



Fleshy Red Algae Mats Influence Their Environment in the Mediterranean Sea

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In the Mediterranean Sea, the fleshy red alga *Phyllophora crispa* forms dense mats of up to 15 cm thickness, mainly located on rocky substrates in water depths below 20 m. Because of the observed density of these mats and some first observations, we hypothesize that *P. crispa* is a yet undescribed ecosystem engineer that provides a multitude of ecological niches for associated organisms along small-scale environmental gradients. Therefore, we conducted an in-situ pilot study in the Western Mediterranean Sea to assess potential influence of the algae mats on the key environmental factors water movement, temperature and light intensity. We comparatively and simultaneously measured in *P. crispa* mats, in neighboring *Posidonia oceanica* seagrass meadows, on neighboring bare rocky substrates without algae mats, and in the directly overlying water column. We used several underwater logging sensors and gypsum clod cards. Findings revealed that *P. crispa* significantly reduced water movement by 41% compared to the overlying water column, whereas water movement was not affected by *P. oceanica* meadows and bare rocky substrates. Surprisingly, *P. crispa* increased the water temperature by 0.3°C relative to the water column, while the water temperature in *P. oceanica* and on bare rocky substrates was reduced by 0.5°C. Light intensity inside the red algae mats was reduced significantly by 69% compared to the water column. This was similar to measured light reduction of 77% by *P. oceanica*. These findings highlight the strong influence of the dense red algae mats on some key environmental factors. Their influence is obviously similar or even higher than for the well-known seagrass ecosystem engineer. This may be a factor that facilitates associated biodiversity similarly as described for *P. oceanica*.

Keywords: macroalgae, seagrass, *Posidonia oceanica*, phytal habitat, hard-bottom communities, environmental gradients

INTRODUCTION

Ecosystem engineers are defined as organisms that control the availability of resources either directly or indirectly by their ability to change the physical state of abiotic or biotic material (Jones et al., 1994, 1997). Therefore, ecosystem engineers can create or modify habitats (Crooks, 2002) by affecting environmental parameters, such as light, temperature, pH, oxygen and availability of substrate. Jones et al. (1994, 1997) define two types of bioengineering organisms: (1) autogenic engineers which modify their environment by endogenous processes, such as growth

(e.g., trees) and (2) allogenic engineers which modify other living or non-living material in their surrounding (e.g., beaver).

Corals are a prominent example of structural engineers, a subgroup of autogenic engineers, which physically create substrate, control resources and shape their environment (Jones et al., 1997; Berke, 2010). For example, the metabolism of both corals and their symbiotic algae (i.e., respiration and photosynthesis) cause oxygen micro-gradients near reefs (Shashar et al., 1993) that can affect a range of associated species (Vogel, 1981; Atkinson, 1992). Mangroves are another example of structural ecosystem engineers that create habitat for numerous aquatic species (Robertson and Blaber, 1992; Kandasamy and Bingham, 2001). The complex structure of their roots provides shelter from predators (Laegdsgaard and Johnson, 2001; Macia et al., 2003). Moreover, kelp algae modify their surroundings' physical state through their morphology in coastal environments worldwide (Jones et al., 1997). Aggregations of such macroalgae form a unique habitat for marine organisms (Christie et al., 2003) by dampening water currents (Jackson, 1997; Gaylord et al., 2007) and diminishing light (Pearse and Hines, 1979; Reed and Foster, 1984; Stewart et al., 2008).

In the Mediterranean Sea, a member of the seagrass family Posidoniaceae, the endemic *Posidonia oceanica* (Delile, 1813) acts as a well-known biodiversity hotspot (Montefalcone et al., 2007; Pergent et al., 2014) and an autogenic ecosystem engineer. It forms wide meadows that can, among others, affect the hydrodynamics of currents and waves (Gambi et al., 1990; Bouma et al., 2005). Further, *P. oceanica* promotes sediment stability by buffering resuspension (Gacia et al., 1999; Terrados and Duarte, 2000; Gacia and Duarte, 2001).

Another potential habitat-building species in the Mediterranean Sea is the fleshy red alga *Phyllophora crispa* (Dixon, 1964). In water depths below 20 m, the alga forms discontinuous mats of at least 5 cm thickness, mainly on rocky substrates, which can cover large parts of the seafloor (Bonifazi et al., 2017). A massive development of these red-algae mats lead to it becoming a dominant benthic habitat around the Island of Giglio since 2012 (Bonifazi et al., 2017).

Bonifazi et al. (2017) provided a first description of the associated fauna of *P. crispa*, and its role as a habitat forming species at the Island of Giglio, Italy, and came to the conclusion that biodiversity of mobile and sessile invertebrates associated with the mats is high. A reason for this finding is likely that *P. crispa* mats create a range of micro-niches by influencing key environmental parameters such as water current exposure, temperature and light availability. Because of the observed density of these mats and some first observations, we hypothesize that *P. crispa* is a yet undescribed ecosystem engineer that provides a multitude of ecological niches for associated organisms along small-scale environmental gradients. This study thus aimed to investigate the potential role of *P. crispa* as an ecosystem engineer and answer the following research question: What are the differences in water movement, temperature and light availability between *P. crispa* mats, *P. oceanica* meadows and rocky substrates without any overlying mats? To answer this question, we conducted a series of comparative and simultaneous in-situ measurements in the Mediterranean Sea.

