

Does mesozooplankton respond to episodic P inputs in the Eastern Mediterranean?

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Abstract

An in situ P addition experiment was carried out in May 2002 in the Levantine basin of the P-limited Eastern Mediterranean that lasted for 10 days. Mesozooplankton abundance, biomass, taxonomic composition and gut fullness were studied from net samples (0–150 m) collected daily at midnight at the center of the fertilized patch starting the day before P addition. Bottle-collected small zooplankton, concentrations of suspended fecal pellets of major grazers and copepod eggs were also examined. Composition, abundance and biomass of bottle-collected zooplankton were also estimated. The following changes were associated with the P addition: higher fecal pellet concentrations in the upper 45 m, a peak in total integrated biomass of suspended fecal pellets, copepod egg concentrations and gut fullness of herbi- and omnivores (but not carnivores) between 3 and 5 days after P release, decreasing thereafter to pre-release levels. These are interpreted as a rapid feeding and reproduction response of the mesozooplankton communities of the Eastern Mediterranean to phosphorus addition. The suggestion is launched that P addition in this ultra-oligotrophic pelagic environment supported a microbial- and phytoplankton-based food web that was instantaneously top-down controlled by zooplankton. Almost no increase in the standing stock of food for mesozooplankton (except for an increase in ciliate abundance) was encountered, but the stimulated production was discernable in an increase in gut fullness, concentrations of copepods eggs and fecal pellets of larger zooplankton forms.

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1. Introduction

The Mediterranean Sea is considered to be one of the most impoverished marine regions. A west–east gradient in nutrient deficiency creates an increasingly oligotrophic environment (Margalef, 1984) being ultra-oligotrophic in the Levantine Sea, its easternmost basin (Berman et al., 1984a, b; Pitta et al., 2005, and references therein). The ultra-

oligotrophic nature of the Levantine Sea is reflected in the low suspended POC concentrations that ranged between 40 and 120 mg C m⁻³, the majority being between 60 and 70 mg C m⁻³ (Krom et al., 2005) and extremely low primary production rates (Psarra et al., 2005). The available evidence reviewed by Berland et al. (1980) supports the conclusion that P is the most limiting factor for primary production in the Mediterranean Sea. This has been verified by Thingstad and Rassoulzadegan (1995) and references therein.

How will such an ecosystem react to episodes of high nutrient supply, such as short-term vertical

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mixing events in late winter (Sur et al., 1992) or aeolian input of Sahara dust? Enhanced nutrient input to oligotrophic water usually leads to increased primary and microbial production and consequently algal/microbial biomass (Martin et al., 1994; Coale et al., 1996; Boyd et al., 2000), but not much is known about the likely response of ultra-oligotrophic offshore regions. In order to test this question a phosphate addition experiment using an SF₆ tracer was carried out in the center of the Cyprus warm core eddy in the SE Levantine basin (Krom et al., 2005; Law et al., 2005). After addition of phosphorus, the patch of P-enriched water was followed successfully for 10 days. There was a rapid biological uptake of phosphate by bacteria and phytoplankton, and an increase in P turnover time (Fonnes Flaten et al., 2005). Is the response confined to the lowest trophic levels or does mesozooplankton respond to such an episodic P supply? These questions are not easy to address because of the lack of knowledge of the functioning of zooplankton communities in the eastern Mediterranean Sea. Previous zooplankton studies in this region were mainly restricted to the taxonomic composition, abundance and distribution of mesozooplankton communities (e.g. Pancucci-Papadopoulou et al., 1992; Mazzocchi et al., 1997; Siokou-Frangou et al., 1997, 1998; Uysal et al., 2002), and there is no data on the cascading effects through zooplankton during episodic increases in nutrient availability. Considering the brevity of natural nutrient additions such as dust storms and their episodic and unpredictable nature, it was considered unlikely that an abundance response by mesozooplankton to an experimentally induced sudden pulse of P could be detectable. However, are they not affected by such episodic nutrient addition? Would there be any changes in the trophic and reproductive responses of dominant zooplankton groups to P addition? This study aimed at answering these questions as part of the CYCLOPS P-addition experiment. A second objective was to collect data on the early summer abundance, biomass and taxonomic composition of the zooplankton community, as well as the concentrations of suspended eggs and fecal pellets in this under-studied region of the Eastern Mediterranean.

2. Materials and methods

Sampling took place in the Cyprus Eddy south of Cyprus (Fig. 1) during a cruise of the R/V *Aegaeo* to

the eastern Mediterranean, between 14 and 26 May 2002. A Lagrangian approach, following a buoy trajectory centered ~3 nautical miles from the eddy center, was applied to study the biological effects of phosphorus addition to a naturally enclosed, ultra-oligotrophic, P limited region. Phosphoric acid diluted by sodium bicarbonate solution was prepared in water collected from the surface mixed layer. SF₆ was used as tracer, and SF₆ saturation was achieved using a novel in-line saturation unit, continuously monitored using a TCD gas chromatograph. On May 17 the saturated SF₆ solution was mixed with the 18,000l phosphate solution using a dual pumping system (see Law et al., 2005). This solution was pumped through a hose which extended ~15m behind the ship and was maintained at a depth of ~10m. The release took 6.5 h and covered an area of <4 × 4 km. The phosphate/SF₆ release was co-ordinated in a Lagrangian mode by reference to the GPS drifter buoy that marked the nominal patch center within the Cyprus Eddy. For information on the location and trajectory of the P-enriched patch, see Fig. 1. For details, see Law et al. (2005). During the experiment the patch increased in size and the P concentration decreased over time, returning to background concentration by day 7 after the release.

2.1. Mesozooplankton sampling

Mesozooplankton was collected within the patch using a WP-2 plankton net (180 μm mesh size). Sampling was first done on May 16, one day before the P addition, then on days 1, 2, 3, 5, 6, 7 and 8 after addition. Vertical hauls were taken from 150 m to the surface at midnight in the center of the patch. Previously, a strong vertical gradient in abundance of both mesozooplankton (Mazzocchi et al., 1997) and small metazoan plankton (Böttger-Schnack, 1997) was found in this region. The upper 50 m layer was most densely populated, and a sharp decrease of total zooplankton abundance was observed below 100 m. Net tows from 150 m to the surface at night ensured sampling of the bulk of the zooplankton. Water temperature was about 21 °C at the surface and 17 °C at 150 m. The samples were preserved with formaldehyde buffered with hexamethyl tetramine and propandiol (4% final concentration). Identification, counting and measuring of zooplankton was carried out under a dissecting microscope. The C-biomass of main zooplankton groups was calculated from the regressions given by

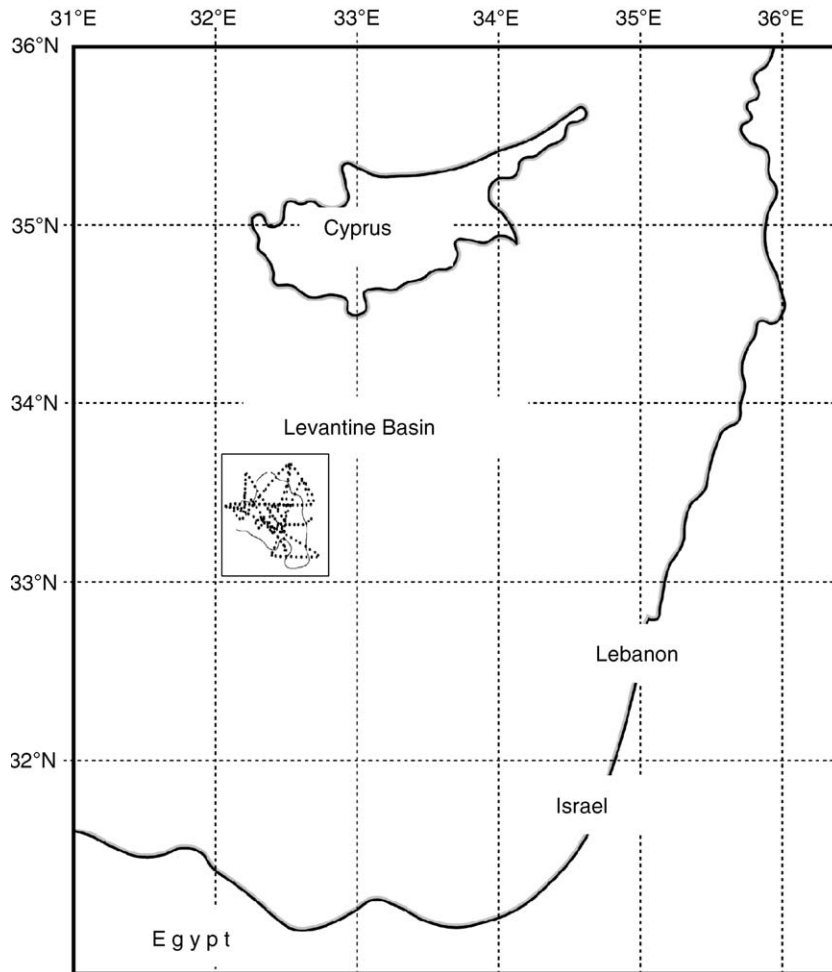


Fig. 1. P release location close to the center of the Cyprus Eddy in the Eastern Mediterranean Sea and buoy trajectory centered ~3 nautical miles from eddy center at 33.27°N32.36°E

Kanaeva (1962) and Vinogradov and Shushkina (1987). We put together Cyclopoida (*Oithona* spp.) and Poecilostomatoida (*Corycaeus* spp., *Oncaea* spp., *Sapphirina* sp., *Copilia* sp.) to be able to compare our data on biomass and abundance with earlier publications, where these genera were considered as Cyclopoida.

