

## Resilience of cold water aquaculture: a review of likely scenarios as climate changes in the Gulf of Maine

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### Abstract

Climate change is one of the biggest challenges facing development and continuation of sustainable aquaculture in temperate regions. We primarily consider the ecological and physical resilience of aquaculture in the Gulf of Maine (GoM), where a thriving industry includes marine algae, extensive and intensive shellfish aquaculture, and a well-established Atlantic salmon industry, as well as the infrastructure required to support these economically important ventures. The historical record of sea surface temperature in the GoM, estimated from gridded, interpolated *in situ* measurements, shows considerable interannual and decade-scale variability superimposed on an overall warming trend. Climate model projections of sea surface temperature indicate that the surface waters in the GoM could warm 0.5–3.5°C beyond recent values by the year 2100. This suggests that, while variability will continue, anomalous warmth of marine heatwaves that have been observed in the past decade could become the norm in the GoM *ca.* 2050, but with the most significant impacts to existing aquaculture along the southernmost region of the coast. We consider adaptations leading to aquacultural resilience despite the effects of warming, larger numbers of harmful nonindigenous species (including pathogens and parasites), acidification, sea-level rise, and more frequent storms and storm surges. Some new species will be needed, but immediate attention to adapt existing species (e.g. preserve/define wild biodiversity, breed for temperature tolerance and incorporate greater husbandry) and aquaculture infrastructure can be successful. We predict that these measures and continued collaboration between industry, stakeholders, government and researchers will lead to sustaining a vibrant working waterfront in the GoM.

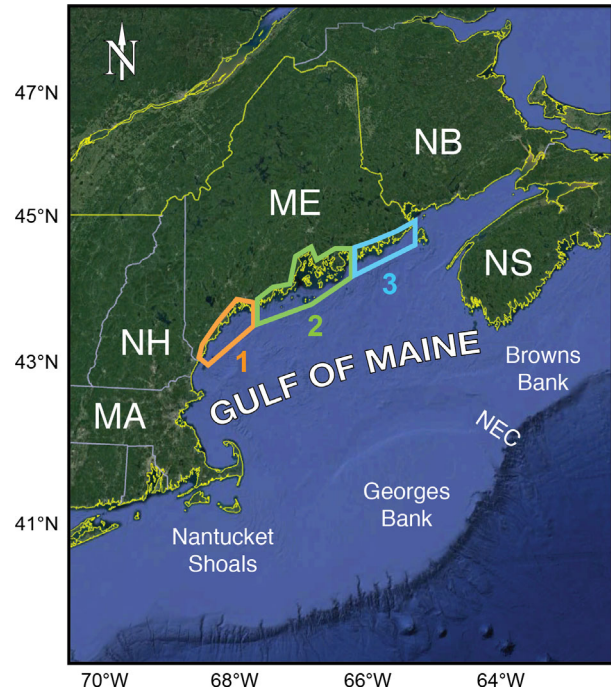
**Key words:** aquaculture, climate change, cold water aquaculture, Gulf of Maine, ocean acidification, resilience.

[Correction added on 5 October 2020, after first online publication: The names of the 5th and final authors contained errors and have been corrected. Redundant section references have additionally been removed throughout the text.]

## Introduction

Marine aquaculture is widely practised in the United States with well-established finfish (Atlantic salmon), shellfish (oysters, mussels and clams) and marine algae (sugar kelp, winged kelp and microalgae) sectors. While much of this is commercial aquaculture, conservation aquaculture is also well-developed, including stocking of both Atlantic and Pacific salmon to support wild stocks as well as other species such as the Devil's Hole pupfish (Feuerbacher *et al.* 2017). Despite the growing size of the domestic industry, aquacultured organisms comprise over 60% of marine foodstuffs imported into the United States each year, leading to an annual seafood deficit of over \$18 billion with about \$9 billion of that deficit coming from aquacultured organisms (Abolofia *et al.* 2017). This deficit affects food biosecurity and public health, because the United States typically has higher standards than many other countries that produce aquacultured foodstuff. The 2012–2018 ban by the USDA of aquacultured shellfish from South Korea due to the high prevalence of norovirus and systematic failings of the testing capability of South Korean laboratories during that period to detect this pathogen were major concerns (Moon *et al.* 2011; Rothschild 2012; USDA 2018). Of equal concern is the mislabelling of marine products, wild and aquacultured, often by substituting less valuable species for high-value foods. Not least is the regular substitution of red snapper, *Lutjanus campechanus* (Poey, 1860), with less valuable species (Marko *et al.* 2004). In some cases, this high-value fish is replaced with much cheaper aquacultured species such as tilapia, and this type of fraud is estimated to affect 30% of all fish consumed worldwide (Black *et al.* 2017). Expanding the marine aquaculture industry in the United States would not only help to reduce this food deficit, but also help to maintain working waterfronts in many coastal states that are impacted by the collapse of commercial fisheries (Hawkins 2002; Gunning *et al.* 2016).

Maine is a mostly rural state (~80,000 km<sup>2</sup>) in the north-eastern United States with 5,600 km of mostly rocky, largely undeveloped coastline along the Gulf of Maine (Fig. 1). The state was historically affected by fisheries declines and is ideally situated for a growing marine aquaculture sector. With the collapse of the historical groundfish fishery, the lobster fishery dominates the remaining capture fisheries in both volume and value (Maine DMR 2019a). Maine needs to improve and diversify its rural economy and increase revenue in these communities. Aquaculture serves as an important socio-economic, resilience-building strategy that offers fishermen and other entrepreneurs an alternative source of income, considering the threat of fisheries decline (Cleaver *et al.* 2018).



**Figure 1** Map showing the Gulf of Maine and adjoining features. Areas outlined in orange, green and blue represent Bioregions 1–3 discussed in the text. U.S. states with coastlines bounding the Gulf of Maine: MA = Massachusetts, NH = New Hampshire, ME = Maine; Canadian provinces: NB = New Brunswick, NS = Nova Scotia. NEC = Northeast Channel. Base map from Google Earth.

Marine aquaculture has developed steadily, as detailed by Maine Department of Marine Resources' harvest reports begun for salmon in 1988, mussels and oysters in 2005 and marine algae in 2015. Total value of marine aquaculture exceeded \$60 million in 9 years between 2010 and 2019 and was reported as \$88,408,714 in 2019 (Maine DMR 2020). Mussels (1,065 metric tons, *Mytilus edulis* L.) and oysters (6,300 mt, *Crassostrea virginica* (Gmelin, 1791)) accounted for \$13,692,925 of this value, and much of the rest can be attributed to Atlantic salmon (*Salmo salar* L.). The value of the salmon harvest was not reported by DMR after 2010, when it was valued at \$55 million (Maine DMR 2020), because of confidentiality requirements triggered by aggregation of the salmon industry into a single large company after 2010. The newest (2015) aquaculture sector increased in value from \$37,897 (2018) to \$176,132 (2019) based on harvest of three kelp species (*Alaria esculenta* (Linnaeus) Greville 1830, *Saccharina angustissima* (Collins) Augyte, Yarish & Neefus 2018, *Saccharina latissima* (Linnaeus) C.E. Lane, C. Mayes, Druehl & G.W. Saunders 2006). Soft-shell clams (*Mya arenaria* L.) have been cultured in Maine since 1987 for public stock enhancement associated with coastal municipalities that manage their wild populations (Beal *et al.* 2016). Additional marine

species are farmed at a small scale (Maine DMR 2020) or are being developed experimentally, but integrated multi-trophic aquaculture (IMTA) remains rare (see below), despite its recognized environmental benefits. In 2019, 610 hectares of Maine coastal waters were farmed at 149 coastal leases for finfish, shellfish and marine algae (Maine DMR 2020).

Given the importance of the emerging aquaculture sector in the United States, a five-year \$20M grant was executed to investigate resilience of the cold water aquaculture sector in the north-eastern United States. The work was funded by the National Science Foundation and titled 'The Nexus of Coastal Social-Environmental Systems and Sustainable Ecological Aquaculture (IIA-1355457)'. This project, 'SEANET', considered likely climate change scenarios and the potential impacts on Maine's coastal communities and cold water aquaculture (SEANET 2020). The following review is based on the findings and the relevance of the research carried out over the five-year SEANET grant.

Due to the economic contributions of the growing aquaculture sector in Maine, it is of great importance to consider the potential impact of climatic and demographic changes on the industry. The vulnerability of Maine's economy is highlighted by the impact of COVID-19, because the major economic drivers of industry, tourism and hospitality have been seriously impacted (Bever 2020). The traditional lobster fishery has suffered a major contraction of income, shrinking by around 70% with the price for lobster hovering around \$4–\$8 kg<sup>-1</sup> (Hall 2020). Lobster has long been considered a luxury food; with the closure of most restaurants, lobstermen are faced with glut of supply and limited outlets. Diversification of these traditional industries to incorporate aquaculture is essential to produce a more robust working waterfront that is less susceptible to global factors such as pandemics. The collapse of lobster fisheries in southern New England highlighted the vulnerability of this industry. A major reskilling of the workforce increased aquaculture activity in that region (Colburn *et al.* 2016), and while only 10–20% of traditional lobstermen remain active, many are still contributing to the marine economy by diversifying into shellfish or seaweed aquaculture.

The Gulf of Maine is vulnerable to a wide variety of climatic shifts, and its warming waters have affected fisheries and marine ecosystems (Pershing *et al.* 2015). In addition, demographic changes such as amenity migration and gentrification, and ageing of the fishing fleet are reshaping Maine's communities (Thompson *et al.* 2016; Johnson & Mazur 2018). Building a resilient industry requires an understanding of the ecological, physical and social characteristics of both the industry itself and the environment in which it is established. To consider the concept of resiliency, it is first necessary to establish a clearly understood

definition in the context of ecological, social and physical parameters.

### Ecological resilience

Ecological resilience has a variety of definitions. Holling (1973) defined ecological resilience as a measure of the persistence of systems and their ability to absorb disturbances while maintaining the same relationships between populations and state variables. This definition has been expanded from the population to the system level by Walker *et al.* (2004) as the ability of a social–ecological system to absorb disturbances and reorganize while undergoing change, so as to still retain essentially the same functions, structures, identity and feedbacks. Gunderson (2000) suggested that an ecological system may possess alternative stable states, and resilience is the amount of disturbance that a system can absorb without changing stability domains. An additional definition is the magnitude of disturbance that can be absorbed before the system changes its structure by changing the variables and processes that control behaviour (Gunderson *et al.* 2002). Finally, Angeler and Allen (2016) defined ecological resilience as the amount of change needed to alter an ecosystem from one set of processes and structures to a different set of processes and structures, which clarified the possibility of existence of alternative regimes and thresholds for the same system.

Ecosystem resilience is the capacity of a system to persist or maintain its function in the presence of a disturbance (Walker *et al.* 2004), such as climate change, and is typically derived from measurable characteristics, such as the variety of genotypes and species, the availability of nutrients or the level of pollution. More specifically, climate resilience can be described as the capacity of ecological, physical (e.g. infrastructural) and social systems to address challenges and to respond to opportunities while maintaining the same function, structure and overall identity (IPCC 2007). Johnson *et al.* (2019) described how aquaculture farming practices may influence the resilience of a marine ecosystem, such as integrated multitrophic aquaculture promoting colocated removal of waste nutrients from one species by another, colocating macroalgal production with bivalves to influence local pH and enhance shell growth rates, or selective breeding of bivalves to increase disease resistance.

A resilient aquaculture industry relies on several ecological characteristics of a coastal ecosystem, including average sunlight and sunlight penetration (e.g. cloud cover and water turbidity), water temperature, salinity (influenced by rainfall and salinity of offshore waters), alkalinity and water quality (e.g. devoid of toxins and nitrogen levels below eutrophication threat). Changes in characteristics such as temperature can have a significant impact on the reproductive cycles of marine biota and are highly influenced by

existing and future climate scenarios (Cartwright *et al.* 2019; Hughes *et al.* 2019; Noor & Das 2019; Rothausler *et al.* 2019; Wilson & Lotze 2019; Azra *et al.* 2020). A significant rain event can transport particulate matter into streams, rivers and estuaries, raising the turbidity of the water and lowering primary production, which can limit bivalve feeding by up to 40% (Lohrer *et al.* 2006). Conversely, the influx of freshwater can reduce environmental pH, limiting the ability of bivalves to form shell and inhibiting several key phases of larval recruitment and development (Kapsenberg *et al.* 2018).

Indirect impacts from changes to system parameters can threaten sustainability of the aquaculture industry, such as pathogen and invasive species introductions/outbreaks (Bush *et al.* 2010). One significant risk under a changing and likely warmer climate is the potential for the Gulf of Maine to become more suitable for diseases that are currently considered exotic to Maine's cold waters. Nonindigenous species (NIS, 'invasive species') are a global challenge, and the economic impacts of NIS in marine ecosystems appear incalculable on either a US or global basis (Ojaveer *et al.* 2018). Warming ocean temperatures allow more invasive species to establish and flourish, adding to the thermal burden on ecological systems (Sorte *et al.* 2010). Climate change and ocean acidification were proposed as causes of increased susceptibility to infectious diseases in farmed and wild stocks, as well as direct adverse effects on physiology (Gubbins *et al.* 2013). The proposed increases in temperature, combined with changes to the ocean's chemistry, will induce a marked physiological stress, and stress is considered to be a major risk factor in susceptibility to infectious diseases (Gubbins *et al.* 2013).

The appearance of new pathogens and increased pressures from invasive species in the Gulf of Maine will drive the need for biotechnological innovation aimed at mitigating the growing vulnerability of the coastal ecosystem and marine-dependent industries. For example, the spread of the European green crab *Carcinus maenas* has led to research and development of new commercial products such as pet food with these crabs as a primary ingredient (Staples 2019). Creating new products can incentivize a new fishery and may reduce NIS damage. While new technologies may help to reduce the vulnerability of coastal ecosystem functioning, it is essential that the direct and indirect impacts of climate change are considered in aggregate in order to assess the current and potential risks for a resilient aquaculture industry.

### Social resilience

The role of social networks, institutions and discourses in supporting industry resilience has been studied using practical (e.g. demographic or regulatory change, and

organizational involvement) and theoretical measures (e.g. social capital and place attachment; Keck & Sakdapolrak 2013; Maclean *et al.* 2014). Among the social determinants of an aquaculture industry's resilience, knowledge and related discourse have received the most attention. In the United States, public knowledge about aquaculture is limited (Murray *et al.* 2017) and reflects much of the information provided in print news media (Rickard & Feldpausch-Parker 2016). Newspaper coverage of aquaculture tends to balance the benefits with the risks of aquaculture development (Rickard & Feldpausch-Parker 2016; Olsen & Osmundsen 2017). When given equal attention in the news, these positions can have negative effects on attitudes, especially among people unfamiliar with aquaculture (Robertson *et al.* 2002).

While there is a broad need for aquaculture literacy in the general public, there must be concerted educational efforts pertaining specifically to aquaculture development in the face of climate change for both farmers and the communities in which farms are embedded. As the human population continues to grow, and, with it, the demand for additional protein sources, global aquaculture production continues to increase (FAO 2018a). The growth of the aquaculture sector is therefore becoming more prominent in communities and increasingly competing for space with other users of the coastal marine zone (Kannen 2014). For example, a variety of organizations in Maine is developing aquaculture-based curriculum for students as young as kindergarten (Island Institute 2016; University of Maine Cooperative Extension 2016, 2018, 2020). Members of Maine's aquaculture industry also participate in ongoing education and community outreach by hosting events with their cultured products and offering farm tours. These various efforts can support the development and maintenance of the community relationships and dialogue needed to facilitate further growth in the industry.

As a rapidly growing sector with many new entrants each year, the cold water aquaculture industry is a socially and economically important resource that must be included in climate change discussions to help fortify coastal communities in the face of a changing environment. The social resiliency of aquaculture is dependent upon the industry's (adaptive) capacity to leverage networks, institutions and discourses to cope with existing changes and adapt to new ones. Community campaigns that engage the public on important matters related to their local coastline, seafood production and working waterfront can help mobilize the action needed to reduce community and industry vulnerability to the adverse impacts of climate change.

### Physical resilience

Aquacultural farming, regardless of species type, is reliant on physical coastal infrastructure (e.g. docks, piers and

anchored farm structures) to support growing and harvesting operations. The design aspects of infrastructure in the face of climate change, including rising sea level and the increased frequency of higher-energy storms, are key aspects of aquaculture resilience. The frequency of extreme storm events is projected to increase from every 100 years to every 10 years by 2050 (Tebaldi *et al.* 2012). Sea-level rise will also enhance storm surge levels (Lowe & Gregory 2005), modify the principal tide (Cai *et al.* 2012; Devlin *et al.* 2017a,b) and increase nonlinear overtides (Holleman & Stacey 2014). Traditional shoreline protection measures (e.g. breakwaters, seawalls and rip rap) not only increase habitat loss and exacerbate erosion (Currin *et al.* 2010), but they also become less effective in deeper mean sea levels (Sutton-Grier *et al.* 2015; O'Donnell 2017), making the coast particularly vulnerable to climate change. Developing more sustainable methods for protecting coastal areas from waves and storm surge will become increasingly necessary. Making use of 'soft' breakwaters to reduce wave energy, such as seaweed or mussel farms, could provide a more resilient and ecosystem-friendly alternative to traditional shoreline hardening.

Climate change will also have profound impacts on aquacultural engineering. Aquaculture structures (e.g. mussel rafts, salmon pens, floating oyster cages and kelp long lines) must withstand loading from water-level fluctuations (i.e. tidal variations and storm surge), current velocities (Nguyen *et al.* 2019) and wave action (Fredriksson *et al.* 2005). Climate change impacts on these forcing mechanisms present a risk to existing aquaculture structures. Increased loading from larger storm tides and/or waves can lead to mooring line and anchor failure. Modifications to the tide can alter flow patterns near structures and may impact nutrient delivery and farm flushing, demonstrating that structural failure is not the only threat to farm design. The vulnerability of aquaculture farms is specific to the type of structure and location (sheltered in an estuary or exposed along a coast). Understanding how climate change will alter forcing parameters, which are used to evaluate the resiliency of aquaculture farm designs and to anticipate how farm designs might need to adapt, is of utmost importance to reduce the vulnerability of the aquaculture industry.

