STUDIES ON SOME ECOLOGICAL ASPECTS OF COPEPODS AND CHAETOGNATHS IN THE SOUTHERN BLACK SEA, WITH PARTICULAR REFERENCE TO *CALANUS EUXINUS*

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ABSTRACT

STUDIES ON SOME ECOLOGICAL ASPECTS OF COPEPODS AND CHAETOGNATHS IN THE SOUTHERN BLACK SEA, WITH PARTICULAR REFERENCE TO *CALANUS EUXINUS*

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The dominant copepods *Calanus euxinus, Pseudocalanus elongatus, Acartia clausi, Paracalanus parvus* and *Oithona similis*, and a chaetognath *Sagitta setosa* were investigated with respect to their abundance, vertical distribution and developmental stage composition during May 1994-December 1996 in the southwestern Black Sea. *P.parvus, O.similis* and *A.clausi* were most abundant in June, while *P.elongatus* and *C.euxinus* reached highest concentration in April and May. The highest number of *Sagitta* was observed in September. The diel vertical migration was pronounced in copepodite-IV, copepodite-V, female *C.euxinus*, female *P.elongatus* and in mature *Sagitta*. The CV individuals of *C.euxinus* were observed in diapause phase at the lower layer of oxygen minimum zone, in June and September samplings.

Gut pigment content of copepod assemblages and grazing impact on primary production were estimated in September 1995. The medium size fraction (1000-500μm) of copepods was important group in terms of numerical abundance and their grazing impact. About 31.5% of primary production was grazed by copepod assemblages.

It was found that, the 14.5% and 9.5% of primary production were consumed by female *C.euxinus* in April and September respectively.

The seasonal differences in total lipid content (TL) of female and copepodite-V *Calanus* were detected in August 1993, May 1994, September 1995-1996, and the maximum TL was found in September 1995, copepodite-V individuals have higher TL than in females. The wax esters was the major lipids in *Calanus*. However, triacylglycerides and phospholipids were found in small amounts.

Keywords: Black Sea, zooplankton, vertical migration, *Calanus*, grazing, lipid.

ÖZ

GÜNEY KARADENİZ'DEKİ KOPEPODLARIN, ÖZELLİKLE *CALANUS EUXİNUS*'UN, VE KETOGNATLARIN BAZI EKOLOJİK ÖZELLİKLERİNİN ARAŞTIRILMASI

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Karadeniz'in baskın kopepodlarından C*alanus euxinus, Pseudocalanus elongatus, Acartia clausi, Paracalanus parvus* ve *Oithona similis*, ve bir ketognat olan *Sagitta setosa* bolluklarına, dikey dağılımlarına ve gelişme evrelerine göre, Mayıs 1994-Aralık 1996 müddetince güneybatı Karadeniz'de incelendi. *C. euxinus* ve *P. elongatus* Nisan ve Mayıs'da çok fazla bulunurken, *P. parvus, O. similis* ve *A. clausi* Haziran ayında çok bulundu. *Sagitta*'nın en yüksek değeri Eylül'de gözlendi. Günlük dikey göç, *C. euxinus*'un dişi, kopepodit-V, kopepodit-IV, *P. elongatus*'un dişisinde ve *Sagitta*'nın ergin bireylerinde oldukça barizdi. Haziran ve Eylül örneklerinde oksijence fakir tabakada duraklama (diapause) evresindeki *C. euxinus* 'un kopepodit-V bireylerine rastlandı.

Eylül 1995'de kopepod topluluğunun mide pigment içeriği ve otlamalarının (grazing) birincil üretim üzerine etkisi hesaplandı. Orta boy grubunu (1000-500μm) sayıca bolluğu ve otlama etkisine dair önemini dikkate alındığında oldukça önemlidir. Birincil üretimin yaklaşık %31.5'ğu kopepod gruplarınca tüketildi.

Birincil üretimin %14.5'ğu Nisan'da ve %9.5'ğunun da Eylül'de dişi *C. euxinus* tarafından tüketildiği bulundu.

Dişi ve kopepodit-V *C. euxinus*'un toplam lipid miktarlarındaki mevsimlik değişiklikler Ağustos 1993, Mayıs 1994, Eylül 1995 ve 1996'da saptandı ve maksimum lipid miktarları Eylül 1995'de bulundu. Kopepodit V'in toplam miktarı dişilerinkinden daha fazladır. *Calanus*'da başlıca lipidler wax esterlerdir. Ancak küçük miktarlarda triasilgliserid ve fosfolipid bulundu.

Anahtar kelimeler: Karadeniz, zooplankton, dikey göç, *Calanus*, otlama, yağ.

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CHAPTER I

INTRODUCTION

1.1. GENERAL INFORMATION ON COPEPODA AND CHAETOGNATHA

The term 'plankton' was first applied by Hensen in 1887 for those plant and animal groups of less than 2cm that inhabit the water column of seas as floaters or weak swimmers. The word is of Greek derivation meaning 'drifter' which infers that these organisms are passive in the aquatic realm. Animal component of the plankton are known as zooplankton of which the majority are not passive, seeking specific depths, responding as schooling animals, regulating their buoyancy and actively seeking or trapping their prey (Steidinger and Walker, 1984).

Among the zooplankton, one of the most abundant form is copepods. Copepods are small crustaceans found in marine and freshwater habitats. Most species in the orders Calanoida, Cyclopoida, and Harpacticoida are free-living planktonic or benthic forms, although parasitic forms occur in the order Cyclopoida (Steidinger and Walker, 1984).

Free-living copepods swim weakly, using their limbs jointed to thorax. They have a characteristics jerky movement. Copepods graze on phytoplankton either by means of a complex filtering mechanism that employs the fine setae (hairs) covering certain appendages around the mouth (maxillae), or else by grasping plants with their appendages. In the filtering process, the swimming movements of the toracic legs create a water current that passes into the midventral line of the body, where it flows through the fine setae of the appendages around the

mouth. Phytoplankton cells are removed from the water and passed to the mouth (Figure 1.1) (Nybakken, 1982).

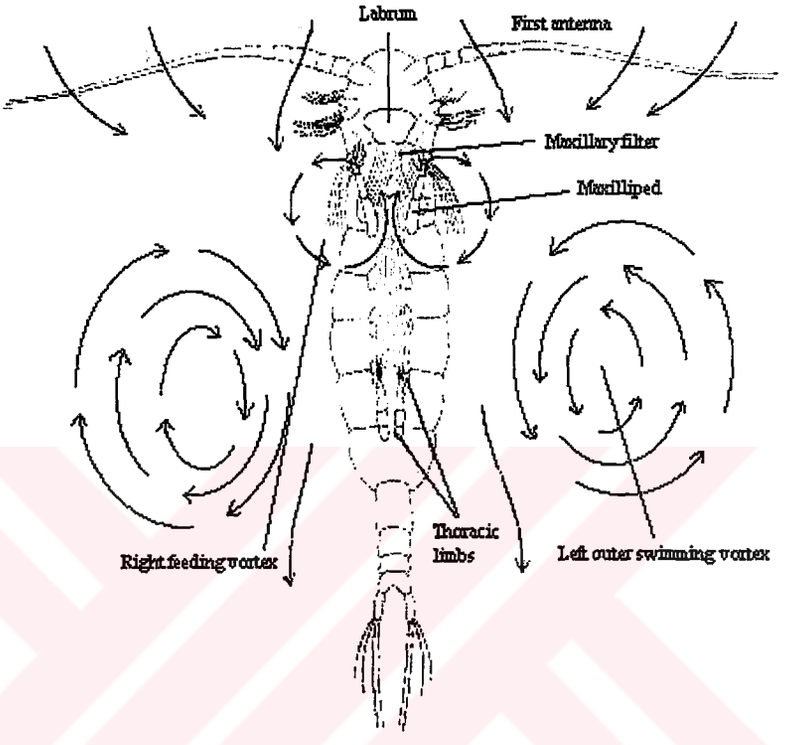

Figure 1.1 : Feeding in a copepod. Ventral view of a copepod showing the currents created in swimming which bring particles in to be filtered in the setae of the maxillae (after Nybakken, 1982).

In copepods, the sexes are separate and sperm are transferred to the female as packaged spermatophores. After fertilisation, eggs hatch as nauplius larvae and progress through several naupliar stages and the several more copepodite stages before becoming adult (Figure 1.2) (Nybakken, 1982).

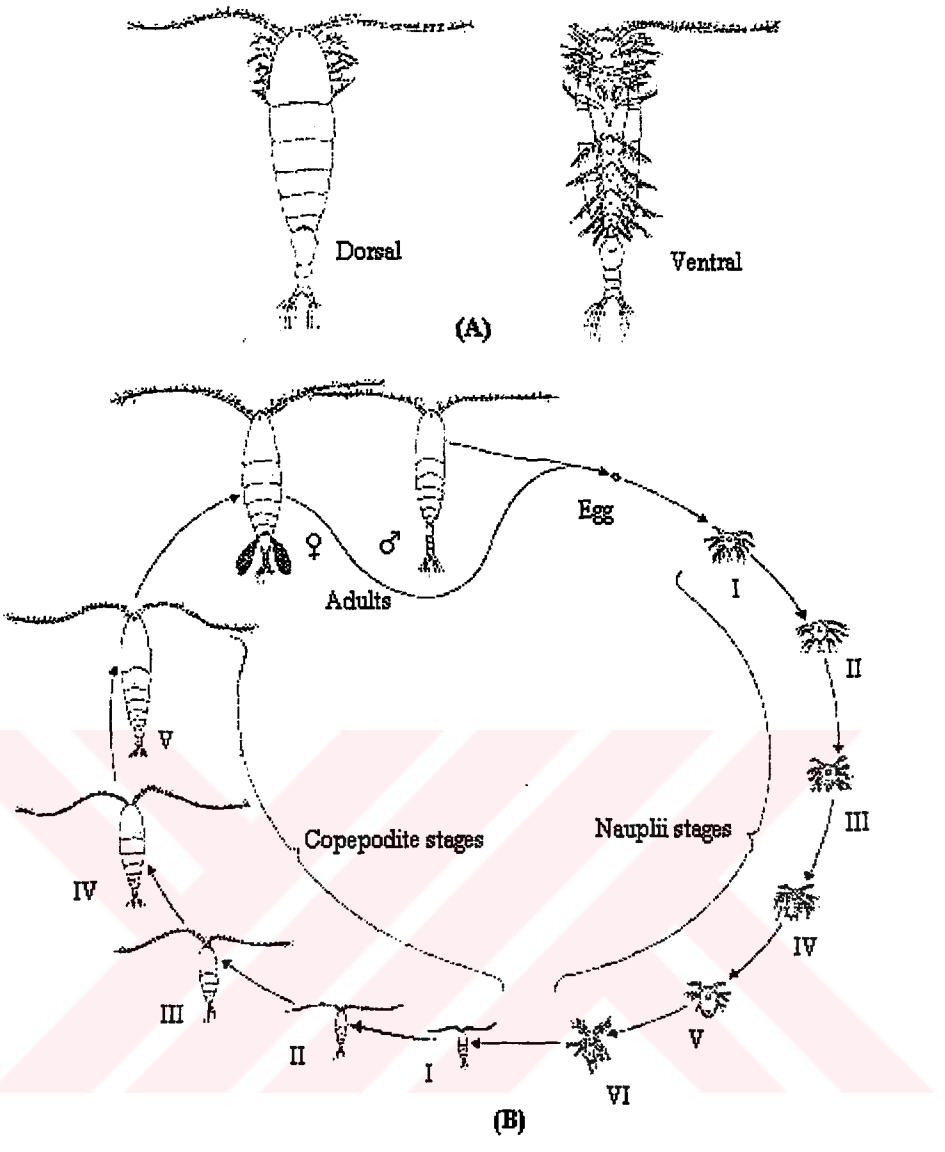

Figure 1.2: Copepods. (A) Typical calanoid copepod showing major morphological features. (B) Outline of the typical life cycle of a copepod (after, Nybakken, 1982).

The chaetognaths, or 'arrow worms' are abundant members of the plankton throughout the world. They are found in every marine habitat, from benthos to all zones of coastal waters and the open oceans. Although small (2-120mm long) they are often abundant, and play an important role in the marine food web as the primary predators of copepods (Barnes *et al.* 1989; Bone *et al.* 1991).

Chaetognaths consist of a head armed with grasping hooks and teeth (see Fig. 2.7). Their body is elongate and filled with fluid. Apart from the gut and gonads there are no internal organs. (Bone *et al.* 1991). The spacious fluid which filled body cavities provide a medium in which diffusion can occur (Brusca and Brusca, 1990). The prey is captured with the hooks and their smaller teeth are perhaps used to puncture prey to aid in paralysing it before ingestion. All chaetognaths are protandrous hermaphrodites, the testis mature before the ovaries (Bone *et al.* 1991).

1.2. BLACK SEA OCEANOGRAPHY

1.2.1. PHYSICAL AND CHEMICAL CHARACTERISTICS

The Black Sea is an unique marine environment, representing the largest land-locked anoxic basin in the world with a maximum depth of ≈2200m, a surface area of 4.2×10^5 km^2 and a volume of 5.3×10^5 km^3. Its waters are almost completely isolated from the world ocean. There is a restricted exchange with the Mediterranean Sea through the Turkish Straits System; the Bosphorus, Dardanelles Straits and the Sea of Marmara.

The general circulation of the Black Sea is a basin-wide cyclonic boundary current (so-called Rim current). This cyclonic circulation is due to the combined effect of cyclonic nature of the wind field, thermohaline fluxes and buoyancy fluxes associated with the river discharges (Oguz *et al.* 1993; Sur *et al.* 1996).

The surface mixed layer has a relatively low salinity, formed as a result of an excess of run-off and precipitation, varies from 17.5 to 18.5‰ depending on the season and the proximity of the river input (Murray, *et al.* 1991; Oguz *et al.* 1992). Below this surface water, saltier Mediterranean water flows northward as an undercurrent into the Black Sea and further sinks to the deeper layers of the Black Sea.

The temperature varies seasonally in the surface layer due to solar heating and decreases with depth to a minimum located at a depth of approximately 50m in the central basin and as deep as 100m near the margins. This temperature minimum is identifiable throughout the Black Sea and has been called as the cold intermediate layer (CIL). The CIL marked by temperatures lower than 8°C, it is formed in the northwestern shelf region, and within the upper layer in the central part of the sea during the winter cooling of the surface water. Below the CIL, permanent halocline (50-200m) separates the surface water from the deep water. The basin-wide distribution of oxygen-carrying CIL waters has important implications on the health and ecology of the Black Sea (Murray *et al.* 1991; Oguz *et al.* 1993; Oguz *et al.* 1994; Ivanov *et al.* 1997).

The basin is completely anoxic, containing oxygenated upper layer (150m depth, 13% of the sea volume) and anoxic deep water with hydrogen sulphide. A permanent halocline separates the oxic and anoxic waters (Ozsoy and Unluata, 1997).

Recent investigators have shown that some 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).

Dissolved oxygen (DO) in the upper mixed layer is nearly at saturated levels (250-350μM). DO concentrations decrease steeply to 20-30μM levels at the 15.4-15.5 density surfaces. Below the main oxycline, the DO values decline slowly from 20-30μM at σ_θ=15.4-15.5 surfaces to <5μM at σ_θ=15.9-16.0 and DO becomes undetectable at about σ_θ=16.15-16.2 density surfaces. At these density surfaces the sulphidic waters appear (Fig.1.3). The DO deficient zone with DO<20μM and H_2S<1μM is called as oxygen minimum zone (OMZ) (Basturk *et al.* 1997).

Nitrate and phosphate concentrations are nearly zero due to consumption by plankton above the seasonal pycnocline (σ_θ=14.2-14.3). Below this surface, their

concentrations increase to a maximum at around the σ_θ=15.4-15.45 density surface because of the microbial oxidation of sinking organic matter and then decrease steadily towards the oxic/anoxic interface (σ_θ=15.85-15.95). Nitrate concentration diminishes completely by heterotrophic denitrification (Fig. 1.3). The lower boundary of the oxic/anoxic interface corresponds to the phosphate maximum depth at σ_θ=16.2±0.05 isopycnal surface, independent of the geographical location and season (Tugrul, *et al.* 1992; Saydam *et al.* 1993; Basturk *et al.* 1994).

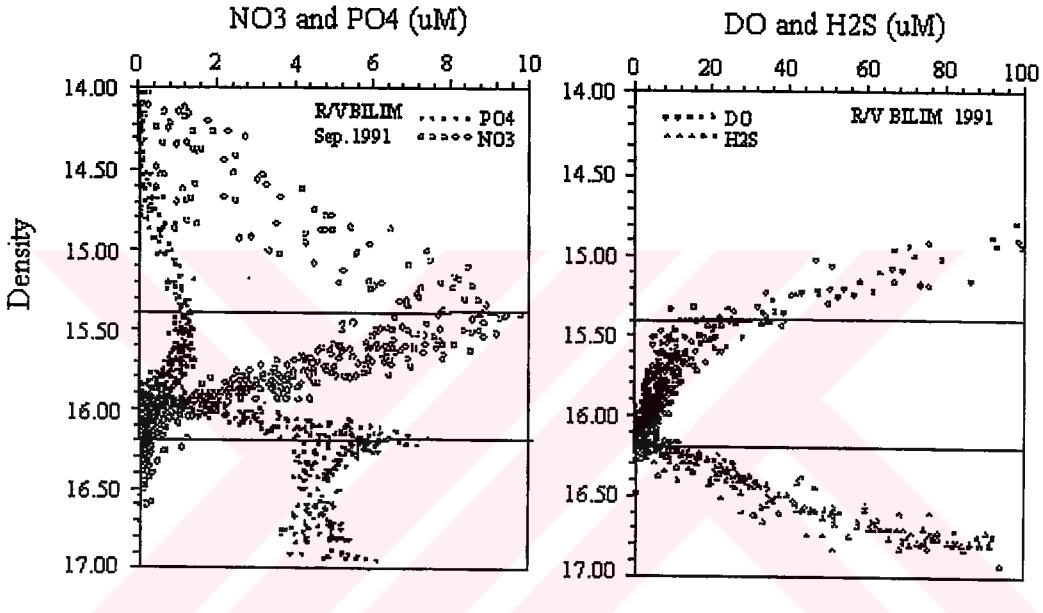

Figure 1.3 : Composite profiles of nitrate (NO_3), phosphate (PO_4), oxygen (DO) and hydrogen sulphide (H_2S) versus density (σ_θ) for 51 stations of the R/V Bilim 1991 cruise. Density is given in terms of kg/m^3, and others by μM (After Saydam, *et al.* 1993).

1.2.2. BIOLOGICAL CHARACTERISTICS

The aerobiotic waters of the Black Sea are biologically productive because of high run-off from rivers around the basin. The major rivers (the Danube, Dnepr and Dnestr) discharge into the northwest shelf of the Black Sea. The Danube River alone is the greatest contributor of river runoff into the Black

Sea accounting for about one half of the total riverine influx. (Sur *et al.* 1996).

The Black Sea is known to be a region of moderate to high productivity since it is fed by river inflow rich in nutrient (Balkas *et al.* 1990; Caddy, 1993). Sorokin (1983) indicated that the primary productivity of the Black Sea were observed twice a year, with a major bloom principally composed of diatoms in early spring, followed by a secondary bloom mainly comprising coccolithophorids in autumn. Additional summer blooms with a predominance of dinoflagellates and coccolithophorids have been increasingly observed in the region in recent years (Bologa, 1986; Hay and Honjo, 1989, Uysal and Sur, 1995).

The eutrophication has started in the northwestern shelf area influenced by the Danube and Dnestr river mouths and progressed south, along the western shelf (Tolmazin, 1985; Musayeva, 1985). It seems that the eutrophication increased sharply in the last decade: for example the long term data for Secchi disc readings in the central parts of the Black Sea illustrate that the Secchi disc visibility has decreased from 20m in the 1920s to about 18m until the 1980s and in the early 1990s it has decreased to 6m (Viladimirov *et al.* 1997). The biomass of phytoplankton and blooming areas have increased more than ten-fold. Corresponding changes in zooplankton population have been observed along with the appearance of some opportunistic species has been invaded (Konsulov and Kamburska, 1997; Zaitsev and Alexandrov, 1997).

The Black Sea mesoplankton is basically derivatives of the Atlantic plankton occurring in the Mediterranean Sea. 425 copepod species are known for the Mediterranean Sea, only ~60 species occur in the Black Sea and distribution of most of them restricted to the Bosphorus adjacent area (Vinogradov *et al.* 1992a). Shushkina *et al.* (1997) divided the last 20 years into two distinct phases of the Black Sea ecosystem; the first one extends

from 1978 to 1988 and the second period starts with the introduction of ctenophore *Mnemiopsis leidyi*. During the first period, the Black Sea ecosystem was mostly affected by the anthropogenic influence with increasing pollutants and nutrients with river discharges. The increase in nutrient discharge accompanied with the increase in biomass of both phytoplankton and zooplankton by at least 1 to 2 orders of magnitude (Caddy, 1993). The introduction of *Mnemiopsis* influenced the structure and biomass of mesozooplankton, e.g. the biomass of *Calanus euxinus*, the main food for fish, decreased since 1989 about 10 times. Kovalev *et al.* (1997) stated that, in 1976 copepods accounted for 67% of the total biomass of zooplankton but by 1990 their contribution was only 14%. *Sagitta* concentration decreased about 100 fold. Total percentage of gelatinous plankton increased from 10-12% in 1978-1984 to 80% in 1992 (Shushkina *et al.* 1997).

1.3. AIM OF THIS STUDY

Zooplankton play a pivotal role in shaping ecosystem structure because grazing by zooplankton is thought to influence or regulate primary production, and variations in zooplankton dynamics may affect biomass of many fish stocks . It was decided to focus initially on copepods because they are the most abundant forms of zooplankton in the Black Sea. There are some studies on the qualitative and quantitative description of the copepods in the food web, production of the populations (Greze and Baldina, 1967; Sazhina, 1987) and their vertical distribution (Vinogradov *et al.* 1985, 1992) carried out in the Black Sea. Along the Turkish side, the studies on the Black Sea copepods focused on their spatial distribution (Ergun, 1994; Niermann *et al.* 1995; Niermann *et al.* 1997).

The main purpose of this work was to collect some information on the ecology (e.g. distribution, grazing) of the common copepods (*Calanus euxinus*, *Pseudocalanus elongatus*, *Acartia clausi*, *Paracalanus parvus* and *Oithona similis*) and the chaetognath (*Sagitta setosa*) population in the

Black Sea in order to help to understand the Black Sea ecosystem. Among them the important role of *Calanus euxinus* on the transferring the organic matter from primary producers to the higher taxa was emphasised.

The specific aims were as follows: In chapter 1 review of the main oceanographic features related to present work and general information on copepods and chaetognaths are given. In chapter 2 the materials and methods used during this work are presented. In chapter 3 the distribution and population structure of copepods and the chaetognath are outlined. The respiration rate of *Calanus* and grazing rates of copepods are estimated in chapter 4 and 5 respectively. The lipid content of *Calanus* is studied in chapter 6. The diapausing period of *Calanus* is discussed in chapter 7. In chapter 8 the results are concluded.

CHAPTER II

MATERIAL AND METHODS

2.1. SAMPLING PERIODS AND PARAMETERS MEASURED

This study is conducted in the southern part of the Black Sea during August 1993, May 1994, April 1995, September 1995, April 1996, June 1996, September 1996, November 1996 and December 1996. The sampling stations during this study are shown in Figures 2.1-2.3.

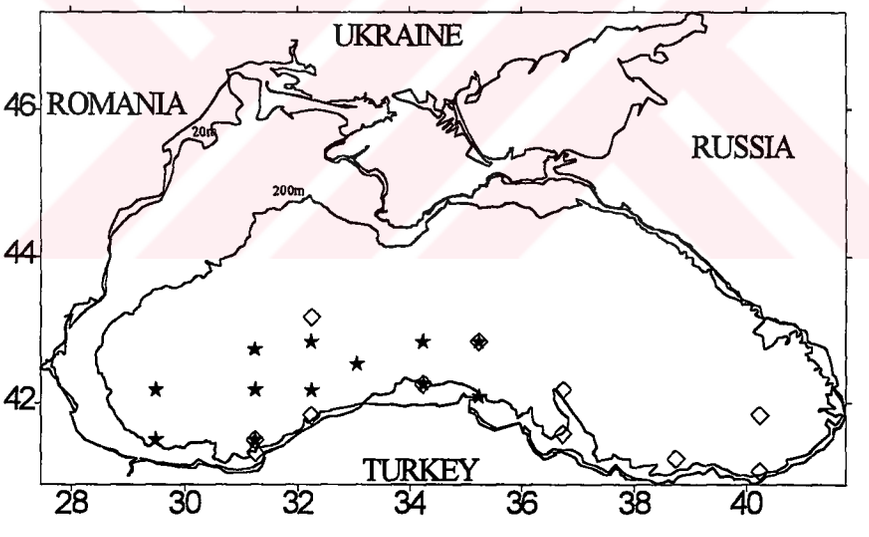

Figure 2.1: Sampling stations during August 1993 (◇) and May 1994 (★).

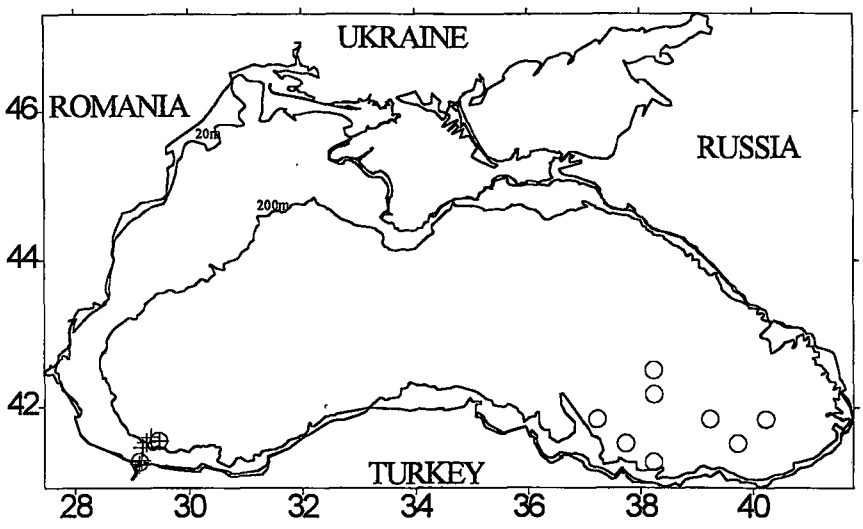

Figure 2.2: Sampling stations during 1995. + April 1995 and ○September 1995.

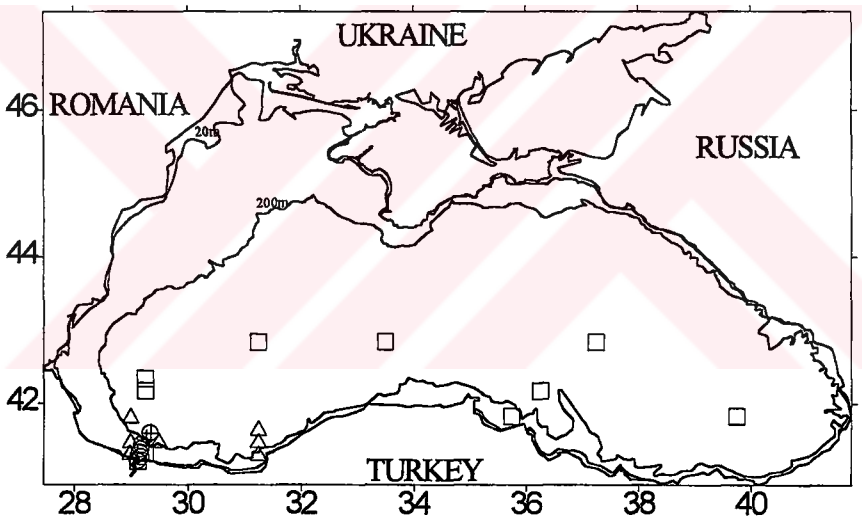

Figure 2.3: Sampling stations during 1996. ○ April 1996, △June 1996, □ September 1996, +November and December 1996.

The parameters measured in each sampling period are summarised in Table 2.1.

Table 2.1: Sampling periods and parameters measured during these periods. CTD=conductivity, temperature, depth; DVM=diel vertical migration; GPC=gut pigment content.

Sampling period	Dates	No. of stations	Mesh size	Parameters measured
Aug. 1993	4-22 Aug.	11	200 µm	CTD, Chl-a, Total Lipid in *Calanus* euxinus
May 1994	25 April-14 May	12	200 µm	CTD, Chl-a, DVM, Total Lipid in *Calanus*, GPC in female *Calanus*
April 1995	25-30 April	6	112 µm	CTD, Chl-a, Abundance, DVM, GPC and Grazing Rate of female *Calanus*
Sept. 1995	26 Sept.-10 October	9	112 µm	CTD, Chl-a, Abundance, DVM, GPC and Grazing Rate of female *Calanus* and copepods assemblages
April 1996	8-17 April	7	112 µm	CTD, Chl-a, Abundance
June 1996	20 June-5 July	7	112 µm	CTD, Chl-a, Abundance, DVM
Sept. 1996	24 Sept.-4 October	10	112 µm	CTD, Chl-a, Abundance, Total Lipid and Lipid classes in *Calanus*, Respiration rate
Nov. 1996	6-7 Nov.	2	112 µm	CTD, Chl-a, Abundance, Respiration rate
Dec. 1996	7-10 Dec.	2	112 µm	CTD, Chl-a, Abundance

2.1.1. DISTRIBUTION OF ORGANISMS

2.1.1.1. SAMPLE COLLECTION AND PRESERVATION

Spatial distribution of species was studied at almost all sampling periods except in August 1993 (Figure 2.4). The stations containing both oxic and suboxic water layers considered as open stations, and others containing only oxic water layers were determined as coastal stations, regardless of their position.

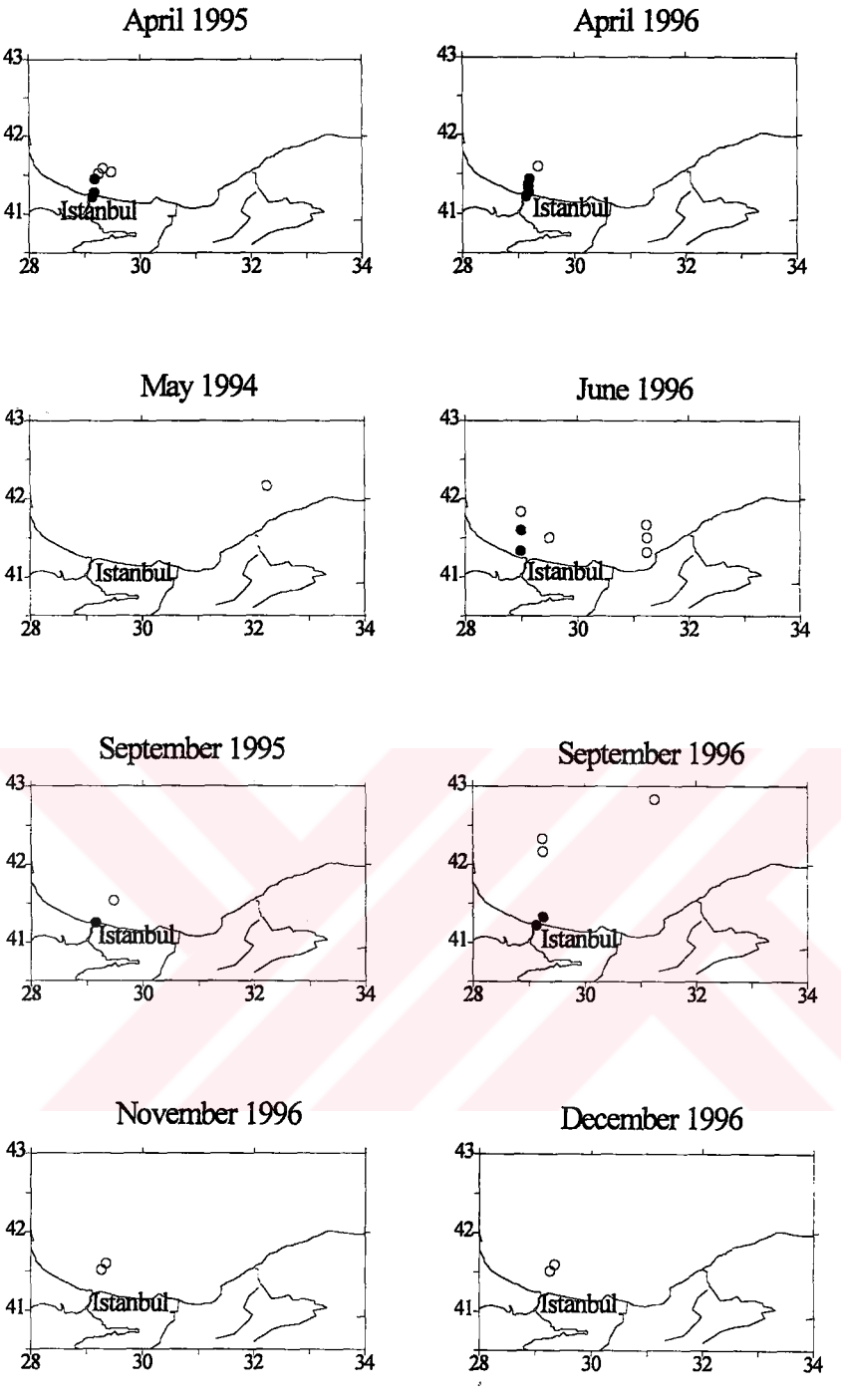

Figure 2.4: Sampling station visited for spatial distribution of copepods and the chaetognath in the southwestern Black Sea. Black circles illustrates coastal stations, open circles show open stations.

The vertical distribution study was based mainly upon a series of hauls made at different depth strata each of which was repeatedly sampled for a continuous period of 12h in May 1994, 30h in April 1995, 21h in September 1995 at a certain station and in June 1996 around 24h cycle were completed from the different stations located in the south-western part of the Black Sea (Figure 2.5).

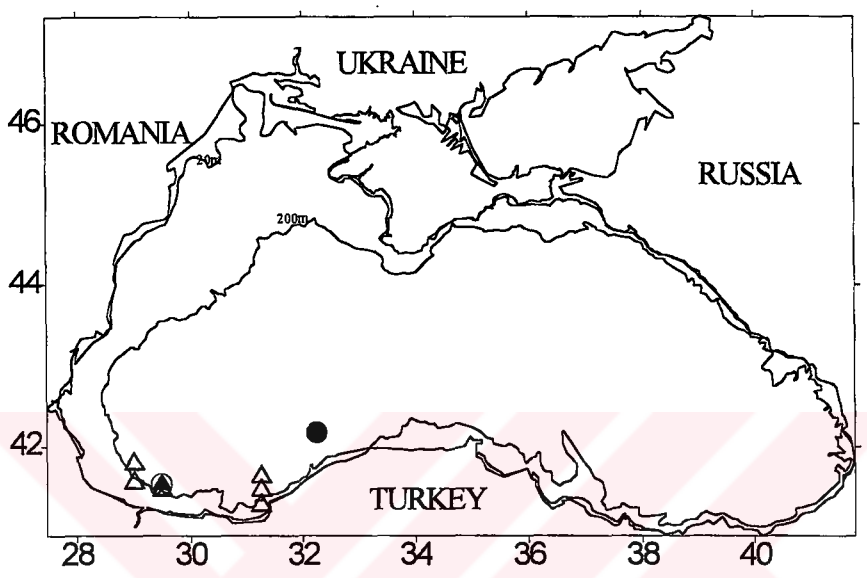

Figure 2.5: Sampling stations for the diel vertical distribution of copepods and the chaetognath in the Black Sea, ● May 1994, ○ April 1995, ▲ September 1995 and △ June 1996.

During the May 1994 cruise, samples were collected from 4 different depth strata down to the beginning of the anoxic layer. In other cruises, the water column was sampled over 5 depth strata in terms of density levels according to major biochemical characteristics of the water column which may affect the distribution of mesozooplankton in the Black Sea (Tables 2.2 and 2.3).

Table 2.2: The sampling depth strata and the characteristics of the layers in May 1994, OMZ= Oxygen Minimum Zone.

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 the seasonal thermocline	2	σ_θ=14.6 roughly corresponds to lowest boundary of the euphotic zone (Oguz *et al.* 1996)
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=16.2 to the depth of σ_θ=15.4	4	denitrification processes begin to occur at the depth of σ_θ=15.4. The depth of σ_θ=16.2 corresponds to the bottom of the oxygenated water column. This water column is called as OMZ. (Saydam, *et al.* 1993)

Table 2.3: The sampling depth strata and the characteristics of the layers in April 1995, September 1995, June 1996. OMZ= Oxygen Minimum Zone.

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 roughly corresponds to lowest boundary of the euphotic zone (Oguz *et al.* 1996)
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	the denitrification processes begin to occur at the depth of σ_θ=15.4 (Bastürk, *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 *Calanus euxinus* (Vinogradov, *et al.* 1992b)

In order to study the vertical distribution of copepods and *Sagitta,* the samples were taken from different depths with a Nansen Closing Net with a mouth opening of 70cm and mesh size of 200μm in May 1994, 112μm in other periods. The haul speed was ≅1m/s. The sampling depths were estimated from the angle and length of the hauling wire. The samples from each depth was preserved with 5% buffered formalin-seawater solution. In the laboratory, samples were

subsampled with a Folsom splitter. The subsamples from 1/1 to 1/128 (usually 1/32) depending on the abundance of individuals in the samples, were identified and counted. *Sagitta* were generally counted without subsampling.

All copepods were enumerated, identified to species (Boltovski, 1969), and staged (i.e. adult, copepodite stages and metanauplii). Their prosome lengths were also measured (Figure 2.6). The mean prosome length of each stage and population were calculated by taking into account the abundance of the organisms. All chaetognaths (*Sagitta*) were enumerated and their total lengths were measured (Figure 2.7).

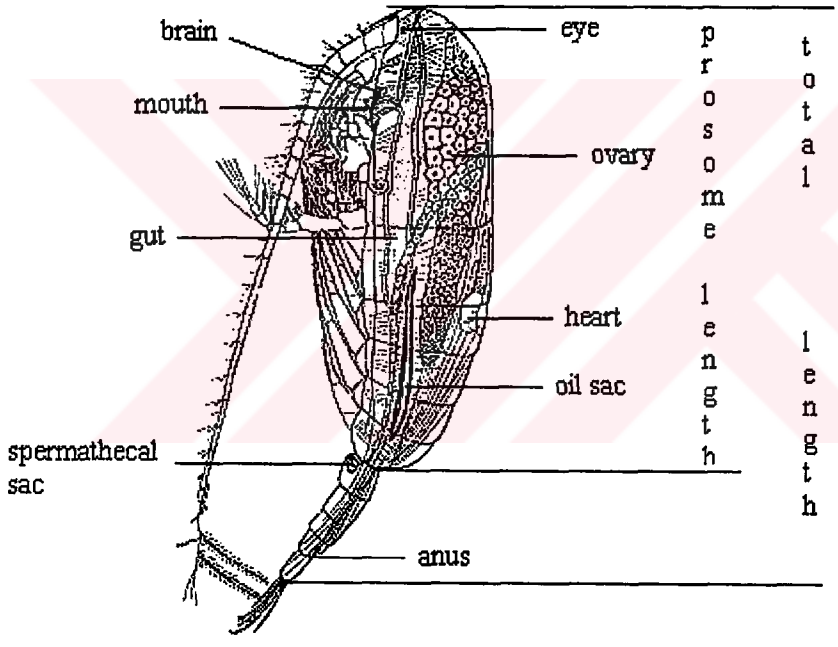

Figure 2.6: Schematic diagram of female *Calanus* from the side (after Marshall and Orr, 1972).

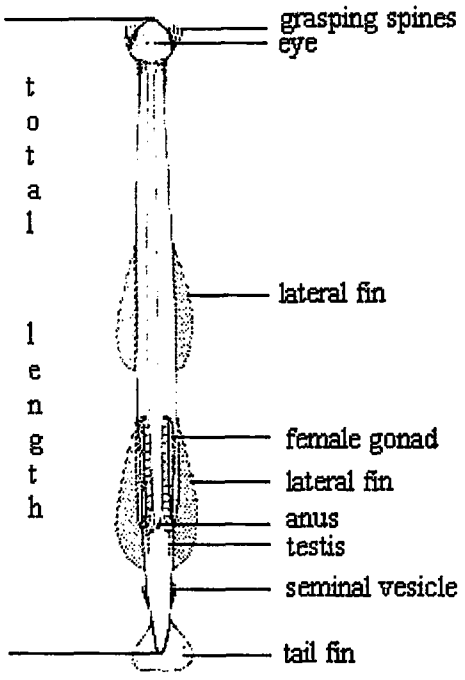

Figure 2.7 : Schematic diagram of chaetognath (*Sagitta*) (after Kapp, 1991).

2.1.2. RESPIRATION OF *CALANUS EUXINUS*

Respiration rates of female and copepodite V *Calanus euxinus* at different temperatures and different oxygen concentrations were measured.

Individuals of *Calanus euxinus* were collected from 50m up to the surface using a Hensen net having 300μm mesh size. Individuals were acclimatised at selected experimental temperatures for 4-5 hours. The measurement of oxygen consumption for female and copepodite V stage of *Calanus* was conducted on board at five different temperatures; 5 °C, 12 °C ,16 °C , 18 °C and 23 °C. These experimental temperatures are within the annual range in the Black Sea. For each temperature 2 to 4 serial replicates (containing 4-7 experimental bottles) were run simultaneously.

Dissolved oxygen concentration was determined by Winkler method (Strickland and Parsons, 1972; Konovalov *et al.* 1994) and the respiration rate was calculated using the equation described by Omori and Ikeda, (1992);

$$R = \frac{(C_{ox} - E_{ox})V}{tN}$$

where C_{ox} and E_{ox} are dissolved oxygen contents (μg-at O_2 $liter^{-1}$) in the control and experimental bottles, respectively; V is the volume of the experimental bottles (liter); t is the incubation time (h); N is the number of animals. Filtered seawater was kept at the experimental temperature before use, then added to glass-stopped Winkler bottles of 29 or 150ml capacity, each containing 4 or 15 individuals of females or copepodite V. Two or three bottles without animals served as controls. All experiments were performed in the dark. The bottles were not rotated as Schindler (1968, *cf.* Heisey and Porter, 1977) noted that this had no detectable effect on respiration.

The increases in temperature prompt increases in respiratory rates. The response of metabolism to temperatures can be represented by,

$$Q_{10} = [r_1/r_2]^{[10/(t_1 - t_2)]}$$

where r_1 and r_2 are O_2 consumption at temperature t_1 and t_2. Q_{10} can be interpreted as the increase in reaction rate for a 10°C change in temperature (McLaren, 1963 *cf.* Valiela, 1995).

To see the effect of oxygen concentration on the respiration rate, the experiments were conducted at constant temperature (at 16 ± 1 °C) in November 1996. Nitrogen was bubbled through 4 litres of filtered sea water for varying periods to obtain the final required oxygen concentration. The experiments were performed at 4 different oxygen concentrations for copepodite V and 5 different oxygen concentrations for female *Calanus* with 5 or 6 serial replicates.

In this study, all experiments were conducted by using unfed individuals of *Calanus*. There are some studies showing that fed individuals have higher DO consumption rates than starved ones (Kinne, 1970; Kideys, 1991).

2.1.3. DETERMINATION OF GUT PIGMENT CONTENT AND GRAZING PRESSURE

Gut pigment contents and the grazing pressure were estimated for copepod assemblages and female *Calanus euxinus* in the Black Sea.

For the estimation of gut pigment contents and grazing pressure of copepod assemblages, the samples were towed from 50 m up to the surface every 3-5 hours in a daily station on 27-28 September 1995 (Figure 2.8). The grazing pressure of copepod assemblages were investigated for three size fractions; large size (range between 2000 and 1000 μm), medium size (1000-500 μm) and small size (500-300 μm). After the towing of net, the cod end was taken immediately, sieved from 2000 μm mesh to remove jelly organisms, washed and rinsed with filtered sea water. They were sieved again through 1000 μm mesh to get large size which was retained on a GF/F filter. The remaining parts of copepods were filtered from 500 μm and 300 μm mesh to get medium and small size organisms respectively and sieved on GF/F filter. The particles and organisms other than copepods on GF/F filters were removed, then the copepods were counted immediately and stored at -20 °C until fluorometric analyses (Mackas and Bohrer, 1976). Duplicate or triplicate samples were taken for each size groups. The numbers of organisms on the filter, ranged from 8 to 28 for large size, 8-41 for medium size and, 46 and 141 for small size on a GF/F filter.

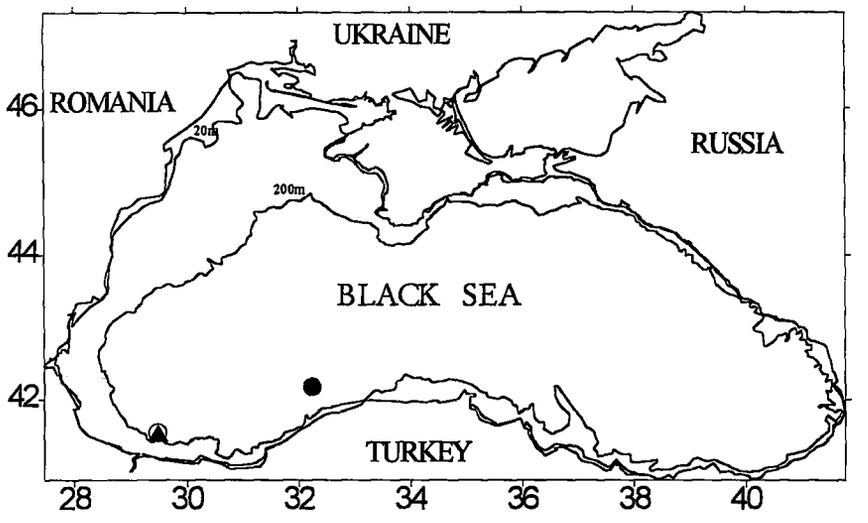

Figure 2.8: Sampling stations visited for gut pigment content analyses of copepods. ●May 1994, ○April 1995 and ▲September 1995.

For the gut-pigment analyses and the grazing pressure estimation of female *Calanus euxinus*, individuals were collected from different depth strata during 10-11 May 1994, 26-28 April and 27-28 September 1995 (Figure 2.8). After towing, the cod end was immediately sieved through 2000 μm and 500 μm mesh size, to remove large (mainly gelatinous) and small organisms respectively to make *Calanus* easily recognisable. The mesh was washed with filtered sea water and under binocular microscope 10-30 individuals (depending on the abundance) of female *C. euxinus* were collected on the GF/F filter paper as soon as possible (around 10-15 min), and stored in deep-freeze at -20°C until laboratory analyses. Duplicate or triplicate samples were collected from each depth stratum.

2.1.3.1. FLUORESCENCE MEASUREMENTS

After thawing the frozen samples on GF/F filter, a standard fluorometric method was used for gut chlorophyll-a determination. The filters and animals were ground in 90% acetone in a grinder for pigment extraction. Samples were diluted with solvent to a final volume 6-10ml and kept overnight in the dark in the refrigerator at 4°C for a complete extraction.

The extract was centrifuged for 10 min. to settle glass fiber pulp and insoluble animal remains. Fluorescence of the extract before and after acidification was measured on Hitachi F-3000 Model fluorometer. Calibration was performed using a commercially available chlorophyll-a standard from Sigma. The standard was dissolved in 90% acetone and its concentration (mg/l) was calculated spectrophotometrically (Strickland and Parsons,1972). A minimum of 4-5 dilutions were prepared from this standard and emission and excitation wavelengths are adjusted using the same standard. Fluorometer readings were recorded before and after acidification with 2 drops of 10% HCl. The linear calibration factors were calculated from the slope of the unacidified fluorometric reading versus Chl-a concentration calculated spectrophotometrically. The fluorometer is zeroed with 90% acetone and fluorescence readings of samples were recorded before and after acidification at 431nm as excitation and 669nm as emission wavelengths.

2.1.3.2. CALCULATION OF GUT PIGMENT CONTENT

The chlorophyll-a and phaeopigment content of each copepod was calculated using equations for in vitro fluorometry (Strickland and Parsons, 1969 *cf.* Dagg and Wyman, 1983),

$$\text{Chlorophyll-a } (\mu g) = \frac{K\,(F_o - F_a)V_x}{n}$$

$$\text{Phaeopigments } (\mu g) = \frac{K\,(AR * F_a - F_o)V_x}{n}$$

where,
K= Calibration constant of the fluorometer
F_o= Fluorescence before acidification
F_a= Fluorescence after acidification
V_x= Volume (ml) of acetone extract used
AR= Acid ratio
n= number of individuals

K value was obtained from the average value of K from standards by following formula;

K= concentration of standard (μg/l)/(F_o-F_a),

To get the AR value, the average value of F_o/F_a was calculated for each standard.

The ingestion rate was estimated using,

$$I = G\,k$$

where,
G= gut pigment content (ng pigment/copepod)
k= gut evacuation rate constant (min^{-1}; Dam and Peterson, 1988)

2.1.4. LIPID MEASUREMENTS

Lipid measurements were conducted in copepodite stage V and female *Calanus euxinus* during these cruises; August 1993, May 1994, September 1995 and September 1996. While the total lipid contents of individuals were measured for all four sampling periods, analyses of lipid classes were performed only for September 1996 samples. The locations of the sampling stations are presented in Figure 2.9.

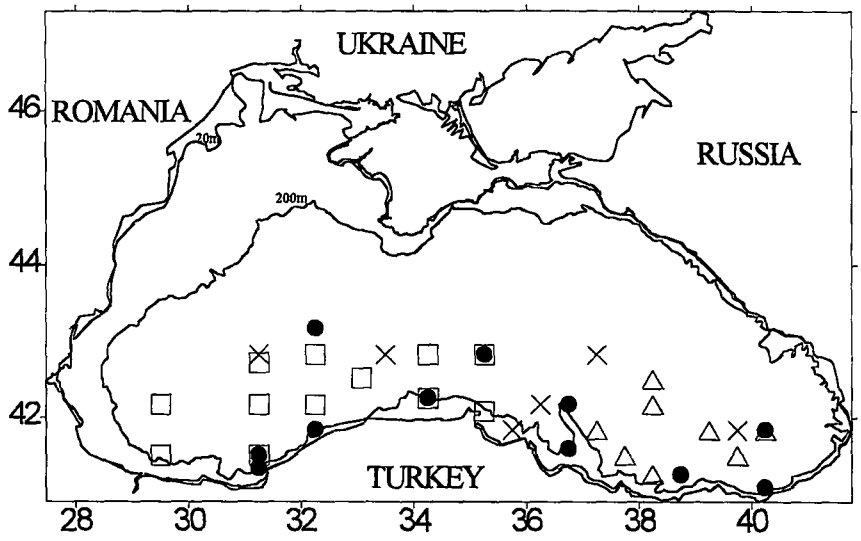

Figure 2.9: Lipid stations. ● August 1993, □May 1994, △September 1995 and × September 1996.

2.1.4.1. TOTAL LIPID CONTENT

2.1.4.1.1. SAMPLE COLLECTION AND PRESERVATION

Total lipid content was measured in copepodite V and female individuals of *Calanus euxinus* . Copepods for lipid analyses were obtained by vertical Nansen net hauls from different depth strata. After the net came on board, the catch was sieved from 500 μm mesh to remove the smaller individuals. Between 8 and 60 alive copepodite V and female specimens were sorted from each net under stereo microscope, put on precombusted and preweighed GF/C filter and stored at -20 ^{o}C until analyses. In September 1996, females and copepodite V stages were put in the Chloroform-methanol (2:1 v/v) mixture in a vialed glass bottles and stored at -20 ^{o}C.

2.1.4.1.2. ANALYTICAL PROCEDURE

Total lipid contents of individuals were determined gravimetrically (Folch *et al.*, 1957) which is known as sulphophosphovanillin method as described by Barnes and Blackstone (1973).

The organisms on the GF/C filter paper were extracted in 2:1 (v/v) chloroform:methanol mixture. The homogenisation was carried out with a glass stick in 12ml graduated tube. The contents were swirled until thoroughly mixed and then put in ultrasonic bath for 10 minutes. Extraction continued overnight in the dark in the refrigerator (4 ^{o}C). Residue was removed by filtration through a GF/C filter paper (precombusted at 450 ^{o}C) then washed three times with chloroform:methanol (2:1 v/v) to achieve a quantitative transfer. An amount of 0.9 % NaCl in H_2O, equivalent to 1/5 of the extract volume was added, shaken vigorously and allowed to stand overnight or until the extract becomes clear, and biphasic system was obtained. The approximate proportion of chloroform, methanol, and water in the upper phase were 3:48:47 by volume, and the respective proportions were 86:14:1 in the lower phase. The upper phase was removed by siphoning and the remaining surface was washed two times with chloroform, methanol, and saline (3:48:47 v/v) to remove traces of the water phase. The remaining chloroform phase was evaporated with a stream of N_2 and water bath (~40 °C). The total lipid contents in samples were measured either by gravimetric or by sulphophoshovanillin methods. Total lipid contents in samples collected in August 1993, May 1994 and September 1995 were measured by gravimetric method, weighed with Mettler-AE 240 electrobalance.

