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REVIEW



Cracking the myth: Bivalve farming is not a CO₂ sink

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Abstract

Bivalve farming was usually considered as a CO₂ source through respiration and calcification, but recent studies suggest its potential as a CO₂ sink, prompting exploration of its inclusion in carbon markets. Here we reviewed the scientific basis behind this idea and found that it is not supported by observational and experimental studies. This idea indeed arises from carbon budget models that are based on theoretical misconceptions regarding seawater carbonate chemistry. The main misunderstanding consists of assuming that the carbon trapped in the shell originates from atmospheric CO₂ when it mostly comes from (bi)carbonate ions. While these ions originate from atmospheric CO2 through the erosion of minerals over geological time scales, their incorporation into shells does not prompt short-term CO₂ compensation. The opposite occurs-calcification releases CO2 in seawater and limits or even prevents the uptake of atmospheric CO₂. Some authors suggest that considering the bivalve farm ecosystem could change the perspective on the source/sink issue but there is no evidence for that now. Most ecosystem-based carbon budget models rely on several unverified assumptions and estimates. Although challenging, field measurements must be conducted for monitoring, reporting, and verifying atmospheric CO2 uptake before qualifying for carbon credits. To achieve scientific consensus, we need reinforcing measurement-based studies of CO₂ fluxes in shellfish ecosystems, integrating carbon balance models with observational and experimental science, and fostering interdisciplinary collaboration. Although bivalve farming provides numerous environmental benefits and is vital for sustainable aquaculture, there is currently no evidence that it contributes to CO₂ capture.

KEYWORDS

carbon credit, carbon dioxide removal, climate change, CO2, mollusc, sustainability

1 | INTRODUCTION

The latest Intergovernmental Panel on Climate Change (IPCC) report delivers a clear message: urgent actions are required to reduce carbon dioxide (CO₂) emissions, mitigate climate change, and ensure the future habitability of our planet.¹ At the current rate of CO₂

emissions, the remaining carbon budget for a 50% chance to reach the Paris Agreement will be spent in 2029. In practical terms, netzero CO_2 emissions must be reached by 2050, necessitating the implementation of carbon dioxide removal (CDR) strategies in addition to deep cuts of CO_2 emissions. CDR is necessary to balance residual emissions that are technically difficult to stop, such as agricultural and

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industrial emissions. Among the most well-known CDR methods are afforestation, reforestation, carbon-sequestering agricultural practices, wetland restoration, as well as blue carbon approaches. Blue carbon is defined by the IPCC as biologically driven carbon fluxes and storage in marine systems that are amenable to management.³ Coastal blue carbon currently focuses on rooted vegetation, such as tidal marshes, mangroves, and seagrasses.⁴

While the traditional view is that shellfish farming (mainly bivalves) acts as a CO_2 source due to respiration and calcification processes, an alternative is becoming increasingly popular. Some recent studies suggest that bivalves could serve as CO_2 sinks with the potential to combat climate change in a way comparable to terrestrial forests or seaweeds (e.g., References [5, 6]). This idea has resonated within the shellfish farming community and made its way into policy in government departments, ministries, and professional organizations. Consequently, there is now a serious exploration of the possibility of incorporating shellfish into carbon markets and, perhaps, offering subsidies or credits to shellfish farmers who may contribute to CO_2 capture and the battle against climate change. Here, we evaluate the concepts behind the idea that bivalve aquaculture acts as a CO_2 sink and conclude that it is based on theoretical misconceptions and, to the best of our knowledge, not supported by observational and experimental studies.

2 | PRINCIPLES GOVERNING AIR-SEA CO₂ FLUXES AND CARBONATE CHEMISTRY

The air-sea CO_2 exchange is driven by the difference in the partial pressure of CO_2 (pCO_2) between these two compartments. Overall, the surface ocean has lower pCO_2 than the atmosphere, allowing it to be a net CO_2 sink capturing about 25% of anthropogenic emissions. Enhancing this sink through marine CDR (mCDR) requires pCO_2 reduction in the surface ocean to allow for more uptake.

The capacity of the ocean to act as a CO_2 sink primarily stems from the transformation of the majority of aqueous CO_2 into carbonic acid (H_2CO_3) which rapidly dissociates in other forms of inorganic carbon, bicarbonate (HCO_3^-) and carbonate (CO_3^{2-}) ions that are not readily re-released into the atmosphere. Reactions are summarized by the following reversible equations:

$$CO_{2(aq)} + H_2O \rightleftharpoons H_2CO_3, \tag{1a}$$

$$H_2CO_3 \rightleftharpoons HCO_3^- + H^+,$$
 (1b)

$$\mathsf{HCO}_3^- \rightleftharpoons \mathsf{CO}_3^{2-} + \mathsf{H}^+. \tag{1c}$$

The sum of these three species is referred to as dissolved inorganic carbon (DIC):

$$\label{eq:DIC} \text{DIC} = \left[\text{CO}_{2(\text{aq})}\right] + \left[\text{HCO}_{3}^{-}\right] + \left[\text{CO}_{3}^{2-}\right]. \tag{2}$$

The uptake of CO_2 by the ocean leads to its acidification (increase in hydrogen ions = decrease in pH), it also increases the

concentrations of CO_2 and HCO_3^- and decreases concentrations of CO_3^{2-} . At the ocean surface (considering a temperature of 15° C, a salinity of 35, a pH level of 8.1 (on the total scale), and a DIC concentration of 2300 μ mol kg $^{-1}$), DIC mainly consists of HCO_3^- (90.9%) and CO_3^{2-} (8.5%), and CO_2 is a relatively minor component (0.6%). Note, however, that CO_2 is the only form of inorganic carbon that is exchanged with the atmosphere.

Total alkalinity (TA), is a measure of the capacity of seawater to resist sudden changes in pH by absorbing hydrogen ions using available bases such as HCO_3^- and CO_3^{2-} . Note that CO_3^{2-} can absorb twice as many hydrogen ions as HCO_3^- . This means that CO_3^{2-} has twice the impact on total alkalinity compared with HCO_3^- . Other ions also contribute to TA, but they are minor contributors. TA is given by the following equation:

$$\mathsf{TA} = \left[\mathsf{HCO}_3^-\right] + 2\left[\mathsf{CO}_3^{2-}\right] + \left[\mathsf{OH}^-\right] - \left[\mathsf{H}^+\right] + \mathsf{minor}\,\mathsf{compounds}. \quad (3)$$

Other things being equal, TA is an indicator of the ocean's capacity to store ${\rm CO_2}$. Differential changes in DIC and TA, mediated by physico-chemical or biological processes, can modify $p{\rm CO_2}$ and control the direction of the air-sea ${\rm CO_2}$ flux^{9,10} (Figure 1). If DIC decreases more rapidly than TA, seawater $p{\rm CO_2}$ decreases, leading to an increased uptake of atmospheric ${\rm CO_2}$ by surface waters. In contrast, if TA decreases more rapidly than DIC, $p{\rm CO_2}$ increases, diminishing the capacity of surface waters to absorb atmospheric ${\rm CO_2}$.

The impact of photosynthesis and respiration on air-sea CO_2 fluxes is intuitive. Indeed, primary production through photosynthesis consumes CO_2 (and thus DIC) to produce organic carbon by releasing dioxygen (O_2) , while conversely, respiration uses organic carbon and O_2 to produce energy and release CO_2 (Equation 4). Photosynthesis and respiration have a negligible effect on TA^{12} (Figure 1) allowing the changes in DIC to be reflected in changes to pCO_2 and air-sea fluxes. Of Summarizing, photosynthesis tends to increase while respiration tends to decrease the capacity of surface waters to absorb atmospheric CO_2 .

$$CO_2 + H_2O \rightleftharpoons CH_2O + O_2. \tag{4}$$

The impacts of calcium carbonate (CaCO₃) precipitation and its reverse process, dissolution, are less intuitive. Marine organisms utilize inorganic carbon to synthesize shells, tests, or skeletons composed of CaCO₃. Calcification is described by the following reversible reaction:

$$Ca^{2+} + 2HCO_3^- \rightleftharpoons CaCO_3 + CO_2 + H_2O.$$
 (5)

This equation shows that CO_2 is generated because of $CaCO_3$ precipitation (Figure 1). The production of 1 mole of $CaCO_3$ consumes 2 moles of HCO_3^- (and TA). Quantitatively, however, <1 mole is released because of the seawater buffering capacity¹³ (see Appendix A). The dissolution of $CaCO_3$ yields the opposite effects. Overall, $CaCO_3$ production tends to decrease while its dissolution tends to increase the capacity of surface waters for atmospheric CO_2

