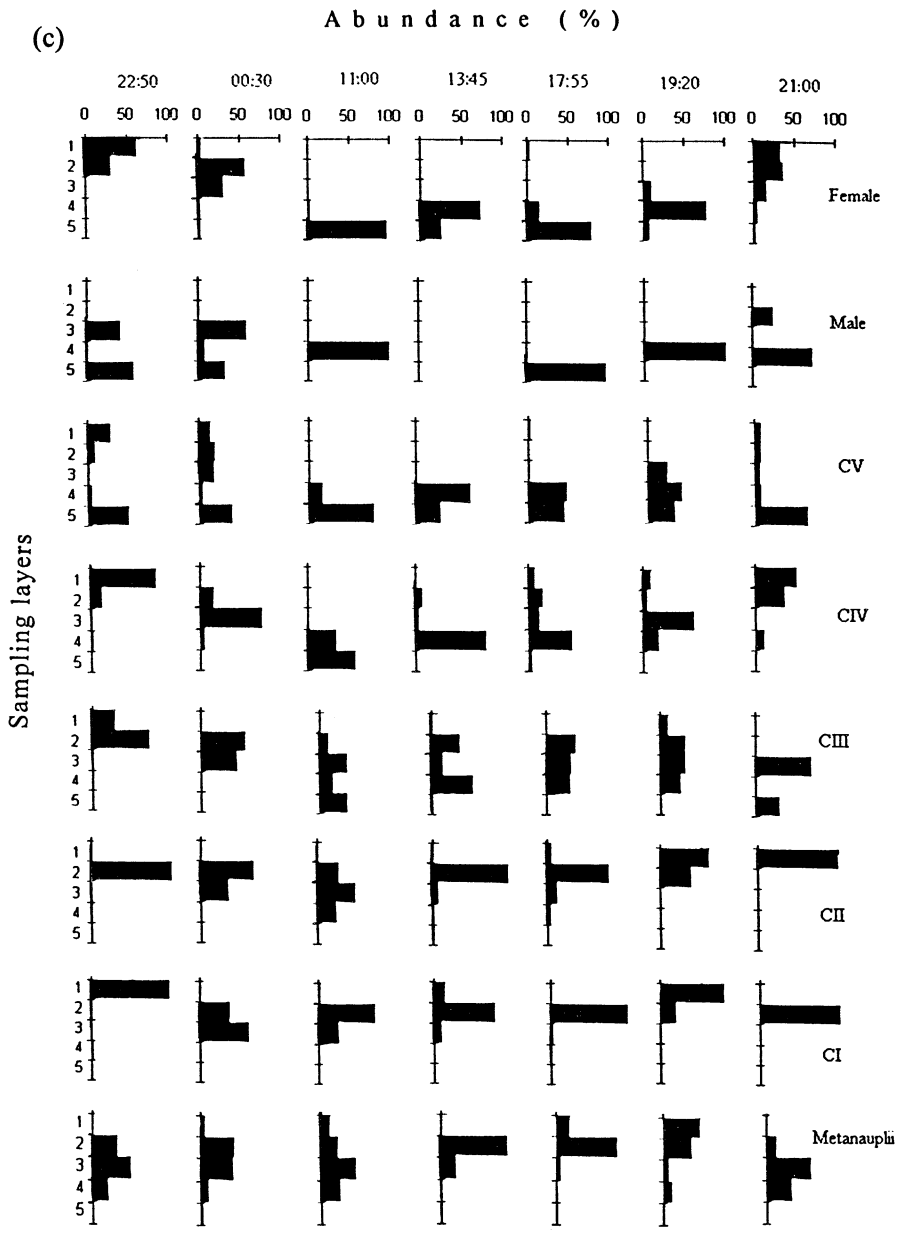

Fig. 5 (*continued*).

ing the expression $I = GR$, where G is the level of gut pigment content (ng pigment copepod^{-1}) and R is the instantaneous evacuation rate (h^{-1}).

Gut evacuation rates (R) were calculated from the relationship of Dam and Peterson (1988), who related gut evacuation rate to temperature, and showed no difference between species. The average temperature was 14.5°C in the water column down to 50 m. Calculated gut evacuation rate (R) was 2.4 h^{-1} for three size fractions. Total ingestion was calculated by taking into account each size's average abundance with ingestion rate. These values were calculated as total pigment, and were converted to carbon by using PC (Phytoplankton Carbon):Chl-*a* ratio.