### Aims of the paper

In order to address the resiliency of the aquaculture industry, it is imperative to assess the various ecological, physical and social parameters on which the sustainability of the industry depends. The impacts of climate change on the Gulf of Maine are expected to be far-reaching, including warmer ocean temperatures, rising sea levels and increases in invasive species and diseases. Therefore, the purpose of

this paper is threefold: (i) to ascertain whether or not a cold water aquaculture industry in its current form in Maine is resilient to changing ocean conditions; (ii) to determine the major risks to and vulnerabilities of sustainable ecological aquaculture; and (iii) to understand how known impacts of climate change will restructure and redefine the future of the aquaculture industry in Maine, with relevance to regions beyond the Gulf of Maine. Because current and predicted temperatures vary regionally across the long Maine coast, we delineated three coastal bioregions (Fig. 1) for our analysis.

### The Gulf of Maine and climate change

The Gulf of Maine is a mid-latitude marginal sea in the north-west Atlantic Ocean (Pettigrew *et al.* 2005), which is bounded (Fig. 1) by the coastlines of New England (Maine, New Hampshire, Massachusetts) and Atlantic Canada (New Brunswick, Nova Scotia). Interior waters of the Gulf are significantly isolated from the North Atlantic Ocean by Nantucket Shoals, Georges Bank and Browns Bank (Townsend 1991). The limited influx of Atlantic seawater (Townsend *et al.* 2015) is from Scotian Shelf Water (cool, relatively fresh flow from the Nova Scotian Shelf), Labrador Slope Water (cold, relatively fresh flow derived from the Labrador Current) and Warm Slope Water (warm, salty flow associated with the Gulf Stream and adjacent waters). Scotian Shelf Water enters the Gulf of Maine as a surface flow, whereas the Labrador and Warm Slope Waters enter at depth via the Northeast Channel. The two Slope Water sources deliver most of the dissolved inorganic nutrients to the Gulf (Townsend *et al.* 2015).

The Gulf of Maine, with its diverse ecosystems and unique morphometry and hydrography, is vulnerable to climate change. For example, the relative composition of the shelf and slope-sourced water fluxes described above has become more variable and unpredictable in the Gulf, possibly due to the Labrador Sea receiving more freshwater from melting sea ice (Townsend *et al.* 2015). Warm Gulf Stream ring water also appears to be entering the Gulf of Maine at depth in some years (Townsend *et al.* 2015). In addition to warmer temperatures from altered water fluxes into the Gulf, ocean acidification is expected to increase and deteriorate habitat for shell-forming organisms crucial to aquaculture (Dupigny-Giroux *et al.* 2018). Further warming and acidification will likely bring major changes to fauna and flora in the Gulf over the course of this century. While it is impossible to predict with certainty how the biota of the Gulf of Maine will change over this century, we can at least expect a significant shift from a boreal to a more temperate ecosystem. All of this underscores the need to better understand historical and future climate trends in order to develop robust resilience strategies for aquaculture.

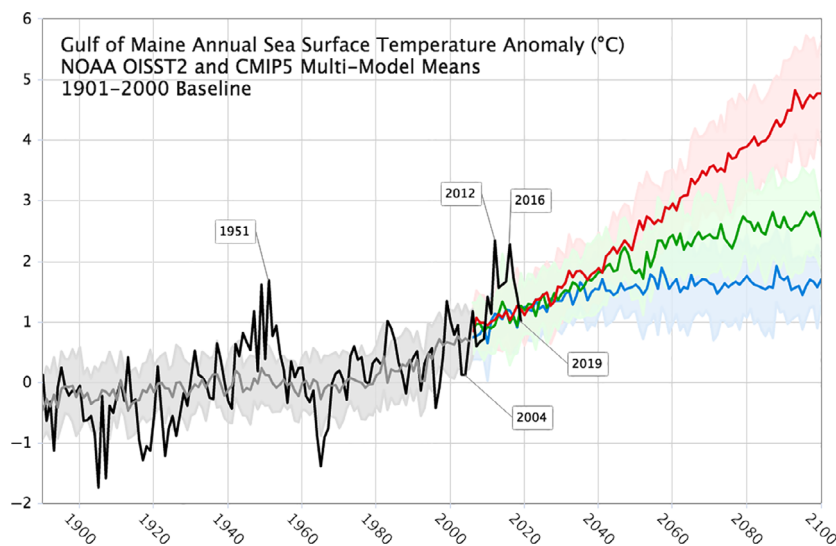
## Sea surface temperature

The historical record of sea surface temperature (SST) in the Gulf of Maine, estimated from gridded, interpolated *in situ* measurements (Huang *et al.* 2017), shows considerable interannual and decade-scale variability superimposed on an overall warming trend (Fig. 2). Similarly, an analysis of shore-based and nearshore measurements indicates that coastal temperatures have warmed at an average rate of  $1 \pm 0.3^\circ\text{C}$  per 100 years (Shearman & Lentz 2010) or approximately  $1.3^\circ\text{C}$  between 1880 and 2010. A continuous record of seawater temperature at West Boothbay Harbour ( $43^\circ50'40''\text{ N}$ ,  $69^\circ38'30''\text{ W}$ ) close to shellfish and macroalgal aquaculture in the Damariscotta Estuary (Bioregion 2) shows a mean annual increase of  $2.4^\circ\text{C}$  between 1905 and 2018 (Maine DMR 2019b).

The past decade is the warmest on record in the Gulf of Maine, and, between 2004 and 2013, surface waters are estimated to have warmed at a rate of  $0.23^\circ\text{C}$  per year, a rate faster than that measured for any other marine water body (Pershing *et al.* 2015). In 2012, a remarkable ‘marine heatwave’ (MHW) developed in association with an extreme northward shift of the Gulf Stream and atmospheric patterns bringing persistent warm weather across the region (Figs 3–5; Gawarkiewicz *et al.* 2012; Mills *et al.* 2013; Chen *et al.*

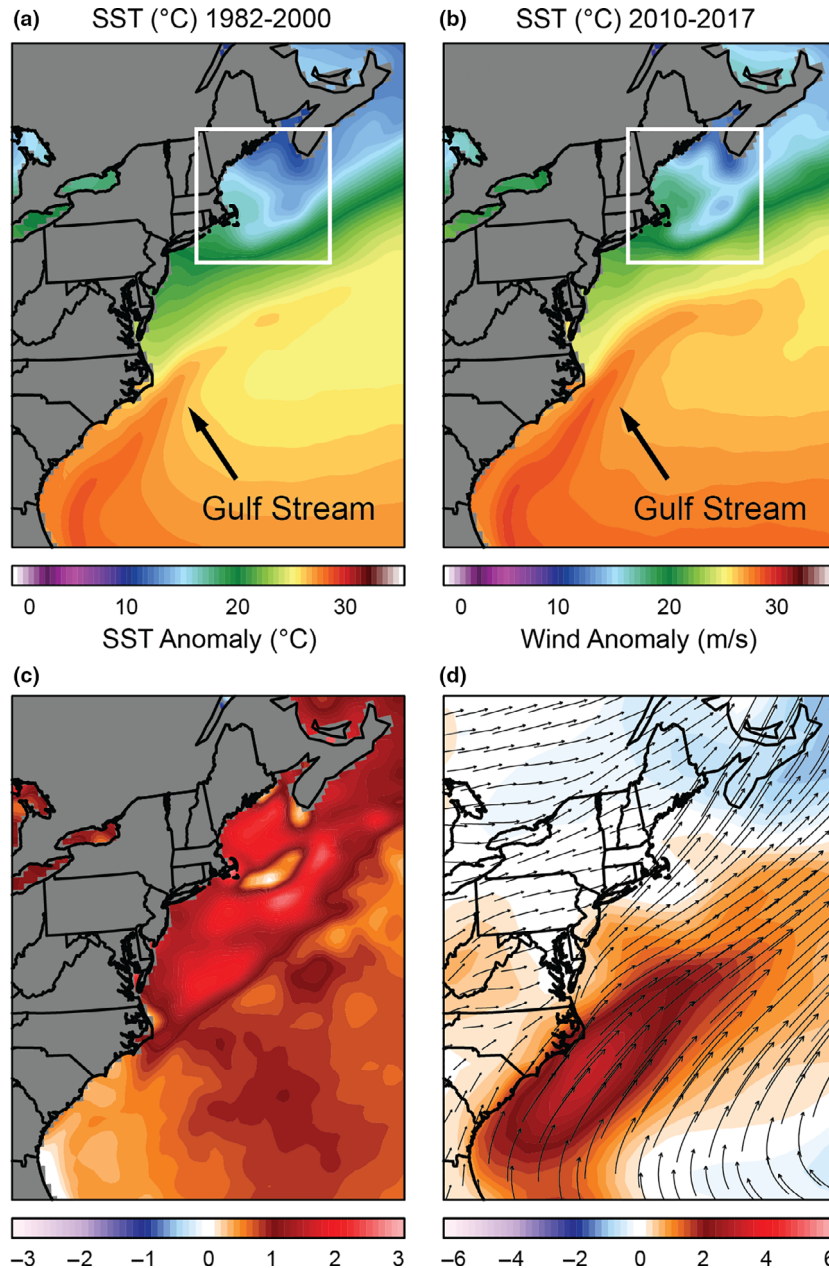
2014, 2015; Pershing *et al.* 2015; Birkel & Mayewski 2018). The event, which lasted more than a year, peaked in August 2012 and brought anomalous warmth throughout the water column (e.g. Chen *et al.* 2014; Pershing *et al.* 2015) that caused significant ecosystem and fisheries impact and human adaptive responses (Pershing *et al.* 2018).

Hobday *et al.* (2016a) define a marine heatwave in general terms as a ‘prolonged, discrete, anomalously warm water event that can be described by its duration, intensity, rate of evolution, and spatial extent’. The authors also suggest a more specific quantification for a marine heatwave as an event lasting five days or longer with temperatures greater than the 90th percentile relative to 30 years climatology. Subsequently, Hobday *et al.* (2018) established a categorical scale (I–V) to define severity of MHWs. Pershing *et al.* (2019) have similarly drawn climatological and economic attention to annual sea surface temperature excursions exceeding 2 standard deviations of the previous 30 year mean, calling these events ‘surprises’. By these definitions, there have been several heatwaves in marine settings around the world in the past decade, including events in the eastern Indian Ocean (2011), north-west Atlantic (2012), the Mediterranean Sea (2012, 2015), the North Pacific (2014–2016) and the Tasman Sea (2015/16, 2017/18), among others (Benthuisen *et al.* 2020).



**Figure 2** Time series of observed (black line) and model-projected (grey and coloured lines) annual sea surface (SST) temperature anomalies ( $^\circ\text{C}$ ) for the Gulf of Maine under different socio-economic/emissions scenarios (RCPs – Representative Concentration Pathways) from the Coupled Model Intercomparison Project version 5 (CMIP5) (Taylor *et al.*, 2012). RCP numbers indicate the projected radiative forcing ( $\text{W m}^{-2}$ ) on the climate system from greenhouse gas emissions by the year 2100. Coloured lines represent multimodel means (one ensemble member per model) for each RCP, whereas the corresponding spread denotes the standard deviation from the mean as calculated from all utilized model outputs. The number of available models is different for each RCP: 14 (RCP 2.6), 20 (RCP 4.5) and 18 (RCP 8.5). The grey line and shaded area represent the multimodel CMIP5 historical simulation (17 models). Observational values shown in black are from the NOAA Extended Reconstructed Sea Surface Temperature version 5 (ERSST5) gridded data set. Some years discussed in text are annotated. CMIP5 multimodel SST time series were obtained using the KNMI Climate Explorer (<https://climexp.knmi.nl>). All time series represent area averages for ocean-only grid cells spanning  $42^\circ\text{N}$ – $45^\circ\text{N}$ ,  $71^\circ\text{W}$ – $66^\circ\text{W}$ . Figure and caption modified from Fernandez *et al.* (2020). — RCP 8.5; — RCP 4.5; — RCP 2.6; — Historical; — NOAA.

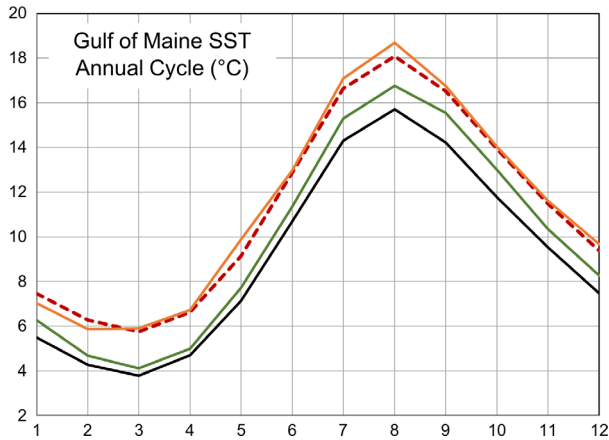




**Figure 3** Maps showing: (a, b) mean summer (June–August) sea surface temperature (SST) for the periods 1982–2000 and 2010–2017; (c) SST warming between those periods; and (d) increase in near-surface wind speed. White box highlights the Gulf of Maine. Data from NOAA Optimum Interpolation SST version 2 (Banzon *et al.*, 2016) and ECMWF ERA-Interim Reanalysis (Dee *et al.*, 2011). Figure and caption modified from Birkel and Mayewski (2018).

The extreme 2012 warming event in the Gulf of Maine was part of the larger 2012 north-west Atlantic marine heatwave (e.g. Chen *et al.* 2014), which was categorized by Hobday *et al.* (2018) as a Category III MHW. Another significant marine heatwave across the region developed in 2016, again peaking in late summer in the Gulf of Maine (Pershing *et al.* 2018). On average

over the past decade, the warm water season in the Gulf of Maine is 3–4 weeks longer in comparison with historical climatology (Thomas *et al.* 2017). In comparison, the 2012 warm water season was about 7 weeks longer than usual, affording a temperature annual cycle similar to that projected by climate models for *ca.* 2050 (Figs 4, 5).



**Figure 4** Comparison of the Gulf of Maine SST annual cycle for three historical (1982–2000, 2010–2019, 2012) and one projected (2041–2060 from RCP 8.5) time period. Historical observations from NOAA Optimum Interpolation SST version 2 (Banzon *et al.*, 2016). The projected values are from a CMIP5 (Taylor *et al.*, 2012) multimodel mean obtained using the KNMI Climate Explorer (<https://climexp.knmi.nl>). All time series represent area averages for ocean-only grid cells spanning 42°N–45°N, 71°W–66°W. — 2041–2060; — 2012; — 2010–2019; — 1982–2000.

Despite recent historically high temperatures in the Gulf of Maine, it is important to consider that variability in the climate system will continue to play a role over economically important timescales (Birkel & Mayewski 2018). This is exemplified by the relatively cool mean annual SST registered in 2019 (Fig. 2). Thus, while both long-term historical trends and climate model projections suggest that significant warming will occur in the Gulf of Maine this century, part of aquaculture resilience should include planning for some seasons or years that bring unexpected cooling.

The temperature increase and lengthening of the warm water season in the Gulf of Maine since the mid-2000s have affected fisheries. Pershing *et al.* (2015) found correlations of warmer temperatures with a marked increase in lobster stock and collapse of cod. It is notable, also, that the invasive European green crab (*Carcinus maenas* L.), present in Maine (Cobscook Bay) since 1905 (Rathbun 1905; Edgell & Hollander 2011), may have larger populations (as now) when the climate warms. A significant warming event in the early 1950s, considerably less severe than the 2012 marine heatwave, was correlated with larger abundances of green crabs in Maine, but subsequent cooling killed many of them to reduce population sizes (Welch 1968).

Climate model projections of sea surface temperature indicate that the surface waters in the Gulf of Maine could warm 0.5–3.5°C beyond recent values by the year 2100 (Fig. 2). At a minimum, this suggests that anomalous warmth of the past decade could become the norm in the

Gulf of Maine by 2050 and that extreme years would present warm temperatures not yet experienced. This represents, in effect, a state of permanent marine heatwave, such as what could develop in the future across other marine settings (e.g. Oliver *et al.* 2019). Moreover, with increased intrusion of warm water into the Gulf of Maine, bulk water salinity is expected to increase, although surface salinity is predicted to decrease (Alexander *et al.* 2020). Local salinity in an estuary is more difficult to predict and considers local factors including geometry and depth of the estuary.

