

Impacts of climate change on aquaculture

C. Collins ¹, E. Bresnan ¹, L. Brown ¹, L. Falconer ², J. Guilder ³, L. Jones ⁴, A. Kennerley ³, S. Malham ⁵, A. Murray ¹ and M. Stanley ⁶

EXECUTIVE SUMMARY

- Aquaculture is a significant industry in UK coastal waters, with annual turnover valued at more than £1.8bn. It particularly important in western and northern Scotland.
- Aquaculture is sensitive to the marine environment and changes therein.
- The dominant contribution of a single species (Atlantic salmon) to production tonnage and value potentially increases vulnerability to climate change.
- Temperature increase is expected to increase growth rates for most species farmed.
- Increased problems associated with some diseases and parasites, notably sea lice and gill disease (which has emerged as a serious problem), are likely to increase in the short term and to get worse in the longer term. Impacts may be synergistic.
- Harmful Algal Blooms (HABs) and jellyfish swarms/invasions may also get worse, however complex ecosystem interactions make responses uncertain.
- The situation for shellfish is similar to finfish, although they are additionally at risk of accumulation of toxins from HABs, and recruitment failure, and, in the longer term, to sea-level rises and ocean acidification.
- Technical and management changes in the rapidly evolving aquaculture industry make long-term impacts of climate change difficult to forecast.

Citation: Collins, C., Bresnan, E., Brown, L., Falconer, L., Guilder, J., Jones, L., Kennerley, A., Malham, S., Murray A. and Stanley, M. (2020) Impacts of climate change on aquaculture. MCCIP Science Review 2020, 482-520.

doi: 10.14465/2020.arc21.agu

Submitted: 10 2019 Published online: 15th January

2020.

1. UK AQUACULTURE

1.1 Introduction

Aquaculture is a key UK food production sector, and it is particularly economically important to rural coastal communities, and in the deprived urban areas where processing takes place (Alexander et al., 2014; UK

^{1.} Marine Scotland Science, 375 Victoria Rd, Aberdeen, AB11 9DB, UK

^{2.} Institute of Aquaculture, University of Stirling, FK9 4LA, UK

^{3.} Centre for Environment, Fisheries and Aquaculture Science, Weymouth, DT4 8UB, UK

^{4.} Centre for Ecology and Hydrology, Bangor, LL57 2UW, UK

⁵ School of Ocean Sciences, Bangor University, LL59 5AB, UK

^{6.} Scottish Association for Marine Science, Oban, PA37 1QA, UK

MNMP, 2015). UK production value exceeds £590 million (Black and Hughes 2017), with £1.8bn turnover and 8800 jobs supported (Alexander *et al.*, 2014), of this £1.4bn turnover and 8000 jobs are in Scotland, making aquaculture particularly relevant there. There is significant potential for aquaculture to develop further throughout the UK (Black and Hughes, 2017).

UK marine finfish aquaculture is dominated by the production off the west coast and islands of Scotland of Atlantic salmon, Salmo salar (156,025 tonnes in 2018; Munro, 2019), and a very small production from Northern Ireland. Freshwater salmon smolt production, for marine on-growing, is more widely Scottish marine production also includes rainbow trout distributed. (Onchorhyncus mykiss), sea (brown) trout (Salmo trutta) and halibut (Hippoglossus hippoglossus). In the past, cod (Gadus morhua) in Scotland, and sea bass (*Dicentrarchus labrax*) in Wales, were farmed. Recently, a major growth in production of lumpfish (Cyclopterus lumpus) and wrasse (various Labridae species) has occurred in Scotland (Munro, 2019), Wales (Anon, 2018) and England, for use as 'cleaner fish' to control sea lice on farmed salmon. The majority of marine salmonid aquaculture takes place in open-sea cages; 86% of freshwater salmonid smolts for marine on-growing are also produced in cages and so can be vulnerable to environmental conditions (Munro, 2019). Other smolts are produced in Recirculating Aquaculture Systems (RAS) that are protected against the environment, RAS are also used for production of other species such as lumpfish.

Bivalve-shellfish farming produces mussels (*Mytilus edulis*), oysters (*Crassostrea gigas* (Pacific) and *Ostrea edulis* (native), scallops (*Pecten maximus*, *Chlamys opercularis*) and clams (*Ruditapes* sp.). Mussels are the main farmed seafood product of Wales, Northern Ireland and England, and, for shellfish, Scotland. Pacific oyster is the second most-farmed shellfish, with minor production of the other bivalves. On-growing or ranching of prawn, lobster and crab and macroalgal farming remain small-scale (Capuzzo and McKie, 2016).

1.2 The future of UK aquaculture

There are aspirations to expand aquaculture, for example doubling the value of Scottish production by 2030 (https://aquaculture.scot/), increasing Welsh shellfish tonnage by 91% (The Welsh Government, Report R.2384, 2015) and mussel production in England (UK MNMP, 2015). Present inshore aquaculture sites will remain important in the medium-term future, at least, and there are continuous developments that may also help mitigate against climate change impacts on growth, disease, pollution and physical damage. However, suitable space for aquaculture expansion in inshore waters is limited. Therefore, offshore production is being developed for bivalves in Lyme Bay and the Irish Sea, and is projected for finfish by 2030 (UK MNMP, 2015; Black and Hughes, 2017); offshore can be defined as >3 km from shore (Holmer, 2010), but definitions vary in practice. Lack of information on

potential impacts of climate change on exposed/offshore aquaculture is a major knowledge gap. Onshore, Recirculating Aquaculture Systems (RAS) are increasingly used for freshwater stages of salmonid production (Munro, 2019) and are being trialled for the marine phase (niri.com). RAS are used throughout the UK for production of other marine fish species, notably cleaner fish, such as lumpfish and wrasse. RAS and Closed Containment System (CCS) production can be made independent of local climate.

Increased production of seaweed is supported in Scotland (Seaweed-cultivation-policy-statement-2017) and Wales. Seaweed aquaculture may mitigate climate change, e.g. producing biofuel or damping wave energy (Duarte *et al.*, 2017). Similarly, Integrated Multi-Trophic Aquaculture (IMTA) may increase the resilience of aquaculture to climate change (Chopin *et al.*, 2012) although research into the practicability of such systems is required before scaling up.

2. SUMMARY OF CURRENT AND PREDICTED CHANGES TO CLIMATE AND OCEAN ACIDIFICATION

2.1 Introduction

Since the early 20th century UK sea levels have risen on average by 16 cm when corrected for isostatic land movement. Future projections for sea-level rises by 2100, compared to 1981–2000, indicate rises of between 0.4 m and 0.7 m for the UK as a whole, depending on emission scenarios, but with considerable variation within these scenarios and regions of the UK and rises over 1 m are possible in southern areas (UKCP18). Temperatures (SSTs) have shown average regional increases of 0.17°C to 0.45°C/decade since 1984, with an average rise of 2.9°C in UK coastal waters expected by the end of the century (Hughes et al., 2017; Tinker et al., 2016). Storms are predicted to increase, but there is a lot of uncertainty in this (Tinker et al., 2016). Rainfall varies regionally across the UK with predicted declines in summer rainfall of up to 47%, particularly in the south, and increases in winter rainfall of up to 35%, particularly in Scotland, however changes are very variable, dependent on area and emissions scenario (UKCP18). Ocean Acidification (OA) has increased in UK coastal waters faster than the North Atlantic average as detailed in the MCCIP report on OA (Williamson et al., 2017).

2.2 Current and predicted impacts of climate change and ocean acidification on UK aquaculture

There is limited evidence of climate change impacts already happening in UK aquaculture, though effects are difficult to disentangle from other factors influencing production (see Section 3). There have been no major changes nor geographical shift in terms of farmed species associated with climate.

There have, however, been a number of recent changes, which (while multifactorial) may be linked to climate change, for example emerging gill disease problems and increasing establishment of feral Pacific oysters. Therefore, the MCCIP review of the impact of climate change on aquaculture is updated here.

This section is divided into subsections based on physical carrying capacity (2.2.1), production carrying capacity (2.2.2), ecological carrying capacity (2.2.3), disease (2.2.4), invasive species (2.2.5) harmful algal blooms (2.2.6) and food safety (2.2.7) and related issues.

2.2.1 Physical carrying capacity (physical suitability of sites) (Low confidence)

Sea-level rise can reduce suitable sites for aquaculture, e.g. intertidal mudflats for shellfish; it is also possible newly flooded land might become available for use. Sediment deposition from runoff, and resuspension during storms, can affect fish and shellfish mortality, health and growth. Suspended particles can cause gill damage in fish (Au *et al.*, 2004). Storms and waves can damage exposed fish cages, leading to escapes or predator access (Jackson *et al.*, 2015). Storms can also damage or detach shellfish from seabed or aquaculture structures (Dankers, 1995), and most present-day shellfish aquaculture is confined to sheltered areas. Furthermore, daily operations and site access can be affected by increased bad weather resulting in health and safety concerns for farm stock and the farm workers (Thorvaldsen *et al.*, 2015).

2.2.1.1. What is happening (Low confidence)

There have been no reports on the loss of aquaculture sites due to climate-change impacts on their physical suitability. Fish escapes are recorded in Scotland together with some data as to causes, including storm damage (Aquaculture Scotland). Taylor and Kelly (2010) indicated that failure of cages and moorings accounted for 16% of fish escapes between 2002 and 2009, some of which were exacerbated by storms. A technical standard for marine and freshwater fish cages was introduced by the Scottish Government in 2015 (Marine Scotland 2015).

2.2.1.2. What could happen in the future (Low confidence)

Projected UK coastal sea-level rise of approximately 40–70 cm by 2100 (UKCP18) is unlikely to have major impacts on coastal space available for finfish production. Shore-based facilities and access points may be affected by increased flood risk. Sea-level rise can result in coastal erosion, affecting coastal geomorphology and hydrodynamics, which may change the availability of suitable areas for shellfish culture, both positively and negatively (Filgueira *et al.*, 2016).

Increased precipitation and storm events may result in higher sediment loading in coastal areas, which may cause stress or physical damage to fish and shellfish, and storms may also increase fish escapes, infrastructure costs and insurance. Mitigation methods include improved cage technology (Thorvaldsen *et al.*, 2015), use of sterile triploid fish (Benfey, 2016), and genetic methods to trace source populations (Gilbey *et al.*, 2018). Co-location of sites with other offshore activities, such as windfarms, can be used to effectively increase capacity (https://maribe.eu/; Gimpel *et al.*, 2018). CRISPR (Clustered Regularly Interspaced Short Palindromic Repeats) DNA sequences have recently been used to generate sterile salmon (Wargelius *et al.*, 2016) and, depending on future policies for use of this technology, may also help mitigate against escape impacts.

2.2.2 Production carrying capacity (Low confidence)

Production carrying capacity is the maximum level of production an area can support. Most production (and ecological) carrying capacity issues are determined by 'local' factors at farm- or waterbody-scale, and it is difficult to generalise climate change impacts.

Temperature is a controlling factor for growth of shellfish and fish (Elliott and Elliott, 2010), affecting metabolism, food conversion, energy expenditure and oxygen requirements (Brett, 1979). Temperature increases within the species' physiological tolerance may increase growth, but growth and feeding reduce and mortality increases if tolerance is exceeded; flesh quality may also be adversely affected by high temperatures (Ørnholt Johnsen *et al.*, 2017).

UK mussel culture is currently dependent on natural settlement of larvae from the environment. Oceanographic features such as stratification and fronts can act as barriers to the movement of larvae, forming in response to warming or freshwater inputs, but they may be disrupted by storms (Woodson and Litvin, 2015), thus climate change may affect bivalve larvae availability. A lack of natural spat could be mitigated by developing hatchery production. Ocean acidification poses a greater risk to bivalve shellfish compared to fish, as shell formation is inhibited by reduced carbonate availability in acidic waters. Bivalves are also poor acid-base regulators (Booth *et al.*, 1984).

2.2.2.1. Finfish: what is happening (Low confidence)

In Scotland, average production times have decreased (Munro, 2019), perhaps reflecting a benefit of warming SSTs. However, changes in husbandry, production (e.g. salmon post-smolts put to sea at larger sizes), feed and breeding have also occurred.

2.2.2.2. Finfish: what could happen in the future (Moderate confidence)

In poikilotherms feeding/growth rates gradually increase towards an optimum temperature and rapidly fall off if temperature exceeds this optimum (Figure 1). Good salmon growth occurs between 10° C and 18° C, decreasing significantly below 6° C and $\geq 18^{\circ}$ C (Handeland *et al.*, 2008; Elliott and Elliott, 2010). SST predictions (Hughes *et al.*, 2017) indicate, with a high

degree of confidence, that temperatures will remain mostly below 18°C and so suitable for salmon farming to 2100 and may be expected to increase growth rates. However, summer and autumn productivity in the south of Scotland and Northern Ireland might decline particularly in sheltered coastal waters with local temperatures substantially different from coastal means (Falconer *et al.*, 2020). Events associated with heat waves could cause episodes of mortality that would need to be managed for (Spillman and Hobday, 2014), such events are likely to remain rare, but risk can be expected to increase. Sustainable densities may also reduce due to coping with lower dissolved oxygen levels, since warmer water holds less oxygen and increases fish metabolism (Vikeså *et al.*, 2016). Modelling studies have predicted a similar outcome for salmon aquaculture along the Norwegian coast, though seasonal and geographical differences in SST are larger (Lorentzen, 2008).

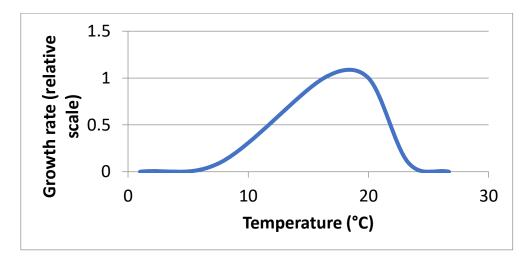


Figure 1: Relative growth rate response of Atlantic salmon to temperature. (From data in Elliott and Elliot, 2010.)

Marine salmon farming does not currently occur in England and Wales and it is likely that prolonged summer seawater temperatures >18°C, particularly on the south coast, would be sub-optimal for production. In general, OA research has not seen significant effects on growth and mortality of adult fish, though studies are limited and there are some exceptions (Gobler *et al.*, 2018). RAS and CCS allow mitigation against climate-change driven changes to freshwater temperature, oxygen and pH levels; however, it may use more energy and so contribute to climate change. Development of exposed/offshore aquaculture may avoid extremes in temperature, salinity, pH and oxygenation experienced closer to the coast.

Increasing SST makes farming of cod and halibut more difficult because optimal growth occurs at lower temperatures (Björnsson and Tryggvadóttir, 1996) but improves the potential for sea bass, sea bream or other species in southern UK waters, though temperatures are still sub-optimal (Besson *et al.*, 2016) even by 2100 predictions. Wrasse production might increase relative



to lumpfish, as the former perform better as cleaner fish relative to lumpfish in warmer water (Costello *et al.*, 1995).

2.2.2.3. Shellfish settlement and growth: what is happening (Low confidence) Shellfish production has declined overall in the UK, though regional increases have occurred. There have been anecdotal reports of poor shellfish spat fall or changes in its timing in recent years (Adamson *et al.*, 2018). However, no studies have been undertaken on links to climate change.

2.2.2.4. Shellfish settlement and growth: what could happen in the future (Low confidence)

Optimal survival of *Mytilus edulis* larvae is at 17–21°C, (Galley *et al.*, 2010) and growth increases up to 21°C (Almada-Villela *et al.*, 1982). UK spat falls, predominately occurring in spring and autumn, may benefit in most parts of the UK, though highest autumn temperatures in the south of England may be suboptimal. Similarly, in the south of England adult *M. edulis* growth may be affected by high summer temperatures, with an associated delay in autumn spawning. Increases of 1°C and 4°C were predicted to reduce production by 10 and 50% for *M. edulis* and 2 and 5% for *Crassostrea gigas* respectively in Strangford Lough, Northern Ireland (Ferreira *et al.*, 2008). In the south of England, *M. galloprovincialis*, with an optimum larvae survival at 20–24°C (Sánchez-Lazo and Martínez-Pita, 2012), may increase its distribution, so even if temperatures become too high for *M. edulis*, production of mussels may continue.

Crassostrea gigas spat is raised in hatcheries where the environment can be controlled. Growth of *C. gigas* occurs between 2–27°C, with the optimum around 20°C (Bougrier *et al.*, 1995). Survival of juvenile oysters was 90% versus 25% during mild and harsh winters respectively (Diederich, 2006). Therefore, predicted increases in UK SST may benefit *C. gigas* growth, but may also result early maturation (Chávez–Vilalba, 2002), resulting in lost production (Deslous-Paoli and Héral, 1988).

Increasing SST may also promote development of the native oyster *Ostrea edulis* in UK waters. Settlement and growth of larvae requires temperatures greater than 15–20°C with optimal temperatures of 25–30°C (Robert *et al.*, 2017). Currently, *O. edulis* populations in UK waters are found in sheltered inlets, where temperatures can reach over 20°C in summer.

