Oysters: the little-known architects of coastal environments

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Oysters are essential marine invertebrates in our coastal ecosystems. These architects of the environment provide many ecosystem services while supporting a flourishing economic activity that structures coastal landscapes. For several million years, they have been responsible for the construction of thick layers of sedimentary rock that are essential to the planetary balance and demonstrate their formidable biogenic capacities. But with the Anthropocene, these geological behemoths are facing relentless overexploitation, habitat destruction, disease introduction, global warming and pollution of all kinds. A bit like the bee in the terrestrial environment, but less photogenic, this engineer species is really a keystone of the marine environment, but it is threatened and should be given more attention. "In his fable about the rat and the oyster, La Fontaine was right: we could well become the ultimate victim of this unbridled decline in biodiversity."

1. The oyster: this essential and threatened marine invertebrate

There are two species of oysters in France: **the flat oyster**, *Ostrea edulis*, [1] native to our European coasts, and **the Pacific cupped oyster**, *Crassostrea gigas*, introduced 50 years ago to save French oyster farming (see Focus: A history lesson). Even if their origin, history, ecology and habits are different, these two species share common destinies: their essential role in the balance of the ecosystem and the same fragility in the face of anthropic pressures (Read The oyster, this sentinel witness of a coastline to preserve).

1.1. Two oyster species, two different biological models

Figure 1. Reef formation of Pacific oysters on the foreshore in a mediolittoral environment (left) and flat oysters underwater in a sublittoral environment (right) [Source: © IFREMER / Stéphane Pouvreau]

By working on these two complementary biological models (Figure 1), the native oyster *Ostrea edulis* and its introduced cousin *Crassostrea gigas*, we seek to understand the key processes in their **life cycle**. In particular, we are interested in their ecology, physiology, reproductive cycle, recruitment determinism, population dynamics and maintenance in the natural environment, and the keys to their rearing performance, all in an ocean that is changing and under multiple pressures. In addition to its interest in aquaculture and fisheries issues, this research also has implications for **conservation biology**: these two species and the reef formations they are capable of building constitute true biodiversity sanctuaries for European coastal environments.

Original reproduction. Like most bivalve molluscs, oysters have a bentho-pelagic life cycle comprising:

a **free larval phase** in the water column (referred to as the pelagic phase) lasting a few weeks;

a **sessile benthic phase** (fixed on the bottom) for the rest of their lives.

They are **hermaphroditic**, either alternatively during their existence for the Pacific oyster, or consecutively at each reproduction season for the flat oyster. On the other hand, they always start their first reproduction with a male phase, which is called protandry.

Pacific oysters are said to be **oviparous** because they release their gametes into the water where fertilization then takes place, whereas flat oysters are **viviparous**!

In summer, the males of *O. edulis* release spermatozoa, grouped in a ball [2]. This gives them a selective advantage because it avoids a too fast dispersion of gametes. They are then filtered by the neighbouring females: the fertilization of the oocytes takes place in their mantle cavity and the larvae develop there for about ten days under cover. The flat oyster is an **incubating** species, a very rare characteristic among molluscs, which constitutes a second evolutionary advantage. During this incubation period, the offspring grows and the mother oyster passes from the “white-sick” stage when the larvae are just formed to the “grey/black-sick” stage when the larvae have acquired their first shell and are then ready to be released into the wild, at the mercy of the currents [3].

In French latitudes, the swarming of flat oyster larvae generally begins in June on the Atlantic coast. This seasonal phenological event is well known by Breton oyster farmers:*"when the chestnut trees are in bloom, oyster farmers put down their collectors*". The Pacific oyster is a little more demanding in terms of temperature, and its spawning on the Atlantic coast does not take place before mid-July. To put it simply, we could say: St John's Day for the flat oyster and July 14th for the Pacific oyster! But the climatic conditions of the current year can advance or delay this precision clock and the climate change already causes unpredictable jolts on the delicate mechanism [4].

