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Spatiotemporal Variation in Environmental Key Parameters within Fleshy Red Algae Mats in the Mediterranean Sea

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Abstract: In the Mediterranean, the fleshy, mat-forming red alga *Phyllophora crispa* creates high-biodiversity habitats that influence light availability, water movement, and temperature. However, knowledge about its influence on other key environmental parameters, such as oxygen availability, chlorophyll, and turbidity, is missing. Therefore, we conducted an in situ study in the Western Mediterranean Sea using multiparameter probes that were placed multiple times on algal *P. crispa* mats, in adjacent *Posidonia oceanica* seagrass meadows, and on bare hard bottoms. We acquired a total of 17 full diel measurements for dissolved oxygen (DO), chlorophyll, and turbidity in September and October 2019. Results showed that *P. crispa* mats influence the investigated parameters differently when compared to *P. oceanica* meadows and that a monthly effect was observed. In September, general DO patterns measured for *P. crispa* mats and *P. oceanica* meadows follow the daily cycle depending on light availability, with the measured DO being lower in the *P. oceanica* meadows compared to the *P. crispa* mats and the hard-bottom habitats. In October, however, no significant difference in DO concentrations was observed between *P. crispa* mats and *P. oceanica* meadows. Results of this study corroborate that *P. crispa* mats can be viewed as an ecosystem engineering species, influencing environmental parameters and, hence, providing a habitat for outstanding associated biodiversity.

Keywords: *Phyllophora crispa*; *Posidonia oceanica*; daily cycles; environmental parameters



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1. Introduction

Ecosystem engineering species are organisms able to physically change the abiotic environment in which they live [1]. This concept depends on the spatial, temporal, and organizational structure of the species with the environment [2]. While native ecosystem engineers are key species for ecosystems [1] and have often been studied when they have decreased dramatically [3], non-indigenous species that act as ecosystem engineers can have profound impacts (positive and negative) on the receiving ecosystem. The presence of ecosystem engineers involves direct physical changes in habitat architecture and indirect changes in the substrate, for example, by trapping sediment particles or changing the light intensity at the bottom [3]. A classic example of an ecosystem engineer is the most common macrophyte in the Mediterranean Sea, the seagrass *Posidonia oceanica* (L.) Delile 1813, an endemic species that forms wide meadows [1]. As such, *P. oceanica* meadows shape a range of variables such as wave exposure [3,4], light availability [5], and temperature [6,7].

Recently, algal assemblages dominated by the red alga *Phyllophora crispa* P.S. Dixon, 1964, received some attention expressed by a growing number of studies [6,8–11]. *P. crispa* develops dense algal mats that harbor high biodiversity [8,9,11–13] and are becoming an important coastal habitat in the Mediterranean Sea [8,11]. As already observed in the Black Sea [13,14], *P. crispa* mats are largely colonizing wide areas of the rocky benthic

communities along the coasts of the Giglio Island (Tuscany, Italy) [8] and in other locations of the Mediterranean Sea [15,16]. Recent observations show that *P. crispa* mats not only replace but also overgrow benthic infralittoral Mediterranean habitats such as seagrass meadows or hard-bottom habitats with gorgonian dominance [17]. The laminal thallus of *P. crispa* mats represents a living substrate suitable for the colonization of solitary sessile species, for example, by increasing the area available for their settlement [9]. The thallus of *P. crispa* mats produces a substrate suitable not only for polychaetes [9], foraminifera [9], and bryozoans [10] but also for encrusting invertebrates (e.g., sponges [8]), as well as for many vagile species, mainly mollusks, crustaceans, and echinoderms [8]. This indicates that *P. crispa* mats may act as ecosystem engineers, thus, likely modifying key environmental parameters. A recent study by Schmidt et al., 2021 [6], found that dense mats of *P. crispa* significantly affect some environmental factors within the algal mats, such as temperature, light availability, and water movement, and their influence is similar to or even greater than that of the well-known ecosystem engineer *P. oceanica* meadow [6]. However, knowledge about the influence of *P. crispa* mats on other major environmental parameters, such as dissolved oxygen (DO) concentration [18] and chlorophyll [19], is still missing.

Thus, we here aim to quantify various environmental key parameters (DO, chlorophyll, turbidity, and temperature) in *P. crispa* mats and two reference habitats, i.e., adjacent *P. oceanica* seagrass meadows and bare hard-bottom habitat, by addressing the following research questions: (i) How do *P. crispa* mats influence DO and chlorophyll along with turbidity and temperature in comparison to neighboring habitats? (ii) What is the daily and monthly variation in these key parameters in *P. crispa* mats in comparison to its neighboring habitats?

