



Copepod communities, production and grazing in the Turkish Straits System and the adjacent northern Aegean Sea during spring

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ABSTRACT

The Mediterranean and the Black Seas are connected through Bosphorus, Marmara Sea and Dardanelles (Turkish Straits System, TSS). In this study, we examined the spatial distribution of copepods and investigate their production and grazing. The aim was to understand the transfer of phytoplankton/microzooplankton production up the food chain in TSS and Aegean Sea during spring. The phytoplankton and microzooplankton biomass and production showed a clear decreasing trend from Bosphorus to the Aegean Sea, whereas copepod biomass did not reveal any distinct trend and only the number of copepod species increased from Bosphorus to the Aegean Sea. Production of copepods and egg production showed similar trends except for the Bosphorus, where production of copepods was very low due to the low copepod biomass in this area. In all areas, the copepod carbon demand was largely met by phytoplankton and microzooplankton production. However, only a low amount of primary production was consumed by copepods and production appeared to flow mostly through other pathways (microbial loop) and/or sediment on the bottom. The results of this study confirm the hypothesis that there is a substantial differentiation within pelagic food web structure and carbon flow from Bosphorus to the Aegean Sea.

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1. Introduction

The Mediterranean and the Black Seas, representing the Southern European Seas, are two interconnected semi-enclosed basins, which, however, have distinct and very different characteristics. The two seas are connected through Bosphorus, Marmara Sea and Dardanelles the so-called Turkish Straits System (TSS). Hydrological, meteorological and biological characteristics are combined forming a distinct ecosystem between the Mediterranean and the Black Seas. The TSS is an important structure specifying the hydrology of the Black and Aegean Seas (Özsoy et al., 2002). Flows through the Turkish Straits are driven by density differences between the Black and the Aegean Seas and the maintained net level difference between these seas (Unluata et al., 1990). The TSS controls the exchange of matter (water, passive or active chemical/biological substances, and fish) between the Black and the Mediterranean Seas. Water masses, exiting through the TSS into the northern Aegean, impact nutrient recycling, productivity and feeding of local and migrating species. While the hydrological aspects of the TSS are well documented (Özsoy et al., 2002), biological data

remain very limited. Studies on the mesozooplankton have focused mainly on the distribution and composition of the mesozooplankton community concluding that zooplankton abundance is primarily controlled by fluctuations in physical environment, eutrophication and pollution (e.g. Tarkan, 2000; Tarkan et al., 2005; Yilmaz et al., 2005; Svetlichny et al., 2006; Isinibilir et al., 2008). Concerning copepod production and grazing as well as food web structure, information is lacking.

The neighboring northern Aegean Sea receives the modified Black Sea Water mass (BSW). The very light, brackish inflow of this water mass usually occupies the uppermost water layer (20–30 m) and it is well detectable in the northern part of the Aegean Sea (Theocharis and Georgopoulos, 1993). The BSW inflow, enriched in dissolved organic carbon and nitrogen (Polat and Tugrul, 1996; Lykousis et al., 2002) induces hydrological complexity (e.g. gyres and fronts) that can be highly mobile in variable time scales (Zervakis and Georgopoulos, 2002). The consequence of this inflow is a plankton production among the highest in the Eastern Mediterranean for both autotrophs and heterotrophs (Ignatiades et al., 2002; Siokou-Frangou et al., 2002). Mesozooplankton standing stock and species composition are affected by the mesoscale features formed from the advection of the BSW and the formation of the halocline/pycnocline (Zervoudaki et al., 2006; Isari et al., 2006; Siokou-Frangou et al., 2009). The carbon flow in

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pelagic food web is very efficient and is expected to affect the production of higher trophic levels (Siokou-Frangou et al., 2002; Zervoudaki et al., 2007). Notwithstanding the influence of the BSW in the northern Aegean Sea has already been addressed in the above studies, a concurrent study of mesozooplankton communities and food web structure from Bosphorus, Marmara Sea and Dardanelles to the northern Aegean Sea is crucial for the clarification of the impact of the BSW inflow into the northeastern Mediterranean Sea.

In this study, we have focused on the copepod communities during the spring period. This group consists of the major mesozooplankton fraction in TSS and northern Aegean Sea (Kovalev et al., 2003; Zervoudaki et al., 2006) and it is well known that copepods play the key role in transferring primary production to higher trophic levels in all pelagic ecosystems (Verity and Smetacek, 1996). Knowledge about their rates (production and grazing) is essential in the scope of understanding the flux of carbon and nutrients through the food chain. Thus, here, we examine the spatial distribution of copepods in the TSS and the northern Aegean Sea, compare their production and grazing on phytoplankton and microzooplankton and finally resolve the carbon flow in the above systems.

2. Materials and methods

2.1. Sampling and hydrography

This study was undertaken from 10 to 15 April 2008 in the northern Aegean Sea aboard the R/V “Aegaeo” (Hellenic Centre for Marine Research) and in the Turkish Straits System (Dardanelles and Bosphorus Straits and Marmara Sea) aboard the R/V “Bilim” (Middle East Technical University). The study area comprised of one station in the northern Aegean Sea (station: AS), one station in Dardanelles (station: DS), three stations in Marmara Sea (stations: MS1, MS2 and MS3) and one station in Bosphorus (station: BS) (Fig. 1). Depth profiles of temperature, salinity and density were measured continuously from surface down to the bottom of each station using a SeaBird Electronics SBE 9/11 plus CTD-General Oceanics Rosette assembly with 51 Niskin bottles. Water samples for chlorophyll *a* (chl *a*), phytoplankton and microzooplankton (ciliates and dinoflagellates) were collected at 2, 10, 20 and 50 m depths depending on the depth of each station, using the Niskin bottles. Also, sampling of these depths was modified in relation to the deep chlorophyll maximum (DCM) as determined with an *in situ* fluorometer (WETStar fluorometer) mounted on the CTD.

2.2. Phytoplankton biomass and production

Water samples (2 l) were size-fractionated by separate filtration on 2- and 0.2- μm polycarbonate Millipore filters. The filters were

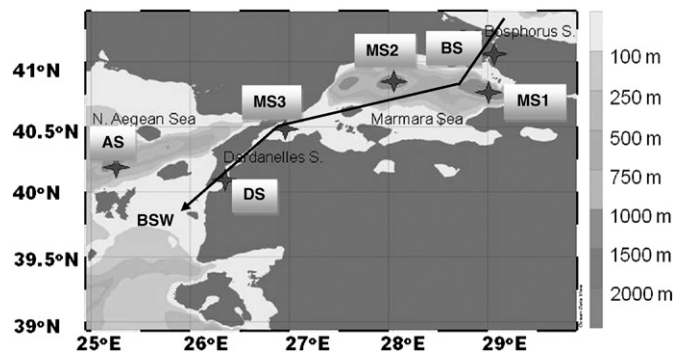


Fig. 1. Sampling station locations (depth contours in meters) investigated during the cruise in the Turkish Strait System (Bosphorus Straits, Marmara Sea and Dardanelles Straits) and in the northern Aegean Sea during April 2008. Line shows the intrusion of the Black Sea Water (BSW) in the northern Aegean Sea.

extracted in 90% acetone for 24 h, and chl *a* was determined using a TURNER 00-AU-10 fluorometer (Holm-Hansen et al., 1965). Chl *a* concentrations were converted to carbon biomass using a conversion factor of 50 (C:Chl *a* = 50). Quantification of phytoplankton was made in an inverted microscope on Lugol-fixed samples, according to the method of Utermöhl (1958).

Photosynthetic productivity was measured at the same depths as chl *a* according to the *in situ* ^{14}C method (Joint et al., 1993). The water samples were taken with clean Go-Flo bottles and dispensed in 250 ml acid washed transparent polycarbonate bottles (four light and one dark for each depth). Each bottle was inoculated with 5 μC ^{14}C - NaHCO_3 and incubated at the collection depths for 2 h at midday (around 11:00–13:00). Fractionation was carried out by filtration through separate 2- and 0.2- μm polycarbonate Millipore filters. Filters were placed in scintillation vials, acidified with 0.5 N HCl and counted in a liquid scintillation counter (Beckman LS 6500). Daily rates were calculated from hourly rates multiplied by the 12 h of the daylight period during sampling. Primary productivity was measured at several discrete depths and integrated over the 50 m of the water column.

2.3. Microzooplankton biomass and production

Water samples for the enumeration of ciliates ($>10\mu\text{m}$) and dinoflagellates ($>20\mu\text{m}$) were fixed with acid Lugol's solution (3% final concentration). Many dinoflagellates have different phagotrophic capabilities (e.g. Jeong, 1999), so in this study, the dinoflagellates $>20\mu\text{m}$ of the genus *Amphidinium*, *Cochlodinium*, *Gyrodinium*, *Gymnodinium*, *Peridinium*, *Proto-peridinium*, *Oxytoxum*, *Gonyaulax*, *Torodinium* and *Warnovia*, were grouped among microzooplankton. The samples were collected at all stations and standard depths, as it is described above. They were stored in a cool (4 °C) and dark environment and were counted within 3 months after their collection dates. In the laboratory, 50 or 100 ml of the sample was transferred into Hydro-Bios Kiel combined plate settling chambers, allowing it to settle for a minimum of 20 h. Cell volumes were estimated assuming simple geometric shapes and converted to biomass using the biovolume-carbon conversion for ciliates of 0.19 $\text{pgC}\mu\text{m}^{-3}$ (Putt and Stoecker, 1989) and the general carbon to volume relationship for dinoflagellates (Menden-Deuer and Lessard, 2000). Integrated values of ciliate and dinoflagellates biomass for the 0–50 m water layer were also calculated by the trapezoid rule.

Microzooplankton production was estimated from maximum specific daily clearance and ingestion rates where maximum clearance (C_{max} , 10^5h^{-1}) Eq. (1) and maximal ingestion (I_{max} , h^{-1}) Eq. (2) were applied (Hansen et al., 1997):

$$\begin{aligned} \text{Ciliates: } \text{Log}C_{\text{max}} &= 1.491 - 0.23\text{log}(P_{\text{vol}}) \text{ and} \\ \text{Dinoflagellates: } \text{Log}C_{\text{max}} &= 0.8514 - 0.23\text{log}(P_{\text{vol}}) \end{aligned} \quad (1)$$

$$\begin{aligned} \text{Ciliates: } \text{Log}I_{\text{max}} &= 0.342 - 0.23\text{log}(P_{\text{vol}}) \text{ and} \\ \text{Dinoflagellates: } \text{Log}I_{\text{max}} &= 0.0034 - 0.23\text{log}(P_{\text{vol}}) \end{aligned} \quad (2)$$

where P_{vol} is the cell volume. The clearance and ingestion were adjusted to the *in situ* temperature by application of a Q_{10} of 2.8 (Hansen et al., 1997). Since protozoan have an overall growth yield of 0.33 (Hansen et al., 1997), the microzooplankton production (P , $\mu\text{g C l}^{-1}\text{day}^{-1}$) could be estimated as:

$$P = I \times 0.33 \quad (3)$$

where I is the ingestion.