Salinity between 10 and 30 psu is reported to have little effect on survival of *M. edulis* larvae, while growth increases to optimum at 25–30ppt (Landes *et al.*, 2015). Temperatures >25°C can impact on survival and growth at salinities <20 ppt (Brenko and Calabrese 1969). *C. gigas* spat can survive and grow at salinities of >15 ppt (Wiltshire 2007), with optimal growth at 25–35 ppt (Fuhrmann *et al.*, 2016). Therefore, increased incidences of high precipitation and freshwater runoff during winter and drought and higher UK SSTs in summer may have greater impact more on oyster and mussel growth respectively.



Salinity and temperature thresholds for bivalves can depend on acclimation (Almada-Villela, 1982) or genotypes (Kinnby, 2015). Higher growth at higher temperature is dependent on food availability (Flores-Vergara *et al.*, 2004), otherwise increased metabolism reduces growth. These interactions make it difficult to predict the net effect of climate change on shellfish production.

OA is detrimental to shellfish, in particular larval stages (Lemason *et al.*, 2017). Effects on post larval and adult shellfish metabolism, growth and shell integrity have also been reported (Callaway *et al.*, 2012; Fitzer *et al.*, 2018), with a predicted reduction of 25% and 10% in shell by 2100 for mussels and oysters respectively (Gazeau *et al.*, 2007). OA effects *Mytilus* byssal threads (Dickey *et al.*, 2018) making some shellfish more susceptible to storm damage and predators. Even if shellfish reach production size, OA may impact on final quality and value, and increase costs of production (Mangi *et al.*, 2018).

Coastal acidification can often exceed the long-term predicted changes in OA but varies greatly on a geographical and temporal scale (Williamson *et al.*, 2017). The frequency, duration and magnitude of coastal acidification events driven by climate change, such as coastal upwellings, phytoplankton blooms and freshwater runoff (Fitzer *et al.*, 2018) and sea-level rises (MEMA, 2017), may increase in future (Gruber *et al.*, 2012). Fluctuating pH may have less impact on bivalves than constant low pH in terms of mortalities or shell damage, though more energy expenditure may be required by the shellfish to maintain homeostasis with changing pH (Mangan *et al.*, 2017).

There is little culture of crustacea in the UK; some hatchery-rearing of lobsters takes place for restocking in the wild. Decapods can regulate their ionic balance with greater control over processes like calcification, though growth may be slowed to maintain homeostasis (Callaway *et al.*, 2012).

Overall, increasing OA and climate change impacts will most likely exacerbate natural fluctuations in coastal pH, with detrimental effects on shellfish in the mid-term. The magnitude of impacts will depend on interactions with other stressors and food-web effects. Impacts at offshore shellfish developments may be dictated by OA alone and only appear by the end of the century.

2.2.3 Ecological carrying capacity (Low confidence)

Ecological carrying capacity is the production level that can be supported without unacceptable ecological impacts (Murray and Munro, 2018). The UK's Westminster and devolved governments' aquaculture policies stress the need to conduct and develop aquaculture in an environmentally sustainable way. Ecological impacts arising, such as reduced benthic oxygen, from aquaculture could be enhanced due to climate-change effects (Kernan, 2015).



2.2.3.1 What is happening

Expansion, including northwards, of invasive species, including feral nonnative Pacific oyster and manilla clam, is discussed elsewhere (see Section 2.2.5). Impact of fish waste on benthic ecosystems can increase as temperatures rise (Tett *et al.*, 2018) and this benthic load already limits consented biomass in many coastal locations. Storm damage can increase escape of farmed fish (see Section 2.12) impacting wild salmon fitness and genetic diversity (Thorstad *et al.*, 2008). Salmonid farming can increase the abundance of infective sea-lice stages in the environment (Shephard *et al.*, 2016) and sea lice can impact on health and behaviour of wild salmonids (Taranger *et al.*, 2016, see Section 2.2.4).

2.2.3.2 What could happen in the future

By the 2050s, warming water temperatures may allow *C. gigas* and *Ruditapes philippinarum* to increase the spread of feral populations and to expand northwards (Cook *et al.*, 2013) with possible impacts on benthic habitats. Warming temperatures increasing their metabolism and food intake could result in limits to allowable shellfish biomass in terms of ecosystem sustainability, due to impacts on food availability for other filter feeders if prey items do not increase in tandem (Guyondet *et al.*, 2015).

Potential increases in escapes of farmed fish associated with storms (see Section 2.2.1) and sea lice associated with warming waters (see Section 2.2.4) are a risk to wild salmonids (Taranger *et al.*, 2014) and associated ecosystems, e.g. the endangered freshwater mussel *Margaritifera margaritifera*. A move to exposed/offshore or RAS/CCS farming could mitigate against impacts due to increased sea lice infestations, assuming lice from offshore sites are dispersed sufficiently to reduce infection pressure.

Climate change may increase pressure on benthic communities in sediments, potentially reducing maximum sustainable production. Higher temperatures could lead to reduced oxygen and increase hypoxia, reducing ability of benthic fauna to cope with farm organic wastes (Tett et al., 2018). These organic wastes could also change as loading from farms changes, given that feed intake, food conversion efficiency and evacuation rate are all affected by temperature (Handeland et al., 2008). Nutrient loading from adjacent terrestrial systems could increase under higher rainfall (Arnell et al., 2015), this can be ameliorated by better terrestrial management. Accumulation of waste under cages may increase in winter/spring due to predicted high rainfall and runoff events, as lower salinities increase settling rate (Chen et al., 1999), as may an increase in winter storms that disperse and dilute wastes. Rising temperature and OA have been shown to increase solubility of heavy metals and other pollutants and their uptake by organisms in sediments (Shi et al., 2016). There may also be changes in coastal hydrodynamics, the ecosystem and the benthic community that will affect dispersion and assimilation (Beveridge, 2004). In Scotland, fjordic systems and basin sills prevent strong



water exchanges (Gillibrand *et al.*, 2006) increasing carrying capacities vulnerability to climate changes.

2.2.3.3 Fish feed

Sourcing of farmed fish feed is another import factor in aquaculture sustainability. Historically a large proportion of this fish feed comes from small pelagic fisheries. Climate has impacted key species previously when El Niño prevented upwelling of nutrients collapsing their phytoplankton food source (Callaway *et al.*, 2012). However, globally salmon feed has gone from 45% fish meal and 25% fish oil in 1995 to 22% fish meal and 12% fish oil in 2010, and proportions continue to drop (Tacon *et al.*, 2011). Plant sources are already, and increasingly, major ingredients for Atlantic salmon feed (Salin *et al.*, 2018), these crops may also be subjected to climate change. Other initiatives include genetic modification of plants to produce fish oil, breeding or programming of fish to adapt to new feed, production of algae or insects for use in fish feed (Roy and Pal 2015; Tran *et al.*, 2015; Sprague *et al.*, 2017), but these would require development in both techniques and public acceptance and must ensure feed retains qualities, such as omega-3 long-chain fatty acids and docosahexaenoic acids.

2.2.3.4 Social carrying capacity (Low confidence)

Social carrying capacity is the level of aquaculture that can occur without unacceptable social impact. These impacts are often subjective and how climate change may affect them is difficult to predict. At a local level, climate change may impact other activities, affecting the perception of aquaculture. For example, climate changes may decrease UK fishing activities leading to loss of employment and income (Fernandes *et al.*, 2017), and therefore prioritisation of aquaculture in national policies. However, changing conditions placing greater pressure on already limited space and resources may increase conflict and animosity towards aquaculture, affecting the ability to establish and operate sites. Marine spatial planning is key to ensure optimal use of an area when adapting to changing conditions (Gimpel *et al.*, 2018) and social planning to ensure societal adaption, for example, creating aquaculture jobs to replace fishing jobs.

2.2.4. Disease (Moderate confidence)

Disease is a major cause of losses in UK aquaculture, accounting for about 30% of losses in salmon aquaculture (Soares *et al.*, 2011) with larger losses during outbreaks (Rodgers *et al.*, 2018). Climate change and OA impacts on disease (Harvell *et al.*, 1999; Marcogliese, 2008) could affect aquaculture, although such impacts can be overstated (Lafferty and Mordecai, 2016) as disease management and technology adapt to climate changes.

2.2.4.1 What is happening (Moderate confidence)

There has been an apparent increase in salmon gill issues due to new pathogens, e.g. the emergence of Amoebic Gill Disease (AGD), caused by

the amoeba *Paramoeba perurans*, is associated with high salinities and temperatures in regions where it is established (Oldham *et al.*, 2016, Hall *et al.*, 2017). AGD likely emerged in Scotland and Norway following a particularly warm summer in 2006 and thereafter outbreaks following mild winters. Industry is increasingly concerned over fish-gill damage due to microalgal and jellyfish blooms, which may reflect increased occurrence, or a decrease in fish ability to deal with these additional stressors (see Harmful Algal Blooms, Section 2.2.6). However, other changing factors can contribute to gill pathology, including breeding, feed composition and production practices. Other pathogens also respond to changing environments, notably sea lice populations grow faster and are more difficult to control in warmer waters (Brooker *et al.*, 2018), although currently industry is controlling numbers (Murray and Hall, 2018) at increasing costs.

Shellfish diseases have also expanded their ranges into and within the UK (Murray *et al.*, 2012). Recent spread of OsHV-1 μ var since 2010 in England and Ireland has been attributed to distribution of infected hatchery spat rather than climate. Nevertheless, the warming of UK waters may have contributed to the spread of the virus and increased disease in infected populations with mass mortality occurring at >16 °C.

2.2.4.2 What could happen in the future

It may be possible to predict the impact of individual climate changes and OA on specific aspects of disease development in relation to specific pathogens/pathogen types. However, it is difficult, as for other life history aspects, to predict impacts in relation to real-life scenarios with multiple temporal, spatial, physical and biological interactions influencing infection rates and disease outcome. To assess sensitivities of diseases to climate change we describe the impacts of climate drivers on pathogen transmission (Section 2.2.4.2.1) and development of disease (Section 2.2.4.2.2) before considering specific case studies of disease likely to be sensitive to climate change (Section 2.2.4.2.3).

2.2.4.2.1 Transmission and persistence in the environment. Pathogens transmit between hosts through the environment. This exposes them directly to that environment and so makes pathogen spread sensitive to climate change and OA. Environmental effects on transmission may be considered as two processes: the physical transport and the decay of pathogens (Salama and Rabe, 2013). The processes of transmission through the environment are similar for pathogens of fish and shellfish.

Currents that transport pathogens are driven by factors such as large-scale circulation patterns, winds, and at a local scale, freshwater inputs in estuaries and sea lochs (Dyer, 1973). Climate change can impact these elements affecting pathogen dispersal and patterns of disease outbreaks, necessitating changes in area management strategies (Gimpel *et al.*, 2018). Conversely, winds also drive turbulent diffusion which disperses pathogens reducing



concentrations potentially below thresholds at which they represent a risk of infection, sea lice are an exception as, because of their ability to swim vertically, they can increase concentrations under appropriate hydrodynamic conditions (Salama and Rabe, 2013; Murray and Salama, 2017).

Once released into the environment obligate pathogens can only decay but opportunistic pathogens can grow while outwith their host. Changing concentration changes the risk to potential new hosts. Environmental drivers therefore affect the environmental dynamics of different pathogens in different way.

Temperature affects the dynamics of all pathogens. Decay rates for viruses tend to increase with temperature (Oidtmann *et al.*, 2017), decay of larval *Bonamia* also increases with temperature (Arzul *et al.*, 2009), whereas, increased SST and OA promote the growth and survival of opportunistic bacterial pathogens such as *Vibrio* (Hernroth and Baden, 2018; Baker-Austin *et al.*, 2017). *Paramoeba perurans* growth increases with temperature to 15°C in culture (Collins *et al.*, 2019). Sea lice maturation-rate increases with temperature (Brooker *et al.*, 2018), so sea lice become infectious sooner, but last for less time as temperature rises; this means they may infect salmonids more rapidly by affect smaller areas under rising temperatures (Samsing *et al.*, 2017). Increased temperatures may increase antimicrobial grazing by shellfish (Burge *et al.*, 2016) and plankton (Gonzalez and Suttle, 1993).

Salinity also affects pathogen survival. Viruses have optimal salinity ranges which differ between viruses (Oidtmann *et al.*, 2017) but many can tolerate substantial ranges. Growth and survival of *Paramoeba perurans* increases at higher salinity (Oldham *et al.*, 2016; Collins *et al.*, 2019), and survival of sea lice (Brooker *et al.*, 2018) and the oyster parasite *Bonamia* (Arzul *et al.*, 2009) also increases at higher salinity so drier hotter summers will potentially increase the abundance and infectivity of these parasites in the environment. Lowered salinity in winter and spring may help counteract increased survival of parasites due to milder temperatures. Fungi and oomycetes tend to be prominent in freshwater (van West, 2006).

Viruses such as ISAV may be particularly sensitive to UV radiation, associated with drier weather (Oidtmann *et al.*, 2017), though other viruses are robust to UV (Kitamura *et al.*, 2004) which attenuates rapidly in water, particularly if it is turbid. Bacteria can also be sensitive to UV.

Although viruses do have optimal pH ranges the response to OA of microbial communities, including pathogens, is largely unknown (Liu *et al.*, 2010).

The environment also provides refuges and reservoirs for pathogens that may change in response to climate changes. Binding to particles provides protection for viruses and bacteria (Pham *et al.*, 2011; Campos *et al.*, 2013); sinking particles may remove pathogens from the water column but create



reservoirs in sediments. Particles also increase turbulence, attenuating UV. Particle availability may depend on wind-driven resuspension and biological creation (Alldredge and Silver, 1988), processes which may themselves increase with temperature. Climate change can affect behaviour and range of wild fish and shellfish (e.g. feral Pacific oyster expansion) which can act as reservoirs for pathogens of farmed animals (Wallace *et al.*, 2017; Jones *et al.*, 2013). Invasive fouling organisms may affect pathogen retention on farms by reducing circulation in cages and making disinfection more difficult (Fitridge *et al.*, 2012).

2.2.4.2.2 Development of infection and disease in hosts. Climate changes and OA can affect pathogen virulence factors or host metabolic and/or immunological activity, impacting on disease development within or on the host itself.

2.2.4.2.2.1 Direct effects of climate change and OA on pathogens in their host environment: Temperature is the most likely factor to have a direct effect on pathogens in a poikilothermic host environment. Optimal growth of many endemic bacterial and parasitic species occurs at temperatures higher than currently found seasonally in UK waters (Uddin et al., 2008; Guijarro et al., 2015; Collins et al., 2019). Viruses depend on host machinery for replication and a temperature induced increase in host metabolism may result in higher viral replication (Gubbins et al., 2013). However, even while promoting growth rate, warmer temperatures may reduce the expression or activity of virulence factors in some species e.g. Flavobactrium psychrophilium (Guijarro et al., 2015), Salmonid Pancreatic Disease virus (Hikke et al., 2014). Environmental changes can also select for new, or for the evolution of existing pathogen strains, differing in virulence or growth rate (Murray and Peeler, 2005; Chen and Shakhnovich 2010; Panzarin et al., 2014; Asrafi et al., 2018). Evolutionary trade-offs between growth ex-host and virulence inhost can occur but may be less pronounced in high host density environments (Pulkkinen et al., 2010). As a generality, in the absence of other factors, increases in average sea water temperatures predicted for the UK will permit faster growth of many aquatic pathogens in their hosts, resulting in an overall increase in their inherent capacity to cause pathological effects.

2.2.4.2.2.2 Indirect effects of climate change and OA on pathogen virulence in the host environment: Skin and mucous barriers are the first lines of defence against infection in fish and shellfish. These barriers may be damaged by climate change effects, giving pathogens a foothold, e.g. increased UV damage during sunny weather (Fabacher *et al.*, 1994), though this may be counteracted by blocking of UV due to turbidity linked to increased storms and runoff (Häder *et al.*, 2015; Williamson *et al.*, 2019). Changes in environmental salinity and pH may affect the immune reactivity of mucosal immune molecules, or may change the viscosity of mucus (Roberts and Powell, 2005), with lowered salinity decreasing viscosity and allowing pathogen entry, or may change the adhesion ability of bacteria to



host surfaces (Balebona *et al.*, 1995). There has been limited study on the effect of predicted climate and OA changes on these aspects of infection. Organisms that cause mechanical damage to fish, such as sea lice, phytoplankton or jellyfish, may increase with sea-water temperature increase, further compromising gills or skin (Ugelvik *et al.*, 2017).

It has been suggested that a potential increase in pathogen replication in fish at warmer temperatures may be counteracted by an increase in innate (nonspecific), but even more so in adaptive (specific) host immune responses (Uribe *et al.*, 2011; Abram *et al.*, 2017). Generation of T_helper cell populations and antibody responses are improved at higher temperatures (Le Morvan *et al.*, 1998; Soto *et al.*, 2014). Higher temperatures resulting in faster and higher expression of antiviral genes in flounder was attributed to control of hirame rhabdovirus infection at 20°C compared to 10°C (Zhang *et al.*, 2017). Higher antiviral and innate immune gene expression or activity were also shown to correlate with higher temperature in shellfish (Green *et al.*, 2014; Rahman *et al.*, 2019), though such effects are not consistently reported (Matozzo and Marin, 2011).