2.2. Small mesozooplankton, fecal pellets and eggs from water bottle samples

Samples of suspended matter were collected with two or three 10-l Niskin bottles at 10, 20, 45, 100 and 150 m depth on days -1, 1, 2, 3, 5, 6 and 7 after P addition. The content was carefully drained in containers with a 20- μ m mesh size and preserved with buffered formaldehyde (2% final concentration). Fecal pellets, copepod eggs, nauplii and small

copepods (that are likely to escape the 180 μ m zooplankton net) were identified, counted and measured under a dissecting microscope in a plankton counting chamber. The whole samples of suspended matter were analyzed to assess the concentration of these items. The length and width of the fecal pellets were measured and the pellet volume calculated using appropriate stereometrical configurations (Edler, 1979). A volumetric carbon conversion factor of 69.4 μ g C mm⁻³ (Riebesell et al., 1995) was applied to estimate the fecal pellet carbon (FPC).

2.3. Mesozooplankton feeding characteristics

Feeding activity was assessed as a percentage of zooplankters with food in the gut. We distinguished three main trophic categories: primarily herbivorous

(copepods of genera *Clausocalanus*, *Ctenocalanus*, *Calocalanus*, *Neocalanus*, and besides copepods, Appendicularia), omnivorous (*Mecynocera*, *Lucicutia*, *Pleuromamma*, *Aetideus*, *Euchirella*, *Scolecithricidae*), and carnivorous (*Haloptylus*, Chaetognatha, *Tomopteris*). This is certainly only an arbitrary division made for the purpose of facilitating the analyses of their gut content. Strictly speaking, almost all calanoids are able to consume protozoans, detritus, eggs and small metazoans in addition to phytoplankton (Mauchline, 1998), and the majority are opportunistic feeders easily switching to the available food (Arashkevich and Pasternak, 1986; Calbet et al., 2000); appendicularians are non-selective grazers, the size of the food items they consume being determined by their sieves (Deibel and Turner, 1985). The published data on the feeding of *Oithona*, *Oncaea* and *Corycaeus* point to the different components of their respective diets and various preferred items and foraging patterns (Pasternak, 1984; Turner, 1986; Metz and Schnack-Schiel, 1995; Calbet et al., 2000; Paffenhöfer and Mazzocchi, 2002). As there is no mutual agreement on their trophic status, we examined them separately. Thirty to 100 specimens of randomly picked zooplankters of each trophic group were analyzed for gut fullness at each station.

To test whether the diets of the dominant zooplankters changed during the course of the enrichment experiment, we dissected the guts of 10 specimens of each group from every sample and analyzed the gut contents under a light microscope. We ranked the occurrence of recognized items according to their proportion in the whole pellet as “few” (1–10%), common (10–50%) and abundant (50–100%). The main part of the guts contents, however, was a non-structured unidentified mass, which can originate from digested soft-bodied organisms (aloricate ciliates and athecate dinoflagellates, nanoflagellates, bacteria) and, sometimes, metazoans. Gut contents analysis usually underestimates the proportion of these groups in the consumed food. All these food items contribute to the unidentified mass in the guts.

3. Results

3.1. Mesozooplankton

The main groups distinguished within the mesozooplankton community together with their occurrence on different sampling dates are presented in

Table 1. Most taxa were registered throughout the study period. Copepods (mostly Calanoida + Cyclopoida) were by far the most important group of zooplankton in terms of abundance (Fig. 2, upper panel), and Calanoida played the main role among copepods. However, the abundance of *Oithona* spp. and *Corycaeus* spp. (regarded here as cyclopoids, see Materials and methods) was also high. Among the Calanoida, the genera *Clausocalanus*, *Calocalanus* and *Ctenocalanus* dominated. *Haloptylus longicornis* was noticeable on some dates.

Although not so pronounced, the dominance of Calanoida in the zooplankton community persisted in terms of biomass (Fig. 2, lower panel; Table 2). Only on the last day of our study, did the cyclopoid biomass exceed that of calanoids. The contribution of rare large zooplankters was, of course, higher in terms of C-biomass. The group of “other” zooplankton, including Cladocera, Ostracoda, Pteropoda, Gastropoda, Heteropoda, Echinodermata, Amphipoda, and Polychaeta, always had a significant share in total C-biomass, but it became dominant with mass appearance of the large pelagic polychaete *Tomopteris* sp. (up to 5000 ind m⁻² or 167 mg C m⁻²) on days 6–8. The contribution of gelatinous zooplankton, appendicularians and doliolids (filter feeders) on the one hand, and siphonophores and medusas (carnivores), on the other, was considerable in terms of abundance and biovolume, but not in terms of C-biomass (Table 2). Although appendicularians dominated gelatinous zooplankton numerically (Fig. 2, upper panel), their contribution together with doliolids (which were scarce) to C-biomass was negligible (Fig. 2, lower panel), due to the much larger size of medusas and siphonophores.

Overall, zooplankton abundance increased from day -1, prior to P addition, to day 2 after addition, reaching a peak of 58×10^3 ind m⁻², after which it decreased, falling below the level prior to the P addition. C-biomass peaked on day 3, staying at the same level for the rest of the experiment (Fig. 2, lower panel). However, only the mass appearance of *Tomopteris* sp. (appearing in Fig. 2 as “others”) compensated for a decrease in biomass of all the other zooplankton at the last 3 days, the maximum value of zooplankton biomass would otherwise have been on day 5. The majority of the regularly occurring copepods increased in abundance from day 2 to day 5 and then decreased (Table 3). The same held true for the total copepod abundance.

Table 1
Main zooplankton groups and their occurrence in the samples

Group (species)	F	O	R
Copepoda	+		
Calanoida	+		
<i>Acartia</i> sp.			+
<i>Aetideus</i> sp.		+	
<i>Calocalanus pavo</i>	+		
<i>Calocalanus</i> sp.	+		
<i>Clausocalanus</i> spp.	+		
<i>Centropages</i> sp.			+
<i>Ctenocalanus</i> sp.		+	
<i>Euchaeta</i> sp.			+
<i>Euchirella messinensis</i>			+
<i>Euchirella</i> sp.			+
<i>Haloptilus longicornis</i>		+	
<i>Heterorhabdus</i> sp.		+	
<i>Lucicutia flavicornis</i>		+	
<i>Mecynocera clausi</i>	+		
<i>Neocalanus gracilis</i>		+	
<i>N. tenuicornis</i>		+	
<i>Paracalanus</i> sp.	+		
<i>Pleuromamma gracilis</i>		+	
<i>Scolecithricella</i> spp.	+		
<i>Scolecithrix</i> sp.		+	
Cyclopoida	+		
<i>Oithona</i> spp.	+		
Poecilostomatoida	+		
<i>Copilia</i> sp.			+
<i>Corycaeus</i> spp.	+		
<i>Oncaea</i> spp.	+		
<i>Sapphirina</i> spp.			+
Copepoda juv.	+		
Copepoda nauplii	+		
Chaetognatha	+		
Euphausiacea		+	
Appendicularia	+		
Doliolida		+	
Siphonophora	+		
Medusa		+	
Other groups	+		
<i>Polychaeta</i>	+	+	
<i>Tomopteris</i> sp.	+		
Polychaeta larvae	+		
Cladocera		+	
Pteropoda		+	
Ostracoda	+		
Decapoda	+		
Euphausiacea	+		
Heteropoda		+	
Amphipoda	+		
Gastropoda larvae	+		
Echinodermata larvae	+		
Pisces larvae	+		

F—frequent groups (present in 6–8 of the sampling dates), O—often occurring (present in 3–5 of the sampling dates), R—rare (present in 1 or 2 the sampling dates).

