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Nutrient Dynamics Across the Israeli Coastal shelf: an Unusual Oligotrophic Coastal System

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Abstract:

The nutrient dynamics and biogeochemical properties of the Pelagic Eastern Mediterranean (EMS), an inland sea with many of the characteristics of a mid-ocean gyre, has been well studied. By contrast there are few studies designed to understand these processes on the coastal shelves of the EMS. In this study the nutrient dynamics were determined using ultra-sensitive analytical procedures together with Primary Productivity (PP) and Chlorophyll across the Israeli Coastal shelf (ICS). This includes 12 monthly cruises over a seasonal cycle at an outer shelf station and several transects from the coast to 100 m depth. Sample preservation tests were carried out for nutrients at the ultra-low concentrations found on the ICS, which found that filtered fresh samples were optimal while confirming that using unfiltered frozen samples gave results for Dissolved Inorganic Phosphorus (DIP) that were too high and NO₃⁻ and NO₂⁻ (N&N) were too low. The extra DIP released from frozen unfiltered samples may be due

to DIP stored in the periplasm of cyano- and other bacteria (Kamennaya et al., 2020). Nutrient data for the ICS showed moderate concentrations of N&N (~300-500 nM) throughout the water column in winter, which decreased to less than 50 nM in mid-late summer. DIP was depleted (<10nM) throughout the year. Net PP at the outer shelf station (120 m) was 30 gC m² y⁻¹. The seasonality and concentration of nutrient concentrations and Net PP as well as the observed seasonal signal of Chlorophyll from remote sensing were similar to that found in the pelagic EMS. The ICS is ultra-oligotrophic and is very different from the eutrophied coastal shelves found in many locations globally because of the unusual anti-estuarine circulation.

Keywords:

Nutrient Dynamics, Coastal Shelf, Seasonal Nitrate Depletion, Phosphate Depletion, Oligotrophic Shelf, Nitrogen Budget

1. Introduction:

The Eastern Mediterranean (EMS) is a highly unusual inland sea which has many characteristics of an ocean gyre (Powley et al., 2017). It has been used as a natural laboratory for globally important biogeochemical processes particularly related to P depleted oceanic systems (Krom et al., 1991). While there has been considerable research to understand nutrient cycling and biogeochemical changes in the pelagic Eastern Mediterranean sea (EMS) (e.g. Ben Ezra et al., 2021; Djaoudi et al., 2018; Kress and Herut, 2001; Powley et al., 2017; Pujo-Pay et al., 2011; Thingstad et al., 2005), there have been very few studies to understand controls on nutrient cycling on EMS coastal shelves in general (Balkis, 2009; Doğan-Sağlamtimur and Tuğrul, 2004; Ignatiades et al., 2002; Ounissi et al., 2018; Psarra et al., 2000; Souvermezoglou et al., 2014; Zaafrane et al., 2019) and the Israeli coastal shelf (ICS) in particular (Berman et al., 1986; Christensen et al., 1988; Townsend et al., 1988). Most of the limited studies which do exist on the EMS coastal shelves, have examined the nature and magnitude of specific point sources of pollution such as fish cages, river outflows (Kress and Herut, 1998; Varkitzi et al., 2018) or factory and/or sewage outfalls (Rekik et al., 2020) or to set

eutrophication standards for sections of the coastal shelf (Kress et al., 2019; Simboursa et al., 2014).

In most parts of the global ocean, the coastal zone is drastically different from the pelagic offshore. Typically, the coastal zone has higher levels of dissolved nutrient supply and concentration, which in turn results in high levels of primary productivity often to the level of eutrophication (e.g. Blog et al. 2009; Berner and Berner 2012 and many others). The nutrients are derived from adjacent rivers discharging natural and anthropogenically derived nutrients, atmospheric inputs and nutrients recycled from labile organic matter deposited in the underlying sediments, which are shallow enough to be in direct contact with overlying biologically active photic zone. There have been a number of studies of nutrient distribution in the ICS, mainly restricted to shallow water (often less than 15-20 m) generally associated with monitoring studies at pollution “hot spots” (Rahav et al. 2018, 2020; Kress et al. 2019 and others). These studies and the more limited studies from the outer ICS (Azov, 1986; Berman et al., 1984; Christensen et al., 1988; Townsend et al., 1988) suggest that the ICS is very different from this global norm in many important characteristics.

In this study we have carried out seasonal and spatial sampling of the water column at an outer shelf station (THEMO1) and in transects across the ICS, to understand the key changes in nutrient concentration and how they relate to biogeochemical characteristics such as chlorophyll-a and primary productivity across the shelf. We aimed to determine to what extent these processes are similar and/or different from the EMS pelagic system and from coastal shelf systems elsewhere. In order to obtain robust measurements of inorganic nutrients at the low levels found in the ICS, we first carried out a series of sample preservation experiments on ICS and EMS.

2. Sampling and methods:

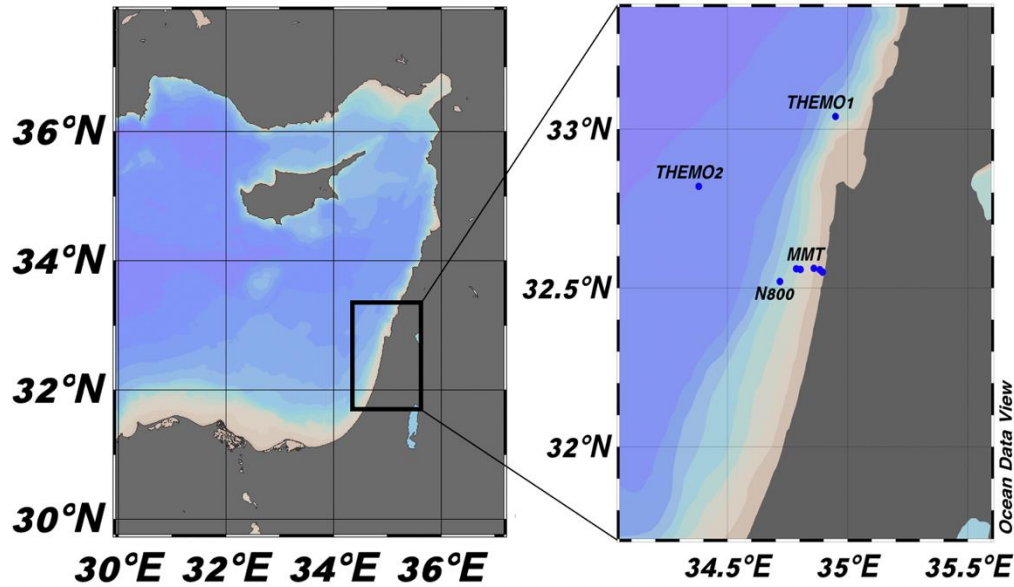


Figure 1: Location of sampling stations across the Israeli coastal shelf in the S.E. Levantine basin of the Eastern Mediterranean Sea. Station THEMO1, the outer coastal shelf station, was at a bottom depth of 135 m. The ICS was sampled in a transect from 10 m to 100 m bottom depth off the coast of Maagan Michael. In addition THEMO2, at a bottom depth of 1450 m, was the pelagic station used for comparative purposes, and N800, was the pelagic station used during the preservation experiment. Isobaths are represented by colors; 10-30 m bottom depth in pink, 30-85 m bottom depth in light yellow, 85-150 m in light blue, Darker shades of blue for over 150 m bottom depth.

2.1 Sampling and analysis:

During monthly cruises from February 2018 until January 2019, samples were collected close to the THEMO1 mooring between midnight and 3AM on board the R/V Mediterranean Explorer or R/V Bat Galim, at a depth of 135 m bottom depth; our sampling station at the edge of the ICS (see Supplementary Files for our definition of the extent of the ICS). These samples are compared to data from a pelagic station at a depth of 1450 m (THEMO2), collected from midday to late afternoon on the same day (Ben Ezra et al., 2021; Reich et al., 2022). In addition, a series of cruises were carried out in a transect off Maagan Michael (MMT; Figure 1) using the R/V Mediterranean Explorer. Samples were taken at 10, 25, 45, 70 and 100 m bottom depth stations on most cruises on Feb 20th, May 29th, Sept 12th and Nov 28th 2018. In all cases the samples were collected using a Seabird carousel system with 12 or 13 Niskin bottles.

A set of samples for the preservation experiment were taken in February 2021. 3 samples (6 replicates) were sampled from the N800 pelagic station (832 m bottom depth) at depths of 10, 50 and 100 m (Figure 1) and 3 samples (6 replicates) were taken from the MMT coastal transect (MMT_100; bottom depth of 100 m), at depths of 10, 50 and 100 m.

Nutrient samples were collected in acid washed 500 ml plastic containers and immediately filtered through 0.22 μ m Nalgene rapid-flow filter units. The first two filtrates were discarded and the final samples for filtered fresh ($n = 6$) were collected in new 50 ml falcon tubes and stored in 4°C in racks. The samples were transported to the lab at Sdot Yam and analyzed for dissolved nutrients within 12-15 hours of sampling.

For the preservation experiments, in addition to filtered fresh samples analyzed within 12-15 hours, a set of filtered samples ($n=6$) in new 50 ml falcon tubes were placed immediately in -20°C freezer in racks. A further set of unfiltered samples ($n = 6$) were also collected in 50 ml falcon tubes and put immediately into the freezer in racks at -20°C. The frozen samples were stored at -20°C for 2 to 3 weeks. They were thawed in a 37°C water bath and shaken thoroughly prior to analysis.

2.1.1. Sample Preservation experiments:

The results of the sample preservation experiments are plotted in Figure 2 and shown in detail in Table S2. The statistical significance of the data in the preservation experiments was assessed using 2 sample paired T-test (Hammer et al., 2001). The results from the filtered frozen samples and the unfiltered frozen samples were compared to the fresh filtered samples analyzed with 12-15 hours of collection (Ben Ezra et al., 2021).

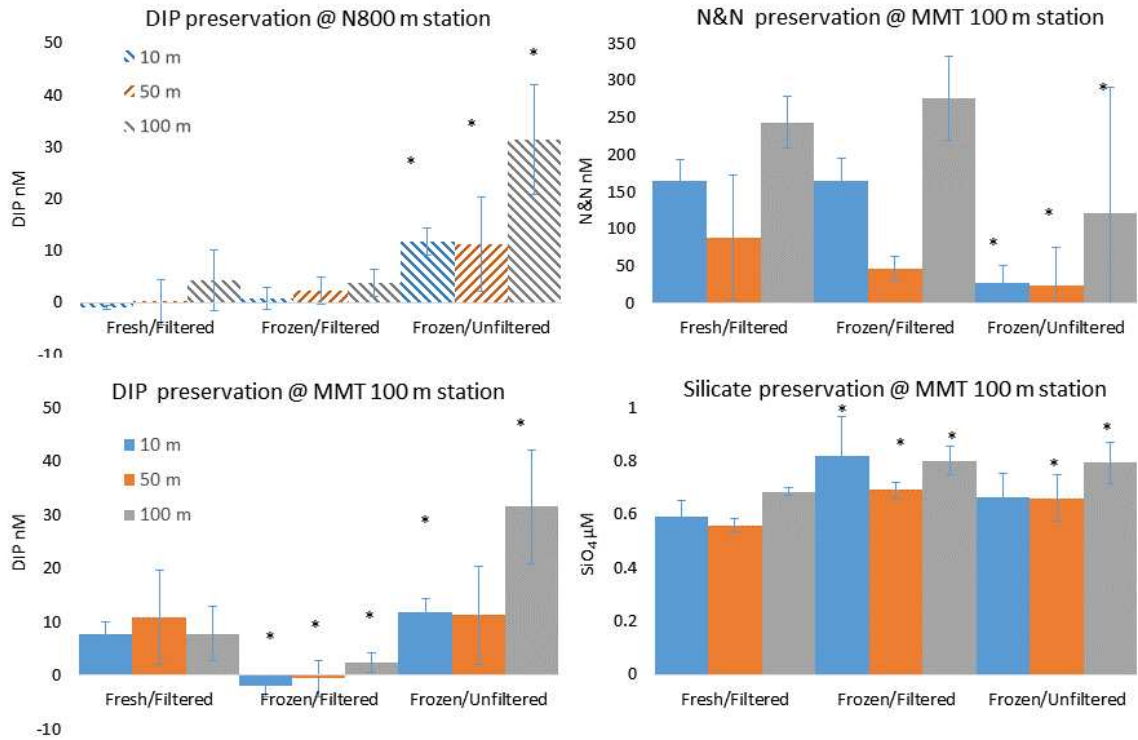


Figure 2: Figure showing the mean ± 1 s.d. of fresh filtered samples, frozen filtered samples and frozen unfiltered samples collected at an N800 pelagic station at a depth of 10m, 50m & 100m (3 samples & 6 replicates) and at the 100m station on the MMT at a depth of 10m, 50m and 100m (MMT; 3 samples & 6 replicates). The samples marked with asterisk are statistically significantly different from the corresponding filtered fresh samples (2 sample paired T-test, $p < 0.05$).

2.1.1.a Filtered frozen vs filtered fresh samples:

In the samples collected from the pelagic station, the frozen filtered sample DIP values were not statistically different from the fresh filtered (i.e. good preservation). Even for the samples collected from the MMT stations, the filtered frozen samples were only a few nanomoles lower than the filtered fresh samples and as long as differences of $< 10 \text{ nM}$ are not being interpreted as important, this preservation technique was considered acceptable. Frozen filtered also gave adequate results for silicate and N&N (adequate preservation but only if used to interpret relatively large changes ($< 50 \text{ nM}$ for N&N & $< 15\%$ for silicate)). This method (Filtered frozen samples) has been used previously for Mediterranean surface samples by Pulido-Villena et al. (2010) and others and is used in our lab as a potential back up if there were problems with the fresh filtered samples on the day when analysis was carried out.

2.1.1.b Unfiltered frozen vs filtered fresh samples:

By contrast, the unfiltered frozen samples gave values for DIP which were consistently significantly higher and for N&N were significantly lower than filtered fresh samples (Figure 2). This agrees with the results presented previously during the CYCLOPS addition experiment which concluded that this method of preservation was only acceptable for samples with values of >400nM N&N and >50 nM DIP, (Krom et al., 2005). Thus unfiltered frozen samples works for samples below the nutricline in the EMS. This is particularly problematic when Nitrate:Phosphate ratios are used to identify the limiting nutrient within the photic zone (e.g. Herut et al., 2000; Rahav et al., 2018).

It is hypothesized that the reason for the higher DIP values with unfiltered frozen samples for DIP, is the presence of 'luxury' consumption and storage of phosphate in the periplasm of cyano and other bacteria (e.g. SAR-11) as has been found in P depleted areas of the N.Atlantic (Kamennaya et al., 2020; Zubkov et al., 2015).

