Mediterranean Marine Science

Vol 16, No 2 (2015)


# Mesozooplankton biomass and abundance in Cyprus coastal waters and comparison with the Aegean Sea (eastern Mediterranean)

*C. C.S. HANNIDES, I. SIOKOU, S. ZERVOUDAKID, C. FRANGOULIS, M. A. LANGE*

doi: 10.12681/mms.1171

Research Article

*Mediterranean Marine Science*
Indexed in WoS (Web of Science, ISI Thomson) and SCOPUS
The journal is available on line at http://www.medit-mar-sc.net
DOI: http://dx.doi.org/10.12681/mms.1171

# Mesozooplankton biomass and abundance in Cyprus coastal waters and comparison with the Aegean Sea (Eastern Mediterranean)

**C.C.S. HANNIDES[1,2,3], I. SIOKOU[4], S. ZERVOUDAKI[4], C. FRANGOULIS[4] and M.A. LANGE[1]**

[1] Energy Environment and Water Research Center, The Cyprus Institute, 20 Konstantinou Kavafi Street, 2121 Nicosia, Cyprus
[2] Department of Geology and Geophysics, University of Hawaii, 1680 East West Road, Honolulu, Hawaii, 96822, USA
[3] Department of Oceanography, University of Hawaii, 1000 Pope Road, Honolulu, Hawaii, 96822, USA
[4] Hellenic Center for Marine Research, Institute of Oceanography, 46.7km Athens, Sounion Ave, Anavyssos, Greece

Corresponding author: ceceliah@hawaii.edu

Handling Editor: Argyro Zenetos

Received: 6 December 2014; Accepted: 25 March 2015; Published on line: 22 May 2015.

**Abstract**

Here we conduct the first comprehensive assessment of mesozooplankton abundance, biomass, and taxa composition in Cyprus coastal waters (Levantine Sea). Mesozooplankton abundance and biomass sampled at several locations around the island ranged from 153 – 498 individuals $m^{-3}$ and 0.7 – 5.2 mg dry weight $m^{-3}$, respectively, with significantly larger biomass observed in winter-early spring (March) than in summer (September). The community was dominated by calanoid and cyclopoid copepods throughout the year (80% of total numbers), with higher abundances of predatory taxa (chaetognaths and medusae) in winter and cladocerans in summer. Overall, we find that coastal mesozooplankton communities around Cyprus appear to be more similar to communities in offshore waters or those around the island of Rhodes than to communities along the mainland Levantine coast. We further highlight regional differences in the Eastern Mediterranean by comparing our data with mesozooplankton in the Western Aegean (Saronikos Gulf) and Northeastern Aegean Sea (NEA). Distinct spatial differences were observed, for example anthropogenic influences in the Saronikos Gulf and the outflow of Modified Black Sea Water in the NEA drove generally greater biomass and abundance in these regions. Overall, our comparison supports the concept of a latitudinal gradient in oligotrophy in the Eastern Mediterranean, with ultra-oligotrophic conditions found in the Levantine Sea.

**Keywords:** Zooplankton ecology, zooplankton community structure, Cyprus, Eastern Mediterranean Sea, Levantine Sea, Northeastern Aegean Sea.

## Introduction

Mesozooplankton influence numerous aspects of ecosystem function in the Mediterranean Sea. These taxa exert a significant grazing impact on phytoplankton and microzooplankton (Siokou-Frangou *et al.*, 2002; Gaudy *et al.*, 2003; Zervoudaki *et al.*, 2007), modulate the response of the microbial food web to nutrient availability (Pasternak *et al.*, 2005), and are the major prey of small pelagic fish (Tudela & Palomera, 1997; Nikolioudakis *et al.*, 2014). Coastal Mediterranean mesozooplankton communities are typically more abundant than in the open Sea, but less diverse in terms of species composition and can differ in terms of species dominance (Gaudy, 1985; Fernández de Puelles *et al.*, 2003). Seasonality in mesozooplankton biomass and community composition has been documented both in coastal and offshore areas (Scotto di Carlo *et al.*, 1984; Mazzocchi *et al.*, 2011). Significant spatial variability has also been observed for mesozooplankton in the Mediterranean, particularly in response to mesoscale structures such as offshore fronts or eddies (Siokou-Frangou *et al.*, 2010 and references therein). For example, Black Sea water entering the northeast Aegean (NEA) continental shelf creates a strong thermohaline front that enhances mesozooplankton standing stocks (Siokou-Frangou *et al.*, 2009).

Here we investigate mesozooplankton communities in the Eastern Mediterranean, focusing on those around the island of Cyprus in the Levantine Sea. Studies of mesozooplankton in the Levantine Sea have been sporadic and focused exclusively on coastal communities along the mainland (El-Maghraby & Halim, 1965; Lakkis, 1990; Zakaria, 2006; Uysal & Shmeleva, 2012), or in epipelagic offshore waters (Mazzocchi *et al.*, 1997, 2014; Siokou-Frangou *et al.*, 1997; Pasternak *et al.*, 2005; Nowaczyk *et al.*, 2011). Mesozooplankton communities off the coast of Cyprus have never been comprehensively assessed. Our aim is to establish a baseline record of Cyprus mesozooplankton abundance, biomass, and taxa composition, and to evaluate potential spatial heterogeneity in plankton populations around the island. We sample mesozooplankton communities along the south and west coast of Cyprus, influenced by the bifurcation of the Mid-Mediterranean Jet, and communities on the northwest coast, influenced by the Asia Minor Current (Menna *et al.*, 2012). We compare our findings to mesozooplankton communities in two relatively well-studied locations of the Eastern Mediterranean: the coastal waters of Saronikos Gulf in the Western Aegean, and the shallow continental shelf waters off the island of Lemnos in the NEA. Our comparison is based on collections made in December-April and August-September, time periods when data was available from all regions and which should highlight the potential mesozooplankton response to seasonal extremes in nutrient entrainment and phytoplankton productivity.

## Materials and Methods

Mesozooplankton were collected along the coast of Cyprus using ships of opportunity (fishing vessels and small research craft) in March 2010 and September 2010 at stations of ~125 m water depth (Table 1). Stations were located along the southern coast of Cyprus at C1 (34.9472°N, 34.0028°E), C2 (34.9142°N, 33.6792°E), and C3 (34.6242°N, 33.0517°E)), on the west coast at C4 (34.7308°N, 32.3789°E), and on the northwest coast at C5 (35.2100°N, 32.5667°E; Fig. 1). 2 – 3 consecutive tows for biomass estimation and another 2 – 3 consecutive tows for abundance estimation were performed at each site by vertical hauls through the water column with a 200 µm mesh size net (1 m mouth diameter). Net tows were conducted in the morning (between 06:00 and 13:00 hours) and tow depths averaged ~100 m. Temperature was also measured on the cruises. Vertical temperature profiles were collected with each tow using a Sea-Bird SBE 39 temperature-depth recorder.

On board, mesozooplankton were filtered onto 200 µm mesh nitex filters for biomass estimation. The samples were dried at 60°C and weighed for total dry weight (dry wt). For abundance and taxa composition, mesozooplankton were preserved in 4.5% borate-buffered formalin and counted using stereomicroscopy. The taxa identified included calanoid copepods, cyclopoid copepods, harpacticoid copepods, ostracods, cladocerans, other crustaceans, molluscs, chaetognaths, thaliaceans, appendicularians, and 'other' mesozooplankton.

Cyprus mesozooplankton were compared with mesozooplankton collected on the R/V AEGAEO in (a) Saronikos Gulf in March 2009 and August 2009 at stations S7 (37.9236°N, 23.5908°E) and S11 (37.8728°N, 23.6383°E) in 70 m water depth and (b) in the NEA in April 2008 and September 2008 at station N2 (39.7850°N, 25.5233°E) in 80 m water depth (Fig. 1; Table 1). At each of these locations mesozooplankton were collected at multiple depth layers (station S7 and S11: 0 – 50 m, 50 – 70 m; station N2: 0 – 20 m, 20 – 50 m, 50 – 80 m) using a WP2 200 µm mesh size net. Samples were split on board, with one subsample used for dry wt estimation and the other used for taxonomic analysis. The subsamples for dry wt estimation collected in Saronikos Gulf were preserved with 4% borate-buffered formalin, while the subsamples collected in NEA were deep frozen. In the laboratory, the above subsamples were handled in a similar manner to those from Cyprus coastal waters (dried at 60°C and weighed for total dry wt). Biomass values issued from formalin-preserved samples were increased by 30% to account for the weight loss due to formalin

**Table 1.** Sampling of mesozooplankton around Cyprus, in Saronikos Gulf (S7 and S11 averaged), and in the northeast Aegean Sea (NEA). For each location, information on sampling date, sea surface temperature (SST), and sea surface chlorophyll (SSChl) during the sampling month, and results concerning mesozooplankton biomass and abundance (± standard deviation) are given.