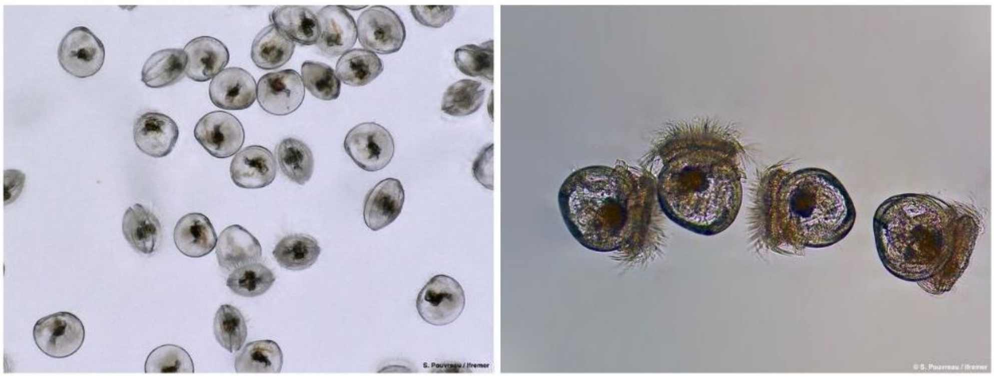

Figure 2. Young larvae of Pacific oysters (left) and flat oysters (right). In both cases, the shell of these young larvae has a characteristic D-shaped structure with a ciliated velum that they use for swimming and feeding. But oviparous oysters release eggs, which after fertilization, will quickly develop into young D-shaped larvae of small size (< 100 µm), whereas viviparous flat oysters release young, more developed larvae, of a size close to 160 µm once they are released [Source: © IFREMER / Stéphane Pouvreau].

Once released, the larva equipped with a "velum" is said to be **veligerous** (Figure 2). It will live a pelagic life of about ten days in the flat oyster, against about twenty days in the Pacific oyster. In both cases, from 240 µm onwards, the shell becomes rounder and heavier, and a foot and an eye are gradually formed. Concentrated in favourable hydrodynamic zones [5], the larva will then search for an optimal substrate on the bottom to settle: rocks, pebbles and other rough supports. But their favourite substrates are above all the shells of fellow oysters, because oyster larvae have a gregarious behaviour; they aggregate with adults by fixing themselves on the perimeter of their shell (see introductory figure). Each season, the magic works and the reef formation grows. The first year of a juvenile oyster's benthic life is then full of pitfalls, between the search for a stable habitat, competition with other neighbouring organisms, daily predation, endemic and emerging viruses and parasites...

Figure 3. Young post-larvae of Pacific oysters (left) and flat oysters (right) attached to their new habitat. In both cases, the larval shell can be clearly distinguished from the post-larval shell by the clear growth streak associated with metamorphosis. These young post-larvae are less than a month old and measure less than 1 mm. They can live for several decades and measure more than 20 cm. [Source: © IFREMER / Stéphane Pouvreau]

A very specific living environment. To ensure the maintenance of populations and the iterative growth of the reef, several conditions must be met.

An optimal nutrition. Oysters feed by filtering matter suspended in the water column from which they extract phytoplankton. An adult oyster can filter between 5 and 10 litres of water per hour from which it retains particles larger than 4-5 µm. Spring is the season when oysters fatten, grow and put a lot of energy into their reproduction: the phytoplankton must therefore be rich and diversified at this time [6].

Specific physico-chemical conditions : optimal salinity (30 - 35 PSU), minimum water temperature in winter around 6°C and maximum in summer around 28°C, water with little turbidity rarely above 50 mg/L of suspended matter [7].

A particular distribution. The two species share the coastal environment equally: the Pacific oyster lives in the tidal zone, whereas the flat oyster prefers the lower foreshore and shallow waters between 0 and 5 metres; it becomes rare beyond a depth of 10 metres.

In these optimal conditions, growth is continuous throughout the life of the animal, oysters can exceed 20 cm and have longevities of several decades: the record for a flat oyster in Wales is 34 years!

1.2. Ecology lesson: strength in numbers

Figure 4. The different stages in the creation of a biogenic flat oyster reef: a first individual settles on the bottom on an available substrate (A); then a second individual takes advantage of the presence of its congener to settle on its shell (B); After several seasons of recruitment, the aggregate counts more than ten individuals of various sizes, weighs more than one kilogram and becomes resilient on the bottom, the reef is in formation; (D) under very favourable conditions and over the long term, this reef becomes very cohesive, counts several hundreds of individuals and shelters many other organisms [Source: © IFREMER / Stéphane Pouvreau].

