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REVIEW

Role of hydrodynamics in shaping chemical habitats and modulating the responses of coastal benthic systems to ocean global change

Fanny Noisette[1,2,3] | Christian Pansch[2,4] | Marlene Wall[2,5] | Martin Wahl[2] | Catriona L. Hurd[3]

[1]Institut des Sciences de la Mer, Université du Québec à Rimouski, Rimouski, Quebec, Canada
[2]Department of Marine Ecology, GEOMAR Helmholtz Centre for Ocean Research, Kiel, Germany
[3]Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania, Australia
[4]Department of Environmental and Marine Biology, Åbo Akademi University, Åbo, Finland
[5]Bentho-Pelagic Processes, Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Bremerhaven, Germany

Correspondence
Fanny Noisette, Institut des Sciences de la Mer, Université du Québec à Rimouski, Rimouski, QC G5L 3A1, Canada.
Email: fanny_noisette@uqar.ca

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Abstract

Marine coastal zones are highly productive, and dominated by engineer species (e.g. macrophytes, molluscs, corals) that modify the chemistry of their surrounding seawater via their metabolism, causing substantial fluctuations in oxygen, dissolved inorganic carbon, pH, and nutrients. The magnitude of these biologically driven chemical fluctuations is regulated by hydrodynamics, can exceed values predicted for the future open ocean, and creates chemical patchiness in subtidal areas at various spatial (µm to meters) and temporal (minutes to months) scales. Although the role of hydrodynamics is well explored for planktonic communities, its influence as a crucial driver of benthic organism and community functioning is poorly addressed, particularly in the context of ocean global change. Hydrodynamics can directly modulate organismal physiological activity or indirectly influence an organism's performance by modifying its habitat. This review addresses recent developments in (i) the influence of hydrodynamics on the biological activity of engineer species, (ii) the description of chemical habitats resulting from the interaction between hydrodynamics and biological activity, (iii) the role of these chemical habitat as refugia against ocean acidification and deoxygenation, and (iv) how species living in such chemical habitats may respond to ocean global change. Recommendations are provided to integrate the effect of hydrodynamics and environmental fluctuations in future research, to better predict the responses of coastal benthic ecosystems to ongoing ocean global change.

KEYWORDS
acidification, boundary layer, deoxygenation, engineer species, global change mitigation, hypoxia, micro-environment, refugia, water motion

1 | INTRODUCTION

The world's oceans are undergoing a range of anthropogenic changes, altering physical and chemical properties such as dissolved oxygen and inorganic carbon concentrations, pH levels, or seawater temperature at an accelerating rate, broadly named the 'ocean global change' (see Box 1). Compared with the relatively stable open ocean, coastal waters are characterized by substantial biological

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BOX 1 **Definition box. All the words between ‘’ in the text are described in the box**

Advection: Bulk transfer of mass, momentum and heat by fluid movement.

Associated species: Species belonging to the community dominated by an engineer species, living under its influence; also called “resident species” after Ninokawa et al. (2020).

Biologically-driven fluctuations: Variation of physical and chemical parameters of the seawater that are generated by the metabolism (physiological processes) of organisms or communities; for instance, photosynthesis of seaweeds during daylight increases the O_2 concentration in the water surrounding the blades.

Diffusive boundary layer = DBL: Concentration gradient that forms within the viscous regions of the velocity boundary layer (VBL); within this layer, the exchange of mass, momentum and heat between an organism and the seawater at their surface is via passive diffusion. Here, we use DBL synonymously with “concentration boundary layer” (CBL), after Denny and Wethey (2001), Hurd et al. (2014).

Diffusion: Net movement of mass, momentum and heat, from a region of higher concentration to a region of lower concentration, driven by the concentration gradient.

Engineer species: Organisms that create, maintain or destroy habitat for other species by either modulating environmental properties (termed autogenic engineers) or by transforming other material (allogenic engineers), after Jones et al. (1994, 1997).

Macrophytes: In our context macrophytes refers to marine macroalgae and vascular plants, i.e. seaweeds and seagrasses, after Olafsson (2016).

Ocean global change: Imprint of climate change on multiple ocean properties, many of which shape the physiology and ecology of marine life, after Boyd et al. (2018).

Influenced-area: Area adjacent to a benthic community that is dominated by a highly productive engineer species and influenced by its metabolic activity. Water masses transformed by the intense metabolic activity of some dense engineer species can be transported by advection to downstream adjacent ecosystems, generating influenced-areas.

Mass transfer limitation: The slow transport rate of a nutrient from seawater to the organism's surface, which can limit its metabolism, after Hurd (2017).

Ocean weather: Local shifts in physico-chemical conditions that occur over weeks, hours and minutes, happening at faster and smaller scales than changes in climate.

Refugia: First described for terrestrial environments, refugia are habitats that some species can retreat to, persist in and potentially expand from under changing environmental conditions, after Keppel et al. (2012). Several authors defined climate change refugia as areas relatively buffered from contemporary climate change over time, in which the vulnerability of species to environmental stressors is reduced, after Kapsenberg and Cyronak (2019), Morelli et al. (2016).

activity, and geochemical processes such as sediment diagenesis, which interact with global change drivers and/or local perturbations (e.g. freshwater discharge, upwelling events, and artificial structures modifying the natural topography; Duarte et al., 2013). Together, biological, geochemical and physical processes govern the complex regulation of local physicochemical parameters at small temporal and spatial scales to produce ‘ocean weather’ that often masks ocean global change trends (Bates et al., 2018; Borges & Gypens, 2010; Chan et al., 2017; Duarte et al., 2013; Johnson et al., 2013; Waldbusser & Salisbury, 2013). Predicting how marine coastal ecosystems will be affected by ocean global changes in the future is, therefore, challenging, in particular because spatially distinct coastal zones may experience different ocean weather conditions (Ghedini et al., 2015; Provost et al., 2017; Wahl et al., 2018, 2021).

Hydrodynamics embodies physical processes related to the motion of water, such as currents, tides, waves, up- and downwelling (Figure 1), occurring from large ocean-basin to small molecular scales, generating turbulent or laminar flow conditions (Mann & Lazier, 2013). Hydrodynamic processes are key drivers of coastal productivity (Egea et al., 2018). They influence the amplitude, frequency and spatial extent of biologically-driven chemical fluctuations such as dissolved oxygen or inorganic carbon concentrations by (i) transporting water bodies away from the source via ‘advection’, (ii) diluting the water body (Gaylord et al., 2012), and (iii) affecting the residence time of the water in a given place (Cyronak et al., 2018). It is well known that hydrodynamics affects the biological processes of planktonic communities (Legendre & Demers, 1984), and also directly impacts benthic organisms (e.g. Boynton et al., 1981; Stewart & Carpenter, 2003). While hydrodynamics has been flagged as a driving force of benthic community structure and functioning since the early 1980s (Nowell & Jumars, 1984; Van Der Wal et al., 2017), the effect of this physical variable has been neglected in multifactorial experiments addressing biological responses to environmental change (Hurd, 2015). This