| Study site | Sampling Date | SST °C | SSChl mg m$^{-3}$ | Biomass mg dry wt. m$^{-3}$ | Abundance ind. m$^{-3}$ |
|---|---|---|---|---|---|
| *Winter* | | | | | |
| Cyprus: C1 | 24-Mar-10 | 17.9 | 0.12 | 2.1 | 306 ± 21 |
| Cyprus: C3 | 17-Mar-10 | 17.7 | 0.10 | 2.6 ± 0.9 | 343 ± 41 |
| Cyprus: C4 | 12-Mar-10 | 17.8 | 0.08 | 3.5 ± 0.6 | 267 ± 19 |
| Cyprus: C5 | 22-Mar-10 | 17.5 | 0.18 | 5.2 ± 0.2 | 532 ± 4 |
| Cyprus: AVG | | | | 3.5 ± 1.3 | 334 ± 83 |
| Saronikos Gulf | Mar-09 | 14.5 | 0.42 | 11.9 ± 3.0 | 708 ± 166 |
| NEA | 4-Apr-08 | 13.6 | 1.08 | 16.2 | 771 |
| *Summer* | | | | | |
| Cyprus: C1 | 29-Sep-10 | 28.4 | 0.04 | 1.8 ± 0.4 | 497 ± 106 |
| Cyprus: C2 | 16-Sep-10 | 28.2 | 0.04 | 2.2 ± 0.6 | 478 ± 92 |
| Cyprus: C3 | 15-Sep-10 | 27.6 | 0.05 | 2.0 ± 0.1 | 421 ± 31 |
| Cyprus: C4 | 17-Sep-10 | 28.0 | 0.04 | 0.8 ± 0.2 | 211 ± 72 |
| Cyprus: C5 | 18-Sep-10 | 28.3 | 0.05 | 1.3 ± 0.6 | 267 ± 64 |
| Cyprus: AVG | | | | 1.5 ± 0.7 | 351 ± 148 |
| Saronikos Gulf | Aug-09 | 25.9 | 0.17 | 11.2 ± 0.8 | 2242 ± 166 |
| NEA | 6-Sep-08 | 22.5 | 0.29 | 4.3 | 912 |

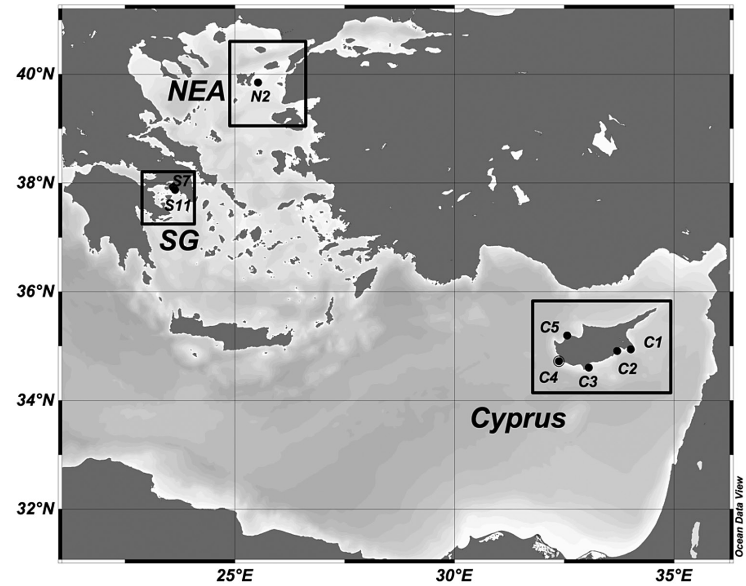


***Fig. 1:*** Mesozooplankton sampling locations in Cyprus coastal waters, in the western Aegean (Saronikos Gulf, SG), and in the northeast Aegean Sea (NEA). Sampling was conducted around Cyprus at stations C1 – C5, in Saronikos Gulf at monitoring stations S7 and S11, and in the NEA at station N2.

preservation (Omori, 1978). Depth integrated values of biomass and abundance ($m^{-3}$) were calculated over the whole water column for Saronikos Gulf and the NEA.

At each study site sea surface temperature (SST) and sea surface chlorophyll (SSChl) were determined from analysis of satellite data. Level 3 SST (MODIS Terra sea surface temperature) and SSChl (MODIS Aqua sea surface chlorophyll *a*) products for each location (a 50 x 50 km coastal region) were acquired from the NASA Goddard Earth Sciences Data Services and Information Center (disc.sci.gsfc.nasa.gov/giovanni). Monthly averaged SST and SSChl were determined for every site for the January 2003 – January 2010 time period. Our approach aimed at a qualitative understanding of environmental conditions rather than a detailed quantitative analysis as several corrections were not applied, e.g. for bias in the calculation of eastern Mediterranean chlorophyll *a* concentrations (Bosc *et al.*, 2004).

In order to investigate differences in mesozooplankton dry wt, total abundance and taxa abundance between locations around Cyprus, the Kruskal-Wallis test was used; the same test was used for testing differences regarding the above parameters between Cyprus, Saronikos Gulf and the NEA. Differences between the two seasons were investigated by application of the Student's *t*-test. The tests were performed using the software package SPSS version 22. Similarities between the sampling regions regarding community composition were further explored using hierarchical clustering and nonmetric multidimensional scaling (MDS), using PRIMER 5 software. Group abundance data were square root transformed, the Bray-Curtis similarity index was used, and the group average method was applied.

## Results

### *Cyprus (Levantine Sea)*

Based on our satellite analysis, Cyprus coastal SST varies between 17°C and 28°C on average over the course of the year. Water column temperature profiles were generally similar at all coastal stations during each quasi-synoptic sampling period, particularly during the winter when water temperatures were vertically homogeneous at 17.3 ± 0.3ºC. In summer a 20 – 25 m thick mixed layer developed in the upper water column. Temperatures in this layer averaged 27.3 ± 0.5ºC at most stations, with the exception of C3 where mixed layer temperatures were lower (24.3 ± 1.2ºC). Average SSChl in the waters around Cyprus was higher in the winter (0.16 – 0.19 mg $m^{-3}$) than in the summer (0.06 – 0.07 mg $m^{-3}$).

Mesozooplankton dry wt biomass ranged from 2.1 – 5.2 mg $m^{-3}$ during the winter (March 2010) and from 0.8 – 2.2 mg $m^{-3}$ during the summer (September 2010; Fig. 2A; Table 1). In winter mesozooplankton biomass was slightly higher along the northwest coast at C5 compared to the other sampling sites, but this difference was not significant (Kruskal-Wallis, $p > 0.05$). However in summer mesozooplankton biomass values on the west and northwest coast (C4 and C5) were significantly lower than those along the southern coast (C1, C2 and C3; Kruskal-Wallis, $p < 0.05$). Seasonal differences in mesozooplankton biomass along the coast were observed when data from all stations were pooled. Summer mesozooplankton biomass around Cyprus was significantly lower than that measured during the winter (*t*-test, $p < 0.001$).

Total mesozooplankton abundances ranged from 267 – 532 ind. $m^{-3}$ in winter and from 211 – 497 ind. $m^{-3}$ in summer (Fig. 2B; Table 1). Similarly to biomass values,

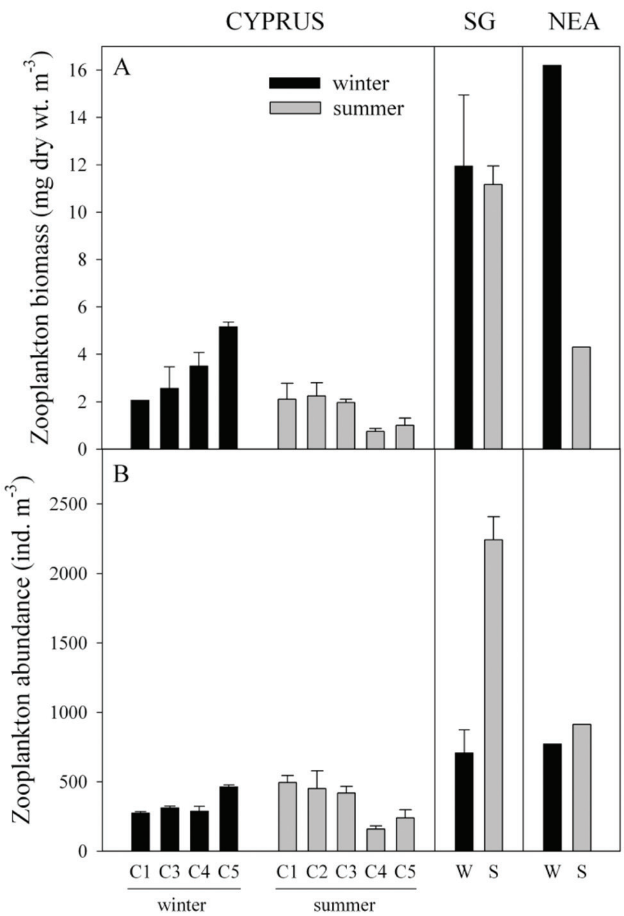


***Fig. 2:*** Mesozooplankton dry weight biomass (A) and total abundance (B) in Cyprus coastal waters, in the Western Aegean (Saronikos Gulf, S7 and S11 averaged), and in the northeast Aegean Sea. Biomass and abundance (± standard deviation) are presented for the following seasons: late winter-early spring (W) and summer (S). Abbreviations as in Figure 1.

mesozooplankton abundance was highest off the northwest coast (C5) in winter, but no significant differences between the different sampling sites were detected during this season (Kruskal-Wallis, $p > 0.05$). However in summer significant differences in abundance were detected between the different sampling sites (Kruskal-Wallis, $p < 0.05$), with mesozooplankton numbers at C4 significantly lower than those at southern stations (C1, C2 and C3) and abundances at C5 significantly lower than those at C1. When data from all stations were pooled, no seasonal differences in mesozooplankton abundance were found ($t$-test, $p > 0.05$).

