

Review



# The World of Edges in Submerged Vegetated Marine Canopies: From Patch to Canopy Scale

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Abstract: This review describes the world of edges in submerged vegetated marine canopies (seagrasses, saltmarshes, and seaweeds) where an edge is a boundary with a frontal area separating the vegetation from the adjacent non-vegetated zones. Plants within the vegetation are made of flexible elements pronating in the direction of the flow and oscillating back and forth in response to wave forcing. Some of them also occupy the full height within the water body. The analysis focuses on both the canopy- and local-patch scales to acquire knowledge about the hydrodynamics and the biophysical interactions in the structural shallows and deep limits of the canopies as well as on the structural edges of vegetation patches and the edges in the gaps within the canopies. The spatial arrangements of both canopy and patch edges are not only well imposed through the modification of hydrodynamics, but so too through small-scale interactions from internal structural causes and modifications. The continuous fragmentation of coastal marine habitats has reduced their structural complexity, thus making habitat edges a prevalent seascape feature, including in the shallow (or upper) and deep (or lower) limits of the canopies, the patch edges, and the edges in the gaps within the canopies. Canopy patches represent a region of high flow resistance where flow deflects and accelerates above and/or next to the canopy, resulting in an increase in water velocity and turbulence, especially at the edges of the patch. At the edges, energy transfer is found in spectral wave velocities from the longer to shorter wave period components. Likewise, at the edges, the net deposition of sediments decreases over a distance to a certain length, relative to the bare bed, which is associated with a region of vertical updraft and elevated turbulent kinetic energy. The edge effects also relate to the influence that a patch edge can have on determining species composition and predation risk, which is additionally mediated by the effect the edges have on habitat complexity within the vegetated patch. Organism feedback within the edges does not simply follow the canopy and local features and, in fact, the intricate interaction between biogeophysical processes is key in explaining the complexity of coastal submerged canopy landscapes. For example, proximity to patch edges has a greater influence on epifaunal density and community structure than structural complexity or predation do. The extent to which edges reduce predation risk depends on the extent to which they support higher structural complexities compared to patch interiors. The canopies' shallow limits and their position in the underwater beach profile are mostly limited by light availability, the intensity of the wave action, and the local nearshore hydrodynamics, but they also depend on the local structural conditions at the vegetated side. The deep limits of the canopies, however, mainly depend on the availability of light and research findings support migration both to the deeper and shallower layers. All structural edges face changes caused by increasing nutrient inputs, development of coastal zones and the increasing impact of climate change. A considerable challenge to managing, restoring, and conserving coastal marine ecosystems stems from understanding how the canopies are able to cope with these natural and anthropogenic disturbances.

Keywords: meadow; canopy; marine; edge; boundary; patch; fragmentation

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## 1. Introduction

The coastal marine seascape has undergone short- and long-term structural changes resulting from increasing nutrient input, the development of coastal zones [1–6], and the ever-increasing impact of climate change. The coastal marine seascape is characterized by, among others, the presence of saltmarshes, seaweeds, and macrophyte canopies that form both submerged and partially emerged habitats which occupy a narrow fringe-from the upper intertidal zone to about 90 m depth, with the shallow limit considered as the landward continuous front settled on the soft bottom [6–8]. Despite their small number, approximately 60 species [9], seagrass communities provide significant and crucial ecosystem services that contribute to human welfare and shoreline protection [8,10,11]. Canopies, for instance, seagrass meadows, also provide ecological services such as attenuating waves, currents, and storms [12–14], mitigating storm surges and marine heat waves, preventing the erosion of coastal beds [12,15,16], promoting sediment accumulation [14,17], contributing to nutrient cycling and carbon sequestration [9], shaping estuarine geomorphology [18], and providing refuge and nursery grounds for the local biota [12,19]. The ability of canopies to deal with both natural and anthropogenic disturbances has become challenging for the management and conservation of coastal marine ecosystems as many of them display patchiness that may persist on long time scales [19,20]. On one hand, seagrass losses associated with heat waves indicate that climate change may compromise the fate of many coastal areas and the services they provide. The loss of seagrasses may increase the impact wind-waves have on coastal areas which, in turn, may effect marsh edges and destabilize estuarine marsh systems [21]. On the other hand, since the productivity of Zostera japonica shows strong positive correlations with air and water temperature, the predicted increases in air and water temperature associated with global climate change might have positive effects on the growth and extension in the distributional range of this species [22]. The reduction in the coverage and limits have also been related to human impact (for example, trawling and mooring activity) that has then led to coastal erosion and turbid waters [23–26] and which is a common situation in the Mediterranean coastal zones. Anchoring patches of Posidonia oceanica may take between 27 and 60 years to be recolonized [27]. The reduction in the structural shallow limits (73%) and extent of Posidiona oceanica meadows over the past 85 years have been linked with the direct or indirect impact of coastal development, namely harbors, ports of refuge, landfills, artificial beaches, groynes and pontoons, submarine pipelines, and aquatic farms [28].

The continuous fragmentation of coastal marine habitats has diminished their structural complexity and has made habitat edges a prevalent seascape feature [29]. Seagrass structural complexity generally increases from patch edges to patch interiors [30] and from patch-to-patch interactions [31,32]. In Posidonia oceanica meadows in the Mediterranean, the shallow limit has been reported to regress, with the proportion of regression ranging from 17.7% to 98.9%, and the highest values have been found in Spain and France and are consistent with the highest levels of fragmentation detected through map analysis and coastal pressures [6]. Ardizzone et al. [25] reported a continuous regression of Posidonia oceanica beds in the central Tyrrhenian Sea, falling from 7,290 ha in 1959 to 2,899 ha in 2005, i.e., a loss of about 60% coverage in 46 years and related to human-mediated coastal impacts. A meadow's shallow limit, which is directly influenced by coastal pressures, is commonly used as an indicator of its health [33–38]. Marbà et al. [39] reported that two thirds (62.0%) of Posidonia oceanica meadows, mainly in the Western Mediterranean, had experienced declines in their real extent. These declines are also found at both the shallow and deep limits. The depth where a wave breaks significantly controls the landward position of the meadow's shallow limit which, in turn, depends on beach morphodynamics, i.e., the distinctive type of beach produced by local geomorphology and wave climate [40– 44]. Furthermore, increased wave intensity has resulted in the offshore migration (into deeper water) of the upper limit of giant kelp canopies [45]. Consequently, the shallow limit of a submerged marine canopy is governed by the morphodynamics of the coastal



areas, the imposed short-term local hydrodynamics, and the long-term modifications resulting from climate change (Figure 1).

