



חקר ימים ואגמים לישראל  
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# דו"חות חיא"ל IOLR REPORTS

**Pelagic habitats in the  
Exclusive Economic Zone of  
the Israeli Mediterranean Sea**

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## **Abstract**

The pelagic habitats of the Israeli EEZ (exclusive economic zone) provide essential ecosystem functions and services, and yet they are increasingly exposed to anthropogenic stressors. This report provides a framework for the inclusion of pelagic habitats in the “Israeli EEZ MPAs masterplan” that aims to use systematic conservation planning, balancing conservation and economic development.

The poor spatial coverage of the biological data from the pelagic zone in the Israeli EEZ has led to the use of physicochemical surrogates for delineating bioregions. Key environmental parameters were obtained from the ISRAMAR database and averaged per significant depth layer, corresponding to distinct water masses. Among layers, summer SST and dissolved oxygen showed high coherence and were used for the delineation of three thermal bioregions and high-low oxygen bioregions. The relative frequencies of cyclonic and anticyclonic eddies were used to delineate two additional bioregions. Such mesoscale eddies form a mosaic of environmental conditions that can facilitate the transport and proliferation of pelagic biodiversity and are especially important in the ultra-oligotrophic, rapidly warming, southeastern Mediterranean Sea. The pelagic waters of the Palmahim disturbance area were defined as a bioregion due to benthic-pelagic coupling. Biological data indicated hotspots of plankton abundance and diversity in the epipelagic zone above the continental slope, which was therefore delineated as a separate bioregion. All pelagic bioregions were provided to the Marxan model for spatial conservation prioritization.

Further updates of the pelagic bioregionalization of the Israeli EEZ should include a larger spatiotemporal coverage of biotic parameters in the water column and incorporate higher trophic levels.

# 1. Introduction

## 1.1 *The ecological importance of marine pelagic ecosystems*

Marine pelagic ecosystems – the physical, chemical and biological features of the marine water column – comprise 99% of Earth’s biosphere and provide essential ecosystem services (Game et al., 2009). These include climate regulation by absorbing nearly 35% of the carbon released into the atmosphere and 80% of the heat (Charlson et al., 1987), acting as the main net source of atmospheric oxygen (Kasting and Siefert, 2002), providing over 60% of the global fish supply (Msangi et al., 2013), provisioning of more than 15% of the animal nutrients consumed (Dickey-Collas et al., 2017), and facilitating transportation of 90% of the international trade (Lee and Meng, 2014).

Anthropogenic threats to pelagic ecosystems include pollution (e.g., oil spills and plastic debris), climate change, overfishing, eutrophication, mining, oil and gas exploration, and the introduction of invasive species (Game et al., 2009; Robison, 2009). These threats can have an additive or synergistic impact on pelagic ecosystems, leading to changes in the composition of species and shifts in ecosystem functioning and services. Such impacts have already manifested in major marine biodiversity declines (Halpern et al., 2008; Díaz et al., 2019; Pörtner et al., 2022).

Despite their evident importance and the major threats facing them, the protection of pelagic ecosystems is widely lagging behind coastal and benthic habitats. Uncertainties surrounding the feasibility and utility of protected areas in pelagic environments have limited the establishment of pelagic protected areas (Game et al., 2009; Kaplan et al., 2010). Only 2% of the global MPA network is located in pelagic waters, while the majority is located in coastal and shelf waters (Halpern et al., 2008; Devillers et al., 2015).

## 1.2 *Pelagic bioregionalization*

Bioregionalization is a process that aims to classify a geographic area into broad-scale, biologically meaningful units, based on a set of physical and biological variables, and/or human-use characteristics. The goal of bioregionalization is to create management units that reflect the unique characteristics and needs of different areas and to ensure that management decisions are tailored to the specific conditions of each bioregion (Costello, 2009; Grantham et al., 2010).

Pelagic bioregionalization classifies water masses at a given spatial scale as habitats with spatially explicit boundaries (Roberson et al., 2017). The bioregionalization of discrete pelagic habitats is a complex and challenging task, mainly due to high levels of spatiotemporal complexity and dynamics of the ocean ecosystems, conveying three-dimensional layers that do not necessarily correspond (Grantham et al., 2011), a lack of data or data-poor deep sea and remote offshore areas (Leathwick et al., 2008), and the wide range of human activities that impact the open ocean (Game et al., 2009). Nonetheless, several global and regional pelagic bioregionalization schemes have been developed, which use surrogate physicochemical variables and related parameters measured in-situ or extracted from remote sensing data and integrated in a cluster analysis (Roberson et al., 2017). These parameters include

depth strata, temperature, turbidity, salinity, nutrients, Chlorophyll *a*, oxygen, and their seasonal and annual variability.

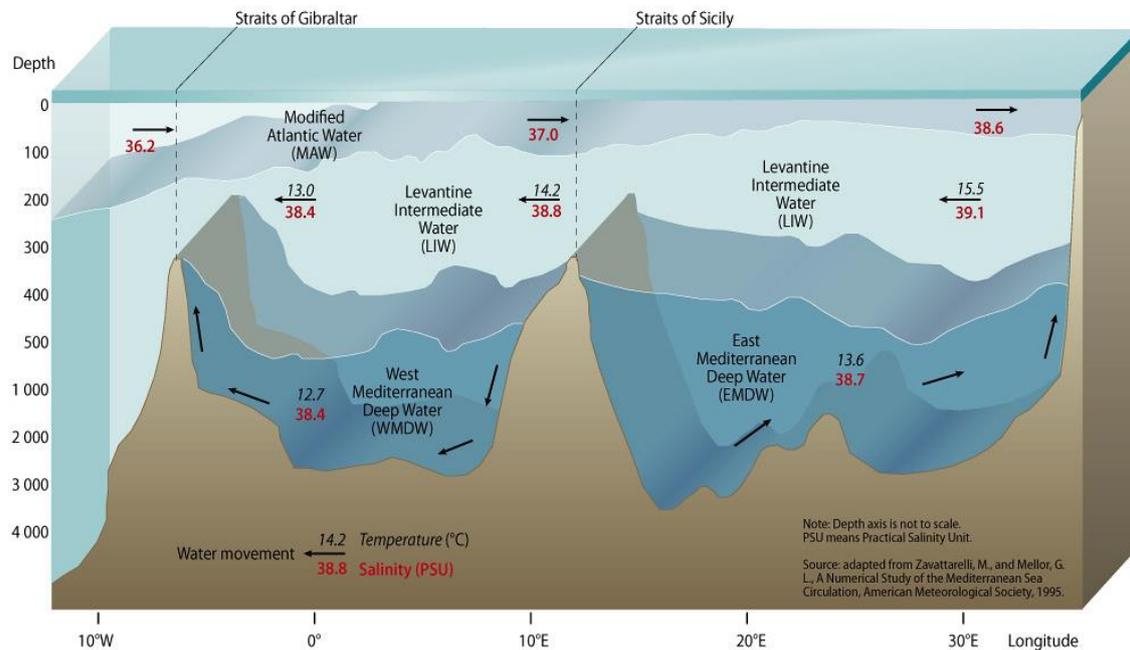
Spatiotemporal variation of currents and eddies has been suggested to have a significant impact on pelagic biomass (Goldthwait and Steinberg, 2008). Mesoscale eddies are closed circular currents, ranging from a few to hundreds of kilometers in diameter. They form partially isolated environments with distinct physical and chemical conditions, supporting and transporting whole plankton communities, including eggs and larvae of many benthic and nekton organisms (Shulzitski et al., 2016). Eddies create attractive pelagic habitats, analogous to oases in the desert, for higher trophic level aquatic organisms through enhanced 3D motion that accumulates and redistributes biomass, contributing to overall bioproduction in the ocean (Owen, 1981). Eddies frequency has been thus recommended as a key parameter in pelagic bioregionalization (Robison, 2009). In the Southeastern Mediterranean Sea, eddy Lagrangian tracking for the period 2000-2018 showed a complex and persistent eddy activity displaying extreme subsurface temperature and salinity anomalies (Barboni et al., 2021). A recent study in the Israeli EEZ found that the biomass and diversity of zooplankton in a cold-core cyclonic eddy was one size of magnitude larger than the surrounding waters (Belkin et al., 2022), supporting the use of eddies frequency as an important parameter for the regional pelagic bioregionalization.

### 1.3 *Vertical water masses as distinct pelagic habitats in the Israeli EEZ*

Oceanic water masses can be considered discrete pelagic habitats based on the distinct physical and biological characteristics that they possess (Sutton, 2013; Johnston et al., 2019). These characteristics include differences in temperature, salinity, oxygen levels, and nutrient concentrations, which in turn can influence the distribution and abundance of marine organisms.

The southeastern Mediterranean is characterized by the highest temperature and salinities in the Mediterranean Sea, and includes four distinct water masses (Fig. 1). The uppermost layer, Levantine Surface Water (LSW, 0-50 m) is created from the Atlantic Water (AW) as they propagate eastward (forming the Modified Atlantic Water, MAW), through heating and evaporation. During the summer, the depth of the LSW is determined by a balance between the mixing of the halocline and the seasonal thermocline, which prevents the vertical mixing of the LSW with the colder, less saline, AW. The formation of Levantine Intermediate Water (LIW) water mass occurs when the LSW cools down and sinks to intermediate depths of 130-400 m, usually in the area of the Rhodes Gyre (Lascaratos et al., 1999) or along the continental margins of the Levantine Basin (Özsoy et al., 1989). The LIW mass flows westward across the entire Mediterranean Sea in the opposite direction below the MAW. The East Mediterranean Deep Water (EMDW) originates from the Adriatic Sea. During the early 1990s, a rapid replacement of the EMDW with a newer, warmer and more saline water mass took place, known as the Eastern Mediterranean Transient (EMT). Decadal reversals in the circulation of the North Ionian Gyre, also known as the Bimodal Oscillating system (BiOS), were suggested as the cause of the EMT. Ozer et al. (2017) found corresponding decadal trends in temperature, salinity, nutrients and primary

productivity levels in the LSW and LIW of the Eastern Basin, suggesting that long-term and interannual analyses of these factors should consider this source of variation.



**Figure 1.** The vertical zonation of Mediterranean Sea water masses. Direction (arrows), temperature (in black) and salinity (in red) are presented for each water mass. Adapted from Zavattarelli and Mellor (1995).