MATERIALS AND METHODS

Study Site and Habitat Characterization

The study was performed in September and October 2019 on the Island of Giglio, Tuscany, Italy. All observational surveys were conducted *in situ via* scuba-diving at a depth of 28–30 m at the dive site “Punta del Morto” (42°23'22.2"N 10°53'24.3"E), which is located at the northern coast of Giglio. The study area was on the west side of the dive site, where, starting at a depth of 20 m, granite blocks cover most parts of the seafloor. In the Mediterranean Sea, the occurrence of small patches of bare granitic rock at water depths of 30 m is common. Additionally, dense *Posidonia oceanica* seagrass meadows, characterized by straight, single leaves, and dense *P. crispa* mats of robust, branched, and entangled structure are present at the study site. All three habitats (i.e., *P. crispa* mats of at least 5 cm thickness, *P. oceanica* seagrass meadows of at least 20 cm height, bare rocky substrate; **Supplementary Figure 1**) were found at the same water depth in an area of about 250 m². Limiting the study to this one sampling site allowed for a direct comparison by quantifying environmental conditions within these three habitats, as we expect that all habitats experienced identical external conditions (e.g., temperature, salinity, insolation, hydrodynamics, etc.). The rhizome part of *P. oceanica*, above and below ground, was not included in this study.

Environmental Parameters

Effects on water movement relative to the water column by *P. crispa* and the other two ecosystem types were measured simultaneously using the gypsum dissolution technique (Eckman et al., 1989; Duggins et al., 1990). While this method is not appropriate to measure absolute water flow, it is well suitable for relative comparison of water movement (Jokiel and Morissey, 1993; Thompson and Glenn, 1994; Evans and Abdo, 2010). Gypsum of smooth consistency (Quick-mix gips, toom # 3050388, CaSO₄) was poured into muffin cups. Air bubbles were removed with continuous finger snapping for 30 s. After a drying period of 24 h at air temperature, gypsum balls were taken out of the cups and dried to constant weight in an oven at 60°C before being glued to plastic cards avoiding gaps between both the cards and the gypsum balls. Then, clod cards were numbered and weighed. Clod cards were placed at heights of 0 cm (seafloor), 1 cm (within *P. crispa* mats), 5 cm (algae-water interface) and 20 cm (above the algal mats) by attaching them to a 30 cm long metal rod with cable ties (**Supplementary Figure 2**). Replication was done primarily temporal, with rods being deployed at four different time points. A total of eleven rods was placed in *P. crispa* at all four timepoints. The same set-up was used at one timepoint on rocky substrates, resulting in two replicates. Since seagrass meadows grow higher than the red algae mats, a metal rod of 80 cm length was used and an additional clod card was placed 30 cm from the ground. This setup allowed selecting the same positions that were used for *P. crispa* and rocky substrates: 0 cm (seafloor), 1 cm (within *P. oceanica* meadow), 5 cm (within *P. oceanica* meadow), 20 cm (meadow-water interface) and 30 cm (above the meadow). A total

of three rods was deployed at three different time points in *P. oceanica*, resulting in a replication of three. The size of the gypsum balls was similar for all environments. The set-ups were prepared before deploying *in situ* and stayed in the water for 6–7 days after deployment. The set-ups were then transported out of the water, clod cards were carefully removed from the metal stick, rinsed with fresh water and placed on a drying rack. Then, clod cards were dried in an oven at 60°C until a constant dry weight was reached. The relative weight loss of gypsum balls [presented as a reduction of daily average weight loss of gypsum balls relative to the overlaying water (%)] was used as an indicator for the strength of relative water movement. We used this relative approach to exclude effects of habitat volume differences on the results. Calculations were made as follows:

$$\text{weight loss [\%day}^{-1}] = \frac{w_l}{\left(\frac{w_l}{t}\right) * 100} \quad (1)$$

reduction of daily average weight loss relative to the overlaying water

$$[\%] = 100 - \left\{100 - \left[\left(\frac{100}{\text{mean}(w_{lw})}\right) * \text{mean}(w_{lp})\right]\right\} \quad (2)$$

with w_1 = weight before water exposure, w_l = total weight loss [g], t = time in the water [days], w_{lw} = weight loss at position [% day⁻¹], w_{lp} = weight loss at position [% day⁻¹].

For light and temperature measurements, the same set-up as for the water movement measurements was used simultaneously in *P. crisa*, *P. oceanica* and on rocky substrates using Onset HOBO Pendant Data Loggers (part # UA-002-64, accuracy temperature: ± 0.53°C, light unit: lux). These loggers are designed for measurements of relative light intensity differences, as they are not accurate for measuring absolute light intensities (Ali et al., 2016). For *P. oceanica*, the loggers were positioned at 0, 1, 5, 20, 35, and 55 cm distance from the seafloor to increase the vertical resolution of measurements. A total of seven rods were placed in *P. crisa* mats at four time points, a total of three rods in *P. oceanica* meadows at three time points, and a total of eight rods were placed at four time points on rocky substrates. Data loggers were exchanged and placed alternately in different habitats and in different heights above the seafloor for each observation to avoid any systematic error. Data collection intervals were set at 15 s, and loggers collected data for five consecutive days. The resulting replication for temperature and light observations in the different habitats is shown in **Supplementary Table 1**. Loggers were read out with the program “HOBOWare” (version 3.7.17).

