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Diel vertical migration of *Sagitta setosa* as inferred acoustically in the Black Sea

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Abstract Swimming trajectories of chaetognaths *Sagitta setosa* Müller in the Black Sea were studied using an echosounder operating at 120 and 200 kHz and an acoustic Doppler current profiler (ADCP) operating at 150 kHz. *S. setosa* were acoustically discriminated with respect to vertical migration and swimming speed, according to dissolved oxygen (DO) concentration and the timing of migrations. *S. setosa* formed a concentration layer thicker than *Calanus euxinus* did (1–3 m). The migration was completed in about 2.5–4 h, upward migration starting before *C. euxinus* and downward migration after *C. euxinus*. Adult *Sagitta* swam fast only in the well-oxygenated layer (subsurface maximum DO). The DO was found to be a significant ($p < 0.05$) variable by partial correlation between the speed and hydrographical parameters. This feature constituted an oxygen-dependent influence on *S. setosa*'s vertical swimming and distinguished *S. setosa* from *C. euxinus*. Chaetognaths migrated daily between the nearsurface and the oxycline or the suboxic zone (OMZ, see Fig. 3b for the layers characterized by DO). Whether the deepest depth limit of migration was the oxycline or the OMZ depended on the relative abundance of adult and immature (young) individuals in the concentration layer. In July and September, individuals belonging to a new generation did not migrate but stayed in subsurface water day and night.

Introduction

Active acoustics provides a powerful tool for revealing the spatial distribution of sound-scattering layers (SSL) in the ocean. Both strong scatterers (organisms and abiotic particles with strong density and sound velocity contrasts relative to the water) and weak scatterers (e.g., many zooplanktors, physical microstructure) can be detected, depending on sound frequency. Acoustic data alone are inherently ambiguous with regard to the identities of the scatterers. With few exceptions the taxonomic identity of scatterers must be verified by supplementary information, such as nets, pumps or optical plankton counters (Foote and Stanton 2000). Nevertheless, some progress has been made in classifying organisms acoustically. Stanton et al. (1994, 1996, 1998a, b) and Stanton and Chu 2000 modeled acoustical scattering of organisms, producing calculations for organisms dominated by three different significant types of scattering: fluid-like, elastic shells, and gas inclusions. Field studies have recently demonstrated that signals from Antarctic krill *Euphausia superba* and the mysid *Antarctomysis maxima* can be separated using multi-frequency acoustic data alone (Brierley et al. 1998). However, direct identification from acoustics without using supplementary information is a rare achievement.

The Black Sea pelagic upper aerobic zone is separated from lower anaerobic layers containing hydrogen sulfide (H_2S) by the main pycnocline, which lies at depths of 70–200 m (Vinogradov et al. 1992). The pycnocline is accompanied by the oxycline, where oxygen concentration decreases from 7.9 to 9.8 $mg\ l^{-1}$ (subsurface maximum oxygen layer; see Table 1, Fig. 3b) at the water density interval, $\sigma_\theta = 14.0$ – 14.7 to 0.47 – $0.84\ mg\ l^{-1}$ at $\sigma_\theta = 15.3$ – 15.9 . The oxycline (OXL; Table 1) generally occurs over a depth change of 50–93 m (Poyarkov 1989). Below this, the oxygen concentration declines slowly to $< 0.16\ mg\ O_2\ l^{-1}$ at $\sigma_\theta = 15.9$ – 16.0 (AOMZ; Table 1), and can no longer be detected at $\sigma_\theta = 16.15$ – 16.20 (OMZ; Table 1, see also Figs. 3b, 5), where sulphide

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Table 1 Temporal distribution of abundance, stage composition, stage depended-lower vertical limit of *Sagitta setosa* collected with the plankton nets in the Black Sea

Months	Abundance (ind m ⁻³)	Abundance in CL (ind m ⁻³)	% Adult in population	LDL of vertical migration of	
				Adult	Juvenile
January (off-in)	0.48–1.3	35–97	96		
February			99		
March	1.12	181	98	OMZ	ML
April	1.5–1.8	250	~100	OMZ	ML
May	0.5	360	~98	OMZ	
June	3.8		~100, 40	OMZ–OXL	ML–TL
July			~10		
August	0.50–0.92	70–128	~5		
September	8.1–9.3		20–40	OXL–AOMZ	ML
October	2.15		56	OMZ–OXL	ML–TL
November	2.1		50		
December	1.9		~45		

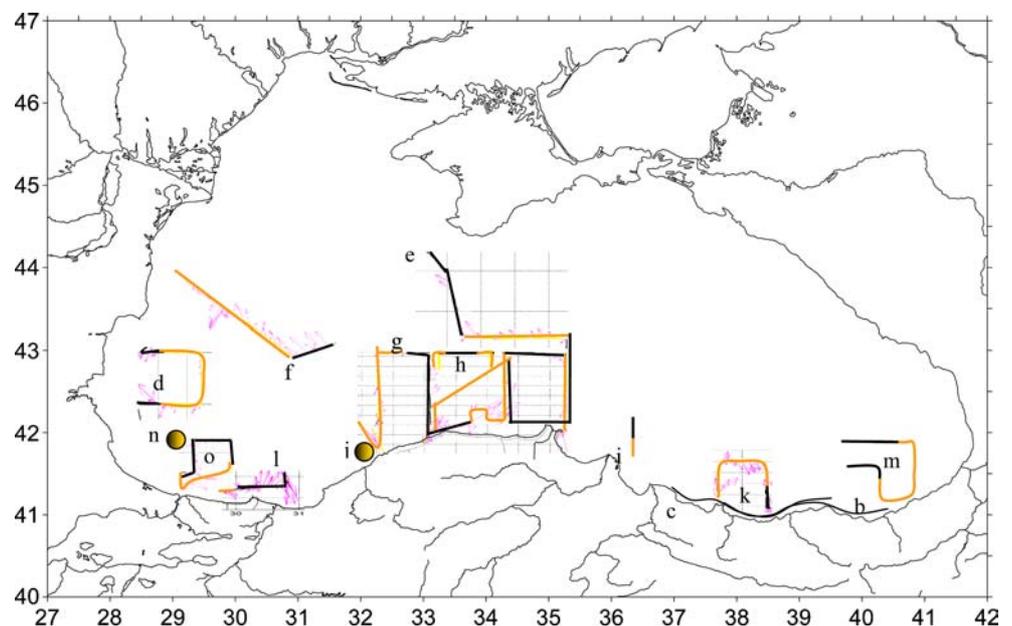
CL concentration layer of the *Sagitta*; LDL Lower depth limit; OMZ Oxygen minimum or suboxic zone, Tugrul et al. 1992; ML Mixed layer; OXL Oxycline; TL Seasonal Thermocline see Figs. 3b, 5; AOMZ Just above OMZ see Fig. 3b for definitions of the layers; off offshore; in inshore or shelf; **Bold layers**, where the specimens generally occurred; Adult specimens has lengths > 5 mm; Niermann et al. 1998, Vinogradov et al. 1985; Besiktepe and Unsal 2000; Erkan et al. 2000; Mutlu 2003a, b)