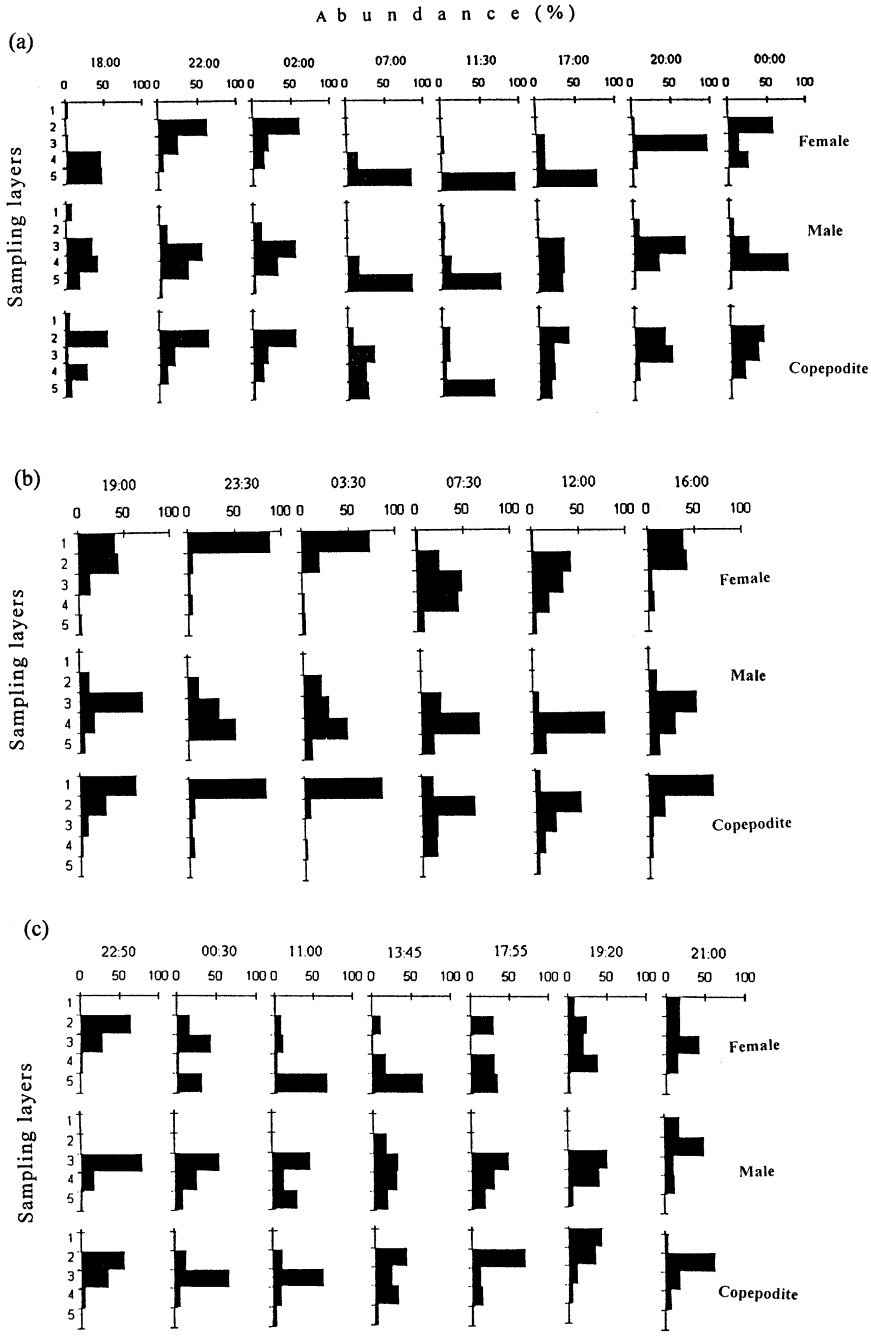

Fig. 6. Vertical distribution of female, male and total copepodite stages of *P. elongatus*. Abundance is expressed as percentage of total population in the water column. Depth intervals are defined in Table 1. The sampling time is presented above the *x*-axis. (a) Samples collected during 26–28 April 1995; sunset = 19:52 h; sunrise = 06:06 h (local time). (b) Samples collected during 27–28 September 1995; sunset = 17:43 h; sunrise = 05:47 h (local time). (c) Samples collected during June 1996; sunset = 20:47 h; sunrise = 05:25 h (local time).