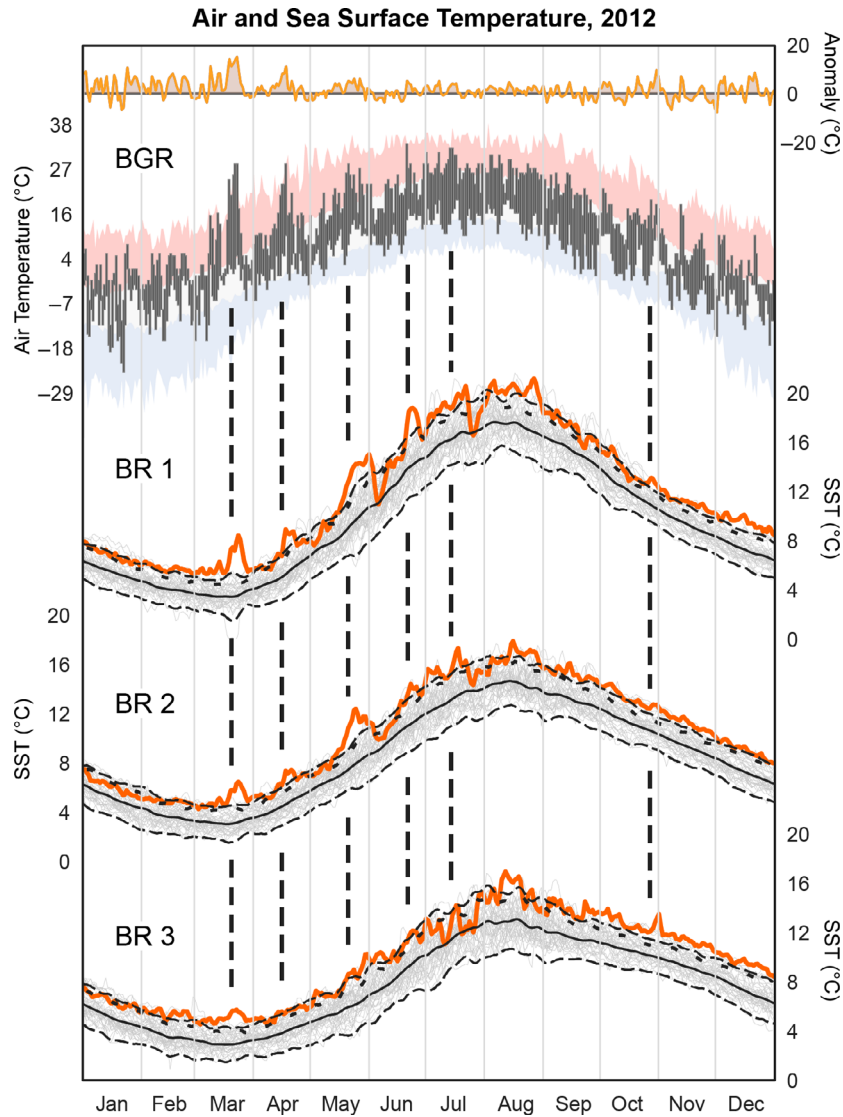
There is uncertainty in future climate for the Gulf of Maine depending on greenhouse gas emission scenarios. The International Panel on Climate Change (IPCC), an intergovernmental body of the United Nations, identified four Representative Concentration Pathways (RCPs) for climate change modelling and research (IPCC 2013), which become realizable depending on future greenhouse gas emissions. The four selected RCPs – 2.6, 4.5, 6 and 8.5 – represent cumulative greenhouse emissions and concentration scenarios, with 2.6 being the most benign and 8.5 being the most extreme.

One recent study utilizing experimental future runs from a high-resolution (~10 km) ocean model shows that coarse-resolution (~100 km) models from the Coupled Model Intercomparison Project (CMIP5, Taylor *et al.* 2012) likely underpredict the amount of warming that could take place in the Gulf of Maine in coming decades (Kleisner *et al.* 2016). Likewise, an analysis of projected marine heatwave intensity and frequency for RCP 4.5 and 8.5 suggests that many parts of the world ocean could attain a near-permanent marine heatwave state by the end of the 21st century with widespread impact to marine ecosystems (Oliver *et al.* 2019). The severity of the effect by 2100, however, depends strongly on the emission pathway, where RCP 8.5 yields nearly double the MHW increases as RCP 4.5 (Oliver *et al.* 2019).

### Sea level

Historical tide gauge measurements from Portland, Maine, show that annual mean local sea level has risen about 180 mm since data collection began in 1912 (2 mm year<sup>-1</sup> on a linear trend; Fig. 6). The record shows considerable variability of 50–76 mm every 3–5 years. The record maximum occurred in 2010, when the mean tide level for that year stood 260 mm above the 1912 baseline. Sea level along Maine's coast could rise 150–300 mm by 2050 and 300–1220 mm by 2100 relative to the present decade's baseline (Walsh 2014; Fernandez *et al.* 2015). The considerable spread in sea-level projections relates to remaining uncertainty with whether ice sheets over Greenland and Antarctica will melt gradually over the coming decades, or whether portions of those ice sheets could become susceptible to rapid collapse (Pachauri & Meyer 2014). Sea-level





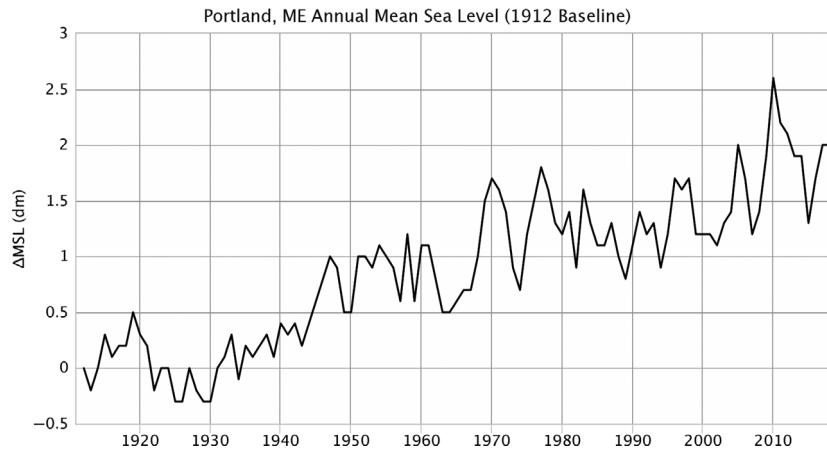
**Figure 5** Qualitative comparison of daily inland Maine air temperature and anomaly (observed at Bangor International Airport [44.8°N, 68.8°W]) (BGR) and offshore bioregion sea surface temperature (SST) (BR 1–3) for 2012, the warmest year on record in the Gulf of Maine and second warmest across Maine. The black bars in the BGR record indicate the observed min-max temperature range for 2012 against all values since 1953. Daily mean SST for 2012 is shown in orange for each bioregion against all values since 1982, along with the mean (solid black),  $\pm 2$  standard deviations (long dash) and 90th percentile (short dash) calculated from the 30 year period 1982–2011. The dashed vertical lines show the general correspondence between atmospheric and marine heatwaves, where a pronounced warm atmospheric pattern tends to elicit a response in the SSTs with only a short lag. Of particular note is the 17–23 March heatwave in which temperatures inland reached above 28°C (~83°F), breaking daily high-temperature records in some places by more than 8°C (~15°F) (Birkel & Mayewski 2018). Air temperature data from the Global Historical Climatology Network (Menne *et al.* 2012). SST data from NOAA Optimum Interpolation SST version 2.1 (Banzon *et al.* 2020).

rise will bring increased potential for erosion, storm surge flooding and saltwater intrusion to coastal communities along the Maine coast.

### Precipitation

Land-based observations of precipitation across Maine show that total annual precipitation has increased by about

150 mm overall since 1895 (Fernandez *et al.* 2015). Much of this increase has occurred since the early 2000s, during which time there was also a documented rise in heavy precipitation across Maine and the broader north-eastern United States (Fernandez *et al.* 2015, 2020; Easterling *et al.* 2017). Recent surpluses in annual precipitation can be attributed to anomalously wet conditions in summer and early fall, which in turn may have teleconnection to changes in large-scale circulation



**Figure 6** Annual mean sea-level anomalies (1912 baseline) from tide gauge measurements at Portland, Maine. Data from the Permanent Service for Mean Sea Level (<https://www.psmsl.org/>).

around the Northern Hemisphere associated with increased frequency of high-pressure blocking over Greenland (Hanna *et al.* 2016; Birkel & Mayewski 2018). Both historical trends and climate projections suggest that the north-eastern United States will continue to get wetter on an annual basis and that heavy rainfall and other extreme events will become more frequent as rising global temperatures drive an intensified hydrologic cycle (Easterling *et al.* 2017). Future precipitation increases are likely to have negative impacts on aquaculture, as more terrestrial runoff and atmospheric deposition from rainfall will contribute to ocean acidification (Dupigny-Giroux *et al.* 2018; Rheuban *et al.* 2019).

### Ocean acidification

While ocean pH is not itself considered a climate attribute, it is vulnerable to anthropogenic climate change. These parallel trajectories create co-occurring conditions that are often jointly considered when discussing potential impacts to aquatic ecosystems. The pH of ocean surface water has decreased by 0.1 units since the beginning of the Industrial Revolution (IPCC 2013), and modelling studies suggest a further decline of 0.3–0.5 pH units by 2100 (Caldeira & Wickett 2005). Similar models were proposed for the Pacific Northwest, with a decline in oceanic pH and an associated drop in aragonite saturation (Holden *et al.* 2019). Further, increased carbon emission scenarios predict pH reductions of 0.8–1.4 units by 2300 (Caldeira & Wickett 2005). However, for the vast majority of marine aquaculture occurring in nearshore waters, large-scale oceanic changes in pH are only a small component of acidification. The acidity of nearshore water is strongly regulated by diel photosynthesis–respiration cycles (Cai *et al.* 2011) and changes in total alkalinity (i.e. the buffering capacity of water) from freshwater flows (Salisbury *et al.* 2008). These

forces lead to daily, seasonal and annual fluctuations in pH in nearshore waters. The combined influences of these dynamic biogeochemical processes are often referred to as coastal acidification. Determining the influence of coastal acidification on aquacultured species will require more complex nearshore biogeochemical models coupled to better models of how these organisms adapt to and are affected by low pH (Waldbusser & Salisbury, 2014).

### Resilience of the aquaculture industry

The following section presents primary, resilience-specific findings from SEANET. This project considered effects of likely climate change scenarios on the aquaculture industry in Maine.

#### Physiological metrics of environmental change

Modelling the predicted outcomes of population health of aquaculture species in response to a changing climate is reliant upon meaningful inputs of both environmental and biological variables. Biological variables assessed in laboratory and field settings can be incorporated into models to determine their usefulness in predicting change. While growth and survival are commonly assessed and decidedly important endpoints, there are many sublethal effects that could challenge the long-term health and resilience of aquaculture species. Here, we identify meaningful variables that can improve modelling predictions and increase the capacity to respond to these changes.

#### Maine bivalve aquaculture

The eastern oyster (*Crassostrea virginica* (Gmelin 1791)) and the blue mussel (*Mytilus edulis* L.) are farmed at



**Figure 7** (a) American lobster in ocean acidification laboratory at the Aquaculture Research Centre, University of Maine. (b) Thousands of soft-shell clams (*Mya arenaria*) that were reared in the Downeast Institute's (Beals, ME) aquaculture programme, transferred to an ocean-based upweller in Freeport (ME) for six weeks and out-planted at the size shown (12–15 mm length) to clam flats for experiments and as part of a training programme for clambers. Photograph courtesy of Brian Beal, Downeast Institute. (c) Eastern oyster (*Crassostrea virginica*) rafts in the Damariscotta Estuary, Maine. (d) Dissected *Crassostrea virginica* from aquaculture farm near the Darling Marine Centre, Walpole, Maine. (e) A line of seed mussels is brought up for inspection in Blue Hill, Maine. Mussels settle naturally on the collector lines, attached by their byssal threads, and will grow until they are ready to be stripped off and redeployed on a mussel raft for grow-out. Photograph courtesy of Dana Morse. (f) The European green crab (*Carcinus maenas*) at sizes beginning >1.9 mm is a strong predator on 0 year class (1 mm) clams (Beal *et al.* 2018). Here, a gravid female (50 mm carapace width, carrying between 100,000 and 125,000 eggs) shows the challenge to Maine shellfish from high recruitment of these well-established non-indigenous crabs. Photograph courtesy of Brian Beal. [Correction added on 5 October 2020, after first online publication: Images for Figures 7 and 8 were reversed and have been corrected.]

commercial levels by aquaculture companies in Maine (Fig. 7). In 2019, 1,065 metric tons of mussels and 6300 metric tons of oysters were harvested from farms (Maine DMR 2020). A recent analysis (Hale Group 2016) projected that Maine's shellfish aquaculture industry would need over 1200 hectares of additional capacity by 2030 to meet product demand, but this may be a conservative estimate. Soft-

shell clams (*Mya arenaria* L.) represent a form of public aquaculture, because 3–5 million seed clams are produced and distributed annually by a coastal hatchery (Fig. 7b) to coastal towns to improve their clam flats (Beal *et al.* 2016). In 2018, 3,233 mt of soft-shell clams were harvested (Maine DMR 2019a). Expansion of bivalve aquaculture, however, is dependent not only on acquiring new hectares for

aquaculture, but also on the ability of the farmed species to withstand acidifying water and sediments.

#### Acidification impacts

Bivalves are particularly vulnerable to the effects of ocean acidification due to their dependence on a calcium carbonate shell for survival (e.g. McCoy *et al.* 2018 and references therein). Calcification rates of the larval, juvenile and adult stages of *C. virginica* will be hindered under the acidic conditions expected to occur within the next century (Miller *et al.* 2009; Ries *et al.* 2009; Waldbusser *et al.* 2011). Larval growth, calcification rates and overall health of *M. edulis* will be inhibited during this same time period (Gazeau *et al.* 2007; Beesley *et al.* 2008; Gazeau *et al.* 2010), but several studies (Beesley *et al.* 2008; Thomsen & Melzner, 2010; Dickey *et al.* 2018) suggest that *M. edulis* metabolism, tissue condition and thread production will not be affected. In contrast, studies with *Mytilus trossulus* (Gould 1850) on the U.S. Washington coast found that byssal thread number and attachment strength were negatively affected by higher temperature (25°C versus 10°C) and secreted adhesives did not cure well at pH < 8 (O'Donnell *et al.* 2013; George & Carrington 2018; Newcomb *et al.* 2019). *Mytilus trossulus* also occurs in Maine (especially in Bioregion 3), suggesting the usefulness of additional studies of adhesive plaques and thread strength in Maine for both *M. edulis* and *M. trossulus*, because failure of these structures due to climate change could have significant negative implications for mussel aquaculture.

Clams (Fig. 7b) are under even greater acidification stress than other bivalves, since postlarval stages (typically 225–300 µm) encounter sediment pore water pH levels < 7.5, which is more acidic than the overlying seawater (Jansen *et al.* 2012; Green *et al.* 2013; Preziosi & Bowden 2019; Preziosi *et al.* 2019). A variety of physical and biological processes ranging from organic matter remineralization (microbial respiration), upwelling, production of gases (NO<sub>x</sub> and SO<sub>x</sub>) due to human activity and biogenic reworking of sediments results in seasonal variability of pore water pH (Green *et al.* 2004; Waldbusser *et al.* 2010). Acidified surface sediments cause shell dissolution and mortality in juvenile hard shell clams (*Mercenaria mercenaria* L.), although their vulnerability to acidified sediments decreases with increasing clam size (Green *et al.* 2009). Soft-shell clam (*M. arenaria*) juveniles are also impacted by surface sediment acidification, but can still achieve survival rates of at least 56% in moderately acidified (pH 7.11) surface sediments (Green *et al.* 2013; Zhao *et al.* 2018; Beal and Otto 2019). At sediment acidification extremes (pH 6.1) though, even adult Manila clams (*Ruditapes philippinarum*, A. Adams & Reeve 1850) suffer 100% mortality within 10 days (Rodríguez-Romero *et al.* 2014). Preziosi and Bowden (2019) found adult razor clams (*Ensis leei* (M. Huber 2015)) are able to tolerate living in acidified surface sediments at pH 6.0 for at least 30 days at both 10°C and 20°C with no

visible shell dissolution or impacts on immune capacity (Preziosi & Bowden 2019; Preziosi *et al.* 2019). The vulnerability to acidified sediments decreases with increasing clam size (Green *et al.* 2009), which may explain why *E. leei* (the largest clam tested so far) is resilient to sediment surface acidification; however, additional research is needed to determine whether juvenile *E. leei* are resilient to sediment acidification effects as well. While community-based aquaculture using cultured juvenile soft-shell clams has been ongoing since 1987 (Beal *et al.* 2016; Beal *et al.* 2018), field grow-out trials along the Maine coast are underway to examine the culture potential for other commercial infaunal bivalves such as hard clam, or northern quahog (*Mercenaria mercenaria*), razor clam (*Ensis leei*), Atlantic surf clam (*Spisula solidissima*) and Arctic surf clam (*Mactromeris polynyma*). *E. leei* has the potential to be the most resilient to sediment acidification of these species and thus the species of choice to use on grow-out sites with particularly acidic sediments. Another threat is green crabs (Fig. 7f); however, the soft-shell clam industry should be resilient to temperature change throughout the 21st century, because this species' range currently extends as far south as North Carolina.

#### Mitigation strategies

Farmers can use a variety of methods to reduce effects of acidification. Selecting a species that has sufficient tolerance to the environmental parameters of the grow-out site is one strategy. Another strategy is to keep the bivalves in the hatchery longer to increase their size and have their feed availability increased before being transferred to the grow-out site. Increased food availability reduces the impact of elevated CO<sub>2</sub> levels on shell growth in *M. edulis* (Melzner *et al.* 2011; Thomsen *et al.* 2013), and shell dissolution rate in acidified sediments decreases with increasing *M. mercenaria* shell size (Green *et al.* 2009). This is an expensive option, however, as extended time in the hatchery also results in more handling time, and those costs are passed along to the farmer. If other options are not feasible, then acidity can be reduced by buffering seawater or sediment pore water with sodium carbonate and crushed shell pieces, respectively. Mook Sea Farm, located in Damariscotta, Maine, found success by buffering the water in their oyster hatchery, and Green *et al.* (2009) found that adding crushed shell to sediment can raise the aragonite saturation state (Green *et al.* 2009; Lockwood 2017). Optimization of the crushed shell buffering method is still underway, although a variety of bivalve shells can buffer sediments successfully including *E. leei* (Preziosi *et al.* 2019) and *M. arenaria* (Green *et al.* 2009). Growers will need to decide on a case-by-case basis which mitigation method(s) will work best for their crop.

To identify suitable endpoints, model organisms are often used that have characteristics favourable for assessment. In this regard, American lobsters (*Homarus americanus* (H.

Milne-Edwards 1837)) have served as an excellent calciferous model to identify novel endpoints and study the effects of environmental change on shellfish physiology. While lobsters are not a traditional model for shellfish aquaculture, we propose that they are well-suited to identify endpoints for exploration in more traditional models (e.g. bivalves). Compared to their molluscan counterparts, lobsters progress quickly through their larval stages, allowing for more rapid assessment of how environmental perturbation may influence larval development. American lobsters are robust and easily maintained in tank-based experimental systems (Fig. 7a). The large sizes reached by subadults and adults allow for the collection of significant volumes of haemolymph at multiple sampling timepoints, permitting the testing of a suite of haemolymph variables not possible with smaller volumes (Basti *et al.* 2010). Further, much of their physiology is conserved with other decapod crustaceans as well as molluscs (Furuhashi *et al.* 2009), and research with lobsters can therefore help to identify promising endpoints to investigate in a variety of aquaculturally important calciferous models such as oysters and mussels.