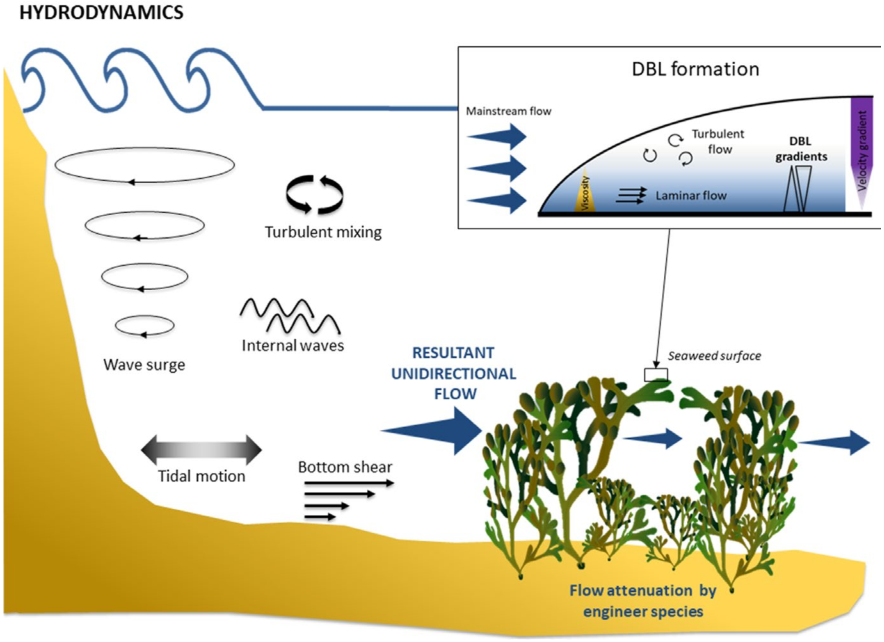

FIGURE 1 Hydrodynamics in subtidal coastal zones. Different hydrodynamic processes occur in coastal areas (left of this sketch). In subtidal zones, hydrodynamic processes generally result in an overall unidirectional flow, which influences benthic organisms and communities. When the flow touches a solid surface, shear stress makes the flow laminar at the surface of the organism and a diffusive boundary layer (DBL) can build up, creating specific chemical conditions at the surface of the organism, different from the bulk seawater (upper right sketch). Engineer organisms (e.g. seaweeds, seagrasses, corals, molluscs) can attenuate the flow depending on their complexity and density. By aggregation of layer on layer of DBLs, a canopy- or community-boundary layer can form (right of this sketch). More details on flow structuring by seagrass and coral communities can be found in Nepf (2012) and Lowe and Falter (2015), respectively

knowledge gap needs to be filled because the magnitude of water velocity can strongly modify the outcome of experiments testing the impacts of ocean global change on benthic marine organisms (Comeau et al., 2014, 2019; Cornwall et al., 2014).

Temporal and spatial fluctuations in chemical conditions in shallow waters mainly result from the interaction between biological activity and hydrodynamic forcing (Cyronak et al., 2018; Kapsenberg & Hofmann, 2016; Saderne et al., 2013; Wahl et al., 2018). Biological activity is the main driver of chemical variations in highly productive systems that are dominated by 'engineer species' (see Box 1) such as seagrass meadows, kelp forests, coral reefs or mollusc beds (Falkenberg et al., 2021). At high population densities, engineer species have the capacity to strongly modulate the chemical and physical conditions of their surrounding waters (Gutiérrez et al., 2003, 2011; Hurd et al., 2014; Kregting et al., 2013; Pujol et al., 2019; Turk et al., 2015; Unsworth et al., 2012). Physiological processes such as respiration, photosynthesis, calcification or excretion shape the chemistry of coastal waters via their influence on inorganic carbon fluxes (e.g. Bordeyne et al., 2015; Chauvaud et al., 2000, 2003; Martin et al., 2007a), nitrogen exchange (e.g. Martin et al., 2006, 2007b), seawater oxygen content (e.g. Smith et al., 2013) and carbonate chemistry variables including pH and alkalinity (e.g. Ninokawa et al., 2020; Takeshita et al., 2018). The intensity of biological activity and the temporal and spatial scale of effects are mainly dependent on the size, biomass, morphology and metabolic rate of organisms and communities in relation to the water volume surrounding them (Figure 2; Lesser et al., 1994; Lowe & Falter, 2015; Stewart & Carpenter, 2003). Biologically driven fluctuations (Figure 2) occur on spatial scales ranging from small (μm to cm) to large (m to hundreds of m), and temporal scales of variation are generally faster at small (seconds) compared with large (hours to days) spatial scales (Boyd et al., 2016; Kapsenberg & Cyronak, 2019; Wahl et al., 2016). Metabolic processes of the organisms are in turn influenced by their physiology, which is regulated by the amount of energy available in the habitat in terms of light, inorganic or organic sources, as well as by other physical factors such as temperature, salinity and hydrodynamics.

An increasing number of publications emphasizes the importance of incorporating fluctuating regimes into experiments testing the responses of organisms and communities to ocean global change, in particular to ocean warming, acidification and deoxygenation (Boyd et al., 2016; Britton et al., 2019; Rivest et al., 2017; Wahl et al., 2016). Furthermore, at this stage, we do not understand how alterations in the metabolism of engineer species due to ocean global change will feedback to shape their surrounding water chemistry, in relation to hydrodynamics (e.g. Hirsh et al., 2020; Noisette & Hurd, 2018; Wahl et al., 2018). In this review, we focus on (i) the influence of hydrodynamics on the biological activity and performances of engineer species, especially under ocean global change. We then describe (ii) specific chemical habitats resulting from the interaction between