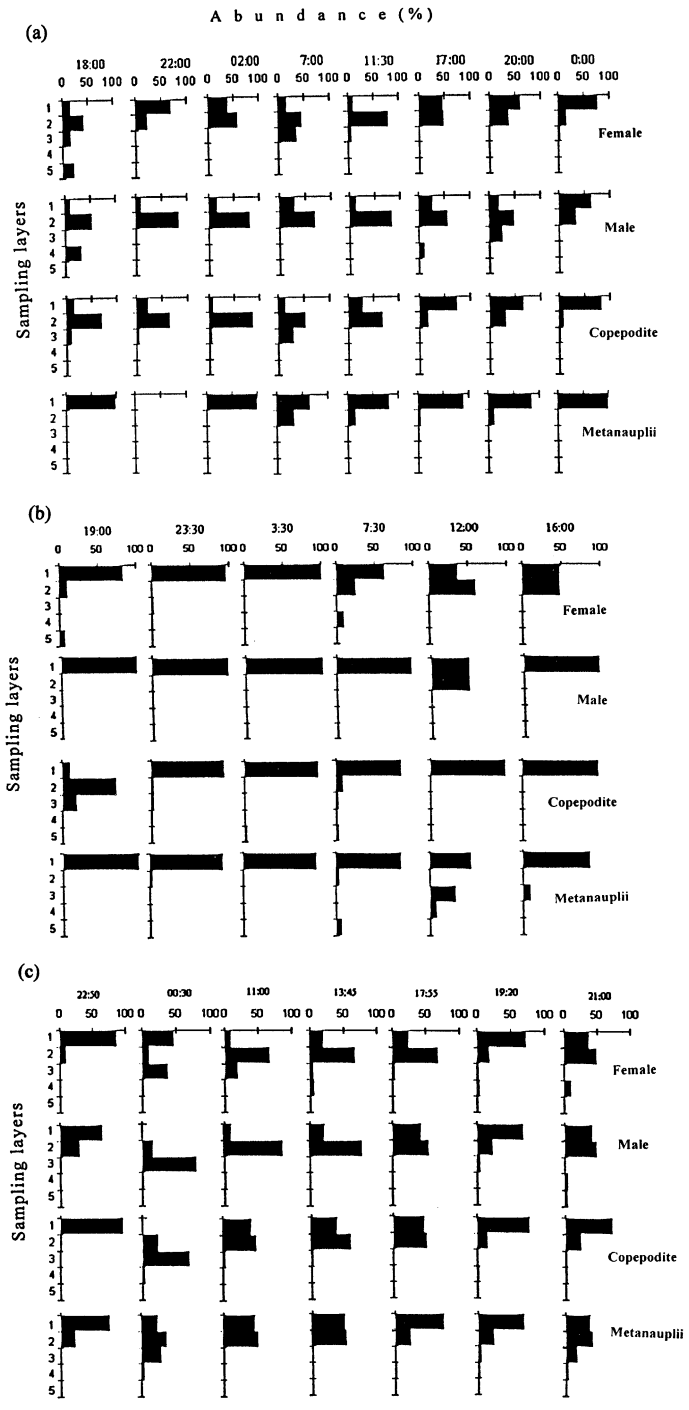

Fig. 7. Vertical distribution of female, male, total copepodite stages and metanauplii of *A. clausi*. Abundance is expressed as percentage of total population in the water column. Depth intervals are defined in Table 1. The sampling time is presented above the *x*-axis. (a) Samples collected during 26–28 April 1995; sunset = 19:52 h; sunrise = 06:06 h (local time). (b) Samples collected during 27–28 September 1995; sunset = 17:43 h; sunrise = 05:47 h (local time). (c) Samples collected during June 1996; sunset = 20:47 h; sunrise = 05:25 h (local time).

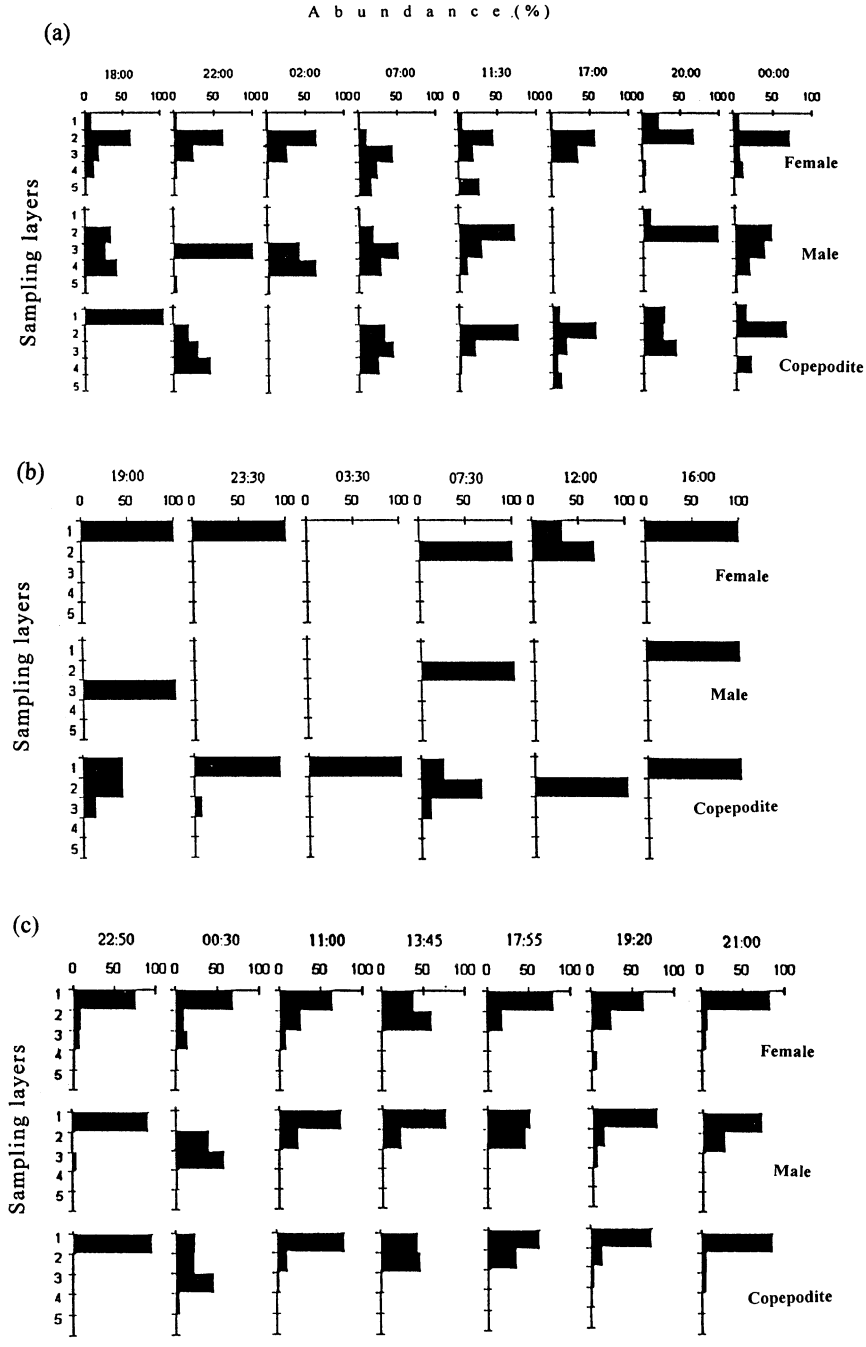

Fig. 8. Vertical distribution of female, male and total copepodite stages of *P. parvus*. Abundance is expressed as percentage of total population in the water column. Depth intervals are defined in Table 1. The sampling time is presented above the *x*-axis. (a) Samples collected during 26–28 April 1995; sunset = 19:52 h; sunrise = 06:06 h (local time). (b) Samples collected during 27–28 September 1995; sunrise = 17:43 h; sunset = 05:47 h (local time). (c) Samples collected during June 1996; sunset = 20:47 h; sunrise = 05:25 h (local time).