**Figure 1.** Photographs of the structural edges of a canopy: the upper limit of a canopy (**a**) and the lower limit of a canopy (**b**). On photograph **c** we present a patch of vegetation and on the photograph **d** a gap within a canopy, with the edge being the boundary between the non-vegetated (sandy bottom) and the vegetated zones. The photographs were taken by Xavier Salvador. Photographs were taken in Cala Vigatà (**b**, **c** and **d**) and in Cala Rostella (**a**), both in the northwestern Mediterranean Sea.

The deep limit of seagrass communities extends from mean sea level down to 90 m, with the differences being attributed to the light attenuation underwater [7]. At the deepest edge, light affects the chlorophyll content and morphological characteristics of leaves such as the changes in leaf thickness [46]. However, as a consequence of modern pollution and water turbidity, in many areas an extensive belt of dead matter limits the deep positions of meadows, [10], as is the case of the *Posidonia oceanica* meadows in the Gulf of Marseille where the limit is found to be between 22 and 30 m deep [10]. Likewise, shoot density and coverage decreases in the regressive deep limits of *Posidonia oceanica* meadows have been found along the coastlines of Corsica [47].

In addition, the fragmentation in most coastal meadows is strongly influenced by human activities, although it is lower in natural meadows than in anthropized ones, and is little influenced by the morphodynamics of the coast [20]. The degree of fragmentation on a landscape scale appears not to affect the hydrodynamics within the inner gaps in the meadow, although both sedimentation rates and hydrodynamics have been found to increase with gap size, but do not show differences at the landscape level with the fragmentation levels of the meadows [48]. Nevertheless, patches of macrophyte species can interact with each other through facilitation of resource uptake [32].

With the increase in exposure to waves, *Posidonia oceanica* meadow habitats have declined and present an increase in meadow fragmentation and a decrease in the deep-depth limit of seagrass distribution [20,25,49]. For example, *Posidonia oceanica* meadows tend to be patchier and have low overall cover, more complex patch shapes, and reduced withinpatch architectural complexity along a wave exposure gradient from low to high energy. The higher the fragmentation degree of the meadow is, the lower the shoot density is in the surrounding vegetation near the gap [50]. The heterogeneity of fragmented meadows is linked to modifications in shoot plant density, leaf morphology, and biomass in fragmented patches, with the shoot density being a good indicator for regression, stability, or progression of seagrass limits [51].

Lateral shoot density, percent cover, and leaf length adjacent to the gaps within the meadows may be up to 20% lower than the structural condition in fully vegetated meadows [52,53]. Fragmentation increases the role edges play and causes a shift from light limitation to phosphorus limitation [54], although infiltration of solutes from the sand to the patch persists [55]. Furthermore, Tanner [56] found that epifauna distribution responded to the shape and orientation of seagrass patches by offering the greatest amount of edge when currents are strong but not when they are weak.

This manuscript provides information on the role the edges (limits) of submerged marine canopies play in terms of the canopy seascape and on the patch or patch/gap scale. The review process has focused on the description of both structural and local edges. First, the description of both the deep limit of a canopy, that is also referred to as the lower limit, and the shallow limit of a canopy, referred to as the upper limit. In addition, this review describes the local edges that are to be found in vegetated patches and in the limit of a gap within a canopy. This review will provide a significant structural description and knowledge on, first, edge hydrodynamics, second, sediment transport across and biophysical interactions at the edges, and, third, the modifications of the temporal and spatial scales of edges and limits of submerged marine seagrasses, saltmarshes, and seaweeds. They are made of highly flexible elements pronating in the direction of the flow and oscillating back and forth in response to wave forcing [57] and present edges with a frontal area separating the vegetation from the adjacent non-vegetated zones [52].

## 2. Materials and Methods

Given that this review is directed towards the role edges play in marine canopies (i.e., both canopy (structure) and patch/gap (local) scales), the hydrodynamics are described in terms of (i) the characteristics of the vegetation that governs the edge processes, namely, the density or cover of the vegetation and the height of plants, and (ii) the characteristic distance of the patch and gap from the edge. The position of the edge is then considered as x = 0, with the edge being deemed the border between habitats in an intermediate boundary in abiotic conditions from the center of adjacent habitat. Therefore, the edge may differ from that of the interior and/or intact habitat, with implications on multiple scales [9,58]. At the canopy scale, edges are differentiated in both the deep and shallow limits [39]. To clarify, in much of the literature, the deep limit is also referred to as the lower limit and the shallow limit as the upper limit. In addition, we consider a patch to be a structure that consists of a single species at a relatively high density whose lateral boundaries or edges are sharp [59,60]. Subsequently, a patch is considered to be a vegetated structure that is smaller than the meadow but larger than an individual element within the patch (i.e., a single plant shoot). A gap is therefore a bare soil area interspersed within a vegetated region. The edge of the gap is the vegetated interface that separates the bare soil from the nearby vegetation. For the best clarification of terms used in the manuscript, a list of definitions is provided in Table 1.

