

Population structure, vertical distribution and diel migration of *Sagitta setosa* (Chaetognatha) in the south-western part of the Black Sea

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Abstract. The population structure of *Sagitta setosa* from the south-western part of the Black Sea was examined between May 1994 and December 1996. In addition, the vertical distribution and diel vertical migration of *S.setosa* were studied for juveniles (≤ 5 mm) and adults (> 5 mm) in April 1995, September 1995 and June 1996. The population structure studies showed that a new generation was introduced in September. Breeding was most intensive from June to November, indicated by the frequency of small-sized individuals. Diel vertical migration from the depth of the oxygen minimum zone to the surface was observed for adult *S.setosa* but not for juveniles. Juveniles were generally distributed above the seasonal thermocline. It is evident that adults are able to tolerate a wide range of oxygen concentrations and temperature.

Introduction

Sagitta setosa is the common chaetognath in the Black Sea and its distribution is well documented (Zenkevitch, 1963; Vinogradov *et al.*, 1990, 1992; Niermann and Greve, 1997). Less abundant in shelf areas and in the central gyres of the Black Sea, *S.setosa* has been observed accumulating along the Black Sea rim current (Niermann *et al.*, 1997). Previous studies have revealed that *S.setosa* performs a strong diel vertical migration from the main pycnocline to the surface (Zenkevitch, 1963; Drits and Utkina, 1988; Vinogradov *et al.*, 1990, 1992). However, vertical distribution and diel migration have not yet been studied for different maturity stages or length classes of this species in the Black Sea. The present study describes the population structure and diel and ontogenetic vertical migrations of *S.setosa* in relation to the physical structures of the water column in the south-western Black Sea.

Characteristics of the Black Sea

The Black Sea is a unique marine environment, representing the largest land-locked anoxic basin in the world. It reaches to a maximum depth of ~ 2200 m, has a surface area of 4.2×10^5 km² and a volume of 5.3×10^5 km³. The Black Sea is almost completely isolated from the world's oceans. There is a restricted exchange with the Mediterranean Sea through the Turkish Straits System: the Bosphorus and Dardanelles Straits and the Sea of Marmara. A strong density stratification inhibits vertical mixing. The oxygenated upper layer extends 150 m down (only 13% of the sea volume) to the completely anoxic basin which contains hydrogen sulphide. A permanent halocline separates the oxic and anoxic waters

(Ozsoy and Unluata, 1997). There is a well defined oxygen minimum zone (OMZ; with $<10 \mu\text{mol l}^{-1} \text{O}_2$) between these waters. The depth of the OMZ varies both seasonally and by location, depending on the circulation and the intensity of eddies. Recent investigations have shown that the location of the OMZ (as well as other chemical and physical characteristics of the water column) could be better explained by water density rather than depth (Murray *et al.*, 1991; Tugrul *et al.*, 1992; Saydam *et al.*, 1993).

Method

Hydrographic data

During all cruises, depth, temperature and salinity of the water column were measured with a Seabird-SBE9 CTD profiler. Dissolved oxygen concentrations in the water column were determined using a modified conventional Winkler titration method (Konovalov *et al.*, 1994).

Sample collection for the study of population structure

Samples were obtained in the south-western part of the Black Sea during May 1994, April and September 1995, and April, June, September, November and December 1996 (Figure 1). At each station, zooplankton were collected by towing vertically a Nansen Closing Net of $112 \mu\text{m}$ mesh size. The net mouth opening was 70 cm. Most of the stations studied were off-shore (Figure 1) and zooplankton samples were towed from the depth of the beginning of the H_2S layer (around the depth of sigma-theta 16.2, or 150–200 m depth, depending on the location of the station) to the surface. The samples from the coastal stations (ranging from 50 to 70 m depth) were taken from the bottom to the surface. The samples were preserved in sodium borate-buffered 4% formaldehyde–seawater solution until

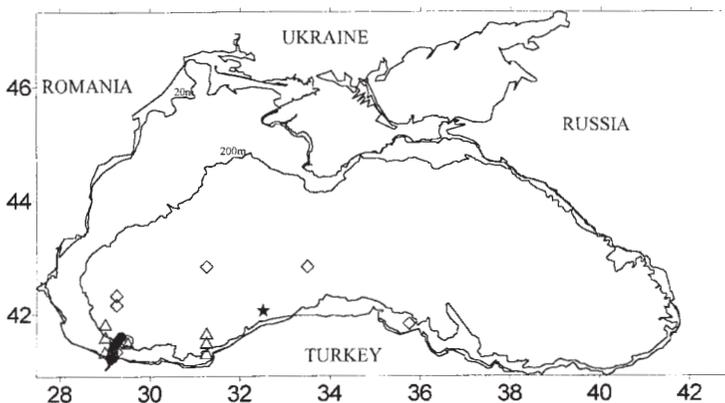


Fig. 1. Sampling stations of this study. ★ in May 1994, ○ in September 1995, △ in June 1996, ◇ in September 1996, ● in April 1995, 1996, November, December 1996. Shown are the 20 and 200 m isobaths.

laboratory analysis. All *S.setosa* individuals in the samples (from 5 to 560 individuals) were counted using a stereomicroscope, and the total body length (excluding tail fin) of all specimens was measured.