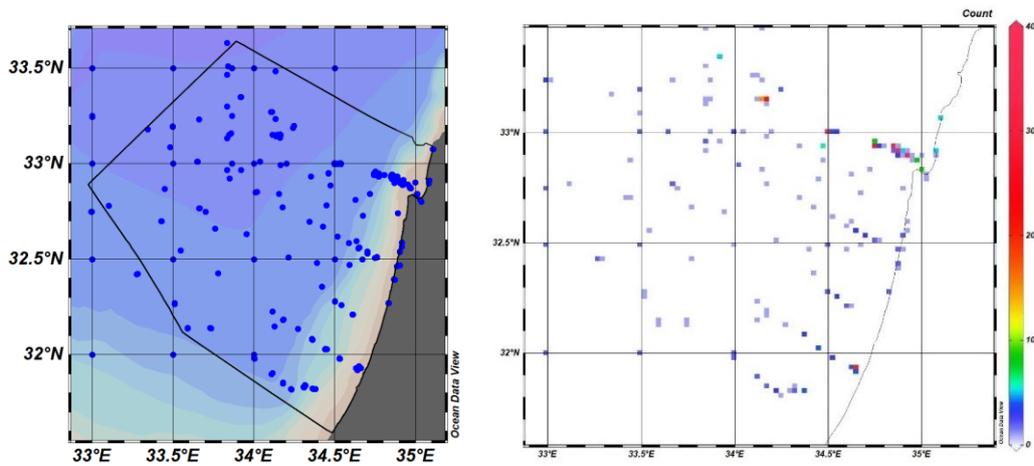
#### 1.4 Benthic-pelagic coupling and lateral transport

Although vertical zonation of discrete water masses can define different pelagic habitats, the use of vertical zoning for defining marine protected areas was not recommended by the IUCN since vertically tiered management is particularly difficult, if not impossible, to effectively police and enforce (Day et al., 2012). Moreover, there is increasing evidence of strong linkages between benthic and pelagic components of the ecosystem. These linkages, termed benthic-pelagic coupling, are characterized by the exchange of energy, mass, or nutrients between benthic and pelagic habitats (Marcus and Boero, 1998). They play a prominent role in marine ecosystems and are crucial to functions from nutrient cycling to energy transfer in food webs. Processes shaping benthic-pelagic coupling include the deposition of organic material, resuspension, the release of inorganic nutrients from the sediment, pelagic predation on benthic fauna, ontogenetic shifts in habitat use, reproductive fluxes, diel and seasonal migrations, nutrient-cycling effects of benthic bioturbation, and filter-feeding by benthic organisms (Griffiths et al., 2017). A holistic food web model of the Mediterranean Sea showed that functional groups that can move on large spatial scales or life history of which is spent between the continental shelf and slope play a key role in linking benthic and pelagic ecosystems (Agnetta et al., 2019). In the Israeli EEZ, the deep-sea megafauna is significantly impacted by carbon sources from the continental shelf margin and slope (Guy-Haim et al., 2022), likely by means of lateral transport (Katz et al., 2020). Also, it has been shown that the biogeochemistry of the water column overlaying the unique chemosynthetic ecosystem in Palmahim disturbance is affected by the methane seeps below (Sisma-Ventura et al., 2022),

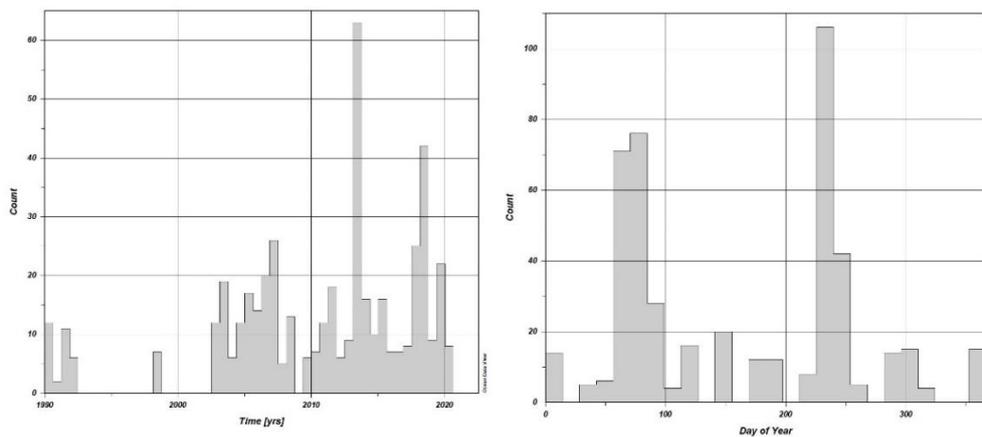
## 2. 2. Materials and methods

### 2.1 Data collection

Cast data was obtained from the Israel Marine Data Center ([ISRAMAR, https://isramar.ocean.org.il/isramar\\_data/CastMap.aspx](https://isramar.ocean.org.il/isramar_data/CastMap.aspx)) from cruises that were included with the Israeli EEZ (Fig. 2). Data collected from the continental shelf was included if it was not limited to the shelf region (e.g., all stations in Haifa Transect monitoring cruises were included). The Data span was 1990-2022, with >95% of the data collected after 2003, during February-April (winter) or July-September (summer) (Fig. 3). Variables were gridded in a 2x2 km resolution using kriging interpolation method.



**Figure 2.** ISRAMAR casts data (1990-2022) used in the analysis. **A.** the location of the sampling stations in the Israeli EEZ. **B.** Sampling data density.



**Figure 3.** ISRAMAR casts data (1990-2022) used in the analysis. **A.** Sampling years. **B.** Sampling dates.

### 2.2 Physicochemical parameters

The following layers were obtained from ISRAMAR based on discrete depths corresponding with LSW, DCM (Deep Chlorophyll Maximum), MAW, LIW, and EMDW. Seasonal data (Winter: December-April, Summer: June-September) was obtained for the upper layers (<200 m).

- 2.2.1 Temperature [°C]:  
depths 3, 100 m (summer/winter); 200, 500 and 1000 m.
- 2.2.2 Salinity [PSU]:  
depths 3, 100 m (summer/winter); 200, 500 and 1000 m.
- 2.2.3 Dissolved Oxygen concentration [ $\mu\text{mol/kg}$ ]:  
depths 3, 100 m (summer/winter); 200, 500 and 1000 m.
- 2.2.4 Nitrate+Nitrite ( $\text{NO}_x$ ) concentration [ $\mu\text{mol/kg}$ ]:  
depths 3, 100 m (summer/winter); 200, 500 and 1000 m.
- 2.2.5 Phosphate ( $\text{PO}_4$ ) concentration [ $\mu\text{mol/kg}$ ]:  
depths 200, 500 and 1000 m. In the surface layers, the concentration of phosphate was below detection level.
- 2.2.6 Silicate ( $\text{SiO}_4$ ) concentration [ $\mu\text{mol/kg}$ ]:  
depths 3, 100 m (summer/winter); 200, 500 and 1000 m.
- 2.2.7 Chlorophyll a concentration [ $\text{mg/m}^3$ ]:  
depths 3, 50, 100 m (summer/winter); 200 m.
- 2.2.8 Eddies frequency was characterized using a 19-year atlas of Mediterranean mesoscale eddies detected with the Angular Momentum Eddy Detection and tracking Algorithm (Le Vu et al., 2018), <https://www.lmd.polytechnique.fr/dyned>. The areas influenced by cyclonic and anticyclonic eddies during 2000-2018 standardized by their lifetimes were calculated as the geometric convex hull of their trajectories buffered by their detected radius at each timestep (Gilboa, Lazar and Guy-Haim, in prep).

### 2.3 *Biological data*

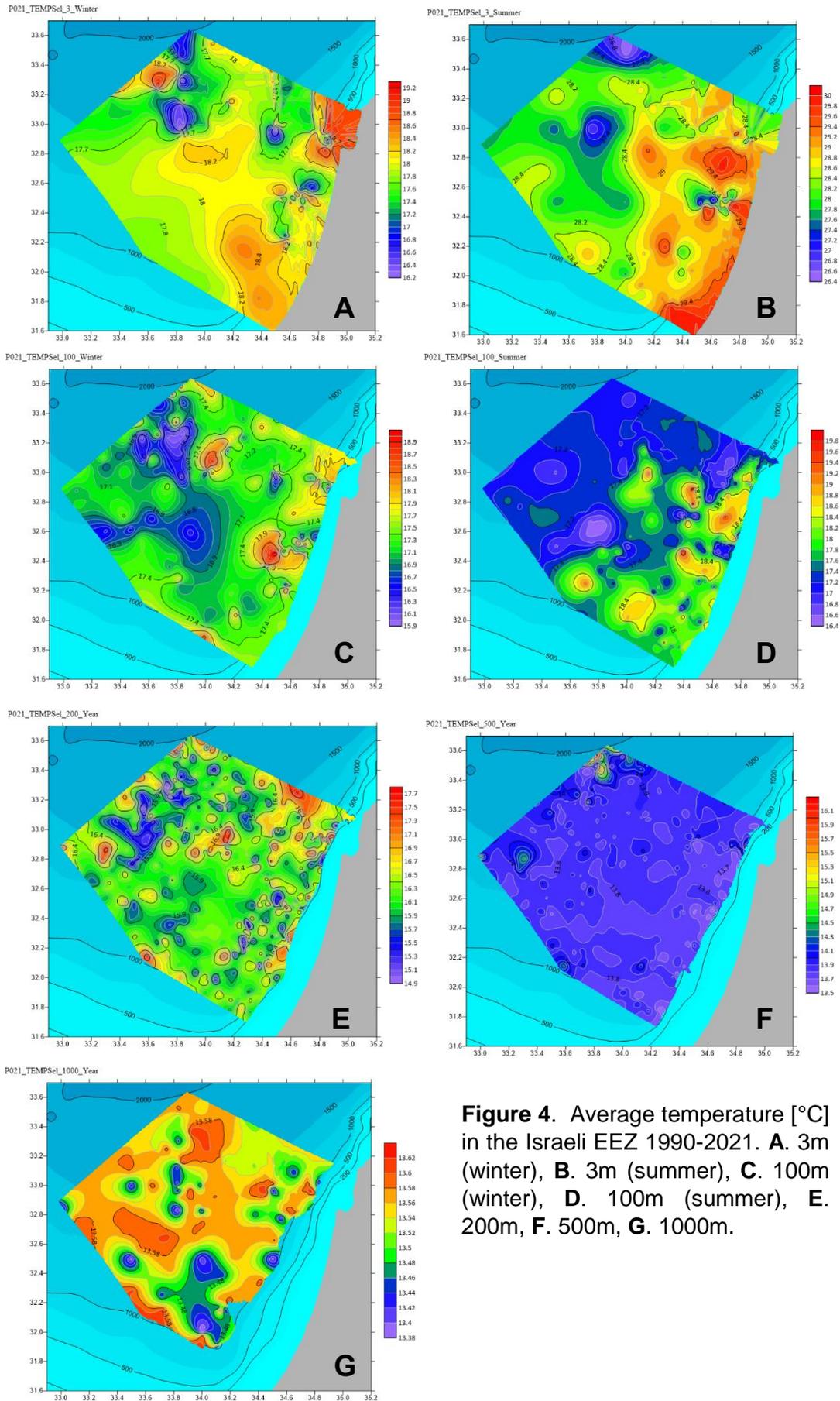
The biological data obtained from ISRAMAR and IOLR monitoring reports (2013-2022) was spatially restricted to IOLR's Haifa Transect (zooplankton) or extended Haifa and Southern Transect (bacterial and primary producer abundance, diversity and productivity), and to haphazard sampling mainly along Haifa Transect (ichthyoplankton).