2.4. Copepod biomass, production and grazing

Zooplankton was sampled vertically at two depth intervals: 0–20 or 0–30 (at Bosphorus station) and 20–50 m with a 200 μm WP-2 net

(UNESCO, 1968). To eliminate differences attributed to vertical migration, samples were taken between 10:00 and 14:00 h. The volume (m^3) of filtered water ($V = A \times DL$) for each tow was estimated taking into account the area of the net mouth (A) and the difference in winch readings $DL = (L_i - L_f)$. After each haul the net was carefully rinsed. The contents of the cod ends were fixed immediately after collection and preserved in a 4% buffered-formaldehyde seawater solution. Zooplankton data were classified at the phyla, class or order level. Copepods and copepodites were identified to species or genus level. The carbon biomass of copepods was calculated from the abundance and the length: weight relationship according to the literature values (Christou and Verriopoulos, 1993; Hirche and Mumm, 1992; Hopcroft et al., 1998; Satapoomin, 1999; Uye, 1982).

Egg production and grazing experiments were conducted at 5 stations (AS, DS, MS2, MS3 and BS). Copepods for the egg production and grazing experiments were collected by vertical tows within the 0–50 m layer, using a 200 μm WP-2 net equipped with a large non-filtering cod-end (10 l). On deck, the content of the cod end was diluted in a 25 l bucket containing seawater collected from the surface, 20 m and 50 m depths and brought directly to the lab on the ship. Within the next few hours, females were sorted under a dissecting microscope. For the estimation of the egg production two–five females for each species were placed in each of three–nine glass jars of 620 ml containing well-mixed 60 μm filtered water collected from the surface and 20 m depth. The females were incubated at the ambient sea temperature for 24 h after which the spawned eggs were counted and female lengths and egg diameters were measured. Egg production (EP) experiments were conducted with *Acartia clausi* (BS, MS1 and MS2), *Centropages typicus* (MS2, DS and AS) and *Calanus helgolandicus* (AS).

Carbon-specific EP (SEP) rates for the copepod species were calculated according to the equation:

$$SEP = EP \times (C_e / C_f) \quad (3)$$

where, EP in terms of egg female $^{-1}$ day $^{-1}$, C_e is the egg carbon calculated from the egg volume and a volume to carbon ratio of 0.14 $\mu g C \mu m^{-3}$ (Kiørboe et al., 1985) and C_f is the female carbon biomass estimated from length–carbon regressions according to the literature (Christou and Verriopoulos, 1993; Hopcroft et al., 1998; Hirche and Mumm, 1992). Copepod production was then calculated by multiplying biomass with SEP, assuming that SEP of adult females equals the growth rates of the juvenile stages (Berggreen et al., 1988).

The grazing rates of copepods were estimated by the incubation method (Båmstedt et al., 2000) and they were conducted with *Acartia clausi* (BS, MS1 and MS2) and *Centropages typicus* (DS and AS). Undamaged individuals were sorted under a dissecting microscope and transferred to 2 l polycarbonate bottles filled with prescreened well-mixed seawater (<150 μm) from the surface, 20 m and 50 m depths. Each experiment was prepared with four replicate treatment bottles for each copepod species, four initials and four bottles without added copepods served as controls. The bottles were placed in a plankton wheel rotated at 0.2 rpm for less than 24 h and incubated at the *in situ* temperature. At the beginning and at the end of each incubation, the water was sub-sampled for assessment of chl *a* (1 l on GF/F filters) and microzooplankton communities (200 ml) and the samples were analyzed in the same way as the water column samples. Copepod clearance rates on phytoplankton (based on chl *a*), on ciliates and dinoflagellates were calculated according to Frost (1972), when the difference in prey concentration between control and experimental bottles proved significant (*t* test, $P < 0.05$). The ingestion rates were calculated by multiplying clearance rates by the initial standing stocks (Båmstedt et al., 2000). The weight-specific ingestion ($\mu g C_{ing} \mu g C_{cop}^{-1} day^{-1}$) rates were estimated using the mean female carbon weight of the respective copepod species.

2.5. Statistical methods

Principal Components Analysis (PCA) was carried out based on the environmental parameters (temperature, salinity, chl *a*) and the abundance of the major planktonic groups (diatoms, dinoflagellates, coccolithophores, small flagellates, ciliates, *Mesodinium* spp. and copepods), in order to identify the principal factors controlling similarities among stations. Copepod abundance was analyzed using both cluster analysis (not shown here) and non-metric multidimensional scaling (NMDS) (Field et al., 1982; Clarke and Warwick, 1994). All copepod species were included in the matrix. Data were transformed using the square root transformation. Hierarchical agglomerative clustering was carried out first, using the Bray–Curtis similarity index coupled with group average linkage. The data set was subsequently subjected to NMDS ordination. The above analyses were performed using the PRIMER software (Plymouth Marine Laboratory, UK).

3. Results

3.1. Hydrography, chl *a* and potential food for copepods

The vertical profiles of temperature and salinity revealed that the water column was characterized by a surface layer (salinity < 35) originated from the brackish Black Sea Water (BSW). Intruding Bosphorus, the BSW is modified along the transect generating a distinct gradient at the surface salinity from Bosphorus (17.6) to the Aegean Sea (33.4). The thickness of this BSW layer was differentiated among stations. At stations in the Marmara Sea the halocline were located between 20 and 30 m. In Dardanelles a thin surface layer of brackish water (~10–15 m) was evident. In the Aegean Sea the signal of low salinity was found within the uppermost 10 m; below 30 m the water column was occupied by the Levantine Waters (Fig. 2). Exception to this pattern was the station in Bosphorus, where the whole water column was occupied by the BSW due to its low depth (35 m). The mean integrated (0–50 m) temperature and salinity in the study area ranged from 10 to 13.5 °C and 17.8 to 36.9 respectively.

The vertical distribution of chl *a* was variable among stations (Fig. 2). The stations in the Aegean Sea and Bosphorus showed maxima at 10 m depth. The highest values of chl *a* were found at the surface layer of stations MS2 and MS3 (2.26 $\mu g l^{-1}$ and 2.09 $\mu g l^{-1}$, respectively) confirming the bloom development recorded in Marmara by satellite imagery during the cruise (unpublished data by Örek). The integrated phytoplankton biomass and production showed a clear decreasing trend from Bosphorus to the Aegean Sea (Table 1). Phytoplankton biomass ranged from 525 to 3986 $mg C m^{-2}$ and production from 292 to 2577 $mg C m^{-2} day^{-1}$. Diatoms were the dominant phytoplankton group throughout the study area (Table 2). Higher abundance values were found in the Eastern Marmara Sea (MS1) and Bosphorus, whereas abundance was lower in Dardanelles. The most abundant genera from the Bacillariophyceae were: *Cerataulina*, *Chaetoceros*, *Coscinodiscus*, *Cylindrotheca*, *Bacteriastrium* (centric diatoms), *Pseudonitzschia* (typical coastal zone pennate diatom) and *Rhizosolenia*.

The microzooplankton (dinoflagellates and ciliates) biomass and production, showed a decreasing trend from Bosphorus to the Aegean Sea (Table 1). The dinoflagellates biomass and production (following the same trend) varied between 340 (DS) and 1798 (BS) $mg C m^{-2}$ and between 2 (AS) and 49 (BS) $mg C m^{-2} day^{-1}$, respectively (Table 1). The dinoflagellates composition differentiated along the study area. Cells < 30 μm clearly dominated in the Aegean Sea (64% of the total), whereas larger cells (> 30 μm) prevailed at the other stations (averaged 89% of the total) (Table 2). The ciliates biomass and production (following the same trend) ranged between 11 and 529 $mg C m^{-2}$ and between 0.2 and 41 $mg C m^{-2} day^{-1}$, respectively, whereas maxima for both were recorded in Bosphorus. The ciliate abundance maximum (9066

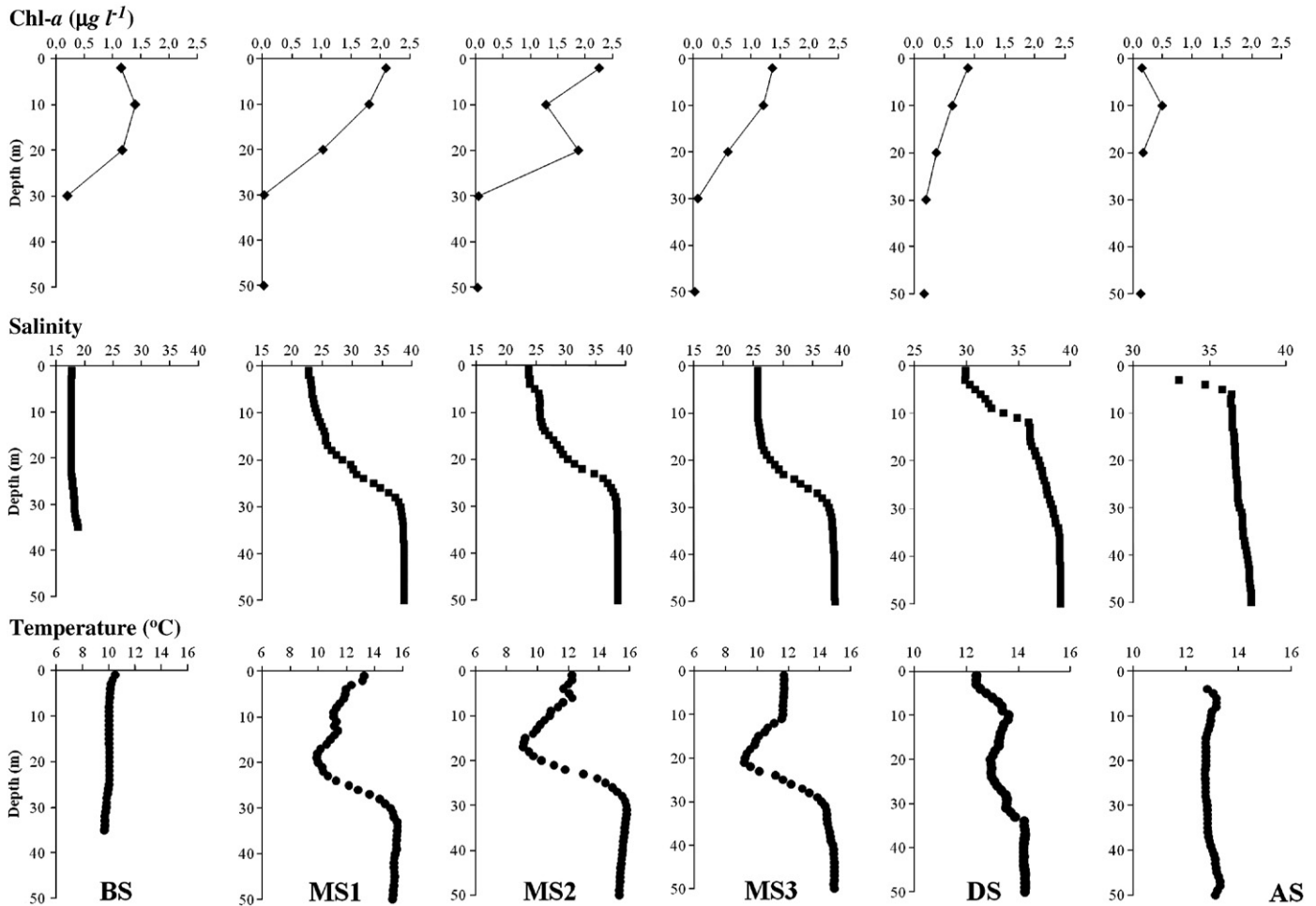


Fig. 2. Vertical profiles of Temperature ($^{\circ}\text{C}$), Salinity and Chl a ($\mu\text{g l}^{-1}$) at all stations from BS to AS following the BSW, up to 50 m of the water column during April 2008. Note the different scale in salinity and temperature at DS and AS stations.

cells l^{-1}) was also recorded in Bosphorus (Table 2). Composition of the ciliate community differed considerably along the study area: $<30 \mu\text{m}$ oligotrich and choreotrich ciliates (*Strombidium delicatissimum*, *S. epidemum*, *S. vestitum*, *S. sphaericum*, *Strombidium sp.* 22 μm , *Lohmaniella oviformis* and *Lohmaniella sp.* 15 μm) clearly prevailed in

the Aegean (AS) and Dardanelles (DS) (70% of total ciliate density): in the Marmara Sea their percentage dropped to 39% and in Bosphorus (BS) they made up only 11% of the total ciliate community (Table 2). Moreover, *Mesodinium* spp. increased their contribution from 33% in the Marmara Sea to 77% in Bosphorus.

