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# Co-culture in marine farms: macroalgae can act as chemical refuge for shell-forming molluscs under an ocean acidification scenario

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## ABSTRACT

With ongoing climate change, aquaculture faces environmental challenges similar to those of natural ecosystems. These include increasing stress for calcifying species, e.g. macroalgae and shellfish. In this context, ocean acidification (OA) has the potential to affect important socioeconomic activities, including shellfish aquaculture, due to changes in the seawater carbonate system. However, coastal environments are characterised by strong diurnal pH fluctuations associated with the metabolic activity of macroalgae; that is, photosynthesis and respiration. This suggests that calcifying organisms that inhabit these ecosystems are adapted to this fluctuating pH environment. Macrophyte-dominated environments may have the potential to act as an OA buffering system in the form of a photosynthetic footprint, by reducing excess of CO<sub>2</sub> and increasing the seawater pH and  $\Omega_{\text{arg}}$ . This can support calcification and other threatened physiological processes of calcifying organisms under a reduced pH environment. Because this footprint is supportive beyond the macroalgal canopy spatial area, this chemical refuge mechanism can be applied to support shellfish aquaculture, e.g. mussels. However, this approach should be tested in commercial shellfish farms to determine critical aspects of implementation. This includes critical factors such as target species and productivity rates. The degree of OA buffering capacity caused by the metabolic activity of macroalgae might depend on community structure and hydrodynamic conditions, creating site-specific responses. This concept might aid the development of future adaptive strategies, supporting marine ecological planning for the mussel aquaculture industry in Chile.

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## INTRODUCTION

The primary driver of climate change, atmospheric CO<sub>2</sub> emissions, is producing dramatic variations in sea surface temperature and in the ocean carbonate system (Intergovernmental Panel on Climate Change 2013). The main effects of ongoing climate change include alterations in biodiversity, shifts in marine ecosystem regimes, increase in diseases, and a reduction of ecosystem services (Kroeker *et al.* 2013; Krumhansl *et al.* 2016; Méléder *et al.* 2010; Müller *et al.* 2009). Climate change may be particularly critical for food ecosystems sustained by coastal ocean processes with subsequent effects on social economy, human health and well-being, and human services to nature (Costa-Pierce 2016; Willett *et al.* 2019). Both wild fisheries and aquaculture, as part of the ocean food system, represent a major contribution to food security and adequate nutrition for the exponentially growing global human population (Food and Agriculture Organization [FAO 2016]; Harvey *et al.* 2017).

After China, Chile is the second largest global producer of mussels, producing 302,000 tonnes in 2018 (SeafoodSource 2019). Production increased by 20% during the 2006–2016 period, contributing approximately 1.2 million tonnes to global production (Servicio Nacional de Pesca y Acuicultura [SERNAPESCA] 2018). In Chile, monocultures of fish and Molluscs have become the main resources for aquaculture,

with a limited production of seaweeds (SERNAPESCA 2018). Therefore, the greatest challenges for Chilean aquaculture are product diversification and improvement of aquaculture techniques (Buschmann *et al.* 1996a, 2008a, 2013). Facing the negative effects of environmental drivers associated with human activities, e.g. climate change on marine ecosystems, aquaculture diversification may become critical for sustaining production (Harvey *et al.* 2017; Troell 2009).

