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## Surprising widespread *Cymodocea nodosa* occurrence along Israel's Mediterranean coast and Implications for Seagrass Conservation in a hotspot of climate change

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### Abstract

*Cymodocea nodosa* is a temperate seagrass that grows in shallow and sheltered waters of the Mediterranean Sea. Although it is found in both the western and eastern basins, it was thought to be absent from the extremely warm and salty waters along the Israeli coastline, the most eastern part of the Mediterranean. We conducted methodical, seasonal, towed-diver surveys along the Mediterranean coast of Israel, recording position, depth, presence/absence of *C. nodosa*, seabed characteristics, and habitat complexity. We used general additive models (GAMs) to understand how the combination of depth, latitude (space), and season (time), explained the distribution of local meadows. We then compared the habitat affinity of these Israeli meadows with other sites in the Eastern Mediterranean by conducting a systematic literature review and using Species Distribution Models (SDMs). Underwater surveys unveiled the extensive distribution of *C. nodosa* over a narrow depth range of 8-21m (with peak occurrence at 14m) in exposed habitats. These locations are distinct from other Eastern Mediterranean populations, in which *C. nodosa* is found in shallower and sheltered habitats. SDMs confirmed the increase in the geographical range also reflects an increase in realized niche breadth into higher values of temperatures, salinity, and current velocity. Considering that the eastern tip of the Mediterranean is a climate change hotspot, finding *C. nodosa* populations surviving these harsh conditions holds implications for seagrass conservation and restoration in the entire Mediterranean. However, the low density of observed meadows suggests that these populations require careful monitoring to prevent local extirpation.

**Keywords:** Seagrass; Levantine Basin; Little Neptune grass; Distribution; Climate Change.

### Introduction

Seagrasses are marine flowering plants (angiosperms) usually found growing in soft sediments where they can form dense and extensive meadows (Short *et al.*, 2016). Seagrass provide a range of ecosystem functions and services. For example, seagrass enrich surrounding water with oxygen, filter nutrients and bacteria, and stabilize sediments (Duffy, 2006; Potouroglou *et al.*, 2017). Seagrass meadows also provide fish nurseries (Nordlund *et al.*, 2016; Maxwell *et al.*, 2017), and it is estimated that seagrass areas support ~20% of the global fishery production (Unsworth *et al.*, 2018). Seagrasses are also efficient at carbon sequestration, and are responsible for the long-term storing of 15% of the “blue” carbon in the ocean (Laffoley & Grimsditch, 2009; Fourqurean *et al.*, 2012; Mazarrasa *et al.*, 2015). However, seagrass meadows are facing global declines due to both direct (e.g., coastal

development, damage from anchors) and indirect (climate change) anthropogenic impacts (Tuya *et al.*, 2014; Nguyen *et al.*, 2021).

The Mediterranean Sea contains rich seagrass communities (Marbà *et al.*, 1996a, b) that include four native species and one Lessepsian migrant (*Halophila stipulacea*; reviewed by Winters *et al.*, 2020). *Cymodocea nodosa* is a small and relatively fast-growing seagrass species native to the Mediterranean and common in both its eastern and western basins (den Hartog, 1970; Green & Short 2003; Orfanidis *et al.*, 2005). Although found in many shallow-water sheltered sites in the Eastern Mediterranean, the distribution of seagrasses in Israel's Mediterranean coast (the most eastern area of the Mediterranean) has been a mystery (Chefaoui *et al.*, 2016). Lipkin *et al.* (2003) mentioned the existence of *C. nodosa* in three sites along the Israeli Mediterranean shore, yet there have been no other records of any seagrasses in the region ever

since (Beer *et al.*, 1998).

The Israeli Mediterranean coastline is characterized by a lack of naturally protected shallow bays. In addition, this region contains extreme salinity and water temperature conditions (Beca-Carretero *et al.*, 2020). The region also suffers from changes in the natural movement of sand following the building of the Aswan dam in the 1970s, and the rapid building of wave breakers and marinas (Almagor *et al.*, 2000; Spanier & Zviely, 2023). Finally, the introduction of herbivore alien species such as gastropods (e.g., *Cerithium* spp.) and rabbitfish (e.g., *Siganus* spp.) (Galil, 2007; Pickholtz 2018), could increase grazing pressure (Cebrián *et al.*, 1996; Vizzini, 2009). All these may be linked to the absence of *C. nodosa* along the Israeli Mediterranean coast. However, limited sampling effort may also have prevented the detection of natural *C. nodosa* meadows.

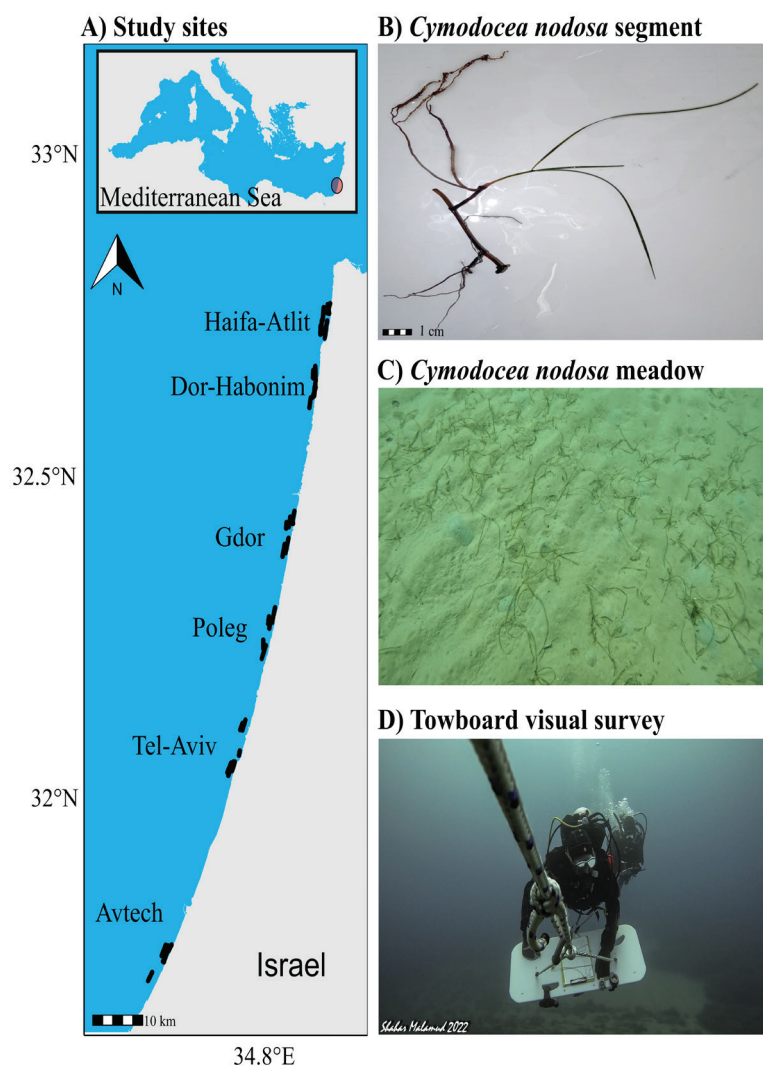
Here we report on the surprisingly wide distribution of *C. nodosa* meadows along the exposed Mediterranean coastline of Israel. We (1) quantified the habitat affinity of this species and mapped its distribution along the Israeli coasts, (2) described seasonal patterns of change in occupancy and depth, and (3) compared the habitat affinity

in Israel to known populations elsewhere in the Eastern Mediterranean. We use this information to discuss reasons for changes in the distribution of this species along the Israeli Mediterranean and implications for the future distribution in light of the rapid environmental changes in this region.