The PC values were estimated from the cell volume measurements of phytoplankton using carbon-volume relationship of Strathmann (1967, data from Eker, 1998). The grazing pressure on primary production

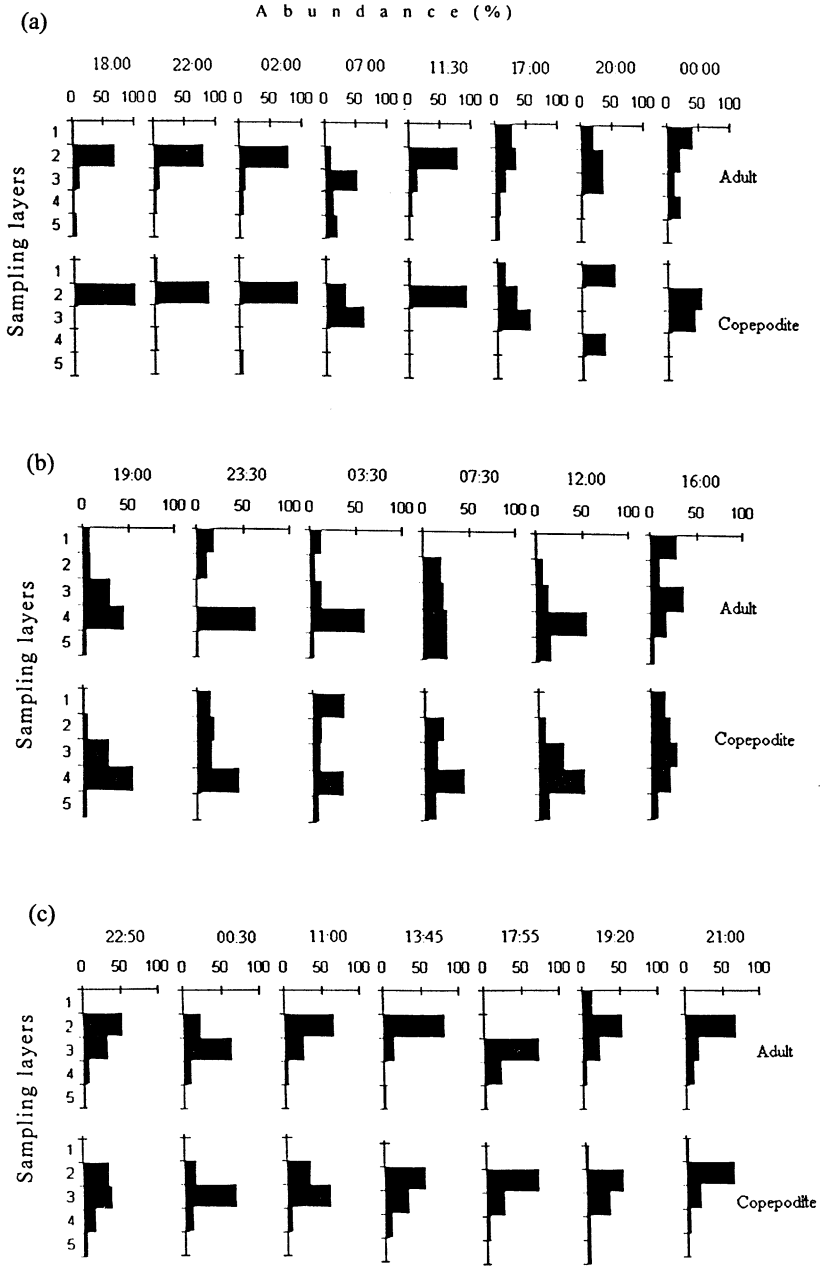

Fig. 9. Vertical distribution of adult and total copepodite stages of *O. similis*. Abundance is expressed as percentage of total population in the water column. Depth intervals are defined in Table 1. The sampling time is presented above the *x*-axis. (a) Samples collected during 26–28 April 1995; sunset = 19:52 h; sunrise = 06:06 h (local time). (b) Samples collected during 27–28 September 1995; sunset = 17:43 h; sunrise = 05:47 h (local time). (c) Samples collected during June 1996; sunset = 20:47 h; sunrise = 05:25 h (local time).

was obtained by dividing the calculated grazing by integrated primary production of the euphotic zone (Yılmaz et al., 1998).

3. Results

3.1. Hydrography

A well-developed thermocline was defined in the warm months, June and September (Fig. 2). The oxygen decreased sharply at about 14.6 density surface, and the core of the OMZ (<10 μM) was between density surfaces of 15.8 and 16.2 during all the sampling periods. The depth of Chl-*a* maxima (0.45 μg l^{-1}) was between 18 and 40 m in April 1995. In September 1995, Chl-*a* concentration was the highest (1.9 μg l^{-1}) in the surface and declined towards the bottom layers. In June 1996, the Chl-*a* maxima (0.7 μg l^{-1}) was below the thermocline (Fig. 2).

3.2. Abundance and population structure

In all sampling periods, five copepod species were observed: *Calanus euxinus*, *Pseudocalanus elongatus*, *Acartia clausi*, *Paracalanus parvus* and *Oithona similis*. Total copepod abundance (total copepodite stages + adults) had a maximum in July 1996 sample (Fig. 3). The most abundant copepod in all sampling periods was *P. elongatus*, except in September 1995 and 1996. In September 1995, the abundance of *P. elongatus* and *O. similis* was almost the same, accounting for around 41% of the total copepod population (965 for *P. elongatus* and 993 for *O. similis* out of 2350 individuals m^{-3}). In September 1996, almost half, 47% (156 out of 329 individuals m^{-3}) of the copepod population was made up of *A. clausi*. *C. euxinus* accounted for 9–12% of the total copepod abundance in almost all sampling periods; it accounted for 4% in June 1996 (Fig. 3).