This study was conducted simultaneously in the three investigated habitats, which means that all habitats experienced identical environmental conditions. Our findings therefore reveal differences in environmental factors resulting directly from the different characteristics of the investigated habitats.

Statistical Analysis

Statistical analysis was conducted using the statistic program “R” (version 3.5.1) and the package “car” (Fox and Weisberg, 2011). One-Way-ANOVA was used to calculate significant differences

between data sets when the sample size was three or higher. Due to the small sample size, differences regarding weight loss of gypsum balls on rocky substrates were calculated with a *t*-test. Differences were considered as significant at *p*-values below 0.05.

For temperature and light analysis, data points used for calculations correspond to the mean of single data points over a period of 5 min [data point_{5 min} = mean (20 × data point_{15 s})]. Light data of light hours, from 6 am to 8 pm, was used for the analysis.

RESULTS

Water Movement

The weight loss of gypsum clod cards was used as an indirect measurement of water movement. Overall, results show a reduction in weight loss of gypsum clod cards relative to the water column by 41 ± 8% in *P. crisa* mats, 25 ± 16% in *Posidonia oceanica* seagrass meadows, and 13 ± 8% on the rocky substrates (**Figure 1**). Only in *P. crisa* mats, the weight loss was significantly different among heights above seafloor (**Supplementary Table 2A**). Gypsum balls placed on the substrate surface inside the *P. crisa* mats showed a significantly lower weight loss of 41 ± 8% compared to the gypsum balls in the overlaying open water (ANOVA: $F_{1,21} = 26.28$; $p \leq 0.001$).

Temperature

The daily temperature cycle was similar in all three habitats, as increasing temperatures from morning (6 am) to evening (6 pm) were observed. Then, temperatures decreased until midnight and remained stable until the morning (**Figure 2**). The temperature in *P. crisa* mats ranged from a minimum of 18.6 to a maximum of 20.4°C, from 17.2 to 19.3°C in *P. oceanica*, and from 18.2 to 20.0°C on rocky substrates. Furthermore, temperature stratifications varied within the investigated habitats. Temperatures at the bottom of *P. crisa* mats (0 cm) were significantly higher than those measured at 1, 5, and 20 cm distance from the seafloor (**Supplementary Table 2B**), which all were in a similar range (**Figure 2A**). For *P. oceanica*, the temperatures observed at the seafloor were significantly (ANOVA: $F_{1,575} = 156.98$; $p \leq 0.001$) lower than temperatures found 35 and 55 cm above the seafloor (**Figure 2B**). On rocky substrates, temperatures measured at the seafloor (i.e., 0 cm) were significantly lower compared to the other positions (**Figure 2C**). The water temperature was 0.31°C higher at the seafloor compared to the water column for *P. crisa*. For *P. oceanica* and the bare rocky substrates, the water temperature was 0.5°C lower at the seafloor compared to the water column, respectively.

Light Intensity

Light stratification was different for the three investigated habitats (**Figure 3**). In *P. crisa* mats (**Figure 3A**), light intensity was consistent at 0 cm and 1 cm above the seafloor, i.e., within the mat, while the light intensity was twofold higher at 5 and 20 cm above the seafloor (**Supplementary Table 2C**). Close to the seafloor, a relative light intensity of 31 ± 0.3%

