Title: Lessons from two high CO_2 worlds – future oceans and intensive aquaculture

Running head: Lessons from two high CO_2 worlds

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Abstract

Exponentially rising CO_2 (currently ~400 µatm) is driving climate change, and causing acidification of both marine and freshwater environments. Physiologists have long known that CO_2 directly affects acid-base and ion regulation, respiratory function, and aerobic performance in aquatic animals. More recently, many studies have demonstrated that elevated CO_2 projected for end of this century (e.g. 800-1,000 µatm) can also impact physiology, and have substantial effects on behaviours linked to sensory stimuli (smell, hearing and vision) both having negative implications for fitness and survival. In contrast, the aquaculture industry were farming aquatic animals at CO_2 levels that far exceed end of century climate change projections (sometimes >10,000 µatm) long before the term "ocean acidification" was coined, with limited detrimental effects reported. It is therefore vital to understand the reasons behind this apparent discrepancy. Potential explanations include: 1) the use of "control" CO_2 levels in aquaculture studies that go beyond 2100 projections in an ocean acidification context; 2) the relatively benign environment in aquaculture (abundant food, disease protection, absence of predators) compared to the wild; 3) aquaculture species having been chosen due to their natural tolerance to the intensive conditions, including CO_2 levels; or 4) the breeding of species within intensive aquaculture having further selected traits that confer tolerance to elevated CO_2. We highlight this issue and outline the insights that climate change and aquaculture science can offer for both marine and freshwater settings. Integrating these two fields will stimulate discussion on the direction of future cross-disciplinary research. In doing so this article aims to optimise future research efforts and elucidate effective mitigation strategies for managing the negative impacts of elevated CO_2 on future aquatic ecosystems and the sustainability of fish and shellfish aquaculture.

Introduction - Climate change, high CO_2 and global food security

In 2015 atmospheric CO_2 concentrations had risen to an annual average higher than 400 µatm the first time in over 800,000 years (Lüthi *et al.*, 2008, Dlugokencky & Pieter, 2016), as a result of anthropogenic CO_2 emissions. The potential implications of this post-industrial rise in CO_2 were predicted over 110 years ago (Krogh, 1904), yet it was only recently that governments agreed to take action on this issue. Despite 196 nations taking an unprecedented stance on climate change last year by signing the COP21 agreement to curtail emissions, CO_2 concentrations are still projected to approach 1000 µatm by 2100 (Pörtner *et al.*, 2014). Around a quarter of anthropogenic CO_2 emissions have been absorbed by the oceans (Pörtner *et al.*, 2014). Whilst this results in a phenomenon commonly referred to as ocean acidification, elevated atmospheric CO_2 is also driving a large elevation in the average aquatic CO_2 in fresh and brackish water systems, regardless of diurnal and seasonal variation. What's more, seasonal oscillations of aquatic CO_2 in the future are predicted to amplify over time which will likely result in CO_2 levels that exceed 1000 µatm for several months each year well before 2100 (McNeil & Sasse, 2016). Occurring simultaneously with warming, pollution, habitat degradation, disease outbreaks and overfishing, this aquatic acidification is therefore threatening not only aquatic ecosystems but also global food security (FAO, 2014, Porter *et al.*, 2014).

Anthropogenic CO_2 emissions accelerate alongside growth of the global human population, which is projected to exceed 9.6 billion by 2100 (Gerland *et al.*, 2014). This same growth has also resulted in at least 80% of world fish stocks being overexploited (FAO, 2014, Pauly & Zeller, 2016). Aquaculture is therefore crucial to ensure the continued provision of fish and shellfish protein for human consumption, particularly for developing countries and small island nations (Bennett *et al.*, 2016). Indeed, aquaculture is one of the fastest growing food producing industries globally (8.8 % annual growth for the last 30 years) (FAO, 2014), and it is the only foreseeable way of increasing seafood† production in the face of this human population expansion. However, to ensure aquaculture is able to maximise its potential for addressing global food security a number of challenges need to be resolved concerning water availability and quality, environmental impacts, and vulnerability to changing climatic conditions. Recirculating Aquaculture Systems (RAS) address many of these issues (Martins *et al.*, 2010) and enable the sustainable intensification of aquaculture. These systems significantly reduce water requirements, relocate production of aquatic organisms away from a natural environmental setting and minimise environmental impacts. They also enable a tighter control of pathogens and other environmental parameters, potentially improving animal welfare and biosecurity, but they create some additional problems, particularly associated with accumulation of CO_2.

A common problem, two perspectives

Physiologists have known for decades that raising the CO_2 partial pressure in water to well above atmospheric levels (e.g. 10,000 µatm) has a direct effect on aquatic organisms in terms of acid-base and ion regulation, respiratory function, and aerobic performance (Cameron & Randall, 1972). More recently, climate change studies have shown that CO_2 levels projected for end of this century (e.g. 800-1,000 µatm), can negatively affect development, physiology and fitness-related behaviours in aquatic animals (see below). Due to the very high stocking densities achieved in most aquaculture settings, as well as the methods employed to control pH and O_2, CO_2 often accumulates, particularly in RAS. However, despite recent evidence on the potential detrimental effects of CO_2 exposure at a level projected for 2100 (1,000 µatm), the aquaculture industry was intensively farming fish and shellfish successfully at much higher

† Seafood in this context refers to all fish and shellfish species produced under fresh, brackish or marine conditions and intended for human consumption

CO_2 levels long before the term “ocean acidification” was coined. The levels at which the effects of CO_2 are perceived as problematic therefore appear to differ greatly between the connected yet traditionally disparate fields of climate change and aquaculture (Fig 1.).