## Methods

### Underwater surveys

We conducted systematic surveys over sandy bottoms along the Mediterranean coast of Israel. Surveys were conducted in six sites along the Israeli coast (from north to south): Haifa-Atlit coastline, Dor-Habonim nature reserve, Gdor nature reserve, Poleg coastline, Tel-Aviv coastline, and Avtech proposed marine reserve (Fig. 1A). Sampling took place at all sites seasonally from December 2021 to June 2023 (winter 2021-2022, spring 2022, summer 2022, autumn 2022, winter 2022-2023 and spring 2023; a total of six surveys at each site). Within each site, and within each season, two transects were



**Fig. 1:** A) map of the different study sites compared to the entire Mediterranean and along Israel's Mediterranean coast (inset). B) Typical *Cymodocea nodosa* segment. C) *C. nodosa* meadow documented in Dor-Habonim nature reserve, Israel. D) An underwater visual survey using a towboard.

performed: a deeper transect (15-20 m) followed by a shallower transect (10-15 m). We sampled in the same area across different seasons, but did not aim to return exactly to the same location. Each survey consisted of towed-diver visual surveys (Fig. 1D). Towing allowed increasing the length of the transect compared to regular diving transects (Miller *et al.*, 2009; Ohayon *et al.*, 2023). In each run, a pair of SCUBA-divers were towed behind a boat using a 70 m rope, about 1-2 m above the bottom. The location, distance, and time of each transect were determined according to the GPS on the boat. A communication system (UDI-14 underwater communication system) between the boat and the divers was used to determine the start and end of each transect as well as meadow coordinates (Lino *et al.*, 2018). The divers were towed long-shore (north-south) for 1 hour at a sailing speed of 1.5-2.5 knots (depending on the sea condition), providing a 1500-4000 m long transect. Divers recorded each minute (one-minute segments) the following information: (1) presence/absence of *C. nodosa*, (2) depth (m), (3) seabed characteristics (sand, rock, gravel, or mud), and (4) habitat complexity, estimated on a 5-point scale: 0- no vertical relief; 1- low and sparse relief; 2- low but widespread relief; 3- moderately complex; 4- very complex with numerous caves and fissures; and 5- exceptionally complex with high coral cover, numerous caves, and overhangs (Polunin & Roberts, 1993). We note that the meadow's coordinates are accurate to a 70 m radius range due to the length of the rope (i.e., the distance to the boat's GPS).

To understand how the combination of depth, latitude (space), and season (time), affected the *C. nodosa* distribution, we used general additive models (GAMs) (Pedersen *et al.*, 2019). The response variable was binomial with the number of one-minute survey segments with the presences of seagrass (number of successes) relative to the number of segments with no seagrass (failures) in the same transect (i.e., the probability of finding *C. nodosa* meadows). We used depth and latitude as continuous predictors and season as a categorical predictor. We used Thin-Plate splines smoothers (Wood, 2017) for the continuous predictors of latitude and depth. We set the knot number (k) as 5 for the depth and 3 for latitude.

### Comparison to other *Cymodocea nodosa* populations

To compare the habitat affinity from other sites in the Eastern Mediterranean to the local affinity in Israel, we conducted a systematic literature review. We searched the Web of Science Core Collection database (accessed 01/06/2023-20/07/2023) for the phrase "*Cymodocea nodosa*" and ("Eastern Mediterranean" or "Tunisia" or "Libya" or "Egypt" or "Cyprus" or "Israel" or "Lebanon" or "Syria" or "Turkey" or "Greece"). We only included studies that focused on *C. nodosa* in the Eastern Mediterranean (studies that just mentioned *C. nodosa* or studies that focus on the western basin, were excluded). The reference lists of each article were also checked and added to the database if relevant. Altogether, this literature review resulted in a total of 80 studies (Table S1-

available at <https://zenodo.org/records/13120938>). From each study, we extracted the following information: (1) Coordinates (in decimal degrees); Each study was given a rank varying between 0-3 to represent the accuracy of the location: 0 - no location information apart from country information, 1 - location at a regional scale (10s of km), 2 - location at a study site scale (several km), 3 - specific coordinates of the study site. (2) Sediment type (sand, rock, mud, or combination between the categories), (3) Minimal and maximal meadow depth (m), and (4) Habitat type (open-shore, bay, semi-enclosed bay, lagoon, protected shore). We then compared the depth and habitat type between the newly discovered populations on Israel's coast to those found in the literature review.

### Environmental profile and mapping of the distribution of suitable habitats

We compared the environmental profiles of the newly discovered *C. nodosa* populations along the Israeli Mediterranean coast to those based on the occurrences from the literature review in the Eastern Mediterranean (east of the Strait of Sicily, excluding the Adriatic Sea; Fig. S1). We adopted two approaches to compare these datasets to ours: simple environmental profile assessments, and species distribution models (SDMs). These comparisons were aimed at clarifying whether our findings represent "just" an increased range distribution or do they also represent an expansion in the ecological niche of this species.

To assess the environmental profile of each population, we first extracted the values of four environmental variables considered relevant for the survival of the species (Pérez & Romero, 1992; Binzer *et al.*, 2005; Tsoli *et al.*, 2021) at all occurrence locations. All variables considered were obtained from BioORACLE (<https://www.bio-oracle.org>), and we selected the values at the maximum depth of the variables because we focus on a benthic species: (1) mean temperature; (2) mean salinity; (3) mean primary productivity; and (4) mean current velocity. We considered including depth as a variable due to its importance for marine photosynthetic organisms (Dennison, 1987), however, the coarse resolution of the available environmental marine data (Turner *et al.*, 2019) hindered this possibility. We then compared the distribution of values for each environmental variable between our data and each of the independent datasets using simple t-tests.

We generated SDMs to map the distribution of suitable areas for *C. nodosa* in the Eastern Mediterranean (full methods provided in Supplementary material SI 1). All analyses were conducted in two steps: we first considered only the occurrences from the literature and then re-ran the analysis after including the newly found populations. The layers used in the SDMs represent the four aforementioned environmental variables. We masked the study area by depth to exclude several non-realistically deep occurrences (Fig. S2). The presence data used in the models underwent pre-modeling steps to ensure their



quality for the SDMs. We used additional background data to run the models (Barbet-Massin *et al.*, 2012; Iturbide *et al.*, 2018).