2.1.2. Chemical analysis of dissolved nutrients:

Dissolved nutrients were determined using a 4 channel SEAL AA-3 autoanalyzer. In order to minimize cross contamination in the laboratory, ammonium was analysed first, using an automated *o*-phthaltaldehyde (OPA) fluorescence method (SEAL Analytical, 2011a). Samples were placed in the sample trays and only opened immediately before the sample probe took the sample. The baseline used for ammonium determination was freshly prepared ultrapure (type 1; Synergy UV, by Merck; MQ) water. The next parameters to be determined were dissolved Nitrate & Nitrite (N&N) and Silicate. The methods used were Cd reduction for N&N and an oxalic acid/molybdate blue method for silicate (SEAL Analytical, 2011b). The baseline used for these determinations was MQ water. Finally a 3rd run was carried out using an ultra-low level phosphate method involving using a 100 cm long flow cell (LWCC) and molybdate blue determination based on Murphy and Riley (1962). The blank used for phosphate determination was surface open-sea water, whose DIP value was determined by either a previous experiment involving determination of refractive index correction by removing the ascorbic acid reagent or measurement of the DIP value using MAGIC (Karl and Tien, 1992). It was not possible to use a MQ water as the blank because the

deionizing system in the lab produced MQ water with ~20 nM DIP. This may be because of the use of desalinated water in Israel which uses phosphonate as a descaler (Kress et al., 2020). The precision and limits of detection for these determinations are given in Table 1.

Table 1: Analytical performance characteristics for nutrient analysis

<i>Determinand</i>	<i>Usual range</i>	<i>Precision (nM)</i>	<i>Limit of detection</i>	<i>Detector device used</i>
	<i>(nM)</i>		<i>(nM)</i>	
<i>DIP</i>	0-125	2	6	LWCC
<i>Nitrate (N&N)</i>	0-1000	20	13	1cm cell spectrophotometer
<i>Ammonium</i>	0-500	6	5	JASCO fluorometer
<i>Silicate</i>	0-2000	7	11	1cm cell spectrophotometer

Table 1. Analytical performance characteristics for the nutrient analyses carried out in this study. Precision was 2 x standard deviation of 6 replicate low-level samples. The limit of detection was determined as 3 x the standard deviation of the blank. LWCC is a WPI Liquid wave guide (see text).

2.2 Primary productivity (PP) and Total Chlorophyll

Net daily photosynthetic carbon fixation rates at the THMO stations were estimated using the ¹⁴C incorporation method (Nielsen, 1952), with several modifications (Hazan et al., 2018). Triplicate 50 ml samples were taken from each depth within the photic zone and from one aphotic depth using sterile vials and kept at surface light and temperature conditions in an onboard tank with running sea water until the following morning. The ‘dark’ sample served as blank and was kept under the same temperature as the ‘light’ samples. Radioactive spiking was done at ~08:00 AM the day following of the cruise in order to start a 24 h incubation (Reich et al., 2022) at the same time. Early work by Letelier et al. (1996) at station HOT showed that prolonged on-deck incubations, similar to the protocol used in this study, may result in underestimated PP rates as it cannot precisely mimic the temperature and illumination levels in-situ. Our

preliminary tests concur with this conclusion and found that ashore incubations underestimate PP rates by up to ~20% compared to incubations on a mooring rope tied to the ship (Reich et al., 2022). Samples were spiked with 50 μ l (5 μ Ci) of $\text{NaH}^{14}\text{CO}_3$ tracer and were incubated for 24 h under 3 light regimes: surface illumination (upper mixed layer samples), 50% illumination (samples from below the mixing depth to the DCM) and ~1% illumination (samples from the DCM and below). Shading was performed using neutral density nets, thus changing light intensity but not spectral properties. Water samples were then filtered through GF/F filters (0.7 μ m nominal pore size, 25 mm diameter) using low vacuum pressure (< 50 mmHg) and rinsed 3 times with filtered sea water. Filters from each sample were then put in scintillation vials where 50 μ l of 32% HCl solution was immediately added in order to remove excess ^{14}C -bicarbonate and kept overnight for incubation. After incubation 5 ml scintillation cocktail (ULTIMA-GOLD) was added to the samples and counted using TRI-CARB 2100 TR (PACKARD) scintillation counter. Three 50 μ L random aliquots were taken from each sample batch and counted immediately after the addition of the radiotracer (without incubation) with ethanolamine to serve as added activity measurements of the reagents.

During the MMT transects, one liter of seawater was collected from all sample depths and was filtered onto GF/F filters (0.7 μ m nominal pore size, 25 mm diameter, Whatman) using a vacuum pump. Filters were frozen in vials in a -20°C freezer until extracted for 24 h in 4 ml buffered acetone and read in Turner instruments fluorometer.

2.3. Satellite data

Time series of sea surface chlorophyll concentrations and temperatures were extracted by averaging satellite data over two regions of interest overlapping the locations of THMO1 and THMO2. The satellite dataset consisted of 1km daily Level 3 products extracted from Copernicus Marine Environment Monitoring Service (CMEMS, <https://marine.copernicus.eu/>) (D'Alimonte et al., 2003; Volpe et al., 2018). The CMEMS chlorophyll product uses merged remote sensing reluctance data from multiple available ocean color sensors (MODIS-AQUA, NOAA20-VIIRS, NPP-VIIRS and Sentinel 3A-OLCI), produced by the Plymouth Marine Laboratory (PML) using the OC-CCI processor version 3. The chlorophyll retrieval algorithm specifically tuned for the

Mediterranean region by using the MedOC4 algorithm (Volpe et al., 2019) for Case I waters, and the AD4 algorithm (Berthon and Zibordi, 2004) for Case II waters.

3. Results:

3.1 Physical structure of the water column

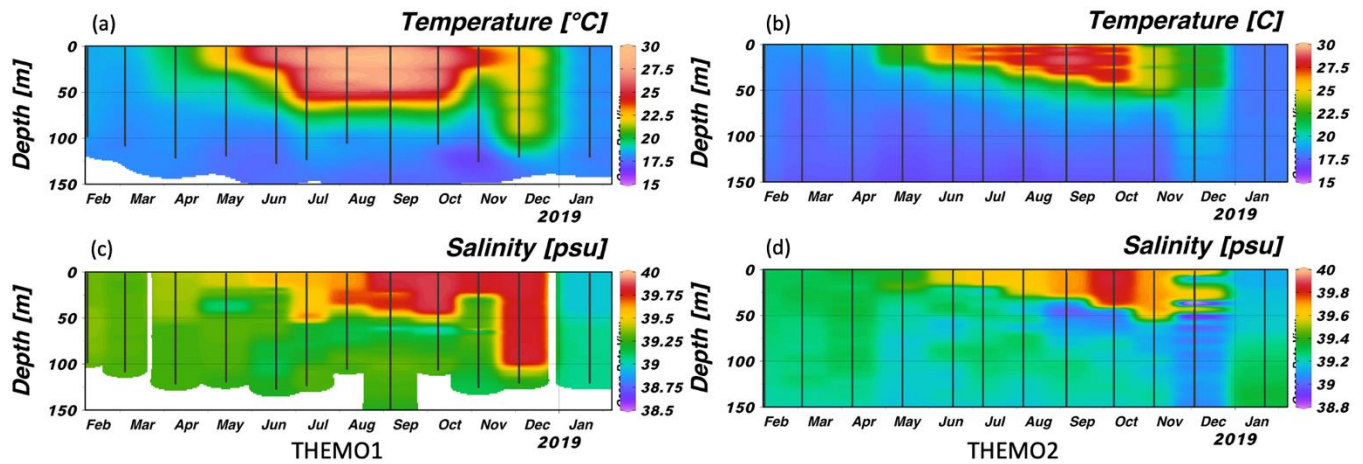


Figure 3: Shows a 12 month time series plots of the Temperature (a, b) and Salinity (c, d) measured over the upper 150 m at THEMO1 (a, c) at the edge of the ICS and THEMO2 (b, d) the pelagic station, sampled from February 2018 to Jan 2019. Data points (binned every 1 m) are shown as black lines; contouring was obtained using Ocean Data View (ODV) weighted average gridding.

The water column at THEMO1 in February and March 2018 was physically mixed to a depth below the 100 m shown in Figure 3. By April there was the start of a seasonal thermocline seen in the temperature signal, which strengthened through the summer months (May-September) when there was a strong pycnocline at 50-60 m depth. This began to weaken in October, with a deeper mixed layer to 100 m in November and a fully mixed cooler water column in January 2019.

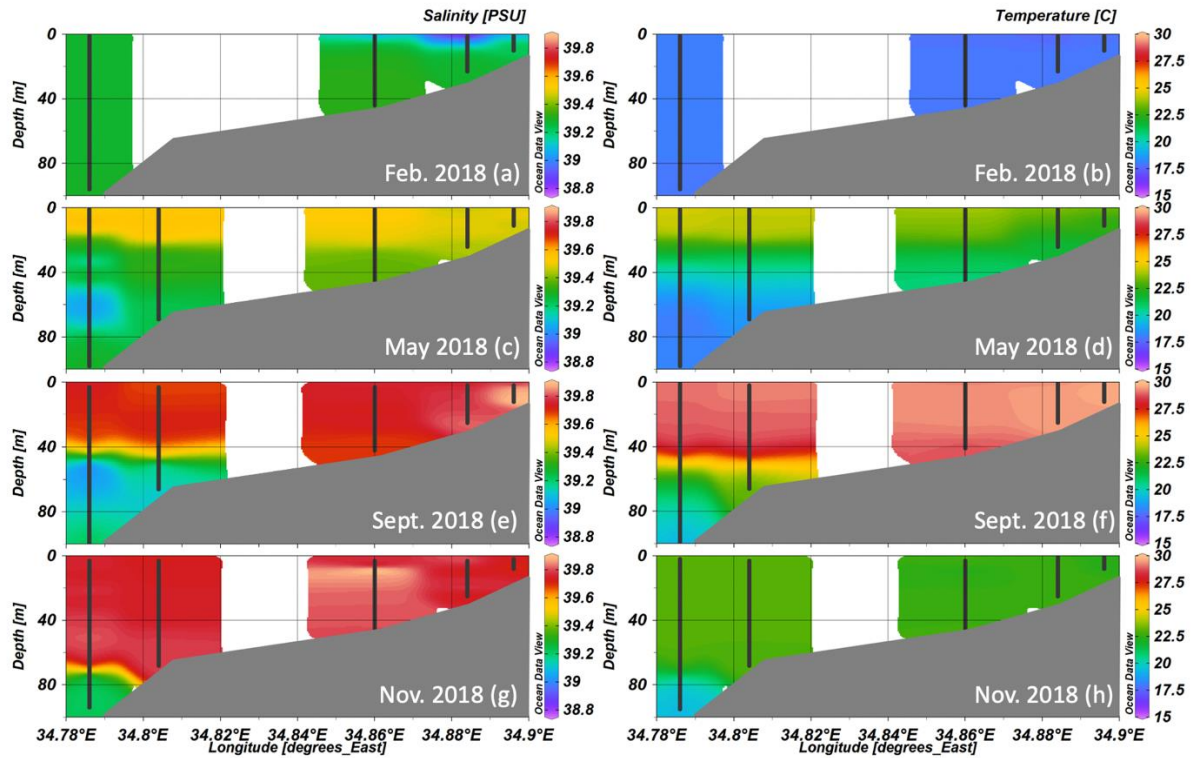


Figure 4: Salinity (left panels) and Temperature (right panels) across the MMT sampled in 2018 on (a, b) Feb 20th (c, d) May 29th, (e, f), Sept 12th and (g, h) Nov 28th. Data points (binned every 1 m) are shown as black lines; contouring was obtained using Ocean Data View (ODV) weighted average gridding.

The physical characteristics of the water column obtained across the shelf (MMT) during 4 seasonally spaced cruises (Figure 4) shows similar patterns to that observed at THEM01 on the edge of the shelf with some specific differences. In February (mid-winter) most of the water column was vertically homogeneous in salinity. An exception was the layer of fresher water (lower salinity & lower temperature) in the uppermost layers close to shore (10 and 25 m depth). By May (Figure 4d) seasonal stratification had been established with a thermocline starting at ~25 m and a similar but rather less clear vertical structure in salinity. The surface layers had somewhat higher salinity than in February. By September both the seasonal pycnocline and the increase in salinity for the shallower water were much clearer with a noticeable increase in salinity towards the shore. In November the water column was mixed above 60m and there was a clear increase in salinity over all of the transect. Note that in temperate parts of the world, November is considered already autumn while here, the physical structure of the water column was a continuation of the summer seasonal pycnocline.

3.2 Seasonal changes in Nutrient distribution across the shelf;

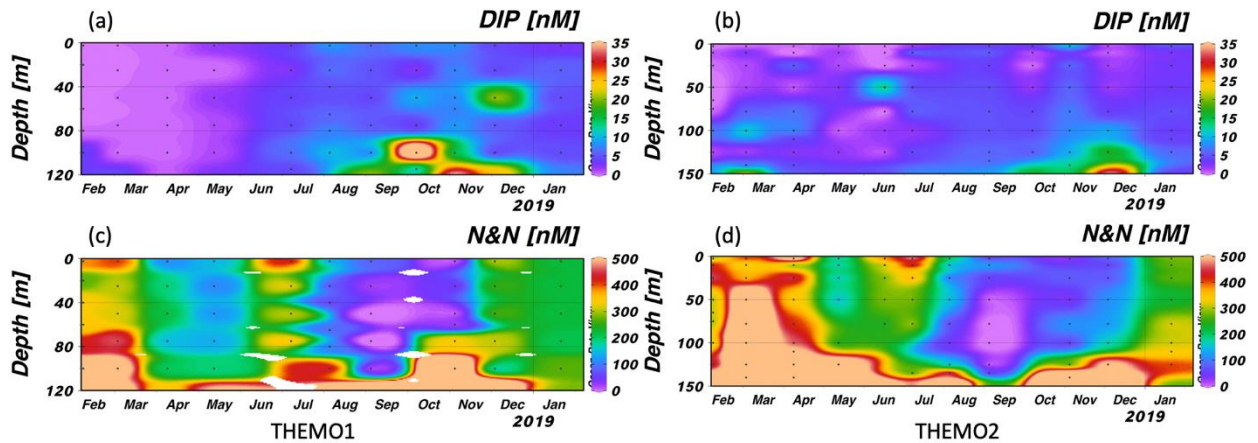


Figure 5: Time series at THEM01 (a, c) of DIP (top) and N&N (bottom) during the 12 months of sampling over the entire water column on the edge of the ICS and for comparison the same time series from pelagic THEM02 station (b, d; 2018-2019; Ben-Ezra et al., 2021) over the upper 150 m. Data points are shown as black dots; contouring was obtained using ODV weighted average gridding.

There were major seasonal changes in the nutrient distribution at THEM01 (135 m; Figures 4). The concentration of N&N was relatively high in the water column above 80 m in winter (February and March; 350-400 nM). This decreased to 140-170 nM in April and May and reached low levels of N&N (8-16 nM) from August until November. The values increased again in winter (December-January) to 220-340 nM. The only exception to this relatively simple seasonal pattern was the increased N&N (360 nM) during the July sampling, which was shown to have sampled a coastal filament confirmed by remote sensing (Lehahn unpublished data). In addition, in all the monthly cruises at THEM01 (except possibly Jan 2019; Figure 5), there was a substantial increase in N&N at the deepest depth sampled (usually 120 m) at this outer shelf station and at the deepest sample of the 100 m sample of the MMT transect (Figure 6) but not at any of the shallower depths across the shelf.