- 2.3.1 Bacterial abundance, diversity and productivity (by vertical layers: LSW, DCM, MAW, LIW, EMDW)
- 2.3.2 Abundance and productivity of primary producers in epipelagic waters
- 2.3.3 Zooplankton biomass concentration and diversity (by vertical layers: LSW, DCM, MAW, LIW, EMDW)
- 2.3.4 Ichthyoplankton (fish larvae and eggs) abundance and richness in the neuston (sea surface boundary layer)

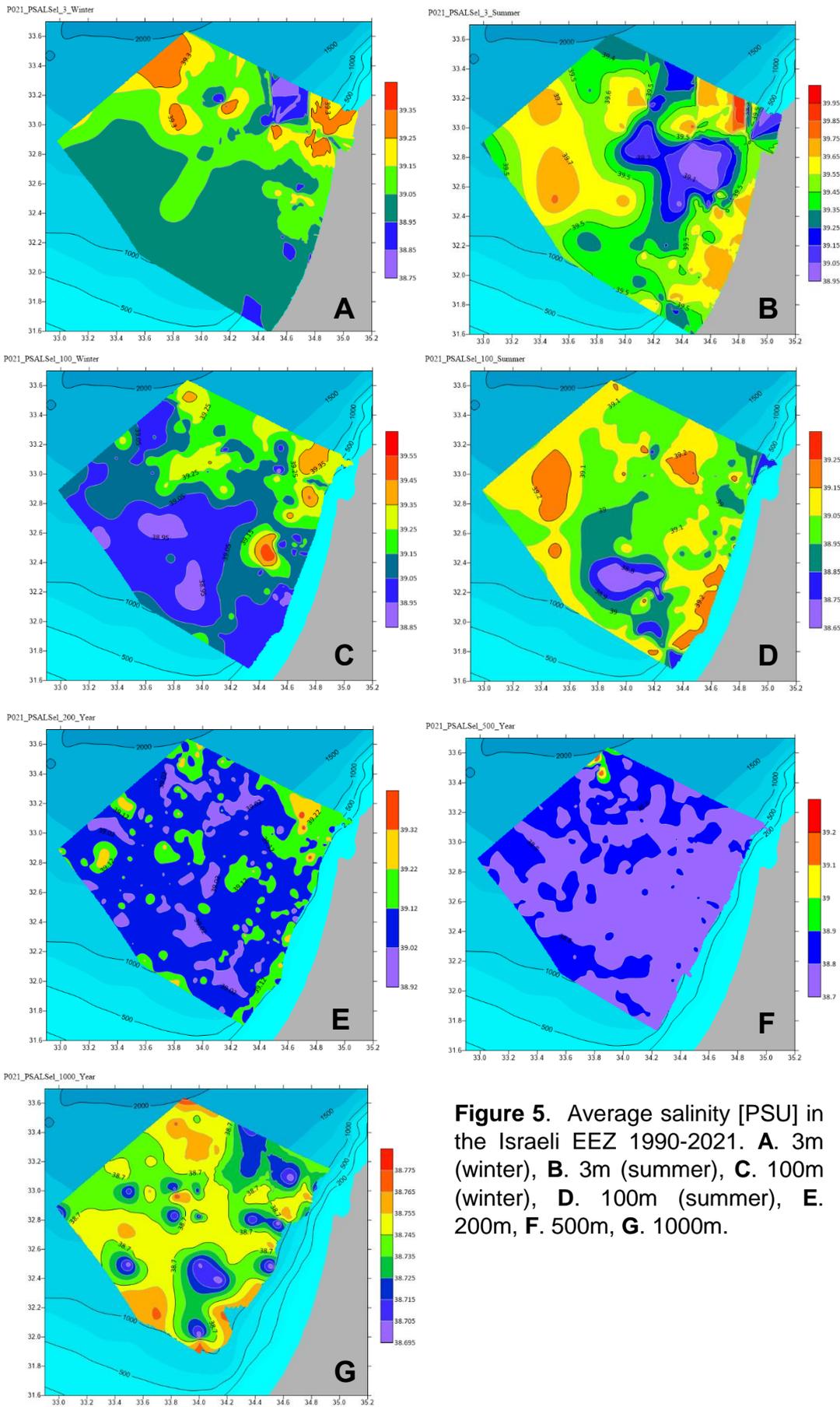
## 3. Results

### 3.1 *Physicochemical layers and corresponding bioregions*

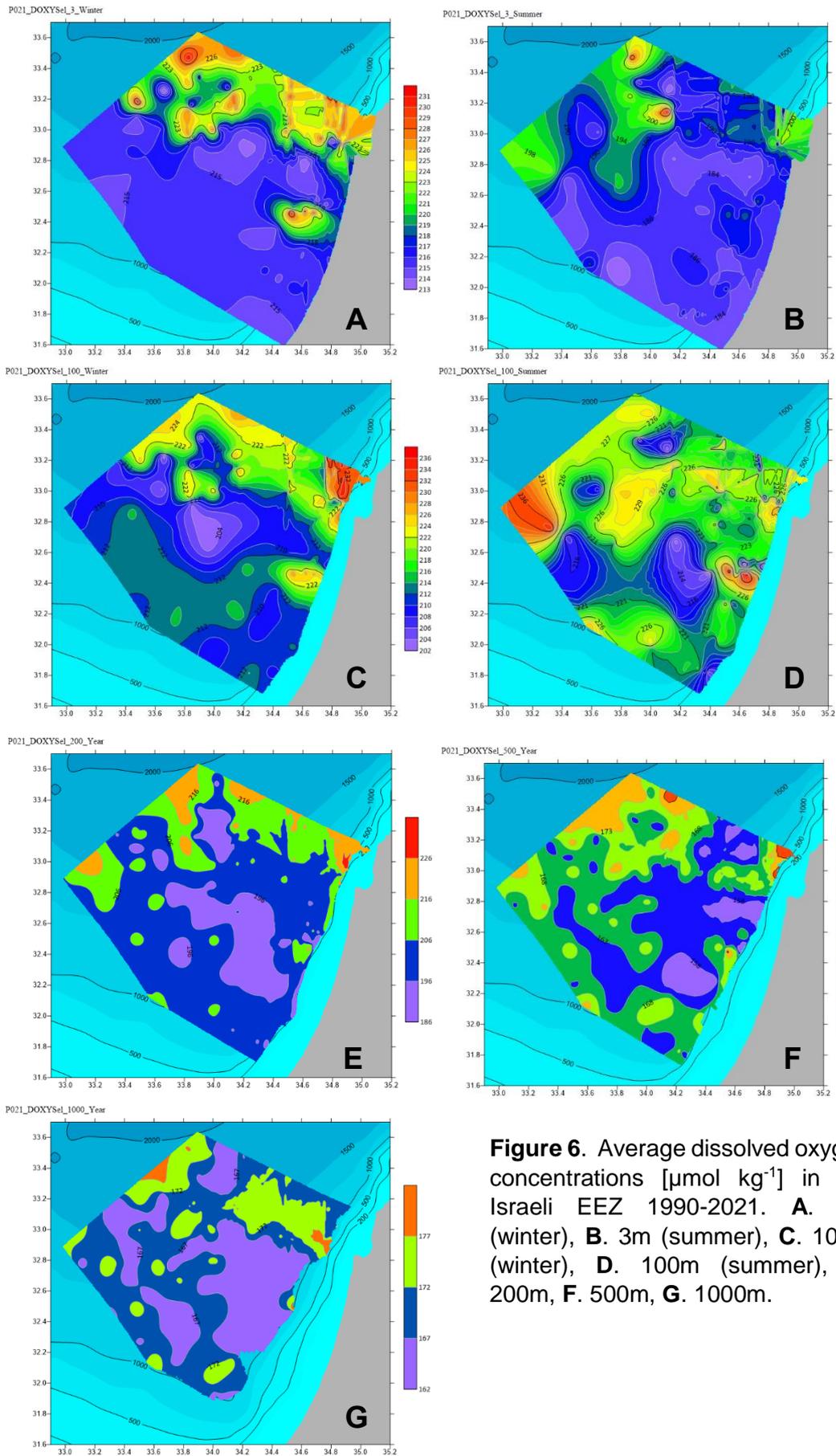
Relevant parameters that best reflect the key ecosystem properties were chosen. The following maps (Figs. 4-9) depict the key parameters per vertical layer averaged per season in the epipelagic zone (0-200 m) or annually in deeper depths (>200 m). The depth layers, corresponding to water mass delimitation, showed marked spatial heterogeneity for the majority of the parameters, which could partly be explained by mesoscale features (Fig. 10).