concentrations are 0.03–0.1 mg H₂S l⁻¹. This oxygen-deficient water, formed within the oxic/anoxic transition layer with oxygen concentration < 0.64 mg O₂ l⁻¹ and H₂S < 0.03 mg H₂S l⁻¹, is called the suboxic zone (Yilmaz et al. 1998). In the surface mixed layer (~0–30 m) see Table 1, Fig. 3b) temperature varies from 7 to 25°C due to seasonal fluctuations (Fig. 5). The temperature of the deeper waters remains consistent throughout the year, with a layer of cold intermediate water (CIL, Figs. 3b, 5), characterized by core temperatures of ~6°C, and a deep layer at 8°C. (Ozsoy and Unluata 1997; Yilmaz et al. 1998).

Previous studies (Vinogradov et al. 1985; Niermann et al. 1998; Besiktepe and Unsal 2000) have described general distribution of *Sagitta* in the Black Sea. The

species *S. setosa* is the dominant chaetognath species in the Black Sea (Niermann et al. 1998; Besiktepe and Unsal 2000). In the southern and western Black Sea, abundances of about 100–1,400 ind m⁻² on average were found between 1991 and 1995. High abundances were found at the shelf edges and in the rim (coastal main) current (Niermann et al. 1998). In the Black Sea, the peak of the *S. setosa* bloom occurs in July/August and September when most of the juveniles remain in the upper layer (Niermann et al. 1998; Besiktepe and Unsal 2000, Table 1, Fig. 2). In July, spawning starts and the number of adult individuals decreases rapidly. By July/August, the adults have virtually disappeared and are replaced by juveniles (Niermann et al. 1998). During summer and early autumn (June–September), the

Fig. 1 Locations (b January 1992, c February 1994, d March 1995, e April 1993, f April 1994, g May 1994, h June 1991, i July 2000 off Samsun, j July 2000 off Zonguldak, k August 1993, l September 1999, m October 1995, n October 1999 and o December 1993) of acoustic studies in the Black Sea (circle fixed stations, Dark line on trackline is nighttime and light line is daytime)



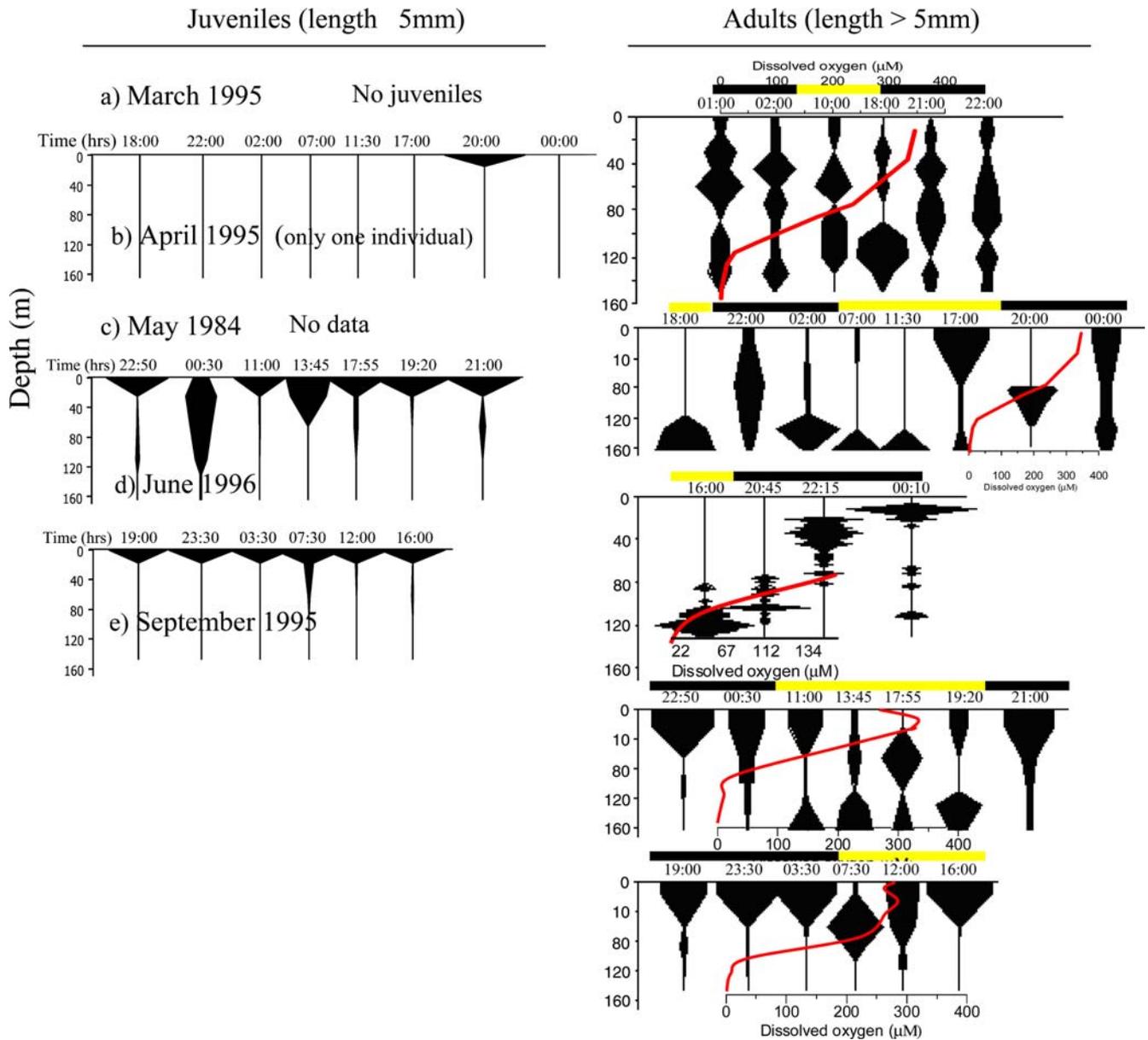


Fig. 2 Vertical distribution and migration of relative abundance (%) of juvenile and adult *Sagitta setosa* in the Black Sea in March 1995 (a); Mutlu 2003b), April 1995 (b), June 1996 (d) and

September 1995 (e); redrawn from Besiktepe and Unsal 2000), and May 1984 (c); Vinogradov et al. 1985; Profile is dissolved oxygen, *Dark line* on trackline is nighttime and *light line* is daytime)

juveniles of *S. setosa* dominate the populations that are generally distributed in the upper layers (Besiktepe and Unsal 2000, Table 1, Fig. 2).

