REVIEWS IN Aquaculture

Reviews in Aquaculture (2016) **0**, 1–16 doi: 10.1111/raq.12140

Ocean acidification and marine aquaculture in North America: potential impacts and mitigation strategies

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Received 3 September 2015; accepted 16 December 2015.

Abstract

Shifting environmental conditions resulting from anthropogenic climate change have recently garnered much attention in the aquaculture industry; however, ocean acidification has received relatively little attention. Here, we provide an overview of ocean acidification in the context of North American aquaculture with respect to potential impacts and mitigation strategies. North American shellfish farms should make ocean acidification an immediate priority, as shellfish and other calcifying organisms are of highest concern in an increasingly acidifying ocean and negative effects have already been felt on the Pacific coast. While implications for various finfish have been documented, our current understanding of how acidification will impact North American finfish aquaculture is limited and requires more research. Although likely to benefit from increases in seawater CO_2, some seaweeds may also be at risk under more acidic conditions, particularly calcifying species, as well as non-calcifying ones residing in areas where CO_2 is not the primary driver of acidification. Strategies to mitigate and adapt to the effects of acidification exist on the regional scale and can aid in identifying areas of concern, detecting changes in seawater carbonate chemistry early enough to avoid catastrophic outcomes, and adapting to long-term shifts in oceanic pH. Ultimately, ocean acidification has already imposed negative impacts on the aquaculture industry, but can be addressed with sufficient monitoring and the establishment of regional mitigation plans.

Key words: finfish aquaculture, mitigation, ocean acidification, seaweed aquaculture, shellfish aquaculture.

Introduction

One of the fastest growing global food sectors is the aquaculture industry. In 2012, aquaculture accounted for more than 40% of the total production of finfish and invertebrates from capture fisheries and aquaculture combined, yielding 90.4 million tonnes of product and revenue upwards of USD$144 billion (FAO 2014). Furthermore, aquaculture accounts for more than 95% of global commercial seaweed production, producing 23.8 million tonnes in 2012 (USD$6.4 billion) (Chopin 2014). Although not as large as in other parts of the world, North American total aquaculture (marine and freshwater) produced 593 496 metric tonnes of food in 2012, highlighting its important role in local and global food production (FAO 2014).

Marine aquaculture in North America is mostly taking place in Canada. In 2013, Canada produced 172 097 metric tonnes of farmed seafood, valued at CAD$962.9 million (Chopin 2015a). Canada's total finfish aquaculture production in 2013 was 130 337 tonnes, valued at CAD $870.3 million, representing 75.7% of the volume and 90.4% of the value of the total Canadian aquaculture production. Farmed salmon, by far the most important finfish grown by Canadian aquaculturists, accounted for 76.7% of the volume and 72.9% of the value of finfish produced in 2013, with a production volume of 100 027 tonnes valued at CAD$634.3 million. Other finfish species currently undergoing aquaculture development or being cultivated on a smaller scale include sablefish, sturgeon, rainbow trout, steelhead trout, halibut and arctic char. Canada's total shellfish aquaculture production in 2013 was 41 760 tonnes, valued at CAD$92.5 million, with mussels accounting for 69.6% of the total Canadian shellfish production and 53.5% of its value in 2013 (29 080 tonnes valued at CAD$49.5 million). In addition, Canada produced 9509 tonnes of farmed oysters in 2013, valued at CAD$27.3 million and accounting for 29.5% of the total value of shellfish production. Other shellfish species under aquaculture development, or cultivated on a smaller scale, include Manila clams, varnish/savory clams, cockles, Japanese scallops, sea scallops, geoducks and quahaugs. With the development of the deposit-feeder component of Integrated Multi-Trophic Aquaculture (IMTA) systems for recapturing the large organic particles from the fed component (fish or shrimps), advances in the aquaculture of other invertebrates such as sea-urchins, sea-cucumbers, polychaetes and lobsters are anticipated. The seaweed aquaculture sector in North America is very small. However, IMTA offers an opportunity to reposition the value and roles seaweeds can have in integrated food production systems and in ecosystem health (ecosystem services), which should contribute to the development of the sector (Chopin *et al.* 2012). In 2013, the value of the total Canadian aquaculture output was CAD$1.114 billion, the aquaculture industry generated a total GDP of CAD$1.064 billion, and the total labour income was estimated at CAD$618 million. Consequently, the cumulative gross value of output generated was CAD $2.796 billion. The aquaculture industry created an estimated 13 070 full time equivalent (FTE) jobs (4812 directly; 5643 indirectly; 2615 being induced).

Given the large value of the aquaculture industry both socially and economically, it is important to understand the risks associated with aquaculture and how particular conditions may impact aquaculture sites and the environments surrounding them. For example, increased nutrient loading as a result of concentrated fish production may have adverse effects on benthic communities around fish farms (Findlay *et al.* 1995; Simenstad & Fresh 1995; Mazzola *et al.* 2000; Nickell *et al.* 2003), although evidence suggests that these effects likely occur on relatively small spatial scales in close proximity to a farmed site and can be negligible (Holmer *et al.* 2005). Diseases and parasites associated with farmed fish are also a concern in aquaculture, as diseased fish can often be of lesser quality and may invoke negative ecological impacts in nearby systems if they are to escape (Lafferty *et al.* 2014). Furthermore, environmental conditions within a given area must suit a species' tolerance range for optimal high-quality growth (Jobling 1988; Jobling *et al.* 1993).

Recently, shifting environmental conditions resulting from anthropogenic climate change have garnered much attention in the world of aquaculture. Climate change can impact aquaculture in a number of ways, as rapidly changing environmental conditions can yield a myriad of biological impacts (both positive and negative; Doney *et al.* 2012). For example, warming waters have been linked to an increased prevalence of diseases among marine organisms, elucidating a key challenge for aquaculture, particularly since diseases are already frequently occurring amongst farmed fish (Lafferty *et al.* 2014). Increased storm severity and other extreme weather events, as well as sea level rise, can also induce challenges for the development and sustainability of aquaculture infrastructure (Cochrane *et al.* 2009). As a result, climate change is expected to result in both physical and biological challenges for aquaculture in the near future.

Anthropogenic climate change affects marine biological processes in two primary ways: ocean warming due to an increasingly warming planet; and ocean acidification due to increasing oceanic CO_2 concentrations and a resultant shift in seawater pH and carbonate chemistry. Although climate change, in general, has received much attention in the realm of aquaculture, warming and acidification have received relatively little independent attention. However, both can independently and synergistically affect marine organisms to various degrees (Byrne 2011; Doney *et al.* 2012). As such, both warming and acidification require special attention regarding their potential impacts to aquaculture and the ways in which the industry can mitigate the relative effects of each.

Here, we provide an overview of ocean acidification in the context of North American aquaculture. The potential impacts of ocean acidification on various types of aquaculture in different regions of the continent are discussed. We also provide suggestions for potential mitigation strategies at the regional level that can help finfish and shellfish farms cope with an increasingly acidifying ocean.