The prediction of suitable areas for *C. nodosa* was assessed by an ensemble forecasting approach (Araújo & New, 2007), which combines results from different algorithms in one consensus model. We generated 25 models for each algorithm (GAM, GLM, MARS, DOMAIN, RF and BRT), amassing 300 SDMs, 150 considering only the occurrences from the literature, and 150 using those combined with the presences found in our surveys. We evaluated the models according to the area under the receiver-operator curve (AUC) and the true skill statistics (TSS). AUC ranges from 0 to 1, and values  $\geq 0.7$  are considered robust predictions (Swets, 1988; Lobo *et al.*, 2008). TSS ranges from -1 to 1, with values  $\geq 0.5$  indicating useful predictions (Zhang *et al.*, 2015). We combined the models with TSS  $\geq 0.5$  in the ensemble forecast models. Finally, we verified whether the occurrence records from each dataset could be predicted correctly by the corresponding final model. We considered the models to predict correctly when more than half the successful models indicated suitability.

## Results

### *Occurrence of Cymodocea nodosa across space and time along the Israeli coast*

Altogether, 56 transects were performed, covering a total length of 120 km. We found *C. nodosa* to be surprisingly common (Fig. 2A). *Cymodocea nodosa* was documented in multiple locations along the Israeli coast; the northernmost point in which we saw plants was in front of Haifa-Atlit coastline (34.94412° N, 32.75678° E) and the southernmost was in front of Tel Aviv (34.57189° N, 31.72122° E). We found a higher probability of occurrence (occupancy) in the northern sites with 30% of all one-minute transect segments containing seagrass, compared with 1% of all one-minute transect segments containing seagrass in the more southern sites such as in Tel-Aviv and Poleg (Fig. 2A). However, no *C. nodosa* was found in the southern Israeli coastline (i.e., south of Tel Aviv). All observed *C. nodosa* were documented growing in exposed habitats, only on sandy bottoms at a depth range of 8.5-21m (a median of 14 m). In terms of seasonality, the highest probability of occurrence was found in the summer 22% (June-August) followed by the autumn 19% (September-November), winter 10% (December-February), and lastly spring 5% (March-May; Fig. 2B).

The GAMs confirmed the single response analyses and showed that depth had a strong effect on the distribution of *C. nodosa*, with peak occurrences at 14-15 m deep (Fig. 2C) (P-value:  $< 0.001$ ; Table S2). The model also supported a latitudinal change in the distribution of the seagrass (P-value:  $< 0.001$ ) with higher occurrences in higher latitudes (Fig. 2D).

### *Comparison to other populations*

We extracted data from 80 studies (Table S1) that documented *C. nodosa* growing in 134 Eastern Mediterranean sites. This data (Table S1) was compared to 292 1-minute sections where we documented *C. nodosa* in the Israeli Mediterranean. For depth (Fig. 3C), we found that in documented sites in the Eastern Mediterranean, the median minimum depth was 1.2 m and a maximum of 4 m. This is significantly shallower than the depth profiles found for the Israeli populations, which was found to be deeper at 14 m ( $p < 2.2e-16$ , t-test). In terms of habitat type (Fig. 3B), in Israel we documented the presence of *C. nodosa* only in open shore habitats, compared with populations in the rest of the Eastern Mediterranean where *C. nodosa* was documented almost exclusively in sheltered habitats, with only one observation from open shore habitat (0.7% from the observations).

Analysis of habitat characteristics found that populations discovered along the Israeli coast had a different environmental profile from those present in other portions of the Eastern Mediterranean. Although the primary productivity values in Israel were nested within the values found elsewhere, all other three variables analyzed (means of temperature, salinity, and current velocity) showed significantly higher values in the Israeli sites compared with other populations of the Eastern Mediterranean ( $p$ -value  $< 0.01$  for all predictors; t-test, Fig. 4B).

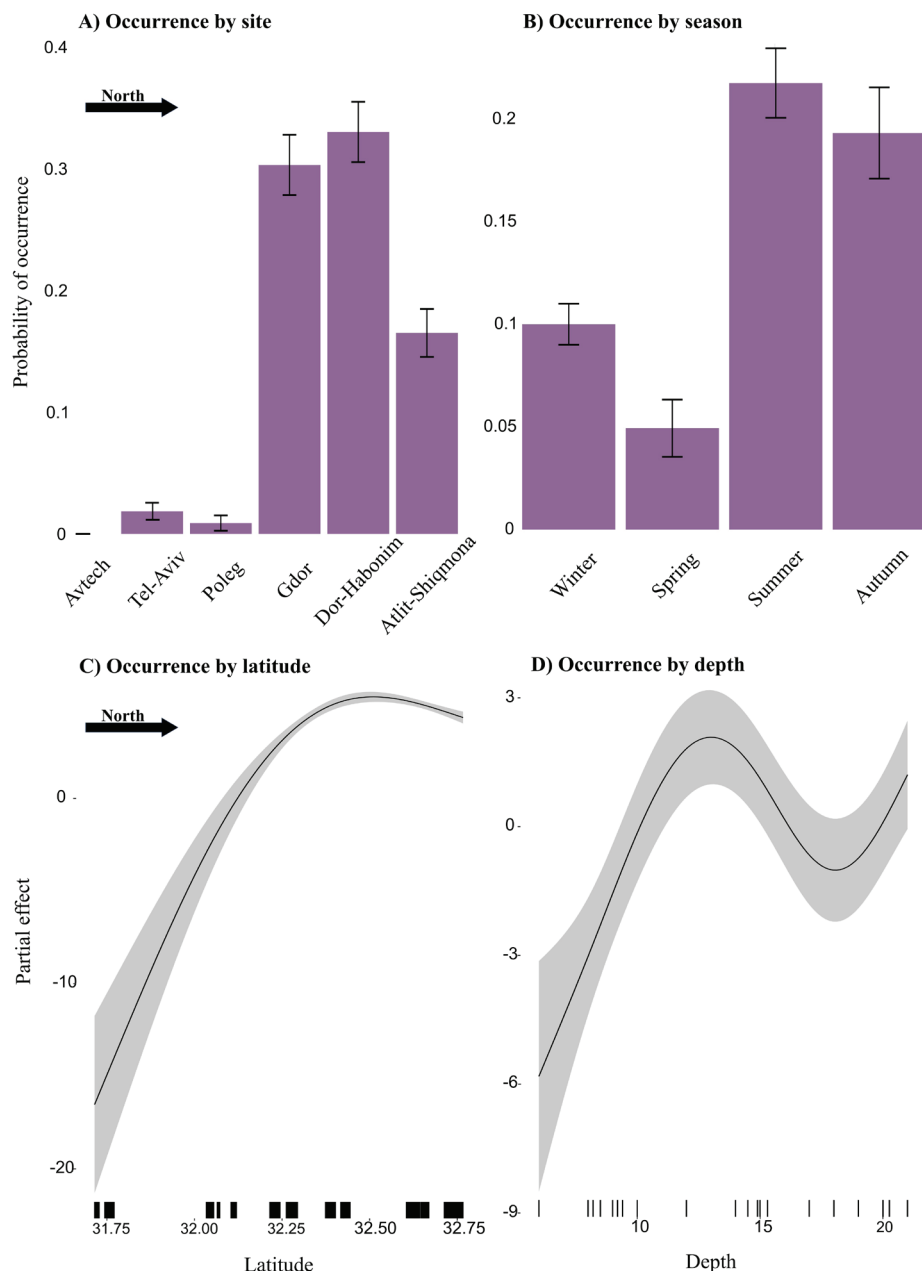
### *Species Distribution Models*

The selected species distribution models were considered good by both evaluation metrics (mean AUC  $> 0.8$ ; mean TSS  $> 0.6$  - Table S3). The final ensemble model produced with data from the literature succeeded in correctly predicting circa 86% of the occurrence data, while it failed to predict all occurrences collected in our survey (Fig. 4C). Conversely, the ensemble model produced with the combined literature and survey data successfully predicted circa 83% of the whole dataset, and more than 99% of the presence data collected in our survey (Fig. 4D).