Upregulated immune genes at higher temperatures in Pacific oysters had no apparent impact on OSHV-1 µvar infection (Green *et al.*, 2014), and both Green *et al.* and Rahman *et al.* suggest that the higher immune gene induction may compromise immunosurveillance or cause pathology in shellfish hosts.

The immune response can be negatively impacted when climate-change- and OA- effects create conflicting demands on energy due to increased host metabolic activity at higher temperatures or maintaining homeostasis in the presence of increased fluctuations in salinity or pH. This effect may be compensated by feeding regime in farmed finfish, but shellfish immune response may be compromised if climate and OA impact negatively on their environmental food sources. Additional stressors including temperature outwith the species tolerated physiological range, as well as extended periods of high temperature, hypoxia and increased UV radiation will result in the production of a stress response in finfish with a direct immune suppressive effect (Markkula et al., 2007; Tort, 2011; Abdel-Tawwab et al., 2019), and these stressors may have even lower thresholds when hosts are infected (Gehman et al., 2018). The effect of these additional environmental factors on shellfish immune response is less clear, with contradictory results observed within and between species (Matozzo and Marin, 2011), though shellfish generally have wider tolerances than finfish (Guo et al., 2015). Additionally, studies using multiple stressors have generated effects on fish and shellfish immune responses different to those using single stressors (MacKenzie et al., 2014, Araujo et al., 2018). Acute and chronic exposures to climate change and OA effects, can also result in different outcomes in relation to immune responses (Bowden et al., 2008). Host stress has also been associated with pathogen virulence emergence (Gadan et al., 2013).



Therefore, beneficial effects of higher temperatures on immune response, especially on that of finfish, may improve the health status of farmed UK species over periods of the year, but it is likely that without intervention then predicted extremes in temperature, hypoxia, salinity or pH fluctuations will result in increased frequency or severity of disease outbreaks at other times. In addition, climate change extends the temporal presence and abundance of pathogens in the environment (or in/on host), then this may increase potential for co-infections to occur, reported to increase mortality risk, e.g. as for coinfection with OSHV-1 uvar and bacteria (de Lorgeril et al., 2018), or to reduce vaccine efficacy (Figueroa et al., 2017). Heterologous, parasite and bacterial pathogen co-infections tend to be synergistic whereas viral coinfections tend to be antagonistic with respect to impact on host (Kotob et al., 2016). Lastly, recent research has highlighted the influence of mucosal microbiome composition on the immune response (Egan and Gardiner 2016). Aquatic animal microbiomes will be influenced by climate and OA changes to environment and host physiology, but an understanding of 'good' and 'bad' microbiomes, and environmental effects on these, is limited.

2.2.4.2.3 Potential changes in specific pathogens: Viruses have optimum temperature windows within which they are most likely to spread or cause disease (Bricknell *et al.*, 2006). Under a warming climate, the times of year of outbreaks may change. For example, Salmon Pancreatic Disease Virus (SPDV), a causative agent of Pancreatic Disease in marine salmon, grows best at 10°C to 15°C, so outbreaks may occur earlier in the year and over extended periods. OSHV–1 μvar causes mortality in oysters when SSTs rise above 16°C with latent infections occurring below 16°C (Pernet *et al.*, 2014). Increasing SST may facilitate its distribution northwards, or increase in outbreaks.

Bacterial responses to climate change are likely to be complex. Some, such as Vibrio salmonicida or Moritella viscosa, may decline under warming temperatures, but other vibrios may increase, especially those affecting shellfish (Thomson et al., 2006), some of which are zoonotic (see Section 2.2.7). Such vibrios are more prevalent at warmer temperatures (>15°C) and lower salinities (<25 ppt) (Baker-Austin et al., 2013), so warmer, wetter winters and springs may increase certain vibriosis during these periods. Vibriosis epizootics may also increase with warmer summers when mollusc hosts are under higher metabolic demands, and bacterial growth rates (and virulence) could also increase (Hernroth and Baden, 2018). Vibrio tubiashii, coupled with an unusual warming event, was associated with 59% mortality in shellfish hatcheries on the US Pacific Coast in 2007 (Elston et al., 2008). infections such as Mycobacterium marinum Mycobacterium chelonae, may increase as warming temperatures allow them to expand their range northwards (Gubbins et al., 2013; Baker-Austin et al., 2017). Many salmonid bacterial diseases are controlled by vaccines, whose introduction was associated with a large drop in mortality (Murray and Munro, 2018), however increased temperature could affect duration of



vaccine efficacy (Eggset *et al.*, 1997), and increases vaccine associated lesions (Grini *et al.*, 2011). Cleaner fish may be susceptible to increased bacterial diseases under warmer climates as available vaccines are limited. *Aeromonas salmonicida*, which tends to occur with increasing temperatures, is controlled in vaccinated salmon but has been reported from wrasse, as has *Vibrio splendidus*.

Fungi and oomycetes may increase under warmer wetter conditions due to runoff as pathogenic fungi are largely freshwater (Van West, 2006). Freshwater fungal diseases could restrict availability of salmonid smolts, but these are relatively rare causes of marine diseases in the UK.

Bonamiasis, caused by the parasite Bonamia ostreae, resulted in a 93% decrease in French production of Ostrea edulis between 1970 and 1982 (Laing et al., 2014). Parasite prevalence is most likely in areas of moderate temperatures (12–20°C) and high salinity, so increasing SSTs and increased salinities due to drier summers may cause the parasite to spread northwards in UK waters (Murray et al., 2012) but to decrease in the south, as the parasite had a lower survival rate at 25°C (Arzul et al., 2009). However, mortality rates for infected oysters may be greater in warmer waters and offset any decrease in parasite levels; B. ostreae although present in Scotland it is not currently associated with disease. Although the UK is free of the parasite Bonamia exitiosa, it has been reported previously from Cornwall (Longshaw et al., 2013). This parasite causes mortality in O. edulis at >26°C and salinities 40 psu, and future predicted warmer drier summers may facilitate establishment and/or outbreaks in the south of the UK. The parasite Maretelia refringens has caused mass mortalities in O. edulis across Europe, and also infects Mytilus edulis and M. galloprovincialis. It is again believed to be temperature dependent, with highest prevalence occurring in the summer (Arzul et al., 2014). Invasive hosts that act as reservoirs may also spread northwards due to increasing SST (Jones et al., 2013).

Sea lice, already the most serious parasite of marine salmonids, are likely to increase with warmer and lower rainfall climates as they mature more rapidly and survive better (Groner *et al.*, 2014; Brooker *et al.*, 2018). Sea lice exhibit seasonal patterns with higher numbers in warmer seasons (Hall and Murray, 2018). They are also found in higher numbers on wild sea trout near farms in warm dry years (Shephard *et al.*, 2016). Warmer conditions may increase stress of mechanical and bath treatments and so make these more likely to induce mortality (Overton *et al.*, 2017). However, cleanerfish wrasse may become more effective delousers as they are active above 10°C (Costello *et al.*, 1995).

Increase in *Paramoeba perurans* population growth occurs between 4°C and 8°C and populations can survive and grow for some time in salinities of >20 ppt and 25 ppt respectively (Collins *et al.*, 2019). Therefore, increasing winter temperatures, despite episodes of lower salinity, may support overwintering

and earlier, faster, disease occurrences in spring and summer. Under warming scenarios AGD (and other gill diseases) may be expected to increase in impact. Freshwater reduces AGD, so drought could reduce treatment options and affect AGD management, particularly if resistance to H₂O₂ treatment emerges (Oldham *et al.*, 2016). Hypoxia due to increased temperature, or algae decay following increased blooms, could reduce ability to perform stressful treatments, and affect fish recovery.

Sea lice and gill diseases may act synergistically to increase problems in response to warming temperatures making problems worse.

Timescales of changes may vary between pathogens. Sea lice and gill disease are already serious problems in the management of fish health and so may be expected to get worse in the short- and moderate-terms (2020s to 2050s). In the longer term, conditions are likely to become inherently become even more suitable for these pathogens, however technological and management changes mean impacts are difficult to predict. Shellfish diseases can also be expected to become more widespread and severe, dependent on the spread of the pathogens, notably Scottish water temperatures are currently generally too low for key pathogens to cause severe shellfish diseases (Murray *et al.*, 2012), but this is more likely to change in the moderate- to long-terms (2050s to 2080s).

2.2.5. Invasive non-native species (INNS) and nuisance species (Low confidence)

2.2.5.1 What is happening (Low confidence)

There is little evidence that invasive non-native species (INNS) are causing significant impact on aquaculture in the UK despite marine INNS including the tunicates Didemnum vexillum and Styela clava being present and spreading. These INNS have the potential to smother and outcompete cultured shellfish species as well as incurring additional husbandry and product-processing costs. D. vexillum has been found on mussel beds and in an oyster hatchery in England, and more recently on oyster farms in Scotland (Cottier-Cook et al., 2019). However, anthropogenic introduction rather than climate change is thought to be the primary cause of these occurrences, though increasing water temperatures above 16°C may support their establishment. In the case of Styela clava, northerly locations reaching summer water temperatures above 16°C may be a contributory factor in the spread of this species northwards in Scotland (Cook et al., 2013). Native fouling species already do cause significant impacts for aquaculture infrastructures (Fitridge et al., 2012) but again there is little reported evidence of climate change effects on their level of impact. Populations of feral Pacific oyster, C. gigas, (originally considered unable to reproduce at UK seawater temperatures) have successfully bred in Northern Ireland (Kochmann et al., 2012). Feral C. gigas have recently been observed as far north as Shetland (Shelmerdine et al., 2017). Spread of C. gigas out with aquaculture sites can have consequences for local biodiversity (Nehls and Buttger, 2007), although these may be positive (e.g. Christianen *et al.*, 2018). Feral oysters can also act as disease reservoirs (for example OsHV has been found in feral oysters in a disease management buffer zone in the Thames estuary), or competition for farmed oysters (Miossec *et al.*, 2009). Increased water temperatures may have contributed to the establishment of feral populations of Manilla clams (*Ruditapes philippinarum*) following introduction for cultivation (Humphreys *et al.*, 2015).

2.2.5.2 What could happen (Low confidence)

Climate change may increase introduction, establishment and secondary dispersal of marine invasive species (Maggs et al., 2010), particularly as species ranges extend further north (Reid et al., 2009). Biofouling of fish and shellfish aquacultures structures is conservatively estimated to contribute 5– 10% of aquaculture production costs (Fitridge et al., 2012). Detrimental effects of biofouling organisms include net occlusion, reduced water flow and oxygen levels, competition for food and space, lesions and disease transmission (Martell et al., 2018) and the added weight to systems increasing structural stress or harvesting effort. The shellfish farming sector is most likely to be impacted by non-native fouling species including the tunicates D. vexillum and S. clava, which are present in the UK and spreading, but hydrozoan biofoulers' stinging cells can damage fish skin and gills (Bloecher et al., 2018). Rising seawater temperatures are likely to provide more optimal conditions for both sexual and asexual reproduction of D. vexillum (Nimmo et al., 2012) contributing to its spread. The slipper limpet Crepidula fornicata is present in coastal water of Wales and southern England. Rising water temperatures could enhance its benthic recruitment (Bohn et al., 2012), with its potential to compete for benthic habitat and foul shellfish species. Similarly, C. gigas recruitment to feral populations is predicted to be high risk by 2040 (Syvret, 2008).

Mytilus trossulus is a native UK 'nuisance species' for aquaculture of M. edulis as its flesh quality is inferior and its weaker shell prone to harvesting and storm damage (Gubbins, 2012). Competition for settlement space in Loch Etive, Scotland, has resulted in significant losses in M. edulis production (Dias et al., 2009). M. trossulus is more tolerant of lower salinities than M. edulis at early life stages (Qiu et al., 2002). Therefore, increased rainfall and freshwater runoff might be expected to promote its expansion. Conversely, M. edulis is more tolerant of higher temperatures, and OA effects on byssus compared with M. trossulus (Dickey et al., 2018), potentially improving ability to withstand storm damage. Therefore, rising SST and OA may limit competition of M. trossulus over M. edulis.

The introduction and establishment of NNS is a complex process influenced by both climatic factors as well as human mediated. There is also insufficient information on the biology of NNS and many native biofoulers. It is therefore



difficult to predict how a changing climate may exacerbate their impacts on aquaculture.

2.2.6. Plankton, HABs and jellyfish (Low confidence)

2.2.6.1 What is happening now

2.2.6.1.1 Harmful Algal Blooms: Plankton are reviewed in an accompaning MMCIP report (Edwards et al., 2020). Harmful Algal Blooms (HABs) have impacted the UK aquaculture industry by causing mortalities and impacting the health of farmed fish, resulting in the enforced closure of shellfish harvesting areas due to concentrations of algal toxins in shellfish flesh above regulatory limits. Mortalities of farmed fish have been caused by high cells densities of a number of different phytoplankton groups. The unidentified 'flagellate x' caused mortalities of farmed fish in Scotland the early 1980s (Ayres et al., 1982). The morphological features of some phytoplankton species such as the diatom Chaetoceros convolutus with spiney setae, can irritate gills of farmed fish, impacting condition (Treasurer et al., 2003). Blooms of the dinoflagellates Karenia mikimotoi have caused mortalies of farmed fish in Scottish waters in the 1980s with impacts on the benthos reported in the late 1990s (Davidson et al., 2009). In 2003, high cell densities of Karenia mikimotoi resulted in mortalities of farmed fish in Shetland although the mechanism during this incident (via toxin production, gill damage or increased O₂ demand once the algae die) is still not clear. A subsequent K. mikimotoi bloom in 2006 which was transported around the Scottish coast resulted in mortalities of the benthos and some wild fish. Farmed fish were not impacted by this event although fish farmers in Shetland reported impacts on fish gills (Davidson et al., 2009). Algal toxins which impact shellfish harvesting areas are discussed under human health impacts (Section 2.2.7).

2.2.6.1.2 Jellyfish blooms: Jellyfish blooms are reviewed in an accompanying MCCIP report (Edwards et al., 2020). In terms of aquaculture, blooms impact the suitability of intermediate and supporting ecosystem services such as suitable seascapes for the rearing of penned finfish (Luisetti et al., 2018). Blooms also impact the suitability of built human capital designed for the purposes of fish farming (Bosch-Belmar et al., 2017). Specifically, jellyfish blooms cause extensive mortalities in finfish due to net obstruction, O₂ reduction and nematocyst liberation that causes gill disorders, which leads to intoxication (Lynam et al., 2011; Lucas et al., 2014). Some evidence also suggests that medusae are a significant carrier of pathogens (Delannoy et al., 2001) and that blooms are a health hazard to aquaculturists (Bosch-Belmar et al., 2017). Extensive blooms of *Pelagia noctiluca* in 2007 across the Celtic Sea were associated with the death of over 100,000 farmed salmon though intoxication, resulting in revenue losses of £1 million (Doyle et al., 2008). In the early 2000s blooms of Cyanea lamarkii in waters surrounding the Isle of Lewis in Scotland were associated with mortality of around 2.5 million



penned salmon, with estimations of total economic loss of £5 million (Johnson 2002).

2.2.6.2 What could happen in the future

2.2.6.2.1 HABs: A review of the last 10 years reveals a strong regional variability in the incidence of HABs in the UK (Bresnan *et al.*, 2017). Over this relatively short time scale, signals from climate change are difficult to disentangle from short-term weather events, e.g. wind-mediated transport influencing sudden or prolonged toxicity in shellfish at some sites in Scotland (Whyte *et al.*, 2014; Morris *et al.*, 2010). Broad-scale modelling studies (Gobler *et al.*, 2017) predict an increase in the occurrence of toxin producing species in the North Sea, however these models need to account for the complexity and differences of life cycles at a species level (Dees *et al.*, 2017). Prediction of the potential for the northern expansion of HAB species in the north-east Atlantic (Townhill *et al.*, 2018) is made difficult by the complexities of application of modelling techniques to plankton (Brun *et al.*, 2016). Changes in toxin producing algae are discussed in Section 2.2.7 under their impact on human health.

2.2.6.2.2 Jellyfish blooms: Jellyfish blooms could occur more regularly under warming scenarios as perceptions exist that link the phenomenon to climate change (Attrill et al., 2007). Evidence of increasing populations includes counts of gelatinous material in data collected by Continuous Plankton Recorder (CPR) tows, that suggest jellyfish biomass has been on the rise since the turn of the century (Licandro et al., 2010). An array of studies in the literature and reports in the media also generally reference patterns of increasing bloom frequencies worldwide (Richardson et al., 2009). However, caution is required when considering this perception, as these relatively shortterm increases could simply have occurred within natural cyclical population patterns (generally over a 20–30 year time period) that jellyfish are known to undergo (Licandro et al., 2010, Condon et al., 2013). Also, biases towards the perception of increasing blooms have recently been identified (Condon, 2012, Sanz-Martin et al., 2016), contributing to a high level of uncertainty in relation to future blooming patterns in response to climate change and the associated impact on aquaculture operations. There is also a lack of long-term population trends data to back up the perception as sampling of jellyfish has been relatively sporadic, but efforts have been underway to expand this since 2012 (e.g. the citizen science reporting tool: <u>jellywatch.org</u>).