2.1.4.1.3. SULPHOPHOSPHOVANILLIN METHOD

The total lipid contents in the samples collected in September 1996 were measured by sulphophoshovanillin method by Dr. T. Yuneva (from Institute of Biology of the Southern Seas, Ukraine). Approximately 100 µg containing total

lipid aliquot from chloroform-lipid was taken in a glass tube and put into the hot water bath until remove the solution then add 0.5 ml H_2SO_4, wait 10min. After cooling the samples add 2.5 ml of fosfovanillin reagent and shake the samples. Wait 15 min. and measure it at 540 nm wavelength by using spectrophotometer (Barnes and Blackstock, 1973). The same procedure is done for the control (chloroform) and the standards. Standards were prepared from *Calanus* gravimetrically.

2.1.4.2. LIPID CLASSES ANALYSES

Measurements of different lipid classes were carried out for the samples collected in September 1996, at the laboratory in Institute of Biology of the Southern Seas, Ukraine, by Dr. T. Yuneva using Kopitov (1983) method. After obtaining the total lipid content, the lipid classes were separated by using thin-layer chromatography. Preparative plates were run in the chromatographic chamber with chloroform:methanol (1:1 v/v) up to the top of the plate to remove any trace of lipids. Thin layer plates covered by Silufol UW254 (Kavalier, Czechoslovakia) which is used as an absorbent were activated at 105 °C and immersed in 10% phosphomolybdic acid in ethanol to make the spots visible by heating at 110 °C after development of classes. After application of lipids to the plates, they were put in chloroform, hexane-diethyl ether (9:1 v/v), hexane solvent system for separating the lipid classes. The solvent was allowed to ascent to within about 1-2 cm of the top of the plate, removed from the tank and allowed to evaporate. After heating at 110 °C, the lipid spots appeared. The lipid classes were measured quantitatively by using a densitometer.

CHAPTER III

DISTRIBUTION AND POPULATION STRUCTURE OF DOMINANT COPEPOD SPECIES AND THE CHAETOGNATH (*Sagitta setosa*) IN THE SOUTHWESTHERN BLACK SEA

3. 1. INTRODUCTION

Survival of a copepod species is an adaptive process with variable selection pressures operating at different developmental stages. Survival means reproductive success to provide future generations. In the marine environment, individual survival is dependent on;

-food availability
-predator pressure or predator avoidance
-competitive advantages (e.g. physiological tolerances and rates, assimilation efficiency) (Steidinger and Walker, 1984).

These factors regulate growth and reproductive effort as well as reproductive and dispersal strategies. Moreover, the regulation of spatial and temporal distribution can confer adaptive advantages. Adaptations include dormancy, size, motility, morphology, vertical distribution, physiological efficiencies and growth, brood size, feeding mechanisms and other adaptive mechanisms (Steidinger and Walker, 1984).

Various species of planktonic copepods occupy certain depths in the water column. These depths, or changes in depths, can be influenced by age, sex, reproductive state, endogenous rhythms, feeding strategies, light intensity and

spectrum, presence of predators, temperature, and other biological and physico-chemical factors. Different ontological stages of copepods often migrate differently. Thus, the weaker swimming abilities of naupliar stages prevent them from making extensive migrations as do copepodites, and especially adults. Migrations can be meager or very extensive depending upon the species. In addition, herbivores may be more responsive to migratory stimuli than omnivores, carnivores or detritivores (Steidinger and Walker, 1984).

Vertical migration in zooplankton has apparently evolved independently in many diverse taxonomic groups, the evolutionist takes it for granted that the migrations involve some major selective advantage for the participants. The nature of that advantage, however, is not immediately evident. Speculation about the issue becomes complex, because certain species do not migrate, although other taxonomically and ecologically similar organisms do; because some species migrate during certain seasons of the year, or in one location and not in others; and because certain life stages of a given species do not migrate, although other stages do. The behaviour is not a universal feature of aquatic life, but instead seems to be of advantage for only certain organisms, any some of the time (Enright, 1977).

Several groups can be distinguished in the Black Sea plankton by the character of their vertical distribution. One group is distributed alike in winter and in summer. The greatest mass of them is usually adapted to a depth of 15 to 50m. Their vertical distribution is only slightly affected by variations of temperature and light, observed throughout the seasons. Examples to this are *Acartia clausi* and *Paracalanus parvus* (Zenkevich, 1963).

The second group is represented by cold water stenothermal forms found in winter at all depths; in summer they sink to the greater depth. This group includes *Calanus euxinus, Pseudocalanus elongatus, Oithona similis* and *Sagitta euxina*. The upper optimum temperature limit in the distribution of *Sagitta* is 10 °C or

11°C, for *Calanus* and *Pseudocalanus* 13 °C, and for *Oithona* 14 °C (Zenkevich, 1963).

The third group develops only in summer, keeping to the upper, warm layer of water. When temperature decreases they become gradually scarcer, disappearing completely from the plankton during the winter. This group includes *Centropages kroeyeri*. The lower temperature of this species is around 10 °C or 14 °C (Zenkevich, 1963).

In the Black Sea, some plankton species have seasonal (ontogenetic) migrations. Nikitin (1929 *cf.* Zenkevitch, 1963) stated that the main factor for this (ontogenetic) migration is temperature, which masks the effect of light. Some of the cold water copepods have the capacity to exist under the Black Sea conditions with little oxygen. In the deepest inhabited layers, where the amount of oxygen is no more than 4% and *Calanus* and *Pseudocalanus* may be present (Zenkevich, 1963).

Apart from the seasonal migrations, daily migrations have been observed for a number of species, conditioned primarily by variations in light. The most pronounced daily migrations are those of *Calanus* and *Sagitta* (Zenkevich, 1963).

Species of the genus *Acartia*, are all inhabitants of the near-surface water layers. *A. clausi* is apparently distributed in a cosmopolitan way and has considerable stocks in tropic waters (Sewell, 1948 *cf.* Fransz *et al.* 1991).

Oithona similis, a boreal, eurythermal, and euryhaline species, is one of the most common copepods in the northern oceans and is widely spread in oceanic as well as in neritic waters (Fransz *et al.* 1991). Vinogradov (1968) considered *O. similis* as an epipelagic species, of which the main proportion during the phytoplankton bloom period is concentrated in a relatively shallow surface layer.

3. 2. RESULTS

The data presented in this chapter were obtained during 1994-1996 from the southwestern Black Sea. Data on *Calanus euxinus* and *Sagitta* complied from 8 cruises; May 1994, April and September 1995, April, July, September, November and December 1996. Data for the other species compiled from 6 cruises; May 1994, April and September 1995, April, June and September 1996. Organisms were collected by the Nansen-closing net having 112μm mesh size, except in May, when the mesh size was 200μm. Each species sampled both from open and coastal stations for each sampling period was examined. The stations containing both oxic and suboxic water layers considered as open stations, and those containing only oxic water layers (not include suboxic water layer) were referred to coastal staions. May 1994, November 1996 and December 1996 periods contain only the open stations (Figure 2.4).

Samples were collected from 4-5 depth strata as was explained in section 2.1.1.1.

3.2.1. *CALANUS EUXINUS*

3.2.1.1. SPATIAL DISTRIBUTION

The total abundance of *Calanus euxinus* showed seasonal variability both at the open and coastal stations. Figure 3.1 shows the abundance of adult and copepodite stages of *C. euxinus* at each station in different sampling periods. There was a significant difference in total abundance of *C. euxinus* between the open and coastal stations in each sampling period. The abundance of *C. euxinus* (adults and copepodites) was generally remarkably higher at open stations than that at coastal stations.

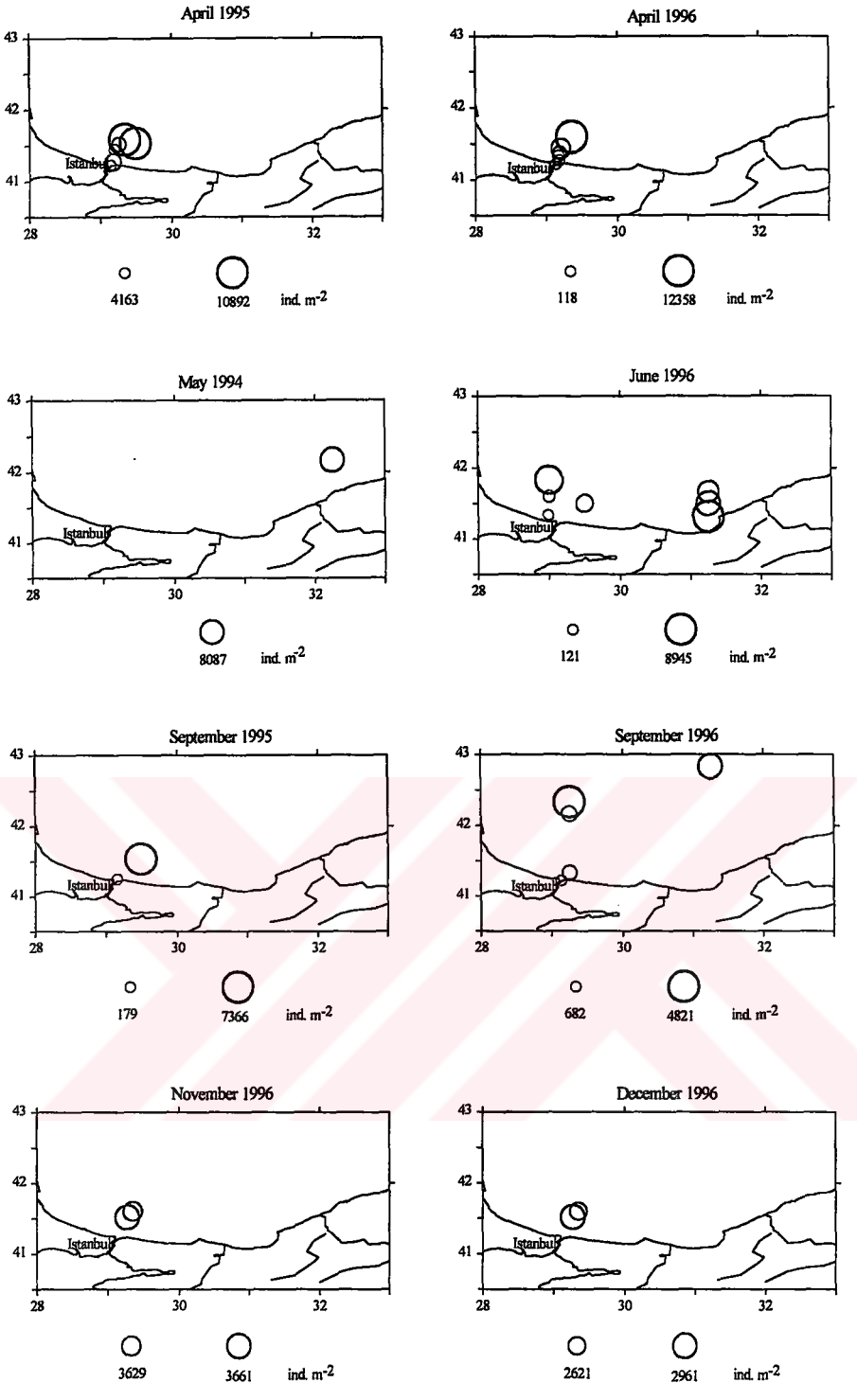

Figure 3.1: Abundance (ind. m^{-2}) of adults and copepodites of *C. euxinus* at each station during sampling periods. Numbers are proportional to the radius of the circle (linear transformation). Minimum and maximum values are given in scale. Open and coastal stations were depicted in Figure 2.4.

Each copepodite stage and metanauplii of *C. euxinus* could easily be identified for all samples. Table 3.1 shows the abundance and mean prosome length of each stage of *C. euxinus*. As it is seen from this table, the total abundance of adults+copepodites peaked with 10263 and 18609 individuals m^{-2} in April 1995 and 1996 at open stations, but decreased dramatically to about half towards December 1996. The lowest value was obtained in December 1996. The highest abundance in metanauplii was observed in April 1995 with a value of 13658 ind. m^{-2} and the lowest value was found in May 1994. It was probably due to the larger mesh size which was 200μm at the later period and caused a lost during this sampling. The second low value in metanauplii for open waters was obtained in November 1996. The seasonal variation in mean prosome length of each stage is also shown in Table 3.1.

As in open stations, the high abundance of *Calanus* excluding metanauplii stages was also found in April 1995 (4891 ind. m^{-2}) and in April 1996 (1689 ind. m^{-2}) in coastal stations. The lowest value was obtained in September 1995 with 148 ind. m^{-2} (Table 3.1). The maximum abundance of metanauplii occurred in April 1995 with 3055 ind. m^{-2} and the minimum value was obtained in September 1995 with 32 ind. m^{-2}.

3.2.1.2. POPULATION STRUCTURE

The size-frequency distribution and mean prosome length of *C. euxinus* population at open and coastal stations during investigation periods is shown in Figure 3.2. In this figure same months (April and September) of different years were pooled.
At open stations, the mean population length was 1.86 mm in April. The sharp increase in the mean length of population was observed in June (2.23 mm) and in September (2.13mm). There were decreases in the population mean length with the values of 1.84 and 1.89 mm in November and in December respectively. At coastal stations, the mean lengths of *Calanus* population were smaller than those at open stations, indicating very little number of late stages (CV, adults) of *Calanus* was present in coastal areas.

Table 3.1: Abundance (ind. m^{-2}) and the mean prosome length (mm) of *Calanus euxinus* in each stage at open and coastal stations during the sampling periods.

	April 1995		April 1996		May 1994	June 1996		September 1995		September 1996		Nov. 96	Dec. 96
Stage	**open**	**coastal**	**open**	**coastal**	**open**	**open**	**coastal**	**open**	**coastal**	**open**	**coastal**	**open**	**open**
Female abundance	2918	9	1832	21	1713	1884	50	1350	--	1208	58	918	808
mean length	2.77	2.82	2.71	2.69	2.67	2.74	2.72	2.7	--	2.71	2.66	2.71	2.7
Male abundance	418	--	695	3	100	32	--	171	--	58	8	134	250
mean length	2.62	--	2.57	2.25	2.61	2.35	--	2.54	--	2.54	2.5	2.56	2.57
CV abundance	2505	35	3747	68	2797	3418	82	2547	11	1829	50	903	429
mean length	2.26	2.25	2.27	2.22	2.18	2.35	2.15	2.31	2.1	2.29	2.23	2.31	2.32
CIV abundance	1003	11	1747	126	1124	347	66	542	11	34	100	218	189
mean length	1.7	1.75	1.76	1.69	1.65	1.74	1.7	1.73	1.6	1.68	1.7	1.81	1.78
CIII abundance	824	929	1789	213	424	266	108	668	63	47	195	426	297
mean length	1.3	1.29	1.33	1.3	1.23	1.32	1.31	1.3	1.32	1.32	1.32	1.46	1.4
CII abundance	1095	2218	1242	405	613	218	55	437	--	42	316	492	366
mean length	0.99	1	0.99	1.01	0.99	0.99	1	1.03	--	1	0.99	1.03	1
CI abundance	1500	1689	1305	853	1318	311	39	563	63	100	389	716	458
mean length	0.74	0.75	0.75	0.75	0.77	0.83	0.76	0.72	0.71	0.76	0.75	0.77	0.76
Total	**10263**	**4891**	**18609**	**1689**	**8089**	**6476**	**400**	**6278**	**148**	**3318**	**1116**	**3807**	**2797**
Metanauplii abundance	13658	3055	7832	2863	255	2521	400	1092	32	1387	2084	776	3029

--; no individuals found

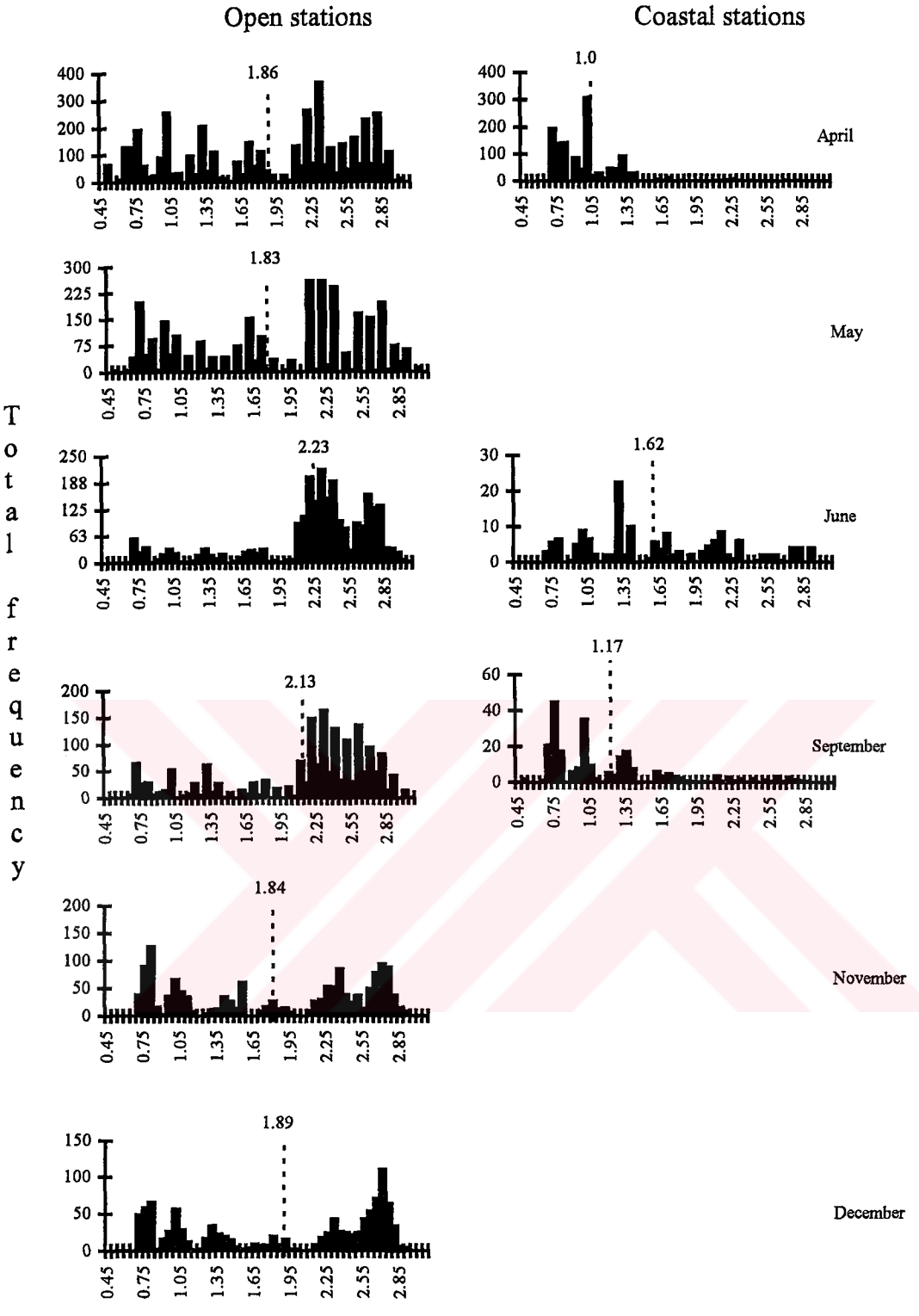

Figure 3.2: The prosome length (mm) - total frequency (ind. number in whole water column) histogram of all stages of *C. euxinus* at open and coastal stations during sampling periods. Vertical dashed lines show the mean prosome length of population.

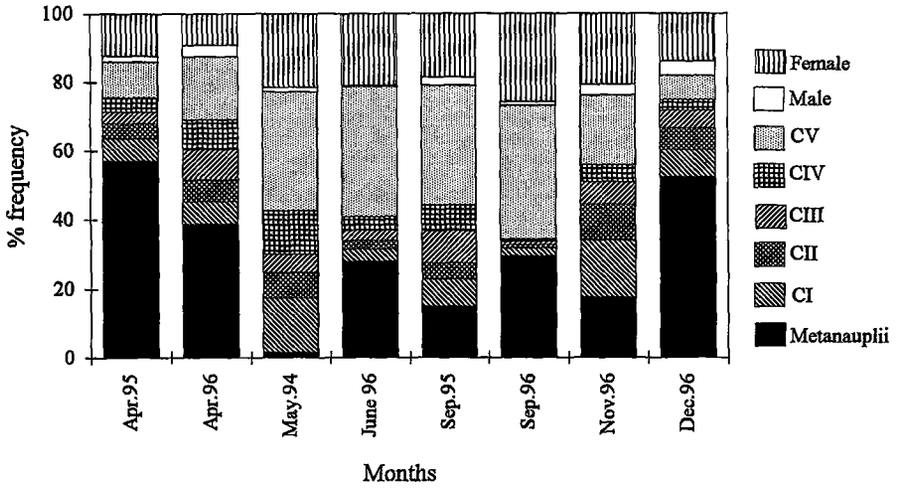

Figure 3.3: Seasonal changes in the developmental stages of *C. euxinus* at open stations.

Figure 3.3 shows the percentage contribution of each developmental stage of *Calanus* population at the open stations throughout the investigation periods. During April and December, *C. euxinus* population was represented mainly by metanauplii (Figure 3.3). The population was youngest (metanauplii, CI, CII and CIII) in April (>60% of the population) and in December (72% of the population) whereas the oldest stages made up >60% of the population in May, June and September. During the latter months CV was the dominant stage. In November, the stage distribution was bimodal with major concentrations of youngest (metanauplii, CI, CII and CIII) and oldest (CIV, CV and adults) stages. During the sampling periods, adults represented 11.5 to 27% of the population and females always outnumbered males. Males had maximum abundance making up 3.4 and 4.3% of the population in April and December 1996 respectively.

Copepods were sampled from the coastal stations in April, September 1995, in April, June and September 1996 (Table 3.1). The population of *C. euxinus* was

generally encountered in low densities from the coastal areas. In three sampling periods (April, June and September), the population was represented mainly (>80%) by youngest (metanauplii, CI, CII and CIII) stages (Figure 3.4). Adult individuals were very rare and constituted 0 to 6.3% of the population. Females occurred in high number only in September 1996. Males were found only in April 1996 (0.07%) and in September 1996 (0.3%), they were absent in April, September 1995 and in June 1996.

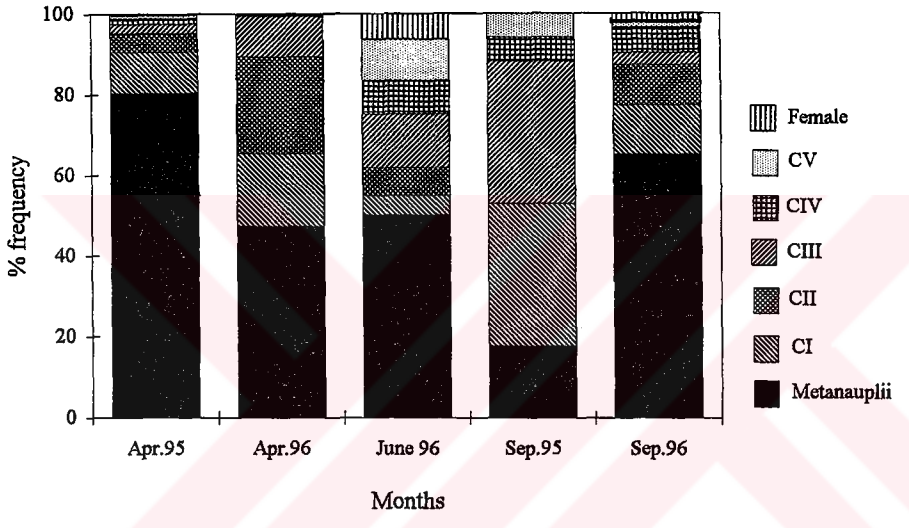

Figure 3.4: Seasonal changes in the developmental stages of *C. euxinus* at coastal stations.

3.2.1.3. VERTICAL DISTRIBUTION

The vertical distribution of species collected from open stations in April 1995, May 1994, June 1996 and September 1995 was studied (for the details of sampling see Chapter 2).

In all sampling periods, the female population of *C. euxinus* was observed to perform diel vertical migration (Figs. 3.5-3.8). The peak in abundance of female occurred at the first layer (from the depth of thermocline to the surface) during the nighttime. They moved to deeper layers during the daytime.

Besides females, males, CV, CIV and CIII also often showed diel vertical migration pattern. In April, the migration of these stages was very well defined (Figure 3.5). They started to migrate to the upper layers before 18:00 h and by 22:00 h most of the population reached the upper layer. The upward migration started approximately 2 h before the sun set which was at 19:52 in this particular day. While most of the CV population were in the upper layers during the daytime, a small percentage of the population kept staying in the 5th (lower layer of the main pycnocline) layer. They started to go deeper layers at 02:00 h, which was 3 and a ½ hours before the sun rise (at 06:06) and stayed there during the daytime. Small copepodite stages (CII, CI) and metanauplii have not shown any apparent diel cycle in their vertical distribution. They did not migrate and stayed mostly in the 2nd layer which corresponds to the depth stratum between σ_θ=14.6 and the seasonal thermocline.

In May 1994, most of the female population was below the main pycnocline (in the Oxygen Minimum Zone: OMZ) at 18:00 h, and the small portion of them still remained in the first layer (Figure 3.6). At 19:30 h they began to go up and all reached in the first layer at 22:00 h. In May, the sun sets at 20:16 h, so they must have began their upward migration approximately 1 hour before the sun sets. After 01:00 o'clock they began to migrate downward, and the majority of the female population reached the OMZ at 06:30 h. Before the sun rise which was at 05:48 h on 11th of May, they began their downward migration. Males were found

generally in the deeper layers during the all sampling time, except at 18:00 h, when they were at the first layer. Copepodite stages of V and IV also showed diurnal vertical migration, but it was not as strong as that of the females. While more than 85% of the CV population were in the first layer during the nighttime, a small percentage of them (~2%) still stayed in the OMZ. In small copepodite stages as CIII, CII, CI and metanauplii there were no regular diel vertical migration. They were generally found in the uppermost two layers.

In June 1996, females and CIV showed a clear daily cycle in their vertical migration between the surface and anoxic layer. CII, CI and metanauplii were mostly distributed in the upper three layers and did not show a well defined vertical migration. While half of the CV population showed apparent diel vertical migration, the other half was still in the 5. layer (i.e. OMZ) during the nighttime (Figure 3.7).

In September 1995, females, CV and CIV showed strong diel vertical migration. While the whole population of female and CIV migrated between the surface and the anoxic layer, 13% of the CV population stayed in the 5^{th} layer which corresponds to oxic-anoxic interface (<20 μM DO). The smaller stages of copepodites (CIII, CII and CI) and metanauplii were mostly at the uppermost two layer (Figure 3.8).

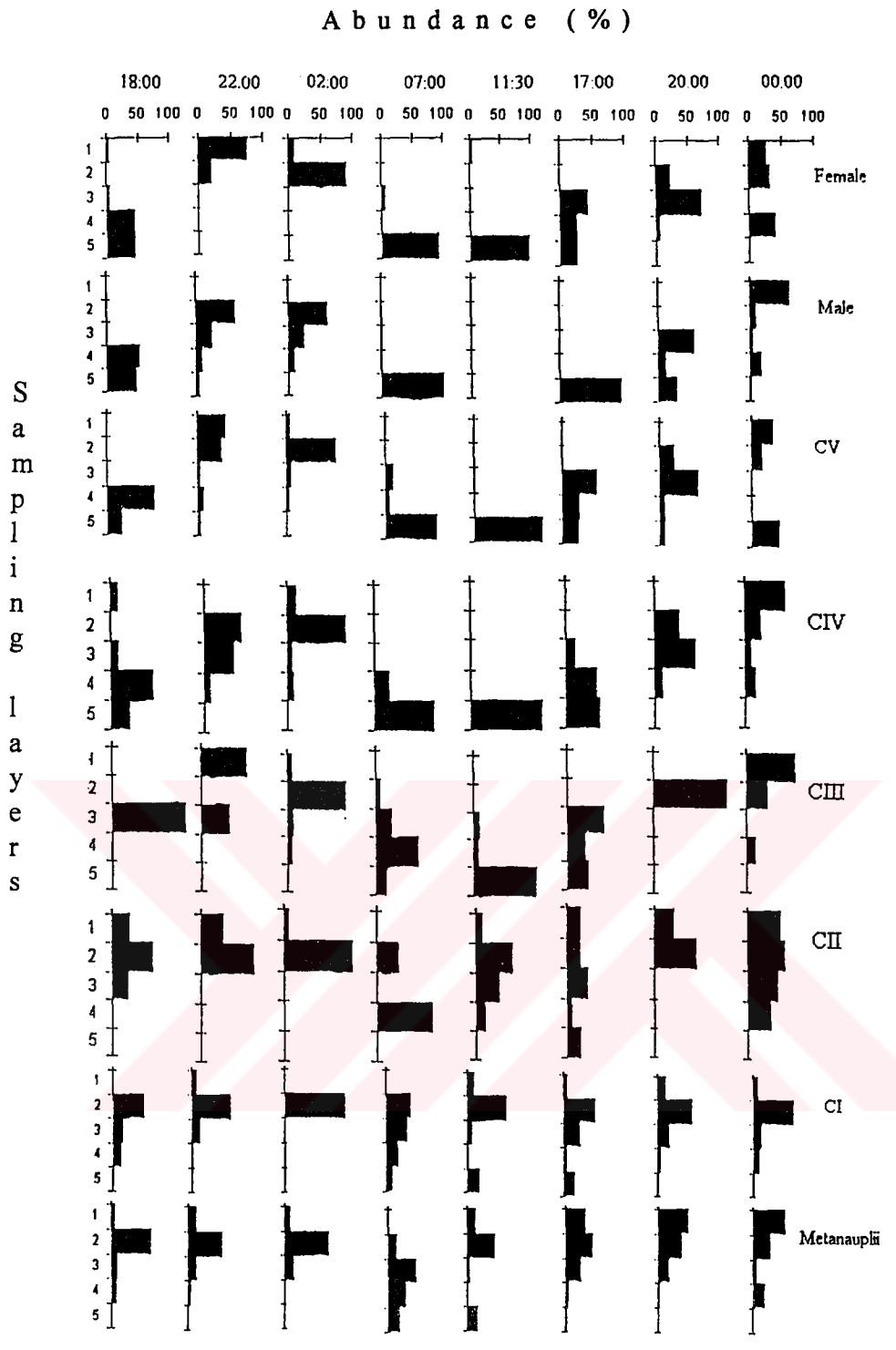

Figure 3.5: Vertical distribution of developmental stages of *C. euxinus* at each sampling time during 26-28 April 1995. Abundance is expressed as per cent of the individuals m^{-3} for the entire profile at 5 depth strata: 1- from the depth of thermocline to the surface, 2- from the depth of σ_θ=14.6 to the thermocline, 3- from the depth of σ_θ=15.4 to the depth of σ_θ=14.6, 4- from the depth of σ_θ=15.8 to the depth of σ_θ=15.4, 5- from the depth of σ_θ=16.2 to the depth of σ_θ=15.8 (for more details see section 2.1.1.1). The sampling time presented at the top of first profiles. Sunset = 19:52 h; Sunrise = 06:06 h (local time).

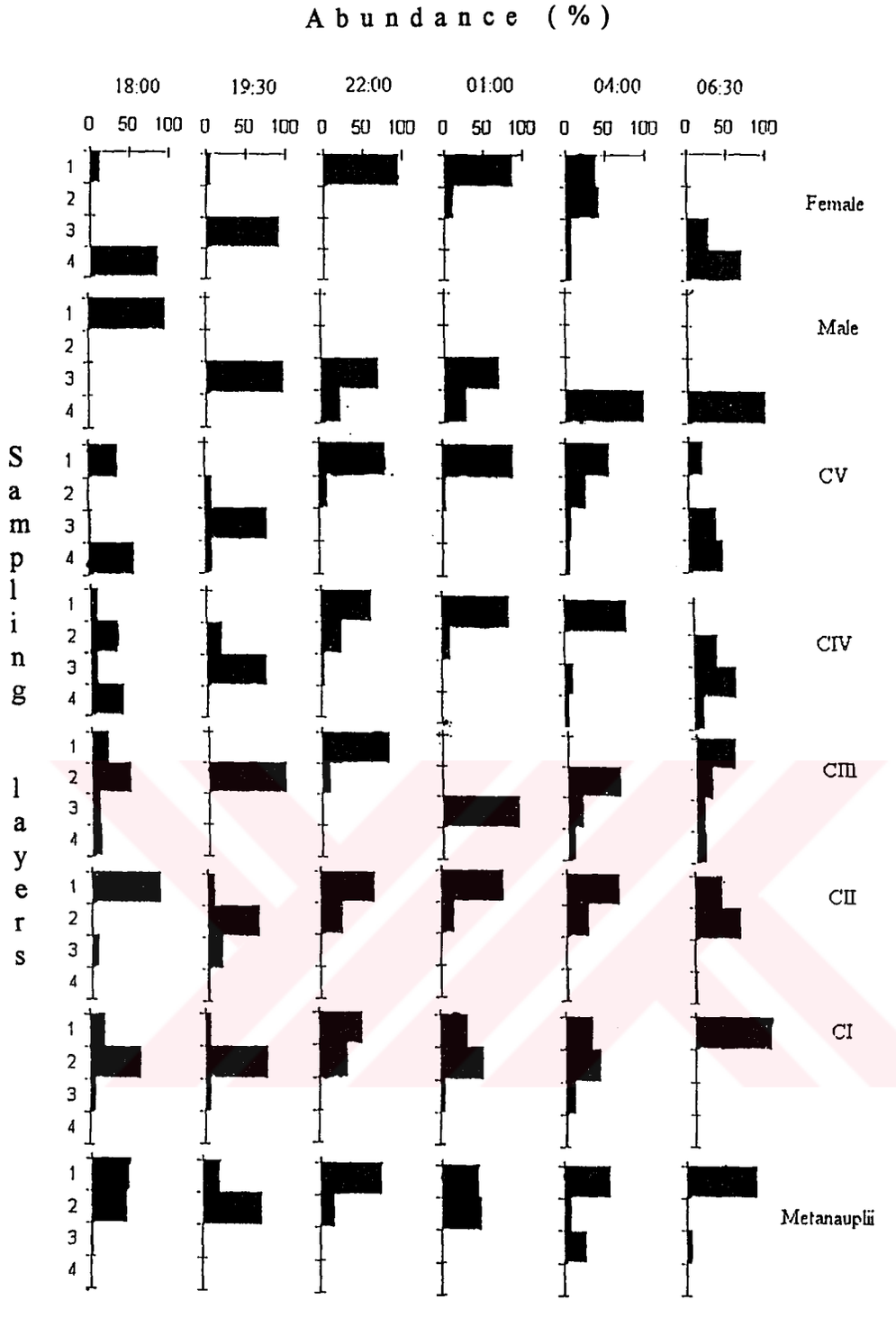

Figure 3.6: Vertical distribution of developmental stages of *C. euxinus* at each sampling time during 10-11 May 1994. Abundance is expressed as per cent of the individuals m^{-3} for the entire profile at 4 depth strata: 1- from the depth of thermocline to the surface, 2- from the depth of σ_θ=14.6 to the thermocline, 3- from the depth of σ_θ=15.4 to the depth of σ_θ=14.6, 4- from the depth of σ_θ=16.2 to the depth of σ_θ=15.4 (for more details see section 2.1.1.1). The sampling time presented at the top of first profiles. Sunset = 20:16 h; Sunrise = 05:48 h (local time).

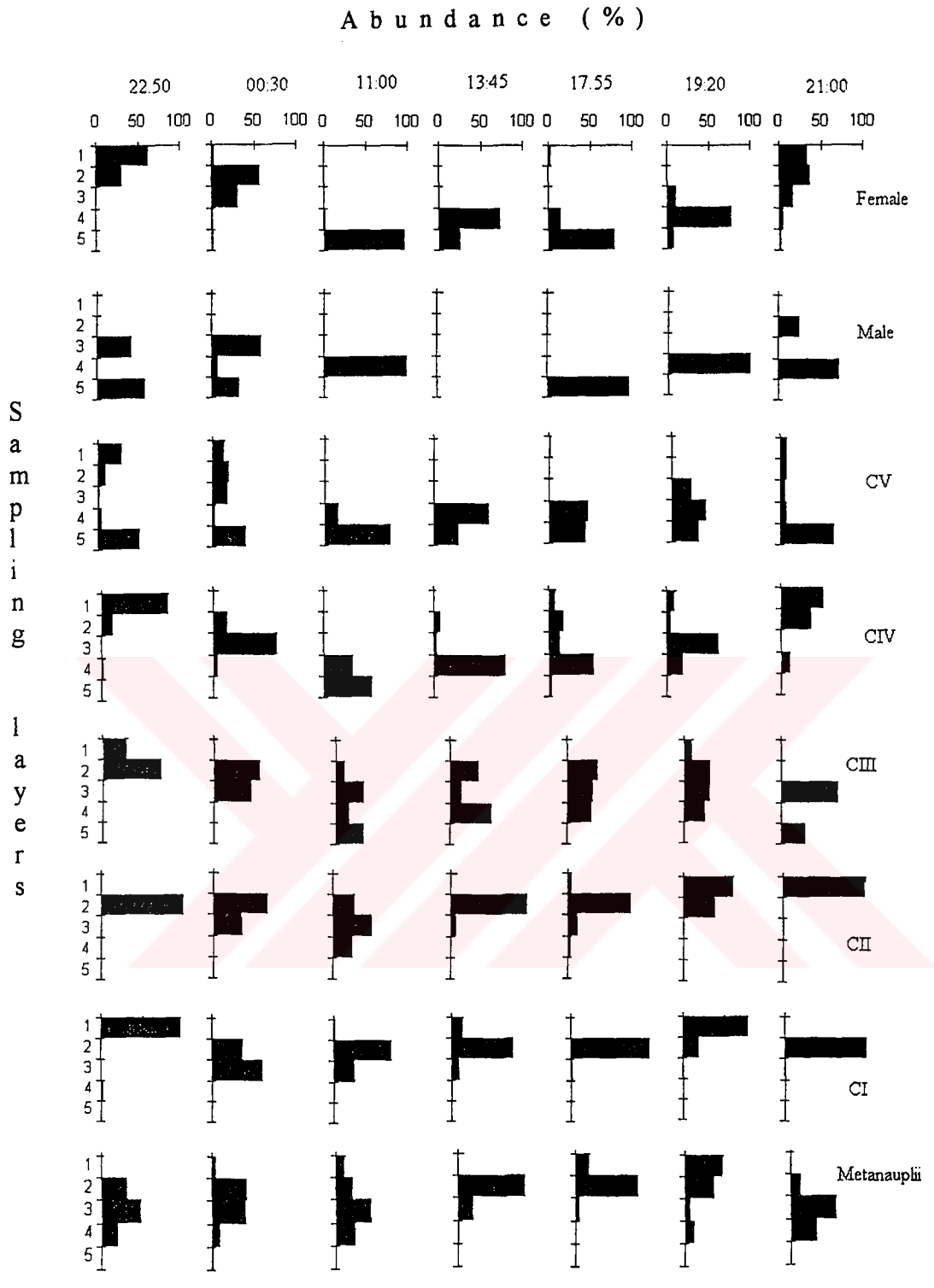

Figure 3.7: Vertical distribution of developmental stages of *C. euxinus* at each sampling time during June 1996. Abundance is expressed as per cent of the individuals m^{-3} for the entire profile at 5 depth strata. The depth of water column for each profile is as in Figure 3.5. Sunset = 20:47 h; Sunrise = 05:25 h (local time).

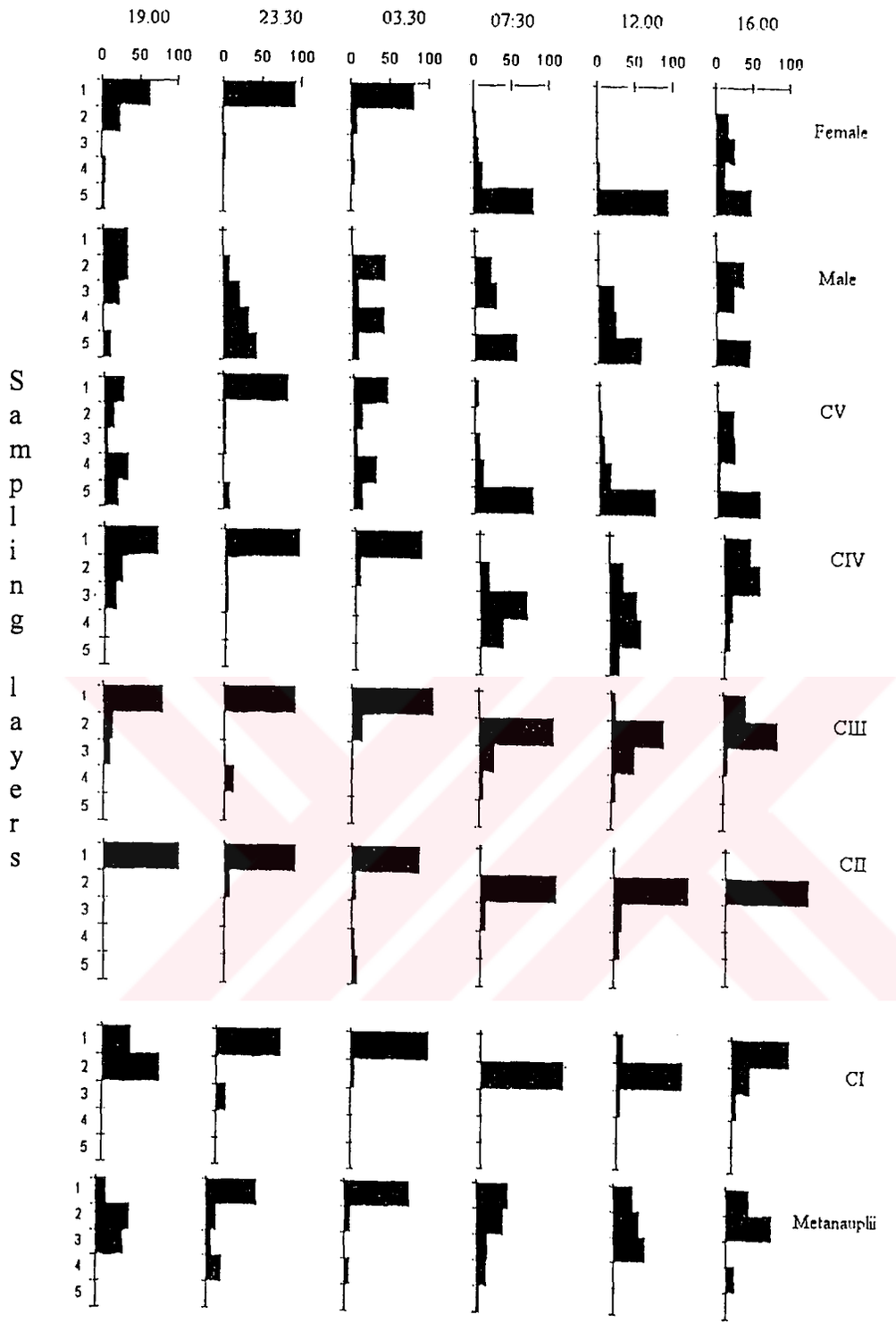

Figure 3.8: Vertical distribution of developmental stages of *C. euxinus* at each sampling time during 27-28 September 1995. Abundance is expressed as per cent of the individuals m^{-3} for the entire profile at 5 depth strata. The depth of water column for each profile is as in Figure 3.5. Sunset = 17:43 h; Sunrise = 05:47 h (local time).

3.2.1.4. DISCUSSION

Calanus is one of copepods whose distribution covers a very large area with temperature ranging between -2 and 22 °C (Marshall and Orr, 1972). *Calanus euxinus* is a cold water species (Boldovski, 1969).

Data, found in this study, on the spatial distribution indicated that they have a higher abundance in the open waters. Niermann and Greve (1997) defined this organism as deep dwelling, so they concluded that *Calanus* is more abundant in the southern Black Sea than in the shallow north western shelf of the Black Sea, because in the southern area the continental slope is very steep.

The maximum abundance of total *Calanus* (including metanauplii) was observed in April sampling. The results of Vinogradov and Shushkina, (1992) and Vinogradov *et al.* (1996) corroborate the results of this study. They found maximum abundance of *C. euxinus* at the end of March in the Black Sea.

From the prosome length distribution results in June and in September, an increase in prosome length of the population (~2.2mm) was apparent which was due to the dominancy of older stages (mostly CV and females), while in spring the smaller stages were dominant (>70% of the population). Vinogradov *et al.* (1995) also showed dominancy of the stage V and IV copepodites of *Calanus euxinus* in net mesoplankton in August. There was a marked decrease in the prosome length of population in November and in December and in these periods again the smaller individuals were dominant. The metanauplii were observed during the all sampling periods but they constituted more than half of the population in April and in December, hence it can be concluded that April and December are the main production seasons of new generations among the studied sampling periods.

Figure 3.9 shows the distribution of average Chl-a concentrations in the first 50m. The chlorophyll concentration was higher at the end of summer and autumn and there was a small peak in April 1995.

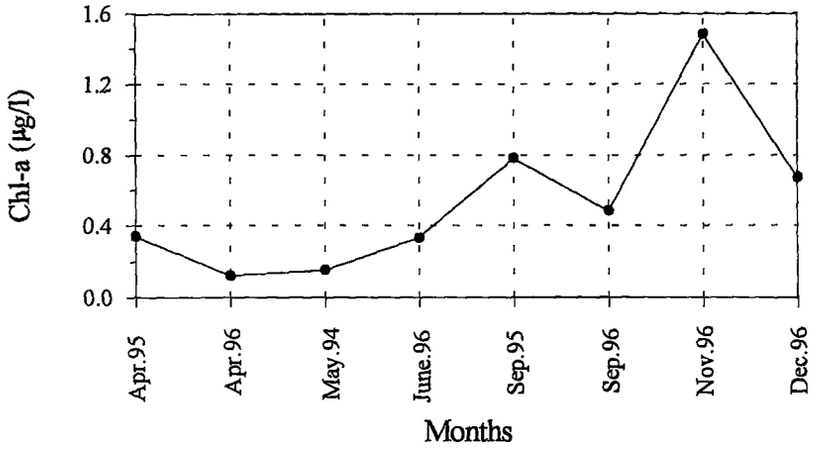

Figure 3.9: Average chlorophyll-a (Chl-a) concentrations in the first 50m at abundance stations in different sampling periods.

Vedernikov and Demidov (1994) analysed the temporal changes in chlorophyll-a concentrations using longterm data (1960-1991) from photosynthetic layer for the open areas in the Black Sea. They showed that there are two main peaks in chlorophyll concentrations; one is in spring (in February and March) and the other in November which was smaller than the spring peak. Yilmaz *et al.* (1997) studied the temporal variations of surface chlorophyll-a in the Black Sea during 1990-1996. According to their results, chlorophyll-a data related to deeper central part of the Black Sea showed different and unusual trends in terms of seasonal and interannual variabilities. A late winter blooming continued with slightly decreasing trend till late spring which collapsed during May. The developments of moderate mid-summer and autumn blooms was observed after May. Three precise peaks of chlorophyll-a

maxima were observed in the surface waters of the shelf region, namely a winter maximum in January-February; a spring-early summer one in May-June and an autumn peak in September-November. Phytoplankton biomass usually expressed as mg Chl-a m^{-3} (Parson *et al.* 1990), so it can be concluded that these Chl-a peaks coincided with the higher phytoplankton biomass. As an ecological rule, in temperate waters breeding of zooplankton cannot start until an increased primary productivity has occurred in spring. In these areas there are generally two maxima in phytoplankton and zooplankton standing stock; a large one occurring in spring and a smaller one in autumn. Thus as a result of increased primary production, there is a temporary increase in the standing stock of phytoplankton followed by a decrease, as the grazing pressure from an increased standing stock of zooplankton becomes effective (Parson *et al.* 1990). Our results corroborate this rule. Temporal changes within a plankton community itself are largely determined by the growth , mortality, sinking and migration rates of the individual plankters and their predators. Vinogradov *et al.* (1992a), mentioned the decreases in abundance of copepods during the summer and autumn periods connected to the increases in abundance of *Mnemiopsis leidyi.* The ratios of abundance in females and males fluctuated greatly during the sampling periods (from 3 to 59). The adult sex ratio was low (females/males= ~3) at the open stations both in April 1996 and December 1996. It may have ensured the rapid fertilisation during these periods. Throughout the summer and autumn the percentage abundance of metanauplii fluctuates from the range of ~15 to 30% of the population, there can be the subsidiary generations throughout the summer and autumn. Zenkevitch (1963), stated that the *C. euxinus* breeds throughout the year producing 5 or 6 generations in the Black Sea. Sazhina (1987) detected *Calanus euxinus* reproduce during the whole year and form 6-7 generation in a year. However she found the maximum abundance of eggs and early nauplii stages in winter and in spring from the Crimean coast. At the beginning of June, she observed lots of young copepodites and after 1.5 months the adults became dominant. Sazhina (1996) concluded that, *C. euxinus* actively reproduce in May. While she also observed the higher fecundity (eggs/female/day) of *Calanus* in

the open waters than the coastal areas, Vinogradov *et al.* (1992a) claimed that reproduction of *C. euxinus* mainly proceeds in the northeastern (shallow shelf) part of the Black Sea during late winter.

Data, obtained in this study, on the population structure and the vertical distribution of *C. euxinus* in the Black Sea are in agreement with the results from Black Sea by Vinogradov *et al.* (1985, 1986, 1990 and 1992a,b) and Zenkevich (1963), and verify that *C. euxinus* is a strong diel and seasonal vertical migrant. Metanauplii and even early copepodite stages (CI, CII and CIII) were concentrated in the uppermost two layers (from the depth of sigma-theta 14.6 to the surface) during the all sampling periods. Vinogradov (1968) stated that the density gradients of two water masses can represent a barrier to the vertical migration of plankton. Banse (1964) showed that salinity gradients of more than 0.2-0.3% per 10m appeared to prevent vertical migration of small copepods. This view is supported by our data; the appearance of seasonal pycnocline during all sampling periods can prevent the vertical migration of small stages. The copepodite stage IV showed an apparent diel vertical migration from the just above the anoxic layer (5^{th} layer) to the above thermocline during all sampling periods. Males showed a pronounced diel vertical migration only in April among the sampling periods. The copepodite stage V and female showed pronounced diel vertical migration throughout the sampling periods. They began to migrate upward to the phytoplankton rich upper layers towards the evening. During the daytime they were concentrated in the lower layer of oxygen minimum zone (OMZ). Obviously, there are no universal patterns of migration. Diel vertical migration is a phenomenon which shows a great deal of plasticity. Ultimately, the causes of this plasticity can only be understood by describing migration under a suite of varying conditions-food availability, presence and absence of predators, light and temperature regime, which might become more or less important in different systems. Diel vertical migration in zooplankton has been linked to predator avoidance in recent literature (Frost, 1988; Lampert, 1989; Bollens and Frost, 1989; Loose, 1993). In zooplankton, the absence of migration

leads to a high mortality as a result of predation. This may be compensated by a high fecundity and birth rate, due to a high food concentration and high temperature. The main predators of *C. euxinus* in the Black Sea are among the planktivorous fishes (as visual predators) especially sprat, mackerel and anchovy (Nalbantoglu, 1955; Acara, 1956; Avsar, 1993) among the jelly organisms, *Mnemiopsis leidyi, Pleurobrachia pileus* and *Aurelia aurita* (Mutlu, 1996); and *Sagitta* as chaetognata (Drits and Utkina, 1988). Avsar (1993), observed the calanoids copepods (especially *Calanus euxinus, Paracalanus parvus, Acartia clausi* and *Pseudocalanus elongatus*) comprised the main food source of sprat in the southern Black Sea. Mutlu (1996), found that the major food item of jelly organisms was copepods in the Black Sea. Among the copepods, they have frequently consumed *Calanus euxinus.* Drits and Utkina (1988) found copepodite stage V and female of *Calanus* and females of *Pseudocalanus* as the principal food of *Sagitta setosa* in the Black Sea. *Sagitta* feed actively in the layers of daytime aggregation layer (lower boundary of oxic zone) as a vertical migratory organism. In spite of, among these predator, *Mnemiopsis leidyi* is the new invader in the Black Sea ecosystem, Vinogradov *et al.* (1992a) confirmed that a definite decreasing trend in *Calanus* population after invasion of *M. leidyi.* Vinogradov *et al.* (1992a), showed that *M. leidyi* population inhabited the thermocline, descending down to the boundary of the pycnocline. Such a strong feeding pressure apparently led to reduction of the *Calanus* population. Vinogradov *et al.* (1992a) stated that the species which remain in the deep water layer most of the time (eg. *Calanus* and *Pseudocalanus elongatus*) are biotopically isolated from *M. leidyi* and are therefore less exposed to its feeding pressure. Considering results of the above mentioned studies, it is evident that there is a high predator stress on *C. euxinus,* so it can not be neglected the effect of predator avoidance hypothesis on the diel vertical migration of *Calanus* in the Black Sea.