The ensemble forecast based solely on data compiled from the literature predicts very low suitability for *C. nodosa* along the coast of Israel, indicating the coasts of the Aegean Sea and the regions near Tunisia as the most suitable for the species' occurrence (Fig. 4A). The final model including the occurrences from our survey predicts higher suitability in all the Levantine coastline and Northern Egypt, with a moderated decrease in the suitability forecasts for the Aegean Sea, and a steep decrease for the Tunisian coastal region (Fig. 4B).

## Discussion

While there have been several reports of *C. nodosa* growing on the Eastern Mediterranean coast, including Lebanon (Sghaier *et al.*, 2014), Egypt (El-Din & El-Sher-



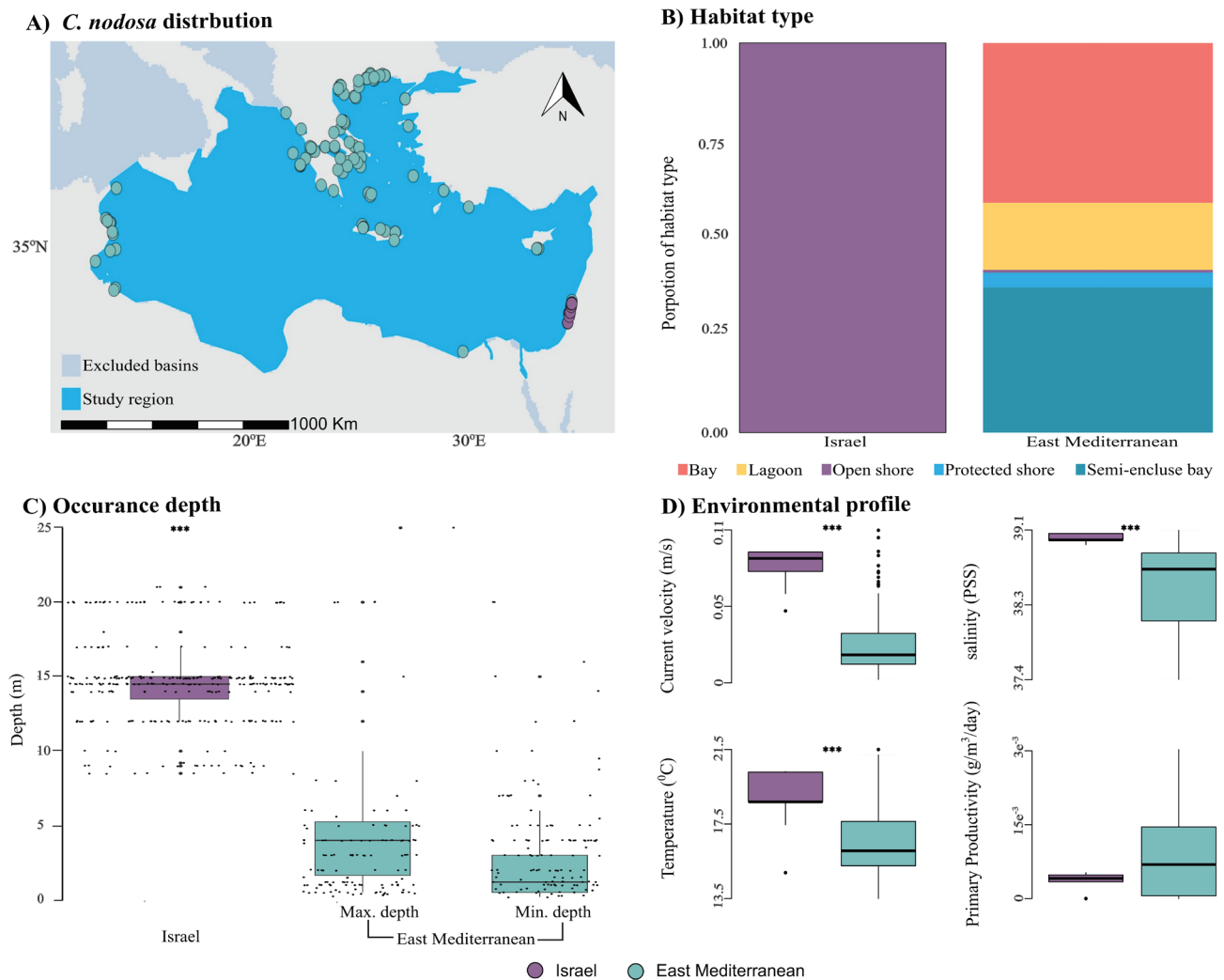
**Fig. 2:** Survey results: A) Average occurrence (the number of one-minute survey segments with the presences of seagrass (number of successes) relative to the number of segments with no seagrass (failures) in the same transect) of *Cymodocea nodosa* in each one of the six sampling sites (ordered from south to north). B) Average occurrence per season. Error bars in A-B represent standard error. C) Relationship between the presence of seagrass meadows and latitude (C) and depth (D). The predictions are partial associations based on GAMs with depth, latitude, and season as predictors. Solid line - mean prediction. The shaded area represents 95% confidence intervals. the number of one-minute survey segments with the presences of seagrass (number of successes) relative to the number of segments with no seagrass (failures) in the same transect (i.e., the probability of occurrence *C. nodosa* meadows).

if, 2013), Turkey (Mutlu *et al.*, 2022) and Cyprus (Konstantinidis *et al.*, 2022), the distribution of seagrasses in Israel's Mediterranean coast has been a mystery. Both Beer *et al.* (1998) and Lipkin *et al.* (2003) mentioned the existence of *C. nodosa* in at least three sites along the Israeli Mediterranean shore; there have been no other records/sightings of any seagrasses in the region ever since.

The presence of *C. nodosa* in our surveys is widespread, and in some transects, it was documented growing along more than 3 km (Fig. 2A). The speed of towing the divers prevented us from accurately estimating *C. nodosa*'s percent of cover along the transects we surveyed.

However, it is clear that the density of *C. nodosa* meadows in this part of the Eastern Mediterranean are relatively low (we estimate the shoots to be ~20 cm apart; Fig. 1C) and that this Israeli population does not form dense meadows as known in other regions. This indicates that while *C. nodosa* is widespread along Israel's northern coastline these populations are in suboptimal conditions, although we could not directly compare these to other deeper meadows.

