



REVIEW

Climate change and aquaculture: considering biological response and resources

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ABSTRACT: The heavy reliance of most global aquaculture on the ambient environment suggests inherent vulnerability to climate change effects. This review explores the potential effects of climate change stressors on aquaculture biology and resources needed to support decision-making for vulnerability assessment, planned adaptation, and strategic research development. Climate change-mediated physiochemical outcomes important to aquaculture include extreme weather, precipitation and surge-based flooding, water stress, ocean acidification, sea-level rise, saltwater intrusion, and changes to temperature, salinity, and dissolved oxygen. Culture practices, environment, and region affect stressor exposure, and biological response between species or populations are not universal. Response to a climate change stressor will be a function of where changes occur relative to optimal ranges and tolerance limits of an organism's life stage and physiological processes; the average magnitude of the stressor over the production cycle; stressor rate of change; variation, frequency, duration, and magnitude of extremes; epigenetic expression, genetic strain, and variation within and between populations; health and nutrition; and simultaneous stressor occurrence. The effects of simultaneous stressors will frequently interact, but may not be fully additive or synergistic. Disease is a major aquaculture limiter, and climate change is expected to further affect plant and animal health through the host and/or infectious agents. Climate change may introduce further complexity to the aquaculture–wild fishery relationship, with over two-thirds of animal aquaculture production dependent on external feed inputs. Higher production costs could be an economic outcome of climate change for many aquaculture sectors. Some aquaculture practices may inadvertently reduce resiliency to climate change, such as a reduction of coastal vegetation, coastal ground-water pumping, and reduction of population variability in pursuit of consistent production traits. Information from the largest aquaculture producers such as China and the top 3 global culture species is still sparse in the literature. This potentially limits thorough understanding of climate change effects on some regional aquaculture sectors.

KEY WORDS: Nutrition · Algae · Genetics · Fish health · Acclimation · Economics · Ocean acidification · Extreme weather

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1. INTRODUCTION

The FAO reports that climate change threatens our ability to ensure global food security, eradicate poverty, and achieve sustainable development (FAO 2018b). Human-driven global warming is already altering our environment, with far-reaching consequences. Much attention has focussed on its implications for terrestrial systems, but climate change is also altering ocean and aquatic ecosystems in profound ways, with consequent impacts on fisheries and aquaculture, and the livelihoods and communities dependent upon these resources. This review aims to explore potential pathways of climate change effects on aquaculture, from alterations to physical systems and how these could affect changes in biology, economics, and resource usage of cultured species, as a prerequisite to guide adaptation.

Capture fisheries and aquaculture provide 3 billion people with 20 % of their average per capita intake of animal protein and a further 1.5 billion people with about 15 % of their animal protein (HLPE 2014). Seafood is the most highly traded food (Smith et al. 2010), and demand is only expected to increase (World Bank 2013). Aquaculture now provides half of all fish for human consumption (FAO 2016). Capture fisheries landings are reported to have either plateaued around 90 Mt annually (FAO 2018a) or decreased (Pauly & Zeller 2016) since the mid-1990s. As of 2013, 31.4 % of global stocks were overfished, 58.1 % were fully fished, and only 10.5 % were underfished (FAO 2016). While some wild fisheries may experience short-term benefits from climate change, overall global landings are predicted to decrease 10 % by 2050 (Barange et al. 2014).

The intersection of these trends has brought increased attention to the potential of aquaculture to fill the gap. Global aquaculture production has been steadily increasing for decades, reaching 110.2 Mt (including aquatic plants), with the first-sale value estimated at US \$243.5 billion in 2016 (FAO 2018a). Aquatic and marine animal production has reached almost 74 Mt, and this is expected to expand to 102 Mt by 2025 (FAO 2016). Almost 600 different aquatic species (FAO 2018a) are cultured in almost 200 countries, nearly a third produced without feed use (e.g. bivalves and filter-feeding carps), and an additional culture of 27.3 Mt yr⁻¹ of seaweeds and other algae (FAO 2016). Global production has largely been driven by China, contributing 60 % to global production, followed by other leading producer nations such as India, Vietnam, Bangladesh, and Egypt. Inland aquaculture systems account for the majority of pro-

duction of aquatic animals (47 Mt), with most finfish culture occurring in earthen ponds, although finfish cage culture is expanding where conditions allow (FAO 2016). In developing countries where there is intense competition for space and resources, expansion of culture-based fisheries is expected in coming years, where extensive aquaculture is based on stock and recapture (De Silva 2016). Areas available for the expansion of marine aquaculture are still largely untapped (Gentry et al. 2017). The vast range of species, environments, regions, systems, and practices suggests that many aquaculture sectors and regions will be susceptible to a variety of climate change impacts, and indeed, some of the largest aquaculture producer nations (e.g. China, Vietnam, Bangladesh, Egypt) are predicted to be highly vulnerable to climate change (Handisyde et al. 2017).

Given the potential range of abiotic and biotic climate change stressors, impacts to resources, the diversity of biological response mechanisms, and the potential for stressor interaction, cost–benefit evaluation of aquaculture adaptation efforts is vital. Research and information are needed to support these efforts. At the global level, the volume of aquaculture-relevant climate research becoming available is encouraging, but also daunting. Research into the multiple dimensions of climate change is increasing exponentially (Haunschild et al. 2016, Pedersen et al. 2016, Xu et al. 2016), and literature specific to climate change impacts on aquaculture is still comparatively limited, but is also increasing exponentially (Dabadie et al. 2018). The rapid publication rate of climate change research makes keeping abreast of aquaculture-relevant literature increasingly difficult, even for experts. This begs the question as to whether there are recurring trends and commonalities that may apply across global aquaculture sectors to help better guide literature searches, decision making, and targeted research to support adaptation. At the sector or farm level, focus can be narrowed by following pathways of effects from changes to regional physical systems, the resultant potential for exposure, and range of biological responses. Therefore, rather than structure this review based on culture systems, country, or species, we explore changes to physical systems, possible mechanisms of exposure to these changes, and biological response examples of aquaculture species (if available). Regions and culture groups are emphasized and examples provided where data are available.

Herein we survey a diverse range of literature to explore possible implications of climate change to aquaculture to support pragmatic decision making

by managers, policy makers, and researchers, needed for vulnerability assessments, planned adaptation, or strategic research development. While there are many potential strategies for adaptation through aquaculture management approaches, this is beyond the scope of this particular review. Studies reviewed herein simulate climate change stressors using projected conditions within, or up to, the end of this century, unless otherwise specified. Where research results are reported, the units of the original study are used. We define a climate change stressor as a physical or biological driver that can be altered by climate change, resulting in the potential for detrimental impacts to an aquaculture species, sector, or resources.

2. STORMS AND WATER

2.1. Sea-level rise

By the end of the 21st century, it is very likely that sea-level rise will occur in more than 95% of the ocean area (Stocker et al. 2013). Global mean sea level rose 1.2 ± 0.2 mm yr⁻¹ between 1901 and 1990 and accelerated to 3.0 ± 0.7 mm yr⁻¹ between 1993 and 2010 (Hay et al. 2015). The rate of sea-level rise over broad regions can be several times larger or smaller than that of global mean sea-level rise for periods of several decades, due to fluctuations in ocean circulation. Oscillations such as the El Niño Southern Oscillations (Cazenave et al. 2014), the Pacific Decadal Oscillation (Mantua et al. 1997), and the Pacific Gyre Oscillation (Di Lorenzo et al. 2008) may cause local convergences of water masses, resulting in higher sea levels (King et al. 2011). Consequently, sea-level rise is not expected to be the same everywhere, and hotspots of accelerated sea-level rise have already been identified, such as the North American Atlantic, where the sea level has risen ~3–4 times higher than the global average (Salenger et al. 2012).

Sea-level rise has the potential to affect coastal aquaculture operations through loss of culture area (Hargreaves 2014), and greater, more distant salt intrusion into coastal groundwater (Smajgl et al. 2015). Small, gradual increases in sea-level rise are not inconsequential, as the influences to flood inundation are not linear. For example, an increase in sea level by 0.1 m will increase flood frequency by approximately 3 times (Church et al. 2006, Zhai et al. 2014). In some aquaculture areas such as coastal Vietnam, the tidal amplitude has changed drastically

(Binh et al. 2017), and this can augment seasonal and episodic flooding via storm surges (Wassmann et al. 2004, Rhein et al. 2013).

Ironically, some previous aquaculture practices may actually exacerbate coastal flooding. Mangroves and other coastal vegetation provide natural barriers to coastal flooding, erosion, and storm surges (Arkeima et al. 2013). Widespread mangrove clearing in Southeast Asia has occurred primarily from agriculture, but also from aquaculture (Giri et al. 2008). Shrimp farming development, in particular, has resulted in extensive historical mangrove destruction in coastal Sri Lanka (Bournazel et al. 2015), Bangladesh (Didar-UI Islam & Bhuiyan 2016), Indonesia (Murdiyarto et al. 2015), Vietnam (Orchard et al. 2015), and many other regions where coastal aquaculture occurs (Hamilton 2013). However, most countries have now banned the clearing of mangrove areas for aquaculture (FAO 2007), and there has been a realization that acid sulphate solids in which mangroves grow do not provide a good environment for shrimp culture (Stevenson et al. 1999), suggesting that mangrove clearing for aquaculture is abating. Some natural mangrove regeneration is now occurring in abandoned shrimp ponds, but growth is expected to be slow (Bournazel et al. 2015). Nevertheless, large areas of coastal mangroves have been removed historically, and remaining mangroves are predicted to be further damaged by climate change (UNEP-WCMC 2006), which may raise additional concerns about their continued effectiveness as coastal defences.

2.2. Saltwater intrusion

With sea-level rise, saltwater is shifting landward into regions that previously have not experienced or adapted to salinity (Tully et al. 2019). Surface and near-surface drinking water in low-lying coastal areas, such as the mega-deltas in Vietnam and Bangladesh–India, are most vulnerable to saltwater intrusion, where more than 25 million people are at risk of drinking ‘saline’ water (Hoque et al. 2016). The rate of intrusion is expected to accelerate, with a 30 cm sea-level rise in the Mekong Delta predicted by 2050 (Smajgl et al. 2015). Salinity changes may not be a concern for cultured euryhaline species, but saltwater intrusion has already proven problematic for less tolerant species. In some areas of Bangladesh, salinization has impacted crops providing a barrier to freshwater prawn farming in rice paddies, also affecting the drinking water of the prawn farmers

themselves (Ahmed 2013). Salinity intrusion has already been experienced by some striped catfish *Pangasianodon hypophthalmus* farmers in Vietnam (Nguyen et al. 2018). In some Vietnamese provinces, sea-level rise from 50 to 75 cm is expected to increase water levels during the rainy season and salt intrusion during the dry season, thereby threatening production (Nguyen et al. 2014). Sea-level rise in combination with some shrimp farming practices may exacerbate saltwater inundation. Prolonged flow of saline water into coastal shrimp ponds can promote saline percolation into the surrounding soils (Didar-Ul Islam & Bhuiyan 2016). Saltwater intrusion may be a possible advantage for some types of aquaculture. Areas rendered unsuitable for agriculture, particularly traditional rice farming, could be repurposed for shrimp farming (De Silva & Soto 2009).

