

Introduction

Contribution to the Themed Section: 'Marine Aquaculture in the Anthropocene'

The future is now: marine aquaculture in the anthropocene

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Aquaculture now produces more seafood than wild capture fisheries and this production is expected to at least double by 2050. Representing almost half of global production, marine aquaculture will contribute to sustainably feeding the growing humanity. However, climate change will undoubtedly challenge the future growth of marine aquaculture. Temperature and sea-level rise, shifts in precipitation, freshening from glacier melt, changing ocean productivity, and circulation patterns, increasing occurrence of extreme climatic events, eutrophication, and ocean acidification are all stressors that will influence marine aquaculture. The objective of this themed article set was to bring together contributions on the broad theme of the potential impacts, adaptation, and mitigation strategies of marine aquaculture to climate change. Here we present 14 papers covering a diverse set of approaches including experimentation, modelling, meta-analysis and review, and disciplines like biology, ecology, economics, and engineering. These articles focus on the impacts of climate change-related stressors on the aquaculture potential itself and on the resulting ecological interactions (e.g. parasitism and predation), on phenotypic plasticity and adaptation potential of species, and on measures to mitigate the effects of climate change on aquaculture and vice versa. Considering this, adaptation of the aquaculture sector relies on anticipating the biogeographical changes in the distribution of species, determining their potential for adaptation and selective breeding for resistance or tolerance to climate-induced stressors, and fostering ecosystem resilience by means of conservation, restoration, or remediation. By will or by force, aquaculture will contribute to the low carbon economy of tomorrow. Aquaculture must move towards a new paradigm where the carbon footprint and the analysis of the life cycle of products are at least as important as economic profitability.

Keywords: adaptation, bivalve, blue economy, carbon, climate change, marine diseases, mitigation, ocean acidification, plasticity, salmon, seaweed, sustainability

Introduction

Officially, Earth is still in the Holocene epoch, which began around 11 700 years ago after the last ice age. This epoch benefitted from stable and mild conditions particularly favourable to the expansion of *Homo sapiens*, which appeared 300 000 years ago. The rapid increase in the human population and the concomitant explosion of agriculture and industry have altered biogeochemical carbon and nutrient cycles, landscapes, and the global climate. The environmental effect

of human activity is increasing at unprecedented rates and at a global scale. At a conference in Mexico in 2000, Paul Crutzen, winner of the Nobel Prize in Chemistry, expressed the idea that we have entered a new geological epoch driven by the impact of human activities on the Earth System: the *Anthropocene* (Crutzen and Stoermer, 2000; Crutzen, 2002; Steffen *et al.*, 2011).

Aquaculture is one of the human activities that accelerated greatly during the latter half of the last century (FAO, 2018a,