Sample collection for the study of vertical distribution and migration

Samples were collected at 3–4 h intervals over a 30 h period in April 1995, and a 21 h period in September 1995, at a drifting station located in the south-western part of the Black Sea (Figure 1). Before each tow, the location of the station was fixed. In June 1996, a 24 h period was completed for the different stations located in the south-western Black Sea (Figure 1). The zooplankton samples were collected from five different depth intervals by a Nansen Closing net of 112 μm mesh size. The specific density (σ_θ) was used to determine sampling depth intervals. Specific density was used because it is related to the major physical and biochemical characteristics of the water column that may affect the distribution of mesozooplankton in the Black Sea (Table I). Before net tows, a CTD cast was carried out to identify depths of density layers. The vertical distribution and migration of both juvenile and adult *S.setosa* were studied. The stage of maturity was determined according to the absence or presence of gonads. Individuals with no visible gonads were considered as juveniles and individuals with gonads with either developing eggs or mature eggs were considered as adults. The minimum length of *S.setosa* observed with gonads was 5.2 mm. Therefore, juveniles were defined as ≤ 5 mm and adults as >5 mm long for the vertical migration study.

In order to examine the relationship between the vertical distribution of *S.setosa* and that of their main prey, copepod samples were collected from each depth interval twice during the sampling duration, once during the day and once during the night within the three sampling periods (April and September 1995, and June 1996). The copepod samples were sub-sampled with a Folsom splitter, identified, and counted using a stereomicroscope after preserving with sodium borate-buffered 4% formaldehyde–seawater solution.

Table I. Sampling depth intervals used in this study and their characteristics

Sampling depth intervals	Depth no.	Characteristics of depth intervals
Seasonal thermocline–surface	1	Mixed layer
$\sigma_\theta = 14.6$ –seasonal thermocline	2	$\sigma_\theta = 14.6$ refers to the beginning of nitrification (Lipp and Kempe, 1993)
$\sigma_\theta = 15.4$ – $\sigma_\theta = 14.6$	3	The majority of nitrification and remineralization of organic matter take place (Lipp and Kempe, 1993)
$\sigma_\theta = 15.8$ – $\sigma_\theta = 15.4$	4	Denitrification processes begin to occur at the depth of $\sigma_\theta = 15.4$ (Bastürk <i>et al.</i> , 1994)
$\sigma_\theta = 16.2$ – $\sigma_\theta = 15.8$	5	This is the daytime aggregation layer for late copepodite stages and the adults of <i>Calanus euxinus</i> (Vinogradov <i>et al.</i> , 1992). $\sigma_\theta = 16.2$ corresponds to the bottom of the OMZ

OMZ = oxygen minimum zone.

Results

Hydrography

Profiles of dissolved oxygen, sigma-theta, temperature and salinity are presented in Figures 2 and 3. Figure 2 shows that the oxygen minimum zone (OMZ) was observed between the depths of sigma-theta 15.8 and 16.2 throughout the sampling periods. A strong thermocline existed in the water column on all sampling dates except in April when it was less pronounced as a result of spring seasonal mixing. Salinity ranged from 17–18 ppt at the surface to 21 ppt in the OMZ.

Abundance and vertical distribution of copepods

In all sampling periods, five copepod species were observed: *Calanus euxinus*, *Pseudocalanus elongatus*, *Acartia clausi*, *Paracalanus parvus* and *Oithona similis*. In April and June, *P.elongatus* was the dominant species in the water column, accounting for almost 70% of the total copepod population in April (1887 ind. m^{-3} out of 2640 ind. m^{-3}) and 30% in June (1615 ind. m^{-3} out of 5604 ind. m^{-3}). In September, *O.similis* was the most abundant species, accounting for 48% of the total copepod population in the water column.

The night and day vertical distributions of copepods are shown in Figure 4. The variability of copepod abundance between night and day samples probably resulted from lateral intrusion of the water masses. In all cases, copepods were more abundant in the shallower waters at night. During the day, copepods were most abundant in the deeper waters only in April. Among the copepods, *P.parvus* and *A.clausii* were generally distributed in the uppermost two layers (for layer definitions see Table I). *Oithona similis* was generally observed in the

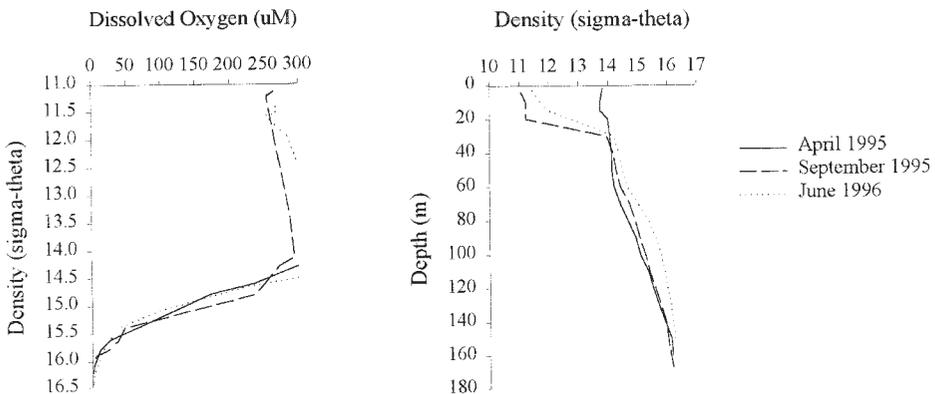


Fig. 2. Vertical profiles of dissolved oxygen and density in April and September 1995, and in June 1996.

