

Thaliacean distribution and abundance in the northern part of the Levantine Sea (Crete and Cyprus) during the eastern Mediterranean climatic transient, and a comparison with the western Mediterranean basin

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Abstract First results are presented on the composition, abundance and vertical distribution of the thaliacean fauna in the Levantine basin obtained from stratified tows at three deep-sea sites in 1993: SE off Crete, and SW and NE off Cyprus. Samples with a 10 m²-MOCNESS (mesh size 1.67 mm) were poor in species and specimens as compared to samples with a 1 m²-double-MOCNESS (0.333 mm). Of the 12 species identified, six species belonged to the most abundant Doliolida, predominated by the phorozooids of *Doliolum nationalis*, five species belonged to the Salpida and one to the Pyrosomatida. Thaliaceans, most abundant by species and numbers SE off Crete, comprised $\leq 0.2\%$ of the local mesozooplankton standing stocks. Presumably, they did not contribute substantially to the vertical flux generating the locally increased biomass and activity of the microbial benthos at the 4,300 m deep Cretean site. Most doliolids and salps were collected from the epipelagic and upper mesopelagic layers, and appeared to be most abundant close to the deep maximum of chlorophyll-*a*. Samples below 150 m were rarely rich in specimens, although two species performed diel migrations from the mesopelagic zone into the surface layers where some vertical segregation was evidenced. The aspect of niche separation is discussed.

Keywords Thaliacea · Eastern Mediterranean Sea · Levantine Sea · Composition · Regional abundance · Vertical distribution

Introduction

Thaliaceans are widespread in the world's oceans, with a preference for tropical and warm temperate waters, except a few species only present south of 50°S (Kashkina 1978; Deibel 1998; van Soest 1998). By virtue of their rapid asexual reproduction (Gibson and Paffenhöfer 2002), they are able to form extensive swarms (Andersen 1998; Deibel 1998; and references therein) with up to tens of thousands of specimens per cubic metre (Deevey 1971), which can affect the trophodynamics in surface waters hampering markedly the development of other zooplankton (Berner 1967; Aldredge and Madin 1982) by the reduction of phytoplankton (Deibel 1982, 1985, 1998; Dubischar and Bathmann 1997). Like in other seas, in the western Mediterranean (CIESM 2001) thaliaceans can thus locally comprise an exceeding portion of the surface zooplankton standing stock in terms of numbers and biomass. By their capability of exploiting small particles over a wide size range, from bacteria to large diatoms and microzooplankton (Silver and Bruland 1992; Caron et al. 1989; Kremer and Madin 1992) and repacking them into large fast-sinking faecal pellets within a resistant peritrophic membrane, thaliaceans contribute substantially to the rapid transfer of energy into deep waters (see Andersen 1998; Deibel 1998; and references therein), in addition to the mass sinking of individual corpses (Wiebe et al. 1979). It has been estimated that in the northwestern Mediterranean up to 74% of the total primary production can be removed by salp blooms from the surface waters (Andersen 1998) which can

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enhance the process of carbon sequestration in the sea's interior—an aspect which is not only of intrinsic biological interest but also relevant to the potential use of the ocean as a carbon repository (Schrope 2007).

Different to the western Mediterranean Sea, thaliacean blooms have not been reported from the eastern Mediterranean which is one of the most oligotrophic water bodies (Redfield et al. 1963; Dugdale and Wilkerson 1988). The only sub-basin wide study on the abundance of thaliaceans is from the Ionian Sea where doliolids and salps accounted for <2% of the zooplankton (Greze 1963).

Data from the Levantine Sea are of taxonomical concern, documenting a diversified thaliacean fauna (Godeaux 1999). Hydrographically, the strong variability of the surface water circulation on different scales (Özsoy et al. 1989) can return nutrients to the exhausted surface water and thereby boost a local phytoplankton bloom (Salihoglu et al. 1990; Krom et al. 1992; Ediger et al. 2005) which may be considered a general prerequisite for a flourishing thaliacean population (e.g. Wiebe et al. 1979; Deibel 1985; Morris et al. 1988). No information, however, is available as to which extent thaliaceans are involved in the observed increase of zooplankton (Salihoglu et al. 1990; Siokou-Frangou et al. 1999).

In 1993, an outstanding increase of zooplankton throughout the water column was reported from a 4,200 m deep site SE off Crete and SW off Cyprus (Elwers 1995; Weikert 1995), which may be attributed (Weikert et al. 2001) to an upward shift of the nutricline in the course of the eastern Mediterranean transient, EMT (Klein et al. 1999). Although the thaliacean population was small relative to other taxa, we present the data on the populations of species and their ontogenetic stages, with a focus on regional abundance and vertical distribution, in order to provide basic information for the evaluation of the yet unknown role of thaliaceans in the Levantine Sea ecosystem.

Material and methods

Thaliaceans were obtained from zooplankton and micro-nekton samples collected during METEOR cruises 25, leg 2, between 11 and 26 June 1993 (Weikert 1994). Three areas were investigated by full depth profiles: the Ierapetra-Deep SE off Crete (site A) at 34°16'N/25°46'E, and one site each SW off Cyprus (B) at 34°05'N/31°47'E and NE off Cyprus (C) at 35°30'N/35°00'E (Fig. 1). The respective depths of sounding were 4,300, 2,700 and 1,200 m.