What is ocean acidification?

Ocean acidification is a predictable outcome of increasing atmospheric carbon dioxide (CO_2) and the subsequent absorption of CO_2 by the oceans. Since the Industrial Revolution, atmospheric CO_2 has risen from an average of 280 ppmv to 399 ppmv in 2014 (Doney *et al.* 2009; NOAA 2014a). As atmospheric CO_2 increases, it is moderated in part by the oceans, which absorb approximately 1/3 of excess anthropogenic CO_2 (Sabine *et al.* 2004; Sabine & Feely 2007). As anthropogenic CO_2 dissolves into the oceans, the CO_2 reacts with seawater to form carbonic acid, which inevitably dissociates into two hydrogen ions (H^+) and one carbonate ion (CO_3^{2-}) (Orr *et al.* 2005). However, as more CO_2 is added to seawater, a disproportionate increase of H^+ and CO_3^{2-} results in an overall increase in the concentration of [H^+] (a reduction in pH) and a decrease in the concentration of [CO_3^{2-}], as it is transformed into bicarbonate (HCO_3^-) (Orr *et al.* 2005). Consequently, reductions in surface-ocean pH (increased H^+)

and calcium carbonate saturation state (decreased [CO_3^{2-}]) have been observed (Feely *et al.* 2004; Caldeira & Wickett 2005; Orr *et al.* 2005; Feely *et al.* 2008, 2009) (Fig. 1), with surface-ocean pH falling by approximately 0.1 units since preindustrial times and expected to drop another 0.2–0.3 units by 2100 (RCP8.5; Hoegh-Guldberg *et al.* 2014).

Coastal vs. open-ocean acidification

Recently, it has been recognized that, unlike the open ocean, coastal areas are subjected to a myriad of CO_2 sources and other sources of acid (Fig. 2). Furthermore, the pH of coastal waters is regulated by a number of processes, including the input of Ca^{2+}, carbonate alkalinity, inorganic and organic minerals (carbon and other nutrients) from surrounding watersheds, ecosystem metabolism, and the degree of mixing between coastal waters and the open ocean (Duarte *et al.* 2013). These processes can act to moderate or amplify the effects of ocean acidification in coastal regions. As a result, coastal waters, particularly estuaries, can experience more acidic and highly variable conditions in relation to the well-buffered open-ocean (Hofmann *et al.* 2011; Duarte *et al.* 2013; Waldbusser & Salisbury 2014). Furthermore, the degree of acidification (or lack thereof) in coastal waters can be highly variable on small spatial and temporal scales (Blackford & Gilbert 2007; Frieder *et al.* 2012).

On the Pacific coast of North America, coastal upwelling events bring CO_2 rich bottom waters to the surface, creating a temporary period of low pH and carbonate undersaturation (Feely *et al.* 2008). On the Atlantic coast, increased nutrient loading, primarily resulting from agricultural

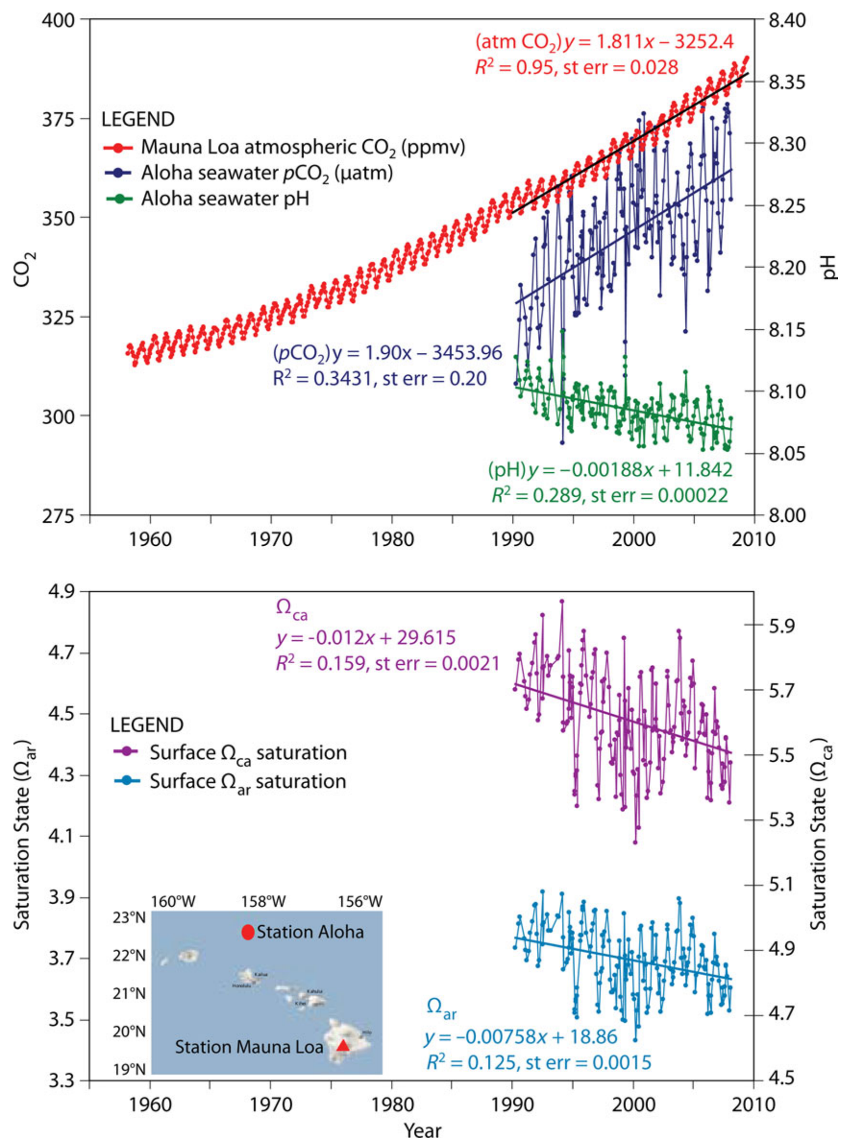

Fig. 1 TOP: Time series of atmospheric CO_2 concentration (ppmv; red) and oceanic pCO_2 (µatm; dark blue) and pH (green) in the subtropical North Pacific Ocean (Hawaii). BOTTOM: Time series of oceanic calcite (purple) and aragonite (light blue) saturation state in the subtropical North Pacific Ocean (Hawaii). Atmospheric CO_2 conditions were recorded from Station Mauna Loa and oceanic carbonate system conditions were recorded at Station Aloha (see insert map). Figure reprinted (with permission) from Feely *et al.* (2009).