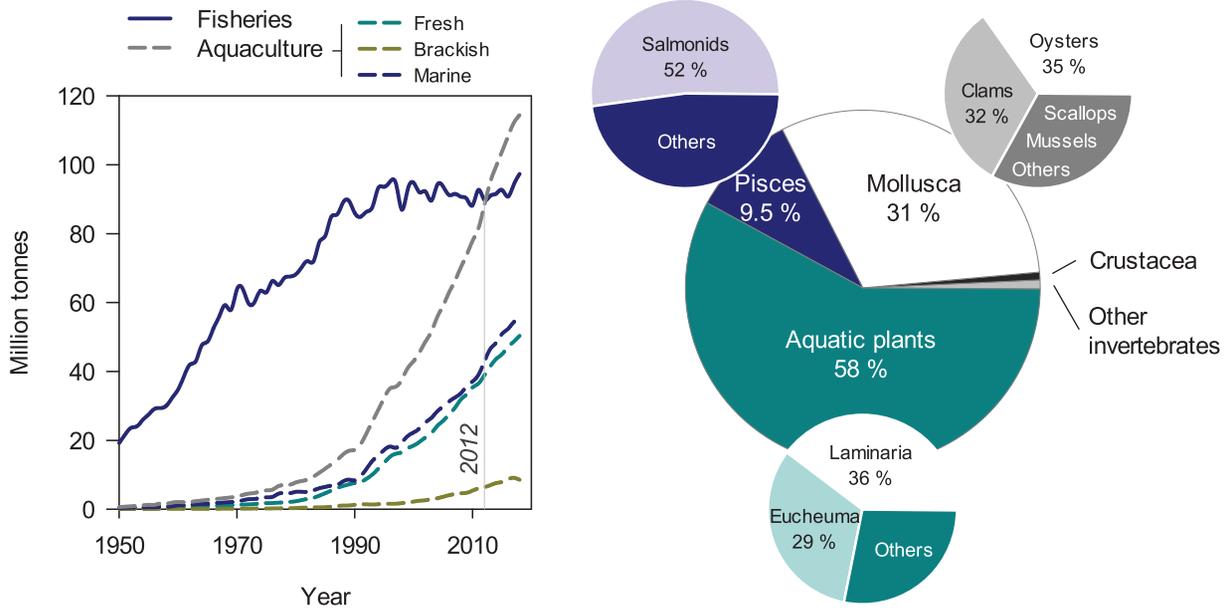


Figure 1. Expansion of global capture fisheries and aquaculture production from 1950 to 2018 (left) and partitioning of marine aquaculture production into taxonomic groupings in 2018 (right). Data are from FAO (2020).

Figure 1). Compared to terrestrial crop and livestock production, aquaculture was the fastest growing food sector for the period 1990–2009 (Troell *et al.*, 2014) and production will continue to grow to meet rising demand (World Bank, 2013; FAO, 2018a). Marine aquaculture, which is focused mainly on aquatic plants, molluscs, and to a lesser extent fish, now accounts for almost half of global aquaculture production, recently exceeding wild capture fisheries (FAO, 2018a, Figure 1). However, climate change and other constraints will undoubtedly challenge future growth of marine aquaculture (Froehlich *et al.*, 2018). Temperature and sea-level rise, shifts in precipitation, freshening from glacier melt, changing ocean productivity and circulation patterns, increasing occurrence of extreme climatic events, eutrophication, and ocean acidification (OA) are some of the stressors that will influence the potential of marine aquaculture production (FAO, 2018b; IPCC, 2019). It is, therefore, critical to anticipate new opportunities and challenges in marine aquaculture production during the anthropocene.

In this context, the *ICES Journal of Marine Science (IJMS)* solicited contributions to the themed article set (TS), “Marine aquaculture in the Anthropocene”. The objective of this TS was to bring together contributions on the broad theme of the potential impacts, adaptation, and mitigation strategies of marine aquaculture in an era of rapid change.

In the call for papers, we solicited contributions on the following topics, among others:

- Impacts of climate change-related factors (warming, acidification, hypoxia, shifts in primary production, to name a few) on aquaculture production and spatial distribution of species-specific aquaculture activities.
- Phenotypic plasticity and adaptation potential of farmed species under climate change, including selective breeding for resilience.
- Impacts and adaptive measures to the increasing occurrence of extreme climatic events like storms and flooding (e.g. physical destruction of aquaculture facilities, escapes, disease spread).

- Climate change as an additional stressor, reinforcing other impacts such as pollution, disease outbreak, and biodiversity loss.
- Indirect impacts of climate change on marine aquaculture (via impacts on aquafeed supplies, on pest and disease emergences and biodiversity).
- Social and economic impacts of climate change on marine aquaculture.
- Vulnerability assessment and development of successful adaptations in local populations.
- Adaptive measures for mitigating the impacts of climate change on marine aquaculture (marine policy and planning measures, research and development, farming practices, ecosystem approach to aquaculture).
- Contribution of aquaculture to climate change and mitigation/remediation strategies (ecological and carbon footprints, life cycle assessment (LCA), blue growth initiative).

