ORIGINAL ARTICLE

A comparison of the contribution of zooplankton and nekton taxa to the near-surface acoustic structure of three Turkish seas

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Abstract

The bioacoustics of upper waters of the Black Sea, the Sea of Marmara, and the Mediterranean Sea were studied in October 1999 with an echosounder with 120 and 200 kHz dual-beam transducers. Net tows were taken to ground-truth the acoustic volume backscattering. A forward solution was applied to determine significant scatterers of the three seas with regard to detection limits of the frequencies and background noise measured in each sea. The noise was 4 dB higher in the Sea of Marmara than in the other two seas. 200 kHz data showed significant correlation between measured and calculated volume backscattering strength, and density (biomass and abundance) of the taxa. Large-sized copepods and chaetognaths in the Black Sea, *Aurelia*, *Beroe*, chaetognaths and large-sized and abundant appendicularians in the Sea of Marmara, and fish larvae in the Mediterranean Sea contributed most to the volume backscattering.

Problem

Bioacoustics have been long used to obtain meaningful information about the length, numerical density, and distribution of zooplankton and fish (Foote & Stanton 2000). In addition, acoustic scattering models need to be used to describe the efficiency with which the animals scatter sound. High frequencies (12 kHz and higher) have been used for different purposes such as determining the distribution of biological sound scatterers, suspended sediments, internal waves and other physical features (Greene & Wiebe 1990; Simmonds *et al.* 1992; Stanton *et al.* 1994, 1998a, 1998b; Wiebe *et al.* 1996, 1997; Stanton & Chu 2000). Generally, zooplankton populations are much more complicated than those of fish. The populations contain a wide variety of animal types, giving rise to great variations in the acoustic reflective or scattering properties. There are several major anatomical categories of zooplankton: fluid-like, gas-bearing, and elastic shelled (Stanton *et al.* 1994). Stanton & Chu (2000) discussed some recommendations on the DWBA-based (Distorted Wave Born Approximation) deformed cylinder model,

which is used to predict acoustic scattering by euphasiids and copepods over a wide range of modeling parameters including shape, material properties, and animal orientation.

The principal objectives of this study were to make acoustical measurements (total volume backscattering and target strength distribution) in three Turkish sea areas (the Black Sea, the Marmara Sea, and the Mediterranean Sea) in order to compare the near-surface backscattering fields and to estimate the contributions to these fields by the zooplankton and nekton community.

Material and Methods

An acoustic and net survey of the seas around Turkey was conducted in October 1999 (Fig. 1) aboard the R/V Bilim. Measurements were performed during day and night to observe daily variation in zooplankton. When the echosounder collected acoustic data, a Nansen Opening-closing net (0.112 mm mesh and 70 cm circle mouth opening) collected zooplankton at five fixed stations: two stations in the Black Sea, one station in the Sea
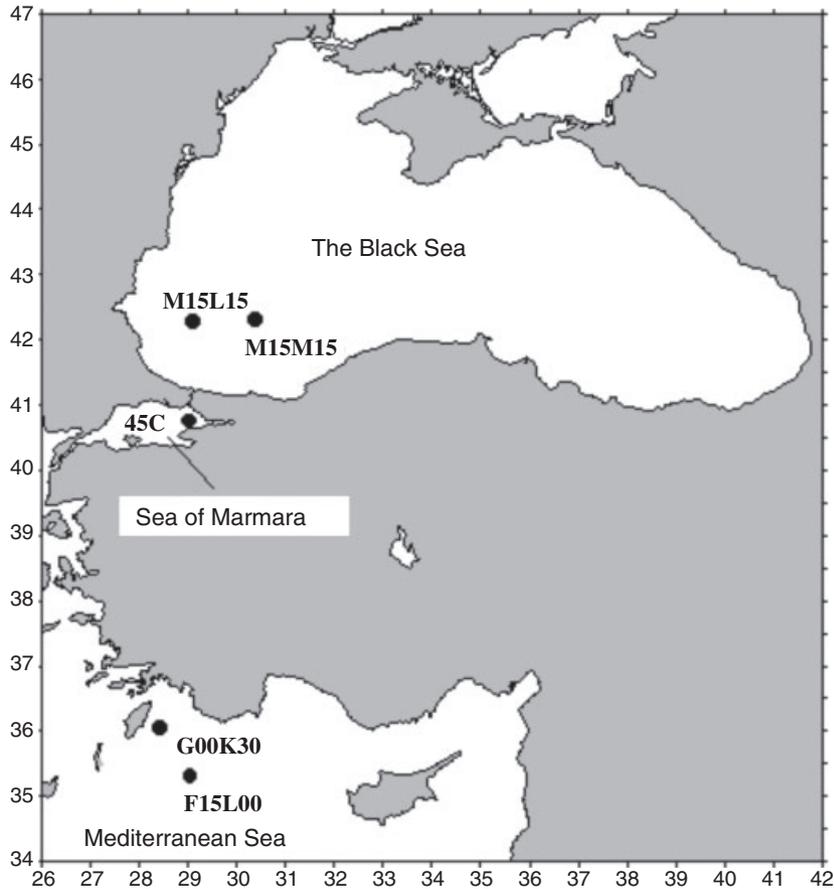
Fig. 1. Stations where zooplankton was collected with the net and acoustical records were made. M15L15 and M15M15 were in the Black Sea; 45C was in the Sea of Marmara; G00K30 and F15L00 were in the Mediterranean Sea.

of Marmara, and two stations in the Mediterranean Sea (Fig. 1). The net tows sampled layers between 15 and 5 m in the Sea of Marmara, mostly between 30 and 10 m in the Mediterranean Sea, and between 30 and 5 m and between 10 and 5 m in the Black Sea (Fig. 2a). The sampling depths were designed to cover only thermocline and mixed layers (excluding the uppermost 5 m) for better comparison of the different hydrographical properties of the seas. These depth ranges were also those in which acoustical background noise was very low. The net was hauled vertically at 1.5 knots; depth was estimated by wire out, and volume filtered by the distance the net traveled and mouth area. Gelatinous macrozooplankton was sized on board. The rest of samples were preserved in 4% formalin solution buffered with borax. Later, numbers [indiv.·m^{-3}] and biomass [mg·m^{-3}] of taxa were determined using standard procedures in the laboratory. Zooplankters were measured for total length and width. The diameters of gastropods, bivalves, jellyfish, and a ctenophore, *Pleurobrachia pileus*, were also measured. Biomasses were calculated from length-weight relationships (Shmeleva 1965).

A dual-frequency (120 and 200 kHz), dual-beam echosounder (Model 102), built by BioSonics Inc., was mounted in a V-finned towed body and deployed so that the towed body was 2 m below the surface. Parameters of the acoustic system during the survey are given in Table 1. The transmitter of the echosounder was disabled to estimate the background noise that would be used to set signal-to-noise threshold during post-processing of the data. Volume backscattering strength, Sv [where Sv = $10 \times \log_{10}(s_v)$ in units of decibels·m^{-1} and s_v is the volume backscattering coefficient], is a measure of the efficiency with which scatterers echo sound back to the source in a cubic meter. These data were collected from 5 to 40 m in 0.1 m depth bins for both frequencies. The data were averaged at 5 s intervals.