3.2. Bottle-collected small zooplankton and eggs

Abundance of small copepods calculated from the water bottles samples was much higher than estimated from the net samples. Nauplii, rarely found in the net samples, were the most abundant group, followed by *Oithona* sp. and *Microsetella* sp. Noticeably lower numbers were found on the last two sampling days (Fig. 3, upper panel). The C-biomass of this group of plankton, about 0.2 g C m^{-2} between days -1 and 3 but declining thereafter, was similar to that of the net-collected mesozooplankton. While the copepod nauplii were most abundant among the “bottle” zooplankton, *Oithona* sp. dominated the biomass and was responsible for its decrease after day 5 (Fig. 3, lower panel). The concentration of copepod eggs followed a bell-shaped curve, reaching maximum around day 5 . It decreased again till day 7 but remained higher than the initial observations (Fig. 4).

3.3. Gut fullness of dominant zooplankton groups

Gut fullness of the primarily herbivorous copepods (*Neocalanus* spp., *Clausocalanus* spp., *Ctenocalanus* spp., *Calocalanus* spp.) gradually increased from the day before phosphorus addition (32%) to day 5 (82%), then decreased again to 31% on day 8 (Fig. 5, upper panel). Similar changes, although less pronounced, were observed in the group of omnivorous copepods. Feeding activity of plankton predators did not show considerable variations during our study (Fig. 5, upper panel).

Appendicularians (fine filter-feeders) always showed a high level of feeding activity, although there was a slight decrease on day 1 and 3 (Fig. 5, lower panel). On all other occasions, gut fullness was 90% and more.

Gut fullness of very abundant *Corycaeus* spp. was always low. A maximum fullness of 20% was observed on day 4 (Fig. 5, lower panel). Changes in the gut fullness of *Oncaea* spp. did not show any temporal trend. Contrary to these zooplankters, gut fullness of *Oithona* spp. gradually increased to a maximum 72% on May 22 before it subsequently decreased (Fig. 5, lower panel).

3.4. Suspended fecal pellet concentration

Concentration of suspended fecal pellets (FP) in the water column gradually increased from day -1

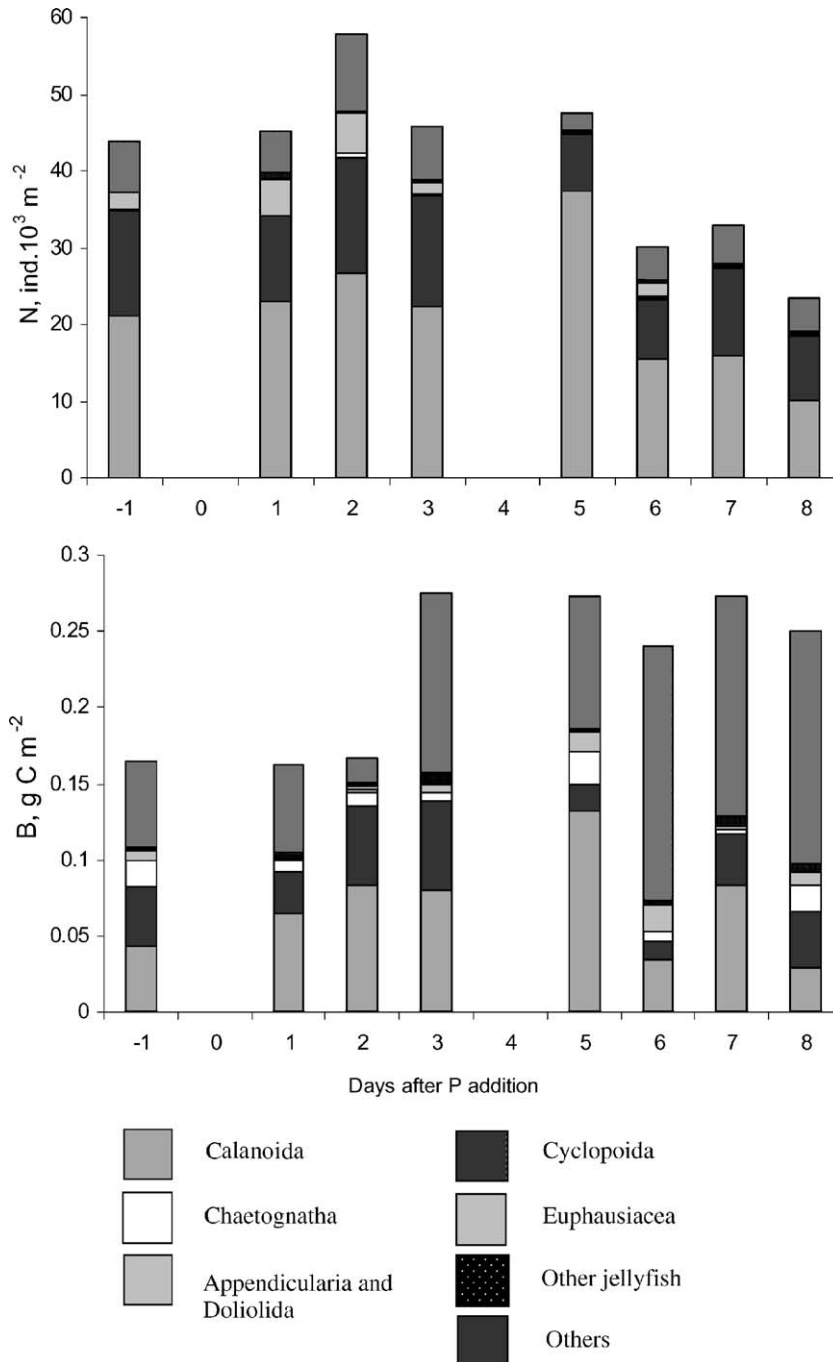


Fig. 2. Mesozooplankton abundance (ind. m⁻², upper panel) and biomass (g C m⁻², lower panel) in the upper 0–150 m layer in the center of the experimental P-enriched patch before (day –1) and after P release. Zooplankton groups distinguished: Calanoida, Cyclopoida, Chaetognatha, Euphausiacea, appendicularians and doliolids, other jellyfish (medusas and siphonophores), and “others” (Polychaeta, including *Tomopteris* sp., and Cladocera, Ostracoda, Pteropoda, Gastropoda, Heteropoda, Echinodermata, Amphipoda).

to a maximum on day 3. Thereafter it decreased, nevertheless remaining higher until the end of the study (Fig. 6). The three distinguished types of FP, cylindrical, oval, and filiform, are believed to be

produced accordingly by copepods, appendicularians and euphausiids together with decapods (Pasternak et al., 2000). Cylindrical pellets were by far the most important fraction of suspended FP,

with the exception of the first sampling day when oval pellets dominated, and the last day when the shares of cylindrical and filiform pellets were similar (Fig. 6). It is worth noting that the maximum concentration of FP was found not in the upper layers, but at 100–150 m depth during the whole period of observations (Fig. 7). This was particularly notable before P addition on day –1 and towards the end of the experiment on days 5–7 (Fig. 7). However, between days 1 and 3 the vertical distribution of FPC changed and FP abundance increased in the upper 50 m (Fig. 7), in particular for cylindrical FP. After day 5 the distribution of suspended FP was similar to that prior to the experiment (day –1).

Table 2
Percentage of different zooplankton groups (C-biomass) during the CYCLOPS study

Group	Range (%)	Mean
Calanoida	12–50	32
Cyclopoida + Poecilostomatoida	5–31	17
Gelatinous plankton	1–2	2
Chaetognatha	1–11	6
Euphausiacea	1–7	3
Others	10–59	40

“Others” include Cladocera, Ostracoda, Pteropoda, Gastropoda, Heteropoda, Echinodermata, Amphipoda, Polychaeta.