Adult *S. setosa* perform diel vertical migrations between the anoxic zone or the oxycline and surface layers (Besiktepe and Unsal 2000, Table 1, Fig. 2). Limits of vertical distribution of *S. setosa* depend on stage composition and body length (Besiktepe and Unsal 2000). The maximum rate of the population's movement upwards was about 1 cm s^{-1} which, assuming the average length of chaetognaths to be about 17 mm, represents $0.6 \text{ body length s}^{-1}$ (Vinogradov et al. 1985). Usually the layer of maximum chaetognath concentra-

tion is more extended vertically and clearly separated from the layer of maximal *Calanus* concentration. *C. euxinus* tends to lag behind the chaetognaths that ascend from the deeper layers during the evening migration in May (Vinogradov et al. 1985).

Mutlu (2003a) identified *C. euxinus* in the Black Sea in June, July and October by looking at acoustical records directly and by using time spent swimming in response to distinct dissolved oxygen concentrations in the water column. A few individuals of *Mnemiopsis* were observed in deeper waters (Mutlu and Bingel 1999; Kideys and Romanova 2001) but at abundances below the acoustical detection threshold (Mutlu 2005). Two

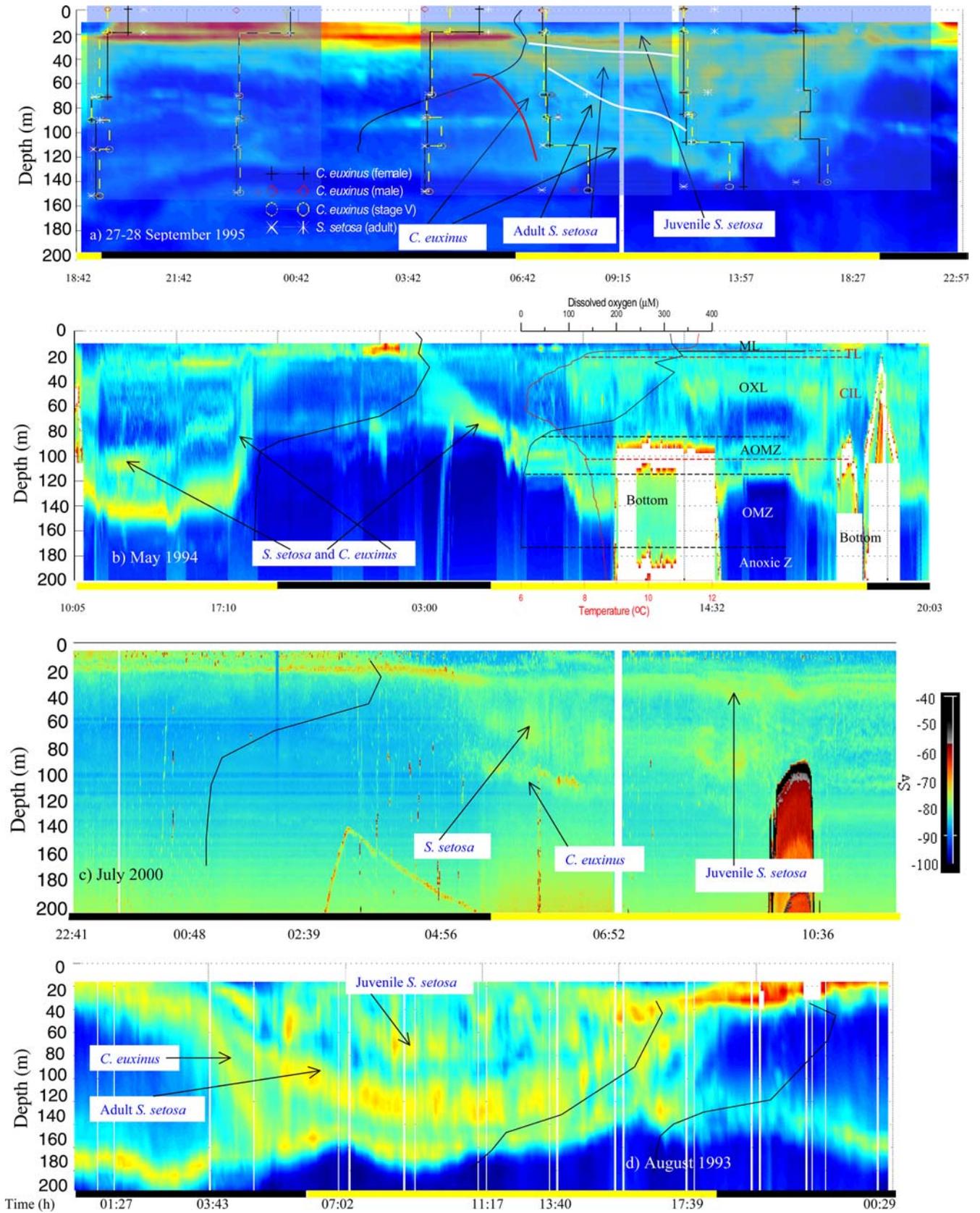


Fig. 3 a Comparison of acoustical (ADCP) results (present study) with plankton net results (Fig. 2e: redrawn from Besiktepe and Unsal 2000; Besiktepe 2001), September 1995. **b** Acoustical (ADCP) observations of upward and downward migration of *Sagitta setosa* (see Table 1), May 1994. **c** Acoustical (Echosounder) observations of upward and downward migration of *Sagitta setosa* off Samsun, July 1992. **d** Acoustical (ADCP) observations of upward and downward migration of *Sagitta setosa*: Black Sea, August 1993. **e** Acoustical (Echosounder) observations of upward and downward migration of *Sagitta setosa*: Black Sea, October 1999 and vertical distribution of meso and macro zooplankton abundances between 1949 and 2008 hours. **f** Acoustical (ADCP) observations of upward and downward migration of *Sagitta setosa*: Black Sea, December 1993 (*Black line* beneath echogram is nighttime and *yellow line* is daytime)

distinct scattering layers that migrated between surface and deep layers have been generally observed in acoustic records for the Black Sea: one has been documented to be composed of *C. euxinus* (Mutlu 2003a).

The aim of the present work was to identify the composition of the unknown scattering layer in the Black Sea from monthly acoustic records, based on the daily behavior of *S. setosa*. This ability would allow in situ monitoring of the species; estimation of biomass and better understanding of spatio-temporal distributional patterns.