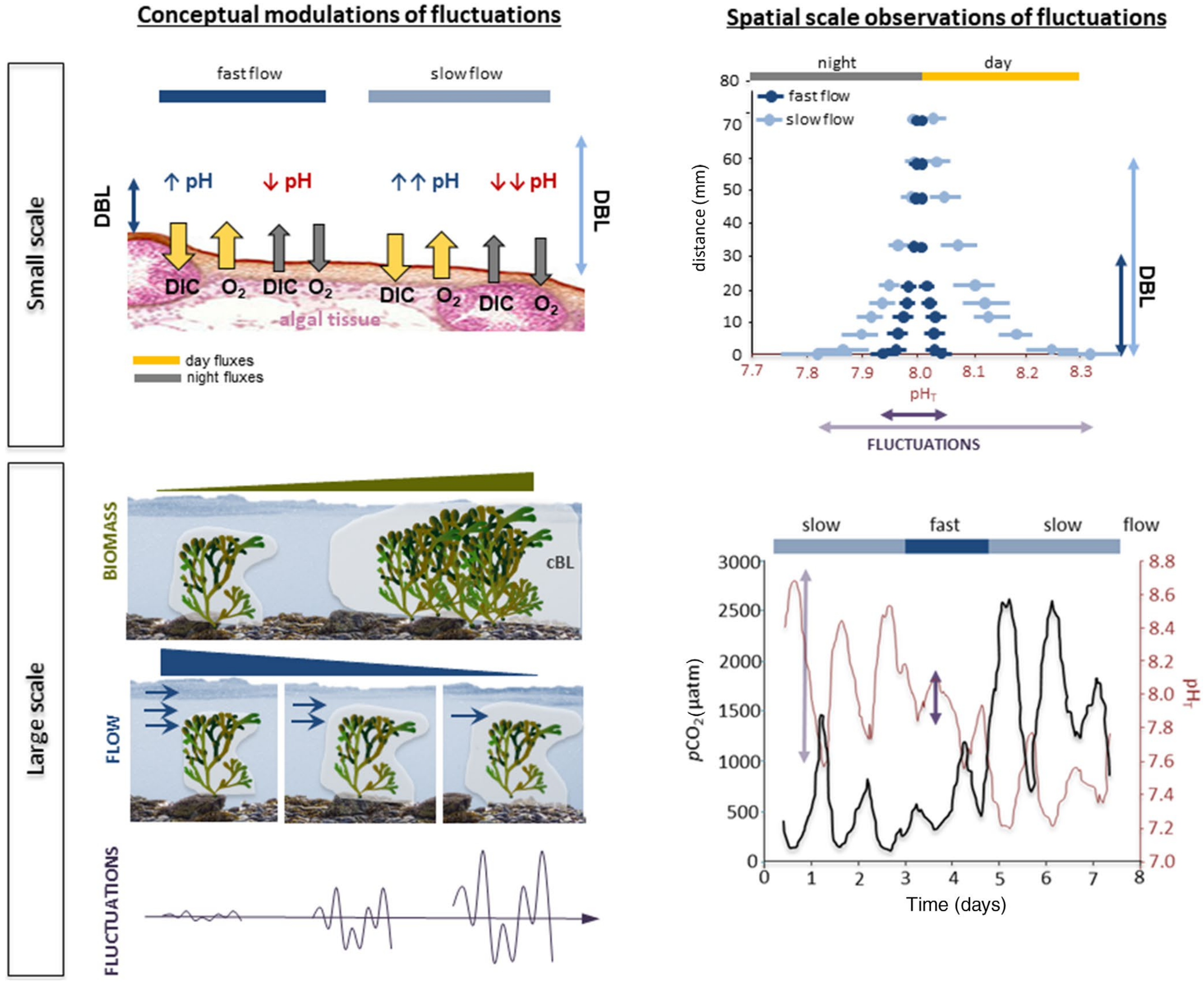

FIGURE 2 Environmental fluctuations and chemical environments at different scales. Organisms modulate their chemical environment at the small-scale up to larger ecosystem scales of hours to days (rights panels). The conceptual basis underlying these fluctuations are illustrated in the left panels. We outline how photosynthetic organisms (i.e. primary producers) modulate their chemical environment within the diffusive boundary layer (DBL, upper panels) up to the community scale (cBL, lower panels). These changes can be large and are usually linked to biomass and/or flow conditions. The amplitude of environmental fluctuations is positively related to increases in biomass (green gradient in bottom left graph shows increasing biomass to the right) and negatively to the intensity of water flow (blue gradient in bottom left graph illustrates increasing flow to the left with constant biomass). Small-scale variation of pH (upper right panel) was measured within the DBL of calcifying red algae as a function of flow (data are adapted from Cornwall et al., 2013, occurring within minutes). At larger scales (lower right panel), these variations are generally slower and less intense (data are adapted from Saderne et al., 2013; changes measured proceeded at this scale over a full day)

engineer species metabolism and hydrodynamics, where environmental fluctuations are different than in the bulk seawater. We highlight (iii) the importance of these specific chemical habitats in providing refugia against ocean acidification and deoxygenation but also (iv) point out how they can facilitate the resistance of populations or decrease species' fitness, depending on species' capacities to respond to large abiotic fluctuations. We deliberately do not address in this review indirect hydrodynamic effects on shifts in species' interactions and interactive impacts of multiple drivers fluctuating asynchronically (see Wahl et al., 2021 for instance).

2 | HYDRODYNAMICS, AN OVERLOOKED DRIVER MODULATING BIOLOGICAL ACTIVITY

2.1 | Hydrodynamics in coastal subtidal environments

Compared with air in terrestrial systems, the higher density and viscosity of seawater causes lower rates of molecular diffusion of essential nutrients and gases. The result is that the fluid medium in which marine organisms grow exerts greater regulation over biological and community performance (Denny, 2015; Sand-Jensen & Krause-Jensen, 1997; Vogel, 1999). Therefore, water motion, which counteracts reduced diffusion rates, is a fundamental regulator of biological activity, at scales ranging from that of the organism to that of entire ecosystems (Nowell & Jumars, 1984). This is particularly the case in coastal habitats, where hydrodynamic processes encompass waves, tidal cycles, storm surges, up- and downwelling. In some coastal ecosystems such as the intertidal zone, wind-driven flows create massive and powerful waves and oscillatory currents (Hurd, 2000). However, the majority of subtidal environments are under the influence of a dominant flow, resulting from cumulative hydrodynamic processes (Nowell & Jumars, 1984; Figure 1).

2.2 | Water flow shapes velocity and DBLs at the organism's surface

The limitation of physiological processes by flow is closely related to what happens at the surface of the organism (De Beer et al., 2000; Hurd, 2015; Kühl et al., 1995; Noisette & Hurd, 2018). The theoretical background of the behavior of a fluid when it touches a solid surface has been reviewed previously (Denny, 2015; Hurd, 2000; Vogel, 1999). Briefly, water flowing over marine organisms generates frictional drag at their surface (Hurd, 2000; Vogel, 1999). A velocity gradient (VBL) forms, with zero velocity at the solid surface due to the no slip condition, and a maximal thickness at a velocity of 99% of the bulk seawater flow overhead. In the viscous sublayer of the VBL, where the flow is laminar, molecules and gases move by the slow process of 'diffusion' from high to low concentrations. This sublayer is termed the 'DBL' (Box 1; Figure 1; Vogel, 1999). The movement of all metabolically important dissolved gases (e.g. CO_2, O_2), dissolved inorganic nutrients (e.g. nitrate, ammonium, phosphorous, bicarbonate), metabolites (e.g. reactive oxygen species, refractory carbon), and metabolic waste (e.g. urea) to and from an organism surface, across the DLB, is via diffusion. Although the seawater flow velocity controls the formation of a DBL and its thickness, the concentration gradient in the DBL is driven by the organism's metabolic activity, the concentration of dissolved substances in the bulk seawater at the outer edge of the DBL, and the thickness of the VBL (Denny, 2015; Stevens et al., 2001). Temperature also changes the transport of dissolved materials across the DBL as it affects fluid viscosity, gas solubility and the diffusion coefficient (Denny, 2015; Vogel, 1999). Increasing temperature usually decreases the DBL thickness and increases diffusion rates, leading to a steeper concentration gradient in the DBL (Wahl et al., 2016). The effects of temperature on the physical properties of the DBL are superimposed to direct effects on organism's metabolism (Brown et al., 2004) and result in specific chemical conditions surrounding the organism.

2.3 | Flow speed impacts metabolic rates and physiology

Physiological and biological rates follow a quadratic response curve as a function of flow speed: they improve with increasing mainstream speed until a maximal rate is reached, when enzymes or organs (like feeding appendices) start being saturated (Hurd et al., 1996; Pujol et al., 2019; Stewart & Carpenter, 2003; Wheeler, 1980). Related to thick DBLs, slow flows can restrict biological performance by impairing the supply of essential dissolved inorganic and organic substances needed for physiological processes. When flow speed increases, convection and advection improve mass transport and decrease DBL thickness, which enhances the supply of essential dissolved substances and the removal of harmful ones, allowing an improvement of an organism's performance. When flow exceeds the optimal velocity, it can be detrimental for the organism, triggering new energetic trade-offs for maintenance or repair (see figure 4 in Pujol et al., 2019). It is important to remember that the concept of *fast* and *slow* flows is relative to the organism studied and the hydrodynamics they experience naturally in their habitat.