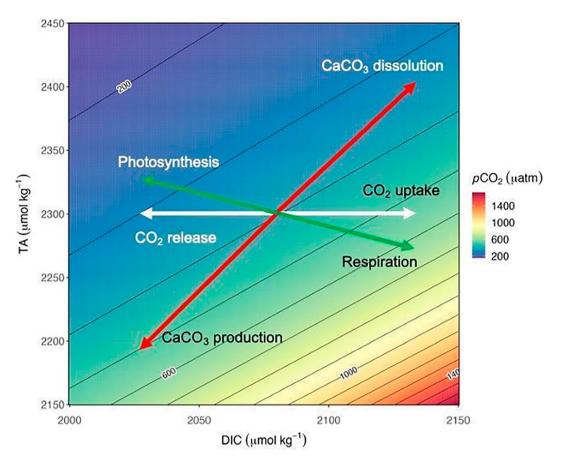


FIGURE 1 Distribution of the partial pressure of CO_2 (pCO_2) in total alkalinity (TA) and dissolved inorganic carbon (DIC) phase space, calculated at temperature = $15^{\circ}C$ and salinity = 35 using the R package seacarb. The black lines are drawn at the pCO_2 values labelled on the colour legend. Vectors represent the effect of biogeochemical processes. Uptake and release of CO_2 into/from the ocean changes only DIC (and therefore pCO_2), whereas photosynthesis and respiration also slightly change TA owing to nutrient uptake and release. Calcium carbonate (CaCO₃) formation decreases TA and DIC in a ratio of 2:1, and increases pCO_2 . CaCO₃ dissolution has the reverse effect. For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.

uptake (see Appendix A for further details). The impact of biogenic calcification on the CO_2 cycle and climate is not trivial: the deposition of $CaCO_3$ within coral reefs may have contributed to the increase in atmospheric CO_2 during the last glacial-interglacial transition (References [13,14] and references therein).

3 | CHALLENGES IN ATTRIBUTING A CO₂ SINK OR SOURCE ROLE TO SPECIES AND ECOSYSTEMS

The intricacy of biogeochemical and physical processes complicates the assessment of whether a species is a net CO_2 source or sink. Although primary producers taken in isolation are CO_2 sinks, and animals, especially heterotrophic calcifiers, are sources, the reality is more nuanced at the ecosystem scale. The distinction between CO_2 source and sink status depends, among other things, on the fate of organisms in the ocean at the end of their life (sequestration or remineralization) and their ecological role in driving other processes. An illustrative example is the case of seagrass beds. Typically, they are

considered as net primary producers contributing significantly to blue carbon in coastal ecosystems. However, recent findings reveal that the decrease in pCO_2 resulting from seagrass photosynthesis may be surpassed by the CO_2 released by the calcification of organisms living in association with them. In that case, the ecosystem becomes a source of CO_2 . Conversely, calcifying species acting as CO_2 sources as taken individually can theoretically favour the growth of primary producers such as seaweeds and therefore promote CO_2 uptake at the ecosystem level. While a species can act as either a source or a sink of CO_2 , its effect can be mitigated, or even reversed by the other species that exert an opposite effect on the carbonate chemistry.

4 | MARINE SHELLFISH AQUACULTURE AS A BLUE CARBON STRATEGY?

Several review papers have explicitly identified ecosystems dominated by calcifiers, such as natural shellfish beds or aquaculture production areas, as potential blue carbon ecosystems. ^{17,18} We, therefore, carried out the most exhaustive literature review possible and found a total

of 51 articles on the role of bivalves in the carbon cycle and their impact on CO_2 levels (Table 1). For each paper, we listed the taxonomic or functional group, the approach used (in situ observation, experimentation, and carbon budget modelling), the type of ecosystem (natural vs. farmed populations), and the conclusion of the study concerning the role of bivalves on the source/sink status.

The idea that bivalve farming is a CO₂ sink originated from the study by Tang et al.,⁶ which investigated carbon removal in a coastal ecosystem dedicated to shellfish and seaweed harvesting. Their estimates relied on the carbon content of these organisms and annual production statistics. From these estimates, authors concluded that cultivating shellfish significantly contributes to carbon sequestration, thereby enhancing coastal ecosystems' ability to absorb atmospheric CO₂. Then, several other papers used similar theoretical carbon budget models and reached similar conclusions (Figure 2).

Of the studies examined, 43 are theoretical budget models and only 8 are based on observational or experimental measurements. Among the theoretical carbon budget studies, 28 conclude that bivalves are CO₂ sinks, while 15 conclude the opposite. Seven out of eight observational and experimental studies also indicate that bivalves are not CO₂ sinks. Among these observational and experimental studies, the sole exception is the paper by Fodrie et al.,²⁸ which concludes that wild oyster reefs can operate as either sources or sinks based on their tidal position. We will see that the majority of the budget model studies were built upon theoretical misconceptions regarding seawater carbonate chemistry.

4.1 | Shell formation is a carbon sink but not a CO₂ sink

Most of the theoretical budget models mentioned in the preceding section consider that the carbon contained in the CaCO $_3$ shell comes from atmospheric CO $_2$ rather than HCO $_3$ -.5.6,22,24-27,29-31,33,36-38,40,43-46,48-50,53-55,58-67 Although some of them explicitly mention Equation 5, they nonetheless assume that, for each mole of CaCO $_3$ produced, 2 moles of CO $_2$ are used in the form of HCO $_3$ -: one mole is incorporated into the shell, and the remaining is released. According to this reasoning, 1 g of CaCO $_3$ would contain 0.12 g of carbon which corresponds to 0.44 g CO $_2$ equivalent. In fact, converting the carbon stored in CaCO $_3$ to CO $_2$ equivalents is incorrect.

This misconception arises from the belief that HCO_3^- in the ocean primarily comes from atmospheric CO_2 . Overall, HCO_3^- comes from two sources: direct CO_2 capture at the ocean surface and chemical weathering of sediments and rocks.

The direct CO_2 capture at the surface ocean represents a minor contribution to the oceanic pool of HCO_3^- . The atmosphere is indeed a relatively small reservoir of carbon compared with the ocean (ca. 600 vs. 38,000 Gt C, respectively). To illustrate this, considering pre-industrial, atmospheric CO_2 concentrations at 280 ppm and in equilibrium with the ocean, HCO_3^- represents 89.5% of the oceanic pool of DIC. At the current atmospheric CO_2 concentrations of 420 ppm, the concentration of CO_2 in seawater increases by 50%

compared with the pre-industrial era, while that of HCO_3^- increases by only 7%, the latter now representing 92% of the DIC pool. Therefore, only 6% of the HCO_3^- pool available to bivalves originates from anthropogenic CO_2 . However, since equilibrium is not achieved, this figure is an overestimate. These calculations were obtained using a TA of 2300 μ mol kg⁻¹, a temperature of 15°C, and a salinity of 35 using the R package sea carb. ¹¹

In contrast to direct atmospheric CO2 capture, mineral weathering is the primary source of HCO₃⁻ for the ocean, as it involves the most important reservoir of carbon on Earth (sediments and rocks: ca. 90×10^6 Gt C).⁶⁸ Weathering is the reaction of atmospheric CO₂ and H₂O with silicate and carbonate rocks. Briefly, CO₂ and rainwater produce carbonic acid (H₂CO₃) which can dissolve silicate and carbonate rocks. The formation of biogenic CaCO3 is the primary process through which a portion of CO₂ sequestered during land weathering cycles returns from the ocean to the atmosphere. However, weathering operates on timescales exceeding 10,000 years and this process is considered stable on shorter timescales such as decades or centuries.⁶⁹ Therefore, the HCO₃⁻ used to build calcareous shells is not compensated by accelerated weathering and capture of atmospheric CO₂ in the short-term. Yet, the emission of CO₂ as a result of CaCO₃ production is immediate, and air-sea CO2 equilibration occurs on timescales of weeks to years. 70 Consequently, calcification is a shortterm CO2-releasing process, with compensation only occurring through accelerated weathering in the long term.