We particularly encouraged the submission of papers reporting complex experimental set ups and modelling approaches that expand from single to multiple drivers, from single organisms to ecosystems/farms, and from acclimation to adaptation. Inter- and trans-disciplinary work linking natural and social science, and economics in tackling effects of climate change were particularly welcome. Thirty manuscripts were submitted for consideration; 14 were accepted and appear in this TS.

An overview of the contributions in this article theme set

Impacts of climate change-related factors on aquaculture production and spatial distribution of species-specific aquaculture activities

Human activities are estimated to have caused $\sim 1^\circ\text{C}$ of global warming above pre-industrial levels (IPCC, 2018). Mean ocean

surface temperature has increased since the 1970s at a rate of 0.11°C per decade (IPCC, 2019). Depending on the future emission scenario, the top 100 m of the ocean is projected to warm by about 0.6–2.0°C by 2100 (IPCC, 2019). The oceans are not only absorbing a large amount of heat, leading to ocean warming, but also about 25% of anthropogenic CO₂ emissions (Le Quéré *et al.*, 2018). Increasing CO₂ concentrations in the atmosphere lower the pH of the oceans, a process referred to as OA (Caldeira and Wickett, 2003; Orr *et al.*, 2005). The pH in the ocean's surface waters has already decreased by 0.1 units since the beginning of the Anthropocene. According to recent projections, an additional decrease is expected by 2100, ranging from 0.06 to 0.32 units, representing an increase in acidity of 15–110% (IPCC, 2019). Simultaneously, aqueous CO₂ concentrations are increasing and carbonate ion concentrations (CO₃²⁻) are decreasing, possibly impacting the growth, physiological rates, immune responses, behaviour, and survival of some marine organisms (e.g. Gazeau *et al.*, 2013; Kroeker *et al.*, 2013; Clements and Hunt, 2015 for reviews).

OA has been the most-studied single topics in marine science in recent times (Browman, 2016). Scientists have conducted many OA experiments, usually exposing organisms to experimental conditions based on scenarios modelled for oceanic waters, typically simulating present and near-future ocean pCO₂ levels (Riebesell *et al.*, 2011). However, most marine organisms are cultivated in coastal areas such as intertidal and upwelling zones, estuaries, fjords, and salt marshes where pH/pCO₂ levels vary far more dramatically than in the open ocean (e.g. Waldbusser and Salisbury, 2014; Vargas *et al.*, 2017). Such variability in coastal environments limits the relevance of applying predictions of CO₂ in the open ocean to these situations. Also, coastal aquaculture is likely to be affected by OA in different ways than open-ocean aquaculture (Clements and Chopin, 2017). Our knowledge of the variability in pH and carbonate chemistry in coastal areas is relatively poor and predictions are lacking. Saavedra *et al.* (2021) use time series of data from an instrument mooring and *in situ* sampling to characterize the variability in oceanographic conditions and the carbonate system at three bivalve aquaculture areas located along a latitudinal gradient off of the Humboldt Current System, Chile. Their results show pH_T below 8 at most coastal sites, and occasionally below 7.5, reflecting upwelling events or freshwater runoff. Therefore, farmed bivalves are occasionally exposed to waters that are undersaturated in aragonite. The authors discuss the growth potential of bivalves along the latitudinal gradient and argue for considering high-resolution pH/pCO₂ time series and growth parameters of farmed bivalves to better anticipate the effects of climate change.

In bivalves, embryonic and larval development are generally sensitive to OA, with reductions in size and survival of larvae and increases in the number of abnormal larvae (Gazeau *et al.*, 2013). On an industrial scale, the most striking illustration of possible OA effects is the correlation between the pH of seawater and the survival of oyster larvae, clearly linking the pH_T/pCO₂ of seawater to hatchery failures (Barton *et al.*, 2012). Espinel-Velasco *et al.* (2021) investigated how OA influenced settlement success in the New Zealand abalone, *Haliotis iris*. They examined direct effects of seawater pH_T at the time of settlement, indirect effects of pH on settlement substrates made of crustose coralline algae (a calcifying organism susceptible to OA) and carryover effects by examining settlement in larvae reared to competency at ambient and reduced pH. They found

no direct or indirect effects, but nearly significant carryover effects with lower settlement in larvae reared at reduced pH_T. This study emphasizes the species-specific response to OA and also the importance of carryover effects for aquaculture operations such as spatfall collection.