The percentage contribution of each developmental stage of *C. euxinus* population is shown in Fig. 4a. In April, the population was youngest (metanauplii, CI, CII and CIII) whereas the oldest stages (CIV, CV, adults) made up $>60\%$ of the population in May, June, and September. During the sampling periods, adults represented 11–27% of the population and females always outnumbered males.

The percentage frequency of developmental stages of *P. elongatus* is shown in Fig. 4b. Total copepodite stages formed $\geq 70\%$ of the population. Females comprised between 13% (in April 1996) and 25% (in September 1995) of the population. Males occurred in high numbers only in April 1996 (10% of the population), but observed very rarely in the other sampling periods.

The percentage frequency of developmental stages of *A. clausi* is shown in Fig. 4c. Metanauplius consisted in the range of 11% (in September 1996) and 27% (in June 1996) of the population. In May, no metanauplius was observed since the mesh size of net used was 200 μm and it would allow them to slip through. Copepodite stages made up a large fraction of the population at almost all sampling periods, except in May when females comprised 47% of the population. Females were generally found in high numbers than males, except in June when the number of females and males was almost the same.

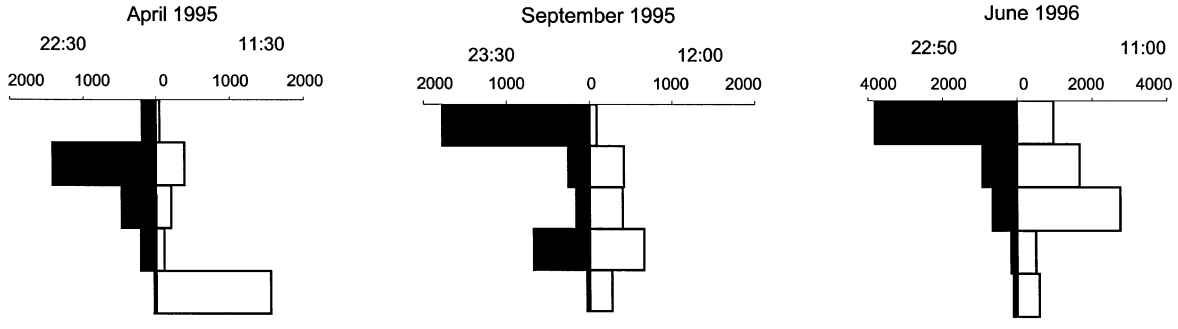

Fig. 10. Vertical distribution of total copepod (individuals m^{-3}) species in 3 different months. Black bars represent samples collected at the nighttime and open bars represent samples collected at the daytime.

Fig. 4d shows the percentage frequency of developmental stages of *P. parvus*. Copepodite stages dominated the population in April, June and in September 1996. In April 1995, adults made up the $> 60\%$ of the population. No copepodite stages were found in May 1994. In September 1995, the stage distribution was bimodal with the equal percentage of adults and copepodites. Females always outnumbered males.

The seasonal changes in population structure of *O. similis* are shown in Fig. 4e. Total copepodite stages dominated the population in June 1996,