Table 1

Biomass (mgC m^{-2}) and production ($\text{mgC m}^{-2} \text{day}^{-1}$) of phytoplankton, microzooplankton and copepods integrated in 0–50 m of the water column during April 2008.

	Bosphorus	Marmara Sea			Dardanelles	Aegean Sea
		MS1	MS2	MS3		
Biomass						
Phytoplankton $<2.0 \mu\text{m}$	2297	1256	1618	612	800	329
Phytoplankton $>2.0 \mu\text{m}$	1690	759	668	736	125	195
Phytoplankton size ratio	0.74	0.60	0.41	1.20	0.16	0.59
Total phytoplankton	3986	2015	2286	1347	925	525
Dinoflagellates	1798	1663	1325	1279	340	405
Ciliates	529	186	285	11	21	45
Total microzooplankton	2327	1849	1610	1290	361	450
Phytoplankton:Microzooplankton	1.71	1.09	1.42	1.04	2.56	1.17
Copepods	27	232	9	45	483	334
Microzooplankton + Copepods/Phytoplankton	0.59	1.03	0.71	0.99	0.91	1.49
Production						
Phytoplankton $<2.0 \mu\text{m}$	1618	484	504	471	199	204
Phytoplankton $>2.0 \mu\text{m}$	959	442	437	361	79	88
Total phytoplankton	2577	926	941	833	202	292
Dinoflagellates	49	17	17	9	3	2
Ciliates	41	7	8	0.2	0.4	0.4
Total microzooplankton	91	25	24	9	3	2
Copepods	7	18	2		17	11

Table 2Abundance (cell l⁻¹) of the dominant phytoplankton and microzooplankton groups in the water column 0–50 m at all stations during April 2008.

	Bosphorus	Marmara Sea			Dardanelles	Aegean Sea
		MS1	MS2	MS3		
<i>Diatoms</i>	28,945	35,580	6580	23,124	5842	8945
<i>Coccolithophores</i>	1005	600	652	36	132	3584
<i>Silicoflagellates</i>			80			200
<i>Other flagellates >10 µm</i>	1335	2772	5712	2052	2482	1426
<i>Dinoflagellates</i>						
20–30 µm	300	1320	1588	2036	60	2046
30–50 µm	2906	7792	5092	15,320	224	602
>50 µm	734	6096	4456	4304	180	549
<i>Total dinoflagellates</i>	3940	15,208	11,136	21,660	464	3197
<i>Diatoms:dinoflagellates</i>	7.35	2.34	0.59	1.07	12.59	2.80
<i>Ciliates</i>						
<i>Oligotrich <20 µm</i>	568	19	465	323	280	712
20–30 µm	389	58	598	2133	169	404
30–50 µm	152	38	235	256	80	98
>50 µm	381	3	139	123	2	16
<i>Tintinnids</i>	16		12		40	2
<i>Non-oligotrich</i>	606	48	523	496	121	242
<i>Mesodinium spp.</i>	6954	108	502	2129	4	18
<i>Total ciliates</i>	9066	274	2474	5460	696	1492

3.2. Copepod communities, production and grazing

Copepod abundance and communities were generally differentiated among stations and layers. Although no distinct pattern/gradient was evident along the whole transect, the dominance of *Acartia clausi* eastwards and that of *Centropages typicus* westwards was a major characteristic (Fig. 3). Total abundance and biomass was lowest at stations BS, MS2 and MS3 (Fig. 3a, Table 1). When the two layers are compared, higher copepod abundance was observed in the upper layer (0–20 m) at all stations except the station MS3. In this layer in the Aegean Sea, in Dardanelles and at station MS3 the copepod community was dominated by the species *Centropages typicus* which accounted for the 30% to 70% of the total (Fig. 3b). Furthermore, species number showed a threefold increase from the Marmara Sea to the Aegean Sea (from 12 to 41 species) (Fig. 3a). *Clausocalanus juveniles* (AS: 12%), *Ctenocalanus vanus* (AS: 13%) and *Oithona similis* (AS: 8%) were the major components of the Aegean copepod community. At the other stations (Marmara and Bosphorus) *Acartia clausi* was dominant accounting for the 61% (BS) to 97% (MS1) of the total, whereas *Paracalanus parvus*, *Oithona similis* and *Calanus spp.* followed, contributed up to 18% of the total (Fig. 3b). In the underlying layer (20–50 m) of stations MS3, DS and AS, the species' composition was similar to that in the upper layer (Fig. 3c). However some differences were observed: the relative abundance of *Centropages typicus* was lower and some copepods such as *Ctenocalanus vanus*, *Paracalanus parvus*, *Oithona similis*, *Oncaea spp.* and *Calanus spp.* were found in higher numbers than in the upper layer. In the same layer (20–50 m) of stations MS1 and MS2 the contribution of *Acartia clausi* dropped, whereas the presence of *Oithona similis* and *Calanus spp.* was evident (Fig. 3c).

The MDS plot revealed two major groups (Fig. 4a). The first group included Bosphorus station, both layers of station MS1 and the surface layer of station MS2. The second layer (20–50 m) of station MS2 and the other stations and layers were grouped together. The ordination of the stations/layers represents the differentiation of the copepod communities based on the hydrographic features of the area revealing similarities according to different water masses.

The Principal Components Analysis (PCA) on environmental variables (temperature, salinity and chl *a*) and abundance of the major planktonic groups (diatoms, dinoflagellates, coccolithophores, small flagellates, ciliates, *Mesodinium spp.* and copepods) showed that the first two axes explained 68% of the variance (Fig. 4b). The station BS was located at the opposite side of the stations DS and AS along the

first axis (PC1), which was correlated very well to both salinity ($r^2=0.93$, $p<0.001$) and *Mesodinium* abundance ($r^2=0.90$, $p=0.004$). The two highest score values (BS and MS3) were positive corresponding to low salinity and high *Mesodinium* abundance. Along

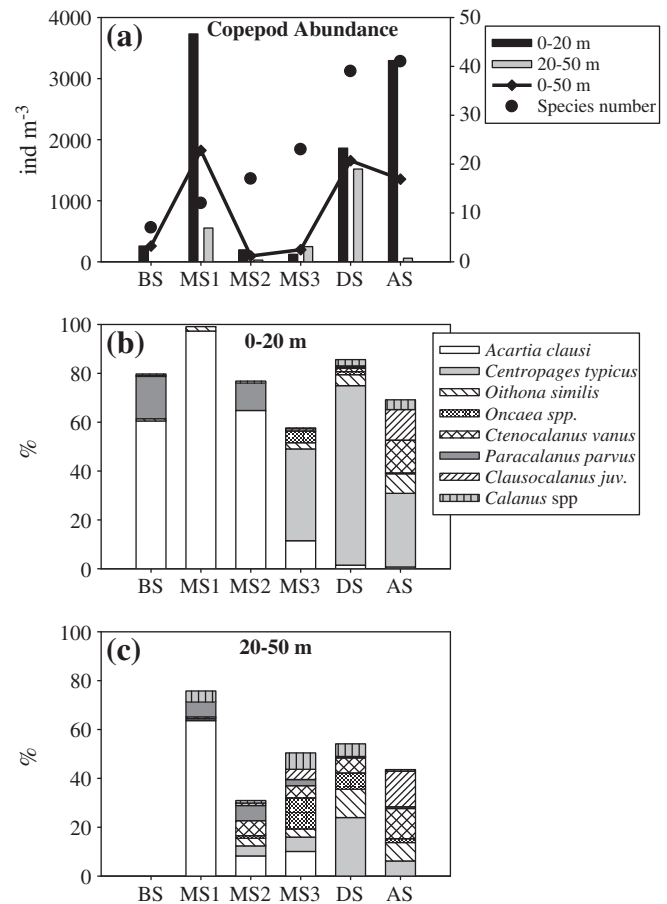


Fig. 3. Copepod abundance (a) (ind m⁻³, bars and line), number of species (a) (symbol) and relative abundance (b and c) (%), stacked bars) of the dominant copepod species on the total copepod population at all stations from BS to AS following the BSW, during April 2008. Note that zooplankton sampling in BS was performed in 0–30 m.

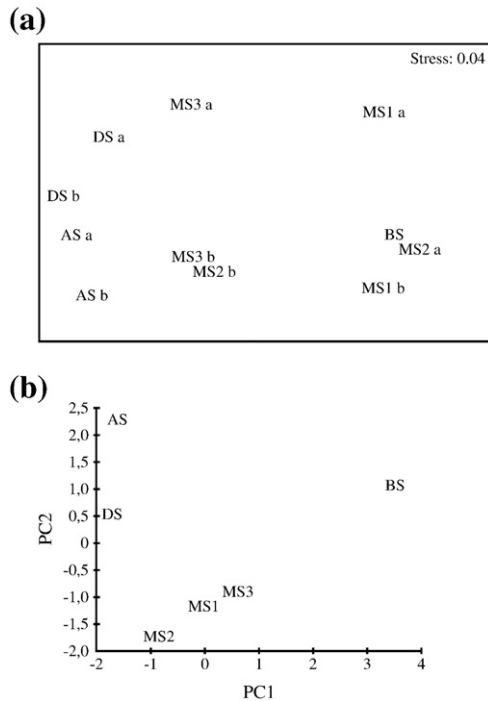


Fig. 4. (a) Ordination plot of copepod species abundance data transformed to square root using nonmetric multidimensional scaling (NMDS) and Bray–Curtis similarity index from the respective cluster. (b) Principal Component Analysis based on the environmental parameters (temperature, salinity, and chl *a*) and abundance of the major plankton components (diatoms, dinoflagellates, coccolithophores, small flagellates, ciliates, *Mesodinium* spp. and copepods).

the second axis, all stations in Marmara Sea (MS1–MS3) exhibited negative score values. The high abundance of dinoflagellates ($r^2=0.66$, $p=0.003$) and of other flagellates $>10\ \mu\text{m}$ ($r^2=0.51$, $p=0.03$) explained these differences. Hence, salinity and composition/distribution of microplankton (phytoplankton and microzooplankton) could account for the differentiation of stations during spring.