To answer these research questions, four multi-probes were positioned multiple times within *P. crispa* mats, in the adjacent *P. oceanica* meadows, and in the bare hard-bottom habitat serving as a reference habitat.

2. Materials and Methods

2.1. Study Area and Experimental Design

The research took place at Punta del Morto on the Giglio Island (Tuscany, Italy; Figure 1), located on the northern side of the island (42°23'22.2" N, 10°53'24.3" E). Four Eureka Manta-2 multi-probes (GEO Scientific Ltd., Austin, TX, USA) were randomly placed in the three target habitats to investigate their physical and chemical characteristics: (i) *P. crispa* mats with a thickness of >5 cm; (ii) *P. oceanica* seagrass meadows with a height of >20 cm; and (iii) in the hard-bottom habitats (Figure 2). All probes were deployed at 28 m depth, where the three target habitats were found in close vicinity being less than 30 m apart from each other. Two sampling periods were chosen, i.e., 7–18 September 2019 and 9–17 October 2019, to evaluate potential monthly variations in the target environmental parameters. During the first sampling period, the probes were placed eight times in *P. crispa* mats, six times in *P. oceanica* meadows, and five times in hard-bottom habitats, for at least 24 h. During the second sampling period, the probes were placed three times in *P. crispa* mats, seven times in *P. oceanica* meadows, and two times in hard-bottom habitats, for at least 24 h. To increase the stability of the probes underwater, the Manta multi-probes were modified with the addition of weights to the basal area of the instrument (Figure 2B). The environmental parameters recorded were dissolved oxygen (DO; mg L⁻¹), chlorophyll (µg L⁻¹), turbidity (NTU), and temperature (°C). Once in the water, the multi-probes acquired simultaneously the values of each parameter with a sampling interval of one minute for at least 24 h. At the end of the acquisition, the multi-probes were recovered and brought to the laboratory for data analyses.

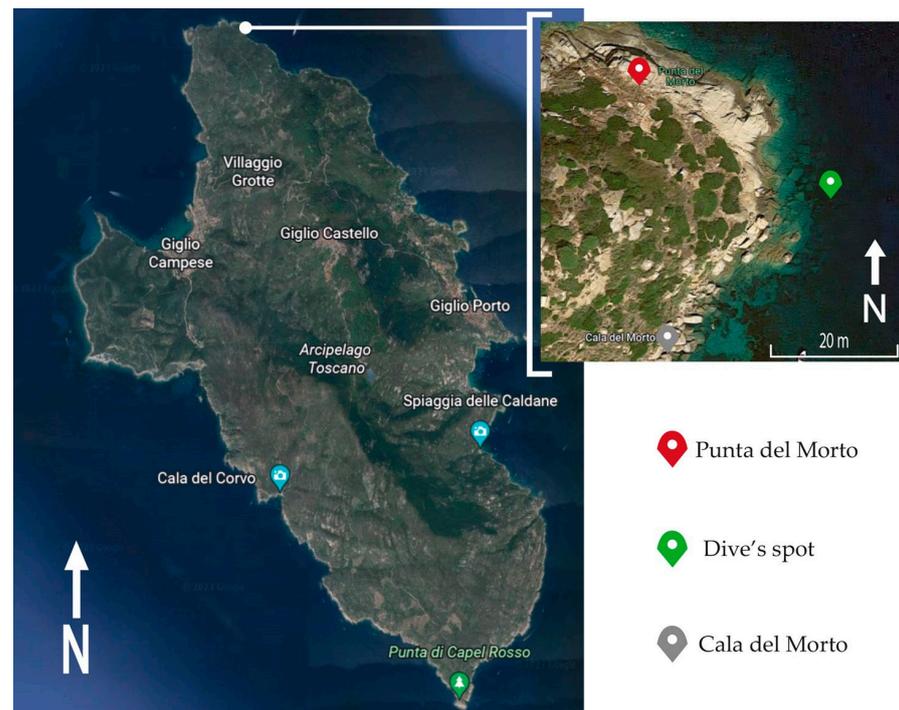


Figure 1. Map of the Giglio Island with the diving spot at Punta del Morto (map of the Giglio Island modified from Google Earth ; aerial image by Google Maps) [20].