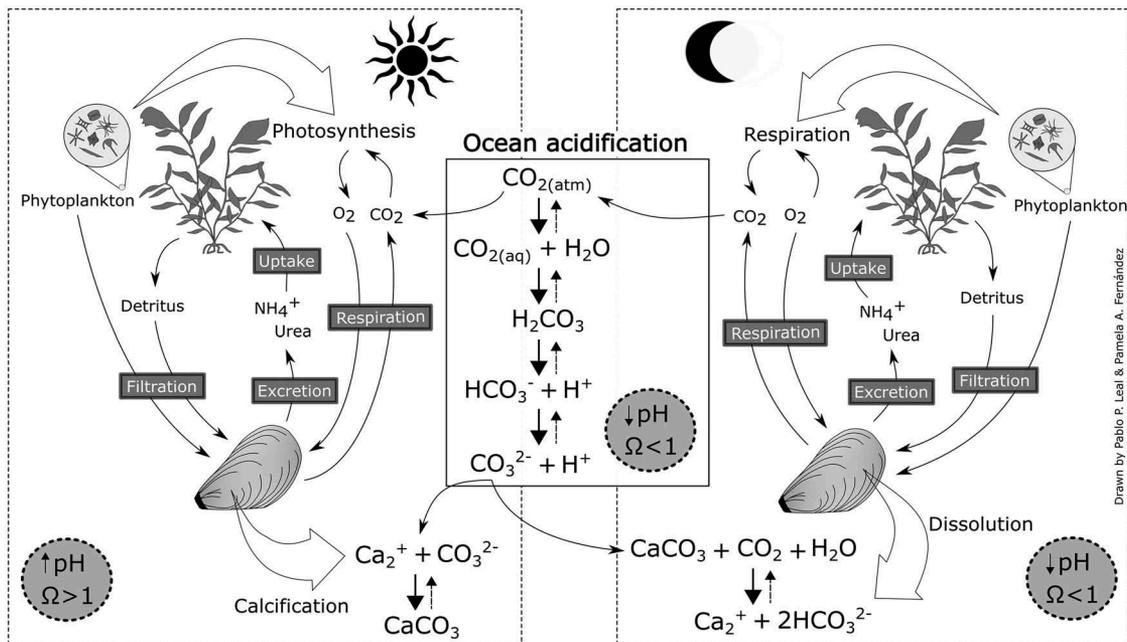
Earth's oceans absorb more than one third of global anthropogenic CO<sub>2</sub> emissions, altering seawater carbonate chemistry and leading to a process known as ocean acidification (OA; Resplandy *et al.* 2018). OA involves a decrease in pH, a reduction in the concentration of carbonate ions (CO<sub>3</sub><sup>2-</sup>), and a decline of the saturation state ( $\Omega$ ) of calcium carbonate (CaCO<sub>3</sub>) mineral forms, i.e. calcite and aragonite (Caldeira & Wickett 2003). These chemical changes in seawater may effect calcifying marine organisms, in particular, corals, coralline macroalgae and shell-forming molluscs (Harley *et al.* 2012; Koch *et al.* 2013). Impacts of OA are particularly strong during the early life stages of marine calcifying species. This has been observed with spores of macroalgae and free-living planktonic larvae of benthic invertebrates, altering biodiversity and productivity of coastal ecosystems (Chen *et al.* 2019; Frieder *et al.* 2014; Leal *et al.* 2018; Przeslawski *et al.* 2015).

Many benthic invertebrates, including calcifying organisms, play an important ecological role in marine ecosystems but are also directly used by humans as fishery resources (Onitsuka et al. 2018). World shellfish production – for example, oysters, cockles, clams, scallops, abalone and mytilids – has reached approximately 16 million tonnes (FAO 2016). Therefore, the expected OA impacts on shell-forming organisms may become a global social–ecological problem (Forsyth et al. 2008). This is particularly relevant for Chilean aquaculture where shellfish molluscs represent 28% of national production (SERNAPESCA 2018). Significantly, Chile’s main cultivated species, the blue mussel (*Mytilus chilensis*), accounts for approximately 15% of global cultivated production (FAO 2016). Moreover, *M. chilensis* and related species (*Choromytilus chorus*, *Aulacomya ater*) play important ecological roles in marine ecosystems, providing biogenic habitats for benthic ecosystems and promoting the recycling of organic matter (Brattström & Johannsen 1983; Häussermann & Försterra 2009). Therefore, strategies to mitigate the negative impacts of OA on ecologically and economically important shell-forming organisms are urgently needed.

The reduction of  $\text{CO}_3^{2-}$  concentration under OA conditions (Fig. 1) increases the vulnerability of early life stages of bivalves. OA affects metabolic energy budgets, impairs neurological function, alters behaviour, and causes shell dissolution, all leading to a reduction in growth and survivorship (Frieder et al. 2014; Green et al. 2013; Kurihara 2008; Waldbusser et al. 2015). In bivalves, calcification is the biochemical production of calcified shells to support and protect their soft bodies (Gazeau et al. 2013; Marin et al. 2000). Adult bivalve shells are typically formed by aragonite and/or calcite, which are sensitive to seawater pH

(Doney et al. 2009; Gazeau et al. 2013; Roleda et al. 2012). In acidified waters, the  $\Omega_{\text{cal}}$  and  $\Omega_{\text{arg}}$  are reduced to below 1.0 because  $\text{CO}_3^{2-}$  concentration also declines (Caldeira & Wickett 2003; Doney et al. 2009). This condition makes the production and maintenance of shell or skeletal structures more difficult because shell production is outcompeted by shell dissolution (Fig. 1). As a result, more energy has to be allocated to support calcification, leading to a potential reduction in other physiological processes such as growth and reproduction (Gazeau et al. 2013; Hendriks et al. 2015; Roleda et al. 2012).