Most studies reporting the effects of hydrodynamics on the metabolism of engineer species are related to photosynthetic primary producers, hereafter called "primary producers" (Hurd, 2017). Seawater velocity has been shown to positively impact primary production rates and nutrient uptake up to the optimum in turf (e.g. Carpenter & Williams, 2007), larger 'macrophytes' such as seagrasses and seaweeds (e.g. Barr et al., 2008; Carpenter et al., 1991; Kregting et al., 2011; Mass et al., 2010) and corals (e.g. Atkinson & Bilger, 1992; Lesser et al., 1994). Indeed, in slow flow, 'mass transfer limitation' (see Box 1) can affect the ability of macrophytes to acquire and use essential dissolved substances, limiting their metabolism and likely causing a reduction in production and growth (Carpenter & Williams, 2007; Pujol et al., 2019). In corals, slow flow can reduce production and calcification rates, when oxygen accumulates in coral tissues at the peak of photosynthesis around midday (Dennison & Barnes, 1988; Jokiel, 1978). The increase in flow speed, thus, turns out beneficial until it becomes too fast and detrimental. For instance, the productivity of marine macrophytes that use an external carbonic anhydrase in their carbon-acquisition mechanism may decline in fast flows as this enzyme could be washed away from the seaweed's surface (Enríquez & Rodríguez-Román, 2006). In corals, fast flow could increase the cost of energetic expenses of light acclimated corals (Patterson et al., 1991) by affecting their carbon translocation process (Edmunds & Davies, 1986). Flow speed can also influence respiration, calcification, and/or the feeding efficiency of heterotrophic engineer species such as cnidarians, (Dennison & Barnes, 1988; Patterson et al., 1991; Rex et al., 1995; Stambler et al., 1991), bryozoans (Hermansen et al., 2001; Okamura, 1985), or molluscs (Saurel et al., 2007; Wildish et al., 1987), affecting their growth (Jokiel, 1978), and likely the local conditions in their surrounding seawater (De Beer et al., 2000). To increase their performance, organisms including seaweeds, mussels, and barnacles, can be morphologically adapted to the prevalent flow regime of their habitat (Hurd & Stevens, 1997; Marchinko & Palmer, 2003). However, the impact of flow speed on morphological changes (e.g. body size, surface topography) is not developed here as it is considered out of the scope of this review.

2.4 | Hydrodynamics can modulate organism responses to ocean global change

An increasing number of studies highlight how prevalent hydrodynamics are in modulating an organisms' responses to ocean global change, including warming, hypoxia or deoxygenation and ocean acidification (Comeau et al., 2014, 2019; Egea et al., 2018; Ho & Carpenter, 2017; Hurd, 2017). For example, Nakamura and Yamasaki (2005) showed that two branched coral species bleached less and grew better under fast (20 cm s^{-1}) compared with slow flow (3 cm s^{-1}), during high sea surface temperature events, which lasted for several weeks. By increasing the diffusion rate and reducing the oxidative stress, fast flow may enable these corals to recover from thermal stress (Finelli et al., 2006; Nakamura & Van Woesik, 2001). Under ocean acidification scenarios, corals and coralline algae have been shown to maintain positive levels of net calcification regardless of the bulk seawater pH decrease, in flows increasing from 2 to 10 cm s^{-1}. The authors hypothesized that this positive effect of fast flow is likely related to an alleviation of mass transfer limitation, which facilitates the uptake of carbonate/bicarbonate ions as well as the export of protons to and from calcification sites (Comeau et al., 2014). Hurd et al. (2011) showed that coralline algae and sea urchins living in slow flows had greater pH variations than in fast flows, and hypothesized that this would support greater physiological flexibility to adjust to environmental changes. This study also suggested that slow flow could create favorable conditions for calcification, a hypothesis later supported by Cornwall et al. (2013, 2015) for coralline algae. These examples reveal the extent to which flow speed can affect the responses of benthic organisms to ocean global changes such as warming and acidification, and therefore highlight the importance of including flow in the design of future experiments examining the effects of environmental changes on species living in highly dynamic coastal environments.

3 | CHEMICAL HABITATS RESULTING FROM HYDRODYNAMICS AND BIOLOGICAL ACTIVITY INTERACTIONS

3.1 | Metabolic processes that drive DBL chemical fluctuations

The nature, rate and rhythm (e.g. diel cycles) of metabolic processes of an organism are the main cause of the chemical fluctuations that occur in the DBL (e.g. Figure 1). Photosynthesis and respiration affect oxygen, CO_2, bicarbonate (HCO_3), hydroxide (OH^-), and proton (H^+, linked to pH) concentrations within the DBL. In light, photosynthesis by primary producers strongly increases oxygen concentration at photosynthetically active surfaces (e.g. Brodersen et al., 2015; Kaspar, 1992; Lichtenberg et al., 2017; Mass et al., 2010; Shashar et al., 1993). Additionally, changes in CO_2: bicarbonate ratio are observed within the DBL (De Beer et al., 2000; Hofmann et al., 2016). These ratio changes depend on the dissolved inorganic carbon uptake strategy of the organism, that is, CO_2-only users versus species that additionally use bicarbonates (Cornwall et al., 2017; Raven, 1997; Van Der Loos et al., 2019). Around most photosynthetic organisms, surrounding seawater pH usually increases over the light period due to (i) CO_2 uptake, which alters the seawater carbonate system, (ii) the accumulation of OH^- ions within the DBL, as a biproduct of bicarbonate uptake used for photosynthesis (Fernández et al., 2014), and/or (iii) light-induced proton pumps (Hofmann et al., 2016). Conversely, respiration releases CO_2, which accumulates within the DBL at night for photosynthetic organisms (Hofmann et al., 2016). The release of CO_2 influences the seawater carbonate system, leading to a pH decrease within the DBL (Hurd, 2000). For heterotrophs, respiration tends to almost exclusively lower pH in the DBL compared with the bulk seawater, regardless of day and night. Calcification and carbonate-dissolution processes at the surface of calcareous species also change the local chemical environment of the DBL by influencing calcium content, carbonate chemistry equilibrium and total alkalinity (De Beer et al., 2000; Ninokawa et al., 2020; Roleda et al., 2012; Wolf-Gladrow et al., 2007).

Nutrient concentrations, nitrogen in particular, can also fluctuate within the DBL, driven by nitrogen uptake in primary producers (Fernández et al., 2017), and ammonium or urea excretion in invertebrates (Hurd et al., 1994). Fluctuations in dissolved nitrogen species can also affect the carbonate chemistry within the DBL, as ammonium and nitrate concentrations influence the alkalinity and the pH of seawater (Wolf-Gladrow et al., 2007). Nitrate assimilation results in a pH increase at the cell surface, whereas ammonium assimilation leads to a pH drop due to influx and efflux of protons, respectively (Raven, 1981; Raven & Michelis, 1980). However, Fernández et al. (2017) showed that nitrogen assimilation did not change pH at the blade surface of the giant kelp *Macrocystis pyrifera*, emphasizing that the co-occurrence of different processes affecting the pH can repress their individual effects.