Table 3
Changes in the abundance of copepods (ind. 10^3 m^{-2}) during the course of the experiment

Copepods	–1	1	2	3	5	6	7	8
<i>Neocalanus gracilis</i> and <i>N. tenuicornis</i>	0.36	0.36	0.36	0.12	2.50	0.36	0.29	0
Small Calanoida (Paracalanidae, Pseudocalanidae)	15.12	18.24	21.24	16.80	12.60	10.56	12.10	7.60
<i>Mecynocera clausi</i>	0.24	1.68	1.68	1.08	20.00	2.52	0.58	0.76
Aetideidae	0.24	0.12	0	0.24	0.30	0.24	0.10	0.31
<i>Heterorhabdus</i> sp.	0	0	0	0.12	0.20	0.24	0.10	0
Scolecithricidae	0.72	0.48	1.08	0.72	0.30	0.60	0.29	0.16
<i>Pleuromamma gracilis</i>	0.24	0.12	0.12	0.12	0.10	0.01	0	0
<i>Lucicutia</i> sp.	0.72	0.60	0.6	0.72	0	0	0.19	0.16
<i>Metridia</i> sp.	0.96	0.12	0	0	0	0	0	0
<i>Haloptylus</i> sp.	0.36	0.48	0.60	1.20	0.90	0.61	1.54	0.76
<i>Candacia</i> sp.	0.24	0.12	0.84	0.12	0	0	0.10	0.15
<i>Euchirella</i> sp.	0	0.12	0	0	0.20	0.01	0.23	0.01
<i>Oithona</i> sp.	5.40	4.32	4.20	3.00	2.60	2.04	5.76	1.98
<i>Oncaea</i> sp.	1.92	1.44	1.08	2.28	0.90	0.84	1.06	0.46
<i>Corycaeus</i> sp.	6.48	5.16	9.60	9.12	3.80	4.80	4.51	5.93
Copepoda juv.	1.68	0.36	0.12	0.72	0.40	0.36	0.29	0.31
Total copepod abundance	34.92	33.97	41.66	36.72	44.80	23.19	27.17	18.56

Column headers indicate the day from P addition which took place on 17 May 2002 (= day 0).

3.5. Gut contents

The percentage of measurable items in the guts of omnivores was higher than in herbivores and carnivores. This could be expected because the primarily herbivorous copepods often consume smaller fine items such as nanoflagellates, dinoflagellates (many of them naked) and detritus. The latter group forages upon larger organisms that are usually severely disrupted in the guts and could not be measured. We paid more attention to the variation of gut contents of herbivores and omnivores.

Gut contents of herbivores and omnivores were dominated by an unidentified mass that could originate from flagellates, aloricate ciliates, athecate dinoflagellates or detritus. In small herbivores (*Clausocalanus*, *Ctenocalanus*, *Calocalanus*, appendicularians), small centric and, less often, pennate diatoms (maximum dimension 6–8 μm) were found, supplemented by larger phytoplankton in the guts of *Neocalanus* species (dinoflagellates of 10–16 μm), the silicoflagellate *Dictyocha speculum* (22 μm), and diatom *Rhizosolenia* sp. (50 μm) (Table 4). Remnants of the diatom *Ditylum brightwellii* were often found in the guts of both herbivores and omnivores, but only the terminal appendices of these cells could be distinguished. In the guts of omnivores, radiolarian remnants as well as larger centric diatoms (30–50 μm), dinoflagellates (16–22 μm) and chiti-

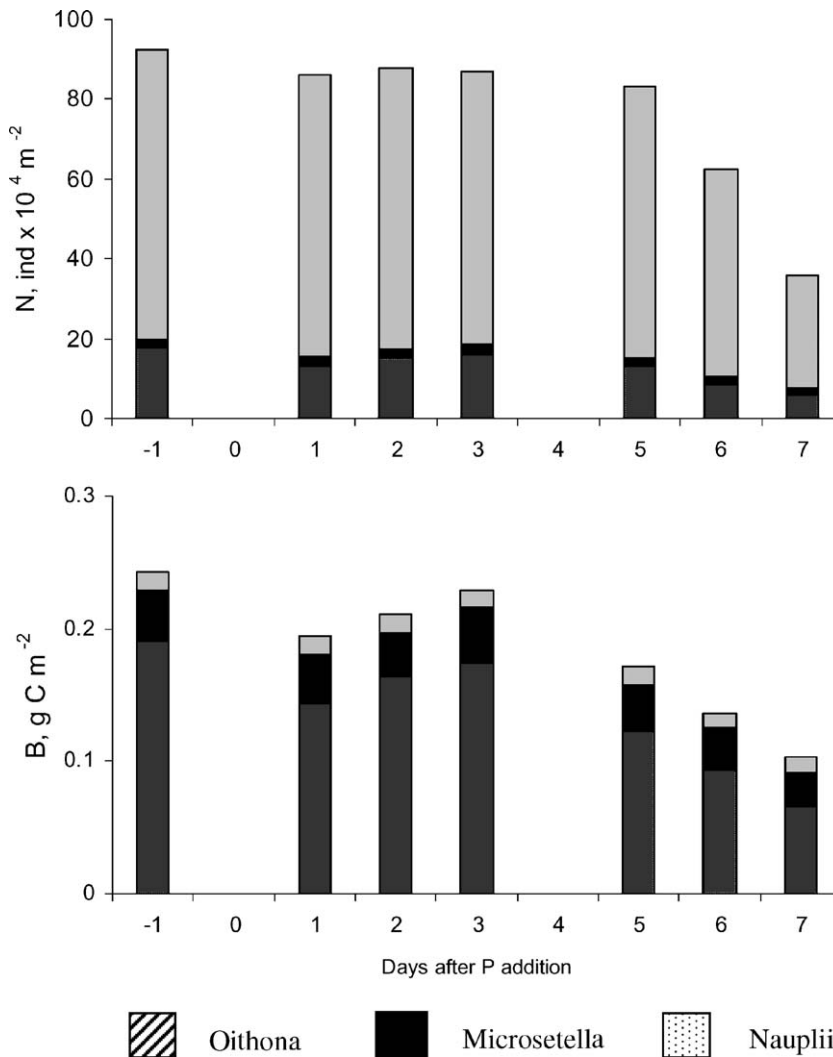


Fig. 3. Abundance of bottle-collected zooplankton (ind. m⁻², upper panel) and biomass (g C m⁻², lower panel) in the upper 150 m layer in the center of the experimental P-enriched patch before (day -1) and after P release.

nous parts and setae of metazoans were often observed (Table 5).

The proportion of unidentified mass in the herbivores was high and stable (around 80%) (Table 4). In omnivores it increased from 60% on day -1 to 74% on day 5, after which it decreased to 70% (Table 5). Diatoms constituted a steady small portion (1–4%) of the gut contents of herbivores (Table 4). Their share decreased in omnivores from 11% to 0% during the study period (Table 5). The abundance of dinoflagellates increased slightly by the end of observation period in herbivores and by day 2 in omnivores. Coccoliths were always present constituting a constant share in gut contents of herbivores (about 6–15%), and decreasing from

17% to 1% in omnivores. Other identified food groups (e.g. radiolarians, metazoans) were only occasionally found in herbivores, but constituted a noticeable portion of the diet of omnivores (Tables 4 and 5).

The gut content of carnivores consisted of an amorphous mass originating from the ingestion of metazoan prey with occasional crumpled chitinous parts (primarily in chaetognaths). No changes in the gut content were recognized during the course of the experiment.

In the guts of *Corycaeus* spp., only an unidentifiable mass was found. More variable gut contents were observed in *Oithona* spp. and, especially, *Oncaea* spp. They contained coccoliths, diatoms,

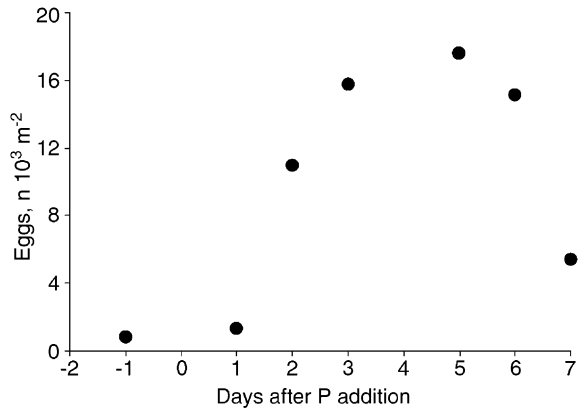


Fig. 4. Abundance of copepods eggs (ind. m⁻²) in the upper 150m layer in the center of the experimental P-enriched patch before (day -1) and after P release.

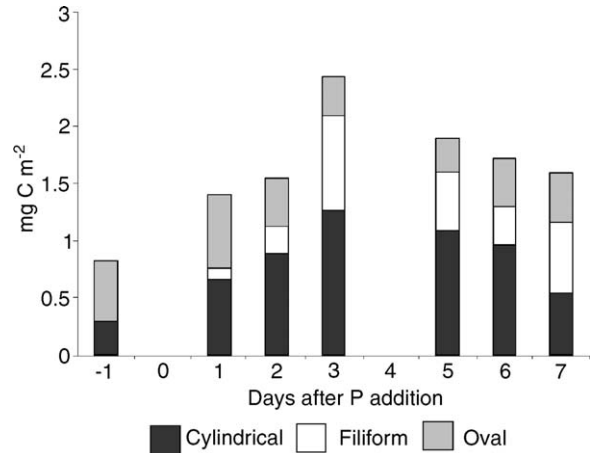


Fig. 6. Fecal pellet carbon in the upper 0–150 m layer (mg C m⁻²) in the center of the experimental P-enriched patch before (day -1) and after P release. Cylindrical, filiform and oval pellets are indicated.