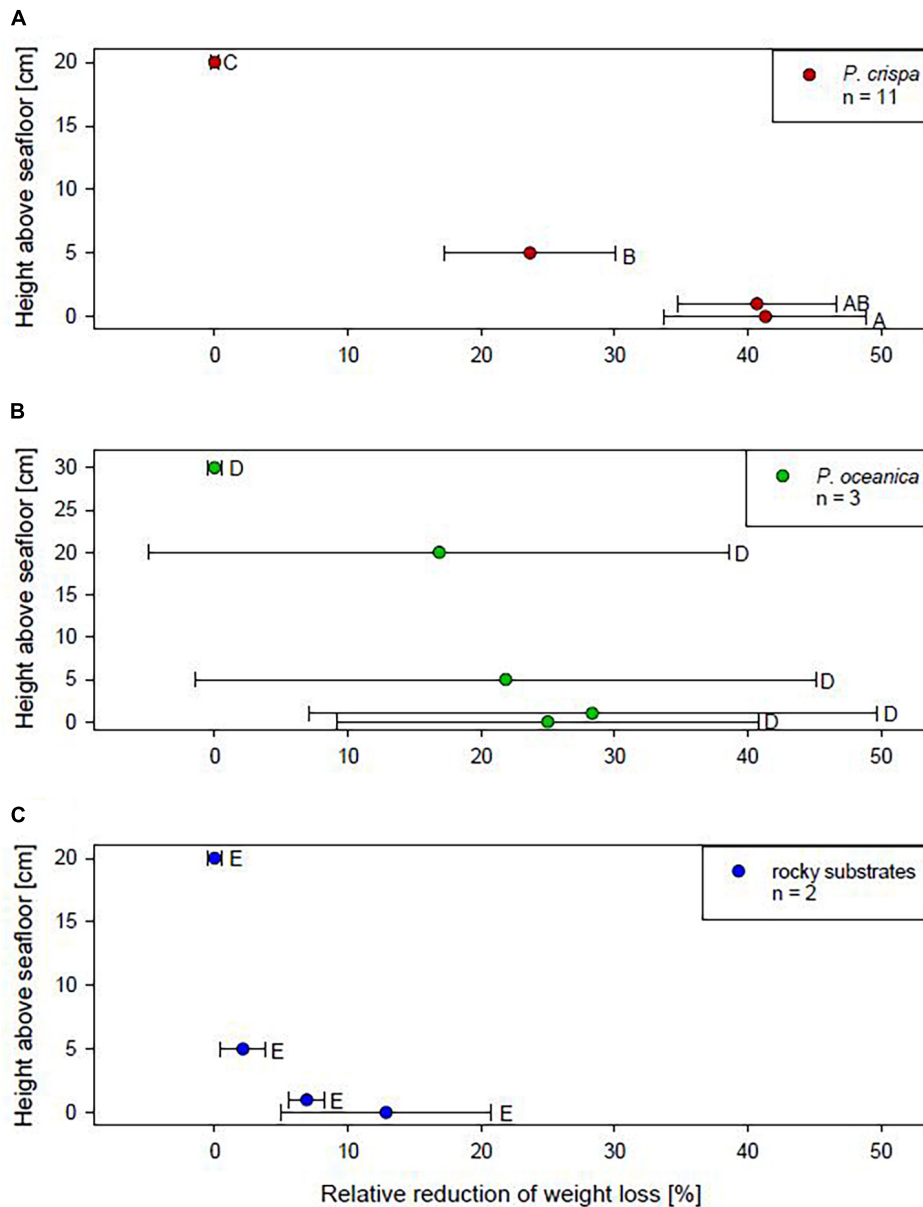


FIGURE 1 | Reduction of daily average weight loss of gypsum balls in *Phyllophora crispa* (A), *Posidonia oceanica* (B) and on rocky substrates (C) relative to the overlying water (0%). Displayed are mean values and standard error. n = number of rods deployed *in situ*. No significant differences are indicated by the same letter, significant differences by different letters.

compared to the overlying water was recorded in this habitat. Similar light values were recorded for *P. oceanica* (Figure 3B) 0, 1, and 5 cm above the seafloor. Higher light intensities occurred 20 cm above the seafloor, while the highest light values were noted 35 cm and 55 cm above the seafloor. Lowest values of minimum $23 \pm 0.2\%$ light intensity relative to the overlying water were recorded close to the seafloor in seagrass. On rocky substrates (Figure 3C), light intensity showed an irregular increase with increasing distance from the seafloor. A reduction of light intensity in the absence of plant canopies, on rocky substrates, was less intense, i.e.,

$58 \pm 0.3\%$ relative to the logger placed furthest away from the seafloor at 20 cm height. Overall, a reduction in light intensity from the highest to the lowest position of $69 \pm 0.3\%$ for *P. crispa*, $77 \pm 0.2\%$ for *P. oceanica* and $43 \pm 0.3\%$ for rocky substrates was noted.

DISCUSSION

It has recently been shown that the red alga *P. crispa* harbors many associated organisms in the north-western