The creation of an oyster reef. Each recruitment of young oysters allows a slow increase in the density of the populations on the bottom, the progressive creation of aggregates and then of delicate reef formations and finally, if left alone, the construction of cohesive and luxuriant biogenic reefs (Figure 4).

These builder organisms, known as "**ecosystem engineers**", thus construct their own habitat. According to the Natura 2000 network classification [8], the habitat created by oysters is called **"biogenic reef**" (Habitat 1170). These reefs are real underwater mini-forests providing habitat, protection and food to many other marine species. They also work to keep the ecosystem clean and resilient. But the process is slow, much like that of corals: it takes years, even decades (Figure 4).

If Pacific oyster reefs are very present on our coasts, 50 years after the introduction of the species, flat oyster beds and reefs (the native species) constitute a **critically endangered** marine habitat on all European coasts [9]. Originally, these reefs constituted vast underwater expanses in all European seas, but they have almost disappeared after 4 centuries of relentless exploitation. They were called "Oyster Ground" in English or "Huitrières" in French. It is surprising to note that these terms have disappeared from our language over the generations and their destruction (Figure 5). (See Biodiversity on rocky coasts: zonation and ecological relationships).

Figure 5. Biogenic oyster reefs in the Arcachon Basin (left) and the first restored flat oyster reef in Brest harbour (right). Note in the background the eelgrass beds in Arcachon, taking advantage of the breakwater effect offered by the Pacific oyster reefs and the numerous ascidians and sponges living in epibiosis on the flat oyster reef [Source: © IFREMER / Stéphane Pouvreau].

Currently, the reef aggregations of *O. edulis*, the first stage in the creation of these ancient reefs, can still be observed, in a sheltered and unexploited environment, on small loose bottoms (0-10 m deep) made up of sandy-muddy sediments, gravels, shellfish debris or directly on boulders. Under geographical protection, biological rest and active restoration, these biogenic reefs can **become flourishing again and particularly rich in biodiversity** (see below).

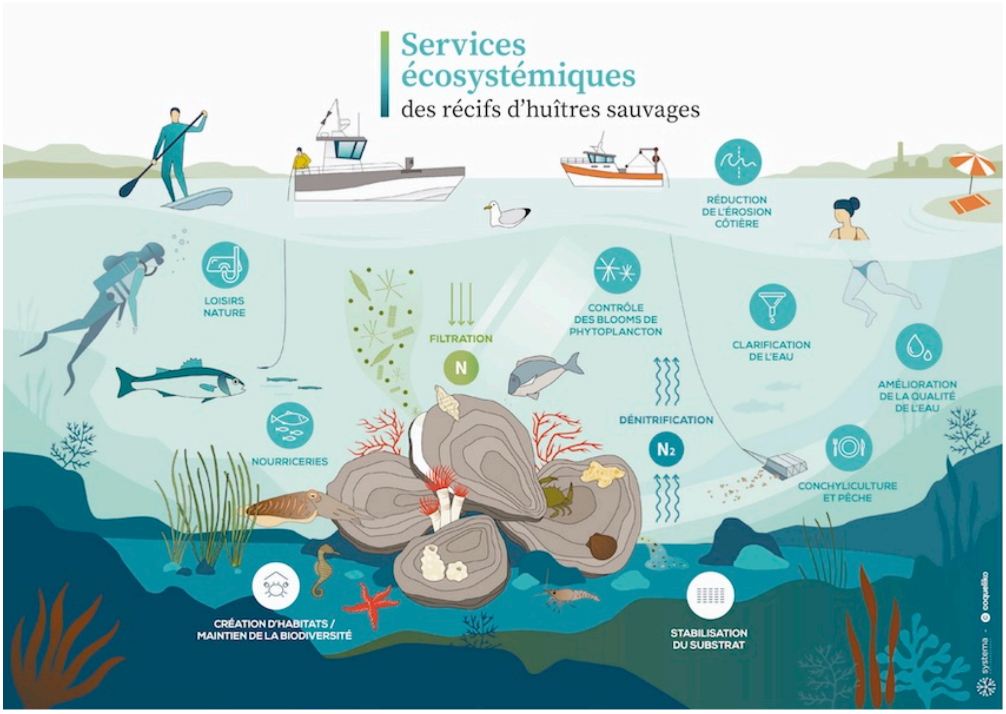

Figure 6. Ecosystem services provided by biogenic oyster reefs [Source: Produced by Systema Environnement ; design by Agence Coqueliko after Pouvreau et al., ref. [4]]