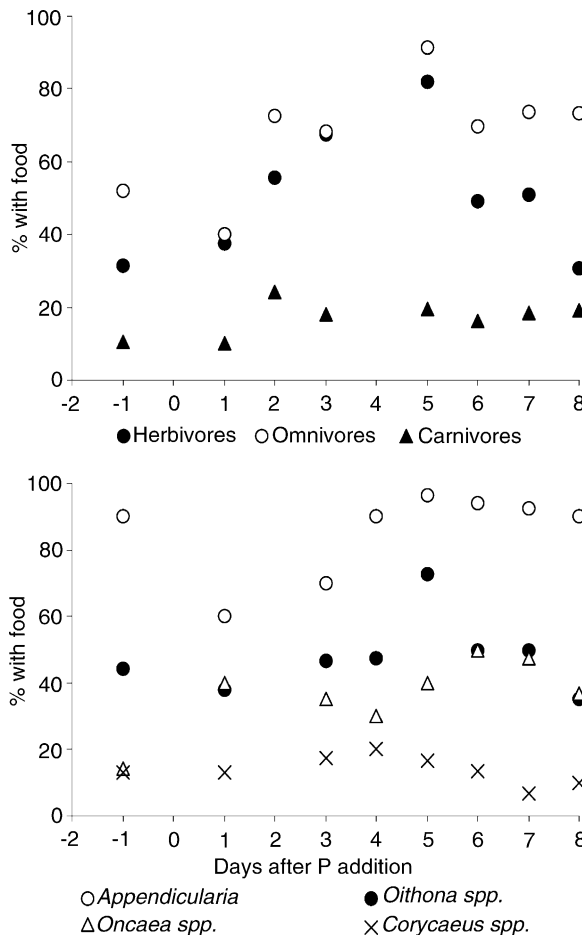


Fig. 5. Gut fullness of zooplankton estimated as percentage of animals with food in the guts in the center of the experimental P-enriched patch before (day -1) and after P release. Upper panel: herbivores, omnivores, and carnivores. Lower panel: selected groups—Appendicularia, *Oithona* sp., *Oncaea* sp., *Corycaeus* sp.

dinoflagellates, and, sometimes, eggs of metazoans with no discernable changes over the length of the investigation period. However, the proportion of unidentified mass (90–99%) dominated their gut contents on all sampling days.

4. Discussion

The zooplankton composition is in general agreement with the published data from the Eastern Mediterranean Sea (Delalo, 1966; Pasteur et al., 1976; Kovalev and Shmeleva, 1982; Pancucci-Papadopoulou et al., 1992; Mazzocchi et al., 1997; Siokou-Frangou et al., 1997, 1998; Uysal et al., 2002). Similarly to the previous studies, copepods comprised the most important group of zooplankton: 72–94% of total abundance in the present study, in comparison with 45–98% at different stations (Mazzocchi et al., 1997), 85–86% (Pasteur et al., 1976; Pancucci-Papadopoulou et al., 1992), more than 70% (Siokou-Frangou et al., 1998). The dominance of Calanoida also agrees with what was reported earlier, although “in some cases the Cyclopoida, represented by one or several species of *Corycaeus*, were dominant” (Pasteur et al., 1976). In all zooplankton studies of the region, *Clausocalanus furcatus* and *Oithona plumifera* were the most abundant species during the summer–autumn period (e.g., Siokou-Frangou et al., 1997), whereas more than one species of these genera are dominant in spring (Siokou-Frangou et al., 1998). The contribution of cyclopoids would have been even

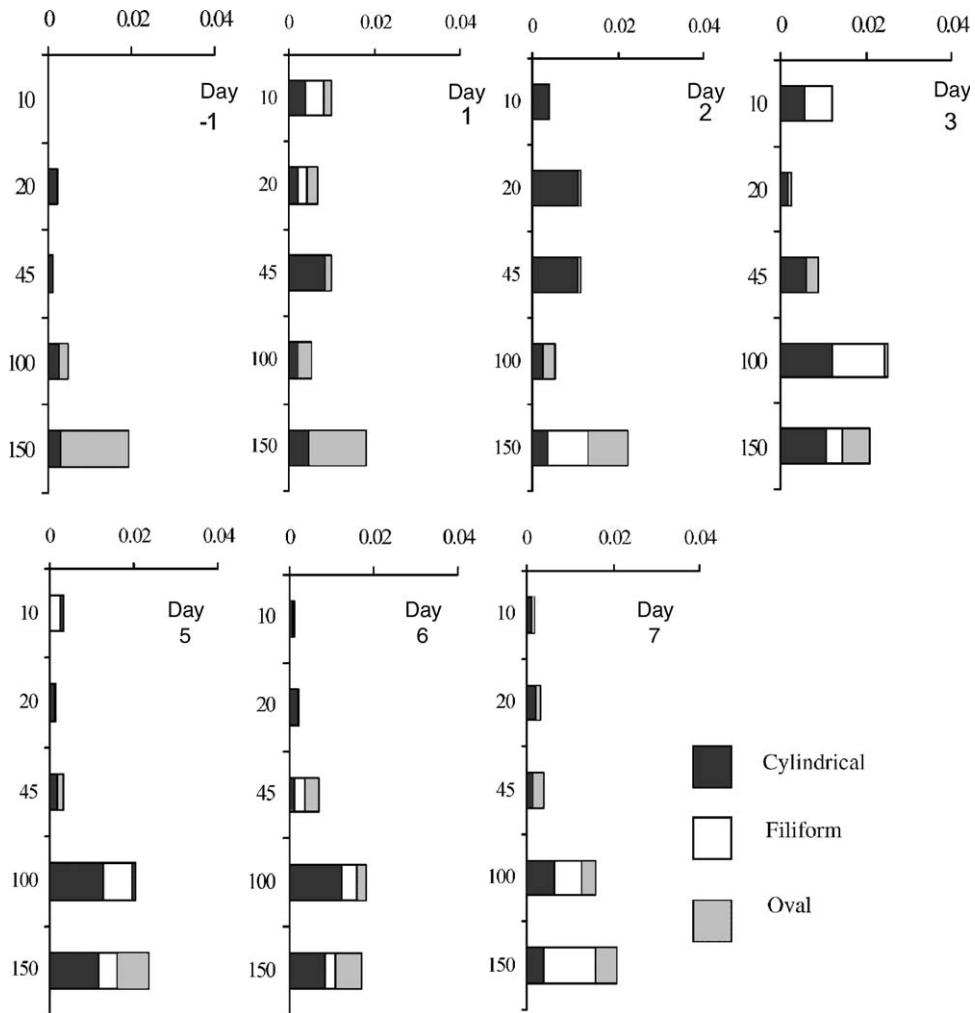


Fig. 7. Vertical distribution of three categories of fecal pellet (mg C m^{-3}) in the center of the P-enriched patch before (day -1) and after P release. Y-axis—depth, m. Cylindrical, filiform and oval pellets are indicated.

Table 4
Percentage of different food items in the guts of herbivores

Day after P addition	Unidentified mass	Diatoms	Dinoflagellates	Coccolithophorides	Silicoflagellates	Radiolaria	Metazoa
-1	82	4	3.5	8	1.2	1	0
1	80	1	4	14	1	0	0
2	82	2	3.5	12	0	0	0
3	82	3	2	11	0.5	1	0.3
5	77	2	5	14.6	0	1.7	0
6	78	3	12	6	0	0.5	0
7	82	1	10	7.2	0	0	0.4

more pronounced if a “bottle” rather than a netting technique would have been applied to sample zooplankton in previous studies (for a comparison of these two sampling techniques, see Pasternak

et al., 2000; Arashkevich et al., 2002). To our knowledge this is the first time that smaller copepods were adequately sampled in this region. Thus, zooplankton biomass in the eastern Mediter-

Table 5
Percentage of different food items in the guts of omnivores

Day after P addition	Unidentified mass	Diatoms	Dinoflagellates	Coccolithophorides	Silicoflagellates	Radiolaria	Metazoa
–1	60	7	8.6	17	0	2	5
2	60	11	10.8	16.6	0	0	1.6
5	74	4	3.6	5.4	0.4	14.4	1.8
7	70	0	1.7	0.8	0	11.8	15.7

ranean Sea could previously have been underestimated.