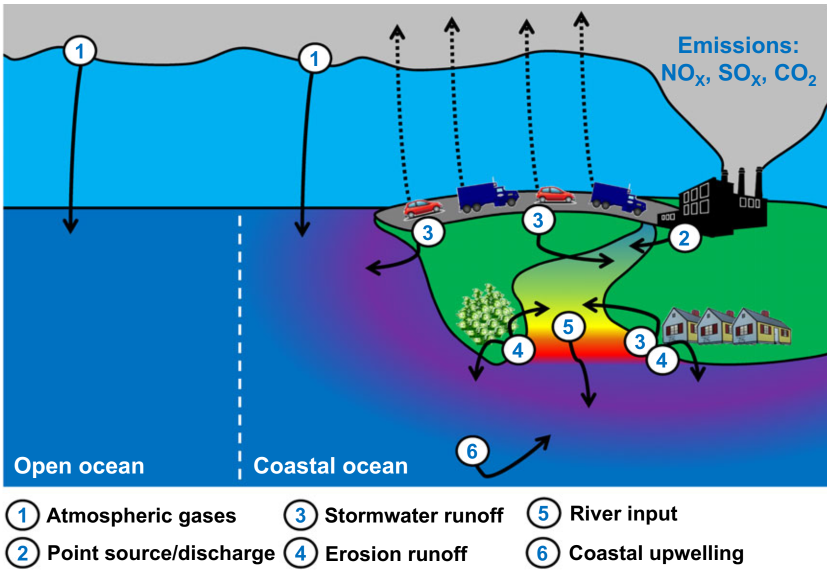

Fig. 2 Sources of seawater acidification in the open and coastal ocean. Coastal zones are exposed to a variety of acidic sources that the open ocean is not. The relative contribution of each acidification source in coastal areas will vary across time and space, often resulting in high carbonate system variability in coastal areas, while the open ocean is more stable.

runoff, drives increases in algal biomass. The subsequent microbial breakdown of the algae reduces oxygen (O_2) and increases CO_2 in coastal zones of the Atlantic (Wallace *et al.* 2014). As a result, organisms not only have to deal with more acidic conditions, but hypoxia (little or no oxygen) as well. Acidic freshwater input from rivers can also contribute to acidification in coastal zones (Salisbury *et al.* 2008), while microbial degradation of organic material in sediments can create acidic porewater conditions which infaunal organisms (e.g. clams, marine worms, amphipods, etc.) must cope with (Green *et al.* 2009, 2013; Clements & Hunt 2014).

Given the differences in acidifying sources between coastal and open-ocean waters, open-ocean aquaculture (both finfish cages and shellfish operations) is likely to be affected by acidification in different ways than coastal aquaculture. Furthermore, the high degree of variability in coastal carbonate chemistry at various spatial and temporal scales suggests that finfish and shellfish sites may be differentially affected in bays or harbours that are in close proximity to one another. Although being explored, the current understanding of pH and carbonate system variability in coastal areas is relatively poor, and an ability to accurately predict such variability into the future is lacking. Thus, understanding the current pH conditions (and associated carbonate chemistry) and the biological implications of coastal and open-ocean acidification on farmed species can help to elucidate and mitigate the impacts of ocean acidification on the aquaculture industry.

Implications for aquaculture

Unlike other consequences of global climate change (e.g. sea level rise and storm severity), ocean acidification will not result in any physical or infrastructural problems. However, the biological implications that ocean acidification can induce are highly problematic for aquaculture. Shellfish and other calcifying organisms are of highest concern under a more acidic ocean, since lower carbonate saturation state can make it more difficult for calcifying organisms to produce shells, while various implications for finfish have also been documented. Conversely, seaweeds and non-calcifying algae are expected to thrive in a CO_2 rich ocean. While some coastal areas in North America (e.g. upwelling zones) already experience temporary periods of low pH and still have relatively good production levels, the biological impacts of chronic exposure to high CO_2 conditions and the associated changes to the carbonate system for cultured species in North America are unknown. Furthermore, acute effects that have already been observed appear to be species specific, elucidating the need to understand the impacts of acute and chronic acidification on the variety of aquacultured species in North America and at various life stages (in particular, larval and juvenile stages). Below, specific problems for cultured species and examples of how ocean acidification is already inducing such problems are discussed.

Shellfish aquaculture

Shellfish have been harvested by humans for millennia. While the Romans farmed oysters in Italy during the first century BC and farming mussels is suggested to have started in the 13th century, clam and scallop cultivation are more recent, arriving only in the last few centuries from Asian nations such as China and Japan (Gosling 2003). Today, shellfish fisheries and aquaculture have been rapidly growing. Furthermore, shellfish aquaculture now provides more than 80% of total shellfish production globally, with >95% of global oyster production coming from aquaculture (FAO 2008). While oysters sit at the top of shellfish in terms of economic value in North America (FAO 2008), clams and mussels are also of great economic importance. For example, soft-shell clams (*Mya arenaria*) are harvested commercially in Maine and other eastern seaboard states, while recreational fisheries exist in both the United States and Canada. Mussels are mostly cultivated in eastern North America as well (*Mytilus edulis*), and to a lesser extent on the west coast (*Mytilus galloprovincialis*) (Canadian Aquaculture Industry Alliance 2015; Chopin 2015a).

Shellfish are considered among the most vulnerable organisms in a more acidic ocean due to their reliance on a calcium carbonate ($CaCO_3$) shell. As the oceans become increasingly acidic, the process of calcification becomes more difficult for marine molluscs and other calcifiers (Orr *et al.* 2005; Hofmann *et al.* 2010; Gazeau *et al.* 2013; Waldbusser *et al.* 2013). Consequently, for many species, shell growth and shell integrity may be compromised under more acidic conditions, leading to higher levels of mortality under current coastal pH conditions (Barton *et al.* 2012; Green *et al.* 2013) and increased vulnerability to diseases and parasites at pH levels predicted for the end of this century (although temperature appears to be more important in controlling disease and parasites; Dorfmeier 2012; McKenzie *et al.* 2014). It has been suggested that calcifying organisms may be able to compensate for low pH and environmental carbonate undersaturation by upregulating calcification internally and maintaining calcium carbonate structures (Wood *et al.* 2008; Gazeau *et al.* 2013). However, this upregulation of calcification is likely to come at the expense of other physiological functions such as metabolism, respiration, somatic growth, tissue condition, excretion, reproduction and immune response (Gazeau *et al.* 2013), and is thought to be a function of calcium carbonate kinetics, energy supply, and life-history characteristics of organisms rather than shell mineralogy and external calcium carbonate thermodynamics (Waldbusser *et al.* 2013).

With respect to cultured species in North America, the impacts of ocean acidification on oysters are among the most studied. In particular, the effects of acidification on the Pacific oyster (*Crassostrea gigas*) have been well documented. Barton *et al.* (2012, 2015) reported negative effects of naturally low pH seawater on hatchery reared *C. gigas* larvae, citing poor shell integrity (hindered calcification) from drastic decreases in seawater saturation state (driven by coastal upwelling) as the cause of severe loss of production at the Whiskey Creek Shellfish Hatchery on the Oregon coast. Negative impacts of near-future (2100) ocean acidification levels to *C. gigas* calcification have also been reported by Gazeau *et al.* (2007), while eastern oyster (*Crassostrea virginica*) calcification has also been reported to be hindered under more acidic conditions expected for 2050 and 2100 (Whitman-Miller *et al.* 2009). More specifically, the availability of carbonate ions (CO_3^{2-}) has been reported to drive negative impacts in the embryonic development of *C. gigas* (pH and saturation state had no impact) (Gazeau *et al.* 2011). Protein expression (Dineshram *et al.* 2012) and metabolism (Lannig *et al.* 2010) in *C. gigas* can also be depressed under more acidic conditions, although the former was tested in conditions beyond those expected by the end of the century (pH 7.5).