Figure 2. Eureka Manta-2 multi-probes deployed at 28 m depth in *Phyllophora crispa* mats (A), hard-bottom habitats (B), and within the *Posidonia oceanica* seagrass meadows (C). Photos taken by Alice G. Bianchi.

2.2. Statistical Analysis

The acquired values of each environmental parameter were displayed through scatter plots using the statistical software R.Studio (version 4.1.3) to highlight the data adaptation curves. Significant differences in the four measured environmental parameters (i.e., dis-

solved oxygen, chlorophyll, turbidity of the water, and water temperature) among the three target habitats (i.e., *P. crispa* mats, *P. oceanica* meadows, and hard-bottom habitats) were analyzed. The averages of the dependent variables (the four parameters) at the levels of the group variable (the investigated habitats) were compared both between environments and between months through a statistical test based on the analysis of variance (ANOVA, results can be seen in Table 1), with significance level $\alpha = 0.05$. To be used, an ANOVA requires the assumptions of normality (the sampled data must come from a population with a normal distribution) and homoscedasticity (the variance of the groups must be the same as that of the population) [21]. To test the assumption of normality, the first transformation of the dependent variables in logarithmic scale was carried out, and then we proceeded to use the Shapiro–Wilk test (Supplementary Material Table S1), while to test the homoscedasticity, the Levine test was used (Supplementary Material Table S2). Since available data are independent samples, we used an ANOVA, which allowed us to verify the significance of the environmental factor. Afterwards, we checked if the effect linked to each type of environment also varied according to the months in which the measurements were recorded (effect of interaction between the month variable and the environment variable). This last goal was managed through the post hoc correction of Tukey HSD, with the Bonferroni adjustment (Supplementary Material Table S3) [22].

Table 1. Analysis of variance (ANOVA) evaluates the significance of the environment variable and the interaction between the latter variable and the month variable for all four chemical-physical parameters. In the specific case of dissolved oxygen and chlorophyll, the impact of temperature, turbidity, and their respective interactions with the environment and month variables is evaluated. Top: *p*-values. Bottom: F-values.

	Dissolved Oxygen	Chlorophyll
Temperature	<0.001 37.406	<0.001 8.412
Turbidity	0.007 7.707	<0.001 301.411
Habitat	<0.001 122.456	<0.001 73.515
Habitat × month	<0.001 18.972	<0.001 88.033
Habitat × Temperature	<0.001 8.467	0.011 5.682
Habitat × Turbidity	0.003 6.501	<0.001 32.536
Month × Temperature	0.010 5.317	0.002 10.252
Month × turbidity	0.011 4.839	<0.001 14.479
	Habitat	Months × Habitat
Turbidity	<0.001 628.3	0.001 7.570
Temperature	0.026 5.298	<0.001 20.447

3. Results

3.1. Temperature

Temperature values ranged from a minimum of 16.8 °C to a maximum of 21.2 °C both detected in *P. oceanica* meadows. The temperatures measured in September showed mostly significant differences among the three habitats (Tukey HSD, $p < 0.001$ for both *P. oceanica*

meadows vs. *P. crispa* mats and hard-bottom habitats vs. *P. crispa* mats; Figure 3A, Table 2). Temperature in all three habitats peaked at 04:00 pm in September, with *P. crispa* mats reaching a temperature of 18.40 °C, *P. oceanica* meadows 19.25 °C, and hard-bottom habitats 19.71 °C (Figure 3A). During October, significant differences between *P. crispa* mats and *P. oceanica* meadows (Tukey HSD, $p = 0.026$; Table 2) were registered. The mean temperature in *P. oceanica* meadows in September was 19.41 ± 0.38 °C, which was significantly lower than in *P. crispa* mats (Tukey HSD, $p < 0.001$; Figure 3B, Table 2).