The copepodite stage V *Calanus* also undergo seasonal (ontogenetic) migration during summer and early autumn (during warmer periods) in the Black Sea. When

they were at the upper layer during the nighttime, some part of the CV population were still staying at lower limit of oxygen minimum zone 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), observed that 60-75% of the stage V remained at the lower limit of the oxygenated layer at the nighttime in August. The rest migrated to the 10-50m layer. They obtained also the overwintering (diapausing) stock in October but at that time more than 1/3 of the CV population did not participate in migrations (for more detail on diapause period of CV, see chapter 7).

3.2.2. PSEUDOCALANUS ELONGATUS

3.2.2.1. SPATIAL DISTRIBUTION

The total abundance of *P. elongatus* showed seasonal variations both at open and coastal stations (Figure 3.10). There was a significant difference (ANOVA) in the abundance of *P. elongatus* between open and coastal stations almost in each sampling period except in June 1996. The total abundances at open stations were significantly higher than those of coastal stations in April 1995, 1996 and in September 1995. However, in September 1996 coastal stations had a significantly higher abundance than open ones.

The data on *P. elongatus* were presented as female, male and total copepodite stages. None of the copepodites and nauplii stages could be identified.

Table 3.2 shows the abundance and mean prosome length of female, male and total copepodite stages of *Pseudocalanus* at open and coastal stations during sampling periods. *P. elongatus* was generally encountered in high densities. At open stations, the maximum abundances of female, male and copepodite stages

were found in April periods. The minimum values were observed in September 1996. At coastal stations, while the abundances of males and females peaked in June 1996, the highest abundance of total copepodite stages occurred in April.

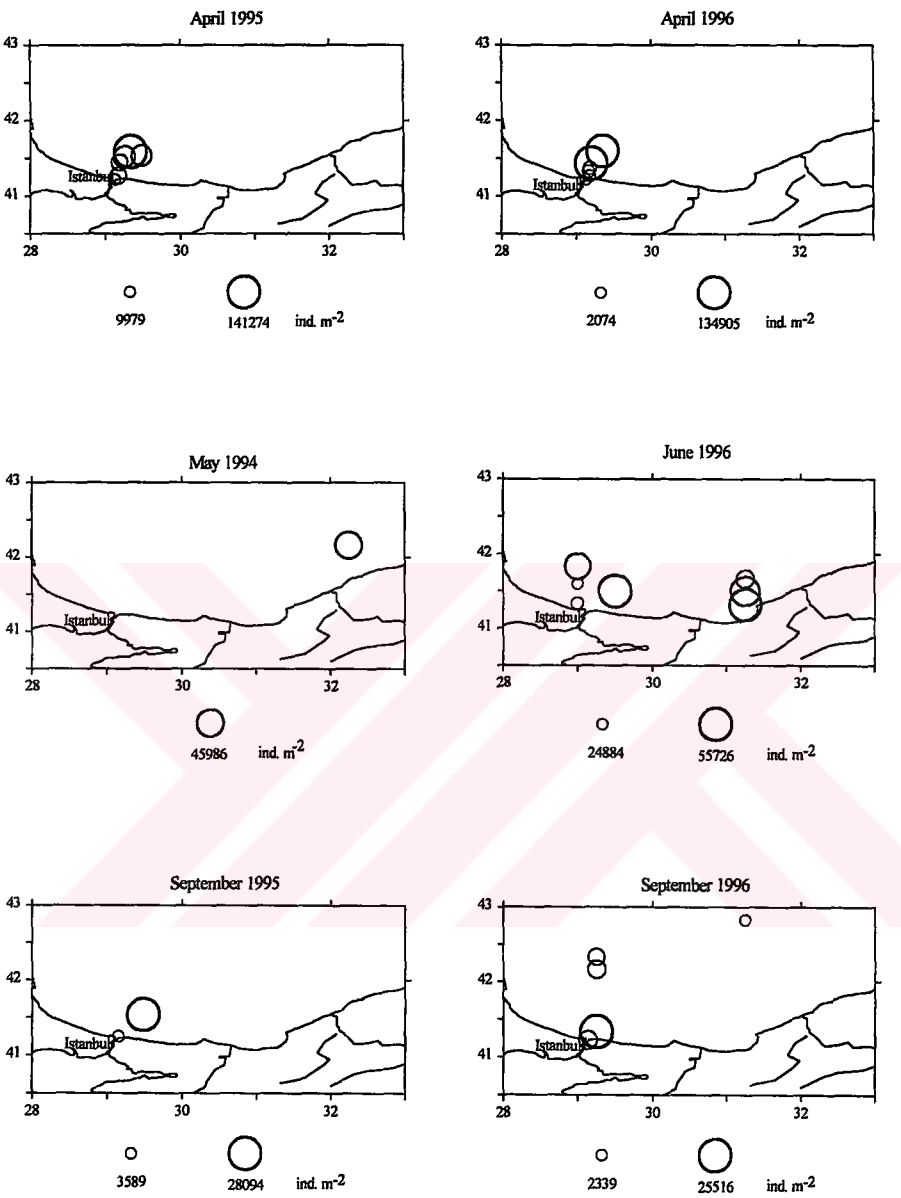

Figure 3.10: Abundance (ind. m^{-2}) of adults and copepodite stages of *P. elongatus* at each station during the sampling periods. Numbers are proportional to the radius of the circle (linear transformation). Minimum and maximum values are given in the scale. Open and coastal stations were depicted in Figure 2.4.

Table 3.2: Abundance (ind. m^{-2}) and the mean prosome length (mm) of *P. elongatus* in female, male and total copepodite stages at open and coastal stations during sampling periods.

Sampling period	Region	Female		Male		Copepodite stages	
		Abundance	Mean length	Abundance	Mean length	Abundance	Mean length
Apr. 1995	open	17252	0.80	2704	0.68	55440	0.53
	coastal	1646	0.87	481	0.76	28993	0.59
Apr. 1996	open	17095	0.88	13053	0.70	100211	0.52
	coastal	2401	0.88	454	0.72	30362	0.51
May 1994	open	10108	0.79	1782	0.68	34096	0.61
June 1996	open	9649	0.79	1439	0.67	37523	0.50
	coastal	2684	0.78	1305	0.64	21842	0.46
Sep. 1995	open	7065	0.83	1404	0.67	19625	0.51
	coastal	1579	0.83	158	0.70	1853	0.52
Sep. 1996	open	1114	0.77	145	0.68	5592	0.52
	coastal	1874	0.84	674	0.68	15263	0.51

3.2.2.2. POPULATION STRUCTURE

The size-frequency distribution and the mean prosome length of the *P. elongatus* population at open and coastal stations during the investigated periods is shown in Figure 3.11. The differences in the mean prosome length of the population in sampling periods were not pronounced at both open and coastal stations. The population reached its higher mean prosome length in May. Minimum prosome length of population was observed in June at coastal stations.

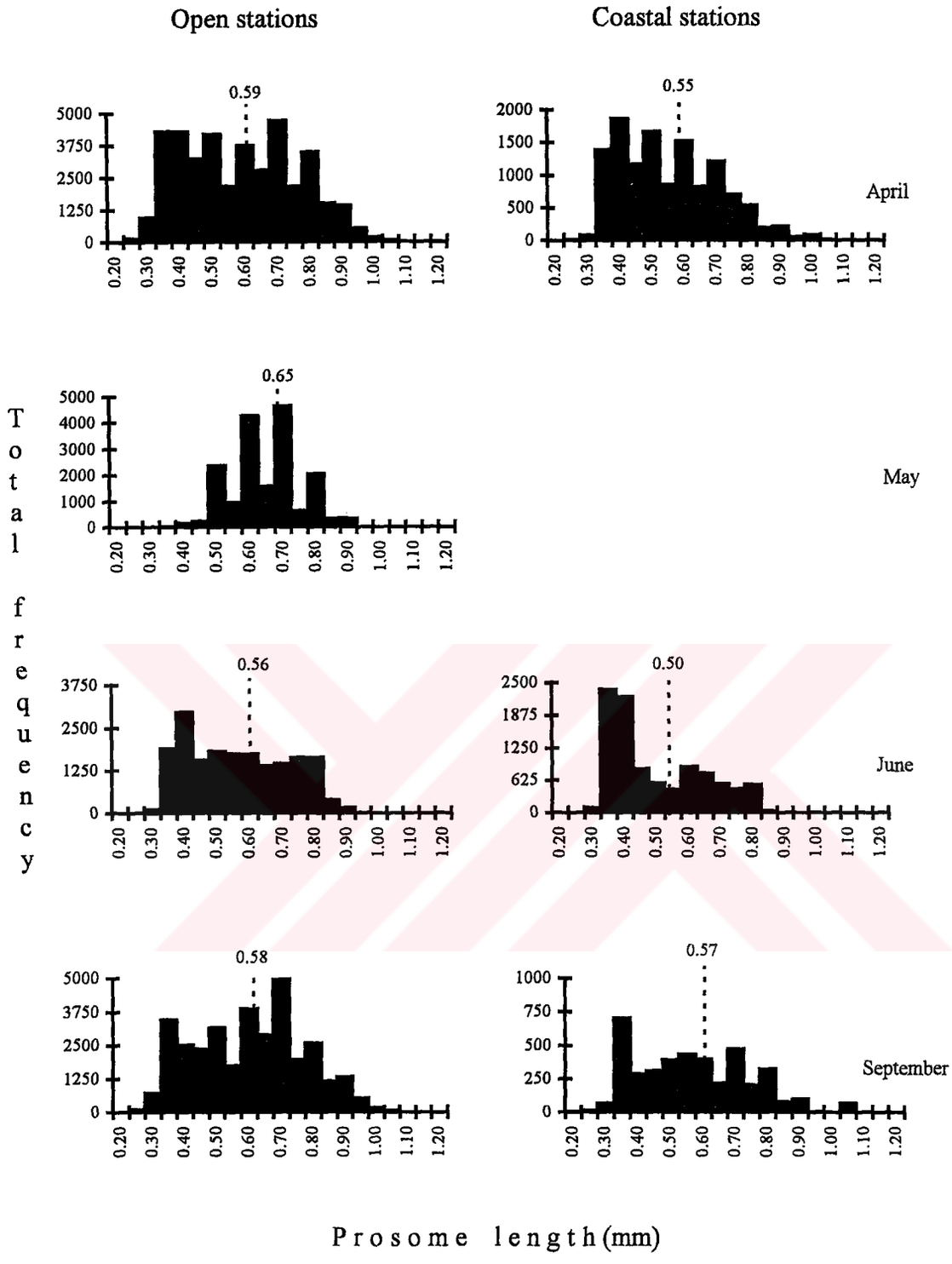

Figure 3.11: The prosome length(mm)- total frequency(ind. number in whole water column) histogram of *P. elongatus* at the open and coastal stations during the sampling periods. Vertical dashed lines show the mean prosome length of population.

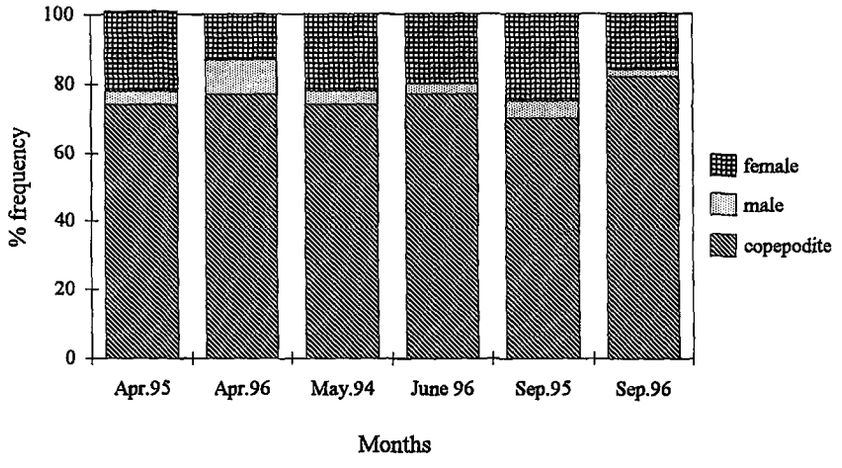

Figure 3.12: Seasonal changes in the developmental stages of *P. elongatus* at the open stations.

The percentage frequency of developmental stages of *P. elongatus* in the sampling periods at open stations is shown in Figure 3.12. In all sampling periods the total copepodite stages formed ≥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 they were almost absent (2% of the population) in September 1996.

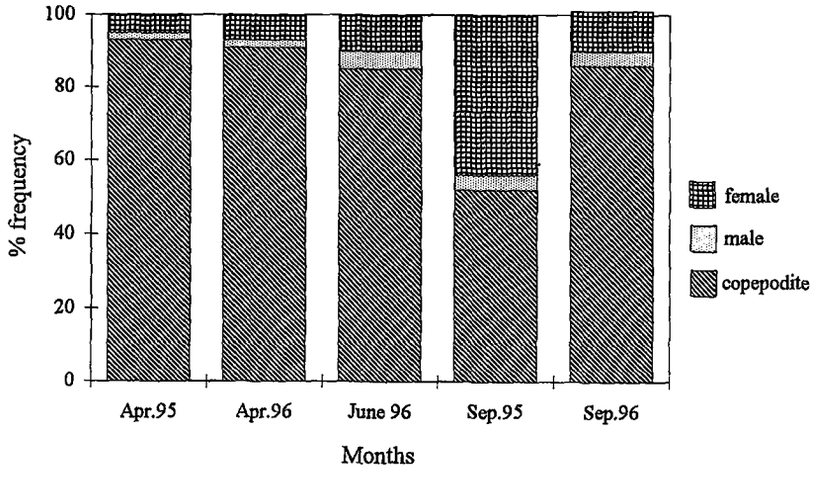

Figure 3.13: Seasonal changes in the developmental stages of *P. elongatus* at the coastal stations.

At coastal stations, total copepodite stages dominated the population in each sampling period (Figure 3.13). Females were always found in much higher numbers than males. In September 1995, they even made up 44% of the population. Males comprised in the range of only 2-5% of the population during the sampling periods.

3.2.2.3. VERTICAL DISTRIBUTION

The diel vertical migration of *P. elongatus* is presented in Figs 3.14-3.17 in each sampling period. The well defined characteristic of diel vertical migration of *Pseudocalanus* was only observed in April 1995 sampling. All specimens migrated between second and fifth layer. This was the only season in which the copepodite stages were observed below the depth of 15.4 sigma-theta.

In April 1995 and in June 1996 there were almost no individuals above the thermocline (i.e. the first layer). In September 1995 and in May 1994, the majority of females and copepodites were in the first layer during the nighttime. Although the peaks in abundance of females were in the deeper layers during the daytime in April and in June, it was in the intermediate layers in September. The lack of daytime sampling, prevents to make definite decision for May 1994 sampling. While the females were found in the deeper layers in the early morning (07:00 h) in April, the peak in abundance was still in the first layer in May. Males showed higher abundance in the intermediate layers (between thermocline and 15.4 sigma-theta) in all sampling periods, except in April 1995. They exhibited small scale periodic migration between the third and the fifth layers. Copepodite stages were distributed in the first and second layers in May and September, while they were mostly in the second and third layers in June. Their peak in abundance was in the lower boundary of the main pycnocline in daytime in April.

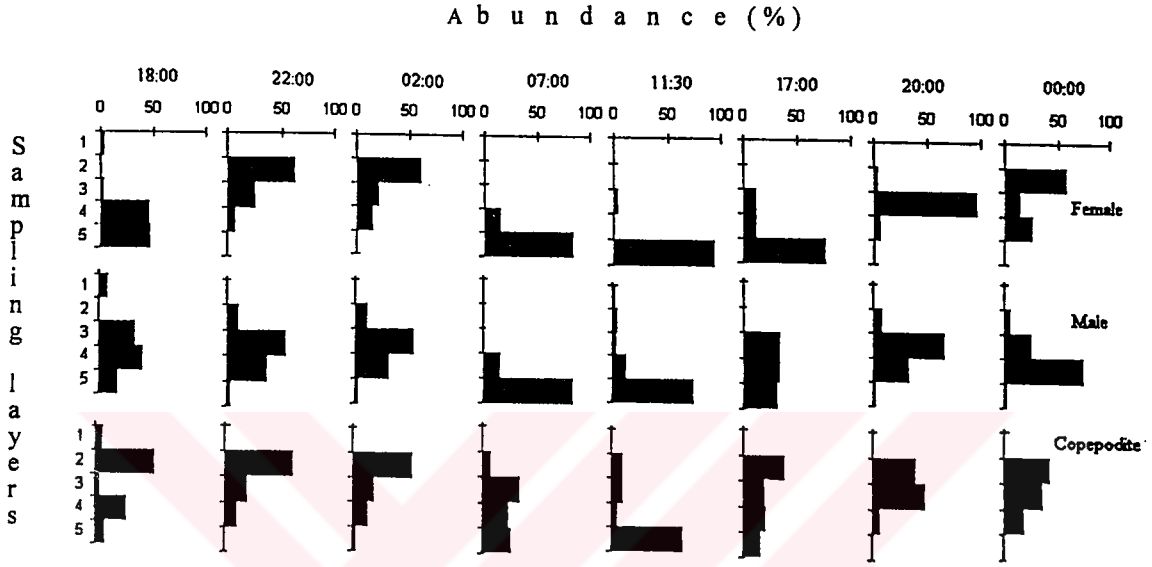

Figure 3.14: Vertical distribution of developmental stages of *P. elongatus* at each sampling time during 26-28 April 1995. Abundance is expressed as per cent of the individuals m^{-3} for the entire profile at 5 depth strata: 1- from the depth of thermocline to the surface, 2- from the depth of σ_θ=14.6 to the thermocline, 3- from the depth of σ_θ=15.4 to the depth of σ_θ=14.6, 4- from the depth of σ_θ=15.8 to the depth of σ_θ=15.4, 5- from the depth of σ_θ=16.2 to the depth of σ_θ=15.8 (for more details on sampling see section 2.1.1.1). The sampling time presented at the top of first profiles. Sunset = 19:52 h; Sunrise = 06:06 h (local time).

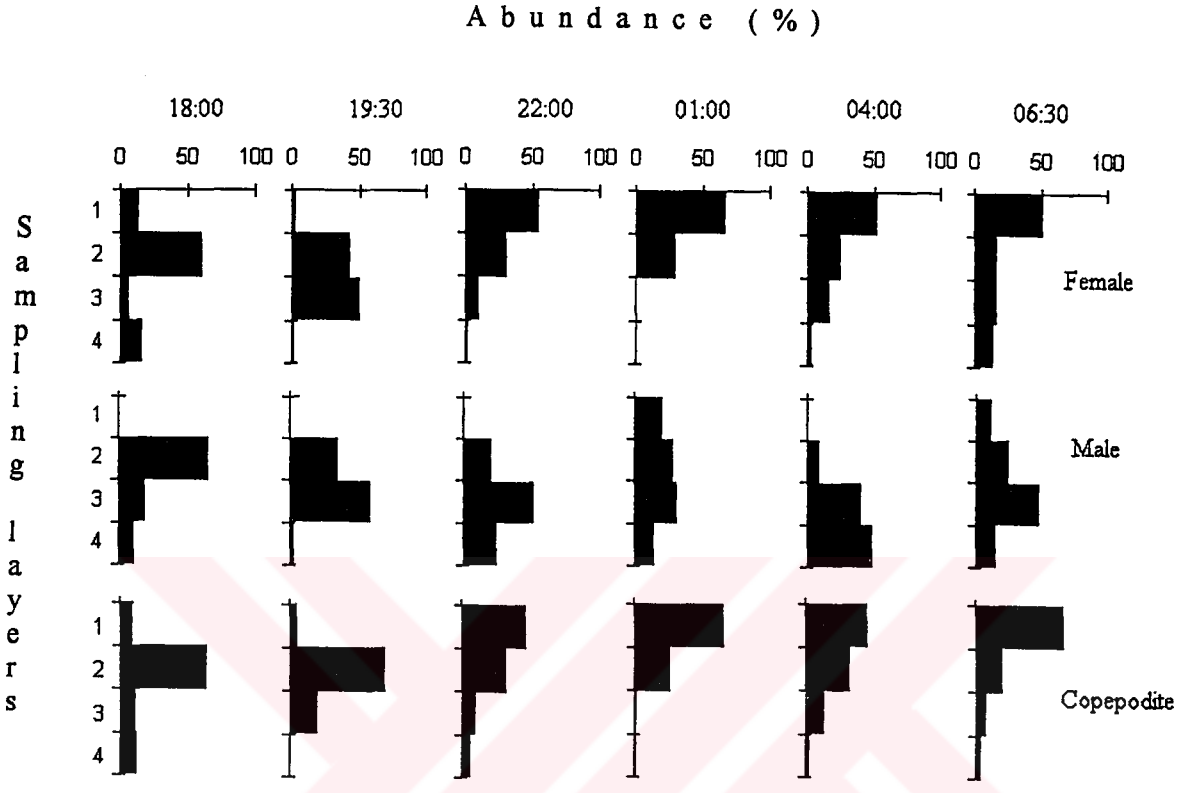

Figure 3.15: Vertical distribution of developmental stages of *P. elongatus* at each sampling time during 10-11 May 1994. Abundance is expressed as per cent of the individuals m^{-3} for the entire profile at 4 depth strata: 1- from the depth of thermocline to the surface, 2- from the depth of σ_θ=14.6 to the thermocline, 3- from the depth of σ_θ=15.4 to the depth of σ_θ=14.6, 4- from the depth of σ_θ=16.2 to the depth of σ_θ=15.4 (for more details on sampling see section 2.1.1.1). The sampling time presented at the top of first profiles. Sunset = 20:16 h; Sunrise = 05:48 h (local time).

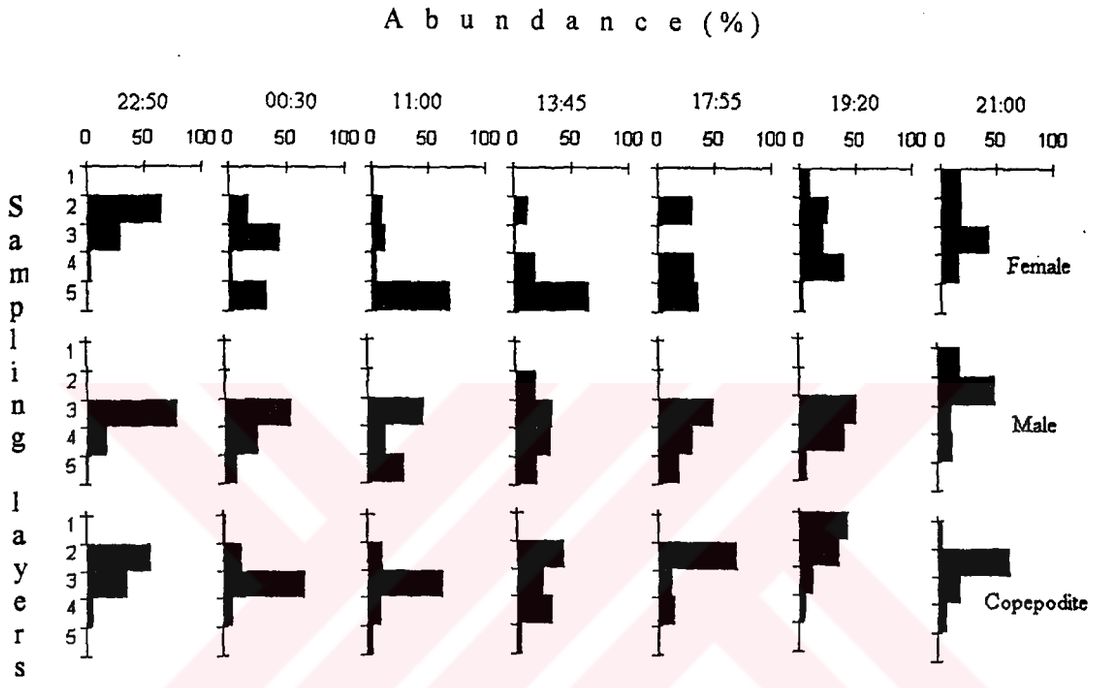

Figure 3.16: Vertical distribution of developmental stages of *P. elongatus* at each sampling time during June 1996. Abundance is expressed as per cent of the individuals m^{-3} for the entire profile at 5 depth strata. The depth of water column for each profile is as in Figure 3.14. Sunset = 20:47 h; Sunrise = 05:25 h (local time).

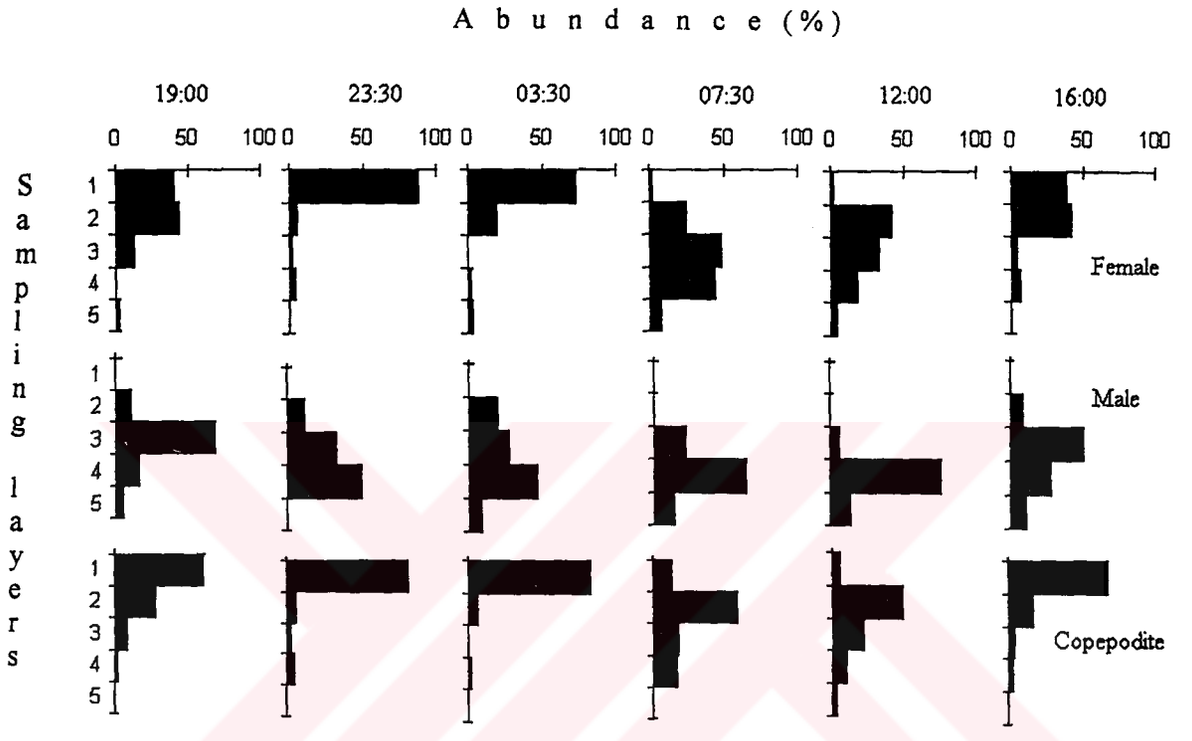

Figure 3.17: Vertical distribution of developmental stages of *P. elongatus* at each sampling time during 27-28 September 1995. Abundance is expressed as per cent of the individuals m^{-3} for the entire profile at 5 depth strata. The depth of water column for each profile is as in Figure 3.14. Sunset = 17:43 h; Sunrise = 05:47 h (local time).

3.2.2.4. DISCUSSION

Pseudocalanus elongatus, being a cold water species, with the optimum temperature of 8-10 °C in the range, is very common throughout the Black Sea (Greze *et al.* 1971; Sorokin, 1983). From results of this study on the spatial distribution of *P. elongatus*, they were found to be dominant at the open areas. The total abundance of *P. elongatus* decrease from April 1996 through September at the open station. Greze *et al.* (1971), analysing their monthly samples from Crimean coast, observed the highest abundances of *P. elongatus* to occur in winter and in spring (from January to May), and after May they found a decrease in abundance of *P. elongatus* until December. In the western Black Sea, also the higher abundance (20000 ind. m^{-2}) was observed in March-April period (Niermann *et al.* 1997). This is probably connected with the spring bloom of phytoplankton.

From the results of the prosome length-frequency histogram of *P. elongatus*, the maximum prosome length of the population was observed in May with the value of 0.65mm, in spite of the total copepodite stages were dominant at that period (Figure 3.12). From Table 3.2 the mean prosome length of total copepodite stages was 0.61mm which was the highest value among all sampling periods. It means that the older copepodite stages (CIV and CV) were the dominant group. Greze *et al.* (1971), suggested that the development of *P. elongatus* takes 35 days from egg to adult, so it could be concluded that spawning must have started at the beginning of April. However, it was observed that the total copepodite stages were dominant during all sampling periods with almost the same prosome length. Greze *et al.* (1971), implied that *P. elongatus* spawns throughout the year, producing 7 or 9 generations depending on the temperature. They also observed the nauplii of *P. elongatus* throughout the year, however, while the 50% of population was constituted by nauplii in summer, and 75-80% of the population was made up by nauplii from October to March.

Zagorodnyaya, (1970) and Vinogradov *et al.* (1986) observed that the diurnal vertical migration was particularly characterised by copepodite stages IV, V and females of *Pseudocalanus elongatus*. Vinogradov *et al.* (1992a) stated that female *P. elongatus* leaves their daytime concentration depths (in the main pycnocline) at night and concentrate in or mostly below the thermocline, and they noticed that these organisms never move to the upper mixed layer in summer. From vertical migration results of this study, its occurrence at all depths was generally erratic. A pronounced diel vertical migration of female, male and total copepodite stages of *P. elongatus* were observed only in April. While there was no individual above the thermocline in April 1995 and in June 1996, the majority of females and copepodite were above the thermocline during the nighttime in September 1995 and in May 1994. Vinogradov *et al.* (1992a) suggested that the daytime concentration layer, its extent and the other factors peculiar to different seasons and areas, as well as the migration pattern of the animals may vary appreciably.

3.2.3. *ACARTIA CLAUSI*

3.2.3.1. SPATIAL DISTRIBUTION

The population of *Acartia clausi* was investigated as female, male, total copepodite stages and the metanauplius. In May 1994, no metanauplius was observed, due to the size of the gauze. The size of metanauplii ranged from 0.17-0.24mm (Boltovski, 1969).

Overall abundance of *A. clausi* showed seasonal variations. Figure 3.18 shows the abundance distribution of adult and copepodite stages (except nauplii) of *A. clausi* at every station in different sampling periods. There was a significant difference in abundance of *A. clausi* between the open and coastal stations in April 1995 and June 1996 samplings. In the other sampling periods the differences in abundance between the open and coastal stations were not significant.

Table 3.3 shows the abundance and mean prosome length of female, male, copepodite stages and the metanauplius of *A. clausi* at open and coastal stations in different sampling periods. *A. clausi* was generally encountered in high densities and reached maximum total abundance in April 1995 (43140 ind. m^{-2}) at coastal stations. At open stations the highest total abundance was observed in June with a value of 31918 ind. m^{-2}. While the abundance of metanauplius was higher in April 1995 at the coastal stations (8323 ind. m^{-2}) , the maximum abundance was found to be 11521 ind. m^{-2} in June at open stations.

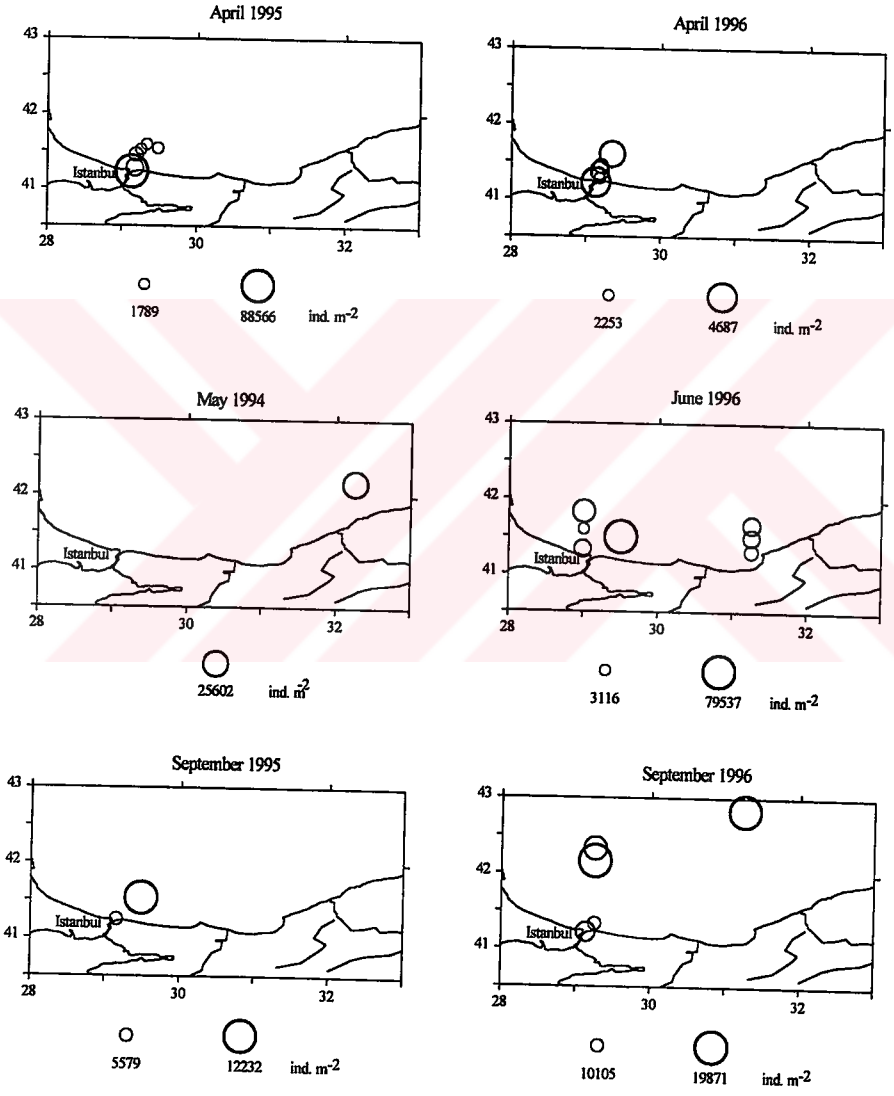

Figure 3.18: Abundance (ind. m^{-2}) of adults and copepodite stages of *A. clausi* at each station during the sampling periods. Numbers are proportional to the radius of the circle (linear transformation). Minimum and maximum values are given in the scale. Open and coastal stations were depicted in Figure 2.4.

Table 3.3: Abundance (individuals m^{-2}) and mean prosome length of *A. clausi* in female, male, copepodite and metanauplius at open and coastal stations during the sampling periods.

Sampling Periods	Region	Female		Male		Copepodites		Metanauplii
		Abundance	Mean length	Abundance	Mean length	Abundance	Mean length	Abundance
	open	1376	0.98	996	0.94	2938	0.60	1651
	coastal	15809	0.98	10018	0.94	17313	0.58	8323
April 1996	open	842	1.00	84	0.90	3284	0.55	674
	coastal	808	0.97	403	0.90	1890	0.55	308
May.94	open	12000	0.97	6166	0.92	7436	0.66	--
June 1996	open	6087	0.85	6142	0.82	19689	0.50	11521
	coastal	2853	0.87	1474	0.82	9526	0.50	4537
Sep. 1995	open	1002	0.87	535	0.84	3111	0.43	2404
	coastal	737	0.85	558	0.79	4284	0.42	1484
Sep. 1996	open	3067	0.83	1519	0.83	13594	0.48	2351
	coastal	3221	0.86	1411	0.82	7074	0.51	758

--; no individuals observed

3.2.3.2. POPULATION STRUCTURE

The size-frequency distribution and mean prosome length of the population of *A. clausi* at open and coastal stations throughout the sampling periods is shown in Figure 3.19. During late spring the mean prosome length of population increased from 0.7 to 0.87 mm at open stations,. In May the population was dominated by the larger individuals. Towards September the population mean length declined to 0.57 mm. In April the population was older with the mean population length of 0.80 mm at coastal stations. In June and September, the population length again declined to 0.60 mm.

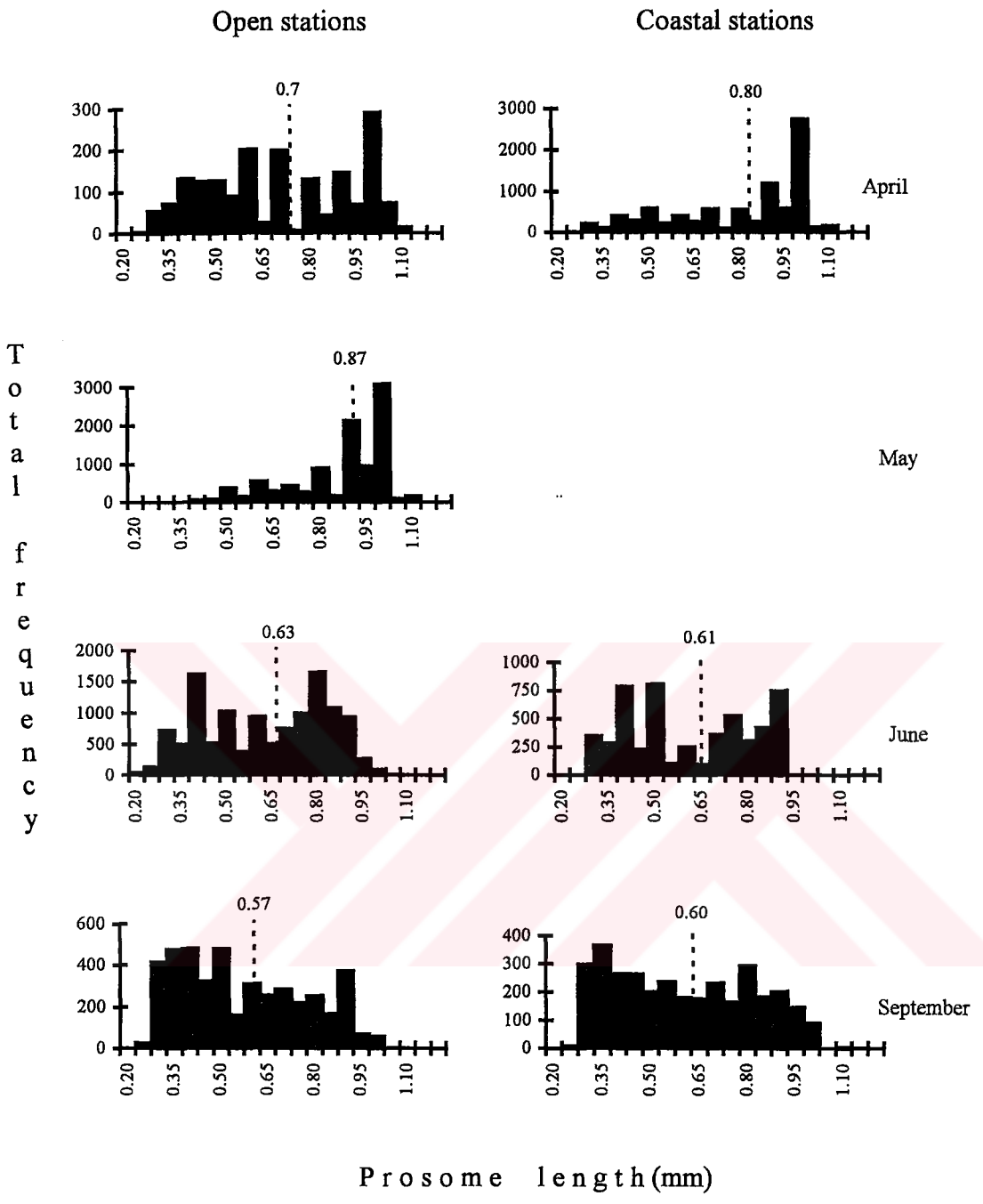

Figure 3.19: The prosome length (mm) - total frequency histogram of *A. clausi* at the open and coastal stations in different sampling periods. Vertical dashed lines show the mean prosome length of population.

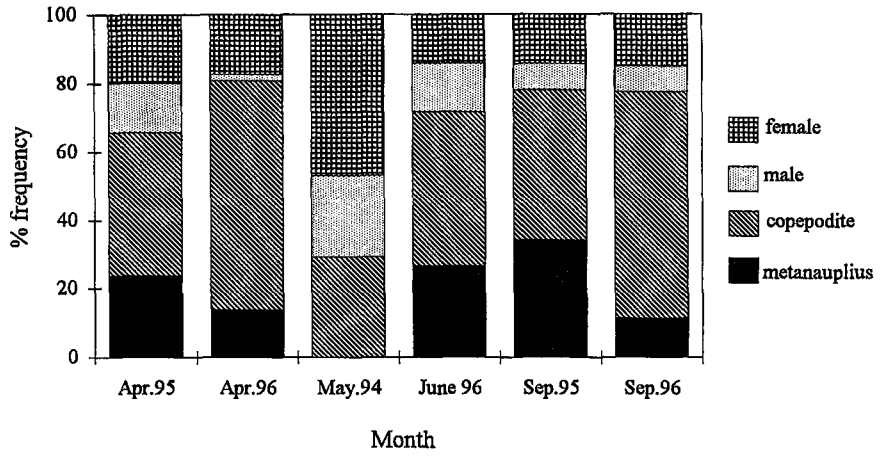

Figure 3.20: Seasonal changes in the developmental stages of *A. clausi* at the open stations.

Figure 3.20 shows the percentage frequency of developmental stages of *A. clausi* in different sampling periods at open stations. The metanauplius consisted in the range of 11% (in September 1996) and 27% (in June 1996) of the population during the sampling periods. In May no metanauplius was observed, since the mesh size used (200μm) was larger than the other sampling periods. 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, expect in June when the number of females and males was almost the same.

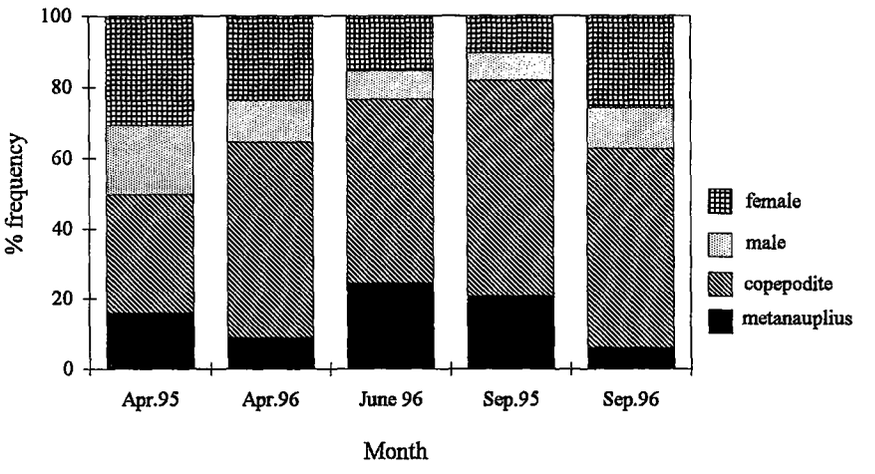

Figure 3.21: Seasonal changes in the developmental stages of *A. clausi* at the coastal stations.

Figure 3.21 shows the percentage frequency of the developmental stages of *A. clausi* in all sampling periods at coastal stations. In April 1995, the stage distribution was bimodal; with 50% of population was comprised by metanauplius and copepodites, and 50% by adults. In other seasons the copepodite stages formed the bulk of the population with the range between 52% (in June) and 61% (in September 1995). Females were more abundant than males in all sampling periods.

3.2.3.3. VERTICAL DISTRIBUTION

There were no apparent diel vertical migration in *A. clausi* distribution in all sampling periods (Figs 3.22-3.25). It occurred frequently in the upper two layers (from the thermocline to the surface and from the depth of sigma-theta 14.6 to the thermocline) in all seasons.

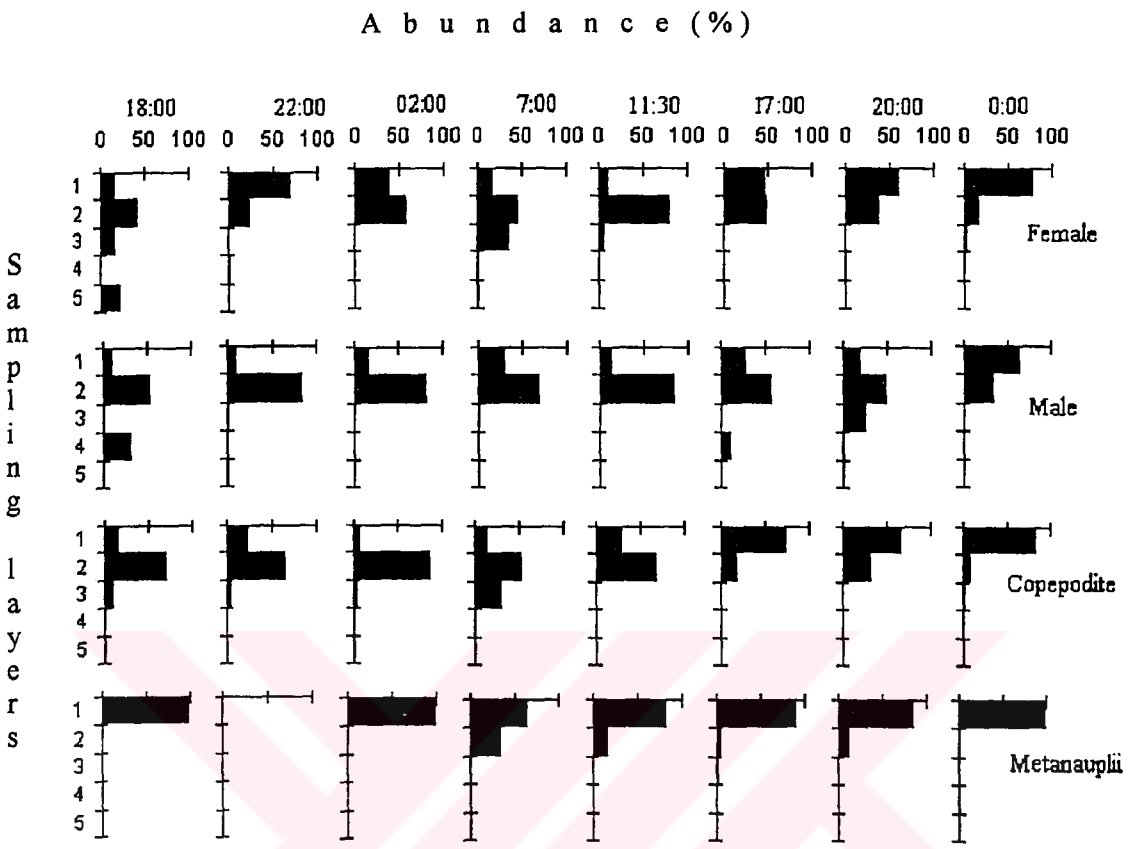

Figure 3.22: Vertical distribution of developmental stages of *A. clausi* at each sampling time during 26-28 April 1995. Abundance is expressed as per cent of the individuals m^{-3} for the entire profile at 5 depth strata: 1- from the depth of thermocline to the surface, 2- from the depth of σ_θ=14.6 to the thermocline, 3- from the depth of σ_θ=15.4 to the depth of σ_θ=14.6, 4- from the depth of σ_θ=15.8 to the depth of σ_θ=15.4, 5- from the depth of σ_θ=16.2 to the depth of σ_θ=15.8 (for more details on sampling see section 2.1.1.1). The sampling time presented at the top of first profiles. Sunset = 19:52 h; Sunrise = 06:06 h (local time).

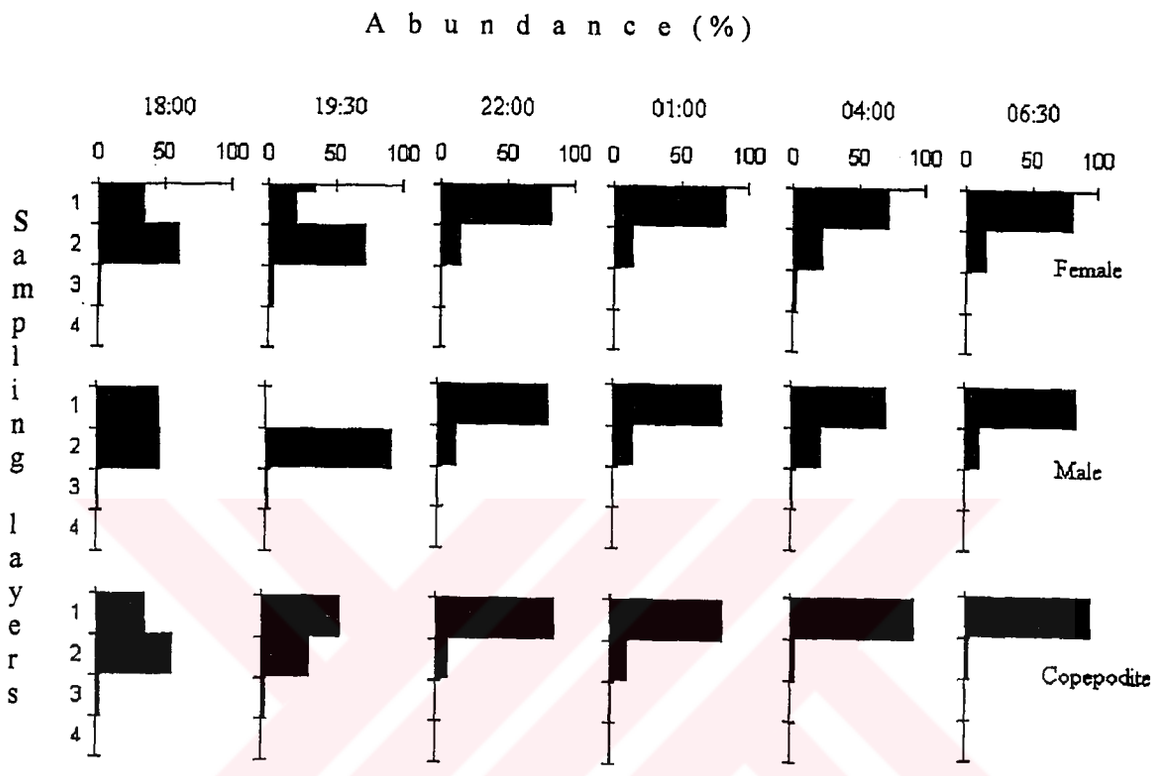

Figure 3.23: Vertical distribution of developmental stages of *A. clausi* at each sampling time during 10-11 May 1994. Abundance is expressed as per cent of the individuals m^{-3} for the entire profile at 4 depth strata: 1- from the depth of thermocline to the surface, 2- from the depth of σ_θ=14.6 to the thermocline, 3- from the depth of σ_θ=15.4 to the depth of σ_θ=14.6, 4- from the depth of σ_θ=16.2 to the depth of σ_θ=15.4 (for more details on sampling see section 2.1.1.1). The sampling time presented at the top of first profiles. Sunset = 20:16 h; Sunrise = 05:48 h (local time).