Although complex environmental factors affect jellyfish blooms (Edwards *et al.*, 2020), increasing temperatures appear to be a key factor for many species (Philippart *et al.*, 2011, Mar-Lopez *et al.*, 2014), increasing temperatures may result in greater frequencies of blooming events within the natural long-term cycles of jellyfish populations. However, there are significant knowledge gaps in species specific physiological information in response to each of the environmental factors of relevance.



2.2.7 Food safety (Moderate confidence)

Food safety is critical for an economically sustainable aquaculture and this can be affected by a range of processes that are themselves sensitive to climate and climate change (Bresnan *et al.*, 2017). These include algal toxins in shellfish, zoonotic or human pathogens, and heavy metals, among others.

2.2.7.1 What is happening (Moderate confidence)

2.2.7.1.1 HAB toxins: Some algal species produce toxins which accumulate in the flesh of shellfish that feed on them and pose a serious risk to human health if consumed. Closures of shellfish harvesting areas are enforced if algal toxin concentrations exceed the permitted concentration defined in the EU Shellfish Hygiene Directive (EU 853/2004). The algal toxins responsible for Paralytic Shellfish Poisoning (PSTs), Diarrhetic Shellfish Poisoning (DSTs), amnesic shellfish poisoning (ASTs) are routinely detected in UK shellfish with the majority of incidences recorded in Scotland and along the south coast of England.

The impacts of climate on the plankton community in the North-east Atlantic has been detailed in Edwards et al. (2006, 2020) with the spatial distribution of some toxin producing genera such as *Dinophysis* changing over a multidecadal timescale. Hinder et al., 2012 revealed an increase in the abundance of the Domoic Acid toxin producing diatom Pseudo-nitzschia associated with changes in wind speed intensity and direction. The complexities of the relationship between HABs and climate change have been highlighted in reviews (Hallegraeff, 2010; Wells et al., 2015). Within the UK, effort has been directed into examining the impact of weather on shellfish toxicity with wind being a driving factor in events associated with DSTs in Shetland (Whyte et al., 2014) and Loch Fyne in Scotland (Morris et al., 2010). Increased effort has been placed in prediction of shellfish toxin events with number of regional alert systems in place or underway to provide an early warning to the aquaculture industry (Davidson et al., 2006; Schmidt et al., 2018, http://www.shellfish-safety.eu/), and historical fish kill events modelled to improve understanding of drivers (Gillibrand et al., 2016).

More recently Tetrodotoxin (TTX) has been detected in shellfish from the south coast of England (Turner *et al.*, 2015; Turner *et al.*, 2017). While no relationship with phytoplankton could be established, the identification of TTX in ribbon worms and associated bacteria has been confirmed (Turner *et al.*, 2018).

2.2.7.1.2 Bacterial and viral pathogens: High levels of human or zoonotic pathogens can result in economic losses for shellfish aquaculture sites. Climate can influence contamination levels. Rainfall is a major driver of pathogen transport into estuarine waters. Intense rainfall can lead to release of untreated sewage from Combined Sewer Overflows (CSO), and to the transfer of animal waste from fields or farm holdings into rivers through overland flow (runoff). Suspended sediment (runoff and storms) can provide



protection from UV radiation, and substrate on which to multiply (Malham *et al.*, 2014; Campos *et al.*, 2013). These processes are similar to those affecting fish and shellfish pathogens, some of which (especially Vibrios) can be zoonotic.

Escherichia coli shellfish contamination in the UK has been correlated with rainfall and suspended sediment (Campos et al., 2017; Malham et al., 2017). Vezzuli et al., (2013; 2016) found a correlation between Vibrio bacteria load (including human vibrio pathogens) in UK and northern European seawater samples and long-term changes in SSTs. This was in parallel with increases in environmentally acquired Vibrio infections in human populations. Vibrio numbers increased in oysters and mussels in Holland with increasing temperatures above 13.5°C (Schets et al., 2010). A clear correlation between shellfish ingestion and human vibriosis is more difficult to establish, possibly due to poor reporting (Bresnan et al., 2017). Norovirus (NoV) levels were positively associated with the frequency and volume of sewage discharges, river flow and storm overflow events and were negatively associated with waters >10°C (Campos et al., 2016; Bresnan et al., 2017). Information on AntiMicrobial Resistance (AMR) in the marine environment in the UK is limited, though antibiotic resistant genes have been detected (Elbashir et al., 2018). Changes in temperature and pH may affect antibiotic persistence in seawater and so impact on antibiotic resistance in bacterial populations.

2.2.7.1.3 Heavy metals and pollutants: Ocean acidification and changes to seawater chemistry could affect the solubility and speciation of metals or contaminants, resulting in greater bioavailability and bioaccumulation in organisms (Ivanina and Sokolova, 2015). pH changes simulating OA have resulted in increased cadmium accumulation in *M. edulis* to levels considered unsafe for human consumption (Shi *et al.*, 2016). Heavy metal and pesticide levels in farmed salmon have however decreased since the 1990s, but this may reflect changes to sources of commercial feed (Nøstbakken *et al.*, 2015).

2.2.7.2 What could happen in the future (Low confidence)

Projected increase in high intensity rainfall has the potential to increase the number and magnitude of Combined Sewer Overflow (CSO) releases and runoff in agricultural areas, leading to increased supply of human pathogens to estuarine areas in winter. Milder winters and springs with increased precipitation may favour increases in Vibrio that grow best at lower salinities and require >15°C (Esteves *et al.*, 2015). NoV outbreaks may decrease overall with increased temperatures, though lower salinities (Lee *et al.*, 2008), and increased loading due to runoff in winter, may counteract any decrease. As NoV can remain viable in sediments for extended periods, the virus may be released by increasing winter storms (Lee *et al.*, 2008). Meanwhile, increased water temperatures, and changing salinities associated with higher river flows could either increase or decrease *E.coli* concentrations, with reports that increased temperature promotes both degradation (Campos *et al.*,



2013) and replication of *E.coli*, and with higher and lower survival at salinities of 25% and 100% respectively (Carlucci and Pramer, 1960).

Increased AMR associated with increased temperatures and density in human populations (MacFadden *et al.*, 2018) which may indirectly impact AMR levels in the marine environment through increased precipitation and CSO overflow. Increases in, or newly emerging, diseases due to climate change may result in increased use of antibiotics in aquaculture and contribute to AMR (Buschmann *et al.*, 2012). However, antibiotic use is low in UK marine aquaculture due to use of effective vaccines. It is difficult to predict if climate change and OA will result in significant changes to metal/pollutant contaminant levels in aquaculture organisms, due to interactions between climate change effects and OA on modulating uptake, metabolism, and elimination processes.

3. QUALITATIVE LEVELS OF CONFIDENCE FOR 'WHAT IS ALREADY HAPPENING' AND 'WHAT COULD HAPPEN IN THE FUTURE'

Globally, climate change and OA has been associated with impacts on aquaculture *in situ*, e.g. seawater influx and storm damage in tropical regions (Barange *et al.*, 2018), summer heatwaves affecting shellfish spat settlement and mortalities in the Mediterranean (Rodrigues *et al.*, 2015), and OA in the Pacific North-west affecting hatchery and wild seed recruitment (Ekstrom *et al.*, 2015).

However, predictions for potential effects of climate change and OA on aquaculture are based for the most part on from experimental or observational data (Callaway et al., 2012; Gubbins et al., 2013). Increasingly multifactorial exposure studies show that climate change and OA effects can be synergistic, dependent on species and on lifecycle stage (Gimenez et al., 2018; Gobler et al., 2018; Ong et al., 2017). Complexity in predicting outcomes not only relates to combined effects on the biology of the host, but on the ecosystem in which it lives, e.g. food supply, pathogens and predators, and the influences climate change and OA may have on these and on their ecosystem interactions. Local geographical or inter-annual variability in conditions make it difficult to predict potential impacts of climate change or OA. In the UK, the North-east Atlantic displays greater variability in SST than the global trend, and this in part may be due to the Atlantic Multi-decadal Oscillation (Hughes et al., 2017), potentially resulting in intermittent periods of lower temperature increase, and associated effects, between now and 2100. The capacity of adaptation by the species tested is also not fully understood (Crozier and Hutchings, 2014).

Climate change impacts will be influenced by other anthropogenic activities, e.g. sources of pollutants, introduction of disease or invasive species and

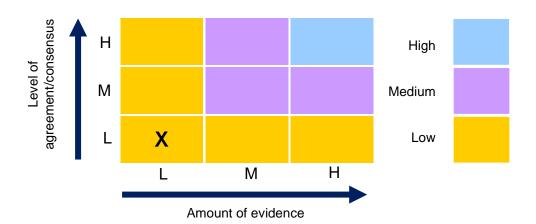


mitigated through technology and spatial planning. In the UK aquaculture sector, in particular for salmon, the rapid advancement of technology and changes in husbandry and production practices potentially mitigate against, and mask impacts. Examples include development of RAS and close containment, vaccines, treatments, functional feeds, selective breeding, shorter marine production cycles and early warning systems e.g. for HABs.

Overall there is a lot of uncertainty on how current impacts and projected impacts of climate change and OA will affect UK aquaculture.

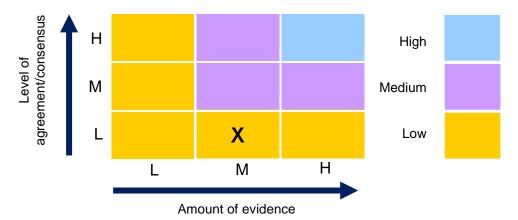
4. CONFIDENCE ASSESSMENT

What is already happening



The evidence for an impact associated with changing climate has increased, particularly for gill disease and *Vibrio* contamination, but there remains a lot of uncertainty and contradictory impacts and the association with climate change cannot be confirmed. Although the evidence that there is an impact has increased since the last MCCIP report (Gubbins *et al.*, 2013) it is not enough to confidently change the status of the evidence to medium, but the evidence is increasing and we do expect medium evidence will be the future situation. Agreement on likely climate-driven changes is also increasing, particularly increased growth rates and disease risks. However large uncertainties remain in changes to risks from HABs and invasive species, so although there are increasing reasons for moving the status to 'Medium', we retain the 'Low' status.

What could happen in the future?



5. KNOWLEDGE GAPS AND EMERGING ISSUES

The following knowledge gaps focus on better understanding potential climate change (CC) and ocean acidification (OA) effects on aquaculture, rather than knowledge gaps relating directly to development of mitigation strategies, though of course one can lead to the other.

- (a) The extent to which sea-level rise and associated coastal habitat loss (including areas suitable for intertidal mollusc culture) will be offset by coastline morphology reformation.
- (b) Understanding causes and ranges of spatio- and temporal fluctuations in coastal acidification and salinity.
- (c) The synergistic effects of CC and OA and the effect of fluctuating compared to continuous exposure to these impacts on settlement (shellfish), growth and survival of aquaculture species.
- (d) The capacity of aquaculture species at individual and population level to adapt to CC and OA.
- (e) Effects of CC and OA on pathogens and disease development and on complex disease outcome.
- (f) Interacting effects controlling transport of pathogens and sediment from terrestrial catchments into estuarine areas, and the persistence of pathogenic organisms in the marine environment.
- (g) Increased information on effects of CC and OA on factors directing phyto- and zooplankton blooms.
- (h) Information on the importance of zooplankton in shellfish diets
- (i) Impacts of climate change on the environmental impacts of aquaculture e.g. assimilative capacity of receiving water bodies, including impacts at potential offshore sites.
- (j) Understanding of the changing environmental factors under altered climate scenarios on the processes involved in invasion, establishment and spread of a range of relevant Non-Native Species.



- (k) Information on offshore environment/ecosystem and potential impacts of CC and OA on sustainable growth of offshore aquaculture.
- (l) Economic predictions on how CC may change aquaculture output elsewhere and increase economic viability of existing/new species in UK planning for future aquaculture development.

The top three *current* priorities for further information are: e, i, and j

The top three *emerging* issues that will require more informationare: k, c, and d.



Table 1: summary of emerging climate change issues in finfish and shellfish aquaculture.

| | Clim | ate ch | ange 8 | k OA | Summary of potential impacts | Confidence | Comments on Confidence Level |
|---|-------------------|-------------------|-------------------|--------------|---|------------|--|
| | Fin | Finfish Shellfish | | | 1 | Level | |
| | 2050 | 2100 | 2050 | 2100 | | (overall) | |
| Physical carrying capacity | | | | | | | |
| Sea level rise | \uparrow | \uparrow | \uparrow | \uparrow | Sea level rise could result in a reduction of | Low | Little information available to predict |
| Sediment deposition (due to | \uparrow | \uparrow | \uparrow | \uparrow | near shore culture sites for shellfish but should | | impact of sea level rises on current shellfish |
| increased precipitation events) | | | | | not impact on finfish. | | sites. |
| Storm frequency and intensity | \uparrow | \uparrow | \uparrow | \uparrow | Sediment runoff may be detrimental through | | Little information on the impact of |
| | | | | | gill damage for finfish and burial and/or impact | | sediment on gill health: particle size, load |
| | | | | | on feeding and primary food production for shellfish. | | etc. Shellfish susceptibility to burial is species specific. |
| Overall production output | \leftrightarrow | \downarrow | \leftrightarrow | \downarrow | • Increased storms could result in increased cage | | Limited information on sediment and food |
| | | | | | damage and fish escapes, loss of shellfish long- lines or damage to shells. | | thresholds at which shells close or when energy expenditire outpaces increase in filtration rates. |
| *Production carrying capacity | | | | | | | |
| Growth: temperature and OA | \uparrow | \leftrightarrow | \downarrow | \downarrow | Increasing SSTs may benefit Scottish salmon | Low | Limited knowledge on how temperatures |
| New aquaculture species | \leftrightarrow | \leftrightarrow | \uparrow | \uparrow | growth in the near to mid term but exceed | | may change impact of larvae and adult |
| Disease | \uparrow | 1 | \uparrow | \uparrow | physiological optima in southern Scotland by the | | shellfish predators. |
| Invasive and nuisance species | \uparrow | 1 | 1 | 1 | end of the century. | | Limited information on synergistic effets |
| Food safety | \leftrightarrow | \leftrightarrow | \downarrow | \downarrow | SST increase may increase shellfish larvae | | of increasing SSTs and OA on pathogen |
| | | | | | development and adult growth (by also increasing food availability), but increasing OA and coastal | | dispersal, survival and infectivity, and on complex infections. |
| Overall production output | \leftrightarrow | \downarrow | \downarrow | \downarrow | acidification fluctuations may result in larvae | | Limited knowledge on how CC and OA |
| | | | | | mortality. | | interactions will impact on shellfish survival |
| | | l | l | l | • Temperature increase may facilitate expansion | | and growth, on invasive species, and on |
| | | | | | of some shellfish species e.g. M. galloprovencialis, | | native nuisence species e.g. hydrozoa. |
| | | | | | but still be insufficient to compete with warmer | | Limited information on local sclae pH |
| | | | | | countries for production of sea bass and sea bream. | | fluctuations in UK coastal waters. |
| | | | | | • Some aquaculture disease issues may increase | | Limited knowledge on how co-inciding |
| | | | | | with rising SSTs such as sea lice, gill pathologies | | positive and negative impacts e.g. |
| | | | | | or shellfish protozoa, while others such as cold | | decreasing salinity but increasing SSTs on |
| | | | | | water vibrios may decrease. | | norovirus survival and infectivity, will impact on outbreak frequencies. |
| | | | | | Warm water invasive species, impacting on | | ' |
| | | | | | aquaculture, may spread northwards and more | | Unknown how future bio/technology development will impact on production, |
| | | | | | widely. | | growth and disease. |
| | | | | | • Increasing precipitation events may lead to | | Unknown how move to offshore farming |
| | | | | | sewage overflow and increased human pathogen load in marine environment. | | will mitigate against or change CC and OA |
| | | | | | | | impacts on aquaculture. |
| | | | | | Higher SSTs and lower salinities may increase incidence of vibriosis and reduce norovirus | | |
| | | | | | outbreaks in winter. | | |
| | | | | | HABs and jellyfish blooms may increase with | | |
| | | | | | increasing SSTs. | | |
| Ecological carrying capacity | | | | | | | |
| Invasion of non-aquaculture | 1 | 1 | 1 | \uparrow | It is likely that with increasing SSTs, feral | Low | Limited information on how increased |
| sites | | | | ı . | populations of Pacific oysters and manilla clams | | SSTs and OA may impact on |
| Escapes | 1 | 1 | \uparrow | \uparrow | will occur more widely potentialy impacting on | | medicine/treatment breakdown, uptake and |
| Disease transfer | <u></u> | <u></u> | <u></u> | ↑ | native fauna. | | retention by fin- and shellfish. |
| Pollution resiliance thresholds | <i>\display</i> | <i>\display</i> | <u>,</u> | ↓ | • Increased frequency and severity of storms may | | Limited information on how SSTs and CC |
| | | ' | | | result in cage damage and farmed fish escapes: | | may impact on hypoxia levels in UK coastal |
| | | | | | increasing integration with wild salmonids and | | sites and on benthic community resilience to pollution. |
| Overall production output | 1 | 1 | \downarrow | 1 | potentially impacting on their biodiversity and health. | | ľ |
| | * | • | * | * | Some diseases and pathogen loads may | | Limited information on how waste from offshore aquaculture developments may |
| | | | | | increase in response to increasing SSTs: warmer | | impact species poor benthic environments. |
| | | | | | temperatures shortens the lifecycle of sea lice, | | Limited information on potential impact of |
| | | | | | allowing more generations: increased lice load in | | aquaculture interaction with new offshore |
| | | | | | environment may impact on wild salmonids. | | wild species, and potential to act as |
| | | | | | Breakdown of medicines and treatments in | | "stepping stones" for new pathogens and |
| | | | | | environment may be affected by increasing SSTs and OA. | | invasive species. |
| | | | | | Exposure thresholds to farm fin- and shellfish | | |
| | ĺ | ĺ | | l | farm waste may be reduced for benthic | | |
| | | l | l | l | communities due to lower oxygen content. | | |
| | | | | | | | |
| Social carrying canacity | 1 | 1 | 1 | 1 | | Low | |
| Social carrying capacity | | | 1 | ' | Detrimental impacts of CC and OA on the | LUW | Social issues can be difficult to measure |
| Increased competition for | ' | | | | | 1 | and are often subjective. |
| Increased competition for resources and concern over | ' | | | | marine environment directly, and via potentially | | and are often subjective. |
| Increased competition for resources and concern over environment. | | • | * | ^ | increasing impact of aquaculture may result in | | and the orien subjective. |
| Increased competition for resources and concern over environment. Support for economic | ↑ | ↑ | ↑ | ↑ | | | one are orien subjective. |
| Increased competition for resources and concern over environment. Support for economic opportunities and food | | 1 | ↑ | ↑ | increasing impact of aquaculture may result in reduced support for aquaculture presence or | | |
| Increased competition for resources and concern over environment. Support for economic opportunities and food security if wild fisheries | | 1 | ↑ | ↑ | increasing impact of aquaculture may result in reduced support for aquaculture presence or expansion. | | |
| Increased competition for resources and concern over environment. Support for economic opportunities and food | | ↑ | ↑ | ↑ | increasing impact of aquaculture may result in reduced support for aquaculture presence or expansion. However, potential reduction of the wild fisheries industry due to CC and OA impacts on fish/shellfish stocks, may encourage support for | | |
| Increased competition for resources and concern over environment. Support for economic opportunities and food security if wild fisheries | | ↑ ↔ | ↑ ↔ | ↑ | increasing impact of aquaculture may result in reduced support for aquaculture presence or expansion. • However, potential reduction of the wild fisheries industry due to CC and OA impacts on | | |