Primary producers like macroalgae have a large capacity to fix  $\text{CO}_2$  via photosynthesis and take up dissolved inorganic nutrients such as phosphorus and nitrogen (Chung et al. 2013; Harrison & Hurd 2001; Hurd et al. 2014). Their growth is also supported by other essential minerals and trace metals (Mišurcová 2012). Therefore, it is not surprising that, due to their large capacity to take up dissolved inorganic nutrients, they have been used in integrated multitrophic aquaculture (IMTA). IMTA combines the cultivation of finfish, filter-feeding shellfish and macroalgae, with the main objective of mitigating the metabolic waste generated by the main cultivated species (Roleda & Hurd 2019; Troell et al. 2009; Turan & Neori 2010). This concept has been extensively studied and developed in several countries, including the United States, China, Canada, and Chile (Abreu et al. 2009; Buschmann et al. 2008b; Chopin et al. 2008, 2012; Fang et al. 2016; Mao et al. 2009; Troell et al. 2009, 2014). However, due to the associated cost of finfish cultivation and/or environmental uncertainty of breeding finfish offshore, IMTA has moved towards a co-culture concept, combining only shellfish and



**Fig. 1.** Conceptual diagram of possible interactions between macroalgae and mussels in co-culture under OA conditions. Seawater pH and aragonite saturation state ( $\Omega_{\text{arg}}$ ) are reduced to unfavourable conditions for calcification. During daytime, macroalgal photosynthesis increases pH in surrounding seawater, counteracting OA effects on calcification. However, during nighttime, macroalgae and mussels release  $\text{CO}_2$  during respiration, contributing to OA conditions. This last condition can be different if appropriate culture proportions are previously determined in, for example, laboratory experiments. Moreover, photosynthetic  $\text{O}_2$  released during daytime and macroalgal detritus can benefit mussels metabolism, and excretion of  $\text{NH}_4^+$ , urea and  $\text{CO}_2$  can support macroalgal growth and photosynthesis. Mussels can also help control phytoplankton blooms by filtration. Note: arrow size indicates direction in which the reaction is favoured (nondashed, negative; dashed; positive).

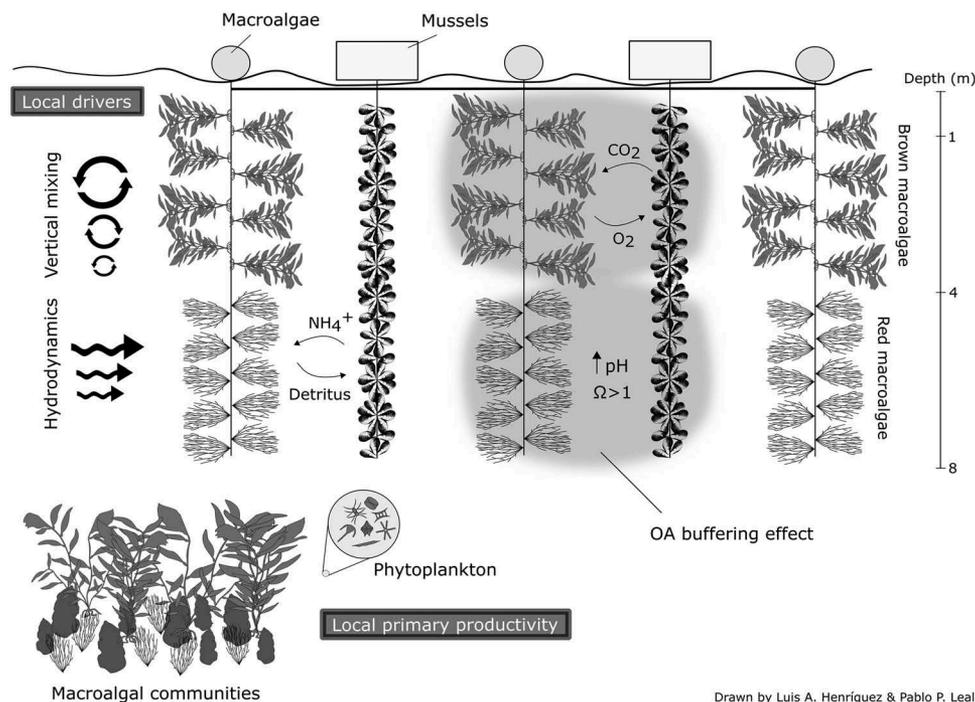
seaweeds (Ladner *et al.* 2018). It has become apparent that the co-culture of these species has important benefits in coastal ecosystems. They absorb high amounts of carbon (C) via photosynthesis and by filter feeding on particulate organic matter (Han *et al.* 2017; Tang *et al.* 2011). Furthermore, the co-culture of shellfish and macroalgae could provide a natural mechanism to buffer the negative impacts of OA on marine ecosystems (Figs 1, 2). This can enhance the early development and growth of wild and farmed shellfish and might also increase the potential for large-scale macroalgal cultivation. Today, this represents only 25% of global aquaculture; however, it is concentrated mainly in China (Chung *et al.* 2013; Fang *et al.* 2016; Xiao *et al.* 2017).