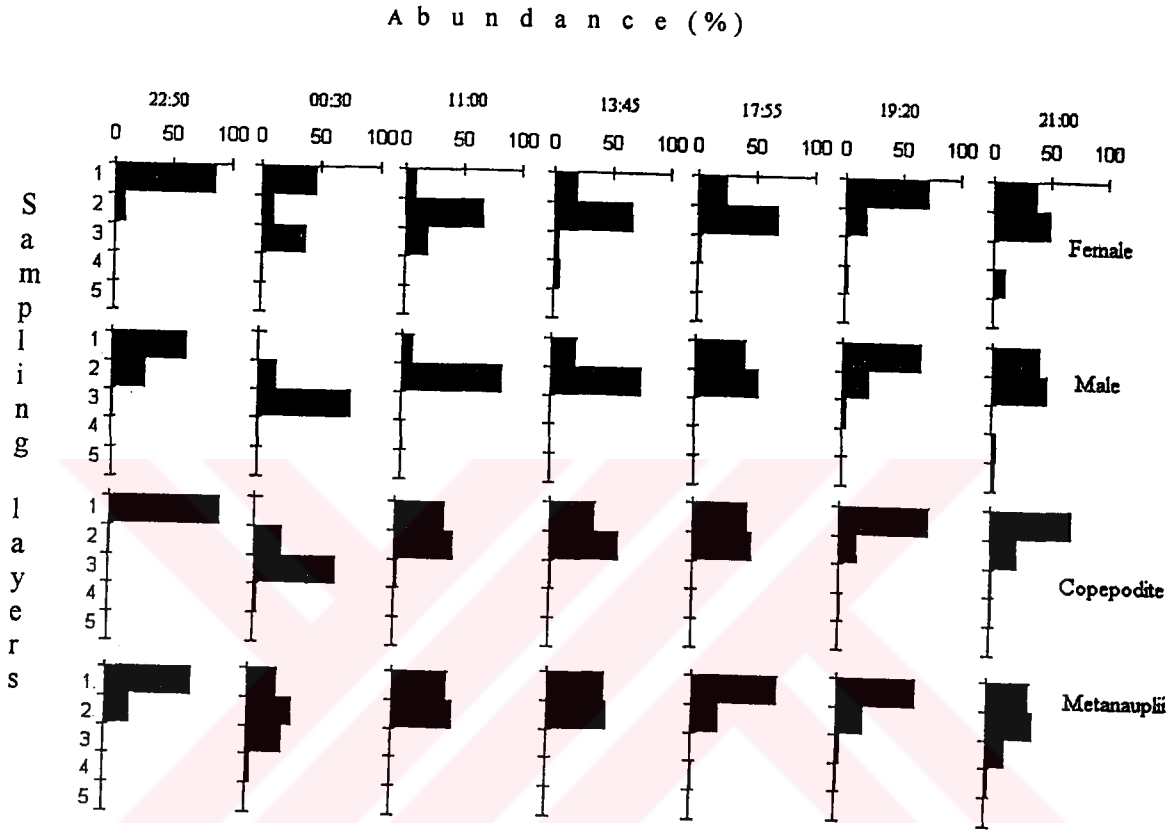

Figure 3.24: Vertical distribution of developmental stages of *A. clausi* at each sampling time during June 1996. Abundance is expressed as per cent of the individuals m^{-3} for the entire profile at 5 depth strata. The depth of water column for each profile is as in Figure 3.22. Sunset = 20:47 h; Sunrise = 05:25 h (local time).

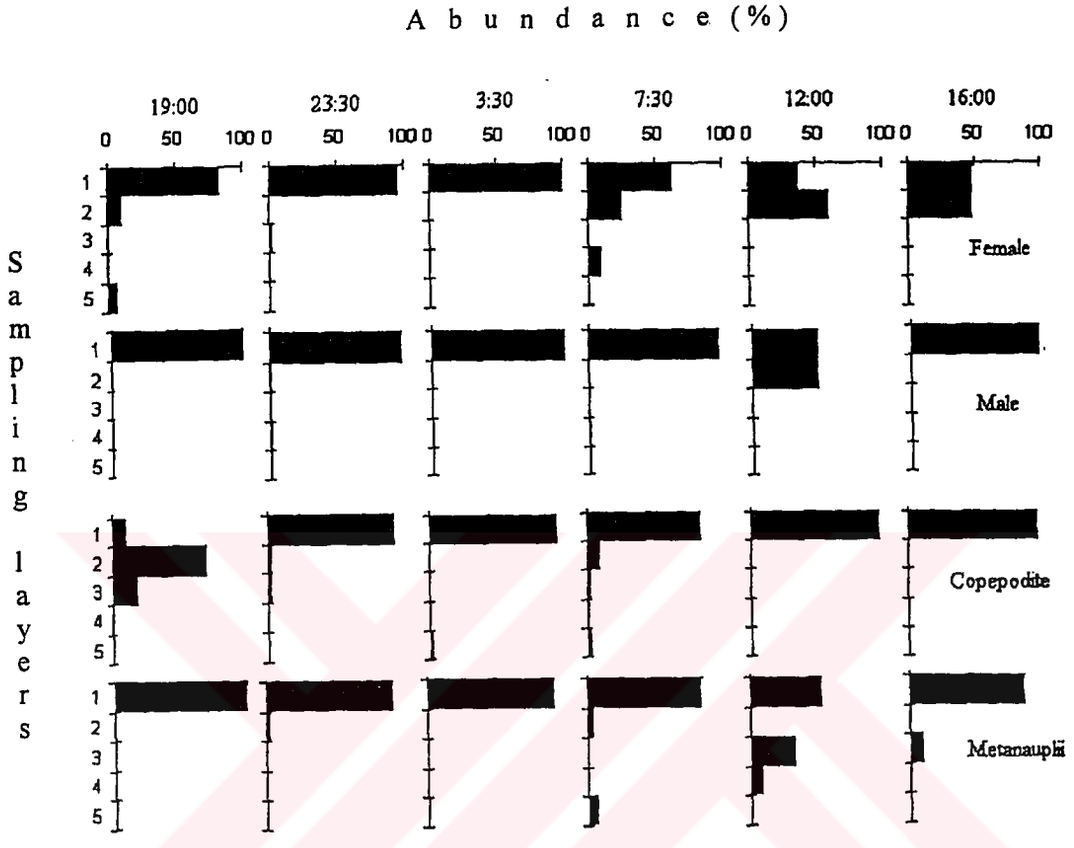

Figure 3.25: Vertical distribution of developmental stages of *A. clausi* at each sampling time during 27-28 September 1995. Abundance is expressed as per cent of the individuals m^{-3} for the entire profile at 5 depth strata. The depth of water column for each profile is as in Figure 3.22. Sunset = 17:43 h; Sunrise = 05:47 h (local time).

3.2.3.4. DISCUSSION

In April, May and June, *A. clausi* was very abundant. With the exception of May, the metanauplii and the copepodite stages dominated the population in all sampling periods. The absence of metanauplii and the low values of copepodite in May resulted probably from the bigger mesh size (200μm) used during this cruise. At open stations, considerable amount of males were observed in all sampling periods except in April 1996. Thus it can be expected the rapid fertilisation especially in April 1995, in May and in June. When looking at the prosome length of the population (Fig. 3.19), in June and in September the prosome length of the population was smaller than that found in other studied seasons, since the smaller individuals were dominant among the copepodite stages; mean length of copepodite was 0.5mm in June and the mean length in September were in the range of between 0.42 and 0.51mm (Table 3.3). Greze and Baldina (1967), suggested that the generation number of *A. clausi* in Sukhumi bay should have been at least 9 per year. They found 7 generation in a year off Sevastopol and concluded that the difference in the generation numbers between Suchumi and Sevastopol is related with temperature. In Suchumi, the temperature is always higher than in Sevastopol. However, they attained from the abundance of developmental stages that the main reproduction period of *A. clausi* is in the spring-summer period.

Considering the vertical distribution of *A. clausi*, it is an epipelagic organism. During all sampling periods, they generally distributed at the two uppermost layers (above the depth of sigma-theta 14.6). They showed small periodicity between these two layers. Zenkevich (1963), Petipa (1967) and Vinogradov *et al.* (1992a) corroborates results found in this study on the vertical distribution of *A. clausi*. They stated that the *A. clausi* is a non-migratory species inhabiting the upper warm layers of the water column. In the Black Sea the mass of the *A. clausi* usually occurs at a depth of 15-50m. Their vertical distribution is only slightly affected by variations in temperature and light conditions observed throughout the seasons (Zenkevich, 1963).

3.2.4. *PARACALANUS PARVUS*

3.2.4.1. SPATIAL DISTRIBUTION

The population of *Paracalanus parvus* was investigated as female, male and total copepodite stages.

The seasonal variability was found in the overall abundance of *Paracalanus*. Figure 3.26 shows the total abundance of *P. parvus* at every station during the sampling periods. The significant differences ($P<0.05$) were observed in its total abundance between open and coastal stations only in April 1996 and June 1996 but not in the other sampling periods.

Table 3.4 shows the abundance and the mean prosome length of female, male and copepodite stages of *P. parvus* at open and coastal stations during the sampling periods. At open stations, while the maximum abundances of female, male and total copepodite stages were obtained in June 1996, the lowest numbers were found in September.

At coastal stations, the highest abundances of females and males were detected in April 1995 with the value of 3250 and 1108 ind. m^{-2} respectively. The highest abundance of total copepodite stages was found in June as 7337 ind. m^{-2} (Table 3.4).

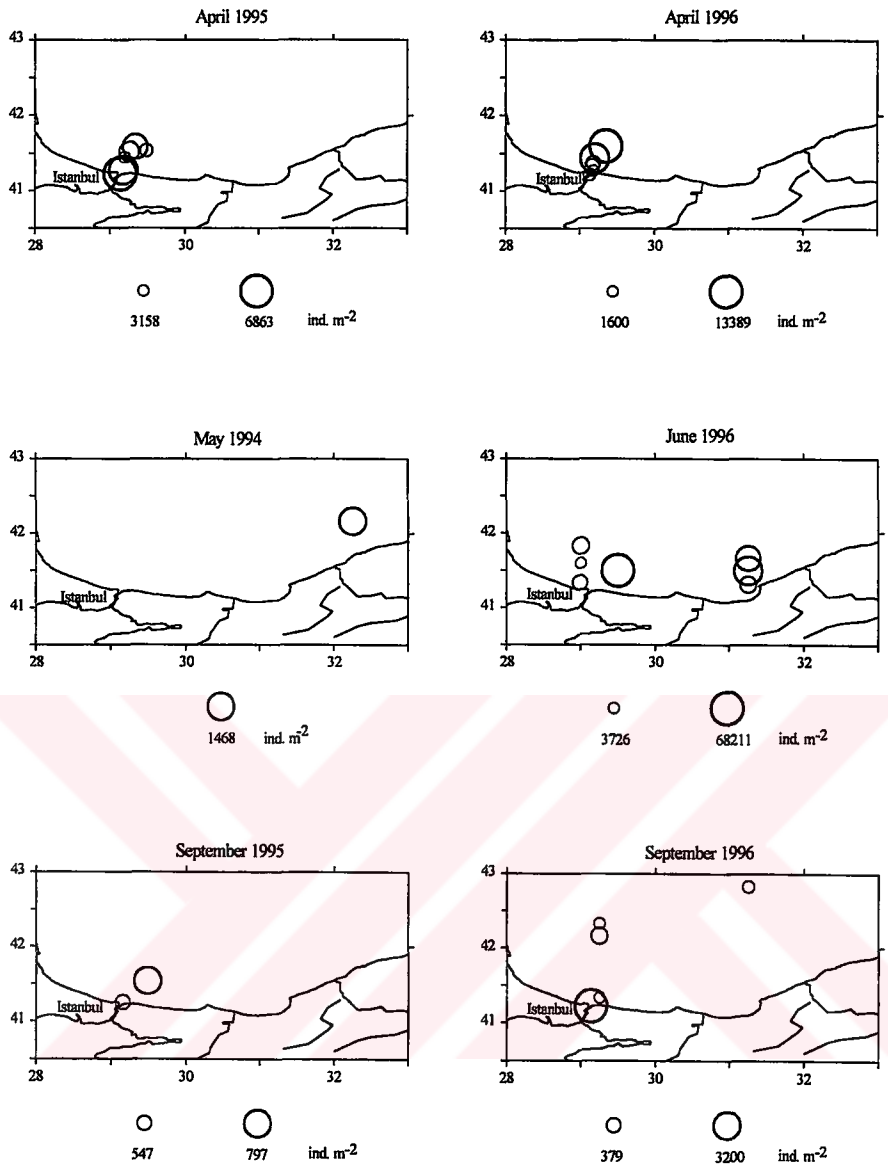

Figure 3.26: Abundance (ind. m^{-2}) of *P. parvus* at each station during the sampling periods. Numbers are proportional to the radius of the circle (linear transformation). Minimum and maximum values are given in scale. Open and coastal stations were depicted in Figure 2.4.

Table 3.4: Abundance (ind. m^{-2}) and mean prosome length of *P. parvus* for female, male and total copepodite stages at open and coastal stations during the sampling periods.

Sampling Period	Region	Female		Male		Copepodite	
		Abundance	Length	Abundance	Length	Abundance	Length
April 1995	open	2368	0.52	350	0.59	1071	0.45
	coastal	3250	0.57	1108	0.61	1034	0.49
April 1996	open	1600	0.57	1095	0.64	10695	0.41
	coastal	1000	0.57	284	0.64	3129	0.42
May.94	open	1100	0.55	368	0.61	--	--
June 1996	open	3516	0.54	1592	0.6	35966	0.36
	coastal	1347	0.55	1095	0.58	7337	0.36
September 1995	open	337	0.53	55	0.53	405	0.43
	coastal	295	0.54	84	0.54	168	0.42
September 1996	open	139	0.58	92	0.62	466	0.42
	coastal	274	0.60	--	--	1516	0.42

--; no individual observed

3.2.4.2. POPULATION STRUCTURE

The size-frequency distribution and mean prosome length of the *P. parvus* population in open and coastal stations in the sampling periods is shown in Figure 3.27. At open stations, the mean prosome length of the population varied from 0.39 mm (in June) to 0.56 mm (in May). At coastal stations, while the lowest mean prosome length was observed in June (0.41 mm), the highest was in April (0.52 mm).

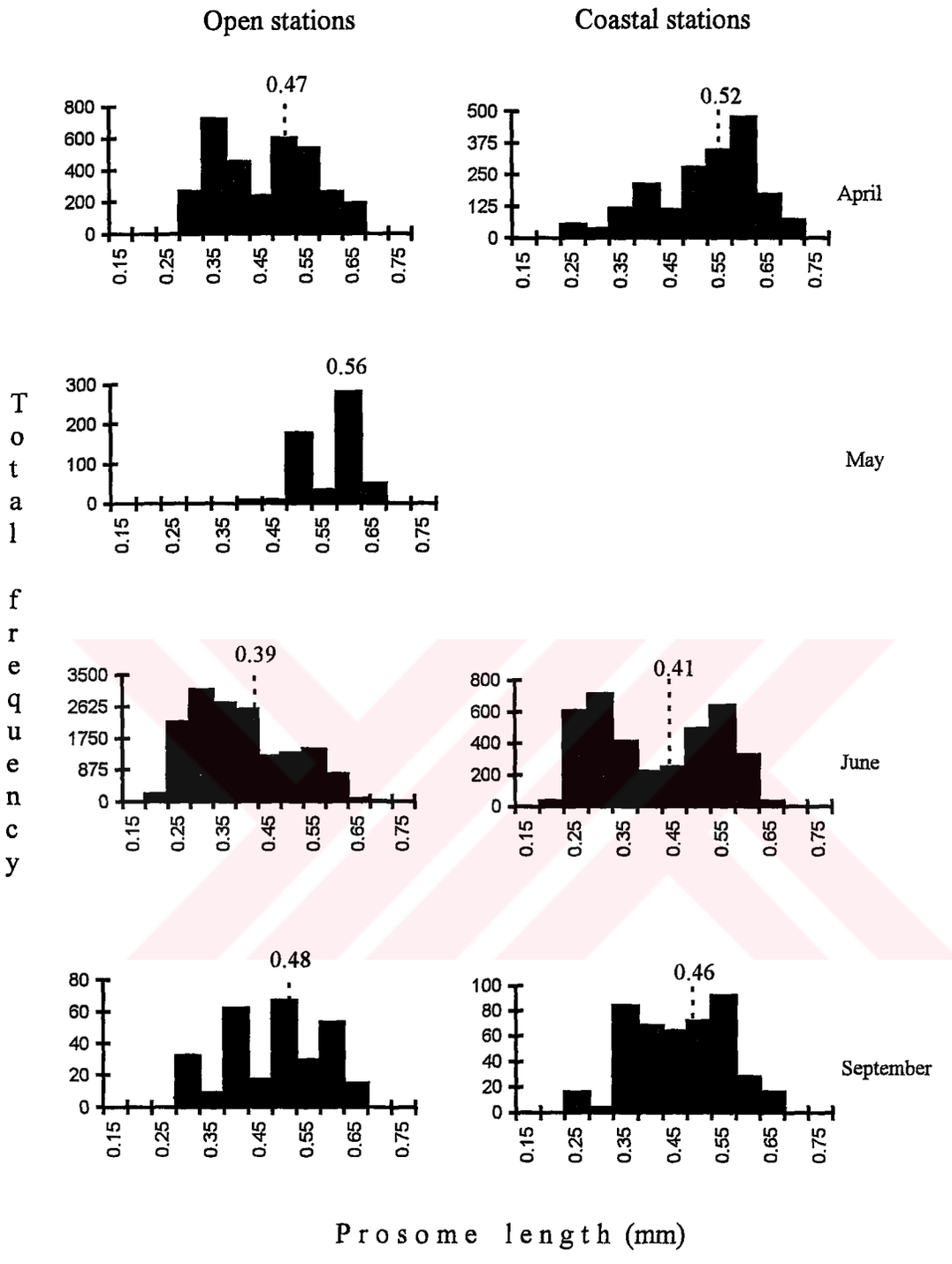

Figure 3.27: The prosome length (mm) -total frequency histogram of *P. parvus* at the open and coastal stations during the sampling periods. Vertical dashes lines show the mean prosome length of the population.

Figure 3.28 shows the percentage frequency of developmental stages of *P. parvus* from the open stations during the sampling periods.

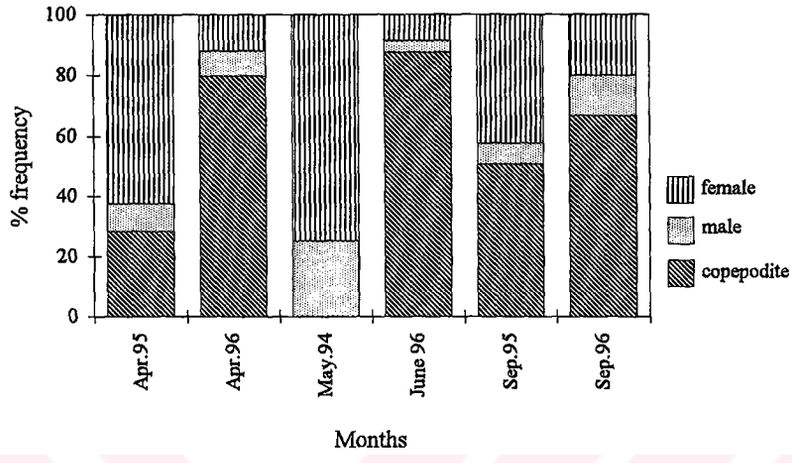

Figure 3.28: Seasonal changes in the developmental stages of *P. parvus* from the open stations.

The copepodite stages dominated the population in April 1996, June 1996 and in September 1996. In April 1995, adults made up the >60% of the population. No copepodite stage was found in May 1994 and females comprised 75% of the population. In September 1995, the stage distribution was bimodal with the equal percentage of adults and copepodites. Females always outnumbered males.

Figure 3.29 shows the percentage frequency of developmental stages of *P. parvus* from the coastal stations during the sampling periods. As at the open stations, the copepodite stages formed also the bulk (>70%) of the population in April 1996, June 1996 and in September 1996 at coastal stations. The population had become older with adults comprising 81 and 69% in April 1995 and in September 1995, respectively.

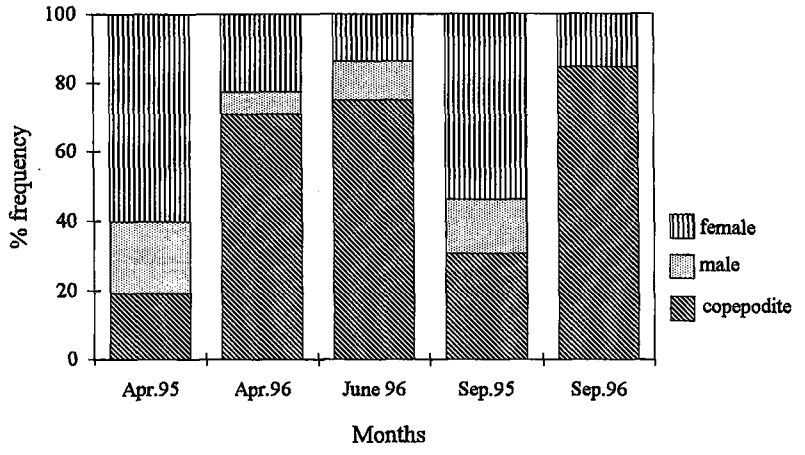

Figure 3.29: Seasonal changes in the developmental stages of *P. parvus* from the coastal stations.

Females accounted for 60% in April 1995 and 54% in September 1995. Males occurred in higher numbers in April 1995 and in September 1995; they were absent in September 1996.

3.2.4.3. VERTICAL DISTRIBUTION

This small species distributed throughout the sampling depth strata (Figs. 3.30-3.33). Its occurrence at all depths was erratic, so there is no evidence for a regular diel vertical migration. In April 1995 during night and daytime their peak in abundance was generally in the second layer and their maximum concentrations were found sporadically in the 3rd and 4th layers. In the other sampling periods (May 1994, September 1995 and June 1996) they occurred frequently in the first layer during night and daytime.

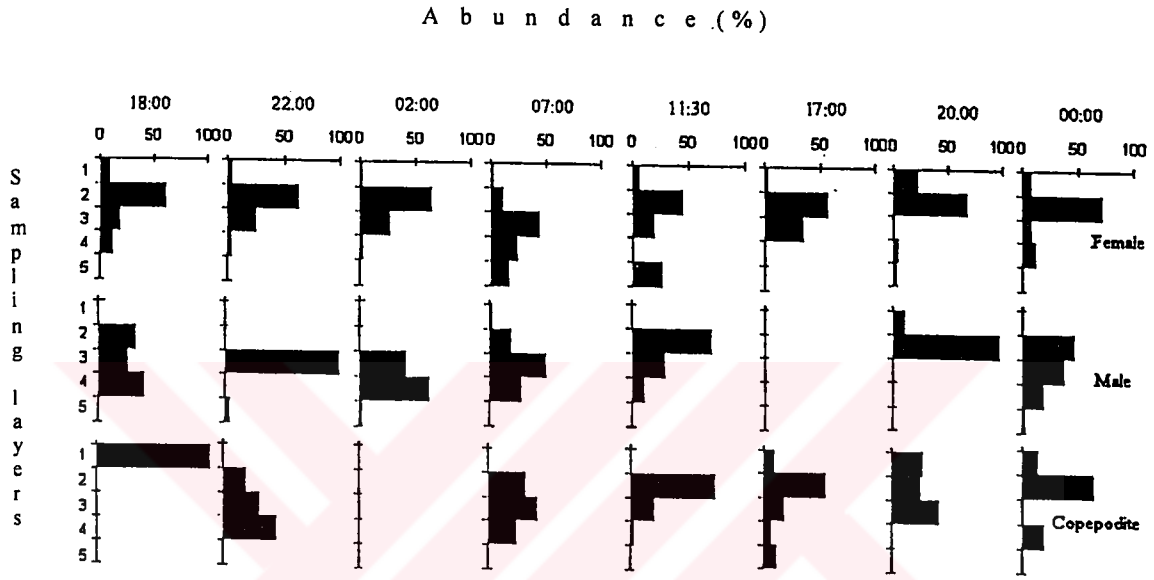

Figure 3.30: Vertical distribution of developmental stages of *P. parvus* at each sampling time during 26-28 April 1995. Abundance is expressed as per cent of the individuals m^{-3} for the entire profile at 5 depth strata: 1- from the depth of thermocline to the surface, 2- from the depth of σ_θ=14.6 to the thermocline, 3- from the depth of σ_θ=15.4 to the depth of σ_θ=14.6, 4- from the depth of σ_θ=15.8 to the depth of σ_θ=15.4, 5- from the depth of σ_θ=16.2 to the depth of σ_θ=15.8 (for more details on sampling see section 2.1.1.1). The sampling time presented at the top of first profiles. Sunset = 19:52 h; Sunrise = 06:06 h (local time).

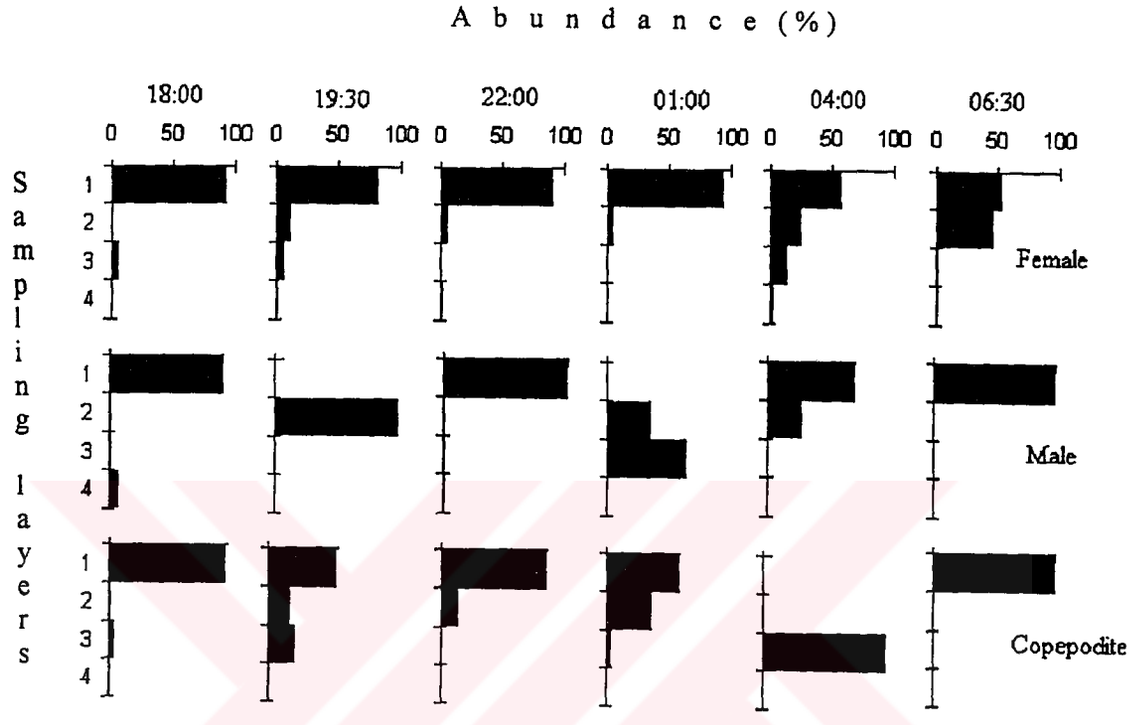

Figure 3.31: Vertical distribution of developmental stages of *P. parvus* at each sampling time during 10-11 May 1994. Abundance is expressed as per cent of the individuals m^{-3} for the entire profile at 4 depth strata: 1- from the depth of thermocline to the surface, 2- from the depth of σ_θ=14.6 to the thermocline, 3- from the depth of σ_θ=15.4 to the depth of σ_θ=14.6, 4- from the depth of σ_θ=16.2 to the depth of σ_θ=15.4 (for more details on sampling see section 2.1.1.1). The sampling time presented at the top of first profiles. Sunset = 20:16 h; Sunrise = 05:48 h (local time).

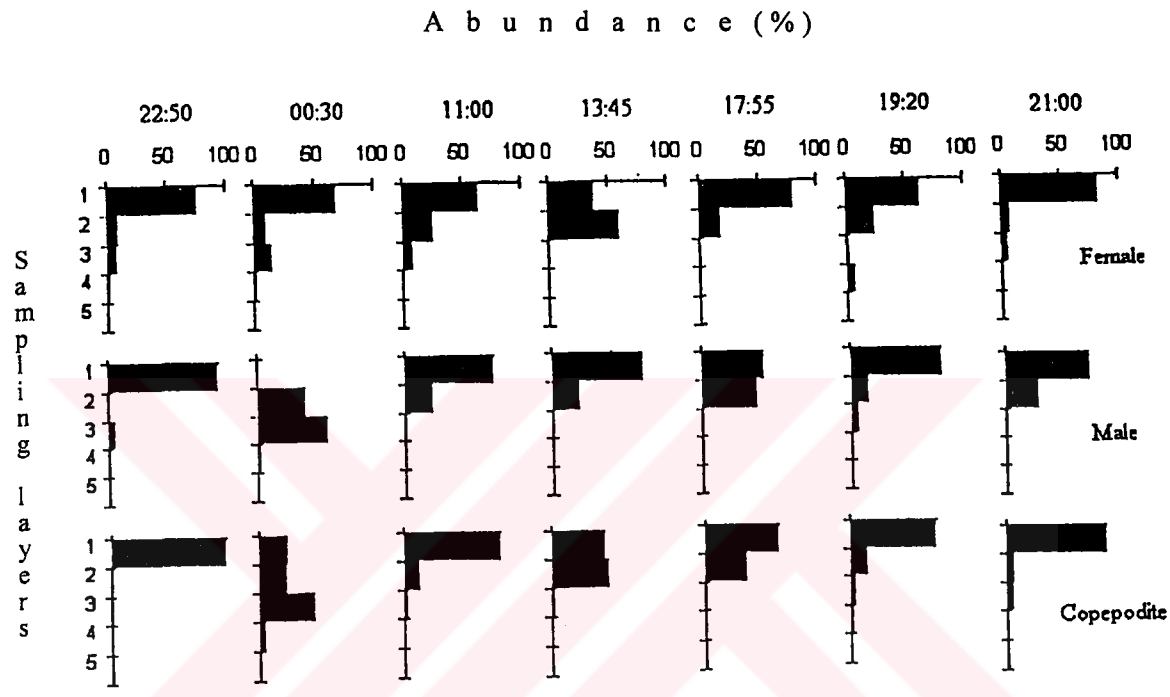

Figure 3.32: Vertical distribution of developmental stages of *P. parvus* at each sampling time during June 1996. Abundance is expressed as per cent of the individuals m^{-3} for the entire profile at 5 depth strata. The depth of water column for each profile is as in Figure 3.30. Sunset = 20:47 h; Sunrise = 05:25 h (local time).

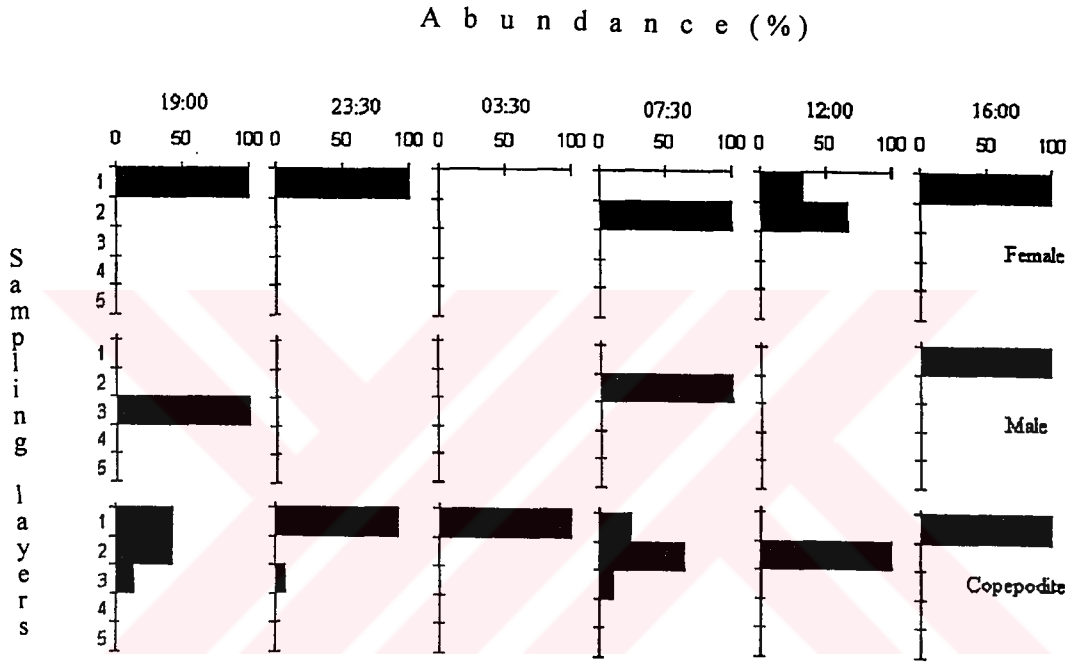

Figure 3.33: Vertical distribution of developmental stages of *P. parvus* at each sampling time during 27-28 September 1995. Abundance is expressed as per cent of the individuals m^{-3} for the entire profile at 5 depth strata. The depth of water column for each profile is as in Figure 3.30. Sunset = 17:43 h; Sunrise = 05:47 h (local time).

3.2.4.4. DISCUSSION

The results, found in this study, on the temporal distribution of *Paracalanus parvus* showed that there is a high variability in its abundance (from the overall average 672 ind. m^{-2} in September 1995 to the 25427 ind. m^{-2} in June). The maximum abundance of this species was found firstly in June and secondly in April. Greze *et al.* (1971) defined this species as a warm-water species (optimum temperature is 10-20°C) and observed its maximum abundance in August, then it decreased through the winter months and increased again in May. Sazhina (1996), observed numerous numbers of copepodite stages of warm water copepods (*Acartia, Paracalanus* and *Centropages*) in July. This species can be observed throughout the year with two main peaks in abundance; in spring and in summer.

From the results of mean prosome length of population, it is clear that the smaller individuals were dominant in June (Fig. 3.27), because the mean prosome length of copepodites had the smallest value as 0.36mm at both open and coastal stations at this period (Table 3.4). It can be concluded that, spawning should have taken place at the beginning of June. According to Sazhina (1987), the developmental time of *P. parvus* from nauplii stage I to the adult is 32 days from the laboratory experiment conducted at 15°C.

P. parvus generally concentrated in two uppermost layers (above the depth of sigma-theta 14.6), but in April they showed erratic distribution throughout the water column. Zenkevich (1963) classified it, as a non-migratory species, inhabiting the upper warm layers (between 15 and 50m) of the water column. Their vertical migration is slightly affected by variations in water temperature and light conditions. It does not occur in deep waters where the temperature is low, but generally accumulates within the thermocline (Sorokin, 1983).

3.2.5. *OITHONA SIMILIS*

3.2.5.1. SPATIAL DISTRIBUTION

The *Oithona similis* population was investigated as adults and total copepodite stages from open and coastal stations during the sampling periods.

The overall abundance of *Oithona* showed seasonal variability. Figure 3.34 shows the total abundance of *O. similis* at each station during the sampling periods. The significant difference ($P<0.05$) between the total abundance at open and coastal stations was found only in September1995, while, no significant difference was observed in other periods.

Table 3.5 shows the abundance and mean prosome length of adult and total copepodite stages of *O. similis* at open and coastal stations during sampling periods. At open stations, the abundance of adults showed a peak in September 1995, while the abundance of total copepodites was highest in June 1996. The minimum abundance was observed in September 1996 for female and in April 1995 for copepodites. No copepodite stage was found in May due to the large mesh size used in this period. At coastal stations, the higher abundance of adults was obtained in June 1996. The maximum abundance of copepodite was found in September 1996. The lowest numbers in abundance were found for adults and copepodites, in September 1995 and in April 1995 respectively.

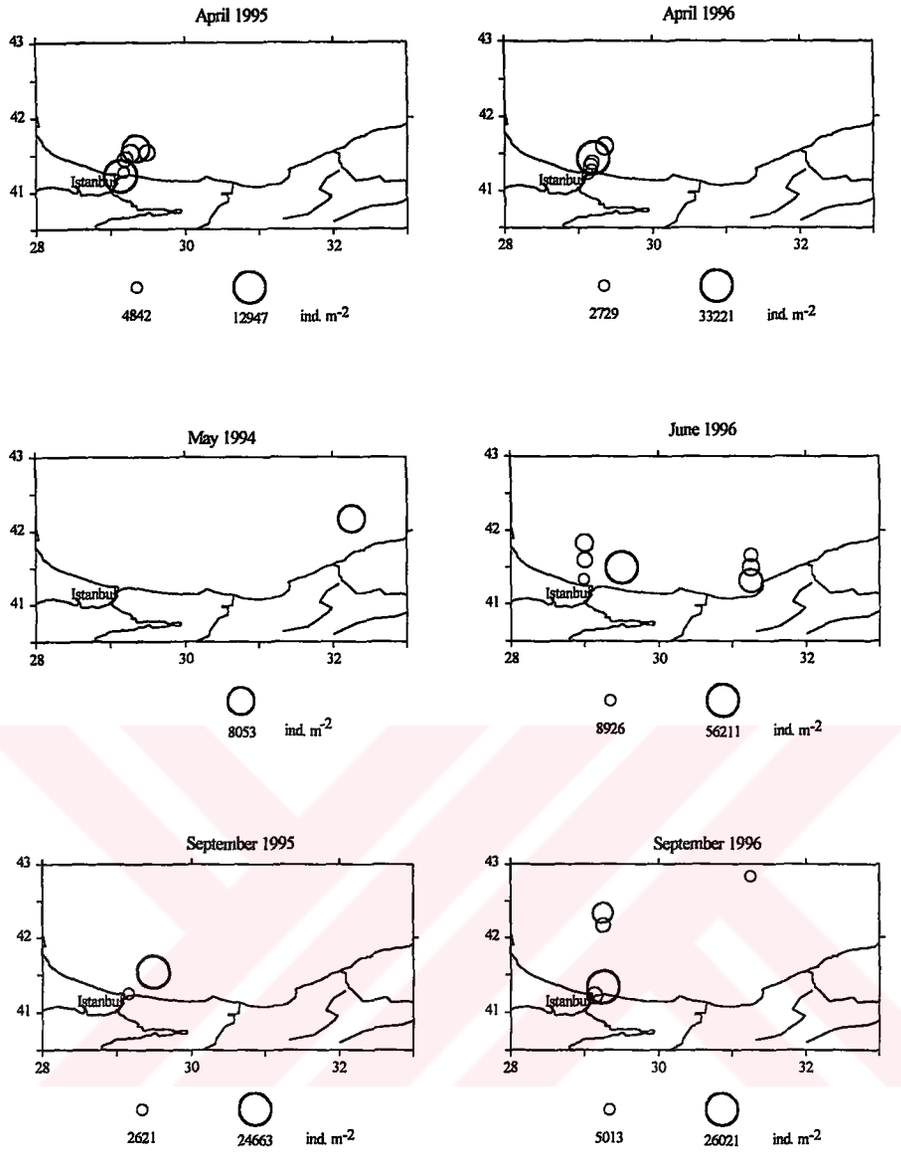

Figure 3.34: Abundance (ind. m^{-2}) of *O. similis* at each station during the sampling periods. Numbers are proportional to the radius of the circle (linear transformation). Minimum and maximum values are given in scale. Open and coastal stations were depicted in Figure 2.4.

Table 3.5:Abundance (ind. m^{-2}) and mean prosome length of *O. similis* for adults and total copepodite stages at open and coastal stations during the sampling periods.

Sampling period	Region	Adult		Copepodite	
		Abundance	Mean length	Abundance	Mean length
April 1995	open	6021	0.43	1076	0.32
	coastal	7324	0.43	845	0.32
April 1996	open	7832	0.43	4295	0.32
	coastal	3053	0.44	2550	0.35
May.94	open	8053	0.44	--	--
June 1996	open	6597	0.44	23718	0.29
	coastal	8821	0.45	4863	0.29
September 1995	open	10834	0.41	13829	0.31
	coastal	1084	0.41	1537	0.30
September 1996	open	2547	0.42	6597	0.32
	coastal	4484	0.42	13495	0.32

--; no individuals observed

3.2.5.2. POPULATION STRUCTURE

The size-frequency distribution and the mean prosome length of the *O. similis* population at open and coastal stations are shown in Figure 3.35.The mean prosome length of the population were almost the same both at open and coastal stations in all periods. In June and September the prosome length was smaller than that measured in May and in April.

The percentage frequency of adults and copepodites in the sampling periods at open stations is shown in Figure 3.36. In June and in September, the copepodites comprised the >55% of the population, while adults were dominant in April. Only adult individuals were found and no copepodites were detected in May. This is probably due to the mesh size of the net, which was 200μm at that period. So the copepodite stages escaped probably through the larger meshes.

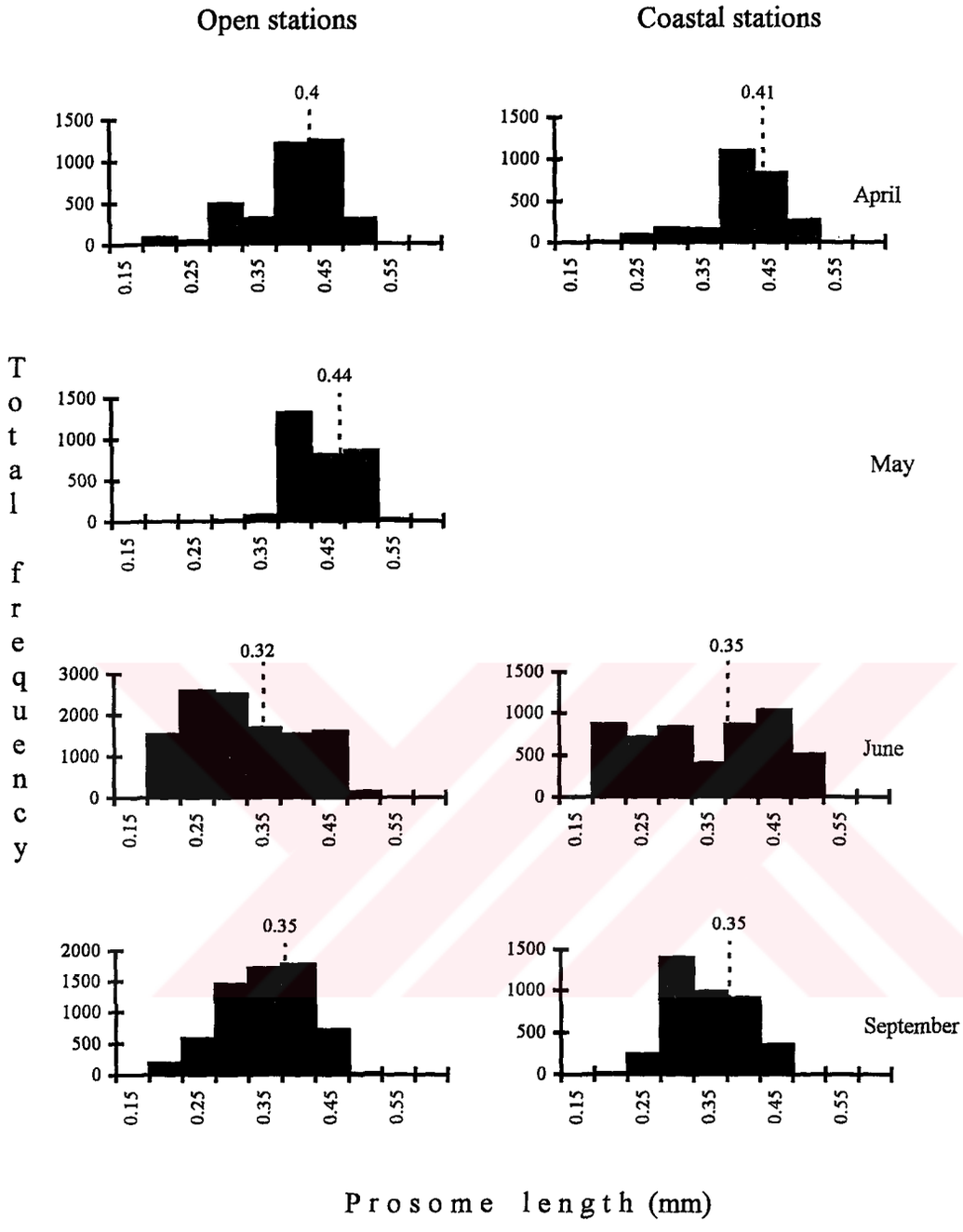

Figure 3.35: The prosome length (mm) -total frequency histogram of *O. similis* at the open and coastal stations during the sampling periods. Vertical dashed lines show the mean prosome length of the population.

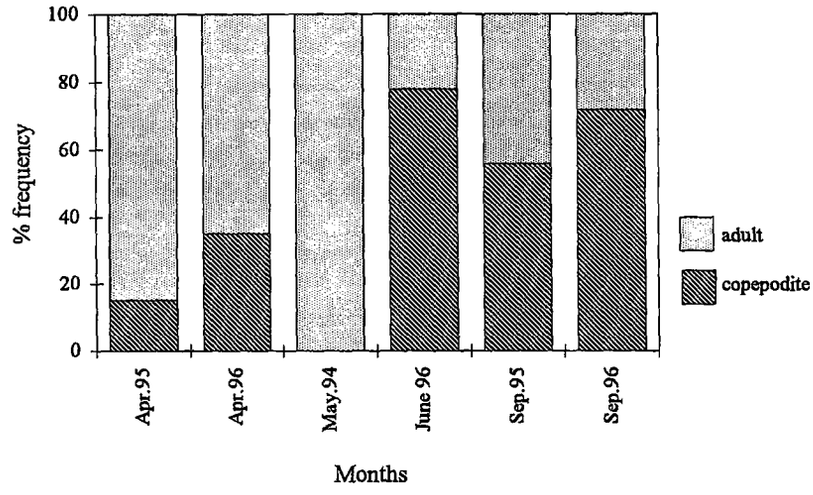

Figure 3.36: Seasonal changes in the developmental stages of *O. similis* from the open stations.

At coastal stations, the total copepodite stages dominated the population in each sampling period, as this is the case at open stations, in June and in September. In April the adults made up >60% of the *O. similis* population (Figure 3.37).

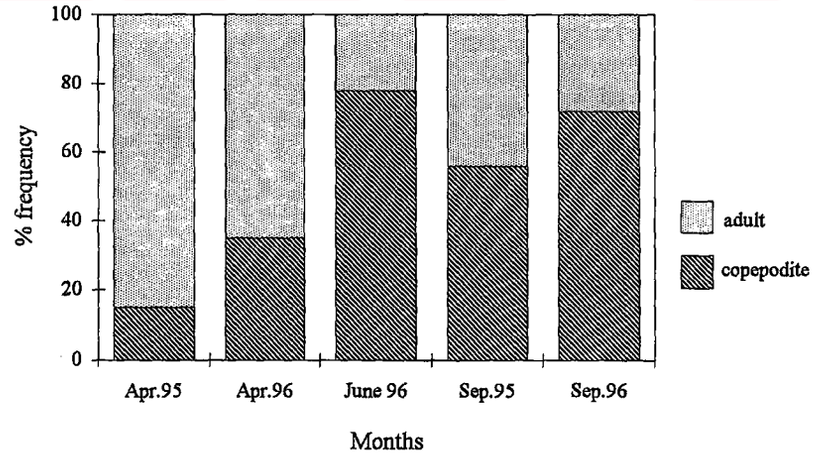

Figure 3.37: Seasonal changes in the developmental stages of *O. similis* from the coastal stations.

3.2.5.3. VERTICAL DISTRIBUTION

This cyclopoid species showed inconsistent distribution throughout the water column. The majority of both adults and copepodites was generally in the first and second layers in April, May and in June, while they were generally found throughout the water column with the maximum concentration in the third and fourth layers in September (Figs. 3.38-3.41).

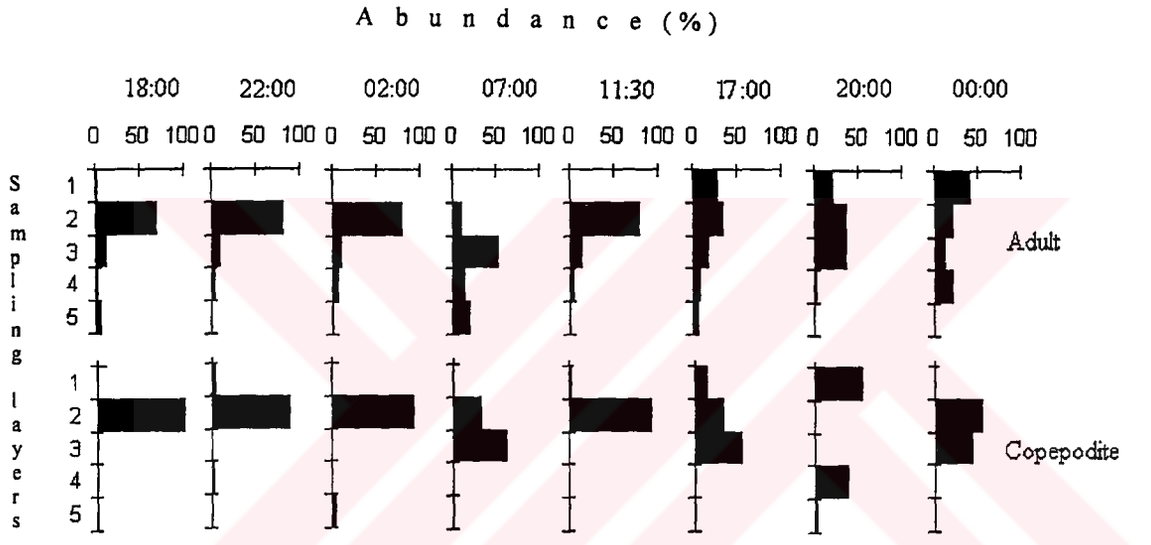

Figure 3.38: Vertical distribution of developmental stages of *O. similis* at each sampling time during 26-28 April 1995. Abundance is expressed as per cent of the individuals m^{-3} for the entire profile at 5 depth strata: 1-from the thermocline to the surface, 2-from the depth of σ_θ =14.6 to the thermocline, 3- from the depth of σ_θ =15.4 to the depth of σ_θ =14.6, 4-from the depth of σ_θ =15.8 to the depth of σ_θ =15.4, 5-from the depth of σ_θ =16.2 to the depth of σ_θ =15. (for more details on sampling see section 2.1.1.1). The sampling time presented at the top of first profiles. Sunset = 19:52 h; Sunrise = 06:06 h.

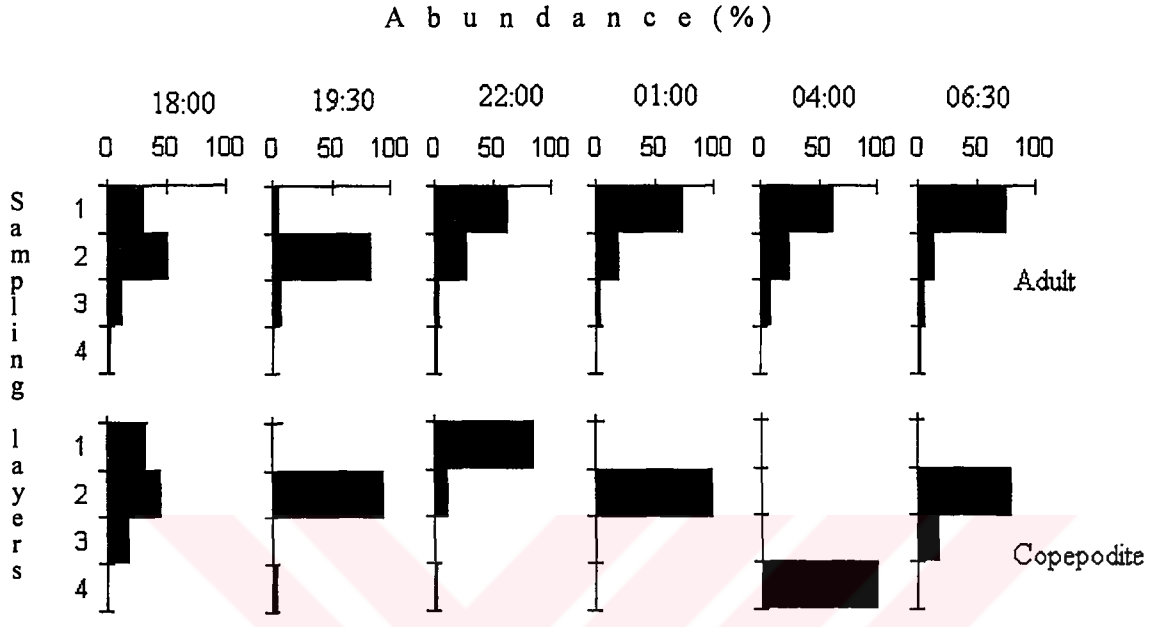

Figure 3.39: Vertical distribution of developmental stages of *O. similis* at each sampling time during 10-11 May 1994. Abundance is expressed as percent of the individuals m^{-3} for the entire profile at 4 depth strata:1- from the thermocline to the surface, 2-from the depth of σ_θ =14.6 to the thermocline, 3- from the depth of σ_θ =15.4 to the depth of σ_θ =14.6, 4-from the depth of σ_θ =16.2 to the depth of σ_θ =15.4 (for more details on sampling see section 2.1.1.1). The sampling time presented at the to of first profiles. Sunset = 20:16 h; Sunrise = 05:48 h.(local time).