Two types of opening/closing devices were used at each site for oblique stratified sampling of the water column at a towing speed of about two knots through the water: a 1 m²-double-MOCNESS (D-MOC) equipped with 18 nets of 0.333 mm mesh size, and a 10 m²-MOCNESS (MOC10)

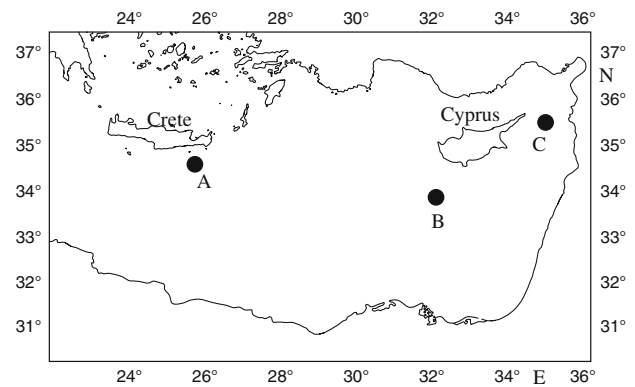


Fig. 1 Sampling sites in the Levantine Sea, June 1993

fitted with five 1.670 mm mesh nets, all nets dark stained (Wiebe et al. 1985). Both devices carried SeaBird CTD probes and sensors to measure flow past the net and net frame angle. We almost exclusively present the findings with the D-MOC, since the number of samples with the MOC10 was small and less specimens and species were collected in general: While the standing stocks of *Salpa fusiformis*, *Thalia democratica* and *Thalia orientalis* were in the same order of magnitude at site A (Mann-Whitney U-test, $P > 0.05$; $n: 7; 2$), they were missing in the MOC10 samples off Cyprus except a few specimens of *T. democratica* at site C. Other species (*Doliolletta gegenbauri*, *Doliolina muelleri*, *Pyrosoma atlanticum*), if present in the MOC 10, were collected in only scattered numbers at the sites.

Thaliaceans were collected from the upper 1,050 m, yet chiefly in the upper 450 m. Within the latter range 50 m-intervals were fished with the D-MOC per haul between 425 and 25 m, in addition to the top 25 m. Off site C, the uppermost layer was 0–35 m, due to an offset of the pressure meter and the depth ranges of the 50 m-intervals had changed accordingly.

The mean water volume filtered at the 50 m-intervals was 332 m³ (SD \pm 105 m³) at the sites A and B and 300 m³ (SD \pm 78 m³) at site C. This is about double as high as the mean filtered in the respective uppermost 25 or 35 m (A 146 \pm 44 m³, B 172 \pm 18 m³, C 156 \pm 38 m³). In total, five day-time and four night-time profiles were available from site A, and two day and two night samples each from sites B and C.

Upon retrieval samples were preserved immediately in a 4% formaldehyde solution buffered with sodium tetraborate and transferred without delay into Steedman's preserving fluid (Steedman 1976) in the homelab prior to subsequent numerical sorting for major taxa and further storage. Samples of the D-MOC were split according to Kott (1953), unless the sample yielded less than 30 thaliaceans.

The species were identified according to Godeaux (1998). Among the species, *D. muelleri* and *Doliolina krohni* display virtually identical stages (cryptic species: Godeaux 1961, 1998) except for the blastozoid stages (phorozoid and gonozoid). But even their species-specific determination is cumbersome. Therefore, the specimens of a rich sample at site A were not discriminated.

The individual numbers were standardized to 1,000 m³ (term “abundance”) or m² (integrals over the upper 1,050 m, “standing stock”) based on volume estimates of filtered water by a calibrated flowmeter, corrected for the net frame angle and the angle of the oblique haul through the water (H.W.). Counts from a day-time haul at site A which encompassed only the deepest layers of regular occurrence of species were accepted for *S. fusiformis* and *P. atlanticum*, because it fully covered the species’ day-time residence depth, whereas the night-time counterpart was omitted. The weighted mean depth (WMD) of species was calculated as

$$\text{WMD} = \sum (ni \times di) / \sum ni$$

where *di* is the depth of a sample *i* (defined as the midpoint of the depth interval), and *ni* is the number of individuals 1,000 m⁻³ in this layer.

The environmental setting at the sites (Fig. 1) as defined by hydrography and phytoplankton distribution is well described (Lenz et al. 1994; Yilmaz et al. 1994; Detmer 1995). At all three sites the upper 50 m of the water column were strongly stratified as exemplified for the site off Crete (Fig. 2). Here, the mixed layer was shallow (4–8 m) with an increase of particles with depth (up to 19×10^5 particles per ml), whereas it was about 20–30 m deep at either site off Cyprus. Temperature was >21°C in general, showing maximum values with >24°C off Cyprus, and salinity increased from 38.73–38.83 off Crete to 38.89–38.99 off Cyprus. Below the thermohalocline, the water was less than 16°C and salinity varied between 38.66–38.77 off Crete and 38.84–38.90 off Cyprus.

The depth of the deep chlorophyll maximum (DCM) approximated or was near the bottom of the euphotic zone. The highest concentrations of 0.4–0.67 µg Chl *a*/l, surpassing background concentrations by an order of magnitude in the upper 150 m, occurred off Crete between 60 and 90 m (Fig. 3), off Cyprus at 90 m (NE) and at 100 m (SW). The basis of the DCM was at 40 m off Crete and at 50–60 m off Cyprus, i.e. in the upper part of the discontinuity layer where a second peak of particle concentrations was measured (Fig. 2). At 200 m, the concentrations of Chl *a* were beyond the limit of detection.