Phenotypic plasticity and adaptation potential of farmed species under climate change, including selective breeding for resilience

Carryover effects can occur between development stages, but also between generations (intergenerational effects). For instance, exposure of adults to OA can produce positive or negative carryover effects in their progeny that influences survival under conditions of lower pH (e.g. Parker *et al.*, 2012; Dupont *et al.*, 2013). Clements *et al.* (2021) tested whether parental exposure to low pH influences reproductive conditioning and early larval development in eastern oysters *Crassostrea virginica*. They found that reduced pH_{NBS} (7.5–7.7) increased the rate of reproductive development in both males and females but did not produce intergenerational effects. They also found that low pH conditions during early development resulted in higher larval survival, reduced shell height, and increased shell deformities. They suggest that the positive effects of low pH on oyster larvae could reflect local adaptation to lower pH conditions due to the geographical proximity of the oyster rearing sites to peat bogs.

Although a growing body of literature documents negative effects of acidification on marine organisms, the majority of this work has focused on the effects of future conditions on current populations, ignoring the potential effects of adaptation (e.g. Kelly and Hofmann, 2013; Bitter *et al.*, 2019). Adaptation to OA will ultimately depend on trade-offs that occur when a relationship between two traits prevents them from being simultaneously optimized. For example, a population might possess genetic variation for tolerance to both OA and disease, but if there is a negative correlation between these two traits it may not be possible to evolve substantially increased tolerance to OA and disease simultaneously. Nordio *et al.* (2021) investigated whether adaptation to OA results in evolutionary trade-offs with *Vibrio* spp. resistance. OA and pathogenic *Vibrio* spp. bacteria both have adverse impacts on the aquaculture production of the Pacific oyster *Crassostrea gigas* in the NE Pacific Ocean (Elston *et al.*, 2008; Barton *et al.*, 2012). They estimated the heritability of survival to a *Vibrio harveyi* infection and larval shell length under OA and normal conditions in oyster larvae. They found moderate heritability of survival to *V. harveyi* challenge and low heritability for shell length in low pH and normal conditions. Interestingly, the estimated breeding values do not correlate between larval shell size in OA conditions and survival to *V. harveyi*, suggesting that genetic selection of oysters for increased resistance to pathogenic *V. harveyi* is unlikely to impact larval sensitivity to OA. Finally, they found that estimated breeding values for larval shell length are correlated between OA and normal conditions, indicating larger larvae tend to do better in low pH seawater. The authors suggest that selection for larger larvae during culling could explain why hatchery oyster populations are less sensitive to OA than wild animals. This study emphasizes the need to investigate the evolutionary potential of marine animals to multiple climate change-related drivers (Riebesell and Gattuso, 2015; Boyd *et al.*, 2018).

The effect of climate change-related drivers on species interactions: the intricate cases of parasitism and predation

Climate change can alter host–pathogen interactions and, therefore, the likelihood of disease outbreaks (e.g. Harvell *et al.*, 1999; Burge *et al.*, 2014 for reviews). For instance, interactions between hosts, pathogens, and the environment govern disease outbreaks, and a change in any of these components can shift the balance towards or away from a high-intensity disease state (Burge *et al.*, 2014). Temperature is the most well-studied climate-related driver of marine disease because it profoundly influences host and pathogen metabolism. Although there are reports of the exacerbating effects of temperature on the risk of disease, it is difficult to attribute a causal link between climate change and the occurrence of disease. Shephard and Gargan (2021) investigated the interaction between climate forcing and parasite infestation by sea lice *Lepeophtheirus salmonis* from coastal aquaculture on returns of wild Atlantic salmon *Salmo salar* to their natal river. The authors analysed annual counts of returning fish from Irish rivers, with or without (= the control) nearby salmon aquaculture. The authors show that salmon returns are decreasing over the long term and are negatively impacted by sea lice infestations associated with aquaculture. They also report a negative relationship between salmon returns in control rivers and climate (NAO effect), suggesting that these fish prefer lower temperatures during marine migration, with evidence of negative impacts from ocean warming. This NAO effect interacted with sea lice infestation: returns decreased with increased NAO, but only when lice infestation was low. The authors discuss the potential mechanisms underlying this complex interaction. This study emphasizes the need for long-term ecological studies examining the consequences of climate-disease interactions for developing management strategies, mitigating disease impacts, and preserving wild populations.