Overall, converting the carbon stored in $CaCO_3$ to CO_2 equivalent is incorrect and reflects a lack of consideration for the carbon cycle and more particularly of the size of carbon reservoirs and the time scales involved in the exchanges between them. For a more comprehensive understanding of the carbonate biogeochemistry, we recommend consulting Ridgwell and Zeebe.⁶⁹

Note, however, that bivalves can convert metabolic CO_2 into (bi) carbonate ions through the action of the enzyme carbonic anhydrase, ^{72,73} thereby contributing to shell formation. While the proportion of metabolic CO_2 integrated into the shell is generally below 10%, it can reach up to 37% depending on factors such as species, age or size, and environmental conditions. ⁷⁴ In specific cases, such as clams exposed to ocean acidification over multiple generations, the contribution of metabolic CO_2 may range from 45 to 61%. ⁷⁵ This pathway reduces the amount of CO_2 released into seawater through respiration. However, in theory, calcification using metabolic CO_2 has the same impact on seawater carbonate chemistry as calcification using HCO_3^- or CO_3^{2-} (see Appendix B). Both processes result in a 2:1 decrease in the TA to DIC ratio and increase in pCO_2 . Despite the potential significance of metabolic CO_2 incorporation into bivalve shells, its contribution is markedly variable and challenging to quantify.

4.2 | Shell dissolution compensates the release of CO₂ from calcification

The above misconception leads to another one: assuming that exporting the carbon contained in the shells through harvesting qualifies as a

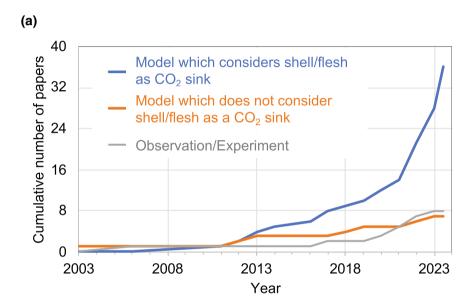
TABLE 1 Summary of the analysis of the scientific literature on the role of bivalves in the carbon cycle and their impact on CO₂ levels.

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References	Group	Approach	Ecosystem	CO ₂ source/sink	$Shell = CO_2 sink$	Flesh = CO ₂ sin
Chauvaud et al. ¹⁹	Clam	Model	Wild	Source	N	N
Martin et al. ²⁰	Limpet	Experiment	Wild	Source	NA	NA
Tang et al. ⁶	Bivalve	Model	Farm	Sink	Υ	Υ
Lejart et al. ²¹	Oyster	Model	Wild	Source	N	N
Mistri and Munari ²²	Clam	Model	Farm	Source	Υ	N
Hily et al. ²³	Calcifier	Model	Wild	Source	N	N
Mistri and Munari ²⁴	Mussel	Model	Farm	Source	Υ	N
Munari et al. ²⁵	Mussel	Model	Farm	Source	Υ	N
Jiang et al. ²⁶	Scallop	Exp./Model	Farm	Source	Υ	N
Wang et al. ²⁷	Abalone	Exp./Model	Farm	Source	Υ	Υ
Fodrie et al. ²⁸	Oyster	Observation	Wild	Both	NA	NA
Han et al. ²⁹	Oyster	Exp./Model	Farm	Source	Υ	N
Zhang et al. ³⁰	Bivalve	Model	Farm	Sink	Υ	Υ
Aubin et al. ³¹	Mussel	Model	Farm	Sink	Υ	N
Ray et al. ³²	Bivalve	Model	Farm	Source	N	N
Filgueira et al. ³³	Mussel	Model	Farm	Source	Y	N
Morris and Humphreys ³⁴	Mussel	Model	Farm	Source	N	N
Han et al. ³⁵	Oyster	Experiment	Farm	Source	NA	NA
Jansen and van den Bogaart ³⁶	Mussel	Model	Farm	Sink	Y	Y
-						
Turolla et al. ³⁷	Clam	Model	Farm	Sink	Y	N
Bertolini et al. ³⁸	Clam	Model	Farm _	Sink	Y	N
Li et al. ³⁹	Mollusc	Observation	Farm	Source	NA	NA
Ren ⁴⁰	Bivalve	Model	Farm	Sink	Y	Υ
Yang et al. ⁴¹	Scallop	Observation	Farm	Source	NA	NA
Álvarez-Salgado et al. ⁴²	Mussel	Model	Farm	Source	N	N
Dong et al. ⁴³	Clam	Model	Farm	Sink	Υ	N
Gu et al. ⁴⁴	Bivalve	Model	Farm	Sink	Υ	Υ
Lai et al. ⁴⁵	Bivalve	Model	Farm	Sink	Υ	Υ
Liu et al. ⁴⁶	Mollusc	Model	Farm	Sink	Υ	Υ
Liu et al. ⁴⁷	Bivalve	Observation	Farm	Source	NA	NA
Martini et al. ⁴⁸	Mussel	Model	Farm	Sink	Υ	N
Sea et al. ⁴⁹	Mussel	Model	Wild	Source	Υ	N
Tamburini et al. ⁵⁰	Bivalve	Model	Farm	Sink	Υ	N
Ye et al. ⁵¹	Clam	Observation	Farm	Source	NA	NA
Bertolini et al. ⁵²	Mussel	Model	Farm	Sink	N	Υ
Feng et al. ⁵	Bivalve	Model	Farm	Sink	Υ	Υ
Le et al. ⁵³	Bivalve	Model	Farm	Sink	Y	Y
Lee et al. ⁵⁴	Oyster	Exp./Model	Wild	Sink	Y	N
Moore et al. ⁵⁵	Calcifier	Model	Farm	Sink	Y	N
Song et al. ⁵⁶	Bivalve	Model	Farm	Source	N	N
Song et al. ⁵⁷						
	Oyster	Observation	Wild	Source	NA	NA
Xu et al. ⁵⁸	Bivalve	Model	Farm	Sink	Y	Y
Zavell et al. ⁵⁹	Bivalve	Model	Wild/Farm	Sink	Υ	N
Gao et al. ⁶⁰	Mollusc	Model	Farmed	Sink	Υ	Υ
Guo and Nie ⁶¹	Mollusc	Model	Farmed	Sink	Υ	Υ
Hao et al. ⁶²						Y

TABLE 1 (Continued)

References	Group	Approach	Ecosystem	CO ₂ source/sink	$Shell = CO_2sink$	$Flesh = CO_2sink$
Li et al. ⁶³	Mollusc	Model	Farmed	Sink	Υ	Υ
Li et al., ⁶⁴	Mollusc	Model	Farmed	Sink	Υ	Υ
Liu et al. ⁶⁵	Scallop	Model	Farmed	Sink	Υ	Υ
Tan et al. ⁶⁶	Oyster	Model	Farmed	Sink	Υ	Υ
Van In and O'Connor ⁶⁷	Oyster	Model	Farmed	Sink	Υ	Υ

Note: For each paper (n = 51), we listed the taxonomic or functional group studied, the approaches implemented (in situ observation, experimentation and modelling), the type of ecosystem (natural or farm environment) and the conclusion of the study concerning the role of bivalves as sources or sinks of CO_2 . For carbon balance model studies, we noted whether the shell and/or the flesh were considered as CO_2 sinks. For experimental studies, no a priori hypothesis concerning the role of shells/tissues as a sink/source of CO_2 is formulated. These a priori hypotheses are therefore considered not applicable. Abbreviations: Exp, experiment; N, no; NA, not applicable; Y, yes.



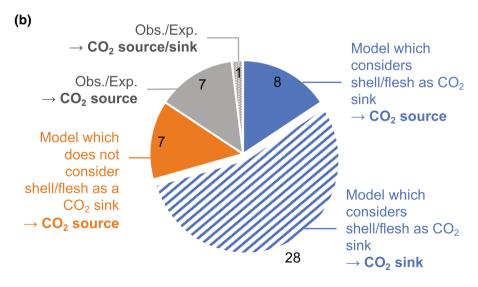


FIGURE 2 Graphical summary of the literature review on the role of bivalves in the carbon cycle and their impact on CO_2 levels. (a) temporal evolution of the cumulative number of articles and (b) current relative proportion of observational/experimental (Obs./Exp.) versus modelling studies (numbers indicate the number of studies). Modelling studies are distinguished depending on whether the shell and/or the flesh were considered as CO_2 sinks. Panel b categorizes studies according to the reached conclusions, indicating whether bivalves are identified as sources and/or sinks of CO_2 (in bold).

form of CO₂ sink or sequestration. This idea contradicts the definition of a CO₂ sink, which refers to any process, activity, or mechanism that removes CO₂ from the atmosphere.³ Removing carbon from the ocean is not necessarily equivalent to removing CO2 from the atmosphere.