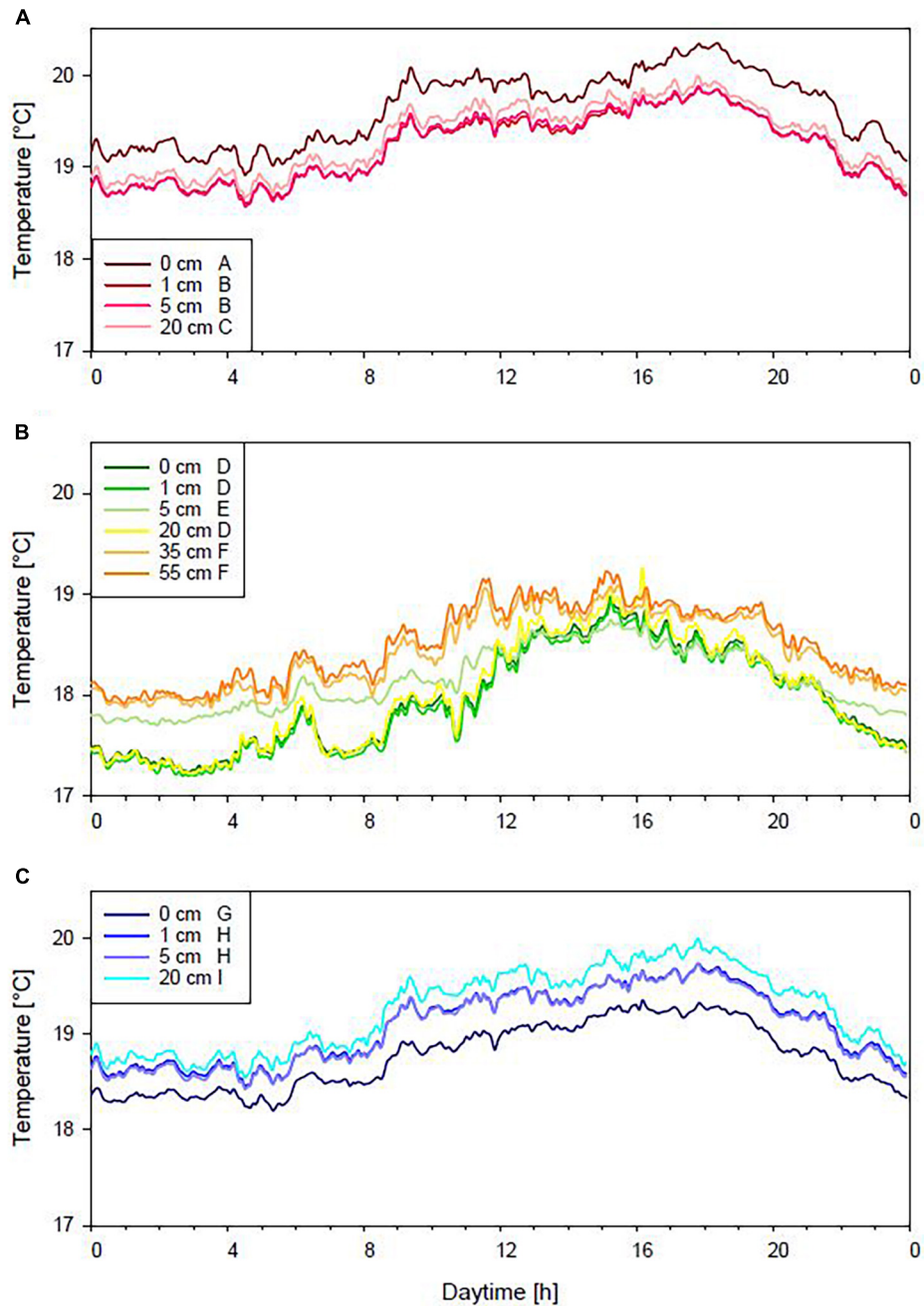


FIGURE 2 | Average temperature in *Phyllophora crispa* (A), *Posidonia oceanica* (B) and on rocky substrates (C). Displayed are mean values. No differences are indicated by the same letter, significant differences by different letters.

part of the Mediterranean Sea (Bianchi et al., 2010; Casoli et al., 2016, 2019; Bonifazi et al., 2017). In this study, we investigated the influence of *P. crispa* on the environmental factors water movement, temperature and light intensity. Furthermore, we related our finding of *P. crispa* to neighboring *Posidonia oceanica* meadows and bare rocky substrates. Our results indicate a potential role of *P. crispa* as an autogenic ecosystem engineer.

Characteristics of Investigated Habitats

The water movement was reduced by 41% at the deepest part of the *P. crispa* mats compared to the water movement 20 cm above the seafloor. Studies on soft-sediment macro algae canopies with a similar structure found similar results, showing reduced water flow and mixing in the lower part of the canopy (Kregting et al., 2011). Both, rocky substrates and *P. oceanica* meadows showed a less intense decrease (13 and 25%, respectively) in relative