The composition of mesozooplankton in Cyprus coastal waters was dominated by copepods (Table 2), which in winter comprised 81% and in summer comprised 80% of total mesozooplankton numbers (Table 3). The copepods were primarily calanoids both in winter (76% of total copepods) and summer (60% of total copepods), although cyclopoids were also abundant during both seasons (24 – 39% of total copepods). Only a very small population of harpacticoids was found (0.3% of total copepods). Groups other than copepods were a minor component of the total community in both seasons (Tables 2, 3). In winter and in summer, respectively, appendicularians were 7% and 6% of the total mesozooplankton numbers, cladocerans 0% and 5% (no cladocerans were observed in winter tows), ostracods 1.5% and 1.5%, and other plankton such as molluscs, chaetognaths, and thaliaceans were each around 1% of total mesozooplankton populations. The remaining other mesozooplankton taxa were 5% of total mesozooplankton numbers.

The abundance of mesozooplankton taxa did not differ significantly between the different sampling sites in winter (Kruskal-Wallis, $p > 0.05$). In summer, differences between the sampling locations were found only for calanoid copepods, cyclopoid copepods, and appendicularians (Kruskal-Wallis, $p < 0.05$). Numbers of calanoid copepods in C1 were significantly higher than in C4 and C5, numbers of cyclopoid copepods in C1 and C2 were significantly higher than those in the C4; finally, numbers of appendicularians were higher in C1 than in C4 and C5. When mesozooplankton abundance from the different sampling sites was pooled together, seasonal differences were observed for cyclopoid copepods, cladocerans, chaetognaths, thaliaceans, and ‘other’ mesozooplankton (including hydrozoan medusa; $t$-test, $p < 0.05$; Table 3). For cyclopoid copepods and cladocerans, the numbers in summer were greater than in winter. In contrast, numbers of chaetognaths, thaliaceans, and ‘other’ mesozooplankton were higher in winter than in summer.

### *Aegean Sea: Saronikos Gulf and Northeast Aegean Sea*

SST in the Saronikos Gulf varies between 14 – 26.5°C and SSChl between 0.17 – 0.52 mg m$^{-3}$, on average. While the temperature range is similar to that in Cyprus waters ($\Delta \equiv 12.5$°C), the range in SSChl is much greater ($\Delta_{SG} \equiv 0.35$ mg m$^{-3}$, vs. $\Delta_{Cyprus} \equiv 0.12$ mg m$^{-3}$). Mesozooplankton dry wt biomass in the Saronikos Gulf was similar during the winter (March 2009) and summer (August 2009), however abundances of total mesozooplankton were lower in the winter than in the summer (Fig. 2; Table 1).

The mesozooplankton community in the Saronikos Gulf was dominated by copepods (84% of total mesozooplankton numbers; Tables 2, 3), specifically calanoids and secondarily cyclopoids, during the winter. Minor components of the community in March 2009 included chaetognaths, euphausiid larvae, gastropod larvae and appendicularians (each < 3.9% of the total mesozooplankton population). In the summer, the community was again dominated by copepods (45% of total mesozooplankton numbers; calanoids and secondarily cyclopoids), but also by significant numbers of cladocerans (30% of total numbers) and appendicularians (14% of total numbers). Minor components of the mesozooplankton community during the summer included doliolids, chaetognaths, euphausiids, and echinoderm larvae (each < 6.6% of the total mesozooplankton population).

**Table 2.** Mean abundance (± standard deviation) of mesozooplankton groups collected around Cyprus (C1-C5), in Saronikos Gulf (S7 and S11 averaged), and in the northeast Aegean Sea (NEA) in late winter-early spring and summer. Mesozooplankton taxa include calanoid copepods (Cal), cyclopoid copepods (Cycl), harpacticoid copepods (Harp), ostracods (Ost), cladocerans (Clad), other crustaceans (O. Crust), molluscs (Moll), chaetognaths (Chaet), thaliaceans (Thal), appendicularians (App), and 'other' mesozooplankton (O. Zoop).

| Study site | **Cal.** ind. $m^{-3}$ | **Cycl.** ind. $m^{-3}$ | **Harp.** ind. $m^{-3}$ | **Ost.** ind. $m^{-3}$ | **Clad.** ind. $m^{-3}$ | **O. crust.** ind. $m^{-3}$ | **Moll.** ind. $m^{-3}$ | **Chaet.** ind. $m^{-3}$ | **Thal.** ind. $m^{-3}$ | **App.** ind. $m^{-3}$ | **O. zoop.** ind. $m^{-3}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Winter* | | | | | | | | | | | |
| Cyprus: C1 | 153 ± 9 | 47 ± 1 | 0.2 ± 0.3 | 3.3 ± 1.1 | 0.0 | 0.8 ± 0.6 | 1.3 ± 0.04 | 3.2 ± 1.0 | 9.1 ± 8.9 | 35 ± 34 | 20 ± 7 |
| Cyprus: C3 | 198 ± 7 | 48 ± 8 | 0.0 | 4.6 ± 2.5 | 0.0 | 1.1 ± 1.5 | 1.4 ± 2.0 | 3.9 ± 2.5 | 0.0 | 41 ± 6 | 13 ± 6 |
| Cyprus: C4 | 195 ± 43 | 54 ± 14 | 0.8 ± 1.1 | 1.8 ± 0.2 | 0.0 | 3.7 ± 3.0 | 1.8 ± 0.2 | 3.7 ± 3.0 | 4.5 ± 1.8 | 4 ± 3 | 18 ± 1 |
| Cyprus: C5 | 278 ± 2 | 112 ± 7 | 0.8 ± 1.1 | 12 ± 1.4 | 0.0 | 4.7 ± 0.8 | 8.1 ± 0.3 | 6.2 ± 0.9 | 4.9 ± 0.9 | 12 ± 5 | 25 ± 12 |
| Cyprus: AVG | 206 ± 51 | 66 ± 30 | 0.4 ± 0.7 | 5.3 ± 4.2 | 0.0 | 2.6 ± 2.2 | 3.1 ± 3.2 | 4.2 ± 2.0 | 4.6 ± 4.9 | 23 ± 21 | 19 ± 7 |
| Saronikos Gulf | 334 ± 98 | 264 ± 92 | 0.0 | 0.5 ± 0.8 | 0.0 | 39 ± 6 | 36 ± 36 | 23 ± 13 | 0.0 | 5 ± 6 | 7 ± 2 |
| NEA | 570 | 140 | 0.5 | 3.8 | 0.0 | 2.9 | 1.3 | 9 | 9 | 16 | 16 |
| *Summer* | | | | | | | | | | | |
| Cyprus: C1 | 252 ± 43 | 148 ± 51 | 1.7 ± 3.0 | 7.8 ± 4.2 | 11 ± 3.2 | 2.8 ± 1.7 | 5.5 ± 7.5 | 3.1 ± 3.8 | 2.5 ± 3.0 | 40 ± 8 | 18 ± 6 |
| Cyprus: C2 | 206 ± 66 | 141 ± 8 | 0.4 ± 0.7 | 2.9 ± 3.0 | 36 ± 28 | 6.4 ± 6.2 | 5.0 ± 3.2 | 3.5 ± 4.2 | 3.1 ± 1.0 | 32 ± 20 | 16 ± 9 |
| Cyprus: C3 | 193 ± 24 | 127 ± 9 | 2.3 ± 0.1 | 7.4 ± 4.9 | 12 ± 12 | 3.5 ± 3.4 | 4.2 ± 2.4 | 1.1 ± 1.1 | 0.7 ± 1.3 | 53 ± 11 | 13 ± 0.3 |
| Cyprus: C4 | 80 ± 9 | 55 ± 9 | 0.4 ± 0.6 | 1.8 ± 0.6 | 6 ± 7 | 1.8 ± 1.2 | 1.1 ± 1.8 | 0.4 ± 0.6 | 1.1 ± 1.8 | 3 ± 3 | 8 ± 4 |
| Cyprus: C5 | 117 ± 45 | 76 ± 12 | 0.7 ± 1.2 | 5.3 ± 1.1 | 18 ± 21 | 2.1 ± 1.8 | 2.8 ± 1.6 | 1.4 ± 1.2 | 0.4 ± 0.6 | 5 ± 3 | 8 ± 2 |
| Cyprus: AVG | 169 ± 74 | 109 ± 44 | 1.1 ± 1.5 | 5.0 ± 3.7 | 16 ± 18 | 3.3 ± 3.4 | 3.7 ± 3.7 | 1.9 ± 2.5 | 1.6 ± 1.8 | 27 ± 22 | 13 ± 6 |
| Saronikos Gulf | 824 ± 109 | 186 ± 81 | 2.2 ± 0.2 | 0.0 | 675 ± 286 | 20 ± 0.9 | 14 ± 16 | 20 ± 19 | 147 ± 30 | 322 ± 47 | 31 ± 4 |
| NEA | 152 | 224 | 1.9 | 1.4 | 78 | 3.8 | 13 | 38 | 299 | 44 | 34 |