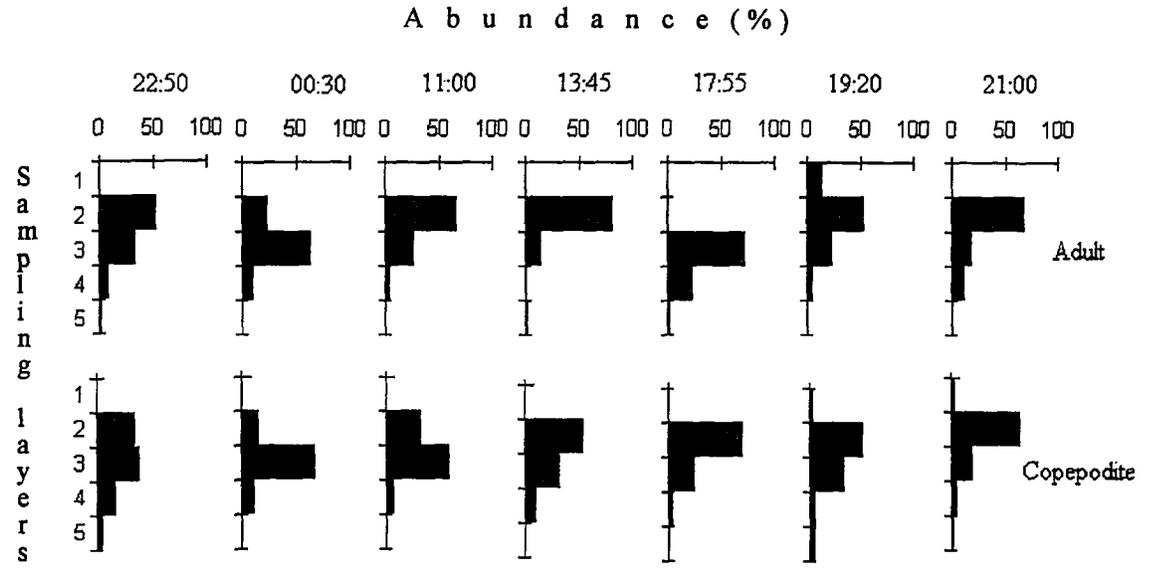

Figure 3.40: Vertical distribution of developmental stages of *O. similis* at each sampling time during June 1996. Abundance is expressed as per cent of the individuals m^{-3} for the entire profile at 5 depth strata. The depth of water column for each profile is as shown in Figure 3.38. Sunset = 20:47 h; Sunrise = 05:25 h.

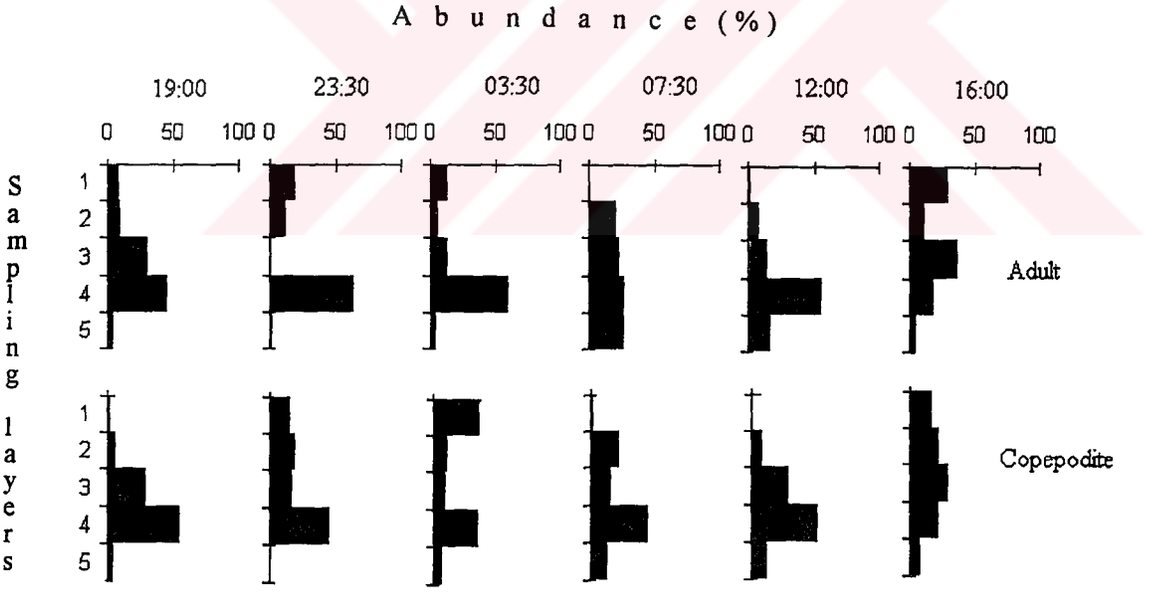

Figure 3.41: Vertical distribution of developmental stages of *O. similis* at each sampling time during 27-28 September 1995. Abundance is expressed as per cent of the individuals m^{-3} for the entire profile at 5 depth strata. The depth of water column for each profile is as in shown Figure 3.38. Sunset = 17:43 h; Sunrise = 05:47 h.

3.2.5.4. DISCUSSION

The total abundance of this cyclopoid copepod, showed seasonal variability. The highest total abundance of *O. similis* was found in warmer periods, in June and in September. During the warmer periods, they were below the thermocline. It was defined by Dritz and Semenova (1984), as cosmopolitan species in distribution, seen in large numbers in open and coastal regions of the world's oceans. Zenkevich (1963) classified it as cold water stenothermal form. Greze *et al.* (1971) found its optimal temperature is in the range of 7-15 °C and they observed its maximum abundance in the second half of the year.

The results of the mean prosome length distribution of *O. similis* population showed that the young copepodites were dominant in June and in September. The mean prosome length of copepodite was 0.29mm in June (Table 3.5). Greze *et al.* (1971), observed the high number of nauplii and copepodites in April, June, July, September and in November and they found the eggs throughout the year with a peak in July. They detected 6-7 generations in a year.

In this study, *O. similis* showed inconsistent vertical distribution throughout the water column. In April, June and in September they were generally below the thermocline and they did not show any pronounced vertical migration and they distributed throughout the water column from the lower layer of pycnocline to the surface. Roman *et al.* (1993) suggest that this cyclopoid copepod has a low metabolism and thus requires less oxygen than *Acartia*. So it could be tolerant the low oxygen concentration as it can be in the oxygen minimum zone. Zenkevich (1963) observed that *O. similis* concentrated from the surface to the lower limit of plankton distribution during cold period of the year (December to April). With the spring warming of surface water, they sink down to the 50m. At the end of November, with decrease in temperature, they move into the upper layers, remaining there until the beginning of May. He concluded that the *O. similis* can be observed throughout the whole water column depending on the season.

3.2.6. SAGITTA SETOSA

3.2.6.1. SPATIAL DISTRIBUTION

The temporal variability and population size structure of *Sagitta* collected from open and coastal stations were studied. Table 3.6 shows the abundance of *Sagitta* for each total length groups taken from the open and coastal stations in different sampling periods.

Overall abundance of *Sagitta* changed among the periods. At the open stations, the abundances were generally higher than coastal stations with the value ranged from 1471 (in September 1995) to 79 ind.m^{-2} (in May 1994). The abundance increased dramatically towards September 1995 when the maximum abundance at open and coastal stations were obtained with the values of 1471 and 3021 ind.m^{-2} respectively. The abundance decreased to 249 ind.m^{-2} and 317 ind.m^{-2} in November and December 1996 respectively, and remained almost at the same level in April.

Figure 3.42 shows the abundance distribution of *Sagitta* collected from the sampling stations in each sampling period. The significant differences ($P<0.05$) in total abundance (individuals m^{-2}) of *Sagitta* occurred between the open and coastal stations during the sampling periods. While total abundance of *Sagitta* from open stations in April 1995, in April 1996, in June 1996 and in September 1996, significantly higher ($P<0.05$) than the coastal ones, in September 1995 the abundances from the coastal stations were significantly higher ($P<0.05$) than those from open stations.

Table 3.6: Abundance (individuals m^{-2}) of *Sagitta* for each total length groups at open and coastal stations during sampling periods.

Length	Apr-95		Apr-96		May-94	June-96		Sep-95		Sep-96		Nov-96	Dec-96
(mm)	open	coastal	open	coastal	open	open	coastal	open	coastal	open	coastal	open	open
1	-	-	-	-	-	56	-	5	-	47	5	-	-
2	-	-	-	-	-	130	7	120	453	345	66	11	-
3	-	-	-	-	-	56	12	330	1066	175	55	1	-
4	-	-	-	-	-	46	13	309	713	139	62	57	-
5	-	-	-	-	-	27	8	176	308	112	88	55	-
6	-	-	3	-	-	26	9	136	124	43	55	33	7
7	1	-	-	-	-	32	3	67	139	60	83	1	5
8	-	3	-	3	-	8	4	62	118	54	47	17	7
9	-	3	3	-	1	5	-	43	50	39	16	25	-
10	2	3	-	-	1	1	-	61	11	17	20	8	30
11	-	-	32	-	1	2	-	21	3	3	4	12	83
12	1	-	26	-	10	2	-	33	32	-	3	21	58
13	3	3	-	-	3	2	-	14	3	-	-	7	82
14	27	-	11	-	4	4	-	8	3	-	1	-	18
15	11	-	18	-	7	3	-	6	-	-	-	1	18
16	31	-	45	-	5	8	-	4	-	-	-	-	7
17	37	-	34	-	10	20	-	6	-	-	-	-	1
18	54	-	37	-	10	24	-	2	-	1	-	-	1
19	50	3	74	-	8	42	-	-	-	-	-	-	-
20	37	-	21	-	11	17	-	-	-	-	-	-	-
21	3	-	18	-	7	5	-	-	-	-	-	-	-
22	-	-	11	-	-	4	-	-	-	-	-	-	-
23	-	-	-	-	-	1	-	2	-	-	-	-	-
24	-	-	-	-	-	2	-	-	-	-	-	-	-
25	-	-	-	-	-	-	-	-	-	-	-	-	-
26	-	-	-	-	-	3	-	-	-	-	-	-	-
27	-	-	-	-	-	-	-	-	-	-	-	-	-
28	-	-	-	-	-	-	-	11	-	-	-	-	-
29	-	-	-	-	-	-	-	-	-	-	-	-	-
30	-	-	-	-	-	-	-	-	-	-	-	-	-
31	-	-	-	-	-	-	-	5	-	-	-	-	-
32	-	-	-	-	-	-	-	53	-	-	-	-	-
total.	256	13	332	3	79	523	55	1471	3021	1033	505	249	317

-; no individuals observed

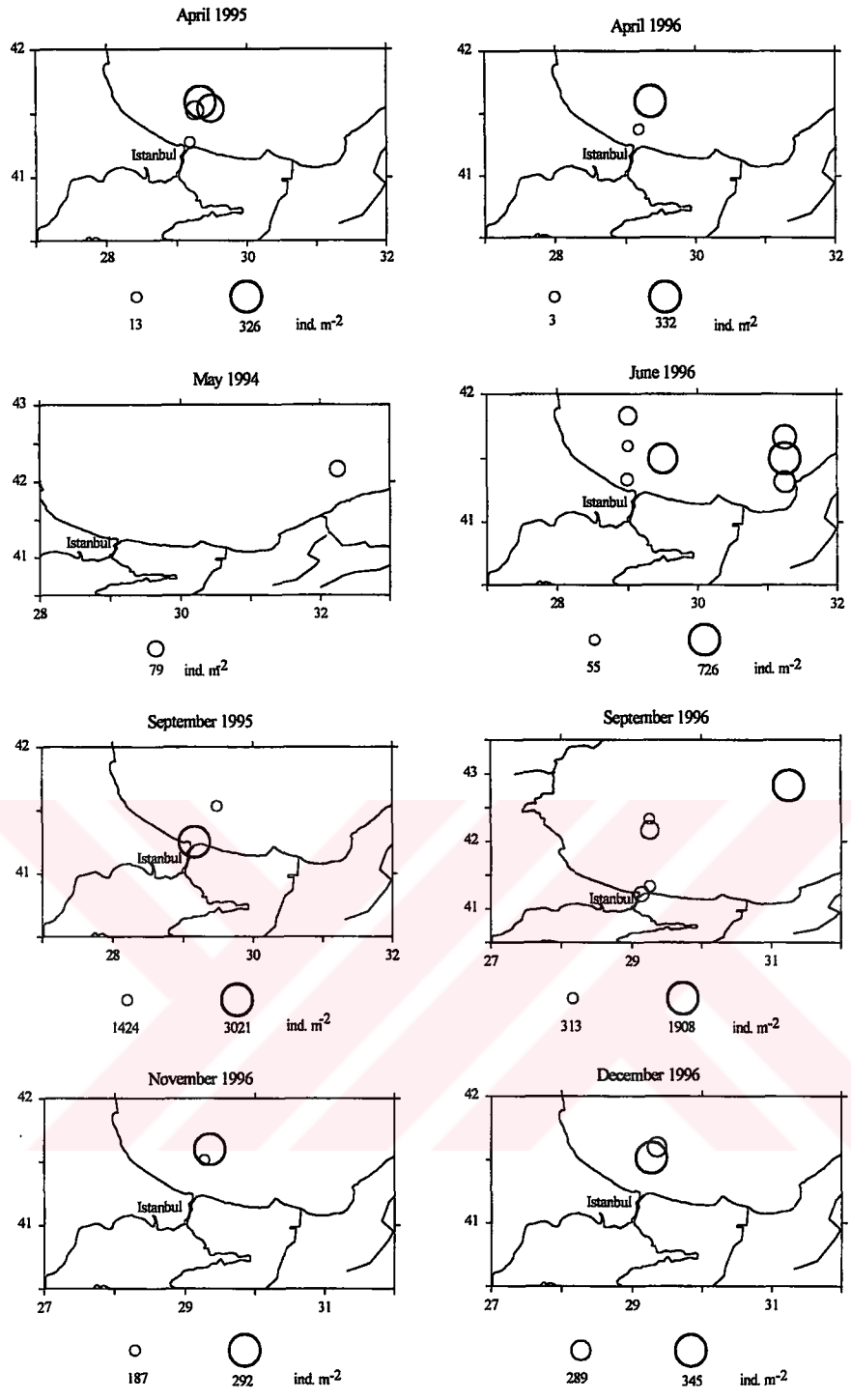

Figure 3.42: Abundance (ind. m^{-2}) of *Sagitta* sampled from each station during the different sampling periods. Numbers are proportional to the radius of the circle (linear transformation). Minimum and maximum values are given in scale. Open and coastal stations were depicted in Figure 2.4.

3.2.6.2. POPULATION STRUCTURE

Based on the mean of total length, the size distribution of *Sagitta* in the Black Sea showed marked seasonal fluctuations. Figure 3.43 shows means of total length (mm) and the total frequency distributions of *Sagitta* from open and coastal stations in each sampling period.

From the Table 3.6, at open stations, the population consists mainly of larger sized groups ranged between 6 and 22mm in length in late spring (April and May). The mean length was 17mm in April and 16.6mm in May (Fig. 3.43). While a few individuals had developing gonads without eggs in April, most of the population had developing eggs in May (from the microscopic observations). A bimodal size distribution were observed with the mean length of 7.2mm by June. In this month, the number of small sized individuals made up the majority of the chaetognaths population and most of the individuals larger than 6mm have ripe eggs in gonads. By early autumn (September), the number of *Sagitta* reached the peak value. In this season a few individuals contained eggs. After June through December the size structure of population became larger and coincided with the development of population. In November and December there was no individual observed with developed gonads.

Although the same trend in the temporal distribution of size was observed in coastal area as in open area, the larger size groups were observed rarely in coastal stations compared to open ones.

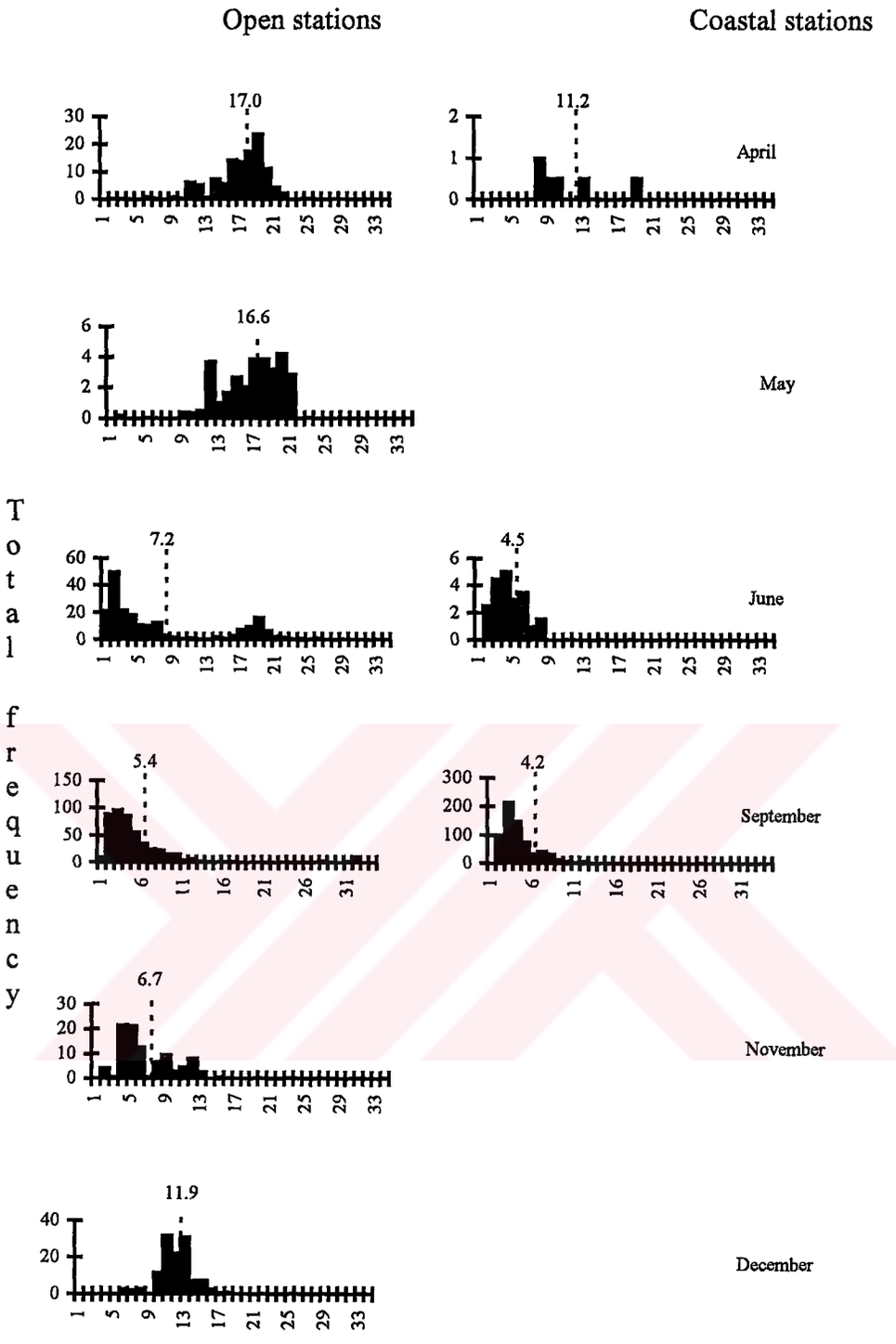

Figure 3.43: Total length (mm)- total frequency histogram of *Sagitta* at the open (left side) and coastal (right side) stations during the sampling periods. Vertical dashed lines show the mean prosome length of the population.

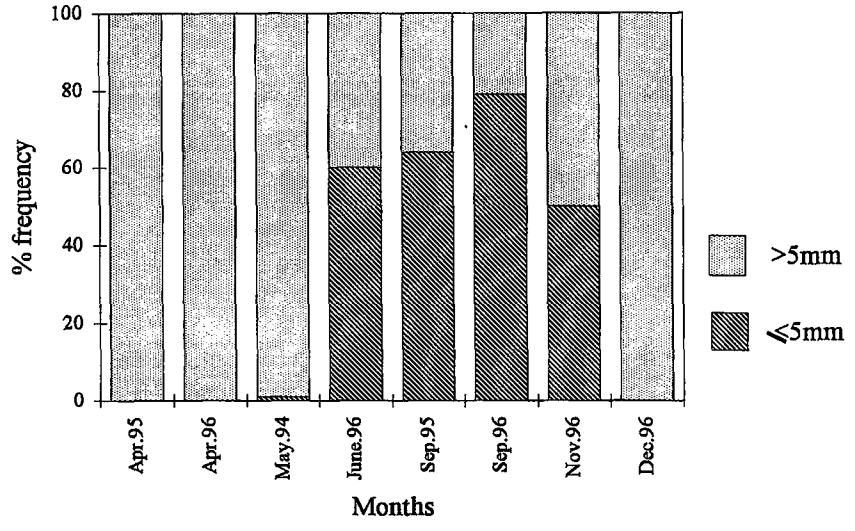

Figure 3.44: Seasonal changes in the developmental stages of *Sagitta* sampled from the open stations.

The percentage frequency of juvenile and mature *Sagitta* from the open stations is shown in Figure 3.44. In April and in May, ~100% of the population was comprised by mature (>5mm long) individuals, while juveniles (≤5mm long) constituted >60% of the population in June and September. However juveniles and adults shared the 50% of the population in November. No juveniles was observed in December and 100% of the population was made up by adults. The same population structure was observed at the coastal stations (Figure 3.45), as at the open stations. Although there were no juveniles in April, they were dominant in June and September.

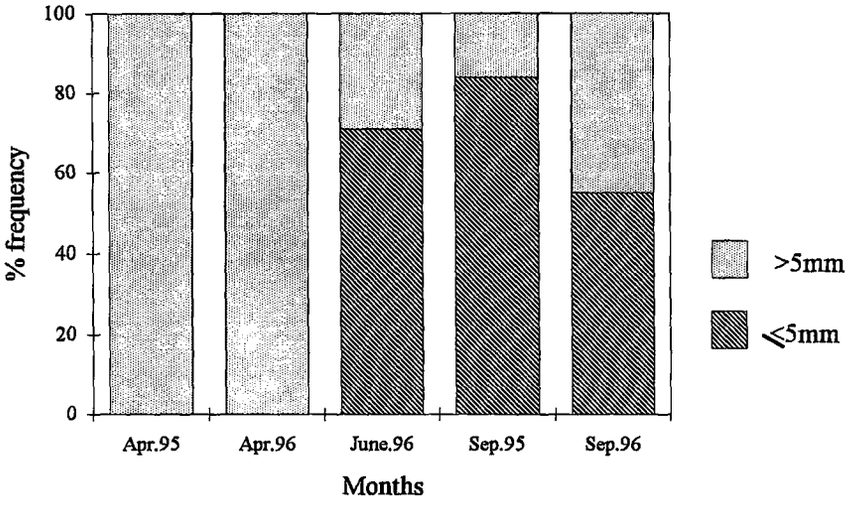

Figure 3.45: Seasonal changes in the developmental stages of *Sagitta* sampled from the coastal stations.

3.2.6.3. VERTICAL DISTRIBUTION

During all sampling periods, the observed minimum length of *Sagitta* with developing ovaries was 5.2mm long, so its vertical distribution was analysed into two groups; ≤5mm as juvenile, >5mm as adult.

Juvenile *Sagitta* had quite different distribution from the adults (Figs 3.46-3.49). During April 1995 and May 1994 there were not much juvenile individuals, only 1 individual was found in the first layer at 18:00 h in May 1994 and at 20:00 h in April 1995. In the other sampling periods (September 1995 and June 1996) the abundance of juvenile individuals was higher than adults. Almost the entire population of juvenile *Sagitta* was located in the first layer, between the thermocline and the surface during both daytime and nighttime in all sampling periods. On the other hand, mature individuals (>5mm long) occupied deeper layers during daytime. The majority of the adult *Sagitta* population showed diel vertical migration in April, May and in June. But this cycle was not obvious in September 1995 in which whole population stayed in the first and second layer.

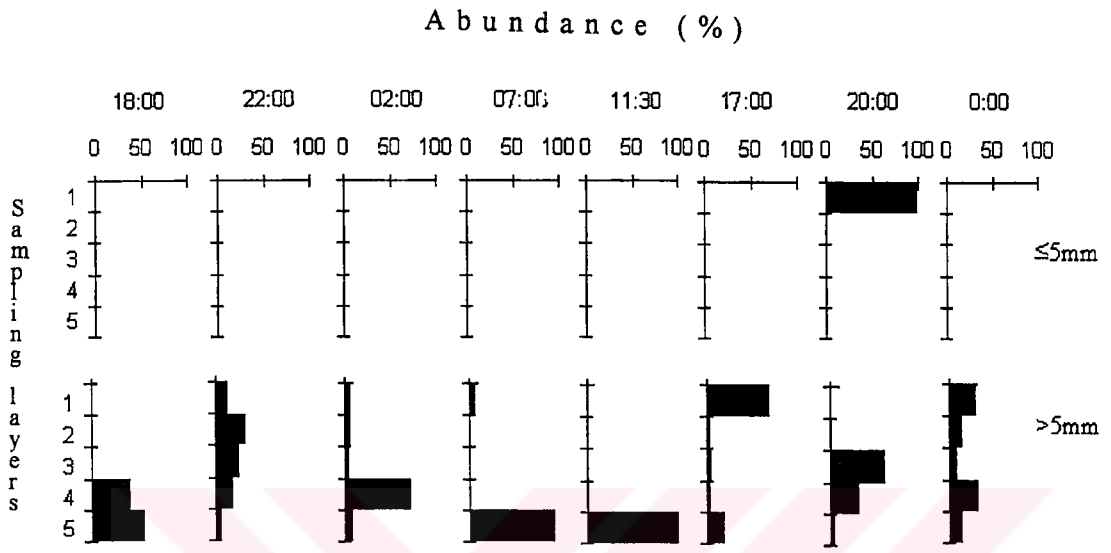

Figure 3.46: Vertical distribution of ≤5mm and >5mm length sized of *Sagitta* at each sampling time during 26-28 April 1995. Abundance is expressed as percent of the individuals m^{-3} for the entire profile at 5 depth strata: 1- from the thermocline to the surface, 2-from the depth of σ_θ =14.6 to the thermocline, 3-from the depth of σ_θ =15.4 to the depth of σ_θ =14.6, 4-from the depth of σ_θ=15.8 to the depth of σ_θ =15.4, 5-from the depth of σ_θ =16.2 to the depth of σ_θ =15.8 (for more details on sampling see section 2.1.1.1). The sampling time presented at the top of first profiles. Sunset = 19:52 h; Sunrise = 06:06h.

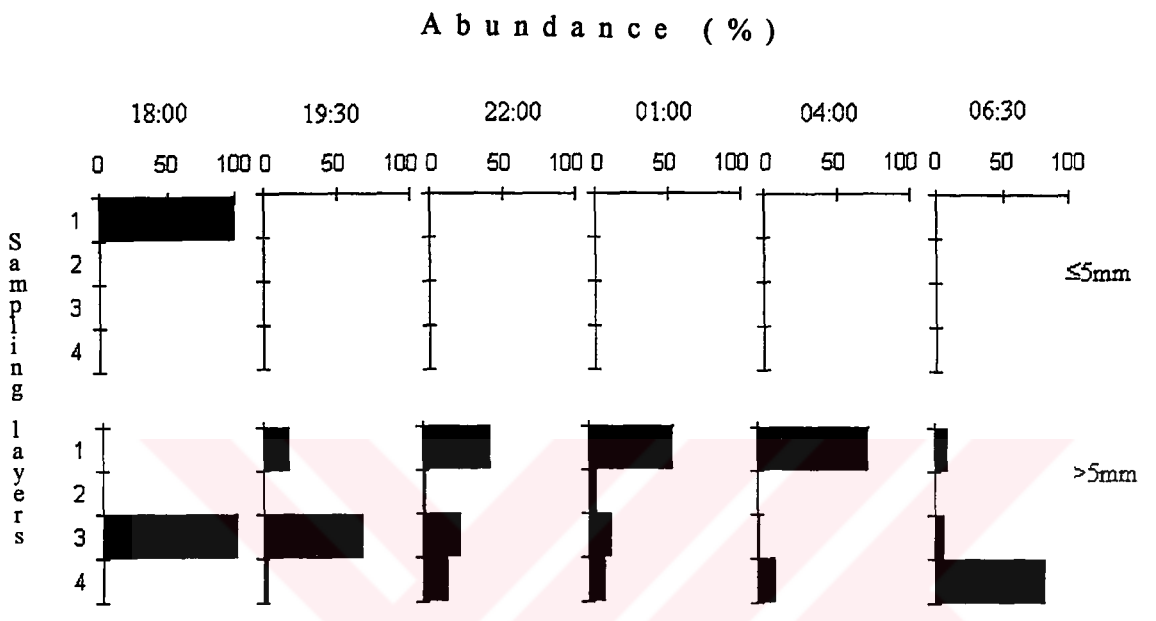

Figure 3.47: Vertical distribution of ≤5mm and >5mm length sized of *Sagitta* at each sampling time during 10-11 May 1994. Abundance is expressed as percent of the individuals m^{-3} for the entire profile at 4 depth strata: 1-from the thermocline to the surface, 2-from the depth of σ_θ =14.6 to the thermocline, 3-from the depth of σ_θ =15.4 to the depth of σ_θ =14.6, 4-from the depth of σ_θ =16.2 to the depth of σ_θ =15.4 (for more details on sampling see section 2.1.1.1). The sampling time presented at the top of first profiles. Sunset = 20:16 h; Sunrise = 05:48 h.(local time).

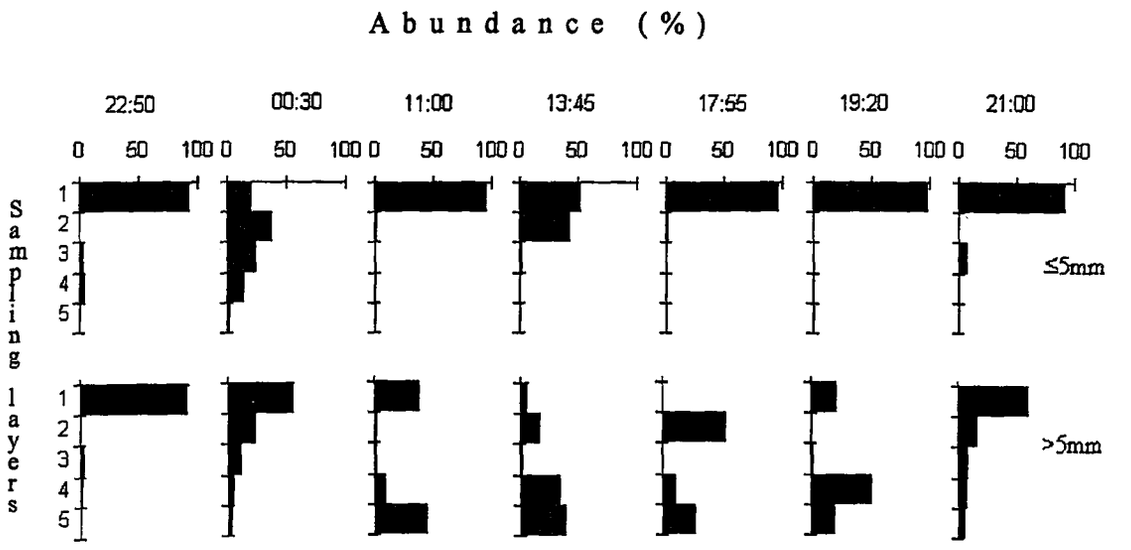

Figure 3.48: Vertical distribution of ≤5mm and >5mm length sized of *Sagitta* at each sampling time during June 1996. Abundance is expressed as per cent of the individuals m^{-3} for the entire profile at 5 depth strata. The depth of water column for each profile is as shown in Figure 3.46. Sunset = 20:47 h; Sunrise = 05:25 h.

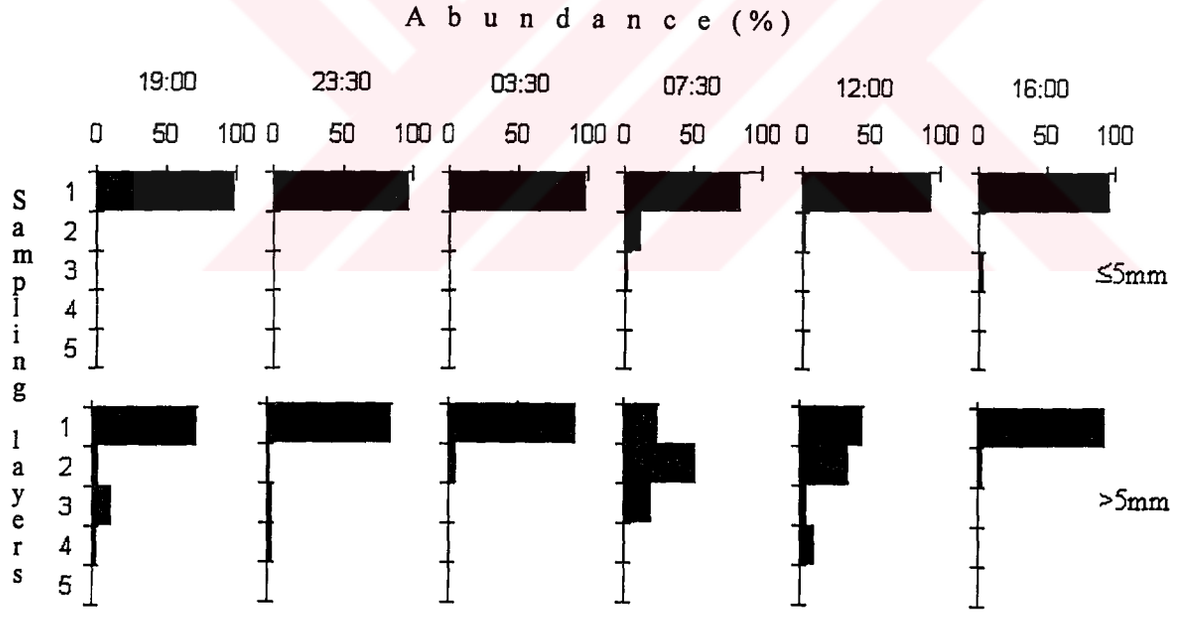

Figure 3.49: Vertical distribution of ≤5mm and >5mm length group of *Sagitta* at each sampling time during 27-28 September 1995. Abundance is expressed as percent of the individuals m^{-3} for the entire profile at 5 depth strata. The depth of water column for each profile is as shown in Figure 3.46. Sunset = 17:43 h; Sunrise = 05:47 h.

3.2.6.4. DISCUSSION

Data, obtained in this study, on the spatial distribution of *Sagitta* in the southwestern part of the Black Sea corroborate the results of previous studies in the Black Sea. The abundance of *Sagitta* was generally higher at open stations than the coastal ones. Niermann *et al.* (1997) showed the accumulation of *Sagitta setosa* in the rim current in the Black Sea. They observed low abundance in the shelf area and in the central gyres. In this study, the maximum total abundance was observed in September. Sazhina's (1987) results confirm our results, she observed a peak in abundance of *Sagitta* in September and in October at Crimean coast, and detected low values in winter and spring. Niermann and Greve (1997) reported that the higher abundance of *Sagitta* was in July/August in the southern part of the Black Sea.

The results of the present study showed that *Sagitta* had a wide length distribution from 1 to 32 mm during the sampling periods. Juvenile individuals dominated the population during summer and early autumn. By September, there was no remaining individuals from the old generation. Similar result was also reported by Niermann *et al.* (1997) and Sazhina (1987). Bainbridge (1963, *cf.* Pearre, 1991) reported two generations per year in the North Sea. They observed replacement of new generation on whole population in August. This may indicate that *Sagitta* dies after breeding (Oresland, 1986; *cf.* Niermann and Greve, 1997). Juvenile individuals were observed from June to November, it is evidence that the *Sagitta* spawns over a long time period. Sazhina (1987) stated that larger form of *Sagitta* dominated in winter, and spawning period is summer and autumn.

Our vertical distribution results showed that, juveniles (≤5mm) generally distributed above the thermocline. They did not display vertical migration. This is also observed by Ukranian scientists (Yu. A. Zagorodnyaya, pers. comm.). Sullivan (1980) observed that while juvenile *Sagitta* was located in between 0 and 25m during both day and nighttime, mature ones were migratory in the subarctic Pacific, and she concluded that the vertical migration of *Sagitta* is related with

food supply. Oresland (1987) showed that the gut content of juvenile *Sagitta* was dominated by nauplii, small copepods and large copepods, while mature *Sagitta* has larger copepods. In May and April, the juveniles were very rare, in relation with the above mentioned reproductive periods. Most of the mature individuals of *Sagitta*, showed diel vertical migration in April, May and June. But this cycle was not obvious in September 1995 in which whole population stayed in the first and second layer. Zenkevich (1963), Vinogradov *et al.* (1990) and Vinogradov *et al.* (1992a) stated that the *Sagitta* shows a strong vertical migration from the lower part of main pycnocline to the surface. They show the same diel vertical pattern with their prey. Drits and Utkina (1988) studied on the feeding of *Sagitta setosa* in the daytime plankton aggregation layer in the Black Sea and they observed that the principal food of *Sagitta* was copepodite stage V and females of *Calanus* and *Pseudocalanus*. They concluded that *Sagitta* feed actively in the daytime plankton accumulation layer (lower layer of the oxygen minimum zone).

CHAPTER IV

RESPIRATION OF *CALANUS*

4.1. INTRODUCTION

Respiration is a process in which every living cell or organism utilises oxygen to convert food compounds into energy releasing carbon dioxide and water (Art, 1993).

Respiration of aquatic organisms is usually measured by the rate of consumed oxygen from the ambient water. Respiration is affected by many factors, such as temperature, salinity, size of organism, level of behavioural activity, amount of oxygen in the surrounding water and biochemical composition of the source of energy (Valiella, 1995).

Respiration rates of poikilotherms are a direct function of temperature. Temperature affects rate of oxygen consumption via the speed of biochemical reactions dependent to temperature (Kinne, 1970).

In biological systems, the temperature coefficient or Q_{10} is the increase in the rate of biological processes (i.e. respiration rate) caused by a 10-degree increase in temperature (Art,1993; Ricklefs, 1990). If Q_{10} is close to 1, it means that respiration do not change with temperature. For several crustaceans such Q_{10} values have been reported to range between 2.0 and 3.0 (Kinne, 1970).

It is well known that *Calanus euxinus* shows diel vertical migration in the Black Sea. During the nighttime they are at the oxygen-saturated upper surface water with the temperature of about 24°C (in summer). During the daytime they stay in

the oxygen deficient lower layer (less than 20 μM dissolved oxygen) with the temperature of about 8°C.

Therefore *Calanus* expose a wide range of temperature (3 fold) and oxygen content (10 fold) variations during their diel cycle. In this study to understand the response of female and copepodite stage V *Calanus* (as the most strong vertical migrants, see section 3.2.1.3) to the changes in temperature and oxygen content in seawater, their respiration rates were estimated.

4.2. RESULTS

As was seen in the previous section 3.2.1.3, *Calanus* especially females and copepodite stage V showed a pronounced diel vertical migration. The vertical profiles of temperature and oxygen in the Black Sea show high variability with depths; temperature change from 23 to 6°C during the water column in summer months and individuals undergo almost 10 times differences in oxygen concentrations during their daily vertical migration. Thus in this chapter, the effects of temperature and oxygen differences on the respiration rate of copepodite V and female *Calanus* were studied.

4.2.1. EFFECTS OF TEMPERATURE ON OXYGEN CONSUMPTION

The dissolved oxygen (DO) uptake (both as μM DO ind.$^{-1}$ h^{-1} and μl DO ind.$^{-1}$ h^{-1}) by copepodite V and female *Calanus euxinus* are presented in Table 4.1. The DO consumption rates of both females and copepodite V increased with increasing temperature. The ranges of DO consumption rates of female were very wide at 12 and 18 °C.

Figure 4.1 and Table 4.1 show that the consumption rates of female *Calanus* were higher than those of the copepodite V at all temperatures.

Table 4.1: Oxygen consumption rates (with their standart deviations) of copepodite stage V and female *Calanus* at 5 different temperatures. (n= the number of replicates. DO= dissolved oxygen).

	Copepodite V Oxygen consumption			Female Oxygen consumption		
T °C	n	µM DO/ind/h	µl DO/ind/h	n	µM DO/ind/h	µl DO/ind/h
5±1	3	0.006±0.0006	0.07±0.007	3	0.011±0.002	0.12±0.019
12±1	3	0.01±0.006	0.11±0.07	3	0.018±0.008	0.2±0.08
16±1	3	0.014±0.001	0.16±0.011	3	0.026±0.0034	0.3±0.038
18±1	2	0.017±0.0007	0.19±0.008	3	0.03±0.015	0.33±0.17
23±1	3	0.02±0.002	0.22±0.02	4	0.034±0.0013	0.38±0.015

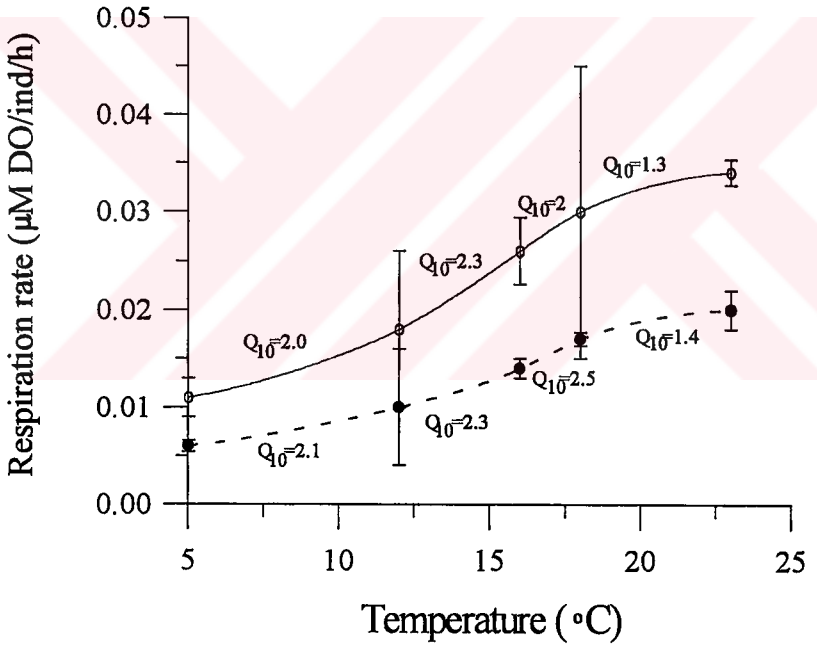

Figure 4.1: Respiration rates (oxygen consumption rates) and temperature coefficient (Q_{10}) of copepodite stage V (dashed line) and females (solid line) of *Calanus* at different temperatures. Vertical lines illustrates error bars of measurements.

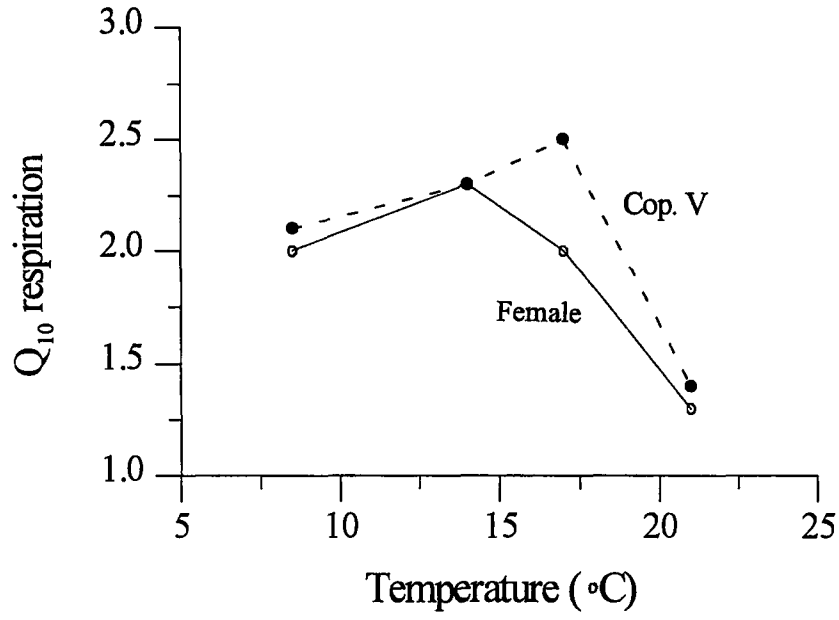

Figure 4.2: Temperature coefficient of copepodite stage V and female *Calanus* at different temperatures.

Metabolic adaptation to the environmental temperature is reflected by the Q_{10} values (McLaren, 1963; 1965 and 1966 c.f. Parsons *et al.* 1990). As seen in Figure 4.1. DO consumption rates of both females and copepodite V were dependent to temperature up to 18°C, above this temperature the DO consumption of the individuals were independent to the temperature hence the Q_{10} values less than 2.0 (Figure 4.2).

4.2.4. EFFECTS OF AMBIENT SEAWATER OXYGEN CONCENTRATION ON OXYGEN CONSUMPTION

The oxygen consumption of copepodite stage V and female *Calanus euxinus* in different oxygen concentrations in the ambient seawater are presented in Tables 4.2 and 4.3.

Table 4.2: Oxygen consumption rates (with their standart deviations) of copepodite stage V *Calanus* at different oxygen concentrations in the ambient water. Experiments conducted at 16±1 °C. (DO= Dissolved Oxygen. n= number of replicates).

DO conc. in ambient water		**Copepodite V Oxygen consumption**		
(µM)	(µl l^{-1})	n	µM ind.$^{-1}$ h^{-1}	µl ind.$^{-1}$ h^{-1}
273.1	3.06	5	0.021±0.004	0.23±0.05
196.5	2.20	5	0.016±0.002	0.17±0.03
142.7	1.60	5	0.007±0.001	0.07±0.01
40.6	0.45	5	0.008±0.003	0.09±0.03

Table 4.3: Oxygen consumption rates (with their standart deviations) of female *Calanus* at different oxygen concentrations in the ambient water. Experiments conducted at 16±1 °C. (DO= Dissolved Oxygen. n= number of replicates).

DO conc. in ambient water		**Female Oxygen consumption**		
(µM)	(µl l^{-1})	n	µM ind.$^{-1}$ h^{-1}	µl ind.$^{-1}$ h^{-1}
273.1	3.06	5	0.04±0.01	0.41±0.07
230.7	2.58	6	0.03±0.01	0.34±0.12
201	2.25	5	0.027±0.003	0.3±0.04
138.5	1.55	6	0.02±0.003	0.24±0.033
36	0.40	5	0.012±0.002	0.13±0.02

There was a linear relationship between the DO consumption of female and DO concentration in the ambient seawater ($P<0.05$) but DO consumption of stage V *Calanus* and the DO concentration in the ambient seawater showed weak relation (Fig. 4.3). The experiments were conducted at a constant temperature of 16 °C. The DO consumption of females and stage V individuals decreased with decreasing DO concentrations in the ambient seawater.

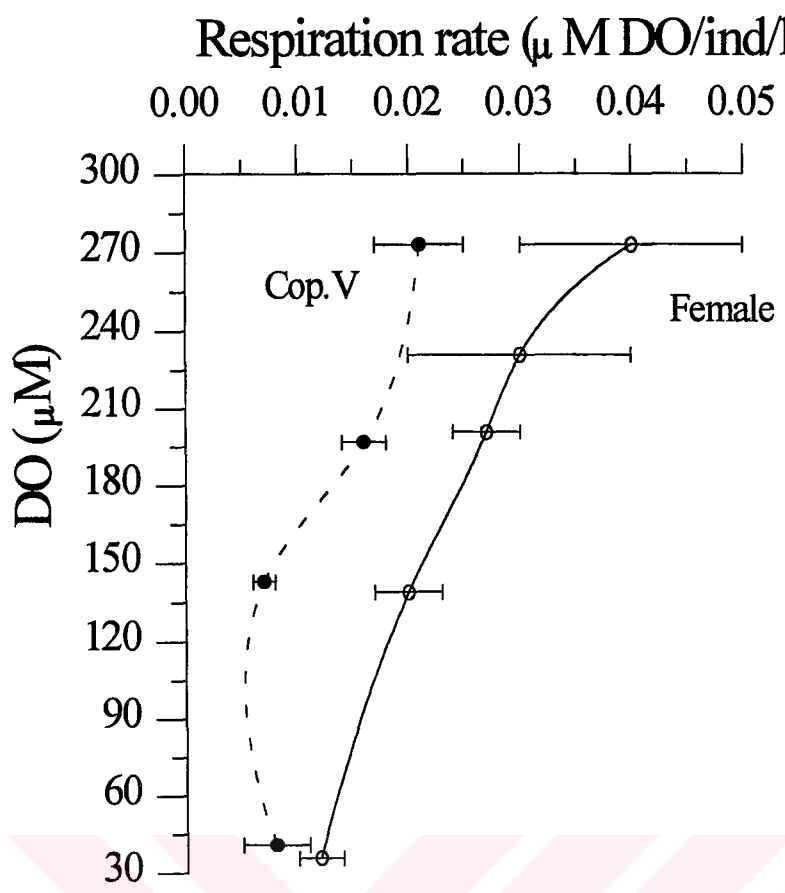

Figure 4.3: Respiration rates of copepodite stage V and female of *Calanus* at different ambient oxygen concentrations. Horizontal lines illustrate error bars. Temperature 16°C.

4.3 DISCUSSION

4.3.1. EFFECT OF TEMPERATURE ON RESPIRATION

Temperature is one of the major environmental variables which influences metabolic activity in poikilothermal animals (Ankaru, 1964; Marshall and Orr, 1958; Haq, 1967). In the present study, there was a remarkably increase at the level of respiration when temperature rose from 5 °C to 18°C, however, there was a slight increase above 18 °C. This slight increase did not show any increase in metabolic activity with temperature. Since temperature affects rate of DO consumption via the speed of biochemical reactions, many authors have expressed

temperature/DO consumption relations in term of Q_{10} values. For several crustaceans Q_{10} values have been reported to range between 2.0 and 3.0 (Kinne, 1970). In this study, both females and stage V individuals' Q_{10} values were between 2 and 2.5 up to 18 °C. Above 18°C, Q_{10} values were close to one. If Q_{10} value is greater than one, it indicates a regular increase of the metabolic rate with temperature and demonstrates a good adaptation of the individual to temperature (Corner and O'hara, 1986). This was the case for the respiration rate between 5 and 18°C. If Q_{10} value is close to one, which means that respiration do not change with temperature (Corner and O'hara, 1986). This happened between 18 and 23°C. Marshall and Orr (1972) mentioned that at 20°C *Calanus* are close to their lethal temperature and there may be harmful effects.

In general, respiration of marine invertebrates increases with the increase of animal size (Conover, 1959; Marshall and Orr, 1958; Marshall and Orr, 1972; Kideys, 1991). Female and stage V *Calanus* confirm to this expected pattern at all five temperatures.

These experiments illustrated that around 5 times increasing in temperature caused increase in the oxygen consumption of both female and copepodite stage V *Calanus* around 3 times.

4.3.2. EFFECT OF AMBIENT OXYGEN CONCENTRATION ON RESPIRATION

Variations in the oxygen content of seawater have effect on the oxygen consumption. In the present study, female and stage V individuals responded to decrease the ambient water oxygen content with decreasing their consumption. From these experiments, it was seen that the around 7 times increase in ambient oxygen concentration caused almost 3 times increase in oxygen consumption in both female and copepodite stage V *Calanus*. Vinogradov *et al.* (1992b) showed that the decrease in oxygen consumption rate of stage V *Calanus* with decreasing oxygen concentration in seawater in the Black Sea. Marshall and Orr (1972)

stated that, female *Calanus* were slightly more resistant than males to oxygen reduction, while stage V withstood oxygen reduction to considerably lower values. The oxygen consumption rate of stage V *Calanus* under different oxygen contents which was studied by Vinogradov *et al.* (1992b) in the Black Sea was much more lower than the value of this study. This may be simply caused by the difference in experimental temperature. They conducted experiments at 8°C as opposed to 16 °C of the present study.

CHAPTER V

DIEL FEEDING BEHAVIOUR AND GRAZING OF COPEPODS

5.1. INTRODUCTION

Planktonic copepod feeding activities play an important role in the transfer of the materials and energy within marine ecosystems. One important goal of numerous feeding behaviour studies in marine planktonic copepods has been to increase the understanding of marine food-chain dynamics and especially to quantify the grazing impact of herbivorous copepods on the phytoplankton community.