2.3. Flooding and extreme weather

Increases in precipitation-mediated flooding will be problematic for some types of aquaculture, but potentially advantageous for other types. Despite some regional uncertainties, climate models consistently project large rainfall changes occurring for a considerable proportion of the tropics by mid-century (Chadwick et al. 2016). Projections suggest that the largest increase in flood frequency will occur in Southeast Asia, peninsular India, eastern Africa, and the northern half of the Andes (Hirabayashi et al. 2013), although flood frequency is still projected to increase in other regions, such as areas of the USA (Rahmani et al. 2016, Prein et al. 2017) and large portions of Europe (Alfieri et al. 2015). Climate-driven causes of floods may be difficult to tease out, as they will also occur together with other catalysts. Global damage due to flooding is expected to increase 20 times by the end of the 21st century, mainly due to climate forcing in Africa and from the effects of socioeconomic growth in Southeast Asia (Winsemius et al. 2016).

Flooding can cause escapes, introduce predator species into culture ponds, and cause contamination of pond water through debris and waste intrusion (Adhikari et al. 2018, Kais & Islam 2018). Flood-related mortalities are not uncommon with pond culture (Bell et al. 2009) and hatcheries. Flood-related fish kills may occur for several reasons, but are predominantly due to low oxygen in flood waters (Idris et al. 2014). While there does not appear to be any documentation on the prevalence of flood damage to aquaculture operations on global or regional scales,

an internet search using the terms 'hatchery', 'fish farm', and 'flood' returned numerous media reports of fish mortalities, escapes, or evacuations due to flooding (e.g. Johnson 2011, Brooks 2013, Booth 2014, 69 News 2014, Lawrence 2016). Many of the floods reported by the mainstream English-language media are flash floods related to heavy rainfall in North America and Europe. This is consistent with the increased frequency and intensity of heavy precipitation events in northern Europe and North America, whereas less precipitation is occurring in other regions such as southern Europe and Central America (IPCC 2013). While flooding is largely seen as detrimental to aquaculture in general, there are some aquaculture fisheries that rely on flooding to fill water bodies with wild fish for culture, such as floodplain ponds in Kenya (Kipkemboi et al. 2010), or Whedo aquaculture systems in west Africa (Hauber et al. 2011). Increased flooding could expand culture opportunities in these areas.

Increasing sediment load and potential for contamination have also been highlighted as flood-mediated threats to aquaculture. Floods can promote high inorganic sediment loads in areas of coastal open-water aquaculture and reduce or arrest the filtration rate of shellfish (Rosa et al. 2012). The re-suspension of contaminated sediments could be an additional problem. In laboratory studies under elevated temperature conditions, sediment resuspension is considered a plausible route for rainbow trout *Oncorhynchus mykiss* contamination (Brinkmann et al. 2013). Increases in rainfall will also increase land run-off, driving nutrients from sewage or agricultural fertilizers into coastal production areas and causing algal blooms, which can reduce dissolved oxygen, again resulting in fish mortalities (Díaz et al. 2009). Shellfish contamination from sewage and agriculture can also be a function of flooding. This is exemplified by a moderate flood event in Tasman Bay, New Zealand, where a low-salinity plume delivered elevated *Escherichia coli* and *Enterococci* concentrations (indicative of raw sewage or manure) to a major shellfish production area, causing terrestrial faecal contamination in shellfish 6 km offshore (Cornelisen et al. 2011).

Flooding through oceanic storm surges can be devastating for aquaculture. Surge-based flooding will be exacerbated by sea-level rise (see Section 2.1). Increased occurrences of tropical cyclones in the Caribbean and landfall typhoons in East Asia are expected, although changes to hurricanes are less certain (Stocker et al. 2013). There is low confidence in any trend of storm systems formed in middle or higher latitudes, but robust evidence exists for

increased intensity of tropical cyclones in the North Atlantic basin since the 1970s (Rhein et al. 2013). El Niño events can modulate the development of tropical cyclones (Chand et al. 2017), and a near doubling in the frequency of future extreme El Niño and reciprocal La Niña events is expected within this century (Cai et al. 2014, 2015). Wind stress has increased in some areas, such as the Southern Ocean, and average winter wave heights have increased in the North Atlantic (since the 1950s), with a reported trend of 20 cm decade⁻¹ (Rhein et al. 2013). Wind intensification is more likely to increase at higher latitudes (Syde-man et al. 2014), which may be linked to stronger warming trends in polar rather than equatorial regions (Baumann & Doherty 2013).

The increased prevalence of extreme weather events will affect coastal fishers, associated services, and infrastructure (IPCC 2007) and can be destructive to coastal aquaculture operations (Allison et al. 2009, Luening 2013). High winds and waves can destroy structures used for coastal aquaculture such as embankments, pond dikes, sluice gates, hatcheries, electricity poles, and rearing structures (Rahman & Hossain 2012). These impacts may not only occur at the farm level but can impact entire aquaculture sectors. In 2009, Cyclone Aila destroyed 80% of shrimp farms in the affected areas of Bangladesh (Kais & Islam 2018), and 2010 storm events in Mexico devastated 1200 farms, reducing the country's annual tilapia production by 80% (Reid & Jackson 2014). Open-water aquaculture is also susceptible to storms, where large-scale escapes from sea cages are correlated with storm events (Jensen et al. 2010). Escapes may promote ecological interactions such as introgression (domesticated ancestry) with wild counterparts (e.g. Bolstad et al. 2017). Counterintuitively, a reduction in wind may also be problematic. McCoy et al. (2017) provided evidence that reduced trade winds during an El Niño in Hawaii decreased surface water mixing, thereby enhancing surface heating and water column stratification in fish ponds, ultimately causing hypoxia and mortalities.

2.4. Water stress

It is difficult to partition out climate change-mediated effects from other anthropogenic effects on aquaculture water use. Water stress is linked largely with land usage, and in many regions, there is fierce competition between aquaculture and other priority needs, such as agriculture and urban demand. The rapid expansion of freshwater aquaculture has led to

major constraints on land use in key producing countries such as China, Indonesia, Bangladesh, Thailand, and India (Liao & Chao 2009). It is anticipated that by 2050, numerous culture ponds will be taken over by urbanization, resulting in more widespread use of cages in small water bodies and greater production moving to open-water coastal areas (Costa-Pierce et al. 2011). At present, however, global inland aquaculture production is greater and still increasing faster than marine aquaculture production, with inland production accounting for 64% of farmed food fish production (FAO 2018a). As most of this production is concentrated in the tropical and subtropical regions of the globe, climate impacts are likely to produce more significant net effects on the freshwater aquaculture subsector in these regions (De Silva & Soto 2009).

Over half of the world's inland fish culture occurs in China (FAO 2014), primarily in ponds and river delta areas of southeast China (Wang et al. 2015), which include 1.55 million hectares of fish-rice culture (Shelton, 2014). Information on climate change and Chinese aquaculture is scant in the English language literature. However, regional climate models project the frequency of heatwaves and rainfall extremes to increase over most of the country (Zhang et al. 2006). How this may affect river water resources depends on the region. Since the 1960s, the Yellow River, a large northern catchment sensitive to drying trends, has experienced reduced flow, while the Yangtze River, frequently flooded by monsoon rains in its middle reach, has had a small but significant flow increase (Piao et al. 2010). Nevertheless, compared to 1971–2000, projections for 2071–2100 suggest that mean Yangtze River flow will be similar but variably will increase, while mean Yellow River flow will increase by 22%, with temperatures in both rivers increasing by 1.8°C (van Vliet et al. 2013). This uncertainty in reconciling observed changes with future river projections in China is considered a major scientific challenge (Piao et al. 2010). However, precipitation-based increases in major aquaculture-producing regions in China are expected to have a positive effect on profitability, but this must also be contextualized with negative effects such as temperature variability (Li et al. 2016). The limited information on climate change and aquaculture water usage in China may reflect more pressing concerns, such as aquaculture-based eutrophic events (Herbeck et al. 2013) and ground subsidence occurring faster than sea-level rise due to hatchery pumping (Higgins et al. 2013). New measures, such as increased regulation and integrated agriculture–aquaculture systems

are gradually being implemented to improve environmental conditions and water usage (Lin et al. 2015, Wang et al. 2015).

Freshwater user conflict may also be exacerbated by climate change. While this has not been clearly quantified, climate change-mediated reduction in water supply or quality is apt to compound existing water stress issues. Some water usage conflicts have reached a crisis point in some of the major aquaculture farming regions of the world, such as Bangladesh, a nation of rivers, whose production has been impacted by upstream dams in India (Costa-Pierce et al. 2011). Western countries have not been immune from freshwater aquaculture conflict either, and conflicts with agriculture are detailed by North American aquaculture industry reports (Dodd 2013).

3. BIOLOGICAL RESPONSE

3.1. Water temperature

Suggestions that aquaculture losses are linked to climate change-driven temperatures are now appearing in the literature, from culture regions such as Vietnam (Binh et al. 2017), Australia (Hobday et al. 2018), and Hawaii (McCoy et al. 2017). The oceans have absorbed over 90% of the increase in energy in the climate system, causing the upper 75 m to warm by $0.11^{\circ}\text{C decade}^{-1}$ between 1971 and 2010 (Rhein et al. 2013), and this has probably been underestimated due to data limitations in the Southern hemisphere (Durack et al. 2014). Marine organisms have, on average, expanded the leading edges of their ranges by $72.0 \pm 13.5 \text{ km decade}^{-1}$, generally poleward, while marine phenology in spring has advanced approximately $4.4 \pm 1.1 \text{ d decade}^{-1}$, but with variability among taxonomic groups (Pinsky et al. 2013, Poloczanska et al. 2013). Depending on the representative concentration pathway (RCP) applied, end-of-century model projections for sea surface temperatures range from $0.71 \pm 0.45^{\circ}\text{C}$ (RCP 4.5) to $2.73 \pm 0.72^{\circ}\text{C}$ (RCP 8.5) (Howes et al. 2015). Some end-of-century projections (RCP 8.5) suggest large increases for some regional 'hot spots', such as the Arctic, tropics, and North Pacific, in excess of 4°C (Bopp et al. 2013, Howes et al. 2015). Marine heat waves will be exacerbated as anthropogenic climate change raises mean temperatures (Schmidt & Boyd 2016). Rivers are of particular concern, given the large portion of global aquaculture production associated with deltas. Global river water temperatures are projected to increase on average

by $0.8\text{--}1.6$ ($1.0\text{--}2.2$) $^{\circ}\text{C}$ (under the IPCC Special Report on Emission Scenarios B1–A2 scenario) by the end of the century compared to 1971–2000, with the greatest warming projected for the USA, Europe, eastern China, and parts of southern Africa and Australia (van Vliet et al. 2013).

Anticipating biological outcomes for culture scenarios under climate driven temperature change is not trivial due to biological response variability and crude predictive temperature resolution. At the organism level, temperature can affect aerobic capacity, reproduction, maturation and development, growth rate, nutrition, immune function, and timing of seasonal activities, as detailed below. Further complexity is introduced when temperature effects may differ for different biological processes and life stages within the same organism. For temperature projections, coarse ocean or river delta scales mean that temperature projections are only partially informative. There are prediction uncertainties for temperature at the smaller biologically relevant temporal and spatial scales (Stock et al. 2011, Brander 2013) at which aquaculture species are grown, although predictive resolution is increasing (Khan et al. 2013).

Increased variability and temporal extremes can act as direct or indirect stressors, increasing production risk and superimposing over potential growth rate benefits (Holst & Yu 2010). Elevated seasonal or annual average temperatures may result in positive effects during some seasons (Morgan et al. 2001) or years, but not in others. In Lake Saroma, Japan, decreasing ice cover and advancing spring phytoplankton blooms in the past decade have promoted good scallop culture production, except during years with East Asian Monsoon and El Niño/La Niña Southern Oscillation events, which promote higher temperatures and decreased production (Liu et al. 2018). Increased winter water temperatures are projected to accelerate the growth rate of 4 abalone species in southern Australia, while the projected summer temperatures are expected to cause a 10-fold increase in juvenile mortality (Russell et al. 2012).