By contrast DIP remained at less than 10 nM in the upper water column (80 m and above) throughout the entire year. In addition, for all monthly cruises the lowest sample (100-120 m) was somewhat higher than the average of the rest of the water column (by a few nM), though only in May, September, November and December this increase was

somewhat greater (17-33 nM). The ammonium and silicate measurements at THOMO1 showed no systematic seasonal or vertical trends (see Supplementary Files).

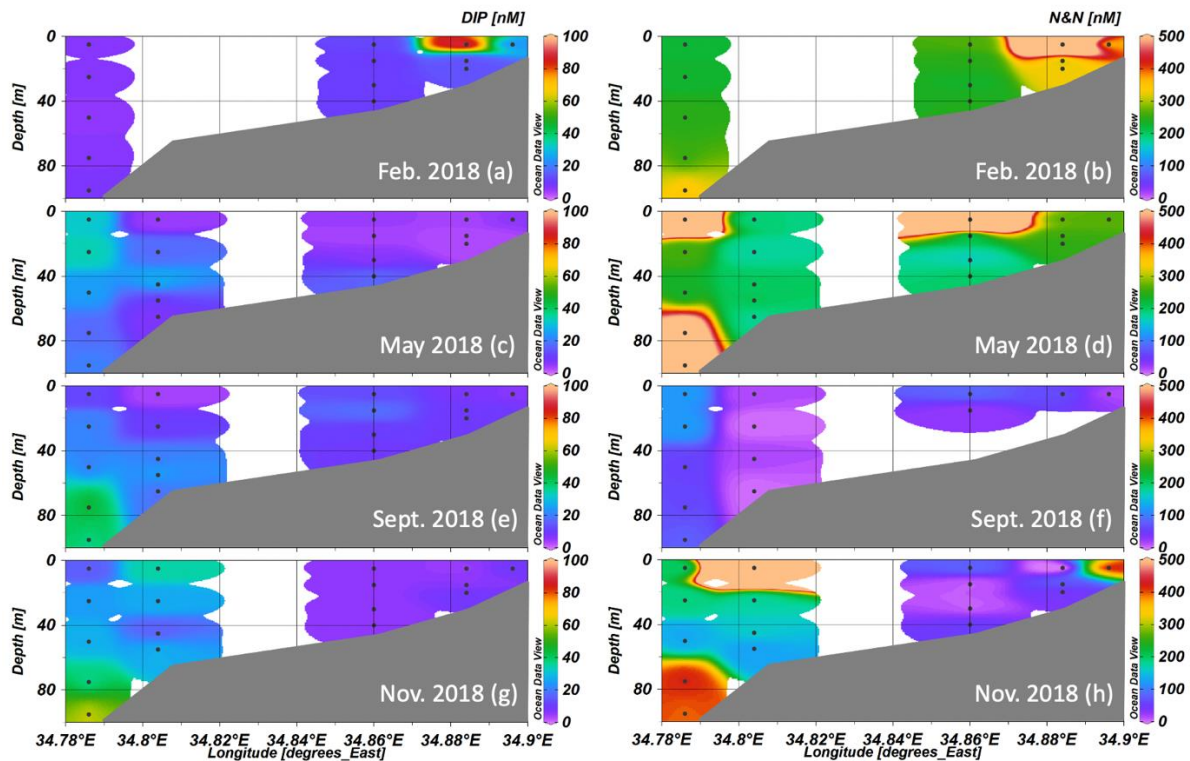


Figure 6: Dissolved inorganic phosphorus (DIP; nM) and Nitrate+Nitrite (N&N; nM) across the MMT, sampled in 2018 on (a & b) Feb 20th; (c & d) May 29th, (e & f) Sept 12th and (g & h) Nov 28th. Data points (binned every 1 m) are shown as black lines; contouring was obtained using Ocean Data View (ODV) weighted average gridding.

In the samples taken across the MMT (Figure 6) there was much higher (and relatively constant) N&N and low nM DIP throughout the water column in February except at the shallowest station where there was layer of higher N&N and DIP, which coincided with a layer of fresher water (Figure 4). In May, after the seasonal thermocline had been established, there was a decrease in N&N to 170-260 nM while DIP remained depleted at low nM concentrations. There was also higher N&N found in the uppermost samples above the seasonal thermocline across the transect. By September the water column across the ICS was depleted in both N&N and DIP. In November the layer depleted in N&N had shrunk and was only observed at the 40 m station in lower depths. There was in addition higher N&N in surface waters at 75 and 100 m and also at the 10 m station. As in all other sampling the DIP remained at extremely low concentrations (5-9 nM)

though there was slightly more DIP in the outer stations than towards the shore (16-62 nM). The ammonium and silicate measured across the MMT showed no systematic seasonal trends though there were occasional patches with higher concentrations particularly in winter (see supplementary files).

3.3 Seasonal changes in Primary Productivity:

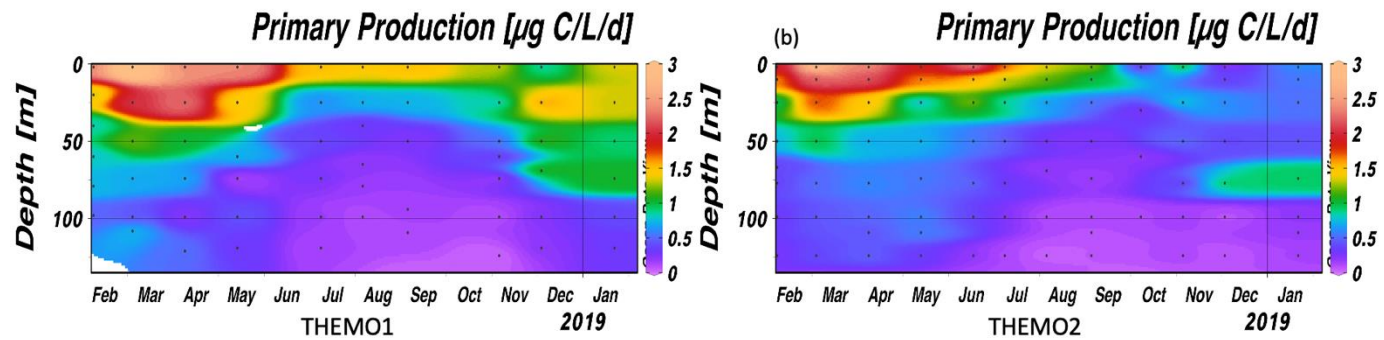


Figure 7: Plot showing monthly changes in potential primary productivity at THEMO1 (a; coastal station) and for comparison at THEMO2 (b; pelagic station; Reich et al., 2022) during 2018-2019.

The net primary productivity (PP) measured at the coastal station was highest in Feb-May 2018, with most of the PP in the upper 50 m of the water column (Figure 7). PP then decreased in magnitude and was restricted mainly to the upper 30 m during the seasonally stratified layer until November, when deeper mixing was reestablished and increased PP reached a depth of ~100 m. The pattern in the pelagic station (THEMO2) was similar with the maximum PP found in the upper 50 m between February and March. There was a decrease and shallowing of the measured PP such that by midsummer, the PP was mainly restricted to the upper 30 m and was considerably reduced from that observed in winter. At THEMO2 (pelagic) there was an increase in PP in November and December but it was mainly restricted to 75 m depth. In total, the annual integrated potential PP in the coastal site was $30 \text{ gC m}^{-2} \text{ y}^{-1}$ at THEMO1, compared with $28 \text{ gC m}^{-2} \text{ y}^{-1}$ at THEMO2, the pelagic station.

Satellite remote sensing data provided a measure of the chlorophyll concentrations in the uppermost part of the water column. These data show a chlorophyll-a maximum in late winter (March) in both 2018 and 2019 at the outer-shelf station (Figure 8), which

was interpreted as the annual phytoplankton increase, followed by a decrease reaching a minimum in late summer. Overall, the satellite chlorophyll followed a similar seasonal cycle at the pelagic station (THEMO2) though with less scatter.

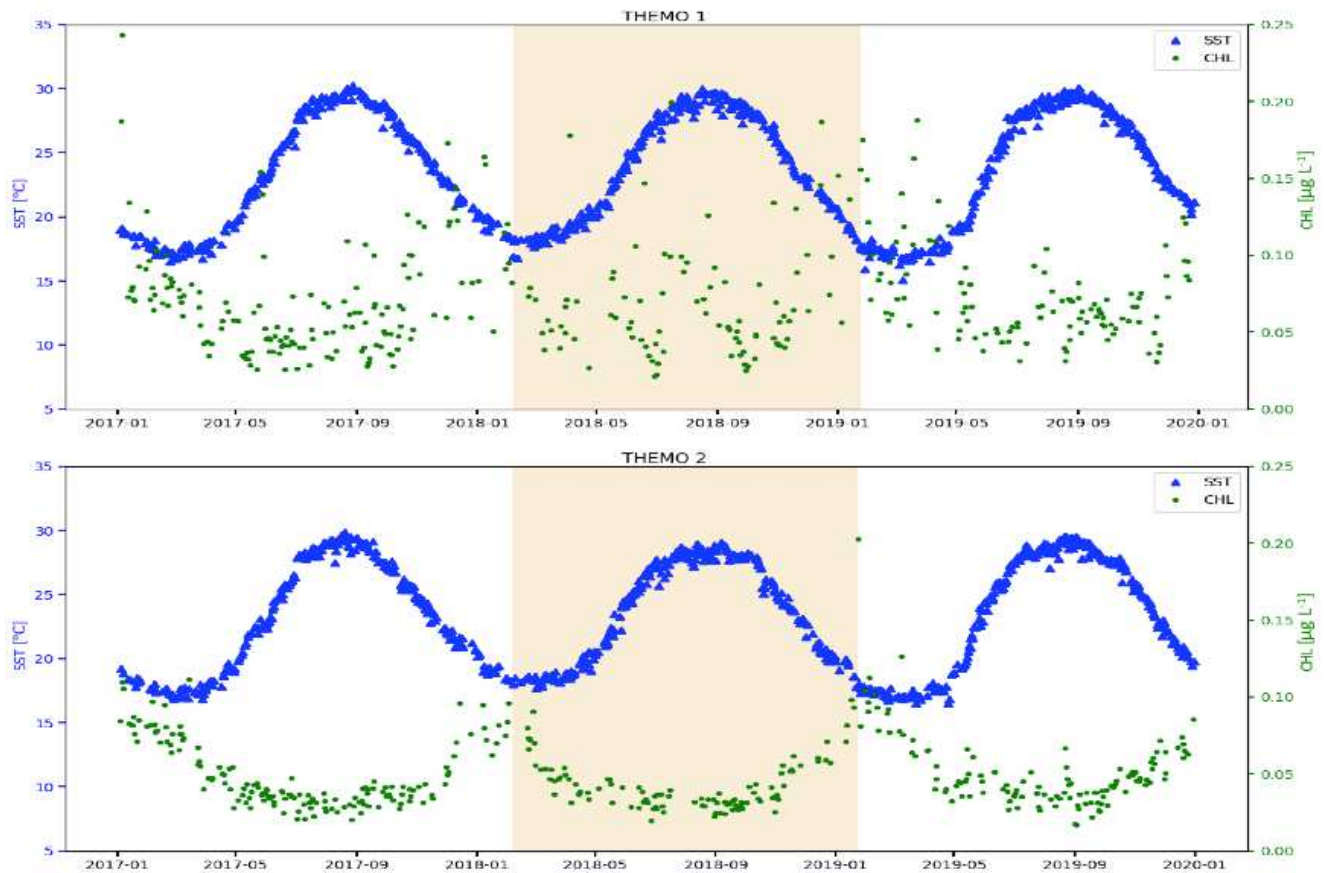


Figure 8: Seasonal changes in satellite-derived temperature (blue) and Chlorophyll-a the outer coastal station (135 m; THEMO1) and for comparison at the pelagic (1450 m: THEMO2) station over a period of three years. The sampling period of 2018-2019 is marked as light brown shading.

4. Discussion:

4.1 Nutrient dynamics across the Israeli Coastal shelf (ICS):

The seasonal changes in dissolved nutrients (especially N&N and DIP) were similar at the edge of the ICS (THEMO1), across the shelf (MMT transects) and at the pelagic station (THEMO2; Figure 5 & 6). In the pelagic station (THEMO2), there are higher values for N&N in winter decreasing in summer such that by September 2018 there was essentially no measurable N&N in the photic zone (Figure 5; Ben Ezra et al. 2021). Simultaneously during the entire year DIP remained at or close to the limit of detection. These seasonal changes in the pelagic waters are driven by physical oceanographic processes (deep mixing) and biological uptake, and not by external nutrient supply (e.g. from rivers or atmospheric supply; Ben Ezra et al. 2021). The coastal waters on the edge of the ICS (THEMO1) also had excess N&N compared to DIP during the winter of 2018 (February and March) and again as the winter of 2019 started (December and January; Figure 5). As the seasonal thermocline developed in April, N&N decreased reaching almost complete depletion in September and October at the end of the seasonally stratified period. This pattern was also seen across the MMT coastal shelf transect. The N&N:DIP was $\gg 16:1$ during winter mixing and decreased during the seasonal stratified period such that by late summer the N&N:DIP ratio was $<16:1$ (Figure S2). Although the nutrient pattern of higher N&N in winter decreasing during the seasonal stratification period at THEMO1 and across the shelf was similar to that at the pelagic station, it was rather more complex in detail. There are patches of nutrients on the shelf, such as the patch of low salinity in Feb 2018 in the shallowest depths (Figure 4) caused by local river and/or atmospheric inputs, which spatially and temporarily result in increased nutrients which rapidly are taken up by the microbial community and/or diluted by mixing.

4.2 Seasonal changes in primary productivity on the ICS;

The monthly potential primary productivity at the outer shelf station (THEMO1) was highest in February-March 2018 during winter mixing, decreased during the period of seasonal stratification (April-November), and then increased again as deeper water column mixing began in December (Figure 7; Reich et al. 2022). This pattern was consistent with observed seasonal nutrient dynamics. The integrated annual PP at the outer shelf station ($30 \text{ gC m}^{-2} \text{ y}^{-1}$) was very similar to the integrated PP at the pelagic station ($28 \text{ gC m}^{-2} \text{ y}^{-1}$) determined on the same sampling day at the pelagic station, and both were similar to previous PP data of $10\text{-}20 \text{ gC m}^{-2} \text{ y}^{-1}$ from ICS (Berman et al., 1986).

These PP values are similar, if not even lower than annual PP determined in the pelagic EMS and the Cretan Sea ($59 \text{ gC m}^{-2} \text{ y}^{-1}$ and $25 \text{ gC m}^{-2} \text{ y}^{-1}$, respectively) and the Ionian Sea ($62 \text{ gC m}^{-2} \text{ y}^{-1}$) as reviewed by Siokou-Frangou et al. (2010). These data confirm that in general the degree of oligotrophy on the ICS was similar to that observed in the EMS pelagic system and much lower than a typical coastal shelf.