Materials and methods

Acoustical backscatter data (echo intensity) were examined to discriminate and identify the concentration layer of *S. setosa* in the Black Sea. Acoustical data were collected with a scientific echosounder (BioSonics Model 120) at 120 kHz (October 1999, July 2000) and 200 kHz (June 1991, January 1992, February 1994, October 1999 and July 2000) and an acoustic Doppler current profiler (ADCP, RD broadband) at 150 kHz (March 1995, April 1993, 1994, 1995, May 1994, July 1997, August 1993, September 1995, 1996, 1999, October 1995, December 1993, Fig. 1). The echosounders were calibrated with a spherical ball of tungsten, and the transmitter of the echosounder was disabled to estimate the background noise that would be used to set the signal-to-noise threshold during post-processing of the data. During acoustical recording, Nansen rosette water samples and conductivity temperature depth profiles (Sea Bird Electronics, Model 9/11) were collected. Dissolved oxygen concentrations were determined using the Winkler titration method. Stratified water column samples ('Argus' submersible; Vinogradov et al. 1985 and Nansen opening-closing net (112 μm mesh size); Besiktepe and Unsal 2000; Mutlu 2003a, b) of meso- and

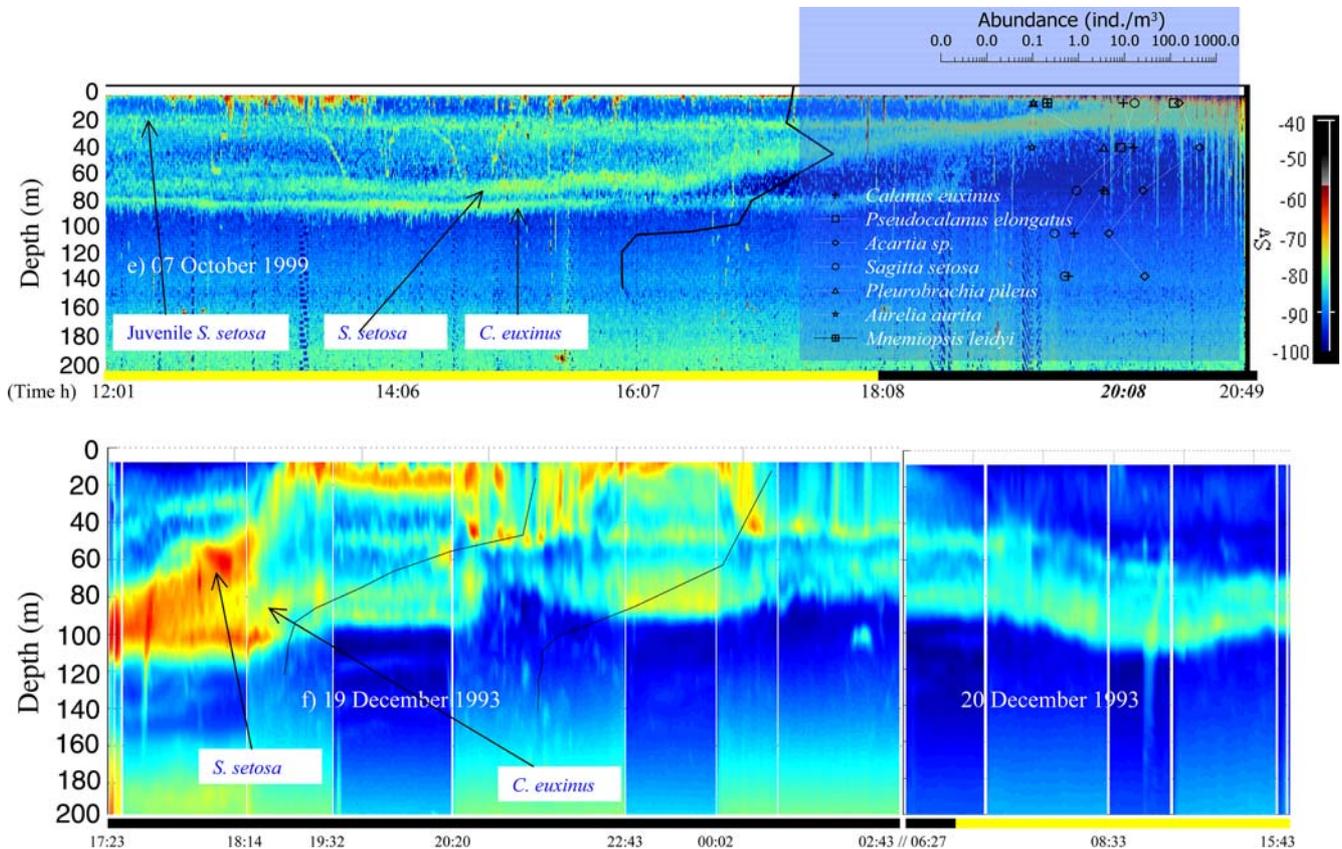


Fig. 3 (contd.)

Table 2 Variations in abundance (ind m^{-3}) of meso and macro zooplankton, which can be detected at 120 and 200 kHz, off Samsun (Fig. 3c) and Zonguldak with different sampling times in July 2000 (Mutlu 2003a)

Location	Time	Depth (m)	Adult <i>Calanus euxinus</i>	<i>Sagitta setosa</i>	<i>Aurelia aurita</i>	<i>Pleurobrachia pileus</i>
Zonguldak	1920	10–20	8.32	23.4	0	0
Zonguldak	2043	30–45	0.87	16.8	0.35	3.12
Samsun	0143	10–20	26.52	46.54	0	0
Samsun	0504	10–20	4.42	6.24	0.26	0.78
Samsun	0728	10–20	1.82	2.86	0.26	0
Samsun	1030	10–20	6.76	5.72	0.26	0

macrozooplankton were examined for indications of vertical migration by *S. setosa* (Tables 1, 2, and Figs. 2, 3d).

The echosounder data, S_v , were converted to volume backscattering strength, S_v , using the following equation:

$$S_v = 10 \times \log_{10}(S_v)$$

Where S_v has units of decibels (dB) m^{-1} , and S_v is the volume backscattering coefficient (a measure of the efficiency with which scatterers echo sound back to the source in a cubic meter) obtained from the transducer.

Acoustical data of the ADCP were converted to echo intensity (dB) using the following formula (RDI 1999).

$$I \text{ [dB]} = \text{EIS} \times I + 20 \log(R) + 2\alpha R$$

where EIS is echo intensity scale (dB/count) = $127.3 / (T_e + 273)$, I is echo intensity (counts), R is distance from transducers to ADCP depth cells in meters, α is the sound absorption coefficient (0.039 dB/m for 153.6 kHz), and T_e is the temperature ($^{\circ}\text{C}$) of the ADCP electronics.