Current guidelines for intensive RAS propose safe CO_2 levels ranging from 15 to 40 mg/l (Fivelstad *et al.*, 1999, Blancheton, 2000, Petochi *et al.*, 2011, Fivelstad *et al.*, 2015). These equate to an upper limit of CO_2 ranging from >5,000 to >30,000 µatm which are 12.5 to 75 times higher than current atmospheric levels respectively. Furthermore, far from being an issue exclusively associated with RAS and finfish production, elevated CO_2 levels appear synonymous with intensive aquaculture more generally. For example, over 40 % of Norwegian salmon smolt hatcheries (flow-through and RAS) report CO_2 levels >5,400 µatm (Noble *et al.*, 2012), whereas Bangladeshi shrimp ponds are shown to experience CO_2 levels averaging >17,000 µatm (Saksena *et al.*, 2006, Sahu *et al.*, 2013).

In stark contrast, recent studies emerging from aquatic acidification research have demonstrated that just 2 to 2.5-fold increases in CO_2 levels projected for the end of this century (e.g. 800–1,000 µatm) can have dramatic and long-lasting effects on the development, physiology and behaviour of both fish and invertebrates (Briffa *et al.*, 2012, Schalkhausser *et al.*, 2012, Heuer & Grosell, 2014, Watson *et al.*, 2014, Welch *et al.*, 2014). For example, exposure to 1,000 µatm during early life cycle stages has been shown to result in reduced survival as well as a number of sub-lethal effects including tissue damage (e.g. Frommel *et al.*, 2012, Chambers *et al.*, 2014, Frommel *et al.*, 2014), altered calcification (e.g. Arnold *et al.*, 2009, Maneja *et al.*, 2013), reduced size (e.g. Talmage & Gobler, 2009, Maneja *et al.*, 2014), reduced metabolic rate (e.g. Small *et al.*, 2016), delayed development and altered gene expression (e.g. Tseng *et al.*, 2013, Goncalves *et al.*, 2016) in a range of different marine organisms. What is more, similar effects are also demonstrated in freshwater, with Ou *et al.* (2015) showing a significant effect of elevated CO_2 (1,000 – 2,000 µatm) on the larval development of pink salmon *Oncorhynchus gorbuscha*. The authors reported a reduction in larval length, total wet and dry mass and reduced production efficiency (conversion of yolk into tissue growth).

In impacting a diverse array of aquatic organisms during early life stages, increased partial pressure of CO_2 in aquatic environments above present day atmospheric levels is a likely bottleneck for organism production. This in turn would significantly impact aquaculture practices that depend upon a reliable source of larvae or juveniles. In 2007, these impacts were realised with the upwelling of elevated CO_2, aragonite under-saturated seawater off the US west coast, significantly impacting oyster hatchery production as a direct result of changing climatic conditions (Barton *et al.*, 2012). In addition to providing a case study in which to investigate the impact of ocean acidification on shellfish production globally, this event highlighted the significant advances achieved when climate change scientists and aquaculture practitioners work closely together. Unifying their research efforts to overcome this phenomenon, the climate change community and shellfish growers were able to successfully identify the root cause of this issue and put in place a number of mitigation strategies and monitoring protocols to minimise impacts in the future (Barton *et al.*, 2015).

Far from being restricted to early life stages, a growing number of studies have also shown sub-lethal physiological impacts of elevated CO_2 (range 1,000 – 2,000 µatm) in a number of species which include impacted respiratory gas transport, acid-base balance and gut carbonate excretion (e.g. Lannig *et al.*, 2010, Esbaugh *et al.*, 2012, Heuer *et al.*, 2012, Wei *et al.*, 2015, Esbaugh *et al.*, 2016). Rapid and efficient acid-base compensation has been demonstrated in a number of species at elevated CO_2 concentrations (e.g. Melzner *et al.*, 2009, Ern & Esbaugh, 2016, Lewis *et al.*, 2016). However, such physiological responses incur energetic costs and could therefore have negative implications for production efficiency and body condition both in aquaculture and natural settings. Likewise, a wide range of behaviours are shown to be disrupted under elevated CO_2, such as those linked to sensory stimuli (including smell, hearing and vision; e.g. Simpson *et al.*, 2011, Nilsson *et al.*, 2012, Roggatz *et al.*, 2016) and cognitive-related functions (such as lateralisation, learning, bold-shy phenotypes and escape behaviour; e.g. Schalkhausser *et al.*, 2012, Jutfelt *et al.*, 2013, Hamilton *et al.*, 2014, Watson *et al.*, 2014), which will have clear detrimental implications at the population level (Munday *et al.*, 2009, Munday *et al.*, 2010, Chivers *et al.*, 2014). However, animals reared in many aquaculture settings are living in a relatively benign environment, being provided with abundant food, relatively constant environmental conditions, protection against disease and absence of a predation threat. Therefore it is perhaps not surprising that the ecologically-relevant physiological and behavioural disruptions caused by end of century CO_2 levels in OA studies have not emerged from aquaculture studies. Equally it may be possible these behavioural effects have not been noted as they are not typically measured in aquaculture studies. Nevertheless, this does not mean that animals reared in an aquaculture setting are not facing problems associated with elevated CO_2 that potentially influence their health and/or production efficiency.

Cross-discipline interaction to improve understanding of CO_2 consequences

Given these contrasting views, combining the knowledge that has arisen from climate change and aquaculture research is crucial to allow a more in-depth understanding of the physiological and ecological responses of aquatic animals to elevated CO_2. The opportunity to compare these two fields directly is appealing, and should enable a more accurate prediction of the consequences of changing climatic conditions for wild populations and intensive aquaculture practices alike. However, at present such comparison is not straightforward. This is partly due to the different experimental measures and reporting protocols typically adopted by each of these scientific fields. To facilitate this process it would be fruitful to develop a collective research agenda and implement standard operating procedures with respect to hypothesis development, experimental outcomes and data reporting.