3.2 | From DBLs (µm-mm) to the formation of larger (cm-m) chemical habitats

The biologically-driven chemical fluctuations occurring in the organism's DBL range from µm to mm depending on the flow velocity (e.g. Hendriks et al., 2017; Noisette & Hurd, 2018; Noisette et al., 2020). These micro-habitats created at the direct surface of organisms represent specific niches with characteristics completely different from the bulk seawater. They provide habitat for microorganisms, hold complex animal assemblages, and may constitute a preferred settlement habitat for bacteria, small larvae and spores (Irwin & Davenport, 2010; Wahl et al., 2016). In favorable conditions, that is, at very slow flow and high metabolic activity, the thickness of the boundary layer at the surface of a macrophyte can even reach a few centimeters (Raven & Hurd, 2012; Wahl et al., 2016), being effective as habitat for also larger epibionts (Saderne & Wahl, 2013).

In dense aggregations of engineering species such as algal canopies or mollusc beds (Ninokawa et al., 2020; Rosman et al., 2010;

Shi et al., 1995), organisms can attenuate the flow speed making the VBLs coalesce (Kregting et al., 2021). In there, biological processes can drive notable chemico-physical differences between seawater in- and outside the formed habitat, leading to the build-up of larger canopy- or community boundary layers from centimeter to meter (Figure 3; Cornwall et al., 2013; Hurd, 2015; Ninokawa et al., 2020). The formation of such thick boundary layers depends on the engineer species' morphology and the complexity of the habitat formed (Hurd & Pilditch, 2011; Kregting et al., 2021; Stewart & Carpenter, 2003). They preferentially build up when the engineer species are large and complex enough to sufficiently slow down the water flow within the habitat (Figure 1; Gutiérrez & Jones, 2006; Jackson & Winant, 1983; Lowe & Falter, 2015).

3.3 | Canopy-boundary layers

To date, research has focused on macrophytes as engineer organisms able to greatly attenuate the flow inside the canopy and changing the hydrodynamic regime for fleshy and calcareous algae in the understory (Cornwall et al., 2015; Jackson & Winant, 1983; Nepf, 2012; Nishihara et al., 2015; Unsworth et al., 2012). In and below the canopy, the seawater residence time increases, while mixing with the water column decreases. The formation of a canopy-boundary layer can reduce the exchange rate of gases, the replenishment of ions and the removal of metabolic by-products, influencing the amplitude and the frequency of the chemical fluctuations within (James et al., 2019; Koweek et al., 2017). Chemical conditions within these habitats are thus defined by the balance between hydrodynamics and biological processes (Ninokawa et al., 2020). For instance, within dense macrophyte communities, pH variability may exceed one pH unit per day (Middelboe & Hansen, 2007; Saderne et al., 2013). These chemical fluctuations can be beneficial or detrimental to the physiological performance of the associated organisms living on the engineer species or in understory (Bergstrom et al., 2019; Cornwall et al., 2013; Garrard et al., 2014; Semesi et al., 2009). Experiencing these fluctuations can therefore modulate an organism's efficiency in coping with ongoing ocean global change such as ocean acidification (Falkenberg et al., 2021; Kapsenberg & Cyronak, 2019; Wahl et al., 2018). This has recently generated much interest in characterizing these chemical habitats and in assessing the responses of "associated species" (see Box 1).

3.4 | Ecosystems influenced by upstream engineer species

Water masses transformed by the intense metabolic activity of some dense populations of engineer species can be transported by advection to downstream adjacent ecosystems (Cyronak et al., 2018),

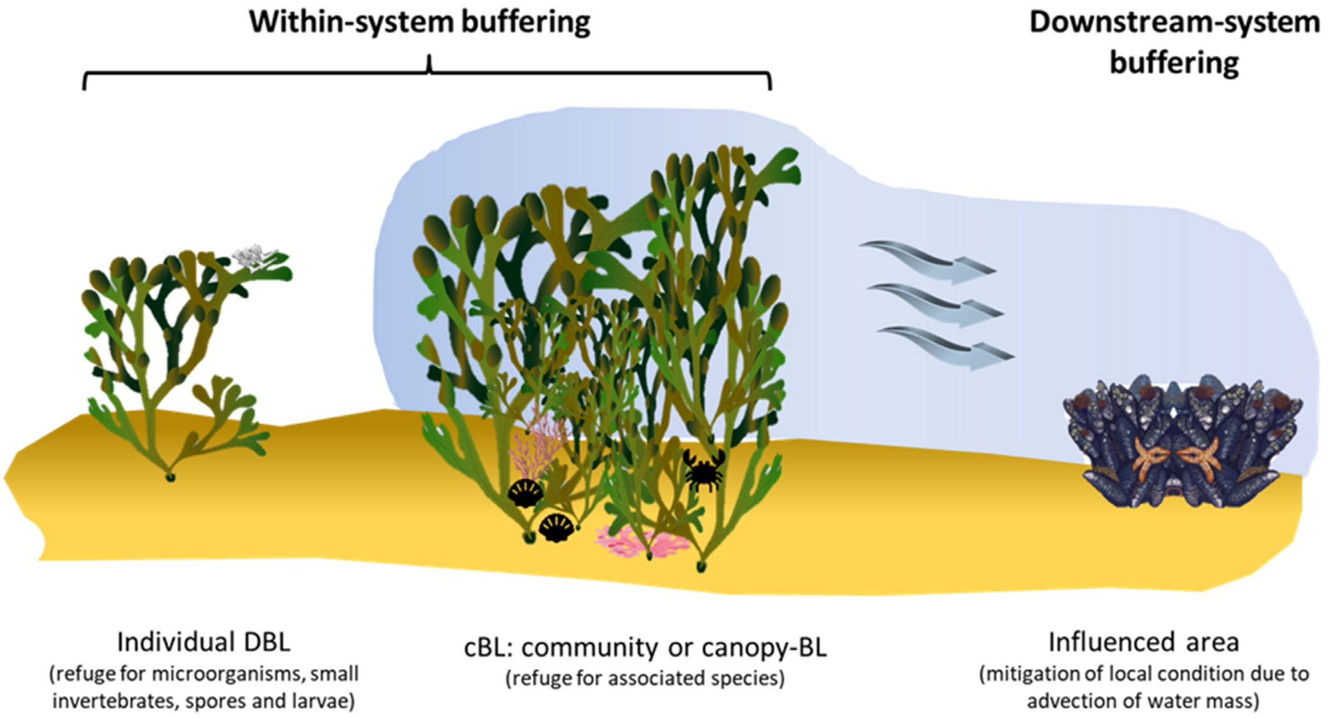

FIGURE 3 Refuge habitats created by engineer species. The interaction between hydrodynamics and biologically driven fluctuations creates chemical micro-habitats of sizes from μm to m, which can provide refuge in the context of global change (particularly ocean deoxygenation and acidification). The chemical conditions can be mitigated around the engineer organism (individual diffusive boundary layer, DBL and canopy or community boundary layer, cBL), also referenced to by Cyronak et al. (2018) as the within-system buffering action. The advection of water masses from main producers' communities to influenced areas located downstream, represent the downstream-system buffering (Cyronak et al., 2018), which could benefit other communities, yet largely depending on the water to biomass ratio

hereafter called influenced-areas (Figure 3; Box 1). This advective transport was shown to affect the local carbonate chemistry of influenced-areas (Krause-Jensen et al., 2015; Saderne et al., 2013), increasing for instance the seawater saturation state of carbonate and likely mitigating ocean acidification effects (Anthony et al., 2013; Unsworth et al., 2012). This phenomenon has been evidenced for ecosystems adjacent to seagrass meadows (Camp et al., 2016; Unsworth et al., 2012), seaweed beds (Delille et al., 2009; Krause-Jensen et al., 2015), coral reefs (James et al., 2019), and mangroves (Yates et al., 2014). Compared with boundary-layer chemical habitats, the local chemistry of influenced-areas is even more dependent on biomass to water ratios and water exchange as current speed and direction (Hirsh et al., 2020; Wahl et al., 2018). Slow flow reduces the exchange rate and dilution of a water body, which permits a higher amplitude in fluctuating variables. Conversely, fast currents result in much lower excursions from the mean (Frieder et al., 2012; Koweek et al., 2017).