Salmon farms act as reservoirs of sea lice that are a source of transmission from farmed to wild salmon. Considering that temperature increases the epidemic potential of the parasite (Groner *et al.*, 2014), Godwin *et al.* (2021) fit a Bayesian model for sea lice population dynamics and management to timeseries data of sea lice on farmed salmon in Pacific Canada and analysed the model under scenarios of warmer climate. They found that in high-temperature years current parasite control policy becomes ineffective as sea-louse abundance is expected to increase. Then, they simulated two alternative parasite management scenarios that rely on additional delousing treatments and observed that both would decrease louse counts on farms in high-temperature years. This study highlights the importance of policies designed to account for future environmental change (also see the next section).

Rapid increase in salmon farming has dramatically altered the disease dynamics between farmed and wild salmon (e.g. Krkosek *et al.*, 2011; Vollset *et al.*, 2018). In Norway, new restrictions on fish farming have been enforced in the south due to the impacts of sea lice on wild salmonids. In northern areas, the effects of pathogens on wild salmonids are lower, reflecting relatively low density of fish farms and low temperatures. However, both factors are now increasing. These areas contain habitats supporting some of the largest remaining wild salmonid populations in the world. Vollset *et al.* (2021) question how these populations will cope with the changes that are coming. They identify research questions emerging from these upcoming changes and discuss

approaches and methods to address them. They conclude that policies related to spatial management of fish farming must consider uncertainties with respect to pathogen dynamics in the north until these research questions are fully addressed.

Temperature can differentially influence species within a community, significantly affecting the outcome of trophic interactions (e.g. O'Connor, 2009). For example, ocean warming is predicted to strengthen plant–herbivore interactions and potentially impact seaweed production. Warming increases the consumption rate of herbivores and also the palatability of macroalgae. This effect might be tempered by other factors such as nutrient availability. Endo *et al.* (2021) investigated the combined effects of ocean warming and nutrient enrichment on the consumption rate of the alga *Undaria pinnatifida* by the isopod *Cymodocea japonica*. They show no significant interaction between elevated temperature and nutrient enrichment on consumption rate, but there were additive effects. The consumption rate doubled in response to elevated temperature and nutrient enrichment and tripled when they were combined. Therefore, nutrient enrichment under warmer conditions is predicted to increase the risk of herbivory during the cultivation of this algal species.

Adaptive measures for mitigating the impacts of climate change on marine resources

The combined accelerated footprint of climate change and anthropogenic pressures on marine life raise the need for restoration programmes worldwide (Duarte *et al.*, 2020). Rinkevich (2021) analyses the recent literature on coral reef restoration from an ecological engineering perspective, linking biology, ecology, and engineering to improve and rehabilitate damaged ecosystems. The author distinguishes ecological engineering applications that integrate all aspects of reef restoration and ecological engineering aspects that deal with assisted genetics, coral chimerism, aquaculture of reef living organisms and consideration of life cycle parameters of the transplanted species. The author emphasizes that the object of study is often the population and the community, and only more rarely the ecosystem. Finally, he concludes that ecological engineering should consider creating new ecosystems that did not exist before rather than seeking to recreate historic ecosystem states.