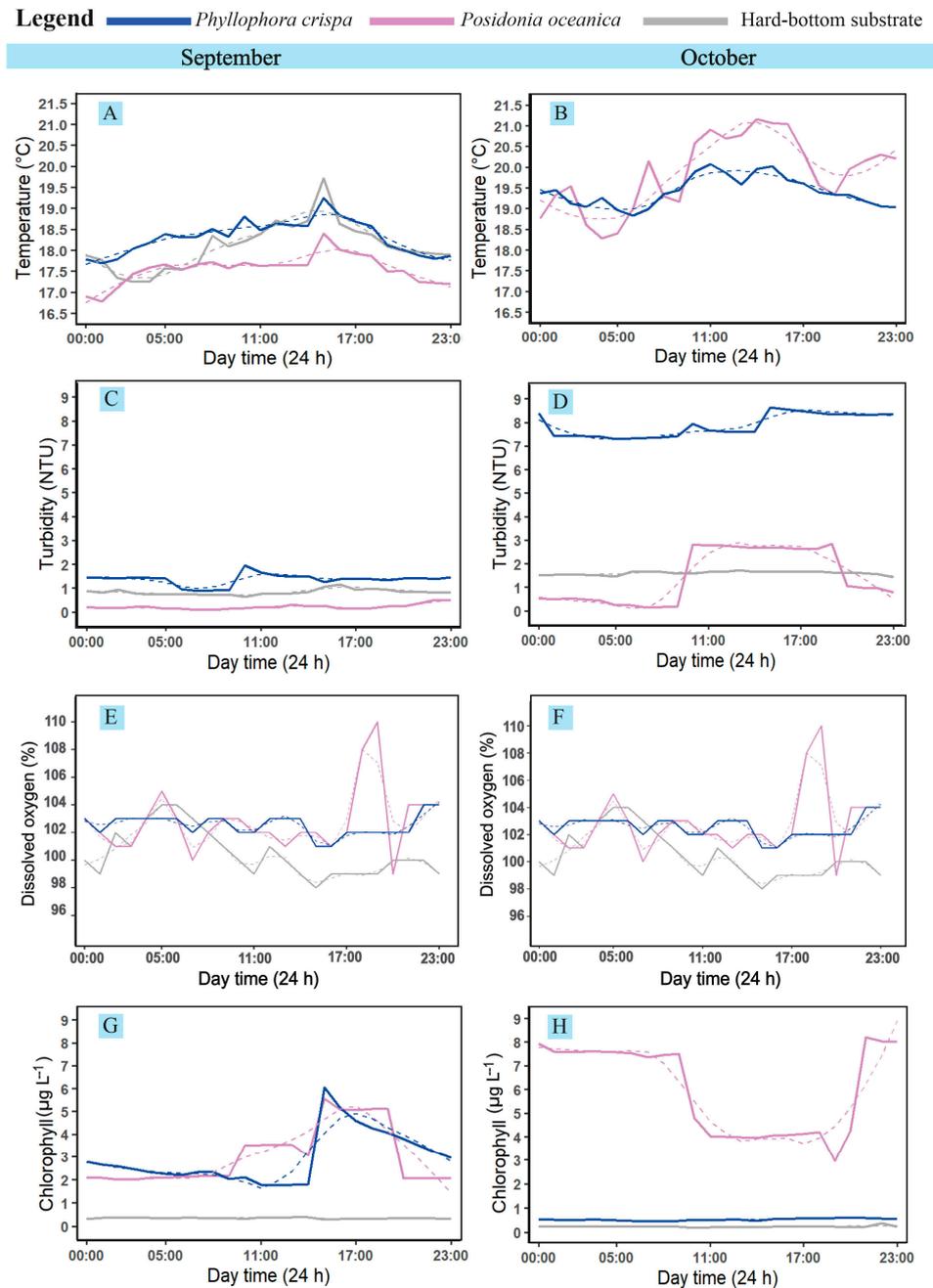


Figure 3. Comparison of temperature (A,B), turbidity (C,D), dissolved oxygen (E,F), and chlorophyll (G,H) in *Phyllophora crispa* mats (blue line), *Posidonia oceanica* meadows (pink line), and hard-bottom habitats (gray line), during September (left) and October (right). Probes were placed for at least 24 h with $n = 8$ for *P. crispa*, $n = 6$ for *P. oceanica*, and $n = 5$ for hard-bottom habitats in September 2019 and $n = 3$ for *P. crispa*, $n = 7$ for *P. oceanica*, and $n = 2$ for hard-bottom habitats in October 2019. The continuous lines are the daily mean values; the dotted lines are the trend line of values. The temperature data for October (B) in the hard-bottom habitats are missing due to technical problems.

Table 2. Post hoc Tukey HSD statistical analysis to evaluate differences between pairs of environments (*Phyllophora crispa* mats, *Posidonia oceanica* meadows, hard-bottom habitats) on the monthly values of environmental parameters.