Both EP and SEP varied among the studied copepod species and showed a decreasing trend from Bosphorus to the Aegean Sea (Table 3). *Acartia clausi* had the highest EP ($38 \pm 2.7\ \text{egg fem}^{-1}\ \text{day}^{-1}$) and SEP ($26.7 \pm 1.9\% \text{body C day}^{-1}$) in Bosphorus and *Centropages typicus* had the highest EP ($47.5 \pm 5\ \text{egg fem}^{-1}\ \text{day}^{-1}$) and SEP ($12.3 \pm 1.9\% \text{body C day}^{-1}$) in the Marmara Sea. Copepod production was highest in Dardanelles ($17\ \text{mgC m}^{-2}\ \text{day}^{-1}$) and Marmara Sea (MS1: $18\ \text{mgC m}^{-2}\ \text{day}^{-1}$) and lowest in Bosphorus ($7\ \text{mgC m}^{-2}\ \text{day}^{-1}$) and Marmara Sea (MS2: $2\ \text{mgC m}^{-2}\ \text{day}^{-1}$) (Table 1).

Table 3
Mean EP (egg female $^{-1}\ \text{day}^{-1}$) \pm SE of the mean and SEP (%body C day $^{-1}$) rates of dominant copepod species at all stations during April 2008. Range (min–max) and number of replicates (n) are given in parentheses.

	Species	BS	MS1	MS2	DS	AS
EP (min–max, n)	<i>C. typicus</i>			47.5 ± 5 (37–59.5, 3)	8.9 ± 1 (5.5–13.1, 7)	4.7 ± 0.9 (1.7–10.3, 9)
	<i>C. helgolandicus</i>					6.6 ± 1 (3.4–8.6, 3)
	<i>A. clausi</i>	38 ± 2.7 (30.2–42.2, 6)	12.9 ± 1.2 (8.7–16, 6)	21 ± 2.4 (12.4–27.3, 6)		
SEP (min–max, n)	<i>C. typicus</i>			12.3 ± 1.9 (10.5–15.3)	3.01 ± 0.5 (2.2–4.6, 7)	1.7 ± 0.3 (0.6–3.7, 9)
	<i>C. helgolandicus</i>					1.5 ± 0.4 (2–0.8, 3)
	<i>A. clausi</i>	26.7 ± 1.9 (21.4–30, 6)	7.8 ± 0.7 (5.3–9.7, 6)	12.03 ± 1.4 (7.1–15.6, 6)		

During the incubation experiments, the initial chl *a* varied between 7.7 ± 0.3 and $32.2 \pm 7.3\ \text{mgC m}^{-3}$, the initial ciliate biomass varied between 0.7 ± 0.01 and $46 \pm 0.1\ \text{mgC m}^{-3}$ and the initial dinoflagellates biomass varied from 0.7 ± 0.02 to $52 \pm 4.5\ \text{mgC m}^{-3}$. The highest clearance rate ($\text{ml cop}^{-1}\ \text{day}^{-1}$) on phytoplankton was measured for *Centropages typicus* ($165 \pm 26\ \text{ml cop}^{-1}\ \text{day}^{-1}$) in Dardanelles (Fig. 5d). Ingestion rates on phytoplankton and microzooplankton were highest in the Marmara Sea and Bosphorus (Fig. 5g–i). *Acartia clausi* obtained on average 60% body C day $^{-1}$ from phytoplankton in the Marmara Sea and Bosphorus, whereas *Centropages typicus* obtained on average 17% body C day $^{-1}$ in Dardanelles and the Aegean Sea.

Based on cell length, ciliates and dinoflagellates were classified into different size classes and finally the clearance and ingestion rates were calculated (Fig. 5). In Bosphorus (BS), clearance by *Acartia clausi* was highest for ciliates and dinoflagellates of 30–50 μm (58 and 86 $\text{ml cop}^{-1}\ \text{day}^{-1}$, respectively), whereas in the Marmara Sea (MS1–MS2) its clearance rates were highest for ciliates $>50\ \mu\text{m}$ and *Mesodinium* spp. (174 and 110 $\text{ml cop}^{-1}\ \text{day}^{-1}$, respectively) (Fig. 5e and f). At the latter area, high ingestion rates of *Acartia clausi* were found for the ciliates $>50\ \mu\text{m}$ and for non-oligotrich ciliates (12.5 and 13% body C day $^{-1}$, respectively), as well as for dinoflagellates 30–50 μm (16% body C day $^{-1}$). In Dardanelles (DS) *Centropages typicus* preferred feeding on ciliates 30–50 μm and dinoflagellates of 20–30 μm (114 and 83 $\text{ml cop}^{-1}\ \text{day}^{-1}$ respectively), whereas in the Aegean Sea (AS) this species cleared ciliates and dinoflagellates of the 30–50 μm size in higher rates (235 and 299 $\text{ml cop}^{-1}\ \text{day}^{-1}$, respectively). Moreover, ingestion by *Centropages typicus* was highest for the dinoflagellates 30–50 μm (9% body C day $^{-1}$) in the latter area.

The relationship between EP and microplankton ingested, mirrored the pattern found between ingestion and food concentration. Overall, there was no correlation between SEP and total carbon ingested (chl *a* and microzooplankton), but a significant correlation was detected between SEP and chl *a* ingestion ($R^2=0.67$, $P<0.05$).

3.3. Carbon partitioning

We described carbon flux budget although data on bacterial and heterotrophic nanoflagellate biomass and production are missing. The partitioning of carbon biomass within different plankton components was strongly differentiated among the areas (Table 1). The ratio of the dominant food source (phytoplankton vs microzooplankton) showed that phytoplankton prevailed against microzooplankton at all stations (Table 1). In Bosphorus the carbon partitioning formed a broad-based pyramid where total phytoplankton biomass overwhelmed that of copepods + microzooplankton and the ratio of copepods + microzooplankton vs total phytoplankton was 0.59. In the Marmara Sea, this ratio ranged from 0.71 (MS2) to 1.03 (MS1). These values imply an increasing contribution of microzooplankton

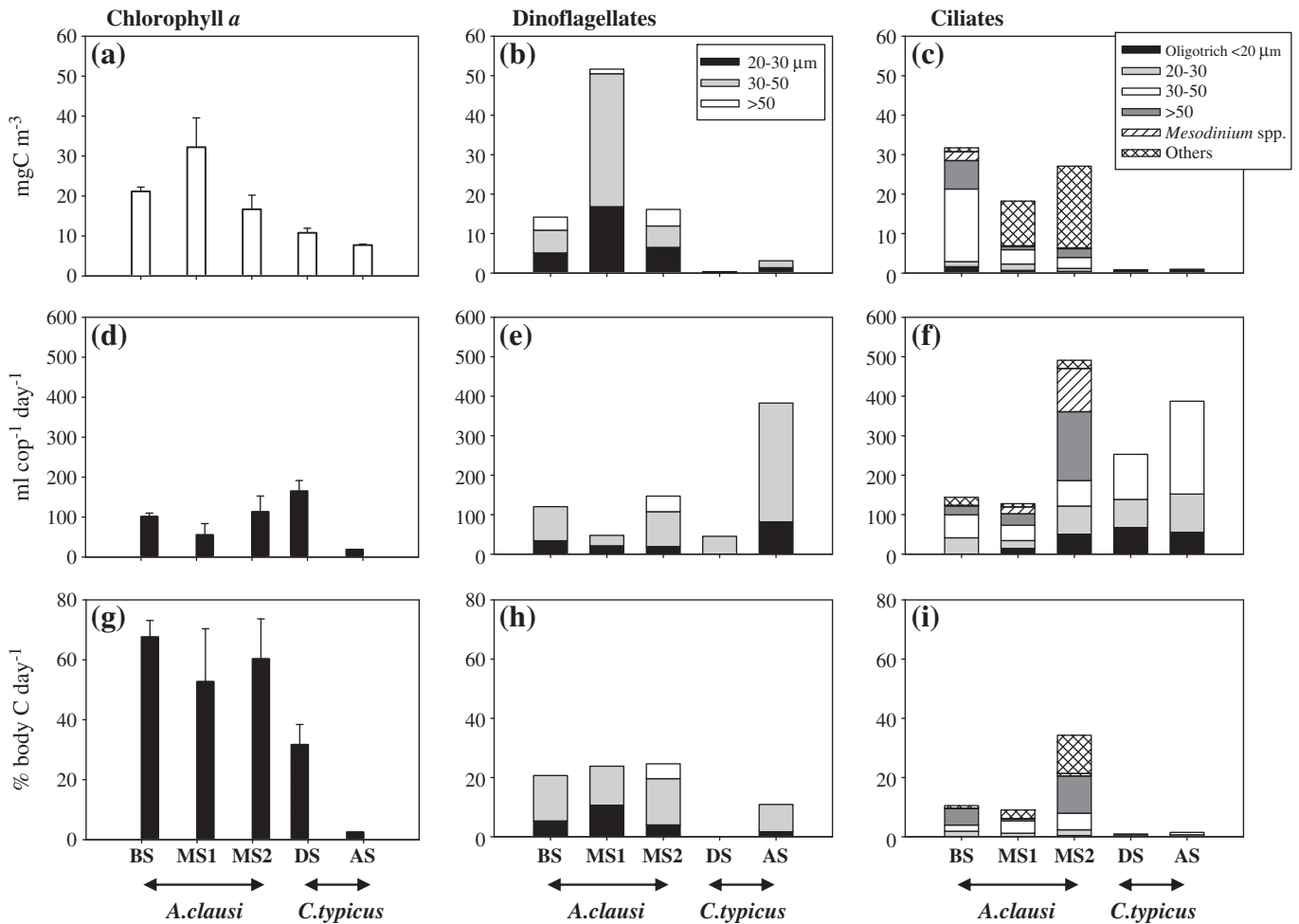


Fig. 5. Initial concentrations of total chl *a* (a) and different size classes of dinoflagellates (b) and ciliates (c) converted to carbon biomass (mgC m^{-3}), clearance rates ($\text{ml cop}^{-1} \text{day}^{-1}$) and specific ingestion ($\% \text{body C day}^{-1}$) of dominant copepod species (*C. typicus* and *A. clausi*) on chl *a* (d and g), Dinoflagellates (e and h) and Ciliates (f and i) during the incubation experiments at all stations on April 2008. Error bars indicate \pm SE of the mean.

and copepods from the Dardanelles (DS) to Bosphorus (BS). In Dardanelles an almost equal contribution of phytoplankton and copepods + microzooplankton was found (0.91), whereas in the Aegean Sea (AS) copepods + microzooplankton prevailed (1.49).