## Table 1. List of terms described in the manuscript and corresponding definitions.

## **Terms and Definitions**

• Canopy: Vegetated area made of highly flexible elements that pronate in the direction of the flow and oscillate back and forth in response to wave forcing. A canopy provides structure, habitat, and processes which support a suite of other species. The structural (architectural) characteristics of a canopy are defined by the shoot density, the coverage, and the leaf length. In this manuscript, the canopy is defined as being formed by submerged elements.

• Flow structure: Flow characteristics within a meadow described by time-averaged velocity, turbulence intensity, or turbulent kinetic energy (TKE).

• Patch: A vegetated structure that is smaller than a meadow but larger than an individual element within the patch.

• Gap: A non-vegetated structure within a canopy. Considering the starting point of a gap at the edge of the gap, two subsequent longshore and onshore lengths are considered, with the longshore length being parallel to the shore and the onshore length being transversal to the shore. Consequently, a longitudinal gap is defined as a gap with the main axis parallel to the wave velocity propagation and the transversal gap is defined as a gap with the main axis per-pendicular to the wave velocity propagation.

- Patchiness: The structure of a meadow at a time t.
- Fragmentation: The evolution of patchiness through time.

• Structural limit: Limit of a designated canopy. In this manuscript, two structural limits are differentiated: the deep limit of a canopy that is also referred to as the lower limit and the shallow limit of a canopy referred to as the upper limit.

• Edge: The border between habitats in an intermediate boundary in abiotic conditions from the center of adjacent habitat. In this manuscript, the edge is considered either as one of the structural limits or the boundary between vegetation and non-vegetation areas.

Roughness length: Characteristic length at the vegetated side of an edge canopy accounting for the bed friction.

• Leading patch edge: Lengths within the longitudinal distances over which advection contributes to a significant sediment source.

Two types of canopies are included in this study: marine micro-canopies and classic marine canopies. Micro-canopies refer mainly to permeable vegetation forming a patch, whereas a classic marine canopy refers to a permeable region forming a canopy. In both cases, the canopies are made of highly flexible elements that pronate in the direction of the flow and oscillate back and forth in response to wave forcing [57].

This paper provides information on marine canopy landscapes which are characterized by vegetated patches or canopies, the hydrodynamics and sediment transport across edges, and the biophysical properties that derive at the edges of canopies. Likewise, the paper offers information about the edges at the level of either natural or anthropogenic derived gaps, therefore providing data on the dynamic features of the edges in the gaps in a fragmented canopy. Next, we analyze multiple canopy scales, given that the role of the edges is manifested both at a local and canopy scale, thus providing information on stable or fragmented marine canopies as well as patches of vegetation from which to further analyze the characteristics of coastal marine environments.

Related literature was analyzed using Scopus and the Web of Science. Searches were carried out for manuscripts that included in their titles, abstracts or keywords, the key words in combination and beginning with "meadow" OR "canop" AND "marine" OR "sea" AND "edge" OR "boundar" OR "patch" OR "margin" OR "front" OR "upper limit" OR "shallow limit" OR "lower limit" OR "deep limit" OR "fringe". For each word, wild-card asterisks were added to the end so that plurals and other related words would be found, i.e., canop\* would pick up the words of canopy and canopies [57]. This search produced hundreds of results that were then filtered by the authors' subjective analysis and by considering those carried out during the last 30 years (1991 as the start date and 2021 as the end date). This provided a list of approximately 200 papers. A close reading of all manuscripts discarded some of them and, together with 10 papers on the hydrodynamics

in the limits of seagrass meadows known to the authors, the final list of papers (see reference section) was obtained.

All the publications cited here have been classified into five-year ranges, resulting in six categories based on five complete years. The last category is based only on the current publications in 2021 (up to June). The number of publications in each category was counted and the number of publications per year has been calculated for each category. From this analysis, it can be seen that and since 1990, interest in the topic has been constantly increasing (Figure 2), because the number of publications in the first five-year range was 2 but then increased to 57 in the last complete five-year range (2016–2020) category. In 2021, 9 publications focusing on this topic were found. This interest in the topic increased following a power trend of  $1.9 \pm 0.1$  and with a p-value < 0.05.



**Figure 2.** Temporal evolution of the number of publications per year focused on the topic studied and classified in five-year ranges.

## 3. The Structural Shallow Limit of Canopies

#### 3.1. Characteristics of the Shallow Limit of Canopies

The structural characteristics (i.e., shoot density and seagrass cover) at the shallow limit of canopies are mostly limited by light availability and water column transparency [61–63], are reworked by wave action, and are mainly controlled by local nearshore hydrodynamics [64–68]. Marbà et al. [39] reported that the shallow limit (Table 1) of most *Posidonia oceanica* meadows in the Mediterranean (26 out of 42 evaluated) has regressed towards deeper waters and this has occurred at an average absolute rate of  $-0.04 \pm 0.1$  m year<sup>-1</sup>, whereas in 8 of 42, meadows it progressed towards the coastline. In the Mediterranean, the discharge of urban effluent into coastal areas adversely affects *Posidonia oceanica* meadows since it induces nutrient enrichment and a decrease in water clarity, resulting in a significant reduction in vegetation cover at their upper limits [69]. Nutrient enrichment may enhance herbivore consumption and decrease the cover and diversity of epizoans at subtidal macroalgal edges, likely by stimulating foraging activity [70].

On the contrary, under reduced tidal ranges, seagrasses may be less exposed to low tide effects, thus, under smaller tidal ranges, *Zostera marina* seagrasses at the shallow edge of the bed suffer less exposure stress, resulting in an expansion of plant distribution shoreward [34,71].

#### 3.2. Hydrodynamics in the Shallow Limit of Canopies

The shallow limits of the meadows were very close to the breaking depth in those sites characterized by lower energy dissipation, whereas higher energy dissipation corresponded to larger distances [67]. Meanwhile, on sandy substrata, the *Posidonia oceanica* meadows' shallow limits lie well offshore from the surf zone, in areas with little morphological activity. On rocky bottoms, the *Posidonia oceanica* meadow can extend up to the outer surf zone of storms, being able to colonize shallow areas subject to stronger hydrodynamic forcings than those observed on sand [72].