In fact, the opposite is true: shells should be left in seawater where their dissolution would absorb CO2, thereby compensating for the emissions from calcification. 34,42,76 Dissolution of shells in seawater raises TA, reduces pCO₂ and increases CO₂ uptake^{77,78} as demonstrated in the sediment of the intertidal zone.⁷⁹ Some papers suggest that shells should be removed from the sea to prevent dissolution (see, e.g., Ref. [17]) or that the integrity of CaCO₃ should be preserved as long as possible. 80 However, principles of the carbonate chemistry tell the opposite.

Shell dissolution indeed represents a facet of another CDR method, Ocean Alkalinisation Enhancement (OAE). OAE consists of the addition of carbonate minerals (or other solid or liquid alkaline materials) to raise TA and therefore decrease pCO2 to promote the uptake of atmospheric CO₂ and its storage as HCO₃⁻ and CO₃²⁻ that do not exchange with the atmosphere. 81-87

4.3 The fate of harvested bivalves: atmospheric CO₂

Not only are shellfish not a CO₂ sink, but the inorganic carbon stored in their tissues and shells is often not sequestered on climate-relevant time scales (100 years or more). In major bivalve-producing countries like China and Europe, shell wastes from human consumption are incinerated as organic wastes, where they undergo high-temperature combustion that releases CO₂ in the atmosphere. 42,80 For these countries, the amount of CO2 released into the atmosphere each year would be equivalent to the emissions from nearly 1 million cars. 80 The carbon stored in the flesh of seafood intended for human consumption is respired and therefore transferred as CO₂ in the atmosphere as well. Therefore, carbon in tissues and shells cannot be considered as sequestered, as reported in some carbon budget models (Table 1).

Advocating for carbon sinks is insufficient. It is indeed imperative to go beyond solely extracting CO2 from the atmosphere; the focus lies on sequestration within geological, terrestrial, or oceanic reservoirs, or in usable products on climate-relevant timescales. Carbon sequestration demands secure, dependable, and verifiable storage. Ideally, carbon sequestration permanently confines CO2, preventing its future release into the atmosphere.^{87,88} This is not what bivalve aquaculture does.

Toward an ecosystem-based carbon budget for bivalve farming

Filgueira et al.⁸⁹ proposed considering bivalve aquaculture within broader ecosystems to account for benthic-pelagic interactions and phytoplankton dynamics in carbon budgets. Secondary effects of bivalve cultivation such as enhanced primary productivity and nutrient cycling as well as the burial of organic carbon in the sediment through bio-deposits should indeed be considered in carbon budgets. According to the authors, a comprehensive analysis of all forms of carbon, as well as significant ecological relationships, feedbacks, and habitats, are required to rigorously quantify the role of cultured bivalves in the CO₂ budget of coastal ecosystems. 33,89

At present, this framework exclusively focuses on assessing the influence of shellfish farming on organic and inorganic carbon, overlooking its potential effects on TA and air-sea CO2 fluxes. This omission is obvious in the few studies that claim using such a comprehensive approach. 5,33,37,50 This limited perspective provides an incomplete picture of the carbon cycle and requires further consideration before including other ecosystem compartments. The only study employing an ecosystem-based approach to carbon budget, considering both DIC and TA budgets, reveals that mussel production is a CO₂ source.⁴² Other studies that investigate in situ air-sea CO₂ flux, pH, and TA in farming ecosystems demonstrate that, in comparison to unfarmed control areas, shellfish sites exhibit a lower TA. higher seawater pCO2 and a lower capacity to absorb atmospheric CO₂^{39,41,47,51} as also reported in wild oyster reefs.⁵⁷

The use of the ecosystem approach often relies on unverified assumptions. For example, it is sometimes assumed that the CO₂ released by respiration and calcification is rapidly used to stimulate primary production, thereby ignoring it in the carbon budget (e.g., Reference [6]). The main problem with this statement is that if photosynthesis uses the CO2 generated by the bivalves, it will not absorb the seawater CO2 it would have absorbed in the absence of bivalves. It is also noteworthy that primary production is rarely constrained by CO₂. Many species of primary producers possess carbonconcentrating mechanisms that render them not responsive to CO₂ enrichment, 90-92 and limiting factors such as inorganic essential nutrients, particularly nitrogen and phosphorus, seawater temperature, and light could play a more decisive role. 93 While the ammonia excretion of bivalves can enhance nutrient cycles and primary production in nutrient-limited ecosystems and the biodeposition can increase denitrification,⁹⁴ thereby potentially acting as indirect CO₂ sinks, it is crucial to verify these effects locally rather than making assumptions.

Likewise, bio-deposits are considered as CO2 sink because they accumulate in the sediment and are therefore permanently separated from the marine water and biosphere. 5,46,53 However, a fraction of the bio-deposit undergo remineralization, leading to CO2 release. The other fraction can store carbon if the environment is suboxic or anoxic. Only a small fraction of benthic organic carbon may ultimately be sequestered within the sediment. 95 While the rate of carbon burial can be elevated under certain conditions, such as in deep anoxic fjords³³ or shallow-subtidal oyster reefs compared with intertidal ones, ²⁸ incorporating bio-deposits into the bivalve aguaculture carbon budget requires a careful assessment of their fate locally.

Filgueira et al.⁸⁹ also propose to make distinct CO₂ budgets for shells, separate from the overall organism, to evaluate the feasibility of incorporating shells into carbon trading systems. This involves allocating the CO₂ emissions associated with respiration to the shell's CO₂ budget (ca., 10%). This approach isolates the carbon footprint of the shells from the rest of the organism and ignores the interdependence between shell formation and soft tissue metabolism, which seems incongruous in the context of the carbon budget of shellfish farming. It also contradicts the fundamental principle of the carbon budget which must include all greenhouse gas fluxes of the manufacturing of the product.

Determining the shellfish ecosystem's net CO₂ contribution—whether as a source or sink—depends on seasonality and local factors like rearing practices, temperature, hydrodynamics and bathymetry, phytoplankton, nutrients, and ecological feedback. Hence, extensive studies on typical shellfish aquaculture ecosystems that consider direct measurement of carbonate chemistry (DIC, but also TA/pCO₂) are needed. Currently, the model-based ecosystem approach of the carbon budget has limited practical utility and opens the door to various approximations and subjective decision-making regarding the inclusion or exclusion of CO₂ emissions in the carbon budget.

5 | CONCLUSION

The claim that shellfish farming can contribute to atmospheric CO_2 sequestration is not scientifically grounded. Stating that bivalves and their culture act as CO_2 sinks does not arise from controversies but from misconceptions, largely stemming from an inaccurate or incomplete understanding of seawater carbonate chemistry. This statement is exclusively based on inaccurate theoretical models and it is not supported by observational and experimental studies. Spreading such misconceptions in the scientific literature and the public could lead to counterproductive policy-making, both for climate protection and for the development of sustainable marine aquaculture.

Most of the carbon contained in the $CaCO_3$ shell comes from HCO_3^- originating from the long-term weathering process on rocks. The contribution of atmospheric CO_2 is negligible. In the short term (<10,000 years), $CaCO_3$ production does not accelerate weathering or atmospheric CO_2 capture. Instead, it increases oceanic pCO_2 , reducing the ocean's capacity to store atmospheric CO_2 and thereby contributing to climate change. Moreover, harvesting and storing shell wastes on land does not contribute to CO_2 sequestration. Shells should be returned to the seawater where their dissolution absorbs CO_2 and offsets emissions resulting from calcification. Currently, most shells are incinerated leading to more CO_2 in the atmosphere. Therefore, the fate of shells following flesh consumption must be considered.