Ecosystem services of oyster reefs. The ecosystem services provided by these engineer-species building their reef formations are summarized in figure 6 (See Biodiversity is not a luxury but a necessity).
They can be grouped into 4 main categories:

support services : creation of habitats and maintenance of marine biodiversity:

The hard substrate of the shells allows the **attachment of** many sessile benthic organisms: bryozoans, tunicates, sponges, annelids, macro-algae settle there generously (Figure 7). [10]

This canopy provides a **refuge** for many invertebrates (gastropods, bivalves, small crustaceans, echinoderms) and this swarming attracts small pelagic organisms (fish and cephalopods) from the surroundings. **All these organisms feed and lay their eggs there**. The reefs thus play essential roles as **nurseries** and **feeding grounds**.

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Figure 7. One of the key services provided by the flat oyster: offering a precious support to numerous organisms that live attached to its shell and form the epibiosis [Source: © IFREMER / Stéphane Pouvreau]

Several hundred different species benefit from these biogenic habitats. Some marine biologists consider oyster reefs to be the equivalent of the coral reefs of our temperate environments, less glamorous but just as useful!

regulation services : But their engineering skills do not stop there:

These biogenic massifs play the role of powerful **biological filters** which, without respite, **purify** the water column of all suspended matter (good or bad) and actively contribute to the regulation of natural biogeochemical cycles: filtration, denitrification, purification, clarification 24 hours a day. They are the "pump and filter of the aquarium" in coastal environments, discreet, silent, hard-working and essential...

production services:

Moreover, their cohesive structures also allow the **stabilization of sediments**, the attenuation of waves energy and the reduction of laminar bottom currents. These physical barriers **structure coastal and underwater landscapes** and encourage the nearby installation of more fragile habitats and/or those requiring clear water, notably eelgrass and maerl beds.

Food products used by humans (fishing and aquaculture)

Natural materials for agriculture (limestone amendment) and for industry (Oystercrete®, oyster glass made from oysters shell, fish concrete, Geocorail®, etc.)

cultural services: finally, [illegible] trail'), diversification [illegible] coastal landscapes and supports recreational activities (diving, fishing) but also educational activities (exploration of marine areas)

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2. Geological colossus with feet of clay in the face of climate change

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If the recruitment of young oysters fails several times in a row, the **population declines** and may disappear, especially if other unfavourable factors are involved, such as multiple and varied anthropogenic pressures. In this particular case of species-ecosystem engineers, the **cascading repercussions** affect distribution, community structure, biodiversity and sometimes the entire ecosystem. On the other hand, as soon as conditions become favourable for larval life and recruitment, the **high individual fecundity** characteristic of these species is an asset that can help them to reconstitute new populations fairly quickly, especially if humans help them a little.

2.1. Identified and manageable local threats

Figure 8. Experiment to assess the dynamics and intensity of predation on an old flat oyster bed in Bay of Brest [Source: © IFREMER/Huber Matthias (2019). Experiment to estimate survival, growth and predation on flat oyster (Ostrea edulis) beds, in bays of Brest & and Quiberon. Ifremer. https://image.ifremer.fr/data/00618/73025/]

Oysters have always been and still are subject to various threats. The **destruction of** their habitat and **overexploitation** by fishing, followed by the introduction of **parasites** or diseases by the world oyster trade, have had disastrous repercussions that can even ruin local maritime economies [11]. These residual and weakened populations quickly become easy prey for natural and introduced predators! This final **regular pressure** can permanently hinder population recovery. Starfish, flatworms, gilthead and king bream, and oyster drills [12] can be particularly devastating [3] (Figure 8).

By combating these identified threats that can "easily be acted upon" locally and by providing **biological rest areas**, certain underwater habitat restoration policies can be envisaged to promote the recovery of former flat oyster beds and thus make the ecosystem more resilient (see 3.2).

2.2. A global, insidious and uncontrollable threat

Among the more global threats is of course that of chronic pollution (see article 2), but above all that of global **warming** and ocean **acidification**.