### Macrophytes as OA refuges for calcifying marine organisms

The concept of chemical refuge has been raised in response to major concerns about the negative effects of OA on calcifying invertebrates (Buapet *et al.* 2013; Greiner *et al.* 2018; Groner *et al.* 2018; Hendriks 2014; Krause-Jensen *et al.* 2016; Unsworth *et al.* 2012). In coastal ecosystems, macroalgal beds are characterised by intense metabolic activity capable of modifying their surrounding environment (Cornwall *et al.* 2013, 2014; Dayton 1985; Hofmann *et al.* 2011; Hurd 2015). For example, during daytime, macroalgae remove CO<sub>2</sub> by photosynthesis from the proximate seawater, increasing the pH of surrounding seawater up to 8.8. This can produce favourable conditions for shellfish calcification (i.e.  $\Omega > 1$ ; Fig. 1; Caldeira & Wickett

2003; Doney *et al.* 2009). During the night, respiration releases CO<sub>2</sub> to the external environment (Fig. 1), which in turn can reduce surrounding seawater pH to 7.8 (Cornwall *et al.* 2013; Hofmann *et al.* 2011). Other studies have indicated that reduced pH during the night within macrophyte assemblages can have negative effects on bivalve calcification (Saderne *et al.* 2015). Hendriks *et al.* (2015) measured a beneficial interaction between these organisms in both natural and controlled environments. For example, under experimental conditions, semidiurnal variations of pH ameliorate the negative effect of static reduced pH on the development of early life stages of mytilid and coral species. This shows that even a short exposure to higher pH might help calcifying organisms tolerate OA conditions (Enochs *et al.* 2018; Frieder *et al.* 2014). Consequently, it has been suggested that calcifying marine organisms living in fluctuating coastal environments have evolved a wide range of mechanisms to cope better with changing pH. These include pH upregulation in extracellular fluids and synchronisation of the calcification window for the most productive hours of the day, when CO<sub>2</sub> is removed via photosynthesis (Hendriks *et al.* 2015; McCulloch *et al.* 2012).

However, field observations have shown contrasting effects of natural assemblages of macrophytes on calcification rates of calcifying organisms. Meadows of the seagrass *Zostera marina* Linnaeus can enhance calcification of the calcareous red alga *Hydrolithon* sp. (Semesi *et al.* 2009). In contrast, beds of the brown macroalga *Padina pavonica* (Linnaeus) Thivy and meadows of *Z. marina* were unable to prevent adverse effects of



Drawn by Luis A. Henríquez & Pablo P. Leal

**Fig. 2.** Schematic representation of co-culture of mussels and macroalgae and its possible relationship with local environment. In this co-culture system, mussels and macroalgae are alternately placed to take advantage of their respective metabolic products. For example, excretion of NH<sub>4</sub><sup>+</sup> and urea by mussels can be used by macroalgae and macroalgal detritus may feed mussels. OA buffering refuge created by macroalgal photosynthesis may benefit calcification of proximate cultured mussels. However, these interactions between co-cultured organisms can be affected by inherent species' production rates and local drivers such hydrodynamics and vertical mixing.

