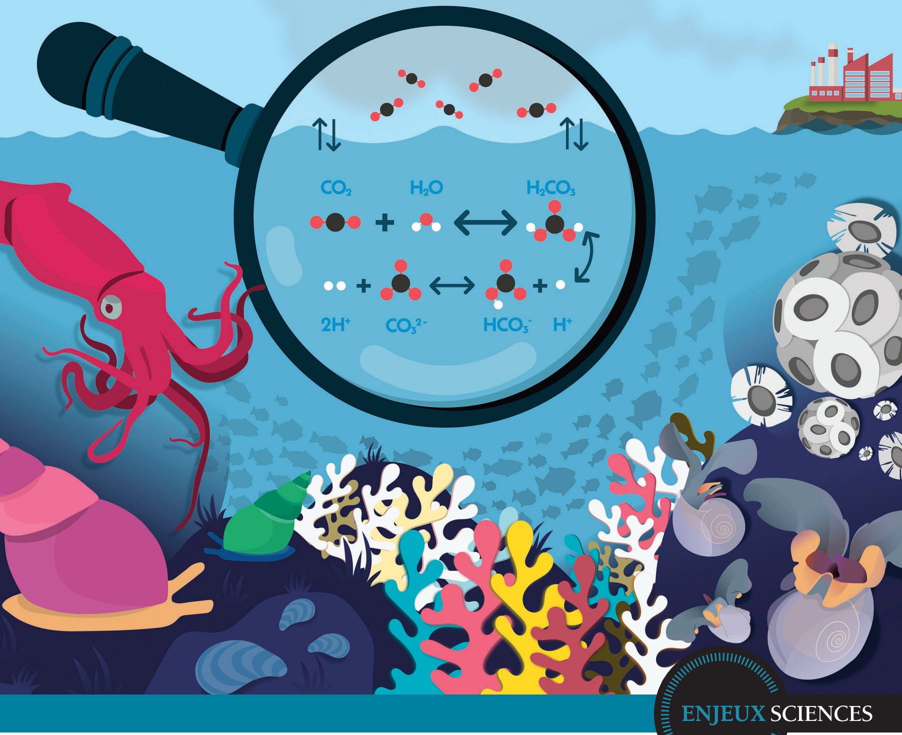

ENJEUX SCIENCES

OCEAN ACIDIFICATION

UNDERSTANDING THE EFFECTS, EXPLORING THE SOLUTIONS

FABRICE PERNET AND FRÉDÉRIC GAZEAU

éditions Quæ

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Introduction
Why a book on ocean acidification?

Human-induced climate change is now a proven fact, no longer in doubt in the scientific community. Heat waves, droughts and floods, storms and hurricanes of unprecedented power are current manifestations of this ongoing climate change, where exceptional events are becoming more and more frequent. The increasing combustion of fossil fuels such as coal, gas and oil, as well as deforestation for agriculture and urbanisation, are enlarging the concentration of greenhouse gases in the atmosphere, warming the planet. Of the greenhouse gases produced by this combustion, carbon dioxide (CO_2) is by far the most abundant.

Climate change is not the only consequence of rising atmospheric CO_2 concentrations. Anthropogenic CO_2 is also partly absorbed by the oceans, where it is transformed into carbonic acid, causing "ocean acidification". This phenomenon really emerged in the scientific literature in the early 2000s, becoming one of the most studied topics in marine science over the last twenty years. Through its effects on water chemistry, ocean acidification has multiple consequences for the marine world and its inhabitants, and consequently for the biological resources on which we depend to live.

However, ocean acidification, often referred to as "the other CO_2 problem" in reference to global warming, remains largely unknown to the general public. The few times the media mention this phenomenon, it is to ask whether we will still be eating oysters in 2100! While this question is relevant, as it suggests that these animals are sensitive to acidification, it deserves to be considerably broadened. In other words, the idea is to understand not only the world *we live from*, but also the world *we live in*, so that we can face the new climate regime with lucidity and pragmatism[1].

The aim of this book is to take a comprehensive look at ocean acidification by answering ten simple questions. It reviews the biogeochemical foundations of acidification; past, current and future trends; impacts on organisms, marine ecosystems and humans; and finally, remediation options and scientific perspectives.

The problem of ocean acidification is transdisciplinary, and finds its answers in biogeochemistry, marine biology and ecology, evolution, aquaculture and fisheries, as well as economics and sociology. May this book make accessible to as many people as possible the magnitude of this little-known phenomenon, which is nonetheless essential to understanding future changes.

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[1] Bruno Latour and Nikolak Schultz, 2022. *Mémo sur la nouvelle classe écologique*, Paris, La Découverte, coll. Les Empêcheurs de penser en rond, 96 p.

WHAT IS OCEAN ACIDIFICATION?

Human influence on the environment dates back to the origin of hominids, almost 3 million years ago. The hunting activities of Paleolithic hunter-gatherers led to the extinction of numerous animal species. Among the most emblematic examples are the extinctions of the megafauna of the last Ice Age, from the woolly mammoth of northern Eurasia to the giant wombats of Australia.

The advent of sedentarisation and agriculture 10,000 to 12,000 years ago reinforced human influence on the environment. During this period, humans intensified the exploitation of natural resources and transformed landscapes through deforestation and the development of irrigation. However, pre-industrial humans lacked the technological or organisational capacity to rival or dominate the great forces of nature. Their impacts remained largely local and transitory, well within the limits of natural environmental variability (Steffen *et al.*, 2007).

From the 18th century onwards, industrialisation turned humanity into a true geological and morphological force, as a number of scientists recognised early on. In 1873, for example, Stoppani described human activity as “a new telluric force whose power and universality may be compared with the greatest forces of the Earth” (quoted in Steffen *et al.*, 2007). Stoppani was already talking about the so-called “anthropozoic” era. However, it was not until the 2000s that the term “Anthropocene” appeared, referring to the current geological epoch marked by humanity’s central role in the great biogeochemical cycles of the elements (Crutzen and Stoermer, 2000).

In this chapter, we will see how the discovery and exploitation of vast quantities of carbon energy buried in the Earth’s subsoil have led to profound transformations in human societies, with major consequences for the carbon cycle, the Earth’s climate and ocean chemistry.

MACHINES, FOSSIL FUELS AND PEOPLE

Since the Industrial Revolution, whose origins broadly correspond to the invention of the internal combustion engine by James Watt in 1758, the number of humans populating the Earth and their level of wealth has increased exponentially (Steffen *et al.*, 2015). The use of more sophisticated and efficient machines greatly increased human capacity to produce goods, communicate and travel, enabling the emergence of the consumer society we know today.

The proliferation of machines and their widespread use in all sectors of production — agriculture, industry and service — was made possible by the discovery of abundant, free energy resources: fossil fuels such as coal, gas and oil. These natural energy resources, non-renewable on our timescales, were formed from plants and animals that lived hundreds of millions years ago. Fossil fuels are carbon-rich compounds that release an extraordinary amount of energy when burned, in addition to carbon dioxide, the famous "CO_2" which we are all familiar with.

This CO_2, naturally present in the atmosphere, is chemically inert, meaning it cannot degrade or react with other compounds to transform itself. Consequently, the CO_2 formed by the combustion of fossil fuels needed to sustain human activities accumulates in the atmosphere or is exchanged with the planet's other compartments, namely the land and the ocean.

GREENHOUSE EFFECT AND CO_2

The sun continuously emits energy in the form of visible light and ultraviolet rays. Some of this energy is absorbed by the Earth's surface, producing heat. The Earth then re-emits this heat as infrared radiation. Certain atmospheric gases, known as greenhouse gases, such as water vapour, CO_2, methane (CH_4), nitrous oxide (N_2O) and ozone (O_3), absorb part of the infrared radiation. The absorption of infrared radiation by these atmospheric gases has the effect of trapping heat in the atmosphere and raising the planet's temperature: this is the greenhouse effect. Without the greenhouse effect, the average global temperature would be – 18°C instead of the current 15°C.

Human activities produce large quantities of greenhouse gases, mainly in the form of CO_2, which increase the amount of heat at the Earth's surface and cause climate change. Despite the stated intentions of governments, CO_2 emissions have been rising steadily for decades, from 2 billion tonnes of CO_2 in 1900, to 6 billion in 1950 and over 37 billion in 2022, a 20-fold increase in just over a century[2]. Our greenhouse gas emissions have never fallen from one year to the next in the last twenty years, except during the financial crisis of 2008 and the COVID-19 pandemic in 2020.

Before the industrial era, the concentration of CO_2 in the atmosphere was around 280 parts per million (ppm), or 0.028% of the gases contained in the atmosphere. Since then, it has exceeded 400 ppm in 2013. The concentration of CO_2 in the atmosphere is currently monitored at numerous sites worldwide, but a series of measurements, started in the 1950s on the Mauna Loa volcano in Hawaii (USA), serves as a benchmark (Figure 1). At the time of writing (August 2023), the CO_2 concentration at this site is 419.68 ppm[3].

Analysis of the composition of ice cores extracted from the Antarctic ice sheet provides information on the climate and composition of the atmosphere going back up to about 800,000 years (Figure 1; Lüthi *et al.*, 2008). Air bubbles trapped in these ice cores at various depths (down to 3,600 m) enable us to assess the atmospheric concentration at the time of formation of these older and younger layers of ice, and thus to go back in time (Figure 1). These glacial climate archives show that CO_2 concentrations have varied periodically between around 180 and 280 ppm, corresponding to glacial and interglacial episodes respectively. These analyses also show that current atmospheric CO_2 concentrations and their rate of increase since 1950 are without historical precedent.

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[2] https://robbieandrew.github.io/GCB2022/PNG/s11_2022_FossilFuel_and_Cement_emissions_1990.png

[3] https://keelingcurve.ucsd.edu

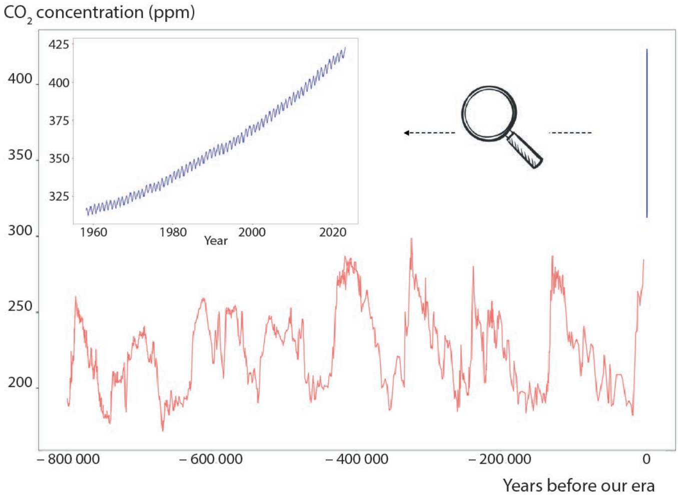

Figure 1. 800,000-year trend in atmospheric CO_2 concentration.

CO_2 concentrations are either estimated from the analysis of air bubbles trapped in ice collected in Antarctica (in red; https://www.ncei.noaa.gov/access/paleo-search/study/17975), or measured since the late 1950s at the Mauna Loa volcano in Hawaii (in blue on the right and enlarged on the graph inserted on the left; https://keelingcurve.ucsd.edu).

SOME LIKE IT HOT!

The increase in global surface temperature observed for decades now leaves no room for doubt. According to the World Meteorological Organisation, every decade since the 1980s has been warmer than the previous one. The average global temperature in 2022 was around 1.15°C higher than its pre-industrial level (period between 1850 and 1900), and the last eight years (2015-2022) are the warmest ever recorded in the world[4]. Although it is always difficult to establish links between cause and effect, the Intergovernmental Panel on Climate Change (IPCC) unambiguously reiterates in its latest synthesis report that global warming is indeed caused by greenhouse gas emissions linked to human activities (IPCC, 2023). In recent years, the

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[4] Press release dated January 12, 2023, available on the WMO website.

media have made the subject their own, resulting in a collective awareness of the phenomenon and its consequences.

THE FATE OF ANTHROPOGENIC CO_2

More than half of the CO_2 emitted into the atmosphere by human activities is captured by the terrestrial and oceanic compartments, considerably limiting the increase in the greenhouse effect and global warming. Terrestrial plants consume CO_2 to form organic matter from the energy provided by solar radiation, releasing oxygen in the process. This is the process of photosynthesis. The Global Carbon Project[5], which annually assesses anthropogenic CO_2 emissions and their redistribution, estimates that, on the one hand, the terrestrial biosphere has captured around 12.8 billion tonnes of CO_2, or 31.4% of emissions linked to human activities in 2021 (Friedlingstein *et al.*, 2022).

On the other hand, around 25% of atmospheric CO_2 dissolves in seawater and is exported to the deep ocean through biological and physical processes. At the ocean surface, dissolved CO_2 is captured by phytoplankton and transformed into organic matter, which eventually sinks to the deep layers, far from the atmosphere. Additionally, dissolved CO_2 is transported by currents from the surface to the bottom *via* the thermohaline circulation, which stirs up water on a global scale, both at the surface and in the deep ocean. The thermohaline circulation is driven by density differences in seawater, which depend on temperature and salinity, hence the term “thermos” for temperature and “halin” for salinity. At high latitudes in the Northern Hemisphere, surface water cools, increasing its density. This water, now denser and therefore heavier than the layers below, sinks to the depths, taking with it the CO_2 it has exchanged with the atmosphere at the ocean surface. The CO_2 thus exported to depths continues its journey southwards through the deep layers of the ocean, following the thermohaline circulation, and is temporarily removed from exchanges with the atmosphere. It is estimated that it takes between 1,000 and

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[5] https://www.globalcarbonproject.org/carbonbudget/

1,500 years for a water molecule to complete this entire circuit. As a result, these waters eventually rise back to the surface and exchange the CO_2 with the atmosphere. The oceanic carbon pump has stored around 10.5 billion tonnes of CO_2, or 26.2% of our emissions in 2021 (Friedlingstein *et al.*, 2022).

When CO_2 dissolves in seawater, the entire chemistry of dissolved inorganic carbon is altered. Dissolved inorganic carbon, or DIC, includes CO_2, bicarbonate ions (HCO_3^-) and carbonate ions (CO_3^{2-}). The chemical reactions that result from CO_2 dissolution are relatively complex and will only be briefly described here (for more information, see Zeebe and Wolf-Gladrow, 2001).

Some of the CO_2 absorbed by the ocean reacts with water (H_2O) to form carbonic acid (H_2CO_3), according to the reaction:

$$CO_{2(aq)} + H_2O \rightleftharpoons H_2CO_3 \text{ (eq. 1)}$$

Carbonic acid is unstable in water and rapidly dissociates into hydrogen ions (or protons H^+) and bicarbonate ions (HCO_3^-):

$$H_2CO_3 \rightleftharpoons HCO_3^- + H^+ \text{ (eq. 2)}$$

Some of the protons released by carbonic acid can react with carbonate ions (CO_3^{2-}) to form bicarbonate ions once again:

$$H^+ + CO_3^{2-} \rightleftharpoons HCO_3^- \text{ (eq. 3)}$$

As the production of hydrogen ions leads to an increase in acidity, the consequence of the absorption of anthropogenic CO_2 by the ocean has been dubbed “ocean acidification”.

pH, or hydrogen potential, is a measure of acidity on a scale of 0 to 14, calculated from proton concentration ($pH = -\log[H^+]$). The pH scale is logarithmic, meaning that a deviation of one unit indicates a division or multiplication of the proton concentration by ten. A liquid is said to be acidic or basic when the pH is respectively below or above 7, the so-called neutral pH value that characterises pure water. The surface ocean is slightly basic, with an average pH of 8.1. The projected decrease over the coming centuries will not cause the surface ocean to fall below neutrality. Strictly speaking, the ocean will not become acidic, nor will it turn into lemon juice! Ocean acidification consists of a shift in pH towards the acidic pole, without actually reaching it.

The above equations clearly show that the uptake of CO_2 by the ocean is not simply a matter of increasing its acidity. Firstly, the addition of CO_2 leads to a rise in the concentration of dissolved inorganic carbon. Secondly, there is an elevation in the proportion of bicarbonate ions and a decrease in the proportion of carbonate ions. These changes are illustrated in Figure 2, which shows the relative proportions of each molecular species of dissolved inorganic carbon as a function of pH. At the ocean surface, dissolved inorganic carbon is composed of 87.6% bicarbonate ions, 11.9% carbonate ions and 0.5% CO_2 at a temperature of 25°C, a salinity of 35 and a pH level of 8.1. As pH decreases, acidity increases; this equilibrium shifts to the left of the graph, with more bicarbonate ions, more CO_2, and fewer carbonate ions.

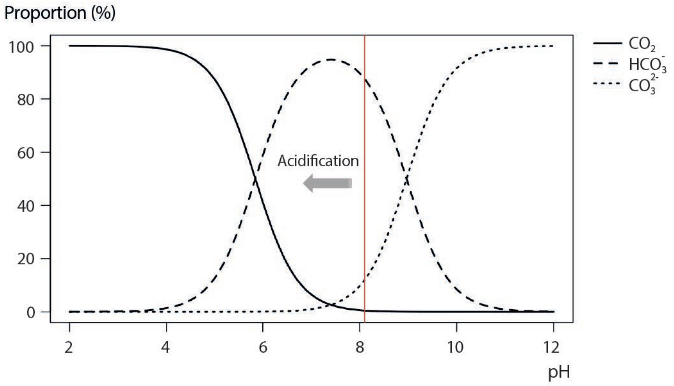

Figure 2. Bjerrum plot showing the relative contribution of carbon dioxide (CO_2), bicarbonate ions (HCO_3^-) and carbonate ions (CO_3^{2-}) to dissolved inorganic carbon (DIC) in seawater, as a function of pH.

The red vertical line represents the average pH of the current surface ocean. In this example, the temperature is set at 15°C and the salinity at 35. The graph is based on the Bjerrum function in the R package "seacarb" (Gattuso *et al.*, 2023).

All these changes in seawater chemistry have repercussions for marine organisms, which we will detail in Chapter 5. In particular, the drop in carbonate ions is problematic for calcifying organisms, such as corals and molluscs, which use this compound along with calcium ions (Ca^{2+}) to produce calcium carbonate ($CaCO_3$ or limestone), the building block of their shells or skeletons. This process, known as "calcification" or "biomineralization", can be summed up in the following chemical equation:

$$Ca^{2+} + CO_3^{2-} \rightleftharpoons CaCO_3 \text{ (eq. 4)}$$

Given the equilibrium that exists between the different species of inorganic carbon dissolved in seawater, the balance equation for calcification and its inverse, dissolution, is written as follows:

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

Thus, calcification consumes bicarbonate ions and produces CO_2 while limestone dissolution produces bicarbonate ions and consumes CO_2. These changes therefore imply a decrease in pH when calcification is favoured and an increase when dissolution dominates.

The ability of organisms to precipitate calcium carbonate depends on the degree to which the seawater is saturated with this element, known as the "saturation state" and expressed by the Greek letter omega (Ω). When the saturation level is greater than 1, calcium carbonate tends to precipitate, i.e. forms a solid molecule. Conversely, when water saturation is less than 1, calcium carbonate tends to dissolve. The saturation state of seawater (Ω) is calculated from the following equation:

$$\Omega = \frac{[Ca^{2+}]\,[CO_3^{2-}]}{[Ca^{2+}]_{sat}\,[CO_3^{2-}]_{sat}} \text{ (eq. 6)}$$

The saturation state is therefore defined as the ratio between observed calcium and carbonate ion concentrations and those expected when the solution is at saturation (*sat*). As a result, ocean acidification leads to a drop in saturation levels, to the point of favouring the dissolution of limestone structures rather than their precipitation in certain regions.

Thus, the uptake of atmospheric CO_2 of human origin by the ocean leads to a series of chemical changes that come under the heading of "ocean acidification", with potential consequences for marine life. Awareness of this "other CO_2 problem" has lagged behind that of global warming.

HOW LONG HAVE WE BEEN TALKING ABOUT OCEAN ACIDIFICATION?

The discovery of the ocean acidification process is closely linked to the recent understanding of the chemical principles of acidity and the development of precise tools for measuring this parameter.

JUST ACIDITY!

The first theory of acidity is attributed to French chemist Antoine Lavoisier, who at the end of the 18th century defined an acid as a compound containing oxygen. This inaccurate theory was corrected a century later by Svante August Arrhenius, who defined an acid as a substance which, when placed in aqueous solution, releases hydrogen or proton ions (H^+), whereas a base is a substance which, when placed in aqueous solution, releases hydroxide ions (OH^-). The Nobel Prize-winning Swedish chemist, who pioneered the understanding of the greenhouse effect, extended the concept of acidity to carbon dioxide (CO_2), which reacts with water molecules to form carbonic acid (H_2CO_3) (eq. 1, Chapter 1, p. 12). Arrhenius' work laid the foundations for understanding CO_2 as an acid and its impact on chemical equilibria in various aqueous systems, including seawater.