The ocean absorbs more than 90% of excess heat and more than 30% of atmospheric carbon dioxide (CO_2) emissions. It therefore plays an essential role in **regulating the** global **climate**. The downside is that the surface ocean (0-300 m) has warmed by about 0.11°C per decade since 1971. At the same time, CO_2 is interacting with seawater, turning into carbonic acid and slowly causing "ocean acidification", the dangerous companion of climate change.

According to the most pessimistic scenario of the Intergovernmental Panel on Climate Change (IPCC; RCP 8.5), the temperature could increase by about 4°C by the end of the century and the pH (hydrogen potential) of the global ocean, currently 8.1, could decrease by another 0.32 units, which would correspond to an increase in its acidity of 110%. These changes have a direct impact on the biology of the oyster.

Oysters facing ocean warming. As an ectothermic animal, the oyster does not regulate its internal temperature and depends on the thermal conditions of its environment. The flat oyster initiates its reproduction as soon as the water masses exceed 17°C, the Pacific oyster waits for 18-19°C. For both species, the warmer water in summer favours larval development:

The "Breton heat waves" are currently favourable to the reproduction of the flat oyster and could therefore facilitate future ecological restoration operations.

From a biogeographical point of view, 50 years after its introduction, rreproduction of the Pacific oyster is now possible almost everywhere in Europe… as far as Norway. This represents a movement of 1400 km northward from its point of introduction in France [13]. Thus, in bay of Brest, spawning and survival of the offspring are now facilitated, and biological modelling exercises for 2100 [14] even indicate that there could be two spawning periods, an early and a late one in this temperate ecosystem where the oyster was not supposed to reproduce at the time of its introduction.

So on the Atlantic coast, we could say that until then, for these two species, all is well.

But on the Mediterranean coast, the heat waves of the last few years are worrying scientists a little more. Thus, in the Thau lagoon - the main oyster farming site in the Mediterranean - during the 2018 and 2019 heat waves, the water reached a record salinity of 42 PSU and a temperature approaching 30°C associated with a drop in dissolved oxygen concentrations in the water [15]. Very close to the physiological limits of the Pacific oyster, these conditions destabilize the benthic biocenoses and modify the planktonic communities on which the oyster feeds. For example, they favour very small species that tolerate these large environmental variations. However, these planktonic species are of no nutritional interest to the oyster, thus causing a halt in their growth, weight loss and increased mortality [16]. Here, climate change is a direct threat to oyster farming!

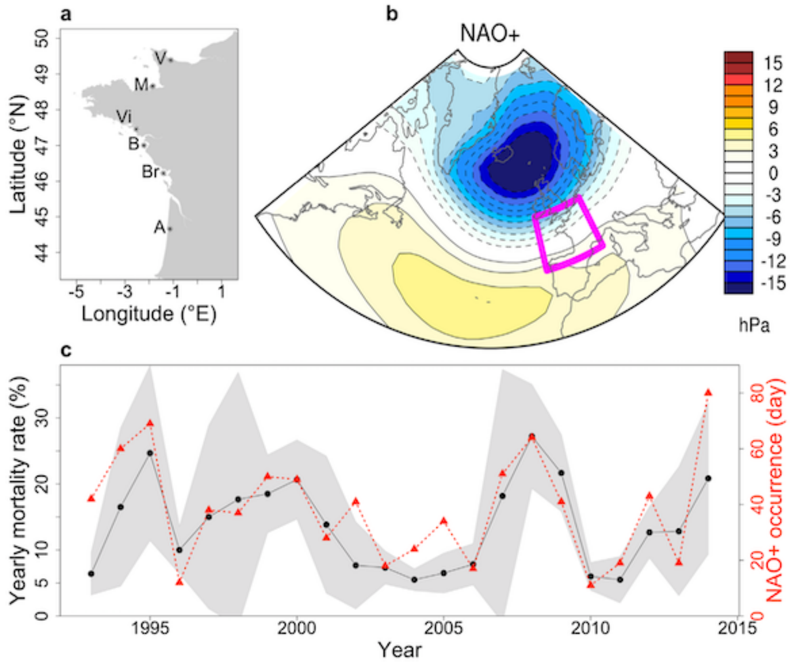

Figure 9. Annual mortality rates of oysters on the French Atlantic coast and winter intensities of the NAO+ climate regime. This regime, characterized by very active oceanic lows, is responsible for mild and wet winters in Western Europe [Source: after Thomas et al., 2018 - https://hal.archives-ouvertes.fr/hal-02530675/document].