The major hint for the shallow limit of canopies developing is a rise in sea level due to global climate change which will automatically induce a withdrawal of the shallow limit of seagrass meadows whenever the limit is beyond the compensation depth [73]. Results from the impact of global warming on seagrasses show an average rate of decline of 0.05 year<sup>-1</sup> associated with both the warming of the seawater and the increase in the water depth [74]. At the shallow limit of a *Posidonia oceanica* meadow, a decline in shoot density and cover is a harbinger of the withdrawal of this limit [51,75].

## 3.3. Sediment Transport in the Shallow Limit of Canopies

Fast currents increase sediment resuspension in sparsely vegetated areas, which further reduces the light available for the growth of rooted submersed macrophytes [15]. That said, aquatic macrophytes, once established, are able reduce the levels of turbidity through the increase in sedimentation. Granata et al. [17] show that in the shallow limit of a *Posidonia oceanica* meadow, the concentrations of particles with characteristic diameters smaller than 10  $\mu$ m were lower in the vicinity of the vegetation of the edge than over the barren sand, while the concentrations of larger particles with characteristic diameters larger than 10  $\mu$ m were lower on the barren sand near the edge. In addition, during a stronger current and wave activity following a storm, near-bed turbulence and orbital wave velocity were elevated, albeit still lower inside the meadow than over the sand [17], proving that in high-energy periods sediment concentration can increase at the edge of canopies, but is still lower towards the edge of the meadow. Gruber and Kemp [76] report higher suspended particle concentrations in the canopy edge compared to the canopy, confirming that the edge of a canopy bed is a dynamic region characterized by deposition and accumulation of sediment particles [17,76,77].

## 4. The Structural Deep Limit of Canopies

## Characteristics of the Deep Limit of Canopies

The deep limit of *Posidonia oceanica* meadows in the Croatian Adriatic Sea is found to range from 24 m in the north to 36 m in the south, with a strong latitudinal gradient, and with the overall differences between the north and the south attributed to water transparency between eutrophic and oligotrophic waters [78].

Most of the reviewed manuscripts report a decline in the depth of the structural deep limit (Table 1) of canopies, that is, an onshore migration of the deep limit. For the few meadows reported by Marbà et al. [39], the maximum colonization depth of *Posidonia oceanica* declined at an overall absolute rate of  $0.61 \pm 0.29$  m yr<sup>-1</sup>, ten-fold faster than the overall rate of regression at their shallow limit. In the central Tyrrhenian Sea, the deep limit of *Posidonia oceanica* beds has been found to have decreased from c. 35 m (in 1959) to between 18 and 25 m, with greater changes for the deep limits as opposed to the shallow limits [25]. Furthermore, Mayot et al. [51] found that in the long term in the northwestern Mediterra-

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nean, a significant shift in the mean density in the early 1990s is consistent with the regression trend of the depth limit of most *Posidonia oceanica* meadows. The regression migration of the deep limit has also been reported in the meadows of *Posidonia oceanica* in the Alicante region (Spain), and is characterized by very low shoot densities [4].

Based on measurements in *Posidonia oceanica* meadows along the coasts of Corsica, two hypotheses, which could not be attributed to the local degradation of the environmental conditions, have emerged to account for the regression of the deep limit. First, the rise in the mean sea level, which may have resulted in a significant regression in sectors where the slope is relatively slight and, second, the North Atlantic Oscillation (NAO), which may mediate the light at the deep limits of the canopies [47]. The regulation of the deep limit by light [79] may indeed delay the response to improved light conditions, with hypoxia/anoxia and nutrients preventing eelgrass from attaining the depth limit that light levels would allow [80]. The reduction in nutrient loads can improve the state of eelgrass beds by ameliorating not only light conditions but also sediment quality and oxygen concentrations [79].

On the contrary, the extent of larger marine meadows in the Semedela Bay (Slovenia) increased in the 2009–2015 period, covering as much as 45.6% of the seabed by moving their deep limits into deeper parts [81]. Likewise, reduced nutrient inputs in fjords have led to an increase in the depth limit (in response to improving water clarity) of the eelgrass meadows found there [82] due to the improvement in waste water treatments.

Under increased tidal ranges, *Zostera marina* meadows at the deep edge of a bed receive less light at high tide, thus resulting in a withdrawal of the deep edge of the bed and a loss in total seagrass area [34,71].

## 5. The Structural Patch

## 5.1. Characteristics of the Edges of Patches

Different types of patches making up the meadows ought to lead to different seascapes according to their shape and their arrangement with one another [83] and with longer-established patches acting as greater sinks of organic carbon [84] (Table 1). The 11 years of observations by Balestri et al. [85] have documented the formation and development of patches by *Posidonia oceanica* seed, and that seedlings occurred more frequently on rocky than on sandy bottoms, and rarely on dead "matte" or *Cymodocea nodosa* meadows. The chance of colonization success on rock was 2 times higher than on sand [85]. For *Zostera marina* patches, however, no difference was found between seed production at the edge of patches versus the center [86], although seed distributions may be altered in fragmented beds when compared to continuous beds, both within and directly outside the bed's boundaries [87].

## 5.2. Hydrodynamics in the Edges of Patches

Canopy patches represent a region of high flow resistance in coastal zones (as in streams), where flow deflects and accelerates above and/or next to the canopy, resulting in an increase in water velocity and turbulence at the edges of the patch [88–91]. Roughness lengths are longer above the canopy than over bare sand and increase with increasing distance from the leading edge of the canopy [92–94]. Dissipation rates outside the vegetation are found to increase with proximity to the bed and are observed to be greater on the incoming tide, even when differences in mean current speeds between flood and ebb tide are accounted for [95].