In a literature review, Daly *et al.* (2021) investigated the implications of phenotypic plasticity for enhancement of crustacean stocks. The main idea is that there are behavioural and morphological differences between hatchery-raised and wild individuals that reflect adaptive responses to an unnatural rearing environment, and this phenotypic plasticity could be used to improve stock enhancement. The authors examine how behavioural and morphological phenotypic plasticity can affect crustacean ecology and recommend consideration of this plasticity in release strategies through adjustments to rearing protocols.

Sustainable development of aquaculture and its contribution to climate change

Concerns over the footprint of the ever-expanding aquaculture industry have motivated a range of approaches focusing on aquaculture impact analysis. The concept of aquaculture carrying capacity, popularized in the 1990s (Chapman and Byron, 2018), is generally framed as the maximum aquaculture intensity an ecosystem can support within limits of an ecological and social change acceptable to stakeholders (McKindsey *et al.*, 2006). Most

studies have focused on the production and ecological components, ignoring the social perspective. Kluger and Filgueira (2021) argue that carrying capacity should be viewed as multidimensional, iterative, inclusive, and just. Hence, the scope of carrying capacity needs to move from industry-driven towards an inclusive vision taking into consideration historical, cultural, and socio-economic concerns of all stakeholders. The authors suggest guidelines to frame a safe operating space for aquaculture based on a multi-criterion, multi-stakeholder approach, while embracing the social-ecological dynamics of aquaculture settings by applying an adaptive approach and acknowledging the critical role of place-based constraints. Carrying capacity approaches should proactively engage with aquaculture-produced outcomes at multiple scales, embracing interdisciplinarity, complexity, and uncertainty. This study highlights the necessity of scoping carrying capacity with the voices of all relevant societal groups, before aquaculture implementation, to jointly develop sustainable aquaculture.

The cultivation and use of seaweeds have high potential to support sustainable jobs and growth, providing biomass for human food, animal feed, and other applications like climate remediation. Although the large majority of seaweed production is located in Asia, interest in Europe is on the rise. van den Burg *et al.* (2021) show that, from a people, planet and profit perspective, the focus is not on producing large volumes of seaweed but on producing the right amount of the right seaweeds, considering the carrying capacity of European seas. They argue that the seaweed sector must avoid developing along the path of traditional economies (i.e. cost-driven decisions) but rather develop in a manner consistent with the emerging circular blue economy. Seaweeds should not be seen as a new product added to the market but become an integral part of the European food system, being used for human consumption, animal feed, and for improving food production processes.

Thomas *et al.* (2021) conducted an environmental LCA of a kelp farm in Sweden. The LCA includes spore production, seeding lines, cultivation at sea, harvesting and preservation and accounts for nutrient bioremediation and carbon capture. They compared two seeding techniques (submersion and spray) and four preservation methods (hang-drying outdoors, heated air-cabinet drying, ensilage, and freezing). The authors found that more nutrients and carbon are absorbed than emitted by the seaweed supply chain. Emissions are most affected by preservation method. The largest impact results from freezing and air-cabinet drying, the two most energy-consuming processes, followed by the cultivation infrastructure. Hatchery processes, harvesting and the ensilage and hang-drying outdoors have relatively small impacts. This study highlights the relevance of LCA to marine aquaculture (Bohnes *et al.*, 2019) and emphasizes the potential of seaweed aquaculture as a solution to mitigate eutrophication and climate change (Froehlich *et al.*, 2019).

Finally, Froehlich *et al.* (2021) ask how the 20 International Council for the Exploration of the Sea (ICES) member nations will sustainably meet the increasing demand for seafood, considering that the majority of these nations have not developed robust aquaculture industries. They evaluated past trends in farmed and wild seafood production and consumption in ICES nations, and the potential and need to increase aquaculture production by 2050. They found that the majority of ICES nations lack long-term strategies for aquaculture, with few plans accounting for climate change and an increasing gap between future production

and consumption. This work highlights the need to prioritize aquaculture policy to set more ambitious domestic production goals and improve sustainable sourcing of seafood from other parts of the world, with a more explicit incorporation of climate change into decision-making.