acidification on epiphytic foraminifera and mussels, respectively (Martin *et al.* 2008; Pettit *et al.* 2015; Saderne *et al.* 2015). To date, only one study has investigated the effects of macrophyte presence close to shellfish cultures and how their OA buffering capacity can support calcification (Greiner *et al.* 2018). This study indicated that the presence of macrophytes does not increase pH or  $\Omega_{\text{arg}}$ , suggesting that this might not be the best strategy to improve carbonate seawater chemistry near clam beds. These contradictory examples on the possible OA chemical refuge for calcifying organisms suggest that further research is needed to determine whether photosynthetic organisms can consistently create a favourable environment for calcification.

The degree of OA buffering capacity might depend on the structure of macrophyte communities and hydrodynamic conditions. This would mean site-specific responses (Comeau & Cornwall 2017; Greiner *et al.* 2018). In a habitat formed by high biomass such as macroalgae or seagrasses, seawater pH can reach optimal values for calcification of associated organisms (Cornwall *et al.* 2013; Pettit *et al.* 2015; Saderne *et al.* 2015). Reciprocally, in natural environments, shellfish excrete  $\text{NH}_4^+$  and urea, which favour growth of macroalgae (Chung *et al.* 2013; Duarte *et al.* 2017). Moreover, shellfish respiration releasing  $\text{CO}_2$  may benefit macroalgal photosynthesis but also reduce seawater pH, which can be detrimental for calcification. Therefore, because metabolic rates are species specific, it is necessary to determine the optimal ratio between the two cultivated species to obtain an efficient utilisation of  $\text{CO}_2$  (uptake) and the extent of the buffering OA effect. Although the introduction of macroalgae near shellfish culture might be a good strategy to mitigate negative impacts of OA on economically important bivalve species such as mussels (Billé *et al.* 2013; Greiner *et al.* 2018; Hendriks *et al.* 2015), this needs to be investigated under laboratory and large-scale field conditions.

Strategies to utilise inorganic carbon (Ci) such as  $\text{CO}_2$  and  $\text{HCO}_3^-$  from seawater to support photosynthesis vary between species. These strategies include carbon concentrating mechanisms (CCMs; Raven *et al.* 2012). Macroalgae that depend on purely diffusive entry of  $\text{CO}_2$  through the plasma membrane (also known as non-CCM species) are thought to benefit under an OA scenario, by increasing their photosynthesis and growth (Cornwall *et al.* 2017). Macroalgae with a CCM (CCM species) have developed different mechanisms to use  $\text{HCO}_3^-$  via external dehydration mediated by the enzyme carbonic anhydrase and/or active uptake through an ATPase pump or anion port. This is predicted to show a neutral or positive response depending on enzyme affinity and mechanisms to use  $\text{HCO}_3^-$  (Fernández *et al.* 2014; Hepburn *et al.* 2011). Similar to the non-CCM species, CCM species with low Ci affinity but high capacity to down-regulate their CCMs may also benefit under elevated  $\text{CO}_2$ . However, CCM species with high Ci affinity but lower capacity to regulate their CCMs may not respond to subsequent changes in  $\text{CO}_2$  (Cornwall *et al.* 2017; Hepburn *et al.* 2011). Experimental surveys have determined that > 50% of red macroalgae are non-CCM and that > 80% of brown and green macroalgae are CCM (Cornwall *et al.* 2015; Hepburn *et al.* 2011). Therefore, we could expect that macroalgae that benefit from elevated  $\text{CO}_2$  via increased Ci availability to

support photosynthesis would have a higher capacity to increase seawater pH and modify seawater carbonate chemistry in their surrounding environment. This may be beneficial for cultivating calcifying organisms under an OA scenario.