However, in detail there are some local observations which suggested higher productivity on the ICS particularly during winter when there was higher nutrient supply from the coast. Thus, the limited chlorophyll data measured in the MMT (see Figure S4; Supplementary files) showed there was an increase during the winter sampling (February 2018) towards the shore, while the May 2018 transect showed only minor changes towards the shore. This coincided with increases in nutrients and was likely due to the effect of storms which caused a plume of fresher water containing nutrients to be input from the coast. Overall the greater scatter of chlorophyll in the coastal system (Figure 8) is because the ICS is both spatially and temporally more inhomogeneous than the pelagic system even though the average total PP is similar.

There is only very limited available data on the nature and seasonal variability of the phytoplankton community on the ICS (Azov, 1986; Berman et al., 1986; Raveh et al., 2015). In general, the autotrophic community on the ICS is dominated by nano and picoplankton (*Synococcus* and *Prochlorococcus*) with a limited fraction of eukaryotes (Reich, unpubl. data). There have been no systematic studies on the important (but minor quantitatively) eukaryote communities comparing the shelf to the offshore. Keuter et al., (2022) found somewhat different coccolith community at THEM01 (Shelf) compared to THEM02 (pelagic) while Kress et al. (2005) sampled a coastal filament and found somewhat higher concentrations of larger eukaryotes ($3.5\text{-}11 \text{ cells ml}^{-1}$) than found in the pelagic waters. Azov (1986) showed that the relative fraction of PP from microplankton at the neritic station (30 m) was 2-20% while at the pelagic station it varied from 5-40% though generally it was $\sim 10\%$ or less.

In addition to these regional differences, there are also local differences in both space and time. For example, Rahav et al. (2020) found higher autotrophic activity in a location on the ICS affected directly by submarine groundwater discharge (SGD). It is

considered highly likely that pulses of nutrients from storms flushing out the micro-estuaries will also result in increased local PP.

5.1 Why is the seasonality of nutrient dynamics on the ICS similar to the Pelagic?

The seasonality of the shelf is driven by a combination of advection of waters from the offshore and external sources to the shelf. In the original study on nutrient dynamics on the Israeli shelf, Townsend et al., (1988) estimated that advection from offshore supplied 90% of the nutrients onto the shelf. However, their calculation did not include SGD, atmospheric inputs or riverine inputs as potential sources to the ICS. In addition they assumed that measurements of net PP represented the entire sink for externally supplied N without taking into account that such measurements include recycled PP which is an unknown quantity on the ICS.

The external inputs of nutrients from atmospheric inputs (Ben-Ezra et al. 2021) and from riverine input (Herut et al., 2000; Suari et al., 2019) to the ICS are higher in winter. Thus the pelagic and ICS have similar atmospheric inputs, which are higher in winter (57%) compared with summer (Ben Ezra et al., 2021). As is typical of a Mediterranean climate area, the rivers and streams tend to flow with much greater volume and nutrient flux in winter (Suari et al., 2019). Although there is no direct evidence it is likely that both SGD and domestic waste discharge would be higher in winter than in summer. While there is no data available to quantify the seasonal flux of water onto the shelf, it has been shown based on the increased nutrients at the deepest waters of THOMO 1 and 100m of MMT have got to have come from the offshore, since there is no increase in nutrients near the sediment-water interface in shallower water. This source of water carries a similar nutrient signal to the pelagic waters, being relatively nitrate rich in winter and a decreasing flux of N (mainly nitrate) in summer (Ben-Ezra et al., 2021, Figure 5 and 6).

In many coastal shelves sedimentation processes are a sink for organic matter. This is also occurring in the ICS (Christensen et al., 1988). But in addition and unusually there is also Benthic Productivity which removes nutrients both from the water column and reduces N fluxes from sediment back into the overlying water. The sediment is within the photic zone and is a sink rather than a source of dissolved nutrients (Christensen et

al., 1988). Direct evidence for the presence of autotrophic organisms on the ICS but not in deeper water has been provided by Rubin-Blum et al. (2022). Understanding the magnitude and seasonality of this bacterial productivity as a key process on the ICS and needs further investigation.

5.2 The unusual nutrient dynamics and oligotrophic status of the ICS:

Most coastal shelves typically have higher nutrient supply and concentrations than offshore waters. This gives rise to much higher PP and chlorophyll values which can cause eutrophic conditions in the water column and sometimes even hypoxic conditions (Andersen et al. 2017; Chen et al. 2019 and many others). For comparison, the range of chlorophyll values in the Baltic coast area, which has a similar external nutrient input per unit area to the EMS (Powley et al., 2017), is 2-15 mg m⁻³ (Wasmund et al., 2001) or 4-25 mg m⁻³ (Babin et al., 2003) i.e. 10-100 times higher values than the ICS. An underlying reason for the typical biogeochemical processes of the coastal shelf is the basic circulation pattern which is in general estuarine, with fresher surface waters derived from rainfall and/or river inputs moving away from the coast to be replaced by deeper upwelling nutrient rich waters. In addition, there is commonly abundant direct input of nutrients from rivers often with additional significant atmospheric input from the adjacent land mass (Berner and Berner, 2012; Chester et al., 1993). Some or indeed most of these inputs nowadays are anthropogenic, even when direct discharge of wastewater onto the coastal shelf is limited. Finally, the sediments in many coastal regions are high in labile organic matter both derived from the adjacent coastal regions and/or produced in the overlying water column and are thus sources of recycled nutrients into the shallow overlying waters. Typically, a consequence of this high primary productivity of coastal waters is high turbidity in the water column which means the sediments are below the photic zone and are dominantly a source of nutrients as respiration and bioturbation processes dominate.

The ICS is a very different coastal shelf. This study shows for the first time that the entire ICS (from the outer shelf to 10 m) has low concentrations of dissolved nutrients generally at similar concentrations to that found in the ultra-oligotrophic pelagic waters (Figure 5 & 6). DIP is consistently less than 10 nM. N&N sampled in 2018-2019 varied seasonally, with moderate levels (~200-500 nM) during winter months while essentially depleted during the late summer stratified period. The PP at the outer shelf

station was approximately equal to the PP of the ultra-oligotrophic pelagic station and well within the range of oligotrophic to ultra-oligotrophic values (Siokou-Frangou et al., 2010). Even using the higher estimate for PP calculated for the ICS (section 4.4.2), the net PP is only ~30% higher than the pelagic values. This generalizes and confirms previous studies on the ICS which identify the ICS as oligotrophic to ultra-oligotrophic (Azov, 1986; Berman et al., 1986; Kress et al., 2019). On the ICS there are no areas of hypoxia and no eutrophication present except possibly close to pollution hot spots in very shallow water (Kress et al., 2019). This implies that the nutrients supplied to the ICS from the rivers, SGD and sewage are not sufficient to change the dominant phytoplankton distribution of pico and nanoplankton which is characteristic of this nutrient depleted systems (Berman et al., 1986; Reich et al., 2022). However although this is true in general, it may not be true in all situations and all times (e.g. Kress and Herut, 1998; Rahav et al., 2020). This system is characterized by patchiness in both space and time indeed that maybe a crucial characteristic of how the higher trophic levels in this nutrient depleted part of the EMS survive.

The fundamental reason for this unusual state is the circulation on the ICS like the pelagic, is antiestuarine. There are limited natural freshwater inputs, which has been further reduced by the critical need and use of essentially all potable freshwater for human uses. This reduces the flux of nutrients from the land. As was found in the MMT, even at a local level the waters across the shelf become more saline as the summer progresses. This suggests that the regional antiestuarine circulation, which is an important characteristic of the EMS (Krom et al., 2014), also applies to the ICS locally. It is hypothesized that like the offshore, even when nutrients are supplied to the photic zone by SGD, rivers or atmospheric supply, most are taken up rapidly by microbial uptake and those small patches of residual nutrients are rapidly mixed and then advected away from the shore. Most studies on coastal shelves elsewhere in the EMS deal with specific pollution hot spots (e.g. Kress and Herut 1998; Neofitou and Klaoudatos 2008; Varkitzi et al. 2018; Rekik et al. 2020). However, in such studies the background nutrients and or chlorophyll/PP are typically low and similar to the values found in the adjacent pelagic EMS. It is suggested here that these general properties of the ICS applies to many coastal shelves in the EMS.

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Reference List:

- Andersen, J.H., Carstensen, J., Conley, D.J., Dromph, K., Fleming-Lehtinen, V., Gustafsson, B.G., Josefson, A.B., Norkko, A., Villnäs, A., Murray, C., 2017. Long-term temporal and spatial trends in eutrophication status of the Baltic Sea. *Biol. Rev.* 92, 135–149.
- Azov, Y., 1986. Seasonal patterns of phytoplankton productivity and abundance in nearshore oligotrophic waters of the Levant Basin (Mediterranean). *J. Plankton Res.* 8, 41–53. <https://doi.org/10.1093/plankt/8.1.41>
- Babin, M., Stramski, D., Ferrari, G.M., Claustre, H., Bricaud, A., Obolensky, G., Hoepffner, N., 2003. Variations in the light absorption coefficients of phytoplankton, nonalgal particles, and dissolved organic matter in coastal waters around Europe. *J. Geophys. Res. Ocean.* 108.
- Balkis, N., 2009. Seasonal variations of microphytoplankton assemblages and environmental variables in the coastal zone of Bozcaada Island in the Aegean Sea (NE Mediterranean Sea). *Aquat. Ecol.* 43, 249–270.
- Ben Ezra, T., Krom, M.D., Tsemel, A., Berman-Frank, I., Herut, B., Lehahn, Y., Rahav, E., Reich, T., Thingstad, T.F., Sher, D., 2021. Seasonal nutrient dynamics in the P depleted Eastern Mediterranean Sea. *Deep. Res. Part I Oceanogr. Res. Pap.* 176, 103607. <https://doi.org/10.1016/j.dsr.2021.103607>
- Berman, T., Azov, Y., Schneller, A., Walline, P., Townsend, D.W., 1986. Extent, transparency, and phytoplankton distribution of the neritic waters overlying the Israeli coastal shelf. *Oceanol. Acta* 9, 439–447.
- Berman, T., Townsend, D.W., Elsayed, S.Z., Trees, C.C., Azov, Y., 1984. Optical transparency, chlorophyll and primary productivity in the Eastern Mediterranean near the Israeli coast. *Oceanol. Acta* 7, 367–372.
- Berner, E.K., Berner, R.A., 2012. Global environment: water, air, and geochemical cycles. Princeton University Press.
- Berthon, J.-F., Zibordi, G., 2004. Bio-optical relationships for the northern Adriatic Sea. *Int. J. Remote Sens.* 25, 1527–1532.
- Blog, B., Business, N., Andersen, J.H., Conley, D.J., 2009. Eutrophication in coastal marine ecosystems: towards better understanding and management strategies, in: *Eutrophication in Coastal Ecosystems*. Springer, pp. 1–4.
- Chen, L., Liu, J., Xu, G., Li, F., 2019. Phytoplankton productivity and community structure variations over the last 160 years in the East China Sea coast in response to natural

606 and human-induced environmental changes. *The Holocene* 29, 1145–1154.
 607 Chester, R., Bradshaw, G.F., Ottley, C.J., Harrison, R.M., Merrett, J.L., Preston, M.R.,
 608 Rendell, A.R., Kane, M.M., Jickells, T.D., 1993. The atmospheric distributions of trace
 609 metals, trace organics and nitrogen species over the North Sea. *Philos. Trans. R.*
 610 *Soc. London. Ser. A Phys. Eng. Sci.* 343, 543–556.
 611 Christensen, J.P., Goldsmith, V., Walline, P., Schneller, A., El Sayed, S.Z., 1988.
 612 Sedimentary nutrient regeneration on the oligotrophic Eastern Mediterranean
 613 continental shelf. *Oceanol. Acta*, Spec. issue 1–27.
 614 D’Alimonte, D., Mélin, F., Zibordi, G., Berthon, J.-F., 2003. Use of the novelty detection
 615 technique to identify the range of applicability of empirical ocean color algorithms.
 616 *IEEE Trans. Geosci. Remote Sens.* 41, 2833–2843.
 617 Davies, A.G., Morales, C.E., 1998. An appraisal of the stoichiometry of dissolved
 618 oxygen/nutrient inter-relationships in the upwelling system off northern Chile. *J.*
 619 *Mar. Biol. Assoc. United Kingdom* 78, 697–706.
 620 Djaoudi, K., Van Wambeke, F., Coppola, L., D’Ortenzio, F., Helias-Nunige, S., Raimbault, P.,
 621 Taillandier, V., Testor, P., Wagener, T., Pulido-Villena, E., 2018. Sensitive
 622 determination of the dissolved phosphate pool for an improved resolution of its
 623 vertical variability in the surface layer: New views in the P-depleted Mediterranean
 624 Sea. *Front. Mar. Sci.* 5. <https://doi.org/10.3389/fmars.2018.00234>
 625 Doğan-Sağlamtimur, N., Tuğrul, S., 2004. Effect of riverine nutrients on coastal water
 626 ecosystems: a case study from the northeastern Mediterranean shelf. *Fresenius*
 627 *Environ. Bull.* 13, 1288–1294.
 628 Ediger, D., Tuğrul, S., Yılmaz, A., 2005. Vertical profiles of particulate organic matter and
 629 its relationship with chlorophyll-a in the upper layer of the NE Mediterranean Sea.
 630 *J. Mar. Syst.* 55, 311–326.
 631 Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. Past: Paleontological statistics software
 632 package for education and data analysis. *Palaeontol. Electron.* 4.
 633 Hazan, O., Silverman, J., Sisma-Ventura, G., Ozer, T., Gertman, I., Shoham-Frider, E., Kress,
 634 N., Rahav, E., 2018. Mesopelagic prokaryotes alter surface phytoplankton
 635 production during simulated deep mixing experiments in Eastern Mediterranean
 636 Sea waters. *Front. Mar. Sci.* 5, 1–11. <https://doi.org/10.3389/fmars.2018.00001>
 637 Herut, B., Almogi-Labin, A., Jannink, N., Gertman, I., 2000. The seasonal dynamics of
 638 nutrient and chlorophyll a concentrations on the SE Mediterranean shelf-slope.

639 Oceanol. Acta 23, 771–782. [https://doi.org/10.1016/S0399-1784\(00\)01118-X](https://doi.org/10.1016/S0399-1784(00)01118-X)

640 Ignatiades, L., Psarra, S., Zervakis, V., Pagou, K., Souvermezoglou, E., Assimakopoulou, G.,
641 Gotsis-Skretas, O., 2002. Phytoplankton size-based dynamics in the Aegean Sea
642 (Eastern Mediterranean). J. Mar. Syst. 36, 11–28. [https://doi.org/10.1016/S0924-](https://doi.org/10.1016/S0924-7963(02)00132-X)
643 7963(02)00132-X

644 Kamennaya, N.A., Geraki, K., Scanlan, D.J., Zubkov, M. V., 2020. Accumulation of ambient
645 phosphate into the periplasm of marine bacteria is proton motive force dependent.
646 Nat. Commun. 11, 1–13. <https://doi.org/10.1038/s41467-020-16428-w>

647 Kanari, M., Tibor, G., Hall, J.K., Ketter, T., Lang, G., Schattner, U., 2020. Sediment transport
648 mechanisms revealed by quantitative analyses of seafloor morphology: New
649 evidence from multibeam bathymetry of the Israel exclusive economic zone. Mar.
650 Pet. Geol. 114, 104224.