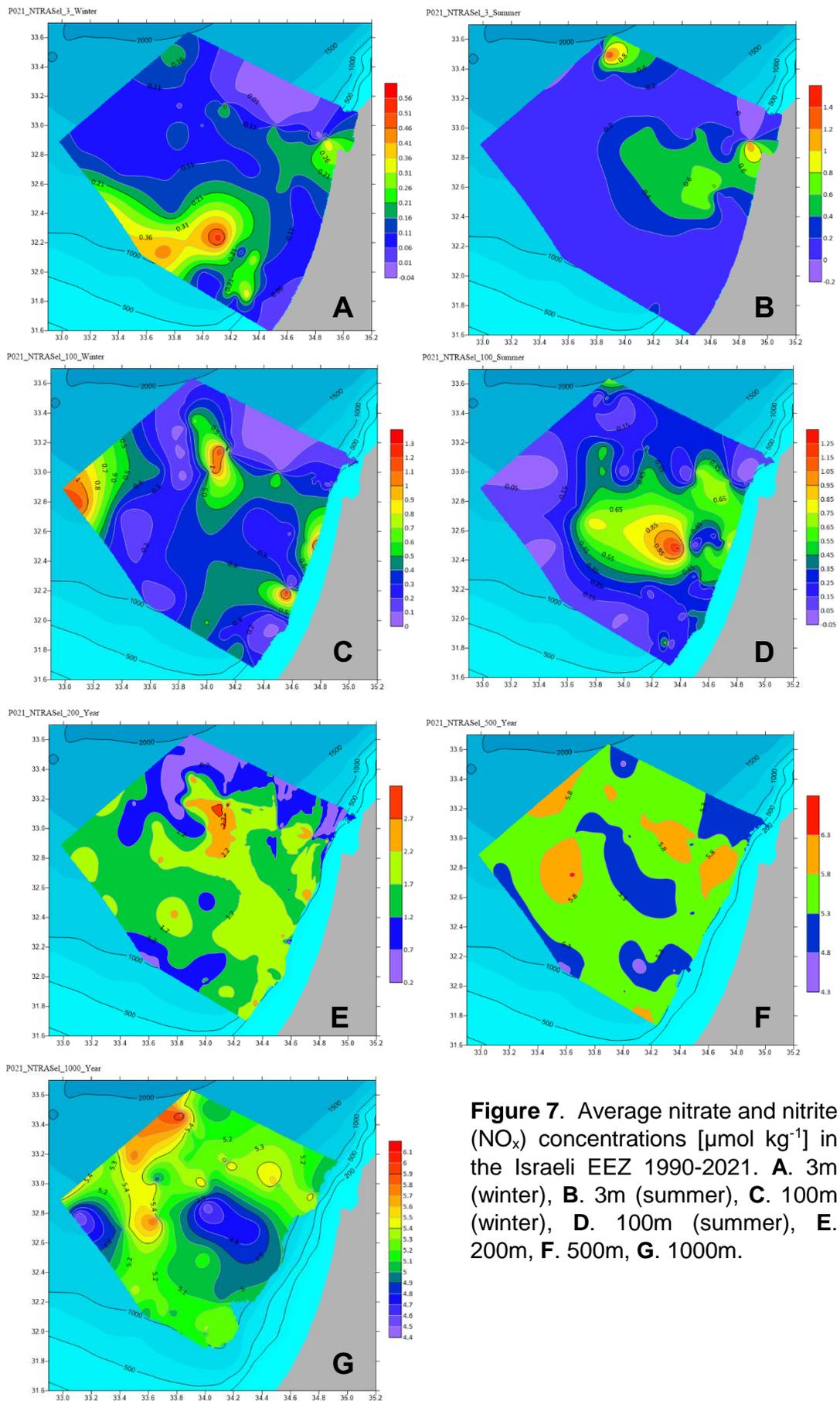
**Figure 4.** Average temperature [ $^{\circ}\text{C}$ ] in the Israeli EEZ 1990-2021. **A.** 3m (winter), **B.** 3m (summer), **C.** 100m (winter), **D.** 100m (summer), **E.** 200m, **F.** 500m, **G.** 1000m.



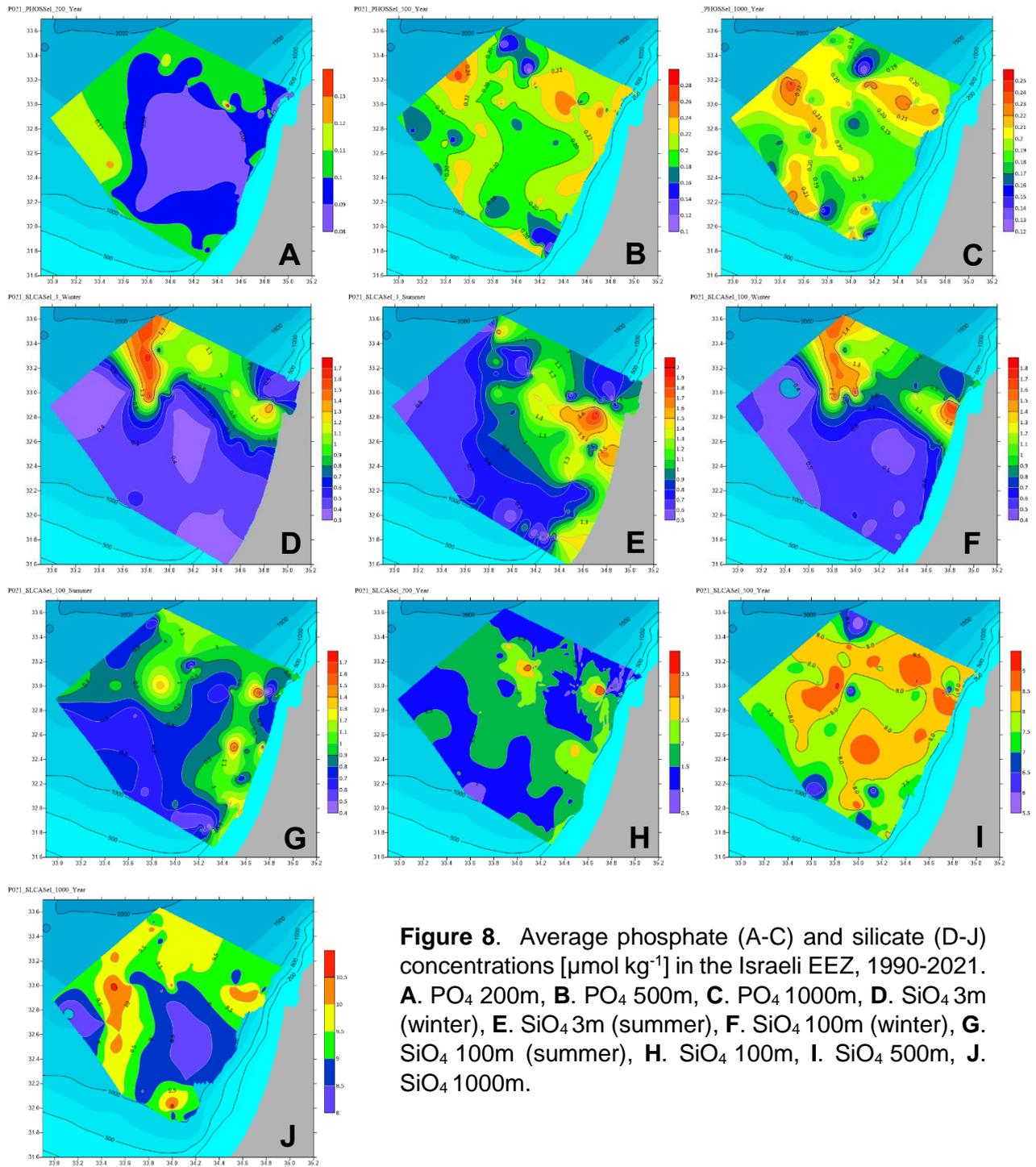
**Figure 5.** Average salinity [PSU] in the Israeli EEZ 1990-2021. **A.** 3m (winter), **B.** 3m (summer), **C.** 100m (winter), **D.** 100m (summer), **E.** 200m, **F.** 500m, **G.** 1000m.



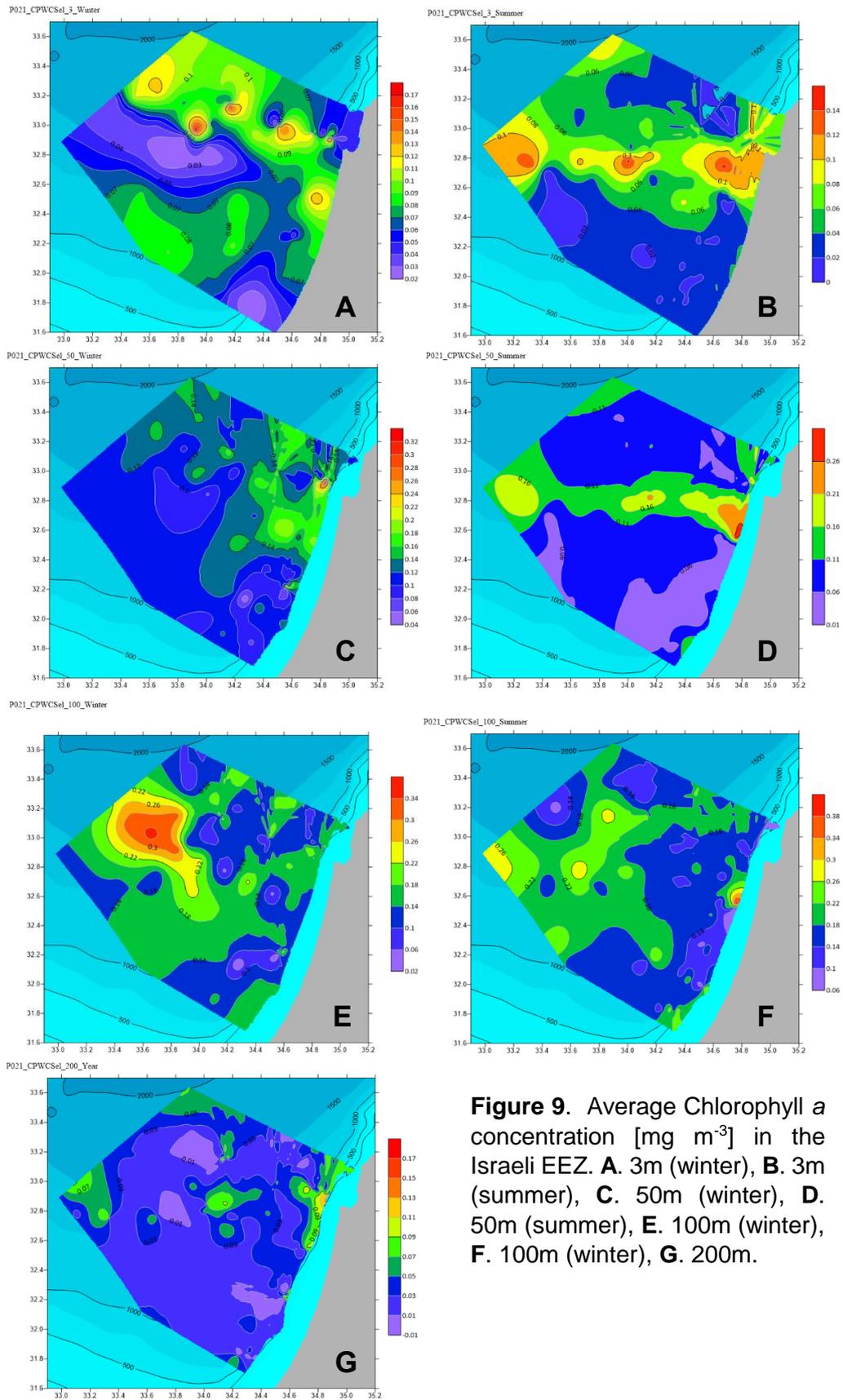
**Figure 6.** Average dissolved oxygen concentrations [ $\mu\text{mol kg}^{-1}$ ] in the Israeli EEZ 1990-2021. **A.** 3m (winter), **B.** 3m (summer), **C.** 100m (winter), **D.** 100m (summer), **E.** 200m, **F.** 500m, **G.** 1000m.