The comparison is also complicated by rather different species often being used in aquaculture compared to OA research, with the former inevitably relying on species that are amenable to domestication, which may go hand-in-hand with greater environmental tolerance. Indeed, when considering contrasting results from aquatic acidification and aquaculture fields it is worth noting that responses from even closely related species can often vary significantly. For example, Ferrari *et al.* (2011) demonstrated a striking and unexpected difference for the impact of CO_2 on the antipredator response of closely related damselfish species. Similarly, Lefevre (2016) and Heuer and Grosell (2014) highlight heterogeneity in physiological responses to elevated CO_2 that argues against a unifying physiological theory for defining CO_2 tolerance, and which needs to be accounted for when modelling and predicting the impacts of climate change. Indeed explaining such interspecies variability with respect to CO_2 tolerance may provide a mechanistic understanding of why species used in aquaculture may be relatively tolerant to the CO_2 levels prevalent within intensive production. However, it is important to note that even cod reared under end of century CO_2 levels (1,000 µatm) exhibit avoidance behaviour towards these conditions when presented with a choice, indicating negligible habituation and suggesting these conditions are unfavourable (Jutfelt & Hedgärde, 2013). Furthermore, a growing body of evidence shows that levels of CO_2 experienced in aquaculture may be more detrimental than traditionally perceived (Heuer & Grosell, 2014). For example Tirsgaard *et al.* (2015) and Ou *et al.* (2015) demonstrated detrimental effects of elevated CO_2 in cod and salmon respectively, species traditionally grown successfully under aquaculture settings. Exposure to 9,200 µatm resulted in longer meal processing time and less efficient digestion in cod (Tirsgaard *et al.*, 2015), whilst exposure to 2,000 µatm reduced growth and production efficiency in salmon larvae (Ou *et al.*, 2015), end-point measures that are of specific importance to aquaculture production. Thus differences between these two fields in the perceived impact of elevated CO_2 cannot be explained solely by variability in interspecific responses. Measuring the impact of elevated CO_2 on a diverse array of physiological and behavioural endpoints, not just those traditionally perceived as important for aquaculture production, is thus vital. It is also crucial to measure these responses in as many species as possible, both finfish and shellfish, as well as those traditionally perceived as CO_2 tolerant and CO_2 sensitive. By doing so it will be possible to optimise water quality parameters within aquaculture, based on a species specific suite of physiological and behavioural CO_2 tolerance endpoints. Targeting these conditions has the potential to maximise growth efficiency and health of aquaculture species, enhancing the sustainability of seafood production. With that aim, it is critical to understand the practical considerations of reducing and maintaining environmental conditions, particularly CO_2, in an aquaculture context. Targets should thus be set that optimise productivity and welfare of the aquaculture species, but which are equally achievable in a practical and economical context (Noble *et al.*, 2012).

In order to optimise research efforts and ensure data are both scientifically robust and comparable, a unified protocol for selecting, manipulating, measuring and finally reporting carbonate chemistry parameters is also needed. This is of particular importance given the methods of carbonate chemistry manipulation employed within intensive aquaculture, for example the addition of a strong alkali to buffer changes in pH, such as sodium hydroxide (NaOH), sodium bicarbonate ($NaHCO_3$), calcium hydroxide ($Ca(OH)_2$) or calcium oxide (CaO). This is the most commonly used of all water chemistry quality management practices in aquaculture, being typically employed in a diverse array of aquaculture settings (Boyd *et al.*, 2016). However, this method of pH compensation additionally elevates alkalinity, often significantly beyond any natural analogue (Ellis *et al.*, in preparation), and depending on the alkali used can have dramatic indirect effects on additional water chemistry parameters, some of which are shown themselves to influence a number physiological processes in aquatic organisms (Boyd *et al.*, 2016, Middlemiss *et al.*, 2016). A further crucial issue is the selection of experimental controls representing present day CO_2 levels (400 µatm), and we propose this should be a common reference point for both climate change and aquaculture researchers. Control levels employed within aquaculture research typically exceed 1,000 µatm (range 1,000–3,000 µatm) (Fivelstad *et al.*, 1999, Petochi *et al.*, 2011), and thus surpass most of the "high CO_2" treatments used as end of century projections in climate change studies. To complicate matters further, reporting CO_2 levels as mg/l in aquaculture studies overlooks the impact of temperature and salinity on the solubility of CO_2 and the resulting impact these have on the partial pressure of this gas (Weiss, 1974, Dickson, 2011). For example, for the same mg/l concentration the actual partial pressure of CO_2 varies by more than 3-fold between cold freshwater and warm seawater (Fig. 2). This is critical because it is partial pressure (not the mg/l concentration) that determines the internal (blood) levels of CO_2 and its impact on physiology, behaviour, growth etc. At present, the scarcity of sufficient water chemistry parameters being presented, the lack of environmentally relevant controls, and the prevalence of reporting CO_2 levels as mg/l in aquaculture literature preclude an unambiguous comparison between data from these two fields.

Finally, understanding and reporting the provenance of the study species/population will be important to enable a more in depth assessment of CO_2 tolerance, i.e. whether animals are wild caught, laboratory-bred or reared within an aquaculture setting (potentially already at very high CO_2 when considered in a climate change experimental context). It is fair to say that many (though not all) laboratory-based climate change studies benefit from easy access to study species available from aquaculture. The systematic selection of traits of interest by the aquaculture industry, such as fast growth and resistance to pathogens, have inherently selected for good performance under intensive farming conditions. In that context it is possible, and even likely, that additional non-target traits have also been selected, potentially including those involved in CO_2 tolerance. Indeed, enhanced CO_2 tolerance has been demonstrated in selectively bred populations of the Sydney rock oyster, compared to its wild type congeners (Parker *et al.*, 2011, Parker *et al.*, 2015, Thompson *et al.*, 2015). Furthermore, as demonstrated by Malvezzi *et al.* (2015) early life survival at elevated CO_2 concentrations can have a significant additive genetic element (i.e. highly heritable), which under sufficient selection pressure could elicit a strong and rapid evolutionary response. It is highly likely therefore, that aquaculture practices operating at elevated CO_2 concentrations would elicit sufficient selection pressure to directly select for CO_2 tolerance during early life stages, leading to the rapid evolution of the population in just a few generations. Thus exploring the traits selected for in broodstock within intensive aquaculture offers a fascinating opportunity to investigate multi-generational adaptation to CO_2 levels experienced under intensive production conditions in aquaculture species. In addition, it will be vital to undertake multigenerational studies in order to discern the transgenerational acclimation to elevated CO_2 of different fish species with respect to different behavioural (e.g. Welch *et al.*, 2014) and physiological (e.g. Miller *et al.*, 2012) endpoints. Combining the understanding from these two fields will therefore help determine the physiological basis for CO_2 tolerance, determine its true ecological consequence and determine its ecological impacts over relevant timescales.