In tropical ecosystems, models and in situ studies showed that the calcification of coral communities could be maintained or increased due to the biologically-driven increase of the mean pH provided by upstream macrophyte beds (Camp et al., 2016; Mongin et al., 2016; Unsworth et al., 2012). It has also been shown that dense oyster beds could modify the alkalinity of an entire bay, likely affecting influenced-areas adjacent to these mollusc beds (Waldbusser et al., 2013). In addition, the capacities of macrophytes in buffering the negative effects of hypoxic events and/or long-term ocean acidification on economically important shellfish (Ricart, Gaylord, et al., 2021; Young & Gobler, 2018) highlights a new role for commercial seaweeds in the context of an integrated multi-trophic aquaculture (Fernández et al., 2019; Troell et al., 2009). This ability of engineer species in shaping the local conditions for adjacent ecosystems is, nevertheless, often underestimated and requires more field studies (e.g. Hirsh et al., 2020; Murie & Bourdeau, 2020) and physical modelling (Mongin et al., 2016) to be better characterized.

4 | ROLES OF CHEMICAL HABITATS TO FACE OCEAN GLOBAL CHANGE (ACIDIFICATION AND DEOXYGENATION)

4.1 | Chemical habitats as refugia

Chemical habitats related to diffusion and community-boundary layers could act to buffer organisms against certain ocean global change-related stressors over time, creating 'refugia' (see Box 1) from unfavorable surrounding seawater conditions like reduced pH due to ocean acidification or hypoxia due to water deoxygenation (Bulleri et al., 2018; Falkenberg et al., 2021; Hurd, 2015; Laffoley & Baxter, 2019). The existence of refugia is primarily dependent on the local hydrodynamics as chemical habitats where fluctuations eclipse bulk seawater conditions can only be shaped when the water flow allows the build-up of boundary layers. Understanding the efficiency of chemical refugia in the context of ocean global change hence requires an excellent characterization of the spatiotemporal variations of local hydrodynamics. When flow conditions permit the formation of boundary layer habitats, the amplitude of chemical fluctuations within such areas can be greater than mean changes projected for the bulk seawater by the end of the century (Wahl et al., 2018). Hence chemical refugia can provide mitigation and temporal buffer, likely alleviating stress relative to conditions without fluctuations (Wahl et al., 2015).

The size of the chemical habitat has to be considered to fully assess its refuge capacity. Some authors suggest that refugia must be large enough to manage a small population (Kapsenberg & Cyronak, 2019; Morelli et al., 2016), while we consider that refugia associated with DBLs are also of importance to very small species (e.g. bryozoans) and some early life stages of larger species (e.g. mollusc larvae or macrophyte spores), which are critical for species persistence. Larger-scale community/canopy-boundary layer habitats can provide wider refugia allowing larger associated species to live, reproduce and interact within these chemical habitats.

4.2 | Ocean acidification refugia provided by primary producers

Biologically-driven processes creating refugia have recently become relevant in understanding species' responses to ocean acidification, focusing mainly on photosynthetic activity by macrophytes (Falkenberg et al., 2021; Hendriks et al., 2015; Hurd et al., 2011; Kapsenberg & Cyronak, 2019). The pH increase caused by photosynthesis during daytime can provide spatial and temporal refuge against the overall pH drop induced by long-term ocean acidification (Hurd, 2015; Krause-Jensen et al., 2015; Noisette & Hurd, 2018; Saderne et al., 2013; Silbiger et al., 2017). While a pH-increase through photosynthesis is limited to daylight, which ranges from hours to weeks at high latitudes (Duarte & Krause-Jensen, 2018; Krause-Jensen et al., 2016), nighttime respiration generally has a lower impact on pH (e.g. James et al., 2019; Ricart, Ward, et al., 2021). The net effect of macrophytes is, thus, an overall rise in the diel mean pH (Krause-Jensen et al., 2016; Wahl et al., 2018) and a reduction of the duration of low pH exposure (Ricart, Ward, et al., 2021). In addition, the range of pH fluctuations driven by macrophytes metabolism along diel cycles could be narrowed in a global change scenario. For instance, Noisette and Hurd (2018) showed that oxygen and pH fluctuations within the DBL of kelp blades would be less broad and shifted towards higher means under ocean acidification scenarios compared with current conditions.

Field studies in temperate and tropical ecosystems dominated by macrophytes have shown that the increase in pH was correlated to an increase in the carbonate saturation state (e.g. Koweek et al., 2017; Pacella et al., 2018; Semesi et al., 2009). Macrophytes could then mitigate the negative impacts of ocean acidification on marine calcifiers in their vicinity by providing buffer from corrosive conditions (Short et al., 2015; Silbiger & Sorte, 2018), as demonstrated on corals (Kleypas et al., 2011; Unsworth et al., 2012), molluscs (Young & Gobler, 2018) and coralline algae (Bergstrom et al., 2019; Cornwall et al., 2014; Short et al., 2015). These local positive effects of macrophyte communities against ocean acidification have been rarely modelled (Pacella et al., 2018) and studied in the field (Ricart, Ward, et al., 2021) and have to be considered with caution. Local natural pH variations have to be carefully characterized (Van Dam et al., 2021a, 2021b) to understand if this buffering effect might help associated species to endure stressful future pH shifts, as experimentally shown in seagrass communities (Cox et al., 2017; Guilini et al., 2017; Ricart, Gaylord, et al., 2021). For more details about the buffering effects of marine macrophytes, see Falkenberg and collaborators (2021) who reviewed the role of seagrass and seaweeds habitats as refugia from ocean acidification and their implementation in management plans. A list of case-studies reporting the effect of engineer species on the chemistry of their surroundings in the context of ocean acidification and deoxygenation is reported in Table 1.

4.3 | Deoxygenation refugia provided by primary producers

Oxygen enrichment as a result of photosynthesis by primary producers such as seaweeds (Irwin & Davenport, 2002, 2010), seagrass meadows (Koopmans et al., 2018; Saderne et al., 2015) and around corals (Shashar et al., 1993; Smith et al., 2013), could also provide refugia in the context of the ocean deoxygenation (Altieri et al., 2021; Keeling et al., 2010; Laffoley & Baxter, 2019). The net daytime increase in oxygen concentration may be beneficial for heterotrophs as it would increase the partial pressure of oxygen (pO_2). Increasing pO_2 facilitates gas exchanges and, thus, also decreases the energy consumption caused by anti-stress mechanisms (Ramajo et al., 2016). For some primary producers, this increase in oxygen level might cause an increase in photorespiration: high pO_2 may decrease the affinity of the Rubisco for carbon dioxide and, thus, reduce photosynthesis (Mass et al., 2010; Nishihara et al., 2015). Nevertheless, numerous coastal regions are predicted to face a future drop in oxygen levels and/or encounter upwelling events that regularly shoal deoxygenated waters (Grantham et al., 2004; Omstedt et al., 2014; Wei et al., 2019). In these regions, the net and, in particular, the daytime increase in oxygen concentration mediated by macrophytes may be particularly beneficial for heterotrophs and might provide important refugia. In tropical ecosystems, which face important deoxygenation episodes (Altieri et al., 2021), an improved understanding of the oxygen variation in boundary to canopy layer habitats could help to better understand coral responses to accelerating future deoxygenation (Hughes et al., 2020).