The concept of pH or "hydrogen potential" was introduced as a quantitative measure of a solution's acidity in 1909 by biochemist Søren Peter Lauritz Sørensen. The first pH measurements in seawater date back to this period. However, these early measurements cannot be used to study acidification trends, as they are too rare and not always reliable.

HOW IS pH MEASURED?

Since the beginning of the 20th century, the pH of seawater has been measured using glass electrodes. Their operating principle is based on the difference in concentration of oxonium ions (H_3O^+) existing on either side of a very thin glass membrane (approx. 0.1 mm), which generates an electrical potential, known as the "membrane potential". This is proportional to the pH of the aqueous solution in which the electrode is immersed. This measurement technique, still used today for experimental laboratory studies, is associated with uncertainties that are too large (0.02 pH units) to allow estimation of inter-annual variations in ocean pH, which are of the order of a few thousandths of a pH unit.

A spectrophotometric method[6] using a specific dye, m-cresol purple, was first proposed in 1988 (Byrne *et al.*, 1988). The colour of the sample mixed with m-cresol changes from yellow to purple when the pH varies between 7.4 and 9.0. Measuring pH spectrophotometrically is much more precise than using glass electrodes, and can achieve uncertainties of the order of 0.003 pH units, making it possible to quantify the ongoing decrease in ocean pH levels.

From the 2000s onwards, autonomous sensors were developed to be installed on instrumented buoys in the ocean to measure pH at high frequency, without the need to visit the site and take samples to the laboratory for measurement. ISFET sensors (for "Ion-Sensitive Field Effect Transistor") use an ion-sensitive field effect transistor. When H^+ protons bind to the surface of the transistor, they alter its conductivity and generate a pH signal. Another technique combines a water sampler with pH spectrophotometric measurement. The idea is to take a water sample automatically at regular intervals using a small programmable pump, inject the dye into the sample and measure its absorbance to determine the pH[7].

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[6] A spectrophotometer is used to determine the concentration of a chemical species in a solution (in the case of pH, protons). To do this, the device measures the intensity of light passing through a sample at a given wavelength. More precisely, the spectrophotometer measures absorbance, i.e. the proportion of light radiation absorbed by the sample. The higher the absorbance, the higher the concentration.

[7] http://www.sunburstsensors.com/products/oceanographic-ph-sensor.html

Recent technological developments have made it possible to miniaturise pH sensors and incorporate them into autonomous devices such as ARGO profiling floats, which have been deployed in the ocean for thirty years to measure salinity and temperature. Several thousand floats drift in all the world's oceans to measure these parameters continuously. For the moment, very few floats are equipped with pH sensors, but current developments are very promising and will, in the near future, greatly increase the spatial and temporal resolution of pH measurements in the ocean.

Finally, it should be noted that, if not measured, pH can be calculated from the measurement of two other carbonate chemistry parameters. Indeed, the carbonate system can be described by six parameters: total dissolved inorganic carbon (DIC), total alkalinity (TA or A_T), and the concentrations of CO_2, HCO_3^-, CO_3^{2-}, and H^+. As these six parameters are linked by four equations, the measurement of two parameters enables the entire system to be solved (Zeebe and Wolf-Gladrow, 2001).

HOW ARE OTHER CARBONATE CHEMISTRY PARAMETERS MEASURED?

The parameters of carbonate chemistry that can be measured in the laboratory are total alkalinity, dissolved inorganic carbon and CO_2 concentration, more precisely referred to as CO_2 partial pressure (pCO_2).

The total alkalinity of seawater is a measure of its ability to neutralise protons and thus resist pH changes. It relies on the weak bases present in the water that can accept these protons. These are largely represented by bicarbonate ions (HCO_3^-) and carbonate ions (CO_3^{2-}). Total alkalinity is measured by adding a strong acid solution (usually hydrochloric acid) of a known concentration. The principle is to add acid until all weak bases have disappeared. This can be detected graphically by a rapid drop in pH, as the protons added by the strong acid can no longer be neutralised by the weak bases. Total alkalinity is thus proportional to the amount of acid added to reach this tipping point.

There are several techniques for analysing the concentrations of dissolved inorganic carbon in a seawater sample. They are all based on the same principle, which also involves adding a strong acid to convert bicarbonate and carbonate ions into CO_2. The techniques for quantifying the quantity of CO_2 present in the sample then differ according to the methods employed, but one of the most common is to rely on the principle of the greenhouse effect: CO_2 absorbs infrared rays. All that needs to be done is to transport the CO_2 produced with an inert gas (which does not absorb infrared rays) to an analyser, which will measure the absorption of infrared rays by CO_2.

Finally, the main technique used to measure the partial pressure of CO_2 in water is to equilibrate a volume of air with a sample of seawater by bubbling. This air, whose initial CO_2 concentration is known (it is also possible to use CO_2-free air by trapping the CO_2 with an absorbent, usually lime), is then sent to an infrared analyser for precise determination of the CO_2 concentration.

pH MONITORING AND THE EMERGENCE OF THE TERM OCEAN ACIDIFICATION

The first reliable monitoring of pH and carbonate chemistry began in the 1980s. At the time, attention was primarly focused on the role of the ocean as a carbon sink, and not on long-term changes in marine pH. It was in the late 1990s and early 2000s that a handful of scientific studies explicitly addressed the effects of CO_2 enrichment in the ocean on calcifying marine organisms. The term “ocean acidification” was introduced and popularised in 2003 by Caldeira and Wickett, who even proposed a projection for the year 2300 (Caldeira and Wickett, 2003).

SCIENTIFIC AWARENESS

The first three IPCC reports, published in 1990, 1995 and 2001, made no mention of the term “ocean acidification”. It was not until the publication of the 4th report, in 2007, that it appeared: "The fixation of anthropogenic carbon emitted since 1750 has lowered the pH of the ocean by an average of 0.1 units. The rise in atmospheric CO_2 concentration has further accentuated the acidity of the marine environment. According to projections based on various socio-economic scenarios, the average surface pH of the ocean is set to fall by between 0.14 and 0.35 units over the course of the 21th century. The effects on the marine biosphere are not yet known, but it is thought that the phenomenon will have a detrimental impact on marine testaceans[8] and crustaceans and the species that depend on them" (IPCC, 2007).

Meanwhile, the first symposium on the Ocean in a High-CO_2 World was held in Paris in 2004, sponsored by the Scientific Committee on Oceanic Research (SCOR) and the Intergovernmental Oceanographic Commission (IOC). The aim of the symposium was to bring together international experts to discuss scientific advances and the impacts of ocean acidification on marine ecosystems. Since this first initiative, the symposium has been held every four years, the most recent edition taking place in 2022 in Lima, Peru.

These symposia were important for several reasons. The second symposium (Monaco, 2008) saw the publication of the Monaco Declaration[9], signed by 155 scientists from 26 nations, calling for a reduction in CO_2 emissions to protect the ocean from the harmful effects of acidification. In 2012, the third symposium (Monterey, USA) produced a summary of the state of knowledge on ocean acidification for decision-makers[10]. Finally, these symposia have contributed to the development of international initiatives such as the Ocean Acidification International Coordination Centre (OA-ICC) or the Global Ocean Acidification Observation Network (GOA-ON) in 2011-2012 to promote coordinated research and societal awareness of ocean acidification.

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[8] Said of an animal with a shell.

[9] https://www.iaea.org/sites/default/files/monacodecl061008.pdf

[10] http://www.igbp.net/download/18.30566fc6142425d6c91140a/1385975160621/OA_spm2-FULL-lorez.pdf

Ocean acidification has thus become an active field of research and a matter of worldwide concern. Since the first laboratory experiments on the effects of acidification on marine organisms in the late 1990s, interest in this subject, which emerged from chemists and physiologists, has gradually spread to ecologists, biogeochemists, palaeontologists and economists — and has grown exponentially in recent years, with the number of publications increasing more than fifty-fold between 2003 and 2023.

PUBLIC AWARENESS

Despite these major advances in the scientific community, public awareness still lags far behind other environmental concerns. Indeed, while public awareness of climate change is now almost universal, a UK study showed that only 20% of people surveyed from a representative sample of 2,500 individuals between 2013 and 2014 had ever heard of ocean acidification (Capstick *et al.*, 2016). More recent studies suggest little change in this situation, both among the general public and at government level (Gallo *et al.*, 2017; Tiller *et al.*, 2019; Insinga *et al.*, 2022), despite the publication of the 5th IPCC Synthesis Report, which discusses ocean acidification and its impacts on marine ecosystems in detail (IPCC, 2014). May the special report on the ocean and the cryosphere published by the IPCC in 2019 (IPCC, 2019) foster this collective awareness.

HOW IS OCEAN ACIDITY EVOLVING?

The definition of the concept of acidity and the development of precise pH measurement tools have shown that the ocean is acidifying. But what is the extent of this acidification? What are the future trajectories of ocean acidification? How do current trends and future projections compare with past variations? This is what we are going to investigate now.

HOW FAR HAS pH FALLEN SINCE THE INDUSTRIAL REVOLUTION?

Between 1960 and 2020, the ocean absorbed an increasing amount of atmospheric CO_2, rising from 1 to 3 Gt C year^{-1} (G for giga = 1 billion), causing a significant drop in pH[11]. Field measurement series covering periods of over 15 years show a decrease of the order of 0.017-0.027 pH units per decade (Figure 3). These local decreases are confirmed by estimates of global ocean pH. According to these estimates, ocean acidification is accelerating. Since the 1960s, pH has fallen by between 0.013 and 0.022 units per decade, compared with just 0.003 units per decade for the period 1850-1900 (Figure 4). Since the industrial revolution, the average pH of the ocean has therefore fallen from 8.16 to 8.05 (– 0.1 pH units), representing a 30% increase in acidity.

WHAT pH VALUES ARE EXPECTED BY 2100?

To answer this question, researchers use mathematical models that convert greenhouse gas emissions into atmospheric concentrations, and then into future warming and acidification.

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[11] Global Carbon Project: https://robbieandrew.github.io/GCB2022/PNG/s54_2022_ESSD21_Fig09.png

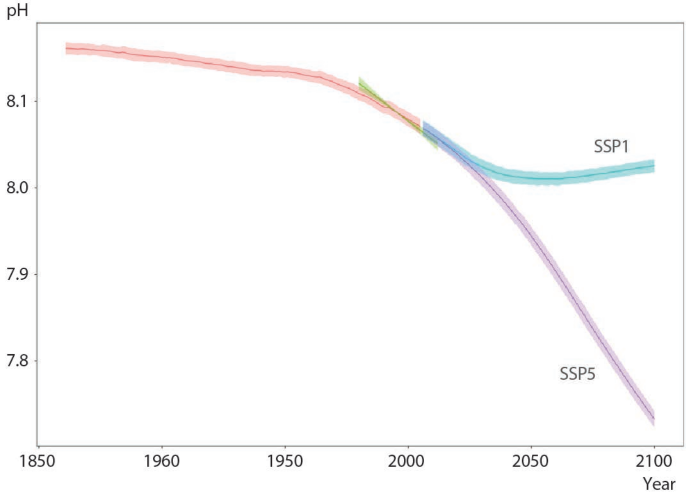

Figure 3. Observed decrease in pH on data series older than 15 years (green), compared with the estimated decrease in pH since the Industrial Revolution (orange) and those projected for the end of the current century according to two distinct scenarios of CO_2 emissions (SSP1 in turquoise and SSP5 in violet). Data taken from Kwiatkowski *et al.* (2020).

SSP1 represents a scenario that can be described as optimistic, leading to a halt in CO_2 emissions over the next few decades, while SSP5 assumes that these emissions will continue to rise at the same rate as at present until the end of the century. A more detailed definition of these scenarios is provided in the following paragraph.

The models are simplified representations of the planet and the interactions between the atmosphere, ocean and continents that influence climate. These models are based on projected anthropogenic CO_2 emission scenarios. With the publication of the IPCC's Sixth Assessment Report (IPCC, 2023), Shared Socio-economic Pathways (SSP) have replaced Representative Concentration Pathways (RCP) scenarios.

SSPs are the most complex emission scenarios ever developed, covering the full range of projections, from very ambitious mitigation measures to continued, unbridled growth in CO_2 emissions. The most ambitious mitigation scenario has been specifically designed to limit the increase in global average temperature to 1.5°C above pre-industrial levels, as set by the Paris Agreement in 2015.

The SSPs represent hypotheses of socio-economic development over the coming century, taking into account factors such as population size, education, urbanisation, Gross Domestic Product[12], economic growth, technological progress, and so on. Five scenarios were created, each with varying assumptions, and used in conjunction with an updated estimate of the radiative forcings[13] (and therefore global warming) that would be reached by the end of the century.

These different SSPs correspond to increasing levels of radiative forcing, from 1.9 to 8.5 $W\ m^{-2}$ (W for watt, the unit of power or energy flux), with higher values representing greater global warming. In IPCC terminology, the climate projections presented on the basis of these scenarios are therefore referenced with the term "SSPx-y", *x* corresponding to the SSP number and *y* to the projected radiative forcing level in 2100.

Five SSPs have been selected by the IPCC. SSP1 is based on sustainable and inclusive development, reducing inequalities and promoting efficient resource consumption. CO_2 emissions fall immediately to zero by 2050-2075, then become negative thereafter. This scenario is therefore based on the capture of atmospheric CO_2. According to this scenario, the temperature rise is in the order of 1.4 to 1.8°C by 2100.

The SSP2 follows the emissions trends observed over recent decades without major changes, with uneven economic growth and limited attention to sustainability. CO_2 emissions only decrease from 2050 onwards, and global warming is limited to 2.7°C by 2100.

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[12] GDP is the economic indicator that quantifies the total value of the annual "production of wealth" by economic agents (households, companies, public administrations) residing within a territory. It therefore reflects a country's internal economic activity.

[13] The term "radiative forcing" ($W\ m^{-2}$) of the climate system refers to any variation in the energy transmitted to the Earth-atmosphere system as a whole, caused by changes in forcing factors. It is therefore the difference between the radiative energy received and the radiative energy emitted by a given climate system. Positive (more energy received than emitted), it tends to warm the system. Negative (more energy emitted than received), it tends to cool the system.

SSP3 focuses on the rise of nationalism and regional competitiveness, with slow economic growth and variable environmental degradation. SSP4 shows increasing inequality, social fragmentation and locally-focused environmental policies. Finally, SSP5 focuses on market-led development and innovation, with rapid economic growth and high fossil fuel use, but a declining world population. These last three scenarios imply that CO_2 emissions will continue to rise, with a warming of between 3.6 and 4.4°C by the end of the century.

According to these scenarios, the pH decreases projected for the end of the century are 0.16 (SSP1-2.6), 0.26 (SSP2-4.5), 0.35 (SSP3-7.0) and 0.44 (SSP5-8.5) compared to the values estimated for the period 1870-1899. These decreases correspond respectively to an average surface ocean pH level in 2100 of 8.0, 7.9, 7.81 and 7.72.

Eventually, the implementation of effective environmental policies or the predicted exhaustion of fossil fuel reserves should reduce our CO_2 emissions into the atmosphere to zero, and a new equilibrium will be established with the ocean. However, it will take hundreds of thousands of years to neutralise the CO_2 that we will have emitted in just a few hundred years.

HAS THE OCEAN EVER BEEN ACIDIFIED?

There is no doubt that ocean chemistry has changed considerably in the past, and that it was once more acidic than it is today. But that is not saying much. We will see that a more “acidic” ocean can be rich in carbonate and favourable to calcifying organisms. Comparisons between the future and the past, made without sufficient knowledge of how the ocean carbon cycle is regulated on geological timescales, will inevitably lead to erroneous conclusions. Although the geological record opens a window onto the future in terms of chemical changes in the ocean and their effects, the analogy must be fair, and comparable situations must be compared. To do this, we need to understand the carbon cycle, the factors that influence it, and the time scales involved. We will start with a brief explanation of the carbon cycle and the factors at work on different timescales, with a closer look at the fate of anthropogenic carbon as described in Chapter 1; we will then take a detour into the methods used by scientists to reconstruct past variations in carbonate chemistry, and finally retrace past trends.

How does the carbon cycle work?

The cycling of an element on Earth is characterised by the existence of reservoirs of different sizes, the flows that link these reservoirs, and the residence times of the element within each reservoir. The atmosphere, the surface layers of soil and ocean, and the biosphere together account for around 4,000 gigatonnes of carbon (Gt C), which are balanced on short timescales of the order of a decade to a century.

By burning fossil fuels, mankind suddenly transfers carbon stored underground into the atmosphere, disrupting the natural cycle described above. Human activities currently emit around 10 Gt C per year. Fossil fuel reserves have been estimated at around 5,000 Gt C. It is therefore clear that the release of several thousand gigatonnes of carbon over a few hundred years exceeds the absorption capacity of the surface reservoirs we have just described.

The deep ocean represents an immense carbon reservoir, estimated at 38,000 Gt. To reach equilibrium between the surface reservoirs and the deep ocean following a disruption of the natural carbon cycle, it takes millennia. A thousand years is roughly the time it takes for the ocean to mix completely (Chapter 1, p. 11). Consequently, this is also the time it will take to reach a new state of equilibrium after the cessation of anthropogenic carbon emissions. In this new equilibrium, atmospheric and oceanic CO_2 levels will rise and the ocean will become acidified.

And this is where deep-sea carbonate sediments come in, a reservoir estimated to be 5,000 Gt in size. Acidification promotes the dissolution of limestone, which consumes CO_2 and raises the pH (eq. 6, Chapter 1, p. 14). As a result, anthropogenic carbon absorbed by the ocean will eventually be neutralised by reaction with carbonate sediments. This is a major process in maintaining the equilibrium of carbonate chemistry in the ocean. However, this process is slow and the elimination of fossil carbon from the atmosphere will take hundreds of thousands of years.

Finally, the largest carbon reservoir, estimated at around 90 million gigatonnes of carbon, is trapped in the Earth's crust. This reservoir, sometimes exposed at the surface due to tectonic plate movements, is relatively inert on timescales of less than a million years.

How can we estimate variations in ocean pH over geological time?

Scientists have several methods at their disposal for reconstructing past CO_2 concentrations in the atmosphere and estimating marine pH levels. The first approach, discussed in Chapter 1, involves analysing the CO_2 content of air bubbles trapped in ice to estimate atmospheric concentrations of this gas and deduce pH. This method makes it possible to go back more than 800,000 years (Figure 1, p. 10).

Another approach, which makes it possible to assess CO_2 concentrations and pH further back in time, is to analyse the isotopes[14] of boron accumulated in calcareous deposits produced by calcifying organisms such as foraminifera. Boron is a mineral element present in seawater in the form of two stable isotopes whose proportions vary according to ocean pH. By analysing the isotopic composition of boron, we can trace the evolution of marine pH back as far as 300 million years!

There are several other methods, which we will not describe here, but it should be borne in mind that each has its advantages and limitations, and reconstructions of past CO_2 or pH concentrations remain uncertain. Consequently, scientists combine several methods to obtain the most reliable estimates possible.

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[14] Isotopes of a chemical element are nuclides that share the same number of protons (characteristic of the element), but have a different number of neutrons.

What do we know about past variations, and what can we learn from them?

During the Holocene, namely the 12,000 years prior to the industrial era, atmospheric CO_2 concentration and all carbonate chemistry parameters have remained remarkably stable (Zeebe, 2012). Atmospheric CO_2 concentrations, ocean surface pH and saturation levels relative to limestone showed variations of around 20 ppm, 0.04 units and 10% respectively. To contextualise these figures, in relation to recent evolution, note that atmospheric CO_2 concentration has increased by 120 ppm, oceanic pH has fallen by 0.1 units and saturation levels have decreased by around 15% over the last 150 years.

Over the last 800,000 years, atmospheric CO_2 levels have fluctuated periodically between 200 and 280 ppm, with alternating glacial and interglacial episodes (Figure 1, Lüthi *et al.*, 2008). These glacial and interglacial cycles were likely accompanied by periodic changes in ocean surface carbonate chemistry, while deep-sea pH and carbonate ion concentration would have remained relatively stable (Zeebe, 2012).

During ice ages, ice formation reduces freshwater inflow, erosion and the input of carbonate ions into the ocean, promoting the dissolution of carbonate marine sediments. This dissolution of limestone consumes CO_2, produces carbonate ions and raises the pH of the water. Thus, during ice ages, the pH of the ocean surface is higher, around 8.3, than during interglacial periods, and the atmospheric concentration of CO_2 is lower, below 200 ppm. In interglacial periods, all the processes described above are reversed: warming causes ice to melt, which increases freshwater inflows, erosion and carbonate ion inputs. The production of limestone by calcifying organisms increases, producing CO_2, consuming carbonate ions and lowering pH. Interglacial periods are thus characterised by a lower pH than glacial periods, around 8.2, and a higher concentration of CO_2 in the atmosphere, of the order of 250 to 300 ppm.