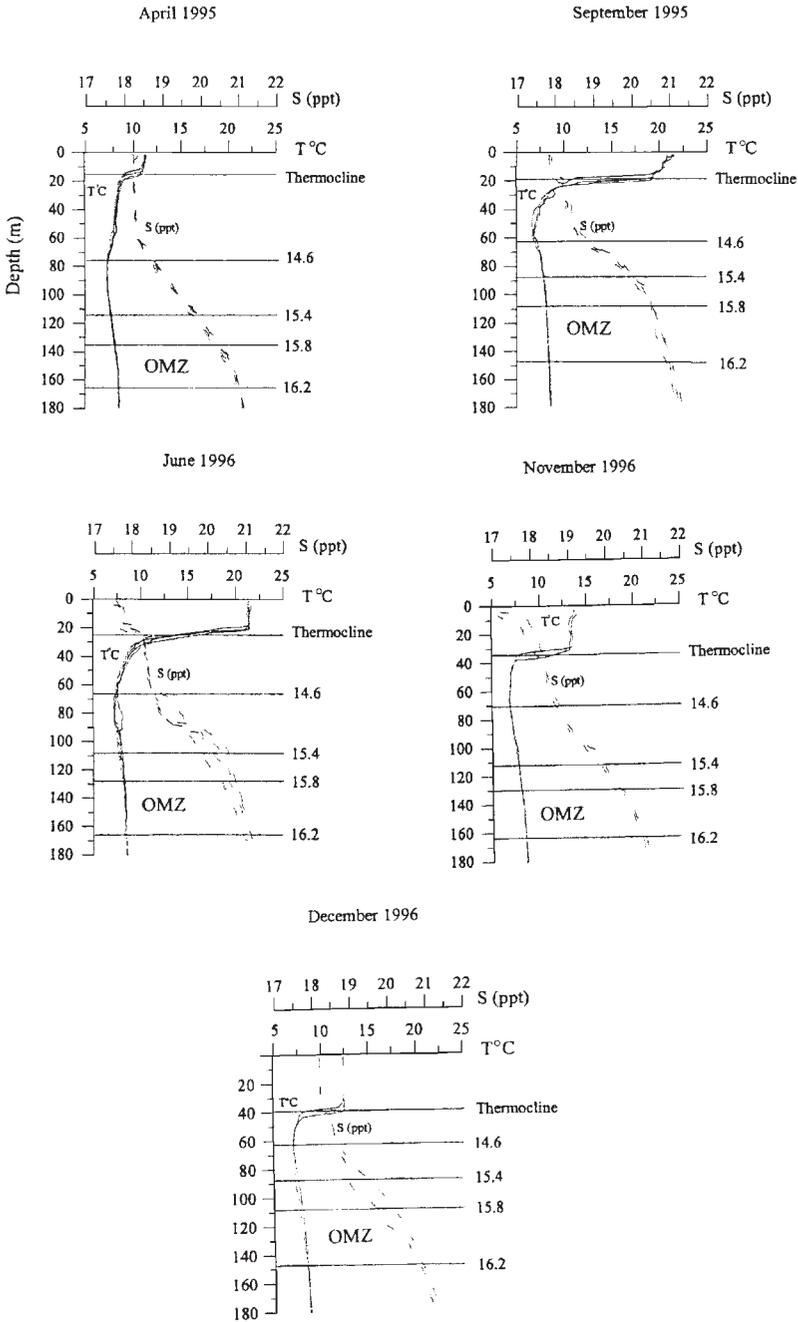


Fig. 3. Potential temperature and salinity from different stations are plotted against depth for each month. Horizontal lines indicate the sampling depths and the corresponding sigma-theta values (see Table I). OMZ = oxygen minimum zone.

intermediate layers during both the day and the night without a consistent migration pattern. Female *P.elongatus*, and female and copepodite stage V of *C.euxinus*, showed strong vertical migration from the surface down to the OMZ during the day (Figures 5, 6 and 7).

Development of the population of S.setosa during the sampling periods

Abundance of *S.setosa* during the sampling periods is presented in Figure 8. Maximum numbers were observed in September 1995 and 1996, with values of 9.3 and 8.1 ind. m⁻³, respectively. Abundance increased from April 1996 to September 1996, then decreased to 1.9 ind. m⁻³ and 2.1 ind. m⁻³ in November and December, respectively.