Invertebrates and other ectotherms rely on the temperature of their environment to regulate growth and metabolism. Growth is accelerated under warming conditions in American lobsters and leads to a more rapid progression through their larval stages. Rapid growth and the commensurate increase in size confer the benefits of increasing the availability of suitable prey as well as reducing the likelihood of predation; however, research shows that there may be costs to rapid growth. Animal growth requires the coordination of numerous cellular processes and is expectedly an energetically expensive process. Accelerating the rate at which growth occurs may impose additional cellular stress and reduce the scope of energy for other processes. One such cost may be the stability of developmental processes and the risk of sub-optimal structural organization. For example, it is thought that in bilaterally symmetric animals, the most optimal condition is that of perfect symmetry, with extreme asymmetry being considered a malformation. Fluctuating asymmetry is a term used to describe random deviations of bilateral traits from perfect symmetry and has been used across a variety of taxa to assess developmental stability under a number of environmental stressors, including temperature stress (Nishizaki *et al.* 2015). While lack of perfect symmetry may not itself pose harm, it could indicate the likelihood of occurrence of potentially harmful effects. For example, fluctuating asymmetry is correlated with parasitism and disease susceptibility, and meta-analyses suggest it is a reliable biomarker of developmental stability and population resilience (Beesley *et al.* 2008). When American lobster larvae were exposed to temperatures that span a wide range of their natural habitat (14, 16, 18, and 22°C), the larvae exposed to the upper and lower temperature extremes of the lobsters' natural

temperature range showed significant variability in the metrics for fluctuating asymmetry (Harrington *et al.* 2019). These changes suggest that warmer temperatures could facilitate faster growth, but at the expense of developmental stability. Further, this novel biomarker could serve as a sensitive metric of response to environmental change and shows utility across a variety of economically important calciferous organisms, including bivalves.

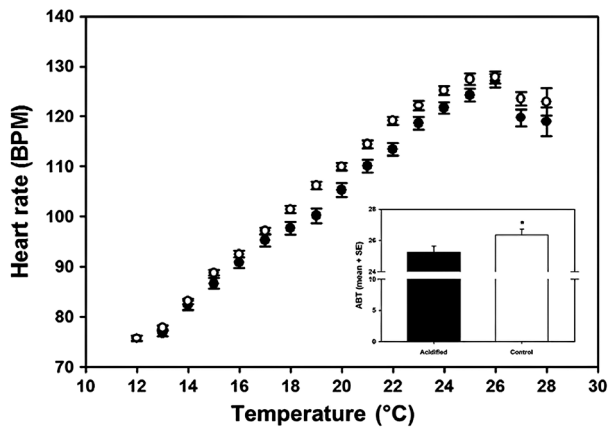
Maintaining a stable internal pH is energetically costly, and the excess energy required in acidic environments may reduce their ability to deal with additional stressors, such as increasing ocean temperature. Therefore, studies that examine the effects of OA independently may not identify this reduced capacity, which could be especially critical in the face of numerous environmental stressors. To address whether lobsters show a limited capacity to deal with subsequent stress following exposure to an acidified environment, lobsters underwent a subsequent rapid temperature ramp, and their cardiac performance was assessed. Increasing temperature is expected to increase heart rate in a linear fashion until the lobster reaches its thermal limit. At this point, the heart rate becomes more erratic and eventually starts to decline. The temperature at which heart rate becomes erratic and begins to decline is termed the Arrhenius break temperature (Harrington & Hamlin 2019). More tolerant animals would be expected to have a higher Arrhenius break temperature, since their heart rate would become erratic at a higher temperature than less tolerant animals. When American lobsters (Figs 7a, 8) were exposed to pH levels of current (pH 8.0) and predicted end-of-century (pH 7.6; IPCC 2013) values, those exposed to the acidified environment showed significantly lower Arrhenius break temperatures than those exposed to current pH levels (Harrington *et al.* 2019). This suggests that the stress of OA will likely compound thermal stress and present additional physiological challenges in the face of future climate change scenarios.

Fluctuating asymmetry and Arrhenius break temperatures could serve as novel and important biological indicators of population resilience in calciferous aquaculture species. While both fluctuating asymmetry and Arrhenius break temperatures have been assessed in various bivalve models, it has not been in the context of aquaculture resilience and the discovery of endpoints that could serve as inputs for forecast modelling. Future efforts should be made to determine whether these endpoints could serve as robust and useful inputs for the predictive assessment of aquaculture species' robustness in the face of a changing climate.

### Macroalgal aquaculture

*Alaria esculenta* (Linnaeus) Greville 1830 (winged kelp), *Saccharina angustissima* (Collins) Augyte, Yarish & Neefus 2018 (skinny kelp), and *Saccharina latissima* (Linnaeus)





**Figure 8** Mean heart rate ( $\pm$ SE) for *Homarus americanus* (50–65 mm carapace length) exposed to acidified (black circles) and control (white circles) treatments during a temperature ramp. The inset shows the mean Arrhenius break temperature ( $\pm$ SE) of acidified (black bar) versus control (white bar) treatment lobsters. The asterisk (\*) indicates significance ( $P < 0.05$ ). Taken from Harrington and Hamlin (2019). ● Acidified; ○ Control. [Correction added on 5 October 2020, after first online publication: Images for Figures 7 and 8 were reversed and have been corrected.]

C.E. Lane, C. Mayes, Druehl & G.W. Saunders 2006 (sugar kelp) have reached the status of true crops (Fig. 9a–c) in Maine aquaculture within the last decade (Grebe *et al.* 2019; Maine DMR 2020). Macroalgal farming expanded over all three bioregions in the last 5 years. Steady annual growth (Maine DMR 2020) in numbers of leases and total wet biomass harvested from coastal macroalgal farms occurred from 2015 (4 leases; 6.6 wet metric tons) to 2018 (9 leases; 24.3 wet metric tons) to 2019 (21 leases, 126 wet metric tons). Of the 2018 farm totals (F. Drury [Maine DMR, personal communication to authors, August 15, 2019]), 1.3 wet metric tons were *Alaria esculenta* and 23 wet metric tons were *Saccharina* (both *S. angustissima* and *S. latissima*). Although the total biomass grown on Maine farms is quite small compared to the 10.3 million metric tons of farmed kelps (*Saccharina japonica* + *Undaria pinnatifida*) produced in China, Japan and Korea in 2015 (FAO 2018b), the techniques and conditions for continuing expansion of the industry are well-established (e.g. nursery production of gametophytes, seeding techniques and optimal times for moving young sporophytes on gametophyte-seeded lines to the field for grow-out). Red macroalgae are still developing as aquaculture crops in Maine (e.g. Blouin *et al.* 2007; Royer *et al.* 2019) because of the need for more investment in infrastructure, but dulse, *Palmaria palmata* (Linnaeus) F. Weber & D. Mohr 1805, is close to attaining crop status in Maine, despite the need for additional technical developments, and is also of keen interest in other areas of the North Atlantic (Grote 2019).

How resilient will these macroalgal crops be to the environmental changes predicted to affect the Gulf of Maine in the 21st century? As reviewed above, sea surface temperatures in the Gulf of Maine under the most extreme model (RCP 8.5) could rise by another 3.5°C by 2100 or slightly decrease (RCP 2.6) from those of the last decade (Fig. 2), and longer summers are predicted. Maine's aquacultured macroalgae (kelps and dulse) are grown from late September to April or early May, however; thus, a fair question is what will happen to wild populations of these species, which are important for breeding and as foundational components of the coastal ecosystem, versus the ability to maintain robust crops of these species in Maine aquaculture through the 21st century? To address this question, we review temperature tolerances and acclimatory potential of our kelp species in the North Atlantic and consider the resilient history of aquaculture of *Saccharina japonica* on the Chinese coast.

#### Temperature tolerances and acclimation potential

Temperature optima vary from the microscopic gametophyte stage of the kelp life history to the large, commercial, sporophyte stage. Temperature optima under nutrient-replete conditions with optimal levels of light are typically close to 10–15°C for sporophytes of *Saccharina* spp. (Lee & Brinkhuis 1988; Gerard 1997; Pang *et al.* 2007) with survival possible at ~20–22°C for short periods (e.g. 4 days to a few weeks), but young sporophytes frequently died at water temperatures >21–22°C (Lüning 1984; Gerard 1997). Optimal temperatures for *Saccharina latissima* gametophytes are near 15°C, with survival limited by 22–23°C (Lüning 1980, Lee & Brinkhuis 1988). In the north-east Atlantic, *A. esculenta* (sporophytes) died after a few weeks of summer temperatures reaching 17°C (Sundene 1962; Munda & Lüning 1977). In summary, these studies suggest that a prolonged rise in sea temperature above 20°C might eliminate *Alaria* and *Saccharina* from our natural ecosystem; however, more information on the acclimatory potential of these species is required to assess their ultimate resilience to climate change. In particular, seasonal acclimation of sporophytes of *Saccharina latissima* in the north-eastern Atlantic was found to increase tolerance by 2°C in summer over early spring (Lüning 1984). Similarly, acclimation of cultures of *A. esculenta* gametophytes to 22°C from a control temperature of 12°C with 1°C steps/12 h had an acclimating effect, which led to some gametophyte survival in response to a later challenge of >30°C (Quigley 2018).

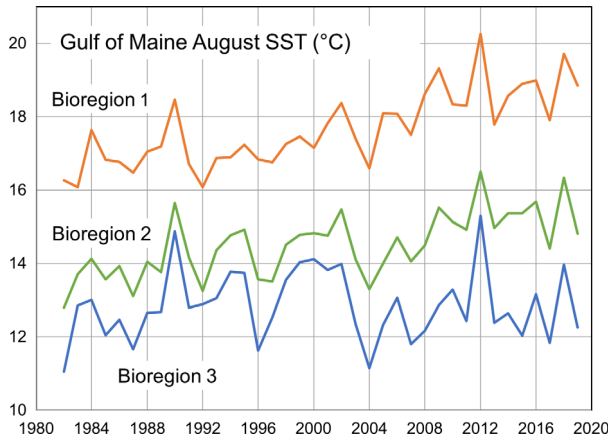
August sea temperatures (Fig. 10) over the last decade for Bioregion 1 (20.3°C) are close to lethal temperature for some life history phases of our aquaculture crops, especially considering predictions for short, extreme ocean heatwaves becoming more common (Oliver *et al.* 2018). MHWs along



**Figure 9** (a) Winged kelp (*Alaria esculenta*) growing in an aquaculture farm in Frenchman's Bay (Bioregion 2). Photograph courtesy of Sarah Redmond, Springtide Seaweed LLC. (b) Skinny kelp (*Saccharina angustissima*) growing in an aquaculture farm in the Damariscotta Estuary (Bioregion 2). Photograph courtesy of Seth Barker, Maine Sea Farms LLC. (c) Sugar kelp (*Saccharina latissima*) growing in an experimental university farm (Bioregion 1). Photograph courtesy of Gretchen Grebe, University of Maine. (d) Sea lice (*Lepeophtheirus salmonis*) copepod, Aquaculture Research Institute, University of Maine. Scale bar = 500 µm. (e) Sea lice attached to an Atlantic salmon. Photograph courtesy of Ian Bricknell, University of Maine. (f) Graduate student inspecting salmon for sea lice, Cobscook Bay, Maine. Note commercial salmon cage in background. Photograph courtesy of Emma Taccardi, University of Maine.

the western shores of Australia and California/Mexico (e.g. Wernberg *et al.* 2011; Smale *et al.* 2017; Wernberg *et al.* 2018; Arafteh-Dalmau *et al.* 2019; Cavanaugh *et al.* 2019; Sanford *et al.* 2019; Straub *et al.* 2019) have devastated kelp canopies and the fish and invertebrate communities associated with them, because, unlike gradual warming, impacts of MHW are too severe and short to allow acclimation or adaptation. The impacts of MHW along south-western Australia have been particularly severe, because after SST returned to levels that would have allowed regrowth of

*Ecklonia* kelps in the northern part of the original 2000 km range, kelp did not regrow. This was attributed to establishment of subtropical herbivorous fish from larvae carried southward by the Leeuwin Current (Verges *et al.* 2019; Zarco-Perello *et al.* 2019) and the inability for *Ecklonia* meiospores to be carried northward from recovered (pole-facing) populations because of this south-flowing current. In contrast, the colder current flowing along the Maine coast to Bioregion 1 from Bioregions 2 and 3 may dampen the effect of MHWs. A common observation associated



**Figure 10** August sea surface temperature, 1982–2019, for the three Gulf of Maine bioregions identified in Figure 1. Data from NOAA Optimum Interpolation SST version 2 (Banzon *et al.* 2016). [Correction added on 5 October 2020, after first online publication: Images for Figures 10 and 11 were reversed and have been corrected.]

with MHWs is an increase in turf algae (e.g. Straub *et al.* 2019) that include invasive species. In this regard, Dijkstra *et al.* (2019) described apparently diminished abundance of kelps at the southern edge of Bioregion 1 and a large increase in filamentous red algae, including the invasive *Dasysiphonia japonica* (Yendo) H.-S.Kim 2012 that may diminish habitat for fish and invertebrates.

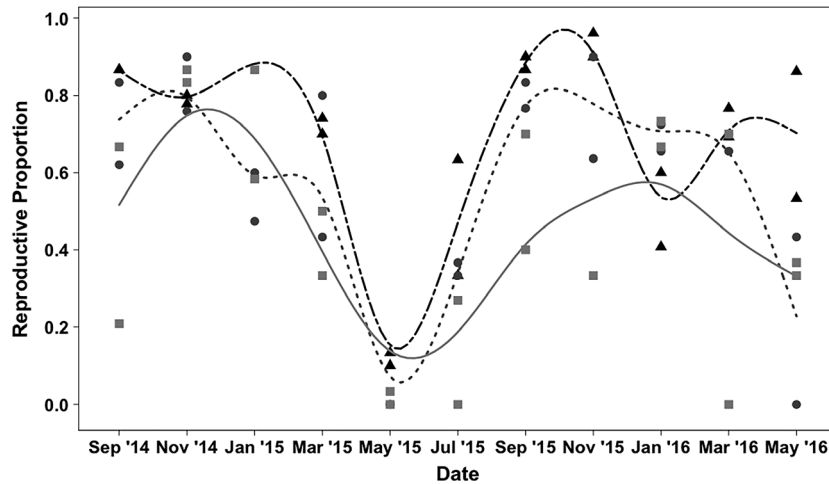
The importance of multiple factors in experiments on temperature tolerance was demonstrated by Gerard (1997), who tested whether heat tolerance and nitrogen supply were correlated in *S. latissima* with an ecotype from Long Island Sound (LIS, New York; exposed to high sea temperatures for a month each year) and a Maine ecotype (ATL, South Bristol, ME). She found they both grew optimally at 12°C but only LIS survived four days at 22°C when both ecotypes were grown under nitrogen limitation. Gerard (1997) found that LIS individuals had the ability to store more N from seawater than ATL before the onset of warm weather. Similarly, field studies on the kelp *Macrocystis* in California (North & Zimmerman 1984) found that survival under heat stress was achieved when nitrogen fertilizer was added to the kelps. In both cases, kelps that had adequate tissue nitrogen could likely synthesize heat-protective molecules (e.g. heat-shock proteins) that led to survival. This emphasizes the need to understand how nutrient supply to coastal aquaculture will be affected by longer periods of stratification (i.e. low nutrients during the extra predicted month of summer), changes in nutrient supply due to new variability in sources of incoming seawater (see above) and whether increased precipitation might decrease nearshore nutrient deficiencies because of more terrestrial runoff.

Longer nutrient limitations in warm weather could accelerate natural loss of *Saccharina* and *Alaria* from Bioregion 1.

How can we improve predictions of performance for macroalgal crops in a warming world? Here, we briefly consider some physiological and molecular techniques. For any photosynthetic organism, one of the quickest, easiest and most economical ways to determine whether elevated temperature is likely to inhibit growth is to employ a pulse amplitude-modulated fluorometer (PAM fluorometer) to measure the efficiency of photosynthetic energy conversion (formally, the maximal quantum yield or  $F_v/F_m$ , see Beer *et al.* 2014). PAM fluorometry is well-established in terrestrial agriculture for assessing stress and has already been applied in many studies of algae (Gerard 1997; Liu & Pang 2010; Roleda 2016; King *et al.* 2017; Hwang *et al.* 2018; Burdett *et al.* 2019). Several types of PAMs are available for use in the field, including underwater in a kelp bed, for example. Another approach to detecting sublethal stress that negatively affects macroalgal growth is to assay whether stress-responsive genes are being expressed at higher than normal levels by quantifying mRNA for the relevant genes (transcriptomic studies) or by direct quantification of the particular protein, often with commercially available antibodies that allow the protein's quantification. Heat-shock proteins (HSP) are a particularly good stress indicator because their role is to repair (refold) other cellular proteins damaged by heat or another stress (Alberts *et al.* 2014). The value in integrating transcriptomic studies with PAM fluorometry to assess resilience was demonstrated by Mota *et al.* (2015, 2018) in studies of effects of climate change on brown macroalgae. Application of molecular techniques requires cooperation between growers and researchers, as do molecular population biology techniques that can assess whether a natural population of a macroalgal crop near a retreating border has lost genetic diversity and might be more susceptible to a heatwave, or whether strains collected from natural populations have enough genetic diversity to support future breeding experiments. These techniques help to determine whether an algal species can acclimate to higher temperature by, for example, producing more HSPs.