Consequently, a deglaciation could be considered as an acidification event, even if its evolution is truly slow and moderate. Nevertheless, deglaciation cannot be compared with current anthropogenic disturbance. Indeed, the average rate of change in ocean surface pH during the most recent deglaciation, estimated at between 0.001 and 0.002 pH units per century, is incomparable with IPCC projections (– 0.35 pH units in two centuries according to SSP3). Thus, chemical changes at the ocean surface during the Anthropocene are expected to be three to seven times greater and 70 times faster than during deglaciation (Zeebe, 2012).

Analysis of glacial and interglacial cycles clearly shows that the Earth system possesses a strong self-regulatory capacity that maintains carbonate chemistry in a quasi-stationary state over long periods, limiting pH variations to 0.1 units. This relative homeostasis[15] underlines the unprecedented aspect of ocean acidification due to human activities on a scale of hundreds of thousands of years.

Looking further back, it appears that carbonate chemistry parameters in the ocean have varied very slowly over the last 4.5 million years. Over this long period, CO_2 levels have fluctuated between around 200 and 500 ppm, while surface ocean pH has oscillated between approximately 8.0 and 8.3 on timescales greater than 10,000 years.

During the Cenozoic, a period between 66 and 2.6 million years ago, marked by the extinction of the dinosaurs, the diversification of mammals, the evolution of primates and the appearance of the first hominids, atmospheric CO_2 concentrations would have decreased gradually from a few thousand ppm (probably due to intense volcanic activity) to around 200 ppm, so that the pH of the surface ocean would have increased from 7.6 to around 8.2. Despite these variations, the saturation state of the ocean surface with respect to limestone was almost constant, thanks to the influx of carbonate ions. This particular situation helped maintaining conditions favourable to the establishment of a high level of biodiversity, including numerous calcifying organisms such as corals, molluscs and foraminifera, which contributed to the formation of limestone deposits. The cliffs of Dover in Great

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[15] Refers to a system's ability to maintain a stable internal state of equilibrium despite external disturbances. This system has internal regulatory mechanisms that act to keep key variables within specific ranges of values, thus promoting stability.

Britain and Étretat in France, for example, were formed during this period by the accretion of calcareous platelets produced by calcifying micro-algae known as coccolithophores. The rate of increase in CO_2 concentrations today makes our era incomparable with this ancient geological period.

DOES THE CURRENT PERIOD HAVE AN EQUIVALENT IN THE GEOLOGICAL PAST?

From what we have just seen, we could quickly answer no. But beware: the evolution of the Earth's climate as presented does not account for geological catastrophes that occurred over short periods of time and could have caused pH changes as rapid as those observed today. So, what exactly is the situation?

The most famous geological and biological catastrophe responsible for the extinction of the dinosaurs occurred around 66 million years ago on a very short time scale at the boundary between two geological periods, the Cretaceous and the Tertiary, known as the KT. Scientists explain KT extinctions by one or more catastrophic events, such as massive asteroid impacts, and increased volcanic activity. Analyses of the chemical content of foraminiferal tests indicate a rapid decrease (over 1,000 years) in pH in the range of 0.25 units, corresponding to an increase in the concentration of CO_2 from around 900 to 1,600 ppm, immediately after the catastrophe. This decrease in pH would have put calcifying planktonic organisms at a disadvantage compared to non-calcifying ones, which explains the selective extinction of these species as observed in sedimentary archives. Climate reconstructions show that surface acidification was compensated for after around 120,000 years, mainly due to the extinction of calcifying organisms and the consequent decrease in calcification, which has the effect of lowering pH.

Another event identified during which ocean chemistry was drastically altered was the Palaeocene-Eocene Thermal Maximum (PETM). This was a period of extreme climatic warming around 55 million years ago. During this period, atmospheric CO_2 levels increased for reasons that are not fully understood. The pH would have decreased by around 0.3 to 0.4 units, with considerable repercussions for ocean life. The concentration of atmospheric CO_2, which was already much higher than today (approx. 1,500 *vs.* 420 ppm today), would have increased by a factor of 2 to 3 in the space of 5,000 to 10,000 years, leading to an increase in global surface temperature of 5 to 9°C. As an example, the temperature and hydrological regime of Antarctica during this period enabled the establishment of temperate forests, and the average surface ocean temperature was around 30°C at latitudes of 60°S, values currently found in the tropics. In the ocean, rapidly decreasing pH and calcium carbonate saturation states have led to extinctions of calcifying species, although the exact extent of these extinctions remains uncertain (McInerney and Wing, 2011). Studies have also shown a decline in the diversity of calcifying planktonic species, foraminifera and other marine organisms such as corals, although the reasons for this are not yet clearly identified.

These profound changes in ocean carbonate chemistry make it possible to estimate the possible impacts on marine organisms and the time required for the Earth system to return to a state of equilibrium, in view of the major changes induced by human activities over the last 150 years. However, even if these two geological accidents are the only known examples of rapid climate change, they are not comparable to the current situation. Indeed, CO_2 emissions during the PETM are estimated at a maximum of 4,500 Gt C over at least 4,000 years, which corresponds to an emission rate into the atmosphere of 0.6 to 1.1 Gt C per year, very far from the current CO_2 emission rates (10 Gt C per year, namely 10 times higher).

As far as we know, the current rate of increase in atmospheric CO_2 is unprecedented in the last 66 million years. In addition to being responsible for the ongoing global warming, the absorption of CO_2 has led to a drop in pH of around 0.1 units since the industrial revolution, representing an increase in acidity of around 30%. This decrease in pH is occurring at a rate around 100 times faster than any change in acidity over the last 55 million years. Ocean acidification will continue inexorably over the coming centuries, and its extent will depend on the ability of human societies to limit the use of fossil fuels.

IS OCEAN ACIDIFICATION A HOMOGENEOUS PHENOMENON ON THE SCALE OF THE GLOBAL OCEAN?

In previous chapters, we have often referred to average values for pH and carbonate parameters at the ocean surface and on an annual scale. However, these parameters are variable within the ocean and on different timescales. As a result, ocean acidification and its potential consequences for marine animals and plants are not homogeneous, depending on where and when we are.

Ocean carbonate chemistry varies according to latitude, proximity to coasts and rivers, origin of water masses and depth. Surface waters exchange CO_2 directly with the atmosphere, and are the site of significant production of organic matter through photosynthesis, or of calcium carbonate by calcifying organisms. Conversely, deep waters are isolated from the atmosphere, and due to the absence of light, lower temperatures and high pressures, biological production is low and the processes of organic matter mineralisation and limestone dissolution dominate.

pH and other ocean carbonate chemistry parameters also vary over time on hourly, diurnal or seasonal scales. The main drivers of this temporal variability are, on the one hand, biological processes associated with ecosystem metabolism, such as photosynthesis, respiration, precipitation and limestone dissolution. On the other hand, physical parameters (temperature, availability of light and nutrients: the essential resources of nitrogen, phosphate and other elements) also play a major role, through their influence on biological processes and *via* changes in water mixing dynamics (variations in tidal coefficients, winds and vertical movements: upwelling and downwelling) and external inputs (precipitation, fluvial inputs, etc.).

HOW DO pH AND CARBONATE PARAMETERS VARY IN THE OCEAN?

From the equator to the poles

Measurements of pH in the ocean over the past thirty years show that geographical variations are around 0.2 units (Figure 4). The lowest surface ocean pH values are found in equatorial regions. This latitudinal variability of oceanic pH is mainly governed by temperature and ocean currents.

Temperature affects pH in two ways. Firstly, as temperature rises, the equilibrium between CO_2, bicarbonate ions and carbonate ions shifts towards a higher proportion of CO_2 and induces a production of hydrogen ions, with the consequence of acidifying the water. In other words, as temperature increases, we move to the left on Bjerrum's plot (Figure 2, p. 13). Secondly, increasing temperature reduces the solubility of gases in water, including CO_2. As a result, the absorption of CO_2 by the ocean diminishes, to the point where CO_2 fluxes can be reversed, from the ocean to the atmosphere. In this case, the ocean becomes a source of CO_2 for the atmosphere with a consequent increase in marine pH. Increasing temperature thus produces two antagonistic effects on carbonate chemistry, which explains the low variability of ocean pH with latitude.

Although temperature has little effect on the latitudinal variability of surface pH, pH levels are generally lower at the equator. This is mainly due to the upwelling of deep waters, enriched in CO_2 and therefore more acidic, as a result of the thermohaline circulation. As water circulates in depth from the poles to the equator, it becomes loaded with organic particles from the surface, which degrade under the action of bacteria, leading to an accumulation of CO_2 and a drop in pH. This deep water eventually rises to the surface as it warms, mainly in equatorial regions.

Unlike pH, carbonate ion concentration shows a strong latitudinal gradient, governed mainly by temperature. Indeed, as we have seen, colder polar waters contain more CO_2 than warmer equatorial waters. Consequently, carbonate ion concentrations are much lower in polar waters than in equatorial waters. This is directly reflected in the saturation state of aragonite, one of

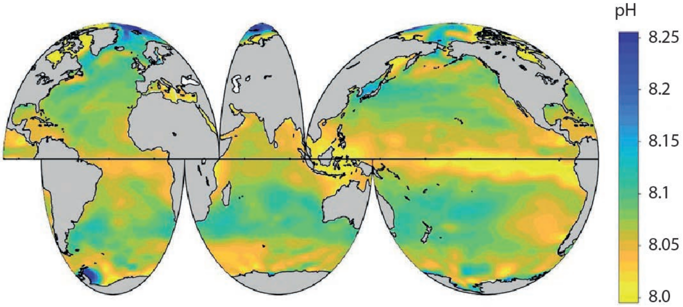

Figure 4. Surface ocean pH distribution in 2000.

pH values are annual average values from the 6th version of the Surface Ocean CO_2 Atlas (SOCATv6; https://socat.info/). Map extracted from Jiang *et al*. (2019).

the main forms of limestone produced by calcifying organisms, which varies on average from 1.4 in polar regions to 3.7 in equatorial regions.

From the surface to the bottom

In general, ocean pH is highest at the surface and decreases with depth. At the ocean surface, the presence of sunlight enables primary producers, such as phytoplankton[16] and algae, to use CO_2 to create organic matter by releasing oxygen. This process, well known as photosynthesis, can be summed up in the following equation:

$$6CO_2 + 6H_2O + \text{light} \rightarrow C_6H_{12}O_6 + 6O_2 \quad \text{(eq. 7)}$$

Consequently, as the photosynthesis reaction consumes CO_2, it can lead to a rise in pH, sometimes very sharp. This is the case, for example, at the end of the day in algal forests, or during seasonal phytoplankton blooms.

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[16] Phytoplankton are all organisms living in suspension in water (plankton), belonging to the vegetal kingdom and invisible to the naked eye. Phytoplankton are autotrophic with regard to carbon, meaning they are capable of producing their own organic matter from minerals. It obtains its energy through photosynthesis. Phytoplankton includes protists such as dinoflagellates, and bacteria such as cyanobacteria.

As we move away from the surface and light, photosynthesis is no longer possible. As particles of organic matter, such as plant and animal debris, sink to the depths of the ocean, they are consumed by animals or decompose under the action of bacteria, which draw energy from them and release CO_2 through respiration, according to the following equation:

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O + \text{energy (eq. 8)}$$

It is partly thanks to this mechanism that the ocean can store anthropogenic CO_2: atmospheric CO_2 is consumed at the surface by phytoplankton to produce organic matter that decomposes on the seabed, far from the atmosphere. This process is slow, and a recent study suggests that around 20% of the anthropogenic carbon drawn by the ocean is currently stored below 1,000 m (Davila *et al.*, 2022).

In the deep ocean, pH is therefore lower and generally much more stable than at the surface, although it remains predominantly basic (pH > 7.6) (Lauvset *et al.*, 2020). As with the surface ocean, however, there are geographical disparities, which can be explained by the movement of deep waters along the thermohaline circulation. The deep waters created mainly in the North Atlantic flow southwards to reach the Indian and Pacific Oceans. It is in the northern Pacific that ocean-bottom pH levels are at their lowest (< 7.8). This is due to the increased accumulation of organic matter from the surface during the transport of these water masses, accumulating as much CO_2 and thus progressively lowering the pH.

Additionally, there are deep-ocean zones that are particularly acidic, such as submarine volcanic or hydrothermal zones found especially along mid-ocean ridges or ripples. Hydrothermal fluids have very high levels of acidity, which can significantly lower the pH of the surrounding seawater.

Seawater calcium carbonate saturation states decrease with depth, under the combined effect of falling pH and temperature, and increasing pressure (Feely *et al.*, 2004). While most of the surface ocean is supersaturated with respect to calcium carbonate ($\Omega > 1$), very large areas of the seafloor exhibit corrosive conditions ($\Omega < 1$)

(Lauvset *et al.*, 2020). This is the case in the North Pacific, where sediments contain little or no limestone, as it dissolves (Hayes *et al.*, 2021). The saturation depth, namely the depth at which calcium carbonate precipitation and dissolution rates are balanced ($\Omega = 1$), varies from 2,000 to 2,500 m in the North Atlantic and from 500 to 1,000 m in the North Pacific (with a minimum of around 300 m in the northernmost region) (Feely *et al.*, 2004).

From the coast to the open ocean

Spatial variations in pH in coastal areas can be much greater than those observed offshore, due to the influence of multiple local factors such as freshwater inputs, bringing nutrients, terrestrial organic matter, or various pollutants. For example, continental freshwater often has a lower pH and can locally acidify coastal marine waters. Freshwater is also less rich in carbonate and bicarbonate ions, reducing the saturation levels of coastal waters with regard to calcium carbonate.

The geology of the watershed plays an important role in determining pH and, more generally, carbonate chemistry. For example, the presence of acidic soils means that runoff brought to the sea greatly reduces its pH. Conversely, a limestone basin will bring in water with a higher carbonate ion content and a higher pH.

In most coastal regions, the input of nutrients such as nitrogen or phosphorus from agriculture, industry or watershed wastewater stimulates primary production and photosynthesis, and can thus raise pH locally and temporarily. In excess, nutrients lead to eutrophication, namely an excessive production of phytoplankton which, as it decomposes, produces CO_2 and acidifies the environment.

The coastal zone is also characterised by diverse communities of bottom-dwelling organisms (benthic organisms, as opposed to pelagic organisms living in the water column), such as corals, seagrass beds, macro-algae, salt marshes and mangroves, which act differently on the chemical and physical conditions of their environment. Whereas seagrass beds are considered CO_2 sinks through photosynthesis, coral reefs and bivalves are considered

CO_2 sources through respiration and calcification (Chapter 3). Consequently, carbonate parameters in the coastal zone depend on the communities that develop there.

The coastal zone can also be the site of upwelling of deep water enriched in CO_2 and acidified (Feely *et al.*, 2008). This generally occurs along coasts where prevailing winds blow parallel to the coast, pushing surface waters offshore, thus favouring deep-water upwelling and lowering surface pH.

Overall, pH in the coastal zone is much more variable than offshore.

HOW DOES pH VARY OVER TIME?

Offshore, pH varies throughout the year depending on temperature, the origin of water masses (surface *vs.* bottom) and biological activity (photosynthesis, respiration, calcification). Some sites are very stable, while others show greater temporal fluctuations, mainly due to more intense biological processes. Overall, at low and mid-latitudes, pH tends to rise in spring with the increase in primary production (photosynthesis), then to fall in summer due to temperature rise, the respiration of organisms, and the drop in primary production. At high latitudes, pH is highest in summer, as summer biological activity outweighs the negative effect of rising temperature. Annual pH amplitudes are rather moderate in open oceans, ranging from 0.02 to 0.07 pH units.

In coastal and estuarine waters, pH is much more variable over time than in the open ocean, depending on the tide, the day-night cycle and the season. In addition to temperature and biological activity, tides and coastal currents can profoundly alter pH. It is generally higher at high tide, when oceanic influences are stronger than freshwater inputs. These marine waters are also richer in carbonate and bicarbonate ions, implying maximum saturation states during high tides. As a result, seasonal pH variations in the coastal zone can reach 0.5 to 1 pH units in certain highly productive regions.

HOW HAS pH EVOLVED IN DIFFERENT REGIONS OF THE OCEAN?

A recent study compared the temporal evolution of pH over periods of 15 to 30 years at seven sites: the Iceland Sea, the Irminger Sea, the Northwest Atlantic (Bermuda), the Northeast Atlantic (Canary Islands), the Southwest Atlantic (Venezuela), the North Pacific (Hawaii) and the South Pacific (New Zealand) (Bates *et al.*, 2014). The pH evolution measured at these stations varies between – 0.0013 and – 0.0026 pH units per year, in line with what is expected given the increase in atmospheric CO_2 concentration. Calcium carbonate saturation states have also fallen at all sites, with the exception of the Iceland Sea. However, the frequency of measurements at sub-polar sites is low, which limits the reliability of the conclusions. The development of autonomous high-frequency sensors and satellite-based surface pH measurements should enable us to extend data resolution and consolidate conclusions at certain sites that are difficult to access.

Below a depth of 1,000 m, ocean pH has not yet been significantly modified by human activity, with the exception of the North Atlantic, Arctic and Southern Oceans, where cold waters rich in atmospheric CO_2 plunge into the ocean depths under the effect of the thermohaline circulation.

It is difficult to identify an acidification trend in the coastal zone, where spatial and temporal variability is high. A compilation of 83 data series acquired in coastal zones shows that the pH of many sites has increased in recent years thanks to the implementation of discharge treatment measures limiting the effects of eutrophication (Carstensen and Duarte, 2019). However, it should be noted that the vast majority of these data sets were obtained from low-precision pH measurements, and very few reliable time series currently exist.

HOW WILL pH EVOLVE IN DIFFERENT REGIONS OF THE OCEAN?

All oceanic regions will see their surface pH fall by the end of the century, according to all models assuming a temperature rise limitation of at least 2°C (Figure 5). Only the SSP1-1.9 scenario, which assumes that global warming will be limited to 1.5°C, combined with a drastic reduction in CO_2 emissions and the capture of atmospheric CO_2, would enable ocean surface pH values to be maintained at current levels. The greatest drops in pH are projected at high latitudes, and in particular in the Arctic Ocean, where a decrease of 0.46 pH units is modelled according to the worst-case scenario for future CO_2 emissions, SSP5-8.5. This drop in pH is amplified in the Arctic due to the increased warming of the surface ocean in this region and the gradual disappearance of sea ice[17].

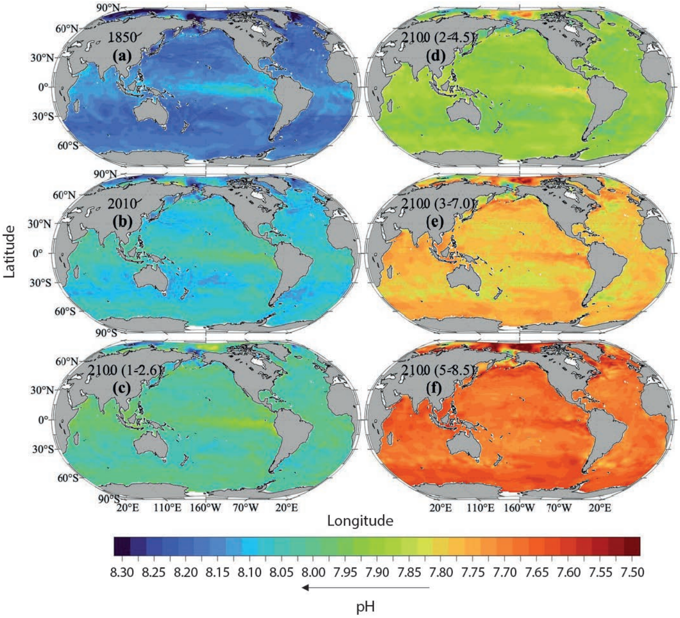

Figure 5. Mapping of ocean surface pH levels in 1850 (a), 2010 (b) and projected for the end of the century according to four CO_2 emission scenarios (SSP, c, d, e, f). Maps extracted from Jiang *et al.* (2023).

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[17] Melting sea ice increases the uptake of anthropogenic carbon and lowers pH, both by providing a larger surface area for air-sea gas exchanges and by enhancing them through dilution of dissolved inorganic carbon concentrations with fresh water.

WHAT ARE THE BIOLOGICAL IMPACTS OF ACIDIFICATION?

Increased atmospheric CO_2 alters seawater carbonate chemistry by increasing dissolved CO_2 concentration, lowering pH (rising acidity) and decreasing carbonate ion concentration. These chemical changes influence several fundamental physiological processes, including acid-base regulation[18], respiration, energy metabolism[19], calcification and photosynthesis.

PHYSIOLOGICAL IMPACTS OF CO_2 ENRICHMENT

Excess CO_2 in seawater diffuses into the body's tissues until a new state of equilibrium is reached. The increased CO_2 content in the body, also known as "hypercapnia", increases the acidity of the blood (for vertebrates, the equivalent being haemolymph for molluscs and crustaceans). This is the phenomenon of *blood acidosis* (Melzner *et al.*, 2009; Pörtner *et al.*, 2004). One function of blood (and haemolymph) is to transport the oxygen (O_2) required for energy production to organs and tissues. To do this, oxygen binds to proteins such as haemoglobin in blood and hemocyanin in haemolymph. However, acidosis reduces the ability of transport proteins to bind oxygen. Hypercapnia thus leads to acidosis, which reduces oxygen transport capacity and impairs gas exchange and energy metabolism. The ability to regulate the acidity of body fluids is considered by physiologists to be the organism's first line of defence against hypercapnia-induced disturbances.