In some instances, increased growth rates due to warmer temperatures have still occurred despite other negative side effects. The annual mean temperature of Lake Huron in Canada has increased, increasing the overall harvest weight of net-pen rainbow trout, irrespective of sub-optimal maximal summer water temperatures (Anon. 2013). Warmer temperatures in Patagonian reservoirs have led to a lack of ovulation and reduced spawning and larval survival of cultured rainbow trout, but ultimately increased overall growth (Báez et al. 2011).

3.1.1. Aerobic capacity

The upper reaches of most ocean regions are experiencing continuous decrease in dissolved oxygen concentration, partially due to increased climate warming (Schmidtke et al. 2017). Oxygen demand to support aerobic processes in ectotherms also increases with temperature, due to its direct effect on metabolic rate. This was clearly demonstrated in a classic study by Fry & Hart (1948), who showed that the oxygen demand of goldfish *Carassius auratus* more than doubles with acclimation from 10 to 20°C, concomitant with a 50% increase in the oxygen tension below which aerobic metabolism is limited by oxygen availability. Similar results have been obtained for aquaculture species, such as post-smolt Atlantic salmon *Salmo salar* (Remen et al. 2013). This effect of temperature on aerobic capacity can severely constrain aquatic ectotherms that have limited or no ability to use atmospheric oxygen because gas solubility declines as water temperature rises, and as a result, dissolved oxygen levels often become insufficient to support aerobic functioning—and ultimately life—at some high temperature. This can have far-ranging impacts in aquaculture that affect stocking densities, feed intake and utilization (e.g. Remen et al. 2016), growth rates, water usage, and other basic husbandry and health management practices. Exploring how temperature affects aerobic capacity will provide a better understanding of how climate change could impact species selection, management, and farm productivity.

Within aquaculture, positive or negative responses to temperature will depend on where the change occurs on the aerobic performance curve for a particular life stage or physiological process (Pörtner & Farrell 2008, Clark et al. 2013). A temperature increase near the lower limit could be beneficial, while an increase near the upper limit will likely be detrimental. The size of the optimal temperature range is also species-specific, with eurythermal species able to operate within a wide range of temperatures, while stenothermal species can only function within a narrow range. Environmental and biotic stressors, such as those expected to accompany climate change (e.g. increased frequency and severity of hypoxic events, changes to salinity, ocean acidification, eutrophication, and changes to pathogen and parasite distributions and abundances), may further reduce the temperature range of aerobic performance, although supporting data are mixed (Lefevre 2016).

Increased oxygen demand may not be problematic in well-oxygenated rearing systems, but could be

where oxygen concentration approaches lower-limit thresholds, potentially during 'slack tides' (low current flow and therefore low oxygen supply) during maximal production periods of marine caged fish (Page et al. 2005) or stratification of aquaculture ponds (Pickering et al. 2011). Froehlich et al. (2016) recently explored thermal and minimum dissolved oxygen tolerance across a range of marine species, reporting that larger, slow-growing species tended to be overall more tolerant, and that tropical species showed reduced capacity to withstand a larger range of temperatures and lower oxygen levels simultaneously. Unfortunately, slow-growing species are not preferred for aquaculture for economic reasons.

Some cultured fish, such as *Pangasius* catfish species (FAO 2018a), are capable of air breathing and are therefore more tolerant of hypoxia. However, there may be other costs of hypoxia, depending on the species of air-breathing fish. These are described in detail by Lefevre et al. (2014) and may include such effects as brachial oxygen loss from the blood to water, increased energy demand, and more surfacing, increasing predator exposure.

3.1.2. Reproduction, growth, and development

Temperature influences reproductive performance in poikilotherms (Pankhurst & Munday 2011). Temperature-mediated changes in embryo survival, fecundity, spawning time, maturation rate, and sex ratio can have major implications for reproductive success and breeding practices. As with other physiological processes, species will have an optional reproductive range (e.g. Fearman & Moltschanivskyj 2010). Outside these optimal ranges, reproductive performance may suffer. For example, elevated temperatures impair gonad steroid synthesis and hepatic vitellogenin production, and can dramatically reduce egg fertility and embryo survival in Atlantic salmon (Pankhurst et al. 2011, Anderson et al. 2012). Fewer eggs are produced by African catfish *Heterobranchus longifilis* under elevated dry season temperatures (Legendre 1986). Egg development time can also be a function of temperature, such as with eggs of the European hake *Merluccius merluccius*, which demonstrate a development power relationship up to a critical temperature threshold (Guevara-Fletcher et al. 2016).

Small increases in average temperatures across a production cycle may have the potential for increases in growth rate for some aquaculture species, such as mussels and salmon (Reid et al. 2015), within optimal

temperature thresholds. However, this cannot be assured for all culture species scenarios. Some species may have the potential for compensatory growth (e.g. sea bass *Dicentrarchus labrax*) where animals cultured at lower temperature will eventually 'catch up' to animals grown at warmer temperatures (Sfakianakis et al. 2013).

Maturation rates can also be influenced by temperature (Wilkinson et al. 2010), which may have positive or negative outcomes for aquaculture, depending on context. Increased maturation can be disadvantageous for some types of production such as salmonid aquaculture, where early maturation redirects energy into gamete production instead of growth, thereby slowing growth and time to reach market weight (McClure et al. 2007). Increases in temperatures for other production systems may be advantageous, such as with the common Japanese conger *Conger myriaster*, where elevated temperatures can induce oocyte maturation without the need for exogenous hormone treatment (Utoh et al. 2013). Sex ratios and early development may also be influenced by temperature, such as in European seabass *D. labrax*, where higher temperatures in early life stages reduced the number of faster-growing females compared to males (Sfakianakis et al. 2013).

3.1.3. Nutritional and digestive metabolism

Temperature has both direct and indirect effects on nutrition, feeding practices, and behaviours. Basal metabolism is the energy used by animals to maintain normal body functions, excluding growth and voluntary activity. As fish are poikilothermic animals, their basal energy needs are directly impacted by the temperature of the water. As temperature rises, so does the standard metabolic rate (e.g. Glencross & Bermudes 2010) and consequently, the maintenance requirement for energy and protein (e.g. Lupatsch & Kissil 2005). However, the degree to which temperatures within an optimum range affect basal metabolism will vary among species (Cho & Kaushik 1990, Glencross 2007, NRC 2011).

Not only will changes in metabolic rate translate into changes for dietary fuel demand, but temperature may also influence the efficiency by which feed is converted into flesh. This is measured by the feed efficiency ratio (FER, gain/feed) or the reciprocal measure, the feed conversion ratio (FCR, feed/gain). For example, FCR increases (less efficient conversion) with temperature in the juvenile hapuku *Polyprion oxygeneios* (Khan et al. 2014). For some spe-

cies, a several-degree temperature difference can translate into large differences in feed conversion. Increased temperature decreased feed conversion efficiency for the cultured juvenile Australasian sea cucumber *Australostichopus mollis* grown at 21°C by 7 times compared to cucumbers grown at 15°C (Zamora & Jeffs 2012). As with other metabolic processes, feed conversion is apt to have optimal temperature ranges, with decreased efficiency occurring at either end of the range (Britz et al. 1997, Siikavuo et al. 2012). An example of this is large-sized barramundi *Lates calcarifer*, which use about a third of their gross energy intake for basic maintenance at 30°C, compared to only 10% at 20°C (Glencross & Bermudes 2012). Temperature-driven changes to FCR may also accompany changes in digestibility of specific nutritional categories, such as with fatty acids in salmonids (Hua & Bureau 2009, Huguet et al. 2015).

The influence of water temperature on nutrient digestibility in aquatic animals is typically minimal. Research on salmonids indicates that changes to protein and lipid digestibility may show minor variations with temperature (Windell et al. 1978, Ng et al. 2004, Amin et al. 2014, Huguet et al. 2015). Some research suggests that gut transit time could be affected by warmer water, as either an increase in the case of yellowtail kingfish *Seriola lalandi* (Miegel et al. 2010) or a decrease, as with greenlip abalone *Haliotis laevigata* (Currie et al. 2015). Generally, these studies suggest that elevated water temperatures associated with climate change will have minimal impact on nutrient or energy digestibility by aquatic animals, at least until the optimum range has been exceeded.

3.1.4. Summary — water temperature

There is an overall warming trend in the world's oceans and freshwaters, with increases in extreme temperature events and variation at multiple scales, but with the greater uncertainty at the farm scale. Global warming is causing species' range shifts, which suggests the potential for introduction of novel predators, invasive species, and pathogens to some aquaculture areas. Climate-driven temperature changes may increase variation in production success, where positive effects may occur in some seasons or years but not in others. While there is the potential for improved growth with increased temperature, there may be other physiological costs such as poorer feed conversion and effects to maturation and reproduction. Some species with the ability for compensatory

growth at lower temperatures may not show prolonged increased growth rates at higher temperatures. There is increased potential for hypoxia with warming waters, and in some regions this may favour more tolerant species, such as air-breathing fishes. Anticipating temperature outcomes will benefit from knowledge of optimal and critical temperature thresholds for both physiological processes and different life stages of the species cultured.

3.2. Ocean acidification

Oceans absorb CO₂ from the atmosphere, providing a buffer to atmospheric levels, but the increased levels of atmospheric CO₂ being produced since the Industrial Revolution mean that the oceans are absorbing more CO₂. This leads to reductions in seawater pH, carbonate ion concentrations, and calcium carbonate (CaCO₃) minerals and is a process called ocean acidification. Ocean acidification is already a major issue in some regions for both wild and cultured populations, particularly when superimposed over already acid-promoting conditions, such as coastal upwelling (Adelsman et al. 2012). Most of the aquaculture focus has been on shellfish, and Ekstrom et al. (2015) showed that 16 out of 23 regions in the USA have been exposed to rapid ocean acidification, with communities highly reliant on shelled molluscs to be currently or in the near future at risk from ocean acidification. In the USA, ocean acidification has already impacted shellfish aquaculture in Washington State (WSBR Panel 2012), an industry which directly or indirectly employs over 3200 people and provides an estimated total economic contribution of US \$270 million (NOAA 2011). The elevated levels of internal CO₂ (hypercapnia; Widdicombe & Spicer 2008) and the reduction in carbonate ions caused by ocean acidification affect the ability of organisms with CaCO₃ shells to build their shells (Gazeau et al. 2007), affecting calcification (Wood et al. 2008, Hofmann et al. 2010), internal acid–base regulation (Miles et al. 2007), shell biomineralization and energy metabolism (Beniash et al. 2010, Ivanina et al. 2013), and the proteome (Dineshram et al. 2012).