Converted acoustical data were plotted as enhanced echograms (Fig. 3) showing the vertical distribution of scattering layers for each sampling period. Migration speed of *Sagitta* and physical data (temperature, density, salinity and dissolved oxygen) of the water column were subjected to the partial correlation of multiple regression analysis used for measuring the relationship between two variables while controlling the possible effect of other variables. Partial correlation is useful for uncovering hidden relationships, identifying intervening variables, and detecting spurious relationships. Wiebe and Greene (1994) formulated relationships between minimum detectable size of the target and the acoustical

frequency such that: ~ 10 mm individuals can be detected at 120 kHz; 4 mm, at 420 kHz; and 1.5 mm, at 720 kHz. However, David et al. (1999) determined that planktonic objects detected at 120 and 38 kHz have size limits, i.e., 3 mm at 120 kHz and 10 mm at 38 kHz, corresponding to one-quarter of the wavelength. Accordingly, the minimum size would be about 2 mm at 200 kHz and 2.5 mm at 150 kHz. “Detectable size of the target is actually a very complex subject and depends on many things. The important factors include diameter of the animal relative to the acoustic wavelength (hence wave number, ‘ka’ value), orientation, material properties, numbers of animals per unit volume, sensitivity of the echosounder, and distance from the transducer. Also, it is important to understand that even if an animal is detectable while isolated, once it is near another animal that has a greater target strength, the latter animal is the one that is detected” (Stanton, personal communication). Accordingly, adult and stage V of the *Calanus* and adult *Sagitta* and juveniles > 2.5 mm in length could be detected in the present studies.

Results

Two deep scattering layers (DSL) are generally observed at these acoustic frequencies to be migrating through the water column (Fig. 3a). Their vertical distribution changes in time and space because of variable layer thickness of the dissolved oxygen (DO) in the upwelling and downwelling regions in the Black Sea. Separation of the layers was very sharp during the diel migration. *Sagitta*’s migration speed as correlated with the oxygen concentration layers differed from those of *Calanus*. One

Table 3 *Sagitta setosa*: overall average migration speed (C) and average migration speed in subsurface maximum dissolved oxygen (CinS)

Months	Upward migration		Downward migration	
	C (cm s^{-1})	CinS (cm s^{-1})	C (cm s^{-1})	CinS (cm s^{-1})
March 1995	1.53	3.15		
April 1993	1.05	1.49		
April 1994	0.87	1.32		
May 1994	0.84	1.52		
July 2000	0.94	0.94	1.43	2.64
August 1993	0.92	2.14	1.50	3.47
August 1993	0.89 ^a	1.15 ^a	0.39 ^a	0.77 ^a
October 1995	0.76	1.33	1.13	2.64
October 1995	0.36 ^a	0.64 ^a	0.51 ^a	1.19 ^a
October 1999	0.62	2.02		
December 1993	1.64	3.05		

^a Marked number of the speed for the juveniles and others for the adult individuals)

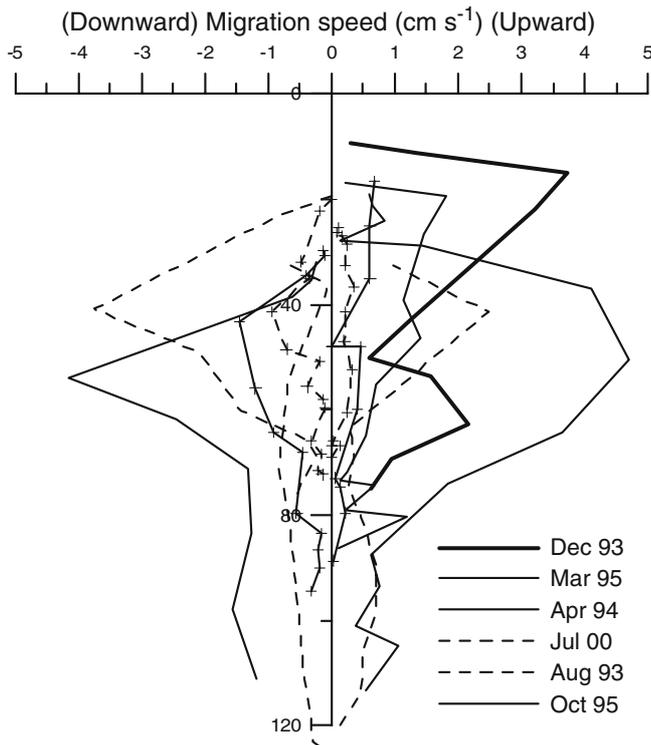


Fig. 4 *Sagitta setosa*: Temporal and stage-based migration speed as function of depth \pm marked line for the speed of the juveniles in the Black Sea

layer, which is known to belong to *C. euxinus* (Mutlu 2003a), migrated very fast at 2.8 cm s^{-1} through normoxic ($\text{DO} > 50 \mu\text{M l}^{-1}$) layers (migrational path along the red line in Fig. 3a, from the surface, through the mixed layer, ML up to $\sim 130 \text{ m}$) oxygen minimum zone, OMZ, Svetlichny et al. 2000; Mutlu 2003a). The other layer rises very fast only through well-oxygenated ($\text{DO} > 250 \mu\text{M l}^{-1}$) layers just above the oxycline (OXL). The pattern of daily upward and downward migration of the two DSL's showed significant differences in timing (migrational path along the white line in Fig. 3a).

Although most of the juvenile population of *S. setosa* appeared to stay in the ML or above OXL, a small part of the population migrated below the layers. This could be midnight sinking as Cushing (1951) described that midnight sinking is one of the five phases of nocturnal vertical migration that is commonly performed by zooplankton. Alternatively, Pearre (1979) suggested that satiation was the cue for sinking, possibly operating through the slowing of swimming speed or the increase in density when satiated. Net sampling disclosed much less vertical migration of juvenile than of adult *S. setosa*. Adults were found to perform diel migrations through the oxygenated water column (Table 1; Figs. 2, 5). The lower depth limit of migration within the oxygenated layer depended on stage (adult and juvenile) composition (Table 1; Fig. 2). Both net and acoustic surveys conducted off Bosphorus (Fig. 2f) in September 1995

revealed diel vertical migration of both *S. setosa* and *C. euxinus* (Fig. 3a). The concentration layer of *S. setosa* moved at a speed of $\sim 1.6 \text{ cm s}^{-1}$ from ~ 100 to $\sim 40 \text{ m}$ between 2045 and 2145 (Fig. 2c) hours.