Acidification, i.e., a decrease in marine pH or an increase in the concentration of protons in the environment, has repercussions for the body. As with CO_2, the excess protons caused by

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[18] Acid-base balance, or pH homeostasis, is the body's function of regulating blood pH.

[19] All the chemical reactions in the body's cells involved in energy production.

acidification diffuse into the body's tissues and can aggravate the acidosis phenomenon described above. Furthermore, these excess protons can bind with carbonates to form bicarbonate, as occurs naturally in the ocean. This reaction has the effect of reducing the availability of carbonate ions and the saturation state (Ω) with regard to limestone, which can disrupt the calcification process (eqs 1-4, Chapter 1, p. 12 and 14).

ANIMAL TOLERANCE TO CO_2 ENRICHMENT

Tolerance to CO_2 enrichment and the resulting effects (hypercapnia and acidosis) vary between animals depending on species, life history and the degree of CO_2 enrichment. Sensitivity to CO_2 is also linked to an animal's level of organisation, energy requirements and lifestyle (Melzner *et al.*, 2009).

Vertebrates, and adult fish in particular, are the most CO_2-tolerant group of marine animals. Indeed, several studies have shown that very high levels of CO_2, well above those expected by 2100, do not have any effect on the growth, swimming performance or metabolism of several fish species. On the other hand, marine invertebrates are generally less tolerant to high levels of CO_2. Several studies have shown reduced growth or calcification of bivalve molluscs, echinoderms and corals at CO_2 levels that have no apparent effect on fish (Kroeker *et al.*, 2013; Gazeau *et al.*, 2013; Leung *et al.*, 2022).

Species that tolerate CO_2 have developed effective protection or compensation mechanisms against acidosis. Among these mechanisms, the accumulation of weak bases such as proton-binding carbonate ions, and the active pumping of protons out of cells, can limit the drop in blood pH, or even maintain it at near-normal levels (Melzner *et al.*, 2009). These ionic regulation capacities are generally well developed in active, mobile species such as cephalopod molluscs and fish. In these species, the alternation between rest and exercise phases induces fluctuations in respiratory activity, i.e. in O_2 consumption and CO_2 production. Such fluctuations in O_2-CO_2 exchanges in active species can occur rapidly, within minutes. These species have effective physiological mechanisms for eliminating CO_2 and excess protons and limiting acid-base disturbances. This is the case, for example, of fish species which hunt their prey by swimming actively in the water column, unlike filter-feeding molluscs, which live attached to the bottom. The physiological constraints imposed by a high metabolic rate in today's environment have led to adaptations that enhance the ability to withstand future ocean acidification.

Conversely, these protective mechanisms against acidosis are much less developed, or even absent, in CO_2-sensitive species (Melzner *et al.*, 2009). The resulting acidosis can cause a drastic drop in metabolism to save energy and survive extreme stress. This is what physiologists call metabolic depression, a phenomenon well known to be at the origin of torpor, hibernation and aestivation states (Guppy and Withers, 1999). This strategy is beneficial in the short term, but incurs energetic costs in the long term by limiting growth and potentially the individual's ability to reproduce.

IMPACTS OF OCEAN ACIDIFICATION ON CALCIFYING ORGANISMS

What are calcifying organisms?

Calcifying organisms precipitate calcium and carbonate ions to produce calcium carbonate ($CaCO_3$), which forms the basis of calcareous structures such as shells, carapaces and other skeletons. As seawater becomes more acidic, the availability of carbonate ions decreases, which can limit calcification and increase limestone dissolution (see eqs 1-4, Chapter 1, p. 12 and 14). The ability of calcifying organisms to build durable, functional calcareous structures is fundamental to their survival, providing protection from predators and supporting the animal's growth and development. If the calcification process is limited by acidification, then the growth, development and survival of calcifying organisms can be impaired and ecosystem functioning severely disrupted (Kroeker *et al.*, 2013; Gazeau *et al.*, 2013; Leung *et al.*, 2022).

Calcifying organisms are extremely abundant in the ocean, belonging to a wide variety of plant and animal groups of different degrees of complexity. These organisms can live in the water column or on the seabed, in coastal or offshore areas, near the surface or in abyssal zones. Coccolithophores, for example, are planktonic micro-algae[20] that form the basis of food chains, while other algae visible to the naked eye (macro-algae) colonise rock faces or form aggregates on the seabed (coralligenous algae).

The best-known calcifying organisms are fixed or mobile animals that alternate between a swimming phase in the water column (planktonic phase) and a fixed or seabed-associated phase (benthic phase), depending on their stage of development (larva, juvenile or adult). This is the case for many species of sponges, corals, molluscs, crustaceans and echinoderms.

Among corals, we find colonial forms that group together to form “superorganisms”. Each individual secretes its own calcareous skeleton, contributing to the formation of a larger, longer-lasting colonial skeleton. Scleractinian corals form reefs, some of which have become the largest complex structures created by living organisms. Today, these coral reefs are considered biodiversity hotspots, helping to protect the coastal zone from erosion.

Bivalve molluscs such as oysters, mussels, scallops and clams are among the most studied calcifying organisms, as they are heavily exploited by fishing and aquaculture and are potentially vulnerable to acidification. Similarly, sea urchins, part of the echinoderm group (which also includes starfish, brittle stars and sea cucumbers), build a calcareous structure covering their entire body (the test) and are consumed by humans. Finally, crustaceans such as amphipods, shrimps, crabs and lobsters are also calcifying organisms of great commercial and ecological interest. However, while these organisms produce limestone, their shells are essentially composed of organic molecules.

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20. Refers to organisms living in the water column and allowing themselves to be carried away by currents, as opposed to “nektonic”, which characterises species capable of moving actively, possibly against the current: cephalopod molluscs, fish, cetaceans, etc.

Calcifying organisms, through their abundance and diversity, are key links in marine food chains, form an integral part of global biogeochemical cycles, and contribute, by their mere presence, to the formation of habitats for other species. In this context, their fate in an acidified ocean is of particular concern, and numerous studies have been conducted to assess their sensitivity (Kroeker *et al.*, 2013).

The composition and crystalline form of the calcareous skeletons of marine organisms vary considerably between species, with consequences for their sensitivity to acidification (Byrne and Fitzer, 2019). Some species have calcareous structures composed mainly of calcium carbonate, while others are a mixture of calcium carbonate and chitin, an organic molecule from the sugar family. This is the case of crustaceans, for example, as mentioned above. Calcifying organisms also precipitate calcium carbonate in various crystalline forms, such as aragonite for corals, calcite or aragonite for molluscs, or magnesian calcite for calcareous algae and sea urchins, a form of calcite that contains a greater or lesser proportion of magnesium to replace calcium. Of these crystals, magnesian calcite is the most soluble in seawater and therefore the most sensitive to acidification, followed by aragonite and calcite.

The production of these different forms of calcium carbonate is biologically controlled by the organism, which secretes specific molecules involved in mineral binding that condition the crystalline form, the orientation and the growth of these minerals (Marin *et al.*, 2008). This is why, depending on the nature of the organic molecules, calcium carbonate crystallises as calcite or aragonite. It should also be noted that some species produce different types of crystals, such as many molluscs that develop a mixed calcite and aragonite shell, and that this can vary depending on the stage of development (Byrne and Fitzer, 2019). Finally, changes in mineralogical composition can also be observed following stunted growth induced by a food shortage or a stress episode such as a drop in pH.

Why are they sensitive to acidification?

The vast majority of calcifying marine organisms are directly or indirectly affected by acidification. Among the negative effects of acidification, declines in growth and calcification are most frequently observed, and in animals, larval stages are particularly sensitive. Systematic reviews of the scientific literature and meta-analyses synthesizing results from hundreds of laboratory and field experiments, as well as observations in naturally high-CO_2 marine environments, have shown lower growth rates, survival or other performance measures for many organisms under future acidification conditions (Kroeker *et al.*, 2013; Gazeau *et al.*, 2013; Leung *et al.*, 2022; Hall-Spencer *et al.*, 2008; González-Delgado and Hernández, 2018). These in-depth analyses of the scientific literature also conclude that there is significant variability between and within species, confirming that some plasticity and adaptation are possible (see Chapter 6).

Warm-water corals are the most studied group of calcifying marine organisms with regard to acidification. At the origin of exceptional ecosystems for their beauty and great biological diversity, these animals precipitate aragonite, a form of limestone that dissolves quickly, making them naturally sensitive to acidification. The overall conclusion is clear: warm-water corals are highly sensitive to ocean acidification, with declines in calcification associated with decreases in aragonite saturation status and seawater pH (Hoegh-Guldberg *et al.*, 2007). However, some major questions remain: how and why is coral calcification so sensitive to ocean acidification? This question is the subject of recent research into the physiological effects of pH on calcification, focusing both on coral tissues (internal pH regulation) and on photosynthetic symbiotic organisms[21] whose metabolism may promote internal pH regulation and resistance to changes in external pH (Ge *et al.*, 2021).

Like tropical corals, cold-water corals form complex and diverse habitats that must cope with ocean acidification. Relatively unknown, these cold-water corals are particularly vulnerable to acidification, as carbonate dissolution increases with depth (Chapter 3). Thus, the aragonite saturation horizon — the depth

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[21] Symbiosis is a lasting, mutually beneficial association between two living organisms. Corals harbour micro-algae in their tissues, called “zooxanthellae”, which photosynthesize and supply nutrients to their host.

at which precipitation and dissolution processes cancel each other out — is likely to decrease as the ocean becomes enriched in CO_2. In some places, the most widespread cold-water coral species[22], found in most of the world's seas and oceans, already lives at depths very close to the aragonite saturation horizon. By the end of the century, it is predicted that 70% of deep-sea corals will be found in water undersaturated with aragonite, below the saturation horizon (Guinotte *et al.*, 2006). Although studies conducted over several months under laboratory conditions at ambient pressure suggest that these organisms can calcify under these conditions, the current low abundance of cold-water corals below the saturation horizon suggests that their long-term survival there is highly unlikely (Büscher *et al.*, 2017). Consequently, if these organisms cannot acclimatise or adapt to CO_2 enrichment, then they will have to colonise new habitats that are increasingly shallower, but also increasingly warmer. The ocean is warmer at the surface than at the bottom, and the depth of the thermocline — the zone of rapid thermal transition between warm surface waters and cold bottom waters — increases with global warming. Acidification and warming would therefore exert antagonistic pressures on these organisms, with the former forcing them to migrate towards the surface, while the latter requires them to move towards the bottom. Between two evils, deep-sea corals will have to adapt to one or the other.

Bivalve molluscs and echinoderms were the subject of the first realistic studies on the effects of ocean acidification, i.e. considering pH levels projected for the end of the century. These studies, conducted from 2007 onwards, have shown that the larval stages of many species are negatively affected by decreases in pH corresponding to the predictions of climate models (Kroeker *et al.*, 2013; Gazeau *et al.*, 2013; Leung *et al.*, 2022). In carbonate-undersaturated conditions, larvae are deformed, growth is reduced and mortality is potentially high. Other indirect effects can also occur. For example, reduced growth may increase the risk of predation. The impact of ocean acidification on larval

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[22] *Desmophyllum pertusum.*

stages is of great importance for the persistence of populations, given the role of these young stages in the colonisation of new habitats. This subject will be covered below.

Finally, crustaceans seem less sensitive to CO_2 enrichment than the above-mentioned groups of organisms, and are more affected by the indirect effects of acidification, such as changes in food quality. This relative resilience to acidification may reflect the fact that their shells are less dependent on carbonate ions, since they also accumulate organic molecules like chitin.

Despite great variability in the observed responses of organisms to CO_2 enrichment between different studies, direct and indirect negative effects predominate. An in-depth analysis of the scientific literature shows that 50% of coral, mollusc and echinoderm species are negatively affected at atmospheric CO_2 levels of between 600 and 1,000 ppm, values that are within the range projected by IPCC scenarios (Leung *et al.*, 2022). For crustaceans, only a third of species are sensitive to these CO_2 enrichment levels. Nevertheless, the effects of acidification are not always observable, suggesting that some calcifying organisms may well tolerate this phenomenon in the decades to come.

LARVAL STAGES, MORE SENSITIVE THAN JUVENILES AND ADULTS

The development cycle of many marine species involves an alternation between a larval phase in the water column, during which the organism disperses with the currents, and a phase on the bottom[23], where it metamorphoses, grows and acquires the ability to reproduce. For example, bivalve molluscs such as oysters, mussels and scallops release their gametes into the water, where fertilisation, embryo and larval development take place. Then, the larvae migrate to the bottom, explore the substrate with their feet, settle in a place chosen according to physical criteria such as the current or the type of substrate (sand, mud

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[23] These stages are called “pelagic” (in the water column) or “benthic” (on the bottom).

or rock), and biological criteria such as the presence of food, the proximity of conspecifics, or the absence of predators, and metamorphose. From this point onwards, the oyster will remain settle all its life; the mussel will also be fixed, but may detach and move locally, while the scallop will be mobile and able to swim short distances.

Analysis of the scientific literature shows that larvae are generally more sensitive than juveniles and adults to acidification (Kroeker *et al.*, 2013; Gazeau *et al.*, 2013; Leung *et al.*, 2022). At this stage, the first shell is formed and calcification is the most intense. In many species, larvae precipitate aragonite, a more soluble form of limestone than calcite, while juvenile and adult stages favour calcite or aragonite. Acidification affects larval growth, calcification and survival, and can produce skeletal deformities. This is the case, for example, of echinoderm larvae, which develop asymmetrical arms under acidified conditions, but also mollusc larvae, which show shell deformities or excess mortality. The greater sensitivity of larvae to acidification compared to other developmental stages could limit population renewal, to the point of threatening their persistence in the environment.

IMPACTS ON BEHAVIOUR

Although the vast majority of scientific studies on the effects of acidification focus on the physiology, calcification and survival of marine organisms, the effects on animal behaviour are attracting growing interest in the literature (Clements and Hunt, 2015). Indeed, behaviour plays a major role in the survival and ability of individuals to reproduce and ensure population renewal in marine ecosystems. Behaviours affected by acidification include predator avoidance by prey, ability to return to breeding sites, habitat selection, auditory response, learning, foraging and swimming behaviour in marine fish. Studies on the subject have mainly focused on coral reef fishes, which, due to their high level of behavioural complexity, naturally lend themselves to observation. Today, there are relatively few studies of this kind on fish species of interest to the fishing industry, or on marine invertebrates.

But how can ocean acidification, caused by the enrichment of seawater with CO_2, affect behaviour? Behaviour is the result of nervous system expression and depends on the chemistry of the environment. It is nothing more or less than a response to visual, tactile, auditory, gustatory or olfactory stimulation, which is transformed into a nerve impulse, i.e. an electrical signal caused by a change in ionic concentrations between the inside and outside of nerve cells, i.e. neurons. We have already seen that CO_2 enrichment induces changes in the ionic composition of body fluids, with the accumulation of bicarbonate ions to compensate for acidosis. These changes in composition have the effect of altering the ionic gradient across the neuronal membrane, and in this way, can alter the transmission of nerve impulses and disrupt behaviour (Clements and Hunt, 2015).

CONTRASTING RESPONSES BY SPECIES

Cuttlefish, a calcifying mollusc tolerant to acidification

The common cuttlefish, *Sepia officinalis*, is a species of cephalopod mollusc widely exploited on our coasts and well known to the general public for its remarkable mimetic and cerebral capacities for an invertebrate. Cuttlefish are calcifying organisms that produce an internal calcareous skeleton, often called “cuttlebone” or “sepion”, composed mainly of aragonite. This porous bone enables the animal to regulate its buoyancy by compressing the gases it contains to a greater or lesser extent. The cuttlefish moves rapidly through the water column thanks to a well-developed muscular system, enabling it to efficiently hunt live prey such as crabs, shrimps and small fish.

Cuttlefish, like other cephalopods (octopus and squid), are less sensitive to ocean acidification than many other marine calcifying organisms (Gutowska *et al.*, 2010). There are three reasons for this. Firstly, unlike other molluscs, cuttlefish have a well-developed ability to regulate their internal pH, enabling them to adapt quickly to variations in surrounding pH. Their metabolism and acid-base regulation mechanisms are designed to maintain a stable internal balance, even in the presence of increased acidity.

Furthermore, although their skeleton is made of aragonite, a particularly soluble form of calcium carbonate, it is not directly exposed to the surrounding seawater. Finally, cuttlefish are highly mobile animals that can adjust their behaviour to avoid areas of higher acidity. In particular, they are able to move rapidly to ocean areas where conditions are more favourable.

Surprisingly, cephalopod population are on the rise in many parts of the world, where they have been monitored for sixty years (Doubleday *et al.*, 2016). Since 2021, the Atlantic coast of Brittany has been colonised by large populations of octopuses, which are devastating shellfish beds. Among the hypotheses put forward to explain this phenomenon are the recent rise in temperature, which accelerates their reproductive cycles, and the worldwide depletion of fish stocks due to overfishing, which reduces predation and competition for food. Although it is not currently possible to predict the future of cephalopod populations, their greater tolerance of ocean acidification could give them a further advantage in a high-CO_2 environment.

Pteropods, canaries in the coal mine

Pteropods[24] are marine gastropod molluscs that spend their entire lives in the water column, thanks to a snail's leg transformed into two wing-like structures that enable them to literally "fly" in the water column. Some species produce a fragile aragonite shell.

Pteropods are an important food source for carnivorous zooplankton[25], exploited fish species, and a number of top predators, such as birds and marine mammals. From a biogeochemical point of view, pteropods play an important role in the direct export of organic carbon and carbonate (for shell species) to the deep ocean through the deposition of dead individuals.

Shelled pteropods have been the focus of global change research because they make their shells from aragonite, a form of calcium

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[24] Pteropods are animals of the gastropod mollusc class. They include the two clades *Thecosomata*, "sea butterflies" with shells, and *Gymnosomata*, "sea angels" without shells.

[25] Zooplankton are animal plankton. They feed on organic matter, some species being herbivorous and others carnivorous.

carbonate that is 1.5 times more soluble than calcite. Many species live in polar regions naturally depleted in carbonate ions. Because their shells are susceptible to dissolution, pteropods have been called "canaries in the coal mine", or sentinel species that warn of the impacts of ocean acidification on marine calcifying organisms.

Various studies show that pteropods are already being negatively affected by acidification in several regions of the ocean, and will be seriously threatened if CO_2 levels continue to rise (Bednaršek *et al.*, 2012).

The negative effects of acidification on pteropods are generally associated with a problem of aragonite saturation, which limits calcification and growth. A few studies have also shown that hypercapnia induced by CO_2 enrichment and lower pH alter their acid-base balance and metabolism. Finally, lower pH seems to induce behavioural changes and reproductive disorders. Acidification therefore affects the survival of pteropods through a number of physiological and behavioural processes.

PHOTOSYNTHETIC ORGANISMS, NOT NECESSARILY WINNERS IN A CO_2-ENRICHED ENVIRONMENT

Like trees and other terrestrial plants, micro-algae (phytoplankton and phytobenthos[26]), cyanobacteria, macro-algae and marine plants capture CO_2 to manufacture organic matter under the action of light, releasing oxygen through photosynthesis (eq. 7, Chapter 4, p. 33). Theoretically, the increase in CO_2 concentration should promote photosynthesis and the growth of the marine organisms that depend on it. In reality, it's not that simple!

Although the stimulating effects of increased CO_2 on photosynthesis and carbon capture have been observed in several non-calcifying phytoplankton species, such as diatoms,

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[26] Phytobenthos are autotrophic organisms that thrive on solid surfaces such as rocks, sediments or even other organisms.

cyanobacteria and dinoflagellates, including many species of harmful and toxic algae, calcifying phytoplankton species are often at a disadvantage (Riebesell *et al.*, 2000). This is the case for several species of coccolithophores, a group of unicellular phytoplankton that produce calcite plates and whose growth is limited in CO_2-enriched conditions.

However, most marine photosynthetic organisms have developed cellular carbon concentration mechanisms, so that intracellular CO_2 concentration is not a limiting factor. Species lacking such mechanisms that could benefit from CO_2 enrichment are generally exposed to other growth-limiting factors, such as a lack of light or nutrients (e.g. nitrogen, phosphorus or iron). CO_2 enrichment can be beneficial for certain algae and diatoms lacking efficient carbon concentration mechanisms and living in otherwise non-limiting conditions.

HOW DO ORGANISMS COMPENSATE FOR THE EFFECTS OF ACIDIFICATION, AND AT WHAT COST?