Pico/nanophytoplankton (cells <20 µm) contributed almost exclusively to the Chl *a* and the total cell numbers (Fig. 3), which were positively correlated ($P < 0.001$,

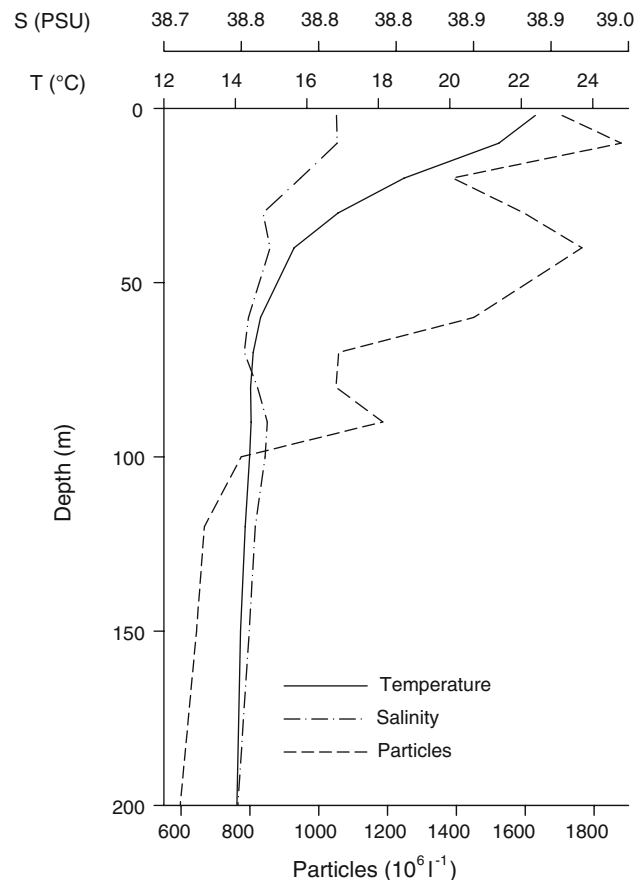


Fig. 2 Distribution of temperature, salinity and particle numbers (2.6–30 µm) in the upper 200 m in the area of the Ierapetra-Deep (site A) in June 1993 (Lenz, unpublished data)

Detmer 1995). The size fraction of autotrophic picoplankton (<2 µm) increased when moving from west to east, averaging 43% off Crete, 62% off SW Cyprus and 76% off NE Cyprus. In the DCM off Crete (Fig. 3), the site which will be referred to almost exclusively in the present study, the numbers of cells <20 µm varied between 3×10^7 and 8×10^7 cells/l. The maxima of eukaryotic autotrophs (up to 1.5×10^7 cells/l) and coccoid cyanobacteria (*Synechococcus*) concurred at 60–80 m. Here, the last group was predominant with up to 4×10^7 cells/l. Prochlorophytes (up to 2.2×10^7 cells/l) climaxed somewhat deeper between 60 and 100 m (Detmer 1995).

Results

Occurrence and standing stocks

The standing stock of thaliaceans and species diversity climaxed at site A (Tables 1, 2), but the individual counts at all sites were small, accounting for only 0.15% of the mesozooplankton off SE Crete (site A), 0.06% off SW

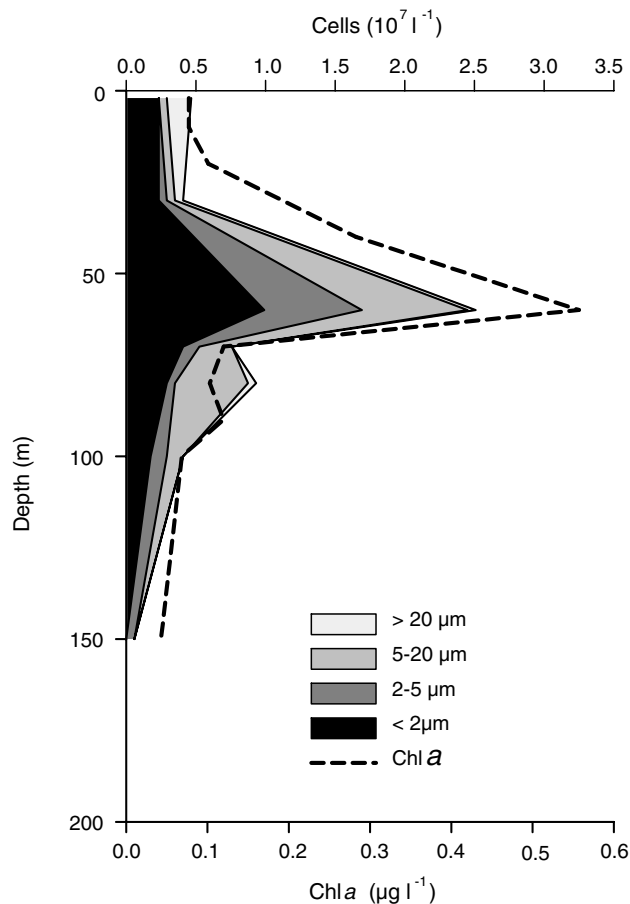


Fig. 3 Distribution of size fractionated chlorophyll *a* ($\mu\text{g l}^{-1}$) and cell numbers (autotrophic pico and nanoplankton, cells 10^7 l^{-1}) in the upper 200 m in the area of the Ierapetra-Deep (site A) in June 1993 (Lenz unpublished cell numbers; modified from Detmer 1995)

Cyprus (B) and 0.2% off NE Cyprus (C). The standing stock at site A was significantly larger (Mann-Whitney *U*-test $P < 0.01$; n : 7; 8) than those at the Cyprian sites B and C which were not different from each other ($P > 0.05$; n : 4; 4). Among the three thaliacean orders doliolids were predominant, comprising 96% of the thaliacean standing stock at site A. Salps ranked second (11%). A total of six doliolid species, one pyrosomatid and four salp species were collected at site A, plus *Cyclosalpa polae* found in the MOC10. Off Cyprus, five doliolid species made up the total thaliacean standing stock, except for a negligible number of *P. atlanticum* at site B (Table 2).