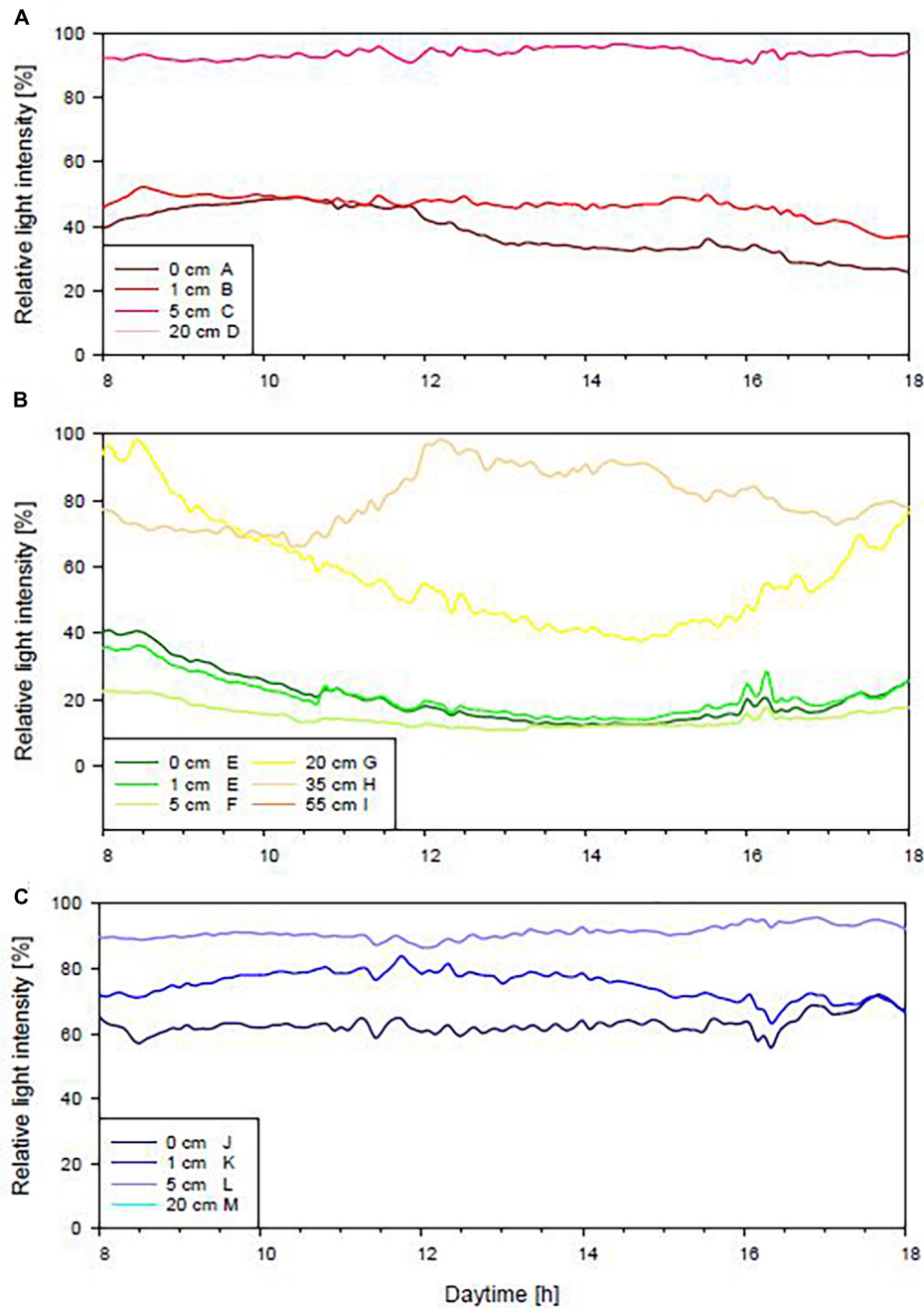


FIGURE 3 | Relative light intensity compared to loggers placed above canopy [%] in *Phyllophora crispa* (A), *Posidonia oceanica* (B) or at similar water depth on rocky substrates (C). Displayed are mean values observed during light hours from 8 am to 6 pm. References (100%) are included in the legend for the display of statistical differences. No statistical differences are indicated by the same letter, significant statistical differences by different letters.

water movement toward the substrate, which was not statistically significant, potentially due to low replication. Previous studies (Koch and Gust, 1999; Arumugam et al., 2013; Bacci et al., 2016) found significant reductions of water currents inside seagrass meadows that were located at a water depth of 10 m (e.g., Peterson et al., 2004; Bouma et al., 2005; Koch et al., 2006). However, investigated seagrass meadows in the present study

were located at a depth of 28 m, in which current is usually weaker than in more shallow areas, which hypothetically explain the absence of statistically significant effects. Water movement in the water column directly above *P. crispa* and *P. oceanica* was similar to rocky substrates, which indicates that the differences between the three investigated habitats are likely caused by the lack of topography of the rocky substrates compared to the structural

complexity of the plant canopy habitats as shown for i.e., seagrass (Fonseca et al., 1982; Gambi et al., 1990). Structural complexity or heterogeneity of a habitat is characterized by the spatial arrangement and diversity of substratum types (McCormick, 1994) and has previously been shown to correlate with lowered water flow (Gorman and Karr, 1978; Willis et al., 2005) and the degree of protection from predation (Hereu et al., 2004). A stronger reduction of water movement was observed in the rather thin *P. crispa* mats over a shorter distance, compared to the *P. oceanica* meadows, suggesting a higher structural complexity of the thalli, which have a relatively high surface area within a small volume compared to seagrass leaves.

Temperatures were significantly higher at the bottom of the algae mats, on average by 0.31°C. Although observed differences were within the range of accuracy of the data logger, all replicates showed similar differences. Since a temperature gradient was observed on the bare rocky substrates with decreasing temperatures toward the seafloor, the observed differences in *P. crispa* likely do not originate from potential temperature differences within the water column. It has been shown for seagrass, that their leaves retain organic matter from the water (Bacci et al., 2016). As the structural complexity seems higher in *P. crispa* mats, the filter capacity may also be higher, resulting in potentially high microbial activity. Habitat complexity also promotes micro-scale heterogeneity (Bell et al., 2001; Ondiviela et al., 2018) and additionally provides a large surface area for high microbial activity. It has been shown that *P. crispa* enlarges the seafloor surface by a factor of 4.9 (YC El-Khaled et al., unpublished data), which could potentially lead to high microbial activity. High rates of microbial replication and activity have been observed to create a heat output in laboratory experiments (Djamali et al., 2012). Potential warming underneath the algae mat could therefore likely be a result of the intense respiration activity of associated (micro) organisms.

Temperatures in *P. oceanica* meadows and on rocky substrates decreased with decreasing distance to the seafloor. The combination of less self-shading, limited water exchange and enhanced microbial activity could cause the temperature differences in *P. crispa* mats as opposed to *P. oceanica* meadows and rocky substrates (Table 1; Arumugam et al., 2013). Although an increase in temperature as indicated for *P. crispa* could not be observed for seagrass leaves, it may potentially occur in the rhizomes, as water current reduction is expected, and the habitat structure becomes more complex (Buia et al., 2000).

TABLE 1 | Environmental gradients in different habitats observed in this study [*] and previous reports by [1] Bacci et al. (2016), [2] Arumugam et al. (2013), [3] Dalla Via et al. (1998).

	Posidonia meadow	Phyllophora mat	Rocky substrates
Water currents	[*] → [1] ↓	[*] ↓	[*] →
Temperature	[*,2] ↓	[*] ↑	[*] ↓
Light	[*,3] ↓	[*] ↓	[*] →

No significant influence on environmental factor is indicated by a horizontal arrow, an increase by an arrow heading upward, a decrease by an arrow heading downward.