A reduction in capacity does not necessarily mean a reduction in production in future, as current capacities may not be utilised fully, and changes to technology may mitigate against CC and OA changes, or improve other aspects.

SSTs: sea surface temperatures; OA: Ocean Acidification; ↑ increase; ↓ decrease; ↔ overall no change



REFERENCES

- Abdel-Tawwab, M., Monier, M.N., Hoseinifar, S.H. and Faggio, C. (2019) Fish response to hypoxia stress: growth, physiological, and immunological biomarkers. *Fish Physiology and Biochemistry*, **45**, 997–1013.
- Abram, Q.H., Dixon, B. and Katzenback, B.A. (2017) Impacts of low temperature on the teleost immune system. *Biology*, **6**, 39.
- Adamson, E., Syvret, M. and Woolmer, A. (2018) *Shellfish Seed Supply for Aquaculture in the UK*: Report on Views Collected from the Industry in 2017. 20 pp.
- Alexander, K.A., Gatward, I., Parker, A., Black, K., Boardman, A., Potts, T. and Thomson, E. (2014)
 An Assessment of the Benefits to Scotland of Aquaculture. A report for Marine Scotland by Imani
 Enterprise Ltd. and SAMS Research Services Ltd., 164 pp,
 http://www.gov.scot/Resource/0045/00450799.pdf
- Alldredge, A.L. and Silver, M.W. (1988) Characteristics, dynamics and significance of marine snow. *Progress in Oceanography*, **20**, 41–82.
- Almada-Villela, P.C., Davenport, J. and Gruffydd, L.D. (1982) The effects of temperature on the shell growth of young *Mytilus edulis* L. *Journal of Experimental Marine Biology and Ecology*, **59**, 275–288.
- Anon (2018) https://www.walesonline.co.uk/business/business-news/welsh-lumpfish-breeder-saving-salmon-15023309
- Aquaculture Growth to 2030. A Strategic Plan for Farming Scotland's Seas. Scotland Food and Drink: https://aquaculture.scot/wp-content/uploads/2017/11/Aquaculture_Growth_2030.pdf
- Araújoa, J.E., Madeira, D., Vitorino, R., Repolho, T., Rosae, R. and Diniz, M. (2018) Negative synergistic impacts of ocean warming and acidification on the survival and proteome of the commercial sea bream, *Sparus aurata*. *Journal of Sea Research*, **139**, 50–61.
- Arnell, N.W., Halliday, S.J., Battarbee, R.W., Skeffington, R.A. and Wade, A.J. (2015) The implications of climate change for the water environment in England. *Progress in Physical Geography*, **39**(1), 93–120.
- Arzul, I., Gagane, B., Bond, C., Chollet, B., Morga, B., Ferrand, S., Robert, M. and Renault, T. (2009) Effects of temperature and salinity on the survival of *Bonamia ostreae*, a parasite infecting flat oysters. *Diseases of Aquatic Organisms*, **85**, 67–75.
- Arzul, I., Chollet, B., Boyer, S., Juliette, G., Yoann, B., Maeva, R., Joly, J.P., Garcia, C. and Bouchouch, M. (2014) Contribution to the understanding of the cycle of the protozoan parasite *Marteilia refringens*. *Parasitology*, 141(2), 227–240.
- Ashrafi, R., Bruneaux, M., Sundberg, L.R., Pulkkinen, K., Valkonen, J. and Ketola, T. (2018) Broad thermal tolerance is negatively correlated with virulence in an opportunistic bacterial pathogen. *Evolutionary Applications*, **11**, 1700–1714.
- Attrill, M.J., Wright, J. and Edwards, M. (2007) Climate-related increases in jellyfish frequency suggest a more gelatinous future for the North Sea. *Limnology and Oceanography*, **52**(1), 480–485.
- Au, D.W.T., Pollino, C.A., Wu, R.S.S., Shin, P.K.S., Lau, S.T.F. and Tang, J.Y.M. (2004) Chronic effects of suspended solids on gill structure, osmoregulation, growth, and triiodothyronine in juvenile green grouper *Epinephelus coioides*. *Marine Ecology Progress Series*, **266**, 255–264.
- Ayres, P.A., Seaton, D.D. and Tett, P.B. (1982) Plankton blooms of economic importance to fisheries in UK waters 1968 1982. ICES CM 82/L38, 10 pp. http://www.ices.dk/sites/pub/CM%20Doccuments/1982/L/1982 L38.pdf
- Balebona, M.C., Morifiigo, M.A., Faris, A., Krovacek, K., Mhsson, I., Bordas, M.A. and Borrego, J.J. (1995) Influence of salinity and pH on the adhesion of pathogenic Vibrio strains to *Sparus aurata* skin mucus. *Aquaculture*, 132, 113–120.
- Baker-Austin, C., Trinanes, J.A., Taylor, N.G.H., Hartnell, R., Siitonen, A. and Martinez-Urtaza, J. (2013) Emerging Vibrio risk at high latitudes in response to ocean warming. *Nature Climate Change*, 3, 73–77.
- Baker-Austin, C., Trinanes, J., Gonzalez-Escalona, N. and Martinez-Urtaza, J. (2017) Non-cholera vibrios: the microbial barometer of climate change. *Trends in Microbiology*, **25**, 76–84
- Barange, M., Bahri, T., Beveridge, M.C.M., Cochrane, K.L., Funge-Smith, S. and Poulain, F. (eds) (2018) Impacts of climate change on fisheries and aquaculture: synthesis of current knowledge, adaptation and mitigation options. FAO Fisheries and Aquaculture Technical Paper, No. 627. FAO, Rome, 628 pp. http://www.fao.org/policy-support/resources/resources-details/en/c/1152846/
- Benfey, T.J. (2016) Effectiveness of triploidy as a management tool for reproductive containment of farmed fish: Atlantic salmon (*Salmo salar*) as a case study. *Reviews in Aquaculture*, **8**, 264–282.



- Besson, M. Vandeputte, M., van Arendonk, J.A.M., Aubind, J., de Boer, I.J.M., Quillet. E. and Komen. H. (2016) Influence of water temperature on the economic value of growth rate in fish farming: The case of sea bass (*Dicentrarchus labrax*) cage farming in the Mediterranean. *Aquaculture*, 46, 47–55.
- Beveridge, M.C.M. (2004) Cage Aquaculture. Third edition. Blackwell Ltd, Oxford, UK, 368 pp.
- Björnsson, B. and Tryggvadóttir, S.V. (1996) Effects of size on optimal temperature for growth and growth efficiency of immature Atlantic halibut (*Hippoglossus hippoglossus L.*). *Aquaculture*, **142**, 33–42.
- Black, K. and Hughes, A. (2017) Foresight Future of the Sea Trends in Aquaculture. Foresight, Government Office for Science. https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/635209/Future_of_the_sea_-_trends_in_aquaculture_FINAL_NEW.pdf
- Bloecher, N., Powell, M., Hytterød, S., Gjessing, M., Wiik-Nielsen, J., Mohammad, S.N., Johansen, J., Hansen, H., Floerl, O. and Gjevre, A-G. (2018) Effects of cnidarian biofouling on salmon gill health and development of amoebic gill disease. *PLoS ONE*, **13**(7), e0199842.
- Bohn, K., Richardson, C. and Jenkins, S. (2012) The invasive gastropod *Crepidula fornicata*: reproduction and recruitment in the intertidal at its northernmost range in Wales, UK, and implications for its secondary spread. *Marine Biology*, **15**, 2091–2103.
- Booth, C.E., McDonald, D.G. and Walsh, P.J. (1984) Acid-base balance in the sea mussel, *Mytilus edulis* I. Effects of hypoxia and air-exposure on hemolymph acid-base status. *Marine Biology Letters*, **5**, 347–358.
- Bougrier, S., Geairon, P., Deslous-Paoli, J.M., Bacher, C. and Jonquières, G. (1995) Allometric relationships and effects of temperature on clearance and oxygen consumption rates of *Crassostrea gigas* (Thunberg). *Aquaculture*, **134**, 143–154.
- Bosch-Belmar M., Azzurro E., Pulis K., Milisenda G., Fuentes V., Yahia O.K.D., Micallef A., Deidun A. and Piraino S. (2017) Jellyfish blooms perception in Mediterranean finfish aquaculture. *Marine Policy*, 76, 1–7.
- Bowden, T.J. (2008) Modulation of the immune system of fish by their environment. *Fish and Shellfish Immunology*, **25**, 373–383.
- Brenko, M.H. and Calabrese, A. (1969) The combined effects of salinity and temperature on larvae of the mussel *Mytilus edulis*. *Marine Biology*, **4**, 224–226.
- Bresnan E., Baker Austin, C., Campos, C.J.A., Davidson, K., Edwards, M., Hall, A., Lees, D., McKinney, A., Milligan, S. and Silke, J. (2017) Human Health. *MCCIP Science Review 2017*, 90–97. http://www.mccip.org.uk/media/1768/2017arc_sciencereview_008_huh.pdf
- Brett, J.R. (1979) In *Environmental Factors and Growth*. [Hoar, W.S., Randall, D.J. and Brett, J.R. (eds)]. Fish Physiology, **8**, 599–675.
- Bricknell, I.R., Bron, J.E. and Bowden, T.J. (2006b) Diseases of fish in cultivation: a review. *ICES Journal of Marine Science*, **63**, 253–266.
- Brooker, A.J., Skern-Mauritzen, R. and Bron, J.E. (2018) Production, mortality, and infectivity of planktonic larval sea lice, *Lepeophtheirus salmonis* (Krøyer, 1837): current knowledge and implications for epidemiological modelling, *ICES Journal of Marine Science*, **75**(4), 1214–1234.
- Brun P., Kiorbe T., Licandro P. and Payne M.R. (2016) The predictive skill of species distribution models for plankton in a changing climate, *Global Change Biology*, **22**, 3170–3181.
- Burge, C.A., Closek, C.J., Freidman, C.S., Groner, M.L., Jenkin, C.M., Shore-Maggio, A. and Welsh, J.E. (2016) The use of filter-feeders to manage disease in a changing world. *Integrative and Comparative Biology*, **56**, 573–587.
- Buschmann, A.H., Tomova, A., López, A., Maldonado, M.A., Henríquez, L.A., Ivanova, L., Moy, F., Godfrey, H.P. and Cabello, F.C. (2012) Salmon Aquaculture and Antimicrobial Resistance in the Marine Environment. *PLoS ONE*, 7(8), e42724, doi:10.1371/journal.pone.0042724
- Callaway, R., Shinn, A.P., Grenfell, S.E., Bron, J.E., Burnell, G., Cook, E.J. *et al.* (2012) Review of climate change impacts on marine aquaculture in the UK and Ireland. *Aquatic Conservation Marine and Freshwater Ecosystems*, **22**, 389–421.
- Campos, C.J.A., Kershaw, S.R. and Lee, R.J. (2013) Environmental influences on faecal indicator organisms in coastal waters and their accumulation in bivalve shellfish. *Estuaries and Coasts*, 36, 834–853.
- Campos, C.J.A., Avant, J., Lowther, J., Till, D. and Lees, D.N. (2016) Human norovirus in untreated sewage and effluents from primary, secondary and tertiary treatment processes. *Water Research*, **103**, 224–232.
- Campos, C.J., Kershaw, S., Morgan, O.C. and Lees, D.N. (2017) Risk factors for norovirus contamination of shellfish water catchments in England and Wales. *International Journal of Food Microbiology*, 241, 318–324.