Of the three scattering layers observed to stay within the upper waters during the generation time (July and September/early October) of *S. setosa*: one scattering layer did not migrate while the other layer moved within well-oxygenated upper water, and a third one (*C. euxinus*) migrated between the surface and OMZ. Non-migratory layers are postulated to belong to juveniles (length $\leq 5 \text{ mm}$, Besiktepe and Unsal 2000) of *S. setosa* in July, September and early October (Figs. 2e, 3a, c, e). But many plankters remain near the surface: presumably these non-migratory layers could include the large *Pleurobrachia*, *Mnemiopsis*, *Aurelia*, or *Beroe*. The limited migratory layer in the upper water column is found to be composed of adult *S. setosa*, individuals with length $> 5 \text{ mm}$, based on the work of Besiktepe and Unsal 2000. Of the migratory layers, the one first descending at dawn was the concentration layer of *C. euxinus* (Fig. 3a). Mutlu 2003a describes the swimming behavior of *C. euxinus* in response to dissolved oxygen. Stratified net samples were dominated by adults of both sexes along with stage V *C. euxinus* within the OXL (Fig. 3a) in the early morning when adult and juvenile *S. setosa* were still in the upper waters (Figs. 2e, 3a). The next layer descending, lagging behind *C. euxinus* in time, was composed of adult *S. setosa* that reached the deeper layers around midday and soon began an upward migration in the early afternoon (1230 hours; Figs. 2e, 3a) when all *Calanus* were in the deeper layers (80–120 m). By twilight, *Calanus* started its upward migration at 1600 hours, thereafter all individuals of the group moved upward very fast (Fig. 3a), although a weak scattering layer alone in the deeper water was found to be composed of male *C. euxinus* (Fig. 3a).

During the cold-water season (December–March, Fig. 3d), the DSL was composed of concentrated layers of *S. setosa* and *C. euxinus* that ascended and descended together in the water column during their daily migration. By April, *S. setosa* started migration before *C. euxinus*. *S. setosa* began ascending from the OMZ by twilight, and reached the surface waters within about 4 h, during which time they ascended at constant speed, and exhibited a different trajectory from that of *C. euxinus*. The same path occurred in May (Fig. 3b). During the warm-water season (June–October) when the juveniles of *S. setosa* were more abundant than the adults, they spent their daylight time just above the OMZ. Generally, they started descending together with *C. euxinus* by dawn, but *C. euxinus* descended down past the CIL more rapidly than *S. setosa* and thus reached their daylight depth earlier than *S. setosa* did (Fig. 3c).

Concentration layers of adult *S. setosa* appeared to be distinct from those of the juveniles in a period of warm water seasons (June–October). Juvenile *S. setosa* first appeared in June and were found in the surface waters. Concentration layers of juveniles appeared to be

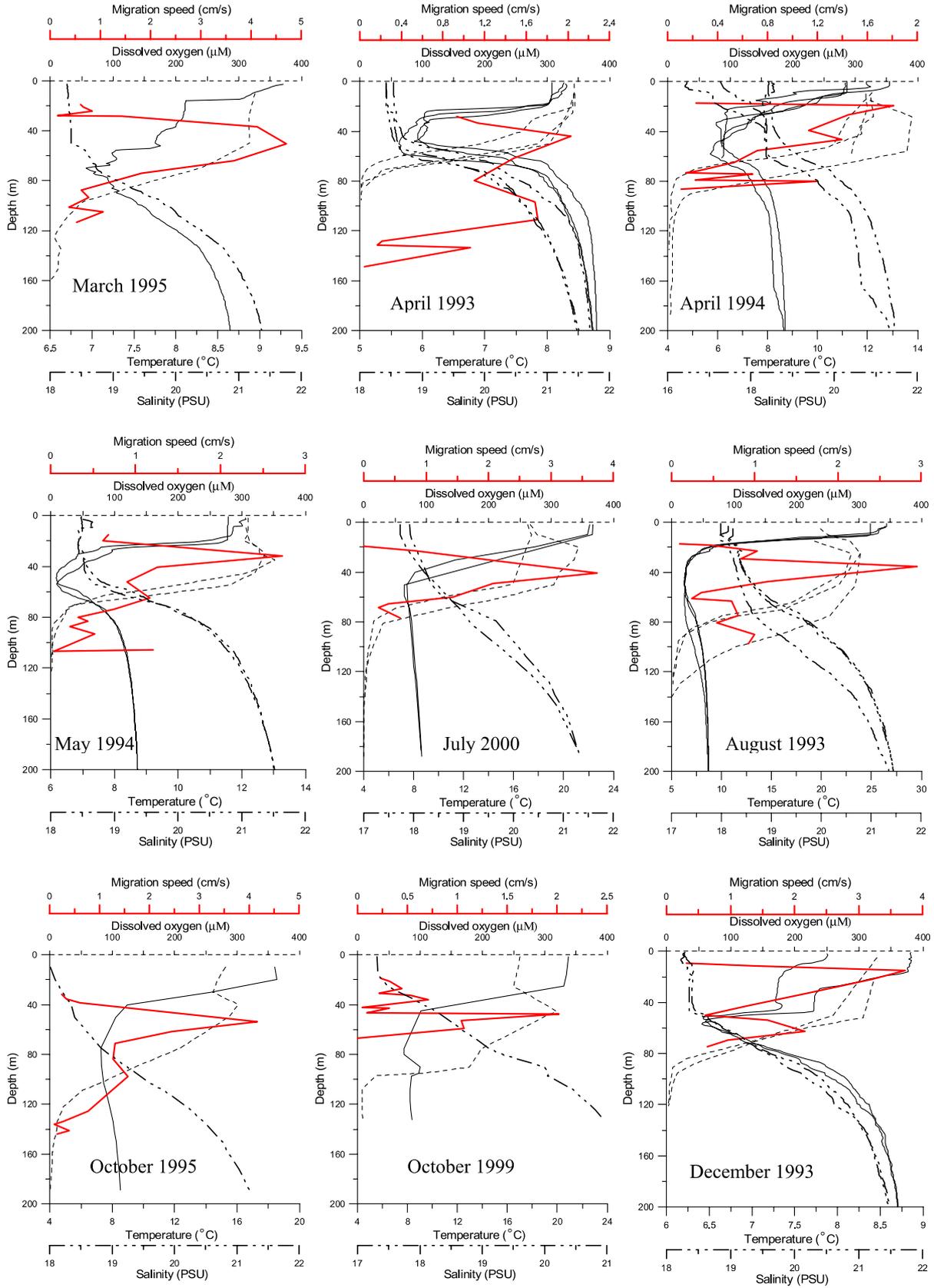


Fig. 5 Temporal vertical migration speeds of adult *Sagitta* individuals against the hydrographical data in the Black Sea

non-migratory during June and July. In August, the juveniles performed a daily vertical migration which had a reduced amplitude compared to that of the adults (Fig. 3d). The adults reached deeper layers than the juveniles during the daylight. The migrational patterns of juveniles and adults during July–August were similar to those found in September–mid October.