651 Karl, D.M., Tien, G., 1992. MAGIC: A sensitive and precise method for measuring
652 dissolved phosphorus in aquatic environments. Limnol. Oceanogr. 37, 105–116.

653 Keuter, S., Silverman, J., Krom, M.D., Sisma-Ventura, G., Yu, J., Tsemel, A., Ben-Ezra, T.,
654 Sher, D., Reich, T., Koplovitz, G., Frada, M.J., 2022. Seasonal patterns of
655 coccolithophores in the ultra-oligotrophic South-East Levantine Basin, Eastern
656 Mediterranean Sea. Mar. Micropaleontol. 102153.
657 <https://doi.org/10.1016/J.MARMICRO.2022.102153>

658 Kress, N., Frede Thingstad, T., Pitta, P., Psarra, S., Tanaka, T., Zohary, T., Groom, S., Herut,
659 B., Fauzi, R., Polychronaki, T., Rassoulzadegan, F., Spyres, G., 2005. Effect of P and N
660 addition to oligotrophic Eastern Mediterranean waters influenced by near-shore
661 waters: A microcosm experiment. Deep. Res. Part II Top. Stud. Oceanogr. 52, 3054–
662 3073. <https://doi.org/10.1016/j.dsr2.2005.08.013>

663 Kress, N., Gertner, Y., Shoham-Frider, E., 2020. Seawater quality at the brine discharge
664 site from two mega size seawater reverse osmosis desalination plants in Israel
665 (Eastern Mediterranean). Water Res. 171, 115402.

666 Kress, N., Herut, B., 2001. Spatial and seasonal evolution of dissolved oxygen and
667 nutrients in the Southern Levantine Basin (Eastern Mediterranean Sea): chemical
668 characterization of the water masses and inferences on the N: P ratios. Deep Sea
669 Res. Part I Oceanogr. Res. Pap. 48, 2347–2372.

670 Kress, N., Herut, B., 1998. Hypernutrification in the oligotrophic Eastern Mediterranean:
671 a study in Haifa Bay (Israel). Estuar. Coast. Shelf Sci. 46, 645–656.

672 Kress, N., Rahav, E., Silverman, J., Herut, B., 2019. Environmental status of Israel's
673 Mediterranean coastal waters: Setting reference conditions and thresholds for
674 nutrients, chlorophyll-a and suspended particulate matter. *Mar. Pollut. Bull.* 141,
675 612–620. <https://doi.org/10.1016/J.MARPOLBUL.2019.02.070>

676 Krom, M., Kress, N., Berman-Frank, I., Rahav, E., 2014. Past, present and future patterns
677 in the nutrient chemistry of the eastern mediterranean, in: *The Mediterranean Sea: Its History and Present Challenges*. Springer Netherlands, Dordrecht, pp. 49–68.
678 https://doi.org/10.1007/978-94-007-6704-1_4

680 Krom, M.D., Kress, N., Brenner, S., Gordon, L.I., 1991. Phosphorus limitation of primary
681 productivity in the eastern Mediterranean Sea. *Limnol. Oceanogr.* 36, 424–432.
682 <https://doi.org/10.4319/lo.1991.36.3.0424>

683 Krom, M.D., Woodward, E.M.S., Herut, B., Kress, N., Carbo, P., Mantoura, R.F.C., Spyres, G.,
684 Thingsted, T.F., Wassmann, P., Wexels-Riser, C., Kitidis, V., Law, C., Zodiatis, G.,
685 2005. Nutrient cycling in the south east Levantine basin of the eastern
686 Mediterranean: Results from a phosphorus starved system. *Deep. Res. Part II Top.*
687 *Stud. Oceanogr.* 52, 2879–2896. <https://doi.org/10.1016/j.dsr2.2005.08.009>

688 Letelier, R.M., Dore, J.E., Winn, C.D., Karl, D.M., 1996. Seasonal and interannual variations
689 in photosynthetic carbon assimilation at Station. *Deep Sea Res. Part II Top. Stud.*
690 *Oceanogr.* 43, 467–490.

691 Murphy, J., Riley, J.P., 1962. A modified single solution method for the determination of
692 phosphate in natural waters. *Anal. Chim. Acta* 27, 31–36.
693 [https://doi.org/10.1016/S0003-2670\(00\)88444-5](https://doi.org/10.1016/S0003-2670(00)88444-5)

694 Neofitou, N., Klaoudatos, S., 2008. Effect of fish farming on the water column nutrient
695 concentration in a semi-enclosed gulf of the Eastern Mediterranean. *Aquac. Res.* 39,
696 482–490.

697 Nielsen, E.S., 1952. The use of radio-active carbon (c14) for measuring organic
698 production in the sea. *ICES J. Mar. Sci.* 18, 117–140.
699 <https://doi.org/10.1093/icesjms/18.2.117>

700 Ounissi, M., Amira, A.B., Dulac, F., 2018. Riverine and wet atmospheric inputs of
701 materials to a North Africa coastal site (Annaba Bay, Algeria). *Prog. Oceanogr.* 165,
702 19–34.

703 Powley, H.R., Krom, M.D., Van Cappellen, P., 2017. Understanding the unique
704 biogeochemistry of the Mediterranean Sea: Insights from a coupled phosphorus

705 and nitrogen model. *Global Biogeochem. Cycles* 31, 1010–1031.
 706 <https://doi.org/10.1002/2017GB005648>
 707 Psarra, S., Tselepides, A., Ignatiades, L., 2000. Primary productivity in the oligotrophic
 708 Cretan Sea (NE Mediterranean): seasonal and interannual variability. *Prog.*
 709 *Oceanogr.* 46, 187–204. [https://doi.org/10.1016/S0079-6611\(00\)00018-5](https://doi.org/10.1016/S0079-6611(00)00018-5)
 710 Pujo-Pay, M., Conan, P., Oriol, L., Cornet-Barthaux, V., Falco, C., Ghiglione, J.-F.F., Goyet, C.,
 711 Moutin, T., Prieur, L., 2011. Integrated survey of elemental stoichiometry (C, N, P)
 712 from the western to eastern Mediterranean Sea. *Biogeosciences* 8, 883–899.
 713 <https://doi.org/10.5194/bg-8-883-2011>
 714 Pulido-Villena, E., Rerolle, V., Guieu, C., 2010. Transient fertilizing effect of dust in P-
 715 deficient LNLC surface ocean. *Geophys. Res. Lett.* 37.
 716 Rahav, E., Raveh, O., Hazan, O., Gordon, N., Kress, N., Silverman, J., Herut, B., 2018. Impact
 717 of nutrient enrichment on productivity of coastal water along the SE Mediterranean
 718 shore of Israel - A bioassay approach. *Mar. Pollut. Bull.* 127, 559–567.
 719 <https://doi.org/10.1016/j.marpolbul.2017.12.048>
 720 Rahav, E., Raveh, O., Yanuka-Golub, K., Belkin, N., Astrahan, P., Maayani, M., Tsumi, N.,
 721 Kiro, Y., Herut, B., Silverman, J., 2020. Nitrate-Enrichment Structures Phytoplankton
 722 Communities in the Shallow Eastern Mediterranean Coastal Waters. *Front. Mar. Sci.*
 723 1127.
 724 Raveh, O., David, N., Rilov, G., Rahav, E., 2015. The temporal dynamics of coastal
 725 phytoplankton and bacterioplankton in the eastern mediterranean sea. *PLoS One*
 726 10, e0140690. <https://doi.org/10.1371/journal.pone.0140690>
 727 Reich, T., Ben-Ezra, T., Belkin, N., Tsemel, A., Aharonovich, D., Roth-Rosenberg, D., Givati,
 728 S., Bialik, M., Herut, B., Berman-Frank, I., Frada, M., Krom, M.D., Lehahn, Y., Rahav, E.,
 729 Sher, D., 2022. A year in the life of the Eastern Mediterranean: Monthly dynamics of
 730 phytoplankton and bacterioplankton in an ultra-oligotrophic sea. *Deep. Res. Part I*
 731 *Oceanogr. Res. Pap.* 182, 103720. <https://doi.org/10.1016/j.dsr.2022.103720>
 732 Rekik, A., Ayadi, H., Elloumi, J., 2020. Spatial and seasonal variability of the planktonic
 733 ciliates assemblages along the Eastern Mediterranean Coast (Sfax coast, Tunisia).
 734 *Reg. Stud. Mar. Sci.* 40, 101529.
 735 Rubin-Blum, M., Sisma-Ventura, G., Yudkovski, Y., Belkin, N., Kanari, M., Herut, B., Rahav,
 736 E., 2022. Diversity, activity, and abundance of benthic microbes in the Southeastern
 737 Mediterranean Sea. *FEMS Microbiol. Ecol.* 98, fiac009.

738 SEAL Analytical, 2011a. Ammonia in water and seawater. AutoAnalyzer Appl. G-327-05.

739 SEAL Analytical, 2011b. Nitrate and Nitrite in water and seawater Total Nitrogen in
740 persulfate digests. AutoAnalyzer Appl. G-172-96.

741 Simboura, N., Zenetos, A., Pancucci-Papadopoulou, M.A., 2014. Benthic community
742 indicators over a long period of monitoring (2000-2012) of the Saronikos Gulf,
743 Greece, Eastern Mediterranean. *Environ. Monit. Assess.* 186, 3809–3821.
744 <https://doi.org/10.1007/s10661-014-3659-z>

745 Siokou-Frangou, I., Christaki, U., Mazzocchi, M.G., Montresor, M., Ribera d’Alcalá, M.,
746 Vaqué, D., Zingone, A., 2010. Plankton in the open Mediterranean Sea: a review.
747 *Biogeosciences* 7, 1543–1586.

748 Souvermezoglou, E., Krasakopoulou, E., Pavlidou, A., 2014. Temporal and spatial
749 variability of nutrients and oxygen in the North Aegean Sea during the last thirty
750 years. *Mediterr. Mar. Sci.* 15, 805–822. <https://doi.org/10.12681/mms.1017>

751 Suari, Y., Dadon-Pilosof, A., Sade, T., Amit, T., Gilboa, M., Gafny, S., Topaz, T., Zedaka, H.,
752 Boneh, S., Yahel, G., 2019. A long term physical and biogeochemical database of a
753 hyper-eutrophicated Mediterranean micro-estuary. *Data Br.* 27, 104809.

754 Thingstad, T.F., Krom, M.D., Mantoura, R.F.C., Flaten, C.A.F., Groom, S., Herut, B., Kress, N.,
755 Law, C.S., Pasternak, A., Pitta, P., Psarra, S., Rassoulzadegan, F., Tanaka, T.,
756 Tselepides, A., Wassmann, P., Woodward, E.M.S., Riser, C.W., Zodiatis, C., Zohary, T.,
757 2005. Nature of phosphorus limitation in the ultraoligotrophic eastern
758 Mediterranean. *Science* (80-.). 309, 1068–1071.
759 <https://doi.org/10.1126/science.1112632>

760 Thingstad, T.F., Skjoldal, E.F., Böhne, R.A., 1993. Phosphorus cycling and algal-bacterial
761 competition in Sandsfjord, western Norway.

762 Townsend, D.W., Christensen, J.P., Berman, T., Walline, P., Schneller, A., Yentsch, C.S.,
763 1988. Near-bottom chlorophyll maxima in Southeastern Mediterranean shelf
764 waters: upwelling and sediments as possible nutrient sources. *Oceanol. Acta SP*
765 235–244.

766 Varkitzi, I., Markogianni, V., Pantazi, M., Pagou, K., Pavlidou, A., Dimitriou, E., 2018. Effect
767 of river inputs on environmental status and potentially harmful phytoplankton in a
768 coastal area of eastern Mediterranean (Maliakos Gulf, Greece). *Mediterr. Mar. Sci.*
769 19, 326–343.

770 Volpe, G., Colella, S., Brando, V.E., Forneris, V., La Padula, F., Di Cicco, A., Sammartino, M.,

771 Bracaglia, M., Artuso, F., Santoleri, R., 2019. Mediterranean ocean colour Level 3
 772 operational multi-sensor processing. *Ocean Sci.* 15, 127–146.

773 Volpe, G., Nardelli, B.B., Colella, S., Pisano, A., Santoleri, R., 2018. Operational
 774 Interpolated Ocean Colour Product in the Mediterranean Sea. *New Front. Oper.*
 775 *Oceanogr.* 227–244.

776 Wasmund, N., Andrushaitis, A., Łysiak-Pastuszek, E., Müller-Karulis, B., Nausch, G.,
 777 Neumann, T., Ojaveer, H., Olenina, I., Postel, L., Witek, Z., 2001. Trophic status of the
 778 south-eastern Baltic Sea: a comparison of coastal and open areas. *Estuar. Coast.*
 779 *Shelf Sci.* 53, 849–864.

780 Zaafrane, S., Maatouk, K., Akrou, F., Trabelsi, I., Drira, N., 2019. Spatio-temporal
 781 distribution of physicochemical and bacteriological parameters in the north area of
 782 Monastir bay, eastern coast of Tunisia. *Arab. J. Geosci.* 12, 1–18.
 783 <https://doi.org/10.1007/S12517-019-4386-0/TABLES/4>

784 Zubkov, M. V., Martin, A.P., Hartmann, M., Grob, C., Scanlan, D.J., 2015. Dominant oceanic
 785 bacteria secure phosphate using a large extracellular buffer. *Nat. Commun.* 2015 61
 786 6, 1–8. <https://doi.org/10.1038/ncomms8878>
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Supplementary files:

Nutrient Dynamics Across the Israeli Coastal Shelf: an Unusual Oligotrophic Coastal System

Ben-Ezra, T., Reich, T , Tsemel, A., Berman-Frank, I., Lehahn, Y., Sher, D., Suari, Y and Krom M.D.

Definition of the Israeli Coastal shelf:

The Mediterranean shoreline of Israel is made up mainly of Nile sand eroded from the delta and transported by long-shore drift. Offshore there is a rather wide continental shelf with gradually decreasing grain size from the coarse sand near the shoreline to silt at the shelf break, which is generally at a depth of 100-130m (Kanari et al., 2020). Berman and co-workers in their studies of biogeochemical processes on the ICS measured transects to a depth of 150m (Berman et al., 1984; Christensen et al., 1988; Townsend et al., 1988). Haifa University in collaboration with Texas A&M university has recently set up two ocean observatory systems, one coastal and the other pelagic. THEMO1 is located off the northern Israeli coast at 130m while THEMO2 is located at 1450m (Figure 1). In this study we consider the monthly sampling at THEMO1 (130m) to represent the outer coastal shelf and the transects from 10-100m off the coast from Maagan Michael (MMT) to represent the rest of the ICS (Figure 1).