4. Discussion

4.1. Patterns in copepod communities, production and grazing

Due to a positive water balance in the Black Sea, its water masses are transferred into the Marmara Sea through the Bosphorus forming a brackish surface layer (15–20 m) with a salinity of 18 to 24 and temperature ranging from 20 to 24 °C in summer and from 8 to 9 °C in winter. Below this brackish water layer lays more saline (about 39) Mediterranean water veof Levantine origin, with a constant temperature of about 15 °C throughout the year (Besiktepe et al., 1994). These water-mass dynamics have been associated with the observed differences in planktonic fauna between the studied areas (Moraitou-Apostolopoulou, 1985; Kovalev et al., 1998; Siokou-Frangou et al., 2004). Our study is in agreement with previous studies in the northern Aegean Sea where the increased abundance of copepods is attributed to the presence of the BSW outflow which has been indicated to control the food supply and offer favorable feeding conditions to zooplankton organisms, enhancing their numbers (Zervoudaki et al., 2006, 2007; Siokou-Frangou et al., 2009). Furthermore our findings on the patterns of copepod

distribution for the Marmara Sea and Bosphorus are similar to those found in Istanbul Strait (Tarkan et al., 2005), as well as in open parts of the Marmara Sea (Unal et al., 2000). The strong stratification at the basin is known to limit diurnal vertical migration pattern of zooplankton with its main biomass concentrated in the upper layer (Mutlu, 2005).

In Bosphorus and Marmara Sea, *Acartia clausi* was dominant. This is a eurythermic and euryhaline copepod which is widely distributed in temperate and warm waters in the Black, Marmara and Mediterranean Seas, reproducing all year round (Tarkan and Erguven, 1988; Gubanova et al., 2001; Tarkan et al., 2005). Although the optimal range of salinity for *Acartia clausi* is 24–30, it has been shown that it can survive within a huge salinity range (1–65) (Cervetto et al., 1995). It has been found that developmental rates of *Acartia* congeners (*A. tonsa*, *A. bifilosa*, *A. discaudata* and *A. clausi*) were not affected even in the lowest saline water (15.5, Chinnery and Williams, 2004). The Bosphorus Straits and the Marmara Sea, (where the abundance maxima of *A. clausi* were recorded) have been subjected to severe eutrophication problems such as wastewater discharges from land-based sources, industrial loads and increased maritime traffic (Orhon, 1995; Okay et al., 1996; Morkoc et al., 2001). *Acartia clausi* is the only copepod species consistently observed in eutrophicated waters (Lakkis, 1974; Gubanova et al., 2001; Isinibilir et al., 2008). The above statements are in agreement with our findings.

Our results on egg production of *Acartia clausi* (Table 3), when compared to other temperate ecosystems at similar temperature,

were found to be: a) higher than those reported in the North Sea, Skaggeak and Kattegat ($0.5\text{--}20\text{ egg fem}^{-1}\text{ day}^{-1}$; Kiørboe et al., 1988; Peterson et al., 1991; Tiselius, 1989; Tiselius et al., 1991; Maar et al., 2004), b) higher than those found in the Aegean Sea ($1\text{--}25.5\text{ egg fem}^{-1}\text{ day}^{-1}$; Zervoudaki et al., 2007) and c) comparable with those found in the NW Mediterranean Sea ($10\text{--}35\text{ egg fem}^{-1}\text{ day}^{-1}$; Calbet et al., 2002). These dissimilarities/similarities in areas with different cell sizes of food, stress the ability of this copepod to use efficiently all available food items. Food quality and cell size are important components for reproductive efficiency and different responses may be related to the dietary diversity (Houde and Roman, 1987; Kiørboe et al., 1990; Vargas et al., 2006; Dutz et al., 2008; Dutz and Peters, 2008). In our study, egg production of *Acartia clausi* was found higher in Bosphorus than in the Marmara Sea and this is supported by the difference in food composition. We found that the ratio between the large ($>2.0\text{ }\mu\text{m}$) and the small ($<2.0\text{ }\mu\text{m}$) phytoplankton fraction in Bosphorus (0.74) and Marmara Sea (mean value: 0.73) was similar (Table 1), whereas the ratio between diatoms and dinoflagellates between Bosphorus (7.35) and Marmara Sea (mean value: 1.33) was different (Table 2). It has a long ago been known that many copepod species feed on diatoms in the sea (Lebour, 1922; Marshall and Orr, 1955) and this, in turn, is related with high egg production rates, which is in agreement with our findings. However, the proportional egg hatching success and naupliar survival has been found to be lower with a diatom-based diet (Ban et al., 1997; Muller-Navarra et al., 2004; Vargas et al., 2006). Dinoflagellates, on the other hand, are ingested at a much lower rate thus reflecting a lower egg production, but in compensation, there is increased egg hatching success (Calliari and Tiselius, 2005). The above relationships on food quality and quantity may enlighten the differentiation and relevance of *A. clausi* production rates and abundance patterns.

The clearance rates of $3\text{ to }165\text{ ml cop}^{-1}\text{ day}^{-1}$ for *Acartia clausi* feeding on various prey items in the Marmara Sea and Bosphorus found in this study fall within the range reported for this species and/or its congeners in various natural ecosystems (Tiselius, 1989; Gifford and Dagg, 1991; Fessenden and Cowles, 1994; Pérez et al., 1997; Bollens and Penry, 2003; Zervoudaki et al., 2007; Dutz and Peters, 2008). We also found that *Acartia clausi* obtained on average 60% body C day^{-1} from phytoplankton, 31% from ciliates and 20% from dinoflagellates (overbalancing requirement). Ciliates including *Mesodinium* spp. and dinoflagellates $>30\text{ }\mu\text{m}$ are considered as an ideal food source for *Acartia clausi* (Tiselius, 1989; Jonsson and Tiselius, 1990; Dutz and Peters, 2008) which is also confirmed by the present study (Fig. 5). The differentiated clearance rates of *Acartia clausi* on the various plankton components found in this study indicate the flexibility of this species to exploit diverse food sources attaining maxima in abundance and egg production (Jonsson and Tiselius, 1990).

Centropages typicus was dominant in the Aegean Sea, and its presence gradually decreased towards central Marmara Sea and Bosphorus where it totally disappeared (Fig. 3). Previous studies in the Marmara Sea have recorded high abundance during the winter–spring period (Benli et al., 2001), but this species has never been found in Bosphorus (Ogdul and Erguven, 1992). However in the Black Sea it has been recorded only two times, characterized as non-indigenous species from the Mediterranean (Kovalev et al., 1998). During our study a phytoplankton bloom was developing in the Marmara Sea with the highest chl α values at stations MS2 and MS1; *Centropages typicus* was present only in the subsurface layer ($20\text{--}50\text{ m}$) of MS2 with the lowest abundance. This is in agreement with the observation of Molinero et al. (2009) that higher abundances of the species were related to low-medium pigment concentration.

Centropages typicus is among the dominant copepods in the Mediterranean Sea with diverse seasonal cycles in population. During spring to early summer (April–June) in the Mediterranean, this species ranks among the most abundant copepods in several coastal (Christou, 1998; Mazzocchi et al., 2007; Molinero et al., 2009) and offshore areas

(Siokou-Frangou et al., 1997; Di Capua and Mazzocchi, 2004; Zervoudaki et al., 2006; Siokou-Frangou et al., 2009). According to the above studies, during this period, *Centropages typicus* predominates the surface communities, accounting for the $10\text{--}50\%$ of the total copepod numbers which is in agreement with our findings ($15\text{--}56\%$). Based on the large ($>2.0\text{ }\mu\text{m}$) to small ($<2.0\text{ }\mu\text{m}$) phytoplankton size ratio, picoplankton prevailed in the Aegean Sea (0.59) and Dardanelles (0.16), whereas large phytoplankton predominated in the Marmara Sea (MS3: 1.20). Diatoms prevailed in the Aegean Sea and Dardanelles, whereas dinoflagellate and diatom densities were comparable in the Marmara Sea (Table 3). Note that the maximum production rate of *Centropages typicus* was recorded in the Marmara Sea (MS3). It has been shown that different diets induce different reproductive responses of *Centropages typicus* as well as that, the food types inducing shortest development times (e.g. *Heterocapsa elongata* and *Strobidium sulcatum*) do not necessarily result in the highest egg production rates (Bonnet and Carlotti, 2001). Unrelated to the maximum abundance values recorded in the Aegean Sea and Dardanelles ($366\text{ and }966\text{ ind m}^{-3}$, respectively), egg production was very low when compared to other areas in the Mediterranean and North Seas (Ianora et al., 2007 and references therein) or to previous studies in the northern Aegean Sea (Zervoudaki et al., 2007). This inverse relationship between individual egg production rates and adult abundance of this species has been also indicated by other authors: Ianora et al. (1992) and Carotenuto et al. (2006) in the Gulf of Naples found a 2–3 month mis-match between maximum reproductive rates and adult female abundances as well as that hatching success was not related to breeding intensity or with environmental variables such as temperature and chl a . Also in the Ligurian Sea, Halsband-Lenk et al. (2001) found that maximum reproductive activity did not coincide with maximum female abundances in spring.

In our study, *Centropages typicus* clearance rates on various prey items varied from $18\text{ to }299\text{ ml cop}^{-1}\text{ day}^{-1}$ which are comparable to a previous study in the northern Aegean Sea ($15\text{--}180\text{ ml cop}^{-1}\text{ day}^{-1}$, Zervoudaki et al., 2007). Nevertheless the highest values in the above range were higher than those found in the NW Mediterranean (*C. typicus* feeding on ciliates: $90\text{ ml cop}^{-1}\text{ day}^{-1}$, Broglio et al., 2004), and in the New York Bight (*C. typicus* feeding on phytoplankton: $94\text{ ml cop}^{-1}\text{ day}^{-1}$, Smith and Lane, 1987). Its preference for large motile prey ($>30\text{ }\mu\text{m}$, ciliates and dinoflagellates, Fig. 5) is in agreement with other studies (Calbet et al., 2007 and references therein). It appears that this copepod successfully exploits different food sources (this study: 17% from phytoplankton, 2% from ciliates and 3% from dinoflagellates) and can benefit of considerable ciliate stocks (Molinero et al., 2009).