Adult *S. setosa* generally descended at higher mean speed ($> 1 \text{ cm s}^{-1}$) than they ascended during their daily migration. *S. setosa* juveniles that showed the limited vertical movement in August 1993 and October 1995 migrated at lower speed than the adults did (Table 3, Figs. 3d, 4). In general, the migration of *S. setosa* was completed in 2.5–4 h. The maximum migration speed of *S. setosa* varied between 2.0 and 4.0 cm s^{-1} and is only observed in well-oxygenated layers ($\text{DO} > 200\text{--}250 \mu\text{M l}^{-1}$). The swimming speed is $< 2 \text{ cm s}^{-1}$ in layers with $\text{DO} < 150 \mu\text{M l}^{-1}$ (Fig. 5). The speed decreases when the individuals reach the surface waters with $\text{DO} > 250 \mu\text{M l}^{-1}$ and complete upward migration (Fig. 5). *S. setosa* starts ascending by dusk during the cold-water season while they begin their ascent during the afternoon in the warm-water season. *S. setosa* exhibited a higher swimming speed only within well-oxygenated subsurface water and appeared unable to sustain the high speed within the oxycline and OMZ (Figs. 3, 5).

Discussion

The dominant sources of acoustical scattering at 120, 150 and 200 kHz in the surface waters of the Black Sea found here are the chaetognath *S. setosa* and the copepod *C. euxinus*. There are three species (*Pleurobrachia pileus*, Ctenophora; *S. setosa*, Chaetognatha; and *C. euxinus*, Copepoda) of adult zooplankton that are $> 2 \text{ mm}$ long (\sim minimum detectable size at 200 kHz, David et al. 1999; Mutlu 2003a, 2005) and migrate through the water column from the deep to the surface in the Black Sea (Vinogradov et al. 1985; Mutlu and Bingel 1999; Besiktepe and Unsal 2000; Besiktepe 2001; Mutlu 2003b). Other larger species (*Aurelia*, *Mnemiopsis*

and *Beroe*) do not penetrate beneath the thermocline during their daily migrations in the Black Sea (Mutlu and Bingel 1999, Mutlu and Bingel 1999; Kideys and Romanova 2001). *Aurelia* is a significant sound scatterer with target strength, $S_v \text{ ind}^{-1} \text{ m}^{-3}$ ($\text{TS} = S_v - 10 \times \log_{10} N$ where N is abundance, ind m^{-3}) varying between -64 and -56 dB , and -60 and -57 dB (*Aurelia* disc diameters from 9.5 to 15.5 cm) at 200 and 120 kHz, respectively (Mutlu 1996) but its vertical depth ranges are restricted to the upper waters. *Pleurobrachia pileus* and *Mnemiopsis* are very similar in acoustical properties to *Bolinopsis* (-75.9 dB at 200–1,000 kHz; -80 dB at 420 kHz; Wiebe et al. 1990; Monger et al. 1998; Benoit-Bird and Au 2001) are very weak scatterers owing to the high water content in the body (97%: Reeve et al. 1978). Chaetognaths are also often considered gelatinous, but have a lower water content. Specifically, water content of *S. setosa* in the Black Sea was reported to be 91.4% (Petipa et al. 1970) and 92% (Greze 1970). Individuals of *P. pileus* were distributed almost throughout the entire water column and had two concentration maxima (Vinogradov et al. 1985; Mutlu and Bingel 1999). Mutlu (2003a) acoustically identified *C. euxinus* in the Black Sea in June/July and October. Background noise levels (the minimum threshold in S_v) of the 120 kHz were -78.5 ± 0.8 (SD) dB in the Black Sea and the noise levels of the 200 kHz were 4 dB lower than those of 120 kHz (Mutlu 2005), which is almost equal to target strength of gelatinous *P. pileus*. Mutlu (2003a) showed that *P. pileus* scattered very little at 120 and 200 kHz in October 1999 (Fig. 3e). At the same time (2008 hours), *P. pileus* was mostly found below 30 m, where no scattering was observed. The rest of the gelatinous organisms were found at the surface in low abundances. Volume back-scattering strength (S_v) of the layers belonging presumably to *S. setosa* was measured to be less than -70 dB (Fig. 3c, e) during migration and daylight time. At night, S_v greater than -70 dB for individual scatterers was measured and varied between -50 and -70 dB (Fig. 3c, e) in the upper waters where all scattering layers were mixed. Individual scatterers with the higher S_v appeared to be seldom in the upper waters during the daytime (Fig. 3c). These could be jellyfish. Toward midnight, *Aurelia* could be found within the CIL (Mutlu 2001) as Mutlu (2005) found the same trend in the Sea of Marmara: *Aurelia* was aggregated in the interface between waters of the Black Sea and Mediterranean Sea between 2200 and 0100 hours, was then distributed throughout the water column until 0600 hours, and then ascended to the surface waters and stayed there during the daylight (the acoustical record stopped at 1300 hours). Such movement of *Aurelia* could also be related with results described by Hammer et al. (1994): *Aurelia aurita* uses a sun compass to migrate in a southeasterly direction during the day. Mutlu (2005) estimated S_v of Chaetognatha by using the sound scattering model inputted with data of individual lengths (2.4–25 mm) and abundance ($1\text{--}100 \text{ ind m}^{-3}$) in the Turkish seas; the S_v varied between -82 and -67 dB . Taking the minimum S_v

Table 4 Partial correlations between migration speed (cm s^{-1}) of adult *Sagitta setosa* and the dissolved oxygen (DO), the density (D), the temperature (T) and the salinity (S)

Months	DO	T	S	D
March 1995	0.791	-0.051	0.538	0.545
April 1993	-0.656	-0.736	-0.962	-0.985
April 1994	0.787	0.506	-0.473	-0.486
May 1994	0.667	-0.539	-0.114	0.128
July 2000	0.802	-0.569	0.334	0.328
July 2000	0.832	0.280	-0.412	0.060
August 1993	0.622	0.559	-0.235	-0.241
October 1995	0.739	-0.711	-0.078	-0.060
October 1999	0.574	-0.638	-0.392	-0.392
December 1993	0.782	0.025	-0.832	0.829

Bold numbers are the correlation coefficients significant at $p < 0.05$

(dependent on the threshold and detection limits of the frequencies, see Mutlu 2003a, 2005 for Stanton, personal communication) into calculation of expected S_v , principal scatterers at 200 kHz in the near-surface of the Black Sea were copepods and chaetognaths; significant correlation were found between the measured S_v and both biomass and abundance of the chaetognaths. In a few samples, the model estimates indicated that chaetognaths could account for a substantial fraction of the total backscattering of the plankton on Georges Bank (Wiebe et al. 1996).