The balance between the flow inertia, canopy drag, and pressure determines the length of the initial adjustment at the leading edge of a patch, with the canopy length not impacting on the flow adjustment near the leading edge [89]. At distances from the leading patch edge that are within the longitudinal distances over which advection contributes to a significant sediment source, the net deposition by flows impacting the patch is laterally uniform [96]. At further distances from the leading patch edge, the net deposition of particles is highest near the flow-parallel edge and decreases into the vegetation area, which is a signature of dispersive transport from the patch edge [96]. Nonetheless, as a whole, seagrass canopies are not only attenuators of wave energy but also serve as low-pass filters, i.e., higher frequencies in the spectra tend to be more attenuated [97].

The hydrodynamics of structural patches depend on the length of the upstream patch in setting the flow regime within the patch [98]. Patchy meadows do not attenuate small and short waves, especially when water levels are high, but are capable of attenuating relatively high and long waves, and this attenuation is particularly notable above the meadow front edge [99]. Near the meadow edge, energy transfer is found in spectral wave velocities from the longer to the shorter wave period components and it has also been found that submerged vegetation attenuates mostly longer waves [100]. Eelgrass beds are found to reduce near-bottom mean velocities by 70 to 90%, while wave heights are reduced by 45 to 70% compared to an adjacent unvegetated region, with longer period waves penetrating effectively into the meadow [101].

Recently, some studies have focused on the concept of minimum patch size, i.e., the patch that is needed to induce in-patch reduction in the velocity, the turbulent kinetic energy, and the fine sediment accumulation [102]. Since streamwise velocity decreases linearly from the edge of the patch, in patches with higher velocities and coarser sediment, the sediment grain size exponentially decreases with the distance from the edge, reaching a minimum value at distances longer than one meter from the edge. In patches characterized by lower velocity and finer sediment, the minimum distances are attained at distances greater than 0.3 m from the edge [103]. As reported by Chung et al. [11], the development of momentum in a vegetated patch is governed by the increased pressure at the canopy front, which occurs on a rapid timescale, while the development of turbulence requires the shear-induced structure above the canopy to grow in size until it reaches the water surface. The vegetation patch can also generate a tidal phase lag between the vegetated and adjacent bare flats with stronger flood currents in the vegetated zone and stronger ebb currents as on the adjacent bare flat [104].

In *Zostera noltii* patches, the edges are characterized by lower plant biomass, shoot density, and aboveground to belowground biomass ratios, and higher leaf elongation rates than the vegetation in the patch interior [105,106], which is in accordance with results of Barcelona et al. [50], for edges in gaps surrounded by *Posidonia oceanica* vegetation. In a patch of *Veronica anagallis-aquatica*, the more exposed edge individuals presented smaller sizes than the sheltered ones, lower relative allocation to stems, higher allocation to roots, and reduced water content in roots and stems [107]. The comparisons between edge and interior vegetation in the eelgrass *Zostera marina* show that inbreeding and clonal dominance would be more likely to occur away from fragment edges, but with tidal cycles moderating differences that might otherwise occur between edge and interior positions in a bed [108].

Differences in the rhizosphere sediment community composition and for eelgrass shoot densities at the patch edge may be correlated with variation in environmental measurements (C:N ratio, dissolved oxygen, pH, and type of sediment, among others) and depend on the release of exudates and oxygen by the roots of the eelgrass, which would increase in concentration with eelgrass density [9]. In a *Zostera mueller* patchy seagrass, carbon stocks were 20% higher in the vegetated zone than at the seagrass–sand edges and bare sediments, and most of the carbon came from allochthonous sources [109]. In *Cymodocea nodosa* and *Zostera noltii*, the spatial patterns in the leading edge correlate with the spatial patterns in NH<sub>4</sub><sup>+</sup> uptakes, with 20% higher uptake rates at the leading edge of both canopies [110]. In *Cymodocea nodosa* meadows, larger organic carbon (Corg) pools were observed in the interior and at the edges of meadow patches than in adjacent unvegetated bottoms [111]. In addition, in the giant kelp *Macrocystis integrifolia*, the reduction in the boundary-layer thickness due to wave-driven flow may impact nutrient uptake and patch development [112].

#### 5.3. Sediment Transport in the Edges of Patches

The vegetation in the patches enhances the deposition of particles transported from adjacent unvegetated sandy areas. This process is dependent on the energy flow regime and the degree of current attenuation, thus showing that the patches can reduce resuspension, promote particle deposition, and carbon burial with distance from the edge patch into the meadow [113–115]. This is the case for seagrass bands of Zostera noltii, where sediment erosion around seagrass shoots increased with distance through the seagrass bands [116]. Deposition fluxes in short flexible seagrass Zostera noltii beds are higher on vegetated beds than on bare sediments, and these fluxes increase with leaf density [117]. At the wave-exposed sandy sites, dense Zostera marina vegetation causes an increase in fine sediments and organic content, i.e., muddification. In contrast, at the sheltered sites with muddy sediments, dense vegetation has no effect on the sediment composition but, in sparse vegetation, sandification (a decrease in fine sediments and organic content) is promoted [118]. Bed sediment deposited within canopy patches by turbidity currents is finer than that in gaps between patches, as has also been reported for currents and waves. This effect might contribute to the development of inter-tidal and shallow sub-tidal landscapes characterized by patches of dense vegetation and fine sediments surrounded by bare regions with coarser sediments [119].