Calcification is an active physiological process biologically controlled by the organism. Indeed, calcifying organisms can themselves create a less acidic microenvironment favouring calcium carbonate precipitation (Gazeau *et al.*, 2013). Thus, calcifying organisms are, up to a certain point, independent of the carbonate ion content of the environment. For example, in molluscs, calcification occurs in a closed compartment where calcium and bicarbonate ions can diffuse or be actively pumped out to increase their concentration in the organism. Calcifying organisms can also directly convert CO_2 from the environment into bicarbonate ions and promote the precipitation of calcium carbonate through the activity of specific enzymes. These compensatory physiological mechanisms explain why calcification can be maintained in conditions that are undersaturated with respect to calcium carbonate.

In addition, the shells of calcifying organisms, like those of molluscs, are covered by a thin organic membrane, the periostracum, which confers flexibility, resistance and protection against external agents such as acids, enzymes and microorganisms. The periostracum is regularly renewed by the cells of the mantle, a tissue that surrounds the soft parts of the organism and forms the different layers of the calcareous shell. The mantle cells continuously produce new layers of periostracum, replacing older layers that have been damaged. Deep-sea mussel shells living near hydrothermal vents, where pH values can reach as low as 5.4, have a literally overdeveloped periostracum that enables them to persist in these environments of extreme acidification (Tunnicliffe *et al.*, 2009). Such a protective role of the periostracum against acidification has been shown for coastal species such as mussels (Gazeau *et al.*, 2013).

Another strategy for reducing calcium carbonate dissolution is to modify the crystalline form by producing a form less sensitive to dissolution. This is possible in certain calcifying organisms known as "bi-mineral", i.e. capable, for example, of producing both calcite and aragonite (Gazeau *et al.*, 2013; Leung *et al.*, 2022). Since calcite is less soluble than aragonite, bi-mineral calcifiers, such as mussels, can precipitate more calcite than aragonite under acidified conditions to reduce the solubility of calcareous structures. Finally, calcifying organisms can also limit dissolution by acting on the mineralogical structure itself. Limestone crystals are arranged hierarchically, with varying degrees of density. In response to acidification, some species can produce denser (or less porous), thicker and smaller limestone structures (Byrne and Fitzer, 2019).

Nevertheless, some of the compensatory mechanisms mentioned above — regulation of internal pH, increased synthesis of periostracum, modification of the mineralogical form of limestone — which enable organisms to live better in acidified conditions, require additional energy input. Although the energy requirements of these various physiological mechanisms are difficult to assess and therefore remain poorly understood (Melzner *et al.*, 2020), the energy budget of animals is, by nature and like everything else, limited. As a result, the surplus energy expended in making limestone under unfavourable conditions cannot be invested in other activities such as reproduction, immunity (which helps fight disease) or locomotion (which enables escape from a predator, hunt prey or colonise a new habitat). Organisms therefore make trade-offs by reallocating available energy to different functions, which influences their fate (Sokolova *et al.*, 2012). For example, a shellfish exposed to an episode of acidification, which allocates more energy to calcification to the detriment of its immune system, will continue to grow at the risk of succumbing to an infectious disease. Just as you're more likely to catch a disease when your body is fighting the cold (you expend energy to maintain your body temperature at 37°C), a shellfish loses energy when it is fighting acidification. It is therefore highly likely that future ocean acidification will have indirect impacts on all the vital processes of marine organisms, such as immunity, reproduction or habitat selection. This could translate into an increased incidence of disease, particularly when combined with other stressors linked to climate disruption, such as warming.

Nor should we lose sight of the fact that an organism's energy budget depends mainly on food intake. So, in order to pay for the extra energy needed to compensate for the effects of stress such as acidification, you'd have to eat more! In practice, this is what has been observed in certain species of coral and bivalve molluscs. However, food must be available in excess, and the organism must have the capacity to assimilate this surplus. For example, we have observed that the food intake of oysters in acidified conditions could not increase, as it was already maximal in ambient pH conditions (Lutier *et al.*, 2022).

Conversely, when food is limiting, the ability of organisms to compensate for the effects of acidification is reduced. Researchers have shown, for example, that mussels reared under acidified, food-limited conditions have more corroded shells than their counterparts fed *ad libitum* (Thomsen *et al.*, 2013). As the vast majority of studies have been conducted under conditions of non-limiting food supply, it is highly likely that the effects of acidification on calcifying organisms are globally underestimated.

CAN MARINE ORGANISMS “ADAPT” TO ACIDIFICATION?

Ocean acidification has an impact on the biology of organisms that can compromise their functioning and survival. However, common sense often says that nature is endowed with a remarkable capacity for adaptation. But is this really true? Can marine organisms really adapt to a rapidly acidifying environment?

WHAT IS ADAPTATION?

In evolutionary biology, adaptation consists of genome modifications induced by natural selection[27], and resulting in morphological, physiological, developmental or behavioural changes within a population[28]. Adaptation is a trait that can be transmitted between generations, increasing the chances of survival and reproduction of individuals in the existing environment. Adaptation takes many forms. It may be a behaviour that enables an individual to escape from a predator, a protein that functions better at the temperature of the environment, or an anatomical characteristic that enables access to a new resource or sexual partners. The peacock’s parade, the giraffe’s neck, the cuttlefish’s camouflage: everything that impresses us in nature is adaptation! Evolutionary adaptation is the result of the selection of existing genetic variations in nature or of new genetic mutations[29]. The potential for evolutionary adaptation is proportional to population size and generation time. The highest rates of adaptation are expected for species with large population sizes and short generation times.

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27. Natural selection is the process defined by Charles Darwin in *The Origin of Species* (1859), whereby the frequency of traits that favour survival and reproduction in a given environment increases from one generation to the next. These hereditary traits are “selected” because the individuals who carry them have more offspring.

28. Group of individuals belonging to the same species.

29. Rare accidental or provoked modification of the genetic information in the genome.

ACCLIMATISATION *VERSUS* ADAPTATION

Acclimatisation is the ability of a living organism to respond to a change in its environment without modifying its genetic heritage, i.e. its genome. In contrast to evolutionary adaptation, acclimatisation takes place over a short period, at most equal to the organism's lifespan, and is often reversible. Acclimatisation is likened to phenotypic plasticity, i.e. the ability to modify the phenotype[30] (physical, behavioural characteristics, etc.) in response to environmental changes. The modification of skin coloration in cuttlefish in response to its immediate environment is an example of phenotypic plasticity. Although plasticity is an adaptive mechanism, it is unlikely to provide a long-term solution for species undergoing sustained directional environmental change, such as ocean warming or acidification. Phenotypic plasticity is possible within well-defined limits, beyond which conditions become stressful, even lethal, for individuals (Figure 6). Beyond the limits of phenotypic plasticity, genetic adjustments[31] are required to persist, and this is likely to be the case for many species. For example, Australian researchers showed no signs of acclimatisation after one year's exposure to different levels of CO_2 enrichment on four species of coral and two species of tropical calcifying algae from the Moorea region of French Polynesia (Comeau *et al.*, 2019). This study highlights the importance of considering adaptation over several generations to assess the vulnerability of species facing ocean acidification.

Yet the vast majority of experimental studies on a species' response to ocean acidification takes little account of the processes of acclimatisation and evolutionary adaptation described above (Riebesell and Gattuso, 2015). These studies generally involve immersing today's animals in tomorrow's conditions, for a few days, weeks or even months, and fail to assess the potential for long-term acclimatisation and adaptation. This is mainly due to

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[30] All the observable, visible characteristics of an organism. Phenotype is often defined in opposition to genotype, which is the set of gene variations.

[31] Or epigenetic, i.e. changes in gene expression that are not caused by modifications to the DNA sequence, but rather by chemical modifications that affect the structure of DNA or DNA-associated proteins. These modifications can be transmitted through cell divisions and, in some cases, from generation to generation.

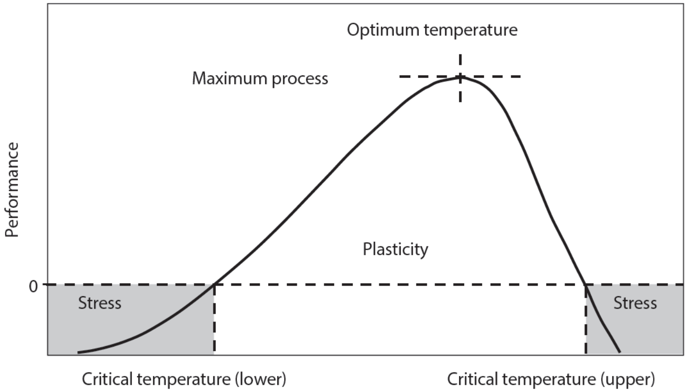

Figure 6. Theoretical performance curve of a physiological process as a function of a forcing factor, in this case temperature.

Performance (growth, respiration, fertilisation, etc.) is generally a non-linear function of temperature, with rates at their maximum when temperature is optimal. The temperature range that maintains physiological rates above a certain threshold represents the organism's range of phenotypic plasticity, while below or above this threshold (critical temperature), physiological performance is so low as to constitute stressful conditions.

the fact that it is very difficult to maintain long-lived organisms in acidified conditions in the laboratory, over several generations.

ADAPTATION IS POSSIBLE, IT'S A MATTER OF TIME!

The few experimental data available suggest that evolutionary adaptation to ocean acidification is possible after a few hundred generations in calcareous microalgae (coccolithophores) (Lohbeck *et al.*, 2012). Members of this group exhibit high genetic diversity, a short reproductive cycle of one day or less, and extremely abundant populations of up to a few thousand and even millions of cells per litre of seawater. Nevertheless, these evolutionary studies are carried out under simplified experimental conditions where predation and competition for resources are non-existent. The question therefore remains to what extent these results are realistic and can be extrapolated to natural conditions.

There are no similar studies on complex, long-lived multicellular organisms. Logically, organisms with long generation times, such as corals, molluscs or fish, will be less able to adapt to the scale and rate of ocean acidification projected for this century. Indeed, the mass extinctions revealed by geological data at times when the rate of change in ocean chemistry was much slower than it is today suggest that the rate of evolution of these species would be far too slow (Chapter 3). In short, the question is not whether adaptation can happen, but whether it can happen fast enough.

Experimentally assessing how marine organisms with generation times of several years will respond to changes in physico-chemical conditions is extremely tedious, if not impossible. Comparative studies using species whose geographic ranges span large pH (or CO_2) gradients can help us to more easily assess the adaptive potential of species. This means examining how organisms adapt locally to assess their future adaptive potential. Indeed, the ability to adapt to an environmental variable in space indicates the ability to cope for changes in that variable over time. Conversely, limits to adaptation in space suggest unsurpassable limits to adaptation in the face of future evolutions.

We have seen that pH and carbonate parameters vary markedly in marine ecosystems, offering a mosaic of diverse habitats to which species have already been able to adapt. Armed with this observation, a German research team compared mussel larvae from the North Sea with those found in an area of the Baltic Sea, which is naturally more acidic (Thomsen *et al.*, 2017). Placing these larvae under the acidity conditions expected in 2100, the researchers found that mussels from the Baltic had better survival than their North Sea counterparts, suggesting a local adaptation to acidification. This is also the case for other species, such as the purple sea urchin in California, and some coral species (Hofmann *et al.*, 2014). While these results breathe optimism into the resilience of these species in a CO_2-enriched environment, they should not obscure the risk of local extinction, precisely where acidity is highest today.

HOW CAN WE STUDY THE PLASTICITY AND ADAPTATION OF MARINE ORGANISMS TO OCEAN ACIDIFICATION?

Imagining the fate of marine organisms in an ocean rich in CO_2, more acidic and depleted of carbonate, is no easy task! Some will imagine a researcher in a white lab coat scrutinizing corals or shellfish immersed in an acid bath day and night. Others will imagine a team busy examining the remains of limestone structures patiently unearthed from marine sediments to glean information about past catastrophic events. In reality, to study the responses of marine organisms to ocean acidification, scientists have developed several approaches, sometimes combined, each with its own advantages and disadvantages.

Analogies with past ocean acidification events

We saw in Chapter 3 that analysis of the evolution of specific community composition depending on pH on geological timescales provides a glimpse of what may lie ahead. There have already been episodes in Earth's history when the ocean was more acidic and warmer than it is today. As such, the Palaeocene-Eocene Thermal Maximum (PETM) is often considered to be the closest past analogue to the future that allows us to imagine what marine life will be like in a high-CO_2 world. Although the fossil record provides a comprehensive overview of the influence of long-term changes, such as extinctions and species emergence, it should be borne in mind that rates of change during the PETM were ten times slower than those in the modern ocean, and therefore more conducive to adaptation, which takes time.

Analogies with local ocean acidification events

We have also seen that the marine environment is heterogeneous, and this applies to pH and carbonate parameters. Following the example of this German team studying the adaptive capacities of mussel populations to acidification, others are describing the communities that live around volcanic CO_2 emissions, very special places in the ocean where this gas naturally escapes from the bottom in the form of clearly visible bubbles, causing local acidification[32]. These cold, shallow emissions, often between 1 and 40 m deep, which are widespread in the Mediterranean off Italy and Greece, offer a window onto a possible future, enabling us to deduce the effects of acidification on biodiversity and the general functioning of the ecosystem, on timescales of several months to several decades, or even centuries.

The best-known natural volcanic emissions of CO_2 are at Ischia, in the Bay of Naples, Italy. On this site, there are zones more or less affected by acidification, which can help us to imagine what marine ecosystems of the future would look like, in a world rich in CO_2. Carbonate parameters in the most affected areas are close to the most extreme acidification scenarios for 2500 (– 1.4 pH units), while in other less affected areas they are comparable to projections for 2100 (– 0.07 to – 0.33 units) (Hall-Spencer *et al.*, 2008). Previous studies of these CO_2 emission sites show an overall decrease in species richness, biomass, structural and trophic complexity, and an increase in the abundance of macro-algae, seagrasses and soft corals, to the detriment of calcifying organisms, with increasing acidification. The conclusion is unanimous: biodiversity decreases with lower pH, both in terms of the number of species (taxonomic diversity) and the biological characteristics of species (functional diversity) (Teixidó *et al.*, 2018).

For example, a recent study carried out at this site shows, on the one hand, that areas unaffected by CO_2 emanations are inhabited by a wide diversity of organisms in terms of size, growth rate, shape, mode of energy acquisition (photosynthetic autotrophs and heterotrophs[33]), and structure (calcifying or not) (Teixidó *et al.*, 2018). On the other hand, low pH zones (7.5-7.8), which represent the conditions expected for 2100, are characterised by small, fast-growing, encrusting and fleshy organisms, rather autotrophic and mainly non-calcifying. Sea urchins are much less abundant. The extreme pH zone (6.6-7.2) is dominated by fast-growing,

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[32] Regarding volcanic CO_2 emissions, see the film: https://youtu.be/sVerGzn_1ME

[33] Feeds on organic substances, cannot synthesise its own constituents (opposite of autotrophic).

encrusting and fleshy organisms, strictly photosynthetic autotrophs and non-calcifying. Sea urchins are completely absent.

However, like past CO_2 enrichment events, CO_2 submarine emission sites cannot be considered as equivalent conditions to current oceanic changes. The first reason is that the effects of warming, which is inseparable from acidification, are not taken into account. Analysis of the communities surrounding submarine emissions gives an idea of the influence of one factor taken in isolation, CO_2 enrichment. The second, more subtle reason is that pH variability at these sites increases with the level of acidification. Thus, the communities living there reflect both the drop in the average pH level, but also an increase in its variability, which can be seen as an additional stress factor.

Experiments on several spatial scales

In the laboratory, scientists routinely carry out experiments under controlled pH conditions, either in “microcosms”, i.e. in aquaria or basins ranging from a few litres to several cubic meters, focusing on single species or strains, or in “mesocosms”, very large-volume structures, sometimes deployed at sea, which incorporate natural biological assemblages. Seawater is generally acidified by bubbling CO_2 gas. The stronger the bubbling, the higher the acidity (lowering the pH). pH manipulation experiments provide highly controlled, mechanistic information on the relationship between one or more factors, such as pH, but also temperature, dissolved oxygen content, diet, etc., and the physiological, ecological or behavioural response of the organisms studied.

However, once again, each of these approaches has drawbacks in terms of cost, degree of replication and ecological relevance (Boyd *et al.*, 2018). Manipulative experiments generally use artificial and simplified systems over short periods (from a few weeks to a few months), making extrapolation to the natural environment and to longer timescales tricky. Microcosm experiments are limited in their ability to predict effects at ecosystem or food web level[34],

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[34] Food chain.

while mesocosm experiments remain limited by their considerable cost and logistical difficulty, and are therefore sometimes hard to replicate. So, as we move along the continuum from simple, small-scale single-species experiments to mesocosm studies to large, open, natural experiments, we increase ecological relevance at the expense of understanding mechanisms. Nevertheless, the ability of manipulative experiments to provide mechanistic insights into how multiple factors will influence marine life in a future ocean makes them powerful and flexible tools, especially when linked to other approaches. Together, these have the potential to generate the mechanistic understanding and predictive power required to assess the effects of acidification on marine organisms and ecosystems.

CAN WE "PROMOTE" EVOLUTIONARY ADAPTATION?

We can try — the tools exist! Genetic selection, which consists in choosing traits of interest and passing them on from one generation to the next, has been practiced for millennia to improve agricultural yields, and is a way of promoting adaptation or accelerating evolution. The vast majority of cultivated plants and livestock are the result of a long process of genetic selection by humans. This selection process, often described as "artificial" as opposed to "natural", can be used to produce organisms that are more tolerant to ocean acidification, notably through traditional selective breeding methods.

To achieve this, firstly the trait must exist in the target species. This may seem obvious, but artificial selection is limited by the existing genetic diversity! This is one of the reasons why it is essential to preserve this diversity in the wild: characteristics observed in wild populations can be introduced into breeding populations to cope with environmental changes. Secondly, the trait must be heritable, i.e. transmissible from one generation to the next. Finally, the desired trait must be selectable independently of other undesirable traits. This is not always the case; health problems or malformations observed in many pedigree dogs are a case in point.

Unlike land-based agriculture, with over 8,000 livestock breeds and an even greater number of plant varieties, aquaculture has developed very few types of farming. The majority of farmed species are of wild origin (FAO, 2019). This explains why many farmed aquatic organisms resemble their wild counterparts as closely as possible, unlike the pig, which has little in common with the wild boar! A farmed oyster is often a wild oyster placed in a mesh bag!

Currently, the development and planned management of marine genetic resources is lacking. The first published breeding experiments in aquaculture began in the 1920s to improve disease resistance in fish (Gjedrem *et al.*, 2012). The first large-scale breeding programs were introduced for salmonids in the 1970s. The implementation of larger-scale breeding programs in aquaculture remains very slow, and despite the spectacular gains that have been demonstrated for a number of species, in 2010 less than 10% of global aquaculture production was based on improved stocks (Gjedrem *et al.*, 2012). Although the feasibility of breeding programs has been widely explored on certain mollusc species such as oysters to increase growth, flesh rate, or disease resistance, few large-scale initiatives have emerged.

Clearly, the aquaculture industry is not equipped to produce organisms selected for greater tolerance to acidification. Although local adaptation to ocean acidification does exist for several species of calcifying organisms (corals, oysters, mussels, sea urchins, etc.), the heritability of this trait and its links with other potentially undesirable traits need to be precisely assessed to enable further progress. The selection of strains or varieties of organisms tolerant to ocean acidification is not for tomorrow!

HOW DOES OCEAN ACIDIFICATION AFFECT US?

Everything we have shown so far in this book suggests that ocean acidification will have serious consequences for marine environments and, consequently, for the millions of people who depend on coastal protection, fishing and aquaculture.

NOTIONS OF ECOSYSTEM SERVICES

This concept, which thinks of ecosystem functioning in terms of goods and services for human beings, emerged in the 1970s to raise public awareness of the need to protect ecosystems (Millennium Ecosystem Assessment, 2005)[35]. Human beings and the economy are placed at the heart of a nature that provides services whose monetary value can be assessed. In 2011, the monetary value of marine and coastal ecosystem services was estimated at $20.9 trillion per year, i.e. almost 60 times French government spending in 2020! The ocean provides provisioning services through the exploitation of marine resources (fishing and aquaculture), support services for living species (habitat), regulating services (climate, carbon storage) and socio-cultural services (recreation, natural heritage).

Acidification will have an impact on all the services provided by the ocean, placing humanity in a situation of vulnerability without historical precedent. The first scientific reports on the impact of acidification on ecosystem services emerged in 2009, focusing mainly on fisheries (Cooley and Doney, 2009; Branch *et al.*, 2013). To illustrate this point, let's look at how acidification generates risks to economic and societal well-being through the reduced supply of seafood products, which could lead to losses

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[35] https://www.ocean-climate.org/wp-content/uploads/2017/02/services-ecosystémiques2.pdf

for the fishing and tourism industries, and thus a threat to the food security of populations who depend on these products as a source of protein.

EXPLOITING MARINE RESOURCES

The potential threat of ocean acidification to seafood farming is twofold, and can be expressed in terms of direct impacts on commercially valuable species (fish, shellfish and crustaceans), and indirect impacts *via* habitat degradation and disruption of the marine food chain.