**Table 3.** Overall percent composition of mesozooplankton collected around Cyprus (C1 through C5 averaged), in Saronikos Gulf (S7 and S11 averaged), and in the northeast Aegean (NEA) in late winter-early spring and summer. Mesozooplankton taxa are those listed in Table 2. Significant differences between winter (W) and summer (S) abundances around Cyprus are indicated.

| Study site | **Cal.** % | **Cycl.** % | **Harp.** % | **Ost.** % | **Clad.** % | **O. crust.** % | **Moll.** % | **Chaet.** % | **Thal.** % | **App.** % | **O. zoop.** % |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Winter* | | | | | | | | | | | |
| Cyprus | 62 ± 6 | 19 ± 5 | 0.1 ± 0.2 | 1.5 ± 0.8 | 0.0 | 0.7 ± 0.6 | 0.8 ± 0.6 | 1.2 ± 0.5 | 1.5 ± 1.9 | 7 ± 7 | 6 ± 2 |
| Saronikos Gulf | 47 ± 3 | 37 ± 4 | 0.0 | 0.1 ± 0.1 | 0.0 | 6 ± 2 | 6 ± 6 | 3 ± 1 | 0.0 | 0.6 ± 0.6 | 0.9 ± 0 |
| NEA | 74 | 18 | 0.1 | 0.5 | 0.0 | 0.4 | 0.2 | 1.2 | 1.2 | 2.0 | 2.0 |
| *Summer* | | | | | | | | | | | |
| Cyprus | 48 ± 6 | 32 ± 6 | 0.3 ± 0.4 | 1.5 ± 1.0 | 5 ± 4 | 1.0 ± 0.7 | 1.0 ± 0.9 | 0.5 ± 0.5 | 0.4 ± 0.5 | 6 ± 5 | 4 ± 1 |
| Saronikos Gulf | 37 ± 8 | 8 ± 4 | 0.1 ± 0 | 0.0 | 30 ± 10 | 0.9 ± 0.5 | 0.6 ± 0.7 | 0.9 ± 0.9 | 6 ± 0.9 | 14 ± 1 | 1.4 ± 0.1 |
| NEA | 17 | 25 | 0.2 | 0.2 | 8.8 | 0.4 | 1.5 | 4.3 | 33.7 | 4.9 | 3.8 |
| *Seasonality*[a] | | | | | | | | | | | |
| Cyprus | ns | S > W* | ns | ns | S > W* | ns | ns | W > S* | W > S* | ns | W > S* |

[a]Significant differences (t-test) between winter and summer abundances when data from all Cyprus stations was pooled. Significance levels: *$p < 0.05$, **$p < 0.01$, ***$p < 0.005$, ns = not significant.

SST near the island of Lemnos in the Northeast Aegean Sea (NEA) varies between 12 – 24°C, and SSChl between 0.29 – 0.93 mg $m^{-3}$, on average. Again the range in SSChl ($\Delta \equiv 0.35$ mg $m^{-3}$) is greater than that observed off Cyprus. Mesozooplankton dry wt biomass in the NEA was higher during early spring (April 2008) and than in summer (September 2008), while the abundance of mesozooplankton was more similar in early spring as compared to summer (Fig. 2; Table 1).

The NEA mesozooplankton community was dominated by copepods in April 2008 (92% of total mesozooplankton numbers; Tables 2, 3). Minor components of the community included appendicularians, thaliaceans, chaetognaths, ostracods, and molluscs (each < 2.0% of the total mesozooplankton population). Copepods were dominated by calanoids (80% of total copepods), with cyclopoids (20%) and harpacticoids (0.1%) forming smaller proportions of the population. In the summer, the community was more heterogeneous and was dominated by copepods (42% of total mesozooplankton numbers), thaliaceans (34%), and cladocerans (8.8%). Less abundant components of the mesozooplankton community during the summer included appendicularians, chaetognaths, molluscs (pteropods), and ostracods (each < 4.9% of the total mesozooplankton population). Summer copepods were dominated by cyclopoids (60% of total copepods) and secondarily by calanoids (40%), with a small contribution from harpacticoids (0.5%).

### *Eastern Mediterranean comparison*

Mesozooplankton biomass and abundance was compared for samples collected in Cyprus coastal waters, in Saronikos Gulf, and in the NEA off the island of Lemnos (Table 1). In summer, mesozooplankton dry wt biomass in the Saronikos Gulf (11.2 mg $m^{-3}$) and the NEA (4.3 mg $m^{-3}$) was higher that that observed around Cyprus (1.5 mg $m^{-3}$), and these differences were significant (Kruskal-Wallis, $p < 0.05$). Similar differences were observed in winter-spring (Saronikos Gulf = 11.9 mg $m^{-3}$; NEA = 16.2 mg $m^{-3}$; Cyprus = 3.5 mg $m^{-3}$) although these differences were marginally significant (Kruskal-Wallis, $p = 0.053$). No differences were found for mesozooplankton biomass in the Saronikos Gulf and the NEA. Mesozooplankton abundance also differed between the different sampling areas. In summer, the differences (Saronikos Gulf = 2242 ind. $m^{-3}$; NEA = 912 ind. $m^{-3}$; Cyprus = 351 ind. $m^{-3}$) were significant (Kruskal-Wallis, $p < 0.05$) and in winter marginally significant (Saronikos Gulf = 708 ind. $m^{-3}$; NEA = 771 ind. $m^{-3}$; Cyprus = 334 ind. $m^{-3}$; Kruskal-Wallis, $p = 0.050$). No significant differences in mesozooplankton abundance were detected between Saronikos Gulf and the NEA.

While mesozooplankton at all sites were dominated by copepods, differences in taxa composition were evident (Table 3). In particular, cladocerans were important components of the summer community in Saronikos Gulf and the NEA, but less abundant around Cyprus. During summer appendicularians and thaliaceans were also significant contributors in Saronikos Gulf and the NEA, respectively, but were not as important in Cyprus coastal waters. In winter, calanoid copepods dominated around Cyprus and in the NEA, however in Saronikos Gulf cyclopoids also were significant components of the community. These differences in taxa composition drove the separation of samples into groups based on hierarchical clustering and nonmetric MDS (Figure 3). At 68% similarity level three groups of samples were distinguished. The first group included samples from Saronikos Gulf and the NEA in summer. Samples from Saronikos Gulf in winter constituted the second group. The remainder of the samples included all samples from Cyprus (winter and summer) and the NEA in winter. Overall, MDS

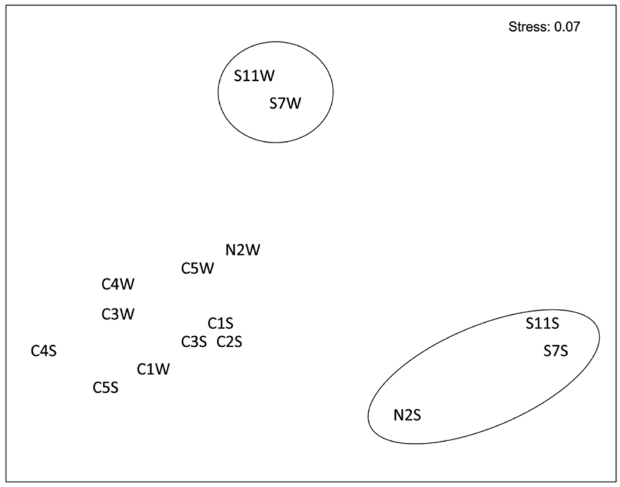


*Fig. 3:* MDS plot of mesozooplankton samples from Cyprus (C1 – C5), Saronikos Gulf (S7 and S11) and the NEA (N2) in winter (W) and summer (S). Example: station C1 in summer = C1S. Cycles include groups of samples identified using hierarchical clustering.

of taxa abundances separated samples from Cyprus and those from the Aegean Sea (Saronikos Gulf and the NEA), while differences between summer and winter were most apparent in Saronikos Gulf and the NEA.