3.2.1. Larval shellfish

As many larval shellfish (defined here as seafood with exoskeletons, including molluscs, crustaceans, and echinoderms) stages contain aragonite, it is

expected that this stage would be the most sensitive to dissolution from ocean acidification (Waldbusser et al. 2010). Negative responses have been reported in numerous commercial aquaculture and fisheries species (Gazeau et al. 2013). These include Pacific oysters *Crassostrea gigas* (Kurihara et al. 2007, Parker et al. 2010, Barton et al. 2012, Timmins-Schiffman et al. 2013), eastern oysters *C. virginica* (Miller et al. 2009, Talmage & Gobler 2009), Sydney rock oysters *Saccostrea glomerata* (Parker et al. 2009, 2010, 2012, Watson et al. 2009), blue mussels *Mytilus edulis* (Gazeau et al. 2010), Mediterranean mussels *M. galloprovincialis* (Kurihara et al. 2008), bay scallops *Argopecten irradians* (Talmage & Gobler 2009, 2011, Gobler & Talmage 2013), gastropods (Tahil & Dy 2016), some crustaceans (Padilla-Gamiño et al. 2013, Small et al. 2016, Emerson et al. 2017), echinoderms (Stumpp et al. 2011, 2013), and hard clams *Merccenaria mercenaria* (Talmage & Gobler 2009, 2011, Gobler & Talmage 2013). Comprehensive summaries including commercial species were presented by Gazeau et al. (2013) and Parker et al. (2013), who reviewed research on the effects of ocean acidification on the fertilization, embryonic, and larval development of commercial gastropod and bivalve species and non-commercial molluscs. Reported responses of bivalve larvae are species-specific and can range from negative to non-significant to positive.

The mechanism by which CO₂ and carbonate undersaturation imparts negative effects on calcifying organisms (Gobler & Talmage 2013) and the dynamics of initial shell formation were, until recently, poorly understood (Barton et al. 2012). Levels of aragonite saturations for Pacific oysters were seen to be stressful at aragonite saturations below 1.7 and corrosive at levels below 1 (Barton et al. 2012), and acute and chronic responses have been documented between 1.2 and 2.0 for other bivalve larvae (Talmage & Gobler 2009, Gaylord et al. 2011, Dineshram et al. 2012, Hettinger et al. 2012). Ekstrom et al. (2015) used a mean aragonite saturation state of 1.5 to represent a conservative threshold and projected when surface seawaters would reach a chronically stressful state for shelled mollusc larvae in Washington State (2016–2021) and Alaska (2006–2015) in the USA, and in British Columbia in Canada (2006–2015).

Ocean acidification can create co-varying inorganic carbon system variables, and seawater manipulations have shown that larval shell development and growth are dependent upon seawater CaCO₃ saturation states and not pCO₂ or pH (Waldbusser et al. 2015). Fassbender et al. (2016) reported

that highly variable coastal carbonate chemistry may affect the ratio of bicarbonate to hydrogen ions in the natural environment and cautioned against the use of aragonite saturation alone for assessing biological ocean acidification exposures and vulnerabilities. Therefore, some conflicting reports on the impacts of ocean acidification on shellfish responses may be related to the decoupling of elements of the carbonate system, highlighting the need to monitor full seawater carbonate chemistry before interpreting results. In addition, an abundance of quality food may assist in buffering the effects of ocean stressors (Thomsen et al. 2010, 2013, Hettinger et al. 2013, Parisi et al. 2017), so care should be taken in assessing organism responses to laboratory acidification experimentation.

Larvae are crucial for sustaining viable populations, and failures will ultimately lead to negative population effects (Jansson et al. 2013). The smaller juvenile larvae with weaker shells may be subject to increased predation risk due to increased time spent in the water column (Waldbusser et al. 2011), and may suffer latent larval effects such as reduced metamorphosis and fitness potential (Miller et al. 2009). This suggests a fundamental ocean acidification bottleneck during early life history for marine keystone species (Waldbusser et al. 2015), and has obvious impacts for aquaculturists reliant on wild seed collection to populate culture farms or the manipulation of hatchery water quality to ensure larval survival. Juveniles that survived under high pCO₂ rearing conditions grew faster when exposed to normal CO₂ levels compared to those control larvae grown under constant ambient conditions; however, such growth rates could not overcome the early larval size differences even after 10 mo (Gobler & Talmage 2013). This highlights how early exposure to high CO₂ fluxes could significantly affect current and future bivalve populations and commercial production.

3.2.2. Juvenile and adult shellfish

Extreme post-settlement loss of juveniles has often been attributed to factors such as predation (Ólafsson et al. 1994), competition (Ahn et al. 1993), and hydrodynamic dispersion (Roegner et al. 1995), but until relatively recently, research had not addressed dissolution mortality (Green et al. 2009). Studies on the impact of lowered pH on post-larval hard clams *M. mercenaria* found a size-dependent mortality factor, where larger individuals were able to withstand dis-

solution through increased rates of calcification (Waldbusser et al. 2010, Talmage & Gobler 2011) or by reaching a size at which corrosive conditions did not affect survival (Green et al. 2009). Studies on the calcification, growth, and mortality of juvenile *Ruditapes decussatus* clams found no effect of pH, which was attributed to naturally elevated total alkalinity and variable physical–chemical characteristics of seawater in coastal, estuarine, and transitional waters, and suggested that biological calcification should not be the only metric for impact (Range et al. 2011). Adults and juveniles may experience reduced calcification and shell growth under acidified conditions (Berge et al. 2006, Gazeau et al. 2007, Miller et al. 2009), but this may vary by populations within a species, as local adaptation may occur (Thomsen et al. 2010, Parker et al. 2011). Transgenerational experimentation has examined the impacts of single and multiple ocean stressor conditioning of broodstock on juvenile offspring (see Section 3.3).

Ocean acidification may also create non-calcium associated problems for aquaculture husbandry. For example, byssus attachment of adult *Mytilid* mussels was weakened under future pCO₂ conditions, which has implications for suspension culture and intertidal communities anchored by mussel beds (O'Donnell et al. 2013). There may be the potential for dwarfing in some species, which would affect production. Studies on non-commercial gastropod species (*Nassarius corniculatus* and *Cyclope neritea*) in shallow-water CO₂ seeps indicate that dwarfing may confer a physiological advantage through a reduced metabolic energy demand, allowing maintenance of calcification and repair of shell dissolution (Garilli et al. 2015). Fundamentally, ocean acidification is likely to impact marine ecosystems over a range of population- and community-level effects, which in turn may affect species' ranges and loss of species diversity (Gaylord et al. 2015) and could result in a change in culture species under aquaculture.

3.2.3. Finfish

While there have been many historical CO₂ studies on finfish, ocean acidification per se has only recently been considered. Ocean acidification may affect foraging behaviour and swimming performance, and wild fish can exhibit tissue damage and malformations when cultured under acidic conditions (Frommel et al. 2012, 2014, Ahnelt et al. 2016, Pimentel et al. 2016, Shao et al. 2016). Numerous studies have demonstrated olfactory impairment under acidifica-

tion in wild fish (Nilsson et al. 2012, Chivers et al. 2014, Chung et al. 2014, Hamilton et al. 2014; reviewed in detail by Leduc et al. 2013). It is unclear if olfactory impairment occurs in cultured fish and what implications this might have. Finfish are routinely raised in high- CO_2 environments in recirculating aquaculture systems, often in excess of end-of-century predictions, with no apparent ill effects (Ellis et al. 2017). This discrepancy with results from studies on wild fish could be for numerous reasons, including improved nutrition and selective breeding for greater tolerance to elevated CO_2 (Ellis et al. 2017). There is also extensive variation among species with respect to innate CO_2 tolerance (Damsgaard et al. 2015).

3.2.4. Macroalgae

Many species of marine macroalgae (seaweeds) have been cultivated for centuries, but intensive algal culture began about 50 yr ago. The FAO reported 37 separate species or species groups cultivated in 50 countries, with a total annual harvest of 30.1 Mt (wet weight) with roughly 9 Mt destined for human consumption (FAO 2016, 2018a). The majority (99.4 %) of seaweed aquaculture occurs in 7 Asian countries, with China as the largest producer of edible seaweeds (Chopin 2018). Cultured seaweeds are used for food, phycocolloids, and other useful chemicals (Chopin & Sawhney 2009).

Macro-algal species, which are currently CO_2 -limited (e.g. Swanson & Fox 2007), are expected to benefit from increases in atmospheric CO_2 and dissolved CO_2 in water compared to species that are already CO_2 -saturated (Beardall et al. 1998). Some fleshy macro-algae, red algae (especially those living in low-light environments), and a few green algae may become more competitive in increased CO_2 environments (Hepburn et al. 2011). By contrast, calcified seaweeds (like crustose corallines) will likely be less competitive, as the maintenance of supersaturated conditions at the site of precipitation for crystalline forms of CaCO_3 will be more difficult in lower- CO_3^{2-} seawater. CaCO_3 already precipitated may also be subject to dissolution (i.e. some species may experience decalcification and reduced survival rate). A meta-analysis by Kroeker et al. (2010) indicated that calcifying macro-algae will be more susceptible to ocean acidification than corals, coccolithophorids, molluscs, echinoderms, crustaceans, fish, fleshy macro-algae, and seagrasses.

3.2.5. Summary—ocean acidification

Anthropogenic CO_2 production has caused reductions in seawater pH, carbonate ion concentrations, and CaCO_3 minerals, collectively described as ocean acidification. Response of shellfish species to experimental ocean acidification has been variable but mostly negative. Experiments suggest that larval stages of shellfish appear most sensitive to dissolution from ocean acidification, with growth and development more dependent upon seawater CaCO_3 saturation states than pCO_2 or pH. Larger juvenile and adult individuals may have greater ability to withstand dissolution through increased rates of calcification or by reaching a size at which corrosive conditions are less impactful. In areas of naturally high CO_2 seeps, some species have adapted by dwarfing. This is presumably not a response desirable for aquaculture species. Economic losses in shellfish hatcheries have already occurred where ocean acidification has superimposed over areas of elevated CO_2 from upwelling. While experimental evidence suggests that some wild finfish species may be susceptible to high CO_2 , negative impacts to finfish raised in routine high CO_2 conditions are not typically seen in aquaculture. This suggests caution in the extrapolation of wild species laboratory studies to aquaculture production scenarios. Some macro-algal species that are CO_2 -limited may benefit from ocean acidification, whereas calcifying species may not, potentially influencing future species selection for culture.

As the bulk of global aquaculture occurs in freshwater, ocean acidification may seem less problematic overall compared to other climate change stressors. However, given the potential limiters for freshwater aquaculture expansion described herein, largescale global expansion is apt to occur in the marine environment. While this circumvents some problematic issues of freshwater culture, climate change effects in marine systems will have greater potential influence on global production as marine-based culture expands.

3.3. Genetics and a changing climate

3.3.1. Acclimation

Within a population, individuals have the capacity to behave, appear, and function (physiologically and phenologically) differently than the average characteristics of an organism within a population, defined as phenotypic plasticity. This suggests that within a

population, there may be individuals which may respond better to climate stressors than others, and this acclimation, or acclimatization, may allow organisms to function in new environments (Sunday et al. 2014). The capacity of a population to buffer a response may be linked to the strength and the rapidity of the change experienced. For example, there may be metabolic shifts to compensate for increased demands in a stressful environment which assist in maintaining growth, but if the change is sudden and large (e.g. extreme events), a tolerance level may be reached. Warmer larval-rearing temperatures cause an irreversible plastic response during early ontogenesis, resulting in increased body masses and hypoxia tolerance in juvenile common sole *Solea solea* (Zambonino-Infante et al. 2013). Temperature change can be linked to specific gene expression such as heat tolerance in Arctic charr *Salvelinus alpinus* (Quinn et al. 2011) and in the spleen transcriptome (Hori et al. 2013) and immune-related genes in blood cells (Pérez-Casanova et al. 2008) of Atlantic cod *Gadus morhua*. Nevertheless, extensive plasticity in finfish is not universal for all traits, species, stressors, or stressor levels. A lack of plasticity in combination with reduced genetic diversity for arrhythmic heart temperature in Chinook salmon *Oncorhynchus tshawytscha* has constrained the upper thermal limit, and catastrophic wild population loss is projected under the year 2100 maximum warming scenario (Munoz et al. 2015). Whether plasticity increases the time available for adaptation or slows the pace of adaptation by shifting the mean phenotype in a direction that weakens selective pressure, remains less clear (Gaylord et al. 2015). Ultimately, plasticity has implications for how entire ecosystems may respond to climate change stressors (Hennon et al. 2015).