The size of *S.setosa* ranged from 1 to 30 mm (Figure 9). Based on the total length, the size distribution of *S.setosa* in the Black Sea showed marked seasonal fluctuations (Figure 9). During the late spring (April and May), the population consisted primarily of individuals between 10 and 22 mm in length. Microscopic

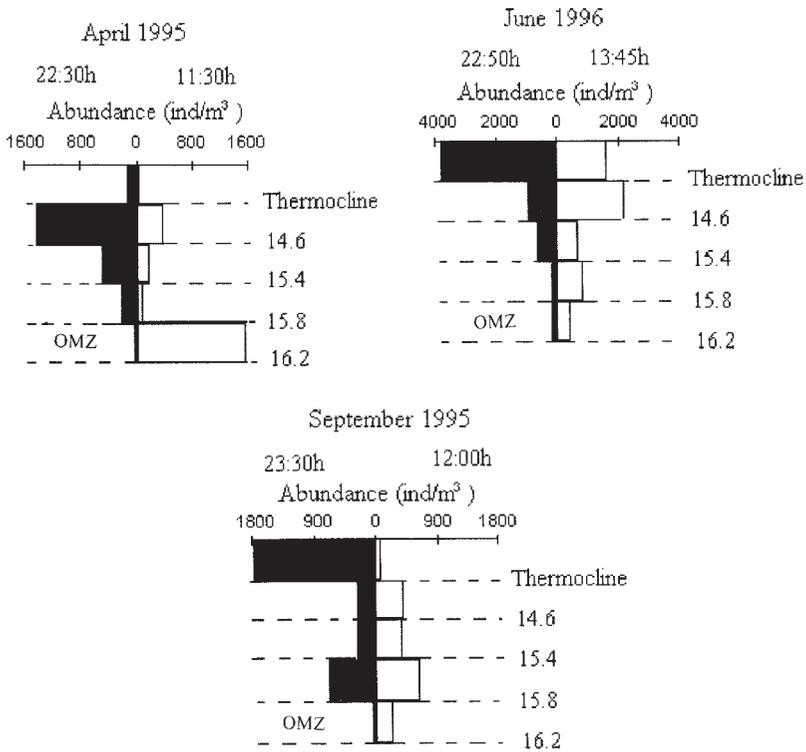


Fig. 4. Day (white bars) and night (black bars) vertical distribution of copepod assemblages in April and September 1995 and in June 1996. Horizontal dashed lines indicate the sampling depths and the corresponding sigma-theta values (see Table I). OMZ = oxygen minimum zone.

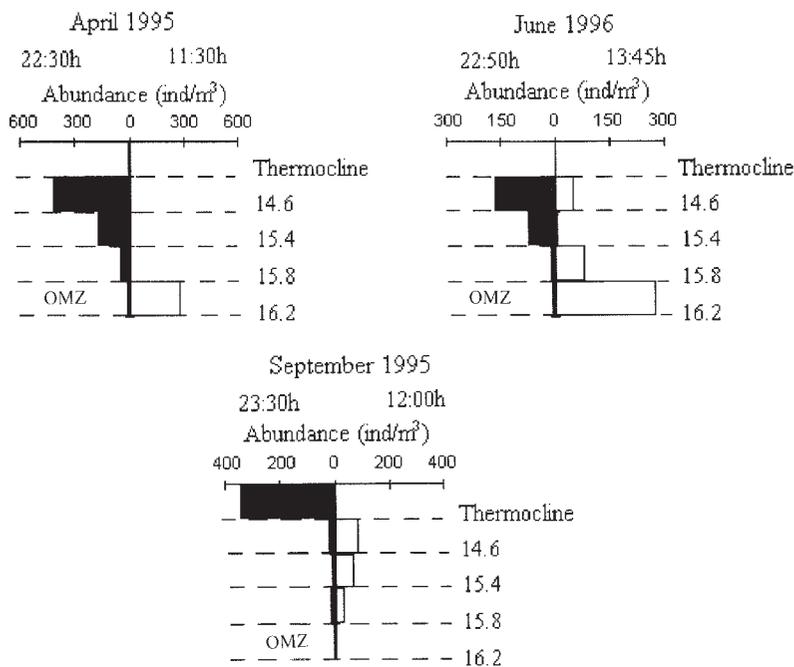


Fig. 5. Day (white bars) and night (black bars) vertical distribution of female *Pseudocalanus elongatus* in April and September 1995 and in June 1996. For details see Figure 4.