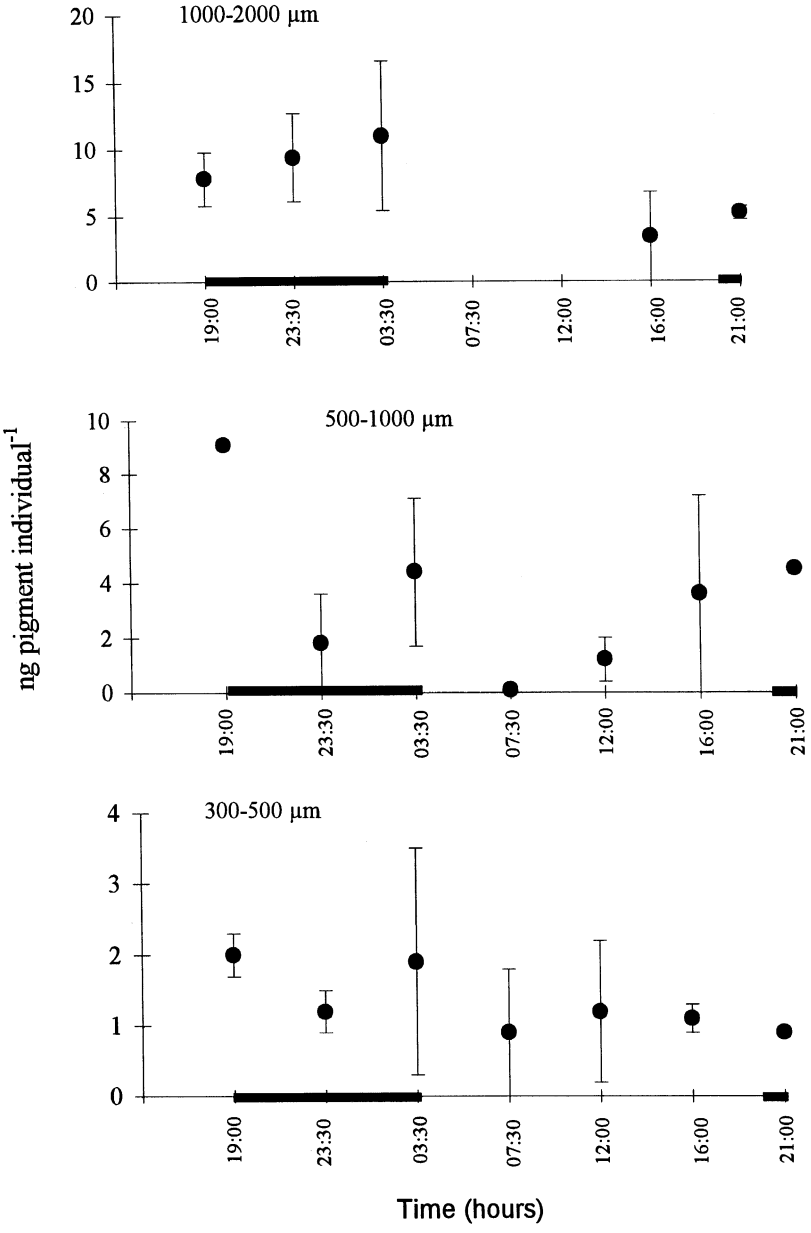

Fig. 11. The diel gut fluorescence for three size fractions of copepods sampled from 50 m to the surface in September 1995. Each point represents mean values $\pm$ S.D. Shaded bar along the *x*-axis indicates the hours of darkness.

September 1995 and 1996. In April samples, the adults made up $>60\%$ of the population, while no copepodite stages were observed in May. In May 1994, the mesh size of the net was 200 μm, and the copepodite stages of *P. parvus* and *O. similis* might have passed through this mesh size.

3.3. Diel vertical distribution of copepods

Vertical distribution of *C. euxinus* was analysed for female, male, all copepodite stages and metanauplii stage (Fig. 5). Females, copepodite V (CV) and copepodite IV (CIV) showed diel vertical migration pattern. They were at the depth of OMZ at daytime and the upper layers at nighttimes. There was no apparent diel vertical migration in males except in April 1995. CIII, CII and CI showed small-scale periodic migration between the third layer and the surface. Metanauplii distributed generally uppermost three layers.

Vertical distribution of *P. elongatus* was studied as female, male and total copepodite stages (Fig. 6). The well-defined characteristics of diel vertical migration of female *P. elongatus* were observed only in April 1995 sampling. In the other seasons, females showed limited diel vertical migration pattern, while the majority of them were in the upper layer at nighttime, deeper layers in the daytime. Males and copepodite stages collected in September and June were found in the intermediate layers as independent on the diel periodicity.

Vertical distribution of *A. clausi* was studied as female, male, total copepodite stages and metanauplii stage. Female *A. clausi* showed limited vertical migration between the first and second layer in April and in June but this migration was not obvious in September. There was no apparent diel vertical migration in male, copepodites and metanauplii stages of *A. clausi* (Fig. 7). They were generally distributed above the thermocline.

All developmental stages (female, male and copepodites) of *P. parvus* showed inconsistent vertical distribution (Fig. 8). In April 1995, during nighttime and daytime, their peak in abundance was generally in the second layer and their maximum concentrations were found sporadically in the third and fourth layers. In the other sampling periods, they occurred frequently in the first layer during nighttime and daytime.

Vertical distribution of *O. similis* population was analysed as adult and total copepodite stages (Fig. 9). This cyclopoid copepod species showed inconsistent distribution throughout the water column.

Total copepod abundance in the water column at one nighttime and one daytime is shown in Fig. 10. In April, the difference of vertical distribution between nighttime and daytime appeared more clearly due to the high contribution of strong vertical migrants (i.e. *C. euxinus* and *P. elongatus*) on the copepod abundance. In September and June, most of the copepods live primarily above the OMZ day and night, and showed small-scale periodic migration.

Table 2
Percentage abundance of three size fractions of copepods sampled from 50 m to the surface in September 1995

Species	2000–1000 μm	1000–500 μm	500–300 μm
C. euxinus			
Female	28.3	–	–
Male	3.3	–	–
Copepodite V	43.7	0.7	–
Copepodite IV	14.1	2.1	–
Copepodite III	2.5	7.5	0.4
Copepodite II	0.8	4	4.7
Copepodite I	0.2	1.9	3.3
P. elongatus			
Female	3.9	44.8	28
Male	–	1.3	0.7
Copepodite stages	1.5	13.2	36.9
A. clausi			
Female	1.1	13.6	2.2
Male	–	5.9	1.8
Copepodite stages	0.3	4	5.2
Par. parvus			
Female	0.2	–	1.3
Male	–	–	0.5
Copepodite stages	–	–	0.9
O. similis			
Female	–	1.0	10.9
Male	–	–	–
Copepodite stages	–	–	3.2

(–) No individuals observed.