The Chilean coast is characterised by wide fluctuations in pH (pulses of high  $\text{CO}_2$  and low pH) associated with upwelling events (Torres *et al.* 2011) and influenced by input of freshwater due to river discharges, generating estuarine systems (Häussermann & Försterra 2009; Pantoja *et al.* 2011; Silva & Vargas 2014; Vargas *et al.* 2016). Estuarine waters are characterised by low alkalinity, pH and carbonate ions (Duarte *et al.* 2013; Waldbusser & Salisbury 2014). These conditions might result in low  $\Omega_{\text{arg}}$ , affecting calcifying organisms that inhabit these coastal systems. In Chile, aquaculture of *M. chilensis* occurs in both coastal and estuarine systems and, hence, is naturally exposed to a fluctuating pH environment, ranging from 7.40 in estuarine areas to 8.10 in areas not influenced by freshwater (Duarte *et al.* 2015). This is important because in environments with naturally reduced pH – for example, estuarine systems – the negative effects of OA may be exacerbated (Cai *et al.* 2011). In addition, the negative effects of OA on physiological responses – that is, growth – of *M. chilensis* suggest that OA might have important consequences on mussel aquaculture in Chile (Duarte *et al.* 2014; Navarro *et al.* 2013, 2016). Nevertheless, intraspecific variability may also be found (Duarte *et al.* 2015). Therefore, in this context, in ecosystems such as Chilean estuaries, the introduction of macroalgae near or within shellfish farms may ameliorate the negative impact of OA (Fig. 3).

### The need for implementing shellfish–macroalgae co-culturing: Towards OA–IMTA aquaculture

The most immediate challenge for the implementation of long-term sustainable integrated aquaculture is preventing environmental impacts. This is possible through efficient utilisation of particulate and dissolved metabolic waste such as N and P generated by the cultivated species (Fang *et al.* 2016; Granada *et al.* 2016; Troell *et al.* 2009). However, the need for carbon fixation has become increasingly important given the increases in  $\text{CO}_2$  concentration and because of the capacity of coastal ecosystems to sequester carbon (Billé *et al.* 2013; Laffoley & Grimsditch 2009). Accordingly, management of coastal carbon by aquaculture could ameliorate the global climate crisis and address adverse scenarios for shellfish production. In this sense, defining an optimal culture design is required to ensure efficient recycling of byproducts in multi-trophic systems; that is, IMTA practice. In addition, it will act as a  $\text{CO}_2$  sink and maximise the seaweed OA buffering effect (Fig. 3). Experience gained from experiments, such as small-scale IMTA operations under controlled conditions, will be instrumental for realising OA strategy mitigation for farmed shellfish. In this context, site- and species-specific responses in different physical conditions are equally relevant to improving biomass production in co-culture farms. These aims may be co-ordinated with successful commercial IMTA systems mainly from the coasts of Canada and China, where co-cultivation of salmon, blue mussel, abalone, scallops and



**Fig. 3.** Mussel culturing sleeve from southern Chile (Auchac, Chiloé Island). Macroalgal species naturally recruit on cultured mussels. Note presence of *M. pyrifera* at the upper part of the sleeve; whereas, red macroalgae appear more frequent towards the end of the sleeve.

macroalgae have both ecological and economic benefits (Granada *et al.* 2016; Ridler *et al.* 2007; Troell 2009).

Optimal co-culturing proportions between macroalgae and bivalves as well as knowledge of the best harvest period for each cultivated species (seasonal variability) need to be considered to realise synergistic growth effects (Ladner *et al.* 2018). Han *et al.* (2017) suggested that a co-culturing ratio *c.* 4:1 between *Crassostrea angulata* and *Gracilaria lemaneiformis* (Bory) Greville results in efficient utilisation of dissolved inorganic carbon by *G. lemaneiformis*. Han *et al.* (2017) showed that a significant increase of pH favoured calcification of *C. angulata* and enhanced the local CO<sub>2</sub> sink. This ratio was comparable to those reported by Mao *et al.* (2009) and Ajjabi *et al.* (2018), who found that a bivalve:macroalgae culturing ratio of *c.* 3:1 was advisable for more efficient NH<sub>4</sub><sup>+</sup> and P uptake for seaweed growth. These results

suggest that at large scales, a substantial OA buffering environment is possible, while maintaining optimal nutrient removal and growth benefits.