4.2. Carbon budget

This is the first attempt to illustrate the fate of pelagic production in both the Turkish Straits System and the northern Aegean Sea simultaneously, taking into account the observed variability in rates and distributions. Carbon budget and estimated flow dynamics are usually exposed to some error factors due to the use of constant carbon conversion factors and growth yields. Given the lack of information on bacteria, the food web structure is also likely to be more complicated than that presented in this study, especially so within microzooplankton (e.g., mixotrophy). Patchiness of plankton, as well as variations in the feeding behavior of plankton organisms, can cause undetectable error in the carbon flow estimation. However, the results of this study confirm our hypothesis that there is a substantial differentiation of the pelagic food web structure and the carbon flow from the Bosphorus to the Aegean Sea (Fig. 6). Based on the established carbon budgets it appears that approximately 55% of the daily phytoplankton production was grazed directly by copepods in Dardanelles whereas less than 1% in Bosphorus. In the Marmara Sea the daily grazing pressure exerted by the copepods on phytoplankton

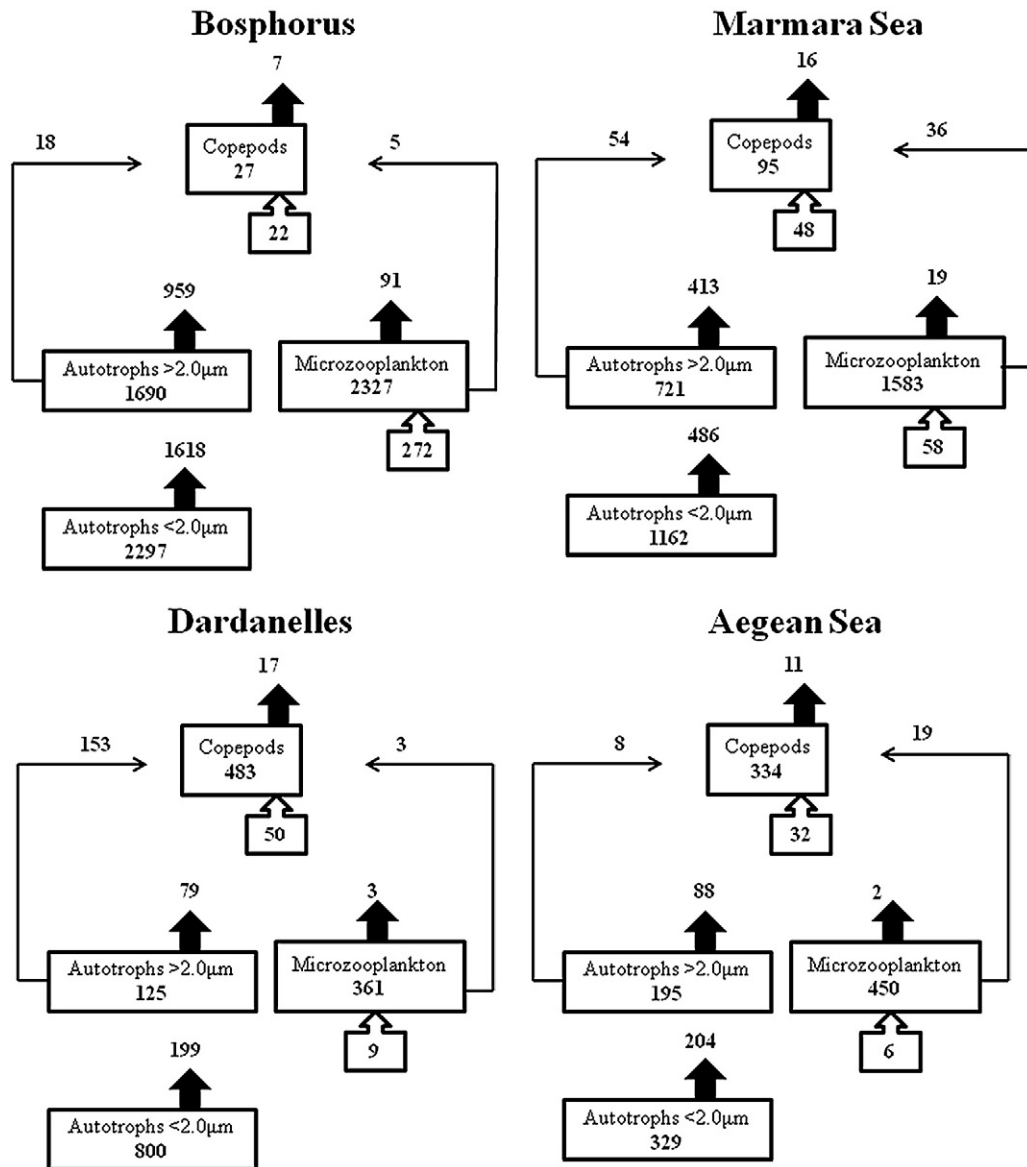


Fig. 6. Carbon flow diagrams of the planktonic food web in April 2008. Numbers in boxes show the biomass (mg C m^{-2}), black thick arrows show the carbon production ($\text{mg C m}^{-2} \text{ day}^{-1}$), the white boxes with arrow show the carbon demand ($\text{mg C m}^{-2} \text{ day}^{-1}$) and narrow arrows show the consumption ($\text{mg C m}^{-2} \text{ day}^{-1}$) of the copepods. Adults and copepodite stages are both included for the calculations of biomass, production and consumption of copepods.

biomass and production were 3 and 6 day^{-1} respectively, whereas the corresponding values for the Aegean Sea were 1.5 and 3 day^{-1} . Our results are in agreement with other studies, confirming that copepods consume less than 50% of the daily phytoplankton production although in cases the grazing impact of copepods exceeds the daily primary production (Richardson et al., 1998; Maar et al., 2002; Gaudy et al., 2003; Siokou-Frangou et al., 2002; Zervoudaki et al., 2007).

The observed low grazing pressure of copepods could be also attributed to the low copepod biomass found in Bosphorus and Marmara Sea. The strong presence of gelatinous zooplankton in these areas such as the residents *Aurelia aurita* and *Pleurobrachia pileus* and the invader *Mnemiopsis leidyi* (all major copepod predators) should be accountable for a substantial decline in copepod biomass. These species were present during the cruise in the Marmara Sea and Bosphorus in relatively high densities ($1\text{--}30 \text{ ind m}^{-3}$, personal observation). Gelatinous zooplankton occurring in the Black Sea all year round are distributed through Bosphorus to the Marmara Sea by the surface Black Sea currents (İşinibilir and Tarkan, 2002; Kovalev and Piontkovski, 1998), while their biomass decreases from the Black

Sea to the northern Aegean Sea (Shiganova et al., 2001; Siokou-Frangou et al., 2004). Experimental work has shown that *Aurelia* may consume ciliates (Stoecker et al., 1987; Omori et al., 1995) suggesting a closer link to the microbial food web (Hansson and Norrman, 1995; Fukuda and Naganuma, 2001).

In Bosphorus and Marmara Sea, the relatively high biomass of microzooplankton available to copepods indicated a strong coupling between copepods and microbial food web (Fig. 6). That was apparent for the Marmara Sea where the grazing impact of copepods on microzooplankton production exceeded 100 day^{-1} . However, in Bosphorus, only 5% of the microzooplankton production was used by the copepods (Fig. 6). The high biomass and production of microzooplankton in Bosphorus in contrast to the very low biomass and production of copepods reflected the low grazing impact of the copepods on microzooplankton. Predation on microzooplankton, on the other hand, is often relaxed during net phytoplankton blooms, and this allows microzooplankton to peak along with the phytoplankton (Nielsen and Kiørboe, 1994). There is a growing consensus in the literature that microzooplankton is able to consume a substantial amount of phytoplankton, especially in

near-shore environments and that their consumption may at times exceed that of larger zooplankton (Gifford and Dagg, 1991; Dagg, 1995; Calbet and Saiz, 2005). The grazing impact of microzooplankton on phytoplankton production in Bosphorus and Marmara Sea was 10 and 6.5% day⁻¹, respectively, whereas copepods and microzooplankton together used less than 13% of the daily primary production in both areas. Hence, it appears that the majority of the produced phytoplankton biomass (mainly derived from large diatoms) is channeled to other pathways leaving euphotic zone ungrazed (Smetacek, 1985; Kiørboe et al., 1994).

In the Aegean Sea microzooplankton appeared to be an important food source for the copepods. Moreover, the low microzooplankton biomass and production suggested that microzooplankton was probably limited by copepod predation, supporting a strong top-down control of its population as has been previously shown for the Aegean Sea (Siokou-Frangou et al., 2002; Zervoudaki et al., 2007). In the Dardanelles, microzooplankton biomass and production was low. However, the low copepod predation on microzooplankton could not explain the observed low biomass and production of microzooplankton. The very low ingestion rates of copepods on dinoflagellates found in the present study support the diminished consumption (Fig. 5). Microzooplankton grazing pressure on phytoplankton production in Dardanelles and Aegean Sea (2 and 3% day⁻¹, respectively) was lower compared to the other stations (this study) or to other seas (Maar et al., 2002, 2004).

Studying copepod grazing pressure, food size structure should be also evaluated. Considering the >2.0 µm fraction as potential phytoplankton food for copepods, we found that production of this fraction could support from 2% (Bosphorus) to more than 100% (Dardanelles) of the daily copepod diet. In the latter area, where copepods consumed more than 100% day⁻¹ of phytoplankton + microzooplankton, the highest copepod biomass and production were recorded, highlighting an efficient exploitation of all available food sources (Fig. 5).

5. Conclusions

This study, based on the copepod communities, analyzed the spatial differentiation of the pelagic food web structure and the carbon flow from Bosphorus to the Aegean Sea during spring. The transition area between the Black Sea and the Aegean Sea is characterized by high gradients in salinity and pelagic fauna compositions. The phytoplankton/microzooplankton biomass and production showed a clear decreasing trend from Bosphorus to the Aegean Sea, whereas copepod biomass and production did not show any clear trend along the transect. However, the number of copepod species dramatically decreased from the Aegean Sea to Bosphorus. The results of this study confirm the hypothesis that there is a substantial differentiation of the pelagic food web structure and the carbon flow from the Bosphorus to the Aegean Sea. A large amount of phytoplankton production appears to pass through other pathways (microbial loop in the Aegean Sea) and/or is might sedimented on the bottom (Marmara Sea, Bosphorus). We strongly recommend further investigations, on: a) carbon cycling (including total microbial loop) and b) importance of gelatinous zooplankton and their impact on carbon cycling in the Turkish Strait System, in order to improve our understanding about the dynamics of the interconnected system between the Black and the Mediterranean Seas.