3.3.2. Adaptation potential

Many desirable aquaculture traits (e.g. disease resistance, growth rate) are dependent on the interaction of numerous genes, gene sequences, or loci. A number of studies on commercial species have examined the impacts of parental exposure on offspring adaptation potential. Transgenerational acclimation potential to ocean acidification has been reported for invertebrates, including the green sea urchin *Strongylocentrotus droebachiensis* (Dupont et al. 2013) and the Sydney rock oyster *Saccostrea glomerata* (Parker et al. 2012). Studies over 3 generations of mussels (*Mytilus edulis*) from CO₂-enriched and non-

enriched habitats have shown short-term selective responses of traits directly affected by ocean acidification and long-term adaptation potential, but it is uncertain if this may actually improve population stability over the longer term (Thomsen et al. 2017). A recent study with the Manila clam *Ruditapes philippinarum* (Zhao et al. 2018) found that transgenerationally acclimated clams may preferentially extract internal metabolic carbon rather than transport external seawater inorganic carbon to build shells, and suggested that these clams may implement a more efficient energy-utilizing strategy for mitigating ocean acidification which may improve future resiliency. However, transgenerational acclimation is not universally assured and may be a function of trait heritability and selection pressure (Hoffmann & Sgro 2011). For example, increased tolerance to ocean acidification was not apparent in next-generation spiny damselfish *Acanthochromis polyacanthus* (Welch et al. 2014), and exposure to multiple climate stressors may actually be maladaptive for the offspring of some species, such as Sydney rock oysters (Parker et al. 2017). Changes in species' range expansions may also lead to hybridization and introgression between closely related species, which may affect the phenotypic variation in the subsequent offspring (Chown et al. 2015), thereby potentially impacting production traits and overall fitness of aquaculture organisms.

3.3.3. Selection

Selective breeding is regularly employed in aquaculture operations to increase desirable production traits. There is good evidence suggesting that significant genetic change in many aquatic species (e.g. salmonids and oysters) can occur over relatively few generations (Allendorf & Phelps 1980, Taris et al. 2006, 2007, Barnes et al. 2011, Crozier & Hutchings 2014). This artificial selection pressure may reduce genetic diversity, overall population fitness, and resiliency to future environmental change (Evans et al. 2015). In shellfish, where broodstock are often sourced from the wild or maintained in wild conditions, environmental change may drive population genetic variability over generations. For example, an analysis of genetic and phenotypic population clines in areas experiencing ocean acidification via upwelling suggests that shellfish may exhibit local adaptation to ocean acidification, but this adaptation may result in reduced genetic variation and therefore capacity for future adaptation to other challenges (Gaitán-Espitia et al. 2017), such as diseases and

pathogens. Therefore, selection through controlled processes, such as hatcheries and breeding programmes, may not be reflective of production traits which are highly sensitive to changes in the coastal growing environment (Sae-Lim et al. 2017).

Epigenetics examines the interaction of phenotype and environment, where phenotypic changes may be heritable. This does not involve changes to the genetic sequence itself, but may generate changes in gene expression through DNA methylation or histone modification. Epigenetic capacity in response to environmental cues has been studied extensively for some species groups, such as teleosts (Pittman et al. 2013, Gavery et al. 2018), intertidal marine invertebrates (Roberts & Gavery 2012, Padilla & Savedo 2013, Olson & Roberts 2014), and aquatic gastropods (Bourdeau et al. 2015), and to a lesser extent, marine plants (Padilla & Savedo 2013). In a review of epigenetic considerations for aquaculture, Gavery & Roberts (2017) discussed areas where epigenetics may be applied, discussing key areas of environmental manipulation and epigenetic selection to produce animals with desired phenotypes, thereby significantly affecting productivity and sustainability. A study of genetics and epigenetics in *Oncorhynchus mykiss* showed differentially methylated genes between hatchery and wild fish, providing support that epigenetic mechanisms in the selective hatchery environment may be linked to adult phenotypes and may be inherited by future generations (Gavery et al. 2018).

Breeding programmes, whether crude or comprehensive, originate out of the necessity to create a captive stock or the desire to improve production traits. Ironically, breeding regimens often aim to decrease variability in production by increasing consistency of desirable traits such as growth rate, improved survival, and enhanced disease resistance. Consequently, the domestication of animals in some breeding programmes may inadvertently reduce variability and stock adaptive capacity or disregard specific traits important to future climate change scenarios (Gurney-Smith et al. 2017).

3.3.4. Summary — genetics and a changing climate

There is a high degree of variation in genetic and epigenetic responses between species and populations, and within populations and life stages. Consequently, some individuals may respond better to climate stressors than others. Environmental exposure can promote plastic responses in early larval stages,

and parental exposure may confer some traits to offspring. Selective breeding may provide an avenue to adapt species to climate change stressors. However, genetic correlations between climate-related traits and those traits presently selected (e.g. specific pathogen or disease resistance) are largely unknown. Also, the rate and capacity at which most aquaculture populations can adapt in response to climate change stressors have not been well quantified, particularly over long-term exposures and multiple generations. Expectations for the natural ability of culture organisms and traditional selective breeding to safeguard against climate change stressors should be tempered given the current state of knowledge.

3.4. Health

Health management and disease control are among the greatest challenges faced by aquaculture producers globally (Costello 2009, Harkes et al. 2015, Cottier-Cook et al. 2016), and this is considered a constraint to aquaculture expansion in many regions (Rosa et al. 2012, Cottier-Cook et al. 2016). As global aquaculture production expands, the effects of large-scale disease outbreaks have become an increasing economic concern (World Bank 2013, Lafferty et al. 2015). In contrast to the terrestrial realm, research on climate change effects on marine and freshwater diseases is still relatively limited (Karvonen et al. 2010, Rowley et al. 2014), and the scarcity of long-term datasets impedes good understanding of climate change influences on disease levels *in situ* (Karvonen et al. 2010, Callaway et al. 2012).

While specific outcomes are neither clearly understood nor well defined, climate change will have significant effects on parasitism and disease in both freshwater and marine ecosystems (Marcogliese 2001, 2008) in which most aquaculture occurs. Some of the most potentially damaging, but least predictable, effects of climate change in these ecosystems relate to the emergence, translocation, and virulence of diseases, parasites, and pathogens (Callaway et al. 2012). As the environment changes, conditions may become more favourable for nonindigenous hosts, and vectors may be translocated through gradual migration (Cook et al. 1998) or sudden events, such as storms (Scheibling & Lauzon-Guay 2010, Buchwald et al. 2015) and tsunamis (Floyd 2016), creating the potential for novel disease emergence (Zell et al. 2008, Okamura 2016).

Along with the locality and magnitude of environmental changes, rates must also be considered.

Changes at the scale of years to decades may provide a good window for biological adaptation or aquaculture management response. However, the seasonality of many aquaculture diseases (Bowden et al. 2007), or their rapid proliferation under extreme environmental conditions, suggest strong potential for climate change to impact aquaculture health through rapid environmental fluctuations (Kautsky et al. 2000, Selvam et al. 2012, Li et al. 2016, Morash & Alter 2016) or the onset of extremes (Callaway et al. 2012). Increasing frequency of extremes, such as anomalous thermal events, may also reduce the capacity for recovery between events (Baker et al. 2008, Eakin et al. 2010, Burge et al. 2014). The projected near-doubling of El Niño (Cai et al. 2014) and La Niña events (Cai et al. 2015) over this century implies increased potential for extreme seasonal changes across the globe, and these will superimpose over more progressive, gradual changes.

It is anticipated that climate change will affect disease through enhanced parasite/pathogen metabolic rates (e.g. affecting development, transmission, survivability, and virulence), changes to the host (e.g. distribution, behaviour, physiology), or compromised host immune function (Marcogliese 2008, Callaway et al. 2012, Chiamonte et al. 2016). Potential pathways of effects are detailed in Fig. 1. However, predicting specific outcomes is highly challenging for the following reasons: different pathogen or parasite life history traits will show varying responses to temperature (Marcogliese 2016); climate change effects will occur simultaneously with other anthropogenic stressors and may work cumulatively or synergistically to exacerbate negative effects on host organisms and populations (Marcogliese 2008); multiple climate change stressors will also occur in combination, both acute and long-term; projected magnitudes of environmental changes at smaller scales of relevance to discrete aquaculture operations are much more uncertain compared to regional-scale projections; hosts, pathogens, and parasites have adaptive capacity either through long-term evolution (Okamura & Feist 2011) or short-term epigenetic response (the extent of which has not been clearly quantified or qualified; see Section 3.3); parental exposure to an environmental stressor may also influence off-

spring resistance, depending on the duration of exposure (Suckling et al. 2014, 2015); and exposure to environmental stressors in early life stages may also direct some species along different developmental pathways with differing capacity for tolerance (see Section 3.3).

The various effects of climate change on aquatic systems (e.g. changes to temperature, precipitation, salinity, acidification, oceanic circulation, water levels and flow, eutrophication, stratification, ice cover, ultraviolet radiation) all have the potential to affect host–parasite interactions (Marcogliese 2001, 2008) and aquatic animal health. Here, we explore possible effects of climate change on physio-chemical stressors and resultant disease and immune function as considerations for potential outcomes.

3.4.1. Water temperature and infection

There is a contrast between the well-documented and forecasted increase in temperature and the paucity of information regarding potential effects on waterborne microbial pathogens in general (Funari et al. 2012). Nevertheless, there are known relationships between disease and temperature (Marcos-López et al. 2010). Burge et al. (2014) reviewed over 30 studies within the marine environment where disease outbreaks have been linked to temperature

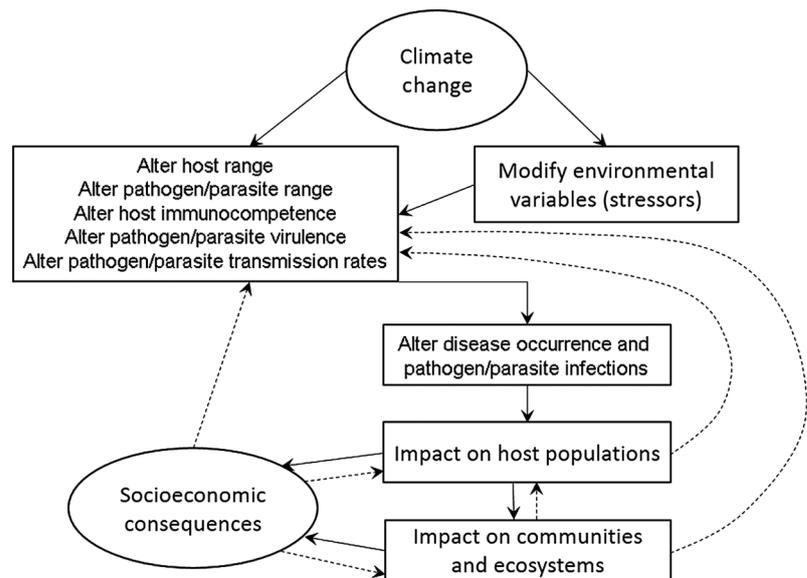


Fig. 1. Schematic representation of climate change effects on pathogens/parasites and their hosts. Effects will cascade, impacting host populations, communities, and ecosystems (solid lines). Effects will be further modified by interactions with other stressors and environmental variables. Population and community effects will feed back to hosts, their pathogens, and parasites (dashed lines). Modified from Marcogliese (2008)

across a range of species groups and infectious agents. Exploring the dynamics of tropical aquaculture diseases suggests that warming waters may generally facilitate infection and mortality. Aquaculture diseases at lower latitudes progress more rapidly and have higher cumulative mortality, with tropical countries suffering proportionally greater losses during disease outbreaks, having less time to mitigate losses (Leung & Bates 2013).