Station	Depth [m]	Lat °N	Long °E
Maagan Michael Transect TSY 10	10	32.550	34.896
Maagan Michael Transect TSY 25	25	32.557	34.884
Maagan Michael Transect TSY 45	45	32.562	34.860
Maagan Michael Transect TSY 70	70	32.559	34.804
Maagan Michael Transect TSY 100	100	32.561	34.786
THEMO1	135	32.820	34.950
THEMO2	1450	32.790	34.380
N800 Pelagic station	832	32.560	34.790

Table S1: The location of sampling stations used in this study. The designation of TSY and the name of the stations as Maagan Michael transect (MMT) is that used in (<https://med-lter.haifa.ac.il/index.php/en/data-base>) where the data is available for use.

Sample Preservation experiments:

The results of the sample preservation experiments are plotted in Figure S1 and shown in detail in Table S2. The statistical significance of the data in the preservation experiments was assessed using 2 sample paired T-test (Hammer et al., 2001). The results from the filtered frozen samples and the unfiltered frozen samples were compared to the fresh filtered samples analyzed with 12-15 hours of collection (Ben Ezra et al., 2021).

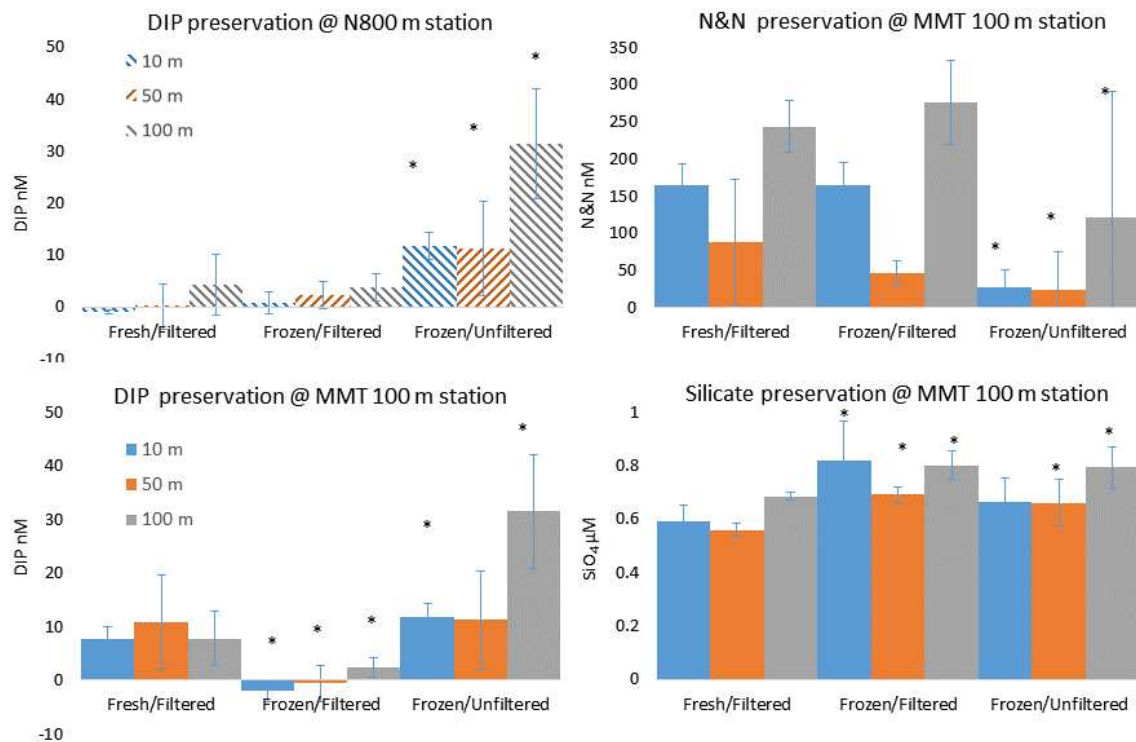


Figure S1: Figure showing the mean $\pm$ 1 s.d. of fresh filtered samples, frozen filtered samples and frozen unfiltered samples collected at an N800 pelagic station at a depth of 10m, 50m & 100m (3 samples & 6 replicates) and at the 100m station on the MMT at a depth of 10m, 50m and 100m (MMT; 3 samples & 6 replicates). The samples marked with asterisk are statistically significantly different from the corresponding filtered fresh samples (2 sample paired T-test, $p < 0.05$).

In the samples collected from the pelagic station the frozen filtered sample DIP values were not statistically different from the fresh filtered (i.e. good preservation). Even for the samples collected from the MMT stations, the preserved samples were only a few nanomoles lower than the fresh samples and as long as differences of < 10 nM are not being interpreted as important, this preservation technique was considered acceptable.

Frozen filtered also gave adequate results for silicate and N&N (adequate preservation but only if used to interpret relatively large changes (<50nM for N&N & <15% for silicate). This method (Filtered frozen samples) has been used previously for Mediterranean surface samples by Pulido-Villena et al. (2010) and others and is used in our lab as a potential back up if there were problems with the fresh filtered samples on the day when analysis was carried out.

The unfiltered frozen samples gave values for DIP which were consistently significantly high and for N&N which were significantly low (Figure 2). This agrees with the results presented previously during the CYCLOPS addition experiment which concluded that this method of preservation was only acceptable for samples with values of >400nM N&N and >50 nM DIP, (Krom et al., 2005) which means for samples below the nutricline in the EMS. This is particularly problematic when Nitrate:Phosphate ratios are used to identify the limiting nutrient within the photic zone (e.g. Herut et al., 2000; Rahav et al., 2018).

It is hypothesized that the reason for the higher DIP values with unfiltered frozen samples for DIP, is the presence of 'luxury' consumption and storage of phosphate within microbial cells. This process is well known from eutrophied waters (Davies and Morales, 1998; Thingstad et al., 1993). It is less well known but present in the P starved waters of the EMS (Ediger et al., 2005; Thingstad et al., 2005) though it is logical that in an environment where there might be occasional pulses of DIP, that organisms will be adapted to accumulate whatever they can.

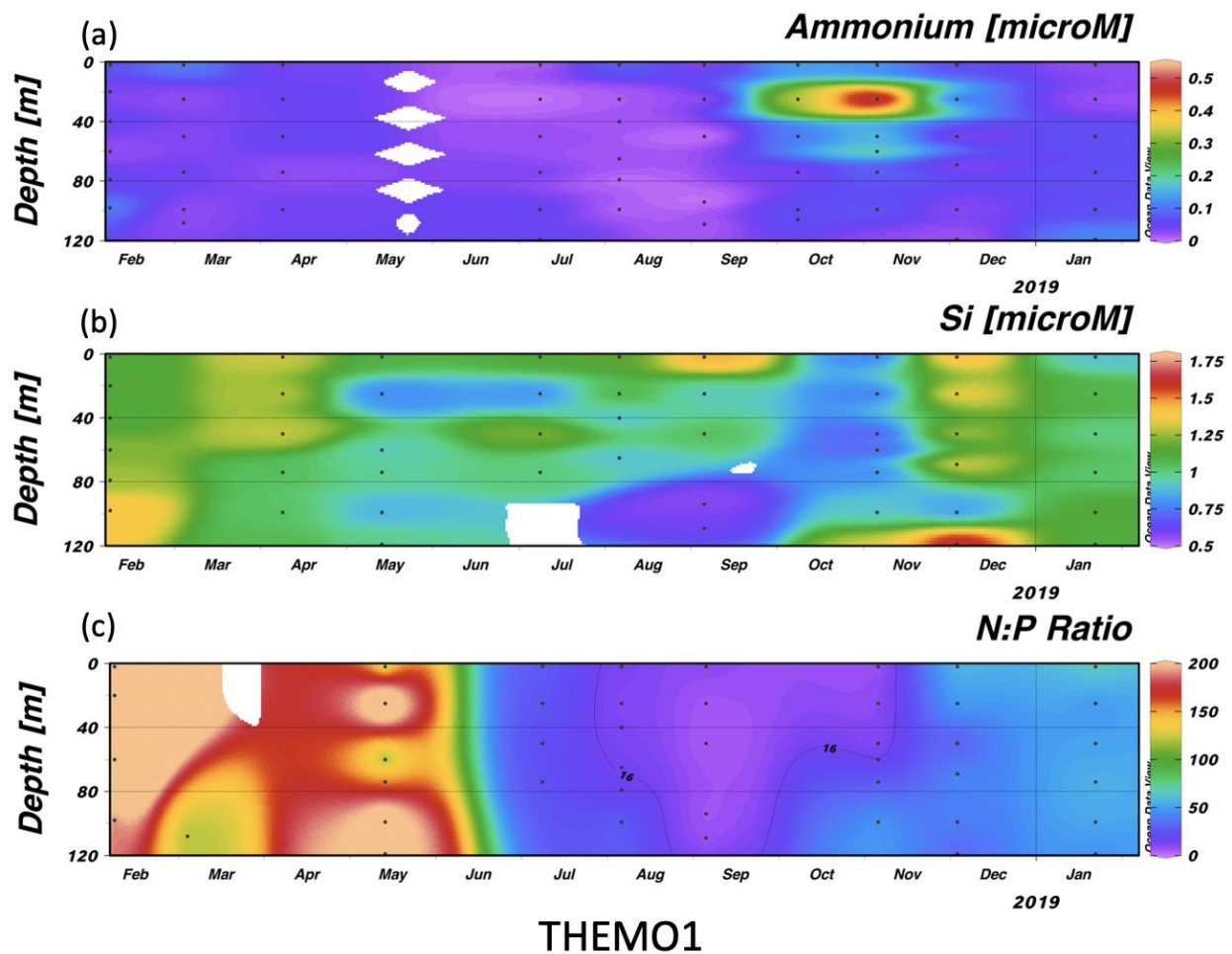
Location	Depth	DIP (nM)			N&N (nM)			Silicate (µM)		
		Fresh Filtered	Frozen Filtered	Frozen unfiltered	Fresh Filtered	Frozen Filtered	Frozen unfiltered	Fresh Filtered	Frozen Filtered	Frozen unfiltered
800m station	10m	-1	1	14				0.777	0.694	0.658
		-1	0	13				0.715	0.658	0.640
		-1	0	10				0.691	0.621	0.655
		-1	3	12				0.683	0.649	0.634
			0	10				0.683	0.656	0.629
			1	11				0.683	0.645	0.648
Average		-1	1	12						

2*Stdev. p		0.49	2.11	2.63						
	50m	-1	2	8				0.66 1	0.60 9	0.637
		-1	0	12				0.65 5	0.61 6	0.619
		5	3	9				0.65 3	0.61 5	0.606
		-1	1	6				0.66 3	0.62 0	0.609
		-1	4	11				0.65 4	0.61 0	
		0	4	21				0.65 3	0.62 1	
Average		0.1	2.3	11.2						
2*Stdev. p		4.3	2.7	9.2						
	100 m	9	4	33						
		3	4	42						
		2	2	30						
		7	3	27						
		2	4	28						
		2	6	29						
Average		4.4	3.8	31.4						
2*Stdev. p		5.8	2.7	10.5						
Maagan Michael transect	10m									
		9	-3	14	0.16	0.14	0.03	0.65	0.98	0.66
		7	-3	13	0.17	0.16	0.02	0.58	0.82	0.63
		8	0	10	0.15	0.16	0.05	0.60	0.80	0.59
		7	-2	12	0.16	0.18		0.58	0.79	0.71
		6	-2	10	0.15	0.18	0.03	0.57	0.78	0.71
		10	-2	11	0.20	0.18	0.01	0.56	0.75	
Average		8	-2	12	0.17	0.17	0.03	0.59	0.82	0.66
2*Stdev. p		2.3	2.0	2.6	0.03	0.03	0.02	0.06	0.15	0.09
	50m	12	-2	8	0.09	0.06	0.03	0.55	0.71	0.68
		19	-3	12	0.18	0.05	0.02	0.55	0.70	0.73
		13	0	9	0.08	0.05	0.02	0.55	0.68	0.63
		8	-2	6	0.06	0.03	0.01	0.56	0.70	0.69
		6	1	11	0.06	0.05	-0.01	0.57	0.67	0.61
		7	2	21	0.06	0.04	0.07	0.57	0.68	0.61
Average		11	-1	11	0.09	0.05	0.02	0.56	0.69	0.66
2*Stdev. p		9	3	9	0.09	0.02	0.05	0.02	0.03	0.09

	100 m	6	1	33	0.25	0.26		0.70	0.77	0.83
		7	2	42	0.26	0.27		0.69	0.77	0.83
		13	2	30	0.21	0.26	0.08	0.68	0.84	0.76
		8	2	27	0.25	0.26	0.07	0.68	0.81	0.75
		8	2	28	0.26	0.26	0.07	0.68	0.83	
		6	4	29	0.24	0.34	0.27	0.68	0.79	
Average		8	2	31	0.24	0.28	0.12	0.69	0.80	0.79
2*Stdev. p		5	2	11	0.04	0.06	0.17	0.01	0.05	0.08

Table S2: Showing the results of the sample preservation experiment in which frozen filtered and frozen unfiltered are being compared with fresh filtered samples (6 samples of each) using 2 sample paired T-test (using past statistics). The results in pale orange as samples in which the preserved samples are significantly higher than the fresh filtered and the samples in pale blue are the samples which are significantly lower than the fresh filtered samples (see Figure S1).

876 *Ammonium and Silicate measured at THEM01 and across the ICS:*



877
 878 *Figure S2: Time series at THEM01 of (a) Ammonium, (b) Silicate (Si) and (c) N:P ratio*
 879 *(N&N [nM]:DIP [nM]) during the 12 months of sampling over the entire water column on*
 880 *the edge of the ICS. Data points are shown as black dots; contouring was obtained using*
 881 *ODV weighted average gridding.*

882
 883 The ammonium levels at THEM01, the outer shelf station (130m) for most of the year
 884 were relatively low ($<100\text{nM}$) and showed no clear depth related trend (Figure S2) The
 885 exception was in October and November where there was a major peak at 25m
 886 supported by increased ammonium values above and below. The Silicate profiles at
 887 THEM01 (Figure S2) showed no systematic vertical or seasonal trends. The average
 888 concentration was $1.06 \pm 0.25 \mu\text{M}$ (range $0.57\text{-}1.71 \mu\text{M}$).