Commercially important clams and mussels can also be impacted by acidification. In blue mussels (*Mytilus edulis*), negative impacts to calcification have been reported under elevated seawater CO_2 expected by 2100 (Gazeau *et al.* 2007), while Beesley *et al.* (2008) suggested that near-future ocean acidification can affect the overall health of *M. edulis*. Immune response (Bibby *et al.* 2008) and embryonic growth (Gazeau *et al.* 2010) in *M. edulis* appear affected by elevated CO_2, albeit at conditions beyond end of century projections, while metabolism (Thomsen & Melzner 2010) and tissue condition (Beesley *et al.* 2008) appear unaffected. Scallops also elicited decreased but variable responses in net calcification to elevated CO_2 conditions predicted for 2050, 2100, and beyond end-of-century predictions (Ries *et al.* 2009), although they are less well studied than other commercially viable shellfish species. The calcification of commercially important clam species can also be reduced under more acidified conditions. Green *et al.* (2009) reported higher shell dissolution rates in settling hard clams (*Mercenaria mercenaria*) under more acidified sediment porewater conditions already experienced by these clams in coastal Maine mudflats. However, these clams may be able to avoid such acidic conditions by refusing to burrow into more acidified sediments and moving elsewhere, as Green *et al.* (2013) reported that settling *M. mercenaria* were less likely to burrow into sediments undersaturated with respect to aragonite (a calcium carbonate mineral). Furthermore, Clements and Hunt (2014) reported a similar pattern in juvenile soft-shell clam (*Mya arenaria*) burrowing, along with subsequent increases in clam dispersal away from more acidic sediments under conditions already experienced by these clams. Although beneficial in avoiding shell dissolution (Green *et al.* 2009), failing to immediately burrow into sediment puts these clams at risk of other mortality factors such as predation, erosion, and burial (Hunt & Scheibling 1997).

Although most of the abovementioned effects of ocean acidification on cultured shellfish are derived from laboratory experiments, the effects of ocean acidification are already being felt by the aquaculture industry. In 2006, the Whiskey Creek Shellfish Hatchery in Oregon suffered catastrophic loss of oyster larvae, leading to drastically reduced production between 2006 and 2008. This loss of larvae was later attributed to extremely low carbonate saturation conditions in the seawater of Netart's Bay, where the hatchery obtained seawater to raise the larvae. Similar die-offs have recently been reported for shellfish hatcheries in other areas of the Pacific coast as well, including Washington State, USA (Taylor Shellfish, Quilcene; water from Hood Canal) and British Columbia, Canada (Island Scallops, Nanaimo; water from Qualicum Bay), and have been attributed primarily to more acidified waters resulting from coastal upwelling (Barton *et al.* 2012). Furthermore, while many of the responses of commercially viable marine calcifiers highlighted above were observed at experimental conditions beyond end-of-century projections, pH and carbonate chemistry in coastal areas can already temporarily reach conditions beyond those projections. If such conditions are sustained or amplified as a result of future ocean acidification, the effects noted above at conditions beyond near-future projections may be felt naturally in coastal regions.

Finfish aquaculture

Finfish aquaculture is an important source of food and income for many regions of North America. Although freshwater species are of high economic value, they are raised under freshwater conditions (which are already acidic) and are not discussed here. While freshwater species dominate the aquaculture market in the United States, the largest marine species contributing to North American aquaculture (primarily farmed in Canada) is Atlantic salmon (*Salmo salar*) (Olin 2001, 2011).

The impacts of ocean acidification on finfish species are less well known than those on shellfish. Although they are shell-less, fish contain calcified otoliths (organs for balance and orientation), which can be impacted by ocean acidification. In general, studies have reported that the morphometry of otoliths in various fish can be altered under more acidified conditions (increased size; Checkley *et al.* 2009; Munday *et al.* 2011; Bignami *et al.* 2013), while others report no changes (Munday *et al.* 2011). The behaviour of marine fish under more acidified conditions has been well studied, with numerous teleost and elasmobranch behaviours being impacted under conditions expected by the end of this century (Clements & Hunt 2015). In addition, fish may experience impaired growth and development (Franke & Clemmesen 2011; Frommel *et al.* 2014), tissue damage (Frommel *et al.* 2012), hindered respiration and aerobic performance (Munday *et al.* 2009), and decreased RNA viability (Franke & Clemmesen 2011) under more acidified conditions, with coastal upwelling scenarios (extreme conditions of low pH and high CO_2) inducing stronger and more negative responses than end-of-century scenarios. However, the magnitude and direction in which acidification induces these changes appears species specific and requires more research.

Although the effects of acidification on pelagic fish are beginning to garner more attention, the effects on farmed fish in North America are virtually unexplored. Of those studies assessing the impacts of acidification on fish, only one has addressed the potential impacts to Atlantic salmon (*Salmo salar*), suggesting no impact of near-future acidification levels on survival (Fivelstad *et al.* 1999). Although these salmon can deal with low pH conditions during their upstream spawning migrations, permanent changes to oceanic pH may induce physiological changes during their time at sea. Furthermore, farmed salmon are typically raised in marine coastal waters, where the biological effects of ocean acidification can be amplified (Duarte *et al.* 2013; Waldbusser & Salisbury 2014). Franke and Clemmesen (2011) reported that acidification conditions beyond 2100 projections did not affect embryonic development in *Clupea harengus*, although RNA concentrations were diminished, potentially leading to reductions in protein synthesis. Furthermore, *C. harengus* embryonic metabolism was negatively impacted under elevated CO_2 (beyond 2100 projections), potentially reducing somatic growth and survivorship in areas of extremely high CO_2 (and low pH) conditions (e.g. areas of coastal upwelling; Franke & Clemmesen 2011). Under near-future and coastal upwelling scenarios, Frommel *et al.* (2014) also reported impaired growth, development and condition in *C. harengus* larvae, along with tissue damage to various organs, while Frommel *et al.* (2012) reported severe tissue damage in Atlantic cod (*Gadus morhua*) larvae under similar conditions, with coastal upwelling scenarios (more extreme conditions) eliciting stronger biological impacts. Additionally, Frommel *et al.* (2013) reported high tolerance for growth and developmental effects in Atlantic cod eggs and larvae.