The most studied direct effect on marine organisms is associated with the calcification process. As described in previous chapters, many calcifying organisms will have difficulty forming their shells or calcareous skeletons in an ocean rich in CO_2, resulting in greater vulnerability.

Shellfish

Among calcifying organisms, shellfish make up a significant proportion of seafood products, making a major contribution to food security in coastal regions. In 2021, marine molluscs from fishing (11%) and aquaculture (89%) accounted for 13.5% of exploited marine biomass and 36.1% of the monetary value generated by global aquaculture production, for a total of $30 billion. Global shellfish production is on the rise, and is largely dominated by China, which accounts for 84.2% of the total. Among the main producing countries, some saw their production grow rapidly between the 1970s and 2000s — this is the case of the most important ones such as China, Chile, South Korea and Vietnam — while others, such as Japan, the United States and France, tend to maintain their historical production levels (FAO, 2020).

French aquaculture

In France, marine aquaculture is largely dominated by shellfish farming, which is a socio-economic element structuring French coastal regions. In 2020, more than 15,000 hectares were farmed by nearly 3,000 companies, in addition to the 1,800 km dedicated to line or "bouchot" culture[36,37]. Historically, French oyster farming has been based on the flat oyster. During the 19th century, episodes of mortality, overfishing and the accidental introduction of parasites led to declining populations and local extinctions. The flat oyster was replaced by the Portuguese oyster in 1925, which was wiped out by a viral disease in the 1970s. The Pacific oyster was introduced and production increased to 120,000 tonnes a year, with a market value of €300 million. In 2008, mass mortalities caused by a virus appeared in almost all farming areas, leading to a 40% drop in annual production. In 2012, a bacterium caused mortalities in adult populations, further weakening the industry. Despite the drop in production due to the mortalities, French oyster production remains at the top of the European Community rankings, and among the top five nations worldwide. French mussel farming is based on the production of blue mussels. French mussel production was on the rise, with over 77,000 tonnes marketed in 2012 (compared with an average of 66,000 tonnes between 2007 and 2012). During the winter of 2014, massive mussel mortality occurred in the Pertuis Breton, and similar episodes were subsequently observed in Brittany, Normandy and Nord-Pas-de-Calais, without the causes being clearly identified.

This summary of the history of French shellfish farming shows that growers have always been able to adapt and integrate risks, given the industry's high exposure to environmental hazards. Until recently, ocean warming and acidification did not appear to growers as a major threat likely to reduce production. A 2014 survey of around 100 French shellfish farmers put the risk of disease emergence and health issues at the top of the list, far ahead of the risks induced by climate change and ocean acidification[38]. Another survey published in 2015 showed that almost half of Mediterranean shellfish farmers said they had not heard of ocean

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36. Bouchots are wooden piles laid out in a line on the foreshore.

37. https://www.info.gouv.fr/organisation/secretariat-general-de-la-mer-sgmer/l-economie-bleue-en-france

38. Source: ANR Gigassat project.

acidification, which also reveals a lack of communication between the scientific community and the industry. And yet, isolated and localised episodes of acidification have already caused significant economic losses in shellfish hatcheries across the Atlantic.

An American story

The most emblematic example of the impact of ocean acidification on aquaculture production is at Whiskey Creek Shellfish Hatchery, on the US west coast in the state of Oregon, where oyster larvae are produced and then sold to oyster farms in the Pacific Northwest (Barton *et al.*, 2012; Barton *et al.*, 2015). In 2007, after 30 years of regular production, entire farms of oyster larvae began to die massively. After believing that this mortality was due to bacterial disease, as is sometimes the case, it turned out that the cause was the chemistry of the seawater itself. In this region, acidified water from the depths of the ocean rises to the surface in seasonal winds and feeds the hatchery that houses the oyster larvae farms. This acidified water kills the particularly sensitive larvae. Although this is a natural phenomenon, ongoing ocean acidification is increasing the acidity level of the deep ocean and seems to have pushed these natural conditions beyond what oyster larvae can withstand.

In response to this problem, the company implemented a strategy to avoid filling the tanks early in the morning, during periods of high-water upwelling, so as to limit production losses. Nevertheless, as the absorption of atmospheric CO_2 shifts the average state towards ever higher CO_2 and more corrosive conditions, the company also chose to adapt by investing in a sodium carbonate-based water treatment system to raise the pH (and Ω) before distributing it to the hatchery. The solution was of minimal cost — although it took a few years and hundreds of thousands of dollars in losses before the problem was understood and remedied.

On the one hand, this is an interesting story, because it projects us today into the world of tomorrow. On the other hand, it underlines the highly variable and fluctuating nature of pH and carbonate parameters in the coastal environment where a significant proportion of humans exploits marine resources.

While ocean acidification is often perceived as a future problem, a distant consequence of CO_2 enrichment of the atmosphere and ocean, punctual episodes of acidification can occur today in many coastal sites. Last but not least, this story illustrates the importance of environmental monitoring, which in this case has certainly helped to limit economic losses.

Research for the French shellfish industry

On the strength of this observation, and on the occasion of COP 21 held in Paris in 2015, France's "Comité national de la conchyliculture" called for monitoring the chemical composition of shellfish waters, with explicit reference to the problem of ocean acidification[39]. Surprising as it may seem, we know more about the current and future evolution of pH and carbonates in the Arctic or the China Sea than we do on our own coasts, where we produce shellfish! This is why Ifremer, as part of its research and public support missions, has been deploying a high-frequency pH measurement sensor at the bottom of the bay of Brest since 2017[40]. The data acquired is unequivocal: pH varies greatly on a seasonal and daily scale, with punctually low values that clearly stand out from the offshore levels on which climate models are based. These data confirm that coastal environments are more vulnerable to acidification than offshore environments, and occasionally present levels below the critical threshold established for oyster larvae in the United States. It is therefore essential to strengthen and extend pH monitoring to other shellfish sites representative of the entire industry, in order to assess their vulnerability to ocean acidification and establish realistic projections.

In partnership with regional and national shellfish farming committees, Ifremer and CNRS have set up a network to monitor pH levels in shellfish farming areas from the Mediterranean to northern Brittany, showing for the first time in France episodes

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[39] https://news-oceanacidification-icc.org/2015/12/04/les-enjeux-environnementaux-de-la-conchyliculture-excerpts-in-french/

[40] Source: Ifremer, Ecoscopa network.

of extreme acidification at different times of the year (Figure 7)[41]. As a result, the pH can occasionally reach values as low as 7.5, corresponding to waters that are corrosive to shellfish. Acidification is therefore an ongoing process that is already potentially affecting shellfish and is set to worsen. Considering measured pH values and future pH and temperature projections according to the IPCC's SSP3-7.0 scenario, we estimate that waters could be corrosive to shellfish up to 10% of the time of year in 2050 and 50% of the time in 2100 at certain sites.

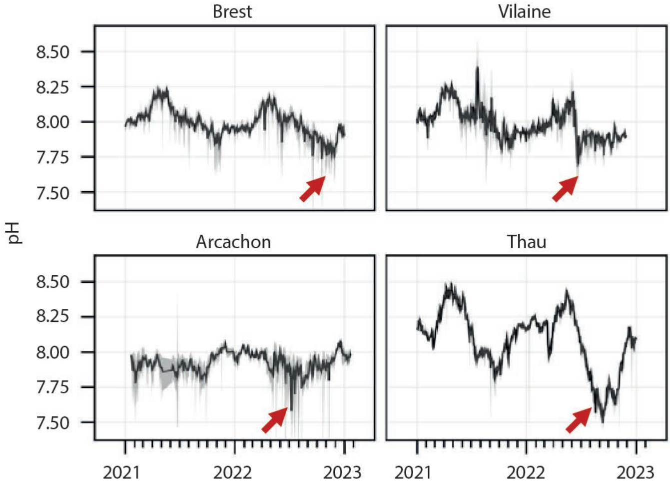

Figure 7. Temporal evolution of average daily pH at four shellfish sites between 2021 and 2023.

The grey area indicates the difference between minimum and maximum values. The red arrows indicate the most marked acidification episodes. Data taken from the project CocoriCO$_2$.

Negative consequences of acidification for shellfish production

Overall, acidification is expected to have negative consequences for shellfish farming and, as indicated in the latest report from the Food and Agriculture Organisation of the United Nations,

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[41] Source CocoriCO$_2$ project "shellfish farming in a high-CO$_2$-rich world", partnership Ifremer/CNRS/CRC-Bretagne-Nord/CRC-Méditerranée/CNC, funded by the European Maritime Affairs and Fisheries Fund (EMFF, 2020-2023).

on the state of world fisheries and aquaculture, scenario planning is becoming essential for developing adaptation strategies (FAO, 2018). The few studies carried out indicate negative economic impacts of climate change, either in terms of net present value, income, consumer welfare, or the nutritional value of products. Regarding the latter, a few recent studies show that acidification has a negative impact on commercial attributes associated with product quality, such as taste, appearance and nutritional composition. For example, the protein, vitamin B_{12} and polyunsaturated fatty acid contents, including the famous omega-3, of mussels are lower in an environment enriched with CO_2 (San Martin *et al.*, 2019).

The impacts of ocean acidification on shellfish farming may have different implications depending on the country and location under consideration. For example, small island developing states, which rely heavily on shellfish farming for food and export, could be particularly vulnerable. Shellfish production could fall by 2060 in most countries due to rapid warming and acidification of the ocean, and even decline over the next decade for the most vulnerable (Stewart-Sinclair *et al.*, 2020).

What about fish?

As we saw earlier, fish are generally less vulnerable than calcifying organisms to ocean acidification. This is reflected in the results of a recent study in which scientists modelled and mapped the effect of changing ocean conditions on the production potential of 180 species of fish and shellfish over the next century. To do this, the authors considered the future evolution of multiple species growth factors, such as temperature, food availability and ocean acidification (Froehlich *et al.*, 2018). Overall, this study shows a higher probability of decline in global aquaculture production. This probability is higher for bivalves than for fish, due to acidification exacerbating the effects of climate change. In fact, fish production could increase locally as the ocean warms up in polar and temperate zones. This study focused on aquaculture only should be taken with caution when extrapolating to fisheries, as these models do not take into account recent discoveries of the effects of acidification on fish behaviour and other indirect effects on habitats and the food chain (Froehlich *et al.*, 2018).

The impacts of ocean acidification have been demonstrated on the behaviour of tropical reef species, and similar experiments have begun to be conducted on temperate species of halieutic interest such as sea bass, a species of strong economic weight with over 150,000 tonnes sold in Europe each year (Porteus *et al.*, 2018). As with reef species, these initial experiments on juvenile sea bass show increased anxiety and reduced olfactory capacity in individuals maintained in acidified conditions. These effects could reduce the survival and reproductive success of the individuals and thus have a long-lasting impact on stocks. If we extrapolate the results of these studies to all exploited species, ocean acidification could have dramatic impacts on commercial fishing that are not currently taken into account.

Additionnally, tropical coral reefs, directly affected by ocean acidification, support important artisanal fisheries in many parts of the world. Ocean acidification weakens coral reefs, which are severely harmed by global warming. As a result, coral reefs will deteriorate by the end of the century, and the consequences for fishing will depend on the type of habitat that replaces them, and the fish species that find refuge there.

While most reef fish can survive predicted increases in acidification and ocean temperature, corals are less tolerant. Some fish species are strictly dependent on corals for food and shelter, suggesting that coral extinctions could lead to secondary fish extinctions. However, these secondary extinctions could extend far beyond these few coral-dependent species. What's more, we don't yet know how these fish declines might evolve worldwide. Mass coral die-offs raise the question of the future of fish communities. A statistical study suggests that fish richness would be around half its current value in a coral-free world (Strona *et al.*, 2021), which would inevitably affect local artisanal fisheries.

Finally, since calcifying organisms, other than the corals mentioned above, are often part of the fish menu, it is possible that the decline of the former in the face of acidification could have repercussions on the abundance of the latter. To test this hypothesis, researchers are using dynamic food web models fed with data on the abundance of species present in the ecosystem, themselves forced by physical, chemical and biological parameters including pH. Using this kind of tool, researchers have studied the direct and indirect effects of acidification on biomass and fishing revenues, and unsurprisingly show that bottom-dwelling invertebrates (crabs, shrimp, benthic grazers, benthic detritus feeders, bivalves) are most affected by lower pH, and that this has repercussions for some of the fish, sharks and other invertebrates that consume these species (Marshall *et al.*, 2017). Although this type of study provides a set of projections that may be useful for managers, the cascading effects of acidification on food chains remain poorly understood.

WILL WE STILL HAVE OYSTERS IN 2100?

Ocean acidification is one of the many factors that will affect the sustainability of seafood products. So, to answer the question above, we will have oysters in 2100, but at what price? Production is likely to decline as a result of acidification and climate change. The question is how to adapt the industry in response to more erratic and less predictable production. As far as fish are concerned, the most worrying possibility is that the loss of the senses observed in tropical reef fish foreshadows the same responses and reduced survival in commercially important species, which provide most of the marine resources consumed by humans. But the greatest uncertainty concerns the impacts of ocean acidification on marine habitats and food webs, with possible repercussions for marine biodiversity and wild populations.

HOW DOES ACIDIFICATION INTERACT WITH OTHER FACTORS IN CLIMATE CHANGE?

Although this book is dedicated to ocean acidification, we cannot ignore the fact that, because of human activities, many parameters are changing at the same time, and that the problems that organisms face as a result of seawater acidification are often compounded by other stressors.

EVERYTHING'S ON THE MOVE!

Ocean warming, deoxygenation, melting glaciers and sea ice, rising sea levels, erosion of biodiversity and pollution of all kinds are all interacting factors that we need to understand in order to better anticipate the future and provide solutions to future problems. While increasing greenhouse gas emissions are making the ocean more acidic, they are also contributing, as we have seen, to their warming, but also to their deoxygenation, which is much less well known! These three parameters — acidification, warming and deoxygenation — are linked by marine physics and chemistry, and their interactions within the ocean risk pushing marine organisms beyond their physiological tolerance limits.

THE OCEAN OVERHEATS

At the time of writing, the average ocean surface temperature is the highest ever measured. As of May 2023, calculated from billions of measurements from submerged sensors, satellites, ships, aircraft and weather stations, it is around 19.7°C, or 0.26°C above the 1991-2020 average. The ocean has absorbed 94% of the excess heat due to human activities and the resulting increase in the greenhouse effect. The latest IPCC report indicates that the average temperature measured at the ocean surface between

2011 and 2020 was 0.88°C above the temperature measured during the period 1850-1900. This increase is less than that observed on Earth, which was 1.59°C, due to the large volume of the ocean and the transfer of heat to the deep layers.

Ocean surface temperature will rise regardless of the future CO_2 emission scenario. Under one of the most optimistic scenarios (SSP2-2.6), average sea surface temperature for the period 2080-2099 will rise by around 1.4°C compared with 1870-1899 (Kwiatkowski *et al.*, 2020). In the high-emissions scenario (SSP5-8.5), the increase will be 3.4°C.

TEMPERATURE GOVERNS SPECIES DISTRIBUTION

Species distribution is intimately linked to temperature gradients, and this temperature-distribution relationship concerns both terrestrial and aquatic environments, and all types of organism. The effect of temperature on organisms is of such magnitude that it imposes strict limits on where life is possible. Temperature influences every aspect of an organism physiology (growth, reproduction, behaviour), from the structure of its macromolecules to the speed of the chemical reactions involved in its metabolism (Hochachka and Somero, 2002). Each species occupies a particular thermal niche, namely the temperature range within which it can thrive, but outside which its survival is compromised (Figure 6, p. 56). A species performance is generally higher in the centre of its range, where temperature is optimal, and decreases as it approaches its limits (Angilletta, 2009).

A particularly important aspect of an organism relationship with its environment is its ability to maintain its body temperature independently of the ambient temperature. Organisms whose body temperature conforms to the temperature of the environment are said to be "ectotherms" (*ecto* is the Greek prefix for "outside"). Marine species are generally strict ectotherms, as they do not have the anatomical or physiological means to maintain a temperature gradient between the external environment and the body. There are a few rare exceptions, such as birds, marine mammals and some fish which are organisms capable of regulating their internal temperature independently of the external environment and called “endotherms” (*endo* is the Greek prefix for “inside”). These organisms are therefore less sensitive to direct thermal disturbances.

Species differ enormously in the range of body temperature they can tolerate, as well as in the temperature limit at which they can live. For example, some species of Antarctic fish, which normally live between 2°C and – 1.86°C, the freezing point of seawater, and die of heat at temperature levels above 4°C, are distinctly “stenothermic” (*steno* is the Greek prefix for “narrow”). Other aquatic species, including many intertidal organisms[42] that undergo long periods of air exposure at low tide, routinely withstand temperature variations of 20 to 30°C on a daily basis, and encounter even greater thermal variations on a seasonal basis. These species are known as “eurytherms” (*eury* is the Greek prefix for “large”).

The thermal preferences of animals and their ability to tolerate greater or lesser variations in outside temperature determine their vulnerability to ocean warming.

COURAGE, LET’S RUN!

The most obvious effect of global warming is the shift of species towards higher latitudes and the modification of their geographic ranges. Species follow their thermal niches. Warming has already altered the distribution of marine species, from phytoplankton to marine mammals, in many parts of the ocean. Pelagic species, which live in the water column, are generally better able to migrate long distances than benthic species that live on the ocean floor. Today, we estimate that the average movement observed since the 1950s is around 60 km per decade for pelagic species, compared with 30 km per decade for benthic species. Marine species richness tends to decrease in latitudes where average

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[42] Living between low and high tide.

annual sea surface temperature exceeds 20°C (Chaudhary *et al.*, 2021). The result is a decline in species richness around the equator that has been accentuated by global warming, particularly for pelagic species.

These shifts in species in response to warmer waters are clearly visible in the Mediterranean. This inland sea, artificially linked to the Red Sea to the south by the Suez Canal built at the instigation of Ferdinand de Lesseps in 1869, is colonised by new species as a result of global warming. The opposite, namely Mediterranean species settling in the Red Sea, has rarely been observed. Observations of so-called “Lessepsian” species, in reference to the eponymous builder, have multiplied in recent decades. These species can pose a threat to local flora and fauna. One example is the rabbitfish, which originates from the Red Sea and destroys the habitat and resources of native species by consuming Mediterranean algae and plants. First spotted in the coastal waters of Israel and southern Turkey, this species was fished for the first time in Italy in 2013, then in France in 2019, and is now listed as an invasive species by the International Union for Conservation of Nature (IUCN).

Another example of climatic migration is the invasion of European coasts by the cupped (or Pacific) oyster. Introduced to France in the 1970s, this species used to reproduce south of the Loire, where water temperature was optimal — it takes several weeks at 18-20°C for adults to lay eggs and larvae to develop to the juvenile stage. During the heatwave of 1976, oyster farmers in Brittany observed mature oysters and juveniles the following year on their rearing beds. What was an exception in 1976 gradually became the rule between 1990 and 2003. Since then, the cupped oyster has reproduced every year in the Brest harbour, where it has made many people happy, since authorisation has been granted to oyster farmers to collect spat, which was unthinkable in the past. The species has colonised northern Europe as far afield as Norway, where it is considered invasive. Although trade-related transfers of live animals have favoured this migration, global warming has contributed to the extension of this oyster range (Thomas *et al.*, 2016).

When species are unable to acclimatise, adapt or move rapidly in response to a rise in temperature, then the risk is of mass mortalities, population collapses or even local extinctions. A study of nearly 25,000 marine species shows that 90% are at high or critical risk of extinction over 85% of their natural range, according to the IPCC's SSP5-8.5 scenario (Boyce *et al.*, 2022). Stenothermic species, less tolerant of variations, are physiologically more at risk of extinction than eurythermic species, which can withstand a wider range of temperatures. This has major consequences for humans, since many stenothermic marine species are heavily exploited through fishing and aquaculture.

MARINE HEATWAVES

In addition to chronic ocean warming, the frequency of marine heatwaves (MHWs) has been on the rise for several decades. Like their terrestrial counterparts, marine heatwaves are defined as periods of several days to several months during which sea surface temperatures are abnormally high. An abnormally warm event is considered a marine heatwave when it lasts five days or more, with temperatures above the 90^e percentile, based on a 30-year historical reference period (Hobday *et al.*, 2016).

This "statistical" definition of marine heatwaves emerged following an unprecedented warming event off the west coast of Australia during the austral summer of 2011. This event resulted in rapid dieback of algal forests and associated ecosystem changes along hundreds of kilometres of coastline (Wernberg *et al.*, 2013). The longest marine heatwave, dubbed "Blob", covered much of the northeast Pacific from 2014 to 2016 and was associated with, among other things, mass mortality events for marine mammals and birds (Cavole *et al.*, 2016) and harmful algal blooms (McCabe *et al.*, 2016), affecting the provision of ecological goods and services for society (Smith *et al.*, 2021; Smith *et al.*, 2023). Over the past 25 years, at least 34 marine heatwaves have affected the provisioning, regulating, habitat and cultural services of ecosystems, resulting in economic losses of several hundred million US dollars in the affected regions.