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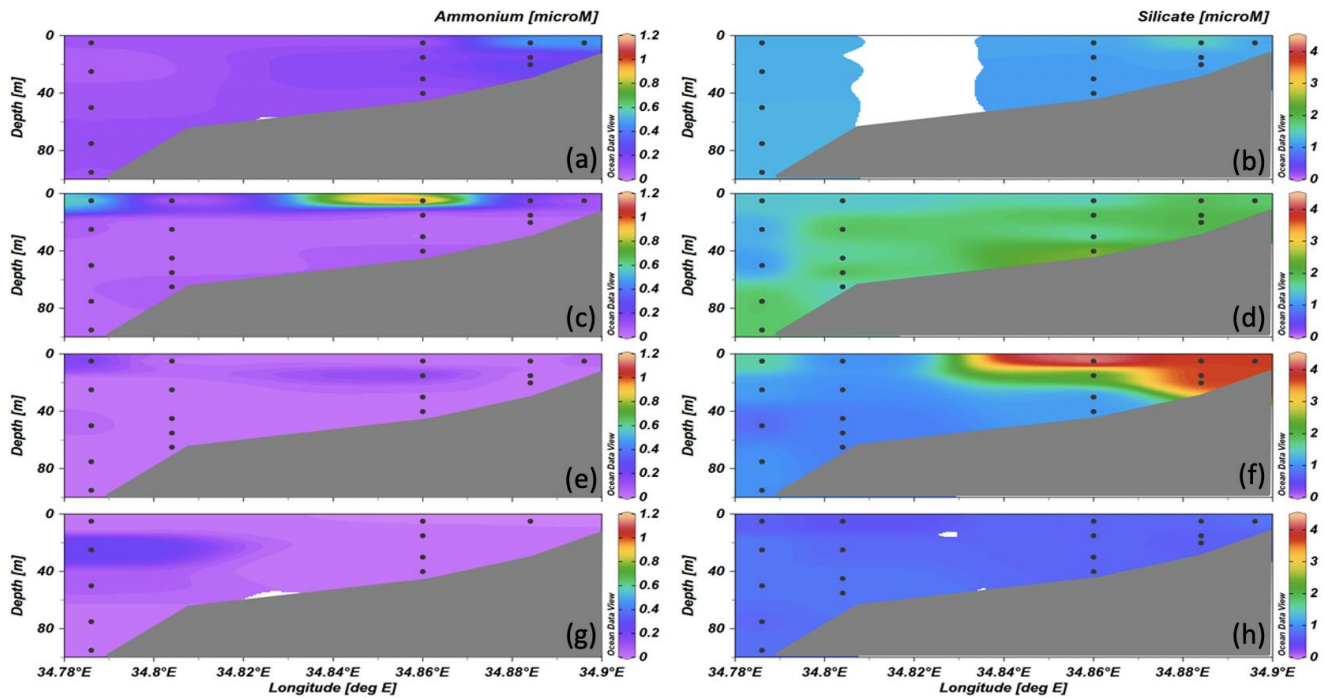


Figure S3: Ammonium (nM) and Silicate (μM) across the MMT, sampled in 2018 on Feb 20th (a, b); May 29th (c, d), Sept 12th (e, f) and Nov 28th (g, h). Data points binned every 1m are shown as black lines; contouring was obtained using Ocean Data View (ODV) weighted average gridding.

In February (which was not sampled at 75m station) there was higher silicate at the 100m station compared to shallower water (Figure S3). As with N&N and DIP, there was a layer of much increased silicate and increased ammonium in the surface layers at the 10 and 25m station. In May there was excess ammonium in the upper layers. In September there was high concentration of silicate as a pulse starting at the coast and floating out as layer near the surface at or beyond the 40m station. The ammonium was relatively low and homogeneous throughout the water column in both September and November.

Extracted Chlorophyll measured across the MMT:

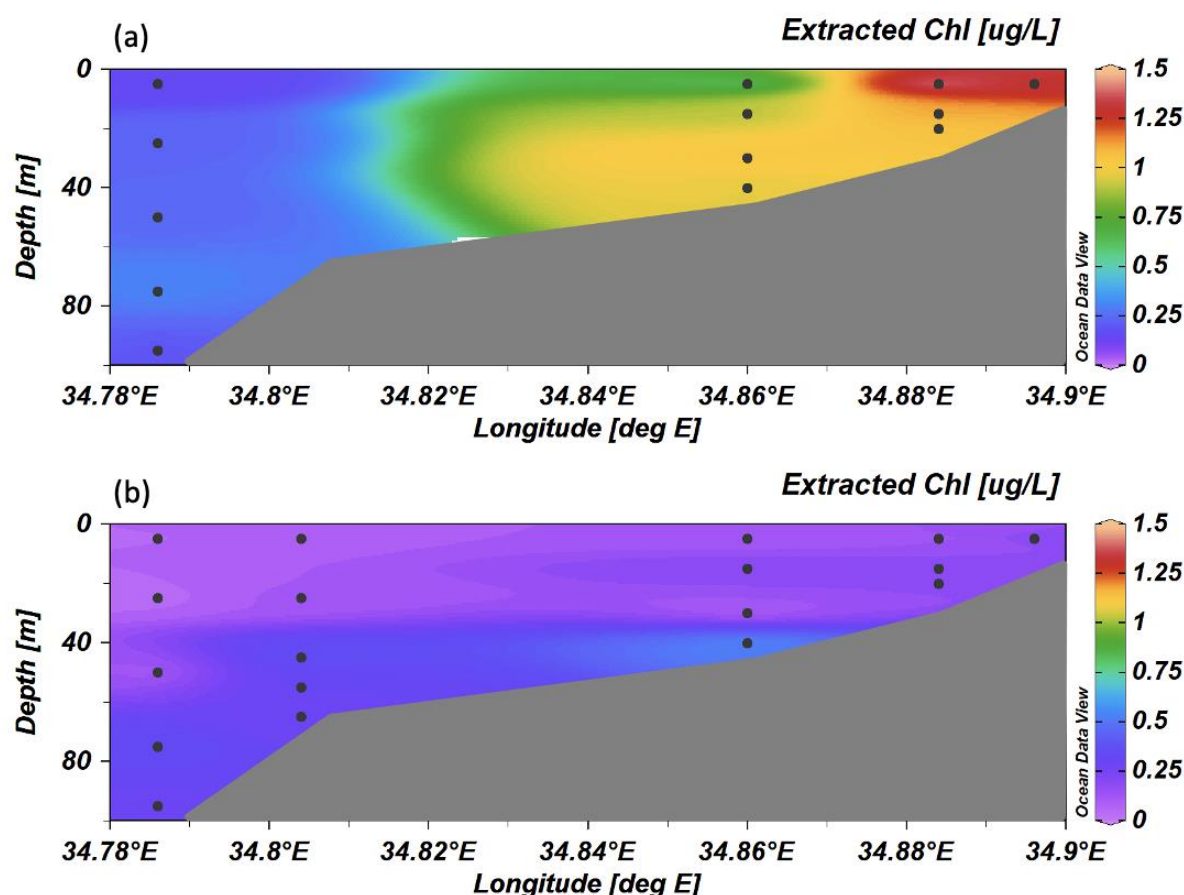


Figure S4: Extracted Chlorophyll *a* across the MMT from Febuary 2018 (top) and May 2018 (bottom) in $\mu\text{g/L}$.

The extracted chlorophyll-*a* during the February cruise decreased from the coast to the offshore (100m). In addition the uppermost samples had higher chlorophyll than deeper samples. For the May cruise there was essentially no trend in chlorophyll from the coast to the offshore and a minor increase in chlorophyll with depth.

Annual nutrient flux from Israeli streams to the sea as determined by IOLR:

Year	Soreq			Lachish			Yarkon		
	Phosphate	Nitrate	Ammon.	Phosphate	Nitrate	Ammon.	Phosphate	Nitrate	Ammon.
2007	0.45	5.43	5.07	0.81	1.14	8.36	4.19	2.29	62.0
2008	0.32	3.14	6.21	1.13	4.29	12.79	0.94	0.29	17.2
2009	0.10	0.07	3.36	0.10	0.21	0.04	3.71	0.07	64.4
2010	0.42	3.79	3.36	0.02	0.01	0.02	0.84	10.29	10.6
2011	0.42	0.00	1.00	0.35	0.50	0.79	1.26	2.71	13.2
2012	1.06	23.14	7.36	1.23	0.79	7.79	0.71	6.71	14.5
2013	2.23	0.86	55.00	0.00	0.14	0.07	0.97	20.50	13.8

2014	0.39	11.00	4.43	3.58	9.50	21.29	1.42	16.50	19.2
2015	1.23	21.07	6.93	0.94	2.00	2.79	2.45	15.14	37.9
2017	0.13	0.57	1.29	0.03	0.07	0.07	3.71	5.21	61.1
10 year average	0.67	6.91	9.40	0.82	1.87	5.40	2.02	7.97	31.4

Year	Alexander			Hadera			Tananim		
	Phosphate	Nitrate	Ammon.	Phosphate	Nitrate	Ammon.	Phosphate	Nitrate	Ammon.
2007	0.68	7.14	1.43	0.32	4.07	8.43	0.00	7.14	0.02
2008	0.68	8.00	2.57	1.32	0.01	20.00	0.00	3.00	0.04
2009	0.35	5.07	0.07	1.39	1.21	16.14	0.00	3.57	0.01
2010	0.26	3.29	2.07	0.32	6.21	3.43	0.06	5.36	0.14
2011	0.03	3.50	2.64	0.65	3.64	32.50	0.00	2.86	0.93
2012	0.26	3.64	11.21	0.58	8.21	10.21	0.00	6.43	0.00
2013	0.32	10.14	25.36	2.35	33.50	9.14	0.00	5.79	0.07
2014	0.03	3.14	0.00	0.06	0.14	1.57	0.00	4.64	0.07
2015	0.03	1.14	0.00	0.16	0.57	1.21	0.00	1.93	0.07
2017	0.35	1.64	4.93	0.02	0.07	0.64	0.01	3.07	0.07
10 year average	0.30	4.67	5.03	0.72	5.77	10.33	0.01	4.38	0.14

Year	Kishon			Naaman			Total Sum		
	Phosphate	Nitrate	Ammon.	Phosphate	Nitrate	Ammon.	Phosphate	Nitrate	Ammon.
2007	0.65	8.36	4.79	0.35	0.50	1.79	7.46	36.07	91.9
2008	0.29	7.43	2.21	0.35	0.18	1.14	5.03	26.33	62.1
2009	0.32	17.93	1.71	0.45	0.86	1.36	6.42	29.00	87.1
2010	0.61	16.43	14.71	0.10	2.71	0.79	2.63	48.08	35.1
2011	0.16	11.43	1.93	0.13	2.29	1.64	3.00	26.93	54.6
2012	0.42	22.86	3.07	0.06	1.86	4.79	4.32	73.64	58.9
2013	1.74	51.00	8.86	0.10	4.21	4.43	7.71	126.14	116.7
2014	0.13	5.93	1.21	0.03	1.93	0.57	5.65	52.79	48.4
2015	0.10	7.64	0.50	0.13	0.43	2.64	5.03	49.93	52.0
2017	0.16	9.64	0.43	0.32	0.21	7.43	4.74	20.50	76.0
10 year average	0.46	15.86	3.94	0.20	1.52	2.66	5.20	48.94	68.3

Table S3: Annual nutrient flux (moles $\times 10^6$ per year) to the sea from the major Israeli streams (data from Herut, 2015) for the years 2007-2017. The flux is calculated by multiplying the concentration measured at the outflow of the stream in March by the total annual discharge as reported by the Israeli Water Authority. Note that the annual discharge includes both baseflow and storm water discharge. The annual total flux of N & N and NH₄ are shown to the right. The total DIN discharged is 117.2×10^6 MolesN y⁻¹.

Reference List:

- Andersen, J.H., Carstensen, J., Conley, D.J., Dromph, K., Fleming-Lehtinen, V., Gustafsson, B.G., Josefson, A.B., Norkko, A., Villnäs, A., Murray, C., 2017. Long-term temporal and spatial trends in eutrophication status of the Baltic Sea. *Biol. Rev.* 92, 135–149.
- Azov, Y., 1986. Seasonal patterns of phytoplankton productivity and abundance in nearshore oligotrophic waters of the Levant Basin (Mediterranean). *J. Plankton Res.* 8, 41–53. <https://doi.org/10.1093/plankt/8.1.41>
- Babin, M., Stramski, D., Ferrari, G.M., Claustre, H., Bricaud, A., Obolensky, G., Hoepffner, N., 2003. Variations in the light absorption coefficients of phytoplankton, nonalgal particles, and dissolved organic matter in coastal waters around Europe. *J. Geophys. Res. Ocean.* 108.
- Balkis, N., 2009. Seasonal variations of microphytoplankton assemblages and environmental variables in the coastal zone of Bozcaada Island in the Aegean Sea (NE Mediterranean Sea). *Aquat. Ecol.* 43, 249–270.
- Ben Ezra, T., Krom, M.D., Tsemel, A., Berman-Frank, I., Herut, B., Lehahn, Y., Rahav, E., Reich, T., Thingstad, T.F., Sher, D., 2021. Seasonal nutrient dynamics in the P depleted Eastern Mediterranean Sea. *Deep. Res. Part I Oceanogr. Res. Pap.* 176, 103607. <https://doi.org/10.1016/j.dsr.2021.103607>
- Berman, T., Azov, Y., Schneller, A., Walline, P., Townsend, D.W., 1986. Extent, transparency, and phytoplankton distribution of the neritic waters overlying the Israeli coastal shelf. *Oceanol. Acta* 9, 439–447.
- Berman, T., Townsend, D.W., Elsayed, S.Z., Trees, C.C., Azov, Y., 1984. Optical transparency, chlorophyll and primary productivity in the Eastern Mediterranean near the Israeli coast. *Oceanol. Acta* 7, 367–372.
- Berner, E.K., Berner, R.A., 2012. *Global environment: water, air, and geochemical cycles.* Princeton University Press.
- Berthon, J.-F., Zibordi, G., 2004. Bio-optical relationships for the northern Adriatic Sea. *Int. J. Remote Sens.* 25, 1527–1532.
- Blog, B., Business, N., Andersen, J.H., Conley, D.J., 2009. Eutrophication in coastal marine ecosystems: towards better understanding and management strategies, in: *Eutrophication in Coastal Ecosystems.* Springer, pp. 1–4.
- Chen, L., Liu, J., Xu, G., Li, F., 2019. Phytoplankton productivity and community structure variations over the last 160 years in the East China Sea coast in response to natural

- and human-induced environmental changes. *The Holocene* 29, 1145–1154.
- Chester, R., Bradshaw, G.F., Ottley, C.J., Harrison, R.M., Merrett, J.L., Preston, M.R., Rendell, A.R., Kane, M.M., Jickells, T.D., 1993. The atmospheric distributions of trace metals, trace organics and nitrogen species over the North Sea. *Philos. Trans. R. Soc. London. Ser. A Phys. Eng. Sci.* 343, 543–556.
- Christensen, J.P., Goldsmith, V., Walline, P., Schneller, A., El Sayed, S.Z., 1988. Sedimentary nutrient regeneration on the oligotrophic Eastern Mediterranean continental shelf. *Oceanol. Acta*, Spec. issue 1–27.
- D'Alimonte, D., Mélin, F., Zibordi, G., Berthon, J.-F., 2003. Use of the novelty detection technique to identify the range of applicability of empirical ocean color algorithms. *IEEE Trans. Geosci. Remote Sens.* 41, 2833–2843.
- Davies, A.G., Morales, C.E., 1998. An appraisal of the stoichiometry of dissolved oxygen/nutrient inter-relationships in the upwelling system off northern Chile. *J. Mar. Biol. Assoc. United Kingdom* 78, 697–706.
- Djaoudi, K., Van Wambeke, F., Coppola, L., D'Ortenzio, F., Helias-Nunige, S., Raimbault, P., Taillandier, V., Testor, P., Wagener, T., Pulido-Villena, E., 2018. Sensitive determination of the dissolved phosphate pool for an improved resolution of its vertical variability in the surface layer: New views in the P-depleted Mediterranean Sea. *Front. Mar. Sci.* 5. <https://doi.org/10.3389/fmars.2018.00234>
- Doğan-Sağlamtimur, N., Tuğrul, S., 2004. Effect of riverine nutrients on coastal water ecosystems: a case study from the northeastern Mediterranean shelf. *Fresenius Environ. Bull.* 13, 1288–1294.
- Ediger, D., Tuğrul, S., Yılmaz, A., 2005. Vertical profiles of particulate organic matter and its relationship with chlorophyll-a in the upper layer of the NE Mediterranean Sea. *J. Mar. Syst.* 55, 311–326.
- Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. Past: Paleontological statistics software package for education and data analysis. *Palaeontol. Electron.* 4.
- Hazan, O., Silverman, J., Sisma-Ventura, G., Ozer, T., Gertman, I., Shoham-Frider, E., Kress, N., Rahav, E., 2018. Mesopelagic prokaryotes alter surface phytoplankton production during simulated deep mixing experiments in Eastern Mediterranean Sea waters. *Front. Mar. Sci.* 5, 1–11. <https://doi.org/10.3389/fmars.2018.00001>
- Herut, B., Almogi-Labin, A., Jannink, N., Gertman, I., 2000. The seasonal dynamics of nutrient and chlorophyll a concentrations on the SE Mediterranean shelf-slope.