- Cao, R., Wang, Q., Yang, D., Liu, Y., Ran, Qu, Y., Wu, H., Cong, M., Li, F., Chenlong, J. and Zhao, J. (2018) CO₂-induced ocean acidification impairs the immune function of the Pacific oyster against *Vibrio splendidus* challenge: An integrated study from a cellular and proteomic perspective. *Science of the Total Environment*, 625, 1574–1583.
- Capuzzo, E. and McKie, T. (2016) Seaweed in the UK and abroad status, products, limitations, gaps and Cefas role. Defra https://www.gov.uk/government/publications/the-seaweed-industry-in-the-uk-and-abroad
- Carlucci, A.F. and Pramer, D. (1960) An evaluation of factors affecting the survival of *Escherichia coli* in sea water: II. Salinity, pH, and nutrients. *Applied Microbiology*, **8**, 247–250.
- Chávez-Villalba, J., Pommier J., Andriamiseza, J., Pouvreau, S., Barret J., Cochard, J.C. and Le Pennec, M. (2002) Broodstock conditioning of the oyster *Crassostrea gigas*: origin and temperature effect. *Aqualture*, 214, 115–130.
- Chen, Y.S., Beveridge, M.C.M. and Telfer, T.C. (1999) Physical characteristics of commercial pelleted Atlantic salmon feeds and consideration of implications of waste dispersion through sedimentation. *Aquaculture International*, **7**, 89–100.
- Chen, P. and Shakhnovich, E.I. (2010) Thermal adaptation of viruses and bacteria. *Biophysical Journal*, **98**, 1109–1118.
- Collins C., Hall M., Fordyce M.J. and White P. (2019) Survival and growth in vitro of *Paramoeba perurans* populations cultured under different salinities and temperatures. *Protist*, **170**, 153–167.
- Condon, R.H., Duarte, C.M., Pitt, K.A., Robinson, K.L., Lucas, C.H., Sutherland, K.R. and Graham, W.M. (2013) Recurrent jellyfish blooms are a consequence of global oscillations. *PNAS*, 110(3), 1000–5.
- Condon, R.H., Graham, W.M., Duarte, C.M., Pitt, K.A., Lucas, C.H., Haddock, S.H. and Mills, C.E. (2012) Questioning the rise of gelatinous zooplankton in the world's oceans. *BioScience*, **62**(2), 160–169.
- Cottier-Cook, E., Minchin, D., Giesler, R., Graham, J., Mogg, A.M.O., Sayer, M.D.J. and Matejusova, I. (2019) Biosecurity implications of the highly invasive carpet sea-squirt *Didemnum vexillum* Kott, 2002 for a protected area of global significance. *Management of Biological Invasions*, 10, 311–323.
- Chopin, T., Cooper, J.A., Reid, G., Cros, S. and Moore, C. (2012) Open-water integrated multi-trophic aquaculture: environmental biomitigation and economic diversification of fed aquaculture by extractive aquaculture. *Reviews in Aquaculture*, **4**, 209–220.
- Christianen, M.J.A., Lengkeek, W., Bergsma, J.H., Coolen, J.W.P., Didderen, K., Dorenbosch, M., *et al.* (2018) Return of the native facilitated by the invasive? Population composition, substrate preferences and epibenthic species richness of a recently discovered shellfish reef with native European flat oysters (*Ostrea edulis*) in the North Sea. *Marine Biology Research*, **14**, 590–597.
- Cohen, R.E., James, C.C., Lee, A., Martinelli, M.M., Muraoka, W.T., Ortega, M., Sadowski, R., Starkey, L., Szesciorka, A.R., Timko, S.E., Weiss, E.L. and Franks, P.J.S. (2018) Marine host-pathogen dynamics: Influences of global climate change. *Oceanography*, **31**(2), 182–193.
- Collins, C., Hall, M., Fordyce, M.J. and White, P. (2019) Survival and growth in vitro of Paramoeba perurans populations cultured under different salinities and temperatures. *Protist*, **170**, 153–167.
- Cook, E.J., Jenkins, S., Maggs, C., Minchin, D., Mineur, F., Nall, C. and Sewell J. (2013) Impacts of climate change on non-native species. *MCCIP Science Review 2013*, 155–166.
- Costello, M.J., Darwall, W.R. and Lysaght, S. (1995) Activity patterns on North European wrasse (Pisces, Labridae) species and precision of diver survey techniques. In *Biology and Ecology of Shallow Coastal Waters*, Olsen & Olsen, Fredensborg, Denmark, pp. 343–350.
- Crozier, L.G. and Hutchings, J.A. (2014) Plastic and evolutionary responses to climate change in fish. *Evolutionary Applications*, **7**, 68–87.
- Dankers, N. (1995). The role of the mussel (*Mytilus edulis* L.) and mussel culture in the Dutch Wadden Sea. *Estuaries*, **18**, 71-80.
- Davidson, K., Miller, P., Wilding, T.A., Shutler, J., Bresnan, E., Kennington, K. and Swan, S. (2009) A large and prolonged bloom of *Karenia mikimotoi* in Scottish waters in 2006. *Harmful Algae*, 8, 349–361.
- Dees, P., Bresnan, E., Dale, A., Edwards, M., Johns, D., Mouat, B., Whyte, C. and Davidson, K. (2017) Harmful algal blooms in the Eastern North Atlantic Ocean. *PNAS*, **114**, 9763–9764.
- de Lorgeril, J., Lucasson, A., Petton, B., Toulza, E., Montagnani, C., Clerissi, C. *et al.* (2018) Immunesuppression by OsHV-1 viral infection causes fatal bacteraemia in Pacific oysters. *Nature Communications*, **9**, 4215, doi: 10.1038/s41467-018-06659-3
- Delannoy, C.M., Houghton, J.D., Fleming, N.E. and Ferguson, H.W. (2011) Mauve Stingers (*Pelagia noctiluca*) as carriers of the bacterial fish pathogen *Tenacibaculum maritimum*. *Aquaculture*, **311**(1), 255–257.



- Deslous-Paoli, J.M. and Héral, M. (1988) Biochemical composition and energy value of 773 *Crassostrea gigas* (Thunberg) cultured in the bay of Marennes-Oléron. *Aquatic Living Resources*, 1, 239–249.
- Dias, P.J., Dordor, A., Tulett, D., Piertney, S., Davies, I.M. and Snow, M. (2009) Survey of mussel (*Mytilus*) species at Scottish shellfish farms. *Aquaculture Research*, **40**, 1715–1722.
- Dickey, G., Preziosi, B.M., Clark, C.T. and Bowden, T.J. (2018) The impact of ocean acidification on the byssal threads of the blue mussel (*Mytilus edulis*). *PLoS ONE*, **13**(10), e0205908.
- Diederich, S. (2006) High survival and growth rates of introduced Pacific oysters may cause restrictions on habitat use by native mussels in the Wadden Sea. *Journal of Experimental Marine Biology and Ecology*, **328**, 211–227.
- Doyle, T.K., De Haas, H., Cotton, D., Dorschel, B. and Cummins, V. (2008) Widespread occurrence of the jellyfish *Pelagia noctiluca* in Irish coastal and shelf waters. *Journal of Plankton Research*, **30**, 963–68.
- Duarte, C.M., Wu, J., Xiao, X., Bruhn, A. and Krause-Jensen, D. (2017) Can Seaweed Farming Play a Role in Climate Change Mitigation and Adaptation? *Frontiers in Marine Science*, 4, 100, doi: 10.3389/fmars.2017.00100
- Duguid, J.P., Marmion, B.P. and Swain, R.H.A. (1978) *Medical Microbiology*, Vol. 1, (13th edn). Churchill Livingstone, Edinburgh, London and New York, 666 pp.
- Dyer, K. (1973) Estuaries: a physical introduction. John Wiley & Sons, London.
- Edwards, M., Johns, D.G., Leterme, S.C., Svendsen, E. and Richardson, A.J. (2006) Regional climate change and harmful algal blooms in the northeast Atlantic. *Limnology and Oceanography*, **51**, 820–829.
- Edwards, M., Atkinson A., Bresnan E., Hélaouët P., Ostle C., Pitois S. and Widdicombe C. (2020) Plankton and Jellyfish. *MCCIP Science Review 2020*, 322–353
- Egan, S. and Gardiner, M. (2016) Microbial Dysbiosis: Rethinking disease in marine ecosystems. *Frontiers in Microbiology*, **7**, 991.
- Eggset, G., Mikkelsen, H., Killie, J-E.A. (1997) Immunocompetence and duration of immunity against *Vibrio salmonicida* and *Aeromonas salmonicida* after vaccination of Atlantic salmon at low and high temperatures. *Fish Shellfish Immunology*, **7**, 247–260.
- Ekstrom, J.A., Suatoni, L., Cooley, S.R., Pendleton, L.H., Waldbusser, G.G., Cinner, J.E., Ritter, J., Langdon, C., van Hooidonk, R., Gledhill, D., Wellman, K., Beck, M.W., Brander, L.M., Rittschof, D., Doherty, C., Edwards, P.E.T. and Portela, R. (2015) Vulnerability and adaptation of US shellfisheries to ocean acidification. *Nature Climate Change*, 5, 207–214.
- Elbashir, S., Parveen, S., Schwarz, J., Rippen, T., Jahncke, M. and DePaola, A. (2018) Seafood pathogens and information on antimicrobial resistance: A review. *Food Microbiology*, **70**, 85–93. doi: 10.1016/j.fm.2017.09.011
- Elliott, J.M. and Elliott, J.A. (2010) Temperature requirements of Atlantic salmon *Salmo salar*, brown trout *Salmo trutta* and Arctic charr *Salvelinus alpinus*: predicting the effects of climate change. *Journal of Fish Biology*, **77**, 1793–1817.
- Ellis, R.P., Widdicombe, S., Parry, H., Hutchinson, T.H. and Spicer, J.I. (2015) Pathogenic challenge reveals immune trade-off in mussels exposed to reduced seawater pH and increased temperature. *Journal of Experimental Marine Biology and Ecology*, **462** (Supplement C), 83–89.
- Elston, R.A., Hasegawa, H., Humphrey, K.L., Polyak, I.K. and Häse, C.C. (2008) Re-emergence of *Vibrio tubiashii* in bivalve shellfish aquaculture: severity, environmental drivers, geographic extent and management. *Diseases of Aquatic Organisms*, **82**, 119–134.
- Esteves, K., Hervio-Heath, D., Mosser, T., Rodier, C., Tournoud, M-G., Jumas Bilak, E., Colwell, R.R. and Monfort, P. (2015) Rapid proliferation of *Vibrio parahaemolyticus*, *Vibrio vulnificus*, and *Vibrio cholera* during freshwater flash floods in French Mediterranean coastal lagoons. *Applied Environmental Microbiology*, **81**, 7600–7609.
- Fabacher, D.L., Little, E.E., Jones, S.B., DeFabo, E.C. and Webber, L.I. (1994) Ultraviolet-B radiation and the immune response of rainbow trout: Chapter 18. In *Modulators of Fish Immune Response:*Models for Environmental Toxicology/Biomarkers, Immunostimulators. SOS Publications, Fair Haven, NJ.
- Falconer, L., Hjøllo, S.S., Telfer, T.C., McAdam, B.J., Hermansen, Ø. and Ytteborg, E. (2020) The importance of calibrating climate change projects to local conditions at aquaculture sites. *Aquaculture*, **514**, 734487.
- Fernandes, J.A., Papathanasopoulou, E., Hattam, C., Qeiros, A.M., Cheung, W.W.W.L., Yool, A., Artioli, Y., Pope, E.C., Flynn, K.J., Merino, G., Calosi, P., Beaumont, N., Austen, M.C., Widdicombe, S. and Barnge, M. (2017) Estimating the ecological, economic and social impacts of ocean acidification and warming on UK fisheries. Fish and Fisheries, 18, 389-411.
- Ferreira, J.G., Hawkins, A.J.S., Monteiro, P., Moore, H., Edwards, A., Goven, R., Lourenco, P., Mellor, A., Nunes, J.P., Ramos, L., Sequeiro, A. and Strong J. (2007) SMILE Sustainable Mariculture in



- Northern Irish Lough Ecosystems: Assessment of carrying capacity for environmentally sustainable shellfish culture in Carlingford Lough, Strangford Lough, Belfast Lough, Larne Lough and Lough Foyle. Institute of Marine Research.
- Figueroa, C., Bustos, P., Torrealba, D., Dixon, B., Soto, C., Conejeros, P. and Gallardo, J.A. (2017) Coinfection takes its toll: Sea lice override the protective effects of vaccination against a bacterial pathogen in Atlantic salmon. *Scientific Reports*, **7**, 17817.
- Filgueira, R., Guyondet, T., Comeau, L.C. and Tremblay, R. (2016) Bivalve aquaculture-environment interactions in the context of climate change. *Global Change Biology*, **2**, 3901–3913.
- Fitridge, I., Dempster, T., Guenther, J. and de Nys, R. (2012) The impact and control of biofouling in marine aquaculture: a review, *Biofouling*, **28**(7), 649–669.
- Fitzer S.C., Gabarda, S.T., Daly, L., Hughes, B., Dove, M., O'Connor, W., Potts, J., Scanes, P. and Byrne M. (2018) Coastal acidification impacts on shell mineral structure of bivalve mollusks. *Ecology and Evolution*, **8**, 8973–8984.
- Flores-Vergara, C., Cordero-Esquivel, B., Nallely Ceró n-Ortiz, A. and Arredondo-Vega, B.O. (2004) Combined effects of temperature and diet on growth and biochemical composition of the Pacific oyster *Crassostrea gigas* (Thunberg) spat. *Aquaculture Research*, **35**, 1131–1140.
- Fuhrmann, M., Petton, B., Quillien, V., Faury, N., Morga, B. and Pernet, F. (2016) Salinity influences disease-induced mortality of the oyster *Crassostrea gigas* and infectivity of the ostreid herpesvirus 1 (OsHV-1). *Aquaculture Environment Interactions*, **8**, 543–552.
- Galley, T.H., Batista, F.M., Braithwaite, R., King, J. and Beaumont, A.R (2010) Optimisation of larval culture of the mussel *Mytilus edulis* (L.) *Aquaculture International*, **18**, 315–325.
- Gadan, K., Sandtrø, A., Marjara, I.S., Santi, N., Munang'andu, H.M. et al. (2013) Stress-Induced Reversion to Virulence of Infectious Pancreatic Necrosis Virus in Naive Fry of Atlantic Salmon (Salmo salar L.). PLoS ONE, 8(2), 54656.
- Gehman, A.L.M., Hall, R.J. and Byers, J.E. (2018) Host and parasite thermal ecology jointly determine the effect of climate warming on epidemic dynamics. *PNAS*, **115**(4), 744–749.
- Gazeau, F., Quiblier, C., Jansen, J.M., Gattuso, J-P., Middelburg, J.J. and Heip, C.H.R. (2007) Impact of elevated CO2 on shellfish calcification. *Geophysical Research Letters*, 34, L07603, doi:10.1029/2006GL028554
- Guijarro, J.A., Cascales, D., García-Torrico, A.I., García-Domínguez, M. and Méndez, J. (2015) Temperature-dependent expression of virulence genes in fish-pathogenic bacteria. *Frontiers in Microbiology*, 6,700.
- Gilbey, J., Cauwelier, E., Sampayo, J., Matej Sova, I., Allen, C., Graham, J., Stradmeyer, L. and Middlemass, S. (2018) Identification of the farm of origin of Atlantic salmon smolt escapees in a freshwater Scottish loch using single-nucleotide polymorphic markers. *ICES Journal of Marine Research*, doi:10.1093/icesjms/fsy072
- Gillibrand, P.A., Cromey, C.J., Black, K.D., Inall, M.E. and Gontarek, S.J. (2006) Identifying the Risk of Deoxygenation in Scottish Sea Lochs with Isolated Deep Water. *SARF 017* Final Report.
- Gillibrand, P., Siemering, B. and Davidson, K. (2016) Individual-Based Modelling of the Development and Transport of a *Karenia mikimotoi* Bloom on the North-West European Continental Shelf. *Harmful Algae*, **53**, 118–134.
- Gimenez, I., Waldbusser, G.G. and Hales, B. (2018) Ocean acidification stress index for shellfish (OASIS): Linking Pacific oyster larval survival and exposure to variable carbonate chemistry regimes. *Elementa: Science of the Anthropocene*, **6**, 1–18.
- Gimpel, A., Stelzenmüller, V., Töpsch, S., Galparsoro, I., Gubbins, M., Miller, D., Murillas, A., Murray, A.G., Pinarbaşi, K., Roca, G. and Watret, R. (2018) A GIS-based tool for an integrated assessment of spatial planning trade-offs with aquaculture. Science of the Total Environment, 627, 1644–1655.
- Gobler, C.J., Doherty, O.M., Hattenrath-Lehmanna, T., Griffith, A.W., Kanga, Y. and Litaker, R.W. (2017) Ocean warming since 1982 has expanded the niche of toxic algal blooms in the North Atlantic and North Pacific oceans. *PNAS*, **114**, 4975–4980.
- Gobler, C.J., Merlo, L.R., Morrell, B.K. and Griffith, A.W. (2018) Temperature, acidification, and food supply interact to negatively affect the growth and survival of the forage fish, *Menidia beryllina* (Inland silverside), and *Cyprinodon variegatus* (Sheepshead minnow). *Frontiers in Marine Science*, 5, 86, doi: 10.3389/fmars.2018.00086
- Gonzalez, J.M. and Suttle, C.A. (1993) Grazing by marine nanoflagellates on viruses and virus-sized particles: ingestion and digestion. *Marine Ecology Progress Series*, **94**, 1–10.
- Green, T.J., Montagnani, C., Benkendorff, K., Robinson, N. and Speck, P. (2014) Ontogeny and water temperature influences the antiviral response of the Pacific oyster, *Crassostrea gigas*. Fish and Shellfish Immunology, **36**, 151–157.