#### *Importance of increased domestication/ husbandry*

It is especially important to conserve genetic diversity of aquaculture crops in areas known to be long-term refuges for marine species during peak glaciations and at retreating southern edges of species (Provan & Maggs 2012; Assis *et al.* 2018; references therein). Because an area off Nova Scotia is predicted as a refuge during the last two glacial maxima (e.g. Li *et al.* 2015, Assis *et al.* 2018), the Maine shore may offer the genetic diversity needed to breed kelp and red algal crops for heat tolerance and a variety of other traits to make them resilient against the environmental



**Figure 11** Proportion of *Alaria esculenta* individuals that were reproductive (fertile sporophylls) over time at three locations (Pemaquid Point, Schoodic Point and Lubec) that span much of Maine's shore. To determine reproductive phenology, random numbers were used along 60 m transects to determine reproductive phenology ( $n = 20$  individuals/transect) at each of two subsites/location. Duplicate symbols/timepoint are the relative proportions that were reproductive on each transect. Cubic spline interpolation was applied to distinguish patterns. From Quigley (2018). ---- ▲ Lubec; ..... ● Schoodic; — ■ Pemaquid. [Correction added on 7 September 2020, after first online publication: Images for Figures 10 and 11 were reversed and have been corrected.]

changes confronting us in the next 50–100 years. Across all bioregions, sporophylls containing meiospores (i.e. zoospores) of *A. esculenta* can be collected even during summer for seeding and conserving genetic diversity in this species (Quigley 2018; Fig. 11). The need to conserve strains is illuminated by the 2011 MHW off south-western Australia, where the degree of kelp resilience was correlated over the 2000 km latitudinal gradient of extirpation, recovery and lack of damage with earlier measured genetic diversity of these kelp populations (Coleman *et al.* 2011; Wernberg *et al.* 2018). Conserving strains that reflect natural genetic diversity can also support 'assisted adaptation' or natural restoration (Coleman *et al.* 2020).

Ecological niche modelling by Assis *et al.* (2018) predicted heavy losses of suitable thermal habitat off Nova Scotia for *Saccharina latissima* under both RCP2.6 and RCP8.5 by 2100, while *Alaria esculenta* had small (21–30%) losses of habitat under RCP2.6 but suffered total loss of habitat in Nova Scotia by 2100 under RCP8.5. Similarly, in Japan, application of RCP 4.5 and RCP 8.5 predicts loss of habitat for natural kelp species due to warming seas, including local extinction of over half of kelp species (Sudo *et al.* 2019). To date, and surprisingly given poleward retreat of some sub-Arctic species and expansions northward of temperate species (i.e. invertebrates, NW Atlantic; macroalgae and invertebrates, NE Atlantic), there does not appear to be a local extinction of any kelp or red alga of aquaculture value in New England from the 1800s to present (i.e. records of Farlow, Collins, Setchell, Cardinal, Scheibling and Adey, among others) as reviewed by

Merzouk and Johnson (2011). This is consistent with findings of only a small decline, with uncertain trend, for kelp forests in the Gulf of Maine and Scotian Shelf that was modelled from data over the last half-century by Krumhansl *et al.* (2016). These researchers found a high probability of declines in 38% of ecoregions surveyed (e.g. central Chile, North Sea and north-central California), no change in 35% of ecoregions and increases in kelp forests in 27% of surveyed ecoregions. Herbarium data can help to increase the accuracy of distributional records, but are subject to the presence of a collector and generally require a baseline monitoring programme that Maine currently lacks, which would reveal changes in abundance versus presence/absence of crop species. Such monitoring programmes are not glamorous but are necessary to identify long-term trends at large spatial scales (Merzouk & Johnson 2011).

Macroalgal aquaculture will be resilient in Maine throughout the 21st century if these steps are taken:

- conserve genetic diversity from natural populations of aquaculture crops/targets across bioregions and genotype isolates using population biology techniques to assure adequate sampling and wide genetic diversity in seed-banked strains (e.g. kelp gametophytes from collected meiospores),
- use seed-banked strains to breed traits of interest,
- develop new crops that may become present in Maine waters from poleward migration of warm temperate species and
- take lessons from agriculture and *Saccharina japonica* aquaculture.



If the Gulf of Maine continues to warm on the trajectory predicted by models based on RCP8.5, the natural marine biota will be negatively impacted, including regional extinctions, but our current aquaculture crops can remain resilient. The development of *Saccharina japonica* (Areschoug) C.E. Lane, C. Mayes, Druehl & G.W. Saunders as an aquaculture crop in China, where it is not native, is relevant. *Saccharina japonica* was accidentally introduced to the northern coast of China (Dalian) in 1927 from Japan and subsequently transplanted to Yantai and Qingdao (Tseng 2001; Shan *et al.* 2017). Just as it had not spread naturally from Japan, because of a warm water barrier (Zhang *et al.* 2015), no wild populations developed south of Qingdao because the seawater is too warm (Tseng 2001). Remarkably, *S. japonica* became the largest macroalgal crop in China following Tseng's development of the summer seeding technique, which involved establishment of land-based nurseries where gametophytes was cultured, fertilization was induced, and the resultant juvenile sporophytes were held in artificially cooled seawater (<10°C) during summer (Tseng 2001). After seawater temperatures dropped below 20°C over large regions of the Chinese coast in October (Tseng 2001; Su *et al.* 2017), juvenile sporophytes were moved to the sea. Also, very important, Wu (1998, as cited in Liu & Pang 2010) cultured gametophytes at 22–24°C, crossed the acclimated gametophytes and produced sporophytes with heat tolerance increased by 2°C (also see Li *et al.* 2008; Liu & Pang 2010). Development of these techniques made it possible to establish large-scale aquaculture of *S. japonica* across more than 1650 km of East China coast from Qingdao to subtropical Fujian Province (Tseng 2001). The original breeding of temperature-tolerant strains was accompanied by inbreeding, which reduced vitality and heat tolerance after a few generations, but improved breeding in the last decade with the benefit of molecular markers (e.g. microsatellites) and related techniques has sustained the large-scale industry (e.g. Zhang *et al.* 2011; Zhang *et al.* 2018; Su *et al.* 2020). Similar high-quality breeding programmes in Japan and Korea have produced excellent cultivars of kelps that are heat-tolerant (e.g. Hwang *et al.* 2017; Hwang *et al.* 2019; Niwa and Kobiyama 2019).

This is the roadmap for resilience of macroalgal aquaculture in Maine. While it is to be hoped that temperatures in the Gulf of Maine will not reach the RCP8.5 level, the strategies employed to make *S. japonica* into a crop for the East China Sea should be sufficient to preserve robust kelp aquaculture if wild *S. latissima* or *A. esculenta* disappear from the Maine coast (e.g. Bioregion 1) by 2100. This is especially true because even under the RCP8.5 scenario, seawater temperatures within the fall to spring farm season for Maine aquaculture crops are predicted (Fig. 4) to range from 14°C (October) to 7°C (April). Scientists working in Maine are beginning to apply this roadmap for resilience

(e.g. Augyte *et al.* 2020; Wade *et al.* 2020), and these efforts need to be applied widely.

#### Product characteristics

Other potential concerns for Gulf of Maine macroalgal aquaculture, not directly related to tolerance of crop species, are change in quality. Xu *et al.* (2019) reported that elevated seawater CO<sub>2</sub> due to ocean acidification enhanced growth in *Saccharina japonica*, but also resulted in higher levels of iodine in blades. At present, the best kelp crop for human consumption from the Gulf of Maine is *Alaria esculenta* because of its nutritional profile, including lower iodine levels compared to *Saccharina* and *Laminaria* kelps (Wells *et al.* 2017), and therefore, monitoring changes in iodine at RCP2.6 and RCP8.5 would be useful to see whether similar results to Xu *et al.* (2019) are evident. Changes in characteristics such as iodine levels may have significant effects on the economic value of these products in the future, even despite their capacity for adaptation and survival.

Similarly, changes in wave action and currents may affect the morphology and retention of some cultivated kelp. For example, wild *S. latissima* thalli grown in higher velocity currents are generally narrower and longer than those grown in low-velocity conditions (Parke 1948a,b). Studies of cultivated *S. latissima* in the eastern Atlantic found that thallus length, blade length and total area of sporophytes grown at a moderately exposed site were significantly greater than those of sporophytes grown at a sheltered site (Peteiro & Freire 2013a, b). Stronger or more frequent wave action can also lead to complete loss of the crop if it is strong enough to tear the holdfasts from the long line. As reviewed above, the Gulf of Maine is expected to experience changes in current patterns, increased storm events and higher sea levels. All of these have the potential to change the hydrodynamic forces acting on cultured macroalgae and may also affect their marketability under a changing climate.

In contrast, *Saccharina angustissima*, until recently thought to be a variety of sugar kelp (Augyte *et al.* 2017, 2018), retains its natural 'skinny' form under different hydrodynamic regimes (Fig 9b). Surprisingly, it grows naturally in a small region of outer Maine shore (Bioregion 1) in areas of very high wave action. Grown in aquaculture farms in Casco Bay (Bioregion 1) and in the Damariscotta Estuary and Frenchman's Bay (Bioregion 2) since 2016, it grows well in the much quieter water of cove and bay habitats and retains its 'skinny' morphology. That is, it can grow in habitats that are quite different from its normal habitat and is acclaimed by Maine farmers and chefs.

#### Macroalgal processing

Different species of macroalgal crops offer one or more of these nutritional benefits: vitamins, minerals, antioxidants, protein, omega-3 fatty acids, carbohydrates and dietary



fibres; Maine kelps are best for carbohydrates, dietary fibres, minerals and antioxidants, and *Alaria* additionally offers a dietary protein contribution (Wells *et al.* 2017). Due to its high moisture content (~92% by weight), freshly harvested kelp is often dried to extend its shelf life by slowing microbial growth and preserving the physical/chemical properties in the final product (Gupta *et al.* 2011). Drying is accomplished either by open-air sun drying or in controlled environments using heated air. The dried product requires less storage volume and allows transportation of more biomass over long distances.

The drying process of seaweeds occurs through a falling rate period and is governed by simultaneous heat and mass transfer with phase change in porous media (Passos & Mujumdar 2000; Sappati *et al.* 2017). The rate of drying is highly dependent on several processing parameters, including air temperature, moisture diffusion coefficient, relative humidity of air, air velocity, material thickness, surface area and phase transition (from glassy to rubbery state; Van Arsdell 1973; Lewicki & Jakubczyk 2004). It is predicted that the sea surface temperature in the Gulf of Maine could increase by 0.5–3.5°C by 2100 due to greenhouse gases (see above). On a smaller scale, local effects are less certain, but could potentially have even greater impact on these processing parameters. This is resulting in prolonged summer conditions lasting four weeks longer than in 1982 on the Maine coast (Thomas *et al.* 2017). With increase in the ambient temperature, the moisture diffusion coefficient, and thus the drying kinetics, will likely increase, resulting in faster moisture migration from seaweeds. In addition, in enclosed greenhouse drying, the increase in ambient temperature will have a net positive effect on the performance of the solar collector with a net reduction in heat loss to the surroundings (Piacentini & Mujumdar 2009). However, in recirculating heat pump-based dryers, the efficiency of condensing out moisture by cooling the exhaust air will decrease with increase in the ambient temperature. Also, the global surface-specific humidity has increased significantly between 1977 and 2003 at the rate of 0.11 and 0.07 g kg<sup>-1</sup> per decade for land and marine areas, respectively (Azis *et al.* 2001). With the rise in water evaporation and transpiration in the Gulf of Maine, there will be more cloud coverage, diminishing the overall solar irradiation. Together, these opposing effects of higher temperature versus greater cloud cover and higher humidity will change the dynamics of open-air drying of seaweeds and could make the drying conditions less predictable. Adding to the unpredictability, it is expected that increase in frequency of storms, more rain events and stronger winds will reduce the times available for open-air drying. Together with the increasing harvest volume associated with seaweed farming, these climate effects may incentivize increased use of closed drying methods. This will require higher capital investments in drying equipment and the added expense of drying energy,

which in turn will likely result in farmers choosing to increase the scale of their operations to justify and make use of this expanded infrastructure.

Some of the environmental changes that affect open-air drying will also have an impact on controlled environment drying, since the ambient air will on average become warmer and more humid, which help and impede drying, respectively. Investigations carried out through the SEA-NET project at the University of Maine show that controlled environment drying can improve the predictability of drying dynamics and preservation of bioactive components in sea vegetables (Sappati *et al.* 2017; Sappati *et al.* 2019). In order to reduce the carbon footprint of the conventional fossil fuel-based dryers, solar dryers with nonconcentrating or concentrating collectors need to be backed up for additional heating using latent heat phase change materials, photovoltaics, wind energy and other renewable sources. This strategy will likely require increased capital investment and infrastructural support but would also increase the reliability of sea vegetable aquaculture faced with unpredictable environmental change.

#### *Ecosystem services*

Seaweed aquaculture installations support ecosystem services such as water purification, and in areas with eutrophication risks, they can be used as tools for intercepting excess nitrogen and phosphorus from impervious surfaces, wastewater treatment plant effluents, agriculture, fertilizer runoff, atmospheric deposition and more (Rose *et al.* 2014; Kim *et al.* 2015; Rose *et al.* 2015a,b; Wu *et al.* 2015; He *et al.* 2019; Mao *et al.* 2019; Liu & Huguenard 2020). These installations can also serve as carbon sinks and provide localized alkalization (Branch *et al.* 2013; Krause-Jensen & Duarte 2016; Pfister *et al.* 2019), habitat for other marine organisms (Skjermo *et al.* 2014; Radulovich *et al.* 2015) and green infrastructure preventing coastal erosion. Anticipating how these ecosystem services might change under the aforementioned climate projections is especially important because the impact could extend far and wide into the natural and human systems that depend on them. The lengthening of warm water conditions may ultimately result in a shifted growing season for kelp and, in turn, a shift in the timing of ecosystem services provided by kelp installations.

In particular, nutrient assimilation offered by macroalgal farms is likely to become an increasingly important management tool in the face of climate change. Globally, it is estimated that the flow of reactive nitrogen, mobilized by anthropogenic activities, needs to be reduced to 25% of its current levels to lie within healthy planetary boundaries (Rockström *et al.* 2009; Gao *et al.* 2019; He *et al.* 2019). The global nitrogen cycle is expected to experience additional stress resulting from climate change (Gruber and Galloway 2008; Suddick *et al.* 2013; Gao *et al.* 2019; He *et al.* 2019). Its

resilience to these stressors will further influence the severity and extent of climate change through additional radiative forcing and shifts in primary productivity influencing C sequestration (Gruber and Galloway 2008; Suddick *et al.* 2013). For example, with increased incidence of high-magnitude storms and changes in river flow in climate change scenarios, the timing and size of anthropogenic nutrient loads moving into estuaries will shift (Suddick *et al.* 2013). As such, the ability of kelp installations to quickly and effectively assimilate nitrogen and phosphorous could be exploited to buffer the Gulf of Maine coastal ecosystems from the undesirable impacts of these pulses (Rockström *et al.* 2009).

Presently, the timing of harvest is dictated by both water conditions and social influences. However, the settlement of fouling organisms (bryozoans, epiphytes, snails, etc.) onto aquaculture infrastructure dramatically increases with warmer waters. Fouling lowers the consumer appeal of the kelp, requiring producers to aim for harvest before the water warms beyond 12–15°C. Under warming water temperatures in a changing environment, fouling organisms such as kelp snails and bryozoans may reproduce earlier in the year, forcing earlier harvest of cultivated kelp. In addition to minimizing fouling, farmers also aim to harvest before phytoplankton begin to compete seasonally with the kelp for nutrients (Flavin *et al.* 2013). Changes in seasonal abundance of phytoplankton have already been attributed to climate change in the North Atlantic (Flavin *et al.* 2013; Barton *et al.* 2016). Similar shifts in phytoplankton distribution in the Gulf of Maine are possible, which will influence the optimal harvesting time for cultivated seaweeds in the region. Lastly, earlier seasonal warming of coastal waters and air temperatures will likely also advance activity of other water users (i.e. lobstermen and recreational boating/fishing). The social resilience of seaweed farming is strongly tied to minimizing conflict with these other users, and therefore, harvest timing and removal of kelp long lines are likely to also be influenced by modified use patterns in the nearshore Gulf of Maine.

### Integrated Multitrophic Aquaculture (IMTA)

Integrated multitrophic aquaculture has long been advocated for its potential to have economic and environmental benefits in marine aquaculture (Ryther *et al.* 1975; Chopin *et al.* 2001; Neori *et al.* 2019). Suitable ratios of fed (fish and crustaceans) and bioextractive (filter-feeding shellfish and macroalgal primary producers) farmed species can remove the potential for coastal eutrophication from nitrogen-rich fish excretions while producing other valuable products (shellfish and macroalgae). Studies throughout the world have demonstrated the nutrient bioextractive benefits of macroalgal aquaculture (e.g. Abreu *et al.* 2009; Sanderson *et al.* 2012; Kim *et al.* 2014; Wu *et al.* 2015; Freitas *et al.* 2016; Wei *et al.* 2017); however, IMTA at the unit of a single

farm remains uncommon in comparison with large-scaled monoculture (e.g. Park *et al.* 2018). Some common problems have emerged in IMTA trials: (i) species selection (e.g. a growing season mismatch between successful monoculture of winter kelp and summer salmon) (Reid *et al.* 2013, Handa *et al.* 2013; Marinho *et al.* 2015; Park *et al.* 2018); (ii) nutrient uptake expectations not achievable without causing gear entanglement, injurious stimulation of epiphyte growth on the macroalgal crop or requiring too much lease acreage to achieve the ratio of macroalgal to animal biomass needed for full nutrient mitigation (e.g. Sanderson *et al.* 2012; Yu *et al.* 2017; Fossberg *et al.* 2018); and 3) lease and crop processing issues (Alexander & Hughes, 2017). Yu *et al.* (2017) published an insightful analysis of discouraged IMTA adopters in Weihai, China, finding that the larger social benefit to the environment of IMTA needed to affect the economics of production more. Kim *et al.* (2019) in a thorough review of the history and present status of open-water seaweed aquaculture in the United States also draw attention to the need for consumers (markets) to appreciate the environmental benefits of seaweed as an aquaculture crop.