Moreover, global warming also affects seasonal weather patterns. Now, during mild, wet winters, which will be increasingly frequent with global warming, there is more mortality of adult oysters and throughout the year that follows [17]. The milder winter temperature allows pathogens to survive in winter and prevents the oyster from resting, making it more fragile in summer. In the flat oyster, the response is more complex: mild, wet winters favour the *Marteilia* parasite but disfavour the *Bonamia* parasite [18]. Climate change could have an impact on these parasitoses, but it is difficult to predict exactly how much.

Oysters facing ocean acidification. An increase in water acidity reduces the availability of calcium carbonate, which is an essential mineral brick used by calcifying organisms, such as oysters, to build their shells. Severe acidification could even lead to the dissolution of these shells. Nearshore waters, populated by our favourite shellfish, are naturally more acidic and variable in pH than the open ocean, but they could become increasingly and permanently so. Currently, oysters are already sometimes confronted with pH levels of 7.7 in the Brest harbour.

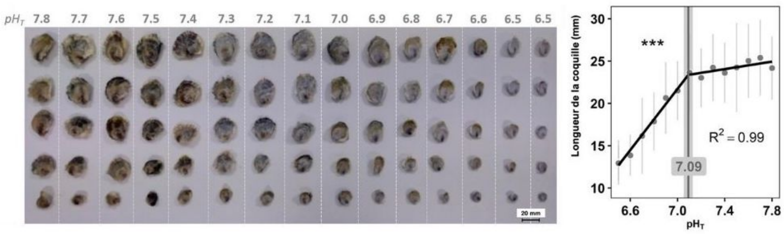

Figure 10. Impact of different pH conditions (full scale, pHT) on the length of Pacific oyster shells exposed for 23 days. On the picture: oysters are sorted from the smallest to the largest within each pH condition; on the figure: the tipping point for growth is at pH 7.09; below this point, oyster growth slows down significantly [Source: © IFREMER / Mathieu Lutier]

However, the Pacific oyster is a "foreshore dweller", continuously covered and uncovered by the tides, and is therefore used to undergoing changing and extreme environmental conditions. Scientific studies show that the juvenile and adult stages of the oyster could resist quite well to the acidification of the oceans expected in 2100. For example, it has been shown that in the laboratory, oyster growth is only affected below a pH of 7.1 (Figure 10). Such conditions of acidification of seawater are not likely to occur in the natural environment [19].

The repercussions of pH on the flat oyster (native, which lives permanently in the water), which is already very fragile, are not well known.

On the other hand, for both species, the larval stage could be a much more sensitive phase: for example, in *C. gigas* larvae, a slowing down of growth and a decrease in survival are observed as soon as the pH goes below 7.6. This critical value has already been reached in some regions of the world, such as on the west coast of the United States, where scientists and shellfish farmers have shown a strong correlation between water acidity and mortality of Pacific oyster larvae [20], forcing them to develop strategies to adapt to it.

3. Reconciling conservation, ecological restoration and uses

3.1. A national observatory to anticipate the effects of climate on the oyster

Figure 11. Assessing annual recruitment in an oyster population. On the left, coated-lime collectors placed on bottom structures during the breeding season are very attractive to oyster larvae, each small black dot in the photo is a newly attached juvenile (spat). On the right, the trained eye can also see these small spat on the shell edges of adult oysters. Annual sampling and counting provide recruitment indices and allow us to evaluate long-term trends [Source: © IFREMER / Stéphane Pouvreau]

In order to anticipate the effects of climate change, a national observatory was created in 2008 at Ifremer to monitor the oyster's life cycle [21], particularly its growth, survival, reproduction and recruitment, throughout the French coastline. These stages are essential links in the dynamics of a population. As an example, recruitment -the cornerstone of community renewal- is scrutinized for both species on several key sectors of the French coast, from the Thau lagoon to the Brest harbour, and allows to better anticipate possible future changes (Figure 11).