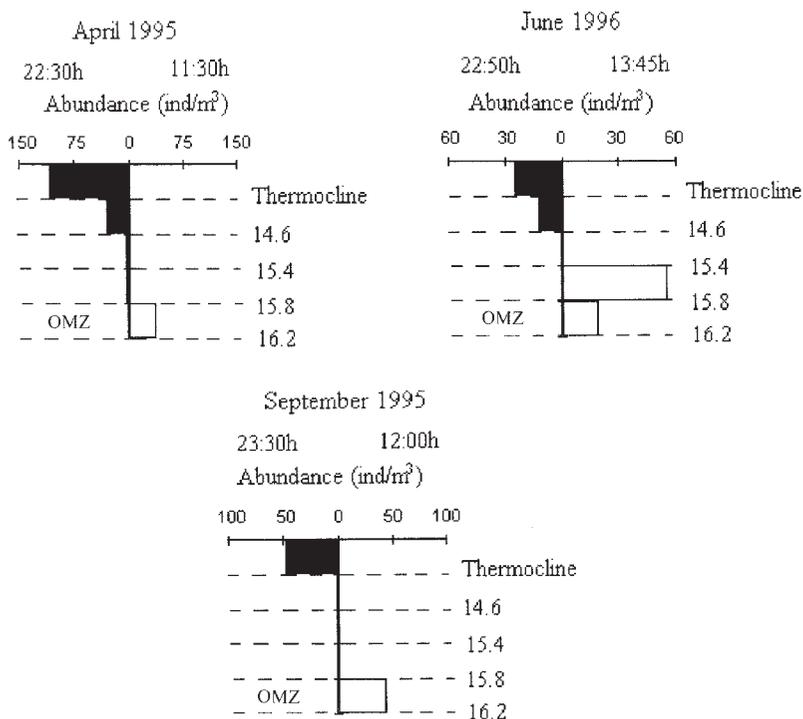


Fig. 6. Day (white bars) and night (black bars) vertical distribution of female *Calanus euxinus* in April and September 1995 and in June 1996. For details see Figure 4.

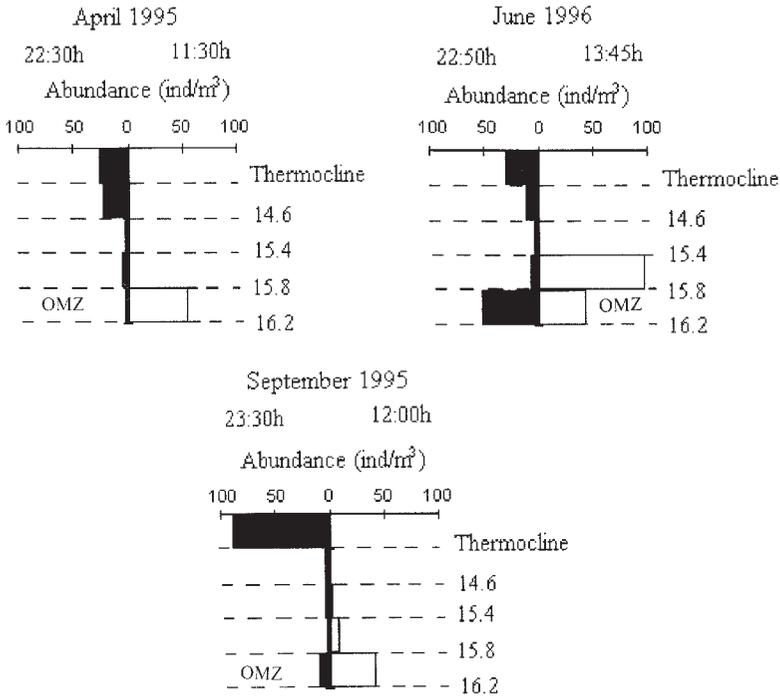


Fig. 7. Day (white bars) and night (black bars) vertical distribution of copepodite stage V *Calanus euxinus* in April and September 1995 and in June 1996. For details see Figure 4.

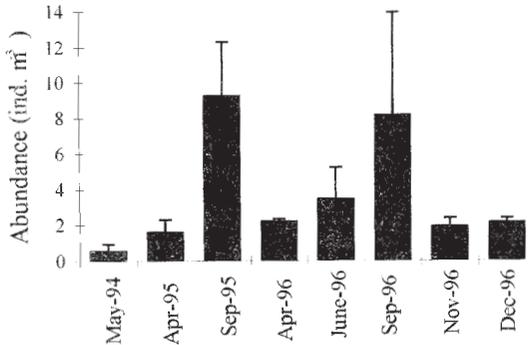


Fig. 8. Abundance of *Sagitta setosa* during the sampling periods.

observations suggested that only a few individuals had eggs in the gonads in April, and most of the individuals had eggs in May. In June, a bimodal size distribution pattern was observed. During this month, juveniles made up the majority of the chaetognath population. By early autumn (September), the abundance of *S.setosa* reached a maximum. The mean length of the population increased from