What are the prospects and challenges for IMTA in Maine? Maine aquaculturists require a diversity of native macroalgal species that can be grown in summer for open-ocean IMTA to prosper. The agarophyte and red alga *Gracilaria tikvahiae* McLachlan 1979 were developed successfully by Yarish and colleagues for bioextraction of nutrients in eutrophic environments in the north-eastern United States (Kim *et al.* 2014). It should be considered for summer IMTA in Bioregion 1, but additional native species are needed. The likelihood that additional companies and sites in Bioregion 2 are poised to expand salmon aquaculture in Maine (Rogers 2020; Whole Oceans 2020) includes one land-based system, which may also offer improved conditions for IMTA in Maine. Shore-side, land-based IMTA facilities that benefit from periodic use of flow-through seawater are well-established in Israel (Ashkenazi *et al.* 2019; Neori *et al.* 2019) and in Portugal (<https://www.algaplus.pt/>; Ghaderiardakani *et al.* 2019). Apart from possible food value, the additional development of salmon aquaculture in Maine might aid consumer acceptance and reward for IMTA, either open-water or land-based. Environmentally conscious consumers provide market value to organic ratings for macroalgal aquaculture crops, so a limitation is that the Maine Organic Farmers and Growers Association (MOFGA 2020) prohibits organic ratings for macroalgae grown closer than 400 m to a fish farm, which is an obvious challenge to IMTA. Thus, to sway consumers and rating organizations, education and system design are needed for either open-water or land-based IMTA. Presently, very few lease holders that have permission are practising IMTA in Maine (but see Bangs Island Mussels (<http://www.bangs-sislandmussels.com/>)).

There is a clear role for the US government to intervene at the same scale (> \$20 million research funding) as in the recent MARINER (Macro Algae Research Inspiring Novel Energy Resources) programme of the US Department of Energy, which is transforming macroalgal aquaculture in the United States (see discussion in Kim *et al.* 2019). A targeted research programme that would require linked research institutions and aquaculture companies could demonstrate achievement of environmentally valuable goals and high-quality aquaculture products in IMTA in Maine. Maine colleges and universities could also encourage ecotourism at several smaller model IMTA farms that would allow training of a cohort of integrated aquaculturists to achieve the promise of IMTA in Maine. Aquafort (<https://seagrant.unh.edu/aquaculture>) is an example of an IMTA training programme for aquaculturists in New Hampshire.

#### Predators, competitors and nonindigenous species (NIS, invasive species)

The historically cooler climate of the Gulf of Maine has historically prevented establishment of many nonindigenous species (NIS) that became established in more southerly areas of the USA's East Coast from vectors such as hull-fouled ships, ballast water discharge and hitchhikers accompanying import of Asian oysters for commercial aquaculture. Nonindigenous species that negatively affect wild and farmed shellfish and macroalgae in Maine and adjacent regions include the European bryozoan *Membranipora membranacea* Linnaeus and green crab *Carcinus maenas*; the Asian shore crab *Hemigrapsus sanguineus* (De Haan 1853); several colonial ascidians including *Botrylloides violaceus* Oka 1927 and *Didemnum* sp. (Dijkstra *et al.* 2007); the green macroalga *Codium fragile* (Suringar 1889) Hariot; the red macroalga *Grateloupia turuturu* Yamada 1941; several filamentous red algae including *Bonnemaisonia hamifera* Hariot 1891, *Dasysiphonia japonica* and *Neosiphonia* spp.; and the brown alga *Colpomenia peregrina* Sauvageau 1927 ('oyster thief') that spread south across the Gulf of Maine from its introduction into Nova Scotia in the 1960s (Mathieson *et al.* 2016).

Warmer temperatures are permitting newer established NIS species to move northward across the Maine coast, and some endanger the resilience of nearshore aquaculture. The effect of many of these NIS algae and ascidians is to foul lines and gear and cause disturbance of the natural community, resulting in decreased abundance of native species. Dijkstra *et al.* (2019, see their Fig. 1) demonstrated waves of colonization of invasive algae into Bioregion 1 in the 1990s, which was correlated at their sites with reductions in *S. latissima* and *Chondrus crispus* Stackhouse 1797 (Irish moss). Subsequent studies suggested degraded habitat for fish and invertebrates due to the large increase in

filamentous red algal turfs that removed sheltering spaces for epibenthic fish (O'Brien & Scheibling 2018), similar to consequences of kelp loss and replacement by turfs during the Australian MHW. General reductions in abundance of *S. latissima* have occurred in southern New England in recent decades (see Kim *et al.* 2019), and greatly reduced densities of coastal *S. latissima* in southern Bioregion 1 were observed compared to offshore kelp beds in the Gulf of Maine at Cashes Ledge (Witman & Lamb 2018). The warm SST/heat waves in 2012 led to colonization of offshore kelps by the harmful *M. membranacea*, and *D. japonica* was found at Cashes Ledge in 2015.

*Codium fragile* and *M. membranacea* have interactive effects in Nova Scotia (Simoson *et al.* 2015; Wilson *et al.* 2015); the bryozoan stiffens kelp blades when it colonizes them, leading to blade breakage and canopy removal in storm waves. *Codium* spreads over the benthos and can prevent new kelp recruitment (Wilson *et al.* 2015). *Codium* is now present in Bioregions 1 and 2 in Maine. Broken wild kelp blades, due to colonization by *M. membranacea*, are common in Bioregions 1 and 2, but uncommon in Bioregion 3. Bryozoan-colonized kelps are unfit for human consumption. Minimizing recruitment of *Membranipora* onto kelps in Gulf of Maine aquaculture requires new research to understand seasonality of larval supply, farm siting and earlier harvest in the spring than temperature *per se* would require. Resilience of our kelp crops under the climate change models discussed here may also be altered by NIS that become established in the future.

The NIS, red macroalga *Grateloupia turuturu*, spread globally from its native range in Asia, often associated with aquaculture of Asian oysters in other parts of the world. It was recognized as number 312 on the IUCN Global Invasive Species Database (Global Invasive Species Database 2020) and was first reported from Maine in 2017 (Capistrant-Fossa & Brawley 2019). This invasion appears to be limited to the upper Damariscotta Estuary in a warm pocket with high residence time; however, frequent boat traffic and seasonal transport of shellfish rafts to lower parts of the estuary may lead to its spread outwards. The ecological impact of this invasion remains unknown, but research from southern New England revealed reductions in invertebrate richness and diversity (Janiak & Whitlatch 2011), competition with native species (Kraemer *et al.* 2017) and host to a unique epiphytic community (Jones & Thornber 2010). It is likely that *G. turuturu* will become more common on the Maine shore, especially in Bioregion 1 (Koerich *et al.* 2020). Previously established invasive macroalgae (*D. japonica* and *C. peregrina*) are also spreading. These NIS are a risk to Maine's aquaculture, as well as native species, through biofouling and/or interspecific competition.

The aquaculture industry is threatened by the green crab *Carcinus maenas* (L.). (Global Invasive Species Database

2020). Green crabs were introduced to New England in 1817 (Kanary *et al.* 2014; O'Connor 2014), and following a subsequent wave of invaders, their population in the north-east Atlantic increased significantly over the last few decades as changing environmental conditions and warming waters allowed for greater dispersal and establishment (Kanary *et al.* 2014; O'Connor 2014). Green crabs (Fig. 7f) prey upon aquaculture species such as shellfish and destroy critical aquaculture habitat through their foraging behaviour (Miron *et al.* 2005; Bloch *et al.* 2015; Lovely *et al.* 2015; Tan & Beal 2015; MacKenzie *et al.* 2015; Beal *et al.* 2016; Goldstein *et al.* 2017; Hobbs *et al.* 2017; Pickering *et al.* 2017). In contrast to the historical *C. maenas* invasion, a second invasive crab appeared in southern Maine in 2002, the Asian Shore crab (*Hemigrapsus sanguineus* De Haan 1853; Jensen *et al.* 2002; Epifanio 2013). The Asian shore crab has spread along the east coast from its 1988 introduction in New Jersey (McDermott 1991). There is direct competition between these two species in their shared invasive range, and in southern New England states, *H. sanguineus* has effectively replaced *C. maenas* in the coastal ecological food web (van den Brink & Hutting 2017; O'Connor 2018; Baillie & Grabowski 2019). The result is declining *C. maenas* abundance accompanied by a dietary shift towards herbivory in areas with *H. sanguineus* (van den Brink & Hutting 2017). The presence of *H. sanguineus* has stimulated *M. edulis* to develop a much thicker shell at the expense of soft tissue growth (Freeman & Byers 2006). In addition, *H. sanguineus* is a more effective predator on bivalves, including on large mussels, than *C. maenas* (Lohrer & Whitlatch 2002; DeGraaf & Tyrrell 2004; Brousseau & Baglivo 2005; Brousseau *et al.* 2014). This could potentially stunt the development of bivalve aquaculture, causing reduction in product quality and slower growth rates. More recently, both the green crab and Asian shore crab have declined in some areas of southern New England, and the Asian shore crab seems to be prone to boom-and-bust population cycles (Bloch *et al.* 2019).

One major risk associated with a changing environment and warmer climate is that the Gulf of Maine will become suitable for diseases that are currently considered exotic to Maine. There are several multifactorial processes by which new diseases might enter the state. Some diseases might see naturally greater dispersion and reproduction after reaching a new habitat, whereas others may be introduced as parasites of other NIS species that are replacing existing biota in the Gulf of Maine in a changing ecosystem. For example, it is possible that southern U.S. populations of striped bass *Morone saxatilis* (Walbaum 1792) will expand northwards in Maine with warming temperatures, as has occurred with northern expansion of the black sea bass *Centropomus striata* L. (DeWitt *et al.* 1981; Bell *et al.* 2015). While the native Maine *M. saxatilis* population has not suffered from extensive mycobacteriosis infections, southern

populations have, and there is potential to introduce this disease into the Gulf of Maine putting both wild and farmed fisheries at risk. The prevalence of mycobacteriosis has been recorded to be as high as 50% in southern populations and is related to warmer water temperatures (Stine *et al.* 2010; Latour *et al.* 2012; Hoening *et al.* 2017). This potentially serious zoonotic pathogen is absent in Maine due to low water temperatures. Low temperatures prevent the pathogen *Mycobacterium marinum* from replicating, because its optimal growth temperature is between 20 and 32°C (Mason *et al.* 2016; Hashish *et al.* 2018). Therefore, it is possible that the future climate in the Gulf of Maine will allow *M. marinum* to become an endemic fish pathogen, potentially impacting wild and farmed fish.

Climate model projections suggest that temperatures across the Gulf of Maine will continue to rise over the next three decades until extremes observed in the last decade become the norm (Fig. 4). By 2050, the Gulf of Maine ecosystem as a whole will likely be in transition and invasive species will be relatively more common (Stachowicz *et al.* 2002; Sorte *et al.* 2010), although many native species will remain. However, by 2100 the ecosystem could lock into an alternate stable state (Verlaque *et al.* 2005; Steneck *et al.* 2013; Morley *et al.* 2018). Additionally, with warmer temperatures, *G. turuturu* may become reproductive year-round, as in Portugal (Violante *et al.* 2005; Araujo *et al.* 2011), strengthening its NIS effects. It is notable that Bioregion 3 has remained relatively cool in comparison with Bioregions 1 and 2 (Fig. 10). To what extent the north-east reaches of the Gulf of Maine will remain sheltered from warming is uncertain.

Resilience for the aquaculture industry and marine ecosystems in Maine requires stricter biosecurity protocols to limit the spread of NIS (Capistrant-Fossa & Brawley 2019). The potential for synergistic impact between the pressure of climate change and other major perturbations to the marine ecosystem, such as overfishing and pollution, will also favour establishment of NIS. One approach to control of invasive species is product development (Kang *et al.* 2019; Puntilla-Dodd *et al.* 2019) to apply fishery pressure on the NIS population (Laubier & Laubier 1993; Taylor *et al.* 1994; Briand *et al.* 2004; Dew & McConnaughey 2005; Bechtol & Kruse 2009; Johnston *et al.*, 2011). As mentioned above, this is ongoing for the green crab, and in addition to consumption as human food, the palatable *G. turuturu* may have commercial value for bioactive compounds (Munier *et al.* 2015).

### Emerging and established diseases in finfish aquaculture

Under a changing environment, disease risks to both the marine environment and aquacultured species are also likely to change. Longer summers will provide a wider

window for pathogen outbreaks (Gubbins *et al.* 2013; Jensen & Kristoffersen 2015; Lyngstad *et al.* 2018; Su & Su 2018). This could cause changes in the epidemiology of endemic and exotic diseases in Maine, resulting in a longer period when aquacultured organisms will be at risk of infection. Initially, the risk may simply stem from water temperatures that are optimal for the pathogen and sub-optimal for the host for longer periods. However, more complex interactions may also occur. The intermediate host of a parasite could potentially perform much better under the new Gulf of Maine climate and cause the parasite intensity to build up to a level where it becomes a challenge to the host's health and survival. Warmer conditions may simply shorten generation times, allowing higher burdens of pathogens to build up within the same time period. Abiotic disease risks may also be amplified through warming temperatures, for example mercury absorption has been shown to increase as temperature rises (Pack *et al.* 2014).

This thermal shift can go both ways, as some diseases are thermally limited. For example, above 12°C the viral haemorrhagic septicaemia virus cannot cause clinical disease (Matejusova *et al.* 2008; Campbell *et al.* 2009), and it may be that the risk from this, presently exotic disease, declines as the Gulf of Maine warms. Some diseases are limited to cold water; for example, the bacterium *Flavobacterium psychrophilum* (Bacteroidetes) causes disease in water below 12°C, as well as winter ulcer disease of Atlantic salmon, which only occurs below 8°C (Lunder *et al.* 1995).

Atlantic salmon have been farmed in open-net pens in Maine since the 1970s. Salmon aquaculture provides a food source that would otherwise not be available through wild fisheries throughout the state, as wild populations in Maine are listed as endangered under the Endangered Species Act and all fishing of the species is prohibited. The majority of salmon farms are located in rural areas of the state, creating jobs for not only farmers, but suppliers, processors and administrators as well (Torrissen *et al.* 2013). Compared to the majority of other aquaculture sectors in Maine, the salmon industry is well-established. However, disease has become increasingly problematic with expansion of the industry throughout the past decades. Persistent, high-intensity and expensive sea lice infections remain the largest impediment to the growth of the sector (Costello 2006). The salmon louse (*Lepeophtheirus salmonis* (Krøyer 1837); Fig. 9d–f) is the most significant economic limitation of salmonid aquaculture, having a greater economic impact than any other disease (Costello 2006). This siphonostomatid copepod has a complex life cycle, which was only described correctly in 2013 (Hamre *et al.* 2013), where the number of attached chalimus stages was correctly determined. In a warming climate, the planktonic nauplii and the host-finding copepodids (Fig. 12) are the stages that are most at risk as they are lecithotrophic. So, warmer

temperatures should increase the metabolism of this store of energy. However, this is likely to be offset by a reduction in generation time in Maine from about 6 weeks to about 4–5 weeks (Tully 1989).

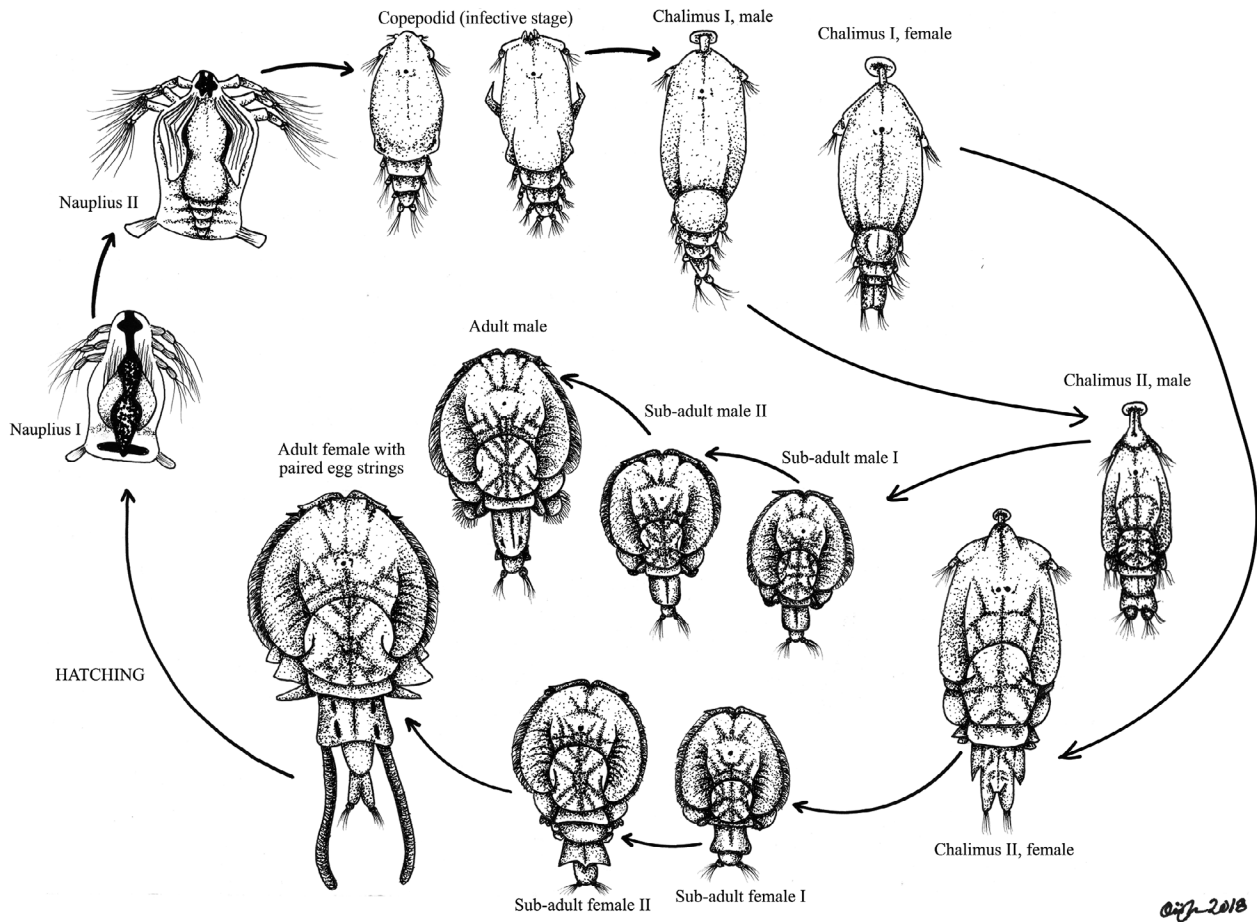
*Lepeophtheirus salmonis* is a species of sea lice that is distributed throughout the Northern Hemisphere, also infecting populations of migrating wild salmon. Although various species of sea lice are found on multiple salmonid species globally, *L. salmonis* is host-specific and is commonly found on salmonids and sticklebacks in Maine (Pietrak *et al.* 2019). Sea lice locate a suitable host, attach using their frontal filaments and feed on fish tissue, mucus and blood (Kabata 1974). With prolonged attachment and high infection intensities, the parasites decrease fish growth, interfere with host osmoregulation and leave open wounds that are susceptible to secondary infections, which at the sublethal level cause economic damage to the value of the product, and can often be the cause of host mortality (Costelloe *et al.* 1999; Mustafa *et al.* 2000).