The habitat of *C. nodosa* in Israel was also unusual as it was restricted to exposed shores, compared to bays, lagoons, and protected habitats in other eastern basin pop-



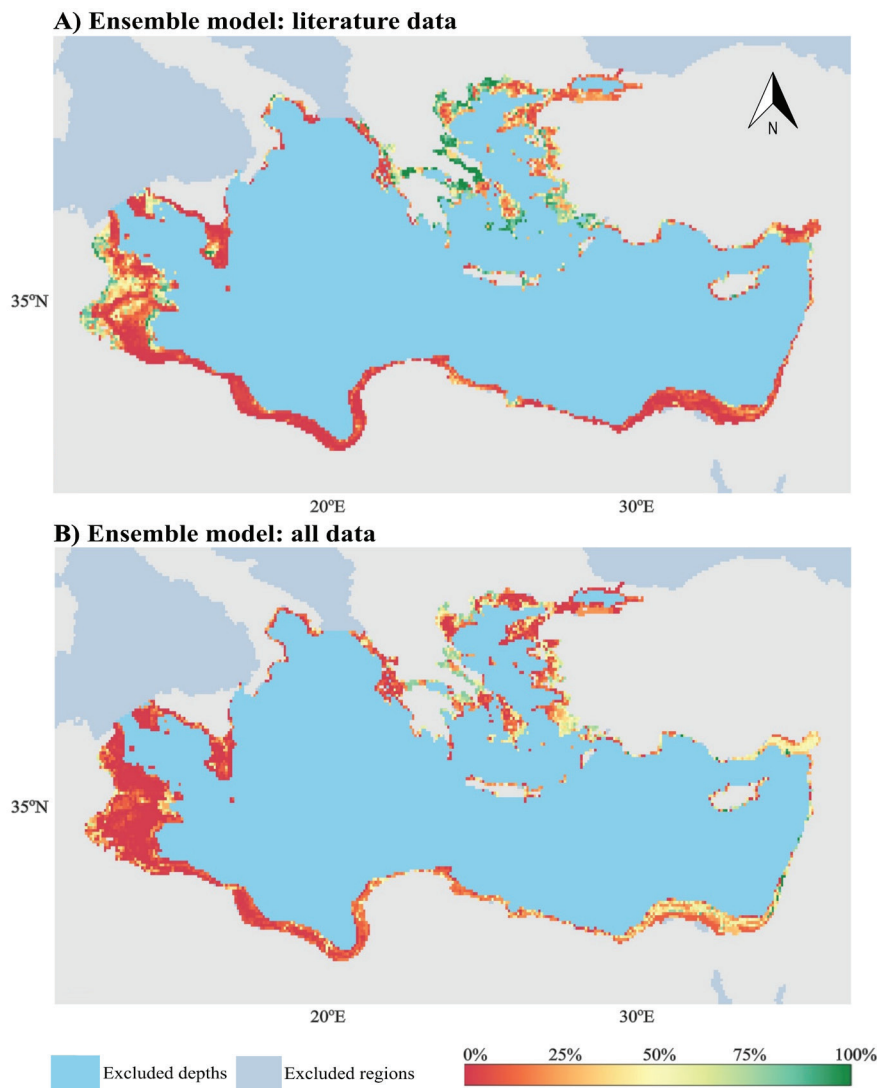
**Fig. 3:** Comparing characteristics of *Cymodocea nodosa* populations documented in this study with known populations from the Eastern Mediterranean. A) Map of the known (published) *C. nodosa* sites in the Eastern Mediterranean (listed in Table S1). Comparisons of B) Habitat type (bay, lagoon, open shore, protected shore or semi-enclosed bay) of *C. nodosa* populations documented in this study and known populations from the Eastern Mediterranean where the meadows were found in Israel and in the Eastern Mediterranean literature review. C) The depth in Israel (n = 292) compared to the minimum and maximum depth that was extracted from the literature (n = 134). D) Environmental profile of Israel meadows (n = 292) compared to other portions of the Eastern Mediterranean (n = 134). Within each box (in C and D), horizontal black lines denote median values; boxes extend from the 25th to the 75th percentile of each group's distribution of values; vertical extending lines denote adjacent values within the 1.5 interquartile range of the 25th and 75th percentile of each group.

ulations (Fig. 3B). The relatively deep habitat in which this species is presently found in the Israeli Mediterranean and the relatively large distance from the shoreline (>1km), may have limited the ability to detect these unique populations in the past.

In addition, we found differences in the condition of the *C. nodosa* meadows during different seasons (Fig. 2B), with a peak of occurrence in the summer followed by a reduction in the occurrence, and apparent vitality, in other seasons. In the literature peak occurrence was documented mostly in the spring (Tuya, 2006; Pérez & Romero, 1992, but see also peaks in summer, Orfanidis *et al.*, 2010). Perhaps this difference is an indirect consequence of the deeper distribution of this species in Israel. Our analyses comparing the environmental profile and the realized niches of *C. nodosa* between the previously

known populations to the occurrences found in our surveys showed that the expansion of the known geographical range of the species also indicates an expansion of the niches associated so far with *C. nodosa*. The inability of the SDMs produced with the occurrences obtained from the literature to predict the species' presence along the Israeli coast supports our assumption that those populations realize a different niche (Booth, 2017). Thus, this species seems to be able to survive in conditions that are much harsher than those that could have been deduced only from its known distribution. Yet, these results are in agreement with lab experiments that showed that this species is capable of surviving under a wide range of environmental conditions (Koch, 1994; Tsioli *et al.*, 2021).

The differences in habitat and depth of the Israeli *C. nodosa* population from other Eastern Mediterranean



**Fig. 4:** Distribution of environmentally suitable conditions for the occurrence of *C. nodosa* in the Eastern Mediterranean Basin. The maps show ensemble forecast predictions, calculated by the percentage of selected models ( $TSS \geq 0.5$ ) predicting environmental suitability for the species at the pixel level in the study area. A) ensemble forecast based solely on data compiled from the literature. B) ensemble forecast based on all occurrence data available for the Eastern Mediterranean Basin (literature and the populations from this study).

populations may be associated with several processes. First, this species may have always been present at deeper depths in Israel. This could be due to the exposed nature of the Israeli coastline, with a lack of sheltered bays, which might have pushed this species into deeper habitats that are less exposed to high wave activity (Fakiris *et al.*, 2023; Chefaoui *et al.*, 2016). However, we could not find *C. nodosa* even in seemingly preferred protected habitats in shallower depths.