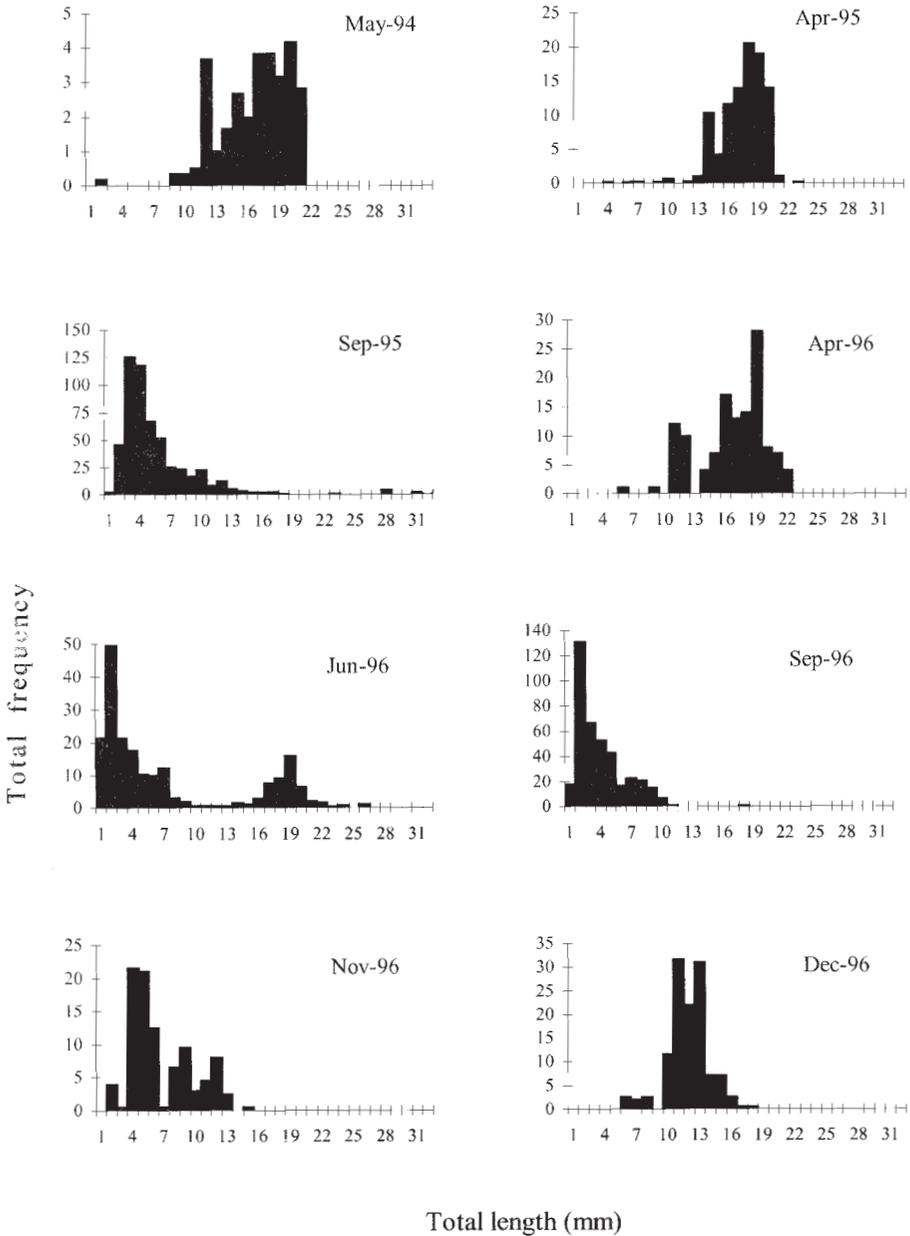


Fig. 9. Frequency distribution of total length (mm) of *Sagitta setosa* during the sampling periods.

June (7.2 mm long) through December (11.9 mm long), indicating growth of a new generation.

The percentage frequency of juvenile and adult *S.setosa* is shown in Figure 10. In April, May and December, the population comprised mainly adults (>5 mm

long). Juveniles (≤ 5 mm long) predominated in June, September and November, accounting for almost 60% of the population.

Vertical distribution and migration of S.setosa

Juvenile and adult *S.setosa* appeared to have quite different vertical distributions (Figures 11–13). Only one juvenile was observed in the water column in April 1995. This individual was collected from the top layer of the water column (Figure 11). In September 1995 and June 1996, juveniles were more abundant than adults.

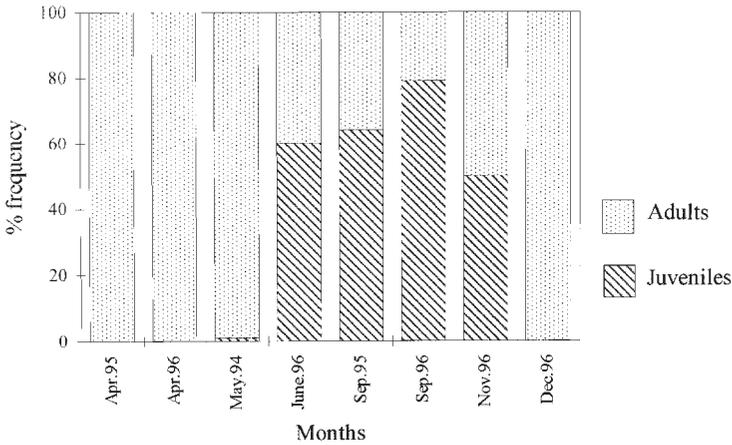


Fig. 10. Age composition of the *Sagitta setosa* population during the sampling periods. Juveniles ≤ 5 mm, adults >5 mm in length.

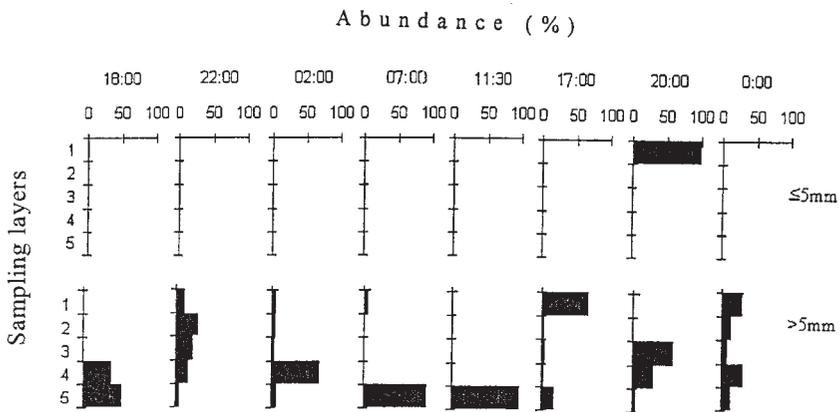


Fig. 11. Vertical distribution of juvenile (≤ 5 mm) and adult (>5 mm) *Sagitta setosa* at each sampling time during 26–28 April 1995. Abundance is expressed as percentage of total population in the water column. Depth intervals are defined in Table I. The sampling time is presented above the x-axis. Sunset = 1952 h; sunrise = 0606 h (local time).