One thing that remains clear is that there is a severe lack of knowledge pertaining to the most valued finfish species in North American aquaculture. Given that growth and development, RNA viability, aerobic performance, and tissue condition can all be negatively impacted by ocean acidification in the early life stages of economically important species, the quality of farmed fish becomes a concern for species raised in coastal bays and estuaries. Furthermore, farmed fish may be more vulnerable to the effects of acidification given that they are raised in large numbers and confined spaces. However, the critical knowledge gap regarding the ways in which acidification will impact farmed finfish prevents any conclusive remarks. Hence, more work is needed to elucidate the ways in which farmed finfish species in North America will be affected by ocean acidification and to determine ways of potentially mitigating any potential impacts, particularly under more realistic near-future (end-of-century) conditions.

Seaweed aquaculture

Seaweed aquaculture is often overlooked in the western world, despite the fact that seaweeds constitute the largest group of organisms cultured at sea since 2004 (Chopin 2014). In 2012, seaweeds represented 49.1% of the world mariculture production (23.8 million tonnes valued at USD$6.4 billion) and were the first group of organisms to pass the 50% farmed/wild harvest threshold in 1971. In 2012, 95.6% of the world seaweed supply came from aquaculture, and only 4.4% was harvested from wild beds. Unfortunately, these data are mostly unknown in the western world, most probably because 96.3% of seaweed aquaculture is concentrated in six Asian countries: China, Indonesia, the Philippines, the Republic of Korea, Japan and Malaysia.

It is therefore important to understand the implications of ocean acidification on seaweeds. The meta-analysis of Kroeker *et al.* (2010) revealed negative yet variable effects of ocean acidification on different groups of marine organisms: interestingly, calcifying macro-algae were found to be more susceptible to the effects of ocean acidification than corals, coccolithophorids, molluscs, echinoderms, crustaceans, fish, fleshy macro-algae and seagrasses. However, unlike many animals, algae do not require $CaCO_3$ or related salts for skeletal support. In fact, $CaCO_3$ deposits may often be a liability rather than an asset (nutrient uptake inhibition and light penetration reduction limiting both photosynthesis and growth). The main advantage of calcification for algae is an anti-grazing strategy.

While there is still a limited database on the effects of ocean acidification on seaweeds and generalization is difficult because of species-specificity, it is likely that a significant fraction of fleshy macro-algae - brown algae, red algae (especially those living in low-light environments), as well as a few green algae (most of the seaweeds being presently cultivated) - will be more competitive in increased CO_2 environments (Palacios & Zimmerman 2007; Martin *et al.* 2008; Vizzini *et al.* 2010; Fabricius *et al.* 2011; Hepburn *et al.* 2011). In contrast, calcified seaweeds (like crustose corallines) will likely be less competitive, since the maintenance of supersaturated conditions at the site of precipitation for the crystalline form of $CaCO_3$ will be more difficult in lower-CO_3^{2-} seawater. Furthermore, the $CaCO_3$ already precipitated will be subject to dissolution and some species may experience reduced survival (Johnson *et al.* 2014).

Fleshy seaweeds may still experience negative impacts as a result of increasing acidification as well. For example, in coastal areas where CO_2 may not be the primary driver of low pH conditions, meiospore germination in kelps can be hindered, although increasing CO_2 conditions can ameliorate the effect of low pH from other sources (Roleda *et al.* 2012). The concentration of phenolic substances in seagrasses and aquatic plants can also be reduced in some species under lower pH conditions (*Cymodocea nodosa* at pH 7.3; *Ruppia maritima* and *Potamogeton perfoliatus* at pH 6.9; Arnold *et al.* 2012), while in terrestrial plants these substances can often accumulate (Coley *et al.* 2002; Bidart-Bouzat & Imeh-Nathaniel 2008; Lindroth 2010). Under near-future conditions, an increase in the cover of non-calcifying species with increasing pCO_2 at the expense of calcifying species was reported in a mesocosm experiment by Hofmann *et al.* (2012), and potential shifts in algal communities have also been reported for a natural kelp forest community in southern New Zealand, although such responses to elevated CO_2 will be influenced by light and energetic constraints on photosynthesis (Hepburn *et al.* 2011). In addition, Connell and Russell (2010) reported an increased potential for phase shifts in kelp forest from kelp- to turf-dominated communities under near-future conditions.

Seaweeds that utilize calcification to carry out biological functions (e.g. anti-grazing) may also be at risk, given that calcification is likely to be impeded under future acidification scenarios. Crustose coralline algae (CCA) are particularly at risk. These are important marine calcifiers (especially on coral reefs in tropical regions where a significant proportion of seaweed aquaculture is taking place) that consolidate reef platforms and facilitate the settlement of larvae; they create habitats, promote diversity, and are important in biogeochemical cycling and carbon sequestration (Ordonez *et al.* 2014). Ocean acidification could lead to species shifts from thick- to thin-crusted species, which may make them unable to cement reefs enough to withstand high disturbance events, which would have significant implications for tropical seaweed aquaculture often conducted in lagoon-sheltered sites protected by reef barriers. Hence, the impacts of ocean acidification will be more on habitat structuring calcifying seaweeds than on aquacultured seaweeds per se, which are often fleshy species.

It should be noted that experiments that have assessed acclimation of macro-algae under different pCO_2 conditions could not, of course, integrate the element of evolutionary adaptations to these conditions by organisms after several generations of acclimation. There will, therefore, always be uncertainty in the conclusions reached. Hall-Spencer *et al.* (2008) attempted to determine how a decrease in pH would affect coralline algae growing near a marine CO_2 vent in the Mediterranean Sea on a more evolutionary scale where genotypic adaptation could occur. They found some corallines growing at a pH of 7.6, well below the pH expected in 2100, and showed that some corallines have already adapted to a large pH decrease of 1.5 units. This field observation emphasized the importance of assessing genotypic adaptation rather than phenotypic acclimation. Moreover, some tropical species appear to have limited scope for acclimation compared with temperate counterparts, presumably due to reduced environmental variability (Harley *et al.* 2012).

One should also consider that interactions between temperature, water stratification and seawater chemistry are likely to make things more complicated. Deeper-growing seaweeds will be exposed to higher nutrient concentrations than intertidal ones. In addition, nutrient concentrations are known to affect the expression of carbon concentrating mechanisms (CCMs) in algae. Seaweeds lacking CCMs are more likely to be C-limited and thus more likely to benefit from increased CO_2 (Harley *et al.* 2012). Modelling photosynthetic rates, Kübler and Dudgeon (2015) concluded that ocean acidification will lead to increased photosynthetic rates in algae using CO_2 as their inorganic carbon source. The magnitude of the benefit will be largest at warmer temperature, greater photon flux densities and high flow (thin boundary layer) conditions. However, ocean acidification is unlikely to increase total productivity of algae lacking CCMs in their current habitats, but may allow for range expansions into brighter habitats. The largest effects will be during warming summers and in shallow and well-mixed waters.