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. 1985, 1990, 1992; Besiktepe and Unsal 2000). The layer containing *S. setosa* can be discriminated from that of *C. euxinus* as Mutlu (2003a) shows different migration patterns during their vertical migration. The swimming speed of *C. euxinus* during migration varies from a passive sinking speed of $\sim 0.57 \text{ cm s}^{-1}$ (Svetlichny et al. 2000) within the suboxic zone to an active speed of 2.3 cm s^{-1} (upward) and to 2.7 cm s^{-1} (downward) by the oxycline through well-oxygenated water. When waters are cooler (December–May), *S. setosa* co-exists with *C. euxinus* within the OMZ during daylight so that these two scatterers appear as a vertically more extended layer than that seen in the warm-period. At this time, the population of *S. setosa* is composed of adult individuals with good swimming capabilities due to well-developed longitudinal epithelium muscle and caudal and lateral fins (Duvert and Salat 1990). Bone and Duvert (1991) pointed out that the locomotor muscles of *Sagitta*'s trunk that oscillate the body in the vertical plane during swimming have an unusual and striking structure and include several different fibre types.

From July to September, acoustical scattering layers belonging to *S. setosa* stayed just above the OMZ during the daylight. At that time interval, the juvenile individuals comprise more than 50% of the total population. In June, Besiktepe and Unsal (2000) observe that almost half of the adults migrate down to the OMZ during the day, whereas the other half show limited vertical migration down to the oxycline or layer just above the OMZ. From these observations, Besiktepe and Unsal (2000) proposed that it was the older adults which migrated down to the OMZ, while young adults showed limited vertical migration down to the oxycline or the AOMZ. This could explain occurrence of three different scattering layers belonging to *S. setosa* in the Black Sea during a year: non-migratory surface layer (1; juveniles) occurred in July and September/early October (Fig. 3a, c, e), migratory layers (2; adults) appeared all the year, and limited migratory layers (3; young adults) occurred in August and October (Fig. 3d). Although chaetognaths appear to grow throughout their life (Bone and Duvert 1991), body growth generally slows down or stops with the onset of maturity (Pearre 1991). In September, the entire population consisted of individuals

from the new generation, and of these almost 20% are adults (6–10 mm long). These adults show restricted diel vertical migration down the oxycline. During September, no individuals were collected from lower end of the oxycline and the OMZ and young individuals stayed in subsurface waters, showing no diel vertical migration (Besiktepe and Unsal 2000; Erkan et al. 2000). A study conducted between January and August showed that in the Black Sea the peak of the *S. setosa* bloom occurred in July/August between years of 1991 and 1994 (Niermann et al. 1998). They observed that all individuals were adults in June 1991 in contrast to observations in June 1996 (Table 1; Besiktepe and Unsal 2000). Pearre (1979) suggested that young stages might have higher specific metabolic demands and lower storage capability and hence, are tied to the surface because they need to feed more often. In contrast to the layer staying in the surface waters, there was a scattering layer staying below the oxycline at nights of some months (more pronounced in March, April, August and less pronounced in late April–August and late October–December). This could be *Calanus*' diapausing layer that occurred in the Black Sea (Vinogradov et al. 1985, 1990; Besiktepe 2001). Usually, the scattering layer of chaetognath concentration was clearly separated from the layer of maximal *Calanus* concentration and was more extended vertically as found by Vinogradov et al. (1985) using a submersible and plankton nets.

In contrast to the pattern observed during downward migration, *C. euxinus* lagged behind *S. setosa* during upward vertical migration. In general, *S. setosa* and *C. euxinus* reached the subsurface water during nighttime at about the same time; however, *S. setosa* started their migration before *C. euxinus* did. This could also be related to possible effects of the trophic link between *S. setosa* and *C. euxinus*. As *C. euxinus* is known to be an important prey of *S. setosa* in the Black Sea (Mironov 1960), this link may well have an important influence on the timing and depths of migrations. *S. setosa* migrated at constant speed varying from 0.38 to 0.70 cm s^{-1} depending on the season until they reach the upper limit of oxycline. Then they speed up through the maximally well-oxygenated subsurface water to speeds comparable to that below the maxima of subsurface water *C. euxinus*. Vinogradov et al. (1985) report the same observation, but did not relate the acceleration to oxygen concentration when the concentration layer of *S. setosa* reached well-oxygenated waters ($\text{DO} > 250 \mu\text{M l}^{-1}$). The faster swimming could be related to the higher oxygen or to feeding movements or activities as a function of metabolic rates. Chaetognaths can produce very rapid, directed movements to catch their prey and avoid predators, and most of the pelagic species that are denser than sea water show regular brief bursts of swimming alternating with passive sinking (Bone and Duvert 1991). Planktonic chaetognaths attack at very short range (Feigenbaum 1991).

Two hypotheses have been put forward to account for the observed decline in metabolic potential with

depth: the food limitation hypothesis and the visual interactions hypothesis (Childress et al. 1990; Thuesen and Childress 1993). In contrast to the rapid declines in metabolic potential with depth that have been observed for pelagic fish and crustaceans, no decline in metabolic rate nor in enzyme activities can be ascribed to depth of occurrence for pelagic chaetognaths (Thuesen and Childress 1993). Pearre (1979) suggested that adult individuals feed intensively in the subsurface water at night and then return to their daytime depth to digest their prey. The present acoustical study showed that the concentration layer of *Sagitta* did not stop passing up throughout the maximally well-oxygenated subsurface water until they reached their feeding depth at night. So observations of the faster migration speed in both upward (for feeding) and downward (for digestion) migrations support the hypothesis that the faster swimming could be dependent on dissolved oxygen of the water column. The migration speed was significantly correlated with only the dissolved oxygen for monthly data (Fig. 5) with a few exceptions (April, August 1993, and October 1999; Table 4), and was correlated with temperature in October 1995, and salinity and density of the water column in December 1993.

In conclusion, taking the minimum background noise threshold and detection limit of acoustical frequencies (120, 150 and 200 kHz) into account, the concentration layer of *S. setosa* can acoustically be identified by observing their diel migrational pattern during different months in the Black Sea. *S. setosa* showed different patterns in time depending on their generation time and stage composition. During the cold-water season when their population consisted mainly of adult individuals, their daytime concentration layer coexisted with that of *C. euxinus* in the OMZ whereas in the warm-water season when the immature individuals (juveniles) comprised more than 60% of the population (Besiktepe and Unsal 2000), the concentration layer stayed in the oxycline. In July and September, detectable individuals of the new generation did not migrate during the day and stayed in subsurface water. *C. euxinus* started accelerating upon entering the oxycline while *S. setosa* accelerated only after entering well-oxygenated subsurface water. This feature distinguishes *S. setosa* from *C. euxinus*. *Sagitta setosa* completed its migration within 4 h.

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