During these periods, most of the juveniles were located above the thermocline throughout the day (Figure 12 and 13). In April, all adults were found at the depth of the OMZ during the day (at 0700 and 1130 h) and in the upper layers at night (Figure 11). In June, adults showed a bimodal vertical distribution, while some exhibited diel vertical migration from the depth of the OMZ to the surface (Figure 12). In September, diel vertical migration was restricted within the uppermost three layers (Figure 13). Adults exhibited small-scale migration; most were

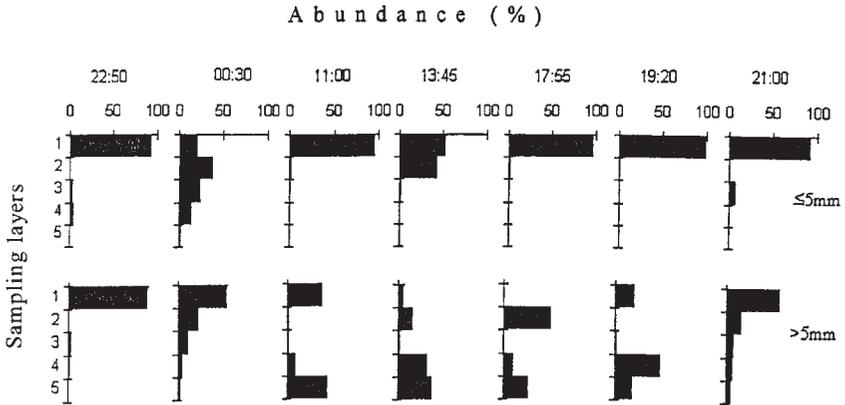


Fig. 12. Vertical distribution of juvenile (≤ 5 mm) and adult (> 5 mm) *Sagitta setosa* at each sampling time during June 1996. Abundance is expressed as percentage of total population in the water column. Depth intervals are defined in Table I. The sampling time is presented above the x-axis. Sunset = 2047 h; sunrise = 0525 h (local time).

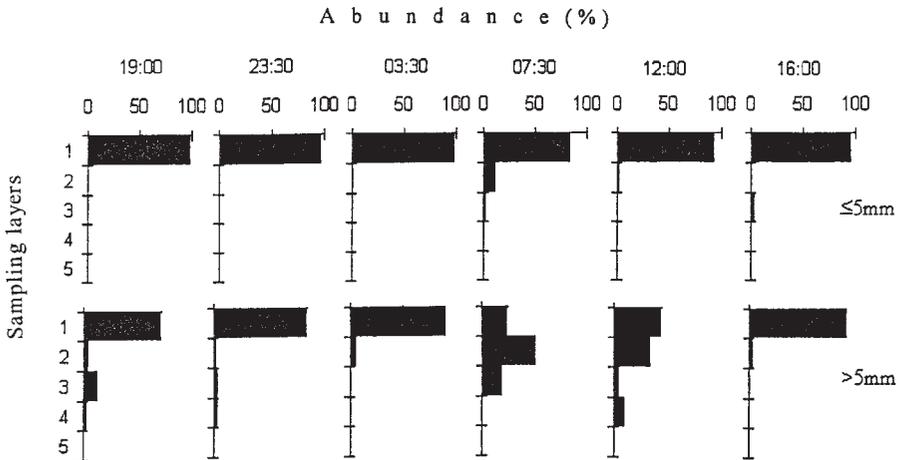


Fig. 13. Vertical distribution of juvenile (≤ 5 mm) and adult (> 5 mm) *Sagitta setosa* at each sampling time during 27–28 September 1995. Abundance is expressed as percentage of total population in the water column. Depth intervals are defined in Table I. The sampling time is presented above the x-axis. Sunset = 1743 h; sunrise = 0547 h (local time).

above the thermocline at night and distributed down to the third layers during the day.

Discussion

Population structure

We observed maximum abundance of *S.setosa* in September. A similar observation was made on the Crimean coast of the Black Sea (Sazhina, 1987). Maximum abundance of *S.setosa* in September coincided with the high abundance of copepods, the principal food for chaetognaths (Feigenbaum, 1991). Large numbers of copepods appear in June. This period of high copepod density and higher temperature is followed by the growth and maturity of *S.setosa*, suggesting that food and temperature are major factors affecting the growth of *S.setosa* in the Black Sea.

Breeding was probably most intensive from June to November (indicated by the frequency of small individuals). Oresland (Oresland, 1987) observed small individuals of *S.setosa*, indicating intensive spawning, from July to early October in the western English Channel. Figure 9 shows that by September, no individuals from the old generation remained in the present study. Niermann *et al.* observed the replacement of the entire population of *S.setosa* by a new generation in August in the Black Sea (Niermann *et al.*, 1997). Microscopic observation suggested that two broods were produced during the breeding period, as most of the adults belonging to the new generation had eggs in their gonads in June.