The majority of the understanding of copepod feeding biology and zooplankton grazing in general is based on the studies of the genus *Calanus*. In the second half of the century, the literature on *Calanus* feeding has expanded rapidly. There are lots of research on the relations between *Calanus* feeding biology and environmental variables (Huntley *et al.* 1987; Dam and Peterson, 1991; Nejstgaard *et al.* 1995).

The basic parameters influencing feeding (for example, temperature affects on the ingestion rate and clearance rate of zooplankton; Dam and Peterson, 1988) are well established. It was recognised that there was a relation between feeding and the ambient light regime. Early studies showed that feeding was higher at night (Huntley, *et al.* 1987; Morales, *et al.* 1993). However, it is still unclear as to the significance of such differences, or whether the differences between day and night result from endogenous rhythms (Dam and Peterson, 1993).

Considering food concentration, and size of food particle, *Calanus* preferentially captures larger food particles. Early studies showed that the ingestion rate of

Calanus increased linearly with food concentration, but a reduction, or even decline, in clearance rate at high food concentration has been observed.

Food quality, in contrast to food concentration, is difficult to define in quantitative terms. However, a number of studies with *Calanus* spp. show that certain algae are preferred in comparison to others of the same size and at the same concentration (Huntley *et al.* 1993 c.f. Harris, 1996), that algae are preferred to non-biological particles and live algae to dead. Dinoflagellates are increasingly recognised as being important in the diet of *Calanus*, there are pronounced interspecific differences which require further investigation. Huntley *et al.* (1986 c.f. Harris 1996) and Gill and Harris (1987, c.f. Harris, 1996) showed that several dinoflagellate species produce compounds that inhibit feeding and may even produce acute physiological responses and death. In contrast other dinoflagellates are actively eaten and may be good diet in laboratory culture.

Feeding or ingestion rate may be defined as the amount of food eaten by an organism per unit of time. Another measure of expressing a copepod's feeding rate is its clearance rate which is expressed as the volume of water swept clear of food particles per unit of time. Feeding rates are a function of the feeder's physiological condition, environmental variables and its behavioural repertoire and ability to deal with changing conditions and variables (Omori and Ikeda,1992; Paffenhofer, 1988).

There are some methods which are representative of feeding rates in nature to examine zooplankton feeding rates. The method longest in use and still applied is that of determining concentrations of food through microscope counts at the beginning and the end of an experiment. This method is time consuming but has certain advantages; rates are obtained not only for different particle sizes but also for particle types. Since this approach is so laborious, an electronic device to rapidly count particles of various sizes found widespread application in freshwater and marine science. One of its disadvantages is that it cannot differentiate particle quality (Paffenhofer, 1988). Another method is developed to

obtain in situ feeding rates (Haney, 1971 c.f. Paffenhofer, 1988). The grazing rate of individual zooplankters and the zooplankton community were estimated from the short-term uptake of radiolabelled yeast. This method was modified by Roman and Rublee (1981 c.f. Paffenhofer, 1988). In addition to ^{14}C for phytoplankton, they used ^{3}H to label bacteria to obtain grazing rates on detritus to which bacteria are thought to be aggregated. The shortcomings of the radiolabel method are the limited period of time (minutes) over which feeding rates are measured and the experiments occur in containers of 2 to 5 liter capacity. In some experiments it was observed that the clearance rate of some carnivorous copepods increased with increasing container volume (Paffenhofer, 1988).

The gut fluorescence method, developed by Mackas and Bohrer (1976), is also considered as an in situ method of determining zooplankton feeding rates. It is based on the 100% molar conversion of chlorophyll to phaeopigment. One of the main criticisms of this approach is the apparently variable degree of pigment destruction during gut passage. Head and Harris (1992) using high pressure liquid chromatography showed a high degree of pigment destruction in *Calanus* spp. grazing on diatoms.

These methods of gut fluorescence, radiolabelling and electronic counting yield primarily data on the consumption of living phytoplankton. Barnett (1974 c.f. Paffenhofer, 1988) suggest that the most reliable methods are still those of visual enumeration.

Kiorboe *et al.* (1985), compared estimates of natural feeding rates obtained by four different methods in seven species of planktonic copepods: gut fluorescence, egg production, removal of chlorophyll and removal of particles from suspension by animals incubated in seawater from the collection depth. They concluded that all four methods seemed to yield reliable and they suggested that the choice of method must, therefore, depend on the environmental conditions as well as the goals of the specific research project undertaken.

The gut fluorescence method has been the subject of considerable development using *Calanus* spp., both as an approach to studying in situ grazing on phytoplankton, and also to estimate cyclical activity and feeding periodicity. Levels of gut pigment in *Calanus* species have been widely reported (Hallberg and Hirche, 1980; Head and Harris, 1992, 1996).

5.2. RESULTS

In this chapter, gut pigment content (GPC) and grazing rate of female *Calanus euxinus* and copepod assemblages on the primary production were presented. GPC of female *Calanus* was investigated from a daily station in May 1994, April 1995 and September 1995 in southwestern part of the Black Sea. Females were collected from 4 depth strata in May and from 5 depth strata in the other seasons (for more details about sampling strata, see section 2.1.1.1). For measuring GPC and grazing rate of copepod assemblages, the samples were collected from 50m to the surface at a daily station only in September 1995. Copepod assemblages was categorised into three size groups; large size (between 2000 and 1000μm), medium size (from 1000 to 500μm) and small size fraction (between 500 and 300μm). The relationships between GPC, chlorophyll-a and phytoplankton composition in seawater were also analysed.

5.2.1. VERTICAL DISTRIBUTION OF CHLOROPHYLL-A, PHYTOPLANKTON AND PARTICULATE ORGANIC CARBON

Figs 5.1-5.3 show the vertical distribution of light transmission, chlorophyll-a and temperature in May 1994, April 1995 and September 1995. In May 1994 (Fig. 5.1) the chlorophyll-a concentration was very low. There was a peak with 0.3 $\mu g\ l^{-1}$ at around 40m. Chlorophyll-a was evenly distributed down to 40m in April 1995 (Fig. 5.2) with the value of 0.4 $\mu g\ l^{-1}$. In September 1995 (Fig. 5.3),

chlorophyll concentration was almost 4 times higher in the upper 20 m, than in May and in April.

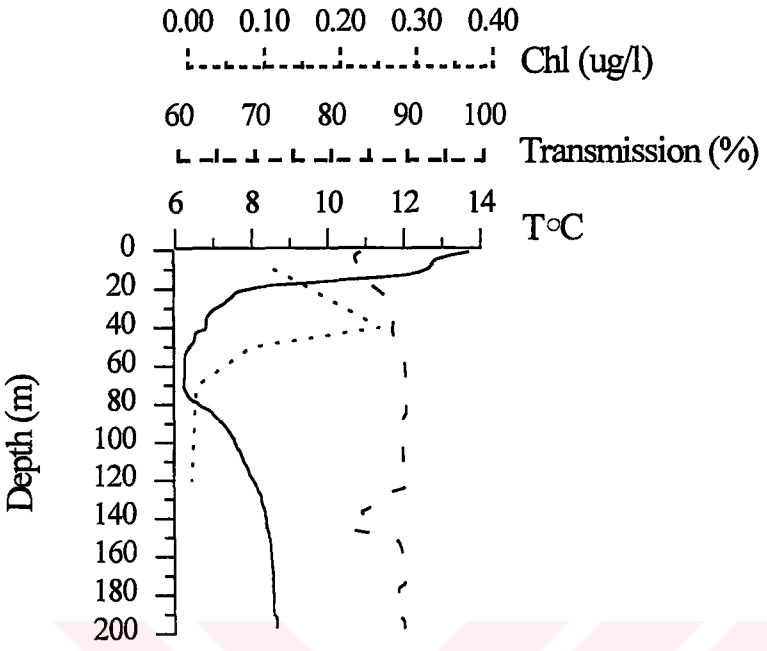

Figure 5.1: Vertical distribution of temperature, light transmission and chlorophyll-a during May 1994.

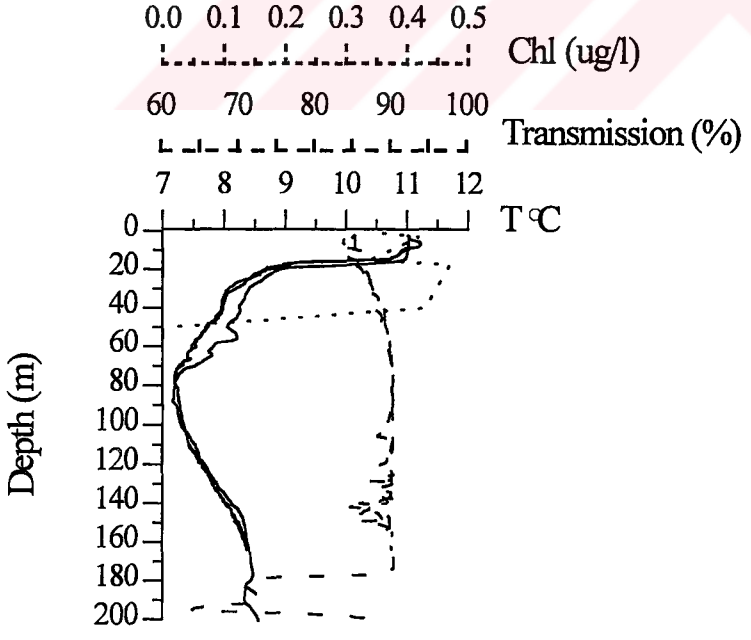

Figure 5.2: Vertical distribution of temperature, light transmission and chlorophyll-a during April 1995.

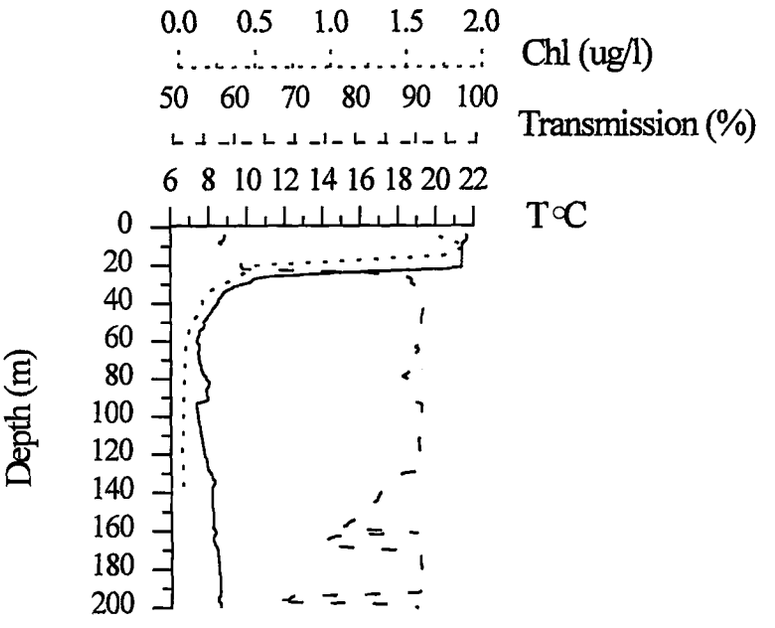

Figure 5.3: Vertical distribution of temperature, light transmission and chlorophyll-a during September 1995.

Figure 5.4 shows the general vertical distribution of particulate organic carbon (POC) in the southwestern part of the Black Sea in August 1993 and in April 1995 taken from Coban, (1997). The maximum concentration of POC was always observed almost in the lower boundary of the thermocline. It decreased sharply at around 20m. The gradual decrease continued down to the ~120m in August 1993 and ~145m in April 1995. Below these depths there was an increase again. These depths almost coincided with the lower boundary of the main pycnocline. In August 1993, the density surface at 120m was 16.0, and in April 1995 the density surface at 145m was ~15.9.

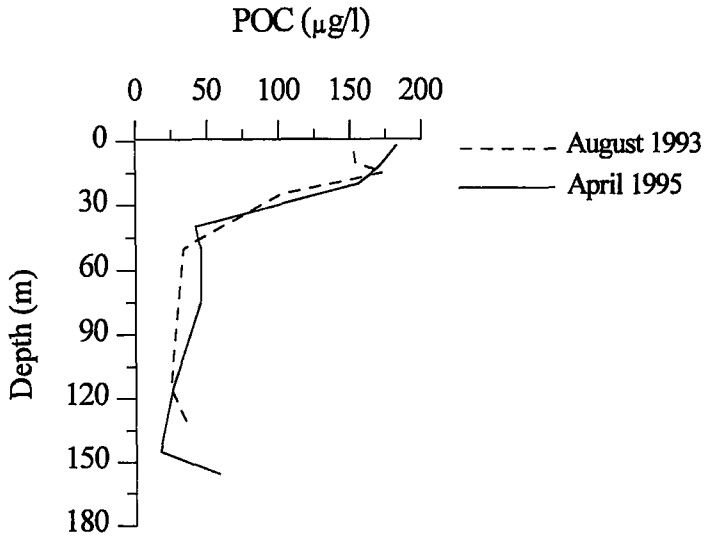

Figure 5.4: Vertical distribution of particulate organic carbon (POC) in the southwestern part of the Black Sea (after Coban, 1997).

The euphotic zone (the depth of 1% light level) depth of stations changed temporally, it was at 30m in May 1994 (Vidal, 1995), at 38m in April 1995 and it was 17m in September 1995 (Yilmaz *et al.* 1996). For determining the phytoplankton abundance, the sample was taken only from the surface and sieved through 55µm mesh size in May 1994. In April 1995 and in September 1995 the phytoplankton samples were taken from several depths within the euphotic layer and analysed by using sedimentation method.

Species numbers, abundance and percentage frequency of dominant groups of phytoplankton during the sampling periods are presented in Table 5.1. In May 1994, only 8 phytoplankton species were found. Diatom was the dominant group in which *Nitzschia longissima* was the most abundant species. Dinoflagellates comprised 11% of the phytoplankton abundance with the dominant species *Peridinium trochoideum* and *P. brevipes* (Dr. Z. Uysal, unpublished data). In April, the coccolithophorid was the most abundant group which was followed by dinoflagellates. Among dinoflagellates *Peridinium triquetrum* and *P. trochoideum* were the main species, and *Nitzschia delicatula* and *N. closterium* were the most dominant ones in Diatomea. Average phytoplankton concentration

in the euphotic layer was $14x10^4$ cells l^{-1} in April (Eker, 1998). This abundance was made up by 53% coccolithophorids, 19% dinoflagellates and 1.3% diatoms (Table 5.1). In September both species number (56 species) and abundance ($11x10^5$ cells l^{-1}) were higher than those in May 1994 and in April 1995. Coccolithophorids made up the bulk of the phytoplankton abundance with 92%. The share of dinoflagellates and diatoms in phytoplankton abundance 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 the diatoms were the most abundant species (Eker, 1998).

Table 5.1: Species numbers, abundance and percentage frequency of dominant groups of phytoplankton in May 1994, April 1995 and September 1995.

	May 1994*	**April 1995◊**	**September 1995◊**
No. of species	8	31	56
No. of cells l^{-1}	2.2×10^4	14×10^4	11×10^5
Dominant groups			
Coccolithophorids	ND	53%	92%
Dinoflagellates	11%	19%	2.8%
Diatoms	89%	1.3%	2.9%

ND=No Data
*, Dr. Zahit Uysal unpublished data
◊, data from Eker, (1998)

From the phytoplankton abundance and volume data, carbon content of phytoplankton was estimated by using Strahtman's equation (1967). In May, phytoplankton carbon (PC) was not estimated. As mentioned before, the phytoplankton samples were collected by sieving from 55μm mesh size at that time so from that phytoplankton carbon will be underestimated than that of other seasons.

The estimated primary production values at the stations were 247 and 405 mg C m^{-2} day^{-1} in April and in September respectively (Yilmaz *et al.* 1996). There is no estimated primary production value in May.

5.2.2. DIEL FEEDING BEHAVIOR OF FEMALE *CALANUS EUXINUS*

5.2.2.1. GUT PIGMENT CONTENT OF FEMALE *CALANUS EUXINUS*

In May 1994, gut pigment content (GPC) of female *Calanus* was collected during 12h time period mostly night times except one sample which was collected early in the morning (at 06:30h) (Table 5.2). GPC in female *Calanus euxinus* varied relatively little over 12 hours periods. At 19:30 the maximum gut pigment content was observed at the first layer with a value of 5.2 ng pigment ind.$^{-1}$. The samples from the deepest layer had also high value with 3.0 ng ind.$^{-1}$ although the chlorophyll-a concentrations were much higher in the upper layers (Fig. 5.1). In May 1994, female *Calanus* showed a pronounced nighttime migration towards the surface layers. (see Fig. 3.6). At 22:00 when most of the population was in the upper two layers, some individuals were still in the OMZ with the GPC value of 0.4 ng pigment ind.$^{-1}$. After midnight, the GPC was observed throughout the water column synchronized with their downward migration. When they were in the lower layers (at 06:30), the high level of gut fullness was observed in deep waters (third layer) where chlorophyll concentration were low. It seems that GPC and chlorophyll concentration in the whole water column were not correlated.

In April, GPC was analysed over 30 hours. The highest amount of GPC was observed during the nighttime at the uppermost two layers synchronising with the diel vertical migration (Table 5.3). During the daytime, they were in the fifth layer (at 07:00, 11:30, 17:00 and 18:00) and their GPC concentration were generally low. However, from morning till evening the GPC gradually increased in spite of low chlorophyll concentration in this layer.

Table 5.2: Average gut pigment content (ng pigment ind.$^{-1}$) in female *Calanus euxinus* from each layers during different sampling times in May 1994. Values in parenthesis are standard deviations. Sunset= 20:16 h; Sunrise= 05:48 h.

		Time of day				
		19:30	**22:00**	**01:00**	**04:00**	**06:30**
Layers	**Depth**	**Average pigment (ng pig. ind.$^{-1}$)**				
from depth of the thermocline to the surface	18m-surface	5.2	1.0 (0.6)	2.4 (1.2)	1.1 (0.7)	ND
from the depth of σ_θ=14.6 to the depth of thermocline	61m-18m	0.4 (0.1)	1.2 (0.2)	2.1 (1.0)	2.3 (0.17)	ND
from the depth of σ_θ=15.4 to the depth of σ_θ=14.6	97m-61m	ND	ND	1.3 (1.2)	3.4 (0.9)	5.0 (0.3)
from the depth of σ_θ=16.2 to the depth of σ_θ=15.8	147m-97m	3.0	0.4	0.3	3.0	1.2 (0.1)

ND=no data available

Table 5.3: Average gut pigment content (ng pigment ind.$^{-1}$) in female *Calanus euxinus* from each layers during different sampling times in April 1995. Values in parenthesis are standard deviations. Sunset=19:52 h, Sunrise=06:06 h.

		Time of day							
		18:00	**22:00**	**02:00**	**07:00**	**11:30**	**17:00**	**20:00**	**0:00**
Layers	**Depth**	**Average pigment (ng pig. ind.$^{-1}$)**							
from depth of the thermocline to the surface	17m-surface	ND	5.5 (2.2)	7.4 (6.4)	ND	ND	ND	22.0 (18.6)	9.1 (3.9)
from the depth of σ_θ =14.6 to the thermocline	76m-17m	ND	13.3 (3.4)	7.5 (2.7)	ND	ND	ND	4.1 (0.9)	16.9 (11.7)
from the depth of σ_θ =15.4 to the depth of σ_θ =14.6	112m-76m	5.1 (2.8)	ND	4.3 (1.3)	ND	ND	ND	ND	ND
from the depth of σ_θ =15.8 to the depth of σ_θ =15.4	136m-112m	3.8 (5.0)	ND	ND	ND	ND	4.2 (2.2)	ND	ND
from the depth of σ_θ =16.2 to the depth of σ_θ =15.8	163m-136m	16.2 (8.1)	ND	ND	0.8 (0.7)	2.4 (0.7)	4.9 (1.6)	ND	ND

ND=no data available

Table 5.4: Average gut pigment content (ng pigment ind.$^{-1}$) in female *Calanus euxinus* from each layers during different sampling times in September 1995. Values in parenthesis are standard deviations. Sunset=17.43 h, Sunrise=05.47 h.

		Time of day					
		19:00	**23:30**	**03:30**	**07:30**	**12:00**	**16:00**
Layers	**Depth**	**Average pigment (ng pig. ind.$^{-1}$)**					
from depth of the thermocline to the surface	25m-surface	9.4 (3.0)	9.4	19.4 (11.4)	ND	ND	20.5 (6.5)
from the depth of σ_θ =14.6 to the thermocline	75m-25m	12.1 (7.9)	0.2	16.5 (1.2)	ND	ND	4.0 (1.2)
from the depth of σ_θ =15.4 to the depth of σ_θ =14.6	95m-75m	15.5	ND	ND	ND	ND	4.0 (5.4)
from the depth of σ_θ =15.8 to the depth of σ_θ =15.4	112m-75m	0.3	5.6	0.5	ND	ND	3.0 (4.2)
from the depth of σ_θ =16.2 to the depth of σ_θ =15.8	153m-112m	1.7	0.3	0.9	4.1 (4.1)	4.0 (4.0)	3.0 (4.2)

ND=no data available

Gut pigment contents of female *Calanus euxinus* varied on a diel cycle in September with highest amounts observed during the nighttime and late afternoon and the lowest amounts observed in the early morning (at 07:30) and at noon. During the nighttime, in the deeper (4^{th} and 5^{th} layers) layers, some individuals were found with the GPC associated with their diel vertical migration. Levels of gut pigment observed during the nighttime in the first layer average approximately 15 ng $ind.^{-1}$. However, there was no apparent relationship between GPC and the chlorophyll concentration of the ambient seawater (Table 5.4).

5.2.2.2. INGESTION RATE AND GRAZING PRESSURE OF FEMALE *CALANUS* ON PRIMARY PRODUCTION

Grazing pressure of female *Calanus* was not estimated for May 1994, because of the lack of primary production data at that time and also incomparable PC to chlorophyll ratio of that station with the others due to the sieving the phytoplankton samples from 55μm mesh. Grazing pressure of female *Calanus euxinus* was calculated for the euphotic zone in April and in September 1995 and its grazing rate was measured from the gut content data collected from the layers which contain the euphotic zone; uppermost two layers in April and first layer in September (Tab. 2.3).

Before calculating grazing pressure, daily feeding duration of female *Calanus* must be clarified in April and in September. It was difficult to define accurately the extent of feeding period (in the sampling layers corresponding to the euphotic zone) due to the long (3-5h) sampling interval; however the feeding duration that female *Calanus* spends in the euphotic zone can be estimated roughly from its vertical distribution figures. 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 upward at around 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 163m and thickness of the euphotic zone was 38m so they should migrate at least 125m to reach the euphotic zone. They spend 5h to transit this 125m resulting an upward speed of about 25 m h^{-1}. At 02:00h, just over the half of the copepods were still in the euphotic zone. According to the estimation of Hardy and Bainbridge, (1954, *cf.* Marshall and Orr, 1972) the downward speed of *Calanus* is about 3 times higher than its upward speed over a long period experiment (i.e. 1h). If this ratio is taken into account the downward speed of *Calanus* will be 75 m h^{-1}, then it must take approximately 2h 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 7.5h in April. With a similar calculation, the duration of stay in the euphotic zone in September would be around 10.5h, with an upward speed of about 34 m h^{-1} and downward speed of 102 m h^{-1}.

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 5.5). Ingestion rate of female *Calanus* estimated by using gut content (G) and evacuation rate (k) constant. Evacuation rate (gut passage time) in copepods is primarily a function of temperature. Using the linear equation of Dam and Peterson (1988), the gut evacuation rate constant was found to be 1.86 h^{-1} in April and 3.0 h^{-1} in September. 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 5.5). 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.

Table 5.5: Gut pigment content (G, 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 (k) were 1.86 h^{-1} in April and 3 h^{-1} in September.

Time of day	Gut Pigment Content in the layers from the thermocline to the surface	from the depth of σ_θ=14.6 to the thermocline	Ingestion Rate
		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.

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. 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 the non-migrating population. By omitting 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 (7.5h in April and 10.5h in September), the number of individuals in the whole water column and 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 5.6). The PC:Chl-a ratios were 76 in April and 65 in September. These 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}, which is equal to 9.5% of the primary production.

Table 5.6: 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 parenthesis.

	April	September
No. of Ind. (m^{-2})	3365	1343
POC ($\mu g\ l^{-1}$)	178.9	188.6
PC ($\mu g\ l^{-1}$)	25.8	85.0
Chl-a ($\mu g\ l^{-1}$)	0.34	1.31
PC:Chl-a	76	65
Average Phytoplankton Conc. (cell l^{-1})	$14x10^4$	$11x10^5$
Consumption (as μg pigment $m^{-2}\ day^{-1}$)	471.6	592.8
Consumption (as mgC $m^{-2}\ day^{-1}$)	35.9	38.5
Primary Prod. (mgC $m^{-2}\ day^{-1}$)	247.0	405.4
Grazing Pressure (%)	14.5 (13.8)	9.5 (3.6)

5.2.3. DIEL FEEDING BEHAVIOUR OF COPEPOD ASSEMBLAGES

5.2.3.1. COMPOSITION AND ABUNDANCE OF COPEPODS

The numeric abundance (ind. m^{-2}) and the percentage of three size fractions of copepods collected from upper 50m in each sampling time in September 1995 are shown in Tables 5.7-5.9.

Table 5.7: Species composition and abundance of large size (2000-1000μm) fraction mesozooplankton during different sampling times in September 1995.

Species composition	19:00		23:30		03:30		07:30		12:00		16:00		21:00	
	ind.m^{-2}	%	ind.m^{-2}	%	ind.m^{-2}	%	ind.m^{-2}	%	ind.m^{-2}	%	ind.m^{-2}	%	ind.m^{-2}	%
C. euxinus female	421.1	22.5	757.9	26.5	463.2	50.0	15.8	9.0	94.7	31.0	505.3	32.4	231.6	26.8
C. euxinus male	21.1	1.1	168.4	5.9	21.1	2.3	15.8	9.0	0.0	0.0	0.0	0.0	42.1	4.9
C. euxinus cop. V	1200.0	64.0	1263.2	44.1	273.7	29.6	57.9	32.8	147.4	48.3	631.6	40.5	400.0	46.3
C. euxinus cop. IV	84.2	4.5	336.8	11.8	126.3	13.6	34.2	19.4	31.6	10.3	379.0	24.3	126.6	14.6
C. euxinus cop. III	0.0	0.0	0.0	0.0	21.1	2.3	10.5	6.0	21.1	6.9	0.0	0.0	21.1	2.4
C. euxinus cop. II	0.0	0.0	84.2	2.9	0.0	0.0	5.3	3.0	0.0	0.0	0.0	0.0	0.0	0.0
C. euxinus cop. I	0.0	0.0	0.0	0.0	0.0	0.0	2.6	1.5	0.0	0.0	0.0	0.0	0.0	0.0
P. elongatus female	126.3	6.7	84.2	2.9	0.0	0.0	26.3	14.9	0.0	0.0	42.1	2.7	0.0	0.0
P. elongatus cop.	0.0	0.0	168.4	5.9	0.0	0.0	2.6	1.5	10.5	3.5	0.0	0.0	0.0	0.0
A. clausi female	0.0	0.0	0.0	0.0	0.0	0.0	5.3	3.0	0.0	0.0	0.0	0.0	42.1	4.9
A. clausi cop.	0.0	0.0	0.0	0.0	21.1	2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
P. parvus female	21.1	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
total	**1873.7**	**100.0**	**2863.2**	**100.0**	**926.3**	**100.0**	**176.3**	**100.0**	**305.3**	**100.0**	**1557.9**	**100.0**	**863.5**	**100.0**

Table 5.8: Species composition and abundance of medium size (1000-500μm) fraction mesozooplankton during different sampling times in September 1995.

Species composition	19:00		23:30		03:30		07:30		12:00		16:00		21:00	
	ind.m^{-2}	%	ind.m^{-2}	%	ind.m^{-2}	%	ind.m^{-2}	%	ind.m^{-2}	%	ind.m^{-2}	%	ind.m^{-2}	%
C. euxinus cop.V	0.0	0.0	168.4	4.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
C. euxinus cop. IV	168.4	2.3	0.0	0.0	42.1	2.2	0.0	0.0	168.4	5.9	168.4	2.3	84.2	2.2
C. euxinus cop. III	0.0	0.0	336.8	9.5	210.5	10.9	84.2	6.9	336.8	11.8	335.8	4.6	336.8	8.9
C. euxinus cop. II	0.0	0.0	252.6	7.1	42.1	2.2	84.2	6.9	84.2	2.9	336.8	4.6	168.4	4.4
C. euxinus cop. I	0.0	0.0	168.4	4.8	42.1	2.2	42.1	3.5	84.2	2.9	0.0	0.0	0.0	0.0
P. elongatus female	3031.6	41.9	1263.2	35.7	968.4	50.0	589.5	48.3	1179.0	41.2	3536.8	47.7	1852.6	48.9
P. elongatus male	0.0	0.0	0.0	0.0	0.0	0.0	84.2	6.9	0.0	0.0	168.4	2.3	0.0	0.0
P. elongatus cop.	2189.5	30.2	589.5	16.7	168.7	8.7	84.2	6.9	84.2	2.9	1179.0	15.9	421.1	11.1
A. clausi female	336.8	4.7	84.2	2.4	210.5	10.9	126.3	10.3	757.9	26.5	1347.4	18.2	842.1	22.2
A. clausi male	1010.5	14.0	0.0	0.0	126.3	6.5	126.3	10.3	168.4	5.9	168.4	2.3	84.2	2.2
A. clausi cop.	505.3	7.0	589.5	16.7	42.1	2.2	0.0	0.0	0.0	0.0	168.4	2.3	0.0	0.0
O. similis female	0.0	0.0	84.2	2.4	84.2	4.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
total	**7242.1**	**100.0**	**3536.8**	**100.0**	**1937.2**	**100.0**	**1221.1**	**100.0**	**2863.2**	**100.0**	**7409.5**	**100.0**	**3789.5**	**100.0**

Table 5.9: Species composition and abundance of small size (500-300μm) fraction mesozooplankton during different sampling times in September 995.

Species composition	19:00		23:30		03:30		07:30		12:00		16:00		21:00	
	ind.m^{-2}	%	ind.m^{-2}	%	ind.m^{-2}	%	ind.m^{-2}	%	ind.m^{-2}	%	ind.m^{-2}	%	ind.m^{-2}	%
C. euxinus cop. III	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	84.2	2.5	0.0	0.0	0.0	0.0
C. euxinus cop. II	0.0	0.0	336.8	1.9	168.4	4.8	0.0	0.0	168.4	5.0	673.7	11.4	252.6	9.7
C. euxinus cop. I	0.0	0.0	673.7	3.8	0.0	0.0	168.4	5.0	168.4	5.0	168.4	2.9	168.4	6.5
P. elongatus female	547.4	16.1	1347.4	7.6	1179.0	33.3	1094.7	32.5	1010.5	30.0	1852.6	31.4	1179.0	45.2
P. elongatus male	0.0	0.0	0.0	0.0	0.0	0.0	84.2	2.5	84.2	2.5	0.0	0.0	0.0	0.0
P. elongatus cop.	1684.2	49.4	11115.8	62.3	1010.5	28.6	1094.7	32.5	1179.0	35.0	1852.6	31.4	505.3	19.4
A. clausi female	42.1	1.2	0.0	0.0	0.0	0.0	84.2	2.5	84.2	2.5	336.8	5.7	84.2	3.2
A. clausi male	0.0	0.0	0.0	0.0	168.4	4.8	84.2	2.5	84.2	2.5	168.4	2.9	0.0	0.0
A. clausi cop.	505.3	14.8	673.7	3.8	252.6	7.1	0.0	0.0	168.4	5.0	336.8	5.7	0.0	0.0
P. parvus female	42.1	1.2	0.0	0.0	84.2	2.4	0.0	0.0	84.2	2.5	0.0	0.0	84.2	3.2
P. parvus male	42.1	1.2	0.0	0.0	0.0	0.0	84.2	2.5	0.0	0.0	0.0	0.0	0.0	0.0
P. parvus cop.	126.3	3.7	0.0	0.0	0.0	0.0	0.0	0.0	84.2	2.5	0.0	0.0	0.0	0.0
O. similis female	294.7	8.6	2021.1	11.3	673.7	19.1	589.5	17.5	168.4	5.0	505.3	8.6	168.4	6.5
O. similis cop.	126.3	3.7	1684.2	9.4	0.0	0.0	84.2	2.5	0.0	0.0	0.0	0.0	168.4	6.5
O. similis female	294.7	8.6	2021.1	11.3	673.7	19.1	589.5	17.5	168.4	5.0	505.3	8.6	168.4	6.5
O. similis cop.	126.3	3.7	1684.2	9.4	0.0	0.0	84.2	2.5	0.0	0.0	0.0	0.0	168.4	6.5
total	**3410.6**	**100.0**	**17852.6**	**100.0**	**3536.8**	**100.0**	**3368.4**	**100.0**	**3368.4**	**100.0**	**5894.7**	**100.0**	**2610.5**	**100.0**

In the large size fraction, *C. euxinus* female, copepodite V and IV were numerically abundant (Table 5.7). In general, the dominant species of the large size fraction showed a diel migration to the surface waters at night (see Fig. 3.8).

The medium size fraction was dominated by female *P. elongatus* and female *A. clausi* throughout the study (Table 5.8). Daytime abundances were generally as high as those at night, suggesting that these copepods were not migrating or they migrated within the 50m.

In the small size fraction, the dominant species were, copepodite stages and the females of *P. elongatus* and also *O. similis* females (Table 5.9). The variations in numbers of these stages appeared to be coupled to those in medium size fraction.

Table 5.10 shows the percentages of species composition in three fractions when all data at each time intervals were poolled.

Table 5.10: Abundance percentage of three size fractions, sampled from 50m to the surface in September 1995.

Species	2000-1000μm	1000-500μm	500-300μm
Calanus 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
Pseudocalanus elongatus			
female	3.9	44.8	28
male	--	1.3	0.7
copepodite stages	1.5	13.2	36.9
Acartia clausi			
female	1.1	13.6	2.2
male	--	5.9	1.8
copepodite stages	0.3	4	5.2
Paracalanus parvus			
female	0.2	--	1.3
male	--	--	0.5
copepodite stages	--	--	0.9
Oithona similis			
female	--	1.0	10.9
male	--	--	--
copepodite stages	--	--	3.2

--; no individuals observed

5.2.3.2. GUT PIGMENT CONTENT OF COPEPODS

A diel sampling cycle consisted of tows from upper 50 m, at 4-5 h intervals, for a 26 h period in September 1995. However, in the large size fraction, when particular categories of copepods were absent from the surface layers during daytime (diel vertical migrants), no data was registered for daytime. All data represent the mean values obtained from 2-3 replicates depending on the abundance of organisms (Table 5.11).

Table 5.11: The gut pigment concentrations (ng pigment individuals^{-1}) in each size fraction during the sampling times in September 1995. Values in parenthesis are standard deviations.

	Gut pigment content (ng pig. ind.$^{-1}$)		
Time of day	Large size (2000-1000um)	Medium size (1000-500um)	Small size (500-300um)
19:00	7.8 (2.0)	9.1 (0.0)	2.0 (0.3)
23:30	9.4 (3.3)	1.7 (1.8)	1.2 (0.3)
03:30	11.0 (5.6)	4.4 (2.7)	1.9 (1.6)
07:30	ND	0.1 (0.1)	0.9 (1.1)
12:00	ND	1.2 (0.8)	1.2 (1.0)
16:00	3.4 (3.4)	3.6 (3.8)	1.1 (0.2)
21:00	5.2 (0.5)	4.5	0.9

ND=no data available

Within the large fraction, there was a trend of increasing gut pigment content during the night feeding period (Table 5.11). The highest value was reached towards the end of the night (at 03:30). In this fraction, around 86% of species abundance was dominated by the vertical migrant organisms i.e. female, copepodite V and copepodite IV stages of *C. euxinus* (see Table 5.10), and during daytime sufficient number of individuals could not be found for GPC analysis.

Within the medium size fraction, during the nighttime the GPC was generally higher than the daytime. The average pigment ranged from 0.1 to 9.1 ng pigment ind.$^{-1}$ and the amount of explained variance was 78.5% among the GPC data. The overall nighttime abundance was 2.4 times higher than daytime abundance.

Within the small size fraction, there was not a pattern of decrease or increase in gut pigment content with time, the coefficient of variation was 32% among the

GPC data. The small copepod species within the small size fraction contained very low levels of pigment in their guts ranging from 0.9 to 2.0 ng pigment ind^{-1}.

Gut pigment content in copepod assemblages showed a trend to increase with increasing body size. When the gut pigment data were correlated with the three average lengths (L) (1500μm as big size, 750μm as medium and 400μm as small size), the equation is;

$$GPC=-0.75 + 5.5L \; ; (r^2=54\%, r=0.73, P<0.001).$$

5.2.3.3. INGESTION RATE AND GRAZING PRESSURE OF COPEPOD ASSEMBLAGES ON PRIMARY PRODUCTION

Ingestion rate of all three size fractions was estimated by using gut content (G) and evacuation rate (k). Gut passage time in copepods is independent of body size and primarily a function of temperature (Morales *et al.* 1990). The average temperature was 14.5 °C in the water column down to 50m. Using Dam and Peterson (1988) linear equation , the estimated gut evacuation rate was calculated as 2.4 min^{-1} for three size fractions.

To estimate the consumption (grazing) on primary production over 50m in September, hourly ingestion rates were multiplied by the corresponding abundances (as ind. m^{-2}) of copepods in the water column (50m) and multiplied by 24 to calculate daily consumption. Medium and small size fractions were observed within the 50m throughout the sampling period (26h cycle). During the daytime (at 07:30 and 12:00) there was no data for large size fraction and so during the daytime there was no detectable grazing for large size then it should be equal to zero. In general there was an increasing ingestion rate with increasing

copepod body size (Table 5.12). The large size fraction had higher ingestion rate with the average value of 12.6 ± 10.5 ng pigment copepod^{-1} h^{-1} while the medium size fraction had an ingestion rate of 8.4 ± 7.1 ng pigment copepod^{-1} h^{-1}. Small size fraction containing mostly copepodites of larger species and female *O. similis*, had an average ingestion rate of 3.1 ± 1.1 ng pigment copepod^{-1} h^{-1}.

The percentage of grazing (consumption) varied widely in each time interval within the size fractions. The highest average grazing pressure was obtained by the medium size fraction with the percentage 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 5.12).

The abundance of female *C. euxinus* constituted ~28.3% of the large size fraction copepods (Table 5.10). We had GPC data of female *Calanus* sampled from 5 depth strata in September from the same station where grazing pressure was estimated for copepod assemblages. To estimate roughly the percentage grazing coming from female *Calanus* among large size fraction, GPC data of female *Calanus* from uppermost 2 layers (from 75m to the surface) where consisted upper 50m, were pooled (Table 5.13). During the daytime female *Calanus* was not observed at the uppermost 2 layers. To estimate daily consumption (grazing) rate, the ingestion rate should be suggested as zero at the uppermost two layers during daytime. Then ingestion rate was found as 18.3 ng pigment ind.$^{-1}$ h^{-1} and female *Calanus* grazed 3.7 % of primary production. Around 45.7% of large size fraction grazing was coming from female *C. euxinus*.

Table 5.12: The gut pigment content (G; ng pigment individuals^{-1}), ingestion rates (I; ng pigment individuals^{-1} hour^{-1}) and the percentage grazing rate of each size fraction of copepod assemblages during the sampling times (SD=Standart deviation) in September 1995.

	Large Size				Medium Size				Small Size			
Time of Day	**G**	**I**	**ind.m^{-2}**	**% Grazing**	**G**	**I**	**ind.m^{-2}**	**% Grazing**	**G**	**I**	**ind.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 (0.3)	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	ND	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	ND	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		**12.6**	**1223.7**	**8.1**	**3.5**	**8.4**	**3999.9**	**16.7**	**1.3**	**3.1**	**5720.3**	**6.7**
SD		**10.5**	**947.0**	**8.8**	**3.0**	**7.1**	**2438.0**	**21.0**	**0.5**	**1.1**	**5447.6**	**5.9**

Table 5.13: Gut pigment content (G; ng pig. ind.$^{-1}$), ingestion rate (I; ng pig. ind.$^{-1}$ h^{-1}) and percentage grazing of female *Calanus* towed from uppermost two layers in September 1995 (SD= standard deviation).

Time of Day	G	I	ind.m^{-2}	% Grazing
19:00	10.8	25.8	1347.4	13.4
23:30	4.8	11.5	610.5	2.7
03:30	18.0	43.1	305.3	5.1
07:30	0.0	0.0	10.5	0.0
12:00	0.0	0.0	10.5	0.0
16:00	12.3	29.4	86.8	1.0
Average	**7.6**	**18.3**	**395.2**	**3.7**
SD	**7.2**	**17.4**	**520.0**	**5.1**

5.2.3.4. GRAZING RATE OF COPEPOD ASSEMBLAGES

To estimate the grazing rate of copepod assemblages, the pigment consumption per individuals was converted into pigment consumption per biomass (mgC m^{-2}). The biomass as wet weight of each size fraction was calculated by using constant value estimated by the Ukranian Scientist for each stage of copepod species in the Black Sea (Niermann *et al.* 1995). The dry weight of each fraction was estimated from the assumption of 80% of wet weight comes from water. Dry weights were converted to carbon assuming that 40% of the dry weight is due to the carbon (Parsons *et al.* 1979 *cf.* Dam and Peterson, 1993). The grazing rate for each size fraction was estimated from the equation (Oguz *et al.* 1998),

Grazing pressure (mgC m^{-2} day^{-1}) = Grazing rate*Biomass (mgC m^{-2})

The grazing rates of small and medium sized copepod fractions were higher than that of large one (Table 5.14). The estimated average grazing rate of copepod assemblages was 0.76±0.26 day^{-1} (Table 5.15).

Table 5.14: Grazing pressure (mgC m^{-2} day^{-1}), biomass (mgC m^{-2}) and grazing rate (day^{-1}) of three size fraction of copepod assemblages in different time of day.

Time of Day	Large size			Medium size			Small size		
	Grazing pressure (mgC m^{-2} day^{-1})	Biomass (mgC m^{-2})	Grazing rate (day^{-1})	Grazing pressure (mgC m^{-2} day^{-1})	Biomass (mgC m^{-2})	Grazing rate (day^{-1})	Grazing pressure (mgC m^{-2} day^{-1})	Biomass (mgC m^{-2})	Grazing rate (day^{-1})
19:00	57.0	116.2	0.49	85.5	24.2	3.53	15.2	4.9	3.1
23:30	100.9	169.8	0.59	14.7	22.1	0.66	40.5	21.8	1.9
03:30	44.3	63.6	0.7	26.6	9.0	2.95	23.8	7.9	3
07:30	0	7.5	0	0.3	5.0	0.05	10.6	7.4	1.4
12:00	0	18.6	0	7.5	16.5	0.45	15.9	8.6	1.8
16:00	20.2	94.1	0.21	44	31.4	1.4	25.2	15.0	1.7
21:00	17.5	52.6	0.33	31.2	17.8	1.75	0.3	7.5	0.04
Average	**34.3**	**71**	**0.33**	**30**	**18**	**1.5**	**18.8**	**10.4**	**1.9**

Table 5.15: Grazing pressure (mgC m^{-2} day^{-1}), biomass (mgC m^{-2}) and grazing rate (day^{-1}) of total copepod assemblages in different time of day.

Time of Day	Total copepod assemblages		
	Grazing pressure (mgC m^{-2} day^{-1})	Biomass (mgC m^{-2})	Grazing rate (day^{-1})
19:00	157.7	145.3	1.1
23:30	156.1	213.7	0.73
03:30	94.6	80.6	1.2
07:30	10.9	20	0.55
12:00	23.4	43.7	0.54
16:00	89.4	140.5	0.64
21:00	49	7.8	0.63
Average	**83**	**103.1**	**0.76**
Stdev	**59**	**67**	**0.26**

5.2.4. DISCUSSION

5.2.4.1. VERTICAL DISTRIBUTION OF PHYTOPLANKTON AND CHLOROPHYLL-A

The maximum abundance of phytoplankton among three seasons (May 1994, April 1995 and September 1995), was found in September (see Table 5.1). In May, diatoms were more abundant than dinoflagellates but probably most of the dinoflagelates escaped from the 55μm mesh size. In April dinoflagellates were much more abundant than diatoms but the dominant group was coccolithophorids. In September both diatoms and dinoflagellates had the same abundance, coccoliths being again the dominant group.

Abundance and species diversity of phytoplankton had a remarkable decrease with increasing depth. Bayrakdar (1994), found that average phytoplankton abundance along the Turkish Black Sea Exclusive Economic Zone from 55μm sieved samples, was 7.9×10^4 and 5.4×10^4 cells l^{-1} in April 1993 and July

1992 in the whole water column respectively. In July 1992, the percentage of the phytoplankton abundance in the Cold Intermediate Layer (CIL) and in the halocline was 9% and 1% of the overall abundance in the water column respectively with the dominancy of dinoflagellates and diatoms in the respective layers. These percentages were lower in April 1993 than in June 1992, with the 6% for CIL and 0.2% for halocline. In April 1993, diatoms were the dominant groups in both layers.

Same as the phytoplankton distribution, chlorophyll in seawater showed a maximum in September and the chlorophyll extended to around 40m. In April, upper 50m was almost homogenous with a value of 0.4 $\mu g\ l^{-1}$. There was a subsurface peak in chlorophyll concentration in May and it was close to the detection limit at around 70m.

5.2.4.2. GUT PIGMENT CONTENT OF FEMALE *CALANUS*

The levels of GPC observed in female *Calanus* varied widely. In May, when chlorophyll concentration was low in the water column, high levels of GPC was not observed, the levels of GPC varied between 0.3 and 5.2 ng pigment/ind and the coefficient of variation was 74%. Although the chlorophyll concentration in April was similar as in May, the GPC in April in the first layer was as high as in September and the GPC in April ranged between 0.8 and 22 ng pigment/ind with the coefficient of variation of 95%. In September although the chlorophyll concentration in the water column was almost 3 times higher than in April, the highest GPC value was almost same as in April with the range of 0.3 to 20.5 ng pigment/ind. This indicates that the high chlorophyll concentration in the water column does not guarantee that grazers will have high GPC. Most of the published reports on the phytoplankton-zooplankton relationships do not show the expected direct relation between GPC and chlorophyll concentrations in seawater (Dagg and Wyman, 1983; Kleppel *et al.* 1985). Two hypotheses are proposed to explain daily variations in copepod gut fullness (Bautista *et al.* 1988): The first is continuous feeding with irregular and discrete food

concentrations, and the second one is, daily variations in feeding activity. Owens *et al.* (1980 c.f. Bautista *et al.* 1988), suggested a third hypotheses as the diurnal variation in gut fullness is the result of continuous feeding on phytoplankton which shows daily variations in the amount of pigments per cell or unit cell volume. This implies that it is possible to find daily variation in gut pigment fullness without a corresponding variation in the amount of food or in the feeding activity. The asynchronous or intermittent feeding by the individuals partly explains the recorded variability in gut pigment level (Kleppel *et al.* 1988; Turner *et al.* 1993; Wang and Conover, 1986; Boyd and Smith, 1980). Even Bamstedt *et al.* (1992, cf. Paffenhofer, 1994) stated that 'much of the variability (in copepod grazing rates) remains unexplained'.

If feeding activity of animals was only a function of food concentration and temperature, one would expect to see greater gut content near the surface than at depth when the water column is stratified because both food concentration and temperature are higher near the surface during the sampling periods. The results of this study support this expectation. The greater GPC was found in the upper layers during the nighttime. However, there were some exceptions; in May during downward migration (at 06:30), *Calanus* sampled from the third layer had high levels of GPC which must come from the second layer (61 to 18m), where chlorophyll concentrations showed maximum. Dagg *et al.* (1989) also observed small amount of pigment remained in the guts of migrating copepods after they had descended to their daytime depth in the early morning. As opposed to in May, in April and September, high GPC were not found in the individuals of female *Calanus* obtained from two lowest depths during descend. However, the respective high GPC may have been missed in these sampling periods because of the sampling intervals. Other exceptional case was in the beginning of the upward migration. As was seen better in April, they were in the lower boundary of the main pycnocline (163 to 136m) during the daytime, the GPC of the individuals increased towards evening. We know from the vertical distribution of POC (Fig. 5.4) that in this layer there was a small increase in POC. Fluorescence of organic compounds and pigments other than chlorophyll and phaeophytin could contribute GPC at this layer. Coble *et al.* (1991) noted two peaks of

chlorophyll throughout the water column in the Black Sea. The primary maximum was between the base of the thermocline and the top of the halocline, and the secondary one at a depth of around 120m in July 1988. The nature of the chlorophyll in the secondary chlorophyll maximum was indeed distinctly different from that found in the primary chlorophyll maximum. Chlorophyll-a was the major pigment present in the primary chlorophyll maximum but the major pigment present in the secondary chlorophyll maximum has spectral properties similar to those of bacteriochlorophyll-e (Bchl-e). The spectrum is typical for Chl-a with the major peaks at 431 and 664nm. The spectrum for Bchl-e is near 466nm, after acidification this peak shift to 441nm. That should be the reason for observing high amount of GPC during daytime depth. Repeta and Simpson (1991) found Bchl-e and the bacterial carotenoids at the deeper zone centered at the chemocline (80-100m) in the Black Sea. Bacteriochlorophyll-e in the H_2S chemocline is associated with anaerobic phototrophs, *Chlorobium phaeobacteroides* and *C. phaeovibroides*, brown sulfur bacteria which typically live as strict anaerobes at shallow oxic/anoxic interface. They suggested that anoxygenic photosynthesis by brown sulfur bacteria occurs when the H_2S chemocline is at depths ≤140m.

In May, there was no sampling during daytime. In September, the GPC from the OMZ did not show any increase during the daytime (at 07:30, 12:00 and 16:00). In May and in September, diapausing female individuals were also observed with the small amount of GPC in the lower boundary of main pycnocline during the nighttime and these values are almost same as the background fluorescence of female individual of *Calanus* (background fluorescence is 0.68±0.39). However, in September, this small amount of GPC in the diapausing stages is observed to increase with the joining of migrating individuals and these values were almost the same (4.0 ng pigment/ind.) during the daytime.

5.2.4.3. INGESTION RATES AND GRAZING PRESSURE OF FEMALE *CALANUS*

There may be several reasons for the higher grazing pressure value found in April (14.5%) compared to that in September (9.5%). First of all, the abundance of copepods is higher and the primary production is lower 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*. Coccoliths were rarely observed as a food item. Harris (1996) mentioned also, while several dinoflagellate species produce compounds that inhibit feeding and may even produce acute physiological responses and death, some other dinoflagellates are actively eaten and may be good diets in laboratory culture for *Calanus*. Although in both seasons coccoliths 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 and 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 and Sugisaki, 1994). In

contrast to many other regions, the contribution of picophytoplankton to the primary production and Chl-a concentration in the Black Sea is low (~20-40%) (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), the bulk of copepod abundance is made up of only five species in the southern Black Sea; *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 surprising. 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.

5.2.4.4. GUT PIGMENT CONTENT AND GRAZING PRESSURE OF COPEPOD ASSEMBLAGES

The highest amount of GPC among the size groups was detected in large size group at 03:30 h. During the daytime sufficient number of organism were not found for GPC analyses. Within the large size group *C. euxinus* female, copepodite V and IV were dominant. These are the strong vertical migrant organisms (see Fig. 3.8). In medium and small size groups, GPC were observed throughout the sampling periods and no apparent feeding cycle was detected in both fractions. The GPC varied widely within the each size fraction.

A clear result of this study is that the trend of increasing gut pigment content with individual length was significant, as was proposed by the literature data (Morales *et al.* 1990; Bautista and Harris, 1992; Morales *et al.* 1991). It is expected that larger animals would have larger digestive systems and therefore accumulation of food is much higher.

The present study has attempted to estimate community grazing rates and 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 GPC between the sampling time. 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. The average medium size fraction abundance was about 3 times higher than the overall average abundance of large size copepods. The estimated grazing rate of total copepod assemblages was 31.5% of the primary production in September 1995. It is possible that copepod grazing rates are underestimated in the present study. Several possible sources associated with the methods applied can be considered for this underestimation. Regarding the possible pigment destruction to the nonfluorescent pigment in copepod guts, the reported values are highly variable from 0 to >100% (Dagg and Walser, 1987; Kiorboe and Tiselius, 1987; Dam and Petersen, 1988; Head and Harris, 1996). An average value of 30% has been estimated (Dam and Peterson, 1988) due to the pigment destruction.