An ecosystem-wide evaluation of the bivalve carbon budget will unlikely change this perspective. There is currently no evidence challenging the idea that bivalve aquaculture acts as a source of CO₂. In fact, the few CO₂ air-sea flux measurements conducted in the field suggest that bivalve farms are net CO₂ sources. Current ecosystem-based carbon budgets exclusively focus on organic and inorganic carbon, overlooking changes in total alkalinity and air-sea CO₂ fluxes, and often rely on unverified assumptions that can minimize CO₂ emissions. Most carbon budgets of bivalve farming are based on models whose parameter estimates are not verified under field conditions. Although challenging, field measurements must be conducted for monitoring, reporting, and verifying CO₂ capture to reliably and honestly qualify for carbon credits. 87,88,96

We acknowledge that our perspective will encounter opposition, reflecting the current division in the scientific literature. To achieve a scientific consensus, we propose three lines of action. First, while studies based on laboratory and field measurements indicate that shellfish are sources of CO2, even when the whole ecosystem is considered, these studies are relatively rare and often outdated compared with carbon balance models. It is therefore necessary to reinforce observational and experimental studies, including the measurement of CO2 fluxes at the interfaces of shellfish farming ecosystems and within them. Second, carbon balance models are frequently dissociated from observational and experimental studies. To bridge this gap, integrative approaches that include observation, experimentation, and modelling are essential. Finally, the aforementioned misconceptions are likely the consequence of a lack of integration between disparate research areas, including biogeochemistry, ecology, physiology, and aquaculture engineering. By fostering collaboration between disciplines, we can advance our knowledge and hopefully resolve the current debate.

While bivalve farming is not a $\rm CO_2$ sink, it should not impede its future development. Cultivated bivalves are among the sources of animal protein with the lowest $\rm CO_2$ emissions, 97,98 and their carbon footprint can be further reduced by either returning their shells in the ocean or by adopting cocultures with algae to partially offset $\rm CO_2$ emissions. 29,35,39,47,99

Moreover, efforts to tackle climate change must be assessed in a broad context that include the preservation of ecological health, ecosystem services, and biodiversity. In this regard, bivalve farming provides many services such as effective seawater filtration and clarification, regulation of nutrient cycles and eutrophication, and the creation of habitats for diverse species. ¹⁸ Therefore, the overall positive impact of bivalves on marine ecosystems makes them an important component of sustainable aquaculture that should not be obscured by the fact that they are CO₂ sources. The conservation of endangered natural oyster reefs should be pursued because they contribute essential ecosystem services and serve as habitats for biodiversity. Conserving these reefs is further justified from a CO₂ perspective as they potentially constitute a buried reservoir of organic carbon that should be prevented from resurfacing and therefore becoming an additional source of CO₂. ²⁸

AUTHOR CONTRIBUTIONS

Fabrice Pernet: Conceptualization; methodology; investigation; funding acquisition; writing – original draft; writing – review and editing.

Sam Dupont: Writing – review and editing. Jean-Pierre Gattuso: Writing – review and editing. Marc Metian: Writing – review and editing. Frédéric Gazeau: Conceptualization; methodology; investigation; funding acquisition; writing – review and editing; writing – original draft.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

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

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REFERENCES

- IPCC. Summary for policymakers. In: Lee H, Romero J, eds. Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC; 2023:1-34.
- Lamboll RD, Nicholls ZRJ, Smith CJ, Kikstra JS, Byers E, Rogelj J. Assessing the size and uncertainty of remaining carbon budgets. *Nat Clim Change*. 2023;13(12):1360-1367. doi:10.1038/s41558-023-01848-5
- IPCC. Annex I: glossary. In: Intergovernmental Panel on Climate, ed. Climate Change 2022—Mitigation of Climate Change: Working Group III Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press; 2023:1793-1820.
- Macreadie PI, Costa MDP, Atwood TB, et al. Blue carbon as a natural climate solution. Nat Rev Earth Environ. 2021;2(12):826-839. doi:10. 1038/s43017-021-00224-1
- Feng J-C, Sun L, Yan J. Carbon sequestration via shellfish farming: a potential negative emissions technology. *Renew Sustain Energy Rev.* 2023;171:113018. doi:10.1016/j.rser.2022.113018
- Tang Q, Zhang J, Fang J. Shellfish and seaweed mariculture increase atmospheric CO₂ absorption by coastal ecosystems. Mar Ecol Prog Ser. 2011;424:97-104. doi:10.3354/meps08979
- Aquaculture Advisory Council. AAC Recommendation on Carbon Sequestration by Molluscs. Retrieved from Brussels, Belgium. 2022. https://aac-europe.org/wp-content/uploads/2022/04/EN_16.AAC_ Recommendation_-_Carbon_Sequestration_by_Molluscs_2022_ 16.pdf
- Friedlingstein P, O'Sullivan M, Jones MW, et al. Global Carbon Budget 2023. Earth Syst Sci Data. 2023;15(12):5301-5369. doi:10.5194/essd-15-5301-2023
- Middelburg JJ, Soetaert K, Hagens M. Ocean alkalinity, buffering and biogeochemical processes. *Rev Geophys*. 2020;58(3): e2019RG000681. doi:10.1029/2019RG000681
- Humphreys MP, Daniels CJ, Wolf-Gladrow DA, Tyrrell T, Achterberg EP. On the influence of marine biogeochemical processes over CO₂ exchange between the atmosphere and ocean. *Mar Chem.* 2018;199:1-11. doi:10.1016/j.marchem.2017.12.006
- Gattuso J-P, Epitalon J-M, Lavigne H, Orr J. Seacarb: Seawater Carbonate Chemistry. R Package Version 3.3.3. (Version 3.3.3.). 2024. https://cran.r-project.org/package=seacarb
- Chisholm JRM, Gattuso J-P. Validation of the alkalinity anomaly technique for investigating calcification of photosynthesis in coral reef communities. *Limnol Oceanogr.* 1991;36(6):1232-1239. doi:10. 4319/lo.1991.36.6.1232
- 13. Frankignoulle M, Canon C, Gattuso J-P. Marine calcification as a source of carbon dioxide: positive feedback of increasing

- atmospheric CO₂. *Limnol Oceanogr*. 1994;39(2):458-462. doi:10. 4319/lo.1994.39.2.0458
- Gattuso J-P, Frankignoulle M, Smith SV. Measurement of community metabolism and significance in the coral reef CO₂ source-sink debate. *Proc Natl Acad Sci.* 1999;96(23):13017-13022. doi:10.1073/pnas.96.23.13017
- Van Dam BR, Zeller MA, Lopes C, et al. Calcification-driven CO₂ emissions exceed blue carbon sequestration in a carbonate seagrass meadow. Sci Adv. 2021;7(51):eabj1372. doi:10.1126/sciadv.abj1372
- Newell RIE, Koch EW. Modeling seagrass density and distribution in response to changes in turbidity stemming from bivalve filtration and seagrass sediment stabilization. *Estuaries*. 2004;27(5):793-806. doi:10.1007/BF02912041
- 17. Jones AR, Alleway HK, McAfee D, Reis-Santos P, Theuerkauf SJ, Jones RC. Climate-friendly seafood: the potential for emissions reduction and carbon capture in marine aquaculture. *Bioscience*. 2022;72(2):123-143. doi:10.1093/biosci/biab126
- van der Schatte Olivier A, Jones L, Vay LL, Christie M, Wilson J, Malham SK. A global review of the ecosystem services provided by bivalve aquaculture. Rev Aquac. 2020;12(1):3-25. doi:10.1111/raq. 12301
- Chauvaud L, Thompson JK, Cloern JE, Thouzeau G. Clams as CO₂ generators: the *Potamocorbula amurensis* example in San Francisco Bay. *Limnol Oceanogr.* 2003;48(6):2086-2092. doi:10.4319/lo.2003. 48.6.2086
- Martin S, Thouzeau G, Chauvaud L, Jean F, Guérin L, Clavier J. Respiration, calcification, and excretion of the invasive slipper limpet, Crepidula fornicata L.: implications for carbon, carbonate, and nitrogen fluxes in affected areas. Limnol Oceanogr. 2006;51(5):1996-2007. doi:10.4319/lo.2006.51.5.1996
- Lejart M, Clavier J, Chauvaud L, Hily C. Respiration and calcification of *Crassostrea gigas*: contribution of an intertidal invasive species to coastal ecosystem CO₂ fluxes. *Estuaries Coast*. 2012;35(2):622-632. doi:10.1007/s12237-011-9462-y
- Mistri M, Munari C. Clam farming generates CO₂: a study case in the Marinetta lagoon (Italy). Mar Pollut Bull. 2012;64(10):2261-2264. doi:10.1016/j.marpolbul.2012.07.010
- Hily C, Grall J, Chauvaud L, Lejart M, Clavier J. CO₂ generation by calcified invertebrates along rocky shores of Brittany, France. Mar Freshw Res. 2013;64(2):91-101. doi:10.1071/MF12146
- Mistri M, Munari C. The invasive bag mussel Arcuatula senhousia is a CO₂ generator in near-shore coastal ecosystems. J Exp Mar Biol Ecol. 2013;440:164-168. doi:10.1016/j.jembe.2012.11.019
- Munari C, Rossetti E, Mistri M. Shell formation in cultivated bivalves cannot be part of carbon trading systems: a study case with Mytilus galloprovincialis. Mar Environ Res. 2013;92:264-267. doi:10.1016/j. marenvres.2013.10.006
- Jiang ZJ, Fang JG, Han TT, Mao YZ, Li JQ, Du MR. The role of Gracilaria lemaneiformis in eliminating the dissolved inorganic carbon released from calcification and respiration process of Chlamys farreri.
 J Appl Phycol. 2014;26(1):545-550. doi:10.1007/s10811-013-0110-8
- Wang H, Ge C, Mao Y, Huang Y, Sui H. Effect of hybrid abalone, Haliotis discus hannai × Haliotis discus discus, cultivation on the carbon cycle: carbon source/sink. J World Aquacult Soc. 2016;47(5): 720-728. doi:10.1111/jwas.12311
- Fodrie FJ, Rodriguez AB, Gittman RK, et al. Oyster reefs as carbon sources and sinks. Proc R Soc B: Biol Sci. 2017;284(1859):20170891. doi:10.1098/rspb.2017.0891
- Han T, Shi R, Qi Z, Huang H, Liang Q, Liu H. Interactive effects of oyster and seaweed on seawater dissolved inorganic carbon systems: implications for integrated multi-trophic aquaculture. *Aquac Environ Interact*. 2017;9:469-478. doi:10.3354/aei00246
- Zhang Y, Zhang J, Liang Y, et al. Carbon sequestration processes and mechanisms in coastal mariculture environments in China. Sci China