Table 3
The gut pigment content (G; ng pigment individuals^{-1}), ingestion rates (I; ng pigment individuals^{-1} h^{-1}) and the percentage grazing rate of each size fraction of copepod assemblages during the sampling times in September 1995

Time of day	Large size				Medium size				Small size			
	G	I	Individual m^{-2}	% Grazing	G	I	Individual m^{-2}	% Grazing	G	I	Individual m^{-2}	% Grazing
19:00	7.8 (2.0)	18.6	1873.7	13.4	9.1 (0.0)	21.8	7242.1	60.6	2.0 (3.0)	4.8	3410.6	6.3
23:30	9.4 (3.0)	22.6	2863.2	24.9	1.7 (1.8)	4.1	3536.8	5.6	1.2 (0.3)	2.9	17852.6	19.6
03:30	11.0 (6.0)	26.4	926.3	9.4	4.4 (2.8)	10.5	1937.2	7.8	1.9 (1.6)	4.6	3536.8	6.3
07:30	0.0	0.0	176.3	0.0	0.1 (0.1)	0.3	1221.1	0.1	0.9 (1.1)	2.2	3368.4	2.9
12:00	0.0	0.0	305.3	0.0	1.2 (0.8)	2.8	2863.2	3.1	1.2 (1.0)	2.8	3368.4	3.7
16:00	3.4 (3.0)	8.2	1557.9	4.9	3.6 (3.8)	8.6	7409.5	24.1	1.1 (0.2)	2.6	5894.7	5.8
21:00	5.2 (0.5)	12.6	863.5	4.2	4.5 (6.0)	10.8	3789.5	15.7	0.9	2.2	2610.5	2.2
Average	5.6 (4.4)	12.6 (10.5)	1223.7 (947)	8.1 (8.8)	3.5 (3.0)	8.4 (7.1)	3999.9 (2438.0)	16.7 (21.0)	1.3 (0.5)	3.1 (1.1)	5720.3 (5447.6)	6.7 (5.9)

Gut evacuation rate = 2.4 h^{-1}; Phytoplankton carbon/Chl-a ratio = 65; Primary production = 405 mg C m^{-2} day^{-1}. Values in parenthesis are standard deviations.

3.4. Gut pigment content and ingestion rates

A diel gut pigment rhythm consisted of tows from the upper 50 m, at 4-h intervals, for a 26-h period in September 1995. Gut pigment content (GPC) of the three size fractions is presented in Fig. 11. All data represent the mean values obtained from two to three replicates depending on the abundance of organisms.

Within the large fraction, there was a trend of increasing gut pigment content during the night feeding period (Fig. 11). The highest value was reached towards the end of darkness (at 03:30). In this fraction, around 86% of species abundance was dominated by the vertical migrant organisms, i.e. female, CV and CIV stages of *C. euxinus* (see Table 2), and during daytime (07:30, 12:00, 16:00) sufficient number of individuals could not be found for GPC analysis.

Within the medium size fraction, variation in gut fluorescence values (Fig. 11) was high especially at nighttime. The average pigment ranged from 0.1 to 9.1 ng pigment individual^{-1} and the amount of explained variance was 78.5% among the GPC data. However, there was evidence of diel patterns in gut fluorescence for the medium size fractions.

Within the small size fraction, there was not a pattern of decrease or increase in gut pigment content with time of the day; the coefficient of variation was 32% among the GPC data. The small copepod species contained very low levels of pigment in their guts ranging from 0.9 to 2.0 ng pigment individual^{-1} (Fig. 11).

The average daily grazing was obtained by the medium size fraction with 16.7% of primary production, and the large fraction had 8.1% grazing on the primary production. The lowest grazing value was found in the small size fraction with the value of 6.7% of primary production (Table 3).

4. Discussion

4.1. Abundance and population composition

The maximum abundance of copepods was observed in June 1996. *P. parvus* made up 28% contribution to the total copepod abundance in this season, whereas they were very rare in the other seasons. Greze et al. (1971) have defined *P. parvus* as a warm-water species (optimum temperature is between 10°C and 20°C) and observed its maximum abundance in August. There was no consistent pattern of abundance with season; abundance in April and September 1995 was higher than those collected in April and September 1996.

Because of the spacing of the cruises it is impossible to identify the generation times of the species. However, metanauplii of *C. euxinus* were observed during all sampling periods, but they comprised more than half of the *C. euxinus* population in April. It can then be concluded that April is the main production season of new generation. During summer, the percentage abundance of metanauplii fluctuates from the range of 15–30% of the population; there can be a subsidiary generation during these periods. Zenkevitch (1963) and Sazhina (1987) reported that *C. euxinus* reproduce during the whole year and form 5–7 generations in a year.

The total copepodite stages of *P. elongatus*, *A. clausi* and *P. parvus* were dominant in almost all sampling periods. It is reported that these species reproduce throughout the year, producing six to nine generations in the Black Sea (Greze and Baldina, 1967; Greze et al., 1971; Sazhina, 1987). In this study, total copepodite stages of *O. similis* were dominant in June and September samples. Greze et al. (1971) observed high number of nauplii and copepodites in April, June, July, and September and November; they found the eggs throughout the year with a peak in July and detected six to seven generations in a year.

4.2. Vertical distribution

Vertical distribution of the species appeared to be related to season, species, stages of species and the oxygen concentration in the water column in the Black Sea. Among small species, *A. clausi* and *P. parvus* were observed mostly uppermost three layers while *O. similis* were found in the OMZ. Low oxygen concentration did not appear to restrict the vertical distribution of *O. similis*. Similar findings

have been reported before for Chesapeake Bay by Roman et al. (1993) and for eastern tropical Pacific by Saltzman and Wishner (1997). Differences in the vertical distribution of the stages of *C. euxinus* and *P. elongatus* have been observed. Female, CV, CIV stages of *C. euxinus* and female *P. elongatus* showed strong diel vertical migration from the surface waters to the OMZ, while the majority of the other stages remained uppermost three layers (~ first 100 m). Data obtained in this study are in agreement with the previous results from the Black Sea by Vinogradov et al. (1985, 1986, 1990, 1992a,b), Zenkevicth (1963) and Zagorodnyaya (1970).