In the Mediterranean Sea, more than 2,300 mass mortality events involving over 90 species of benthic invertebrates were recorded between 1979 and 2020, mostly associated with marine heatwaves (Garrabou *et al.*, 2019). According to a study published in July 2022, the 2015-2019 marine heatwaves in this region caused massive mortalities in some 50 benthic species, including corals, gorgonians, sea urchins, molluscs, Posidonia, etc. (Garrabou *et al.*, 2022). Finally, the most recent, which hit the Mediterranean almost entirely in the summer of 2022, generated temperature anomalies of almost 5°C, causing massive mortalities of benthic organisms (Marie *et al.*, 2023). In the spring of 2023, the North Atlantic as a whole showed an average temperature anomaly of +1.3°C, with record-breaking temperatures at the end of July — 24.9°C on average — whereas the ocean is usually warmest at the beginning of September.

Ocean warming and marine heat waves can be the cause of a well-known phenomenon: coral bleaching. Corals live in association with symbiotic micro-algae, the zooxanthellae, which provide the nutrients needed for growth. Under stress, these coloured algae are expelled from the animal, revealing its white skeleton. Bleaching does not necessarily lead to the death of the coral; some individuals recover their symbionts once the stress has passed. Nevertheless, bleaching increases the coral vulnerability, as it no longer benefits from the nutrients provided by micro-algae. Numerous bleaching episodes have been reported in recent years, notably on the Great Barrier Reef in Australia. The most recent, which took place during the austral summer of 2022, affected almost 90% of its extent when temperature was 0.5 to 2°C above normal. However, the increasing frequency of these heat waves suggests the worst for these emblematic ecosystems, with the risk that animals will no longer have time to recover between two heatwaves. The IPCC is therefore sounding the alarm: 70-90% of coral reefs could disappear if temperature rises by 1.5°C, and we risk almost total extinction at 2°C of warming (IPCC, 2023).

Warming has direct effects on marine organisms, with major consequences for ecosystem functioning. Ocean warming will also have secondary effects, notably on dissolved oxygen levels.

I BREATHE, THEREFORE I AM!

Oxygen, by enabling the production of energy through respiration, is essential to aerobic life[43]. And yet, we do not talk about it much, but since the middle of the 20th century, oxygen levels have been declining both in the open sea and in coastal waters to an alarming degree. What scientists call "ocean deoxygenation" is one of the most significant changes to have occurred in marine ecosystems. The open ocean has lost around 2% of its oxygen over the past 50 years, and global warming is the cause of this phenomenon in many places (Breitburg *et al.*, 2018).

In the open ocean, oxygen content in the upper layers of the ocean is negatively correlated with temperature. From the mid-1980s onwards, strong deoxygenations coincide with large increases in ocean heat content (Ito *et al.*, 2017). "Deep-sea oxygen minimum zones", where concentrations are below 2 mg per litre (also known as *hypoxic* conditions), occur naturally at depths of around 200 to 1,500 m, usually along the west coast of continents. Over the past 50 years, the extent of these zones has increased by an area equivalent to the size of the European Union. The volume of water totally devoid of oxygen — referred to as "anoxic" — has more than quadrupled over the same period.

In coastal waters, this phenomenon is exacerbated by nutrient runoff, particularly nitrogen and phosphorus, linked to agricultural activities and human waste disposal. This phenomenon stimulates primary production (phytoplankton, algae), which in turn leads to the accumulation of organic matter on the seabed, where decomposition by aerobic microbial respiration consumes oxygen. Hypoxia has now been reported at over 500 sites, whereas less than 10% were affected before 1950 (Diaz and Rosenberg, 2008). Thus, the current rate of oxygen decline in coastal areas exceeds that of the open ocean, reflecting the combined effects of increased warming of shallow waters and higher nutrient concentrations.

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[43] The term "aerobic" is most often applied to a system (e.g. a living organism, but also a chemical reaction) that requires oxygen.

HOW ARE GLOBAL WARMING AND OCEAN DEOXYGENATION LINKED?

Warming increases the risk of deoxygenation due to reduced oxygen solubility, increased stratification intensity and duration, and accelerated breathing.

The first reason, which accounts for around 15% of the current worldwide loss of oxygen, is linked to the fact that the solubility of gases in water decreases with increasing temperature. Oxygen is no exception to this elementary rule. So, the hotter it is, the less oxygen water contains; it is a physical fact.

The second reason, which accounts for the remaining 85%, is related to the intensification of ocean stratification, itself caused by global warming. Indeed, in many parts of the globe, the ocean is made up of a relatively homogeneous upper layer of warmer, lighter water, and a deeper layer of cold water, originally formed at the surface in the polar regions. These different layers mix together as the temperature becomes more homogenous under the action of winds, currents and tides. With climate change, warmer, lighter surface waters are warming up faster than deeper, denser cold waters. Differences in density between the surface and the bottom are increasing, reducing exchanges and, consequently, oxygenation of the ocean depths. The intensification of stratification is accentuated by another consequence of climate change: the melting of glaciers and polar ice caps. By bringing in freshwater that is naturally lighter than saltwater, the density of surface seawater decreases and the density difference with deep waters increases. This is yet another obstacle to the mixing of waters and deep ocean oxygenation.

Finally, the third reason, which is biological and difficult to quantify, is linked to the fact that higher temperatures increase the respiratory oxygen demand of organisms, which in turn reduces the quantity of oxygen available in the environment.

The ocean will continue to be depleted of oxygen as a result of further warming. According to the IPCC most pessimistic scenario (SSP5-8.5), ocean oxygen reserves are set to decline by 3 to 4% by the end of the century. This may not seem like much, but most of this loss is concentrated in the top 1,000 meters of the ocean, where species richness and abundance are the greatest.

SOME EFFECTS OF OXYGEN DEPLETION

Given that hypoxia limits the acquisition of energy through respiration, ocean deoxygenation can influence all the vital processes of aerobic organisms to the point of reducing their survival, growth and reproductive capacities, and altering their behaviour. However, tolerance to oxygen depletion and behavioural responses vary according to species, taxa and trophic groups. As a result, ongoing ocean deoxygenation can alter marine food chains and ecosystem functioning. Like temperature, the distribution of organisms depends on the dissolved oxygen content of the water, and any change in this parameter can cause species to move. Oxygen-depleted zones are often referred to as “dead zones”, as they are literally deserted by strict aerobic organisms such as fish, zooplankton and coral.

Mass mortality due to temporary oxygen deficiency has been observed for decades, particularly on the French coast. A well-known case of anoxic or hypoxic crises concerns Mediterranean lagoons, where episodes of *malaïgue* — “bad water” in Occitan (a French regional language) — recur year after year. These anoxic crises are local phenomena mainly due to high temperature and the absence of wind allowing water mixing. In the summer of 2018, *malaïgue* literally wiped out mussel production and caused the loss of 30% of oyster production in the Thau lagoon. This is not the first time this phenomenon has hit the shellfish farming profession, but global warming, with increasing marine heat waves, is likely to lead to increasingly frequent anoxic episodes.

ACIDIFICATION, WARMING AND DEOXYGENATION: A DEADLY TRIO?

Acidification, warming and deoxygenation are mechanically linked by antagonisms and positive feedback loops. On the one hand, rising temperature increases aerobic respiration and thus the demand for oxygen, whose availability decreases due to its lower solubility in warm water. On the other hand, the increase in respiration favours the production of CO_2 and hence acidification, further reducing the ocean capacity to absorb the anthropogenic CO_2 responsible for global warming.

The effects of acidification, warming and deoxygenation can interact in different ways on marine organisms (Figure 8). The effects of interaction are termed additive, synergistic or antagonistic, depending on whether they are equal to, greater than or less than the sum of the individual effects.

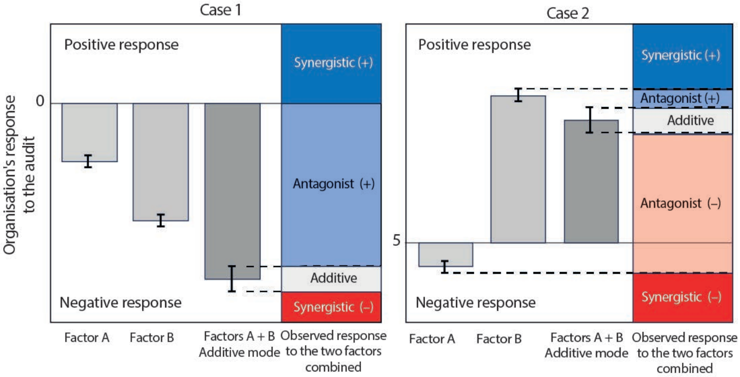

Figure 8. Description of interactions between environmental factors (A or B, e.g. warming and acidification) on a marine organism.

The cumulative effects of these factors can be additive, synergistic or antagonistic. Note that these effects are not necessarily negative; the example on the right shows the case of an organism reacting favourably to factor B. Diagram adapted from Lopez *et al*. (2022).

To test the interaction of three factors such as acidification, warming and deoxygenation, we need to assess the effects of the single factors in isolation, but also their mutual interactions, which leads to complex experimental designs that are sometimes impossible to implement. Let's imagine that we assign three levels to each factor — each level corresponding to model projections from greenhouse gas emission scenarios; we would then need to test 27 combinations of treatments (3 temperature levels × 3 oxygen concentrations × 3 pH). As each combination would have to be repeated at least three times to allow generalisation of results and the use of statistical analyses, this would require a minimum of 81 independent experimental units, which is very complicated to set up in a laboratory. Although it is possible to obtain valid answers by limiting the interactions tested or by constructing specific scenarios, this complexity explains why the vast majority of studies conducted to date focus on one factor, sometimes two, rarely three (Boyd *et al.*, 2018).

The few studies involving two or more factors generally show negative additive or synergistic effects. For example, a study assessing the combined impacts of three factors on abalone showed that the combination of hypoxia and acidification induced a more marked narrowing of the thermal niche than hypoxia alone (Tripp *et al.*, 2017). More generally, the temperature range tolerated by organisms tends to decrease in response to acidification or hypoxia (Figure 9; Pörtner and Farrell, 2008). This effect is particularly marked in polar and tropical species, whose particularly stable habitat means they can tolerate small temperature variations. In temperate and

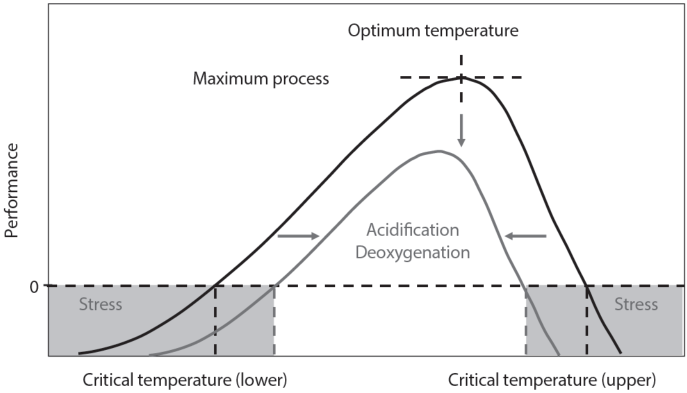

Figure 9. Theoretical performance curve of a physiological process as a function of temperature.

The zone of optimal performance decreases under the pressure of other environmental factors, in this case ocean acidification and deoxygenation. Diagram adapted from Pörtner and Farrell (2008).

subtropical species, accustomed to fluctuating environments, warming and acidification have generally negative effects, but the acceleration of metabolism caused by warming can offset the effects of acidification when the organism is maintained in its thermal niche and well fed (Dworjanyn and Byrne, 2018).

The vast majority of multifactorial studies have focused on the combined effects of warming and acidification. Hypoxia is a factor that has generally been studied in isolation, *via* short laboratory exposures. However, a recent meta-analysis of the scientific literature shows that hypoxia always has an aggravating effect, outweighing the effects of both warming and acidification (Sampaio *et al.*, 2021).

The effect of multiple factors on marine organisms is difficult to generalise, as there are too few studies that take into account more than two factors combined. Moreover, responses differ according to the species studied and the intensity of the stressors. Nevertheless, our knowledge of how organisms perform in response to environmental factors, and how they manage available energy, enables us to define a theoretical framework for assessing multifactorial effects (Figure 10). Energy allocation plays an essential role in tolerance to environmental stress and in setting limits to the survival of organisms and their populations.

Under normal conditions, the amount of energy available covers the maintenance costs required to keep the organism strictly alive, and the activity costs associated with digestion, growth, locomotion, immunity and reproduction, among other things (Sokolova *et al.*, 2012). When exposed to a moderate stressor, maintenance costs increase to the detriment of other functions to protect and repair damage inflicted to the organism. This is, for example, what can happen when CO_2 enrichment is compensated for by the addition of bicarbonate to the blood. Exposure to a greater stress factor — such as prolonged hypoxia or critical temperature — can reduce the amount of energy acquired by the organism. As maintenance costs take priority and are incompressible, the energy allocated to other functions is reduced. The combination of these two factors increases stress and can lead to both higher maintenance costs and a reduction in available energy. This temporary physiological state prolongs the survival of individuals in the short term, but fails to maintain the population in the long term due to the lack of energy allocated to activities other than maintenance (Figure 10).

Based on the aforementioned physiological mechanisms and paleoclimate reconstruction models, researchers have shown that warming and deoxygenation are responsible for the majority of extinctions that wiped out 95% of marine species at the end of the Permian[44] (Penn *et al.*, 2018). In this article, the authors draw a parallel with our current situation. The warming predicted by the IPCC by 2300 under the SSP5-8.5 scenario would correspond to 35-50% of what occurred at the end of the Permian. These projections highlight the possibility of a future mass extinction resulting from the ongoing depletion of the ocean aerobic capacity. We would be well advised to take note.

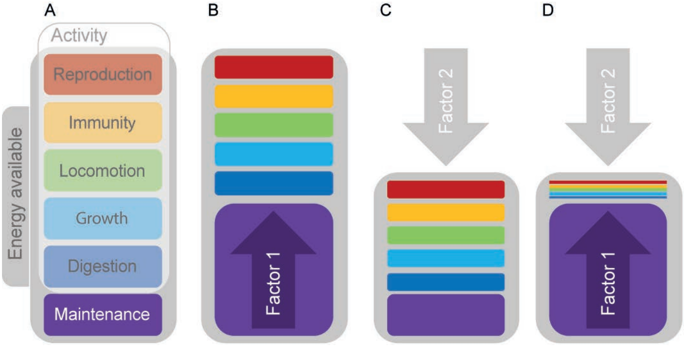

Figure 10. Assessment of multifactorial effects in an energy context.

In a favourable environment, aerobic metabolism provides sufficient energy to support the maintenance and activity costs represented by the different-coloured boxes (A). Exposure to an environmental factor increases maintenance costs (B) or reduces available energy (C), which in both cases reduces activity potential. Exposure to both factors simultaneously increases maintenance costs, while available energy is reduced, virtually eliminating activity potential (D). The size of the boxes does not reflect actual energy allocation. Figure inspired by Sokolova *et al*. (2012).

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[44] The Permian is the sixth and last geological epoch of the Palaeozoic. It extends from 299 million years ago to 251 million years ago.

Ocean acidification is a factor exacerbating the effects of climate change, which can push an individual beyond its physiological tolerance limits and drive entire populations to extinction. Nevertheless, the effects of climate change remain dominated by warming, which acts directly on the metabolism and indirectly on the oxygen availability of marine organisms. Deoxygenation is also a dominant factor compared to acidification, as it is the very acquisition of energy that is directly compromised. However, experimental studies evaluating the joint impact of the three stress factors on marine fauna are still rare, leaving a gap to be filled by the scientific community. It is vital to move towards multifactorial scenarios to better predict biological responses to tomorrow's ocean.

HOW TO TAKE ACTION?

Everything we've shown so far in this book suggests that ocean acidification is a factor exacerbating the effects of climate change, which will impact marine organisms and ecosystems, and have a long-lasting effect on the millions of people who depend on them. The natural question is whether we can, individually and collectively, act to mitigate and adapt to this phenomenon.

MITIGATION *VERSUS* ADAPTATION

Let's imagine we're in a boat that's taking on water. To avoid sinking, we need to solve two problems. The first, which is the very cause of the sinking, is to plug up the waterways. The second, which is a consequence of the first, consists in evacuating the water present to stay dry and avoid damaging the ship. In the same way, faced with CO_2 emissions and the resulting acidification of the ocean, mankind must act on two complementary fronts at once: mitigation, which involves tackling the problem at source by reducing our emissions of greenhouse gases or trapping those present in the atmosphere, and adaptation, which involves overcoming and reducing the effects of the changes underway.

REDUCING OUR GREENHOUSE GAS EMISSIONS

The first measure that springs to mind is to tackle the problem at source and reduce our greenhouse gas emissions by cutting our consumption of fossil fuels such as coal, oil and natural gas, making renewable energy sources more widespread, improving energy efficiency and promoting energy conservation. The adoption of such measures depends on the implementation of incentive-based public policies, but also on more energy-efficient individual behaviour. The emissions scenario humanity adopts will have a major impact on climate trajectory, as it will on ocean acidification. But in the meantime, are there local and more specific actions we can take to adapt?

GREENING THE OCEAN

To reduce acidification, we need to lower the concentration of CO_2 in seawater. As on land, marine primary producers — macro-algae, phytoplankton and marine plants — use CO_2 to manufacture organic matter, under the action of light, through photosynthesis (eq. 7, Chapter 4, p. 33). Photosynthetic activity consumes CO_2 and therefore increases pH and carbonate ion concentration (CO_3^{2-}). Consequently, one strategy for limiting ocean acidification would be to increase primary production, in other words, to revegetate the oceans.

But it works as long as there is light! At night, photosynthesis stops, CO_2 is released into the surrounding seawater *via* respiration, and the pH drops. In this way, macro-algae and marine plants provide a "temporary" refuge from acidification, and vary the pH on a daily basis.

A few days' monitoring of pH in macro-algae forests near Dunedin in New Zealand shows variations of up to 1 pH unit between day and night (Cornwall *et al.*, 2013). Similarly, in seagrass systems[45] in the Philippines, the Great Barrier Reef in Australia, and the Mediterranean, pH varies daily by 0.5 to 0.7 units, with maximum values reached around midday when photosynthesis is at its peak (Falkenberg *et al.*, 2021). These natural variations in pH generally have no negative effect on the organisms occupying these habitats (Kapsenberg and Cyronak, 2019). On average, the pH measured around macro-algae and seagrass beds is higher than in adjacent non-vegetated areas. Thus, despite daily fluctuations in pH linked to the intermittence of photosynthesis, primary producers can relieve calcifying organisms from the harmful effects of acidification. Given the high tolerance of algae and seagrass beds to acidification, it is highly likely that these organisms will continue to provide important refugia for many of the species associated with them.

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45. In reference to seagrasses, aquatic marine plants belonging to the genus Zostera (family Zosteraceae) that grow in sandy and sandy-muddy sediments in the tidal and infralittoral zone.

A recent example shows that a species of brown algae belonging to the genus Fucales increases the overall average pH of seawater in the Kiel fjord in Germany by 0.01 to 0.2 units, with a diurnal variability of 1.2 units. Mussels living in the vicinity take advantage of this natural pH modulation by producing shell during diurnal periods, when pH is highest (Wahl *et al.*, 2018).

Such refuges based on the biological elimination of CO_2 potentially exist in all areas of intense primary production. The protective effect of algae and seagrass beds varies in time and space according to their productivity, which depends on the season, time of day, currents and availability of nutrients. In temperate and polar regions, characterised by strong seasonality, macroalgal productivity — and thus their capacity to fix CO_2 and increase pH — is highest in spring and summer, when light intensity and daylight duration peak.

The spatial extent of the protective effect of algae and marine plants can range from a few centimetres, limited to the interface between water and plant, to several metres or kilometres. The extent of the refuge depends mainly on the stock, primary productivity and currents. Refuge potential is particularly important in dense, fast-growing macro-algae assemblages, characterised by a complex canopy that slows currents and thus increases water residence time.

The modification of seawater carbonate chemistry by seagrasses and algae grown alongside acid-sensitive organisms is a field of research that has been emerging over the last decade or so, and now needs to be considered from a conservation and aquaculture perspective in a CO_2-enriched ocean. If algae and seagrass beds can form true underwater forests and mitigate acidification, then it is all the more important to conserve and protect them to increase the resilience of marine ecosystems.

Growing algae and raising shellfish: a win-win relationship!

The co-culture of seaweed and shellfish is nothing new. What could be likened to marine agroforestry — the association of trees and animals on the same plot of land — has been practiced since ancient times in many Asian countries. This is the case, for example, in Daya Bay, located in the north-eastern part of the South China Sea. This semi-enclosed, shallow bay, 600 km^2 long, has been home to one of the country's most intensive oyster-growing areas for over three decades, with an estimated stock of 66,000 tonnes in 2016 — just over two-thirds of French production! At the same time, the Chinese produce 270,000 tonnes of red algae.