Temperature variability may affect disease dynamics to a greater degree than simple increases in temperature (Rohr et al. 2011, Altizer et al. 2013). Indeed, epizootics of marine trematodes in coastal host populations are predicted to be more common during years when the North Atlantic Oscillation index is high (Mouritsen & Poulin 2002). However, while modelled increase in seasonal temperature variation has predicted increased growth rate of sea lice populations, the response was of lesser magnitude compared to increases in mean temperature (Groner et al. 2014). Temperature variability, its magnitude and frequency, and acclimation temperatures can differentially affect parasite and host life history traits (Marcogliese 2016).

Not all infectious organisms are expected to thrive under warming waters (Harvell et al. 2002, Karvonen et al. 2010). Using a 21 yr dataset on bacterial and protozoan pathogens in fish farms from northern Finland, the latter authors showed that while the prevalence of 2 agents (the ciliate *Ichthyophthirius multifiliis* and the bacterium *Flavobacterium columnare*) increased with mean water temperature over time, others decreased (the flagellate *Ichthyobodo necator*) or showed no change (the ciliate *Chliodonella* sp.). Parasites and pathogens are subject to many of the same environmental constraints as other aquatic organisms, and their ranges tend to be much narrower (Callaway et al. 2012). Some marine viruses infect their hosts across a very narrow temperature window of only a few degrees, suggesting that rapid temperature changes through this range would reduce the time available for infection (Gubbins et al. 2013). Pathogens associated with cooler water suggest lesser potential for spread under warming conditions, such as some salmonid cold-water diseases (Harvell et al. 2002, Gubbins et al. 2013).

However, there is no assurance that pathogen temperature ranges or virulence will remain static under environmental change. Bacteria, fungi, and viruses have short generation times (Gubbins et al. 2013), with arguably greater opportunity for evolution compared to their hosts (Martin et al. 2010). Warming temperatures within optional ranges are apt to

increase the growth rates of aquaculture species (see Section 3.1). Increasing growth rate compresses the host's rearing cycle, and this could favour evolution of increased pathogen virulence (Kennedy et al. 2016). For parasites with complex life cycles, one must consider the net effects of temperature over the parasite's entire life cycle, as physiological tolerances, optimal thermal conditions, and host pathology vary among stages within species (Marcogliese 2016).

3.4.2. Water quality

While temperature is an intuitive environmental focus for aquaculture health, other water quality parameters can become health stressors, including changes in pCO₂, salinity, dissolved oxygen, and eutrophication. Changes in pH along with other parameters such as oxygen and temperature have been linked to infections, such as saprolegniasis in carp (Das et al. 2012) and white spot syndrome virus in shrimp and prawns (Selvam et al. 2012). In the marine environment, research on observed and projected effects of ocean acidification suggests potential for negative effects on structural formation of calcifiers, tissue damage, reproduction, development, and growth in numerous species, as detailed in Section 3.2). Research on ocean acidification and effects to marine aquaculture parasites or pathogens is still in its infancy. While it is expected that ocean acidification will affect marine microbial life, impact specifics are poorly understood (Das & Mangwani 2015, O'Brien et al. 2016), and most host–parasite studies in ocean acidification research have occurred under the umbrella of ecology, not aquaculture (MacLeod 2017). Nevertheless, some recent laboratory simulations may have some relevance to aquaculture. Under ocean acidification conditions, the abundance of *Vibrio* spp. (a major group of pathogens for numerous marine organisms) appears to increase (Zha et al. 2017), and immune functions of Pacific oysters *C. gigas* can become impaired, making them more susceptible to *Vibrio* (Cao et al. 2018). Simulated ocean acidification conditions also appear to impact haemocyte functionality of the blue mussel *M. edulis* (Bibby et al. 2008). While most ocean acidification research associated with disease potential appears negative, there is evidence that the longevity of different life cycle stages of marine trematodes is reduced by decreasing pH (Marcogliese 2016).

As with temperature and other abiotic parameters, effects of salinity vary among stages of the same par-

asite species (Löhmus & Björklund 2015). Changing salinity may even control certain disease outbreaks. A relative reduction in salinity may control infections as such as Dermo disease in oysters (Burge et al. 2014) and sea lice on salmon (Groner et al. 2016), whereas a relative increase in salinity has been reported to control certain infections such as *V. vulnificus* in hybrid tilapia (*Oreochromis* sp.) (Chen et al. 2006) and to decrease infection with the parasitic nematode *Anguillicoloides* (= *Anguillicola*) *crassus* in Atlantic eels (*Anguilla* spp.) (Lefebvre & Crivelli 2012). Saltwater intrusion and storm surge-based flooding may also increase disease susceptibility of coastal freshwater species. Saltwater intrusion into freshwater prawn culture areas in Bangladesh has already been linked to several viral and bacterial infections (Ahmed 2013), but may also lead to reductions in parasite abundance and diversity (Overstreet 2007, Marcogliese 2016).

In some instances, competing environmental effects will affect water quality and have implications for health with uncertain outcomes. For example, higher temperatures are likely to increase stratification in shrimp ponds with low water exchange, potentially increasing hypoxia, reducing production, and increasing the risk of disease, but increased pond mixing is expected with projected rainfall increase (Pickering et al. 2011).

3.4.3. Immune functionality

Climate change-mediated immuno-suppression is complicated, hard to measure, and difficult to tease out from other anthropogenic or environmental stressors at the wider population or ecosystem level (MacKenzie & Köster 2004). While temperature may affect pathogen growth rates, it is also a principal environmental cue stimulating changes in the immune response of fish (Chiaromonte et al. 2016), affecting both innate and acquired immune responses (Bowden et al. 2007, Buchtíková et al. 2011). It is suggested that innate parameters are active at the lower temperature range of finfish, while acquired immune parameters (e.g. lymphocyte activity, antibody production) are more effective at higher temperatures (Magnadóttir 2006). Above an optimum, immune function can be impaired by increasing temperature (Löhmus & Björklund 2015). Shellfish, however, lack a true adaptive immune system and must depend on their innate immune system to overcome disease (Renault 2009). Given the role of temperature in immune functionality, outcomes from seasonal modi-

fication by climate change can be expected. Nevertheless, immune response to temperature may vary widely between related species (Matozzo et al. 2012, Branco et al. 2013). One generality that appears robust, however, is that temperature extremes are detrimental to immune function and contribute to disease outbreaks (Martin et al. 2010). Apart from temperature, concurrent changes in water quality parameters, such as ocean acidification and changes in dissolved oxygen, also have implications for immune functionality in various fish (Choi et al. 2007) and shellfish (Mydlarz et al. 2006, Bibby et al. 2008, Hernroth et al. 2012, 2016, Sui et al. 2016).

The interpretation of apparent competing effects reported in the literature introduces further complexity. Exposure to sub-lethal stress may enhance tolerance to a consequent stressor or incur epigenetic changes that lead to sensitivity to other stressors. Physiological stress decreases disease resistance, but stress-induced heat shock proteins may also enhance the tolerance of aquatic organisms to disease (Sung et al. 2011). While temperature is expected to decrease generation time of many bacterial, viral, and fungal diseases, the acquired immune system of finfish is expected to operate more effectively at warming temperatures (assuming the fish are operating within their thermal limits) and, therefore, with greater potential to overcome infection (Gubbins et al. 2013).

3.4.4. Summary — health

Disease is a major aquaculture limiter globally, and climate change is expected to further affect plant and animal health through the host and/or infectious agents with uncertain, but potentially profound, outcomes. Environmental conditions may become more favourable for some nonindigenous hosts, and translocated vectors may create the potential for novel disease emergence. Temperature is the most investigated environmental parameter affecting aquatic disease, and numerous studies have linked water temperature with infection potential. Climate change-mediated immuno-suppression of hosts is hard to measure and difficult to tease out from other stressors, but temperature extremes are generally detrimental to immune function of aquatic species. The faster progression of diseases in tropical aquaculture regions suggests that globally warming waters may generally facilitate infection, although many tropical culture areas are in developing regions with limited access to health professionals and treatment, which could also be a contributing factor. Nevertheless, not

all infectious agents will thrive under changing environmental conditions. Parasites and pathogens are subject to many of the same environmental constraints as other aquatic organisms, and their ranges tend to be much narrower. This aspect may seem like a potential equalizer, but shorter life cycles of infectious agents compared to their hosts may provide greater opportunity for evolutionary adaptation. Research on the effects of ocean acidification on aquatic diseases is still in its infancy. Disease is apt to continue as a major aquaculture limiter under climate change, and additional fish health challenges are expected.

4. BIOLOGICAL RESPONSE TO MULTIPLE STRESSORS

Until recently, most research on biological response to climate change stressors has focussed on single stressors. As simultaneous increases in CO₂ (reduced pH and aragonite saturation) and temperature will occur together with changes to salinity and in some instances reduced oxygen (Stramma et al. 2012, Boyd et al. 2015), exploring responses to combined stressors will provide important insights for aquaculture adaptation. Stressor combinations that are negatively synergistic may not always be fully additive (i.e. there is interaction), with the greatest biological response often being attributed to a single dominant driver (Brennan & Collins 2015). Multi-stressor studies have been initiated only relatively recently, and thus studies focussing on aquaculture species are still limited. We have therefore also drawn examples from the ecological literature to explore the scope of potential effects.

4.1. Ocean acidification and temperature

Increased temperature has been referred to as the 'evil twin' of ocean acidification, given the potential for negative synergy (Miller et al. 2015). In the autotrophic world, increased CO₂ is expected to enhance productivity. In the Arctic Ocean, for example, this may have a positive fertilization effect on marine autotrophs, while increased temperature should lead to increased planktonic gross primary production; however, the greatest enhancement of primary production is expected to occur under lower temperatures, constrained by spring nutrient and light availability (Holding et al. 2015). In some instances, ocean acidification effects may be mediated by moderate

warming by altering the physiology and seawater geochemistry, such as with growth rates of the Mediterranean mussel *Mytilus galloprovincialis* (Kroeker et al. 2014). In the case of macro-algae, seasonality may affect how pH and temperature interact. Elevated pCO₂ positively affected growth of the bladderwrack seaweed *Fucus vesiculosus*, alone and/or interactively with warming, although the response pathway (additive, synergistic, or antagonistic) was a function of season and day length (Graiff et al. 2015).