3.2. A global approach and a European alliance to save the flat oyster

Climate change is having a growing impact on ecosystems, but the erosion of biodiversity and the increased degradation of environments are reducing their resistance and making them even more fragile. Alongside measures to reduce CO_2 emissions, nature-based solutions (NBS) offering greater resilience are also proving to be complementary responses.

The degradation of the seabed, the mechanization of fishing, pollution, massive soil erosion and increased sedimentation of estuaries, not to mention the introduction of allochthonous species that are sometimes invasive or pathogenic, are causing native species and their habitats to decline or disappear (see The oyster, the sentinel of a coastline to be preserved). In such a context, conservation biology and restoration ecology have also become essential multidisciplinary research topics in the marine environment, especially since the European Habitat Directive in 1992.

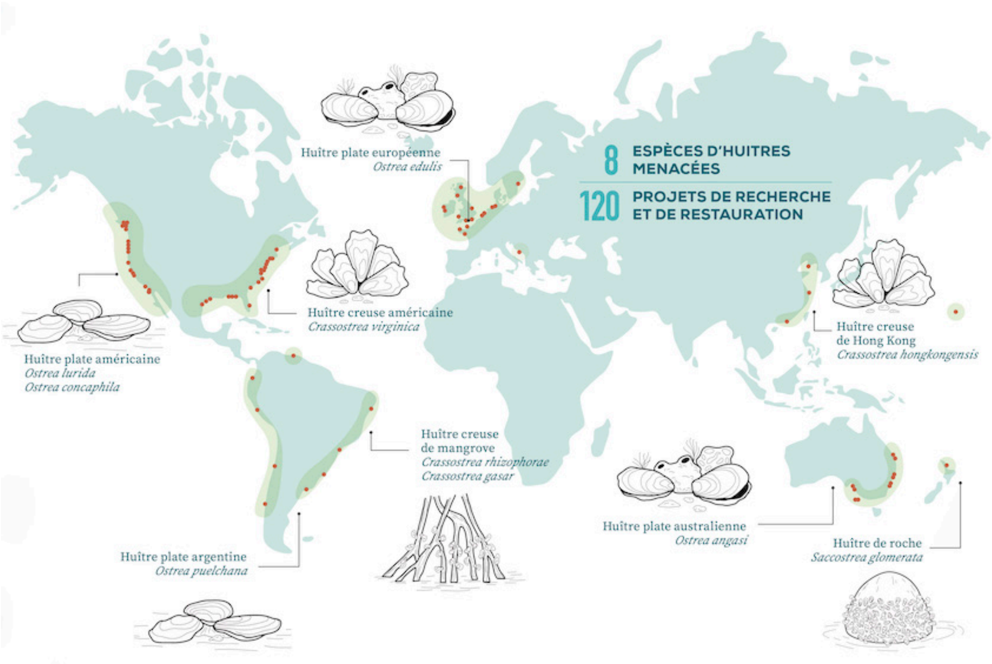

Figure 12. Overview of ecological restoration projects on native oyster reefs worldwide [Source: Produced by Systema Environnement; design by Agence Coqueliko after Pouvreau et al., ref. [4]]

On an international level, native oyster reefs are the subject of very special attention organised within different scientific networks and through the annual ICSR *(International Conference on Shellfish Restoration*) congress. More than 100 restoration projects can be listed around the world (Figure 12).

In France, the flat oyster, the only native and endemic oyster in Europe, has long been overlooked by the environmental code. Since 1992, the *European Directive on Habitats, Fauna and Flora* provides for "maintaining a favourable state of habitats or even restoring them" and since 2008, the OSPAR Convention [22] (Oslo-Paris) lists flat oyster reefs as a "critically endangered" habitat. However, in 2021, the **ecological restoration** of this species and its habitat is still in its infancy, but things are moving a little [23].

Figure 13. Restoring the former oyster beds of the past: implantation of concrete shell reefs in order to favour recruitment and revitalise the flat oyster populations of the Roz bank in Brest bay and the Penthièvre bank in Quiberon bay. [Source: © IFREMER / Stéphane Lesbats (left) & Stéphane Pouvreau (right)]

Some **pioneering scientific projects** in Brittany and Corsica have started to bear fruit in recent years [23] (Figure 13). In addition, a recently established European-wide alliance (*NORA - Native Oyster Restoration Alliance*) is also becoming increasingly active on these restoration issues [24]. This craze is expected to grow from 2021 onwards as part of the United Nations Decade *on Ecosystem Restoration (UNDER*). Gradually, the flat oyster, in the twilight of its existence, could become a real mascot, a pioneer ambassador of restoration ecology in the marine environment.