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References

- Båmstedt, U., Gifford, D.J., Irigoien, X., Atkinson, A., Roman, M., 2000. Feeding. In: Harris, R., Wiebe, P., Lenz, J., Skjoldal, H.R., et al. (Eds.), ICES Zooplankton Methodology Manual. Academic Press, London, pp. 297–399.
- Ban, S.H., Burns, C., Castel, J., et al., 1997. The paradox of diatom-copepod interactions. *Marine Ecology Progress Series* 157, 287–293.
- Benli, H.A., Tarkan, A.N., Sever, T.M., 2001. Comparison of the mesozooplankton composition the southwestern Black Sea, Sea of Marmara and eastern Aegean Sea. *Turkish Journal of Marine Science* 7, 163–179.
- Berggreen, U., Hansen, B., Kiørboe, T., 1988. Food size spectra, ingestion and growth of copepod *Acartia tonsa*, implications for the determination of copepod production. *Marine Biology* 99, 341–352.
- Besiktepe, S.T., Sur, H.I., Ozsoy, E., Latif, M.A., Oguz, T., Unluata, U., 1994. The circulation and hydrography of the Marmara Sea. *Progress in Oceanography* 34, 285–334.
- Bollens, G.C.R., Penry, D.L., 2003. Feeding dynamics of *Acartia* spp. copepods in a large, temperate estuary (San Francisco Bay, CA). *Marine Ecology Progress Series* 257, 139–158.
- Bonnet, D., Carloti, F., 2001. Development and egg production in *Centropages typicus* (Copepoda: Calanoida) fed different food types: a laboratory study. *Marine Ecology Progress Series* 224, 133–148.
- Broglio, E., Saiz, E., Calbet, A., Trepas, I., Alcaraz, M., 2004. Trophic impact and prey selection by crustacean zooplankton on the microbial communities of an oligotrophic coastal area (NW Mediterranean Sea). *Marine Ecology Progress Series* 35, 65–78.
- Calbet, A., Saiz, E., 2005. The ciliate-copepod link in marine ecosystems. *Aquatic Microbial Ecology* 38, 157–167.
- Calbet, A., Saiz, E., Alcaraz, M., 2002. Copepod egg production in the NW Mediterranean: effects of winter environmental conditions. *Marine Ecology Progress Series* 237, 173–184.
- Calbet, A., Carloti, F., Gaudy, R., 2007. The feeding ecology of the copepod *Centropages typicus* (Krøyer). *Progress in Oceanography* 72 (2–3), 137–150.
- Calliari, D., Tiselius, P., 2005. Feeding and reproduction in a small calanoid copepod: *Acartia clausi* can compensate quality with quantity. *Marine Ecology Progress Series* 298, 241–250.
- Carotenuto, Y., Ianora, A., Di Pinto, M., Sarno, D., Miralto, A., 2006. Annual cycle of early developmental stage survival and recruitment in the copepods *Temora stylifera* and *Centropages typicus*. *Marine Ecology Progress Series* 314, 227–238.
- Cervetto, G., Pagano, M., Gaudy, R., 1995. Adaptation aux variations de la salinité chez le copepode *Acartia clausi*. *Journal de la Recherche Océanographique* 20, 42–49.
- Chinnery, F.E., Williams, J.A., 2004. The influence of temperature and salinity on *Acartia* (Copepoda: Calanoida) nauplii survival. *Marine Biology* 145, 733–738.
- Christou, E.D., 1998. Interannual variability of copepods in a Mediterranean coastal area (Saronikos Gulf, Aegean Sea). *Journal of Marine Systems* 15, 523–532.
- Christou, E.D., Verriopoulos, G.C., 1993. Length, weight and condition factor of *Acartia clausi* (Copepoda) in the Eastern Mediterranean. *Journal of the Marine Biological Association of the United Kingdom* 73, 343–353.
- Clarke, K.R., Warwick, R.M., 1994. Change in marine communities: an approach to statistical analysis and interpretation. Plymouth Marine Laboratory, Plymouth: Natural Environment Research Council.
- Dagg, M.J., 1995. Copepod grazing and the fate of phytoplankton in the northern Gulf of Mexico. *Continental Shelf Research* 15 (11/12), 1303–1317.
- Di Capua, I., Mazzocchi, M.G., 2004. Population structure of the copepods *Centropages typicus* and *Temora stylifera* in different environmental conditions. *ICES Journal of Marine Science* 61, 632–644.
- Dutz, J., Peters, J., 2008. Importance and nutritional value of large ciliates for the reproduction of *Acartia clausi* during the post spring-bloom period in the North Sea. *Aquatic Microbial Ecology* 50, 261–277.
- Dutz, J., Koski, M., Jonasdottir, S.H., 2008. Copepod reproduction is unaffected by diatom aldehydes or lipid composition. *Limnology and Oceanography* 53 (1), 225–235.
- Fessenden, L., Cowles, T.J., 1994. Copepod predation on phagotrophic ciliates in Oregon coastal waters. *Marine Ecology Progress Series* 107, 103–111.
- Field, J.G., Clarke, K.R., Warwick, R.M., 1982. A practical strategy for analysing multispecies distribution patterns. *Marine Ecology Progress Series* 8, 37–52.
- Frost, B.W., 1972. Effect of size and concentration of food particles on the feeding behaviour of the marine planktonic copepod *Calanus pacificus*. *Limnology and Oceanography* 17, 805–815.
- Fukuda, Y., Naganuma, T., 2001. Potential dietary effects on the fatty acids composition of the common jellyfish *Aurelia aurita*. *Marine Biology* 138, 1029–1035.
- Gaudy, R., Youssara, F., Diaz, F., Raimbault, P., 2003. Biomass, metabolism and nutrition of zooplankton in the Gulf of Lions (NW Mediterranean). *Oceanologica Acta* 26 (4), 357–372.
- Gifford, D.J., Dagg, M.J., 1991. The microzooplankton link, consumption of planktonic protozoa by the calanoid copepods *Acartia tonsa* Dana and *Neocalanus plumchrus* Murokawa. *Marine Microbial Food Webs* 5, 161–177.
- Gubanov, A.D., Prusova, I.Yu., Niermann, U., Shadrin, N.V., Polikarpov, I.G., 2001. Dramatic change in the copepod community in Sevastopol Bay (Black Sea) during two decades (1976–1996). *Senckenbergiana Maritima* 31, 17–27.