The current annual global cost of sea lice treatments to the industry is estimated at nearly \$1 billion (Abolofia *et al.* 2017). As a result, the sector continues to seek innovative physical and biological methods to curb and prevent sea lice infections. Although antiparasitic chemicals have been effective in reducing lice loads in the short term, *L. salmonis* has quickly become more resistant to the treatments, rendering them ineffective as a long-term solution. Larval dispersal models are proactive tools that may be used to predict the timing and intensity of lice infections. However, the models must be biologically accurate, and the larval stages of the parasite are difficult to assess directly in field studies (Brooker *et al.* 2018).

Despite the fact that the salmon louse is widely studied and has a profound impact on salmon aquaculture, its baseline biology remains relatively unclear beyond its overall life cycle (Fig. 12). Additionally, the changing environment of the Gulf of Maine further confounds knowledge of how the parasite may perform under future environmental conditions. The maternally derived lipid reserves of sea lice run out once they reach the infective copepodid stage, and at that point, they can no longer survive without attaching to a fish. Therefore, sea lice are attached to a host throughout most of their life stages. It is unknown whether the high fecundity of *L. salmonis* is due to natural selection because of high losses at the early planktonic stages or to access to an essentially unlimited food source (Brooker *et al.* 2018), or to a mix of both.

Temperature, salinity and pH are the most commonly studied environmental parameters that affect sea lice. Tucker *et al.* (2000a) found that copepodid settlement was significantly greater at salinity of 34 compared to 24, and development was faster at the higher salinity. In 2006, Bricknell *et al.* (2006) reported that copepodid





**Figure 12** Life cycle of *Lepeophtheirus salmonis*. The planktonic stages (e.g. Nauplii I & II and the host-seeking copepod) are likely to be vulnerable to climate change as they are lecithotrophic and do not feed until they find a host. Thus, warmer temperatures will shorten the planktonic stage, potentially reducing the infectivity period. However, this is likely to be more than offset by a reduction in generation time in Maine as the seawater temperature rises, leading to maturation of the infective larva in about 4.5 weeks in 2050, compared to 6 weeks now. (image courtesy of Olivia Joyce)

survival in the same general region as that of Tucker *et al.* (2000a), western Scotland, was significantly lower after short-term exposure to salinities below 29. Compromised survival at lower salinities is a result of osmoregulatory failure (Bricknell *et al.* 2006). In comparison, Crosbie *et al.* (2019) compared salinity preferences of both nauplii and copepodid larvae and found that both increasingly avoided water layers that were more brackish. They also found that nauplii strongly avoided salinities below 30, and some copepodids were even found in water layers that had salinities of 16–20. These results differ from the results of Bricknell *et al.* (2006), but, on closer inspection, copepodids in the 2019 study were from Norway and from fish populations that were routinely exposed to freshwater as a louse treatment, which may have selected for tolerance to low salinity.

Thompson *et al.* (2019) demonstrated that *L. salmonis* larvae are tolerant to the predicted end-of-century  $p\text{CO}_2$

levels (RCP 8.5) and the estimated pH values. Again, this study was carried out on European *L. salmonis* larvae (Norwegian stocks). However, currently there is little reason to assume the physiology of these animals will differ from Scottish, Icelandic or North American stocks of *L. salmonis*. This is especially true as low pH has not been used as a method for sea lice control and the previous long-term stability of oceanic pH 8.1–8.4 has provided little evolutionary pressure for *L. salmonis* to have developed regional tolerances to low pH.

Temperature also influences developmental rates and survival of sea lice. Johannessen (1978) found that eggs developed for 33–39 days, 25 days and 10–14 days at 9°C, 9.5°C and 11.5°C, respectively. Tucker *et al.* (2000a,b) also reported that copepodids developed more rapidly at 12°C compared to 7°C. The nauplius I stage of *L. salmonis* in the northern Pacific lasted 9 hours, 30 hours and 52 hours at 15°C, 10°C and 5°C, respectively (Johnson & Albright

1991). The nauplius II stage in the same experiment lasted 35, 56 and 170 hours respective at the same temperatures. Boxaspen and Naess (2000) reported that time to hatching incrementally ranged from 45 to 8 days at temperatures that ranged from 2°C to 10°C, respectively. Similarly, Samsing *et al.* (2016) suggested that there is a predictable effect of temperature on sea lice development, as water temperatures were negatively correlated with development times. However, nauplius larvae in the same study were unable to moult into the copepodid stage at 3°C. Temperature also appears to influence reproductive output of *L. salmonis* adult females. Ritchie *et al.* (1996) found that the average number of eggs per egg string was negatively correlated with water temperature, as the number of eggs per string peaked at approximately 240 in March, a month after lowest average water temperature. These trends are indicative of how the *L. salmonis* population in the Gulf of Maine will respond to the predicted changes in water temperature. Increasing water temperature may lead to a lower number of eggs per egg string and will likely result in more rapid development of *L. salmonis* larvae and could increase the parasite's virulence.

The current literature lacks the baseline sea lice developmental data for the north-east Atlantic. Many published developmental studies investigate sea lice from European waters or western Canadian waters. This is due, at least in part, to the Atlantic salmon industries in Scotland, Norway, Iceland and Ireland that have been producing salmon since 1968 (Eileen 2018) and first encountered an epizootic outbreak of sea lice two decades earlier than Maine. Existing data suggest that sea lice will develop faster in warming waters, which may influence the timing of treatments on farms in the short term. However, the relationship between temperature and the overall population dynamics of salmon lice is not straightforward, as annual peaks and troughs in the abundance of mobile lice appear delayed relative to annual temperature maxima and minima (Jansen *et al.* 2012). Furthermore, although comparisons of results across geographical regions may be useful, investigations of sea lice in the immediate region are necessary for making effective future predictions. A better understanding of current and predicted developmental timing and survival, fecundity and infection success will be key for ultimately creating pest management plans that will persist through the impending environmental changes. The resilience of salmon aquaculture will, in part, depend on the ability of the industry to overcome disease hurdles, and in order to address the problem in the long term, we must proactively account for the influence of a changing environment on sea louse populations.

### Forecasting

The value of seasonal forecasting for finfish aquaculture is an important area for research. Seasonal and annual

forecasts are extremely useful in predicting likely crop outcomes and potential risks. The more traditional, long-term forecasts that predict major change to the ecosystem are of little use to the aquaculturist whose crop cycle may be 1–3 years. These outcomes can be beneficial if the seasonal water temperatures support optimum fish growth but are at the limits for certain pathogens. For example, amoebic gill disease would be of less concern when wet rainy summers are predicted because dilute surface seawater inhibits the pathogen. Similarly, predictions of a cold winter and spring would be expected to delay the onset of parasitic sea lice in salmon farms (Heuch *et al.* 2002). Hobday *et al.* (2016b) make a very strong case that accurate quarterly forecasts are of more use to finfish producers than the longer 10, 25 or even 100 year predictions that are made in many climate change models (Birkel & Mayewski 2018). Such seasonal forecasts should include water temperature, rainfall and air temperature to allow accurate economic decisions to be made. Currently, this type of forecasting is only accurate for 10 days or so (Mase & Prokopy 2014), and it is a clear research deficit in the study of the relationship between climate change and aquaculture resilience. The Maine Climate Office ([https://mco.umaine.edu/gom\\_sst/](https://mco.umaine.edu/gom_sst/)) provides an interface for viewing daily sea surface temperature by bioregion from September 1981 to present. While not completely meeting the need for full forecasting, this utility should be helpful for aquaculturists to place current conditions and trends within a historical context.

### Aquaculture and coastal infrastructure

Climate change will physically modify the estuaries that house many aquaculture farms. The capacity of aquaculture infrastructure to respond to climate stressors while maintaining functionality is an underlying concern of the industry. Here, the general resiliency of aquaculture infrastructure is explored through the lens of Maine aquaculture farms.

#### *Sea-level rise*

The Damariscotta River Estuary (DRE), located in Mid-coast Maine, is a thriving estuary for shellfish aquaculture, and more than half of all current oyster landings from aquaculture occur here (Maine DMR 2020). In particular, the northern reach of the estuary is optimal for shellfish due to low freshwater input, long residence times, warm temperature and high primary production of chlorophyll. Climate change will modify some features of the estuary, which may have implications for the resiliency of the farming industry. Lieberthal *et al.* (2019) proposed that the ideal conditions in the northern reach are likely influenced by a 'curved sill constriction' that separates the northern and mid-reaches. The constriction forces a lateral gyre that

promotes landward-directed flow for a longer period than seaward-directed flow. This influence, along with the generation of overtide currents near the bottom, causes long-term landward transport of dense, suspended particulate matter and reduces the seaward transport of surface material (e.g. plankton). The predicted sea-level rise (see above) has the potential to modify the principal tide, either through amplification or attenuation, depending on the depth of the estuary (Cai *et al.* 2012), which changes flow patterns and long-term material transport. An analytical model has been developed which predicts that by the year 2100, the tidal amplitude in the DRE will be reduced by 0.8 cm (~ 0.5%) (Fig 13b). Weaker tidal forcing leads to a 7.1 cm/s (18.6%) reduction in tidal currents when comparing Fig. 13c.1 and c.2 with Fig. 13d.1 and d.2, which suggests that the optimal particle retention in landward portions of the estuary may decrease, as the blocking effect of the gyre will diminish. Therefore, the productive section of the estuary may be less resilient under extreme sea-level rise as its unique characteristics are diminished. Reduced current velocities will also impact tidal fluctuations in water quality. Intratidal asymmetry in currents within an estuary promotes tidal asymmetries in water quality and is linked to turbulent kinetic energy dissipation (Huguenard *et al.* 2019).

As sea level rises and tidal energy is reduced, the bottom boundary layer and upward flux of sediment may no longer reach the surface, which will reduce the intratidal variability of turbidity, chlorophyll and pH. This aligns with a common facet of aquaculture siting. It is ideal to place farms over locations that are deep enough so that bottom and surface boundary layers do not overlap, limiting the upward flux of sediment into the farm, considering that current speed is reduced over the entire water column underneath the farm with sea-level rise (Fig. 13d.2). This could indicate that as environmental change alters hydrodynamic forces within estuaries, current farm sites may see a reduction in factors contributing to their success, while new regions may become more suitable for aquaculture lease siting.

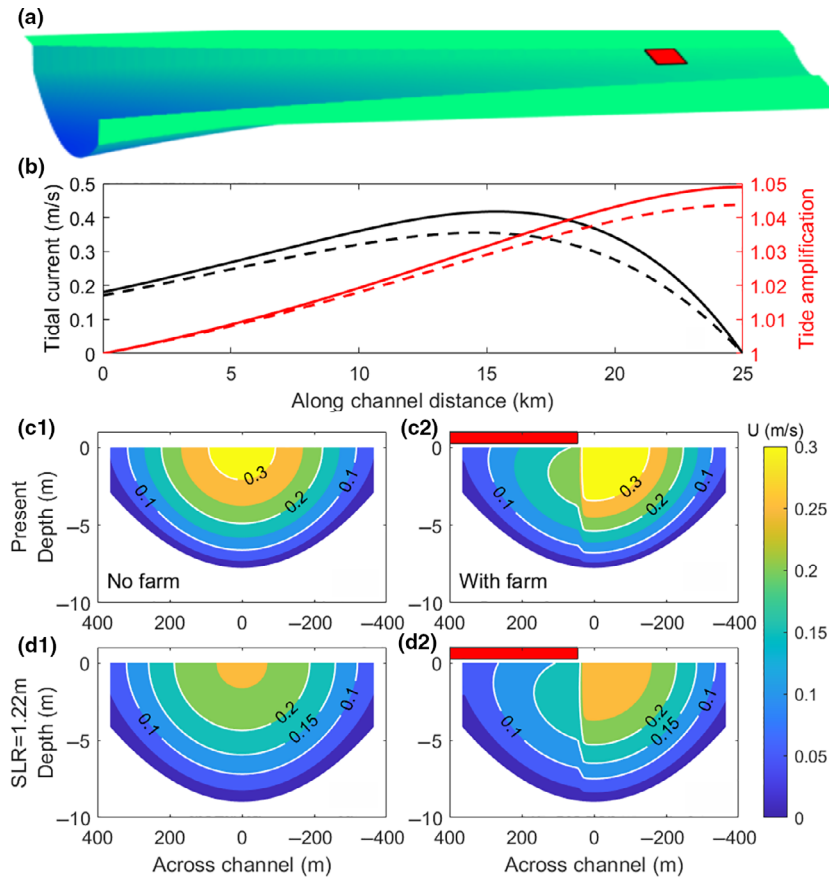
In addition to design considerations for extreme events, the optimal design of an aquaculture farm is also highly dependent on hydrodynamic conditions, which influences the delivery of food to the entire farm. Aquaculture farms (e.g. floating oyster rafts) impose friction that reduces flow directly under the farm compared to the channel (Fig. 13c.2), which causes the flow in the channel to accelerate compared to no farm conditions (Fig. 13c.1). It is expected that this general flow response will be exacerbated from rising sea levels. As sea levels rise, the farm-induced reduction in flow from the channel to the farm will increase from 35.3% in present-day conditions to 37.5% by 2100. The resulting change of flow in the channel from flow bypassing around the farm slightly increased from 14.4

% in present-day conditions to 15.8% by 2100 as less flow travels through the farm (Fig. 13d.2). Farm designs may need to be altered (i.e. long-line length or position) in the future to accommodate weaker currents that deliver food through the farm. While these results are specific to the Damariscotta River Estuary, they highlight how changes in hydrodynamic forcing can influence the physical conditions upon which aquaculture farms are indirectly reliant.

#### Storm surge

Aquaculture farms located in estuarine environments tend to be sheltered from storm-related, enhanced wave energy. Field measurements on a floating oyster farm in the northern reach of the Damariscotta Estuary identified mooring line loads to be highly dependent on water level (Nguyen *et al.* 2019). Peak loads tended to occur during high tide, though loads from current velocities were also significant at low to mid-tide. Asymmetry in line loads was observed before and after the farm, suggesting that mooring loads are highly dependent on local flow interaction with the farm. While mooring lines can be extended to accommodate sea-level rise, excess water levels from extreme weather events may induce line or anchor failures. When farms are located upstream in shallow estuaries, they are susceptible to extreme total storm surge values that are exacerbated by higher frequency tide–surge–river interaction. During a significant storm surge event on 30 October 2017, total surges of roughly 1 m were observed in the Bagaduce River Estuary. The low-frequency component of storm surge (black line in Fig. 14) is related to wind stress and atmospheric pressure and accounted for only half of the measured total storm surge levels. The other half was related to tide–surge–river interaction (magenta line in Fig. 14), which is a mechanism that only occurs inside of estuaries, inland of the immediate coast. The Bagaduce River Estuary houses an oyster farm located upstream of B2, where the tide–surge–river interaction mechanism was shown to increase from B1 to B2, demonstrating that this forcing mechanism needs to be considered in farm mooring design. Flooding due to tide–surge–river interaction can be even more pronounced in short, relatively straight and shallow estuaries. High-frequency tide–surge–river interaction, which is caused by friction and resonance, amplified the wind and pressure-driven (low-frequency) storm surge to over 2 m during a storm event at the head of the Penobscot River (Spicer *et al.* 2019), which is adjacent to the Bagaduce River Estuary.

High-frequency tide–surge–river interaction is expected to intensify as a result of sea-level rise, as mean depth approaches the resonant frequency of the system. If this level of surge coincides with high tide, this could impose



**Figure 13** Idealized 3D analytical model that shows how a farm and sea-level rise (SLR = 1.22m) predicted at 2100 will change tidal characteristics. (a) Idealized bathymetry showing a shallowing and narrowing of the river from mouth to head. A floating oyster farm (marked by red square) is imposed at 20–21 km. (b) Tide amplification is defined as the ratio of tidal amplitude (half the tidal height) at any point along the estuary to the tidal amplitude at the mouth. Values larger than 1 indicate the tidal range is amplified along the estuary. The tide amplifies the estuary due to the funnel shape, though increased sea level reduces that amplification at 2100 (red dashed line) compared to present day (red solid line). The tidal velocity amplitude in the main channel without the presence of the farm is largest at 15 km up the estuary (black lines). SLR will decrease tidal currents (black dashed line) compared to present day (black solid line). (c–d) show how the presence of the farm (red rectangle) changes the along-channel velocity amplitude,  $U$  (m/s), across the estuary. During present day, the farm-imposed friction causes the flow under the farm to decrease (blue contours) and the flow to increase (yellow contours) in the channel (c.2) as compared to no farm case (c.1). At 2100 under 1.22 m of SLR, the currents under the farm are reduced even more significantly (d.2) compared to no farm (d.1), which is important for food delivery and farm flushing.