- Oceanol. Acta 23, 771–782. [https://doi.org/10.1016/S0399-1784\(00\)01118-X](https://doi.org/10.1016/S0399-1784(00)01118-X)
- Ignatiades, L., Psarra, S., Zervakis, V., Pagou, K., Souvermezoglou, E., Assimakopoulou, G., Gotsis-Skretas, O., 2002. Phytoplankton size-based dynamics in the Aegean Sea (Eastern Mediterranean). *J. Mar. Syst.* 36, 11–28. [https://doi.org/10.1016/S0924-7963\(02\)00132-X](https://doi.org/10.1016/S0924-7963(02)00132-X)
- Kamennaya, N.A., Geraki, K., Scanlan, D.J., Zubkov, M. V., 2020. Accumulation of ambient phosphate into the periplasm of marine bacteria is proton motive force dependent. *Nat. Commun.* 11, 1–13. <https://doi.org/10.1038/s41467-020-16428-w>
- Kanari, M., Tibor, G., Hall, J.K., Ketter, T., Lang, G., Schattner, U., 2020. Sediment transport mechanisms revealed by quantitative analyses of seafloor morphology: New evidence from multibeam bathymetry of the Israel exclusive economic zone. *Mar. Pet. Geol.* 114, 104224.
- Karl, D.M., Tien, G., 1992. MAGIC: A sensitive and precise method for measuring dissolved phosphorus in aquatic environments. *Limnol. Oceanogr.* 37, 105–116.
- Keuter, S., Silverman, J., Krom, M.D., Sisma-Ventura, G., Yu, J., Tsemel, A., Ben-Ezra, T., Sher, D., Reich, T., Koplovitz, G., Frada, M.J., 2022. Seasonal patterns of coccolithophores in the ultra-oligotrophic South-East Levantine Basin, Eastern Mediterranean Sea. *Mar. Micropaleontol.* 102153. <https://doi.org/10.1016/J.MARMICRO.2022.102153>
- Kress, N., Frede Thingstad, T., Pitta, P., Psarra, S., Tanaka, T., Zohary, T., Groom, S., Herut, B., Fauzi, R., Polychronaki, T., Rassoulzadegan, F., Spyres, G., 2005. Effect of P and N addition to oligotrophic Eastern Mediterranean waters influenced by near-shore waters: A microcosm experiment. *Deep. Res. Part II Top. Stud. Oceanogr.* 52, 3054–3073. <https://doi.org/10.1016/j.dsr2.2005.08.013>
- Kress, N., Gertner, Y., Shoham-Frider, E., 2020. Seawater quality at the brine discharge site from two mega size seawater reverse osmosis desalination plants in Israel (Eastern Mediterranean). *Water Res.* 171, 115402.
- Kress, N., Herut, B., 2001. Spatial and seasonal evolution of dissolved oxygen and nutrients in the Southern Levantine Basin (Eastern Mediterranean Sea): chemical characterization of the water masses and inferences on the N: P ratios. *Deep Sea Res. Part I Oceanogr. Res. Pap.* 48, 2347–2372.
- Kress, N., Herut, B., 1998. Hypernutrification in the oligotrophic Eastern Mediterranean: a study in Haifa Bay (Israel). *Estuar. Coast. Shelf Sci.* 46, 645–656.

- Kress, N., Rahav, E., Silverman, J., Herut, B., 2019. Environmental status of Israel's Mediterranean coastal waters: Setting reference conditions and thresholds for nutrients, chlorophyll-a and suspended particulate matter. *Mar. Pollut. Bull.* 141, 612–620. <https://doi.org/10.1016/J.MARPOLBUL.2019.02.070>
- Krom, M., Kress, N., Berman-Frank, I., Rahav, E., 2014. Past, present and future patterns in the nutrient chemistry of the eastern mediterranean, in: *The Mediterranean Sea: Its History and Present Challenges*. Springer Netherlands, Dordrecht, pp. 49–68. https://doi.org/10.1007/978-94-007-6704-1_4
- Krom, M.D., Kress, N., Brenner, S., Gordon, L.I., 1991. Phosphorus limitation of primary productivity in the eastern Mediterranean Sea. *Limnol. Oceanogr.* 36, 424–432. <https://doi.org/10.4319/lo.1991.36.3.0424>
- Krom, M.D., Woodward, E.M.S., Herut, B., Kress, N., Carbo, P., Mantoura, R.F.C., Spyres, G., Thingsted, T.F., Wassmann, P., Wexels-Riser, C., Kitidis, V., Law, C., Zodiatis, G., 2005. Nutrient cycling in the south east Levantine basin of the eastern Mediterranean: Results from a phosphorus starved system. *Deep. Res. Part II Top. Stud. Oceanogr.* 52, 2879–2896. <https://doi.org/10.1016/j.dsr2.2005.08.009>
- Letelier, R.M., Dore, J.E., Winn, C.D., Karl, D.M., 1996. Seasonal and interannual variations in photosynthetic carbon assimilation at Station. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 43, 467–490.
- Murphy, J., Riley, J.P., 1962. A modified single solution method for the determination of phosphate in natural waters. *Anal. Chim. Acta* 27, 31–36. [https://doi.org/10.1016/S0003-2670\(00\)88444-5](https://doi.org/10.1016/S0003-2670(00)88444-5)
- Neofitou, N., Klaoudatos, S., 2008. Effect of fish farming on the water column nutrient concentration in a semi-enclosed gulf of the Eastern Mediterranean. *Aquac. Res.* 39, 482–490.
- Nielsen, E.S., 1952. The use of radio-active carbon (c14) for measuring organic production in the sea. *ICES J. Mar. Sci.* 18, 117–140. <https://doi.org/10.1093/icesjms/18.2.117>
- Ounissi, M., Amira, A.B., Dulac, F., 2018. Riverine and wet atmospheric inputs of materials to a North Africa coastal site (Annaba Bay, Algeria). *Prog. Oceanogr.* 165, 19–34.
- Powley, H.R., Krom, M.D., Van Cappellen, P., 2017. Understanding the unique biogeochemistry of the Mediterranean Sea: Insights from a coupled phosphorus

- and nitrogen model. *Global Biogeochem. Cycles* 31, 1010–1031.
<https://doi.org/10.1002/2017GB005648>
- Psarra, S., Tselepides, A., Ignatiades, L., 2000. Primary productivity in the oligotrophic Cretan Sea (NE Mediterranean): seasonal and interannual variability. *Prog. Oceanogr.* 46, 187–204. [https://doi.org/10.1016/S0079-6611\(00\)00018-5](https://doi.org/10.1016/S0079-6611(00)00018-5)
- Pujo-Pay, M., Conan, P., Oriol, L., Cornet-Barthaux, V., Falco, C., Ghiglione, J.-F.F., Goyet, C., Moutin, T., Prieur, L., 2011. Integrated survey of elemental stoichiometry (C, N, P) from the western to eastern Mediterranean Sea. *Biogeosciences* 8, 883–899.
<https://doi.org/10.5194/bg-8-883-2011>
- Pulido-Villena, E., Rerolle, V., Guieu, C., 2010. Transient fertilizing effect of dust in P-deficient LNLC surface ocean. *Geophys. Res. Lett.* 37.
- Rahav, E., Raveh, O., Hazan, O., Gordon, N., Kress, N., Silverman, J., Herut, B., 2018. Impact of nutrient enrichment on productivity of coastal water along the SE Mediterranean shore of Israel - A bioassay approach. *Mar. Pollut. Bull.* 127, 559–567.
<https://doi.org/10.1016/j.marpolbul.2017.12.048>
- Rahav, E., Raveh, O., Yanuka-Golub, K., Belkin, N., Astrahan, P., Maayani, M., Tsumi, N., Kiro, Y., Herut, B., Silverman, J., 2020. Nitrate-Enrichment Structures Phytoplankton Communities in the Shallow Eastern Mediterranean Coastal Waters. *Front. Mar. Sci.* 1127.
- Raveh, O., David, N., Rilov, G., Rahav, E., 2015. The temporal dynamics of coastal phytoplankton and bacterioplankton in the eastern mediterranean sea. *PLoS One* 10, e0140690. <https://doi.org/10.1371/journal.pone.0140690>
- Reich, T., Ben-Ezra, T., Belkin, N., Tsemel, A., Aharonovich, D., Roth-Rosenberg, D., Givati, S., Bialik, M., Herut, B., Berman-Frank, I., Frada, M., Krom, M.D., Lehahn, Y., Rahav, E., Sher, D., 2022. A year in the life of the Eastern Mediterranean: Monthly dynamics of phytoplankton and bacterioplankton in an ultra-oligotrophic sea. *Deep. Res. Part I Oceanogr. Res. Pap.* 182, 103720. <https://doi.org/10.1016/j.dsr.2022.103720>
- Rekik, A., Ayadi, H., Elloumi, J., 2020. Spatial and seasonal variability of the planktonic ciliates assemblages along the Eastern Mediterranean Coast (Sfax coast, Tunisia). *Reg. Stud. Mar. Sci.* 40, 101529.
- Rubin-Blum, M., Sisma-Ventura, G., Yudkovski, Y., Belkin, N., Kanari, M., Herut, B., Rahav, E., 2022. Diversity, activity, and abundance of benthic microbes in the Southeastern Mediterranean Sea. *FEMS Microbiol. Ecol.* 98, fiac009.

- SEAL Analytical, 2011a. Ammonia in water and seawater. AutoAnalyzer Appl. G-327-05.
- SEAL Analytical, 2011b. Nitrate and Nitrite in water and seawater Total Nitrogen in persulfate digests. AutoAnalyzer Appl. G-172-96.
- Simboura, N., Zenetos, A., Pancucci-Papadopoulou, M.A., 2014. Benthic community indicators over a long period of monitoring (2000-2012) of the Saronikos Gulf, Greece, Eastern Mediterranean. *Environ. Monit. Assess.* 186, 3809–3821.
<https://doi.org/10.1007/s10661-014-3659-z>
- Siokou-Frangou, I., Christaki, U., Mazzocchi, M.G., Montresor, M., Ribera d'Alcalá, M., Vaqué, D., Zingone, A., 2010. Plankton in the open Mediterranean Sea: a review. *Biogeosciences* 7, 1543–1586.
- Souvermezoglou, E., Krasakopoulou, E., Pavlidou, A., 2014. Temporal and spatial variability of nutrients and oxygen in the North Aegean Sea during the last thirty years. *Mediterr. Mar. Sci.* 15, 805–822. <https://doi.org/10.12681/mms.1017>
- Suari, Y., Dadon-Pilosof, A., Sade, T., Amit, T., Gilboa, M., Gafny, S., Topaz, T., Zedaka, H., Boneh, S., Yahel, G., 2019. A long term physical and biogeochemical database of a hyper-eutrophicated Mediterranean micro-estuary. *Data Br.* 27, 104809.
- Thingstad, T.F., Krom, M.D., Mantoura, R.F.C., Flaten, C.A.F., Groom, S., Herut, B., Kress, N., Law, C.S., Pasternak, A., Pitta, P., Psarra, S., Rassoulzadegan, F., Tanaka, T., Tselepides, A., Wassmann, P., Woodward, E.M.S., Riser, C.W., Zodiatis, C., Zohary, T., 2005. Nature of phosphorus limitation in the ultraoligotrophic eastern Mediterranean. *Science* (80-.). 309, 1068–1071.
<https://doi.org/10.1126/science.1112632>
- Thingstad, T.F., Skjoldal, E.F., Böhne, R.A., 1993. Phosphorus cycling and algal-bacterial competition in Sandsfjord, western Norway.
- Townsend, D.W., Christensen, J.P., Berman, T., Walline, P., Schneller, A., Yentsch, C.S., 1988. Near-bottom chlorophyll maxima in Southeastern Mediterranean shelf waters: upwelling and sediments as possible nutrient sources. *Oceanol. Acta SP* 235–244.
- Varkitzi, I., Markogianni, V., Pantazi, M., Pagou, K., Pavlidou, A., Dimitriou, E., 2018. Effect of river inputs on environmental status and potentially harmful phytoplankton in a coastal area of eastern Mediterranean (Maliakos Gulf, Greece). *Mediterr. Mar. Sci.* 19, 326–343.
- Volpe, G., Colella, S., Brando, V.E., Forneris, V., La Padula, F., Di Cicco, A., Sammartino, M.,

- Bracaglia, M., Artuso, F., Santoleri, R., 2019. Mediterranean ocean colour Level 3 operational multi-sensor processing. *Ocean Sci.* 15, 127–146.
- Volpe, G., Nardelli, B.B., Colella, S., Pisano, A., Santoleri, R., 2018. Operational Interpolated Ocean Colour Product in the Mediterranean Sea. *New Front. Oper. Oceanogr.* 227–244.
- Wasmund, N., Andrushaitis, A., Łysiak-Pastuszek, E., Müller-Karulis, B., Nausch, G., Neumann, T., Ojaveer, H., Olenina, I., Postel, L., Witek, Z., 2001. Trophic status of the south-eastern Baltic Sea: a comparison of coastal and open areas. *Estuar. Coast. Shelf Sci.* 53, 849–864.
- Zaafraane, S., Maatouk, K., Akrouf, F., Trabelsi, I., Drira, N., 2019. Spatio-temporal distribution of physicochemical and bacteriological parameters in the north area of Monastir bay, eastern coast of Tunisia. *Arab. J. Geosci.* 12, 1–18.
<https://doi.org/10.1007/S12517-019-4386-0/TABLES/4>
- Zubkov, M. V., Martin, A.P., Hartmann, M., Grob, C., Scanlan, D.J., 2015. Dominant oceanic bacteria secure phosphate using a large extracellular buffer. *Nat. Commun.* 2015 616, 1–8. <https://doi.org/10.1038/ncomms8878>