The total mesozooplankton abundance (160–390 ind. m⁻³), although somewhat higher in our study, is close to the 120 ind. m⁻³ reported previously for October–November in the Levantine basin (Siokou-Frangou et al., 1997). It is, however, about twice that reported for this area for the late March–early April period (Pancucci-Papadopoulou et al., 1992). According to Scotto di Carlo and Ianora (1983), Mediterranean zooplankton is characterized by two similar abundance maxima, one in early spring and one in autumn. The highest zooplankton displacement volume was obtained in May–June for the offshore Eastern Mediterranean (Pasteur et al., 1976). The present investigation seems to have taken place at a time close to the seasonal maximum of mesozooplankton abundance.

A slight increase in “net” copepod abundance and biomass was observed on days 2–5 after P addition, followed by a considerable decline during the last 3 days of the experiment. This decline is also obvious in the bottle-collected small zooplankton. However, it is hard to tell what reasons were responsible for these changes. It could be the patchy distribution of zooplankton, or some lateral migration. The high biomass of zooplankton during the last 3 days (despite a reduction in abundance) was due to a considerable number of the predatory (Kucheruk, personal communication) polychaete *Tomopteris* sp. that was not encountered in such abundance on the earlier days of the experiment. In a patch with a high concentration of *Tomopteris* sp. smaller zooplankton could be suppressed.

An increased abundance of fecal pellet carbon in the upper 50 m around day 3 was mainly due to cylindrical pellets, suggesting that feeding of copepods in the upper layers intensified. Gut content of both primarily herbivorous and omnivorous zooplankters increased until day 5, followed by a

gradual decrease (Fig. 5). There was also a certain delay between gut content of herbivores that increased very soon after the P addition and gut content of omnivores that increased somewhat later and then remained high throughout the experiment. The integrated FPC increased after P addition, reaching a maximum on day 3 and then, gradually decreasing. All these observations point to an increased feeding activity of zooplankton after P addition, suggesting that the concentration of their potential food could be higher than prior to addition. However, enrichment with P was not followed by increase of either primary production or chlorophyll *a* concentration (Psarra et al., 2005). Prior to the enrichment, phytoplankton abundance of the larger cells was dominated by coccolithophorids <15 µm in size, followed by dinoflagellates, and diatoms constituting only 8% of abundance (Psarra et al., 2005). At the end of the experiment, the relative proportion of coccolithophorids and dinoflagellates in the water was inverted. The proportion of diatoms remained at about 8% (Psarra et al., 2005). In the guts of herbivores, coccoliths and diatoms constituted a stable share throughout the course of the experiment. The proportion of dinoflagellates in the guts of herbivores increased towards the end of the observation period. In omnivores, the percentage of silicoflagellates and diatoms was reduced, coccolithophorids decreased towards the end of the experiment and, as it could be expected, the share of larger prey items, i.e., metazoans and radiolarians, was larger than in herbivores. Thus, gut contents of mesozooplankton mirror, to some extent, the subtle changes that occurred in ambient phytoplankton. At the same time, the proportion of unidentified mass dominated gut contents at all sampling dates. This suggests that the role of soft-bodied prey and detritus prevailed constantly over all other food sources during the experiment.

The microbial loop has been proposed as a second major pathway of energy and carbon flow in the pelagic food web (Pomeroy, 1974; Azam et al., 1983) as opposed to the classic grazing food chain (phytoplankton–copepods). In oligotrophic seas, the microbial loop is usually assumed to dominate over the classic food chain (Reckermann and Veldhuis, 1997; Thingstad and Rassoulzadegan, 1995; Caron et al., 1999; Van Wambeke et al., 1996). Copepods, the main component of mesozooplankton in oligotrophic seas, possess a poor ability to feed directly on bacteria and picoplankton, but are forced to rely on protozoans as a major food source or on episodic blooms of larger algae (Sommer et al., 2002).

Both phytoplankton and bacteria in the Mediterranean Sea are limited by the availability of phosphorus (Thingstad and Rassoulzadegan, 1995). The bacteria with their small size and favorable surface:volume ratio are supposed to have the highest affinity for dissolved phosphate (Thingstad and Rassoulzadegan, 1995) and could, therefore, outcompete phytoplankton. Although no increase in the abundance of bacteria was observed in our experiment, a considerable increase in bacterial activity was reported soon after nutrient enrichment (Pitta et al., 2005; Fonnes Flaten et al., 2005). Heterotrophic flagellates, ciliates, and then, copepods could have used an increased bacterial production. No changes were observed in heterotrophic flagellates that could have thrived on the increased bacterial production. This was probably due to the grazing pressure exerted by ciliates, whose abundance and biomass quickly and significantly increased (Pitta et al., 2005). Compared to copepods, ciliates show a very rapid numerical response to increased food availability in laboratory, as well as in mesocosms experiments (Olsson et al., 1992; Kivi et al., 1996; Nejstgaard et al., 1997, 2001; Pitta et al., 1998; Gismervik et al., 2002). Indeed, ciliate population was most abundant during the first 3 days after P addition (Pitta et al., 2005). By that time, it could provide an important source of food for mesozooplankton.

Based on the previous and present data, we can assume that phosphate enrichment in our study has strengthened the “microbial loop”. Gradual increase in copepod feeding activity demonstrated by an increase in animals with full guts and increased concentration of their fecal pellets, which was observed until day 5, could result from copepod enhanced grazing rate on ciliates. The dominance of

aloricate ciliates (Pitta et al., 2005) could partly be responsible for a high percentage of unidentified mass in the guts of copepods.

Ciliates are known to be preferred food for some copepods and to have a positive effect on egg production (Stoecker and Egloff, 1987; Wiadnyana and Rassoulzadegan, 1989). An increase of egg production by *Acartia* spp. after nutrient enrichment has been reported, although variation was high (Gismervik et al., 2002). A similar increase in egg concentration around days 3–6 was observed in the present study. This apparently points to the elevated food quality that the reproducing females were exposed to after the P addition. The ingestion and egg production of copepods are closely coupled. Gonad formation and maturation can be fuelled by internal energy reserves (previous feeding success), but major egg-laying activities are supposed to rely on current feeding conditions (e.g., Tande, 1982; Plourde and Runge, 1993; Hirche, 1996). Thus, egg production should be the result of interactions of two factors: (a) previous feeding success and (b) presently available food, or actual ingestion, which explains the relation between ingestion and egg production rate frequently observed (Marshall and Orr, 1952; Runge, 1985; Hirche, 1990, 1996; Hirche et al., 1997; Niehoff et al., 1999). In the present study, concentration of copepod eggs coincided with gut fullness trend in herbivorous and omnivorous copepods. However, this response was short-lived and not pronounced. It was not followed by a change in nauplii abundance, but then, all components of zooplankton community except *Tomopteris* sp. declined over the last 3 days of observation.

There was thus a rapid and conspicuous response of mesozooplankton to P addition in the eastern Mediterranean. The major portion of the added P was channeled not through autotrophs, but from bacteria through the microbial food web towards copepods. Almost no increase in the standing stock of food for mesozooplankton (except for an increase in ciliate abundance) was encountered, but stimulated zooplankton production was indicated by increased egg production, fecal pellet abundance and gut fullness of larger zooplankton forms.

The decline in zooplankton abundance observed at days 6–8 after enrichment, accompanied by a mass appearance of *Tomopteris* sp., could not be adequately explained with our set of data. The patchy spatial distribution is a well-known characteristic of zooplankton. With samples taken only

at one station (the center of the patch) once per day we cannot describe the extent of the phenomenon.

An alternative mechanism explaining the apparent increase in zooplankton feeding activity and egg production was suggested by Thingstad et al. (2005): P addition led to a change in food quality rather than food concentration. Both phytoplankton and bacteria rapidly consumed phosphate but phytoplankton, because of a lower than bacteria access to the pool of the next limiting element (N), soon became N-limited and was unable to grow. Thus, P-content of phytoplankton but not its abundance increased. Food enriched with P could trigger enhanced feeding and egg production of zooplankton. These two proposed mechanisms (microbial loop and “luxury consumption” of food enriched with P) do not exclude each other and both could be responsible for the observed changes in zooplankton feeding and egg production activity.