Copepodite stage V *Calanus* undergoes seasonal migration during summer and early autumn (during warmer period) in the Black Sea. When some of them were at the upper layer during nighttime, some part of the CV population were still staying at the OMZ as in the diapause period. In June, around 50% of the CV population was in the diapausing period, while in September only 13% of the population was observed in diapausing period. Vinogradov et al. (1990) reported that 60–75% of stage V remained at the lower limit of the oxygenated layer at nighttime in August. The OMZ may be used a refuge from predation by diapausing stage or vertical migrants as pointed out before by Alldredge et al. (1984) and Vinogradov et al. (1986).

4.3. Gut pigment content and grazing pressure

In the present study, gut pigment concentrations fell between 0.1 and 11 ng pigment individual^{-1} of copepod for the 300–500, 500–1000, 1000–2000 μm fractions. These pigment concentrations were similar to values measured in other field studies of mesozooplankton grazing. For example, gut pigment content measured for *Neocalanus cristatus* CV ranged from ~ 1 to 15 ng pigment copepod^{-1} (Tsuda and Sugisaki, 1994).

Our grazing estimates were derived from gut fluorescence method. The degree of pigment destruction during the digestion processes is highly variable in this method (Dam and Peterson, 1988; Head and Harris, 1996). An average value of 33% has been estimated (Dam and Peterson, 1988). No correction for pigment destruction was made on the assumption that there was little pigment destruction at the low food concentration (1000 cells ml^{-1}) (Penry and Frost, 1991). The average number of phytoplankton cell was 1100 cells ml^{-1} at the station (Eker, 1998). Increase in gut pigment concentration at night hours in the large and medium size fraction was in good agreement with the previous studies (Mackas and Bohrer, 1976; Morales et al., 1993; Atkinson, 1996). However, this increase at night hours was not obvious in small size fraction.

Daily removal of the primary production by total mesozooplankton was 32% (see Table 3); this corresponds to 128 of 405 mg C m^{-2} day^{-1} in this study. The limited impact of grazing by mesozooplankton on the primary production has been reported in several studies for the other regions. Morales et al. (1991) estimated removal rates of 1–2% of the primary production in north-east Atlantic, while Dagg (1993) estimated removal rates of the primary production of 6–15% for the subarctic Pacific Ocean. Other estimates of rates of removal of primary production by large copepods during spring bloom ranged from 4% to 100% day^{-1} in shelf waters off the New York Bight (Smith and Lane, 1988).

The present study has attempted to estimate community grazing impact on primary production by employing measurements of ingestion rates, copepod abundances and primary production. The variability in grazing impact during the study was mainly a result of differences in both copepod abundances and gut pigment content among the sampling times. Although large copepods showed the highest daily ingestion rates on an individual basis, the overall highest grazing on primary production was performed by the medium sized copepods, due to their numerical abundance. It is calculated that 53% of the community grazing was due to medium size fraction. In contrast to Morales et al. (1991) and Dam et al. (1993), whom discussed the relative importance of small size fraction grazing on primary production in the North Atlantic, the medium sized copepods grazing was considerably most important among the three size classes in September 1995 in the Black Sea. Regarding the estimation of copepod abundances, the small size fraction of copepods only included those larger than 300 μm. Many copepodites and *O. similis* individuals might have passed through the 300-μm mesh filter and thus have not been considered in calculating grazing rates. The

Table 4
Grazing pressure, biomass and basic metabolic requirements of copepods from the first 50 m in September 1995

Time of day	Large size			Medium size			Small size		
	GP	B^a	R^b	GP	B	R	GP	B	R
19:00	54.3	116.2	7.3	245.7	24.2	2.2	25.5	4.9	0.5
23:30	100.9	169.8	10.7	22.7	22.1	1.8	79.5	21.8	2.1
03:30	38.1	63.6	4.0	31.6	9.0	0.8	25.5	7.9	0.7
07:30	0.0	0.0	0.0	0.4	5.0	0.4	11.8	7.4	0.7
12:00	0.0	0.0	0.0	12.6	16.5	1.4	15.0	8.6	0.8
16:00	18.9	94.1	5.9	97.7	31.4	2.7	23.5	15.0	1.4
21:00	17.0	52.6	3.3	63.6	17.8	1.5	8.9	7.5	0.7

GP = Grazing pressure (mg C m^{-2} day^{-1}), B = Biomass (mg C m^{-2}), R = Respiration (mg C m^{-2} day^{-1}).

[a]The wet weight of copepods for each size fraction was calculated by using a constant value estimated by Ukranian Scientists for each stage of the copepod species in the Black Sea (Niermann et al., 1995). The dry weight was estimated from the assumption of 20% of wet weight, and converted to carbon assuming that 40 % of the dry weight is due to carbon (Parsons et al., 1990).

[b]Respiration rates were estimated using Dagg et al.'s (1982) equation: $R = 0.101W_c^{0.884}$, where R is the respiration rate as μg C $animal^{-1}$ day^{-1}, W_c is the animal size as μg C.

estimated percentage abundance of loss from 300-μm mesh filter was 15% of the total abundance of small-sized copepods. When considering this loss, the ingestion rate of small size fraction was still lower than that of large size fraction.

The grazing rate estimated in this study is relatively high. For example, the daily carbon ration ranged from 20% to 70% of the body carbon for large size fraction, from 10% to 360% for medium size fraction and from 4% to 310% of the body carbon for small size fraction. In general, our data show that the phytoplankton carbon ingested apparently met all fraction of basic metabolic requirement when respiration rate was estimated using the Dagg et al. (1982) equation (Table 4). These results imply that the food source of mesozooplankton was mainly phytoplankton in September 1995 in the Black Sea.

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