- Halsband-Lenk, C., Nival, S., Carlotti, F., Hirche, H.J., 2001. Seasonal cycles of egg production of two planktonic copepods, *Centropages typicus* and *Temora stylifera*, in the north-western Mediterranean Sea. *Journal of Plankton Research* 23, 597–609.
- Hansen, P.J., Bjornsen, P.K., Hansen, B., 1997. Zooplankton grazing and growth, scaling within the 2–2000 mm body size range. *Limnology and Oceanography* 42, 687–704.
- Hansson, L.J., Norrman, B., 1995. Release of dissolved organic carbon (DOC) by the scyphozoan jellyfish *Aurelia aurita* and its potential influence on the production of planktonic bacteria. *Marine Biology* 121, 527–532.
- Hirche, H.J., Mumm, N., 1992. Distribution of dominant copepods in the Nansen basin, Arctic Ocean, in summer. *Deep Sea Research* 39 (2A), S485–S505 Suppl.
- Holm-Hansen, O., Lorenzen, C.J., Holmes, R.N., Strickland, J.D.H., 1965. Fluorometric determination of chlorophyll. *Journal de Conseil pour l'Exploration de la Mer* 30, 3–15.
- Hopcroft, R.R., Roff, J.C., Lombard, D., 1998. Production of tropical copepods in Kingston Harbour, Jamaica: the importance of small species. *Marine Biology* 130, 593–604.
- Houde, S.E.L., Roman, M.R., 1987. Effects of food quality on the functional ingestion response of the copepod *Acartia tonsa*. *Marine Ecology Progress Series* 40 (1–2), 69–77.
- Ianora, A., Mazzocchi, M.G., Grotoli, R., 1992. Seasonal fluctuations in fecundity and hatching success in the planktonic copepod *Centropages typicus*. *Journal of Plankton Research* 14, 1483–1494.
- Ianora, A., Miralto, A., Halsband-Lenk, C., 2007. Reproduction, hatching success, and early naupliar survival in *Centropages typicus*. *Progress in Oceanography* 72, 195–213.
- Ignatiades, L., Psarra, S., Zervakis, V., Pagou, K., Souvermezoglou, E., Assimakopoulou, G., Gotsis-Skretas, O., 2002. Phytoplankton size-based dynamics in the Aegean Sea (Eastern Mediterranean). *Journal of Marine Systems* 36, 11–28.
- Isari, S., Ramfos, A., Somarakis, S., Koutsikopoulos, C., Kallianiotis, A., Fragopoulou, N., 2006. Mesozooplankton distribution in relation to hydrology of the Northeastern Aegean Sea, Eastern Mediterranean. *Journal of Plankton Research* 28, 241–255.
- İsinibilir, M., Tarkan, A.N., 2002. Distribution of the Invasive Ctenophore *Mnemiopsis leidyi* (Agassiz, 1865) in the North-eastern Aegean Sea in August 1998. *Turkish Journal of Fisheries and Aquatic Sciences* 2, 129–132.
- İsinibilir, M., Kideys, A.E., Tarkan, A.N., Yilmaz, I.N., 2008. Annual cycle of zooplankton abundance and species composition in Izmit Bay (the northeastern Marmara Sea). *Estuaries, Coastal and Shelf Science* 78, 739–747.
- Jeong, H.J., 1999. The ecological roles of heterotrophic dinoflagellates in marine planktonic community 1. *Journal of Eukaryotic Microbiology* 46, 90–996.
- Joint, I., Pomroy, A., Savidge, G., Boyd, P., 1993. Size-fractionated primary productivity in the northeast Atlantic in May–July 1989. *Deep Sea Research II* 40, 423–440.
- Jonsson, P.R., Tiselius, P., 1990. Feeding-behavior, prey detection and capture efficiency of the copepod *Acartia tonsa* feeding on planktonic ciliates. *Marine Ecology Progress Series* 60 (1–2), 35–44.
- Kjørboe, T., Møhlenberg, F., Hamburger, K., 1985. Bioenergetics of the planktonic copepod *Acartia tonsa*, relation between feeding, egg production and composition of specific dynamic action. *Marine Ecology Progress Series* 26, 85–97.
- Kjørboe, T., Møhlenberg, F., Tiselius, P., 1988. Propagation of planktonic copepods: production and mortality of eggs. *Hydrobiologia* 167 (168), 219–225.
- Kjørboe, T., Kaas, H., Kruse, B., Møhlenberg, F., Tiselius, P., Ærtebjerg, G., 1990. The structure of the pelagic food web in relation to water column structure in the Skagerrak. *Marine Ecology Progress Series* 59, 19–32.
- Kjørboe, T., Landsgaard, C., Olesen, M., Hansen, J.L.S., 1994. Aggregation and sedimentation processes during a spring bloom: A field experiment to test coagulation theory. *Journal of Marine Research* 52, 297–323.
- Kovalev, A.V., Piontkovski, S.A., 1998. Interannual changes in the biomass of the Black Sea gelatinous zooplankton. *Journal of Plankton Research* 20 (7), 1377–1385.
- Kovalev, A.V., Besiktepe, S., Zagorodnyaya, J., Kideys, A., 1998. Mediterraneanization of the Black Sea zooplankton is continuing. In: Ivanov, L., Oguz, T. (Eds.), *Ecosystem modeling as a management tool for the Black Sea*. NATO ASI Ser 1 *Global Environmental Change*, pp. 199–207.
- Kovalev, A.V., Mazzocchi, M.G., Kideys, A.E., Toklu, B., Skryabin, V.A., 2003. Seasonal changes in the composition and abundance of Zooplankton in the Seas of the Mediterranean Basin. *Turkish Journal of Zoology* 27, 205–219.
- Lakkis, S., 1974. Considerations on the distribution of pelagic copepods in the Eastern Mediterranean of the coast of Lebanon. *Acta Adriatica* 18, 39–52.
- Lebour, M.V., 1922. The food of plankton organisms. *Journal of the Marine Biological Association of the United Kingdom* 12, 644–677.
- Lykousis, V., Chronis, G., Tselepidis, A., et al., 2002. Major outputs of the recent multi-disciplinary biogeochemical researches in the Aegean Sea. *Journal of Marine Systems* 33 (34), 313–334.
- Maar, M., Nielsen, T.G., Richardson, K., Christaki, U., Hansen, O.S., Zervoudaki, S., Christou, E.D., 2002. Spatial and temporal variability of food web structure during the spring bloom in the Skagerrak. *Marine Ecology Progress Series* 239, 11–29.
- Maar, M., Nielsen, T.G., Gooding, S., Tønnesson, K., Tiselius, P., Zervoudaki, S., Christou, E.D., Sell, A., Richardson, K., 2004. Trophodynamic function of copepods, appendicularians and protozooplankton in the late summer zooplankton community in the Skagerrak. *Marine Biology* 144, 917–933.
- Marshall, S.M., Orr, A.P., 1955. The biology of a marine copepod *Calanus finmarchicus*. Gunnerus. Oliver and Boyd, Edinburgh.
- Mazzocchi, M.G., Christou, E.D., Di Capua, I., Fernandez de Puelles, M.L., Fonda-Umani, S., Molinero, J.C., Nival, P., Siokou-Frangou, I., 2007. The temporal variability of *Centropages typicus* in the Mediterranean Sea: from seasonal to decadal scales. *Progress in Oceanography* 72, 214–232.
- Menden-Deuer, S., Lessard, E.J., 2000. Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. *Limnology and Oceanography* 45, 569–579.
- Molinero, J.C., Vukanic, V., Lucic, D., et al., 2009. Mediterranean marine copepods: basin-scale trends of the calanoid *Centropages typicus*. *Hydrobiologia* 617, 41–53.
- Moraitou-Apostolopoulou, M., 1985. The zooplankton communities of eastern Mediterranean (Levantine Basin, Aegean Sea); influence of man-made factors. In: Moraitou-Apostolopoulou, M., Kiortsis, V. (Eds.), *Mediterranean marine ecosystems*. Plenum, New York, pp. 303–329.
- Morkoc, E., Okay, S.O., Tolun, L., Tüfekçi, V., Tüfekçi, H., Legović, T., 2001. Towards a clean Izmit Bay. *Environmental International* 26, 157–161.
- Muller-Navarra, D.C., Brett, M.T., Park, S., Chandra, S., Ballantyne, A.P., Zorita, E., Goldman, C.R., 2004. Unsaturated fatty acid content in seston and tropho-dynamic coupling in lakes. *Nature* 427, 69–72.
- Mutlu, E., 2005. A comparison of the contribution of zooplankton and nekton taxa to the near-surface acoustic structure of three Turkish seas. *Marine Ecology* 26, 17–32.
- Nielsen, T.G., Kjørboe, T., 1994. Regulation of zooplankton biomass and production in a temperate coastal ecosystem: 2. Ciliates. *Limnology and Oceanography* 39, 508–519.
- Ogdul, R.G., Ergüven, H., 1992. A study on the abundance and composition of zooplankton groups in the bay of Beykoz (Bosphorus). *Istanbul University Journal of Aquatic Products* 1, 105–120.
- Okay, S.O., Legović, T., Tüfekçi, V., Egesel, L., Morkoc, E., 1996. Environmental impact of land-based pollutants on Izmit Bay (Turkey): short-term algal bioassays and simulation of toxicity distribution in the marine environment. *Archives of Environmental Contamination and Toxicology* 31, 459–465.
- Omori, M., Ishii, H., Fujinaga, A., 1995. Life history strategy of *Aurelia aurita* (Cnidaria, Scyphomedusae) and its impact on the zooplankton community of Tokyo Bay. *ICES Journal of Marine Science* 52, 597–603.
- Orhon, D., 1995. Evaluation of the impact from the Black Sea on the pollution of the Marmara Sea. *Water Science and Technology* 32 (7), 191–198.
- Özsoy, E., Gregg, M., Latif, M.A., et al., 2002. Turkish Straits System. Proc. of the “Second Internat. Conf. on the Eastern Mediterranean and Black Sea: Similarities and Differences of the Two Interconnected Basins.” TÜBITAK, Ankara, pp. 89–94.
- Pérez, M.T., Dolan, J.R., Fukai, E., 1997. Planktonic oligotrich ciliates in the NW Mediterranean: growth rates and consumption by copepods. *Marine Ecology Progress Series* 155, 89–101.
- Peterson, W.T., Tiselius, P., Kjørboe, T., 1991. Copepod egg-production, molting and growth-rates, and secondary production, in the Skagerrak in August 1988. *Journal of Plankton Research* 1, 131–154.
- Polat, C., Tugrul, S., 1996. Chemical exchange between the Mediterranean and the Black Sea via the Turkish Strait. Dynamics of Mediterranean Strait and Channels. *CIESM Science Series* no. 2. Bulletin de l'Institut Océanographique Monaco 17, 167–186.
- Putt, M., Stoecker, D.K., 1989. An experimentally determined carbon volume ratio for marine oligotrichous ciliates from estuarine and coastal waters. *Limnology and Oceanography* 34, 1097–1103.
- Richardson, K., Nielsen, T.G., Pedersen, F.B., Heilmann, J.P., Lokkegaard, B., Kaas, H., 1998. Spatial heterogeneity in the structure of the planktonic food web in the North Sea. *Marine Ecology Progress Series* 168, 197–211.
- Satapoomin, S., 1999. Carbon content of some common tropical Andaman Sea copepods. *Journal of Plankton Research* 21, 2117–2123.
- Shiganova, T.A., Mirzoyan, Z.A., Studenikina, E.A., Volovik, S.P., Siokou-Frangou, I., Zervoudaki, S., Christou, E.D., Skirta, A.Y., Dumont, H.J., 2001. Population development of the invader ctenophore *Mnemiopsis leidyi*, in the Black Sea and in other seas of the Mediterranean basin. *Marine Biology* 139 (3), 431–445.
- Siokou-Frangou, I., Christou, E.D., Frangopoulou, N., Mazzocchi, M.G., 1997. Zooplankton distribution from Sicily to Cyprus (Eastern Mediterranean) II. Copepod assemblages. *Oceanologica Acta* 20 (3), 537–547.
- Siokou-Frangou, I., Bianchi, M., Christaki, U., et al., 2002. Organic carbon partitioning and carbon flow along a gradient of oligotrophy in the Aegean Sea (Mediterranean Sea). *Journal of Marine Systems* 33 (34), 325–353.
- Siokou-Frangou, I., Shiganova, T., Christou, E.D., Kamburska, L., Gubanova, A., Konsulov, A., Musaveva, E., Skryabin, V., Khoroshilov, V., 2004. Mesozooplankton communities in the Aegean and Black Seas: a comparative study. *Marine Biology* 144, 1111–1126.
- Siokou-Frangou, I., Zervoudaki, S., Christou, E.D., Zervakis, V., Georgopoulos, D., 2009. Variability of mesozooplankton spatial distribution in the North Aegean Sea, as influenced by the Black Sea waters outflow. *Journal of Marine Systems* 78, 557–575.
- Smetacek, V., 1985. Role of sinking in diatom life-history cycles: ecological, evolutionary and geological significance. *Marine Biology* 84, 239–251.
- Smith, S.L., Lane, P.V.Z., 1987. On the life history of *Centropages typicus*: responses to a fall diatom bloom in the New York Bight. *Marine Biology* 95, 305–313.
- Stoecker, D.K., Michaels, A.E., Davis, L.H., 1987. Grazing by the jellyfish, *Aurelia aurita*, on microplankton. *Journal of Plankton Research* 9, 901–915.
- Svetlichny, L., Hubareva, E., Kideys, A., İsinibilir, M., Shmeleva, A., 2006. Zooplankton community state in the Northeastern Marmara Sea during early autumn with comments on mass mortality of the Black Sea species due to the salinity gradient. *Journal of Black Sea/Mediterranean Environment* 12, 213–231.
- Tarkan, A.N., 2000. Abundance and distribution of zooplankton in coastal area of Gökçeada island (Northern Aegean Sea). *Turkish Journal of Marine Science* 6, 201–214.
- Tarkan, A.N., Ergüven, H., 1988. The main copepod species of Marmara Sea. *Istanbul University Journal of Aquatic Products* 2, 71–72.
- Tarkan, A.N., İsinibilir, M., Tarkan, A.S., 2005. Seasonal variations of the zooplankton composition and abundance in the Istanbul Strait. *Pakistan Journal of Biological Science* 8, 1327–1336.

- Theocharis, A., Georgopoulos, D., 1993. Dense water formation over the Samothraki and Limnos plateaus in the North Aegean Sea (Eastern Mediterranean-Sea). *Continental Shelf Research* 13 (8–9), 919–939.
- Tiselius, P., 1989. Contribution of aloricate ciliates to the diet of *Acartia clausi* and *Centropages hamatus* in coastal waters. *Marine Ecology Progress Series* 56, 49–56.
- Tiselius, P., Nielsen, T.G., Breuel, G., Jaans, A., Korshenko, A., Witek, Z., 1991. Copepod egg production in the Skagerrak during SKAGEX, May–June 1990. *Marine Biology* 111, 445–453.
- Unal, E., Shmeleva, A.A., Zagordnyaya, J., Kideys, A.E., 2000. Zooplankton structure and copepod species of the Sea of Marmara in spring 1998. In: Ozturk, B., Kadioglu, M., Ozturk, H. (Eds.), *Marmara Sea 2000 Symposium*. Turkish Marine Research Foundation (TUDAV) Publications 5, Istanbul, pp. 450–460.
- UNESCO, 1968. Zooplankton sampling. The UNESCO Press, Paris, p. 174.
- Unluata, U., Oguz, T., Latif, M.A., Ozsoy, E., 1990. On the physical oceanography of the Turkish Straits. *The Physical Oceanography of Sea Straits*, NATO/ASI Series. Kluwer Academic Publishers, The Netherlands, pp. 25–60.
- Utermöhl, H., 1958. Zur Vervollkommung der quantitative phytoplankton-methodik. *Mitteilungen der Internationale Limnologische Vereinigung* 9, 1–38.
- Uye, S.-I., 1982. Length-weight relationships of important zooplankton from the Inland Sea of Japan. *Journal of the Oceanographical Society of Japan* 38, 149–158.
- Vargas, C.A., Escribano, R., Poulet, S., 2006. Phytoplankton food quality determines time windows for successful zooplankton reproductive pulses. *Ecology* 87 (12), 2992–2999.
- Verity, P.G., Smetacek, V., 1996. Organism life cycles, predation and the structure of marine pelagic ecosystems. *Marine Ecology Progress Series* 130, 277–293.
- Yilmaz, I.N., Okus, E., Yuksek, A., 2005. Evidence for influence of a heterotrophic dinoflagellate (*Noctiluca scintillans*) on zooplankton community structure in a highly stratified basin. *Estuaries Coastal Shelf Science* 64, 475–485.
- Zervakis, V., Georgopoulos, D., 2002. Hydrology and circulation in the North Aegean (Eastern Mediterranean) throughout 1997 and 1998. *Mediterranean Marine Science* 3, 5–20.
- Zervoudaki, S., Nielsen, T.G., Christou, E.D., Siokou-Frangou, I., 2006. Zooplankton distribution and diversity in frontal area of the Aegean Sea. *Marine Biology Research* 2, 149–168.
- Zervoudaki, S., Christou, E.D., Nielsen, T.G., et al., 2007. The importance of small-sized copepods in a frontal area of the Aegean Sea. *Journal Plankton Research* 29, 317–338.