Alternatively, this species may have been once widespread and declined in abundance, being pushed into deeper waters and exposed habitats. For example, the currently warm water temperatures in Israel may have pushed *C. nodosa* into deeper waters, as has been documented for fish and invertebrates (Chaikin *et al.*, 2022). If this is the case, it is possible that the ongoing rapid warming of the local waters (Ozer *et al.*, 2017; Ozer *et al.*, 2022) may eventually cause the extirpation of the newly discovered populations. However, we note that in lab conditions this species tolerates temperatures of up to

34–35 °C (Tsioli *et al.* 2019). The rapid building of wave breakers and marinas (Almagor *et al.*, 2000; Spanier & Zviely, 2022) might have also limited the presence of this species in shallow waters. Finally, herbivorous rabbitfish (*Siganus* spp.), which were introduced from the Red Sea, are very abundant in the shallow waters of the Israeli coast and cause severe overgrazing (Cebrián *et al.*, 1996; Sala *et al.*, 2011; Vergés *et al.*, 2014; Yeruham *et al.*, 2020) possibly preventing the growth of *C. nodosa* in the shallow parts of the coastline. These shallow areas of the coastline are now protected by wave breakers. However, these wave breakers have been observed to be the preferred habitat of these invasive, meaning that grazing pressure near these shallow shelters is particularly high.

*Cymodocea nodosa* occurs more in the northern sites in Israel, with no occurrences south of Tel Aviv. This could be related to commercial fisheries, since trawl fishing can cause degradation of seagrass meadows (Nordlund *et al.*, 2017). In 2016, trawl fishing in Israeli waters was restricted, including a prohibition of fishing north of



the Dor-Habonim line (at all depths). The limited activity of trawl fishing boats in the north may partially explain the higher *C. nodosa* abundance. However, we note that most trawl fishing activities take place in deeper depth (>30m; Edelist *et al.*, 2013; van Rijn *et al.*, 2020; Chaikin & Belmaker, 2023) especially since the 2016 regulation and hence this is unlikely to affect the observed populations directly. Alternatively, southern sites are known to be more turbid, and this species may suffer as a result (Najdek *et al.*, 2020). Finally, the southern sites are generally closer to developed urban areas and may be more exposed to stressors such as pollution, runoff, and light pollution (Todd *et al.*, 2019).

Regardless of the underlying reasons for the unique distribution of *C. nodosa* in Israel, the findings described in this study hold both local and regional conservation implications. In terms of local implications, the widespread occurrences of the meadows in Israel, with some specific meadows stretching longer than 3 km, may have important contributions to local biodiversity. These meadows are also likely to contribute to carbon sequestration to local sediments (Maxwell *et al.*, 2017). Findings of widespread *C. nodosa* meadows in unusually deep depths and exposed habitats highlights the need for conserving also soft-bottom habitats that are frequently overlooked in local conservation planning.

However, finding these meadows has also important regional conservation implications. The Mediterranean is a hotspot for climate change, going through a rapid tropicalization process (becoming warmer and saltier), with the Eastern Mediterranean characterized by the most extreme conditions (Milot *et al.*, 2006; Schröder *et al.*, 2006). Recent work by Beca-Carretero *et al.* (2024) predicted that *C. nodosa* growing in the Eastern Mediterranean will not be able to survive warming temperatures and its current distribution in the Mediterranean will be reduced. Previous studies have found significant genetic variation among *C. nodosa* populations (Alberto *et al.*, 2008; Masucci *et al.*, 2012; Konstantinidis *et al.*, 2022). Similarly, genetic studies on the newly found populations thriving under conditions that are so different from those documented before may unveil new genetic variations. Thus, these newly found populations may be a “treasure chest” in terms of their potential adaptation to the local warming conditions, providing future restoration monitoring of *C. nodosa* providing future restoration projects with seagrasses that will survive the harsh conditions predicted for the region. Long-term monitoring of *C. nodosa* distributions is needed to assess its conservation risk and understand the driver of this distribution change over time.

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## References

- Alberto, F., Massa, S., Manent, P., Diaz-Almela, E., Arnaud-Haond, S. *et al.*, 2008. Genetic differentiation and secondary contact zone in the seagrass *Cymodocea nodosa* across the Mediterranean–Atlantic transition region. *Journal of Biogeography*, 35 (7).
- Almagor, G., Gill, D., Perath, I., 2000. Marine sand resources offshore Israel. *Marine Georesources & Geotechnology*, 18 (1), 1–42.
- Araújo, M.B., New, M., 2007. Ensemble forecasting of species distributions. *Trends in Ecology and Evolution*, 22 (1), 42–47.
- Barbet-Massin, M., Jiguet, F., Albert, C.H., Thuiller, W., 2012. Selecting pseudo-absences for species distribution models: how, where and how many? *Methods in Ecology and Evolution*, 3 (2), 327–338.
- Beca-Carretero, P., Teichberg, M., Winters, G., Procaccini, G., Reuter, H., 2020. Projected rapid habitat expansion of tropical seagrass species in the mediterranean sea as climate change progresses. *Frontiers in Plant Science*, 11, 555376.
- Beca-Carretero, P., Winters, G., Teichberg, M., Procaccini, G., Schneekloth, F. *et al.*, 2024. Climate change and the presence of invasive species will threaten the persistence of the Mediterranean seagrass community. *Science of the Total Environment*, 910, 168675.
- Beer, S., Vilenkin, B., Weil, A., Veste, M., Susel, L. *et al.*, 1998. Measuring photosynthetic rates in seagrasses by pulse amplitude modulated (PAM) fluorometry. *Marine Ecology Progress Series*, 174, 293–300.
- Binzer, T., Borum, J., Pedersen, O., 2005. Flow velocity affects internal oxygen conditions in the seagrass *Cymodocea nodosa*. *Aquatic Botany*, 83 (3), 239–247.
- Booth, T.H., 2017. Assessing species climatic requirements beyond the realized niche: some lessons mainly from tree species distribution modelling. *Climatic Change*, 145 (3–4), 259–271.
- Cebrián, J., Duarte, C.M., Marbà, N., 1996. Herbivory on the seagrass *Cymodocea nodosa* (Ucria) Ascherson in contrasting Spanish Mediterranean habitats. *Journal of Experimental Marine Biology and Ecology*, 204 (1–2), 103–111.
- Chaikin, S., Belmaker, J., 2023. Fish depth redistributions do not allow maintenance of abundance in a region of rapid change. *Oikos*, 2023 (8), e09650.
- Chaikin, S., Dubiner, S., Belmaker, J., 2022. Cold-water species deepen to escape warm water temperatures. *Global Ecology and Biogeography*, 31 (1), 75–88.
- Chefaoui, R.M., Assis, J., Duarte, C.M., Serrão, E.A., 2016. Large-Scale Prediction of Seagrass Distribution Integrating Landscape Metrics and Environmental Factors: The Case of *Cymodocea nodosa* (Mediterranean–Atlantic). *Estuaries and Coasts*, 39 (1), 123–137.
- Dennison, W.C., 1987. Effects of light on seagrass photosynthesis, growth and depth distribution. *Aquatic Botany*, 27 (1), 15–26.
- Duffy, J.E., 2006. Biodiversity and the functioning of seagrass ecosystems. *Marine Ecology Progress Series*, 311, 233–250.
- Edelist, D., Rilov, G., Golani, D., Carlton, J.T., Spanier, E., 2013. Restructuring the Sea: profound shifts in the world’s most invaded marine ecosystem. *Diversity and Distribu-*