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References

- Arashkevich, E.G., Pasternak, A.F., 1986. Food size composition in the different trophic groups of zooplankton in the eastern Pacific. In: Vinogradov, M.E. (Ed.), *Frontal Zones of the South-Eastern Pacific Ocean: Biology, Physics, Chemistry*. Nauka, Moscow, pp. 247–256.
- Arashkevich, E., Wassmann, P., Pasternak, A., Wexels Riser, C., 2002. Seasonal and spatial variation in abundance, composition, and development of zooplankton community in the Barents Sea. *Journal of Marine Systems* 38, 125–145.
- Azam, F., Fenchel, T., Field, J.G., Meier-Rei, L.A., Thingstad, F., 1983. The ecological role of water column microbes in the sea. *Marine Ecology Progress Series* 10, 257–263.
- Berland, B.R., Bonin, D.J., Maestrini, S.Y., 1980. Azote ou phosphore? Considerations sur le “paradoxe nutritionelle” de la mer mediterrannee. *Oceanologica Acta* 3, 135–142.
- Berman, T., Azov, Y., Townsend, D.W., 1984a. Understandable oligotrophic oceans: can the eastern Mediterranean be a useful model? In: Holm-Hansen, O., Bolis, L., Gilles, R. (Eds.), *Marine Phytoplankton and Productivity*. Springer, Berlin, pp. 101–112.
- Berman, T., Townsend, D.W., El-Sayed, S.Z., Trees, C.C., Azov, Y., 1984b. Optical transparency, chlorophyll and primary production in the Eastern Mediterranean near the Israeli coast. *Oceanologica Acta* 7 (3), 367–371.
- Böttger-Schnack, R., 1997. Vertical structure of small metazoan plankton, especially non-calanoid copepods. II. Deep Eastern Mediterranean (Levantine Sea). *Oceanologica Acta* 20, 399–419.
- Boyd, P.W., Watson, A.J., Law, C.S., Abraham, E.R., Trull, T., Murdoch, R., Bakker, D.C.E., Bowie, A.R., Buesseler, K.O., Chang, H., Charette, M., Croot, P., Downing, K., Frew, R., Gall, M., Hadfield, M., Hall, J., Harvey, M., Jameson, G., LaRoche, J., Liddicoat, M., Ling, R., Maldonado, M.T., McKay, R.M., Nodder, S., Pickmere, S., Pridmore, R., Rintoul, S., Safi, K., Sutton, P., Strzepek, R., Tanneberger, K., Turner, S., Waite, A., Zeldis, J., 2000. A mesoscale phytoplankton bloom in the polar Southern Ocean stimulated by iron fertilization. *Nature* 407, 695–702.
- Calbet, A., Landry, M.R., Scheinberg, R.D., 2000. Copepod grazing in a subtropical bay: species-specific responses to a midsummer increase in nanoplankton standing stock. *Marine Ecology-Progress Series* 193, 75–84.
- Caron, D.A., Peele, E.R., Lim, E.L., Dennett, M.R., 1999. Picoplankton and nanoplankton and their trophic coupling in surface waters of the Sargasso Sea south of Bermuda. *Limnology and Oceanography* 44, 259–272.
- Coale, K.H., Johnson, K.S., Fitzwater, S.E., Gordon, R.M., Tanner, S., Chavez, F.P., Ferioli, L., Sakamoto, C., Rogers, P., Millero, F., Steinberg, P., Nightingale, P., Cooper, D., Cochlan, W.P., Landry, M.R., Constantinou, J., Rollwagen, G., Trasvina, A., Kudela, R., 1996. A massive phytoplankton bloom induced by an ecosystem-scale iron fertilization experiment in the equatorial Pacific Ocean. *Nature* 383, 495–501.
- Delalo, E., 1966. Zooplankton in eastern part of the Mediterranean Sea (the seas of Sirt and Levant). In: *Investigations of Plankton in the South Seas*, vol. 7. Science, Moscow, pp. 62–81 (in Russian).
- Deibel, D., Turner, J.T., 1985. Zooplankton feeding ecology: contents of fecal pellets of the appendicularian *Oikopleura vanhoeffeni*. *Marine Ecology-Progress Series* 27, 67–78.
- Eidler, L., 1979. Recommendations on Methods for Marine Biological Studies in the Baltic Sea. Phytoplankton and Chlorophyll. The Baltic Marine Biologists Publication No. 5. Gotub, Malmö, 32pp.
- Fonnes Flaten, G.A., Skjoldal, E.F., Krom, M.D., Law, C., Mantoura, R.F.C., Pitta, P., Psarra, S., Tanaka, T., Tselepidis, A., Woodward, E.M.S., Zohary, T., Thingstad, T.F., 2005. Studies of the microbial P-cycle during a Lagrangian phosphate-addition experiment in the eastern Mediterranean. *Deep-Sea Research II*, this volume [doi:10.1016/j.dsr2.2005.08.010].
- Gismervik, I., Olsen, Y., Vadsstein, O., 2002. Micro- and mesoplankton response to enhanced nutrient input—a mesocosm study. *Hydrobiologia* 484, 75–87.
- Hirche, H.-J., 1990. Egg production of *Calanus finmarchicus* at low temperature. *Mar. Biol.* 106, 53–58.
- Hirche, H.-J., 1996. The reproductive biology of the marine copepod, *Calanus finmarchicus*—a review. *Ophelia* 44, 111–128.