- Earth Sci. 2017;60(12):2097-2107. doi:10.1007/s11430-017-9148-7
- Aubin J, Fontaine C, Callier M, Roque d'orbcastel E. Blue mussel (Mytilus edulis) bouchot culture in Mont-St Michel Bay: potential mitigation effects on climate change and eutrophication. Int J Life Cycle Assess. 2018;23(5):1030-1041. doi:10.1007/s11367-017-1403-y
- Ray NE, O'Meara T, Wiliamson T, Izursa J-L, Kangas PC. Consideration of carbon dioxide release during shell production in LCA of bivalves. *Int J Life Cycle Assess*. 2018;23(5):1042-1048. doi:10.1007/s11367-017-1394-8
- Filgueira R, Strohmeier T, Strand Ø. Regulating services of bivalve molluscs in the context of the carbon cycle and implications for ecosystem valuation. In: Smaal AC, Ferreira JG, Grant J, Petersen JK, Strand Ø, eds. *Goods and Services of Marine Bivalves*. Springer International Publishing; 2019:231-251.
- Morris JP, Humphreys MP. Modelling seawater carbonate chemistry in shellfish aquaculture regions: insights into CO₂ release associated with shell formation and growth. Aquaculture. 2019;501:338-344. doi:10.1016/j.aquaculture.2018.11.028
- Han T, Shi R, Qi Z, Huang H, Wu F, Gong X. Biogenic acidification of Portuguese oyster Magallana angulata mariculture can be mediated through introducing brown seaweed Sargassum hemiphyllum. Aquaculture. 2020;520:734972. doi:10.1016/j.aquaculture.2020.734972
- Jansen H, van den Bogaart L. Blue Carbon by Marine Bivalves: Perspective of Carbon Sequestration by Cultured and Wild Bivalve Stocks in the Dutch Coastal Areas. 2020. https://edepot.wur.nl/537188
- Turolla E, Castaldelli G, Fano EA, Tamburini E. Life cycle assessment (LCA) proves that manila clam farming (Ruditapes Philippinarum) is a fully sustainable aquaculture practice and a carbon sink. Sustainability. 2020;12(13):5252. doi:10.3390/su12135252
- Bertolini C, Bernardini I, Brigolin D, Matozzo V, Milan M, Pastres R. A bioenergetic model to address carbon sequestration potential of shellfish farming: example from *Ruditapes philippinarum* in the Venice lagoon. *ICES J Mar Sci.* 2021;78(6):2082-2091. doi:10.1093/icesjms/ fsab099
- Li J, Zhang W, Ding J, et al. Effect of large-scale kelp and bivalve farming on seawater carbonate system variations in the semienclosed Sanggou Bay. Sci Total Environ. 2021;753:142065. doi:10. 1016/j.scitotenv.2020.142065
- Ren W. Study on the removable carbon sink estimation and decomposition of influencing factors of mariculture shellfish and algae in China—a two-dimensional perspective based on scale and structure. Environ Sci Pollut Res. 2021;28(17):21528-21539. doi:10.1007/s11356-020-11997-1
- 41. Yang B, Gao X, Zhao J, et al. Massive shellfish farming might accelerate coastal acidification: a case study on carbonate system dynamics in a bay scallop (*Argopecten irradians*) farming area, North Yellow Sea. *Sci Total Environ*. 2021;798:149214. doi:10.1016/j.scitotenv. 2021.149214
- Álvarez-Salgado XA, Fernández-Reiriz MJ, Fuentes-Santos I, Antelo LT, Alonso AA, Labarta U. CO₂ budget of cultured mussels metabolism in the highly productive Northwest Iberian upwelling system. Sci Total Environ. 2022;849:157867. doi:10.1016/j. scitotenv.2022.157867
- Dong S, Wang F, Zhang D, Yu L, Pu W, Shang Y. Growth performance and ecological services evaluation of razor clams based on dynamic energy budget model. *J Environ Manage*. 2022;306:114392. doi:10.1016/j.jenvman.2021.114392
- Gu Y, Lyu S, Wang L, Chen Z, Wang X. Assessing the carbon sink capacity of coastal mariculture shellfish resources in China from 1981–2020. Front Mar Sci. 2022;9:1-10. doi:10.3389/fmars.2022. 981569
- 45. Lai Q, Ma J, He F, Zhang A, Pei D, Yu M. Current and future potential of shellfish and algae mariculture carbon sinks in China. *Int J*

- Environ Res Public Health. 2022;19(14):8873. doi:10.3390/iierph19148873
- Liu C, Liu G, Casazza M, et al. Current status and potential assessment of China's ocean carbon sinks. Environ Sci Technol. 2022; 56(10):6584-6595. doi:10.1021/acs.est.1c08106
- Liu Y, Zhang J, Wu W, et al. Effects of shellfish and macro-algae IMTA in North China on the environment, inorganic carbon system, organic carbon system, and sea-air CO₂ fluxes. Front Mar Sci. 2022; 9:1-11. doi:10.3389/fmars.2022.864306
- Martini A, Calì M, Capoccioni F, et al. Environmental performance and shell formation-related carbon flows for mussel farming systems. Sci Total Environ. 2022;831:154891. doi:10.1016/j.scitotenv. 2022.154891
- Sea MA, Hillman JR, Thrush SF. The influence of mussel restoration on coastal carbon cycling. *Glob Chang Biol.* 2022;28(17):5269-5282. doi:10.1111/gcb.16287
- Tamburini E, Turolla E, Lanzoni M, Moore D, Castaldelli G. Manila clam and Mediterranean mussel aquaculture is sustainable and a net carbon sink. Sci Total Environ. 2022;848:157508. doi:10.1016/j. scitotenv.2022.157508
- Ye W, Sun H, Li Y, et al. Greenhouse gas emissions from fed mollusk mariculture: a case study of a Sinonovacula constricta farming system. Agr Ecosyst Environ. 2022;336:108029. doi:10.1016/j.agee. 2022.108029
- Bertolini C, Pastres R, Brigolin D. Modelling CO₂ budget of mussel farms across the Mediterranean Sea. Ambio. 2023;52(12):2023-2033. doi:10.1007/s13280-023-01900-w
- Le C-Y, Feng J-C, Sun L, et al. Co-benefits of carbon sink and low carbon food supply via shellfish and algae farming in China from 2003 to 2020. J Clean Prod. 2023;414:137436. doi:10.1016/j. iclepro.2023.137436
- Lee HZL, Davies IM, Baxter JM, Diele K, Sanderson WG. A blue carbon model for the European flat oyster (Ostrea edulis) and its application in environmental restoration. Aquat Conserv: Mar Freshw Ecosyst. 2024;34(1):e4030. doi:10.1002/aqc.4030
- 55. Moore D, Heilweck M, Fears W, et al. Potential of ocean calcifiers to sequester atmospheric carbon in quantity and even reverse climate change. *J Fish Res.* 2023;7(1):132.
- Song C, Xiong Y, Jin P, et al. Mariculture structure adjustment to achieve China's carbon neutrality and mitigate climate change. Sci Total Environ. 2023;895:164986. doi:10.1016/j.scitotenv.2023. 164986
- Tomasetti SJ, Doall MH, Hallinan BD, Kraemer JR Jr, Gobler CJ. Oyster reefs' control of carbonate chemistry—implications for oyster reef restoration in estuaries subject to coastal ocean acidification. *Glob Chang Biol.* 2023;29(23):6572-6590. doi:10.1111/gcb. 16960
- Xu C, Su G, Zhao K, et al. Assessment of greenhouse gases emissions and intensity from Chinese marine aquaculture in the past three decades. J Environ Manage. 2023;329:117025. doi:10.1016/j. jenvman.2022.117025
- Zavell MD, Lindahl O, Filgueira R, Shumway SE. An estimate of carbon storage capabilities from wild and cultured shellfish in the Northwest Atlantic and their potential inclusion in a carbon economy. J Shellfish Res. 2023;42(2):325-342. doi:10.2983/035.042. 0214
- Gao Y, Fu Z, Yang J, Yu M, Wang W. Spatial-temporal differentiation and influencing factors of marine fishery carbon emission efficiency in China. *Environ Dev Sustain*. 2024;26(1):453-478. doi:10.1007/s10668-022-02716-6
- Guo S, Nie H. Estimation of mariculture carbon sinks in China and its influencing factors. J Mar Sci Eng. 2024;12(5):1-20. doi:10.3390/ jmse12050724
- 62. Hao Y, Tan Z, Cai Y, et al. Assessment of carbon sink capacity and its value accounting for a farmed shellfish in the coastal wetland of the