**Figure 7.** Average nitrate and nitrite ( $\text{NO}_x$ ) concentrations [ $\mu\text{mol kg}^{-1}$ ] in the Israeli EEZ 1990-2021. **A.** 3m (winter), **B.** 3m (summer), **C.** 100m (winter), **D.** 100m (summer), **E.** 200m, **F.** 500m, **G.** 1000m.



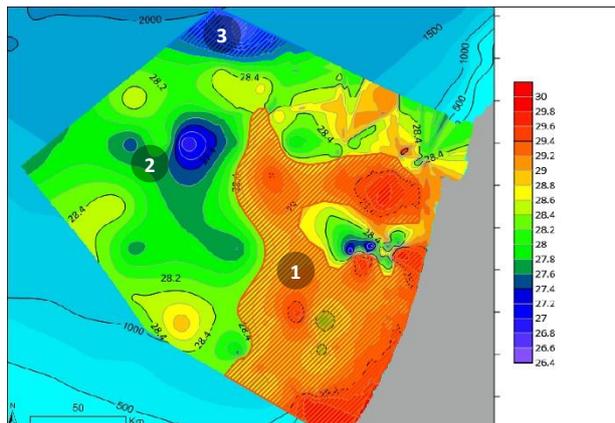
**Figure 8.** Average phosphate (A-C) and silicate (D-J) concentrations [ $\mu\text{mol kg}^{-1}$ ] in the Israeli EEZ, 1990-2021. **A.** PO<sub>4</sub> 200m, **B.** PO<sub>4</sub> 500m, **C.** PO<sub>4</sub> 1000m, **D.** SiO<sub>4</sub> 3m (winter), **E.** SiO<sub>4</sub> 3m (summer), **F.** SiO<sub>4</sub> 100m (winter), **G.** SiO<sub>4</sub> 100m (summer), **H.** SiO<sub>4</sub> 100m, **I.** SiO<sub>4</sub> 500m, **J.** SiO<sub>4</sub> 1000m.



**Figure 9.** Average Chlorophyll a concentration [mg m<sup>-3</sup>] in the Israeli EEZ. **A.** 3m (winter), **B.** 3m (summer), **C.** 50m (winter), **D.** 50m (summer), **E.** 100m (winter), **F.** 100m (summer), **G.** 200m.

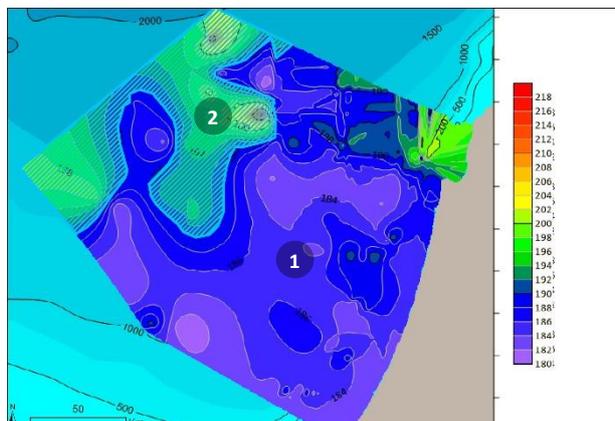
Since the stability of the physicochemical layers and their coherence are greater during summertime, summer SST and dissolved oxygen levels were chosen for bioregion delineation.

Summer SST isotherms 28.4 °C and 27.6 °C were chosen to delineate three thermal bioregions (Fig. 10): (1) warm region at the south and center of the continental shelf and slope extending to the continental rise in the central EEZ, with a protrusion in front of Haifa and an enclave south of it, likely caused by the consistent cyclonic activity of that area (Fig. 12D); (2) cold region at the northmost EEZ tip; (3) mid-thermal region.



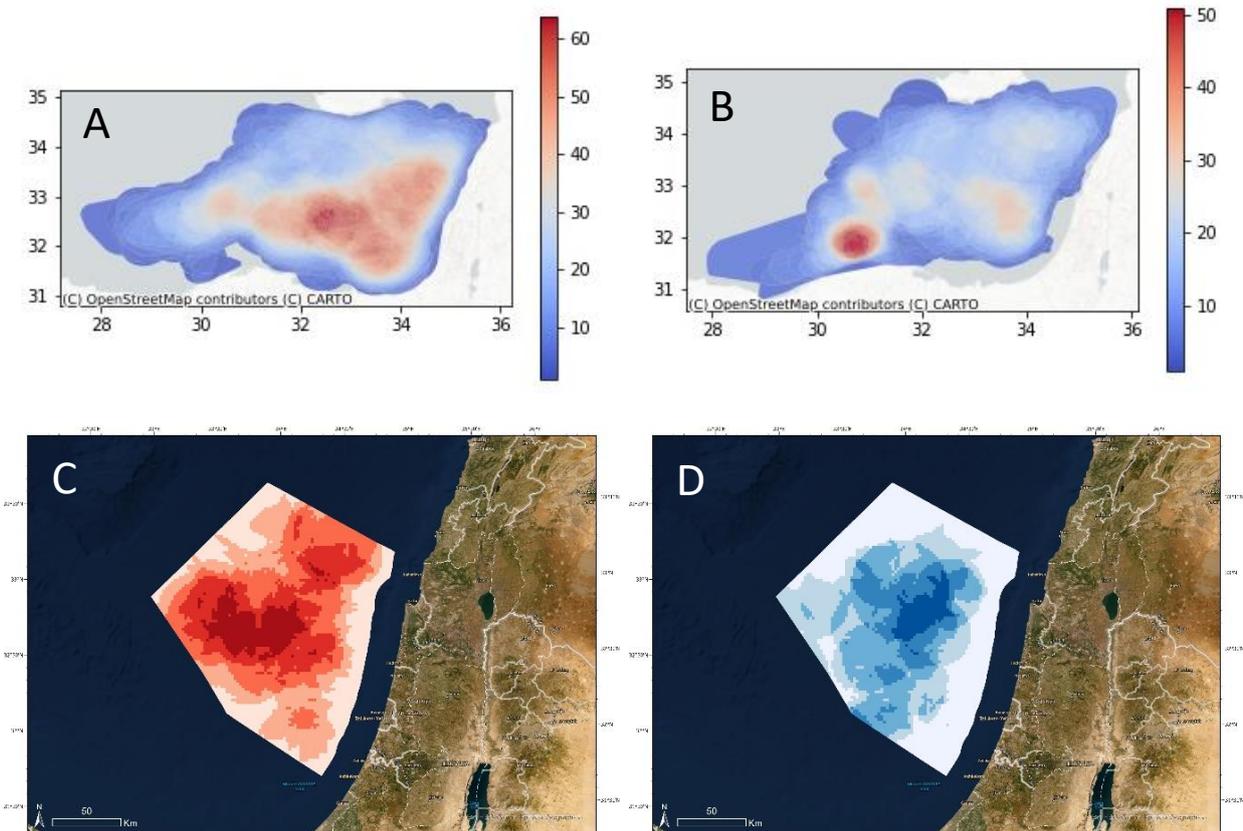
**Figure 10.** Thermal bioregions based on summer average SST data.

Similarly, two bioregions were delimited based on summer average surface dissolved oxygen levels, delineating the lower (1) and higher (2) oxygen regions at the northeast EEZ (Fig. 11).



**Figure 11.** Bioregions based on summer average surface dissolved oxygen data.

The frequency of cyclonic mesoscale eddies based on the DYNED atlas was highest in the mid-EEZ region, and of anticyclonic eddies – in the mid-west (Fig. 12C,D), with an average longevity of 100-125 days.

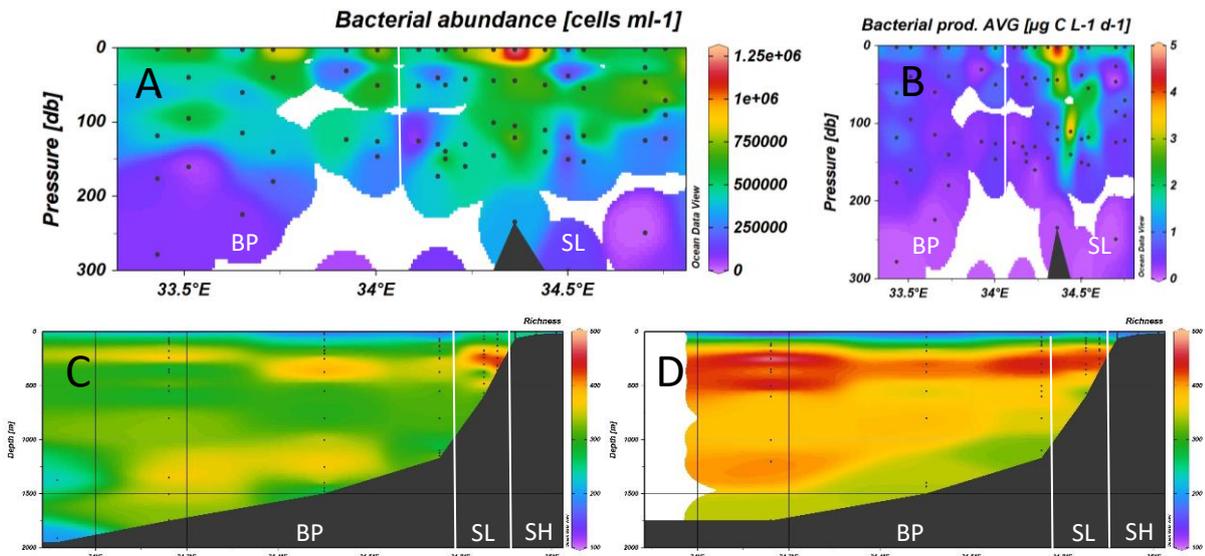


**Figure 12.** Mesoscale eddies frequency (A – anticyclones; B – cyclones) in the Southeastern Mediterranean Sea and the corresponding bioregions in the Israeli EEZ (C – anticyclones; D – cyclones). Color scales represent the number of eddies standardized by their duration.