The backscattering data were ground-truthed with the taxonomic data from microscopic analyses in order to determine relative contributions of different functional groups to backscattering intensity. The length and width measurements for each individual were used in equations appropriate for the taxonomic groups developed by Stanton *et al.* (1996, 1998a, 1998b), Monger *et al.* (1998),
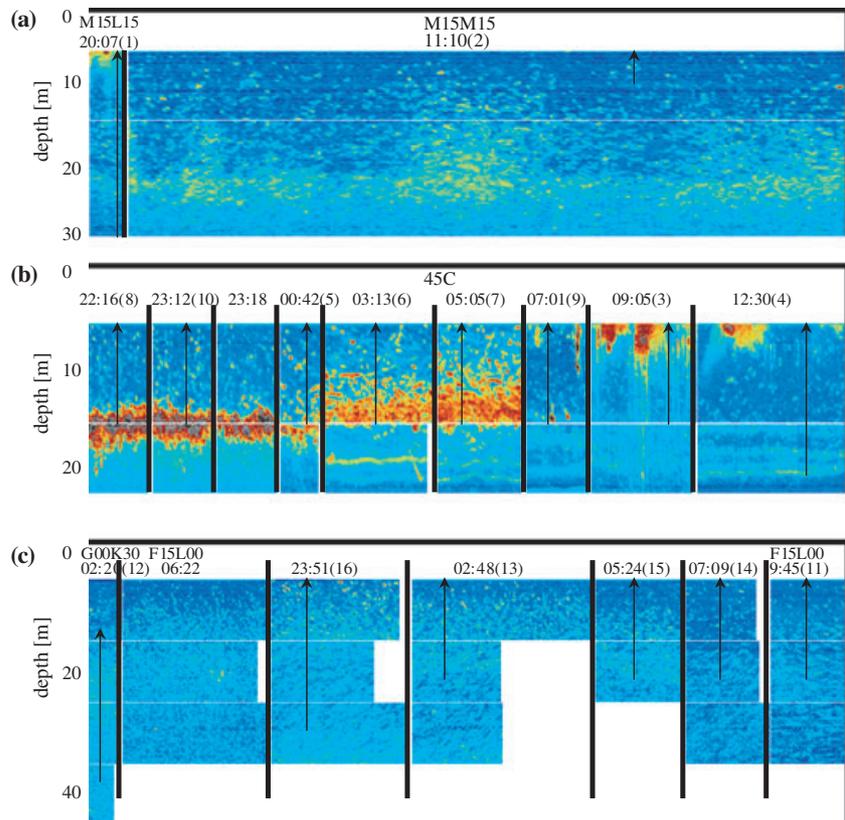
Fig. 2. Enhanced echograms (200 kHz) of sound scatterers of area to be purposed for the models in the Black Sea (a), the Sea of Marmara (b), the Mediterranean Sea (c) (arrows show net sampling depth intervals). Numbers in parentheses denote station number used in Figs 6–11.

Table 1. Calibration data and processing parameters for hydroacoustic system (PW, pulse width).

sounder parameters			
pulse width [ms]	0.4		
trigger interval [s]	0.5		
speed of sound [m·s⁻¹]	1500		
receiving gain [dB]	0		
transmit power [dB]	0		
	processing criteria		
noise threshold [V]	based on *in situ* measurements only listening		
frequency [kHz]	120		200
source level [dB]	223.51		222.69
receive sensitivities	narrow	wide	narrow	wide
20 log(R) [dB]	−154.53	−154.56	−149.59	−149.69
40 log(R) [dB]	−184.21	−184.21	−179.23	−179.23
simultaneous [dB]	−160.51		−149.55	
wide beam dropoff [dB]	1.0678		1.1989	
nominal angle [N/W beams]	7°	18°	6°	15°

Mutlu (1996), and Love's formula (Love 1971) to estimate their contribution to the volume backscattering (Table 2). Non-physonect siphonophores were modeled as weakly scattering fluid targets. Assuming that gelatinous salp tissue would approximate that of non-gas-bearing gelatinous siphonophores as well, in these calculations R (reflection coefficient) was set to 0.0041 to match the R used for salp tissue in Stanton *et al.* (1994).

The fluid-like model was applied to Amphipoda, Appendicularia, Chaetognatha, Cladocera, Copepoda, copepod nauplii, decapod larvae, euphausiids, fish eggs, Mysidacea, Ostracoda, Polychaeta, and salps; hard

Table 2. Values for reflection coefficients (R) used in the models (Ressler 2002).

organisms	R	model types
Salps non-physonect Siphonophora	0.0041	fluid-like
Copepoda (mixed)	0.0178	fluid-like
Euphausiacea	0.0341	fluid-like
Amphipoda	0.037	fluid-like
Beroe, *Mnemiopsis*, *Pleurobrachia*	0.056	Monger's model
Appendicularia, Chaetognatha, Cladocera, Decapoda larvae, fish eggs, Mysidacea, nauplii, Ostracoda, Polychaeta	0.058	fluid-like
Gastropoda and Bivalvia larvae	0.5	elastic shell
jellyfish		Mutlu's equation
fish larvae		Loves' formula

elastic-shell model to Gastropoda and bivalve larvae; Monger *et al.*'s (1998) model to *Pleurobrachia pileus*, *Mnemiopsis leidyi* and *Beroe*; Mutlu's equations (Mutlu 1996) to jellyfish (*Aurelia aurita*) and Love's formula to fish larvae. Equivalent diameters of *Mnemiopsis* and *Beroe* were converted to that of *Pleurobrachia* using the volume-length relationships (Mutlu & Bingel 1999; Mutlu 1999; Finenko *et al.* 2001).

Target strength was calculated first for each individual of the taxa due to the significant differences found in the ratio of body length/body width among individuals of the same taxa. Expected volume backscattering (Sv) was estimated:

$$Sv = TS + 10 \times \log_{10}(N)$$

where Sv is volume backscattering strength [dB], TS is target strength [dB] calculated from the models, N is abundance [number of individuals·m^{-3}].

Before calculating the expected volume backscattering, two criteria are discussed: detection limit of the frequencies and minimum Sv as threshold. "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, note 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" (T. K. Stanton, pers. comm.). Greene & Wiebe (1990) provided approximate 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. David *et al.* (1999), however, 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. Mutlu (2003) identified acoustically a concentrated layer of the copepod *Calanus euxinus* (length <4 mm) at 120 and 200 kHz. The Sv of the taxa was calculated for individuals larger than a length corresponding to one-quarter of the wavelength of the frequencies. Minimum threshold in Sv was measured by switching the transmitter of the echosounder off and measuring the received sound. Background noise levels of 120 kHz were −78.5 ± 0.8 (SD), −75.5 ± 1.2 and −78.5 ± 0.8 dB in the Black Sea, the Sea of Marmara, and the Mediterranean Sea, respectively. The noise levels of 200 kHz were 4 dB lower than those of 120 kHz (Fig. 3a). However, the noises were 3–4 dB higher in the Sea of Marmara than those in the other seas (Fig. 3b). This might have been due to the presence of Black Sea water overlying Mediterranean water (below 20 m depth) in the Sea of Marmara. The ambient noise may have been enhanced by reflection occurring between the surface and the interface of the two water types in the Sea of Marmara. Individual calculated Sv less than the noise was not incorporated into the comparison between expected and measured Sv. Possible reasons for the high ambient noise present in the Sea of Marmara are discussed later.