## Discussion

### *Mesozooplankton communities around Cyprus and in the surrounding Levantine Sea: Standing stock and community composition*

Mesozooplankton assemblages in the Levantine reflect the depauperate nature of the region, with abundance and biomass values among the lowest measured in the Mediterranean Sea (Siokou-Frangou *et al.*, 2010; Nowaczyk *et al.*, 2011; Mazzocchi *et al.*, 2014). In the Levantine Sea, mesozooplankton abundance measured during several field campaigns has ranged from 93 – 370 ind. $m^{-3}$, and mesozooplankton biomass measured during the same studies has ranged from 1.1 – 3.8 mg dry wt $m^{-3}$ (when using 200+ μm mesh nets; Table 4). Our observations indicate that Cyprus mesozooplankton abundance and biomass are similar in magnitude to these offshore populations, suggesting that Cyprus coastal waters are similarly extremely oligotrophic and that coastal plankton assemblages are strongly influenced by the open Mediterranean Sea. Chlorophyll *a* levels along the Cyprus coast are also low (Bianchi *et al.*, 1996) and analogous to those found in offshore waters (Vidussi *et al.*, 2000). Previous studies indicate coastal and shelf waters in the Levantine are dominated by the energetic mesoscale flow phenomena found in neighboring deep waters (Zodiatis *et al.*, 2003). In the case of Cyprus, the coast is primarily influenced by the bifurcation of what has been termed the Mid-Mediterranean Jet (Robinson *et al.*, 1991), with one portion of the flow moving north along the west coast of the island, and the other moving east along the south coast

**Table 4.** Mesozooplankton populations in offshore and coastal waters of the Levantine Sea. For each study, information on plankton net mesh, season (Sp: spring; Su: summer; Au: autumn; Yr: year round), water depth, and ranges in biomass and abundance are listed.

| Locale | Net mm | Season | Water depth m | Biomass mg dry wt. $m^{-3}$ | Abundance ind. $m^{-3}$ | Reference[a] |
|---|---|---|---|---|---|---|
| *Levantine (offshore)* | | | | | | |
| central Levantine | 200 | Au | >1000 | | 115 | Mazzocchi *et al.* (1997) |
| central Levantine | 200 | Au | >1000 | | 216 | Siokou-Frangou *et al.* (1999) |
| central Levantine | 200 | Su | >1000 | 1.1 | 93 | Siokou-Frangou (2004) |
| W Levantine (Crete) | 333 | Sp | >1000 | 2.1 - 3.5 | | Koppelmann *et al.* (2004)[b] |
| Cyprus eddy | 180 | Sp | >1000 | 3.0 | 293 | Pasternak *et al.* (2005)[b] |
| offshore Egypt | 220 | Yr | offshore | | 370 | Zakaria (2006)[c] |
| central Levantine | 120 | Su | >1000 | 6.8 ± 2.2 | 872 ± 93 | Nowaczyk *et al.* (2011) |
| central Levantine | 200 | Sp | >1000 | 3.8 | 274 | Mazzocchi *et al.* (2013)[b] |
| central Levantine | 200 | Au | >1000 | 2.2 | 217 | Mazzocchi *et al.* (2013)[b] |
| *Levantine (coastal)* | | | | | | |
| Cyprus | 200 | Yr | ≤ 150 | 0.7 - 5.2 | 158 - 493 | This study |
| Egypt (Alexandria) | 200 | Yr | ≥ 20 | | 3660 - 39000 | El-Maghraby & Halim (1965) |
| Lebanon (Byblos) | 200 | Yr | 200 | 2 - 20 | 82 - 3350 | Lakkis (1984, 1990) |
| Egypt | 220 | Yr | inshore | | 2081 | Zakaria (2006)[c] |
| Turkey (Mersin Bay) | 112 | Yr | 20 | 5 - 68 | 1648 - 14198 | Yilmaz & Besiktepe (2010) |
| Turkey (Mersin Bay) | 112 | Yr | 200 | 1.4 - 4.6 | 238 - 1556 | Yilmaz & Besiktepe (2010) |
| Turkey (Mersin Bay) | 112 | Yr | 150 | 4 - 22 | 215 - 2221 | Uysal & Shmeleva (2012)[d] |
| *South Aegean (coastal)* | | | | | | |
| Rhodes | 200 | Yr | 50 - 350 | | 33 - 646 | Siokou-Frangou & Papathanassiou (1989) |

[a]cited in Reference section.
[b]data extracted using PlotDigitizer (http://sourceforge.net/projects/plotdigitizer/).
[c]1984 - 1985 data only.
[d]copepods only.

(Zodiatis *et al.*, 2008). Clearly this significant open Sea influence, and the fact that Cyprus coastal regions have no significant fluvial inputs (Abousamra, 2003) and are generally narrow with an open shoreline (Zodiatis *et al.*, 2003), underlie the oligotrophic nature of Cyprus waters.

We can further compare Cyprus mesozooplankton assemblages with those found in coastal waters of the Levantine mainland, communities that have been studied sporadically over the past ~ 50 years (Lakkis, 1990; Zakaria, 2006; Yilmaz & Besiktepe, 2010; Table 4). Greater mainland populations appear to be found in Egyptian inshore waters (Zakaria, 2006), likely related to the anthropogenic input of nutrients in the region (Nixon, 2003). Populations of mesozooplankton along the Lebanese coast (Lakkis, 1984, 1990) are as abundant as those found off Cyprus, with large numbers found off Lebanon only in the spring (Lakkis, 1984, April – June; 1990). Mesozooplankton abundance and biomass off the southern coast of Turkey (Iskenderun and Mersin bays) are relatively high (Yilmaz & Besiktepe, 2010; Uysal & Shmeleva, 2012; Terbiyik Kurt & Polat, 2013). These large numbers could be due to the significant river discharge of nutrients in both locations and the anthropogenic impact in Iskenderun Bay (Koçak *et al.*, 2010; Terbiyik Kurt & Polat, 2013). High values in Mersin Bay may also be the result of using a small (112 µm) mesh net (which would more effectively sample abundant small copepods and copepodites; Calbet *et al.*, 2001; Zervoudaki *et al.*, 2006). Interestingly, mesozooplankton abundance measured in the present study is of the same order of magnitude as that found on Rhodes, another eastern Mediterranean island (Siokou-Frangou & Papathanassiou, 1989; Table 4). Both islands are subject to energetic flow phenomena from the surrounding waters (Theocharis *et al.*, 1993; Zodiatis *et al.*, 2008) and have narrow continental shelves, factors that clearly underlie the strong influence of offshore waters on these island mesozooplankton communities.

The general similarity between coastal Cyprus and offshore Levantine mesozooplankton populations can be extended to their taxa compositions. We have found that copepods by far dominate Cyprus mesozooplankton assemblages, as has previously been noted for mesozooplankton in the Levantine Sea (Mazzocchi *et al.*, 1997, 2014; Nowaczyk *et al.*, 2011). In spring and autumn, Levantine Sea epipelagic copepods were mainly comprised of small calanoids (e.g. *Clausocalanus paululus*, *C. furcatus*, and *Mecynocera clausi*) and cyclopoids (e.g. *Oithona plumifera, O. setigera*, and *Farranula rostrata*; Siokou-Frangou *et al.*, 1997; Mazzocchi *et al.*, 2014). Our samples from Cyprus were similarly dominated by calanoid and cyclopoid copepods, with the percentage contribution of each of these orders during September remarkably similar to that found in autumn in the 0 – 100 m layer of offshore Levantine waters (i.e., 68% calanoid and 30% cyclopoid; Siokou-Frangou *et al.*, 1997). Cyclopoids (*Oithona* spp., *Corycaeus* spp., and *Farranula* spp.) as well as *Clausocalanus* spp. and *Paracalanus* spp. have also been found to dominate south and west of Cyprus (Pasternak *et al.*, 2005; Mazzocchi *et al.*, 2014) and across the Levantine Sea (Nowaczyk *et al.*, 2011). The cyclopoids *Farranula rostrata, Oncaea media* and *O. mediterranea* are mentioned as first dominant species among copepods in Lebanon coastal waters from December to March (Lakkis, 1990), while *Oithona plumifera*, *O. nana* and *F. rostrata* are among the ten most abundant species in the Egyptian coastal waters (Zakaria, 2006). The important contribution of cyclopoids in Cyprus coastal waters, particularly during the warm season, reflect the very oligotrophic conditions in which this taxon can thrive (Paffenhöfer, 1993).