Conclusions

The yield from wild-capture fisheries has plateaued since the late 1980s and human consumption from aquaculture exceeded that from wild sources for the first time in 2014 (FAO, 2014). Furthermore, as stated previously, aquaculture is likely to be the only pathway for increasing seafood production in the future. Moving from a capture to a culture mentality requires a shift in attitude that will require time, a luxury that is ill-afforded in the rapidly changing environment of the Anthropocene. Creating opportunities for the aquatic acidification community and the aquaculture industry to work together should help to speed up this process and enable the aquaculture industry to rapidly adapt by using better-informed decisions to; a) optimise the water chemistry conditions within intensive aquaculture to suit the species, and/or b) select traits within the species to suit intensive aquaculture conditions. This will help address the environmental, economic and social impacts of this developing sector towards a sustainable intensification of production, enhancing food security and its resilience to climate change. Equally, this cross-discipline interaction should also improve our capability to predict and mitigate the consequences of the changing chemistry for natural ecosystems in a future “high” CO_2 world.

References

Arnold, KE, Findlay, HS, Spicer, JI, Daniels, CL, Boothroyd, D (2009) Effect of CO_2-related acidification on aspects of the larval development of the European lobster, *Homarus gammarus* (L.). Biogeosciences, **6**, 1747-1754.

Barton, A, Hales, B, Waldbusser, GG, Langdon, C, Feely, RA (2012) The Pacific oyster, *Crassostrea gigas*, shows negative correlation to naturally elevated carbon dioxide levels: Implications for near‐term ocean acidification effects. Limnology and Oceanography, **57**, 698-710.

Barton, A, Waldbusser, GG, Feely, RA, Hales, B, Langdon, CJ (2015) Impacts of coastal acidification on the Pacific Northwest shellfish industry and adaptation strategies implemented in response. Oceanography, **28**, 146-159.

Bennett, NJ, Blythe, J, Tyler, S, Ban, NC (2016) Communities and change in the anthropocene: understanding social-ecological vulnerability and planning adaptations to multiple interacting exposures. Regional Environmental Change, **16**, 907-926.

Blancheton, JP (2000) Developments in recirculation systems for Mediterranean fish species. Aquacultural Engineering, **22**, 17-31.

Boyd, CE, Tucker, CS, Somridhivej, B (2016) Alkalinity and hardness: Critical but elusive concepts in aquaculture. Journal of the World Aquaculture Society, **47**, 6-41.

Briffa, M, de la Haye, K, Munday, PL (2012) High CO_2 and marine animal behaviour: Potential mechanisms and ecological consequences. Marine Pollution Bulletin, **64**, 1519-1528.

Cameron, JN, Randall, DJ (1972) The Effect of Increased Ambient CO_2 on Arterial CO_2 Tension, CO_2 Content and pH in Rainbow Trout. Journal of Experimental Biology, **57**, 673-680.

Chambers, RC, Candelmo, AC, Habeck, EA *et al.* (2014) Effects of elevated CO_2 in the early life stages of summer flounder, *Paralichthys dentatus*, and potential consequences of ocean acidification. Biogeosciences, **11**, 1613-1626.

Chivers, DP, McCormick, MI, Nilsson, GE *et al.* (2014) Impaired learning of predators and lower prey survival under elevated CO_2: a consequence of neurotransmitter interference. Global Change Biology, **20**, 515-522.

Dickson, AG (1990) Standard potential of the reaction: and the standard acidity constant of the ion HSO_4^- in synthetic sea water from 273.15 to 318.15 K. The Journal of Chemical Thermodynamics, **22**, 113-127.

Dickson, AG (2011) The carbon dioxide system in seawater: equilibrium chemistry and measurements. In: *Guide to best practices for ocean acidification research and data reporting.* (eds Riebesell U, Fabry VJ, Hansson L, Gattuso JP) pp Page., European Union.

Dickson, AG, Millero, FJ (1987) A comparison of the equilibrium constants for the dissociation of carbonic acid in seawater media. Deep-Sea Research, **34**, 1733-1743.

Dlugokencky, E, Pieter, T (2016) Trends in Atmospheric Carbon Dioxide. (ed Division N-E-GM) pp Page.

Ern, R, Esbaugh, AJ (2016) Hyperventilation and blood acid–base balance in hypercapnia exposed red drum (*Sciaenops ocellatus*). Journal of Comparative Physiology B, **186**, 447-460.

Esbaugh, AJ, Ern, R, Nordi, WM, Johnson, AS (2016) Respiratory plasticity is insufficient to alleviate blood acid–base disturbances after acclimation to ocean acidification in the estuarine red drum, *Sciaenops ocellatus*. Journal of Comparative Physiology B, **186**, 97-109.

Esbaugh, AJ, Heuer, R, Grosell, M (2012) Impacts of ocean acidification on respiratory gas exchange and acid–base balance in a marine teleost, *Opsanus beta*. Journal of Comparative Physiology B, **182**, 921-934.

FAO (2014) The state of world fisheries and aquaculture - Opportunities and challenges. pp Page, Rome, Italy.