Ecosystem responses will also be difficult to decipher (Harley *et al.* 2012). Herbivores are key structuring agents in algal communities and can devastate some algal crops. However, complex scenarios under climate change projections yield much uncertainty regarding the ways in which whole ecosystems will respond. For example, will increasing temperatures reduce herbivore defenses in seaweeds and increase some herbivore populations, or will elevated CO_2 increase the carbon:nitrogen ratio in algal tissues and reduce their palatability, all the while decreasing populations of heavily calcified and efficient herbivores such as sea-urchins? Furthermore, it is still unclear as to how such changes in multiple factors will interact to elicit ecosystem-wide impacts. There will most certainly be changes in productivity, diversity and resilience of the different components of the ecosystem, but predicting these changes remains difficult.

Understanding impacts in the context of co-occurring environmental changes

Most studies assessing the biological impacts of ocean acidification have employed controlled laboratory studies that are typically defined by "best practice guides" (Dickson *et al.* 2007; Riebesell *et al.* 2010) and, until recently, assessed the effects of acidification in isolation. Consequently, accurately determining realistic effects of ocean acidification proves difficult, given that shifting pH conditions do not occur in isolation (they occur along with other environmental changes; Breitburg *et al.* 2015) and are not static, particularly in coastal zones. For example, ocean warming can interact with declining pH to exacerbate or amplify the biological effects of acidification alone (Byrne 2011; Kroeker *et al.* 2013), while nutrition and source population can also impact the magnitude of organismal response to acidification (Kroeker *et al.* 2013). Furthermore, how organisms will respond to acidification in highly variable environments also poses a challenge in accurately predicting the impacts of ocean acidification. Given that variability can modulate the amount of time that an animal spends above or below a threshold of effect (either positive or negative), variability can also act to lessen or worsen the impacts of acidification (Shaw *et al.* 2013). Although such conditions are highly pronounced in the coastal zone and can act to alleviate or amplify the effects of ocean acidification (Waldbusser & Salisbury 2014), the open-ocean is more buffered against changes in pH than these areas (Duarte *et al.* 2013). It is thus likely that open-ocean aquaculture will be more resilient to ocean acidification than coastal aquaculture. However, it is crucial to enhance our understanding of how cultured species will react to synergistic changes in multiple environmental factors and associated changes in their variability in order to accurately determine the impacts of ocean acidification on marine aquaculture.

Mitigation

Although ocean acidification is a global issue, it is one that is difficult to address on a global scale. The processes contributing to ocean acidification in coastal areas are much broader than atmospheric CO_2 alone. Furthermore, the complex processes occurring in coastal areas result in an immense degree of variability on different spatial and temporal scales. As such, coastal acidification will occur at different magnitudes within coastal areas depending on the regional processes contributing to acidification (Duarte *et al.* 2013; Waldbusser & Salisbury 2014). Given that marine aquaculture takes place primarily in coastal areas, it is thus necessary to address ocean acidification in the context of aquaculture on a regional, site-by-site scale. Below, potential mitigation strategies are discussed, which can help the aquaculture industry reduce the impacts of an acidifying ocean. While some of these strategies have already been implemented (for example, some shellfish hatcheries in Washington State, USA, have begun buffering their seawater during production and others have relocated a subset of their operations to more optimal areas), other strategies appear viable and beneficial, although more work is needed to gain a better understanding of their viability and efficacy.

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Monitoring and early detection

Arguably the first and most important step in mitigating the effects of ocean acidification is to implement adequate monitoring. Although various monitoring programs are in effect (particularly on the Pacific coast; NOAA 2014b), the small-scale spatial variability in carbonate chemistry within coastal areas requires more monitoring to accurately model, predict, and ultimately prevent the negative implications of acidification at aquaculture sites (e.g. loss of production, increased prevalence of disease, lower quality product). Aquaculture industries should, thus, undoubtedly begin monitoring pH and carbonate chemistry at their sites.

Increased monitoring is easier said than done, however. For example, although specialized instruments have been developed to monitor ocean chemistry and the physico-chemical impacts of ocean acidification (Hardman-Mountford *et al.* 2008; Moore *et al.* 2009; Hofmann *et al.* 2011; Burke-O-Lator 3000 (see Barton *et al.* 2015)), these instruments need to be calibrated consistently and matched to manual measures of ocean chemistry to ensure their accuracy, creating much work for fish and shellfish farmers to embrace alone. As such, it is critical that the aquaculture industry and the scientific community work closely together to implement adequate monitoring programs across North America.

Although more monitoring is required and ways of efficiently implementing small-scale monitoring are needed, there are examples of such programs generating positive results. A great example of such a partnership is the IOOS Pacific Regional Ocean Acidification Data Portal, where monitoring programs at various hatcheries on the Pacific coast have been implemented through collaboration between NOAA (and other scientific partners) and various shellfish farms/hatcheries. As a result of this partnership, hatcheries have been able to buffer the seawater (with respect to pH and carbonate chemistry) that they use in their hatcheries and avoid instances of annual production loss as they had in the past (Barton *et al.* 2012, 2015). Furthermore, real-time pH data at various hatcheries is now publicly available for all fish farmers to use in an attempt to prevent more acidification-driven shellfishery crashes from occurring on the Pacific coast. Although volunteer pH monitoring in Maine has been motivated by increasingly unproductive clam flats (Reid 2015), direct aquaculture-science partnerships are lacking along the Atlantic coast. Furthermore, the United States is far ahead of Canada when it comes to ocean acidification knowledge, awareness, and monitoring. Ultimately, small-scale monitoring programs are necessary to understand the current trends in coastal seawater chemistry around aquaculture sites and to detect harmful conditions before they impose detrimental impacts on aquaculture farms across North America. Furthermore, the open sharing of monitoring data can help facilitate awareness and preparedness of aquaculture managers and stakeholders in the wake of ocean acidification effects. These programs are most needed on the Atlantic coast and in Canada.

Site-specific buffering

One strategy for dealing with more acidic seawater in aquaculture is to buffer the seawater pH and carbonate chemistry. For example, adding sodium bicarbonate or other basic compounds to seawater can enhance pH conditions and potentially mitigate the impacts of acidification. Adding natural buffers to an environment can also enhance carbonate chemistry. For example, adding crushed shell hash to sediments in clam flats can enhance pore water pH and carbonate geochemical conditions within the sediment (Green *et al.* 2009) .

Such buffering has been reported to have positive results for shellfish operations on the Pacific coast. After devastating losses of production occurred at the Whiskey Creek Shellfish Hatchery and more acidic waters were isolated as the primary cause, the hatchery started using chemical buffers to enhance the carbonate chemical conditions of the water in their tanks, which prevented further losses even when seawater pH in Netart's Bay (source of hatchery's seawater) remained low (Barton *et al.* 2012, 2015). Additionally, on the Atlantic coast, buffering mudflat sediment with crushed shell hash can enhance the pH and carbonate geochemical conditions within sediment pore water and has been reported to increase clam settlement and survival in comparison to unbuffered sediments (Green *et al.* 2009, 2013).