Results

1. Biological characteristics of the three seas

The 16 individual net samples from the three seas yielded 21 taxa of meso- and macro-zooplankton. Eight taxa were found in the Black Sea, namely, Copepoda (*Calanus euxinus*, *Pseudocalanus elongatus*, *Acartia* sp., *Oithona* sp., and *Paracalanus parvus*), copepod nauplii, Chaetognatha (*Sagitta setosa*), Gastropoda larvae, Appendicularia (*Oikopleura dioica*), Cladocera (*Pleopis polyphemoides*, *Podon* sp.), Scyphozoa (*Aurelia aurita*), and Ctenophora (*Mnemiopsis leidyi*, *Beroe ovata*, and *Pleurobrachia pileus*). Eleven taxa composed of Appendicularia (*Oikopleura* sp.), Chaetognatha, Cladocera (*Pleopis* sp., *Penilia* sp.), Copepoda (*Acartia* sp., *Microsetella* sp., *Oncaea* sp., *Oithona* sp., *Paracalanus* sp., *Centropages* sp.), copepod nauplii, fish larvae, Polychaeta, Gastropoda and Bivalvia larvae, Scyphozoa (*Aurelia aurita*), and Ctenophora (*Beroe ovata*) were found in the Sea of Marmara. The 19 Mediterranean taxa were Amphipoda (Hyperidae), Appendicularia (*Oikopleura dioica*, *Stegosoma magnum*), Chaetognatha (*Krohnitta subtitü*), Cladocera (*Podon*, *Pleopis*, *Penilia* sp.), Copepoda (well diversified), copepod nauplii, Decapoda larvae, Euphausiacea (*Stylocheiron suhmii*), fish eggs, fish larvae, Mysidacea (*Loghogaster typicus*), Ostracoda (*Conchoecia spinirostris*), Polychaeta, Salpa (*Salpa maxima*), Gastropoda and Bivalvia larvae, Siphonophora (*Eudoxioides spiralis*,

(a)

(b)
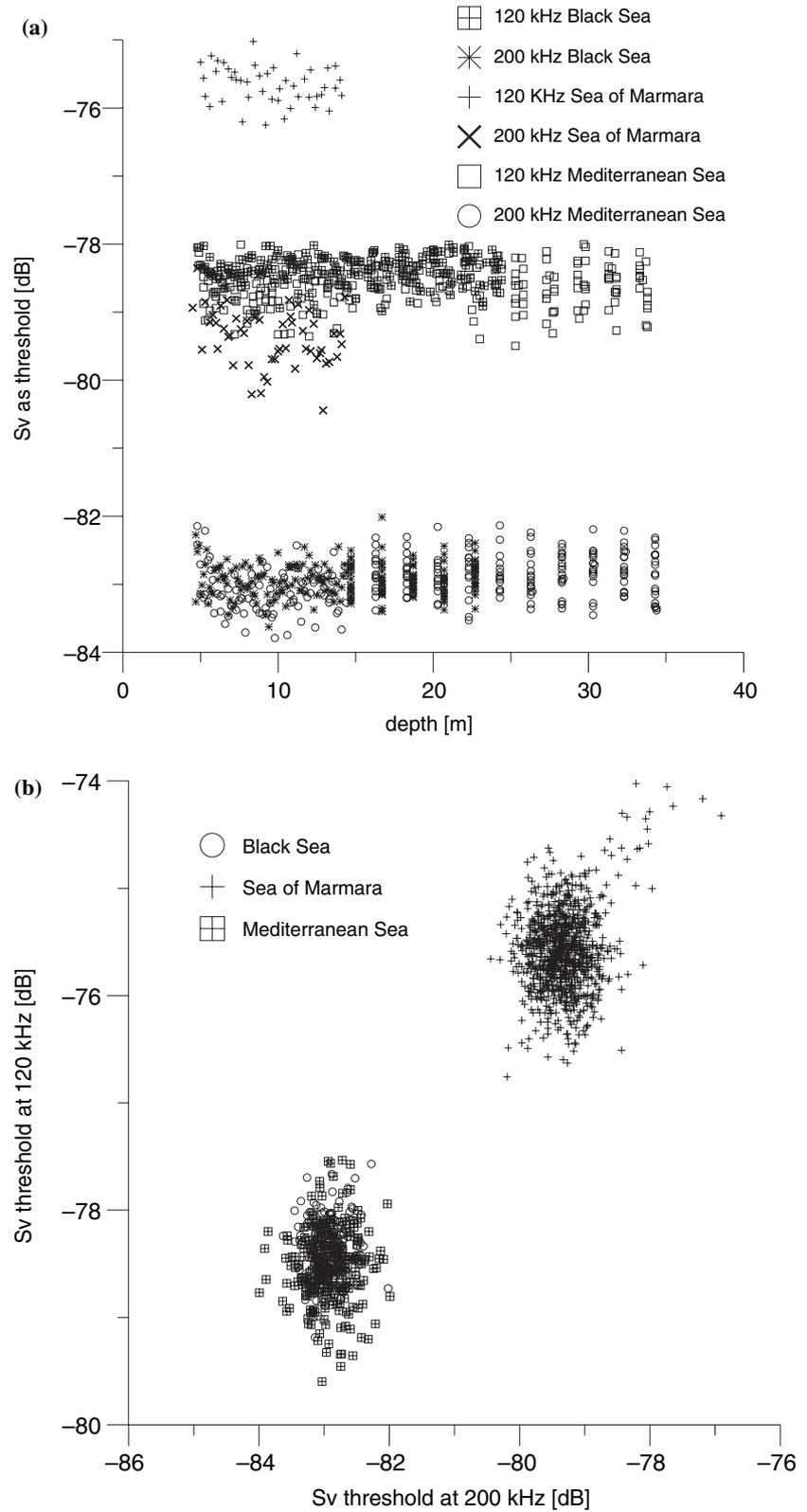
Fig. 3. Background noise (minimum Sv as threshold, dB) as function of depth (a), and for comparison between 120 and 200 kHz (b) in the three seas.
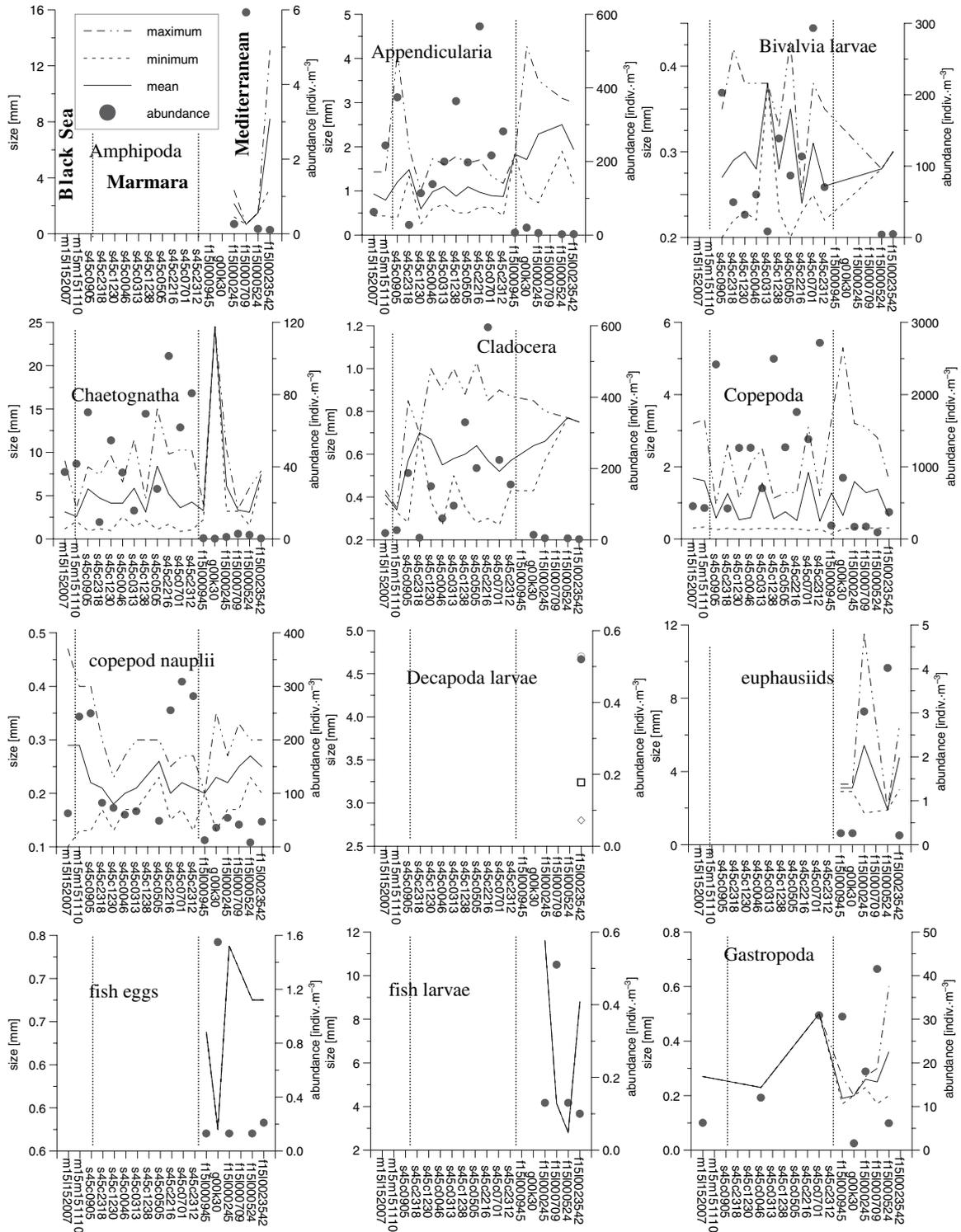
Fig. 4. Minimum, maximum and mean lengths, and abundances (number of individuals·m^{-3}) of specimens (Station code: *e.g.* F15L000709 means that F15L00 is station code and 0709 is sampling time at 07:09 h; see Figs 1 and 2).