Overall, a statistically significant gradient in light intensity occurred on rocky substrates, and in the observed plant canopy habitats of *P. crispa* and *P. oceanica*. Light intensity gradients observed on rocky substrate were presumably the same as in the open water for all substrates. *P. crispa* mats decreased the light intensity by 69% from the overlaying water to the bottom of the mat, which is a strong environmental light gradient across the relatively thin mat of about 5 cm thickness. For *P. oceanica* meadows, a decrease in light intensity of 77% compared to the overlaying water was observed. Previous studies also showed strong light gradients in habitats of macrophyte dominance, i.e., *P. oceanica* meadows, of up to 70% and confirm self-shading effects (Dalla Via et al., 1998). These structures reduced the incidence of the blue, green and red wavelengths by, respectively, 57–58%, 61–63%, and 51–53% within the seagrass stands, additionally to light attenuation of the water column. A third interconnected light gradient occurs due to direct shading of macrophyte structures caused by epiphytes (Riedl, 1966; Dalla Via et al., 1998), which can reach a thickness of up to 6 cm on *P. crispa* mats (Bonifazi et al., 2017). In combination with self-shading induced by the entangled thalli of the alga and horizontally lying blades, this can explain the exceptional strong light gradient.

Potential Relevance for Ecosystem Functions

Based on several studies, lowered water movement inside *P. crispa* mats potentially promotes sediment trapping and reduces resuspension, as described for seagrass meadows (Gacia et al., 1999; Gacia and Duarte, 2001; Hendriks et al., 2008). Subsequently, this could affect the associated biodiversity, as large amounts of sediment trapped within *P. crispa* mats provide a heterogeneous habitat for infauna species and offer building material and food in form of organic and inorganic matter for tube-building species (Prathep et al., 2003). Previously, the global occurrence of algal turfs has been related to stressful habitats (Hay, 1981; Benedetti-Cecchi et al., 2001; Piazzzi and Cinelli, 2001) and their structural characteristic of sediment trapping (Piazzzi and Cinelli, 2001). However, the coast of Giglio island is affected by sediment deposition, which consists of fine terrigenous particles controlled by rainfall and larger particles derived from erosion of granite rocks (Bonifazi et al., 2017). Sedimentary processes in this area are therefore a natural scenario rather than the result of anthropogenic stressors, such as pollution (Bonifazi et al., 2017).

Moreover, the community composition can be affected by reduced water movement within the algae mat. A similar pattern has been observed for the eelgrass *Zostera marina* (L.), where lowered water movement enhances the accumulation of planktonic organisms, such as invertebrate larvae and protozoans (Eckman, 1987). The settlement of invertebrate larvae is greatly affected by small-scale fluid dynamics (Koehl, 2007) and thus by changing these parameters, *P. crispa* mats consequently change the community composition. Reduced water movement could favor the settlement of e.g., certain bryozoan species (Ryland, 1970; McKinney and Jackson, 1991).

and other sessile invertebrates. Experimental studies have shown that low water turbulence and velocity enhance the settlement of some species of e.g., hydroids (Mullineaux and Garland, 1993), bryozoans (Mullineaux and Garland, 1993; Qian et al., 1999, 2000), barnacles (Mullineaux and Butman, 1991; Mullineaux and Garland, 1993), bivalves (Judge and Craig, 1997), and polychaetes (Qian et al., 1999), while it decreases the settlement of other species of the same taxa (Mullineaux and Garland, 1993; Judge and Craig, 1997; Qian et al., 1999). In general, we expect a high number of settling invertebrate larvae in *P. crispa*, as low water movement increases the acceptance of surfaces by post-settled larvae and therefore the attaching of certain species, e.g., barnacles (Mullineaux and Butman, 1991; Jonsson et al., 2004; Larsson and Jonsson, 2006). Further, high numbers of mobile organisms, particularly larvae and juveniles, may be attracted to this habitat as it offers protection from water turbulences.

Observed higher temperatures at the bottom of *P. crispa* mats could potentially indicate a thermal insulation effect of *P. crispa*. However, future studies are required to confirm this hypothesis. While many studies focused on the effect of temperature on algae growth (e.g., Butterwick et al., 2004; Baker et al., 2007; Martin and Gattuso, 2009), the effects of algae on the habitat's temperature are so far unstudied. Studies of another important ecosystem engineer, however, report similar effects on temperature: shallow water scleractinians increased water temperatures in their microenvironment, due to solar radiation and water holding capacities by surface heterogeneity (Jimenez et al., 2008; Ong et al., 2017). While solar radiation plays only a minor role in the deep layer of *P. crispa* mats, we showed that water movement is low in the algae mats, which could indicate a long water residence time and explain a similar effect on the thermal microenvironment of this habitat.

P. crispa provides a habitat that differs in light intensity to bare rocky substrates, as the plant structures create shade. The alga's phylloids hinder light to reach the seafloor, which limits requirements for primary production within the red algae mats. Light availability is most important for photoautotrophic organisms and therefore an important factor for overall oxygen availability. Hence, in seagrass meadows, oxygen availability generally increases with the distance to the rhizome (Borum et al., 2007). Other macroalgae mats have been shown to inhabit a high abundance of microphytobenthos along a vertical gradient, which is a food source for associated organisms (Shadrin et al., 2019, 2021; Prazukin et al., 2020) and causes high phototrophic activity. In the present study, we found a 1.1-fold stronger light gradient over a shorter distance in *P. crispa* mats, which implies that the layer of high phototrophic activity is in closer proximity to the deeper layer of heterotrophic activity. This could lead to higher oxygen availability for heterotrophic organisms, especially heterotrophic microbes, and hence fuel the potential warming effect of microbial activity inside the mats. High microbe abundance is beneficial for suspension feeders, such as certain Porifera (Larsen and Riisgård, 1994), ascidians (Jørgensen et al., 1984; Riisgård, 1998), bryozoans (e.g., Ryland, 1976; Grünbaum et al., 1998; Lisberg and Petersen, 2000), bivalves (e.g.,

Beninger, 2000; Riisgård and Larsen, 2000; Silverman et al., 2000), cnidarians (Miglietta et al., 2000), crustaceans (Trager et al., 1990; Riisgård, 2015), and polychaetes (Emlet, 1990; Hansen, 1993), that feed on microbes. The aforementioned active benthic filter feeders create their own currents, e.g., by using their cilia or muscles (Jørgensen, 1966; Riisgård and Larsen, 2000), and are therefore not affected by the lowered water movement inside *P. crispa* mats.