	September			October		
	<i>P. crispa</i> Mats vs. Hard-Bottom Habitats	<i>P. crispa</i> Mats vs. <i>P. oceanica</i> Meadows	<i>P. oceanica</i> Meadows vs. Hard-Bottom Habitats	<i>P. crispa</i> Mats vs. Hard-Bottom Habitats	<i>P. crispa</i> Mats vs. <i>P. oceanica</i> Meadows	<i>P. oceanica</i> Meadows vs. Hard-Bottom Habitats
Dissolved oxygen	0.590	<0.001	<0.001	<0.001	0.856	<0.001
Chlorophyll	<0.001	0.969	<0.001	<0.001	<0.001	0.074
Turbidity	<0.001	<0.001	<0.001	0.707	<0.001	<0.001
Temperature	<0.001	<0.001	0.223	-	0.026	-

3.2. Turbidity

Turbidity values fluctuated between a minimum of 0.09 NTU detected in *P. crispa* mats to a maximum of 8.63 NTU registered in the *P. oceanica* meadows. In both September and October, significant differences in the turbidity values among the three habitats were detected (Tukey HSD, $p < 0.001$; Table 2). In September, turbidity was constant during the 24 h in all three habitats (Figure 3C) with daily mean values of 0.22 ± 0.11 NTU for *P. crispa* mats and 136 ± 0.24 NTU for *P. oceanica* meadows. Turbidity measured in October within the *P. crispa* mats increased to 2.86 NTU at 11:00 am and then remained stable until 9:00 pm (Figure 3D). In *P. oceanica* meadows, turbidity was higher, peaking at 04:00 pm at a value of 8.63 NTU and then remaining stable (Figure 3F).

3.3. Dissolved Oxygen

The range of dissolved oxygen (DO) values between the three environments ranges from a minimum of 98% O₂ detected in the hard-bottom habitats to a maximum of 110% O₂ found in the *P. crispa* mats. The DO concentration was similar for *P. oceanica* meadows and hard-bottom habitats in September (Figure 3E), whereas a different daily DO concentration cycle was observed for *P. crispa* mats. In September, DO concentrations in the *P. oceanica* meadows were significantly higher during the 24 h compared to *P. crispa* mats (Tukey HSD, $p < 0.001$; Table 2), with DO concentrations peaking at 105% O₂ in *P. crispa* mats at 08:00 pm, followed by a decrease at 09:00 pm when the minimum value of 99% O₂ was recorded. During October, no significant differences in DO between *P. crispa* mats and *P. oceanica* meadows were registered but between hard-bottom habitats and both *P. oceanica* meadows and *P. crispa* mats (Tukey HSD, $p < 0.001$; Table 2; Figure 3F).

3.4. Chlorophyll

Chlorophyll concentrations in the three environments ranged from a minimum of $0.19 \mu\text{g L}^{-1}$ recorded in the hard-bottom habitats to a maximum of $8.19 \mu\text{g L}^{-1}$ detected in *P. crispa* mats. The values registered in the hard-bottom habitats were constant, with an average value of $0.29 \mu\text{g L}^{-1}$. In September, chlorophyll concentrations were similar in *P. crispa* and *P. oceanica* (Tukey HSD, $p = 0.969$; Table 2, Figure 3G). The daily average of chlorophyll registered in *P. crispa* mats was $3.00 \pm 1.26 \mu\text{g L}^{-1}$. It peaked at 04:00 pm with a concentration of $5.55 \mu\text{g L}^{-1}$, followed by a decrease until 9:00 pm to constant values of about $2.05 \mu\text{g L}^{-1}$. Chlorophyll concentrations measured in the *P. oceanica* meadows during September peaked at 04:00 pm at a value of $6.05 \mu\text{g L}^{-1}$. In October, the chlorophyll showed significant differences only between *P. crispa* mats and *P. oceanica* meadows and between *P. crispa* mats and the hard-bottom habitats (Tukey HSD, $p < 0.001$; Table 2). Additionally, the chlorophyll concentration measured within the *P. crispa* mats decreased drastically from 11:00 am to 09:00 pm in October, reaching a minimum value of $2.97 \mu\text{g L}^{-1}$ at 08:00 pm (Figure 3H). In this month, the mean daily value of chlorophyll was $0.053 \pm 0.04 \mu\text{g L}^{-1}$ for *P. oceanica* meadows and $0.24 \pm 0.03 \mu\text{g L}^{-1}$ for hard-bottom habitats.