Eudoxioides sp., *Eudoxia* sp., *Sulculeolaria quadrivalvis*), squid (*Todarodes sagittatus*), and gelatinous organisms (*Turritopsis nutricula*) (Fig. 4).

Lengths of Amphipoda species – Hyperidae and one Caprellidae species – that were found only in the Mediterranean Sea varied between 1 and 3.5 mm, and between

Fig. 4. Continued.

3.5 and 12 mm, respectively. Lengths of appendicularian species measured between 0.4 and 1.5 mm, with an abundance of 75 to 250 indiv.·m^{-3} in the Black Sea, between 0.5 and 4 mm (abundance: 25–580 indiv.·m^{-3}) in the Sea of Marmara, and between 1.75 and 4.5 mm (abundance: 1–10 indiv.·m^{-3}) in the Mediterranean Sea. Shell diameters of bivalve larvae varied between 0.15 and 0.375 mm (abundance: 10–300 indiv.·m^{-3}) in the Sea of Marmara, and between 0.225 and 0.25 mm (abundance: 5 indiv.·m^{-3}) in the Mediterranean Sea, while no bivalves were found in the Black Sea. Chaetognath lengths varied between 2.4 and 10 mm (38–40 indiv.·m^{-3}), 2.5 and 15 mm (10–100 indiv.·m^{-3}), and 2.5 and 25 mm (0.1–2 indiv.·m^{-3}) in the three seas. The corresponding values for cladocerans were 0.3–0.45 mm (5–10 indiv.·m^{-3}), 0.3–1.25 mm (5–600 indiv.·m^{-3}), and 0.45–0.9 mm (5–10 indiv.·m^{-3}), for copepod specimens 0.25–3.2 mm (400–500 indiv.·m^{-3}), 0.25–3 mm (40–2750 indiv.·m^{-3}), and 0.25–3.25 mm (10–40 indiv.·m^{-3}) (Fig. 4).

2. Acoustic characteristics

The enhanced echograms were very different among the three seas. Clear changes in the plankton composition and hydrography in these seas caused the differences in the acoustic levels. The regions that were acoustically tracked in this study (Fig. 5) were biologically very productive and were associated with divergence zones due to upwelling. Biological scattering was vertically distributed between the surface and suboxic zone (here 120 m) in the Black Sea (Fig. 5a), whereas it was confined to a narrow layer in a range from the surface to the interface at 20 m formed between waters of the Black Sea and Mediterranean Sea in the Sea of Marmara (Fig. 5b). The Mediterranean Sea was very different in terms of the volume backscattering due to the absence of the shallow interface (Fig. 5c).

Acoustic scattering was layered in and above the suboxic zone during the daytime in offshore waters of the Black Sea, while it was aggregated in the mixed layer at night hours. As the bottom depth was shoaled, the volume backscattering strength became homogeneous (Fig. 5a). In the Sea of Marmara, the scattering was much intensified and layered just above the interface during the daytime, whereas it was homogeneously distributed within the mixed water characterizing the Black Sea above the interface. During daytime, the layer between interface and transducer depth was deserted by the plankton. Aggregations by the scatterers were observed just underneath the transducers

Fig. 5. Enhanced echograms of sound scatterers around the study areas at 200 kHz in the Black Sea (a), at 120 kHz in the Sea of Marmara (b), at 200 kHz in the Mediterranean Sea (c), and vertical profiles of the hydrography. T: temperature in °C; S: salinity; D: density in sigmatheta; F: fluorescence in Volts; L: light transmission in %.

(Fig. 5b). Moderately high scattering was observed in the upper 100 m in the Mediterranean Sea at night, while the scattering observed in the upper 60 m layer during the day was less intense because vertical migratory species deserted the upper layers (Fig. 5c).

3. Characteristics of model outputs

Taking the minimum Sv (dependent on the threshold and detection limits of the frequencies) into calculation of expected Sv, six taxa contributed mainly to the acous-
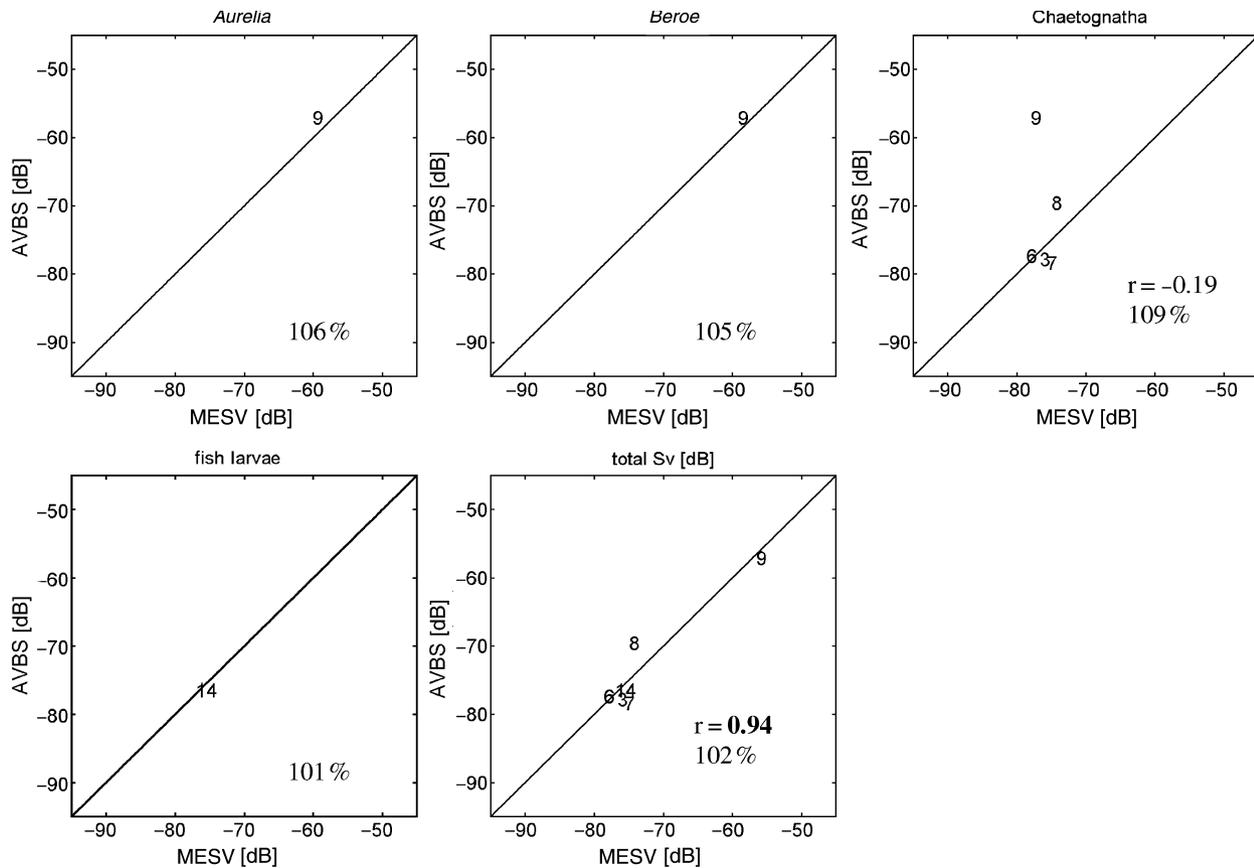
Fig. 6. A comparison of estimated acoustic volume backscattering based on the individual size and abundance of individual taxa and the measured volume backscattering at each net location at 120 kHz. AVBS: acoustic volume backscattering; MESV: model estimated Sv; see Fig. 2 for denotation of numbers. r = correlation coefficient and **bold** means significant at P < 0.05, and number below r is average percent contribution of taxa to total measured acoustic volume backscattering strength.