Regarding the estimation of copepod abundances, the small size fraction of copepods only included those larger than 300μm. Many copepodites and *Oithona similis* individuals might have passed through the 300μm mesh filter and thus have not been considered in calculating grazing rates. The estimated percentage abundance of loss from 300μm mesh filter was 15.0% of the total abundance of

small sized copepods. When considering this loss the grazing rate of small size fraction was still lower than those large size fraction. In contrast to Morales *et al.* (1991) whom discussed the relative importance of small size fraction grazing filterred from 200μm mesh on primary production in the northeast Atlantic, the medium sized copepods grazing was considerably most important among the three size classes at this study. Bautista and Harris (1992), found high phytoplankton consumption by medium sized copepods (ranged from 350 to 710μm) in the coastal waters off Plymouth.

One of the important results of this study indicates that the importance of female *C. euxinus* grazing in the large size fraction. Female *C. euxinus* sampled from the two uppermost layers was responsible for about 46% of large size fraction grazing. This emphasise the importance of *Calanus* transferring the organic matter through pelagic trophic levels in the Black Sea.

When considering the overall average grazing pressure of copepod assemblages (31.5% of primary production), it is close to the upper limits of the reported range of values by Conover and Mayzaud (1984, c.f. Sautour, *et al.* 1996) and Sautour, *et al.* 1996 for copepod species (Table 5.16).

The maximum grazing rate of zooplankton was taken as 0.8 day^{-1} by Oguz *et al.* (1998) for their model. The estimated average grazing rate was found as 0.76±0.26 day^{-1} (Table 5.15) in this study. Therefore Oguz *et al.* (1998)'s assumption is in agreement with the value estimated here for grazing rate.

Table 5.16: Summary of herbivoruos planktonic daily grazing rate on primary production

Reference	Species	Grazing Pressure Primary Production	Areas	Period
Nicolajsen *et al.* 1983.	Mesozooplankton (dominated by *Centropages hamatus* and *Pseudocalanus* sp.	6%	Oresund	from January through May
Baars and Fransz, 1984.	Copepods (copepodite and adult stages of *Temora longicornis, C. hamatus, A. clausi, Calanus finmarchicus*	14%	Central North Sea	from May to September
Conover and Mayzaud, 1984 (c.f. Sautour *et al.* 1996)	Zooplankton	10-30%	Nova Scotia Inlet	Spring bloom
Morales *et al.* 1991	mesozooplankton	2%	NE Atlantic	June-July
Dam and Peterson, 1993	*Temora longicornis* (female)	1-49%	Long Island Sounds	from March to July
Morales et.al. 1993	mesozooplankton	<10%	NE Atlantic	spring
Tsuda and Sugisaki, 1994	copepod population (dominated by *Neocalanus cristatus, N. flemingeri* and *Eucalanus bungii*)	1.4-2%	North Pacific	spring
Sauteur *et al.* 1996.	Zooplankton community (*C. helgolandicus, P. parvus, T.longicornis* and *Evadne* sp.)	17-21%	Gronde Estuary (France)	April
Present study	copepod population (*C.euxinus, P. elongatus, A. clausi, P. parvus* and *O. similis*)	31.5%	Southern Black Sea	September

CHAPTER VI

LIPIDS IN *CALANUS EUXINUS*

6.1. INTRODUCTION

The lipid components of planktonic organisms are the major metabolic fuels in the sea (Lee *et al.* 1971) and the lipid content of marine organism has been intensively studied for more than 150 years. A large body of data has been accumulated over the years on marine lipid (Corner and O'Hara, 1986).

Ontogenetic development is strongly interlinked with seasonal productivity in polar as well as in temperate regions (Kattner *et al.* 1994). As known from other calanoids, lipid storage is most pronounced in the older stages (copepodite V and adults). The lower lipid contents of the younger copepodite stages show that they do not conserve their dietary energy primarily in lipid deposits; instead they invest it in rapid development and growth (mainly as proteins) to reach a stage capable of overwintering. The younger copepodite stages utilise their dietary energy more for somatic growth than for lipid storage, and hence are more vulnerable to periods of low food supplies. In contrast, the older copepodite stages are well adapted to survive long starvation periods due to their extensive lipid reserves. (Kattner *et al.* 1994).

The calanoid copepods occupy a key position in the marine food chain because they feed directly on phytoplankton which are the primary producers in the oceans. The copepods constitute the largest single fraction of the biomass of the zooplankton in most waters and they are the principal food at some stage in the life of many fish species of nutritional and economic importance to man, such as the herring, sardine and anchovy (Benson and Lee, 1975).

Lipid content of organisms fluctuates according to; season, age, physiological conditions (including degree of maturity of the genital products) and food supply. The lipid content of *Calanus* is directly proportional to abundance of food. So it is expected to find the highest lipid content during the bloom time. Lipid content of *Calanus* also varies among sex and developmental stages. Lipid rich eggs of *Calanus* develop into nauplii that rapidly consume their remaining lipid reserves through the subsequent nauplii stages. The emerging early copepodite stages C-I and C-II have relatively low levels of lipid. Until stage IV and especially stage V, large amounts of lipids are deposited by the animal. Both male and female increases its total lipid content, presumably by depositing lipid in maturing eggs during the final stages of egg production. The seasonal variations of lipid components in *Calanus* are dependent on environmental conditions such as food supply, which is highly variable owing to for example, stratification of water column, nutrient supply and growth of phytoplankton blooms (Kattner and Krause, 1989; Sargent and Falk-Peterson, 1988).

It has been widely accepted that temperate and polar herbivorous copepods utilise their massive lipid reserves for basic metabolic needs to endure long periods of food scarcity, eg. during overwintering (Hagen and Schnack-Schiel, 1996). Tande and Hopkins (1981, c.f. Hagen and Schnack-Schiel, 1996) emphasised the importance of lipid reserves for fuelling reproductive processes before the spring phytoplankton bloom becomes available. Only a smaller portion of the accumulated energy stores appears to be utilised for metabolic maintenance during the food-limited winter period.

Kattner and Krause (1989) observed two population of *Calanus finmarchicus* in North Sea in summer; one is surface-living and the other is deep-living populations. The deep stock is build up throughout the summer and consists mainly of copepodite stage V and of some females. The overwintering stages with large oil sacs are very rich in lipids.

Hakanson (1984), measured the wax ester and triglyceride contents of *Calanus pacificus* as indices of feeding condition. He has suggested that quality of food is very important and that Chl-a or particulate carbon are poor indicators of food for late stage *C. pacificus*.

The triglycerides, are esters of the alcohol-glycerol and fatty acids , in natural waxes a long chain fatty acid is esterified to a long chain alcohol. They are extraordinarily efficient for energy storage because they contain carbon in fully reduced form and will therefore yield a maximum amount of energy on oxidation. Because they are uncharged, acylglycerols (glycerides), waxes, cholesterol and cholesteryl esters are termed neutral lipids. Phospholipids contain in addition to fatty acids and an alcohol, a phosphoric acid residue and they are polar lipids (Mathews and Holde, 1990; Murray *et al.* 1990).

In contrast to phospholipids, neutral storage lipids, namely wax esters and triacylglycerids are assumed to be a reflection of both anew synthesis and dietary fatty acids (Lee, 1974a).

Copepods especially from temperate and polar latitude store both fats and wax as metabolic fuel. This alternative food-storage system provides the copepod with a food reserve that can be controlled separately from its day-to-day metabolism. The control appears to rely on the relative activity of two enzymes: triglyceride lipase and wax lipase. The triglyceride lipase, which catalyses the metabolism of fat, is normally active in the animals at all times. In freshly caught copepods triglyceride-lipase activity can readily be detected, but wax-lipase activity is virtually zero. Wax-lipase is activated only under the stress of starvation. This provides the control that prevents the early depletion of the wax reserve (Benson and Lee, 1975). Phospholipid forming the cell membranes, constitute a fairly constant biochemical property, comprising a few percent of dry mass of copepods (Norrbin *et al.* 1990).

The energy-rich wax ester reserves are mobilised during unfavourable food conditions. This results in a mobilisation of lipids which starts with the

consumption of triacylglycerols, followed by the short-chain wax esters which were also used up and/or served as a reserve for the hibernating stages. Therefore the wax esters with the highest energy content are stored as long as possible (Kattner and Krause, 1987).

In addition, these wax esters may also play an important role in buoyancy regulation (Hirche, 1996).

6.2. RESULTS

The results have to be considered in view of some limitations during sampling and shipboard sorting of *Calanus*. Sometimes animals were not sufficient to obtain representative material for lipid analyses. On the other hand it was impossible to sort a large number of parallel samples on the board. Therefore at some stations results of one sample are given.

6.2.1. VARIATIONS IN TOTAL LIPID CONTENT WITH DEVELOPMENTAL STAGE AND SEASON

Total lipid content of *Calanus euxinus* was examined in two developmental stages; copepodite stage V and female, collected from different depths and time of day in May 1994, August 1993, September 1995 and in September 1996 in the Black Sea.

Tables 6.1-6.4 show the total lipid contents as mg mg^{-1} dry weight (DW) in copepodite stage V and female *C. euxinus* from different depth strata at different sampling periods.

Table 6.1: Total lipid content in copepodite stage V (CV) and female *Calanus euxinus* collected from different times and different depths at each station in May 1994. Values in parentheses are standard deviations.

Stations	Time	Coordinates		Sampling layers (m)	Sigma-theta values of sampling layers	Total lipid (mg mg^{-1} DW)	
		Lat.	Lon.			CV	Female
M50P15	09:10	42.50	32.15	113m-72m	16.2-15.4	0.61 (0.37)	0.16 (0.04)
M10P15	22:00	42.10	32.15	18m-0m	14.1-13.4	0.41 (0.14)	0.24 (0.02)
				61m-18m	14.6-14.1	0.41 (0.18)	0.24 (0.12)
				97m-61m	15.4-14.6	0.25 (0.17)	0.13 (0.03)
				147m-97m	16.2-15.4	0.5 (0.18)	0.19
M10P15	12:00	42.10	32.15	97m-61m	15.4-14.6	0.33	--
				147m-97m	16.2-15.4	0.41 (0.08)	0.16 (0.2)
M50S15	21:40	42.50	35.15	20m-0m	14.4-13.7	0.36	0.26 (0.08)
				52m-20m	14.6-14.4	0.38 (0.25)	0.23
				83m-52m	15.4-14.6	0.85	--
				130m-83m	16.2-15.4	0.49 (0.04)	--
M10L30	15:00	42.10	29.30	145m-100m	16.2-15.4	0.26 (0.06)	0.20 (0.02)
M10N15	03:00	42.10	31.15	15m-0m	14.2-13.3	0.10	0.33 (0.13)
				56m-15m	14.6-14.2	0.18	0.11 (0.06)
				141m-91m	16.2-15.4	0.49 (0.04)	--
M50R15	05:00	42.50	34.15	72m-21m	15.4-14.6	0.4 (0.14)	0.26 (0.01)
				116m-72m	16.2-15.4	0.44 (0.22)	0.24 (0.16)
M43N15	21:30	42.43	31.15	20m-0m	13.6-13.3	0.14	0.27 (0.02)
				60m-20m	14.6-13.6	0.44 (0.28)	0.26 (0.11)
				92m-60m	15.4-14.6	0.45	0.12
M05S15	12:30	42.05	35.15	173m-118m	16.2-15.4	0.35 (0.13)	0.18 (0.02)
M30Q04	24:10	42.30	33.04	30m-0m	14.4-13.5	0.14 (0.08)	0.20
				43m-30m	14.6-14.4	0.23	0.17 (0.06)
L30N15	09:30	41.30	31.15	113m-71m	15.4-14.6	0.46	--
				163m-113m	16.2-15.4	0.28 (0.05)	0.18 (0.02)
L30L30	20:55	41.30	29.30	25m-0m	14.1-13.03		0.14 (0.12)
				75m-25m	14.6-14.1	0.36 (0.25)	0.2 (0.05)
L19M55	16:00	41.19	30.55	152m-114m	16.2-15.4	0.78	--

DW= dry weight; -- = no data available

Table 6.2: Total lipid content in copepodite stage V (CV) and female *Calanus euxinus* collected from different times and different depths at each station in August 1993. Values in parentheses are standard deviations.

Station	Time	Coordinates		Sampling layers (m)	Sigma-theta values of sampling layers	Total lipid (mg mg^{-1} DW)	
		Lat.	Lon.			CV	Female
L20N15	7:00	41.20	31.15	161m-94m	16.2-15.4	0.24 (0.08)	0.33 (0.12)
L30N15	0:00	41.30	31.15	0m-10m	11.4-11.1	0.49	--
				25m-10m	14.2-11.4	0.42	0.19 (0.01)
				25m-100m	15.4-14.2	0.44	0.32
				145m-100m	16.2-15.4	0.46 (0.06)	0.4 (0.07)
L30N15	15:30	41.30	31.15	142m-95m	16.2-15.4	0.43	0.38
N10P15	6:30	43.10	32.15	0m-20m	11.3-10.8	0.53	0.42
				130m-80m	16.2-15.4	0.46	0.24 (0.11)
L50P15	19:30	41.50	32.15	95m-20m	15.4-14.3	0.45	0.22
				150m-95m	16.2-15.4	0.46 (0.04)	0.22 (0.01)
M15R15	13:00	42.15	34.15	145m-90m	16.2-15.4	0.44 (0.05)	0.22 (0.06)
M50S15	7:15	42.50	35.15	90m-65m	15.9-15.3	0.58 (0.13)	0.36 (0.06)
M10T45	4:50	42.10	36.45	10m-30m	14.5-10.5	--	0.28
				70m-30m	15.4-1456	0.35	0.32
				120m-70m	16.2-15.4	0.45 (0.04)	0.26
L50Y15	5:30	41.50	40.15	100m-20m	14.6-14.2	0.30	0.09
				220m-110m	16.2-15.4	0.43 (0.11)	0.13 (0.05)
L05Y15	21:30	41.05	40.15	50m-25m	14.3-10.6	0.37	0.18
L15W45	23:00	41.15	38.45	10m-0m	10.6-10.5	--	0.13
				30m-10m	14.3-10.6	--	0.26
				110m-30m	15.4-14.3	0.37	0.18
L35T45	0:00	41.35	36.45	15m-0m	13.3-10.6	--	0.23
				30m-15m	14.4-13.3	--	0.19
				100m-30m	15.4-14.4	0.30	0.31 (0.18)
				150m-100m	16.2-15.4	0.42 (0.03)	--

DW= dry weight; -- =no data available

Table 6.3: Total lipid content in copepodite stage V (CV) and female *Calanus euxinus* collected from different timess and different depths at each station in September 1995. Values in parentheses are standard deviations.

Station	Time	Coordinates		Sampling layers (m)	Sigma-theta values of sampling layers	Total lipid (mg mg^{-1} DW)	
		Lat.	Lon.			CV	Female
L50V15	20:00	41.50	37.15	50m-25m	14.6-14.0	--	0.63
				73m-50m	14.6-15.4	0.49	--
				123m-91m	16.2-15.8	0.55 (0.01)	--
L30V45	2:00	41.30	37.45	63m-25m	14.6-12.7	0.53 (0.03)	0.35 (0.1)
M10W15	11:00	42.10	38.15	88m-68m	15.8-15.4	0.52 (0.06)	0.44 (0.11)
				120m-88m	16.2-15.8	0.55 (0.08)	0.39 (0.01)
L50Y15	5:00	41.50	40.15	113m-78m	15.4-14.6	0.43	0.25
				134m-113m	15.8-15.4	0.51	0.24
				170m-134m	16.2-15.8	0.29 (0.28)	0.33
L30X45	0:10	41.30	39.45	40m-0m	13.2-11.7	0.74	0.26
				82m-40m	14.6-13.2	0.49 (0.15)	0.32 (0.01)
L15W15	16:00	41.15	38.15	113m-74m	15.4-14.6	0.40	0.30
				147m-113m	15.8-15.4	0.51	0.35
				173m-147m	16.2-15.8	0.55	0.24
L50X15	23:00	41.50	39.15	45m-20m	14.6-14.1	0.46 (0.13)	0.35 (0.06)
				125m-92m	16.2-15.8	0.47 (0.04)	--

DW= dry weight; --=no data available

Table 6.4: Total lipid content in copepodite stage V (CV) and female *Calanus euxinus* collected from different times and different depths at each station in September 1996. Values in parentheses are standard deviations.

Stations	Time	Coordinates		Sampling layers (m)	Sigma-theta values of sampling layers	Total lipid (mg mg^{-1} DW)	
		Lat.	Lon.			CV	Female
M50N15	22:00	42.50	31.15	80m-30m	15.7-14.2	0.58	0.42
				130m-80m	16.4-15.7	0.75	--
M50Q30	20:00	42.50	33.30	80m-30m	15.8-14.2	0.72	0.37
				130m-80m	16.3-15.8	0.78	0.55
M10T15	1:30	42.10	36.15	35m-0m	14.2-12.1	0.66	0.21
				120m-40m	15.9-14.3	0.54	0.29
				170m-130m	16.3-16.0	0.64	0.50
M50V15	21:00	42.50	37.15	40m-0m	14.5-12.4	0.53	0.28
				90m-40m	15.8-14.5	0.73	0.30
				140m-90m	16.3-15.8	0.61	0.38
L50X45	22:00	41.50	35.45	30m-0m	13.6-11.4	0.63	0.13
				160m-30m	15.7-13.6	0.54	0.21
				210m-160m	16.3-15.7	0.70	--
L30X45	22:00	41.30	39.45	30m-0m	13.6-11.4	0.57	0.19
				150m-30m	15.8-13.6	0.55	0.20
				200m-150m	16.4-15.8	0.64	--

DW= dry weight; -- =no data available

Because of the pronounced diel vertical migration of CV and female *Calanus*, during the daytime, individuals were sampled from the main pycnocline layer (between the depth of σ_θ=16.2 and the depth of σ_θ=15.4), they distributed throughout the water column at dawn and dusk.

The spatial distribution of the average lipid content (% DW) of copepodite stage V and female *Calanus euxinus* in each sampling periods were exhibited in Figures 6.1-6.4.

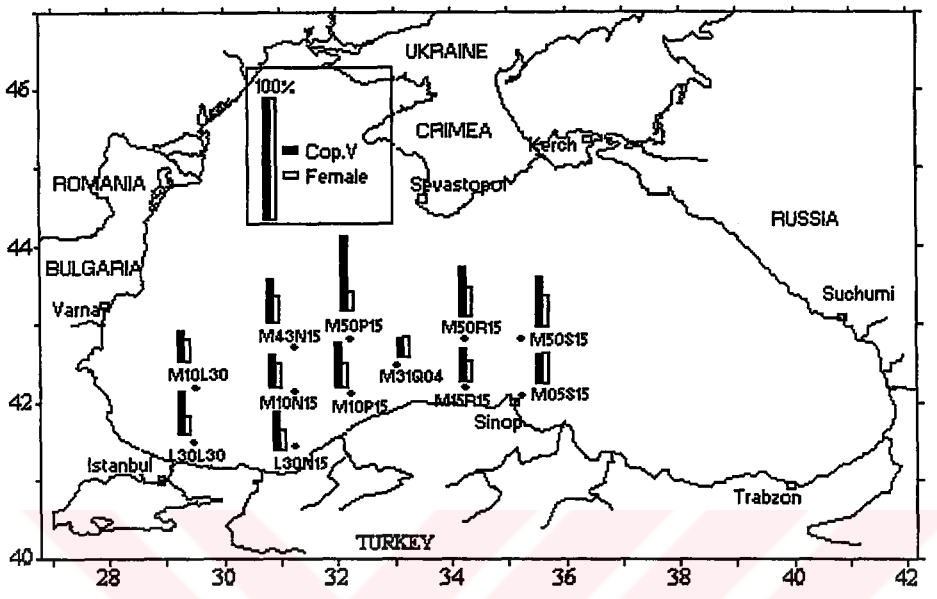

Figure 6.1: Total lipid content as percentage of dry weight of copepodite stage V and female *Calanus euxinus* in May 1994 in the southwestern Black Sea.

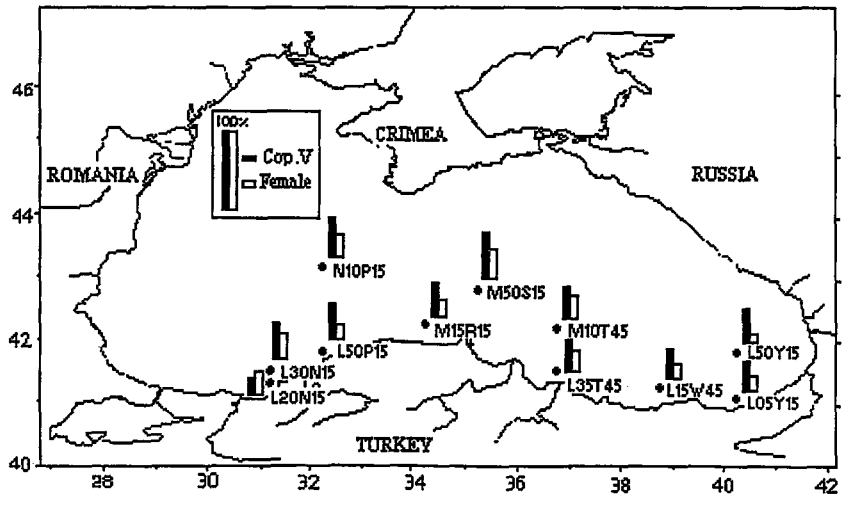

Figure 6.2: Total lipid content as percentage of dry weight of copepodite stage V and female *Calanus euxinus* in August 1993 in the southern Black Sea.

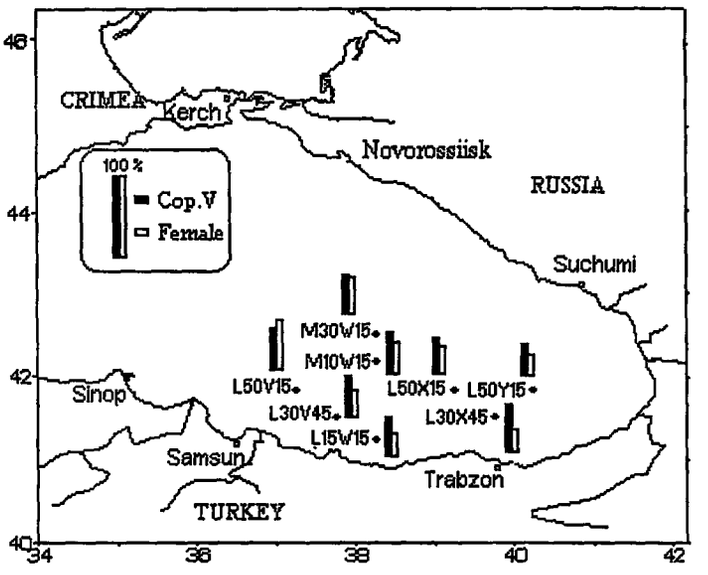

Figure 6.3: Total lipid content as percentages of dry weight of copepodite stage V and female *Calanus euxinus* in September 1995 in the southeastern Black Sea.

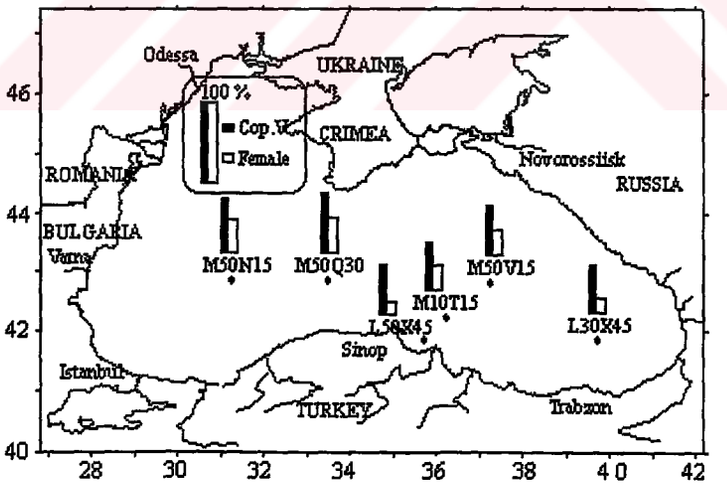

Figure 6.4: Total lipid content as percentage of dry weight of copepodite stage V and female *Calanus euxinus* in September 1996 in the Black Sea.

As seen in the spatial distribution of total lipid content figures, the copepodite stage V have higher total lipids content than that of females almost at all stations in each sampling periods.

Total lipid levels in females and in CV showed more or less seasonal variation. Lipid levels of females constituted a smaller percentage of dry weight. When all lipid data collected from each stations were pooled, the minimum total lipid content was detected in May as 0.2 mg mg^{-1} DW and there was a gradual increase in lipid content from May through September (Figure 6.5). The lipid content of females was intermediate in August (0.26 mg mg^{-1} DW) and maximum average value was observed in September 1995 with the averaged value of 0.37 mg mg^{-1} DW (Figure 6.5).

Total lipid content in CV was significantly higher compared to female. In May and August, the coefficient of variations in the total lipid content in CV among stations were 41% and 20% respectively and the average data was around 0.4 mg mg^{-1} DW in both seasons. In September 1995 and 1996 the lipid contents of CV almost 1.5 times higher (0.5-0.6 mg mg^{-1} DW) than in May and August (Figure 6.5).

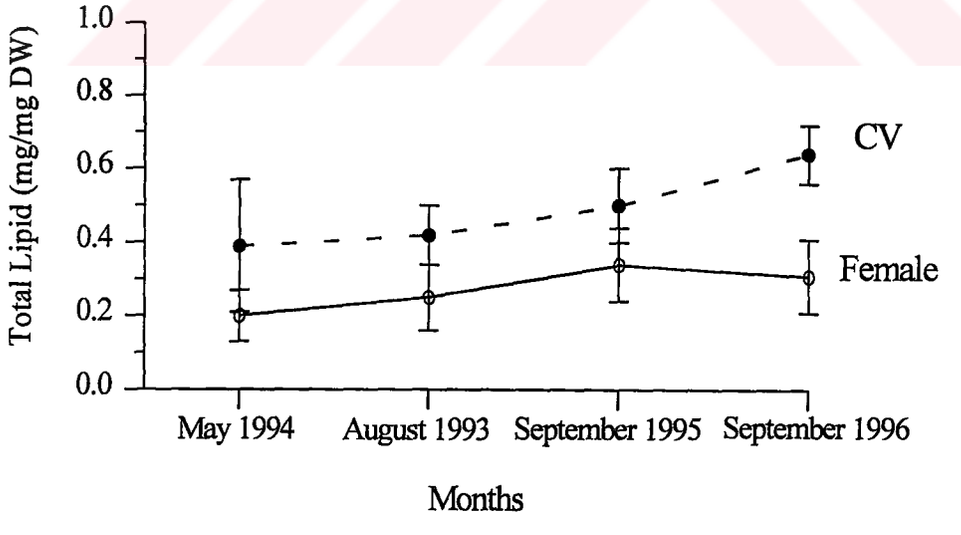

Figure 6.5: The overall average of total lipid contents (mg mg^{-1} DW) in CV (dashed line) and female (solid line) *Calanus euxinus* in each sampling period. Vertical lines illustrate error bars of measurements.

6.2.2. TOTAL LIPID CONTENT IN MIGRATING AND NON-MIGRATING INDIVIDUALS OF *CALANUS*

In terms of vertical migration of CV and female *Calanus euxinus* showed that, they apparently migrate and live in the lower layer of main pycnocline at daytime (see section 3.2.1.3). During the sampling periods two groups of CV and females were recognised; the first group shows migration to upward at nighttime and the second one which is called in the overwintering period, inhabited in the lower layer of OMZ during nighttime.

To differentiate migrating group from that of diapausing (overwintering) individuals, the nighttime samples were taken into account. Individuals distributed in the water column above the OMZ during the nighttime were considered as migrating and those stayed in the OMZ as overwintering individuals. While plenty number of CV were found in the main pycnocline during the all sampling periods, females were found only in August and September 1996 in that layer. Females generally do not enter overwintering periods (E. Arachkevich, pers. comm.). So it is decided to call the females collected from lower layer of the OMZ during nighttime as 'non-migrating' females.

As it is seen from the Figure 6.6, the overwintering CV contained higher total lipid than the migrating individuals during the sampling periods but this difference was not high as to be expected. The variation in the total lipid contents of the diapausing stage CV among the sampling periods was smaller than the migrating individuals. For the former group the coefficient of variation ranged between 5% (in August 1993) and 23% (in May 1994). For migrating individuals the coefficient of variation changed from 12 (in September 1996) to 56% (in May). The lipid contents of CV in both overwintering and migrating groups were higher in September samples.

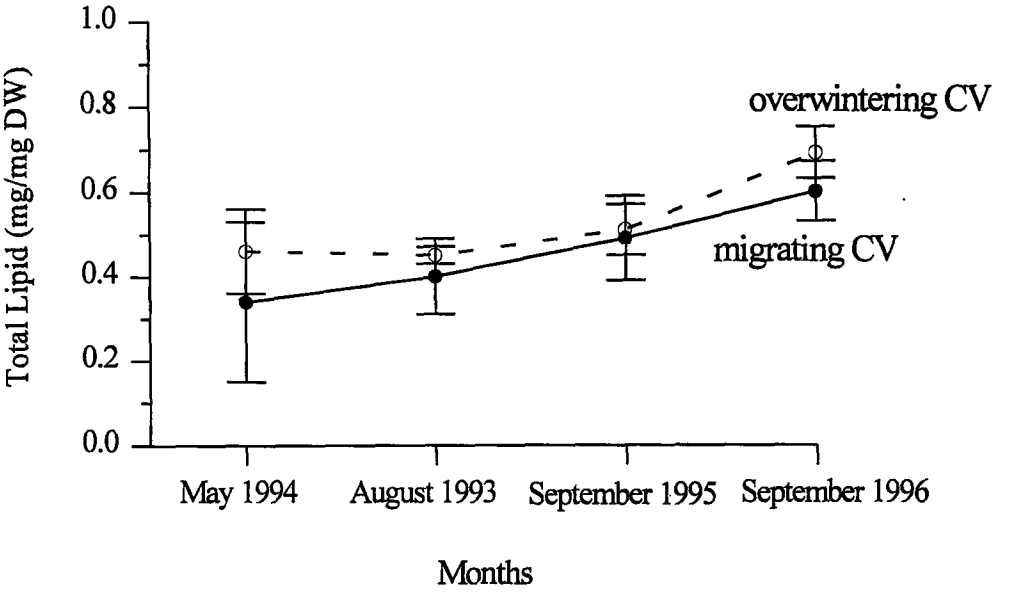

Figure 6.6: Total lipid contents in migrating (solid line) and diapausing (overwintering) copepodite stage V (dashed line) of *Calanus euxinus* at different sampling periods. Vertical lines illustrate the error bars.

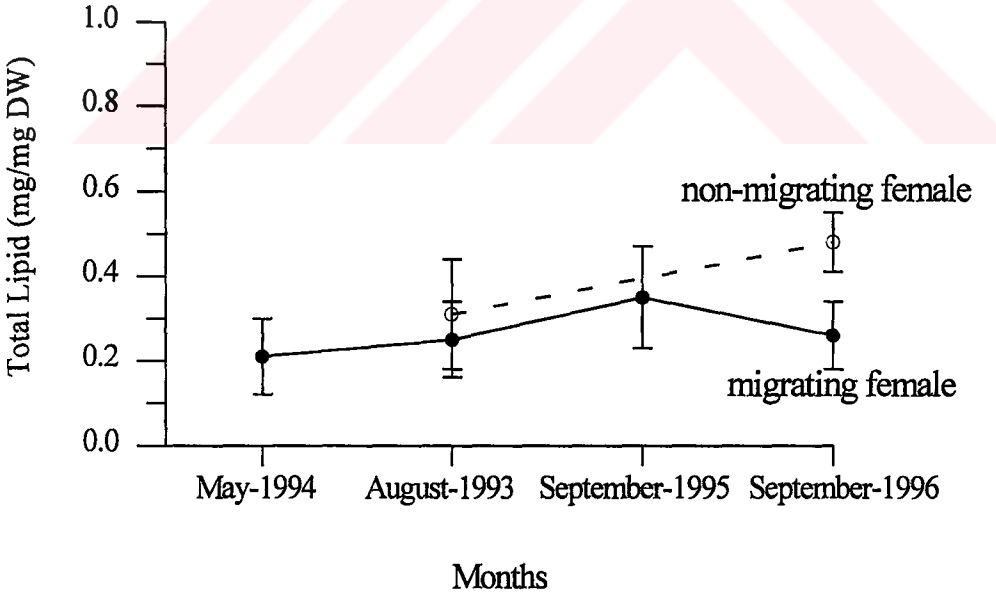

Figure 6.7: Total lipid contents in migrating (solid line) and non-migrating females (dashed line) *Calanus euxinus* at different sampling periods. Vertical lines illustrate the error bars.

Figure 6.7 shows the total lipid contents of migrating and non-migrating females. While sufficient number of non-migrating females was found in August 1993 and September 1996 in the lower layer of OMZ, the number of individuals was not enough for lipid analyses in the other sampling periods. The non-migrating females had the higher amount of lipid content than the migrating ones as was observed for CV stage. All female samples collected in September have higher total lipid content.

6.2.3. LIPID CLASS COMPOSITION

The lipid compositions of CV and female *Calanus euxinus* were performed only in the samples collected in September 1996. Three main groups of lipids were investigated; triacylglycerids (TAG), wax esters (WE) and phospholipids (PL). Tables 6.5 and 6.6 present the lipid composition of CV and female *Calanus* respectively.

Table 6.5: Total lipid content (µg ind.$^{-1}$) and lipid compositions in copepodite stage V *Calanus euxinus* in September 1996 (TL= Total lipid, TAG= Triacylglycerids, WE= Wax esters, PL= Phospholipids).

Station	Time	Depth	TL	TAG		WE		PL	
			µg ind.$^{-1}$	µg ind.$^{-1}$	% TL	µg ind.$^{-1}$	% TL	µg ind.$^{-1}$	% TL
M50N15	22:00	80-30	93.24	11.14	11.95	71.33	76.50	6.36	6.82
		130-80	120.45	7.85	6.52	97.05	80.57	9.35	7.76
M50Q30	20:00	80-30	114.71	8.39	7.31	91.34	79.63	8.70	7.58
		130-80	124.32	9.90	7.96	101.05	81.28	7.96	6.40
M10T15	1:30	35-0	105.75	6.93	6.55	84.08	79.51	10.30	9.74
		120-40	85.87	4.58	5.33	69.18	80.56	7.02	8.18
		170-130	103.07	6.76	6.56	83.92	81.42	6.86	6.66
M50V15	21:00	40-0	84.57	7.96	9.41	63.77	75.40	8.30	9.81
		90-40	116.79	11.64	9.97	85.92	73.57	8.86	7.59
		140-90	97.38	7.70	7.91	78.90	81.02	6.60	6.78
L50X45	22:00	30-0	100.14	10.14	10.13	70.28	70.18	13.02	13.00
		160-30	85.90	3.75	4.37	71.65	83.41	6.74	7.85
		210-160	112.65	4.56	4.05	97.90	86.91	6.52	5.79
L30X45	22:00	30-0	91.53	5.96	6.51	69.12	75.52	10.12	11.06
		150-30	88.35	6.24	7.06	68.65	77.70	9.36	10.59
		200-150	102.98	5.58	5.42	84.58	82.13	8.77	8.52

Table 6.6: Total lipid content (µg ind.$^{-1}$) and lipid compositions in female *Calanus euxinus* in September 1996 (TL= Total lipid, TAG: Triacylglycerids, WE= Wax esters, PL= Phospholipids).

Station	Time	Depth	TL	TAG		WE		PL	
			µg ind.$^{-1}$	µg ind.$^{-1}$	% TL	µg ind.$^{-1}$	% TL	µg ind.$^{-1}$	% TL
M50N15	22:00	80-30	118.14	16.53	13.99	84.75	71.74	12.35	10.45
		130-80	--	--	--	--	--	--	--
M50Q30	20:00	80-30	103.21	11.50	11.14	76.14	73.77	10.31	9.99
		130-80	154.36	13.68	8.86	116.74	75.63	18.25	11.82
M10T15	1:30	35-0	57.49	7.63	13.27	36.85	64.10	7.46	12.98
		120-40	80.76	6.89	8.53	56.09	69.45	10.60	13.13
		170-130	139.33	14.17	10.17	106.52	76.45	9.85	7.07
M50V15	21:00	40-0	78.11	13.34	17.08	52.26	66.91	7.24	9.27
		90-40	84.92	16.85	19.84	55.57	65.44	7.74	9.11
		140-90	107.08	14.66	13.69	74.67	69.73	10.12	9.45
L50X45	22:00	30-0	36.17	14.77	40.83	21.18	58.56	6.14	16.98
		160-30	59.50	7.51	12.62	39.38	66.18	7.76	13.04
		210-160	--	--	--	--	--	--	--
L30X45	22:00	30-0	52.74	4.30	8.15	38.42	72.85	6.13	11.62
		150-30	57.23	5.61	9.80	42.56	74.37	5.92	10.34
		200-150	--	--	--	--	--	--	--

-- = no available data

Lipid analyses showed that the female and CV *Calanus euxinus* had a large amount of wax esters constituting about >70% of total lipid (TL) and a low percentage of phospholipids (Figure 6.8).

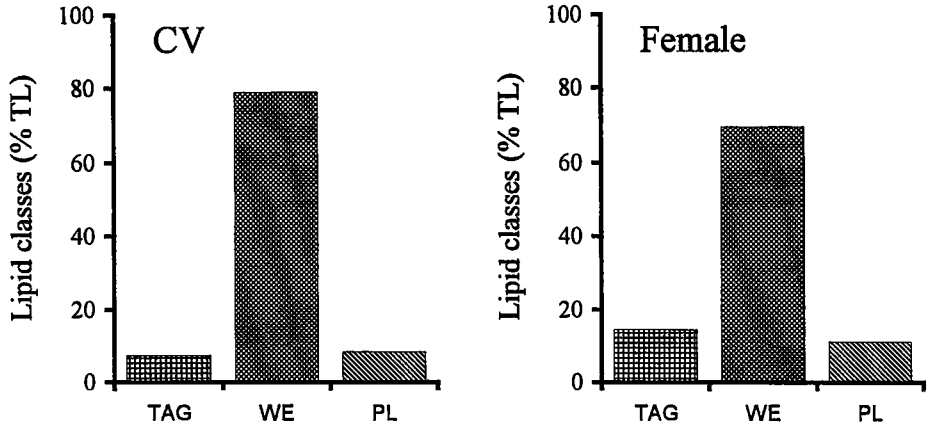

Figure 6.8: The averaged lipid class composition (as % TL) of copepodite stage V and female *Calanus euxinus* in September 1996 (TAG= Triacylglycerids, WE= Wax esters, PL= Phospholipids).

In September 1996, the diapausing and migrating groups were easily separated by collecting the samples from the OMZ and the above water column respectively during nighttime. In both CV and female, the percentage of TAG and PL were lower in overwintering stages than in migrating groups. In contrast to TAG and PL, the percentage of WE in overwintering stages of CV and females were higher than that in migrating individuals (Figure 6.9 and 6.10).

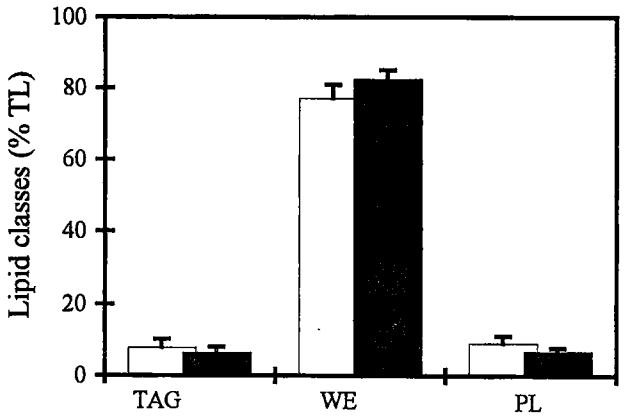

Figure 6.9: Lipid class compositions in copepodite stage V *Calanus euxinus*. Black bars shows individuals in diapausing periods, white bars shows migrating individuals. Vertical lines illustrates positive error bars.

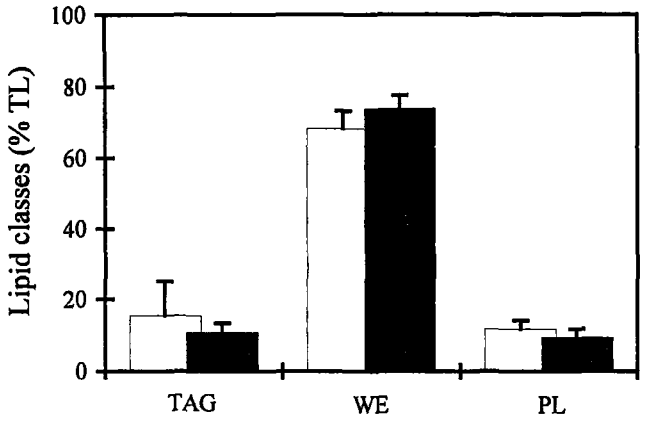

Figure 6.10: Lipid class compositions in female *Calanus euxinus*. Black bars shows lipids in non-migrating individuals, white bars shows lipids in migrating individuals. Vertical lines illustrates positive error bars.

6.3. DISCUSSION

The calanoid copepod *Calanus euxinus* which is a dominant species in terms of biomass in the Black Sea, is known for its extensive capability to accumulate lipids, which is also reflected by their large oil sacs (Vinogradov *et al.* 1992b; Shulman *et al.* 1997; Arachkevich *et al.* 1997). It is clear that the percentage lipid in a sample of calanoid zooplankton depends both on the developmental stage and on the season (Lee *et al.* 1972; Lee, 1974a; Kattner and Krause 1989). Stage IV and V animals will invariably have lipid levels higher than those of earlier stages (Corner and O'Hara, 1986). The younger copepodite stages of calanoids utilise their dietary energy for somatic growth rather than for lipid storage (Kattner *et al.* 1994). Kattner and Krause (1987) studied the changes in lipids during the development of *Calanus finmarchicus* from copepodite I to adult. They found that the total lipid increased exponentially until copepodite V, and the females have sometimes lower lipids than the stage V. Gatten *et al.* (1980) also showed that the total lipid levels were higher in stage V copepodites than in females of *Calanus helgolandicus*. The total lipid content in CV is being higher than that in females in all sampling periods, the results of the present study are in agreement with those mentioned above.

Lee (1974b) and Kattner and Krause (1989) found a correlation between the lipid storage in copepods and phytoplankton bloom. Shul'man et al. (1997) found significant correlation between lipid contents in *Calanus euxinus* and chlorophyll-a concentration in the Black Sea. Sampling periods in this study comprise three seasons; May as late spring, August as summer and September as early autumn. The primary productivity in the Black Sea was known to occur twice a year, with a major bloom principally composed of diatoms in early spring, followed by a secondary bloom mainly comprising coccolithophorids in autumn. Additional summer blooms with a predominance of dinoflagellates and coccolithophorids (*Emiliana huxleyi*) have been increasingly observed in the region in recent years (Uysal and Sur, 1995; Sur *et al.* 1994). The overall averages of the chlorophyll-a concentrations in the first 50m during the sampling periods are shown in Figure 6.11. The chlorophyll-a concentrations was higher in August 1993 and September 1996. The lowest value was found in September 1995. Whereas the lipid content of both CV and female individuals were higher in September 1995 than that in August.

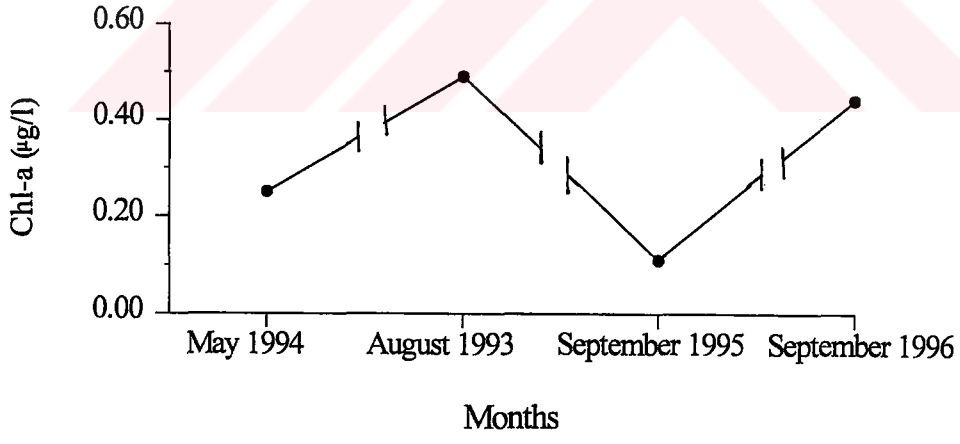

Figure 6.11: The overall average of chlorophyll-a concentration in the first 50m at lipid stations during the sampling periods.

So no significant correlation was found between the chlorophyll-a concentration in particulate materials and total lipid content in both stages of *Calanus euxinus* in the Black Sea during the sampling periods in contrast to Shul'man et al.'s (1997) results. Hakanson (1984), suggested that quality of food is very important and that chlorophyll-a or particulate carbon are poor indicators of food for late stage *Calanus pacificus*. Wainmann *et al.* (1993) also did not found any correlation between food availability, edible phytoplankton biomass and zooplankton lipid concentrations in freshwater lakes. Gatten *et al.* (1980) compared the lipid content in stage V, female and male *Calanus helgolandicus* during spring periods in 1977 and in 1978 from coastal area near the entrance to Plymouth Sound. They found higher amount of total lipid in 1978 than that in 1977, although the chlorophyll-a levels in the particulate material were similar. However, they showed a good correlation between the total lipid in particulate material and the total lipid in *C. helgolandicus*. They concluded that the lipid levels in the organism were dependent on the amount of total lipid present in the microparticulate materials, mainly phytoplankton in the water.

During the sampling periods, the stage V and female *Calanus euxinus* were separated into non-migrating (in the overwintering period) consisting mainly stage V and migrating populations. Hirche (1983, 1996) stated that whole population does not always enter diapause together at the same time. Thus often during summer diapausing stages accumulate in deep waters, while new generations are still growing in the surface waters. In this study, the overwintering individuals of CV and non-migrating females have higher total lipid content than the migrating ones but these differences were not high as was expected. However, Vinogradov *et al.* (1992b) measured total lipid in both migrating and overwintering copepodite stage V of *Calanus euxinus* in the Black Sea in August and in September 1989 and they observed considerably higher amount of lipid content in the overwintering (114.6 µg/ind.) individuals than the

migrating ones (50.9µg/ind.) in September. Gatten *et al.* (1979, c.f. Kattner and Krause, 1989) studied total lipid and lipid classes of males, females and copepodite stage V of *C. helgolandicus* and described the high variability of all components in the annual cycles which were not the same from year to year. Arashkevich *et al.* (1997) considered two groups of migrating *Calanus euxinus* copepodite stage V in September 1996 in the Black Sea. One has accumulated lipids with no gonad development, second one with small oil sac but with gonad development. They suggested that the first group is likely to enter diapause. The overwintering individuals are not feeding and have to rely on stored energy. Lipids, mostly deposited as wax esters in a conspicuous oil sac prior to descending to overwintering depth, are the main energy source for the overwintering period (Hirche, 1996). Marshall and Orr (1955, cf. Kattner and Krause,1987) showed that females contained fewer wax esters than CV, especially that of older populations, because the lipid reserves were used up during the moulting process, growth of ovaries, egg production and spawning. Arashkvich *et al.* (1997) showed a strong negative correlation between gonad size and the oil sac volume of overwintering CV of *Calanus euxinus* in the Black Sea. During egg production wax esters had to be converted into triacylglycerids, since wax esters were not detected in the eggs (Lee *et al.* 1972 c.f. Kattner and Krause, 1987). Our study comes to an agreement with this, the wax ester levels in CV was considerably higher than females . Tande and Hopkins (1981, c.f. Hagen and Schnack-schiel, 1996) suggested that prior to spring bloom gonad build-up must depend largely on internal energy reserves, mainly wax esters. However, they hypothesised for *C. finmarchicus* that in contrast to the initial processes the completion of gonad development and spawning is supported externally by sufficient phytoplankton input.

Table 6.7 illustrates the results of this study and some of the published values for the percentages and class compositions of total lipid in *Calanus* together with the developmental stages of animals analysed at different sampling seasons.

Table 6.7: Content and composition of lipid in *Calanus* from the various periods and regions of the world. F= female, M= male, -= No data (retabulated from Corner and O'Hara, 1986).

Species	Stage	Region	Month	Lipid (%DW)	WE (%TL)	TAG (%TL)
C. hyperboreus	F	Arctic	Nov.	73	92	2
C. plumchrus	F	Temper.	-	59	86	7
C. helgolandicus	F	Subtrop.	-	14	33	4
C. helgolandicus	CV	Subtrop.	-	37	50	3
C. helgolandicus	Adult	Subtrop.	-	28	41	12
C. helgolandicus	CV	Temper.	June	34	85	0
C. helgolandicus	M	Temper.	June	34	90	0
C. helgolandicus	CV	Temper.	Jan.	16	70	4
C. helgolandicus	F	Temper.	Jan.	3	9	8
C. finmarchicus	F	Arctic	-	50	63	11
C. pacificus	CV	Temper	-	45	41	5
C. pacificus	CV	Temper	-	27	20	2
C. gracilis	F	Subtrop.	-	26	21	17
C. gracilis	F	Tropic.	-	11	31	8
C. cristatus	CIV	Temper.	-	51	80	5
C. robustior	F	Subtrop.	-	8	21	3
C. euxinus	CV	this study	May-94	40	-	-
C. euxinus	CV	this study	Aug-93	43	-	-
C. euxinus	CV	this study	Sept-95	51	-	-
C. euxinus	CV	this study	Sept-96	44	77	8
C. euxinus	F	this study	May-94	20	-	-
C. euxinus	F	this study	Aug-93	26	-	-
C. euxinus	F	this study	Sept-95	37	-	-
C. euxinus	F	this study	Sept-96	32	68	16

As it is seen from Table 6.7, *Calanus* can accumulate remarkably high levels of total lipid and that this lipid is largely wax esters, although substantial amounts of triacylglycerids do also occur. Total lipid contents in *Calanus euxinus* measured in this study are in the reported range of values for *Calanus* measured at the other regions in the world (Table 6.7). Lipid class analyses demonstrate that wax esters were the major neutral lipids in *Calanus euxinus*. The triacylglycerids and phospholipids were found in small amounts. Wax esters are accumulated in large amounts by those marine animals that experience short

periods of food abundance followed by prolonged periods of food shortage (Corner and O'Hara, 1986). Hakanson (1984), showed that the triglyceride content in *Calanus pacificus* seemed a good indicator of recent feeding, being completely lost after 3 days of starvation. The wax ester content was a good indicator of feeding over a period of a week.

The phospholipids are viewed having a structural role that components of membranes. Phospholipid composition shows little variation within the zooplankton species regardless of changes in the quantity or type of food and revealed that the phospholipid data for the same species obtained by different investigators should be comparable even though the area of collection and the time of the year may be different (Lee, 1974b). Hakanson (1984), found that the polar lipid content of *Calanus pacificus* copepodite stage IV was not significantly different at the three food concentrations. Lee (1974b) measured the phospholipid content of *Calanus plumchrus* from Bute Inlet in British Columbia as 4 % of total lipid.

CHAPTER VII

DIAPAUSE IN *CALANUS EUXINUS*

7.1. INTRODUCTION

The terms such as resting phase or stage, dormancy, quiescence, hibernation and overwintering are frequently encountered in descriptions of the diapausing of calanoid copepods. Diapause is characterised by a suspension of growth and development. It may be observed in different developmental stages ranging from eggs to adults (Ohman, 1988). In general, resting phases in development caused by internal and external factors, are grouped together under the concept of dormancy (Hirche, 1996). The majority of published data provide evidence that diapause is an adaptation to avoid physically harsh environments in which deviation of environmental factor(s) from the optimum such as cold, heat, light intensity or drought (Mansingh, 1971; Art, 1993; Marcus, 1982; Pijanowska and Stolpe, 1996). Diapause stage is a critical phase in the life cycle of species because they make possible long-term survival during periods unfavourable for continuous development. The diapausing phase is commonly observed in as seasonal or ontogenetic vertical migration of copepods. Ontogenetic vertical migration occur in some harpacticoids, cyclopoids and calanoid copepods. Among the calanoid copepods a number of species, for example the genera *Calanus, Eucalanus, Calanoides* and *Rhincalanus* enter diapause. Ontogenetic vertical migration is characteristic of cold-water species that are primarily herbivorous (Steidinger and Walker, 1984).

Hirche (1996) observed that the diapause stages of *Calanus finmarchicus* begin to accumulate in early summer in Gullmarfjord in Sweden. Grigg and Bardwell (1982) concluded from observations of time from capture of CV to ecdysis

(moulting), that seasonal changes in photoperiod were implicated in the initiation of diapause. The diapause individuals undergo dramatic physiological and behavioural changes. They are torpid and utilise little oxygen. Their digestive enzymes activities are reduced (Hallberg and Hirche, 1980). While they are not feeding during the diapause phase, they have to rely on stored energy. The main source of energy for overwintering period is lipids. Lipids mostly deposited as wax esters and wax esters may also play an important role in buoyancy regulation (Butler *et al.* 1970; Grigg and Bardwell, 1982; Hirche 1983, 1996).