The averaged species counts were highest at site A, except for *P. atlanticum* (Tables 1, 2), but the species-specific variability at the sites was consistently high. Only two species exhibited an overall data set allowing for a Mann-Whitney *U*-test. It revealed a significantly increased standing stock for *D. muelleri* at site A versus site C ($P = 0.05$; n : 7; 4), while the latter stock was larger than that at site B ($P < 0.05$; n : 4; 4). The standing stocks of

D. gegenbauri were not significantly different ($P > 0.05$) among sites. The outstanding large standing stock of *Doliolum nationalis* at site A is self-explanatory.

D. nationalis, all of them phorozoids, comprised 67% of the doliolids at site A, and contributed with 62% substantially to the local thaliacean fauna. In contrast to this species, the other doliolids were represented by different stages, with nurses prevailing off Cyprus (Tables 1, 2). Among the Salpida, Salpidae were predominant, and aggregate forms (*proles gregata*, PG) outnumbered solitary forms (*proles solitaria*, PS). Only three specimens of Cyclosalpidae were encountered (site A): a damaged and doubtful PG of *Helicosalpa virgula*, and two specimens of *C. polae* (PG) in a MOC10 sample. The rare *P. atlanticum* (Pyrosomatida) were represented by all stages of development, from the tetrazoid colonies to mature colonies.

Vertical distribution and migration of species

Among the rare species, *D. krohni* (if clearly identified) and *Doliolum denticulatum* were exclusively found at 25–75 m and *H. virgula* at 75–125 m. *C. polae* was found in a MOC10 sample at 50–100 m. *P. atlanticum* was collected at the sites between 575 and 750 m by day and within the upper 135 m by night. Apart from *D. nationalis* which was represented solely by phorozoids, stages other than nurses at site A were most abundant in the 25–75 m-layer ($206.0 \pm 508.6 \text{ ind. } 1,000 \text{ m}^{-3}$) as compared to the adjacent 0–25 and 75–100 m-layers ($8.7 \pm 22.5 \text{ ind. } 1,000 \text{ m}^{-3}$ and $17.3 \pm 32.9 \text{ ind. } 1,000 \text{ m}^{-3}$, respectively), but the differences were not significant (Mann-Whitney *U*-test, $P > 0.05$; n : 8; 8).

The remaining seven species were abundant enough at site A to allow for a day/night comparison of their respective standing stocks, with no significant differences in abundance between the two time periods (Mann-Whitney *U*-test, $P > 0.05$; Table 3), and to allow for illustrating their vertical distribution (Fig. 4). In order to determine the vertical partitioning of a species at day and at night in the water column, the average weighted mean depths (WMD) for the day and night were calculated for each species (Table 4). When compared by a Bonferroni-adjusted *t*-test ($P > 0.05$) no significant differences were found, except for *S. fusiformis* ($P \leq 0.03$). *Doliolinetta intermedia* was excluded from the test since only one positive sample was available for the night-time.

By exclusion of the day-time data for the diel migrator *S. fusiformis*, significant differences were found between the WMDs of the epipelagic species (Kruskal Wallis test, $P < 0.05$), allowing for a consecutive Tukey-Kramer test at $P < 0.1$ (Sachs 1999). This revealed a significant difference between the centres of abundance occupied by *T.*

Table 1 Standing stocks (means and standard deviation) of thaliaceans (ind./m²) at site A, SE off Crete

Taxon	Standing stock	%	N	PS	PG	PZ	GZ	Ooz	Larvae
<i>Doliolletta gegenbauri</i>	8.2 ± 13.9	8.5	2.7			0.1	<0.1	2.6	2.9
<i>Doliolina krohni</i> ^a	0.9	0.9	<0.1				0.8		
<i>Doliolina muelleri</i>	12.1 ± 7.2	12.6	11.2				0.1	0.8	
<i>Doliolina muelleri/D. krohni</i> ^a	7.2	7.5	1.6				1.4	3.7	0.6
<i>Doliolinetta intermedia</i>	0.6 ± 1.0	0.6	0.5			0.2			
<i>Doliolum denticulatum</i> ^a	0.2	0.2					<0.1	0.2	
<i>Doliolum nationalis</i>	67.2 ± 69.0	69.7				67.2			
Doliolida, total	96.4	89.5	16.0			67.5	2.3	7.3	3.5
<i>Helicosalpa virgula</i> ^a	<0.1				<0.1				
<i>Salpa fusiformis</i>	0.6 ± 0.6	5.3		0.2	0.5				
<i>Thalia democratica</i>	3.0 ± 5.0	26.5		1.0	2.1				
<i>Thalia orientalis</i>	6.2 ± 6.1	54.9		1.9	4.3				
Unidentified	1.5	13.2							
Salpida, total	11.3	10.5		3.1	6.9				
<i>Pyrosoma atlanticum</i> ^a	<0.1								
Pyrosomata, total	<0.1								
Total standing stock	107.7 ± 102.9	100.0	16.0	3.1	6.9	67.4	2.4	7.3	3.4
Zooplankton standing stock	73,931.0								

Percentages refer to the nearest higher-ranking unit. Total zooplankton standing stock from Weikert et al. 2001

N nurses, PS proles solitaria, PG proles gregata, PZ phorozooids, GZ gonozooids, Ooz oozoids

^a Erratic or singular findings

orientalis and *D. nationalis* ($P < 0.05$) as well as between those of *T. orientalis* on the one hand and *T. democratica* and *D. muelleri* on the other hand ($P < 0.1$; Table 5). Obviously, *T. orientalis* showed a lesser affinity to the uppermost 25 m over the whole day as compared to the other three species.