- Hirche, H.-J., Meyer, U., Niehoff, B., 1997. Egg production of *Calanus finmarchicus*: effect of temperature, food and season. *Mar. Biol.* 127, 609–620.
- Kanaeva, I.P., 1962. Average weight of Copepoda from the central and northern Atlantic, the Norwegian and Greenland Seas. *Trudy VNIRO* 46, 253–288 (in Russian).
- Kivi, K., Kuosa, H., Taskanen, S., 1996. An experimental study on the role of crustacean and microprotozoan grazers in the planktonic food web. *Limnology and Oceanography* 38, 893–905.
- Kovalev, A.V., Shmeleva, A.A., 1982. Fauna of Copepoda in the Mediterranean. *Ekologiya Morya* 8, 82–87 (in Russian).
- Krom, M.D., Woodward, E.M.S., Herut, B., Kress, N., Carbo, P., Mantoura, R.F.C., Spyres, G., Thingstad T.F., Wassmann, P., Wexels-Riser, C., Kitidis, V., Law, C.S., Zodiatis, G., Zohary, T., 2005. Nutrient cycling in the south east Levantine basin of the Eastern Mediterranean: results from a phosphate starved system. *Deep Sea Research*, this volume [doi:10.1016/j.dsr2.2005.08.009].
- Law, C.S., Abraham, E.R., Woodward, E.M.S., Liddicoat, M.I., Fileman, T.W., Thingstad, T.F., Kitidis, V., Zohary, T., 2005. The fate of phosphate in a Lagrangian enrichment experiment in the Eastern Mediterranean. *Deep Sea Research II*, this volume [doi:10.1016/j.dsr2.2005.08.017].
- Margalef, R., 1984. *Western Mediterranean*. Pergamon Press, New York, 353pp.
- Marshall, S.M., Orr, A.P., 1952. On the biology of *Calanus finmarchicus*. VII. Factors affecting egg production. *Journal of Marine Biological Association of the United Kingdom* 30, 527–547.
- Martin, J.H., Coale, K.H., Johnson, K.S., Fitzwater, S.E., Gordon, R.M., Tanner, S.J., Hunter, C.H., Elrod, V.A., Nowicki, J.L., Coley, T.L., Barber, R.T., Lindley, S., Watson, A.J., Van Scoy, K., Law, C.S., Liddicoat, M.I., Ling, R., Stanton, T., Stockel, J., Collins, C., Anderson, A., Bidigare, R., Ondrusek, M., Latasa, M., Millero, F.J., Lee, K., Yao, W., Zhang, J.Z., Friederich, G., Sakamoto, C., Chavez, F., Buck, K., Kolber, Z., Greene, R., Falkowski, P., Chisholm, S.W., Hoge, F., Swift, R., Yungel, J., Turner, S., Nightingale, P., Hatton, A., Liss, P., Tindale, N.W., 1994. Testing the iron hypothesis in ecosystems of the equatorial Pacific Ocean. *Nature* 371, 123–129.
- Mauchline, J., 1998. The biology of calanoid copepods. *Advances in Marine Biology* 33, 1–710.
- Mazzocchi, M.G., Christou, E.D., Fragopoulou, N., Siokou-Frangou, I., 1997. Mesozooplankton distribution from Sicily to Cyprus (Eastern Mediterranean): I. General aspects. *Oceanologica Acta* 20 (3), 521–535.
- Metz, C., Schnack-Schiel, S.B., 1995. Observations on carnivorous feeding in Antarctic calanoid copepods. *Marine Ecology-Progress Series* 129, 71–75.
- Nejstgaard, J.C., Gismervik, I., Solberg, P., 1997. Feeding and reproduction by *Calanus finmarchicus*, and microzooplankton grazing during blooms of diatoms and the coccolithophore *Emiliania huxleyi*. *Marine Ecology-Progress Series* 147, 197–217.
- Nejstgaard, J.C., Hygum, B.H., Naustvoll, L.-J., Bamstedt, U., 2001. Zooplankton growth, diet and reproduction success compared in simultaneous diatom- and flagellate-microzooplankton-dominated plankton blooms. *Marine Ecology-Progress Series* 221, 77–91.
- Niehoff, B., Klenke, U., Hirche, H.-J., Irigoien, X., Head, R., Harris, R., 1999. A high frequency time series at Weathership M, Norwegian Sea, during the 1997 spring bloom: the reproductive biology of *Calanus finmarchicus*. *Marine Ecology-Progress Series* 176, 81–92.
- Olsson, P., Graneli, E., Carlsson, P., Abreu, P., 1992. Structuring of a postspring phytoplankton community by manipulation of trophic interactions. *Journal of Experimental Marine Biology and Ecology* 158, 249–266.
- Paffenhöfer, G.-A., Mazzocchi, M.G., 2002. On some aspects of the behaviour of *Oithona plumifera* (Copepoda: Cyclopoida). *Journal of Plankton Research* 24, 129–135.
- Pancucci-Papadopoulou, M.-A., Siokou-Frangou, I., Theocharis, A., Georgopoulos, D., 1992. Zooplankton vertical distribution in relation to the hydrology in the NW Levantine and the SE Aegean seas (spring 1986). *Oceanologica Acta* 15, 365–381.
- Pasternak, A.F., 1984. Feeding of copepods of genus *Oncaea* (Cyclopoida) in the southeastern Pacific Ocean. *Oceanologia* 24, 609–612.
- Pasternak, A., Arashkevich, E., Wexels Riser, C., Ratkova, T., Wassmann, P., 2000. Seasonal variation in zooplankton and suspended faecal pellets in the subarctic Norwegian Balsfjorden, in 1996. *Sarsia* 85, 439–452.
- Pasteur, R., Berdugo, V., Kimor, B., 1976. The abundance, composition and seasonal distribution of epizooplankton in coastal and offshore waters of the Eastern Mediterranean. *Acta Adriatica* 18 (4), 55–80.
- Pitta, P., Giannakourou, A., Divanach, P., Kentouri, M., 1998. Planktonic food web in marine mesocosms in the Eastern Mediterranean: bottom-up or top-down regulation? *Hydrobiologia* 363, 97–105.
- Pitta, P., Stambler, N., Tanaka, T., Zohary, T., Tselepidis, A., Rassoulzadegan, F., 2005. Biological response to P addition in the Eastern Mediterranean Sea. A race against time in the microbial side. *Deep Sea Research II*, this volume [doi:10.1016/j.dsr2.2005.08.012].
- Plourde, S., Runge, J.A., 1993. Reproduction of the planktonic copepod *Calanus finmarchicus* in the lower St. Lawrence Estuary—relation to the cycle of phytoplankton production and evidence for a Calanus pump. *Marine Ecology-Progress Series* 102, 217–227.
- Pomeroy, L.R., 1974. The ocean foodweb, a changing paradigm. *BioScience* 24, 499–504.
- Psarra, S., Zohary, T., Krom, M., Mantoura, F., Polychronaki, T., Stambler, N., Tanaka, T., Tselepidis, A., Thingstad, T.F., 2005. Phytoplankton response to a Lagrangian phosphate addition in the Levantine Sea (Eastern Mediterranean). *Deep Sea Research II*, this volume [doi:10.1016/j.dsr2.2005.09.002].
- Reckermann, M., Veldhuis, M.J.W., 1997. Trophic interactions between picophytoplankton and micro- and nanozooplankton in the western Arabian Sea during the NE monsoon 1993. *Aquatic Microbial Ecology* 12, 263–273.
- Riebesell, U., Reigstad, M., Wassmann, P., Noji, T., Passow, U., 1995. On the trophic fate of *Phaeocystis pouchetii* (Hariot): VI. Significance of *Phaeocystis*-derived mucus for vertical flux. *Netherlands Journal of Sea Research* 33, 193–203.
- Runge, J.A., 1985. Egg production rates of *Calanus finmarchicus* in the sea of Nova Scotia. *Archiv für Hydrobiologie (Beih. Ergebn. Limnol.)* 21, 33–40.
- Scotto di Carlo, B., Ianora, A., 1983. Standing stocks and species composition of Mediterranean zooplankton. In: Hopkins, T.S.,

- Leftic, L., Morcos, S. (Eds.), Quantitative Analysis and Simulation of Mediterranean Coastal Ecosystems: The Gulf of Naples, a Case Study. UNESCO Reports on Marine Science 20, 59–69.
- Siokou-Frangou, I., Christou, E.D., Fragopoulou, N., Mazzocchi, M.G., 1997. Mesozooplankton distribution from Sicily to Cyprus (Eastern Mediterranean): II. Copepod assemblages. *Oceanologica Acta* 20 (3), 537–548.
- Siokou-Frangou, I., Gotsis-Skretas, O., Christou, E.D., Pagou, K., 1998. Plankton characteristics in the Aegean, Ionian and NW Levantine Seas. In: Malanotte-Rizzoli, P., Eremeev, V.N. (Eds.), *The Eastern Mediterranean as a Laboratory Basin for the Assessment of Contrasting Ecosystems*, NATO Science Series, Series 2, vol. 51. Kluwer Academic Publishers, Dordrecht, pp. 205–223.
- Sommer, U., Berninger, U.G., Böttger-Schnack, R., Cornils, A., Hagen, W., Hansen, T., Al-Najar, T., Post, A.F., Schnack-Schiel, S.B., Stibor, H., Stubling, D., Wickham, S., 2002. Grazing during early spring in the Gulf of Aqaba and the northern Red Sea. *Marine Ecology-Progress Series* 239, 251–261.
- Stoecker, D.K., Egloff, D.A., 1987. Predation by *Acartia tonsa* on planktonic ciliates and rotifers. *Journal of Experimental Marine Biology and Ecology* 110, 53–68.
- Sur, H.I., Ozsoy, E., Unluata, U., 1992. Simultaneous deep and intermediate convection in the Northern Levantine Sea, winter 1992. *Oceanologica Acta* 16, 33–43.
- Tande, K.S., 1982. Ecological investigation on the zooplankton community of Balsfjorden, northern Norway: general life cycles, and variations in body weight and body content of carbon and nitrogen related to overwintering and reproduction in the copepod *Calanus finmarchicus* (Gunnerus). *Journal of Experimental Marine Biology and Ecology* 62, 129–142.
- Thingstad, T.F., Rassoulzadegan, F., 1995. Nutrient limitations, microbial food webs, and “biological C-pumps”: suggested interactions in a P-limited Mediterranean. *Marine Ecology-Progress Series* 117, 299–306.
- Thingstad, T.F., Krom, M.D., Mantoura, R.F.C., Flaten, G.A.F., Groom, S., Herut, B., Kress, N., Law, C.S., Pasternak, A., Pitta, P., Psarra, S., Rasoulzadegan, F., Tanaka, T., Tselepidis, A., Wassmann, P., Woodward, E.M.S., Wexels Riser, C., Zodiatis, G., Zohary, T., 2005. Nature of phosphorus limitation in the ultraoligotrophic Eastern Mediterranean. *Science* 309, 1068–1071.
- Turner, J.T., 1986. Zooplankton feeding ecology: contents of fecal pellets of the cyclopoid copepods *Oncaea venusta*, *Corycaeus amazonicus*, *Oithona plumifera*, and *O. simplex* from the Northern Gulf of Mexico. *Marine Ecology-Pubblicazioni della Stazione Zoologica di Napoli I* 7, 289–302.
- Uysal, Z., Kideys, A.E., Shmeleva, A., Zagorodnyaya, A., Gubanov, A.D., 2002. Checklist of copepods (Calanoida and Podoplea) from the northern Levantine basin shelf waters. *Hydrobiologia* 482, 15–21.
- Van Wambeke, F., Christaki, U., Gaudy, R., 1996. Carbon fluxes from the microbial food web to mesozooplankton. An approach in the surface layer of a pelagic area (NW Mediterranean Sea). *Oceanologica Acta* 19, 57–66.
- Vinogradov, M.E., Shushkina, E.A., 1987. Functioning of Plankton Communities in Epipelagic Zone of the Ocean. Nauka, Moscow, 240pp. (in Russian).
- Wiadnyana, N.N., Rassoulzadegan, F., 1989. Selective feeding of *Acartia clausi* and *Centropages typicus* on microzooplankton. *Marine Ecology-Progress Series* 53, 37–45.