The retention of particles increases with distance from the leading edge (Table 1), which is associated with the decrease in vertical updraft, with the retention being greater for larger particles [120]. The net deposition of sediments decreases over a distance to a certain length, relative to the bare bed, which is associated with a region of vertical updraft and elevated turbulent kinetic energy [121]. Net deposition increases with distance over further distances, associated with a decrease in vertical velocity and turbulent kinetic energy [121]. Due to flow obstruction by the seagrass meadows, tidal flows may be deflected around the meadow and concentrated at the edge [122]. Although flow velocity may increase by 30% at the meadow edges, it is not able to offset the loss of water flux within the meadow and the total water flux discharged through the cross-meadow may be reduced by 10% [122]. Posidonia oceanica meadows significantly buffer sediment resuspension, which may be reduced more than three-fold compared to the unvegetated sandy bottom [115]. However, in the presence of small patches of Zostera marina, the critical erosion threshold may start within the patch at lower velocities than on bare sediment, including sand and mud treatments, with the particle resuspension reducing the light level below the minimum requirement of the plants. A patch that is too small is not able to reduce waves and instead exhibits enhanced turbulence and scouring at meadow edges [123]. During the summer when seagrass density is high, pronounced sediment accumulation (>6 mm/month) may occur at the edges of the seagrass bed and decrease logarithmically with distance into the meadow [122]. Saltmarsh Ruppia maritima patches are characterized by a reduction in the turbulent kinetic energy and resuspended sediment concentrations decrease as the vegetation densities increase [124].

In simulated model vegetation at high channel velocity, resuspension occurred in the bare regions and a non-uniform spatial distribution of net deposition was observed around and within the patch. In contrast, at low channel velocity, there was no (or limited) resuspension, and a uniform distribution of net deposition was observed around and within the patch [125]. Flow divergence begins upstream of the patch and extends some distance into the patch [126].

## 5.4. Habitat Structures in the Edges of Patches

Edge effects also relate to the influence that a patch edge can have in determining species composition [127–129], the distribution of predators, and strategies for predation and processes within patch edges [130,131], although the literature still shows the opposite results for fauna interacting with canopy edges [132]. Algal patches organize themselves to define edge habitat structures that may define the margins of large persistent sea

urchin barrens and likely the dynamics of sea urchin feeding and movement [133]. On the contrary, the removal of urchins by human harvesting fosters the spread of fleshy algae and the recruitment of *Cystoseira* from the edge of vegetated patches [134].

Habitat patches may house small mesopredators that benefit from an increased structure, with the center of the patch experiencing higher predation and therefore presenting fewer epifauna in contrast to patch edges [135]. Likewise, the abundance of epifauna and gastropods may be significantly greater at the edges of seagrass beds, whereas species diversity is higher in the interior, with the differences being exacerbated with increasing patch size [136]. Proximity to patch edges has a greater influence on epifaunal density and community structure than structural complexity or predation [30,137]. Zooplankton and meiofauna also increase in abundance around the seagrass edge compared to the sand [138].

Fish densities were found to be greater in individual species' densities at seagrass edges [139–142] than in the middle. While in continuous configurations, pipefish were found to be 3 times more abundant at the edges (due to greater food availability) than in the interiors, although in patchy configurations there was no difference [143]. The total number of fish sampled at a seaward *Heterozostera nigricaulis* seagrass edge was found to be greater than in the seagrass interior, with little difference between the seagrass middle and the shoreward seagrass edge [130]. Faunal assemblages in the proximities to *Zostera* patch edges may show no (infauna) or negative (epifauna) responses to hydrodynamic stress [142]. Additionally, while shoot density and plant biomass were greater in interior portions of patches of *Thalassia testudinum* beds than at the edges, mean faunal density was significantly greater at the edges, resulting in specific habitat differences in secondary production among the major taxonomic groups [144]. Significantly different fish assemblages in kelp forests have been found at edges compared to interior locations with the relative abundance of fishes, explaining 91.4% of the variability [145].

Additionally, fragmented seagrass landscapes hold significant refuge value for juvenile blue crabs with crab survival increasing with habitat complexity regardless of patch size [146]. In patches of Zostera marina, juvenile blue crabs are more abundant in the interior of patches than at the edge [147]. In Zostera marina patches across the Atlantic and Pacific oceans and the Mediterranean Sea, the predation risk for crustaceans (crabs or shrimps) was lower along patch edges than in patch interiors, regardless of the extent of habitat degradation. However, the extent to which edges reduced predation risk depended on the extent to which edges supported higher structural complexities compared to patch interiors [29]. Ecologically significant edge effects on predation rates of tethered blue crabs and pinfish have been found, with blue crabs surviving >2.5 × longer, and pinfish surviving >2 × longer along the meadow edge relative to the patch interior [148]. The strength of the predation-related edge effects was most notable for blue crabs within patches with higher shoot density, while the opposite pattern was true for pinfish [148]. Additionally, predation on tethered cod was highest at the edge of eelgrass patches, compared with barren and eelgrass locations, with predation generally decreasing with distances from the patch boundary [149].

Scallop settlement was significantly enhanced along seagrass edges, regardless of patch type, while survival was elevated within patch interiors, but the scallop recruitment (the net result of settlement and post-settlement loss) did not vary significantly from edge to center [150]. Scallop growth was consistently fastest in bare sand and slowest at patch centers, and survival showed the opposite trend. Scallops in patch edges displayed intermediate growth and survival [151,152].

In addition, the effect of distance from the meadow edge on macrobenthic invertebrate abundance has been found to be relevant, with higher abundances towards the interior of seagrass meadows [153].

All these results suggest an indirect component to edge effects in which the impact of edge proximity on predation risk is mediated by the effect of edges on other key biotic factors such as habitat complexity within the vegetated patch [29,154–160]. Taxon-specific responses to shoot structure seemed more important than landscape structure for distribution and behavior [161]. Indeed, higher taxon richness and gastropod abundance were recorded in the patch edges but no significant differences were found among patch sizes [162]. In addition, the sharpness of transitions influences the interactions in the patch landscape due to the increased number of species in edges [155].