4. Discussion

Mats formed by *Phyllophora crispa* are of growing interest, as this key structural and fast-growing alga of the Mediterranean [8] is replacing many classical Mediterranean habitats [17], harboring outstanding associated invertebrate biodiversity [8,11]. The parameters investigated in this study extend the findings of a recent study by Schmidt et al., 2021 [6], by showing that relevant environmental parameters, such as dissolved oxygen (DO), chlorophyll, turbidity, and intense solar radiation differ among months and corroborate the concept that *P. crispa* mats can be considered as an ecosystem engineer.

4.1. How Do *P. crispa* Mats Influence Oxygen and Chlorophyll along with Turbidity and Temperature in Comparison to Neighboring Habitats?

Throughout the sampling period, higher values of DO, temperature, turbidity, and chlorophyll (registered global minimum or maximum values depending on the different parameters) were recorded within *P. crispa* mats compared to adjacent *P. oceanica* meadows and hard-bottom habitats. The temperature in all three target habitats was higher in October compared to September, especially during the central hours of the day, when the sun is warmer. Variations in water temperature can create conditions that lead to ecological change, for example, the invasions of alien species [23] with important associated physical and geomorphic interactions [24]. The DO concentrations and temperatures found in *P. crispa* mats did not differ significantly from the hard-bottom habitats, probably due to an effective mixing of overlaying waters. The lower values of DO found in *P. oceanica* meadows compared to *P. crispa* mats may be explained by the positioning of the probes in the rhizoidal zone of the meadow, a part of the plants that does not carry out photosynthetic activity but respiration [25]. The recorded patterns of DO concentrations, although they reflect the daily cycle with increasing DO concentrations during the daytime and decreasing during the night hours (visible especially in September), are generally lower in *P. oceanica* meadows than in *P. crispa* mats and hard-bottom habitats. The increase in temperature in October could explain the observed patterns in the trend of DO, which is inversely proportional to the temperature [26]. Both DO and chlorophyll significantly differed between the two investigated periods in each habitat. It should also be noted that, although statistical analyses indicate that in October there is no significant difference in the amount of DO between *P. crispa* mats and *P. oceanica* meadows, some differences occur: while *P. crispa* mats reveal peaks of DO at certain times of the day, *P. oceanica* meadows have a more uniform trend during the daily span of October. The increase in temperature during autumn can affect the increase in sediment suspension [24]. In *P. crispa* mats, the increased turbidity during the middle hours of the day in October probably contributed to a decrease in the chlorophyll released by its fronds. Suspended sediments may be responsible for the attenuation of sunlight [27] and, consequently, the decrease in benthos-reaching light [28] influencing photosynthetic activity [29] and the release of chlorophyll into the environment. The higher and constant turbidity values measured in October in the *P. oceanica* meadows may be due to weather conditions [30]. Comparatively low water movement inside the red algae mats, as observed in the same sampling period [6], could lead to a suspension of sediment within the *P. oceanica* meadows due to its dense rhizomes that reduce water current and, in turn, lead to higher turbidity [31]. Increased turbidity during the hottest hours of the day (11:00 am–9:00 pm) in *P. crispa* mats was observed. This increase could negatively impact light availability [6], which in turn could influence photosynthetic activity [32], thus explaining the lower DO values measured in *P. oceanica* meadows in September. The high turbidity values recorded in *P. crispa* mats in October are concomitant with a decrease in chlorophyll. This contradicts reciprocal patterns in *P. oceanica* meadows and previous findings, demonstrating a link between turbidity and chlorophyll production [33]. Our data show that both turbidity and temperature may cause changes in DO and chlorophyll levels. The interaction effect of these two variables both with the environment and with the months is significant, highlighting how the impact of turbidity and oxygen varies in relation to the environment and with months. Our results

indicate that in September the average level of DO in the environment of *P. crispa* is similar to the average level found in the hard-bottom environment, while in October it is similar to the average value visible in the *P. oceanica* environments.

For chlorophyll, the average concentration measured within *P. crispa* mats in September is similar to that in the *P. oceanica* meadows, while in October it differs from that of both other environments. However, the daily trend of DO and chlorophyll for *P. crispa* mats changes in the two months, above all if compared with that of the other environments as it presents more extreme peaks during certain phases of the day. We assume that this is due to an effect of turbidity and temperature.