The findings at either site off Cyprus appear to fit the species' vertical patterns at site A except for *D. muelleri* (nurses), the most abundant species at site C (90% of thaliaceans). Two positive night-time hauls out of three hauls performed in the area of an intermittent anticyclonic gyre (Yilmaz et al. 1994) yielded considerable counts between 225 and 875 m comprising some 70% of the standing stock. The respective abundances varied between 0.5 ind. 1,000 m⁻³ at 725–875 m and 74.5 ind. 1,000 m⁻³ at 375–425 m.

Discussion

Composition and standing stock of thaliaceans

Our data on the populations of thaliacean species in the Levantine Sea are a snapshot. Only a limited set of species from the livestock reviewed in Godeaux (1999) was recorded. *H. virgula*, on the other hand, so far known from the central Mediterranean (Godeaux 1999), may be the first

record from the eastern basin, but the sole and severely damaged specimen could not be identified with certainty. *P. atlanticum*, one of the main blooming thaliaceans in the western Mediterranean (Franqueville 1971; Andersen and Sardou 1994), was recorded with all developmental stages for the first time from northern Levantine waters and appears to have established an indigenous population. Earlier findings were from the southern part of the basin and the central Mediterranean (Galil and Goren 1994; Godeaux 1987, 1999). Colonies not identified to species level have been reported from off Rhodes and the Levantine Basin (Mazzocchi et al. 1996). No Lessepsian species was found, although a number of thaliacean species in the Red Sea are considered potential migrants to the basin (Godeaux 1999).

In January 1998, the collection of zooplankton was repeated at site A. Due to unspecified losses when counted specimens were transferred into vials for taxonomic identification, quantitative statements are impossible. *P. atlanticum* was again present with a complete biological cycle. Among the Doliolidae, *D. gegenbauri* (N) and *D. intermedia* (N) were the commonest, accompanied by *D. muelleri* (Ooz, N), *D. nationalis* (PZ), and *D. denticulatum* (Ooz, PZ, GZ). Salps were represented by *S. fusiformis*, *T. orientalis* and the dominant *T. democratica*. In the sparsely investigated northern Aegean Sea, a few specimens of *D. muelleri* (Ooz, N), *D. denticulatum*

Table 2 Standing stocks (means and standard deviation) of thaliaceans (ind./m²) at sites B, SW off Cyprus (I) and C, NE off Cyprus (II)

Taxon	Standing Stock	%	N	PZ	GZ	Ooz
I SW off Cyprus						
<i>Dolioletta gegenbauri</i>	1.2 ± 1.2	66.7	1.2			
<i>Doliolina krohnii</i> ^a	0.1	5.6			0.1	
<i>Doliolina muelleri</i>	0.5 ± 0.4	27.8	0.4			0.1
<i>Doliolum nationalis</i> ^a	<0.1			<0.1		
Unidentified	<0.1					
Doliolida, total	1.8 ± 1.7	94.7	1.6	<0.1	0.1	0.1
<i>Pyrosoma atlanticum</i> ^a	0.1	100				
Pyrosomata, total	0.1	5.2				
Total standing stock	1.9 ± 1.7	99.9	1.6	<0.1	0.1	0.1
Zooplankton standing stock	3,239.0					
II NE off Cyprus						
<i>Dolioletta gegenbauri</i> ^a	0.2	4.0	0.2			
<i>Doliolina muelleri</i>	4.5 ± 4.3	90.0	4.0			0.4
<i>Doliolinetta intermedia</i> ^a	0.2	4.0	0.2			
<i>Doliolum nationalis</i> ^a	0.1	2.0		0.1		
Unidentified	<0.1					
Doliolida, total	5.0 ± 4.0	100.0	4.4	0.1		0.4
Total standing stock	5.0 ± 4.0	100.0	4.4	0.1		0.4
Zooplankton standing stock	2,236.0					

Percentages refer to the nearest higher-ranking unit. Species of the orders are being ranked according to Table 1. Total zooplankton standing stock from Elwers 1995

^a Erratic or singular findings

Table 3 Mean number and standard deviation of individuals m⁻² for the most abundant thaliacean species in the upper 400 m of the water column at site A, SE off Crete

Species	Day (n = 4)	Night (n = 3)
<i>Dolioletta gegenbauri</i>	12.4 ± 18.0	2.1 ± 1.7
<i>Doliolina muelleri</i>	10.4 ± 4.5	14.1 ± 10.7
<i>Doliolinetta intermedia</i>	0.6 ± 1.0	0.7 ± 1.2
<i>Doliolum nationalis</i>	88.1 ± 86.9	38.7 ± 30.3
<i>Salpa fusiformis</i> ^a	0.7 ± 0.7	0.5 ± 0.1
<i>Thalia democratica</i>	5.1 ± 6.1	0.3 ± 0.3
<i>Thalia orientalis</i>	8.8 ± 7.1	2.8 ± 2.1

Day-night differences (*U*-test) not significant at the 0.05 level

n number of samples

^a *S. fusiformis*: n day = 5 (see “Material and methods”)

(Ooz, N), *D. gegenbauri* (N) and *T. orientalis* (PS) were caught in the Sporades Basin, around 39°17'N/23°33'E. *T. democratica*, reported to be dominant in the eutrophic north Aegean Sea (Kiortsis 1974), was not found.