### 3.2 *Biological parameters and bioregionalization*

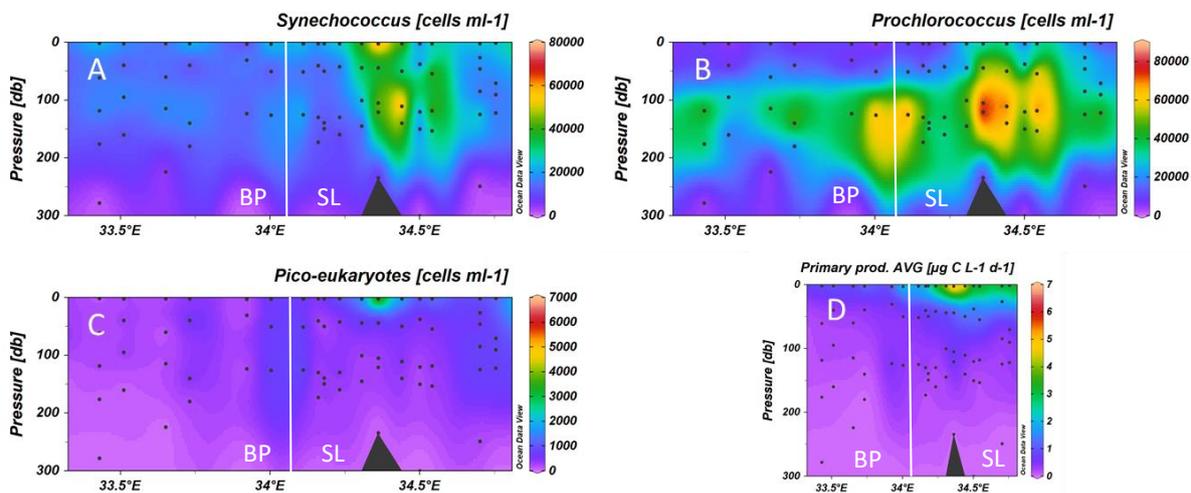
The spatial resolution of the biological data samples restricts the bioregionalization analysis to vertical and longitudinal trends.

Bacterial abundance and productivity in the epipelagic zone (Fig. 13A-B) showed a general decreasing trend from the surface to 300 m depth. The highest bacterial diversity was found in the mesopelagic LIW waters from the deep shelf to the slope and the bathyal plain (Fig. 13C-D). The epipelagic waters above the continental slope (34.35°E on average, Fig. 13A-B) are a hotspot of bacterial abundance, productivity and diversity (in winter). Similarly, the epipelagic waters above the continental slope had a high abundance of primary producers and primary productivity (Fig. 14A-D), and of zooplankton biomass in the summer (Fig. 15B).

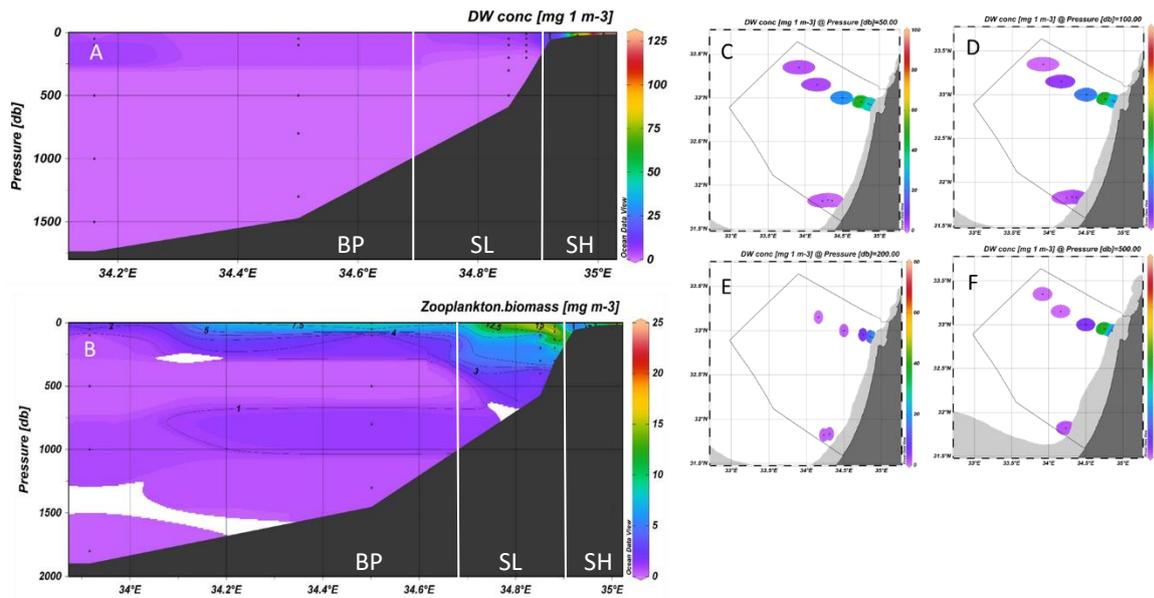


**Figure 13.** **A.** Epipelagic bacterial abundance [ $\text{cells ml}^{-1}$ ], **B.** epipelagic bacterial productivity [ $\mu\text{g C L}^{-1} \text{d}^{-1}$ ], **C-D.** bacterial diversity (C – winter, D – summer) along the Haifa (A-D) and Southern (A-B) transects. SH – shelf, SL – slope, BP – bathyal plain.

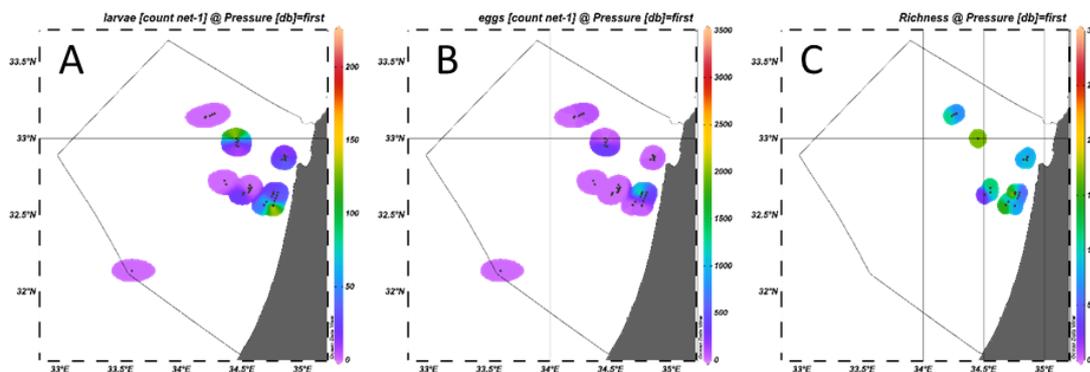
In all seasons, zooplankton biomass (Fig. 15) showed two general decreasing trends – a horizontal decreasing trend from the continental shelf to offshore waters, and a vertical decreasing trend from the epipelagic surface waters to the deep sea. The horizontal decreasing trend was less apparent in the ichthyoplankton abundance and diversity (Fig. 16).



**Figure 14.** **A-C.** Average abundance of primary producers [ $\text{cells ml}^{-1}$ ], and **D.** primary productivity [ $\mu\text{g C L}^{-1} \text{d}^{-1}$ ] in the epipelagic waters along the Haifa (A-D) and Southern (A-D) transects. SH – shelf, SL – slope, BP – bathyal plain.



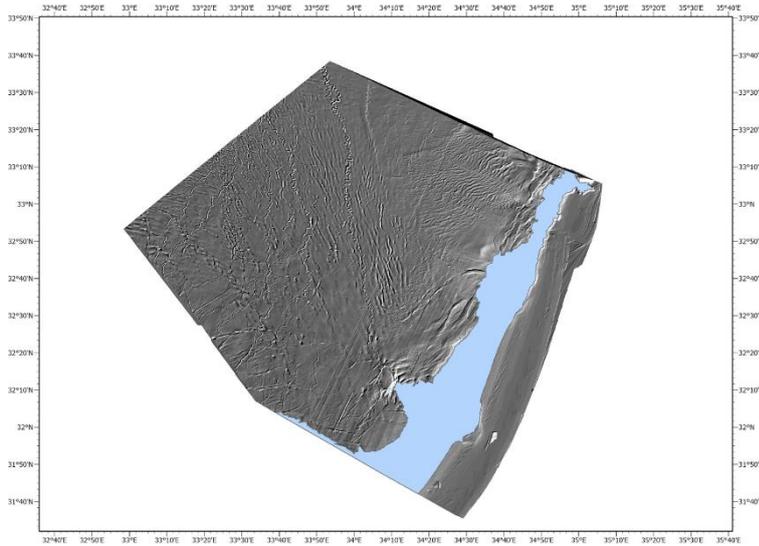
**Figure 15.** A-B. The average concentration of zooplankton biomass [mg dry weight m<sup>-3</sup>] in winter (A) and summer (B) along the Haifa transect. C-F. average zooplankton biomass per depth layers 50, 100, 200, 500 m. SH – shelf, SL – slope, BP – bathyal plain.