- tions, 19, 69-77.
- El-Din, N.G.S., El-Sherif, Z.M., 2013. Nutritional value of *Cymodocea nodosa* and *Posidonia oceanica* along the western Egyptian Mediterranean coast. *Egyptian Journal of Aquatic Research*, 39, 153-165.
- Fakiris, E., Giannakopoulos, V., Leftheriotis, G., Dimas, A., Papatheodorou, G., 2023. Predictive Mapping of Mediterranean Seagrasses-Exploring the Influence of Seafloor Light and Wave Energy on Their Fine-Scale Spatial Variability. *Remote Sensing*, 15, 2943.
- Fourqurean, J.W., Duarte, C.M., Kennedy, H., Marbà, N., Holmer, M. *et al.*, 2012. Seagrass ecosystems as a globally significant carbon stock. *Nature Geoscience*, 5 (7), 505-509.
- Galil, B., 2007. Seeing Red: Alien species along the Mediterranean coast of Israel. *Aquatic Invasions*, 2, 281-312.
- Green, E.P., Short, F.T., 2003. *World atlas of seagrasses*. University of California, Berkeley, Los Angeles & London, 298 pp.
- den Hartog, C., 1970 *The sea-grasses of the world*. North-Holland Publishing Company, Amsterdam, 275 pp.
- Iturbide, M., Bedia, J., Gutiérrez, J.M., 2018. Background sampling and transferability of species distribution model ensembles under climate change. *Global and Planetary Change*, 166, 19-29.
- Koch, E.W., 1994. Hydrodynamics, diffusion-boundary layers and photosynthesis of the seagrasses *Thalassia testudinum* and *Cymodocea nodosa*. *Marine Biology*, 118, 767-776.
- Konstantinidis, I., Gkafas, G.A., Papathanasiou, V., Orfanidis, S., Küpper, F.C. *et al.*, 2022. Biogeography pattern of the marine angiosperm *Cymodocea nodosa* in the eastern Mediterranean Sea related to the quaternary climatic changes. *Ecology and Evolution*, 12 (5), e8911.
- Laffoley, D.d'A., Grimsditch, G. (Eds). 2009. *The management of natural coastal carbon sinks*. IUCN, Gland, Switzerland. 53 pp.
- Lino K., Asher J., Ferguson M., Gray A., McCoy K. *et al.*, 2018. *Ecosystem Sciences Division standard operating procedures: data collection for towed-diver benthic and fish surveys*. Pacific Islands Fisheries Science Center, National Marine Fisheries Service, Administration Report H; 18-02, 76 pp.
- Lipkin, Y., Beer, S., and Zakai, D., 2003. The Eastern Mediterranean and Red Sea. p. 65–73 in: *World Atlas of Seagrasses*. Green, E. P., Short, F. T. (Eds). Berkeley, California: University of California Press.
- Lobo, J.M., Jiménez-Valverde, A., Real, R., 2008. AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography*, 17, 145-151.
- Marbà, N., Duarte, C.M., Cebrián, J., Gallegos, M.E., Olesen, B. *et al.*, 1996a. Growth and population dynamics of *Posidonia oceanica* on the Spanish Mediterranean coast: elucidating seagrass decline. *Marine Ecology Progress Series*, 137, 203-213.
- Marbà, N., Cebrián, J., Enríquez, S., Duarte, C.M., 1996b. Growth patterns of Western Mediterranean seagrasses: species-specific responses to seasonal forcing. *Marine Ecology Progress Series*, 133, 203-215.
- Masucci, A.P., Arnaud-Haond, S., Eguíluz, V.M., Hernández-García, E., Serrão, E.A., 2012. Genetic flow directionality and geographical segregation in a *Cymodocea nodosa* genetic diversity network. *EPJ Data Science*, 1, 11.
- Maxwell, P.S., Eklöf, J.S., van Katwijk, M.M., O'Brien, K.R., de la Torre-Castro, M. *et al.*, 2017. The fundamental role of ecological feedback mechanisms for the adaptive management of seagrass ecosystems - a review. *Biological Reviews*, 92, 1521-1538.
- Mazarrasa, I., Marbà, N., Lovelock, C.E., Serrano, O., Lavery, P.S. *et al.*, 2015. Seagrass meadows as a globally significant carbonate reservoir. *Biogeosciences*, 12 (16), 4993-5003.
- Miller, I.R., Jonker, M.J., Coleman, G., 2009. *Crown-of-thorns starfish and coral surveys using the manta tow and SCUBA search techniques*. Australian Institute of Marine Science, Long-term monitoring of the Great Barrier Reef standard operation procedure number 9, edn 3, 74pp.
- Millot, C., Candela, J., Fuda, J.L., Tber, Y., 2006. Large warming and salinification of the Mediterranean outflow due to changes in its composition. *Deep Sea Research Part I: Oceanographic Research Papers*, 53, 656-666.
- Mutlu, E., Olguner, C., Özvarol, Y., Gökoğlu, M., 2022. Spatiotemporal biometrics of *Cymodocea nodosa* in a western Turkish Mediterranean coast. *Biologia*, 77 (3), 649-670.
- Najdek, M., Korlević, M., Paliaga, P., Markovski, M., Ivančić, I. *et al.*, 2020. Dynamics of environmental conditions during the decline of a *Cymodocea nodosa* meadow. *Biogeosciences*, 17, 3299-3315.
- Nguyen, H.M., Ralph, P.J., Marín-Guirao, L., Pernice, M., Proccaccini, G., 2021. Seagrasses in an era of ocean warming: a review. *Biological Reviews*, 96, 2009-2030.
- Nordlund, L.M., Koch, E.W., Barbier, E.B., Creed, J.C., 2016. Seagrass Ecosystem Services and Their Variability across Genera and Geographical Regions. *PLoS ONE*, 11, e0163091.
- Nordlund, L.M., Unsworth, R.K.F., Gullström, M., Cullen-Unsworth, L.C., 2017. Global significance of seagrass fishery activity. *Fish and Fisheries*, 19, 399-412.
- Ohayon, S., Homma, H., Malamud, S., Ostrovsky, I., Yahel, R. *et al.*, 2023. Consistent edge effect patterns revealed using continuous surveys across an Eastern Mediterranean no-take marine protected area. *ICES Journal of Marine Sciences*, 80 (6), 1594-1605.
- Orfanidis, S., Panayotidis, P., Siakavara, A., 2005. Benthic macrophytes: main trends in diversity and distribution. P. 226-235. In: *State of the Hellenic Environment*, Papathanassiou, E., Zenetos, A., (Eds). HCMR Publication, Athens.
- Orfanidis, S., Papathanasiou, V., Gounaris, S., Theodosiou T., 2010. Size distribution approaches for monitoring and conservation of coastal *Cymodocea* habitats. *Aquatic Conservation Marine and Freshwater Ecosystems*, 20 (2), 177-188.
- Ozer, T., Gertman, I., Kress, N., Silverman, J., 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., Gertman, I., Gildor, H., Herut, B., 2022. Thermohaline Temporal Variability of the SE Mediterranean Coastal Waters (Israel) – Long-Term Trends, Seasonality, and Connectivity. *Frontiers in Marine Science*, 8:799457.
- Pedersen, E.J., Miller, D.L., Simpson, G.L., Ross, N., 2019. Hierarchical generalized additive models in ecology: an intro-