## 6. The Structural Edges in Gaps within Canopies

#### 6.1. Characteristics of the Edges in Gaps within Canopies

The fragmentation (the evolution of patchiness) of the submerged marine meadows leads to contrasted and complex seascapes with an increase in the number of gaps [52,83] and sand corridors [163]. The anthropogenic processes (anchoring, trawling) impact fragmentation more quickly than pollution [83]. The balance between the growth of the vegetation in the vicinity of a gap and the degree of spatial patchiness depends on the frequency and amplitude of the natural disturbances [7,164]; however, when human activities exceed the natural disturbance regime, the balance may be upset and vegetative growth may not compensate for meadow fragmentation [20]. Canopies with large gaps present more mixing than canopies with small gaps despite having the same total gap area in the canopy [165].

## 6.2. Hydrodynamics of the Edges in Gaps within Canopies

Gaps within rigid submerged model canopies enhance turbulence, provided that Aw/S < 0.35 [165,166], where  $A_w$  is the orbital length scale and S is the plant-to-plant distance. In such cases, the role of plants is to dampen seabed generated turbulence. Conversely, for Aw/S > 0.35, plants generate turbulence at the stem scale, decreasing the wave velocity of the flow. Observations also show that turbulence does not remain local within the gap, but is transported throughout the water column and is then transported downstream and thereby perturbs the canopy flow [11]. In more detail, gaps may enhance turbulence production and also turbulent transport as turbulent kinetic energy is mixed and redistributed over the depth through turbulent wake production [11]. In relatively fast unidirectional flows, the mean flow profile is logarithmic above the canopy and has an inflection point near its top and uniformly low values within it [167]. Within the gap, a recirculation is formed, and the length of leaves overhanging the gap from the upstream canopy is found to be the key parameter to locate the flow recirculation cells within the gap [168]. In slower flows, the flow at the gap is more uniform. Sweeps dominate both high and low flows in the region near the top of the canopy and within the gap [167].

The patch is divided into two regions, first, the turbulent, high-momentum upper region above the canopy and, second, the low-turbulence (in the x–z plane), low-momentum lower region below the canopy height. A significant amount of total energy is dissipated when the flow entrains and mixes from the top to the lower layer within the gap, although for a canopy that is continuously fragmented this process might be limited [11]. At the gap/patch scale, fragmentation induces a stream-wise discontinuity in shear that results in the restructuring of the turbulence locally, with the turbulent flow at the gap/patch edge depending on both the dimensions of the gap and the characteristics of the vegetation in close vicinity to the gap [11,48,52,167]. The length of the gap may enhance or limit the level of gap-induced increased shear, or the turbulence being introduced to vicinity gaps [11].

Within seagrass meadows at leaf length distances from the edge, wave attenuation by the lateral vegetation next to the gap is found to be the same as attenuation by fully vegetated areas and the wave attenuating capacity of the near-gap vegetation is independent of gap width [52]. Gaps with widths less than twice the leaf length exhibited 8% wave attenuation and 11% turbulent kinetic energy attenuation, confirming that vegetation shelters, at least, small gaps [52]. Under oscillatory flows, vegetation in the vicinity of a longitudinal gap (i.e., with its main axis aligned to wave direction) may reduce wave velocity and the turbulent kinetic energy at the edge with distance into the canopy, with the attenuation increasing as the density of the vegetation increases [169]. Compared to flexible plants, an edge of plants with high rigidity would present even higher wave velocity attenuation but with an increase in the turbulent kinetic energy with distance into the canopy [169]. In canopies with rigid plants, the lateral vegetation may modify the wave attenuation in the nearby gap, while there is no attenuation in the gap for flexible plants in the vicinity of the gap [170]. In addition, numerical models on how emergent and submerged vegetation affects coastal hydrodynamics show that in a scenario of waves on tidal flow, the speed increases at the lateral edges of the vegetation patch [171].

For a transversal gap within a canopy (i.e., a gap oriented perpendicular to the wave direction), the wave velocity was found to increase with gap width. Additionally, the turbulent kinetic energy within the gap increased but was more attenuated by the adjacent vegetation than the wave velocity. Denser canopies, compared to sparse canopies, in the vicinity of the edge produced a greater attenuation of both the wave velocity and the turbulent kinetic energy within the adjacent gap [165].

## 6.3. Habitat Structures of the Edges in Gaps within Canopies

The level of fragmentation is unlikely to determine any identification of any taxonomic group in terms of fauna differentially using edge or core areas of seagrass patches [19] unless extensive areas of meadows are deformed by human disturbances such as boat propeller damage [19]. However, a reduction in both infaunal and epibenthic organisms at the 1 m edges of seagrass meadow relative to interior areas has been found [19]. Likewise, crustaceans inhabiting fragmented *Zostera* seagrass meadows have shown the greatest abundance at the boundary between sand and seagrass, at scales of 0.25–1 m at the patch edge [106]. In contrast, the infaunal polychaete and bivalve groups showed very little or no response at the patch edges due to the presence of substantial quantities of seagrass root and rhizome material in the sand habitat [106].

#### 7. Discussion

### 7.1. The Impact of Edges on Submerged Marine Canopies

Heterogeneity due to multispecific spatial patchiness has crucial implications for macrophyte species interactions and aquatic ecosystem functions such as nitrogen retention [32], although the impact of edge proximity exacerbated by fragmentation is mediated by the effect edges have on the habitat complexity within the vegetated patch, albeit at the local scale rather than at the canopy scale [48]. The local changes in the spatial structural patterns of patches (shoot density, vegetation coverage, and leaf length, Table 1) to changing abiotic conditions (waves, turbulence, flows), dynamically affecting the patch edge, suggest the potential use of the spatial patterns in the edge of meadows as an indicator for describing the level of meadow stress under long-term changes in hydrodynamics.