Site selection

Selecting optimal sites for aquaculture activities is an important aspect for insuring the success of a fish farm or hatchery. Given the strong degree of spatial variability in coastal pH and carbonate chemistry, coupled with the likely increase in such variability as ocean acidification and climate change worsen (Easterling *et al.* 2007; Hoegh-Guldberg *et al.* 2014), site selection will be a key component in mitigating the impacts of acidification. For example, seawater near river mouths is known to be much more acidic than seawater further away from rivers (Salisbury *et al.* 2008), so choosing sites away from river mouths can lessen the impact of low pH. Likewise, avoiding areas where large-scale agricultural activities are prominent can reduce the risk of acidification-driven impacts to aquaculture sites, given that intense agriculture tends to lead to more acidic coastal waters resulting from increased terrestrial runoff and nutrient loading (White *et al.* 1997). However, it is important to note that selecting an optimal site at a particular time period may not be sufficient for mitigating the effects of ocean acidifciation beyond that time period, as conditions in a given area will likely change (either positively or negatively) over time. Thus, choosing sites with well predicted future conditions can help establish successful, long-term aquaculture activities in a given area with minimal concern for negative effects. Ultimately, understanding the current pH and carbonate conditions in a given coastal area, along with an area's susceptibility to future acidification, can play a key role in mitigating acidification in aquaculture. Frequent monitoring of pH and carbonate chemistry, as well as other environmental parameters (e.g. temperature, salinity, oxygen, eutrophication, etc.), at current and potential aquaculture sites is thus necessary to elucidate optimal areas for aquaculture activities, once again highlighting the need for more industry-science partnerships.

Selective breeding

Selective breeding – breeding plants and animals for specific traits – is a technique that is often used in terrestrial farming and aquaculture to optimize production. Although aquaculture generally lags behind terrestrial farming in terms of selective breeding (Gjedrem *et al.* 2012), aquaculture species have been bred to increase productivity and disease resistance. For example, selective breeding of Pacific white shrimp (*Litopenaeus vannamei*) in the United States was observed to enhance growth and resistance to Taura Syndrome Virus (TSV), although negative correlations between growth and TSV suggested that selection for multiple traits may be difficult (Argue *et al.* 2002).

Alongside elevated growth and disease resistance, selective breeding can also be used as an adaptive tool against climate change and ocean acidification in aquaculture. For example, Parker *et al.* (2011) demonstrated that selective breeding significantly reduced the magnitude of effect that ocean acidification induced on Sydney rock oyster (*Saccostrea glomerata*) shell growth, as selectively bred populations elicited only a 25% reduction in shell growth under more acidic conditions, while wild populations suffered a 64% reduction. Similarly, adult exposure to more acidic conditions can help to alleviate impacts to offspring in shellfish (Parker *et al.* 2012) and finfish (Miller *et al.* 2012; Allan *et al.* 2014). For some organisms, however, adult exposure to acidification may have no impact on offspring responses (Welch *et al.* 2014), can reverse positive adult-generation effects in offspring (that is, positive effects of acidification observed in parents are reversed in offspring) (Schade *et al.* 2014), or, in some instances, can amplify the negative effects of acidification on subsequent generations (although acclimation time appears important in modulating the biological responses for both parents and offspring) (Dupont *et al.* 2013). Unfortunately, our current understanding of how selective breeding and transgenerational acclimation can serve aquaculture with respect to mitigating the effects of ocean acidification are limited and require further investigation before strategies are implemented.

Nutritional enhancement

It has become increasingly recognized that increased food availability can modulate the biological impacts of ocean acidification to varying degrees (Kroeker *et al.* 2013). For example, Melzner *et al.* (2011) reported that increased food availability reduced the impact of elevated pCO_2 on shell growth (length) and internal (nacreous) shell dissolution in blue mussels (*Mytilus edulis*). Additionally, Thomsen *et al.* (2013) found that increased food availability completely alleviated the effects of acidification on *M. edulis* shell growth in both the laboratory and field.

Although relying on environments to naturally contain enough food for organisms to modulate the negative impacts of acidification is not sufficient, increasing the amount of food and/or enhancing food quality may help to alleviate the impacts of ocean acidification in cultured populations of various finfish and shellfish. Increasing food availability may work in land-based aquaculture, but may be difficult to implement in open-water aquaculture, as negative impacts to the benthos and surrounding areas may increase. Furthermore, it is important to note that ocean acidification may directly impact the amount and quality of food available in an area (Rossol *et al.* 2012). However, if food supply and/or quality is sufficient enough to allow an adequate amount of energy to be allocated into modulating the effects of ocean acidification, many species will likely be able to overcome the negative effects that ocean acidification will induce (Melzner *et al.* 2011; Pan *et al.* 2015).

Integrated multi-trophic aquaculture

Integrated multi-trophic aquaculture (IMTA) is a method of aquaculture whereby species from various trophic levels and serving complementary ecosystem functions are incorporated into a single farm or area, allowing the wastes and by-products of one species to be utilized by one or a number of other species (Chopin 2013). IMTA is typically comprised of four components: fed aquaculture (e.g. finfish or shrimps), small organic particle suspension extractive aquaculture (e.g. shellfish), dissolved inorganic nutrient suspension extractive aquaculture (e.g. seaweeds and aquatic plants), and large organic particle deposit extractive aquaculture (other invertebrates), with the goal of having each group of organisms enhance both the eco-

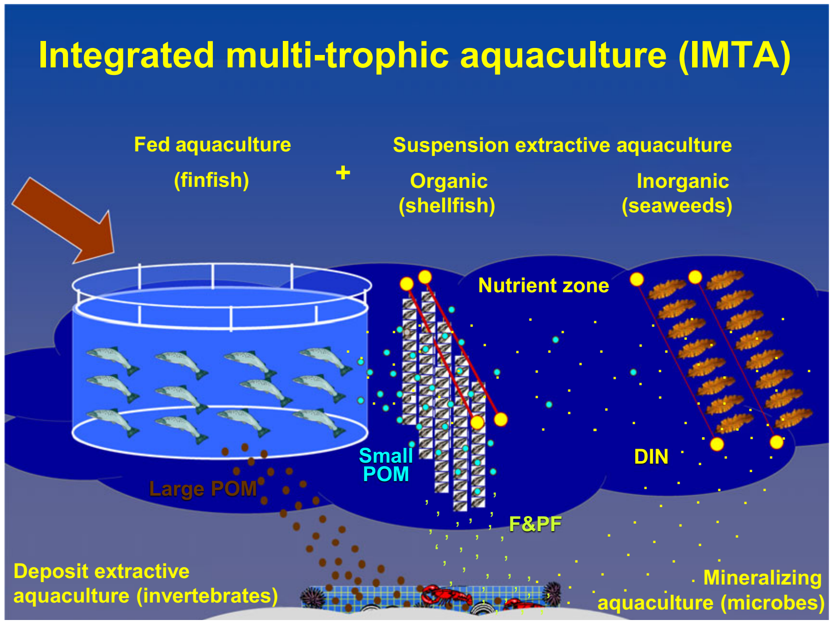

Fig. 3 A simplified schematic of an IMTA-based aquaculture operation. Finfish are fed and their wastes are consumed by organic (mussels, oysters, scallops, etc.) and inorganic (seaweeds) suspension feeders, as well as organic deposit feeders (sea urchins, sea cucumbers, decapods, polychaetes, etc.). Large particulate organic matter (POM) is consumed by organic deposit feeders located under or very close to the finfish cages, while small POM is consumed by organic suspension feeders cultivated in proximity to the finfish cages. Dissolved inorganic nutrients (DIN) are captured by the inorganic suspension feeders, which are cultivated more downstream. Faeces and pseudo-faeces (F&PF) from the organic suspension feeders are consumed by the organic deposit feeders. More DIN, from bioturbation and microbial mineralization on the bottom, are consumed by the seaweeds.