Another positive bivalve–macroalgal trophic relationship is algal detritus as a source of C for bivalves (Peterson *et al.* 1984; Wiedemeyer & Schwamborn 1996). In an IMTA system, Xu *et al.* (2016) established, via the carbon isotope method, that 14%–42% of C in the scallop *Chlamys farreri* was obtained from the kelp *Saccharina japonica* (Areschoug) C.E.Lane, C.Mayes, Druehl & G.W.Saunders. This enhancement of the food supply may be beneficial for growth under a reduced pH environment by allowing for the allocation of more energy resources for calcification (Hendriks *et al.* 2015). These relationships are tied to complex interactions within the environment (Chopin *et al.* 2008; Fang *et al.* 2016; Newell 2007) and to the physiological responses of each species. These can be modulated by factors such as light, stocking density, water depth, water flow and renewal rate (Buschmann *et al.* 1996b; Huo *et al.* 2012; Mao *et al.* 2009). This should be investigated in the context of the OA buffering effect by macroalgae.

Prevailing hydrodynamic regimes and vertical mixing may be critical for the design of an effective cultivation layout. Studies on the seagrass *Posidonia oceanica* (Linnaeus) Delile indicated that the footprint of the OA buffering effect can be detected approximately 10 m from the meadow boundary. Furthermore, mussel farms tend to reduce current speeds, which affects water residence times (Hendriks *et al.* 2014; Keeley *et al.* 2009). This may accentuate the effects of the macroalgal OA buffering effect within the limit of the farm (Fig. 3). However, reduced current speed might affect macroalgal nutrient uptake via increasing the diffusion boundary layer (Hurd 2000). In turn, bivalves and associated fauna (i.e. from fouling) release NH<sub>4</sub><sup>+</sup>, faeces and pseudofaeces directly into the water column (Coen *et al.* 2007; Dumbauld *et al.* 2009; Ferriss *et al.* 2016; Keeley *et al.* 2009), increasing nutrient concentration in the seawater. This counteracts the effects of slow nutrient transport across a thicker diffusion boundary layer (Hurd 2000). However, large-scale co-culturing of shellfish–macroalgae in a relatively static system may promote accumulation of faeces and pseudofaeces on macroalgal thalli (Newell 2007), affecting physiological processes such as photosynthesis. For example, Jiang *et al.* (2015) showed that excess suspended particulate matter (e.g. < 63 µm grain size) reduced the viability of microscopic stages of foliose and crustose coralline algae by reducing their photosynthetic efficiency (Airoldi 2003; Harrington *et al.* 2005). In addition, biodeposition can enhance ephemeral macroalgae with stronger effects on sheltered coastal areas (Kotta *et al.* 2009; Madsen *et al.* 2001). These studies highlight the importance of investigating hydrodynamic regimes when considering the location for a co-culture of shellfish and macroalgae.

In channels and fjords from southern Chile (41° to 56°S), local current speed and water circulation are influenced by tidal oscillations, freshwater inputs, and wind variation (Castillo & Valenzuela 2008). Tidal currents tend to vary from relatively weaker in deep fjord systems (*c.* 0.1 m<sup>-1</sup> s<sup>-1</sup>) to stronger (*c.* 0.7 m<sup>-1</sup> s<sup>-1</sup>) in shallower channels (Instituto de Fomento Pesquero 2019; Valle-Levinson *et al.* 2007). This is relevant for developing an efficient mechanism to recapture inorganic and organic metabolic waste generated by the cultivated carnivore species and to identify the dispersal and retention zones across

the region. In Chile, as in other countries, mussel aquaculture encompasses two production cycles: a seeding period (from early to late spring) and a growth period (from early autumn to late spring). Accordingly, the mussel growth period seems to be more relevant for introduction of macroalgae and the attenuation of adverse impacts from particulate waste on macroalgal thalli. Southerly winds dominate from early autumn to early spring and tend to be stronger than in late spring and summer, promoting surface turbulence and vertical mixing (Valle-Levinson *et al.* 2007). This agrees with the season (autumn–spring) for optimum seeding and growth for farming *Macrocystis pyrifera* (Linnaeus) C.Agardh (Camus *et al.* 2019). In addition, the limited light environment during the low productivity period (autumn–winter) restricts the growth of nuisance epiphytic algae in pilot crops of commercial macroalgae (Avila *et al.* 1999; Lüning & Pang 2003; Romo *et al.* 2001; Westermeier *et al.* 1993). However, as mentioned above, temporal constraints should be considered because the optimum growth season can vary among cultivated species.

