



Topic
Aquaculture
Author(s)
Matt J. Gubbins & Ian Bricknell
Organisation(s) represented
Fisheries Research Services, Marine Laboratory, 375 Victoria Road, Aberdeen AB11 9DB
Executive summary
<p>Given the current predictions, climate change is unlikely to have a significant effect on Scottish mariculture over the next decade. However, within the next 50 years or more, the forecast changes are likely to result in noticeable effects. Rising average water temperatures will result in faster growth rates for some species (e.g. Atlantic salmon, mussels and oysters) but prolonged periods of warmer summer temperatures may cause thermal stress, particularly for cold water species (e.g. cod and Atlantic halibut) and intertidal shellfish (oysters). However, warmer waters may provide opportunities to culture new species, or species that are currently economically marginal in UK waters.</p> <p>Diseases of cultured fish and shellfish including bacterial, viral, parasitic and fungal diseases, will be affected by a changing thermal regime, but in a largely unpredictable manner. However, under conditions of thermal stress, cultured species are likely to be more susceptible to disease and warmer conditions may allow the establishment of exotic diseases, while diseases such as cold water vibriosis, may become much rarer. Sea lice are likely to remain a problem in salmon culture and rising temperatures will extend their season and may increase infective pressure, requiring more treatments. Increased storminess (higher frequency of strong wind speeds) predicted for certain seasons in some regions will increase the risk of escapes through equipment failure and may necessitate site relocation or changes to equipment design.</p> <p>The forecast warmer waters with calmer, drier summer months will have an effect on planktonic communities, although this will be difficult to predict in detail. There may be an increase in the frequency of harmful algal and jellyfish</p>

blooms, potentially causing more fish kills and closures of shellfish harvesting areas, but the forecast reduction in summer precipitation may benefit classification of shellfish growing areas. Increased temperatures and more abundant plankton could also enhance early spawning success and spat fall of cultured shellfish species, to the benefit of the shellfish industry.

Full review

Introduction

In 2006, Scottish marine aquaculture (mariculture) produced over 99% of the UK's cultured marine finfish. For shellfish, 18% was cultured in Scotland, with 39% in England and Wales and 43% in Northern Ireland. (Marine Fisheries Agency, 2006). The dominant species currently produced in Scotland are Atlantic salmon, mussels and oysters. In England and Wales, mariculture is primarily focussed on the culture of oysters and mussels, with some effort being put into the rearing of species such as lobsters. To date, there has been little published research or consensus opinion on the effects of climate change on UK mariculture. However, much can be inferred from the published literature on the effects of environmental variables on cultured species. Although the impacts suggested below are made predominately with respect to the Scottish aquaculture industry, many of the impacts may also be relevant for aquaculture based in other UK coastal waters.

Ocean climate change in mariculture areas

Scottish aquaculture in the marine environment (mariculture) is concentrated around the West coast of mainland Scotland and the Western and Northern Isles. In England and Wales, culture of oysters and mussels mainly takes place along the southern coast of England and around the southern and northern coastline of Wales. Predictions of climate variables in these areas taken from the UKCIP published forecasts on www.ukcip.org/scenarios/ukcip02/scenarios/maps, were used to derive the subsequent predictions of effects on aquaculture. The following points relating to the predicted climate change in the key Scottish mariculture areas were used as the basis for predicting effects on mariculture:

All areas around Scotland are predicted to experience rises in annual and seasonal mean water temperature of up to 0.5 °C by 2020 and up to 2.5 °C by 2080. Over the same timescales, the summer precipitation is predicted to decrease (0-10% by 2020 and 10-30% by 2080) and winter temperature are predicted to increase (10-15% by 2080). Similar predictions are expected for England and Wales in the same time period.

Direct effects of temperature increase. Medium confidence

An increase of 2°C may well adversely affect some species currently being farmed in Scotland as the thermal optima for the animals physiology may be exceeded for long periods of time during the summer months. Aquaculture of species such as Atlantic cod and Atlantic halibut may not be possible in the south of the country or be limited to areas of deep-water up-welling where the water is cooler than normal. Salmonid species are more tolerant of higher temperatures (Reddin *et al.*, 2006, Cano & Nicieza, 2006; Tackle *et al.*, 2006; Goniea *et al.*, 2006; Galbreath *et al* 2006; and Larsson & Berglund 2006) than Atlantic cod (Levesque *et al.*, 2005; Claireaux *et al.*, 1995 and Neat & Righton, 2006) and Atlantic halibut (Hurst *et al.*, 2005; Imsland *et al.*, 2000; Aune *et al.*, 1997 and Bjornsson & Tryggvadottir, 1996) but higher peak temperature in the summer months, which may well be of longer duration than present could cause issues with thermal stress and potentially make some sheltered, warmer sites unsuitable for those species during the summer months.

Optimal temperatures for on-growing large cod are generally low (approximately 7°C) (Neat & Righton, 2006) and although rising temperatures in Scottish waters may have some benefit to the growth rates of juveniles, growth rates of adults are likely to suffer.

Predicted increased growth rates of shellfish species (mussels and oysters) are dependent on the continued availability of the planktonic food supply. It is recognised that mussels around the UK are comprised of at least two species that are able to hybridise, and therefore, it is possible that they will be able to tolerate the expected wider temperature fluctuations. Intertidal shellfish, notably Pacific oyster (*Crassostrea gigas*), are currently susceptible to occasional mortality events during prolonged periods of hot weather. These would be likely to increase in frequency under warmer conditions. This species of oyster is not endemic to the UK and our current thermal regime is not optimal for spawning and natural recruitment from cultured stocks to establish wild populations. Under conditions of increased temperature, this may change.