Vertical distribution and migration

The variation in vertical distribution and migration of *S.setosa* throughout the sampling periods appears to be related to the body length (maturity status) of the individuals. Core populations of juveniles (≤ 5 mm) were distributed generally above the thermocline and did not display significant vertical migration. However, the mean length of juveniles in the uppermost layer showed differences between day and night in April and June samples, indicating small-scale migration which cannot be discerned with our sampling depth intervals. Adult *S.setosa* (> 5 mm), however, underwent extensive migration between the surface and the depth of the OMZ. During their vertical migration, individuals of *S.setosa* were exposed to a large change in oxygen concentration (~ 20 -fold) and temperature (\sim threefold). This implies that the adults can tolerate a very wide range of temperature and oxygen concentration. Terazaki and Marumo showed a wide range of temperature tolerance in *Sagitta elegans* in the north Pacific Ocean [(Terazaki and Marumo, 1979) cf. (Conway and Williams, 1986)]. Saltzman and Wishner found chaetognaths to be a secondary dominant taxon in the core of the OMZ of the eastern tropical Pacific (Saltzman and Wishner, 1997), indicating that they can tolerate low oxygen concentrations.

It is thought that adult chaetognaths show more active migration than juveniles because of their increased swimming ability with size (Pearre, 1973; Conway and Williams 1986). The difference in vertical migration between the juveniles

and the adults in our study supports this hypothesis. In the subarctic Pacific, juvenile *S.elegans* were located within the upper 25 m during both day and night, while adults were migratory (Sullivan, 1980). Studies on the gut contents of chaetognaths showed that juveniles contained nauplii, small copepods and a few large copepods, while adults had larger copepods in their guts (Sullivan, 1980; Oresland, 1987; Stuart and Verheye, 1991). The gut contents of *S.setosa* were not analysed in this study, but Drits and Utkina (Drits and Utkina, 1988) studied the feeding of *S.setosa* in the Black Sea and observed *C.euxinus* and *P.elongatus*, as well as some nauplii, polychaetes and cyclopoids, in the guts of *S.setosa* (size range from 16 to 21 mm) collected from the surface at night. In the daytime when individuals of *S.setosa* resided in the OMZ, they contained *C.euxinus* and *P.elongatus* in their guts (Drits and Utkina, 1988). However, in the present study, a significant correlation was found ($P \leq 0.05$) between the vertical distribution of all copepods and adult *S.setosa* in the April samples, but this correlation was not obvious in the June and September samples. A significant correlation was observed between the vertical distribution of female *P.elongatus* and adult *S.setosa* in April, but not in June and September.

Diel vertical migration in adult *S.setosa* was observed from the upper layers down to the OMZ in April, when the entire population was made up of adults longer than 10 mm (from 10 to 22 mm length). In June, we observed that almost half of the adults migrated down to the OMZ during the day, whereas the other half showed limited vertical migration down to the third or fourth layers. In September, when the entire population consisted of individuals from the new generation and of these, almost 20% were adults (from 6 to 10 mm long), these adults showed restricted diel vertical migration down to the third layer. During September, no individuals were collected from the two lowest layers. From these observations, we can conclude that while older adults can migrate down to the depth of the OMZ, young adults show limited vertical migration down to the third or fourth layers. There may be some explanation for the limited vertical migration of young adult individuals of *S.setosa* in June and September. Firstly, because of high temperature and high food supply in June and September, they might have matured earlier, before completing their body growth. Although chaetognaths appear to grow throughout their life (Bone and Duvert, 1991), body growth generally slows down or stops with the onset of maturity [(Alvarino, 1965) and (Sameoto, 1971) cf. (Pearre, 1991)]. Their muscle fibre formation might not have been completed sufficiently to allow the individuals to swim down to the depth of the OMZ in June and September. Pearre (Pearre, 1979) suggested that young stages might have higher specific metabolic demands and lower storage capability and hence, are tied to the surface because of the need to feed more often. In addition, young adults might not be able to tolerate the low oxygen concentration in the OMZ.

Diel vertical migration of zooplankton has been linked to predator avoidance in past decades (Ohman, 1988, 1990; Bollens and Frost, 1989; Lampert, 1989; Loose, 1993). The common planktivorous fish in the Black Sea are sprat, mackerel and anchovy (Nalbantoglu, 1955; Acara, 1956; Sirotenko and Danilevskiy, 1977; Sirotenko and Istomin, 1978; Avsar, 1993). *Sagitta* was observed in the gut

of sprat (*Sprattus sprattus phalericus*) (Sirotenko and Sorokalit, 1979), and the vertical distribution of sprat is limited to the upper 70 m (Avsar, 1993). Low oxygen concentration in the OMZ may form a barrier to deeper penetration for these fishes in the Black Sea. Alldredge *et al.* (Alldredge *et al.*, 1984) suggested that low oxygen concentration may reduce predation on zooplankton. However, we need more information on the predation pressure on *S.setosa* at different depths and different times of the day to explain the reason for their diel vertical migration in the Black Sea.

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