Macroalgal growth might be limited by the vertical attenuation of photosynthetically active radiation and shading by adjacent lines and culture sleeves. Depth is a limiting factor for the cultivation of macroalgae and restricts productivity to the first few metres of the water column (Beer *et al.* 2016). Therefore, we propose that macroalgal cultivation on vertical lines be tested to determine both OA buffering effects and resulting productivity rates (Fig. 2). This is critical for important commercial species such as *Agarophyton chilensis* (C.J.Bird, McLachlan & E.C.Oliveira) Gurgel, J.N.Norris & Fredericq (formerly *Gracilaria chilensis*; Gurgel *et al.* 2018), in which productivity may vary from 84 to 132 t ha<sup>-1</sup> year<sup>-1</sup> by increasing culturing depth from 0.75 to 1.5 m, respectively (Buschmann *et al.* 1997; see Espi *et al.* 2019 for review of seaweed aquaculture in Latin America). For *M. pyrifera*, effective suspended growth has been determined to occur at *c.* 3-m depth (Varela *et al.* 2018). However, the presence of accessory pigments phycoerythrin and phycocyanin in red macroalgae (Rhodophyta) becomes relevant for cultivation under light limitation and can help determine optimal cultivation depth (Fig. 3). For instance, during early growth of *Gigartina skottsbergii* Setchell & N.L. Gardner optimal depths are between 4 and 6 m (Romo *et al.* 2006); *Sarcothalia crispata* (Bory) Leister had higher growth rates at 12–13 m (Westermeier *et al.* 2012); and *Chondracanthus chamosii* (C.Agardh) Kützing can be found growing naturally at depths up to 15 m on the central coast of Chile (Hoffmann & Santelices 1997). Overall, these outcomes suggest that culturing red macroalgae below 4-m depth along with filter-feeder sleeves may provide a successful strategy. This can maximise both the macroalgal OA buffering effect in greater portions of the water column and the adaptive mechanisms to grow under attenuated light (Fig. 3). In addition, red algae are characterised by using both CO<sub>2</sub> and HCO<sub>3</sub><sup>-</sup> as Ci forms to support photosynthesis (Maberly *et al.* 1992); hence, depending on their CCMs, some red algae might have increased photosynthetic rates under elevated CO<sub>2</sub>. Therefore, preliminary studies investigating the CCMs of the target species will be necessary to select the best candidate with respect to capacity to improve seawater carbonate chemistry.

Finally, another issue to be examined is the potential relationship of macroalgae as substrata for shellfish during

recruitment. The use of a biogenic habitat, provided by sea-grasses, drifting algae and algal rafts, for recruitment and dispersion has been documented for mussel larvae and spat in New Zealand (Alfaro *et al.* 2004; Jeffs *et al.* 2018). However, this may also increase the effects of epibionts and opportunistic macroalgae such as *Desmarestia* sp. (Phaeophyceae), which can affect mussel cultures during spring in southern Chile (local mussel growers, personal communication, November 2018).

## CONCLUSIONS

OA is occurring faster than expected, and mitigation strategies are urgently needed to reduce anthropogenic CO<sub>2</sub> emissions and their associated negative effects on marine ecosystems, coastal communities (e.g. calcifying organisms), and economic sectors (e.g. fisheries and aquaculture). Coastal environments are characterised by strong diurnal pH fluctuations associated with metabolic activity of macroalgae. Marine organisms inhabiting coastal zones have developed a wide range of mechanisms to cope with this changing pH environment. In this context, mimicking the natural OA buffering effect created via the photosynthetic footprint (i.e. reduction of CO<sub>2</sub> and increase in seawater pH and Ω<sub>arg</sub>), which favours calcification, may be a strategy to mitigate the negative effects of OA on shell-forming molluscs. Beneficial interactions between macroalgae and calcifying organisms have been observed in natural environments and in co-culturing conditions; for example, efficiency of macroalgae to remove excess inorganic and organic metabolic waste generated by the cultured animals. However, these positive synergistic effects have not been investigated under an OA scenario. In this context, important factors related to hydrodynamic regimes and physiological responses of cultivated species (e.g. nutrient uptake, excretion rates, buffering effects and CO<sub>2</sub> sink capacity) must be tested when considering a co-culture design. Thus, any potential benefit between these organisms may be both site specific and species specific and affect final biomass production. In addition, an ecosystem-based marine planning approach is needed in Chile to optimise different local possibilities. Policy is needed to maximise the benefits of multitrophic aquaculture for an industry that may need to adapt rapidly under climate change.

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