Summary and forward look

We hope that the articles in this TS will be seen as a small step forward in supporting a better understanding of the challenges and potential of “marine aquaculture in the Anthropocene”.

As is clear from the preceding, this TS attracted a very diverse set of articles in terms of the approaches taken (experimentation, modelling, meta-analysis, review) and the disciplines covered (biology, economics, engineering), reflecting the complexity of the topic.

The call for papers solicited submissions that used approaches ranging from a single to multiple drivers, a single organism to an ecosystem, and acclimatization to adaptation. Indeed, these approaches are essential for understanding the effects of climate change and providing guidelines to policymakers (Riebesell and Gattuso, 2015). The research articles that we received were generally multi-factorial (Endo *et al.*, 2021; Espinel-Velasco *et al.*, 2021; Godwin *et al.*, 2021; Nordio *et al.*, 2021; Shephard and Gargan, 2021) and several address adaptation issues (Clements *et al.*, 2021; Espinel-Velasco *et al.*, 2021; Nordio *et al.*, 2021). However, they focus on the species of interest and pay relatively little attention to other ecosystem components. This reflects the slow uptake of ecosystem-based aquaculture (Brugère *et al.*, 2019). The exception was pathogens and parasites (Godwin *et al.*, 2021; Nordio *et al.*, 2021; Shephard and Gargan, 2021; Wiik Vollset *et al.*, 2021), probably because they pose major challenges to aquaculture production. The change of scale from single organism to ecosystem remains a daunting challenge.

Inter- and trans-disciplinary work linking natural and social science, and economics, in tackling effects of climate change on aquaculture were particularly welcome. Although taking a trans-disciplinary approach is a key component of sustainability science (Hirsch Hadorn *et al.*, 2006), we did not receive any trans-disciplinary contributions. Work of this nature is still in its infancy.

From all these articles and the associated scientific literature, it seems that three types of action are possible for adapting aquaculture operations to climate change. First, we must anticipate the biogeographical changes in the distribution of species. Species are indeed distributed over geographic areas where physical and biotic conditions fit their physiological range (Pörtner, 2002), and any changes in these conditions may locally alter the potential for aquaculture production (Froehlich *et al.*, 2018). Second, we must determine if species can adapt to a range of stressors via evolution. Then, the selection of robust phenotypes, which are resistant or tolerant to these stressors would be an option for the aquaculture industry, although trade-off with other traits and maintaining the genetic diversity need to be carefully considered (Reid *et al.*, 2019; Tan *et al.*, 2020). Third, we must consider ecosystem conservation, restoration or remediation strategies to foster resilience to climate change stressors. Biodiversity indeed limit disease risk (Keesing *et al.*, 2010), an upcoming threat under climate change (Harvell *et al.*, 1999). Macroalgae and plant act as a carbon sink and create local refugia against acidification for calcifying organisms (Groner *et al.*, 2018; Young and Gobler, 2018). These examples suggest that the combination of species that

interact favourably with each other can mitigate the effects of climate change. These three options are not mutually exclusive and should be considered together.

To limit the effects of climate change, human activities, including aquaculture, are currently being imposed new constraints. According to the Paris agreements signed by 196 government representatives in 2016, anthropogenic greenhouse gas emissions must decrease rapidly to keep the increase in global average temperature to well below 2°C by 2100. This effort, which is based on limiting our consumption of fossil fuels, is promoting a low-carbon economy. Aquaculture will have to adapt to this new standard. From this point of view, not all aquaculture productions are created equal. For example, intensive culture of shrimp or carnivorous fish is highly energy demanding, while production of omnivorous fishes, bivalve molluscs or macroalgae have a low or even negative carbon footprint (Cochrane *et al.*, 2009). Therefore, aquaculture will undoubtedly contribute to the low carbon economy of tomorrow. Development choices should be based on carbon footprint and product LCAs in addition to traditional profitability analyses. Aquaculture can help make our planet great again, this is a matter of choice.

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