5 | POTENTIALS AND LIMITATIONS OF CHEMICAL REFUGIA

5.1 | Boundary layer fluctuations as an additional stress

The refuge capacity of boundary layer chemical habitats must be evaluated by balancing any benefits of periodic relief from environmental stress, with any potential deleterious effect due to intensifying exposures to harmful conditions (alternating phases of high stress and recovery; see figure 1 in Wahl et al., 2015). For instance, conditions around macrophytes can be improved compared with the surrounding bulk seawater during day (light) time but also become unfavorable at night (Cyronak et al., 2018; Koweek et al., 2017; Pacella et al., 2018). Even though daily net increases in pH and oxygen levels are recorded around macrophytes, often steep and strong changes over relatively short time scales may not always provide mitigation from mean stress but may challenge an organisms' capacity for physiological adjustments (Middelboe & Hansen, 2007; Wahl et al., 2018). These fluctuating conditions (see Figure 2b) may actually add an additional component to the stress portfolio of the environment, strongly driven by the amplitudes of fluctuations, but also their rates of change, in diurnal to weekly to seasonal patterns of shifts (Sabine, 2018; Wahl et al., 2016).

Intensity and duration of such deviations from the mean would, therefore, determine whether fluctuations alleviate or aggravate stress in boundary layer chemical habitats, relative to conditions without variability. Overall, fluctuation effects may be determined by different aspects: (i) Jensen's inequality, mathematically differentiating the impacts from variable versus stable environmental conditions (Ruel & Ayres, 1999), (ii) relaxation from stress might provide temporal release (refuge) from stress allowing physiological or community recovery (Wahl et al., 2016), and (iii) intense peak stress that might drive organisms to their limits, leading to selection, mortality, and/or detrimental population collapse (Wernberg et al., 2016). Typical performance curves in response to environmental variables such as temperature or oxygen concentration have mono-modal quadratic or modified Gaussian shapes (Angilletta, 2006; Woodin et al., 2013). Fluctuations may, therefore, enhance or decrease an organisms' performance depending on whether fluctuations are based within the ascending or the descending part of the curve (Ruel & Ayres, 1999). In the stress range of the environmental variables (outside the optimum), the net effect of the fluctuations depends on the position of the mean relative to the energetic break-even point, and the proportional time the variable resides below or above this point (Camp et al., 2016; Woodin et al., 2013). To understand the effects of fluctuating regimes on organisms living within chemical habitats, it is important to determine whether their biological responses are more dependent on the mean condition of exposure or the time they spend below a critical threshold (Sabine, 2018).

5.2 | Fluctuations can promote resistance to ocean global change

Recent reviews, out of the context of boundary layer chemical habitats, compiled the effects of fluctuations on the physiology of benthic organisms in the context of ocean global change (Boyd et al., 2016; Rivest et al., 2017). With respect to ocean acidification scenarios, pH fluctuations may improve survival (Hurd et al., 2011) or increase the growth rate of fleshy algae (Britton et al., 2016, 2019). These variable

TABLE 1 Case-studies illustrating the effects of engineer organisms in shaping the chemistry of their surrounding environment with specific reference to ocean acidification and/or deoxygenation context. Environmental parameters related to ocean acidification and/or deoxygenation mitigation or worsening are reported (Ω, calcium carbonate saturation state; DIC, dissolved inorganic carbon; DO: dissolved oxygen; pCO_2, carbon dioxide partial pressure; TA, total alkalinity). References in italic specifically refer to studies mentioning deoxygenation

Ecosystem type	Engineer species	References	Parameters investigated
Kelp forest	*Macrocystis pyrifera* and *Nereocystis luetkeana*	Delille et al. (2009)	DIC, pCO_2
		Frieder et al. (2012)	DO, pH
		Hirsh et al. (2020)	DO, pH, pCO_2, TA, Ω
		Murie and Bourdeau (2020)	DO, pH, DIC, pCO_2, Ω
	Saccharina latissima and *Agarum clathratum*	Krause-Jensen et al. (2016)	pH, pCO_2
	Brown algae	Krause-Jensen et al. (2015)	DO, pH, Ω
Seaweed bed	*Arthrocardia corymbosa*	Cornwall et al. (2014)	pH
	Carpophyllum maschalocarpum	Cornwall et al. (2015)	DO, pH
	Seaweed farm	Mongin et al. (2016)	Ω
Seagrass meadow	*Zostera marina* and *Fucus vesiculosus* or *F. serratus*	Buapet et al., 2013)	pH, DIC, pCO_2, Ω
		Cyronak et al. (2018)	DO, pH, DIC, TA, Ω
		Greiner et al. (2018)	pH, Ω
		Pacella et al. (2018)	pH, pCO_2, Ω
		Ricart, Gaylord, et al. (2021)	pH, TA, Ω
		Ricart, Ward, et al. (2021)	pH
		Saderne et al. (2015)	DO, pH, DIC, pCO_2, Ω
		Saderne et al. (2013)	DO, pH, DIC, pCO_2, Ω
		Wahl et al. (2018)	DO, pH, pCO_2, Ω
	Halodule wrightii	Bergstrom et al. (2019)	pH, DIC, pCO_2, Ω
	Posidonia oceanica	Cox et al. (2017)	pH, pCO_2, Ω
		Garrard et al. (2014)	pH, pCO_2, TA, Ω
		Koopmans et al. (2018)	DO
	Thalassia species	Camp et al. (2016)	pH, TA, DIC, pCO_2, Ω
		Cyronak et al. (2018)	DO, pH, DIC, TA, Ω
		James et al. (2019)	pH
		Semesi et al. (2009)	pH, DIC, pCO_2, Ω
	Undefined	*Altieri et al. (2021)*	DO
		Unsworth et al. (2012)	pH, DIC, TA, Ω
Macrophyte DBL	*Posidonia oceanica*	Guilini et al. (2017)	DO, pH, DIC, TA, Ω
	Ecklonia radiata	Noisette and Hurd (2018)	DO, pH
Mangrove		*Altieri et al. (2021)*	DO
		Camp et al. (2016)	pH, TA, DIC, pCO_2, Ω
		García-Troche et al. (2021)	pH, TA, DIC, pCO_2, Ω
		Sippo et al. (2016)	DO, pH, DIC, pCO_2, TA
		Yates et al. (2014)	DO, pH, DIC, pCO_2, TA, Ω
Tidal pool		Duarte and Krause-Jensen (2018)	DO, pH, pCO_2, TA
		Krause-Jensen et al. (2015)	DO, pH, Ω
		Silbiger and Sorte (2018)	DO, pH, DIC, TA
Coral reef		*Altieri et al. (2021)*	DO
		Anthony et al. (2013)	Ω
		Hughes et al. (2020)	DO
		Kleypas et al. (2011)	DIC, pCO_2, TA, Ω
		Silbiger et al. (2017)	pH, DIC, TA, Ω
		Smith et al. (2013)	DO, pH
Mollusc bed	*Mytilus californicus*	Ninokawa et al. (2020)	DO, pH, TA
	Crassostrea virginica	Waldbusser et al. (2013)	TA

regimes might also lead to an increased resilience of calcareous species because of an acclimation to a wider pH range than normally experienced (Semesi et al., 2009; Short et al., 2015). In the context of fluctuations based on a diel light cycle, it has been observed that species might develop mechanisms to endure phases of stress and relaxation by shifting their metabolic rates (Price et al., 2012). A study from

Wahl et al. (2018) has suggested that mussels were able to shift the majority of their costly physiological processes such as calcification to day times, when the surrounding chemical conditions were the most favorable, driven by the biological activity of the habitat-forming bladder wrack (*Fucus vesiculosus*).