In Atlantic halibut *Hippoglossus hippoglossus*, different temperatures can result in differences in down- or up-regulation of immune system-related proteins under elevated CO₂ (Bresolin de Souza et al. 2014), whereas increased temperature has been associated with increased aerobic scope and cardiac performance, but more so under elevated CO₂ (Gräns et al. 2014). For the anemonefish *Amphiprion melanopus*, elevated temperature had a much stronger influence on reproductive traits compared to a minimal influence of elevated CO₂, but offspring quality declined under both increased temperature and CO₂ (Miller et al. 2015). Experimental increases in temperature and CO₂ each significantly depressed survival, development, growth, and lipid synthesis in 3 species of calcifying bivalves (*Mercenaria mercenaria*, *Crassostrea virginica*, and *Argopecten irradians*), and in *M. mercenaria* and *A. irradians* larvae, the effects were additive. While reported outcomes of increasing temperature and decreasing pH for invertebrates are often negative, they are not always additive. Additive negative effects have been reported for the fluted giant clam *Tridacna squamosa* (Watson et al. 2012) and larvae of the invasive sea star *Patiriella regularis* (Byrne et al. 2013). However, increased temperature, but not reduced pH, compromised purple sea urchin *Heliocidaris erythrogramma* fertilization and early development (Byrne et al. 2009). Interactive effects of temperature and pH have been reported to immunomodulate the striped venus clam *Chamelea gallina* and the mussel *M. galloprovincialis* (Matozzo et al. 2012), with effects that were not always linear. Culture experiments with adult Antarctic sea urchins *Sterechinus neumayeri* demonstrated that with a sufficient acclimation period, there were minimal effects of combined pH and increased temperature (Suckling et al. 2015).

4.2. Ocean acidification and dissolved oxygen

CO₂-induced climate change is increasing the extent and severity of both eutrophication-induced hy-

poxia in coastal ecosystems and naturally occurring oceanic hypoxic zones (Levin & Breitburg 2015). Eutrophication is expected to increase in the 21st century due to changes in precipitation (Sinha et al. 2017). Neither the occurrence nor the strength of synergistic impacts of low pH and low dissolved oxygen on biological response is currently predictable nor fully understood (Gobler & Baumann 2016), although some generalizations are reported. Hypoxia and acidification typically have synergistic negative effects on the growth, survival, and metamorphosis of early life stage bivalves (Gobler et al. 2014), and reduced respiration in various other marine invertebrates (Steckbauer et al. 2015). A handful of species-specific responses have been reported to date.

Both hypoxia and low pH have negative effects on the Korean mussel *M. coruscus*, but with significant interaction, where the effects of low pH are not as strong as dissolved oxygen and do not seem to aggravate effects of induced hypoxia (Sui et al. 2016). In 3 species of Northwest Atlantic forage fish, acidification alone significantly depressed the post-hatch survival of *Menidia beryllina*, but not that of *M. menidia* nor of *Cyprinodon variegatus*, while hypoxia alone significantly reduced the length of *M. menidia* and *C. variegatus* (DePasquale et al. 2015). Both acidification and hypoxia together had a negative synergistic effect on length of *M. beryllina* larvae, and hypoxia alone delayed hatching of embryos for all 3 species. This suggests a greater sensitivity of early life-stage estuarine fish to low dissolved oxygen compared to low pH conditions. However, acidified conditions may increase mortality in *M. beryllina* and *M. menidia* when under hypoxic conditions. (Miller et al. 2016).

4.3. Salinity change and concurrent effects

Salinity is expected to decrease in most ocean regions (except the north Southern Ocean, South Atlantic, northern subtropical Atlantic), and inland saltwater intrusion is expected to accompany sea-level rise (Boyd et al. 2015, Hoque et al. 2016). As with other combined stressor studies, salinity also has species-specific optimal ranges in combination with other parameters, such as with the red algae *Gracilaria verrucosa* and *G. chorda* (Choi et al. 2006) and the green-lipped mussel *Perna viridis* (Wang et al. 2011).

Interaction with salinity has also been reported for oxygen, temperature, and pH. Wang et al. (2012) discovered significant interactive effects of oxygen and salinity in the green-lipped mussel *P. viridis*, with

haemocyte mortality increasing under low salinity and low dissolved oxygen. Guzmán-Agüero et al. (2013) reported a significant interaction effect of temperature and salinity in the Cortez oyster *Crassostrea corteziensis*, with scope for growth increasing with temperature but decreasing with increased salinity. Interaction between salinity and temperature has been reported in channel catfish *Ictalurus punctatus*, hybrid catfish (channel catfish female × blue catfish *I. furcatus* male) and transgenic catfish (Abass et al. 2016). In a 3-factor experiment, assessing effects of different salinity, pH, and temperature, the shell area of Portuguese oyster *C. angulata* larvae increased under low salinity and elevated temperature but not in other combinations (Thiyagarajan & Ko 2012). The oxidative status and metabolic capacity of the mussel *M. galloprovincialis* were negatively affected by low pH and salinity change, with the potential for impairment of reproductive output, disease resistance, and growth (Freitas et al. 2017). Some salinity response studies have reported that despite interaction with temperature, one parameter may act as the greatest driver. Salinity is more important than temperature for egg hatching success of the barramundi parasite *Lernanthropus latis* (Brazenor & Hutson 2013), but temperature is more important than salinity for yolk utilization of sac fry Nile tilapia *Oreochromis niloticus* (Hui et al. 2015). However, interaction between salinity and temperature does not occur in all situations. Fertilization and hatching success of the noble scallop *Chlamys nobilis* had a linear relationship with temperature, but not salinity, and with no interaction between them (Lü et al. 2017).

5. AQUACULTURE ECONOMICS

Marine and freshwater aquaculture can anticipate various impacts from climate change, some more severe than others, as detailed elsewhere in this review. A key impact from climate change of pertinence for aquaculture is its potential influence on the severity and frequency of extreme weather events. These events can have extensive effects on aquaculture whether climate change is a factor or not. For example, tropical cyclones Sidri in 2007 and Aila in 2009 devastated shrimp aquaculture in coastal Bangladesh. Kais & Islam (2018) cited damages from the former at US \$36 million from the loss of up to 54 000 shrimps (integrated fish and farm production system), while the latter resulted in damages to 80–90 % of the shrimps in key coastal districts, leading to a reduction in shrimp production of as much as 80 %.

While the influence from climate change on extreme weather events is hotly debated and difficult to isolate, some researchers have suggested that it will have more pronounced effects on the severity of events and less so on their frequency (Allison et al. 2011). However, increasing intensity of hurricanes in the future appears not to have been studied in terms of economic effects. Nonetheless, Hernandez-Llamas & Zarain-Herzberg (2011) examined the influence of hurricane frequency on the economic returns from shrimp raised in floating cages off the northwest coast of Mexico by simulating economic returns with and without the occurrence of hurricanes. They found that the effect of hurricanes on economic returns is pronounced, but can be ameliorated partly by using partial-and-final harvests and by altering grow-out schedules. While we might expect that more severe hurricanes in the future would have a negative impact on economic returns as well, this was not discussed by the authors.

To date, the more technical investigation of economic impacts of climate change on aquaculture has involved intensive modelling exercises of Norwegian salmon farming or more general investigations of effects for aquaculture in the Tropical Pacific region. Lorentzen (2008) analysed the effect of more volatile sea surface temperature on the economics of salmon farming in Norway, while Hermansen & Heen (2012) considered the impact of temperature changes on the spatial distribution of production and employment. One result is the shift of production further north in response to increasing temperatures, with potential effects on production and transportation costs. A more indirectly related area of research has examined the impact of climate change on important feed fisheries (i.e. reduction fisheries) for salmon, especially the anchoveta *Engraulis ringens* fisheries of Peru. Increased climate volatility could raise feed costs (Daw et al. 2009), although any such effects would be moderated by increasing use of alternative feed inputs by the industry.

Climate change could lead to a number of other important impacts on the profitability of aquaculture operations. This observation inevitably arises from a casual review of the many physical and biophysical impacts of climate change outlined in earlier sections. For example, Handisyde et al. (2008) argued that changes in sea surface temperature may accelerate fish growth, thereby improving profitability, but if rising ambient sea temperature also leads to declining dissolved oxygen, stocking densities may have to be reduced, yielding offsetting effects from changing sea temperatures on profitability. Besson et al. (2016)

examined these influences on cage farming of sea bass *Dicentrarchus labrax* in the Mediterranean and found that higher than ambient temperatures (to 19.5 and 21°C) created positive effects on profits, while for smaller increases in temperature (to 18°C) the reverse was true. Meanwhile, the prospect of rising sea temperatures and changing salinity levels for the oyster industry in Rhode Island, USA, was analysed by Sproul et al. (2013), who found that the best response was a mix of slow-growing, disease-resistant varieties and fast-growing, less resistant varieties, akin to diversifying an investment portfolio; the appropriate mix depended on the severity of climate change effects. Finally, Gubbins et al. (2013) suggested that with greater climate volatility and the greater occurrence of extreme events, damages to aquaculture infrastructure would increase, resulting in larger stock losses. They further suggested that other types of disturbances, such as harmful planktonic events or fouling of equipment, may worsen and increase costs for restocking, insurance, and cleaning.

Increasing sea levels under climate change will have additional economic impacts. Pickering et al. (2011) pointed out that coastal pond operations affected by sea-level rise will have greater difficulty with rapid drainage and drying of ponds, requiring heightening of pond walls and floors or costly relocation (if possible at all). Nguyen et al. (2014) argued that sea-level rise will worsen the influence of seasonal increases in water level and salt intrusion for catfish farming in Vietnam; aside from the expense of raising protective dykes, they found that farmers may need to switch to more salt-tolerant and potentially less profitable varieties of catfish. In a separate paper, Nguyen et al. (2016) reported that the associated costs for such a breeding programme for saline-tolerant striped catfish *Pangasianodon hypophthalmus* could require long-term investments of up to 0.40% of production costs, and for upstream *Pangasius* farms outside the upgraded dyke-protected areas, additional dyking would cost up to 0.34% of variable costs per hectare. However, Kam et al. (2012) suggested that catfish farmers may be unable to invest in modifying on-farm infrastructure (e.g. raising dykes) due to the industry's marginal profitability, so that public investment at the regional level may be necessary.

Handisyde et al. (2008) cited rising insurance costs as another potential consequence of rising sea levels and a more volatile climate in general. Opportunities may exist in the future for innovative insurance products such as the 'Extreme El Niño Insurance' being

promoted in Peru, cited as ‘the world’s first regulated insurance product that makes payouts before losses are incurred’ (GlobalAgRisk 2012). Also, changes in disease prevalence and virility add an increased risk to aquaculture operations that reduces potential profits because losses from disease or costs for preventive and treatment measures may increase (Pickering et al. 2011). For example, Álvarez-Salgado et al. (2008) reported that climate change has reduced the upwelling season in northwest Spain and induced longer water retention times in local bays where 15% of the world supply of marine mussels are cultivated. Consequences include increased disease prevalence and reduced windows for safe harvesting, both of which can have an impact on the industry’s economic returns.

Ocean acidification will have substantive repercussions for various farmed species in the aquaculture sector, as detailed in previous sections. Many impacted species are high-valued, so that the economic losses, at least regionally, could be significant. Reported impacts of ocean acidification in the US Pacific region has already resulted in an estimated US \$110 million of lost revenue, and jeopardized 3200 jobs in the shellfish industry (Ekstrom et al. 2015). The ability of a system to respond to such threats will be a result of the level of ecosystem exposure (how real is the threat), social vulnerability (market value of product and number of related jobs), and adaptive capacity (scientific support, political capacity, and diversification potential) (Ekstrom et al. 2015). Bell et al. (2013) cited the case of the lucrative black pearl *Pinctada margaritifera* industry in the tropical Pacific Ocean, which may be particularly sensitive to increases in sea surface temperature and ocean acidification, since these affect nacre deposition and pearl quality, and increase the susceptibility of pearl oysters to disease.