- duction with mgcv. *PeerJ*, 7, e6876.
- Pérez, M., Romero, J., 1992. Photosynthetic response to light and temperature of the seagrass *Cymodocea nodosa* and the prediction of its seasonality. *Aquatic Botany*, 43, 51-62.
- Pickholtz, R.S.M., Kiflawi, M., Friedlander, A.M., Belmaker, J., 2018. Habitat utilization by an invasive herbivorous fish (*Siganus rivulatus*) in its native and invaded range. *Biological Invasions*, 20, 3499-3512.
- Polunin, N.V.C., Roberts, C.M., 1993. Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. *Marine Ecology Progress Series*, 100, 167-176.
- Potouroglou, M., Bull, J.C., Krauss, K.W., Kennedy, H.A., Fusi, M. *et al.*, 2017. Measuring the role of seagrasses in regulating sediment surface elevation. *Scientific Reports*, 7, 11917.
- van Rijn, I., Kiflawi, M., Belmaker, J., 2020. Alien species stabilize local fisheries catch in a highly invaded ecosystem. *Canadian Journal of Fisheries and Aquatic Sciences*, 77, 752-761.
- Sala, E., Kizilkaya, Z., Yildirim, D., Ballesteros, E., 2011. Alien marine fishes deplete algal biomass in the Eastern Mediterranean. *PLoS ONE*, 6, e17356.
- Schröder, K., Gasparini, G.P., Tangherlini, M., Astraldi, M., 2006. Deep and intermediate water in the western Mediterranean under the influence of the Eastern Mediterranean Transient. *Geophysical Research Letters*, 33 (21).
- Sghaier, Y.R., Limam, A., Samaha, L., Bitar, G., Khalaf, G. *et al.*, 2014. *Cymodocea nodosa* distribution along the Lebanese coast. p. 248-249. In: Proceedings of the 5th Mediterranean Symposium on Marine Vegetation, Portoroz, Slovenia, 27-28 October 2014. UNEP-MAP-RAC/SPA, Tunis.
- Short, F.T., Short, C.A., Novak, A.B., 2016. Seagrasses. p. 1-19. in: *The Wetland Book: II: Distribution, Description and Conservation*. Finlayson, C.M., Milton, G.R., Prentice, R.C., Davidson, N.C. (Eds.). Springer Netherlands, Dordrecht.
- Spanier, E., Zviely, D., 2023. Key Environmental Impacts along the Mediterranean Coast of Israel in the Last 100 Years. *Journal of Marine Science and Engineering*, 11, 2.
- Swets, J.A., 1988. Measuring the accuracy of diagnostic systems. *Science*, 240, 1285-1293.
- Todd, P.A., Heery, E.C., Loke, L.H.L., Thurstan, R.H., Kotze, D.J. *et al.*, 2019. Towards an urban marine ecology: characterizing the drivers, patterns and processes of marine ecosystems in coastal cities. *Oikos*, 128, 1215-1242.
- Tsioli, S., Orfanidis, S., Papathanasiou, V., Katsaros, C., Exadactylos, A., 2019. Effects of salinity and temperature on the performance of *Cymodocea nodosa* and *Ruppia cirrhosa*: A medium-term laboratory study. *Botanica Marina*, 62, 97-108.
- Tsioli, S., Papathanasiou, V., Rizouli, A., Kosmidou, M., Katsaros, C. *et al.*, 2021. Diversity and composition of algal epiphytes on the Mediterranean seagrass *Cymodocea nodosa*: a scale-based study. *Botanica Marina*, 64, 101-118.
- Turner, J.A., Babcock, R.C., Kendrick, G.A., Hovey, R.K., 2019. How does spatial resolution affect model performance? A case for ensemble approaches for marine benthic mesophotic communities. *Journal of Biogeography*, 46, 1249-1259.
- Tuya, F., 2006. Seasonal cycle of a *Cymodocea nodosa* seagrass meadow and of the associated ichthyofauna at Playa Dorada (Lanzarote, Canary Islands, eastern Atlantic). *Ciencias Marinas*, 32, 695-704.
- Tuya, F., Ribeiro-Leite, L., Arto-Cuesta, N., Coca, J., Haroun, R. *et al.*, 2014. Decadal changes in the structure of *Cymodocea nodosa* seagrass meadows: Natural vs. human influences. *Estuarine, Coastal and Shelf Science*, 137, 41-49.
- Unsworth, R.K.F., Nordlund, L.M., Cullen-Unsworth, L.C., 2018. Seagrass meadows support global fisheries production. *Conservation Letters*, e12566.
- Vergés, A., Tomas, F., Cebrian, E., Ballesteros, E., Kizilkaya, Z. *et al.*, 2014. Tropical rabbitfish and the deforestation of a warming temperate sea. *Journal of Ecology*, 102, 1518-1527.
- Vizzini, S., 2009. Analysis of the trophic role of Mediterranean seagrasses in marine coastal ecosystems: a review. *Botanica Marina*, 52, 383-393.
- Winters, G., Beer, S., Willette, D.A., Viana, I.G., Chiquillo, K.L. *et al.*, 2020. The Tropical Seagrass *Halophila stipulacea*: Reviewing What We Know From Its Native and Invasive Habitats, Alongside Identifying Knowledge Gaps. *Frontiers in Marine Science*, 7:300.
- Wood, S.N., 2017. "GAMs in Practice: mgcv." *Generalized additive models: an introduction with R*. 2nd ed. New York: Chapman and Hall/CRC. 80pp.
- Yeruham, E., Shpigel, M., Abelson, A., Rilov, G., 2020. Ocean warming and tropical invaders erode the performance of a key herbivore. *Ecology*, 101, e02925.
- Zhang, L., Liu, S., Sun, P., Wang, T., Wang, G. *et al.*, 2015. Consensus forecasting of species distributions: the effects of niche model performance and niche properties. *PLoS ONE*, 10, e0120056.

## Supplementary Data

The following supplementary information is available online for the article:

### 1. Detailed SDM methods.

**Table S2.** GAM results. The binomial response variable was the presence of seagrass meadows in a transect (number of successes) relative to the number of absences of the meadows (failures). Depth, latitude and season were used as predictors.

**Table S3.** SDM results for the models built based solely on data extracted from the literature (B), and for those including the data collected in our surveys (B). Each table shows the number of selected models according to the criterion of yielding TSS  $\geq 0.5$ , and the means

**Fig. S1:** Mediterranean Sea. The darker shade of blue represents the study area adopted in this work - the Eastern Mediterranean Basin. The lighter shade represents the areas that were excluded from our study, namely the portions of the Mediterranean Sea located East to the Strait of Sicily, and the Adriatic Sea.

**Fig. S2:** Eastern Mediterranean Basin. The darkest shade of blue represents the study area masked by depth, adopted for the SDMs - the cells within the Eastern Mediterranean Basin where the maximum depth was within the 95th quantile of occurrences records. The intermediate shade of blue represents the cells within the study area that were excluded by the depth criterion. The lightest shade represents the aforementioned areas that were excluded from our study.