Positive and negative feedbacks between the spatial patterns and the abiotic conditions will predictably account for the responses of canopies and patches (physiological responses, morphological traits, and meadow architecture) and their edges under moderate to high natural and anthropogenic stressors. In homogeneous canopies, the habitat configuration has a greater influence on species at intermediate values of habitat quantity, where the variability in fragmentation metrics (longer length of edges) is greater [172], suggesting that all species are, to a certain degree, sensitive to the structural modifications of edges and, therefore, to landscape changes [173,174]. As canopy-forming seaweeds provide essential habitats, carbon storage, and nutrient cycling, understanding their response to continued climate warming is critical to inform coastal management and conservation planning [175]. However, the lack of edge effects in patchy configurations for seagrass fishes might be because patchy seagrass consists entirely of edge habitat [143]. Special attention should be paid to how the coastal marine seascape and associated shallow and deep canopy limits undergo short- and long-term structural changes due to increasing nutrient inputs, and the increasing impact of climate change, i.e., sea level increase, increased water temperature, acidification, and the interplay between abiotic and biotic factors in determining the distribution of canopies and patches of vegetation. Research suggests that the shallow edge of the meadow is primarily maintained by vegetative recruitment, whereas the deep edge, to a larger extent, relies on sexual recruitment [176]. The predicted increases in temperature during this century may lead to local extinctions of or reductions in marine ecosystems through the combination of increased physiological stress at both upper and lower canopy limits and patch edges [74,177].

Within canopies, the interaction between the hydrodynamics and light availability can induce biostability [178], i.e., the presence of seagrass may reduce the suspended sediment concentrations through the reduction in resuspension of particles and the capture of particles by plant leaves [179], associated with the reduction in energy to increase the benthic light availability, thereby favoring growth, but, on the contrary, at edges, increased wave action may increase resuspension of particles that increases turbidity, thereby reducing growth of vegetation.

Characteristic high animal species richness in the seagrass relative to adjacent sand is not closely related to the characteristics of the seagrass habitat as a whole, but rather to the presence or absence of individual plants at the very edge, with marked differences in assemblage composition within short distances from the edge in both the vegetated and the non-vegetated sides [157,158,180,181]. Differences in faunal densities and secondary production between edges and interiors of seagrass patches represent a potentially vital link in seagrass trophic dynamics. If this elevated secondary production leads to increases in trophic transfer, then edges may serve as a significant trophic conduit to higher-level consumers within patches [144]. While trophic levels are differentially affected, the impact of habitat fragmentation may be greater on intermediate rather than top trophic levels in fragmented seagrass seascapes [182]. Predators increase their success by searching patch edges, and this results in the greatest predation risk being for prey in isolated intermediate-sized patches rather than larger ones [149]. The increase in fragmentation leads to an increase in the area of edges over the inner canopy areas. Edge habitats may benefit some organisms by maximizing risk versus reward [151]. Some fish species have been found to be more abundant at seagrass edges due to greater food availability, therefore providing experimental support for the resource distribution model as an explanation for edge effects [138]. The strong positive edge effect (higher densities at the edge rather than the interior) for taxa such as copepods implies some benefit of patchy landscapes although, during patch fragmentation, the minimized effect of the edge itself highlights the importance of the mechanisms by which habitats become patchy [183].

## 7.2. The Knowledge of Edges on Submerged Marine Canopies for Coastal Management

The restoration efforts of coastal canopies might best focus on locating coastal areas with similar landscape contexts or patch characteristics other than patch size at both deep and shallow canopies [19,184], although for fragmented seagrass meadows, the intensity of species interactions has been found to depend on the proximity to the patch edge where the risk of grazing is high and the restoration through seagrass transplants may be compromised [185]. For example, recovering plants growing on the edges of eelgrass beds displayed a low capacity for resilience to excavation [186]. This is exacerbated by seagrasses near the edges of their biogeographical ranges being more vulnerable to stress events, local-scale burial, erosion events, and sediment deposition caused by water pollution and/or eutrophication [187–189], although shoots growing in interior patches are denser than shoots in the edge of the patches and are subject to marked self-shading and competition for space [80].

Although water quality conditions that are suitable for recovery of existing seagrass canopies are likely better than those required for continued survival, the levels needed for

restoration and recovery of many currently unvegetated sites contiguous to the patch can be compromised due to reduced complexity at the patch edge [190]. Fragmentation of marine landscapes can reduce biodiversity dominance, but even small patch sizes can be important for the conservation of macroinvertebrate diversity [162] as well for mesopredators and epifaunal communities [191]. Although meadow degradation greatly affects trophic structuring and nutrient pathways within the food web [192], some authors report higher species richness in fragmented *Posidonia oceanica* and *Cymodocea nodosa* meadows, through habitat diversification, in comparison with homogeneous habitats [127]. However, at the same time, edge vegetation can present 14 times higher vulnerability than within a canopy, as is the case of the mapped invasion of the invasive green alga *Caulerpa racemose* on margin meadows and within gaps in fragmented meadows of *Posidonia oceanica* [193].

## 7.3. Suggestions for Further Analysis

Finally, the analysis of the 3661 manuscripts that resulted from the search of manuscripts in both the databases of Scopus and Web of Science showed that research on edges in marine ecosystems was mainly focusing on seagrasses, with a lack of studies on saltmarshes and seaweeds. This implies the necessity of focusing research on both saltmarshes and seaweeds for a general interpretation of hydrodynamics, a general description of habitat at the edges of canopies, and the definition of relevant scales at the edge of marine canopies (saltmarshes, seagrasses, and seaweeds). Furthermore, the interaction between hydrodynamics (waves, currents, or turbulence only) and edges of different canopy types (saltmarshes, seaweeds, and seagrasses) needs more investigation. The structural distributions of patches and their interactions in terms of their impact on hydrodynamics need to be further addressed. With such information, restoration plans might better succeed and management strategies can be consistently applied to make seascapes more resilient in the face of anthropogenic disturbances.

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