Other mesozooplankton taxa found in Cyprus coastal waters include appendicularians, cladocerans, ostracods, molluscs, chaetognaths, and thaliaceans. Appendicularians were the most significant minor contributor to the Cyprus mesozooplankton assemblage, reaching up to 20% of total mesozooplankton abundance in winter. Their contribution was by far lower in Mersin Bay and coastal Egyptian waters during the relevant seasons or months (Zakaria, 2006; Yilmaz & Besiktepe, 2010), whereas in Iskenderun Bay they represented almost 19% of total abundances in summer (Terbiyik Kurt & Polat, 2013). Appendicularians are able to feed on submicron particles (Scheinberg *et al.*, 2005), and their populations in the Mediterranean have been linked to those of autotrophic picoplankton (Calbet *et al.*, 2001; Yilmaz & Besiktepe, 2010) and water rich in dissolved organic carbon (and therefore microbial populations; Isari *et al.*, 2007). Thus it is possible that the relatively large proportion of appendicularians around Cyprus is related to the dynamics of the microbial loop in these waters. Cladocerans were an important minor component of the Cyprus coastal community during the summer, similar to Iskenderun and Mersin bays (Yilmaz & Besiktepe, 2010; Terbiyik Kurt & Polat, 2013), but in contrast this taxa comprised 0.1 – 1.25% of mesozooplankton in offshore waters (0 – 200 m layer) of the Levantine Sea in spring to autumn (Mazzocchi *et al.*, 1997, 2014; Nowaczyk *et al.*, 2011). The importance of resting eggs to cladoceran population dynamics likely constrains the range of this taxon to predominantly neritic waters (Egloff *et al.*, 1997). Finally, ostracods were comparatively rare in our coastal samples. This may be attributed to our relatively shallow (< 100 m) sampling depth, as their relative abundance in the Eastern Mediterranean is generally higher in the 100 – 300 m layer as compared to surface layers (Mazzocchi *et al.*, 1997; Siokou *et al.*, 2013). Ostracods were also found to be more abundant at deeper rather than shallow stations off the island of Mallorca (Fernández de Puelles *et al.*, 2003).

***Mesozooplankton communities around Cyprus and in the surrounding Levantine Sea: Seasonality in plankton dynamics***

Our analysis of general trends in satellite-derived SST and SSChl around Cyprus indicates a similar seasonal evolution as that found in the greater Levantine (D'Ortenzio & Ribera d'Alcalá, 2009), with maximum pigment concentrations observed in winter (January – March) and minimum concentrations observed in late summer (July – September). At the same time, mesozooplankton biomass was significantly higher around the island in March as compared to September, suggesting a potential strong seasonal response from these populations. Interestingly, mesozooplankton abundance did not show the same seasonal signal. This discrepancy may be attributed to the large numbers of cyclopoid copepods found in Cyprus waters in the summer, which contribute little biomass due to their small size and/or thin shape (i.e. *Oithona plumifera*, *Oithona setigera*). Another summer signal was the presence of cladocerans, which are small and grow rapidly during this season's favorable environmental conditions (warm temperatures and a stable water column; Siokou-Frangou, 1996; Ribera d'Alcalá *et al.*, 2004; Atienza, 2008). In contrast, larger taxa including predatory chaetognaths and medusae were more abundant around Cyprus in winter. The increase in these groups could indicate a larger amount of energy available for higher trophic levels during the winter bloom. In concert with these changes, mesozooplankton community trophic position as measured using compound-specific stable isotope analysis also increased in winter around Cyprus (Hannides *et al.*, 2015).

An interesting finding of our study was that mesozooplankton populations at our different sampling sites exhibited quantitatively similar seasonal changes, despite their exposure to different current regimes. As discussed above, mesozooplankton along the southern coast (at stations C1, C2 and C3) are primarily influenced by the eastward branch of the Mid-Mediterranean Jet, as well as by eddies and local current systems that form south of the island. In contrast mesozooplankton along the northwest coast of Cyprus (at C5) are influenced by the westward moving Asia Minor Current and associated local flow phenomena. Despite this, similar variability in abundance and biomass, and similar changes in taxa composition (i.e., the appearance of cladocerans in summer) were observed in all locations. Small-scale differences between the different sampling sites were found significant only in summer, e.g., abundances and biomass off C5 and C4 (north and west coast) were lower than those found south of the island (C1, C2 and C3). This pattern may have been caused by the local upwelling phenomena typically observed in the region of station C3 in summer (Zodiatis *et al.*, 2003, 2008). Upwelling brings nutrient-rich deep water into the euphotic zone, spurring an increase in phytoplankton biomass (as is observed in SSChl images; Zodiatis *et al.*, 2008) and apparently larger mesozooplankton populations in these coastal waters. Mesozooplankton communities downstream of this location (i.e., stations C2 and C1) may also be impacted, as the upwelling signal (low SST and high SSChl) can extend along the southern coast in summer (Zodiatis *et al.*, 2008).

Unfortunately for comparative purposes, few data on seasonality exist for Levantine mesozooplankton populations and most studies were performed during only one season (Table 4). In coastal communities along the Levantine mainland, mesozooplankton populations appear to increase in spring, e.g., high numbers were observed in Lebanese waters in April – May (Lakkis, 1990), peak biomass and abundances were found in February – March in Mersin Bay (Yilmaz & Besiktepe, 2010; Uysal & Shmeleva, 2012) and maximum abundances were observed in April in Iskenderun Bay (Terbiyik Kurt & Polat, 2013). In offshore waters west of Cyprus, total mesozooplankton abundance was slightly higher in April than in October, while biomass values were almost double in the former month than in the latter (Mazzocchi *et al.*, 2014). Thus evidence indicates generally larger mesozooplankton populations in the Levantine during the winter – spring, although significant interannual variability has been observed (Yilmaz & Besiktepe, 2010). To explore the seasonal cycle in more detail, a comprehensive multi-year time-series of mesozooplankton in Cyprus waters should be attempted.

***Regional differences in Eastern Mediterranean mesozooplankton communities***

Longitudinal transects across the Mediterranean have routinely documented differences in plankton biomass and productivity between the eastern and western basins (Siokou-Frangou *et al.*, 2010; Nowaczyk *et al.*, 2011), with the eastern basin generally considered 'ultra-oligotrophic'. However the trophic status of the Mediterranean Sea is not homogeneous (D'Ortenzio & Ribera d'Alcalá, 2009), and Mazzocchi *et al.* (2014) recently documented a clear heterogeneity in mesozooplankton communities in both basins. Furthermore, in the Eastern Mediterranean the trophic nature of coastal environments can be strongly impacted by anthropogenic influences, for example in the Saronikos Gulf near Athens (Siokou-Frangou, 1996). Offshore ecosystems in the Eastern Mediterranean also exhibit spatial differences in trophic state. For example, Siokou-Frangou *et al.* (2002) documented a latitudinal gradient of oligotrophy in the Aegean Sea, with plankton biomass and production in the NEA (which is strongly influenced by the outflow of Modified Black Sea Water (MBSW)) higher than that in the southern Aegean off Crete. Here we attempt to place our findings regarding Cyprus mesozooplankton in the context of this regional variability.

In Saronikos Gulf, we found mesozooplankton populations at both stations to be larger than those in Cyprus waters, as one might expect given the mesotrophic nature of the Gulf (Siokou-Frangou, 1996) and the fact that plankton around Cyprus are strongly influenced by ultra-oligotrophic Levantine offshore waters. Differences between the two coastal systems were especially pronounced in summer, with numbers of all dominant taxa (copepods, cladocerans and appendicularians) much larger in Saronikos Gulf. While the water column at both sites is well stratified during this season (this study; Zeri *et al.*, 2009), our satellite analysis indicates SSChl is greater in the Gulf throughout the year. Thus the large numbers of mesozooplankton observed in the Gulf in this and previous studies (Siokou-Frangou, 1996) could be a function of the higher baseline chlorophyll *a* levels. Moreover cladocerans and appendicularians were particularly significant components of the Gulf mesozooplankton assemblage during summer, and much more dominant than in any of our Cyprus collections. Large numbers of cladocerans in the Gulf were previously attributed to a food chain based on the microbial loop (Siokou-Frangou, 1996) and in fact very high bacterial production levels were found in summer by Zeri *et al.* (2009) near station S7. Thus the relatively large Saronikos Gulf mesozooplankton populations are likely also a function of the anthropogenically-influenced growth of microbial loop components and the taxa (cladocerans, appendicularians) that can efficiently feed on them.