It is in this context of hyperproduction that researchers at the Chinese Academy of Fisheries Sciences in Guangzhou are studying in the laboratory the effect of co-cultivating oysters and algae, and suggesting a reciprocal benefit (Han *et al.*, 2017). The oyster calcifies and breathes, both processes excreting CO_2 which is used during the day by algae to manufacture their material. In doing so, algae limit biogenic acidification, i.e. they counteract the drop in pH that is normally caused by the excretion of CO_2 by oysters. In this way, the algae raise the pH and availability of carbonate ions required for shell production. In addition, oysters filter phytoplankton and clarify seawater, enabling better light penetration essential for photosynthesis and macro-algae growth.

These researchers also show, on the one hand, that monoculture oyster production releases CO_2 *via* respiration and calcification, which ends up in the atmosphere. On the other hand, when co-cultured with algae, the situation can be reversed, as the algae make direct use of dissolved CO_2. While oyster farming is a source of CO_2, co-culture with algae can be a sink for CO_2.

Another study conducted on the US east coast, off Long Island near New York, shows that oysters co-cultured with the well-known brown seaweed Kombu royal are exposed to higher pH levels and grow faster than their counterparts cultivated on sites some 50 m away from seaweed beds (Young *et al.*, 2022).

Collectively, these results suggest that bivalve farming and nearby algae cultivation not only promote atmospheric CO_2 capture, but also cross-species synergies that could increase the resilience of shellfish farms in the years and decades to come.

Act local, think global: growing algae to save the climate?

In addition to adapting to ocean acidification, large-scale algal cultivation can therefore also be a means of increasing the potential for CO_2 capture and sequestration by the ocean, and thus contribute to mitigating climate change.

This approach is considered a geoengineering technique[46] because, unlike local adaptation practices, the idea is to correct human's effects on the environment by involving mechanisms that have a global impact on the planet. Although controversial, geoengineering techniques based on CO_2 capture and long-term storage in geological, terrestrial or oceanic reservoirs ("carbon dioxide removal", or CDR) are today considered complementary and indispensable approaches to efforts to reduce greenhouse gas emissions in order to achieve the climate goals set out in the Paris Agreement (IPCC, 2023).

On the one hand, the CO_2 dissolved in the upper ocean that is captured and transformed into organic matter by algae can be sequestered permanently on the seafloor, away from the atmosphere (Krause-Jensen and Duarte, 2016). On the other hand, as algae grow, they release large quantities of dissolved organic carbon into the upper ocean layer, which remains stable over long periods of time, offering an additional carbon sequestration pathway.

Given the progress made over the past decade in developing algae crops for human consumption, animal feed and biofuel production, it is conceivable today to create large-scale farms specifically dedicated to deep-sea CO_2 capture and sequestration. The available surface area suitable for seaweed cultivation is estimated at nearly 48 million km^2 (Froehlich *et al.*, 2019). According to a report by the US National Academy of Sciences, an area of around 73,000 km^2 is needed to sequester 0.1 Gt of CO_2 per year with algae, or a 100 m-wide strip dedicated to algae cultivation spread over 63% of the world's coastline (National Academies of Sciences, Engineering, and Medicine, 2021). In other words, it would take approximately 29 million km^2 to sequester the 40 Gt (approx.) of CO_2 we emit every year, or twice the surface area of Europe. Large-scale algae cultivation can help us achieve carbon neutrality, but it probably won't be enough. Large sources of energy will also be needed

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[46] A set of techniques designed to manipulate and modify the Earth's climate and environment.

in the process to transport and maintain these facilities. To this end, offshore algae farms can involve a combination of renewable energy sources. There are currently two seaweed farm pilot projects off Belgium and the Netherlands that use wind farms[47].

In summary, the cultivation and sequestration of algae on the ocean floor appears to be effective in sequestering CO_2. We have a good understanding of the biology and decades of experience in algae cultivation. However, there is still uncertainty about the quantity and sustainability of the carbon sequestered by algae. There are likely to be both positive and negative societal and environmental impacts from algae cultivation and sequestration.

Seaweed farming will clearly enhance aspects of the blue economy[48], while constraining other marine economic activities if there is competition for coastal space and resources, and the question of the extent of the net benefit to coastal communities remains open. On the negative side, vast seaweed farms could pose a risk to navigation and generate conflicts of use for space and resources. In particular, these algae capture nutrients and light that are no longer available to other photosynthetic organisms such as phytoplankton, which form the basis of the food chain.

BOOSTING OCEAN ALKALINITY

Initially, a climatic geoengineering technique

Ocean Alkalinity Enhancement (OAE), also known as "enhanced erosion", was first proposed in 1995 to increase the potential of the ocean to capture and sequester CO_2 and thus limit the effects of climate change (Kheshgi, 1995). In this context, alkalinisation is seen as a geoengineering technique that incidentally combats acidification (Renforth and Henderson, 2017).

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[47] https://www.norther.be/offshore_seaweed_farm/

[48] The blue economy is an economic concept relating to economic activities linked to ocean, seas and their coasts.

How does it work?

This technique is largely inspired by the modulation of the Earth's alkalinity over geological time scales, during which the slow dissolution of silicate and carbonate minerals increases ocean alkalinity and decreases CO_2 concentrations. More specifically, the increase in alkalinity leads to the consumption of protons and an increase in pH, resulting in a decrease in the partial pressure of CO_2 in seawater, a net reduction in atmospheric CO_2 and an increase in the oceanic carbon reservoir. It should also be remembered that increased carbonate ion concentrations promote limestone precipitation in calcifying organisms (eq. 4, Chapter 1, p. 14).

In practical terms, OAE involves accelerating the naturally slow erosion process by adding large quantities of pulverised silicate (olivine, basalt), carbonate rock (limestone) or their dissolution products (lime) to seawater to raise the pH and lower the CO_2 concentrations in the water. These alkaline substances come from land-based mineral or synthetic chemical sources, or from locally available marine materials such as shellfish. These substances have to be processed beforehand, ground into fine particles to facilitate dissolution, and transported on board ships to be dissolved in the ocean.

What are the constraints?

The rate at which olivine and limestone dissolve in seawater under natural conditions is very slow, as the medium is often supersaturated with respect to limestone. On the other hand, when the concentration of carbonate ions decreases as a result of CO_2 enrichment, the rate of dissolution increases. As a result, limestone dissolution is a potentially effective method to apply to acidified waters, enriched in CO_2, and undersaturated in carbonate ions.

An alternative to the problem of limestone dissolution is to use quicklime (CaO), a product derived from the combustion of limestone at high temperatures. Lime is easily soluble in seawater, but the limestone transformation process releases CO_2 and energy is required to power the combustion process, which itself emits CO_2. Consequently, producing large quantities of quicklime without capturing and storing the CO_2 emitted would result in an undesirable additional release of CO_2 that needs to be accounted for.

A final option for increasing dissolution speed is to reduce these compounds to the smallest possible particles. At average seawater temperatures of 15 to 25°C, an olivine sand with a grain size of 0.3 mm takes 700 to 2,100 years to dissolve, and is therefore of little practical value. To obtain useful and stable CO_2 absorption rates within 15 to 20 years, grains with a diameter of less than 0.01 mm are required. However, preparing and transporting the necessary material raises major economic, infrastructure and public health issues. For example, the energy required to extract rock and transform it into millimetre-sized particles is relatively low and common practice, but it takes three times as much energy to grind particles to diameters of less than 0.01 mm.

What is the potential of OAE?

To date, the potential of OAE has mainly been deduced from modelling and techno-economic laboratory studies. Models use simplified representations of marine biogeochemistry, rudimentary descriptions of marine ecosystems, and generally simulate OAE as the addition of "pure" alkalinity, i.e. olivine or limestone minerals. The first experimental studies have only recently begun, and have already generated new information on questions concerning the actual addition of alkalinity and ecological impacts.

The main unknown is how OAE deployments would alter the biogeochemical cycling of elements on a local and global scale, and the impact of these alterations on marine ecosystems, given the permanence of these chemical changes. The impacts of alkalinity addition and other confounding effects such as the addition of impurities like certain trace metals to the marine environment are unknown.

Putting shells back in the sea: a form of "permaculture" to mitigate acidification locally and adapt at the same time!

Shellfish are made of limestone by the precipitation of calcium and carbonate ions (eq. 6, Chapter 1, p. 14). Today, consumed shellfish often end up in the trash, headed for the incinerator, where they will be transformed into atmospheric CO_2. This is biogeochemical and ecological heresy, as well as economic, because transporting and burning shells is expensive!

Incinerating shellfish is equivalent to converting what was marine limestone into CO_2. Not only are we adding greenhouse gases to the very atmosphere we're trying to reduce, but we're also exporting to the atmosphere the ocean carbonates used in the calcification process.

It is also important to note that shellfish are not CO_2 sinks, but rather sources. The processes of calcification and respiration emit CO_2, which means that the production of shellfish results in a net CO_2 debt. This debt is further increased when the shells are reduced to ash and enter the atmosphere as CO_2. One way to offset this CO_2 debt would be to return the shellfish to the ocean where they were produced, as their dissolution sequesters CO_2.This practice could attenuate acidification locally and maintain the alkalinity of the environment by avoiding the export of carbonates. This circular process would have the virtue of returning to the ocean some of what it has produced, and more specifically, its alkalinity.

Unlike olivine or inorganic limestone from quarries, the materials on which current OAE models are based, shells can dissolve in seawater even in carbonate supersaturated conditions (Ries *et al.*, 2016). Nevertheless, this process remains very slow and it is highly likely that the reduction of shells to particles accelerates their dissolution.

As with OAE, we need to evaluate the ability of different shell materials (shells, grains, powders, dusts) to dissolve and raise pH and alkalinity in the laboratory, test the best-performing products in the laboratory on pilot sites *in situ*, and assess the environmental impact and societal acceptability of this kind of practice.

Generally speaking, shellfish production sites lend themselves well to this type of OAE experiment. These environments are, on the one hand, generally sheltered, and the hydrodynamics are favourable to particle retention. On the other hand, they are often characterised by wide variations in pH, with biogenic acidification phenomena (i.e. acidification caused by the respiration of organisms) likely to promote shell dissolution. This form of amending shellfish farming sites with shell residues could constitute both a climate change mitigation measure, thanks to the sequestration of CO_2 linked to the dissolution of limestone, and an adaptation measure for shellfish farming thanks to the increase in pH, carbonate ions and alkalinity that is favourable to calcifying organisms.

THE LIMITS OF KNOWLEDGE

Ocean revegetation and enhanced alkalinisation techniques could help mitigate the effects of climate change and acidification, while adapting shellfish farms by maintaining favourable conditions for shellfish development. While the potential of revegetation seems limited by the cultivation surfaces required, that of OAE may appear to be an attractive solution for reducing oceanic CO_2 concentration and curbing ocean acidification.

Nevertheless, the current state of knowledge on these carbon capture techniques is insufficient. They are mainly based on theories and concepts, laboratory experiments and numerical models. Consequently, it is important to pursue research in parallel with multiple approaches, favouring *in situ* experimentation. This is to assess the potential effectiveness of the techniques discussed, the sustainability of carbon sequestration, environmental impacts, as well as other factors governing possible deployment decisions, such as technological readiness, development timescales, energy and resource requirements, economic costs and potential social policies. At present, geoengineering therefore appears to be an imperfect solution to the challenges of climate change, and in no way replaces the urgent need to reduce CO_2 emissions at source[49].

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[49] On this subject, see the article published in *Le Monde* by the Ocean and Climate platform on July 12, 2021: https://www.lemonde.fr/blog/oceanclimat/2021/07/12/geo-ingenierie-marine-nouvelle-frontiere-debats-scientifiques-politiques-ethiques-lutte-changement-climatique/

WHAT'S NEXT?

As we have seen, ocean acidification is mainly caused by the increase in anthropogenic emissions of CO_2 into the atmosphere. This gas is partly absorbed by the ocean, causing its acidity to increase at an unprecedented rate. This problem, which has been well known to scientists since the early 2000s, is now being monitored at high frequency in many parts of the world, and its effects have been extensively studied over the last twenty years. We now know that acidification compromises the shell and skeletal formation of many organisms, making their survival and reproduction more difficult. We also know that the behaviour of many fish species and their prey can be altered, with consequences for food chains and fisheries. Analysis of the past shows that the ocean has already experienced episodes of acidification, but current changes are probably too rapid for species with long generation times to adapt. Acidification, coupled with other climate change factors such as warming and ocean deoxygenation, will increase the risk of extinction, with repercussions for societies that depend on marine resources. To combat this phenomenon, we have no choice but to mitigate our emissions and to adapt by increasing the resilience of marine ecosystems. To achieve this, we need to strengthen observation networks, assess impacts in a more integrated way, develop mitigation and adaptation strategies, and reinforce the protection and conservation of marine ecosystems.

REINFORCING OBSERVATION

The aim of operational observation systems is to record data on a regular and permanent basis in order to establish the basic conditions and natural variability of a system, identify trends and anomalies, anticipate developments, and assess the progress made towards achieving a set objective. These permanent observation systems are also intended to meet the demands of the public and decision-makers by providing them with scientifically-based information.

While temperature is well monitored, this is less the case for pH, whose reliable measurement is relatively recent and complex to implement. Yet the need to monitor ocean acidification has been recognised at intergovernmental level, notably by the UN General Assembly, the UN Convention on the Law of the Sea, the Convention on Biological Diversity and the Intergovernmental Panel on Climate Change (IPCC). In 2015, the UN General Assembly made ocean acidification one of the ten targets of Sustainable Development Goal 14 for the ocean. Unesco's Intergovernmental Oceanographic Commission (IOC) is the custodian agency of the indicator for Target 14.3, which calls for minimizing the effects of ocean acidification. In 2018, the World Meteorological Organisation made ocean acidification a leading climate indicator for reporting to the United Nations Framework Convention on Climate Change (UNFCCC), and included ocean acidification in its annual State of the World Climate statement. Today, the Global Ocean Acidification Observation Network (GOA-ON) pools data acquired on an international scale, reporting nearly 400 pH measurement points worldwide[50]. Despite this pooling effort, acidification observation networks are operated on a national or even regional scale, and often rely on funding whose precariousness threatens the sustainability of data sets.

Observation is also essential for assessing and implementing mitigation and adaptation strategies. For example, if we decide to revegetate or alkalinise shellfish farming areas to combat acidification, we need reliable measurements of pH and carbonate chemistry before and after to assess the effects of the actions taken. Nevertheless, such monitoring must be maintained for at least ten years to assess annualised acidification rates and take informed management measures.

Additionnally, we need to observe in order to inform, train, raise awareness and take action. Marine heatwaves have received a great deal of media coverage in recent years, because water temperatures have been monitored for over fifty years in some places, enabling us to establish benchmarks and trends, and show

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[50] A map of pH measurement stations is available on the GOA-ON website: http://portal.goa-on.org/Explorer

anomalies to which we can give warning. Today, when we observe pH drops lasting several days, we are still unable to distinguish the norm from the exception, for lack of reference data.

EXPANDING THE SCALE OF EXPERIMENTS

Despite more than twenty years of assessing the impacts of acidification, we have mostly studied short-term effects, often at the scale of a species, on a given developmental stage, and without considering the additive, synergistic or antagonistic effects of other factors such as warming or deoxygenation (Boyd *et al.*, 2018; Riebesell and Gattuso, 2015). In order to provide a clearer picture of the future of species, we need to consider long-term experiments that capture both acclimatisation and adaptation effects between generations, during which organisms are placed in the most realistic conditions possible, within complex communities that include several links in the food chain, and finally where pH is controlled according to natural levels. These experiments require substantial financial and human resources over the long term, which is not necessarily compatible with current public research funding arrangements.

To achieve these ambitious goals, several initiatives are underway around the world. In France, we have recently developed mesocosms to study the joint impacts of acidification and warming on shellfish over several generations, directly in the farming areas, under real-life conditions, and taking into account natural variations in food, oxygen, salinity, turbidity, etc. These mesocosms consist of tanks of seawater taken directly from shellfish farming sites, more or less heated and acidified depending on the emission scenario being tested. In an experiment that began in October 2022 in the Mediterranean Thau lagoon, we placed oyster and mussel spat under current and projected temperature and acidification conditions for 2050, 2075 and 2100 according to the IPCC's SSP3-7.0 emission scenario, applying a temperature or pH offset to ambient conditions, thus respecting the natural fluctuations of the environment. The results show that future temperature and acidification conditions will have a negative effect as early as 2050 on shellfish growth and reproduction, which could have repercussions on their offspring. Monitoring of the offspring is currently underway and should enable us to see whether these species are able to adapt. Another experiment underway at "Océanopolis" in Brest involves maintaining living reefs of flat oysters with associated fauna and flora in several mesocosms exposed to different scenarios of warming and acidification by 2100, so as to assess the impacts on organisms and biodiversity. This original project associates researchers with scientific mediation activities, creating an indispensable link with society.

ASSESSING AND IMPLEMENTING MITIGATION AND ADAPTATION STRATEGIES: THE JOB OF THE CENTURY

Until now, research into acidification has focused mainly on observing the phenomenon and its impacts. However, it is high time to move on to developing strategies for mitigating and adapting to climate change.

Geo-engineering techniques such as ocean revegetation and alkalinisation appear interesting, but must be preceded and accompanied by rigorous scientific assessment of their ecological and environmental impacts. The development of these strategies requires further experimentation in laboratory and real-life conditions, in order to assess the effectiveness and scalability of these techniques, their impacts and their potential for large-scale application. In addition, given the societal stakes involved in all potential solutions, social science research is needed to understand the factors that hinder or encourage the implementation of solutions. We have little time to carry out these studies, which are essential if we are to achieve carbon neutrality by 2050, and which require the mobilisation of substantial human and financial resources. So let's get started!

PROTECTION, CONSERVATION AND RESTORATION: NATURE-BASED, NO-REGRET SOLUTIONS

In the previous chapter, we discussed the role of algae and marine plants as temporary refuges against acidification. This observation naturally raises the question of the importance of protecting, conserving and restoring ecosystems — so-called "nature-based" solutions[51] — in the fight against acidification and climate change. In fact, these solutions can contribute to the sequestration of CO_2 in the ocean. This seems relatively obvious for algae and marine plants that consume CO_2 during photosynthesis, much less so for animals that excrete CO_2 throughout their lives through respiration and calcification, at least for those that manufacture limestone.

And yet, it is estimated that pelagic animals export more than 2 Gt C per year, by emitting their excrement into the deep sea (Boyd *et al.*, 2019). Another example, less significant but much more tangible: whales that sink to the seabed at the end of their lives sequester carbon for hundreds or even thousands of years. In fact, restoring whale populations would naturally remove 160,000 tonnes of carbon from the seabed every year (Pershing *et al.*, 2010). Despite significant uncertainties concerning, among other things, the global extent of macroalgae, the role of marine animals in nutrient cycles, and the fraction of carbon that is actually sequestered during many ecological processes, nature-based solutions focused on conservation and restoration are likely to contribute to carbon capture, in part because they offer a panel of low-regret solutions[52], with many perceived co-benefits and the potential for global governability (Gattuso *et al.*, 2018).

Among the actions to be taken, we can mention the significant reduction of pollution and eutrophication, the mapping of sensitive ecosystems and their protection, the maintenance and development of marine protected areas to reinforce the resilience of marine ecosystems, the promotion of sustainable fishing and aquaculture practices, and of course the unfailing support of public authorities for scientific research.

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[51] According to IUCN, nature-based solutions are actions that rely on ecosystems to meet the challenges posed by global change to our societies, such as the fight against climate change. https://www.iucn.org/fr/notre-travail/solutions-fondees-sur-la-nature

[52] The term "no-regret measures" is used to describe actions that deliver benefits even when the impact on climate change or carbon sequestration is less than expected.

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Acronyms and abbreviations

UNFCCC: United Nations Framework Convention on Climate Change.

IOC: Intergovernmental Oceanographic Commission of UNESCO.

IPCC: Intergovernmental Panel on Climate Change.

GOA-ON: The Global Ocean Acidification Observing Network.

Gt C: Gigatonne of carbon, corresponding to one billion tonnes of carbon.

KT: Cretaceous-Tertiary boundary.

OA-ICC: Ocean Acidification International Coordination Centre.

SDGs: Sustainable Development Goals.

WMO: World Meteorological Organisation.

PETM: Paleocene-Eocene Thermal Maximum.

SCOR: Scientific Committee on Oceanic Research.

IUCN: International Union for Conservation of Nature.

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Carbon dioxide (CO_2) emissions, resulting from the combustion of fossil fuels by human activity, reinforce the greenhouse effect and cause climate disruption. While public awareness of this global problem is growing, ocean acidification, described as "the other CO_2 problem", is still considerably unknown.

In this book, the authors answer ten key questions on the biogeochemical basis of acidification, on past, current and future trends, on the impact on marine organisms and humans, and finally on remediation measures.

It draws its answers from fields as diverse as biogeochemistry, ecology, physiology, evolution, aquaculture and fisheries, economics and sociology.

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