Ferrari, MCO, Dixson, DL, Munday, PL, McCormick, MI, Meekan, MG, Sih, A, Chivers, DP (2011) Intrageneric variation in antipredator responses of coral reef fishes affected by ocean acidification: implications for climate change projections on marine communities. Global Change Biology, **17**, 2980-2986.

Fivelstad, S, Kvamme, K, Handeland, S, Fivelstad, M, Olsen, AB, Hosfeld, CD (2015) Growth and physiological models for Atlantic salmon (*Salmo salar L.*) parr exposed to elevated carbon dioxide concentrations at high temperature. Aquaculture, **436**, 90-94.

Fivelstad, S, Olsen, AB, Kloften, H, Ski, H, Stefansson, S (1999) Effects of carbon dioxide on Atlantic salmon (*Salmo salar*) smolts at constant pH in bicarbonate rich freshwater. Aquaculture, **178**.

Frommel, AY, Maneja, R, Lowe, D *et al.* (2012) Severe tissue damage in Atlantic cod larvae under increasing ocean acidification. Nature Climate Change, **2**, 42-46.

Frommel, AY, Maneja, R, Lowe, D *et al.* (2014) Organ damage in Atlantic herring larvae as a result of ocean acidification. Ecological Applications, **24**, 1131-1143.

Gerland, P, Raftery, AE, Ševčíková, H *et al.* (2014) World population stabilization unlikely this century. Science.

Goncalves, P, Anderson, K, Thompson, EL, Melwani, A, Parker, L, Ross, PM, Raftos, DA (2016) Rapid transcriptional acclimation following transgenerational exposure of oysters to ocean acidification. Molecular Ecology.

Hamilton, TJ, Holcombe, A, Tresguerres, M (2014) CO_2-induced ocean acidification increases anxiety in Rockfish via alteration of GABAA receptor functioning. Proceedings of the Royal Society of London B: Biological Sciences, **281**.

Heuer, RM, Esbaugh, AJ, Grosell, M (2012) Ocean acidification leads to counterproductive intestinal base loss in the Gulf Toadfish (*Opsanus beta*). Physiological and Biochemical Zoology: Ecological and Evolutionary Approaches, **85**, 450-459.

Heuer, RM, Grosell, M (2014) Physiological impacts of elevated carbon dioxide and ocean acidification on fish. American Journal of Physiology-Regulatory, Integrative and Comparative Physiology, **307**, R1061-R1084.

Jutfelt, F, Bresolin de Souza, K, Vuylsteke, A, Sturve, J (2013) Behavioural disturbances in a temperate fish exposed to sustained high-CO_2 levels. PLoS One, **8**.

Jutfelt, F, Hedgärde, M (2013) Atlantic cod actively avoid CO_2 and predator odour, even after long-term CO_2 exposure. Frontiers in Zoology, **10**, 1-8.

Krogh, A (1904) On the tension of carbonic acid in natural waters and especially in the sea. Meddelelser om Grønland, **26**, 231-342.

Lannig, G, Eilers, S, Pörtner, HO, Sokolva, IM, Bock, C (2010) Impact of ocean acidification on energy metabolism of oyster, *Crassostrea gigas* - changes in metabolic pathways and thermal response. Marine Drugs, **8**, 2318-2339.

Lefevre, S (2016) Are global warming and ocean acidification conspiring against marine ectotherms? A meta-analysis of the respiratory effects of elevated temperature, high CO_2 and their interaction. Conservation Physiology, **4**, cow009.

Lewis, C, Ellis, RP, Vernon, E, Elliot, K, Newbatt, S, Wilson, RW (2016) Ocean acidification increases copper toxicity differentially in two key marine invertebrates with distinct acid-base responses. Scientific Reports, **6**, 21554.

Lüthi, D, Le Floch, M, Bereiter, B *et al.* (2008) High-resolution carbon dioxide concentration record 650,000-800,000 years before present. Nature, **453**, 379-382.

Malvezzi, AJ, Murray, CS, Feldheim, KA *et al.* (2015) A quantitative genetic approach to assess the evolutionary potential of a coastal marine fish to ocean acidification. Evolutionary Applications, **8**, 352-362.

Maneja, R, Frommel, A, Geffen, A, Folkvord, A, Piatkowski, U, Chang, M, Clemmesen, C (2013) Effects of ocean acidification on the calcification of otoliths of larval Atlantic cod *Gadus morhua*. Marine Ecology Progress Series, **477**, 251-258.

Maneja, RH, Dineshram, R, Thiyagarajan, V *et al.* (2014) The proteome of Atlantic herring (*Clupea harengus* L.) larvae is resistant to elevated pCO_2. Marine Pollution Bulletin, **86**, 154-160.

Martins, CIM, Eding, EH, Verdegem, MCJ *et al.* (2010) New developments in recirculating aquaculture systems in Europe: A perspective on environmental sustainability. Aquacultural Engineering, **43**, 83-93.

McNeil, BI, Sasse, TP (2016) Future ocean hypercapnia driven by anthropogenic amplification of the natural CO_2 cycle. Nature, **529**, 383-386.

Mehrbach, C, Culberson, CH, Hawley, JE, Pytkowicz, RM (1973) Measurements of the apparent dissociation constants of carbonic acid in seawater at atmospheric pressure. Limnology and Oceanography, **18**, 897-906.

Melzner, F, Göbel, S, Langenbuch, M, Gutowska, MA, Pörtner, H-O, Lucassen, M (2009) Swimming performance in Atlantic Cod (*Gadus morhua*) following long-term (4–12 months) acclimation to elevated seawater. Aquatic Toxicology, **92**, 30-37.

Michaelidis, B, Spring, A, Pörtner, HO (2007) Effects of long-term acclimation to environmental hypercapnia on extracellular acid–base status and metabolic capacity in Mediterranean fish *Sparus aurata*. Marine Biology, **150**, 1417-1429.

Middlemiss, KL, Urbina, MA, Wilson, RW (2016) Effects of seawater alkalinity on calcium and acid–base regulation in juvenile European lobster (*Homarus gammarus*) during a moult cycle. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology, **193**, 22-28.