tic volume backscattering (AVBS) at 200 kHz as well as four taxa at 120 kHz (Figs 6 and 7). Individually, none of the taxa showed significant correlations between model estimated Sv (MESV) and AVBS, whereas there was significant correlation between total MESV and AVBS at P < 0.05 (Figs 6 and 7). MESV and AVBS were higher in the Sea of Marmara than those in both the Mediterranean and Black Sea. Main contributors to the total AVBS at 120 kHz were *Beroe*, *Aurelia* and Chaetognatha in the Sea of Marmara, and fish larvae in the Mediterranean Sea. No taxon, however, was found to be a significant 120 kHz-scatterer in the Black Sea. Principal scatterers at 200 kHz in the Black Sea were copepods and chaetognaths in addition to others that contributed at 120 kHz. However, other macrozooplanktonic gelatinous organisms, *Mnemiopsis leidyi* and *Pleurobrachia pileus*, salps, and non-physonect siphonophores were not significant scatterers at either frequency (Figs 4, 6 and 7). Other taxa were not significant because their MVBS were less than the mini-

mum Sv of the echosounder and their sizes were less than one-quarter of the wavelengths at both the frequencies.

Among the potential correlations between AVBS and density (abundance and biomass) of significant scatterers at 120 and 200 kHz, only chaetognaths showed significant correlations. Since MVBS of *Beroe* and *Aurelia* were in good agreement with AVBS, 200 kHz might be considered the lowest frequency to use in studying mesozooplankton acoustically because there were significant correlations between total density and AVBS only for 200 kHz (Figs 8–11). Clearly, this statement could change depending mainly on material properties, abundance, and size of targets and ambient noises in the water, which is an issue related to Rayleigh versus geometric scattering.

Discussion

Acoustic records revealed that the depth limit for the vertical distribution of zooplankton was confined to 100 m
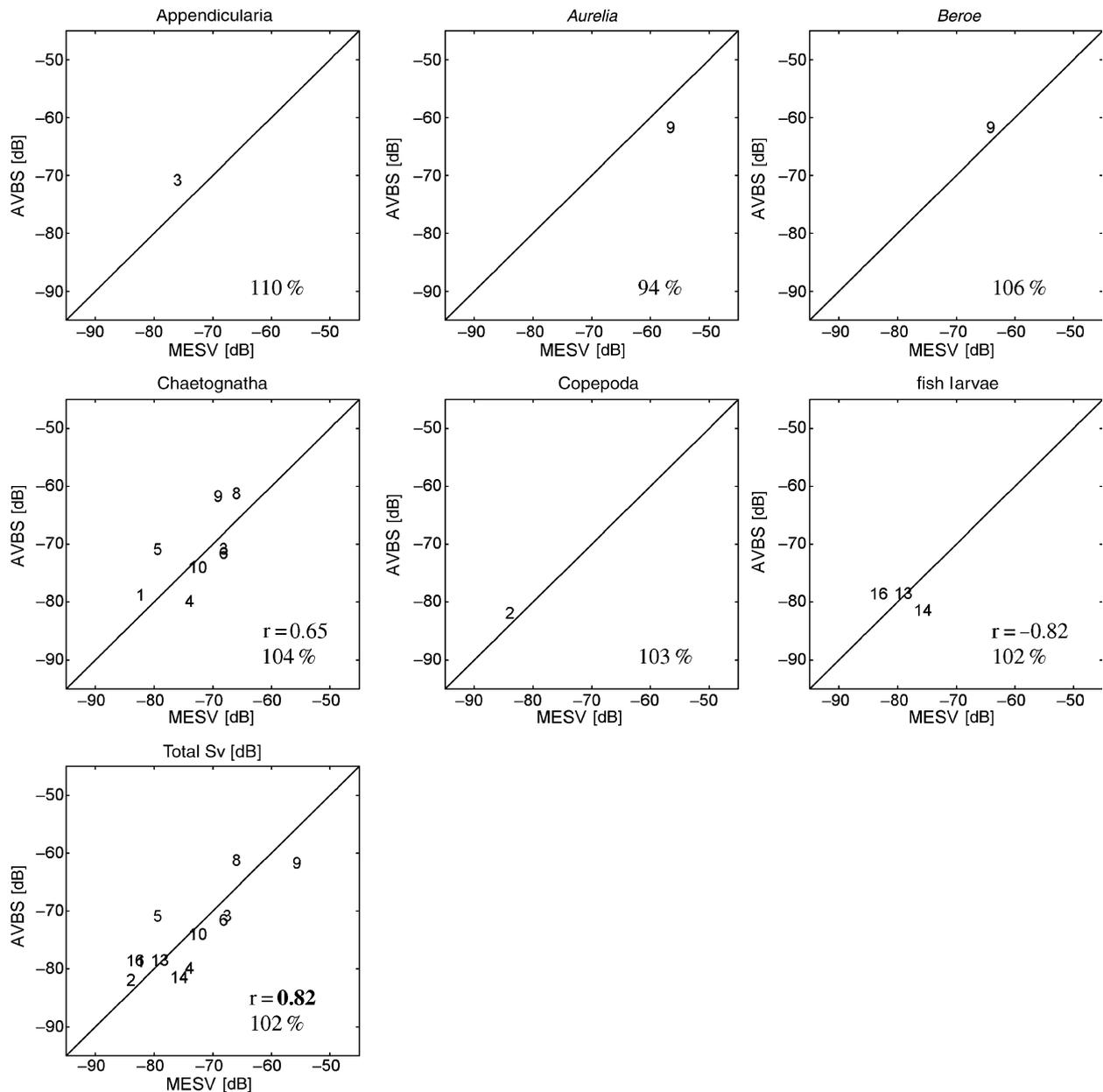
Fig. 7. A comparison of estimated acoustic volume backscattering based on the individual size and abundance of individual taxa and the measured volume backscattering at each net location at 200 kHz (see Fig. 6 for explanation).