Early research recognized the quantitative and qualitative distinctiveness of plankton assemblages in the northern Aegean (Moraitou-Apostolopoulou, 1972), and more recent evaluations have highlighted the relatively large NEA plankton abundances, biomass, and production (Siokou-Frangou *et al.*, 2002) and characteristic species assemblage (Zervoudaki *et al.*, 2006; Siokou-Frangou *et al.*, 2009). Plankton production in the NEA appears to be fueled by the rapid uptake of nutrients and dissolved organic material from low-salinity MBSW flowing through the Dardanelles Strait (Lykousis *et al.*, 2002), particularly at the associated thermohaline front (Zervoudaki *et al.*, 2007; Siokou-Frangou *et al.*, 2009). The latter study indicates the NEA may be considered meso-oligotrophic, and correspondingly we found higher SSChl levels and larger mesozooplankton populations in this region compared to Cyprus waters. Hannides *et al.* (2015) also found differences in trophic structure between the two regions, based on their stable isotope composition. Interestingly, the taxa driving the large northern Aegean populations changed with the seasons. In winter-early spring, NEA mesozooplankton were clearly dominated by small to large sized calanoid copepods including *Centropages typicus, Ctenocalanus vanus,* and *Calanus helgolandicus*. Because of their large size, *C. helgolandicus* may have contributed disproportionately to the high biomass levels found in the NEA in April. In September, the assemblage was characterized by the very significant presence of salps. These filter-feeders have the potential to graze on submicron particles (Sutherland *et al.*, 2010), and can efficiently take advantage of autotrophic production in the Northern Aegean, which is dominated by < 3 μm cells (Ignatiades *et al.*, 2002). While a picoplankton-based food web also likely dominates around Cyprus (as is found in the offshore Levantine; Psarra *et al.*, 2005), the stimulation of autotrophic production in the NEA by the MBSW outflow and efficient channeling of this energy to mesozooplankton populations (Siokou-Frangou *et al.*, 2002) appear to support higher overall biomass levels and occasionally large populations of filter feeders such as salps (this study), appendicularians, and cladocerans (Zervoudaki *et al.*, 2006). Differences between regions and seasons in terms of taxa composition were confirmed by hierarchical clustering and MDS results. Interestingly, the seasonal differentiation was found to be more important in Saronikos Gulf and in NEA than around Cyprus. Overall, our comparison of mesozooplankton in the NEA and in Cyprus waters suggests that the 'latitudinal gradient in oligotrophy' described by Siokou-Frangou *et al.* (2002) for the Aegean Sea may be extended southward, with ultra-oligotrophic conditions found in the Levantine Sea.


## Acknowledgements

We sincerely thank the numerous individuals who helped with sample collection and analysis. We specifically thank Dr. A. Hannides, A. Petrou, E. Paschali, P. Leonida, S. Kyriakou and the THETIS Foundation for their help with sample collection in Cyprus, and the captain and crew of the R.V. AEGEAO for their help with sample collection in the northeast Aegean Sea. M. Argyrou and others at the Cyprus Department of Fisheries and Marine Research provided some of the equipment used in sample processing. Our manuscript was significantly improved with help from Dr. A. Hannides and two anonymous reviewers. We thank Drs. G. Georgiou and G. Zodiatis at the University of Cyprus Oceanography Center for their input concerning physical oceanography. This study was funded by a Cyprus Research Promotion Foundation (RPF) fellowship to C. Hannides (RPF DESMI 2008 Programme ΠΡΟΣΕΛΚΥΣΗ/ΠΡΟΝΕ/0308). Monitoring in Saronikos Gulf was financed by the Athens Water Supply and Sewerage Company (EYDAP SA) and sample collection in the northeast Aegean Sea was performed within the EU projects SESAME (FP6) and MEDEX (MARINERA). This is University of Hawaii School of Ocean and Earth Science and Technology contribution number 9402.


**Disclosure**: C.C.S.H. designed the study in Cyprus and M.L. helped with implementation. C.C.S.H. and I.S. designed the Aegean comparison and I.S., S.Z. and C.F. contributed data and helped with implementation. All authors have commented on the manuscript and approved the final paper.

## References


Abousamra, F., 2003. Riverine transport of water, sediments and pollutants to the Mediterranean Sea, No. 141. MAP Technical Reports Series. UNEP/MAP, Athens, Greece.

Atienza, D., 2008. Life history and population dynamics of the marine cladoceran *Penilia avirostris* (Branchiopoda:Cladocera) in the Catalan Sea (NW Mediterranean). *Journal of Plankton Research* 30, 345-357.

Bianchi, T.S., Demetropoulos, A., Hadjichristophorou, M., Argyrou, M., Baskaran, M. *et al.*, 1996. Plant pigments as biomarkers of organic matter sources in sediments and coastal waters of Cyprus (Eastern Mediterranean). *Estuarine Coastal and Shelf Science* 42, 103-115.

Bosc, E., Bricaud, A., Antoine, D., 2004. Seasonal and interannual variability in algal biomass and primary production in the Mediterranean Sea, as derived from 4 years of SeaWiFS observations. *Global Biogeochemical Cycles* 18. doi:10.1029/2003GB002034

Calbet, A., Garrido, S., Saiz, E., Alcaraz, M., Duarte, C.M., 2001. Annual zooplankton succession in coastal NW Mediterranean waters: the importance of the smaller size fractions. *Journal of Plankton Research* 23, 319-331.

D'Ortenzio, F., Ribera d'Alcalá, M., 2009. On the trophic regimes of the Mediterranean Sea: a satellite analysis. *Biogeosciences,* 6, 139-148.

Egloff, D.A., Fofonoff, P.W., Onbe, T., 1997. Reproductive biology of marine cladocerans, p. 79-167. In: *Advances in Marine Biology, Vol 31.* Blaxter, J.H.S., Southward, A.J. (Eds.),. Elsevier Academic Press Inc, San Diego.

El-Maghraby, A.M., Halim, Y., 1965. A quantitative and qualitative study of the plankton of Alexandria waters. *Hydrobiologia,* 25, 221-238.

Fernández de Puelles, M.L., Pinot, J.M., Valencia, J., 2003. Seasonal and interannual variability of zooplankton community in waters off Mallorca island (Balearic Sea, Western Mediterranean): 1994-1999. *Oceanologica Acta,* 26, 673-686.

Gaudy, R., 1985. Features and peculiarities of zooplankton communities from the Western Mediterranean, p. 279-301. In: *Mediterranean Marine Ecosystems.* Moraitou-Apostolopoulou, M., Kiortsis, V. (Eds.), Plenum Press, New York.

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, 357-372.

Hannides, C.C.S., Zervoudaki, S., Frangoulis, C., Lange, M.A., 2015. Mesozooplankton stable isotope composition in Cyprus coastal waters and comparison with the Aegean Sea (Eastern Mediterranean). *Estuarine Coastal and Shelf Science,* 154, 12-18.

Ignatiades, L., Psarra, S., Zervakis, V., Pagou, K., Souvermezoglou, E. *et al.,* 2002. Phytoplankton size-based dynamics in the Aegean Sea (Eastern Mediterranean). *Journal of Marine Systems,* 36, 11-28.

Isari, S., Psarra, S., Pitta, P., Mara, P., Tomprou, M.O. *et al.,* 2007. Differential patterns of mesozooplankters' distribution in relation to physical and biological variables of the Northeastern Aegean Sea (Eastern Mediterranean). *Marine Biology,* 151, 1035-1050.

Koçak, M., Kubilay, N., Tuğrul, S., Mihalopoulos, N., 2010. Atmospheric nutrient inputs to the Northern Levantine Basin from a long-term observation: sources and comparison with riverine inputs. *Biogeosciences,* 7, 4037-4050.

Koppelmann, R., Weikert, H, Halsband-Lenk, C., Jennerjahn, T., 2004 Mesozooplankton community respiration and its relation to particle flux in the oligotrophic eastern Mediterranean. Global Biogeochemical Cycles 18, GB1039 DOI: 10.1029/2003GB002121 GB103.

Lakkis, S., 1984. On the presence of some rare copepods in the Levantine Basin. *Crustaceana,* suppl. 7, 286-304.

Lakkis, S., 1990. Composition, diversity and successions of planktonic copepods in the Lebanese waters (Eastern Mediterranean). *Oceanologica Acta,* 13, 489-501.

Lykousis, V., Chronis, G., Tselepides, A., Price, N.B., Theocharis, A. *et al.,* 2002. Major outputs of the recent multidisciplinary biogeochemical researches undertaken in the Aegean Sea. *Journal of Marine Systems,* 33, 313-334.

Mazzocchi, M.G., Christou, E.D., Fragopoulu, N., Siokou-Frangou, I., 1997. Mesozooplankton distribution from Sicily to Cyprus (Eastern Mediterranean). I. General aspects. *Oceanologica Acta,* 20, 521-535.