- Yalu River Estuary. Front Aquac. 2024;3:1-10. doi:10.3389/faquc. 2024;3:5741
- 63. Li W, Li X, Song C, Gao G. Carbon removal, sequestration and release by mariculture in an important aquaculture area, China. *Sci Total Environ*. 2024;927:172272. doi:10.1016/j.scitotenv.2024. 172272
- 64. Li X, Yang J, Zhao Y, Zhou S, Wu Y. Prediction and assessment of marine fisheries carbon sink in China based on a novel nonlinear grey Bernoulli model with multiple optimizations. *Sci Total Environ*. 2024;914:169769. doi:10.1016/j.scitotenv.2023.169769
- 65. Liu S, Li F, Liu Y, Zhang J, Wu S, Zhang J. Assessment of carrying capacity and carbon sink capacity of *Argopecten irradians*: taking Qinhuangdao as an example. *Proc Engr.* 2024;24(1):6.
- Tan K, Liu X, Yan X, et al. Performance of fishery carbon sink of oyster aquaculture (mainly *Crassostrea hongkongensis*) in Guangxi, China: a long-term (2003–2022) analysis. *Estuar Coast Shelf Sci.* 2024;300: 108707. doi:10.1016/j.ecss.2024.108707
- 67. Van In V, O'Connor W. Blue Economy: Valuing the Carbon Sequestration Potential in Oyster Aquaculture. ACIAR; 2024.
- Berner RA, Lasaga AC, Garrels RM. Carbonate-silicate geochemical cycle and its effect on atmospheric carbon dioxide over the past 100 million years. Am J Sci. 1983;283(7):641-683. doi:10.2475/ajs. 283.7.641
- Zeebe RE. History of seawater carbonate chemistry, atmospheric CO₂, and ocean acidification. *Annu Rev Earth Planet Sci.* 2012;40(1): 141-165. doi:10.1146/annurev-earth-042711-105521
- Jones DC, Ito T, Takano Y, Hsu W-C. Spatial and seasonal variability
 of the air-sea equilibration timescale of carbon dioxide. *Global Bio-geochem Cycles*. 2014;28(11):1163-1178. doi:10.1002/2014GB004813
- Ridgwell A, Zeebe RE. The role of the global carbonate cycle in the regulation and evolution of the earth system. *Earth Planet Sci Lett*. 2005;234(3):299-315. doi:10.1016/j.epsl.2005.03.006
- 72. Greenaway P. Calcium regulation in the freshwater mollusc *Limnaea stagnalis* (L.) (Gastropoda: Pulmonata): II. calcium movements between internal calcium compartments. *J Exp Biol.* 1971;54(3):609-620. doi:10.1242/jeb.54.3.609
- Roleda MY, Boyd PW, Hurd CL. Before ocean acidification: calcifier chemistry lessons. *J Phycol.* 2012;48(4):840-843. doi:10.1111/j. 1529-8817.2012.01195.x
- McConnaughey TA, Gillikin DP. Carbon isotopes in mollusk shell carbonates. Geo-Mar Lett. 2008;28(5):287-299. doi:10.1007/s00367-008-0116-4
- Zhao L, Yang F, Milano S, Han T, Walliser EO, Schöne BR. Transgenerational acclimation to seawater acidification in the Manila clam Ruditapes philippinarum: preferential uptake of metabolic carbon. Sci Total Environ. 2018;627:95-103. doi:10.1016/j.scitotenv.2018. 01.225
- Waldbusser GG, Powell EN, Mann R. Ecosystem effects of shell aggregations and cycling in coastal waters: an example of Chesapeake Bay oyster reefs. *Ecology*. 2013;94(4):895-903. doi:10.1890/ 12-1179.1
- Ries JB, Ghazaleh MN, Connolly B, Westfield I, Castillo KD. Impacts of seawater saturation state (ΩA = 0.4–4.6) and temperature (10, 25°C) on the dissolution kinetics of whole-shell biogenic carbonates. Geochim Cosmochim Acta. 2016;192:318-337. doi:10.1016/j.gca.2016.07.001
- Waldbusser GG, Steenson RA, Green MA. Oyster shell dissolution rates in estuarine waters: effects of pH and shell legacy.
 J Shellfish Res. 2011;30(3):659-669. doi:10.2983/035.030.
 0308
- Doyle B, Bendell LI. An evaluation of the efficacy of shell hash for the mitigation of intertidal sediment acidification. *Ecosphere*. 2022; 13(3):e4003. doi:10.1002/ecs2.4003