Calanus populations inhabiting the open ocean overwinter at greater depths, which vary with geographic location. The greatest depth was recorded in Westspitsbergen Current (Greenland Sea, 75°N) at 1500 to 1000m for *Calanus finmarchicus*. The temperature of overwintering habitat of *C. finmarchicus* ranged from -1 to 11 °C (Hirche, 1996; Kaartvedt, 1996). The temperature of the overwintering habitat is important because respiration is temperature dependent. Internal energy resources essential for development and maturation of gonads should last longer in cold water (Kaartvedt, 1996). In shallow seas, the accumulation of overwintering *C. finmarchicus* is close to the bottom (Williams, 1985).

The beginning of favourable conditions does not bring an immediate end to diapause. Termination of diapause is associated with the significant changes in biochemical reactions. There is a brief period when endocrinological and biochemical preparations occur (Mansingh, 1971 ;Hirche, 1996). For example, Hirche (1979, cf. Hallberg and Hirche, 1980) found that towards the end of diapausing period, the digestive enzyme activity of CV slightly increased.

7.2. RESULTS

Evaluations of overwintering habitats and strategies of *Calanus* have mainly focused on physical factors and food availability (bottom-up factors) (Kaartvedt, 1996). The results of the present study and some more results from literature about *Calanus euxinus* in the Black Sea will be presented here. The possible

reason(s) initiating the diapausing period of *Calanus euxinus* in the Black Sea will also be discussed.

7.2.1. TEMPORAL AND VERTICAL DISTRIBUTION OF COPEPODITE V

It was deduced from the results of vertical migration of *Calanus euxinus* (see section 3.2.1.3) in the Black Sea that copepodite stage V is the main group entering diapause phase. Figure 7.1 shows the appearance of the CV in the water column during night-time in five different sampling periods. In this figure only data from the cruises in which samples were collected vertically from five different depth strata were presented. Considerable amount of overwintering population was observed only in June 1996 and September 1995.

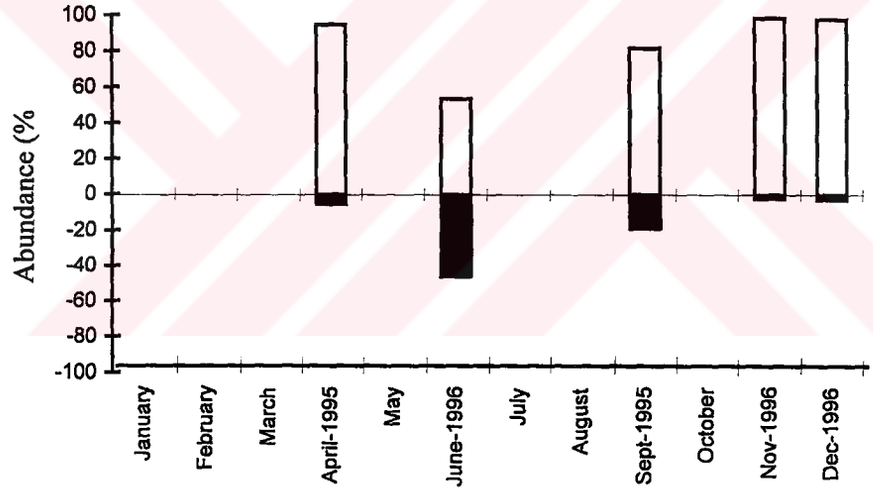

Figure 7.1: Nighttime distribution of CV (% abundance) in different sampling periods. 0 line indicates boundary between upper and lower layers which is defined by sigma-theta 15.8. Positive and negative scales represent occurrence of CV in the upper and lower layers respectively. Black bars illustrate the percentage of overwintering CV in the lower layer of the OMZ. White bars show the percentage of migrating CV distributed over the OMZ.

Vertical distribution of CV through 5 depth strata at night and daytime in June 1996 and September 1995 is shown in Figure 7.2. In June during the daytime, the CV population is concentrated in the OMZ, while at night-time around the half of the population still stay in the lower layer of OMZ. Almost the same figure was observed for September with about 13% of population overwinter in the lower layer of OMZ.

7.2.2. GUT PIGMENT CONTENT IN COPEPODITE V

Gut pigment contents (as ng Chl-a/individual) in CV are shown in Figure 7.3. The migrating CV has considerably higher gut pigment content (GPC) with 1.1±0.78 ng pigment/ind., while the overwintering individuals has very low GPC as 0.3±0.26 ng pigment/ind. The background pigment value of CV was 0.21±0.06 ng pigment/ind., which is almost same as GPC in overwintering CV.

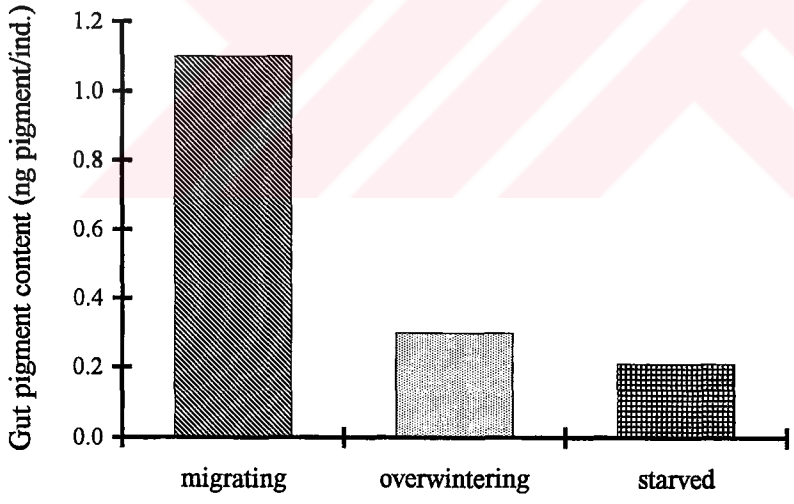

Figure 7.3: Gut pigment content (ng pigment/ind.) in migrating, overwintering and starved (background pigment content) CV collected from the Black Sea in September 1996.

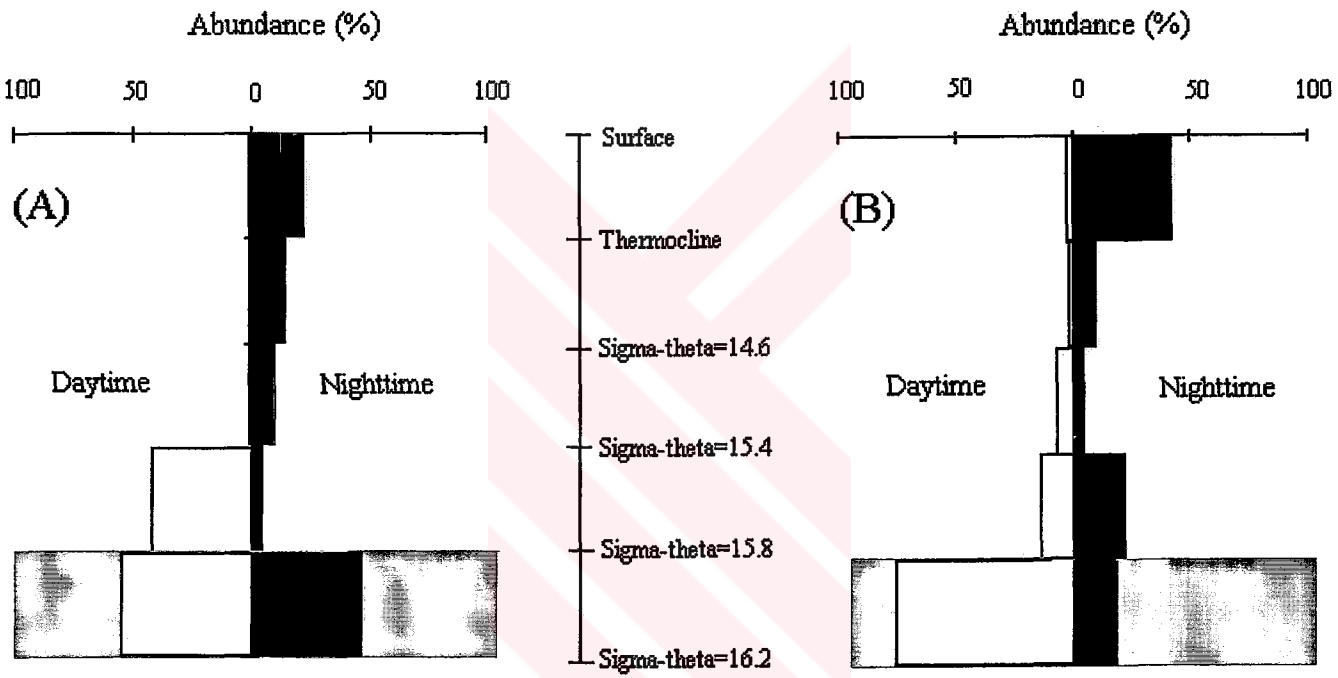

Figure 7.2: Vertical distribution of CV at daytime (white bars) and nighttime (dark bars) in June 1996 (A) and in September 1995 (B). Vertical scale (between the figures) illustrates the density values of the sampling strata. Shaded area indicates the lower boundary of OMZ.

7.2.3. PROSOME LENGTH DISTRIBUTION OF COPEPODITE V

The prosome length distribution of migrating and overwintering CV was compared in Figures 7.4 and 7.5 in June and September 1996 respectively. In both sampling periods the mean prosome lengths of overwintering CV were slightly higher than those of migrating individuals.

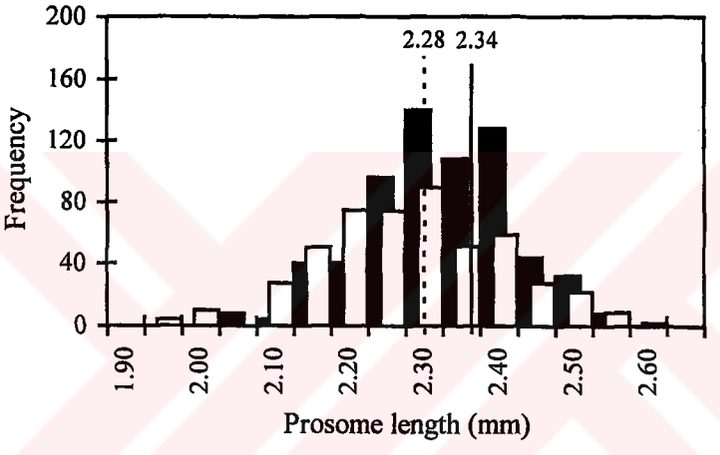

Figure 7.4: Prosome length (mm)-frequency histogram of migrating (white bars) and overwintering (black bars) CV in June 1996. Dashed vertical line shows the mean prosome length of migrating CV and solid vertical line indicates the mean prosome length of overwintering CV.

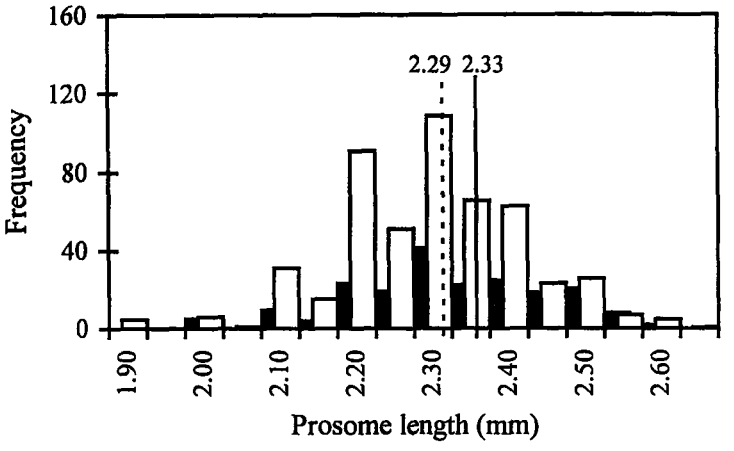

Figure 7.5: Prosome length (mm)-frequency histogram of migrating (white bars) and overwintering (black bars) CV in September 1996. Dashed vertical line shows the mean prosome length of migrating CV and solid vertical line indicates the mean prosome length of overwintering CV.

7.3. DISCUSSION

Among the five different sampling periods, only in June and in September, the considerable amount of CV was found in the overwintering period. Vinogradov *et al.* (1990), emphized that in March and April almost all copepodite CV of *Calanus euxinus* in the Black Sea belong to the migrating group, while 60-75% of the CV belonged to the overwintering population in August and in October.

Occurrence of diapause phase during warm summer-early autumn months denotes that temperature and light could be the most important environmental factors, triggering the diapause.

The most important physical environmental parameter which affect metabolism of an organism is temperature. Figure 7.6 shows the monthly fluctuations of surface temperature along the Bulgarian coast of the Black Sea.

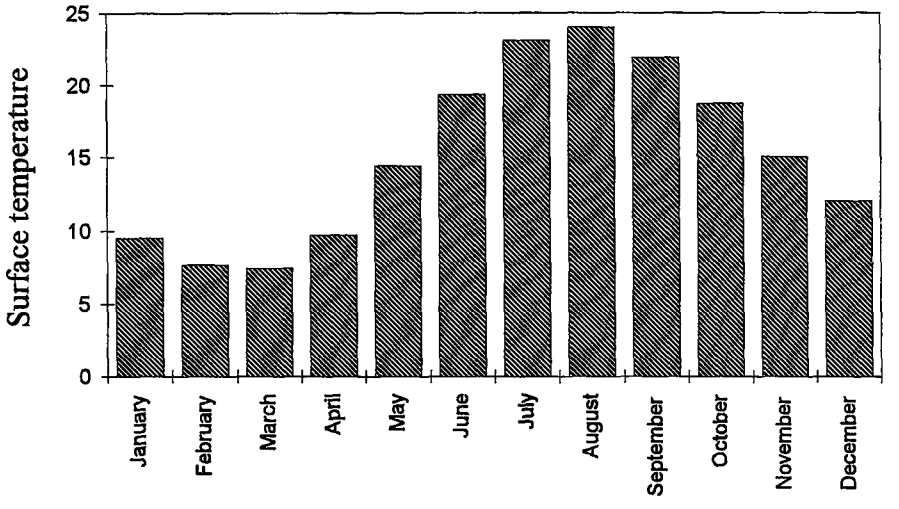

Figure 7.6: Monthly variations of the sea surface temperatures (°C) along the Turkish coastal zone of the Black Sea (constructed using data from Oguz *et al.* 1992).

During the summer period (June, July, August and September) temperature was higher than 20 °C, and the maximum temperature was observed in August and September with 23 °C. Zenkevich (1963) defined *Calanus euxinus* in the Black Sea as cold-water species with the upper limit of temperature is 13 °C. Marshall and Orr (1972) emphasised that *Calanus* distribution covers areas with temperature ranging between -2 and 22 °C. The high summer temperature may trigger the overwintering period of *Calanus euxinus* in the Black Sea.

Figure 7.7 shows the general oxygen and temperature profiles in summer in the Black Sea. The oxygen concentration is usually <20μM in the overwintering habitat.

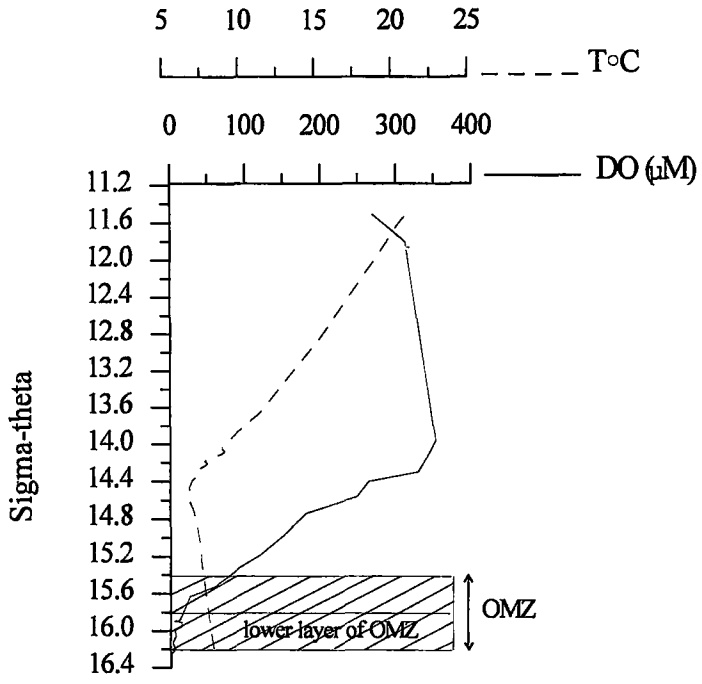

Figure 7.7: Potential temperature and dissolved oxygen (DO) profile against density surfaces in June 1996 in the Black Sea. OMZ= Oxygen Minimum Zone.

The temperature of overwintering habitat is important, because copepods have lower metabolic rates at low temperatures and therefore use stored lipids longer than if they diapaused in colder waters. When the results of gut pigment content in overwintering CV taken into account, it is seen that they are not feeding during overwintering period. Arashkevich *et al.* (1997) investigated gut fullness visually under microscope, they observed that there were no remains of food and the guts were so compressed that the midgut looked like a narrow tube in diapausing CV of *Calanus euxinus* in the Black Sea. Hallberg and Hirche (1980) also mentioned the reduced epithelium of midgut and low digestive enzyme activities in the overwintering copepodite stage of *Calanus finmarchicus* and *Calanus helgolandicus* in the Gullmarfjord in Sweden.

Low oxygen concentration in the overwintering habitat also reduces the metabolic rates in CV (section 4.2.4). Arashkevich *et al.* (1997) showed that the diapausing CV became torpid at 0.3 mg O_2/l, while migrating CV at 0.5 mg O_2/l.

The respiration and ammonium excretion rate of migrating CV was higher than diapausing CV. However, the effect of low oxygen content on metabolism is not as strong as temperature effect (see section 4.3). Alldredge *et al.* (1984) confirmed that low temperature in the overwintering habitat reduce metabolism and low oxygen may reduce predation. Dark habitats provide safety from visual predators, and by diminishing the mobility, they may reduce non-visual invertebrate predation (Kaartvedt, 1996). In the Black Sea, *Pleurobrachia pileus* and *Mnemiopsis leidyi* as non-visual predators of *Calanus*, extent their vertical distribution down to the OMZ.

Changes in photoperiod are suggested as an important factor regulating the phenology of the organisms (Mansingh, 1971). Grigg and Bardwell, (1982) suggested that overwintering behaviour, metabolism and moulting are to a large extent under endocrine control, and are possibly triggered by the photoperiod. Photoperiod directly influences some physiological, behavioural, developmental and reproductive processes. The results of Marcus (1982), indicated that a short day-length photoperiod is the primary cue triggering diapause egg production by *Labidocera aestiva* (calanoida) in Vineyard Sound, MA.

Figure 7.8 shows the monthly average air light intensity in Sinop during 1994. The maximum light intensity was observed in June, July and in August. In those months the day-time length is greater than night-time. It was recently indicated in the literature (Koslow, 1979; Frost, 1988; Ohman, 1988, 1990) that the diel vertical migration is mainly due to the visual predation. Kremer and Kremer (1988) concluded this migration pattern with the following principle 'better hungry than dead'. During the summer, the daytime length is longer than nighttime length. If the energetic and demographic costs of continuous diel vertical migration of *C. euxinus* is taking into account, it may be adapted the Kremer and Kremer's (1988) principle for the overwintering strategy as 'better long term hungry than extinction' for *Calanus euxinus*. When it is considered the importance of CV in the creation of new generation this principle becomes more meaningful. Visual predators have of great significance in the overwintering

period and habitat of *Calanus euxinus*, and therefore the importance of zooplanktivorous pelagic fishes being the main visual predators in the Black Sea should be discussed.

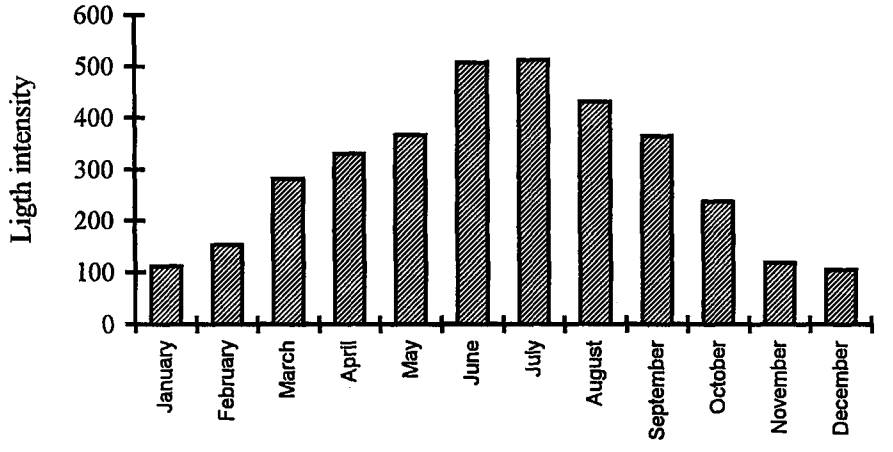

Figure 7.8: Monthly average air light intensity (cal/m^2/min) in Sinop during 1993 (data obtained from Monthly Meteorological Bulletin, 1993).

The Black Sea fishery of the riparian countries is dominated by anchovy, sprat and horse mackerel (Ivanov and Beverton, 1985, cf. Avsar, 1993). The most dominant fish species is anchovy. It comprises more than 50% of total landings from the Black Sea (Gucu, 1997). According to the Statistics of the State Institute of Turkey the total fish yield was 557,138 tons in 1995 from the surrounding seas (from Black, Marmara, Aegean and Mediterrenean Seas) of Turkey. Anchovy made up about 2/3 of total landing with 387,574 tons. There are two subspecies of anchovy in the Black Sea; the Black Sea anchovy, *Engraulis encrasicolus ponticus* and the Azov anchovy, *E. encrasicolus maeoticus*. The Black Sea anchovy overwinter mainly in the south and spawn during summer, the Azov anchovy spawn in the Azov Sea during summer and migrate to the northern Black Sea for overwintering from November to April (Shul'man, 1974; Chashchin, 1995; Gucu, 1997). In winter, anchovy does not

During summer, the Black Sea anchovy is distributed in the whole sea. They feed more actively especially in July and August (Slastenenko, 1955/56), mostly on copepods, especially on *Acartia clausi* (Acara, 1956).

The second important pelagic fish in the Black Sea is sprat (*Sprattus sprattus phalericus*). This is a cold water species. They migrate to shelf area during the late spring and summer months, their gonads develop during summer and they spawn in winter months. The young prefer the warm water and widely distribute in the warm water layers over the entire Black Sea. Adults tend to remain below thermocline and penetrate above thermocline for spawning and feeding. Vertically they mostly distribute down to 70m in September. This can be explained by their preference of cold water as a cold water species. Copepods form the main food item of sprat. *Calanus helgolandicus, Paracalanus parvus, Acartia clausi* and *Pseudocalanus elongatus* constitute the largest proportion of copepods (Avsar, 1993). The fat content of sprat reach maximum in June-July (Shul'man, 1974) depending on the intensive feeding at that time.

The effect of predation pressure on shaping life history strategies of copepods documented well in freshwater. Fulton, (1973, cf. Kaartvedt, 1996) found that the *Neocalanus plumchrus* developed in the surface waters during the spring bloom and descended to overwintering habitats by early June in the Strait of Georgia, British Columbia. There are largest salmon-producing rivers of the world surrounding the Strait of Georgia, and each spring and summer a predictable pulse of planktivores is introduced into this strait (Kaartvedt, 1996). Hairston (1987) suggested that the production of benthic resting eggs by copepod *Diaptomus sanguineus* is approximately timed to minimize seasonal predation by planktivorous sunfish. The results of a natural experiments were also consistent with this hypothesis. When a drought eliminated sunfish from a shallow pond but not a deeper pond, the timing of resting egg production shifted later in the year only in the shallow, fishless pond (Hairston, 1987).

Among the above mentioned parameters which thought to affect on choosing the diapause habitat in *C. euxinus* in the Black Sea, the temperature seems to have effect on the beginning of diapause phase. They choose the lower layer of OMZ for the overwintering habitat where the temperature is around 8 °C. However, if only the low temperature would be important for choosing diapausing habitat, copepods need not go so deep instead they could stay in the upper layers such as cold intermediate layer. Two other parameters may have effect on choosing the lower layer of OMZ as the overwintering habitat: (1) Vinogradov *et al.* (1992b) assumed that diapausing CVs have the neutral buoyancy at that layer, (2) The vertical distribution of above mentioned planktivores pelagic fishes is limited down to the 70m, and therefore low oxygen concentration in the OMZ forms a barrier for them. Alldredge *et al.* (1984) also suggested that low oxygen may reduce predation.

During the overwintering period that is during the summer-autumn months in the Black Sea, two behaviorally different groups of CV have been observed; one is overwintering, other group is still continue to their diel vertical migration. Arachkevich *et al.* (1997) mentioned two groups of migrating CV *Calanus euxinus* in the Black Sea. One had with large oil sac without gonad development second group had development in gonad without oil storage and they suggested that the individuals belonging the first group is likely to enter diapause. Furthermore from the results of the size class distribution of diapausing CVs, they observed two different diapausing groups presumable belong to different generations. Arachkevich (per.comm) suggested that the whole population of copepodite CV *Calanus euxinus* does not enter diapause together at the same time. Some of the migrating CV join the diapausing groups at different time and some of them continue to their diel vertical migration and to give new generation in the surface waters. Den Boer (1968, cf. Ohman, 1988) described that a population is more likely to survive in the extreme conditions, if a range of traits occurs within a population than is one with a single expression of a trait. Different zooplankton patches within the same interbreeding population may encounter pronounced differences in thermal regime, food supply and

planktivorous fish. Further attention is needed to the distribution of genetic variability in behavioral traits in planktonic population. Weider (1984) identified clonal differences in diel vertical migration behavior of *Daphnia pulex* co-occuring within a single pond. Two clones, identified by allozyme markers, differed in both vertical and horizontal distribution. One clone predominated in shallow strata while a separate clone predominated in deeper strata. Marcus (1984) identified geographic differentiation in the diapause response of the pontellid copepod *Labidocera aestiva*. Populations in the low latitude rarely enter diapause.

The return to favourable conditions does not bring an immediate end to diapause in insects. There is a brief period when endocrinological and biochemical preparations occur (Mansingh, 1971). The wide variety of natural stimuli; such as, intensity and spectral quality of light, a constant or available range of temperature or photoperiod etc., are capable of terminating diapause (Hirche, 1996). The animal should recognise seasons at great depths in an unknown way, so that they terminate the overwintering period (Banse, 1964). Both the ovarian maturation and moult cycle in crustaceans are important processes in overwintering physiology. Both are controlled by endocrine system in crustaceans (Quackenbush, 1986, cf. Hirche, 1996). These endocrinological changes triggers DNA synthesis and mitotic activity (Mansingh, 1971). Arashkevich *et al.* (1997), concluded that the development of gonads marks the termination of diapausing phase of *Calanus euxinus* in the Black Sea.

CHAPTER VIII

CONCLUSIONS

During this study five copepod species and a chaetognath species were investigated. The results obtained through this study have shown:

1- The abundance of organisms varied with season and related with their range of tolerance to the environmental factor(s). The studied organisms showed different seasonal distributional pattern. The highest total abundance (adults and copepodite stages) in *Calanus euxinus* population was found in April sampling which is similar to the findings cited in the literature. After a sharp decrease during summer months, there was a small peak in abundance in November (section 3.2.1). Throughout the sampling period, the metanauplii comprised more than half of the *C. euxinus* population in April and December samplings which leads to the conclusion that the main reproduction of this species takes place in April and in December.

Population structures of copepods other than *Calanus* were studied in April 1995, 1996; May 1994; June 1996 and in September 1995, 1996. The maximum total abundance of *Pseudocalanus elongatus* as a cold water species was observed in April. There was a decrease in warmer periods (June and September).

The seasonal cycle in the mean abundance of *Acartia clausi* contrasted to those of *Calanus* and *Pseudocalanus* species. The total abundance of *A. clausi* peaked in May and in June which is similar to the findings of Greze and Baldina (1967). The highest total abundance of *Paracalanus parvus* was found in June which is in agreement with the statements of Greze *et al.* (1971) and Sazhina (1996). The second small peak was found in April sampling.

The maximum total abundance of the cyclopoid copepod *Oithona similis* occurred during warmer periods (June and September), although Zenkevich (1963) defined it as a cold-water stenothermal species. But they tolerate the warmer periods by migrating below the thermocline.

Similar to the observation of Sazhina (1987), an increase was found in the abundance of *Sagitta* in September. Juvenile individuals dominated the population during summer and early autumn. In September, there was a replacement of new generation on whole population.

2- Various species of zooplankters occupy certain depths in the water column. These depths, or changes in depths, can be influenced by age, sex, reproductive state, feeding strategies, light intensity and spectrum, presence or absence of predators, temperature, daytime length and other biological and physical factors. In the present work, the studied copepod and chaetognath species showed different vertical distribution pattern depending on the time of day.

The data on the vertical distribution of *Calanus euxinus* obtained in this study are in the agreement with the results attained by Vinogradov *et al.* (1985, 1986, 1990 and 1992a,b) and Zenkevich (1963) and verify that C. euxinus is a strong diel and seasonal vertical migrant. The individuals of female, copepodite V (CV) and copepodite IV (CIV) *Calanus euxinus* showed strong diel vertical migration compared to smaller stages (CIII, CII, CI). In daytime they concentrated between the depth of σ_θ =15.8 and σ_θ =16.2, while in nighttime they were dominant between the depth of thermocline and the surface (Figure 8.1). However, males exhibited inconsistent distribution over 24 hours. Although smaller copepodite stages (CIII, CII, CI) occurred mostly in the uppermost two layers (above σ_θ =14.6), in nighttime they concentrated mainly in the first layer throughout the all sampling periods.

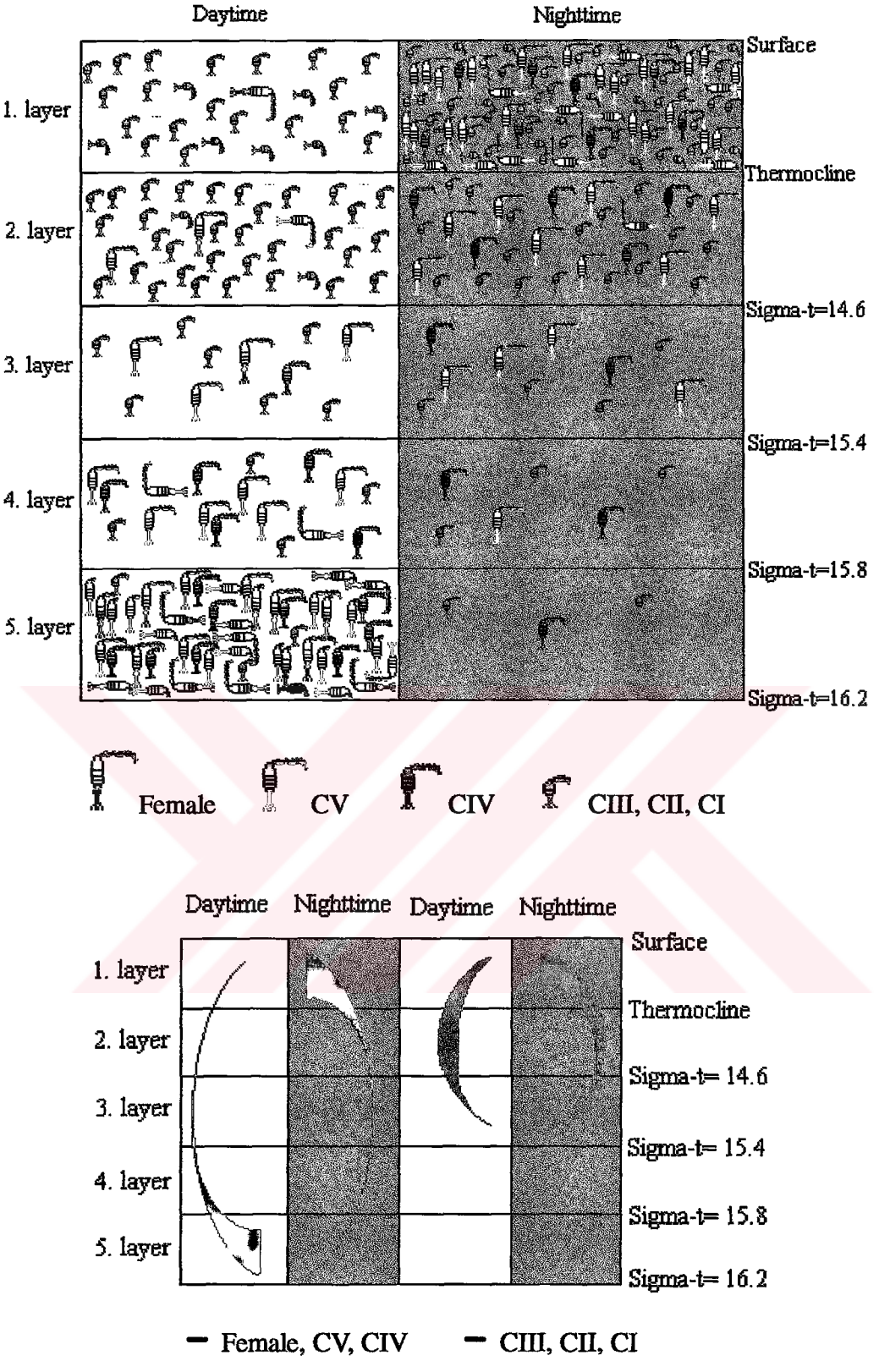

Figure 8.1: Relative diel vertical distribution in abundance of *Calanus euxinus* at day and night-times in the Black Sea.

During the warmer periods (June and September), the vertical distribution was different from the general pattern due to the ontogenetic migration; during nighttime, some individuals were found still in the lower layer of the main picnocline (between the depth of σ_θ =15.8 and σ_θ =16.2), as recognised in the overwintering period (Figure 8.2).

The vertical migration of *Pseudocalanus elongatus* was generally erratic. With some exceptions female *P. elongatus* showed a noticeable vertical migration. The majority of females were in the uppermost two layers in daytime. Males showed higher abundance in intermediate layers with small scale diel vertical migration (Figure 8.3). Copepodite stages were generally dominant in the uppermost three layers and they exhibited small scale periodic migration (Figure 8.3). Zagorodynyaya (1970) and Vinogradov *et al.* (1986) found similar vertical distribution for adults and older copepodite stages of *P. elongatus*.

Parallel to the finding of Zenkevich(1963), Petipa (1967) and Vinogradov *et al.* (1992a), *Acartia clausi* and *Paracalanus parvus* generally distributed at the uppermost two layers, above the depth of sigma-theta 14.6. *A. clausi* showed small periodicity between these two layers (Figure 8.4). *Oithona similis* showed inconsistent vertical distribution throughout the water column from the lower layer of pycnocline to the surface. They were generally observed in the intermediate layers at both day and nighttime (Figure 8.4).

The mature *Sagitta* showed a marked diel vertical migration from the lower layer of the oxygen minimum zone (5^{th} layer) to the surface. During the daytime they condensed in the lower layers, while they dominated in the first layer during nighttime. Juveniles were mostly found in the uppermost two layers, concentrated between the depth of thermocline and the surface (Figure 8.5).

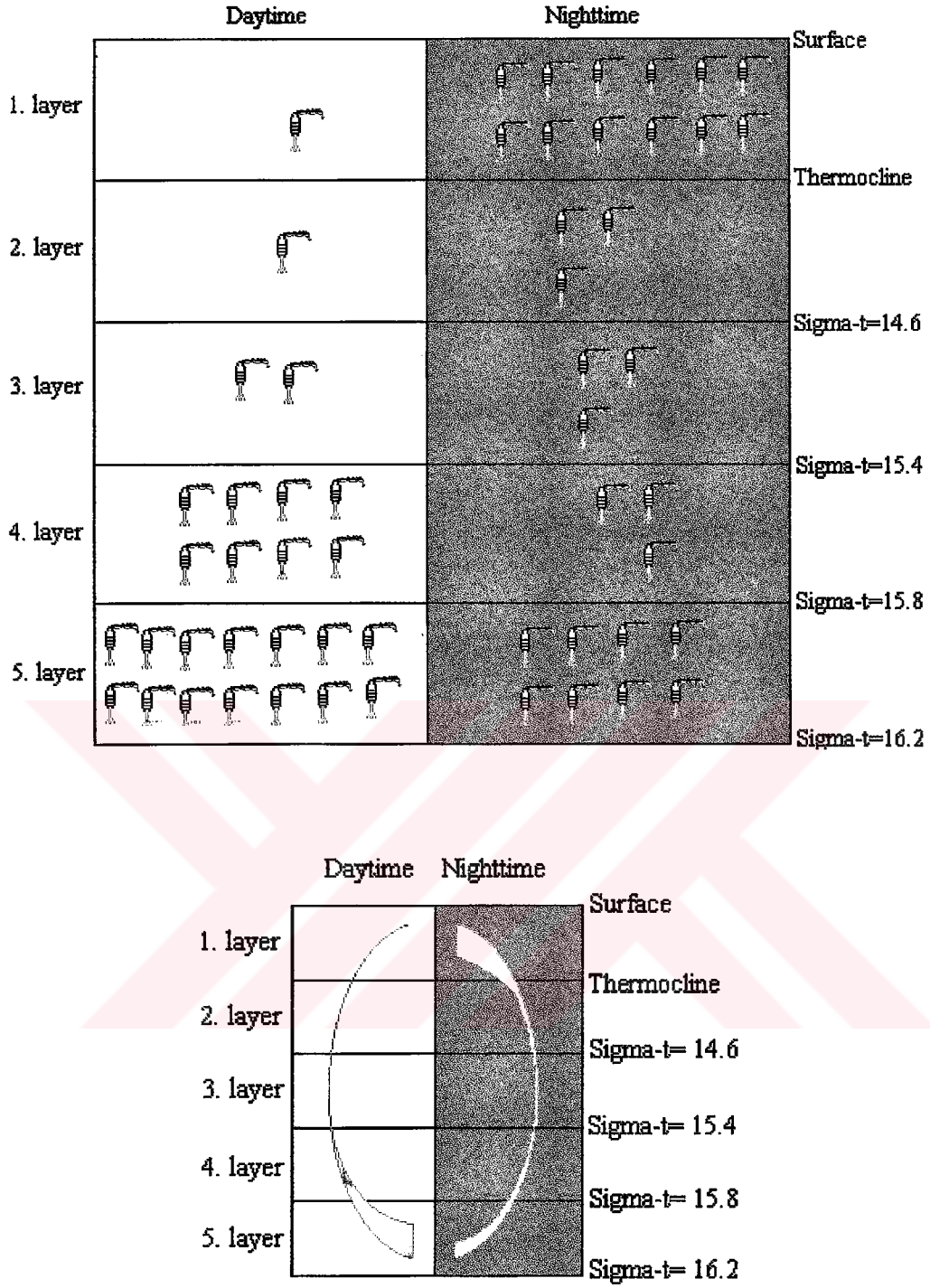

Figure 8.2: Relative diel vertical distribution in abundance of copepodite V *Calanus euxinus* at day and night-times due to ontogenetic migration in June 1996 and September 1995/1996 in the Black Sea.

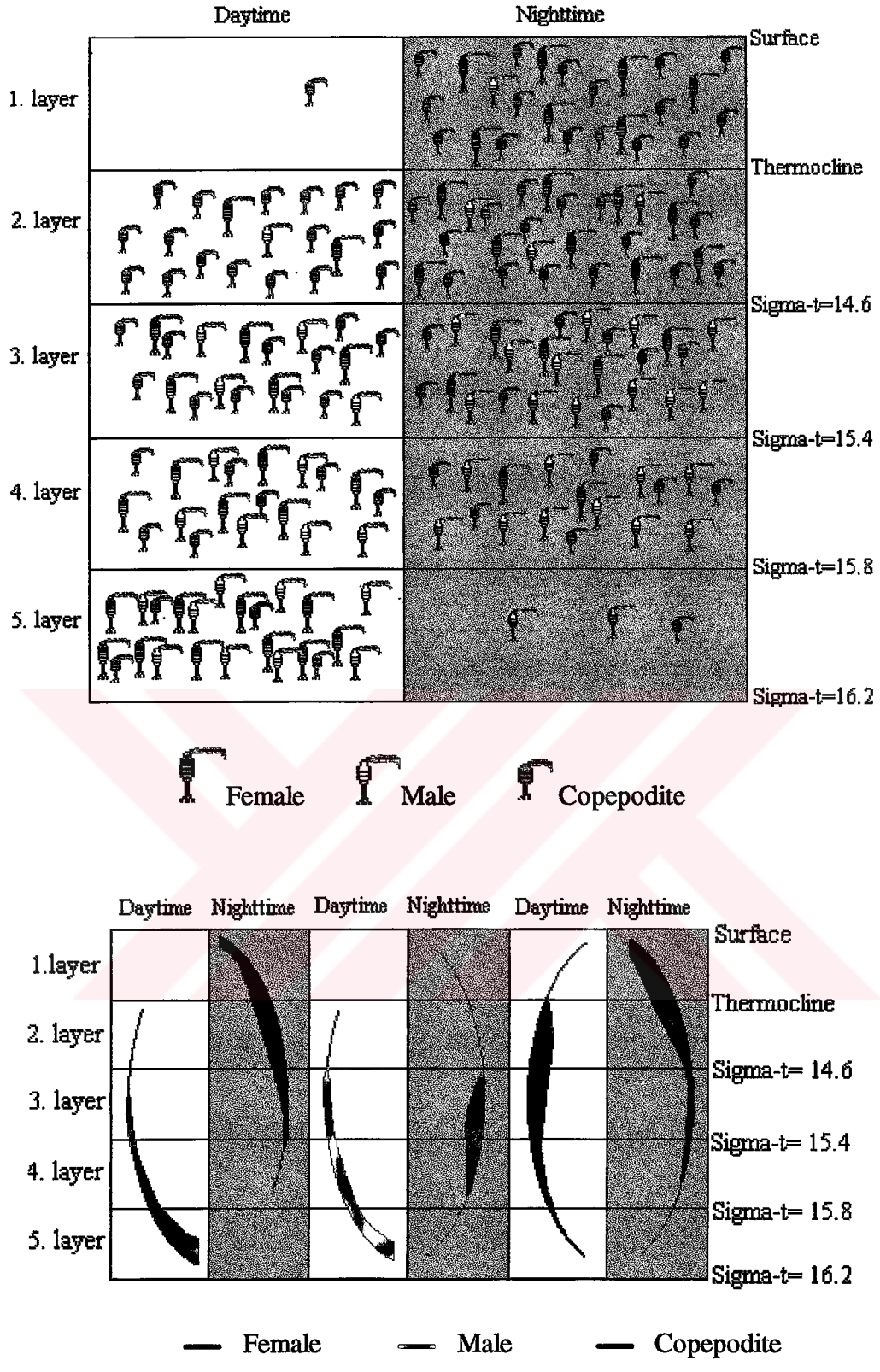

Figure 8.3: Relative day and night-time vertical distribution in abundance of *Pseudocalanus elongatus* in the Black Sea.

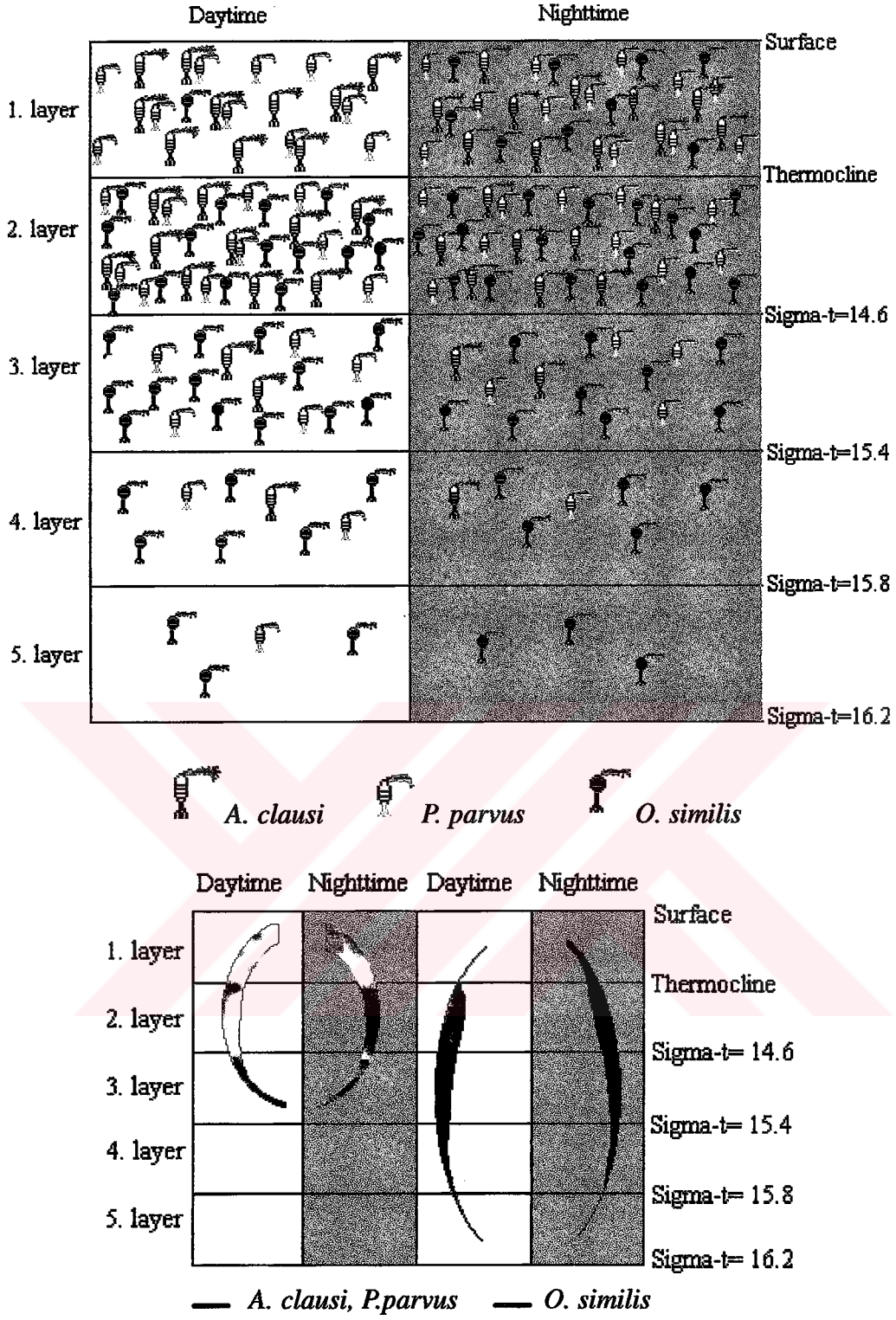

Figure 8.4: Relative vertical distribution in abundance of *Acartia clausi, Paracalanus parvus* and *Oithona similis* at day and night-time in the Black Sea.

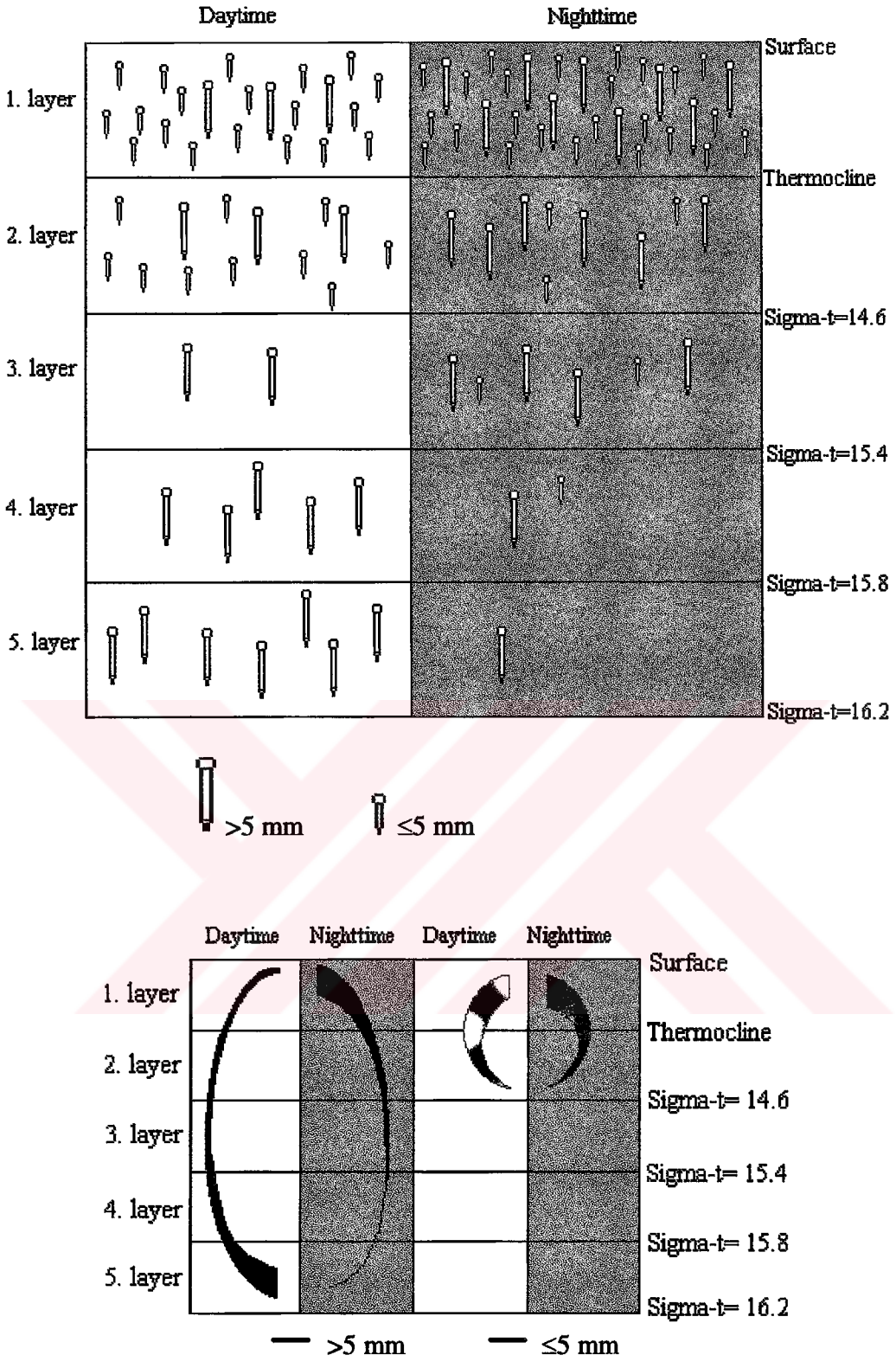

Figure 8.5: Relative diel vertical distribution in abundance of *Sagitta* at day and night-time in the Black Sea.

3- During the diel vertical migration of *Calanus euxinus*, from the surface to the lower layer of the oxygen minimum zone, they undergo almost 10 times oxygen and about 3 times (during summer months) temperature changes. Similar to the observation of Araschkevich *et al.* (1997), it is found that, the respiration rates of the female and CV of *C. euxinus* increase with increasing temperature and oxygen concentration in the ambient seawater. As a conclusion, their metabolic rates decrease while they stay in the lower layer of OMZ. The respiration rate of females was higher than that of CV.

4- The gut pigment content (GPC) in female *C. euxinus* was found to be higher in the upper layers during the nighttime. The grazing pressure of female *Calanus* was found 14.5% and 9.5% of primary production in April and in September respectively.

Gut pigment content (GPC) and grazing pressure of copepod assemblages were studied in the three size fractions; small (300-500μm), medium (500-1000μm) and large (1000-2000μm). The highest amount of GPC, among the size groups of copepod assemblages was detected in the large size fraction. A positive relationship was observed between the GPC and the individual length. Although large sized copepods showed the highest daily ingestion rate, the overall highest grazing on primary production was performed by the medium sized copepods. It is found that 31.5% of primary production was grazed by copepod assemblages.

The average grazing rate of copepod assemblages was estimated as 0.76±0.26 day^{-1} in September 1995.

5- Similar to the findings indicated in the Shul'man *et al.* (1997), the total lipid content in copepodite V stage of *Calanus euxinus* was higher than that of females. No significant correlation was found between the Chl-a concentration and total lipid content in both stages (female and CV). The wax esters was the dominant lipid class, whilst the triacylglycerids and phospholipids contributed little to the lipid reserves in both stages.

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