Production losses from disease may be accentuated by climate change, resulting in increasing operator losses. Diseases in farmed oysters, shrimp, abalone, and finfish (particularly salmon) already cost the aquaculture industry billions of dollars annually (Lafferty et al. 2015), as detailed below. In economic terms, diseases impact aquaculture through outcomes such as decreased productivity, reduction in product quality, and increased processing and treatment or restocking costs. For example, outbreaks of white spot disease, which are associated with warmer temperatures, resulted in economic losses that were as high as US \$6 billion in Asia in 1992–1993 and US \$1 billion in Ecuador in 1999. More generally, mitigation costs for the industry in combatting

disease and parasitic outbreaks can be enormous. For example, disinfecting and vaccination to prevent infectious haematopoietic necrosis virus in farmed Atlantic salmon in the Pacific Northwest can cost US \$4 million per farm, while annual global costs to combat sea lice exceed US \$400 million (Costello 2009). To the extent that these problems are worsened by climate change, the costs would rise further. In addition, where climate change leads to greater risks of contamination of shellfish cultured in coastal and estuarine areas, there will be a concomitant rise in human health concerns (Gubbins et al. 2013), leading to various measurable health costs and lowered economic productivity.

Many balanced assessments of climate change impacts find some potential positive effects, and this would also apply to aquaculture. For example, increased growth rates for some species could improve profitability for some aquaculturists. Moreover, improved surface conditions for freshwater aquaculture species such as tilapia, carp, and freshwater prawns could support expanded livelihood opportunities for inland populations providing that feed supplies are not an issue (Pickering et al. 2011). In China, Li et al. (2016) modelled provincial-level freshwater aquaculture profits as a function of climate variables and showed that profits predominantly will be positively influenced by climate change at more northerly latitudes, at least in the short run. In the worst case, rapidly advancing impacts of climate change, such as rising sea levels, could produce ‘environmental refugees’ for whom new opportunities may open up in freshwater aquaculture further inland. This perspective identifies aquaculture as a potential adaptive strategy in the face of advancing climate change, as Dey et al. (2016) argued for Fiji. Similarly, it has been suggested that coastal households possessing aquaculture assets are better poised to rebound after extreme events, leading researchers to propose that aquaculture be promoted for income and food security in coastal areas (Karim et al. 2014).

Overall, there has been relatively little exploration of the potential economic consequences of climate change for aquaculture, and more research is needed. While some modelling of the economics of climate change effects has been carried out for Norwegian salmon farming and for a few other species (e.g. *Pangasius* sp. and shrimp), most aquaculture sectors remain unstudied. Key policy questions with an economic component need further study as well. Examples include the role of subsidies, both destructive subsidies that increase aquaculture production in vulnerable areas and involve susceptible species,

and needed subsidies for investments in infrastructure and predictive tools to aid in responding to the climate change threat. Dulvy & Allison (2009) provided several suggestions for 'mainstreaming' marine fisheries and aquaculture into climate change policy processes and emphasized the need to build resilience in these systems and assess vulnerabilities of not just the production operations, but also of the dependent human populations.

6. FINFISH AND INVERTEBRATE DIETS

How climate change will affect ingredient sourcing for aquafeeds (De Silva & Soto 2009, Brugère 2015) and feed management (Shelton 2014) is a pressing concern. Approximately 70% of total global aquaculture production by weight is dependent upon the supply of external feed inputs (Tacon & Metian 2015), and a major challenge for long-term sustainability is to reduce dependence on capture fisheries as a source of raw materials for feed formulations (Tacon et al. 2009). Despite great strides in identification and development of alternative ingredients (e.g. meals derived from soy or corn), small pelagic fish (De Silva & Soto 2009) are still heavily used for aquafeeds, and the reduction fisheries accounted for about 17% of the global fisheries landings in 2014 (Tacon & Metian 2015). Climate change may therefore further complicate the relationship between aquaculture and the capture fisheries.

Population fluctuation of reduction-fisheries species, such as sardine *Sardinops sagax* and anchovy *Engraulis mordax*, are explained by interacting density-dependent processes and climate forcing (Lindegren et al. 2013, Buchheister et al. 2016). Merino et al. (2010) modelled the interacting effects of climate-driven fluctuations on reduction-fisheries stocks and expansion of fish meal demand under various management schemes. Model projections suggested that regional stocks could recover from climate-driven fluctuations, but only if increased fish meal demand and sub-optimal management did not occur simultaneously. As demand for fish meal and oil are increasing (Tacon & Metian 2015) and sub-optimal management of fisheries worldwide is a continuing challenge (World Bank 2015, Vivekanandan et al. 2016), fisheries decline cannot be ruled out.

Climate change influences on micro-algae, either as a direct food source or indirectly through food webs (Doney 2006), may have major implications for some types of aquaculture. Micro-algae (phytoplankton) are commonly used as feed for cultured finfish

larvae (through zooplankton), bivalve molluscs, and crustaceans (Wikfors & Ohno 2001). On a global scale, the production of major non-fed species contributed 30.7% by weight to world food fish aquaculture production in 2013 and consisted mainly of filter-feeding bivalves and carps, with 14 Mt of bivalves cultured in marine systems (FAO 2015).

Phytoplankton species account for less than 1% of the Earth's photosynthetic biomass, but contribute approximately 50% of the global carbon biogenic fixation (Field et al. 1998), with the global population replaced, on average, every 2 to 6 d (Falkowski et al. 1998, Behrenfeld et al. 2006). Warmer and more stratified oceans are expected to shift phytoplankton communities towards smaller sizes with reduced adaptive capacity (Acevedo-Trejos et al. 2014) and to shift cold-water species' ranges poleward (Hallegraeff 2010). The increase in global sea surface temperatures is also projected to reduce phytoplankton abundance in tropical and mid-latitude regions, while there may be greater phytoplankton abundance in higher-latitude regions. This is because tropical areas are typically nutrient-limited, whereas polar areas are typically light-limited (Richardson & Schoeman 2004, Doney 2006). However, impacts will vary with location (Doney 2006), possibly benefitting filter-feeding species of shellfish aquaculture in currently nutrient-limited areas (De Silva & Soto 2009). Some micro-algae can form harmful algal blooms, which are toxic to aquaculture species or which have impacts for human consumption, but the effects of climate change on the severity and frequency of these blooms is uncertain (Wells & Trainer 2016). Nevertheless, El Niño events have been linked to massive harmful algal blooms in Chile in 2015 and 2016, and, in combination with extreme heat and low dissolved oxygen, impacted Central American tilapia production (Soto et al. 2018). Climate change effects on 'green water' for fish ponds have also warranted consideration. Takarina et al. (2017) reported that during peak high temperatures and consequent oxygen decline in west Java fish ponds, the phytoplankton population was significantly reduced, but not the diversity. There may be qualitative effects to phytoplankton diets as well. Climate warming is predicted to reduce n-3 long-chain, polyunsaturated fatty acid production in micro-algae (Hixson & Arts 2016).

Data on ocean acidification effects on nutrition are limited, although there has been some suggestion that increased dietary demand by the larval stages of some species under future pH conditions may be affected. Acidified conditions may compromise the feeding energetics of the sea urchin *Strongylocentro-*

tus droebachiensis. Larvae exposed to seawater with lower pH had lower gastric pH, leading to reduced digestive efficiencies and higher food consumption (Stumpp et al. 2013).

The cost of feed is one of the largest expenses for fed aquaculture production, and dynamics that affect the availability of key ingredients, like fish meal, have greater potential to influence overall production costs. Climate change is expected to further complicate this relationship between aquaculture and climate-sensitive reduction fisheries. While the source materials used to generate ingredients for feed production varies by culture species, the impact of climate change may make traditional sources more challenging to obtain. Fortunately, research on alternate ingredients has been undertaken for many decades, often driven by reductions in periodic availability of fishmeal and fish oil brought about by episodic large-scale oceanic conditions (e.g. El Niño), irrespective of climate change. However, non-fed species typically source food in the local environment and are arguably more vulnerable to climate change if local dietary sources are affected.

7. CONCLUSIONS

Information specific to climate change and aquaculture is still in its infancy, but there have been exponential increases in climate change publications in areas of importance to aquaculture. Summarizing relevant global research and reports, with vast differences in regional environments, culture systems, and species, in combination with uncertainties of effects, is not trivial. However, there are some recurring trends and generalities that may have application across the aquaculture spectrum. These are as follows:

- (1) The heavy reliance of most global aquaculture on the ambient environment and ecosystem services suggests inherent vulnerability to climate change effects.
- (2) Biological response to climate change stressors between related species or even between populations of the same species is not universal.
- (3) The magnitude of response, whether positive or negative, as well as negligible responses of a species or population to changes in the climate system, will be a function of:
 - (a) where changes occur relative to optimal ranges and tolerance limits of an organism's life stage and physiological processes
 - (b) the average magnitude and duration of the stressor over the production cycle

- (c) stressor rate of change
 - (d) variation, frequency, duration, and magnitude of extremes
 - (e) interaction with other stressors
 - (f) organism capacity for epigenetic expression or plasticity
 - (g) genetic strain and population variation
 - (h) diet quality and quantity
- (4) Multiple climate change stressors will occur together and frequently interact. Interaction may not be fully additive or linear but may be synergistic, and one dominant driver may have the greatest effect depending on species and life stage.
 - (5) There is some potential for epigenetic or short-term acclimation to climate change stressors, but this has not been well quantified or qualified for most aquaculture species and populations. For some species:
 - (a) Exposure to environmental stressors during early rearing may have a major influence on successful adaptation to similar or different stressors in later life stages.
 - (b) Parental exposure to environmental change may influence the adaptation potential of offspring.
 - (6) Climate change may affect plant, algal, and animal health through the host, and/or infectious agents, with uncertain, but potentially profound, outcomes.
 - (7) Some aquaculture practices (current and previous) may inadvertently reduce resilience to climate change, such as:
 - (a) reducing coastal protection through historical removal of coastal vegetation
 - (b) increasing the rate of ground subsidence (lowering) through pumping
 - (c) reducing genetic variability through domestication in pursuit of consistent production traits, which may impact acclimation and adaptation to climate stressors
 - (8) Higher production costs at aquaculture operations could be an expected economic impact of climate change for many aquaculture sectors.
 - (9) Climate change is apt to add additional complexity to the sourcing of ingredients for aquafeeds and affect phytoplankton dynamics for marine filter feeders.
 - (10) Competition for freshwater resources is apt to be augmented under climate change.

There are gaps in knowledge and/or data accessibility on climate change effects for large portions or world aquaculture, and these form 2 potential limitations of this review. The first limitation is that this review draws primarily upon the scientific English language literature, which is heavily focussed on marine systems in developed regions. As such, this

review may not be fully reflective of large segments of world aquaculture production. The second limitation is that aquaculture research on the top 3 globally produced species by weight is not well represented in the climate change literature. Grass carp *Ctenopharyngodon idellus*, silver carp *Hypophthalmichthys molitrix*, and common carp *Cyprinus carpio* contribute to 29% of global aquaculture production (FAO 2018a). These species are heavily produced, in part, due to their resilience and versatility. This robustness reflects their success as invasive species and difficulties eradicating them from novel habitats (e.g. Crichigno et al. 2016, Weber et al. 2016, Erickson et al. 2018, Prechtel et al. 2018), suggesting some potential for tolerance to multiple stressors. Nevertheless, potential resistance to climate change stressors would benefit from explicit quantification in these species to better support planned adaptation for such a large portion of world aquaculture.

Various aquaculture sectors are already being affected by climate change, and greater effects are anticipated. Global-scale consideration of the differences, commonalities, and knowledge gaps of biological responses and resource effects from climate change stressors can guide pragmatic focus on specific aquaculture sectors to better anticipate consequences and prioritize response efforts.

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