logical and economic status of a fish farm or an area (Chopin 2013; Fig. 3). While IMTA approaches are still being refined (for example, the role of the fifth group of organisms, the microbial mineralizing component), it has been developed in eastern and western Canada with promising ecological, economic and societal results (Chopin 2015b).

Although the ecological and economic benefits of IMTA have been highlighted, its applications to mitigating the impacts of oceanic climate change have yet to be understood. Theoretically, IMTA could contribute to mitigating ocean acidification in two primary ways: 1) CO_2 buffering and 2) ecosystem resilience. A key component of IMTA is seaweeds (Chopin 2014, 2015b). Seaweeds will not only be affected by climate change and ocean acidification, but they can also be part of the solution – maybe not when considering large-scale ocean acidification impacts, but certainly at a local scale. Being photosynthetic, seaweeds are the only aquaculture component with a net production of oxygen, hence reducing coastal hypoxia. While photosynthesizing, seaweeds also absorb carbon dioxide and, hence, participate in carbon sequestration, even if in a transitory manner. As such, by sequestering carbon dioxide dissolved in seawater, seaweeds could play a significant role in reducing ocean acidification and its biological effects. For example, on a local scale, when pH was observed to increase from 7.9 to 8.9 in a tropical seagrass meadow due to rapid photosynthesis, calcification rates of *Hydrolithon* sp. increased several fold (Semesi *et al.* 2009). Furthermore, changes in pH and thus CO_2 availability are most pronounced in intertidal tide pools where pH can increase as a consequence of photosynthetic activity, or drop when respiration prevails. Confined tide pools with a high level of seaweed biomass will see their pH rising easily to values > 10 over a 12 h period (Chopin, pers. obs.). Translated to a shellfish hatchery situation, the development of an IMTA system, in which in-coming seawater would go first through tanks filled with photosynthesizing seaweeds before being moved to shellfish tanks, can buffer low pH seawater and act as an alternative to chemical buffering. Furthermore, this use of seaweeds can provide an additional crop for farms to sell, ultimately increasing revenue. In fact, ocean acidification can even benefit some species (Palacios & Zimmerman 2007; Martin *et al.* 2008; Vizzini *et al.* 2010; Fabricius *et al.* 2011; Hepburn *et al.* 2011), but may negatively affect growth and biomass (but not nutritional quality) in other species (Gutow *et al.* 2014). While it is important to note that the contribution of seaweeds after their use will determine their mitigation capacity relative to their contribution to global carbon cycling (and thus to ocean acidification), as is the case for any adaptation/mitigation strategy, it is likely that seaweeds, at least when photosynthesizing, will buffer seawater and optimize the production of other species. However, it is important to understand just how much seaweed biomass would be necessary to biologically buffer seawater pH at an aquaculture farm, or hatchery, of a given size to dependably predict the mitigating potential of seaweeds.

In addition to buffering seawater pH with seaweeds, IMTA also increases biodiversity at aquaculture sites. Given that increased biodiversity can enhance the resilience of marine ecosystems and communities to stressors (Peterson *et al.* 1998; Worm *et al.* 2006; Levin & Lubchenco 2008), the ecological and economic resilience of IMTA sites to the effects of ocean acidification may be higher than that at farmed sites employing only a single species. Thus, the role of IMTA in mitigating the impacts of future ocean acidification at aquaculture sites and in shellfish hatcheries deserves attention. It remains unclear, however, as to how much diversity would be needed to increase resiliency to stressors such as ocean acidification at an IMTA site or area. For example, having only a single species in each component of an IMTA site may not be sufficient to increase system resiliency, while having a number of co-cultured species in each component may provide sufficient biodiversity to add resiliency to these sites. Thus, further work is needed to determine just how much diversity would be required at an IMTA site, or coastal management area with IMTA activities, to increase resiliency in order to fully understand the viability of this mitigation approach.

Ultimately, the bio-buffering services of seaweeds, coupled with the potential for increased ecosystem resilience and economic diversification may make IMTA a formidable mitigation strategy in the face of ocean acidification. Furthermore, it is clear that, in some regions, the scope for expansion of monoculture activities is limited and that diversification of the aquaculture industry is imperative to maintain its competitiveness. Developing IMTA systems should not only bring increased profitability per cultivation unit through economic diversification of co-cultivating several value-added marine crops, it could also bring environmental sustainability and societal acceptability. Moreover, the IMTA multi-crop diversification approach (fish, seaweeds, invertebrates and microbes) could be an economic risk mitigation and management option to address pending climate change and ocean acidification impacts (Chopin 2015a).

Final remarks

Ocean acidification has already imposed negative impacts on the aquaculture industry, primarily in product loss at shellfish operations on the Pacific coast (although unproductive clam flats have been associated with low pH sediments on the Atlantic coast). The impacts of acidification on commercially harvested shellfish have been relatively well-described (Gazeau *et al.* 2013), but much more work is needed to address the implications of acidification on cultured finfish. Although likely to benefit from increases in seawater CO_2, some seaweeds may be at risk under more acidic conditions, particularly calcifying seaweeds, as well as non-calcifying ones existing in areas where increasing acidity is not primarily driven by increases in seawater CO_2.

While many experiments assessing the impacts of ocean acidification on cultured species in North America employ carbonate system conditions beyond those projected by the end of this century, coastal areas may experience more prolonged exposure to extreme conditions (low pH and high CO_2). As such, the responses observed under extreme scenarios cannot be ignored, but more experiments employing more realistic acidification scenarios are needed.

Although ocean acidification should be a concern for the aquaculture industry, it is a concern that can be addressed at the regional scale. Proper monitoring can provide early detection of changes in pH and seawater carbonate chemistry around aquaculture sites and negative instances (like those recently observed on the Pacific coast of North America) can be avoided by implementing proper mitigating strategies (site buffering, site selection, selective breeding, nutritional enhancement and IMTA). However, more elaborate monitoring programs are needed, particularly on the Atlantic coast, in order to avoid such scenarios in the future.

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