4.2. What Is the Daily and Monthly Variation in These Key Parameters in *P. crispa* Mats in Comparison to Neighboring Habitats?

The parameters recorded in the three habitats vary with the investigated months. September 2019 was a month in which no storm surges or bad weather were recorded [20]. In September, the temperatures recorded in the three habitats were a few degrees Celsius lower than in the following month, and this month is characterized by greater sun exposure being the last month of the summer season [20]. Intense daily light hours and weather contributed to greater photosynthetic activity, visible with the increase in chlorophyll and DO concentrations in the target habitats, an increase that coincides with the hours of maximum sun exposure and then decreases at sunset. October 2019 was a month that recorded several days of bad weather, wind, and high waves that did not facilitate the acquisition of data. The increased current intensity influenced the mixing of water by increasing turbidity and affecting the production of dissolved oxygen and chlorophyll at the bottom. In addition, even slightly higher temperature values contributed to a decrease in dissolved oxygen. In both months, we assume that the monthly variations affect the trend of the physical and chemical values and we hypothesize that the latter are interconnected in each habitat. In particular, the interaction between chlorophyll and turbidity is visible in *P. crispa* mats in October, where a sharp increase in suspended sediments during daylight hours (10 am–10 pm) reduced the amount of light on the bottom, potentially resulting in reduced photosynthetic activity [27]. In fact, one of the physical properties of the suspended sediment is precisely that of dispersing and absorbing even solar photons, modifying the radiation of the underwater field and consequently the thermal characteristics and the primary production within the water body [27]. The trends of the parameters in the *P. crispa* habitats appear to be more different from those of the nearby habitats in October. It can also be noted that the trend of chlorophyll is opposite in the two months: chlorophyll concentrations increase during the day and then progressively decrease during the night in September, while in October they decrease during the day and then increase again overnight. Some sites may be characterized by a mild seasonal effect of sediments more in summer and coarser in winter, explained by the seasonality of waves, currents, and storms [34]. The load of suspended sediments was greater in autumn than in September, particularly in *P. oceanica* meadows where the turbidity is greater than in the other investigated habitats. One of the reasons for greater turbidity may be the predominant adverse weather and marine conditions throughout the month of October 2019. The Mediterranean Sea is a basin whose temperature is strongly influenced by seasonal changes [35]. The sea has a very high heat capacity [35] that generates a temperature difference between the sea and the land, causing heat exchanges between the two systems, so that in summer the sea absorbs heat from the coast, and in winter it releases it gradually. On a physical level, the concept of water thermoregulation may explain the increase of a few degrees in temperature in late October compared to early September in *P. crispa* mats, *P. oceanica* meadows, and hard-bottom habitats. The graphs (Figure 3) show how the parameters in the three habitats are similar to each other; for example, the maximum values are reached in the same time slot, and the curves decrease in a similar way. Nevertheless, the comparison of pairs of parameters of each habitat performed with ANOVA (Table 1) found that the trends are different for each environment. In particular, in the case of DO, it can be assumed that the

differences found between pairs of parameters can be caused by turbidity and temperature, which from ANOVA appear to affect the levels of DO.