Quantitative information on thaliaceans from sub-basins adjacent to the Levantine Sea is rare. Near to the coast of northern Rhodes, the share of thaliaceans in total zooplankton collected during four months with 0.200 mm nets in the upper 50–350 m varied between virtual absence (0.03%) and 3.27%, with maxima in February and May and minima in August and November (Siokou-Frangou and Papathanassiou 1989). Estimated averages of salps calculated from that study are about 24 ind. 1,000 m⁻³ in summer, and 1,100 ind. 1,000 m⁻³ in winter. Doliolids were always present. Except in autumn (60 ind. 1,000 m⁻³) when no salps were collected, the averaged counts varied between 200 and 300 ind. 1,000 m⁻³. In the open Ionian Sea, samples (mesh size no. 46, which corresponds to 0.170 mm according to Scotto di Carlo and Ianora 1983) averaged up to 24,600 salps 1,000 m⁻³ in the 10–25 m layer and 9,500 doliolids 1,000 m⁻³ in the 50–100 m layer of maximum occurrence in summer, possibly indicating the existence of blooms (Greze 1963). *D. denticulatum* and, like near to Rhodes, *T. democratica* were conspicuous. In either study the finer mesh sizes used may have resulted in higher numbers as compared to our study, especially concerning the small-sized oozoids of doliolids.

In the northwestern Mediterranean, thaliaceans have been observed weekly over some 25 years at a site in the Bay of Villefranche-sur-mer, using a 0.680 mm mesh size. The surface temperature seems to be the only environmental factor which significantly influences the distribution of salps. The most common *S. fusiformis* and *T. democratica* were most abundant in spring/early summer, the first species showing a strong decrease in August/September (Licandro et al. 2006). The doliolids begin to be numerous from May–June, with peaks of abundance in summer and autumn when the numbers of salps decrease (Braconnot et al. 1990; Braconnot and Dallot 1995) and the environment is most oligotrophic (Menard et al. 1997). In samples based on a 0.700 mm mesh size, *S. fusiformis* may reach 20,000 ind./1,000 m³ in the upper 75 m (Braconnot et al. 1990), and numbers of the most abundant *D. nationalis* may be even twice as high (Braconnot and Dallot 1995). Counts of *P. atlanticum* based on 0.500 mm meshes varied between rare findings and up to 187 colonies 1,000 m⁻³ according to season (Andersen et al. 1994). Possible seasonal variations included and corroborating previous faunistic studies (Godeaux 1999, and references therein), the thaliacean fauna is richer in species and specimens as compared to the eastern Mediterranean, where phytoplankton and bacterial production is up to three times less than in the western Mediterranean Sea (Turley et al. 2000). Notwithstanding, the seasonal fluctuations of salps and doliolids in the SE Aegean Sea (Siokou-Frangou and Papathanassiou 1989) seem to fit the respective pattern in the western Mediterranean Sea.

Fig. 4 Vertical distribution of abundant thaliacean species in June 1993 above the Ierapetra Deep (site A). The bars represent the mean and the sticks the standard errors. Shaded bars day-time, black bars night-time