Thus, chemical habitats created by biologically driven fluctuations may alter the intensity and direction of the effects caused by superimposed ocean global change like ocean acidification and deoxygenation (Gunderson et al., 2016). It could in the long run facilitate a "hardening" of populations throughout processes of individual and transgenerational acclimation and adaptation (Bulleri et al., 2018; Eriander et al., 2016; Pansch et al., 2014; Rivest et al., 2017). Fluctuating regimes may select for physiological generalists' that can endure a wide range of environmental variables through acclimatization processes, that is, the change in physiological performances in response to environmental changes driven by phenotypic plasticity (Kroeker et al., 2020). In fact, organisms from environments characterized by greater heterogeneity have more phenotypic plasticity, that is, an ability to express different phenotypes based on the same genotype (Boyd et al., 2016; Pansch et al., 2014). However, the transient transgressions of tolerance thresholds followed by relaxation periods may not only selectively favor high phenotypic plasticity but may also select for more robust genotypes (Frieder et al., 2014; Melzner et al., 2009). Populations locally adapted to highly fluctuating environmental conditions, like in boundary-layer chemical habitats, might help coastal ecosystems in enduring or tolerating ocean global changes via the conservation and the migration of resistant genotypes (Rivest et al., 2017; Thomsen et al., 2017).

5.3 | Can heterotrophs provide refugia against ocean global changes?

Although photosynthetic organisms are now recognized to provide potential refugia in the context of ocean acidification and deoxygenation, the role of heterotroph engineer species is barely studied (Table 1). Their contribution to the local raise of $p\mathrm{CO}_2$ is even considered detrimental (Ninokawa et al., 2020). However, changes in carbonate chemistry driven by dense populations of calcareous heterotrophs such as bivalves and reef-forming corals may induce specific conditions around them such as alkalinity regeneration (Waldbusser et al., 2011). These local changes in chemistry can be perceived as favorable cues for larval recruitment in zones submitted to intense pH decrease or drastic changes in alkalinity (Green et al., 2013; Waldbusser et al., 2013). In addition, shell debris enrichment was shown to increase local pH and aragonite saturation state likely providing a chemical refuge that would promote a better recruitment of mollusc larvae (Greiner et al., 2018). Nevertheless, measurements of vertical gradients within and above mussel beds over a range of several flow velocities showed that reduction in pH and oxygen concentration inside dense mussel beds may negatively impact the species associated (Ninokawa et al., 2020). This latest study counteracts the few previous outcomes supporting that heterotroph engineer species may provide refugia to face ocean global change. Better exploring the frequency and the amplitude of the chemical fluctuations generated by invertebrate reefs and their beneficial and deleterious effects for the associated species is, therefore, an avenue worth to be investigated in the future.

6 | CONCLUSION

In coastal environments, local abiotic conditions are strongly shaped by the metabolism of benthic communities, which themselves are regulated by the conditions of the surrounding environment based on small-scale (diurnal to seasonal) cycles and on global mean changes (temperature, light, salinity, carbonate chemistry). Variations in these abiotic conditions are under the influence of hydrodynamics, which directly control biological responses and shape the rate and amplitude of abiotic fluctuations induced by biological activity. In this review, we emphasized a lack of knowledge concerning the effects of hydrodynamics in coastal benthic environments. We also identified the role of chemical habitats engineered by different species in the context of ocean global change. These specific chemical habitats may mitigate the negative effects caused by global changes by providing temporal and/or spatial refugia, modulating exposure to harmful ocean acidification and deoxygenation conditions. As highly fluctuating habitats, however, they could also be detrimental and/or constitute selective arenas enhancing adaptive capacities (i.e. concept of adaptive refugia: Kapsenberg & Cyronak, 2019) and facilitating the hardening of some populations.

In the context of ocean global change, there are still major gaps of knowledge which prevent a better understanding of how hydrodynamics can shape chemical habitats and impact coastal benthic system functioning. Hydrodynamics at a relevant scale for chemical habitats description remain poorly characterized (Kregting et al., 2021). Biologically-driven fluctuations are highly dependent on abiotic drivers and can change drastically according to the season (Falkenberg et al., 2021): seasonality of the variations is rarely assessed. The spatial extent of chemical refugia in situ is complex to assess (Ricart, Gaylord, et al., 2021) and often prevented by technical and logistical limitations. To overcome these identified gaps and to provide accurate data for better understanding the future of coastal benthic ecosystems, we advise the scientific community to pay attention to the following main points:

1. Accurately report the intensity and type of hydrodynamics (e.g. laminar vs. turbulent, unidirectional, oscillatory, wave-induced) in an experiment or in a field study, as water motion controls individuals' physiology and might be partly accountable for the observed wide variations in responses of organisms to ocean global change.
2. Assess the effects of hydrodynamics on the biological responses of benthic organisms and communities using in situ open water determination of metabolism and seawater chemistry (e.g. James et al., 2019; Takeshita et al., 2016) or experimental flumes in the laboratory (e.g. Carpenter et al., 2018), and in particular under different ocean global change scenarios (e.g. Comeau et al., 2019; Noisette & Hurd, 2018).

3. Better characterize the temporal and spatial abiotic fluctuations occurring in the field (Cyronak et al., 2018) and incorporate them into experimental designs of studies addressing the effect of ocean global change. Especially for perennial species, more attention should be paid to seasonal variations because both environmental baselines (i.e. means) and their distance to specific optima change with seasons (Ricart, Ward, et al., 2021; Wahl et al., 2021). These measurements require new technical developments in autonomous loggers and infrastructure (Pansch & Hiebenthal, 2019), as well as publication of best practice guides to standardize procedures (Lorenzoni et al., 2017).
4. Dedicate more attention to the chemical habitats resulting from the interaction of flow and metabolism (e.g. James et al., 2019) in order to better characterize the magnitude of buffering/amplification, the area impacted, and the frequency of the fluctuations generated.

Addressing these different points more carefully will be key to understand the complicated feedback loops within coastal benthic communities, often dominated by engineer species with high metabolic rates, under ocean global change. It could also permit to elucidate whether or not biologically-driven chemical habitats (boundary-layer associated and influenced areas) can fulfill the role of refugia or merely provide additional stress for organisms that leads to strong selection pressure in the ocean of tomorrow.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

ORCID

Fanny Noisette https://orcid.org/0000-0002-9672-2870
Christian Pansch https://orcid.org/0000-0001-8442-4502
Marlene Wall https://orcid.org/0000-0003-2885-1301
Martin Wahl https://orcid.org/0000-0001-8703-3857
Catriona L. Hurd https://orcid.org/0000-0001-9965-4917

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