- Grini, A., Hansen, T., Berg, A., Wargelius, A., Fjelldal, P.G. (2011) The effects of water temperature on vertebral deformities and vaccine-induced abdominal lesions in Atlantic salmon, *Salmo salar L. Journal of Fish Diseases*, **34**, 531–546.
- Groner, M.L., Gettinby, G., Stormoen, M., Revie, C.W. and Cox R. (2014) Modelling the Impact of Temperature-Induced life history plasticity and mate limitation on the epidemic potential of a marine ectoparasite. *PLoS ONE* **9**(2), e88465, doi:10.1371/journal.pone.0088465
- Gruber N., Hauri C., Lachkar Z., Loher D., Frölicher T.L., Gian-Kasper P. (2012) Rapid progression of ocean acidification in the California Current System. *Science*, **337**, 220–223.
- Gubbins, M. (2012) Mytilus trossulus: Managing Impact On Sustainable Mussel Production In Scotland, ICES CM 2012/Q:08. ISBN: 978-1-907266-47-8
- Gubbins, M., Bricknell, I. and Service, M. (2013) Impacts of Climate Change on Aquaculture. *MCCIP Science Review 2013*, 318–327.
- Guo, X., He, Y., Zhang, L., Lelong, C. and Jouaux, A. (2015) Immune and stress responses in oysters with insights on adaptation. *Fish and Shellfish Immunology*, **46**, 107–119.
- Guyondet, T., Comeau, L.A., Bacher, C., Grant, J., Rosland, R., Sonier R. and Filgueira, R. (2015) Climate change influences carrying capacity in a coastal embayment dedicated to shellfish aquaculture. *Estuaries and Coasts*, **38**, 1593–1618.
- Häder, D.P., Williamson, C.E., Wängberg, S-A., Rautio, M., Rose, K.C., Gao, K., Helbling, E.W., Sinha, R.P. and Worrest, R. (2015) Effects of UV radiation on aquatic ecosystems and interactions with other environmental factors. *Photochemical and Photobiological Sciences*, **14**, 108–126.
- Hall, L.M. and Murray, A.G. (2018) Describing temporal changes in adult female *Lepeophtheirus* salmonis abundance in Scottish farmed Atlantic salmon at the national and regional levels. *Aquaculture*, **489**, 148–153.
- Hall, L.M., Duiguid, S. and Noguera, P.A. (2017) Utilising pathology codes to detect increases in aquatic animal disease occurrence: a retrospective study. *Bulletin European Association of Fish Pathologists*, 37, 183–189.
- Hallegraeff, G.M. (2010) Ocean climate change, phytoplankton community responses and harmful algal blooms: a formidable predictive challenge. *Journal of Phycology*, **46**, 220–235.
- Handeland, S.O., Imsland, A.K. and Stefansson, S.O. (2008) The effect of temperature and fish size on growth, feed intake, food conversion efficiency and stomach evacuation rate of Atlantic salmon post-smolts. *Aquaculture*, **283**, 36–42.
- Harvell, C.D., Kim, K., Burkholder, J.M., Colwell, R.R., Epstein, P.R., Grimes, D.J., Hofmann, E.E., Lipp, E.K., Osterhaus, A.D.M.E., Overstreet, R.M., Porter, J.W., Smith, G.W. and Vasta, G.R. (1999) Emerging marine diseases – climate links and anthropogenic factors. *Science*, 285, 1505–1510.
- Hernroth, B. and Baden, S. (2018) Alteration of host-pathogen interactions in the wake of climate change Increasing risk for shellfish associated infections? *Environmental Research*, **161**, 245–438.
- Hikke, M.C., Braaen, S., Villoing, S., Hodneland, K., Geertsem, C., Verhagen, L., Frost, P., Vlak, J.M., Rimstad, E. and Pijlman, G.P. (2014) Salmonid alphavirus glycoprotein E2 requires low temperature and E1 for virion formation and induction of protective immunity. *Vaccine*, **32**, 6206–6212.
- Hinder, S.L., Hays, G.C., Edwards, M., Roberts, E.C., Walne, A.W. and Gravenor, M.B. (2012) Changes in marine dinoflagellate and diatom abundance under climate change. *Nature Climate Change*, **2**, 271–275.
- Holmer, M. (2010) Environmental issues of fish farming in offshore waters: perspectives, concerns and research needs. *Aquaculture Environment Interactions*, **1**, 57–70.
- Hughes, S.L., Tinker, J., Dye, S., Andres, O., Berry, D.I., Hermanson, L., Hewitt, H., Holliday, N.P., Kent, E.C., Kennington, K., Inall, M. and Smyth, T. (2017) Temperature. MCCIP Science Review 2017, http://www.mccip.org.uk/media/1750/2017arc_sciencereview_003_tem.pdf
- Humphreys, J., Harris M., Herbert, R.J.H., Farrell, P., Jensen, A. and Cragg, S. (2015) Introduction, dispersal and naturalisation of the Manila clam *Ruditapes philippinarum* in British estuaries, 1980–2014. *Journal of the Marine Biologicak Association of the UK*, **95**, 1163–1172.
- Hutchison, Z.L., Hendrick, V.J., Burrows, M.T., Wilson, B. and Last, K.S. (2016) Buried Alive: The Behavioural Response of the Mussels, *Modiolus modiolus* and *Mytilus edulis* to Sudden Burial by Sediment. *PLoS ONE*, **11**(3), e0151471, doi:10.1371/journal.pone.0151471
- Ivanina, A.V. and Sokolova, I.M. (2015) Interactive effects of metal pollution and ocean acidification on physiology of marine organisms. *Current Zoology*, **61**, 653–668.
- Jackson, D., Drumm, A., McEvoy, S., Jensen, Ø., Mendiola, D., Gabiña, G., Borg, J.A., Papageorgiou, N., Karakassis, Y. and Black, K.D. (2015) A pan-European valuation of the extent, causes and cost of escape events from sea cage fish farming. *Aquaculture*, 436, 21–26.



- Jones M.C., Dye, S.R., Pinnegar, J.K., Warren, R. and Cheung, W.W.L. (2013) Applying distribution model projects for an uncertain future: the case of the Pacific oyster in UK waters. *Aquatic Conservation*, 23, 710–722.
- Johnson, P. (2002). Jellyfish, algae take toll on Scottish salmon. Fish Information Service, Europe, https://www.fis.com/
- Kernan, M. (2015) Climate change and the impact of invasive species on aquatic ecosystems. *Aquatic Ecosystem Health and Management*, **18**, 321–333.
- Kinnby, A. (2015) Effects of reduced salinity on fertilization and larval development in the Pacific Oyster, *Crassostrea gigas* (Thunberg, 1789). MSc thesis, Department of Biological and Environmental Sciences, University of Gothenburg, pp. 1–36.
- Kitamura, S-I., Kamata, S.I., Nkano, S.I. and Suzuki, S. (2004) Solar UV radiation does not inactivate marine birnavirus in coastal seawater. *Diseases of Aquatic Organisms*, **58**, 251–254.
- Kochmann, J., Carlsson, J., Crowe, T.P. and Mariani, S. (2012) Genetic evidence for the uncoupling of local aquaculture activities and a population of an invasive species a case study of Pacific oysters (*Crassostrea gigas*). *Journal of Heredity*, **103**, 661–71.
- Kotob, M.H., Menanteau-Ledouble, S., Kumar, G., Abdelzaher, M. and El-Matbouli, M. (2016) The impact of co-infections on fish: a review. *Veterinary Research*, 47, 98.
- Lafferty, K.D. and Mordecai, E.A. (2016) The rise and fall of infectious disease in a warmer world. *F1000 Research*, **5**, 2040, https://f1000research.com/articles/5-2040/v1
- Laing, I., Dunn, P., Peeler, E.J., Feist, S.W. and Longshaw, M. (2014) Epidemiology of Bonamia in the UK, 1982 to 2012. *Diseases of Aquatic Organisms*, **110**, 101–111.
- Landes, A., Dolmer, P., Poulsen, L.K., Petersen, J.K. and Vismann, B. (2015) Growth and Respiration in Blue Mussels (*Mytilus* spp.) from Different Salinity Regimes. *Journal of Shellfish Research*, 34, 373–382.
- Lee, J.E., Zoh, K.D. and Ko, G.P. (2008) Inactivation and UV Disinfection of Murine Norovirus with TiO2 under Various Environmental Conditions. *Applied Environmental Microbiology*, **74**, 2111–2117.
- Lemasson, A.J, Fletcher, S., Hall-Spencer, J.M. and Knights, A.M. (2017) Linking the biological impacts of ocean acidification on oysters to changes in ecosystem services: a review. *Journal of Experimental Marine Biology and Ecology*, 492, 49–62.
- Le Morvan, C., Troutaud, D. and Deschaux, P. (1998) Differential effects of temperature on specific and nonspecific immune defences in fish. *The Journal of Experimental Biology*, 201, 165–168.
- Licandro, P., Conway, D.V.P., Yahia, M.N.D., Fernandez de Puelles, M.L., Gasparini, S., Hecq, J.H., Tranter, P. and Kirby, R.R. (2010) A blooming jellyfish in the northeast Atlantic and Mediterranean. *Biology Letters*, **6**, 688–691.
- Liu, J., Weinbauer, M.G., Maier, C., Dai, M. and Gattuso, J.B. (2010) Effects of ocean acidification on microbial diversity and on microbe-driven biogeochemistry and ecosystem functioning. *Aquatic Microbial Ecology*, 61, 291–305.
- Longshaw, M., Stone, D.M., Wood, G., Green, M.J. and White, P. (2013) Detection of *Bonamia exitiosa* (Haplosporidia) in European flat oysters *Ostrea edulis* cultivated in mainland Britain. *Diseases of Aquatic Organisms*, **106**, 173–179.
- Lorentzen, T. (2008) Modelling climate change and the effect on the Norwegian salmon farming industry. *Nature Resource Modelling*, **21**, 416–435.
- Lucas, C.H., Gelcich, S. and Uye S-.I (2014) Living with Jellyfish. Management and adaptation strategies. In *Jellyfish Blooms*, [Pitt K.A. and Lucas C.H. (eds)], Springer Science+Business Media, Dordrecht, pp. 129–15, doi: 10.1007/978-94-007-7015-7_6
- Luisetti, T., Kennerly, A. and Lorenzoni, I. (2018) Jellyfish bloom impacts on human welfare: what do we know is happening vs what do we think is happening. In *Engaging Marine Scientists and Fishers to Share Knowledge and Perceptions Early Lessons*. CIESM Monograph 50 [Briand, F. (ed)] CIESM Publisher, Monaco and Paris, pp. 181–186.
- Lynam, C.P., Lilley, M.K.S., Bastian, T., Doyle, T.K., Beggs, S.E. and Hays, G.C. (2011) Have jellyfish in the Irish Sea benefited from climate change and overfishing? *Global Change Biology*, **17**, 767–782.
- MacFadden, D.R., McGough, S.F., Fisman, D., Santillana, M. and Brownstein J.S. (2018) Antibiotic resistance increases with local temperature. *Nature Climate Change*, **8**, 510–514.
- Mackenzie, C.L., Lynch, S.A., Culloty, S.C. and Malham, S.K. (2014) Future oceanic warming and acidification alter immune response and disease status in a commercial shellfish species, *Mytilus edulis* L. *PLoS ONE*. **9**(6), e99712.
- Maggs, C.A., Mineur, F., Bishop, J.D.D., McCollin, T. (2010) Non-natives, *MCCIP Science Review* 2010, 11 pp. www.mccip.org.uk/arc
- Malham, S.K., Rajko-Nenow, P., Howlett, E., Tuson, K.E., Perkins, T.L., Pallett, D.W., Wang, H., Jago, C.F., Jones, D.L. and McDonald, J.E. (2014) The interaction of human microbial pathogens,



- particulate material and nutrients in estuarine environments and their impacts on recreational and shellfish waters. *Environmental Science: Processes and Impacts*, **16**, 2145–2155.
- Malham, S.K., Taft, H., Cooper, D., Ladd, C., Seymour, M., Robins, P.E., Jones, D.L., McDonald, J.E., Le Vay, L. and Jones, L. (2017) Review of Current Evidence to Inform Selection of Environmental Predictors For Active Management Systems In Classified Shellfish Harvesting Areas. Report to Food Standards Agency, Project FS103001.
- Mangan, S., Wilson, R.W., Findlay, H.S. and Lewis, C. (2019) Acid-base physiology over tidal periods in the mussel Mytilus edulis: size and temperature are more influential than seawater pH. *Proceedings of the Royal Society. B*, **286**, doi/10.1098/rspb.2018.2863
- Mangi S.C., Lee J., Pinnegar J.K., Law R.J., Tyllianakis E., Birchenough S.N.R. (2018) The economic impacts of ocean acidification on shellfish fisheries and aquaculture in the United Kingdom. *Environmental Science Policy*, **86**, 95–105.
- Mar-López, M., Mitchell, S.O. and Rodger, H.D. (2014) Pathology and mortality associated with the mauve stinger jellyfish *Pelagia noctiluca* in farmed Atlantic salmon *Salmo salar L. Journal of Fish Disesases*, **39**, 111–115.
- Marcogliese, D.J. (2008) The impact of climate change on the parasites and infectious diseases of aquatic animals. *Scientific and Technical Review of the Office International des Epizooties*, **27**, 467–484
- Marine Scotland (2015) A Technical Standard for Scottish Finfish Aquaculture. The Scottish Government, Edinburgh, https://www.gov.scot/publications/technical-standard-scottish-finfish-aquaculture/
- Markkula, E.S., Kavonen, A., Salo, H., Valtonen, E.T. and Jokinen, E.I. (2007) Ultraviolet B irradiation affects resistance of rainbow trout (*Oncorhynchus mykiss*) against bacterium *Yersinia ruckeri* and trematode *Diplostomum spathaceum*. *Photochemistry and Photobiology*, **83**, 1263–1269.
- Martell, L., Bracale, R., Carrion, S.A., Purcell, J.E., Lezzi, M., Gravili, C., Piraino, S. and Boero, F. (2018) Successional dynamics of marine fouling hydroids (Cnidaria: *Hydrozoa*) at a finfish aquaculture facility in the Mediterranean Sea. *PLoS ONE*, **13**, e0195352.
- Matozzo, V., Chinellato, A., Munari, M., Finos, L., Bressan, M. et al. (2012) First evidence of immunomodulation in bivalves under seawater acidification and increased temperature. PLoS ONE 7(3), 33820.
- MEMA (2017) NSW Marine Estate Threat and Risk Assessment Background Environmental information, 409 pp. ISBN 978-1-74256-983-3.
- Miossec, L., Le Deuff, R-M. and Goulletquer, P. (2009) Alien species alert: *Crassostrea gigas* (Pacific oyster). *ICES Cooperative Research Report* No. 299, 42 pp.
- Morris, S., Stubbs, B., Brunet, C. and, Davidson, K. (2010) Spatial Distributions and Temporal Profiles of Harmful Phytoplankton, and Lipophilic Toxins in Common Mussels and Pacific Oysters from Four Scottish Shellfish Production Areas (2009). Final project report to the Food Standards Agency Scotland (FSAS), 57 pp.
- Munro, L.A. (2019) The Scottish Fish Farm Production Survey 2018. The Scottish Government, Edinburgh.
- Murray, A.G. and Munro, L.A. (2018) The growth of Scottish salmon (*Salmo salar*) aquaculture 1979–2016 fits a simple two-phase logistic population model. *Aquaculture*, **496**, 146–152.
- Murray, A.G. and Peeler, E.J. (2005) A framework for understanding the potential for emerging diseases in aquaculture. *Preventative Veterinary Medicine*, **67**, 223–235.
- Murray, A.G. and Salama, N.K.G. (2017) Modelling disease in aquatic systems that are spread by processes operating at different temporal and spatial scales: Examples from salmon aquaculture. *CABI Reviews: Perspectives in Agriculture, Veterinary Science, Nutritional and Natural Resources*, **12**(32), doi: 10.1079/PAVSNNR201712032
- Murray, A.G., Marcos-Lopez, M., Collet, B. and Munro, L.A. (2012) A review of the risk posed to Scottish mollusc aquaculture from *Bonamia*, *Marteilia* and oyster herpesvirus. *Aquaculture*, **370**–**371**, 7–13.
- Nehls, H. and Buttger, G. (2007) Spread of the Pacific Oyster *Crassostrea gigas* in the Wadden Sea. Causes and consequences of a successful invasion. *HARBASINS Report for The Common Wadden Sea Secretariat*, Wilhelmshaven, 54 pp.
- Nimmo, F., Cook, E. J., Moxey, A. P., Hambrey, J. and Black K. (2012) *Cost-Benefit Analysis of Management Options for* Didemnum vexillum (*Carpet Sea Squirt*) in *Scotland*. Hambrey Consulting in association with the Scottish Association for Marine Science and Poseidon Aquatic Resource Management. Scottish Government, Edinburgh, 69 pp.
- Nøstbakken, O.J., Hove, H.T., Duinker, A., Lundebye, A-K., Berntssen, M.H.G., Hannisdal, R., Lunestad, B.T., Maage, A., Madsen, L., Torstensen, B.E. and Julshamn, K. (2015) Contaminant levels in Norwegian farmed Atlantic salmon (*Salmo salar*) in the 13-year period from 1999 to 2011. *Environment International*, 74, 274–280.