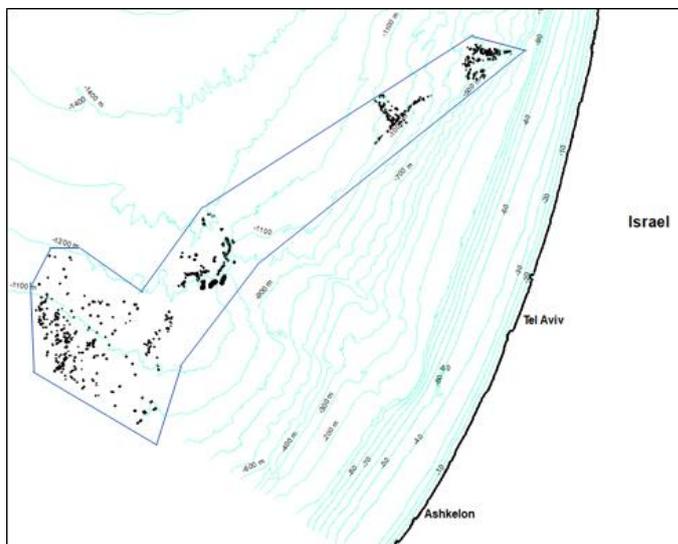
**Figure 16.** Ichthyoplankton abundance and diversity from surface waters (neuston). A. fish larvae. B. fish eggs. C. species richness.

Due to the higher abundance, biomass and richness of the various biological components in the waters overlaying the continental slope, this region was determined as a separate pelagic biohabitat (Fig. 17).

Another pelagic biohabitat was delimited based on the occurrence of pockmarks, indicating gas seepage, that has been shown to affect the overlaying water column (Fig. 18).



**Figure 17.** The bioregion of the pelagic waters above the continental slope (in blue).



**Figure 18.** The Palmahim bioregion of the pelagic waters above pockmarks/seepage.

#### 4. Discussion

Pelagic habitat delineation presented in this report was based on the physicochemical surrogates – temperature, oxygen and the frequency of mesoscale eddies, as well as unique bathymetric zones and benthic habitats with evident effects on the water column. The biological data in terms of bacterial, phytoplankton, zooplankton, and fish larvae abundance and diversity, had poor spatial coverage, accounting for <5% of the Israeli EEZ area, yet, showed coherent vertical zonation. The vertical structuring of the water column to discrete water masses in the Eastern Mediterranean Sea based on their physical properties is well-established (Malanotte-Rizzoli et al., 2003; Kress et al., 2014; Ozer et al., 2020), and its effects on the biogeochemical characteristics, bacterial diversity (Keuter and Rinkevich, 2016), and plankton abundance and productivity are known (Ozer et al., 2022). The high diversity of bacterioplankton in the LIW, including mostly copiotrophic bacteria (exploiting nutrient-rich microhabitats), corresponds with the high abundance of zooplankton, and can be explained by the high availability of organic carbon sources provided by zooplankton-mediated fluxes. Nonetheless, the bioregionalization of distinct vertical pelagic habitats was not recommended due to

management and enforcement difficulties (Day et al., 2012) and benthic-pelagic coupling (Roberson et al., 2017). Therefore, in this analysis, pelagic habitats were defined for the extent of the whole water column.

The Southeastern Mediterranean Sea is the hottest, saltiest region, with the lowest primary productivity in the Mediterranean (Coll et al., 2010). Within this ecoregion, the Israeli EEZ represents the trailing, warm distribution edge of most Mediterranean and Atlanto-Mediterranean native species (Rilov et al., 2022). Warming can therefore drive these species beyond their thermal tolerances and lead to extirpations, whereas colder areas can serve as climatic refugia (Chaikin et al., 2022). Temperature is, therefore, a key factor in shaping the biodiversity in the pelagic habitats of the Israeli EEZ. In this analysis, summer SST levels were used to delineate three thermal bioregions in the Israeli EEZ, and similarly, summer surface oxygen levels were used to differentiate between high and low (relative) oxygen zones. Oxygen levels are often coupled with temperature and indicate oceanic water masses.

Despite poor spatial coverage, hotspots of bacterial diversity, abundance of primary producers, primary productivity and zooplankton biomass were found in the water column overlaying the continental slope. Continental slopes in the European Seas were previously shown to be benthic biodiversity hotspots (Danovaro et al., 2009). A recent review found that the narrow slope regions contribute to ecosystem functioning disproportionately to the size of the habitat area (Bluhm et al., 2020). Lateral currents transport particle loads from the continental shelf along the slope, creating connectivity gradients in water mass properties and biomass. In the Israeli EEZ, evidence for this mechanism was obtained from the offshore mooring site DeepLev by Katz et al. (2020) who found that lateral transport from the continental margin contributes the greatest fraction of particulate flux to the seafloor. This flux fuels the diverse microbial communities at the seafloor (Rubin-Blum et al., 2022). The comparison of carbon and nitrogen stable isotopes in demersal crustaceans and fish in the shelf margin, slope and bathyal of the Israeli EEZ showed that the majority of the deep-sea megafauna is supported by neritic (shelf) carbon sources, transported across the slope via currents (Guy-Haim et al., 2022). Thus, due to its central role in the transport of organic material, the continental slope of the Israeli EEZ was delineated as a discrete bioregion.

Natural gas seepage from the deep seafloor has a major impact on the marine environment, supporting unique communities. In the Israeli EEZ, gas seeps and brine pools that are characterized by unique geomorphological properties and fauna were found at the toe of the Palmahim disturbance region, now considered as VME (Vulnerable Marine Ecosystem) in the bioregionalization analysis of benthic habitats (Shabtay et al., 2022). Benthic-pelagic coupling between the seabed and the overlying waters in vents and seeps sites can play a major role in marine biogeochemistry. A recent study in Palmahim seeps showed that the biogeochemical fluxes and microbial community in the water column overlaying the seeps and in their vicinity are affected to the extent of tens of meters beyond the seepage hotspots (Sisma-Ventura et al., 2022). Therefore, the pelagic waters in the Palmahim region are delineated as a bioregion.

The frequency of cyclonic and anticyclonic mesoscale eddies based on the DYNED atlas was used to delineate two bioregions. The frequency of cyclonic eddies was highest in the mid-EEZ region, and of anticyclonic eddies – in the mid-west, with an average longevity of 100-125 days. Such temporal scales can have a profound impact on the resident biodiversity. The mosaics of conditions within and outside mesoscale eddies create areas where environmental conditions can provide physiological relief from stress, potentially allowing species to persist locally during long-term change, serving as a climate refuge. Cyclonic cold-core eddies are often associated with a slow upwelling flow in their interior connecting convergent flow at depth with divergent flow near the surface, bringing cold, nutrient-enriched water to the surface, whereas anticyclonic eddies are associated with vertical downwelling flow in their interior that connects convergent flow near the surface with divergent flow at depth, pushing surface water below the euphotic zone. In the ultra-oligotrophic Southeastern Mediterranean, the importance of cyclonic eddies as “high productivity islands” for fish reproduction and recruitment might be high. A recent study of mesoscale eddies in the Israeli EEZ found that zooplankton biomass, supporting the higher trophic levels, was one order of magnitude larger in the epipelagic waters of a cold-core cyclone than the surrounding waters (Belkin et al., 2022). Warm-core anticyclonic eddies reduced epipelagic zooplankton biomass and diversity but increased the richness of non-indigenous species. Nonetheless, warm-core anticyclonic eddies were shown to facilitate the aggregations of top predators by increasing mesopelagic prey (Arostegui et al., 2022).

Further updates of the pelagic bioregionalization of the Israeli EEZ presented here should include a larger spatial coverage of biotic parameters in the water column as well as incorporate higher trophic levels (e.g., pelagic fish, sea turtles, marine mammals).

## 5. References

- Agnetta, D., Badalamenti, F., Colloca, F., D’anna, G., Di Lorenzo, M., Fiorentino, F., Garofalo, G., Gristina, M., Labanchi, L., and Patti, B. (2019). Benthic-pelagic coupling mediates interactions in Mediterranean mixed fisheries: An ecosystem modeling approach. *PLoS One* 14, e0210659.
- Arostegui, M.C., Gaube, P., Woodworth-Jefcoats, P.A., Kobayashi, D.R., and Braun, C.D. (2022). Anticyclonic eddies aggregate pelagic predators in a subtropical gyre. *Nature* 609, 535-540.
- Barboni, A., Lazar, A., Stegner, A., and Moschos, E. (2021). Lagrangian eddy tracking reveals the Eratosthenes anticyclonic attractor in the eastern Levantine basin. *Ocean Science* 17, 1231-1250.
- Belkin, N., Guy-Haim, T., Rubin-Blum, M., Lazar, A., Sisma-Ventura, G., Kiko, R., Morov, A.R., Ozer, T., Gertman, I., Herut, B., and Rahav, E. (2022). Influence of cyclonic and anticyclonic eddies on plankton in the southeastern Mediterranean Sea during late summertime. *Ocean Science* 18, 693-715.
- Bluhm, B.A., Janout, M.A., Danielson, S.L., Ellingsen, I., Gavrilov, M., Grebmeier, J.M., Hopcroft, R.R., Iken, K.B., Ingvaldsen, R.B., and Jørgensen, L.L. (2020). The Pan-Arctic continental slope: Sharp gradients of physical processes affect pelagic and benthic ecosystems. *Frontiers in Marine Science* 7, 544386.
- Chaikin, S., Dubiner, S., and Belmaker, J. (2022). Cold-water species deepen to escape warm water temperatures. *Global Ecology and Biogeography* 31, 75-88.