Mazzocchi, M.G., Licandro, P., Dubroca, L., Di Capua, I., Saggiomo, V., 2011. Zooplankton associations in a Mediterranean long-term time-series. *Journal of Plankton Research,* 33, 1163-1181. Mazzocchi, M.G., Siokou, I., Tirelli, V., Bandelj, V., Fernandez de Puelles, M.L. *et al.,* 2014. Regional and seasonal characteristics of epipelagic mesozooplankton in the Mediterranean Sea based on an artificial neural network analysis. *Journal of Marine Systems,* 135, 64-80.

Menna, M., Poulain, P.-M., Zodiatis, G., Gertman, I., 2012. On the surface circulation of the Levantine sub-basin derived from Lagrangian drifters and satellite altimetry data. *Deep-Sea Research Part I-Oceanographic Research Papers,* 65, 46-58.

Moraitou-Apostolopoulou, M., 1972. Occurence and fluctuation of the pelagic copepods of the Aegean Sea with some notes on their ecology. *Hellenic Oceanology and Limnology* 11, 325-402.

Nikolioudakis, N., Isari, S., Somarakis, S., 2014. Trophodynamics of anchovy in a non-upwelling system: direct comparison with sardine. *Marine Ecology Progress Series,* 500, 215-229.

Nixon, S.W., 2003. Replacing the Nile: Are anthropogenic nutrients providing the fertility once brought to the Mediterranean by a great river? *Ambio,* 32, 30-39.

Nowaczyk, A., Carlotti, F., Thibault-Botha, D., Pagano, M., 2011. Distribution of epipelagic metazooplankton across the Mediterranean Sea during the summer BOUM cruise. *Biogeosciences,* 8, 2159-2177.

Omori, M., 1978. Some factors affecting on dry weight, organic weight and concentration on carbon and nitrogen in freshly prepared and preserved zooplankton. *Internationale Revue der gesamten Hydrobiologie,* 62, 261-269.

Paffenhöfer, G.A., 1993. On the ecology of marine cyclopoid copepods (Crustacea, Copepoda). *Journal of Plankton Research,* 15, 37-55.

Pasternak, A., Wassmann, P., Riser, C.W., 2005. Does mesozooplankton respond to episodic P inputs in the Eastern Mediterranean? *Deep Sea Research Part II: Topical Studies in Oceanography,* 52, 2975-2989.

Psarra, S., Zohary, T., Krom, M.D., Fauzi, R., Mantoura, R.F.C. *et al.,* 2005. Phytoplankton response to a Lagrangian phosphate addition in the Levantine Sea (Eastern Mediterranean). *Deep Sea Research II,* 52, 2944-2960.

Ribera d'Alcalá, M., Conversano, F., Corato, F., Licandro, P., Mangoni, O. *et al.,* 2004. Seasonal patterns in plankton communities in a pluriannual time series at a coastal Mediterranean site (Gulf of Naples): an attempt to discern recurrences and trends. *Scientia Marina,* 68, 65-83.

Robinson, A.R., Golnaraghi, M., Leslie, W.G., Artegiani, A., Hecht, A. *et al.,* 1991. The Eastern Mediterranean general circulation: features, structure and variability. *Dynamics of Atmospheres and Oceans,* 15, 215-240.

Scheinberg, R.D., Landry, M.R., Calbet, A., 2005. Grazing of two common appendicularians on the natural prey assemblage of a tropical coastal ecosystem. *Marine Ecology Progress Series,* 294, 201-212.

Scotto di Carlo, B., Ianora, A., Fresi, E., Hure, J., 1984. Vertical zonation patterns for Mediterranean copepods from the surface to 3000m at a fixed station in the Tyrrhenian Sea. *Journal of Plankton Research,* 6, 1031-1056.

Siokou-Frangou, I., 1996. Zooplankton annual cycle in a Mediterranean coastal area. *Journal of Plankton Research,* 18, 203-223.

Siokou-Frangou, I., 2004. Epipelagic mesozooplankton and copepod grazing along an east-west transect in the Mediterranean Sea. Rapports de la Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée, 37, 439.

Siokou-Frangou, I., Bianchi, M., Christaki, U., Christou, E., Giannakourou, A. *et al.,* 2002. Carbon flow in the planktonic food web along a gradient of oligotrophy in the Aegean Sea (Mediterranean Sea). *Journal of Marine Systems,* 33-34, 335-353.

Siokou-Frangou, I., Christaki, U., Mazzocchi, M.G., Montresor, M., d' Alcalá, M.R. *et al.,* 2010. Plankton in the open Mediterranean Sea: A review. *Biogeosciences,* 7, 1543-1586.

Siokou-Frangou, I., Christou, E.D., Fragopoulu, N., Mazzocchi, M.G., 1997. Mesozooplankton distribution from Sicily to Cyprus (Eastern Mediterranean). II. Copepod assemblages. *Oceanologica Acta,* 20, 537-548.

Siokou-Frangou, I., Gotsis-Skreta, O., Christou, E., and Pagou, K., 1999. Plankton characteristics in the Aegean, Ionian and NW Levantine seas, p.205-223. In: *The Eastern Mediterranean as a Laboratory Basin for the Assessment of Contrasting Ecosystems,* Malanotte-Rizzoli, P. Eremeev, V. (Eds), Kluwer Academic Publishers, Dordrecht.

Siokou-Frangou, I., Papathanassiou, E., 1989. Aspects of coastal zooplankton of the Rhodes island (Aegean Sea, Greece). *Vie Milieu,* 39, 77-85.

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.

Sutherland, K.R., Madin, L.P., Stocker, R., 2010. Filtration of submicrometer particles by pelagic tunicates. *Proceedings of the National Academy of Sciences of the United States of America,* 107, 15129-15134.

Terbiyik Kurt, T., Polat, S., 2013. Seasonal distribution of coastal mesozooplankton community in relation to the environmental factors in İskenderun Bay (north-east Levantine, Mediterranean Sea). *Journal of the Marine Biological Association of the United Kingdom* 93, 1163-1174.

Theocharis, A., Georgopoulos, D., Lascaratos, A., Nittis, K., 1993. Water masses and circulation in the central region of the Eastern Mediterranean - Eastern Ionian, South Aegean and Northwest Levantine, 1986-1987. *Deep-Sea Research Part II-Topical Studies In Oceanography,* 40, 1121-1142.

Tudela, S., Palomera, I., 1997. Trophic ecology of the European anchovy *Engraulis encrasicolus* in the Catalan Sea (northwest Mediterranean). *Marine Ecology Progress Series,* 160, 121-134.

Uysal, Z., Shmeleva, A.A., 2012. Species composition, abundance and biomass of Copepoda in plankton of the Northern Levantine Basin (Eastern Mediterranean). *Crustaceana,* 85, 909-935.

Vidussi, F., Marty, J.C., Chiaveini, J., 2000. Phytoplankton pigment variations during the transition from spring bloom to oligotrophy in the Northwestern Mediterranean Sea. *Deep-Sea Research Part I-Oceanographic Research Papers,* 47, 423-445.

Yilmaz, A.Z., Besiktepe, S., 2010. Annual variations in biochemical composition of size fractionated particulate matter and zooplankton abundance and biomass in Mersin Bay, NE Mediterranean Sea. *Journal of Marine Systems,* 81, 260-271.

Zakaria, H.Y., 2006. The zooplankton community in Egyptian Mediterranean waters: A review. *Acta Adriatica,* 47, 195-206.

Zeri, C., Kontoyiannis, H., Giannakourou, A., 2009. Distribution, fluxes and bacterial consumption of total organic carbon in a populated Mediterranean Gulf. *Continental Shelf Research,* 29, 886-895.

Zervoudaki, S., Christou, E.D., Nielsen, T.G., Siokou-Frangou, I., Assimakopoulou, G. *et al.,* 2007. The importance of small-sized copepods in a frontal area of the Aegean Sea. *Journal of Plankton Research,* 29, 317-338.

Zervoudaki, S., Nielsen, T.G., Christou, E.D., Siokou-Frangou, I., 2006. Zooplankton distribution and diversity in a frontal area of the Aegean Sea. *Marine Biology Research,* 2, 149-168.

Zodiatis, G., Lardner, R., Hayes, D.R., Georgiou, G., Sofianos, S. *et al.,* 2008. Operational ocean forecasting in the Eastern Mediterranean: implementation and evaluation. *Ocean Science,* 4, 31-47.

Zodiatis, G., Lardner, R., Lascaratos, A., Georgiou, G., Korres, G. *et al.,* 2003. High resolution nested model for the Cyprus, NE Levantine Basin, Eastern Mediterranean Sea: implementation and climatological runs. *Annales Geophysicae,* 21, 221-236.