Miller, GM, Watson, S-A, Donelson, JM, McCormick, MI, Munday, PL (2012) Parental environment mediates impacts of increased carbon dioxide on a coral reef fish. Nature Climate Change, **2**, 858-861.

Munday, PL, Dixson, DL, McCormick, MI, Meekan, M, Ferrari, MCO, Chivers, DP (2010) Replenishment of fish populations is threatened by ocean acidification. Proceedings of the National Academy of Science USA, **107**.

Munday, PM, Dixson, DL, Donelson, JM, Jones, GP, Pratchett, MS, Devitsina, GV, Døving, KB (2009) Ocean acidification impairs olfactory discrimination and homing ability of a marine fish. Proceedings of the National Academy of Science USA, **106**, 1848-1852.

Nilsson, GE, Dixson, DL, Domenici, P, McCormick, MI, Sørensen, C, Watson, S-A, Munday, PL (2012) Near-future carbon dioxide levels alter fish behaviour by interfering with neurotransmitter function. Nature Climate Change.

Noble, C, Kankainen, M, Setälä, J, Berrill, IK, Ruohonen, K, Damsgård, B, Toften, H (2012) The bio-economic costs and benefits of improving productivity and fish welfare in aquaculture: utilizing CO_2 stripping technology in norwegian atlantic salmon smolt production. Aquaculture Economics & Management, **16**, 414-428.

Ou, M, Hamilton, TJ, Eom, J *et al.* (2015) Responses of pink salmon to CO_2-induced aquatic acidification. Nature Climate Change, **5**, 950-955.

Parker, L, Ross, PM, O'Connor, WA (2011) Populations of the Sydney rock oyster, *Saccostrea glomerata*, vary in response to ocean acidification. Marine Biology, **158**, 689-697.

Parker, LM, O'Connor, WA, Raftos, DA, Pörtner, H-O, Ross, PM (2015) Persistence of positive carryover effects in the oyster, *Saccostrea glomerata*, following transgenerational exposure to ocean acidification. PLoS One, **10**, e0132276.

Pauly, D, Zeller, D (2016) Catch reconstructions reveal that global marine fisheries catches are higher than reported and declining. Nature Communications, **7**.

Petochi, T, Di Marco, P, Priori, A, Finoia, MG, Mercatali, I, Marino, G (2011) Coping strategy and stress response of European sea bass *Dicentrarchus labrax* to acute and chronic environmental hypercapnia under hyperoxic conditions. Aquaculture, **315**, 312-320.

Pierrot, EC, Lewis, E, Wallace, DWR (2006) CO_2SYS Dos program developed for CO_2 system calculations. ORNL/CDIAC-105. Carbon Dioxide Information Analysis Centre, Oak Ridge National Laboratory, US Department of Energy, Oak Ridge, TN.

Pope, EC, Ellis, RP, Scolamacchia, M *et al.* (2014) European sea bass, *Dicentrarchus labrax*, in a changing ocean. Biogeosciences, **11**, 2519-2530.

Porter, JR, Xie, L, Challinor, AJ *et al.* (2014) Food security and food production systems. In: *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* (eds Field CB, Barros VR, Dokken DJ, Mach KJ, Mastrandrea MD, Bilir TE, Chatterjee M, Ebi KL, Estrada YO, Genova RC, Girma B, Kissel ES, Levy AN, Maccracken S, Mastrandrea PR, White LL) pp Page, Cambridge, United Kingdom and New York, NY, USA.

Pörtner, HO, Karl, DM, Boyd, PW *et al.* (2014) Ocean systems. In: *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* (eds Field CB, Barros VR, Dokken DJ, Mach KJ, Mastrandrea MD, Bilir TE, Chatterjee M, Ebi KL, Estrada YO, Genova RC, Girma B, Kissel ES, Levy AN, Maccracken S, Mastrandrea PR, White LL) pp Page, Cambridge, United Kingdom and New York, NY, USA.

Roggatz, CC, Lorch, M, Hardege, JD, Benoit, DM (2016) Ocean acidification affects marine chemical communication by changing structure and function of peptide signalling molecules. Global Change Biology.

Sahu, BC, Adhikari, S, Mahapatra, AS, Dey, L (2013) Carbon, nitrogen, and posphorous budget in scampi (*Macrobrachium rosenbergii*) culture ponds. Environmental Monitoring and Assessment, **185**, 10157-10166.

Saksena, DN, Gaidhane, DM, Singh, H (2006) Limnology of Kharland (saline) ponds of Ratnagiri, Maharashtra in relation to prawn culture potential. Journal of Environmental Biology, **27**, 49-53.

Schalkhausser, B, Bock, C, Stemmer, K, Brey, T, Pörtner, H-O, Lannig, G (2012) Impact of ocean acidification on escape performance of the king scallop, *Pecten maximus*, from Norway. Marine Biology, **160**, 1995-2006.

Seidelin, M, Brauner, CJ, Jensen, FB, Madsen, SS (2001) Vacuolar-Type H^+-ATPase and Na^+, K^+-ATPase expression in gills of Atlantic Salmon (*Salmo salar*) during isolated and combined exposure to hyperoxia and hypercapnia in fresh water. Zoological Science, **18**, 1199-1205.

Simpson, SD, Munday, PL, Wittenrich, ML, Manassa, R, Dixson, DL, Gagliano, M, Yan, HY (2011) Ocean acidification erodes crucial auditory behaviour in a marine fish. Biology letters, **7**, 917-920.

Small, DP, Calosi, P, Boothroyd, D, Widdicombe, S, Spicer, JI (2016) The sensitivity of the early benthic juvenile stage of the European lobster *Homarus gammarus* (L.) to elevated pCO_2 and temperature. Marine Biology, **163**, 1-12.