in the Black Sea (Fig. 5a). This depth corresponds to the upper end of the suboxic zone characterized with a depth of sigmatheta = 16.2 (Tugrul *et al.* 1992). The vertical distribution of zooplankton was restricted to the zone above the oxygen minimum (<0.5 mg O_2 l^{-1}; Tugrul *et al.* 1992), which depends on season, species, stages, and the oxygen concentration in the water column (Vinogradov *et al.* 1985; Mutlu 1999, 2001, 2003; Mutlu & Bingel 1999; Besiktepe & Unsal 2000; Besiktepe 2001). The verti-

cal distribution of zooplankton in the Sea of Marmara was characterized as belonging to two ecosystems (Fig. 5b). The first ecosystem ranged from the surface to the interface between the Black Sea and the Mediterranean Sea water masses (here at 20 m) and the second from the interface to the bottom. The two-layer exchange flow characteristic of the straits permits material transport between the Black Sea and the Mediterranean Sea while creating an unusual marine ecosystem in the transition
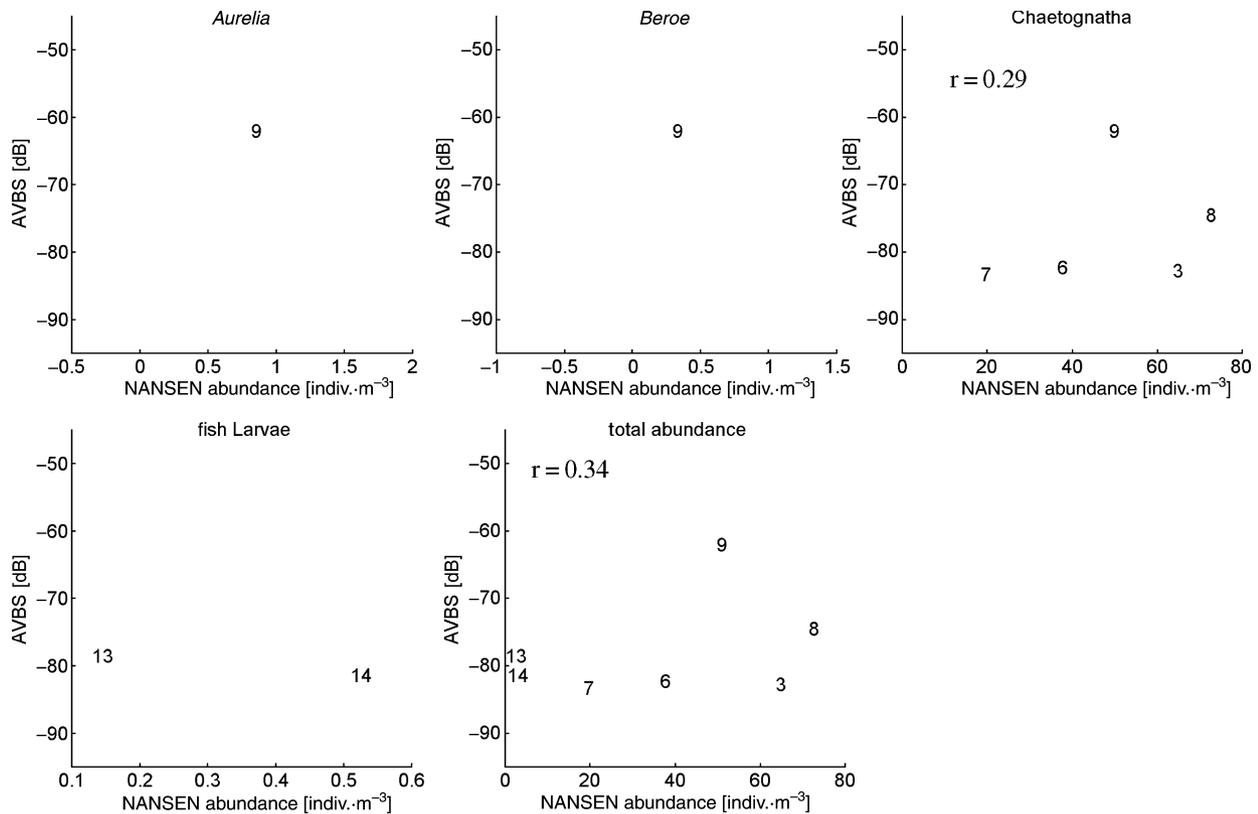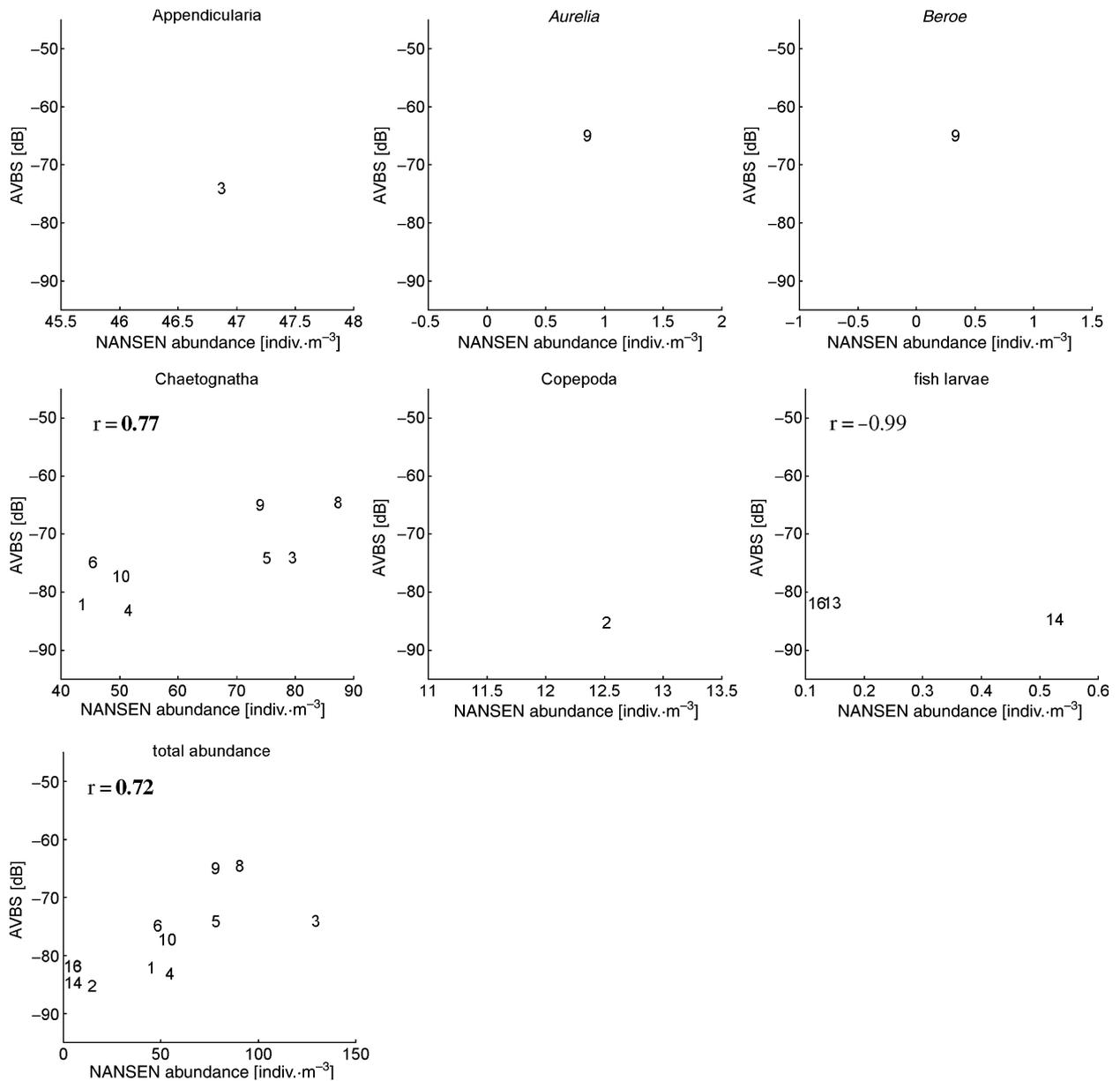
Fig. 8. The relationship between volume backscattering (120 kHz) and abundance of taxonomic categories (see Fig. 2 for denotation of numbers). r = correlation coefficient and **bold** means significant at P < 0.05.

between them (Polat *et al.* 2000). Acoustic records showed that there was no significant difference in the day and night vertical distribution of biological scatterers below the interface in contrast to the layer above the interface. During the present study, at 12:30 h the layered samples taken by the net revealed dead specimens between 80 and 150 m and between 20 and 80 m. The specimens were all alive above the interface. The water column below the interface has not, however, been well studied biologically. There was only one striking scattering layer between 40 and 80 m, where the light transmission dropped to 44%. The physical parameters appeared to be homogeneous beneath the interface. A high abundance of dead chaetognaths (length > 1.5 cm) and larger calanoid copepod (length > 2 mm) predominated in the layer between 80 and 150 m. Low numbers of small-sized copepods, polychaete larvae, and cladocerans were present between 20 and 80 m.