4. Messages to remember

Oysters, which have been present on our coasts for millions of years, could well be added to the list of **species threatened** by man;

These marine organisms, not very photogenic, reveal a biology much more **complex** than it seems, in particular in their strategy of reproduction, which enables them to quickly colonize an environment when the conditions are favorable;

Oysters play a role as architect species, **ecosystem engineers**, biodiversity supports and suppliers of numerous regulation services (biological filters purifying the water column, stabilizing sediments, structuring coastal and underwater landscapes);

The **resilience** that these **biogenic fortresses** bring to the marine environment is a valuable tool for adaptation and mitigation to the pressures of climate change.

Continued **globalisation** will favour the emergence of new pathogens, parasites and predators, and the inherent inertia of the climate machine will have age-old **repercussions** on the maintenance of oyster ecosystems;

In this context, the pragmatic solution of **protecting**, or even **restoring**, part of the surface of the globe (a golden figure of around 30% by 2030 [25]) is an objective that can easily be transposed to our coastal environments, and one that is easy enough to understand collectively and to consolidate together in order to maintain regional and planetary integrity;

The active restoration of oyster beds is part of a whole, of a **future strategy**, that of nature-based solutions [26] promoted by the IUCN;

Just like the bee in terrestrial environment, the polar bear in polar environment, the coral reefs in tropical environment, the oyster plays the role of a victim, a **sentinel** and an alerting agent for the coastal environment of our temperate latitudes. We just have to "listen to it" to avoid being "caught who thought he was caught".

Notes and References

Cover image. Fragile reef colony of flat oyster in the heart of a former oyster beds destroyed in the 19th century and now being renatured in bay of Brest [Source: © IFREMER / Stéphane Pouvreau]

[1] The flat oyster, *Ostrea edulis*, is locally called Belon (southern Brittany), Gravette (Arcachon) or Pied de Cheval (for the wild ones that have grown).

[2] These structures are called "spermatozeugmata"; SUQUET, M. *et al.* (2018). Biological characteristics of sperm in European flat oyster (*Ostrea edulis*). Aquatic Living Resources, 31, 20 (7p).

[3] Duchene, J., Bernard, I., Pouvreau, S. (2015). Vers un retour de l'huître indigène en rade de Brest. *Espèces*, 16, 51-57.

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[5] Petton, S., Pouvreau, S., Dumas, F. (2020). Intensive use of Lagrangian trajectories to quantify coastal area dispersion. *Ocean Dynamics,* 70, 4, 541-559 .

[6] Bernard, I., De Kermoysan, G., Pouvreau, S. (2011). Effect of phytoplankton and temperature on the reproduction of the Pacific oyster *Crassostrea gigas*: investigation through DEB theory. *Journal of Sea Research*, 66, 349-360.

[7] Especially for the flat oyster, which does not appreciate turbidity or sedimentation.

[8] http://www.natura2000.fr/outils-et-méthodes/guides-ouvrages/cahiers-habitats

[9] Pouvreau, S. *et al.* (2021). Current distribution of the residual flat oyster beds *(Ostrea edulis*) along the west coast of France. SEANOE. https://doi.org/10.17882/79821

[10] The shell of the flat oyster is particularly flaky and offers a support capacity four times richer than a standard mineral hard

substrate but also twice as rich as its introduced cousin.

[11] Bosseboeuf, L. (2019). Étude de la variation des ressources marines en rade de Brest : 1866-1963. HistoRade project. Univ. Bretagne Occidentale, Master 2 report. 80p.

[12] Oyster drills are destructive winkles (small gastropods) that bore holes in the shells of bivalves to feed on their flesh. The action of their rasping tongue combined with the secretion of enzymes allows them to drill a small circular hole in a few hours (or even two days for the thickest shells). There was a native species, the cormaillot *Ocenebra erinacea*, but the two species introduced during the 20th century, *Urosalpinx cinerea* and especially *Ocinebrellus inornatus*, are much more voracious.

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