4.3. Ecological Implications

In the Black Sea, *P. crispera* is considered a key species as it creates a habitat for many species of marine fauna and flora, which reproduce and recruit within the three-dimensional structure provided by this red alga [14,36]. The different chemical-physical factors that influence the possible presence of epiphytes include nutrient availability, temperature, salinity, depth, current, and the amount of light [37]. The production of oxygen by plants and seaweeds determines the amount of the epiphytic community associated with them [25]. The community of sessile and vagile animals can create oxygen fluctuations within algal mats and lawns and can attenuate the flow of light [38,39] and increase the resistance of the transfer of dissolved substances between their mass and the surface of the plant [40]. The abundance of some vagile or sessile organisms can also depend on variations in environmental parameters, according to the monthly payments [37,38]. In September, the lower production of chlorophyll may be associated with seasonal sessile organisms that occupy the thallus of *P. crispera* mats. In October, chlorophyll concentrations were high, potentially indicating fewer organisms present on the thallus of *P. crispera* mats. During that month, however, a decrease in DO concentrations and an increase in turbidity may also be associated with seasonal vagile organisms that live on the thallus of *P. crispera* mats. The abundance of foraminifera found in *P. crispera* mats [9] may be due to the characteristics of DO [41,42], from organic material within sediment and chlorophyll concentration [34]. The higher chlorophyll values recorded in October compared to September may have also been influenced by the possible presence of associated seasonal biodiversity [37,38]; some foraminifera are seasonal, and their abundance is moderated by temperature variations [43] and by the deposition and removal of sludge [34]. The suspension of organic material may be due to bioturbation activities such as those carried out by polychaetes [34], which feed rapidly on organic material [44–46] and increase the suspended sediment, favoring the penetration of DO into the seabed [34,44]. *P. crispera* mats with their ability to retain sediment could function as a food source and create habitat for its associated organisms [6]. As in the Black Sea [14], *P. crispera* mats could serve as a biodiversity hotspot in the Mediterranean Sea for invertebrates, to a certain extent also surpassing *P. oceanica* meadows in species richness and diversity since a range of sessile, colonial, and aggregate species can be found almost exclusively in *P. crispera* mats [8,9,11]. In this context, *P. crispera* mats have recently been proposed as an ecosystem engineer [6]. The high primary production and the wide supply of labile organic matter over a prolonged period favor the development of foraminifera [44]. The higher concentrations of chlorophyll recorded in the *P. crispera* mats compared to *P. oceanica* meadows (for both months of sampling) may contribute to a greater abundance of foraminifera found in the algal mat than in the seagrass [11]. The three-dimensional structure of *P. crispera* mats with a large surface area enlargement factor [11], in addition to influencing the chemical and physical environmental parameters, can also influence any communities present [10]. Given the possible presence of resident organisms on the thallus of *P. crispera* mats [8,10,45], several sessile, colonial, and mobile species may also benefit from these changes.

4.4. Limitations and Conclusions

Spatiotemporal research, such as monitoring key environmental parameters, is often limited by technical and logistical issues. These limitations can be addressed and reduced by following a scientifically robust experimental design [46], including a maximum amount of spatiotemporal replication and a statistical analysis using mixed models, useful in contexts where repeated measurements are made on the same statistical units, especially for their advantage of dealing with missing values [47]. Here, we were able to deploy the respective probes with the following replication: $n = 8$ for *P. crispera*, $n = 6$ for *P. oceanica*, and $n = 5$ for hard-bottom habitats in September 2019 and $n = 3$ for *P. crispera*, $n = 7$ for *P. oceanica*,

and $n = 2$ for hard-bottom habitats in October 2019. All probes consecutively collected data for 24 h covering a full daily cycle. We acknowledge that two of the aforementioned six deployments ($n = 3$ and $n = 2$ for *P. crispa* and hard-bottom habitats, respectively, in October 2019) range at the lower end of an appropriate replication. However, working at a depth of ~30 m limits the bottom time for divers without exceeding decompression limits. Therefore, prioritizing divers' safety while deploying the probes led to a reduced number of deployments during the second half of the experimental period, thus resulting in a lower replication. Nevertheless, we assume that the collected data still provide valuable insights that corroborate the previously characterized role of *P. crispa* mats as ecosystem engineers. We here were able to demonstrate that several key environmental parameters are significantly modified by *P. crispa* mats, and seasonal changes within these parameters are likely to subsequently affect the associated biodiversity. We conclude that despite its surprising function as an ecosystem engineer, further investigations should aim to include a higher spatial and temporal resolution to understand (i) to what extent the environmental parameters may vary over seasons and (ii) whether the observed patterns can be found at other reported locations in which *P. crispa* mats occur, such as the Mediterranean, the Black Sea, or the Atlantic.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/oceans4010007/s1>, Table S1: Shapiro–Wilk test for the analysis of normality. The assumption of normality is a requirement for the execution of ANOVA for repeated measures, Table S2: Mauchly test for the verification of sphericity. The assumption of sphericity is a requirement for the execution of ANOVA for repeated measurements, Table S3: Bonferroni adjustment for the verification of the monthly influence on the environmental parameters recorded in the three habitats. The Bonferroni adjustment is considered an extension to the case of repeated measurements of the post hoc correction of Tukey for the classic ANOVA [22].

Author Contributions: Y.C.E.-K., A.G.B. and C.W. conceptualized and designed the research. A.G.B. and Y.C.E.-K. performed the research. A.G.B., E.B. and Y.C.E.-K. analyzed the data. A.G.B., C.W., M.M. and Y.C.E.-K. wrote the manuscript. All authors have read and agreed to the published version of the manuscript.

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