The Mediterranean Sea exhibited rather different acoustic scatterings than the other two seas. Two plankton concentration levels existed daily in the epipelagic of the Mediterranean Sea. Plankton that ascended from deep

layer towards the surface at nighttime tended to reside at night in a layer between 40 and 80 m, where the fluorescence peaked. Non-migrating plankton was distributed in the upper 40 m, corresponding to the depth of the thermocline (Fig. 5c). Andersen *et al.* (2001) showed that some species of zooplankton ascended from the deep layer towards the surface at night while others stayed in the epipelagic zone during the day.

Taxon-specific model equations (Love 1971; Stanton *et al.* 1994; Mutlu 1996; Monger *et al.* 1998) were used to estimate the relative contribution of the animals to the total acoustic energy at 120 and 200 kHz, as done by Wiebe *et al.* (1996). Solving this forward problem and comparing the result to *in situ* acoustic scattering measurements can be used to test the robustness of the scattering models and to verify their use in field application (Wiebe *et al.* 1996; Stanton *et al.* 1997). Figures 6 and 7 clearly show that the estimated volume backscattering showed better correlation with the measured Sv and a larger contribution to the total energy at 200 kHz than those at 120 kHz. The acoustic process is a complex function of animal size, shape, orientation, and material properties as

Fig. 9. The relationship between volume backscattering (200 kHz) and abundance of taxonomic categories (see Fig. 2 for denotation of numbers). r = correlation coefficient and **bold** means significant at P < 0.05.

well as acoustic frequency or wavelength (Stanton & Chu 2000). The principal acoustic scatterers changed between the different seas, as did the taxonomic composition, size, abundance of targets, and background noise. In the Black Sea, significant contributors to total AVBS were *Beroe*, *Aurelia*, and *Sagitta*. Other ctenophores, however, especially *Pleurobrachia*, which occurred below the thermocline in high numbers remained below the background noise. Mutlu (2003) showed that *Pleurobrachia pileus* was mostly

found below 30 m, where no scattering above the noise thresholds was observed. Although a high concentration layer of the copepod *C. euxinus* was acoustically discriminated previously in the Black Sea (Mutlu 2003), in the present study copepods were not significant scatterers because the sampling depth ranges did not cover the layer except for a few large-sized copepods at station 2 in the Black Sea. Copepods were not important scatterers in the Sea of Marmara, although they were concentrated within
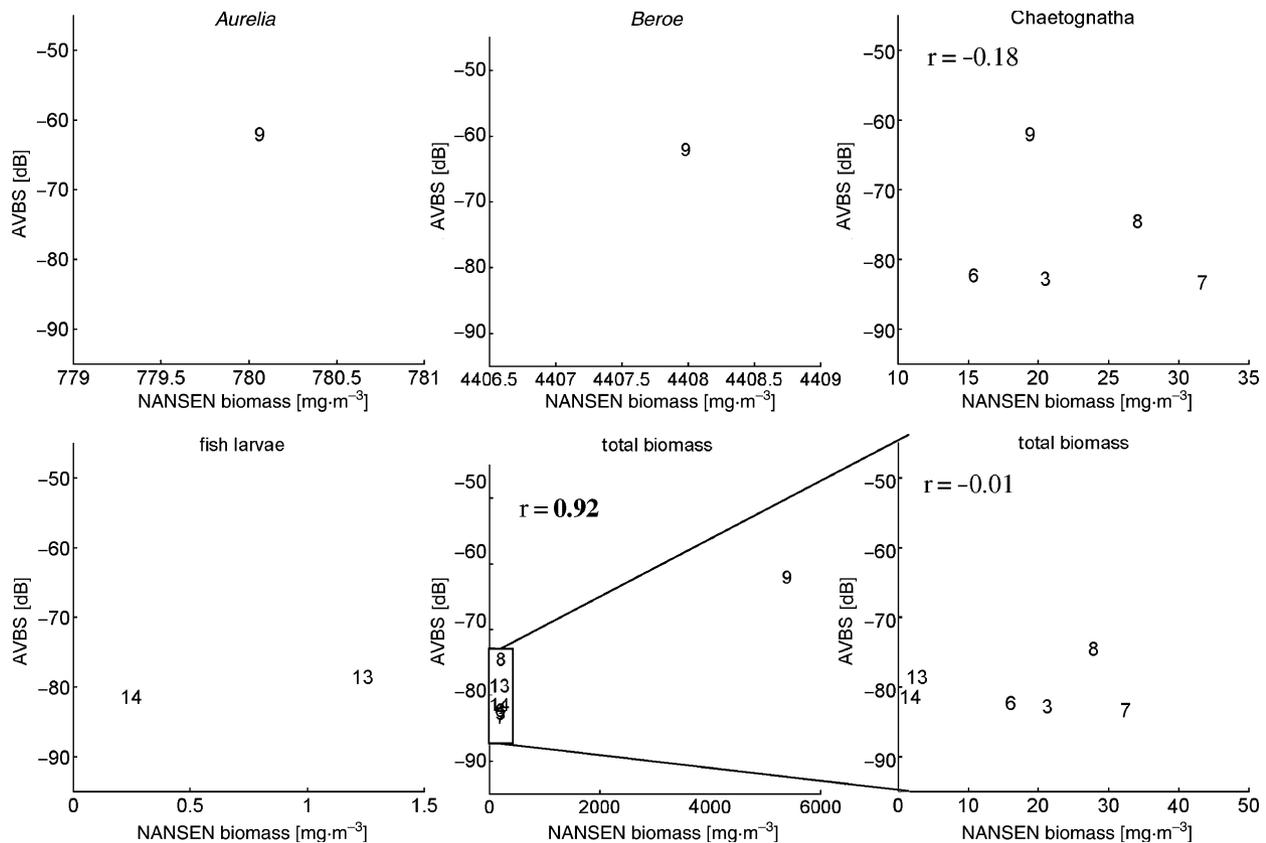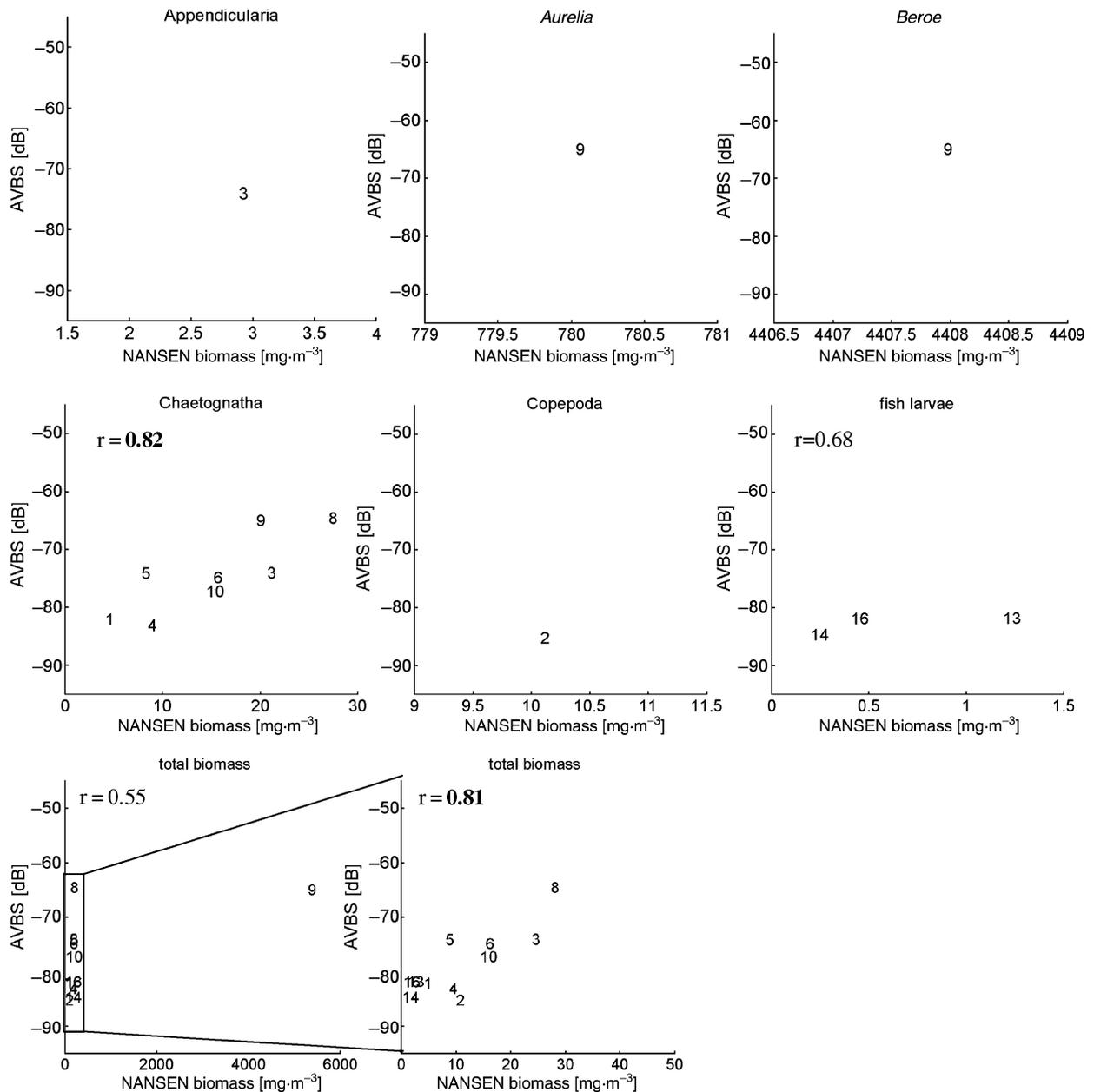
Fig. 10. The relationship between volume backscattering (120 kHz) and Nansen biomass (see Fig. 2 for denotation of numbers). r = correlation coefficient and **bold** means significant at P < 0.05.