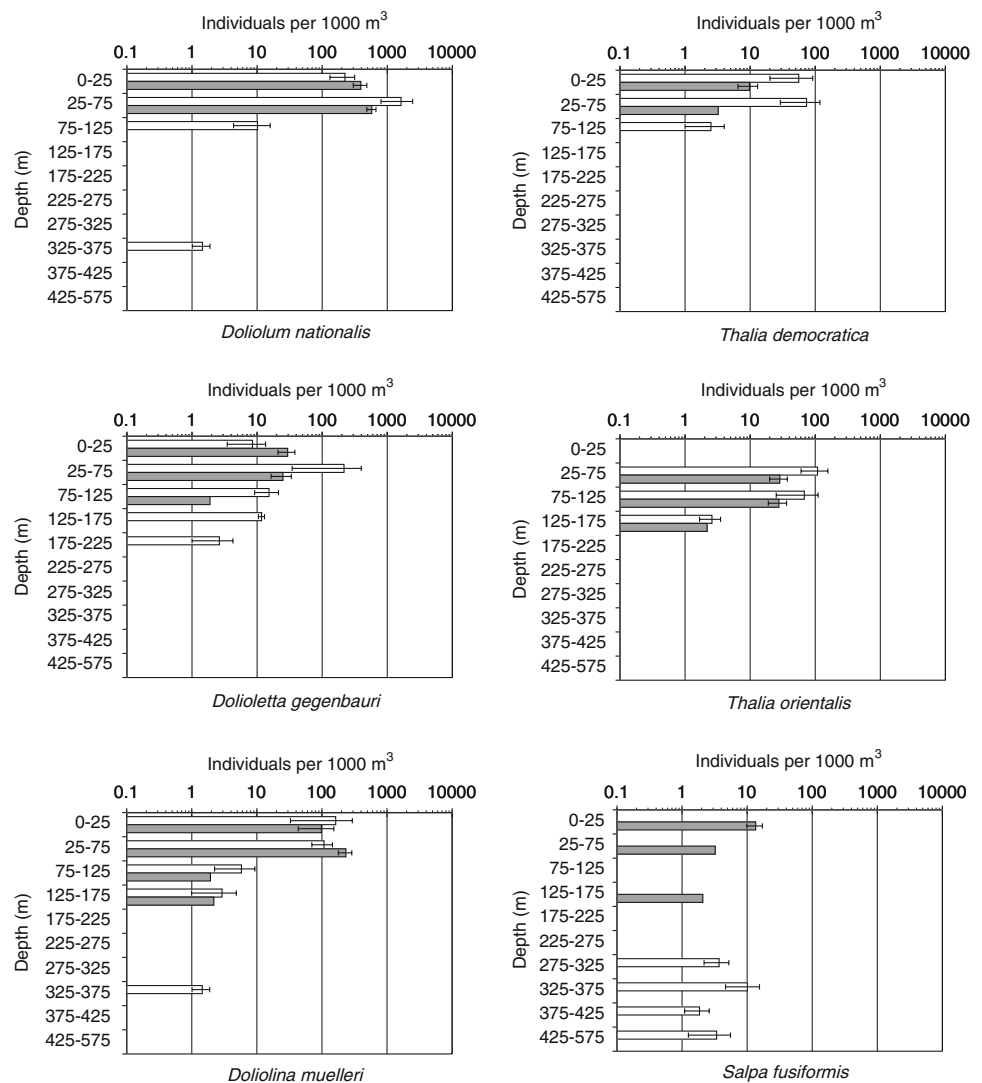


Table 4 Average weighted mean depths (WMD) \pm standard deviations at day-time and night-time for the most abundant thaliacean species at site A, SE off Crete

Species	WMD (day)	WMD (night)
<i>Doliolletta gegenbauri</i>	75.9 \pm 19.4	45.1 \pm 13.1
<i>Doliolina muelleri</i>	47.8 \pm 19.5	45.5 \pm 3.1
<i>Doliolinetta intermedia</i> ^a	64.9 \pm 21.0	33.1
<i>Doliolum nationalis</i>	47.2 \pm 3.8	40.7 \pm 3.1
<i>Salpa fusiformis</i>	362.7 \pm 43.7	39.0 \pm 23.2
<i>Thalia democratica</i>	44.4 \pm 6.5	37.5 \pm 21.7
<i>Thalia orientalis</i>	68.4 \pm 16.4	67.2 \pm 17.8

Day-night differences (*t*-test) not significant at the 0.05 level except for *S. fusiformis*

^a Not tested, see text

Our data from June 1993 indicate also a decline in species and individual richness from SE of Crete (site A) to SW and NE of Cyprus (sites B and C, respectively). The

conspicuous predominance of the blastogenetic *D. nationalis* over salps at site A apparently features the phenology of the summer season (Table 1). Even though this neritic species was not entrained by the local anticyclonic eddy in high numbers, expatriates into the oceanic Ierapetra-Deep area may have benefitted from a high phytoplankton availability by rapid budding which is a competitive advantage over oceanic species. Yet, even the high counts of *D. nationalis* of 4,095 ind. 1,000 m⁻³ in a rich 25–75 m-sample are by a factor of ten less as compared to blooms in the western Mediterranean.

Aside from a supra-regional comparison, the counts of thaliaceans at the studied sites were low in absolute numbers and relative to the local zooplankton. This is typical of oceanic sites for most of the time when there are no blooming events. In June 1993, when the EMT was at its climax (Roether et al. 2007), the population of thaliaceans was insignificantly increased (Table 6) as compared to studies before (1987) and after (1998, 1999, 2001) the

Table 5 Significance of the Tukey-Kramer test applied for the most abundant species of thaliaceans at site A, SE off Crete

	<i>Doliolina muelleri</i> <i>n</i> = 7	<i>Dolioletta gegenbauri</i> <i>n</i> = 7	<i>Doliolum nationalis</i> <i>n</i> = 7	<i>Salpa fusiformis</i> <i>n</i> = 3	<i>Thalia democratica</i> <i>n</i> = 7	<i>Thalia orientalis</i> <i>n</i> = 7
<i>Doliolina muelleri</i>	–	12.43 < 15.37	1.57 < 15.37	1.76 < 19.85	1.0 < 16.93	16.43 > 15.37
<i>Dolioletta gegenbauri</i>	12.43 < 16.93	–	14.00 < 15.37	14.19 < 19.85	11.43 < 16.93	4.00 < 16.93
<i>Doliolum nationalis</i>	1.57 < 16.93	14.00 < 16.93	–	0.52 < 19.85	2.71 < 16.93	19.29 > 15.37
<i>Salpa fusiformis</i>	1.76 < 21.85	14.19 < 21.85	0.52 < 21.85	–	2.71 < 16.93	19.81 < 19.85
<i>Thalia democratica</i>	1.0 < 16.93	11.43 < 16.93	2.71 < 16.93	3.24 < 21.85	–	16.14 > 15.37
<i>Thalia orientalis</i>	16.43 < 16.93	4.00 < 16.93	19.29 > 16.93	19.81 < 21.85	16.14 < 16.93	–

Bold numbers indicate difference between the centres of vertical distribution: upper part at the 0.1 level, lower part at the 0.05 level. Diel migrator *S. fusiformis* only night data

n number of samples

Table 6 The standing crop (mean \pm SD) and relative abundance (% of zooplankton) of thaliaceans in the upper 1,050 m of the water column at site A, SE off Crete, in different years.

Year, month	Ind./m ²	%	<i>n</i>	Data referring to
1987, January	44.9 \pm 43.0	0.3	4	Weikert and Trinkaus 1990
1993, June	107.7 \pm 102.9	0.2	7	Weikert et al. 2001
1998, January	48.1 \pm 29.1	0.4	3	Weikert, unpublished
1999, April	53.1 \pm 16.2	0.3	4	Koppelman and Weikert 2007
2001, October/November ^a	66.4 \pm 40.2	0.4	2	Koppelman and Weikert 2007

Number of profiles (*n*). Sampling devices: D-MOC, 1987 single MOC; all nets of 0.333 mesh size. Standing crop differences (Kruskal and Wallis-Test; ^anot included) are not significant at the 0.05 level ($3.025 < 5.991 = \chi^2_{3;0.05}$)

climatic change in hydrography, although a phytoplankton bloom prior to our study was evidenced. Chloroplastic pigment equivalents as well as bacterial biomass and activity at the abyssal sea floor were significantly elevated as compared to contiguous sites and previous years (Boetius et al. 1996). The zooplankton standing stock was exceptionally large, almost exclusively supported by resting stages of the herbivorous calanoid copepods *Calanus helgolandicus* and *Eucalanus monachus* at mainly mesopelagic and bathypelagic depths as deep as 4,000 m (Weikert 1995, Weikert et al. 2001). Species of the respective genera are well-known to take full advantage of phytoplankton blooms and to diapause at depth during oligotrophic conditions.