- Charlson, R.J., Lovelock, J.E., Andreae, M.O., and Warren, S.G. (1987). Oceanic phytoplankton, atmospheric sulphur, cloud albedo and climate. *Nature* 326, 655-661.
- Coll, M., Piroddi, C., Steenbeek, J., Kaschner, K., Ben Rais Lasram, F., Aguzzi, J., Ballesteros, E., Bianchi, C.N., Corbera, J., and Dailianis, T. (2010). The biodiversity of the Mediterranean Sea: estimates, patterns, and threats. *PloS one* 5, e11842.
- Costello, M.J. (2009). Distinguishing marine habitat classification concepts for ecological data management. *Marine ecology progress series* 397, 253-268.
- Danovaro, R., Canals, M., Gambi, C., Heussner, S., Lampadariou, N., and Vanreusel, A. (2009). Exploring benthic biodiversity patterns and hotspots on European margin slopes. *Oceanography* 22, 16-25.
- Day, J., Dudley, N., Hockings, M., Holmes, G., Laffoley, D.D.A., Stolton, S., and Wells, S.M. (2012). *Guidelines for applying the IUCN protected area management categories to marine protected areas*. IUCN.
- Devillers, R., Pressey, R.L., Grech, A., Kittinger, J.N., Edgar, G.J., Ward, T., and Watson, R. (2015). Reinventing residual reserves in the sea: are we favouring ease of establishment over need for protection? *Aquatic conservation: marine and freshwater ecosystems* 25, 480-504.
- Díaz, S.M., Settele, J., Brondízio, E., Ngo, H., Guèze, M., Agard, J., Arneeth, A., Balvanera, P., Brauman, K., and Butchart, S. (2019). The global assessment report on biodiversity and ecosystem services: Summary for policy makers.
- Dickey-Collas, M., Mcquatters-Gollop, A., Bresnan, E., Kraberg, A.C., Manderson, J.P., Nash, R.D., Otto, S.A., Sell, A.F., Tweddle, J.F., and Trenkel, V.M. (2017). Pelagic habitat: exploring the concept of good environmental status. *ICES Journal of Marine Science* 74, 2333-2341.
- Game, E.T., Grantham, H.S., Hobday, A.J., Pressey, R.L., Lombard, A.T., Beckley, L.E., Gjerde, K., Bustamante, R., Possingham, H.P., and Richardson, A.J. (2009). Pelagic protected areas: the missing dimension in ocean conservation. *Trends in ecology & evolution* 24, 360-369.
- Goldthwait, S.A., and Steinberg, D.K. (2008). Elevated biomass of mesozooplankton and enhanced fecal pellet flux in cyclonic and mode-water eddies in the Sargasso Sea. *Deep Sea Research Part II: Topical Studies in Oceanography* 55, 1360-1377.
- Grantham, H.S., Game, E.T., Lombard, A.T., Hobday, A.J., Richardson, A.J., Beckley, L.E., Pressey, R.L., Huggett, J.A., Coetzee, J.C., and Van Der Lingen, C.D. (2011). Accommodating dynamic oceanographic processes and pelagic biodiversity in marine conservation planning. *PLoS One* 6, e16552.
- Grantham, H.S., Pressey, R.L., Wells, J.A., and Beattie, A.J. (2010). Effectiveness of biodiversity surrogates for conservation planning: different measures of effectiveness generate a kaleidoscope of variation. *PLoS One* 5, e11430.
- Griffiths, J.R., Kadin, M., Nascimento, F.J., Tاملander, T., Törnroos, A., Bonaglia, S., Bonsdorff, E., Brüchert, V., Gårdmark, A., and Järnström, M. (2017). The importance of benthic–pelagic coupling for marine ecosystem functioning in a changing world. *Global change biology* 23, 2179-2196.
- Guy-Haim, T., Stern, N., and Sisma-Ventura, G. (2022). Trophic Ecology of Deep-Sea Megafauna in the Ultra-Oligotrophic Southeastern Mediterranean Sea. *Front. Mar. Sci* 9, 857179.
- Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., and Fox, H.E. (2008). A global map of human impact on marine ecosystems. *science* 319, 948-952.
- Johnston, M.W., Milligan, R.J., Easson, C.G., Derada, S., English, D.C., Penta, B., and Sutton, T.T. (2019). An empirically validated method for characterizing pelagic habitats in the Gulf of Mexico using ocean model data. *Limnology and Oceanography: Methods* 17, 362-375.
- Kaplan, D.M., Chassot, E., Gruss, A., and Fonteneau, A. (2010). Pelagic MPAs: The devil is in the details. *Trends in ecology & evolution* 25, 62-63.

- Kasting, J.F., and Siefert, J.L. (2002). Life and the evolution of Earth's atmosphere. *Science* 296, 1066-1068.
- Katz, T., Weinstein, Y., Alkalay, R., Biton, E., Toledo, Y., Lazar, A., Zlatkin, O., Soffer, R., Rahav, E., and Sisma-Ventura, G. (2020). The first deep-sea mooring station in the eastern Levantine basin (DeepLev), outline and insights into regional sedimentological processes. *Deep Sea Research Part II: Topical Studies in Oceanography* 171, 104663.
- Keuter, S., and Rinkevich, B. (2016). Spatial homogeneity of bacterial and archaeal communities in the deep eastern Mediterranean Sea surface sediments. *Int. Microbiol* 19, 109-119.
- Kress, N., Gertman, I., and Herut, B. (2014). Temporal evolution of physical and chemical characteristics of the water column in the Easternmost Levantine basin (Eastern Mediterranean Sea) from 2002 to 2010. *Journal of Marine Systems* 135, 6-13.
- Lascaratos, A., Roether, W., Nittis, K., and Klein, B. (1999). Recent changes in deep water formation and spreading in the eastern Mediterranean Sea: a review. *Progress in oceanography* 44, 5-36.
- Le Vu, B., Stegner, A., and Arsouze, T. (2018). Angular momentum eddy detection and tracking algorithm (AMEDA) and its application to coastal eddy formation. *Journal of Atmospheric and Oceanic Technology* 35, 739-762.
- Leathwick, J., Moilanen, A., Francis, M., Elith, J., Taylor, P., Julian, K., Hastie, T., and Duffy, C. (2008). Novel methods for the design and evaluation of marine protected areas in offshore waters. *Conservation Letters* 1, 91-102.
- Lee, C.-Y., and Meng, Q. (2014). *Handbook of ocean container transport logistics: making global supply chains effective*. Springer.
- Malanotte-Rizzoli, P., Manca, B., Marullo, S., Ribera D'alcala', M., Roether, W., Theocharis, A., Bergamasco, A., Budillon, G., Sansone, E., and Civitarese, G. (2003). The Levantine Intermediate Water Experiment (LIWEX) Group: Levantine basin—A laboratory for multiple water mass formation processes. *Journal of Geophysical Research: Oceans* 108.
- Marcus, N.H., and Boero, F. (1998). Minireview: The importance of benthic-pelagic coupling and the forgotten role of life cycles in coastal aquatic systems. *Limnology and Oceanography* 43, 763-768.
- Msangi, S., Kobayashi, M., Batka, M., Vannuccini, S., Dey, M., and Anderson, J. (2013). Fish to 2030: prospects for fisheries and aquaculture. *World Bank Report* 83177, 102.
- Owen, R.W. (1981). Fronts and eddies in the sea: mechanisms, interactions and biological effects. *Analysis of marine ecosystems*, 197-233.
- Ozer, T., Gertman, I., Gildor, H., Goldman, R., and Herut, B. (2020). Evidence for recent thermohaline variability and processes in the deep water of the Southeastern Levantine Basin, Mediterranean Sea. *Deep Sea Research Part II: Topical Studies in Oceanography* 171, 104651.
- Ozer, T., Gertman, I., Kress, N., Silverman, J., and Herut, B. (2017). Interannual thermohaline (1979–2014) and nutrient (2002–2014) dynamics in the Levantine surface and intermediate water masses, SE Mediterranean Sea. *Global and Planetary Change* 151, 60-67.
- Ozer, T., Rahav, E., Gertman, I., Sisma-Ventura, G., Silverman, J., and Herut, B. (2022). Relationship between thermohaline and biochemical patterns in the levantine upper and intermediate water masses, Southeastern Mediterranean Sea (2013–2021). *Frontiers in Marine Science* 9, 1333.
- Özsoy, E., Hecht, A., and Ünlüata, Ü. (1989). Circulation and hydrography of the Levantine Basin. Results of POEM coordinated experiments 1985–1986. *Progress in Oceanography* 22, 125-170.
- Pörtner, H.-O., Roberts, D.C., Adams, H., Adler, C., Aldunce, P., Ali, E., Begum, R.A., Betts, R., Kerr, R.B., and Biesbroek, R. (2022). Climate change 2022: Impacts, adaptation and vulnerability. *IPCC Sixth Assessment Report*, 37-118.

- Rilov, G., Klein, L., Iluz, D., Dubinsky, Z., and Guy-Haim, T. (2022). Last snail standing? superior thermal resilience of an alien tropical intertidal gastropod over natives in an ocean-warming hotspot. *Biological Invasions* 24, 3703-3719.
- Roberson, L.A., Lagabrielle, E., Lombard, A.T., Sink, K., Livingstone, T., Grantham, H., and Harris, J.M. (2017). Pelagic bioregionalisation using open-access data for better planning of marine protected area networks. *Ocean & coastal management* 148, 214-230.
- Robison, B.H. (2009). Conservation of deep pelagic biodiversity. *Conservation Biology* 23, 847-858.
- Rubin-Blum, M., Sisma-Ventura, G., Yudkovski, Y., Belkin, N., Kanari, M., Herut, B., and Rahav, E. (2022). Diversity, activity, and abundance of benthic microbes in the Southeastern Mediterranean Sea. *FEMS Microbiology Ecology* 98, fiac009.
- Shabtay, A., Goren, L., Slavenko, A., Idan, T., Neuman, A., Bialik, O., and Makovsky, Y. (2022). Environmental data collection and analyses to support conservation planning in the Israeli EEZ. *Report submitted to the Israeli EEZ MPAS masterplan project scientific committee.*
- Shulzitski, K., Sponaugle, S., Hauff, M., Walter, K.D., and Cowen, R.K. (2016). Encounter with mesoscale eddies enhances survival to settlement in larval coral reef fishes. *Proceedings of the National Academy of Sciences* 113, 6928-6933.
- Sisma-Ventura, G., Bialik, O.M., Makovsky, Y., Rahav, E., Ozer, T., Kanari, M., Marmen, S., Belkin, N., Guy-Haim, T., Antler, G., and Herut, B. (2022). Cold seeps alter the near-bottom biogeochemistry in the ultraoligotrophic Southeastern Mediterranean Sea. *Deep Sea Research Part I: Oceanographic Research Papers* 183, 103744.
- Sutton, T. (2013). Vertical ecology of the pelagic ocean: classical patterns and new perspectives. *Journal of fish biology* 83, 1508-1527.
- Zavatarielli, M., and Mellor, G.L. (1995). A numerical study of the Mediterranean Sea circulation. *Journal of Physical Oceanography* 25, 1384-1414.