the upper 20 m. The background noise and minimum Sv was, however, very high at 21:00 h in the Sea of Marmara. Korneliussen (2000) showed that the noise is inherently frequency dependent and also depends on bottom depth. The water mass interface during nighttime reflected echo energy as much as the bottom did. Daytime Sv from the interface was very low compared to that of the nighttime because the biological scatterers around the interface changed with time (Fig. 2b). This could have changed the 'hardness' of the interface, and thus the noise increased due to the biological variations as Korneliussen (2000) suggested for the bottom variations. The hardness of the interface could be associated with the density of the jellyfish *Aurelia aurita*. Although jellyfish avoid capture by net, according to Mutlu (1996) the swimming rhythms of the observed organisms showed that they could be jellyfish (Fig. 12). A variation of about 10–15 dB (dependent on the disc diameter of the jellyfish) and the occurrence of a peak every 25–30 s due to swimming jellyfish were observed in individual scatterers rising from the interface (stations 6 and 7; Figs 2b and 12). In addition, *Aurelia* individuals with disc diameters varying between 10 and

24 cm (captured by a scoop net) were observed in the surface waters of the Sea of Marmara during the daytime.

Bioacoustical properties depended on taxa composition, material properties, size of the scatterers, and minimum threshold of the echosounders, all related with the frequencies and with the physical and biological density of the water. Wiebe *et al.* (1997) suggested that size and/or taxa distribution of the zooplankton, and not the quantity of biomass, was the critical determinant for differences in the volume backscattering. The orientation of the scatterers is also a critical determinant. Data on orientation were not available for the present study. Stanton & Chu (2000) showed that some acoustic predictions were more sensitive to animal shape and orientation than others. Thus, for elongated animals, the pattern of backscattering versus angle of orientation at a fixed frequency is strongly dependent upon shape. Recently, Benfield *et al.* (2000) reported that the orientation distribution of freely swimming copepods peaked at about 90° (*i.e.* the animal body axis was vertical with the head up), with a standard deviation of 30°. There was a discrepancy between the predicted and observed regression. This offset could be

Fig. 11. The relationship between volume backscattering (200 kHz) and Nansen biomass (see Fig. 2 for denotation of numbers). r = correlation coefficient and **bold** means significant at P < 0.05.

due to a combination of factors including system calibration, net avoidance (particularly for the macrozoogelatinous organisms at stations 6 and 7; Fig. 2b), accuracy of acoustic models, accuracy of input parameters into the models, and the failure of the frequencies to detect mesozooplankton. Stanton & Chu (2000) concluded that the scattering predictions showed a very strong dependence upon shape, orientation, and frequency for the euphausiids and copepods.

Summary

The three seas exhibited significant differences in overall levels of acoustic volume backscattering; the Sea of Marmara and the Black Sea had higher values than the Mediterranean Sea. The acoustic patchiness structure differed among the seas due to a clear difference in hydrographic peculiarities. Large-sized meso- and macrozooplankton (jellyfish, chaetognaths, ctenophores)
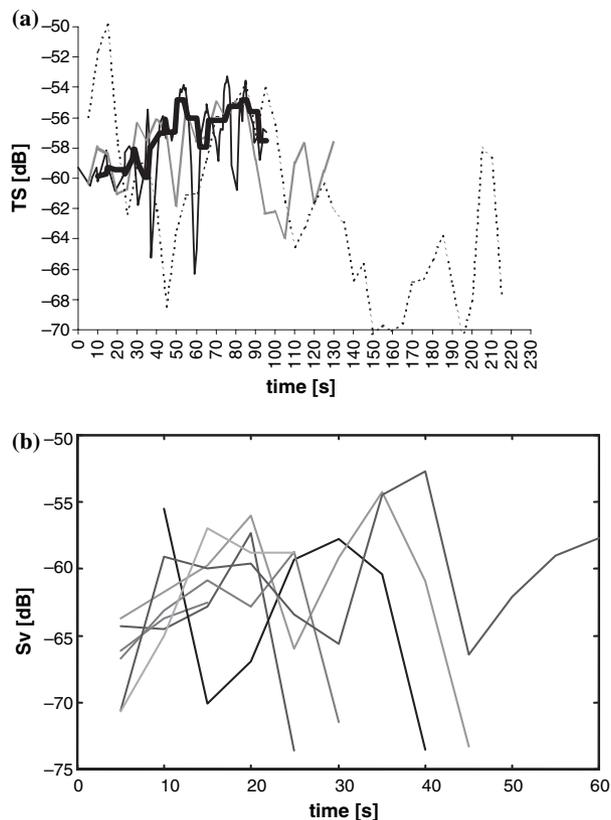
Fig. 12. Comparison of swimming rhythm of *Aurelia aurita* (Mutlu 1996) with that obtained from the scatterers arising from the interface in the Sea of Marmara (a, b). Thin black line, variation of TS due to the swimming behavior of *A. aurita*; thick black line, the variation averaged over 5 s (Mutlu 1996); variation of Sv of the individual scatterers observed for long time (a; gray line, station 6; dashed black line, station 7; see Fig. 2b) and short-time duration of individuals below the transducers (b, each line denotes different individual at station 6). All acoustical data were at 120 kHz.

contributed most to the total volume backscattering strength.

Acknowledgements

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