Talmage, SC, Gobler, CJ (2009) The effects of elevated carbon dioxide concentrations on the metamorphosis, size, and survival of larval hard clams (*Mercenaria mercenaria*), bay scallops (*Argopecten irradians*), and Eastern oysters (*Crassostrea virginica*). Limnology and Oceanography, **54**, 2072-2080.

Thompson, EL, O'Connor, W, Parker, L, Ross, P, Raftos, DA (2015) Differential proteomic responses of selectively bred and wild-type Sydney rock oyster populations exposed to elevated CO_2. Molecular Ecology, **24**, 1248-1262.

Tirsgaard, B, Moran, D, Steffensen, JF (2015) Prolonged SDA and reduced digestive efficiency under elevated CO_2 may explain reduced growth in Atlantic cod (*Gadus morhua*). Aquatic Toxicology, **158**, 171-180.

Tseng, Y-C, Hu, MY, Stumpp, M, Lin, L-Y, Melzner, F, Hwang, P-P (2013) CO_2-driven seawater acidification differentially affects development and molecular plasticity along life history of fish (*Oryzias latipes*). Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology, **165**, 119-130.

Watson, S-A, Lefevre, S, McCormick, MI, Domenici, P, Nilsson, GE, Munday, PL (2014) Marine mollusc predator-escape behaviour altered by near-future carbon dioxide levels. Proceedings of the National Academy of Sciences B, **281**, 20132377.

Wei, L, Wang, Q, Ning, X *et al.* (2015) Combined metabolome and proteome analysis of the mantle tissue from Pacific oyster *Crassostrea gigas* exposed to elevated pCO_2. Comparative Biochemistry and Physiology Part D: Genomics and Proteomics, **13**, 16-23.

Weiss, RF (1974) Carbon dioxide in water and seawater: the solubility of a non-ideal gas. Marine Chemistry, **2**, 203-215.

Welch, MJ, Watson, S-A, Welsh, JQ, McCormick, MI, Munday, PL (2014) Effects of elevated CO_2 on fish behaviour undiminished by transgenerational acclimation. Nature Climate Change, **4**, 1086-1089.

Figure 1*:* Diagrammatic representation of the levels at which elevated carbon dioxide is considered problematic within recirculating aquaculture systems (RAS) (caused by accumulation of excreted CO_2 due to high stocking densities) and under global aquatic acidification (marine and freshwater; caused by rising atmospheric CO_2). Numbered arrows, and corresponding key, indicate the levels at which CO_2 is demonstrated to have significant impacts on fish development, physiology and behaviour. The expanded view on the right side highlights CO_2 levels in relation to climate change scenarios in greater detail (0–3,000 µatm or 0–4 mg/l). Conversion of CO_2 levels between µatm and mg/l in this diagram is based on 35 psu seawater at 15°C. Fish images Kovalevska & Kazakov maksim /shutterstock.com. References corresponding to numbered arrows indicating levels of CO_2 shown to have a significant impact of fish development, physiology or behaviour; 1) Hamilton *et al.* (2014), Jutfelt and Hedgärde (2013), Simpson *et al.* (2011), Nilsson *et al.* (2012); 2) Chambers *et al.* (2014), Frommel *et al.* (2012), Frommel *et al.* (2014), Maneja *et al.* (2014), Tseng *et al.* (2013); 3) Esbaugh *et al.* (2016), Esbaugh *et al.* (2012), Heuer *et al.* (2012); 4) Pope *et al.* (2014); 5) Ou *et al.* (2015); 6) Michaelidis *et al.* (2007); 7) Tirsgaard *et al.* (2015); & 8) Seidelin *et al.* (2001).

Figure 2: Schematic representation of the conversion of 1 mg L^{-1} dissolved CO_2 concentration into partial pressure (µatm) at a range of different temperatures and salinities. This shows the very large influence of temperature in particular (up to 3.2-fold higher partial pressure at the warmest temperature compared to the coolest) but also salinity (up to 26% higher partial pressure at the highest salinity compared to freshwater) on the CO_2 partial pressure due to the impact these abiotic factors have on the solubility of CO_2 in water (Weiss, 1974, Dickson, 2011). Conversion of dissolved CO_2 in mg L^{-1} to partial pressure in µatm were undertaken using the CO2SYS program (Pierrot *et al.*, 2006), using dissociation constants from Mehrbach *et al.* (1973), refit by Dickson and Millero (1987), and KSO_4 using Dickson (1990), with values for CO_2 solubility at different temperatures and salinities checked against Weiss (1974).