Ecological Implications

Phyllophora crispa widely covers rocky substrates and increases in abundance with increasing water depth beyond 25 m (Sagarra and François, 2015; Bonifazi et al., 2017). Loss of *P. oceanica* meadows and rocky substrate communities threaten the overall high biodiversity in the Mediterranean Sea (Coll et al., 2010). *P. crispa* potentially recolonizes these degraded habitats following the concept of algal phase shifts. The importance of *P. crispa* as an autogenic ecosystem engineer was stated by Zaitsev (2008) in the Black Sea, where *P. crispa* is a key species along the north-western rocky coasts. More than 100 species of invertebrates and 40 species of fish, some of which are endangered or rare (Shcherbak et al., 1994), inhabited the *P. crispa* mats in this area. This associated community benefits from the algal habitat as a food source, substratum for spawning, material for the construction of nests, or shelter from predators (Zaitsev, 2008). Provision of food or protection for rich associated communities are also characteristics of other algal habitats, such as *Cladophora* mats (Shadrin et al., 2019, 2021; Prazukin et al., 2020) or *Cystoseira* beds (Mineur et al., 2015).

The term “ecosystem engineer” is often associated with large-scale bioengineers, such as corals, mangroves, and seagrasses, which create extensive contiguous habitats covering wide areas (e.g., Copper, 1994; Kandasamy and Bingham, 2001; Duarte, 2002). However, referring to Jones et al. (1994, 1997), scale is not a parameter defining “ecosystem engineers.” Bivalves for example, such as mussels or oysters, are well-recognized structural small-scale bioengineers that form dense beds or reefs (Ruesink et al., 2005; Bouma et al., 2009), which create habitats of smaller volume and act mainly on a local scale (Kelaheer and Castilla, 2005). Their shells provide substrate for other organisms to colonize (Padilla, 2010), alter the local water flow regime (Widdows et al., 2009), as well as the local dynamics of sediment (Padilla, 2010). This study showed that *P. crispa* influences its environment in a similar way, i.e., by reducing water movement and creating habitat. Despite reaching heights of only about 15 cm, this red alga therefore acts as a small-scale ecosystem engineer, forming dense but thin mats, that can cover areas of up to 10,000 km², as shown for the Black Sea (Zaitsev, 2008).

Our study showed that key environmental parameters are shaped by *P. crispa*, thus a complex and valuable habitat is likely provided in the Mediterranean Sea. As the complexity of a habitat increases biodiversity (Russ, 1979) and *P. crispa* mats show highly complex structures and environmental gradients, they could act as a biodiversity hotspot in the Mediterranean Sea, similar to the Black Sea, as already indicated by the pilot study of Bonifazi et al. (2017). A total of 99 non-colonial invertebrate taxa were collected in *P. crispa* mats in the Mediterranean Sea,

while polychaetes were the most abundant group, followed by Mollusca and Crustacea (Bonifazi et al., 2017). Additionally, that study reports 37 taxa of colonial invertebrates, which were dominated by Bryozoa and Porifera, but also included Tunicata and Anthozoa. Further, Bonifazi et al. (2017) state that *P. crispa* mats significantly increase species richness and abundance of sessile filter feeders in contrast to shallower areas without the red algae mats. This could be the result of enhanced invertebrate larvae settlement due to reduced water movement in *P. crispa* mats observed in this study, which has been previously shown for seagrass meadows (Eckman, 1987). The dominance of sessile filter feeders within *P. crispa* mats observed (Bonifazi et al., 2017) strengthens our hypothesis of high oxygen availability due to high microphytobenthos abundance in the mats that enhances overall microbial abundance resulting in a higher food availability for active filter feeders.

This study provides the first attempt to investigate the potential role of the red alga *P. crispa* as an autogenic ecosystem engineer, which may harbor high associated biodiversity. Our results indicate the possibility that *P. crispa* provides resources for associated organisms by retaining sediment, providing food, and creating habitat. While we were able to show that *P. crispa* serves a habitat by influencing the key environmental factors water movement and light intensity, its effect on temperature needs to be studied further.

Future studies should investigate the diversity of infauna in Mediterranean *P. crispa* mats to understand their role as potential biodiversity hotspots and also confirm the abundance of *P. crispa* in other regions of the Mediterranean coast. Further, studies on the turnover rate of *P. crispa* mats are needed to understand the ability to generate refuge for organisms, which may suffer from habitat loss due to anthropogenic pressure and climate change.

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DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

NS, YE-K, FR, and CW: conceptualization, methodology, investigation, and writing—review and editing. NS: formal analysis, writing—original draft preparation, and visualization. CW: supervision. All authors have read and agreed to the published version of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2021.721626/full#supplementary-material>

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