Faecal pellets of large copepods as a potential transport vehicle of phytoplankton to the sea floor can sink at similar rates as doliolid faeces (Small et al. 1979). The processes which favour the likely competitive outbreaks of copepods and thaliaceans are poorly understood (Licandro et al. 2006), but particle size of food might be an important agent. Calanoid copepods, in general, feed most effectively on particles $>5 \mu\text{m}$ in size. Thus, the overwhelming abundance of the dormant coarse filterers *C. helgolandicus* and *E. monachus* argues against a preceding bloom of

mainly small-sized autotrophs and a food web dominated by thaliaceans.

Vertical distribution and migration

Vertically habitat-partitioning was evident among species of salps. In the epipelagic zone, the centre of distribution of *T. orientalis* was significantly different from that of *T. democratica* (Table 5, Fig. 4). The first species appeared to be closer associated with the DCM and the broad, deep maximum of particles (Figs. 2, 3), while the latter species abounded also in the phytoplankton-poor but particle-rich 0–25 m surface layer (Fig. 2). Salps can be regarded as ecological equivalents due to an apparent overlap in diet among species (Madin and Deibel 1998). The restricted occurrence of *T. orientalis* may reduce food competition on *T. democratica*, whereas competition pressure by *S. fusiformis* in the surface layers is restricted to the night-time. In the mesopelagic zone, the population of the diel migrator was observed at depths ≤ 575 m at day-time (Fig. 4, Table 4), at shallower depths than the rare findings of *P. atlanticum*. In the southern Levantine Sea, Galil and Goren (1994) caught three colonies of *P. atlanticum* below 1,400 m, i.e. 500 m deeper than our utmost record.

Among the doliolid species (Fig. 4) and their stages, a segregation in space could not be proved statistically, although *D. intermedia* was not collected in the top 25 m at day-time, and feeding stages (phorozooids, oozoids, gonozooids) of the *D. muelleri-krohni* group, *D. gegenbaui*, *D. intermedia* and *D. denticulatum* were most abundant at depths below 25 m contrasting to the extended vertical distribution of the neritic, blastogenetic *D. nationalis*, which was represented solely by phorozooids (Table 1). Its occurrence throughout the euphotic zone at varying cell concentrations (Fig. 4) might be hypothesized from feeding experiments: unlike neritic species (*T. democratica*), larger oceanic salps (*S. fusiformis*) which live in diluted particle concentrations cannot adjust filtration to changing particle concentrations (Deibel 1982; Madin and Deibel 1998). Nurses, which do not feed as deprived of any digestive tract, showed a vertically extended distribution similar to *D. nationalis*.

It is impossible to correlate statistically the species' abundances with the phytoplankton and particle concentrations. Irrespectively of the fact that we do not have access to the original data, the above concentrations were measured with a time lag ranging from some hours to four days relative to the MOC tows and at differing geographical positions, since the sampling strategy for zooplankton was designed for deep-sea studies (Weikert et al. 2001). Also, the coarse subsampling of the upper 200 m by 25 m and 50 m layers inevitably blurred vertical biological structures. Dives, for example, showed a doliolid abundance decreasing by two orders of magnitude over a vertical distance of only 2 m (Paffenhöfer et al. 1991). However, time-series suggest that the depth where reproduction takes place and thaliacean stages are distributed seasonally, may be related to environmental variables such as temperature, salinity and food (Licandro et al. 2006), depending on species (Paffenhöfer et al. 1995; Tew and Lo 2005). But the coupling may be subject to environmental disturbance as exemplified by the conspicuous mesopelagic findings of thaliaceans at site C (see above). Paffenhöfer and Gibson (1999) reported on asexually reproducing *D. gegenbaui* in the top 1–13 m before, and their vertical dispersion after, a storm-induced turbulence.

Differential grazing in thaliaceans would allow spatial coexistence of salps and doliolids, although some vertical separation is indicated for *T. orientalis* versus the doliolids *D. nationalis* and *D. muelleri* (Table 5). Madin and Deibel (1998) and Bone et al. (2003) related the most recent results on thaliacean feeding experiments to observations in the field. They suggested that small doliolid stages should at least be capable of filtering small nanoplankton and even picoplankton particles efficiently, and doliolids “are thus apparently significantly different from salps” (Madin and Deibel 1998, page 85). Such a difference

would not only explain the dominance of doliolids over salps during our study, when the portion of nanoplankton and picoplankton was large, but also the diverging horizontal distribution pattern of both groups. The virtual absence of salps from the sites off Cyprus was associated with low cell numbers and a relative decrease of cells sizes $>2\ \mu\text{m}$, from 57% off Crete to about 38% off SE Cyprus and 24% off NE Cyprus (Detmer 1995), which are most efficiently grazed by salps (Madin and Deibel 1998; Bone et al. 2003; Vargas and Madin 2004). Under the increased oligotrophic conditions doliolids were almost exclusively represented by non-feeding stages (nurses).

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