- Alonso AA, Álvarez-Salgado XA, Antelo LT. Assessing the impact of bivalve aquaculture on the carbon circular economy. *J Clean Prod.* 2021;279:123873. doi:10.1016/j.jclepro.2020.123873
- Bach LT, Gill SJ, Rickaby REM, Gore S, Renforth P. CO₂ removal with enhanced weathering and ocean alkalinity enhancement: potential risks and Co-benefits for marine pelagic ecosystems. Front Climate. 2019;1:1-21. doi:10.3389/fclim.2019.00007
- 82. Gattuso J-P, Magnan AK, Bopp L, et al. Ocean solutions to address climate change and its effects on marine ecosystems. *Front Mar Sci.* 2018;5(337):1-18. doi:10.3389/fmars.2018.00337
- Kheshgi HS. Sequestering atmospheric carbon dioxide by increasing ocean alkalinity. Energy. 1995;20(9):915-922. doi:10.1016/0360-5442(95)00035-F
- 84. National Academies of Sciences, Engineering, & Medicine. A Research Strategy for Ocean-Based Carbon Dioxide Removal and Sequestration. The National Academies Press; 2022.
- 85. Oschlies A, Bach LT, Rickaby REM, Satterfield T, Webb R, Gattuso JP. Climate targets, carbon dioxide removal, and the potential role of ocean alkalinity enhancement. In: Oschlies A, Stevenson A, Bach LT, et al., eds. *Guide to Best Practices in Ocean Alkalinity Enhancement Research*. Copernicus Publications; 2023:1-9. doi:10.5194/sp-2-oae2023-1-2023
- Renforth P, Henderson G. Assessing ocean alkalinity for carbon sequestration. Rev Geophys. 2017;55(3):636-674. doi:10.1002/ 2016rg000533
- 87. Smith SM, Geden O, Nemet GF, et al. The State of Carbon Dioxide Removal. 1st ed. MCC; 2023.
- Boyd PW, Bach L, Holden R, Turney C. Carbon offsets aren't helping the planet - four ways to fix them. *Nature*. 2023;620(7976):947-949. doi:10.1038/d41586-023-02649-8
- 89. Filgueira R, Byron C, Comeau L, et al. An integrated ecosystem approach for assessing the potential role of cultivated bivalve shells as part of the carbon trading system. *Mar Ecol Prog Ser.* 2015;518: 281-287. doi:10.3354/meps11048
- Giordano M, Beardall J, Raven JA. CO₂ concentrating mechanisms in algae: mechanisms, environmental modulation, and evolution. *Annu Rev Plant Biol.* 2005;56(1):99-131. doi:10.1146/annurev.arplant.56. 032604.144052
- 91. Hurd CL, Hepburn CD, Currie KI, Raven JA, Hunter KA. Testing the effects of ocean acidification on algal metabolism: considerations for experimental designs. *J Phycol*. 2009;45(6):1236-1251. doi:10.1111/j.1529-8817.2009.00768.x
- 92. Reinfelder JR. Carbon concentrating mechanisms in eukaryotic marine phytoplankton. *Ann Rev Mar Sci.* 2011;3(1):291-315. doi:10. 1146/annurev-marine-120709-142720
- 93. Bristow LA, Mohr W, Ahmerkamp S, Kuypers MMM. Nutrients that limit growth in the ocean. *Curr Biol.* 2017;27(11):R474-R478. doi:10. 1016/j.cub.2017.03.030
- Smaal AC. The ecology and cultivation of mussels: new advances.
 Aquaculture. 1991;94:245-261. doi:10.1016/0044-8486(91)90121-M
- 95. Chen Z, Nie T, Zhao X, et al. Organic carbon remineralization rate in global marine sediments: a review. *Reg Stud Mar Sci.* 2022;49: 102112. doi:10.1016/j.rsma.2021.102112
- Ho DT, Bopp L, Palter JB, et al. Monitoring, reporting, and verification for ocean alkalinity enhancement. In: Oschlies A, Stevenson A, Bach LT, et al., eds. Guide to Best Practices in Ocean Alkalinity Enhancement Research. Copernicus Publications; 2023:12. doi:10.5194/sp-2-oae2023-12-2023
- Gephart JA, Henriksson PJG, Parker RWR, et al. Environmental performance of blue foods. *Nature*. 2021;597(7876):360-365. doi:10. 1038/s41586-021-03889-2
- Naylor RL, Hardy RW, Buschmann AH, et al. A 20-year retrospective review of global aquaculture. *Nature*. 2021;591(7851):551-563. doi: 10.1038/s41586-021-03308-6

- Liu Y, Wang X, Wu W, Yang J, Wu N, Zhang J. Experimental study of the environmental effects of summertime cocultures of seaweed Gracilaria lemaneiformis (Rhodophyta) and Japanese scallop Patinopecten yessoensis in Sanggou Bay, China. Fishes. 2021;6(4):53. doi: 10.3390/fishes6040053
- Gattuso JP, Lavigne H. Technical note: approaches and software tools to investigate the impact of ocean acidification. *Biogeosciences*. 2009;6(10):2121-2133. doi:10.5194/bg-6-2121-2009
- Lewis E, Wallace D. Program Developed for CO₂ System Calculations. NCEI; 1998.
- Wolf-Gladrow DA, Zeebe RE, Klaas C, Körtzinger A, Dickson AG. Total alkalinity: the explicit conservative expression and its application to biogeochemical processes. *Mar Chem.* 2007;106(1):287-300. doi:10.1016/j.marchem.2007.01.006
- Zeebe RE, Wolf-Gladrow D. CO₂ in Seawater: Equilibrium, Kinetics, Isotopes. Gulf Professional Publishing; 2001.

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APPENDIX A

For illustrative purpose, we conducted simulations involving the production or dissolution of 100 µmol of CaCO $_3$ kg $^{-1}$ (i.e., 10 mg) to observe the impact on pCO $_2$ and seawater carbonate chemistry. This simulation was performed using the seacarb package in the R software, 11 although similar analyses can be carried out with other carbonate chemistry characterization programs such as CO $_2$ SYS. 100,101

The simulation was conducted under conditions of 15°C and salinity 35 and the assumption that seawater is equilibrated with the atmosphere with respect to CO_2 (i.e., 397 μ atm). Initial TA and DIC concentrations were set at 2300 and 2080 μ mol kg $^{-1}$, respectively. These two parameters, together with salinity and temperature, allow determining the remaining parameters of the carbonate chemistry 102,103 (Table A1).

The production of 100 μ mol of CaCO₃ results in a reduction of TA and DIC by 200 and 100 μ mol kg⁻¹, respectively, reaching

concentrations of 2100 and 1980 μ mol kg⁻¹. In a closed system without contact with the atmosphere, this leads to an increase in pCO_2 by 241 μ atm and a decrease in pH by 0.22 units.

In an open system, pCO_2 in seawater tends to equilibrate with the atmosphere. Consequently, seawater degasses, allowing excess CO_2 to escape to the atmosphere until equilibration is attained (i.e., 397 μ atm) and a new equilibrium is reached in the seawater carbonate chemistry. Under these conditions, final concentration of DIC is reduced by 171 μ mol kg $^{-1}$, of which 100 μ mol kg $^{-1}$ are due to $CaCO_3$ production and 71 μ mol kg $^{-1}$ are due to CO_2 degassing to the atmosphere. The latter corresponds to the value ψ , defined by Frankignoulle et al. 13 as CO_2 released into the atmosphere: precipitated carbonate ratio of 71/100 = 0.71. It is also worth noting that pH remains lower compared with the initial condition.

Dissolving 100 μ mol of CaCO₃ leads to opposite results: TA, DIC, and pH increase, while pCO₂ decreases (Table 1). Upon equilibration with the atmosphere, the water will have absorbed 71 μ mol kg⁻¹ of DIC and pH_T will remain slightly higher compared with the initial condition.

APPENDIX B

As many calcifying organisms, bivalves have the ability to use metabolic CO_2 produced through the respiration as an alternative carbon source for shell production. This energy consuming pathway involves the activity of the carbonic anhydrase, an enzyme which catalyses the transformation of bicarbonate ions (HCO_3^-) to CO_2 . Here we show that using metabolic CO_2 has the exact same consequence on seawater carbonate chemistry than by using seawater HCO_3^- or carbonate $(CO_3^{\,2-})$ ions.

The reaction of incorporating metabolic CO_2 that was enzymatically transformed to HCO_3^- , into the shell is:

$$CO_2 + H_2O + Ca^{2+} \Leftrightarrow CaCO_3 + 2H^+.$$

This reaction releases 2 hydrogen ions into seawater. The equilibration of the carbonate system involves the titration of these newly formed hydrogen ions by the most abundant base in seawater, HCO₃⁻ according to the following reversible reaction

TABLE A1 Seawater carbonate parameters under initial conditions and following production or dissolution of 100 μ mol of calcium carbonate (CaCO₃) before and after equilibration with the atmosphere.

Condition	System (open/closed)	DIC (μmol kg ⁻¹)	TA (μmol kg ⁻¹)	pΗ _T	pCO ₂ (μatm)	HCO_3^- (µmol kg $^{-1}$)	CO_3^{2-} (µmol kg $^{-1}$)
Initial		2080	2300	8.05	397	1907	159
Production	Closed	1980	2100	7.83	638	1862	94
	Open	1909	2100	8.01	397	1759	135
Dissolution	Closed	2180	2500	8.20	284	1940	230
	Open	2250	2500	8.08	397	2052	184

Abbreviations: CO_3^{2-} , concentration in carbonate ions; DIC, dissolved inorganic carbon; HCO_3^{-} , concentration in bicarbonate ions; pCO_2 , partial pressure of CO_2 ; pH_T , pH on the total scale; TA, total alkalinity.

$$2HCO_3^- + 2H^+ \Leftrightarrow 2CO_2 + 2H_2O$$
.

The overall reaction can therefore be written as:

$$2\mathsf{HCO}_3^- + \mathsf{Ca}^{2+} \Leftrightarrow \mathsf{CaCO}_3 + \mathsf{CO}_2 + \mathsf{H}_2\mathsf{O}.$$

This equation shows that calcification based on metabolic ${\rm CO}_2$ leads to the consumption of 2 moles of ${\rm HCO}_3^-$ (decrease of total alkalinity by 2 moles) and the consumption of 1 mole of dissolved inorganic carbon (2 ${\rm HCO}_3^-$ consumed - 1 ${\rm CO}_2$ produced), therefore shifting the system to a higher proportion of ${\rm CO}_2$ in seawater.