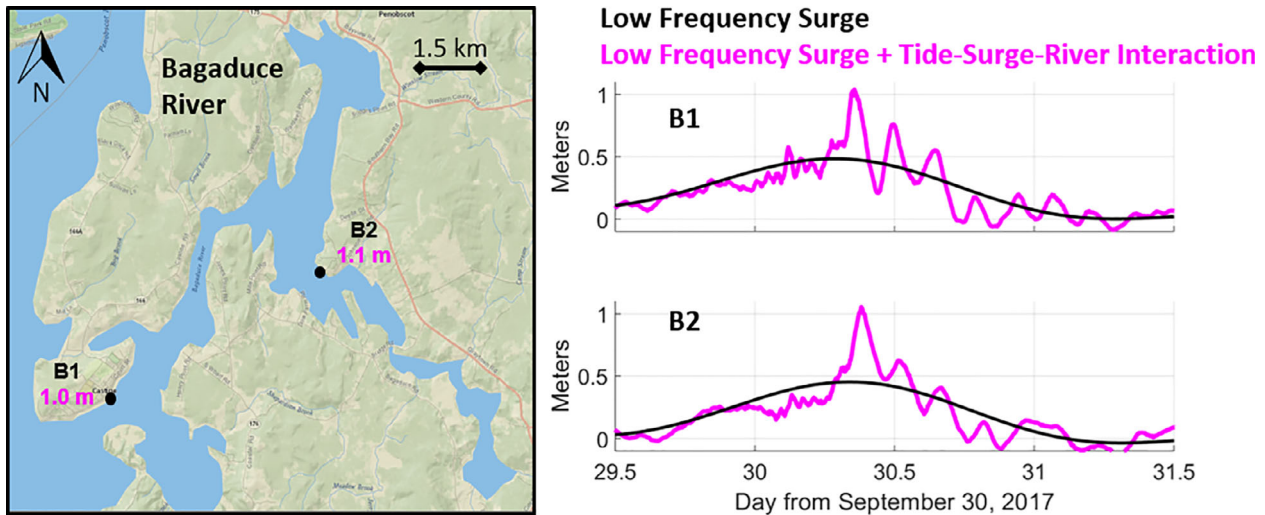
extreme loads on the mooring lines and anchor systems. Predictions from the National Oceanic and Atmospheric Association's Extratropical Storm Surge (ETSS) model during large tide–surge–river interaction events revealed significant (~1.6 m) discrepancies between predicted and observed total surge levels (Spicer *et al.* 2019). The ETSS model only predicts wind- and pressure-driven storm surge and does not account for tide–surge–river interaction, which suggests that actual flooding may far exceed anticipated surge levels.

The understanding of tide–surge–river interaction is in its infancy. Currently, a high-resolution 3D regional modelling system, such as the Regional Ocean Modelling System or the Finite-Volume, primitive equation Community

Ocean Model, is required to capture the tide–surge–river interaction mechanism responsible for the discrepancies between the observations and the ETSS model, though regional modelling systems are computationally expensive and require detailed validation with observations. Once the tide–surge–river interaction mechanism is better understood, a nonlinear forcing term may be included into simpler modelling systems, such as ETSS, in order to improve predictions of storm surge in estuaries.

#### *Coastal erosion mitigation*

As storms become more frequent and intense, existing shoreline protection will become less effective due to rising sea level, and coastlines will become more vulnerable to



**Figure 14** Comparison of low-frequency storm surge (predictable by the Extratropical Storm Surge model) and total surge (including tide–surge–river interaction). Left panel is a map of the Bagaduce River Estuary in Maine, where B1 is the seaward station and B2 is the interior station. Total storm surge was 1 m at B1 and increased to 1.1 m at B2. The right-hand panels compare the low-frequency surge (black line) with the total storm surge in magenta during a storm event in October 2017. The low-frequency storm surge (predictable by ETSS) underrepresented the flood levels by as much as 0.6 m on day 30, because it does not capture tide–surge–river interaction.

erosion. A green and sustainable alternative is to use floating aquaculture as living breakwaters off the coast. Modelling has been performed (Zhu *et al.* 2020) to determine whether floating mussel droppers can be used in conjunction with submerged aquatic vegetation to reduce wave energy and potentially mitigate coastal erosion. Results showed that the mussel droppers are better at attenuating shorter waves, such as those occurring in sheltered environments, compared to longer waves that may be observed at an exposed coastline. Floating mussel droppers are not impacted by large fluctuations in water levels in the same way that submerged aquatic vegetation is, because of their suspension from the surface. Using floating mussel droppers in conjunction with submerged aquatic vegetation along vulnerable sheltered coastlines offers a sustainable alternative to shoreline armoring by attenuating waves in storm tide conditions. It remains to be determined if shoreline armoring with floating mussel droppers will be suitable for harvest for commercial purposes in Maine, and may serve primarily as shoreline protection.

## Conclusions

This paper focuses on the resilience of the cold water aquaculture industry in the face of impending environmental change, which was defined as the capacity of the ecological, physical and social systems of the sector to address challenges and respond to opportunities, while maintaining the same function and identity under climate change (IPCC

2007). The Gulf of Maine is warming, is likely to experience future acidification and is also a significant case study for mitigating the effects of environmental change. By studying the impacts of climate change on the cold water aquaculture industry, we will gain a better understanding of potential impacts on other regions. Resiliency of the marine aquaculture sector will be subject to factors such as warming waters, decreased pH levels, changes in precipitation, and increased storm frequency and severity, which could negatively impact both the cultured species and the gear on an aquaculture farm. Such risks are summarized in Table 1.

Current research has highlighted several stressors to the aquaculture industry as well as potential paths forward. New models and model organisms are being developed that will give more reliable and detailed measurements of physiological effects of environmental change, thus giving way to novel physiological metrics that provide a more nuanced base of information to inform research initiatives in the future. While bivalve aquaculture is threatened by increasing ocean acidification, and macroalgal aquaculture in Bioregion 1 could be threatened by increasing ocean temperatures, recent research suggests that a combination of new species and greater focus on domestication of the aquaculture industry (e.g. breeding, public repository of strains, nurseries and hatcheries) will provide resilience against climate change. Physical effects of climate change have the potential to influence the characteristics of the products themselves and may change the most efficient methods and practices, as in the case of seaweed drying.



**Table 1** Risk factors to the resiliency of the marine aquaculture sector in a changing climate

Class	Potential impact	Exposure factors	Sensitivity magnitude	Strategy to improve adaptive capacity
Biological	Changing disease profiles in cold water sectors and risk of new disease and parasite introduction.	Warming waters will reduce the incidence of thermally limited disease, that is cold water vibriosis. Some warm water diseases will become established, for example mycobacteriosis and parasites, such as sea lice will have more generations in a season. Increasing the infectious pressure on wild and farmed fish.	High	<ul style="list-style-type: none"> <li>• Develop and accurately utilize proactive tools such as larval dispersal models to predict and prevent infection risk.</li> <li>• Increase resolution of epidemiology research to create regionally specific and effective pest management plans.</li> <li>• Improved biosecurity plans for aquaculture sites.</li> </ul>
Biological	Changing oceanic conditions may exclude the growth and production of certain commercial aquaculture species.	Will the upper thermal limit for Atlantic salmon be reached by 2050 in the Gulf of Maine?	Medium	<ul style="list-style-type: none"> <li>• Evaluate new aquaculture species for open-water aquaculture.</li> <li>• Evaluate and invest in onshore RAS aquaculture systems.</li> <li>• Maintain a research programme for alternative species for cultivation.</li> </ul>
Biological	Increased risk of new invasive species and accelerated invasion progress, disrupting aquaculture species and infrastructure.	<p>NIS green crabs and Asian shore crabs prey on aquaculture species and negatively affect growth rate of bivalves.</p> <p>NIS green crabs and Asian shore crabs damage salt marsh and eelgrass beds adding to coastal erosion and habitat degradation.</p> <p>NIS <i>Membranipora</i> (bryozoan), <i>Grateloupia</i>, filamentous algae such as <i>Dasyatisiphonia</i>, and colonial ascidians create biofouling on macroalgal crops and gear and/or outcompete native macroalgae.</p> <p>Asian shore crabs are currently colonizing Bioregion 1 and competing with the established invasive green crab. This could lead to Asian shore crabs outcompeting green crabs and forcing them to become predominantly herbivorous. However, they are more aggressive towards native crabs and target immature blue mussels as their preferred diet.</p>	<ul style="list-style-type: none"> <li>• High, Bioregion 1</li> <li>• Medium, Bioregion 2</li> <li>• Medium, Bioregion 3</li> </ul> <ul style="list-style-type: none"> <li>• High, Bioregion 1</li> <li>• Medium, Bioregion 2</li> <li>• Medium, Bioregion 3</li> </ul> <ul style="list-style-type: none"> <li>• High, Bioregion 1</li> <li>• Medium, Bioregion 2</li> <li>• Low, Bioregion 3</li> </ul> <ul style="list-style-type: none"> <li>• High Bioregion 1</li> <li>• Medium, Bioregion 2</li> <li>• Medium, Bioregion 3</li> </ul>	<ul style="list-style-type: none"> <li>• Nursery production of larvae and seed clams followed by distribution to farmers for seeding intertidal sediment.</li> <li>• Use of crab deterrent equipment to protect small bivalves until they out-grow their crab predators.</li> <li>• Develop and protect crab-free refugia.</li> <li>• Develop a fishery or biological control measures for the reduction in the intensity of invasive crabs.</li> <li>• Strengthen enforcement of existing regulations and consider new regulations to prevent transfer of aquaculture gear and organisms that may be fouled to NIS-free areas.</li> <li>• Apply decision tree analysis to cost/benefit of earlier harvest of kelp crops.</li> <li>• Education for local governments, conservation groups, recreational users and aquaculturists across all sectors about dangers of NIS on Maine aquaculture production.</li> <li>• Consider biosecurity knowledge requirements for lease awards.</li> <li>• Strengthen enforcement of legislation to prevent accidental introduction of this species northwards.</li> <li>• Increase monitoring for the presence of <i>H. sanguineus</i> in Maine.</li> <li>• Education for local governments, conservation groups, recreational users and aquaculturists across all sectors on the impact this crab will have on the endemic fauna and flora and aquaculture activities.</li> </ul>

Table 1 (continued)

Class	Potential impact	Exposure factors	Sensitivity magnitude	Strategy to improve adaptive capacity
Biological	Ocean and sediment acidification causing reduced health and growth rates in aquacultured species.	Acidification reduces mineral availability by changing the saturation state in the water column and increases shell erosion rates, especially in juvenile bivalves.	High	<ul style="list-style-type: none"> <li>• Exploration of alternative commercial species that are more resilient to the anticipated conditions.</li> <li>• Extended hatchery periods to increase fitness before moving to grow-out site.</li> <li>• Seawater buffering with sodium carbonate and crushed bivalve shells.</li> <li>• Examine mechanisms that enable juveniles of some bivalve species to survive in acidic pore water.</li> </ul>
Biological	Trophically unbalanced development of aquaculture.	Increased number of fish farms without colocated shellfish and marine algae, a situation that could lead to eutrophication of embayments, and potential seasonal mismatch of main aquaculture species that limits application of IMTA.	Medium	<ul style="list-style-type: none"> <li>• Consider IMTA for open-ocean or land-based aquaculture of marine finfish with seasonally matched animal/algal species.</li> <li>• Achieve IMTA by infusion of new U.S. programme to couple companies and researchers to solve IMTA bottlenecks.</li> </ul>
Biological	Warming sea water temperatures negatively affect natural populations of kelps.	Lack of diversification of species used in macroalgal aquaculture, and slow move to 'agricultural models' to acquire and seed bank natural genetic diversity for future breeding.	High	<ul style="list-style-type: none"> <li>• Develop commercial potential of acclimation treatments to increase heat tolerance, including study of epigenetic effects.</li> <li>• Introduce baseline monitoring to reveal changes in kelp abundance and presence/absence of natural populations to reveal changes in algal crop species.</li> <li>• Move to established husbandry in kelp aquaculture (e.g. establishment of permanent gametophyte seed banks of each commercial kelp species, definition of genotypes to assure genetic diversity among seed-banked strains, breeding to produce strains with desired crop traits).</li> <li>• Invest in human capital and farm infrastructure to develop commercial aquaculture of native red algae.</li> </ul>
Biological/ Societal	Inadequate financial benefit for IMTA growing operations preventing expansion of IMTA technology.	Environmental benefits of IMTA not recognized in market value of IMTA aquaculture crops, discouraging farmers' interest in nutrient extraction by trophically balanced aquaculture.	Medium	<ul style="list-style-type: none"> <li>• Consider private and public mechanisms to add economic value to products/crops produced with certified IMTA.</li> <li>• Overcome bottleneck for organic certification of crops grown in IMTA with fish.</li> <li>• Establish University/Sea Grant IMTA demonstration farms (1+/Bioregion) for training new cohort of aquaculturists, while emphasizing ecotourism.</li> </ul>

**Table 1** (continued)

Class	Potential impact	Exposure factors	Sensitivity magnitude	Strategy to improve adaptive capacity
<i>In silica</i>	Inadequate modelling predictions and low capacity for anticipating the multifactorial effects of climate change.	Inaccurate simulations of future change could substantially hinder planning. For example, underestimating the magnitude of future acidification could delay the development of hatcheries for bivalve species with early life stages susceptible to acidification.	Medium	<ul style="list-style-type: none"> <li>• Coupling global climate models (GCM) to high-resolution nearshore models of biogeochemistry and aquaculture production extensively validated with historical data will increase confidence in projections.</li> <li>• Laboratory and field studies that mechanistically determine the response of organisms to multiple stressors induced by climate change will be vital to couple future environmental changes to biological systems that are adaptable.</li> <li>• Encourage farmers to monitor environmental trends through the Maine Climate Office's interactive tool: <a href="https://mco.umaine.edu/gom_sst/">https://mco.umaine.edu/gom_sst/</a></li> </ul>
<i>In silica</i>	Sea-level rise leads to reduction of food availability for aquaculture operations.	Reduced tidal current velocities in estuaries due to sea-level rise, together with frictional farm drag force influence, may lead to a localized reduction in food supply, depending on farm orientation relative to current and bathymetry.	Medium	<ul style="list-style-type: none"> <li>• Given sea-level rise can alter hydrodynamics of an estuary and the interaction between farm geometry and local hydrodynamic conditions (i.e. food availability and waste transport characteristics), farmers should periodically review local hydrodynamics in close proximity to the farm and assess need to alter farm location, orientation and/or size.</li> <li>• Animal density is another factor to consider simultaneously.</li> </ul>
<i>In silical</i> Societal	Increased coastal erosion from storm events.	Increased coastal erosion from storm tides reduces the shoreline width, causes property loss of the coastal communities and adversely impacts tourism.	High	<ul style="list-style-type: none"> <li>• Utilize suspended mussel droppers offshore to dissipate wave energy.</li> <li>• Utilize surface-suspended macroalgae or mussels, to dissipate wave energy, recognizing that harvesting the product during storm season will negate dissipation benefits.</li> </ul>
<i>In silical</i> Societal	Storm surge imposes additional structural loading on aquaculture farms.	Enhanced storm surge upstream in estuaries relative to the coast increases the hydrodynamic load on the aquaculture infrastructure, resulting in mooring line and/or anchor failure, limiting aquaculture production.	High	<ul style="list-style-type: none"> <li>• Optimize mooring line configurations and anchor designs, considering local morphology and peak high-frequency tide–surge–river interactions.</li> <li>• Avoid upstream farm placement in shallow and short estuaries with orientation parallel to storm wind, which is understood to lead to vulnerabilities during storm surge conditions.</li> <li>• Incorporate nonlinear tide–surge–river interaction in storm surge predictive models.</li> </ul>

**Table 1** (continued)

Class	Potential impact	Exposure factors	Sensitivity magnitude	Strategy to improve adaptive capacity
Physical/ Societal	Decreased efficiency and predictability of sea vegetable drying processes.	Changing precipitation, humidity and temperature in coastal areas will elevate risk of poor or unpredictable drying conditions.	Low	<ul style="list-style-type: none"> <li>• Transition from open-air drying methods to more resource-intensive and predictable closed-system drying methods.</li> <li>• Research and development of green methods such as solar dryers and other renewable energy sources.</li> </ul>
Physical/ Societal	Inadequate drying and processing methodology for macroalgal crops.	Inadequate capital for infrastructure with majority of farm sites in Maine, and limited knowledge of alternative methods to sun drying within the sector.	Medium	<ul style="list-style-type: none"> <li>• Entrepreneurs needed to develop new products/markets.</li> <li>• Cooperative collaboration across farm clusters could reduce barriers to equipment investment.</li> <li>• Enhanced training opportunities to reduce knowledge gap for alternative drying methods.</li> </ul>
Societal	Change in market characteristics of sea vegetable products.	Changing growing environments result in different species and cultivars entering market.	Medium	<ul style="list-style-type: none"> <li>• Establish baselines and continual monitoring of product and market characteristics to detect changes as they occur.</li> <li>• Effective marketing of new or replacement products.</li> </ul>

Nonindigenous, invasive species and diseases will continue to threaten the health of the local ecosystems and aquacultured products, with even small levels of warming enhancing these threats. The effects of these new invasive species are yet to be discovered, but past events such as the devastating NIS crab invasions provide insight into the potential impacts on coastal ecology.

Despite ongoing efforts to understand the changing environment and socio-cultural context within which aquaculture occurs, there remains much uncertainty regarding climate change scenarios. This paper has reviewed a variety of initiatives in the cold water sector. Despite these efforts, the aquaculture industry's adaptive capacity and potential resilience in the face of the adverse impacts of climate change would benefit from additional research and development in ecological, social and physical sciences. In particular, given that many of the adaptive strategies identified to enhance the resilience of aquaculture are inherently social, particular attention must be paid to understanding the industry's (adaptive) capacity to leverage networks, institutions and discourses to cope with existing changes and adapt to new ones.

These complex and ongoing efforts will require sustained funding, effort, and support to reach fruition. The catalyst of the recently concluded SEANET project united aquaculturists across species and bioregions in Maine. This collaboration advanced the pace of aquacultural development and has drawn other players to Maine. By continuing the new collaborations between researchers, farmers, industry

and government at both federal and state levels, we expect our industry to be resilient to future climate change.

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- [Correction added on 5 October 2020, after first online publication: Fernandez *et al.* (2020) has been amended. The references Lüning & Mortensen (2015); Munda (1997); Wilson, Mortazavi & Kiene (2015); and Wilson & Whitney (2015) have been removed from the list. The references Lüning (1984); Munda & Lüning (1977); and Wilson, Kay, Schmidt & Lotze (2015) have been added. All in-text citations have been corrected accordingly.]