- Oidtmann, B., Dixon, P., Way, K., Joiner, C. and Bayley, A.E. (2017) Risk of waterborne virus spread review of survival of relevant fish and crustacean viruses in the aquatic environment and implications for control measures. *Reviews in Aquaculture*, 641–669.
- Oldham, T, Rodger, H, Nowak, BF (2016) Incidence and distribution of amoebic gill disease (AGD) An epidemiological review. *Aquaculture*, **457**, 35-42.
- Ong, E.Z., Briffa, M., Moens, T. and Van Colen, C. (2017) Physiological responses to ocean acidification and warming synergistically reduce condition of the common cockle *Cerastoderma edule. Marine Environmental Research*, **130**, 38–47.
- Ørnholt-Johansson, G., Frosch, S. and Jørgensen, B.M. (2017) Variation in some quality attributes of Atlantic salmon fillets from aquaculture related to geographic origin and water temperature. *Aquaculture*, **479**, 378–383.
- Overton, K., Samsing, F., Oppedal, F., Stein, L.H. and Dempster, T. (2017) Lowering treatment temperature reduces salmon mortality: a new way to treat with hydrogen peroxide in aquaculture. *Pest Management Science*, **74**, 535–540.
- Panzarin, V., Cappellozza, E., Mancin, M., Milani, A., Toffan, A., Terregino C. and Cattoli, G. (2014) *In vitro* study of the replication capacity of the RGNNV and the SJNNV betanodavirus genotypes and their natural reassortants in response to temperature. *Veterinary Research*, **45**, 56.
- Pham, P.H., Jung J., Lumsden J.S., Dixon B. and Bols N.C. (2011) The potential of waste items in aquatic environments to act as fomites for viral haemorrhagic septicaemia virus. *Journal of Fish Diseases*, **35**, 73–77.
- Philippart, C.J.M., Anadon, R., Danovaro, R., Dippner, J.W., Drinkwater, K.F., Hawkins, S.J., Oguz, T., O'Sullivan, G. and Reid, P.C. (2011) Impacts of climate change on marine ecosystems: observations, expectations and indicators. *Journal of Experimental Marine Biology and Ecology*, 400, 52–69.
- Pitt, K.A., Lucas C.H., Condon R.H., Duarte C.M. and Stewart-Koster B. (2018) Claims that anthropogenic stressors facilitate jellyfish blooms have been amplified beyond the available evidence: a systematic review. *Frontiers in Marine Science*, **5**(451), doi: 10.3389/fmars.2018.00451
- Pulkkinen, K., Suomalainen, L-R., Read, A.F., Ebert, D., Rintamaki, P. and Valtonen, E.T. (2010) Intensive fish farming and the evolution of pathogen virulence: the case of columnaris disease in Finland. *Proceedings of the Royal Society B*, **277**, 593–600.
- Pernet, N., Lagarde, F., Jeannee, N., Daigle G., Barret, J., Le Gall, P., Quere, C. and D'Orbcastel, E.R. (2014) Spatial and temporal dynamics of mass mortalities in oysters is influenced by energetic reserves and food quality. *PLoS One*, **9**, https://doi.org/10.1371/journal.pone.0088469
- Qiu, J-W., Tremblay, R. and Bourget, E. (2002) Ontogenetic changes in hyposaline tolerance in the mussels *Mytilus edulis* and *M. trossulus*: implications for distribution. *Marine Ecology Progress Series*, 228, 143–152.
- Rahman, M.A., Henderson, S., Miller-Ezzy, P., Li, X.X. and Qin, J.G. (2019) Immune response to temperature stress in three bivalve species: Pacific oyster *Crassostrea gigas*, Mediterranean mussel *Mytilus galloprovincialis* and mud cockle *Katelysia rhytiphora*. *Fish and Shellfish Immunology*, **86**, 868–874.
- Reid, P.C., Cook, E.J., Edwards, M., McQuatters-Gollop, A., Minchin, D. and McCollin, T. (2009) Marine Non-Native Species. *MCCIP Ecosystem Linkages Report Card*, 27 pp.
- Richardson, A.J., Bakun, A., Hays, G.C. and Gibbons, M.J. (2009) The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. *TREE*, **24**(6), 312–322.
- Robert, R., Vignier, J. and Petton, B. (2017) Influence of feeding regime and temperature on development and settlement of oyster *Ostrea edulis* (Linnaeus, 1758) larvae. *Aquaculture Research*, **48**, 4756–4773.
- Roberts, S.D. and Powell, M.D. (2005) The viscosity and glycoprotein biochemistry of salmonid mucus varies with species, salinity and the presence of amoebic gill disease. *Journal of Comparative Physiology B*, **175**, 1–11.
- Rodgers, C., Arzul, I., Carrsco, N. and Furones Nozal, D. (2018) A literature review as an aid to identify strategies for mitigating ostreid herpesvirus 1 in *Crassostrea gigas* hatchery and nursery systems. *Reviews in Aquaculture*, **11**(3), 565–585, https://doi.org/10.1111/raq.12246
- Rodrigues, L.C., Van Den Bergh, J.C.J.M., Massa, F., Theodorou, J.A., Ziveri, P. and Gazeau, F. (2015) Sensitivity of Mediterranean bivalve mollusc aquaculture to climate change, ocean acidification, and other environmental pressures: findings from a producer survey. *Journal of Shellfish Research*, **34**, 1161–1176.
- Roy, S.S. and Pal, R. (2015) Microalgae in aquaculture: a review with special references to nutritional value and fish dietetics. *Proceedings of the Zoological Society of London*, **68**, 1–8.



- Salama, N.K.G. and Rabe, B. (2013) Developing models for investigating the environmental transmission of disease-causing agents within open-cage salmon aquaculture. *Aquaculture Environment Interactions*, **4**, 91–115.
- Salin, K.R., Arun, V.V., Nair, C.M. and Tidwell, J.H. (2018) Sustainable Aquafeed. In *Sustainable Aquaculture*, [Hai, F.I., Visvanathan, C., Boopathy, R (ed)]. Springer, pp. 123–151.
- Samsing, F, Johnsen, I, Dempster, T, Oppedal, F, Treml, EA (2018) Network analysis reveals strong seasonality in the dispersal of a marine parasite and identifies areas for coordinated management. *Landscape Ecology*, **32**, 1953–1967.
- San-Martín, M., Pitt, K.A., Condon, R.H., Lucas, C.H., Novaes, de Santana C. and Duarte, C.M. (2016) Flawed citation practices facilitate the unsubstantiated perception of a global trend toward increased jellyfish blooms. *Global Ecology and Biogeography*, **25**(9), 1039–1049.
- Sánchez-Lazo, C. and Martínez-Pita, I. (2012) Effect of temperature on survival, growth and development of *Mytilus galloprovincialis* larvae. *Aquaculture Research*, **43**, 1127–1133.
- Schets, F.M., van den Berg, H.H., Rutjes, S.A. and de Roda Husman, A.M. (2010) Pathogenic Vibrio species in Dutch shellfish destined for direct human consumption. *Journal of Food Protection*, 3, 734–738.
- Schmidt, W., Evers-King, H.L., Campos, C.J.A., Jones, D.B., Miller, P.I., Davidson, K. and Shutler, J.D. (2018) A generic approach for the development of short-term predictions 2 of *E. coli* and biotoxins in shellfish, *Aquaculture Environment Interactions*, **10**, 173–185.
- Scottish Government's Seaweed Cultivation Policy Statement (2017)
 https://beta.gov.scot/publications/seaweed-cultivation-policy-statement-2017/
- Shelmerdine, R.L., Mouat, B. and Shucksmith, R.J. (2017) The most northerly record of feral Pacific oyster *Crassostrea gigas* (Thunberg, 1793) in the British Isles. *BioInvasions Records*, **6**, 57–60.
- Shephard, S., MacIntyre, C. and Gargan, P. (2016) Aquaculture and environmental drivers of salmon lice infestation and body condition in seatrout. *Aquaculture Environment Interactions*, **8**, 597–610.
- Shi, W., Zhao, X., Han, Y., Che, Z., Chai, X. and Liu, G. (2016) Ocean acidification increases cadmium accumulation in marine bivalves: a potential threat to seafood safety. *Scientific Reports*, **6**, 20197, doi: 10.1038/srep20197
- Syvret, M. L. (2008) Project report Pacific oyster aquaculture protocol for the UK. *Shellfish News*, **26**, 9–11.
- Soares, S., Green, D.M., Turnbull, J.F., Crumlish, M. and Murray, A.G. (2011) A baseline method for benchmarking mortality losses in Atlantic salmon (*Salmo salar*) production. *Aquaculture*, **314**, 7–12
- Soto, E., Brown, N., Gardenfors, Z.O., Yount, S., Revan, F., Francis, S., Kearney, M.T. and Camus, A. (2014) Effect of size and temperature at vaccination on immunization and protection conferred by a live attenuated *Francisella noatunensis* immersion vaccine in red hybrid tilapia. *Fish and Shellfish Immunology*, **41**, 593–599.
- Spillman, C.M. and Hobday, A.J. (2014) Dynamical seasonal forecasts to aid salmon farm management in a climate hotspot. *Climate Risk Management*, **1**, 25–38
- Sprague, M., Betancor, M.B. and Tocner, D.R. (2017) Microbial and genetically engineered oils as replacements for fish oil in aquaculture feeds. *Biotechnology Letters*, **39**, 1599–1609.
- Tacon G.J., Hasan M.R., Metian M. (2011) Demand and supply of feed ingredients for farmed fish and crustaceans Trends and prospects. Food and Agricultural Organisation of the UN, Rome, http://www.fao.org/3/ba0002e/ba0002e.pdf
- Taranger, G.L., Karlsen Bannister, R.J., Glover, K.A., Husa, V., Karlsbakk, B., Kvamme, B.O., Boxaspen, K.K., Bjørn, P.A., Finstad, B., Madhun, A.S., Morton, H.C. and Svåsand, T. (2014) Risk assessment of the environmental impact of Norwegian Atlantic salmon farming *ICES Journal of Marine Science*, 72, 997–1021.
- Taylor, M. and Kelly, R. (2010) Assessment of Protocols and Development of Best Practice Contingency Guidance to Improve Stock Containment at Cage and Land-based Sites Volume 1.74 pp. ISBN: 978-1-907266-30-0.
- The Welsh Government (2015) A Spatial Assessment of the Potential for Aquaculture in Welsh Waters.

 Report No. R.2384, ABP Marine Environmental Research Ltd.

 http://gov.wales/docs/drah/publications/150702-a-spatial-assessment-ofthe-potential-for-aquaculture-in-welsh-waters-en.pdf
- Thompson, F.L., Austin, B. and Swing, J. (2006) *The Biology of Vibrios*. American Society for Microbiology, 423 pp.
- Thorstad, E.B., Fleming, I.A., McGinnity, P., Soto, D., Wennevik, V. and Whoriskey, F. (2008) Incidence and impacts of escaped farmed Atlantic salmon *Salmo salar* in nature. *NINA Special Report* 36, 110 pp.
- Thorvaldsen, T., Holmen, I.M. and Moe, H.K. (2015) The escape of fish from Norwegian fish farms: causes, risks and the influence of organisational aspects. *Marine Policy*, **55**, 33–38.



- Tinker J., Lowe J., Pardaens A., Holt J. and Barciela R. (2016) Uncertainty in climate projections for the 21st century northwest European shelf seas. *Progress in Oceanography*, **148**, 56–73.
- Tett, P., Verspoor, E., Hunter, D-C., Coulson, M.W., Hicks, N., Davidson, K., Fernandes, T.F., Nickell, T., Tocher, D.R., Benjamins, S., Risch, D., Wilson, B., Wittich, A. and Fox, C.J. (2018) Review of the environmental impacts of salmon farming in Scotland. Report for the Environment, Climate Change and Land Reform (ECCLR) Committee. *The Scottish Parliament Technical Report*, January 2018, 196 pp.
- Tort, L. (2011) Stress and immune modulation in fish. *Developmental and Comparative Immunology*, **35**, 1366–1375.
- Townhill, B.L., Tinker, J., Jones, M., Pitois, S., Creach, V., Simpson, S.D., Dye, S., Bear, E. and Pinnegar, J. (2018) Harmful algal blooms and climate change: exploring future distribution changes, *ICES Journal of Marine Science*, 75, 1882–1893.
- Turner, A.D., Powell, A., Schofield, A., Lees, D.N. and Baker-Austin, C. (2015) Detection of the pufferfish toxin tetrodotoxin in European bivalves, England, 2013–2014. *Eurosurveillance*, **20**(2), 21009.
- Turner, A.D., Dhanji-Rapkova, M., Coates, L., Bickerstaff, L., Milligan, S., O' Neill, A., Faulkner, D., McEneny, H., Baker-Austin, C., Lees, D.N. and Algoet, M. (2017) Detection of Tetrodotoxin Shellfish Poisoning (TSP) Toxins and Causative Factors in Bivalve Molluscs from the UK, *Marine Drugs*, 15, 1–17.
- Turner, A.D., Fenwick, D., Powell A., Dhanji-Rapkova M., Ford C., Hatfield R., Santos A., Martinez-Urtaza J. and Bean T.P. (2018) New Invasive Nemertean Species (*Cephalothrix Simula*) in England with High Levels of Tetrodotoxin and a Microbiome Linked to Toxin Metabolism. *Marine Drugs*, **16**, 1–20.
- Tran, G., Heuzé, V. and Makkar, H.P.S. (2015) Insects in fish diets. Animal Frontiers, 5, 37-44.
- Treasurer, J.W., Hannah F. and Cox D. (2003) Impact of a phytoplankton bloom on mortalities and feeding response of farmed Atlantic salmon, *Salmo salar*, in west Scotland, *Aquaculture*, **218**, 103–113.
- Uddin, M.N., Al-Harbi, A.H. and Wakabayashi, H. (2008) Optimum temperatures for the peak growth of some selected bacterial fish pathogens. *Asian Fisheries Science*, **21**, 205–214.
- Ugelvik, M.S., Skorping, A., Moberg, O. and Mennerat, A. (2017) Evolution of virulence under intensive farming: salmon lice increase skin lesions and reduce host growth in salmon farms. *Journal of Evolutionary Biology*, 30, 11361142.
- Uribe, C., Folch, H., Enriquez, R. and Moran, G. (2011) Innate and adaptive immunity in teleost fish: a review. *Veterinarni Medicina*, **56**(10), 486–503.
- UK MNMP (2015) United Kingdom multiannual national plan for the development of sustainable aquaculture,
 - $\frac{https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/480928/sustainable-aquaculture-manp-uk-2015.pdf$
- UKCP18 (2018) UK Climate projections, https://www.metoffice.gov.uk/news/releases/2018/ukcp18-launch-pr
- Van West, P. (2006) *Saprolegnia parasitica*, an oomycete pathogen with a fishy appetite: new challenges for an old problem. *Mycologist*, **20**, 99–104.
- Vezzulli, L., Colwell, R.R. and Pruzzo, C. (2013) Ocean warming and spread of pathogenic Vibrios in the aquatic environment. *Microbial Ecology*, 65, 817, http://dx.doi.org/10. 1007/s00248-012-0163-2
- Vezzulli, L., Grande, C., Reid, P.C., Helaouet, P., Edwards, M., Hofle, M.G., Brettar, I., Colwell, R. and Pruzzo, C. (2016) Climate influence on *Vibrio* and associated human diseases during the past half century in the coastal North Atlantic. *PNAS*, 113(34), E5062–E5071, doi/10.1073/pnas.1609157113
- Vikeså, V., Nankervis, L. and Hevrøy, E.M. (2016) Appetite, metabolism and growth regulation in Atlantic salmon (*Salmo salar* L.) exposed to hypoxia at elevated seawater temperature. *Aquaculture Research.* **48**(8), 1–16.
- Wallace, I.S., McKay, P. and Murray, A.G. (2017) A historical review of the key bacterial and viral pathogens of Scottish wild fish. *Journal of Fish Diseases*, **40**, 1741–1756
- Wells, M.L., Trainer, V.L., Smayda, T.J., Karlson, B.S.O., Trick, C.G., Kudela, R.M., Ishikawa, A., Bernard, S., Wulff, A., Anderson, D.M. and Cochlan, W.P. (2015). Harmful algal blooms and climate change: learning from the past and present to forecast the future. *Harmful Algae*, 49, 68–93
- Whyte, C., Swann, S. and Davidson, K. (2014) Changing wind patterns linked to unusually high *Dinophysis* blooms around the Shetland Islands, Scotland. *Harmful Algae*, **39**, 365–373.



- Williamson, P., Turley, C. and Ostle, C. (2017) Ocean Acidification. *MCCIP Science Review 2017*, 1 14, doi:10.14465/2017.arc10.001-oac,
 - http://www.mccip.org.uk/media/1760/2017arc_sciencereview_001_oac.pdf
- Wargelius, A., Leininger, S., Skaftnesmo, K.O., Kleppe, L., Andersson, E., Taranger, G.L., Schulz, R.W. and Edvardsen, R.B. (2016) *Dnd* knockout ablates germ cells and demonstrates germ cell independent sex differentiation in Atlantic salmon. *Scientific Reports*, 6, 21284.
- Wiltshire, K. (2007) Ecophysiological tolerances of the Pacific oyster, *Crassostrea gigas*, with regard to the potential spread of populations in South Australian waters. *SARDI Research Report Series Number* 222, SARDI Aquatic Sciences Publication Number F2007/000499-1.
- Woodson, C.B. and Litvin, S.Y. (2015) Ocean fronts drive marine fishery production and biogeochemical cycling. *PNAS*, **112**, 1710–1715.
- Zhang, J., Tanga, X., Sheng, X., Xing, J. and Zhan, W. (2017) The influence of temperature on viral replication and antiviral-related genes response in hirame rhabdovirus-infected flounder (*Paralichthys olivaceus*). Fish and Shellfish Immunology, **68**, 260–265.