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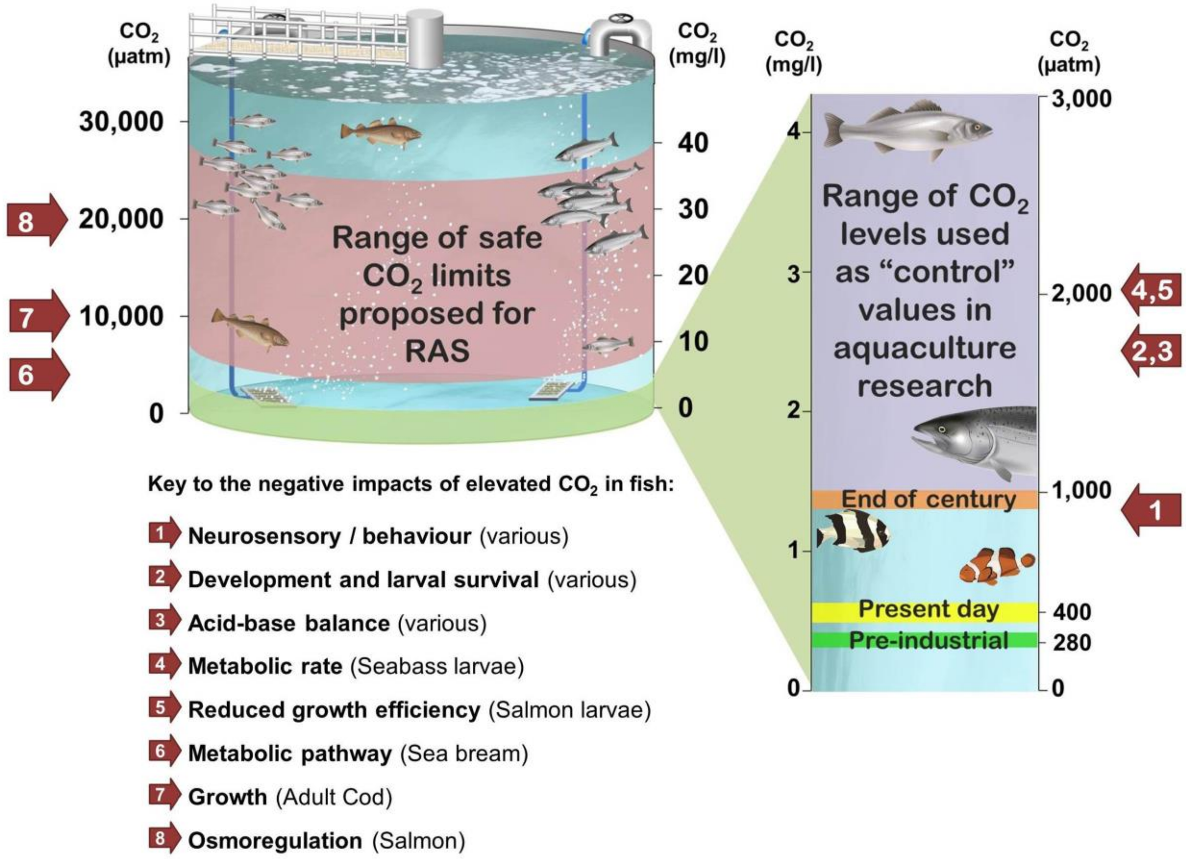
Author contributions

R.W.W. won the funding for aquaculture and aquatic acidification projects that stimulated this article and produced figure 2. R.E led the formulation of the paper and produced figure 1. M.U compiled the initial draft. All authors contributed equally to discussions, figure development, editing and production of the final manuscript.

Competing financial interests

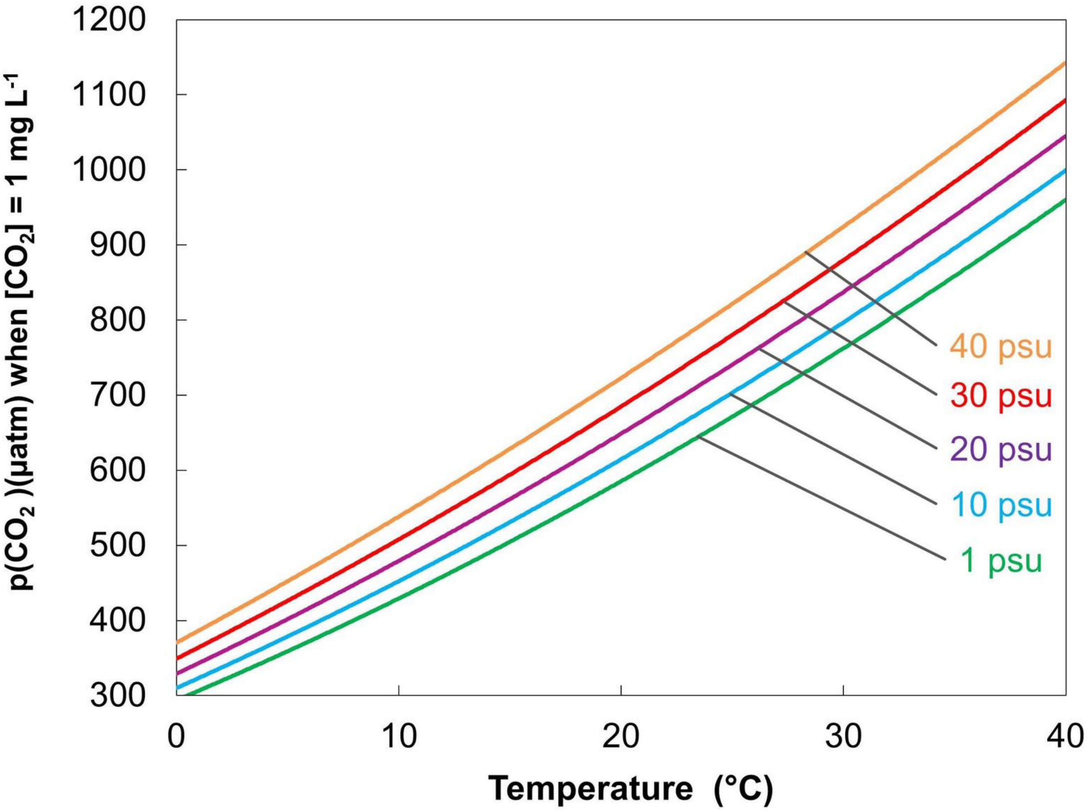
The authors declare no competing financial interests.

Figure 1



CO_2 (µatm)
30,000
20,000
10,000
0
CO_2 (mg/l)
40
30
20
10
0
8
7
6
Range of safe CO_2 limits proposed for RAS
CO_2 (mg/l)
4
3
2
1
0
CO_2 (µatm)
3,000
2,000
1,000
400
280
0
Range of CO_2 levels used as "control" values in aquaculture research
End of century
Present day
Pre-industrial
4,5
2,3
1
Key to the negative impacts of elevated CO_2 in fish:
1 Neurosensory / behaviour (various)
2 Development and larval survival (various)
3 Acid-base balance (various)
4 Metabolic rate (Seabass larvae)
5 Reduced growth efficiency (Salmon larvae)
6 Metabolic pathway (Sea bream)
7 Growth (Adult Cod)
8 Osmoregulation (Salmon)

544 Figure 2



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