Broodstock of some species (e.g. Atlantic halibut, Arctic charr) require low winter temperatures (3 months <6°C) for egg maturation. Production of high quality ova could require increased energy costs and capital expenditure associated with temperature control of broodstock and the availability of suitable broodstock sites may be restricted in the future.

Opportunities for new species. Low confidence.

Warmer water conditions could, potentially, allow new species to be cultured in the UK where the current temperature maximums and minimums are marginal for the species, such as sea bass, sea bream, turbot, hake, scrombiforms (e.g. blue fin tuna), nori, ormer and Manilla clams.

Diseases of fish and shellfish. Low confidence.

From a disease point of view an increase in temperature can have many affects. Bacterial, viral and fungal disease will, in general, have shorter generation times. It is possible that some diseases, which transmit above a minimum temperature, will increase in prevalence. Not all effects on disease will be detrimental. For example the seasonal window of infectivity of some serious infectious conditions such as viral haemorrhagic septicaemia virus (VHSV) or the freshwater viral disease Infectious pancreatic necrosis virus (IPNV) could be shortened, whilst others that require a minimum temperature to cause clinical symptoms and transmission, such as Bacterial Kidney disease (BKD) in freshwater salmonids, could be lengthened. However, as most fish are **poikilothermic** their physiology is largely governed by the temperature of their surrounding environment and warmer water will mean the immune system of these animals will function more effectively in preventing the establishment of infections (up to the thermal optimum of the animal) (Bowden *et al.*, 2007). It is therefore possible that clinical infections will not increase as fewer infections become established in the host. Once the thermal optimum is exceeded, then the function of the immune system will decline and physiological stress and oxygen depletion (warmer water holds less oxygen in solution than cold water) may well lead to disease and welfare issues.

Some viral infections can only occur between narrow temperature ranges, often 10-12°C, usually during spring and autumn. Under warmer conditions this temperature window may decrease in the spring (and occur earlier in the year) as more rapid warming of water occurs in spring. Conversely if cooling of the environment is delayed during the autumn this temperature window may become extended and occur later in the year. Additionally, warmer water conditions may allow the establishment of exotic diseases, which are currently excluded as the climate is too cool to permit transmission. Beneficially, diseases that occur under cool environments, e.g. cold water **vibriosis**, may become much rarer if the ecosystem is not cold enough for their biology.

If shellfish experience super-optimal thermal conditions (as will be more likely, particularly for inter-tidally cultivated species, given the predicted changes in temperature for the regions where they are cultivated) they will also be more susceptible to bacterial, viral and parasitic infections.

By their nature it is difficult to understand the response of diseases of unknown **aetiology** to increase in temperature. Some may become established in the UK, new ones may develop as a result of the warmer conditions while others that occur under cooler water regimes may decline.

Bacterial infections

As a rule of thumb as temperature increases the generation time of bacteria decreases (Duguid *et al.*, 1978) so under higher temperature regimes most bacterial infections would be predicted to progress faster once the host was infected, however, as mentioned above, assuming the animal is not at its thermal limit the fishes immune system will be operating more effectively and may well overcome the infection (Le Morvan *et al.*, 1996; Lillehaug 1997; Van Muiswinkel and Wiegertjes 1997 and Eggset *et al.*, 1997a).

Under a rising temperature regime some bacterial diseases of fish, such as *Moritella viscosa* (Benediktsdottir *et al.*, 2000 and Coyne *et al.*, 2006) and cold water vibriosis (Nordmo & Ramstad 1999; Nordmo *et al.*, 1997 and Steine *et al.*, 2001), may decline in abundance as these diseases are characteristically seen in winter under cold water conditions and the new warmer environment may well adversely affect these bacteria. *Aeromonas salmonicida* and BKD, however, tend to occur under rising temperature regimes and during the summer months (Nordmo & Ramstad 1999; Lillehaug *et al.*, 2000; Eggset *et al.*, 1997b; Rose *et al.*, 1989; Roberts 1976; Hirvela-Koski *et al.*, 2006; Bruno 2004; Jacobson *et al.*, 2003; Nagai & Lida 2002; Piganelli *et al.*, 1999 and Jonsdottir *et al.*, 1998). If the environment warms by 2°C then it is possible that diseases such as these will occur earlier in the year (as the spring will be warmer and earlier) and the period in which these diseases are common may well be extended, increasing the infectious pressure of these pathogens in the environment. Warmer conditions may also favour currently rare bacterial infections such as *Clostridia*, allowing this pathogen to extend its range further north.

Viral diseases

Viruses effectively hijack the host's cells to replicate and the rate of replication is governed by the animal's physiology (Duguid *et al.*, 1978). As most fish are **poikilothermic** (Bond, 1996) their physiology is largely governed by the temperature of their surrounding environment and warmer water will mean the animals will have a faster metabolism, which in turn will lead to increased viral replication within the host. It is worth pointing out again that, assuming the animal is not at its thermal limit, the fishes' immune system will be operating more effectively and may well overcome the infection as described above.

Some viruses can only infect their host during a very narrow temperature window (usually 10-12°C for most viruses currently of interest in Scotland

(Bricknell *et al.*, 2006; Skall *et al.*, 2005a; Skall *et al.*, 2005b; Einer-jensen *et al.*, 2004; Bowden 2003; Park & Reno 2005; Bowden *et al.*, 2002; Kollner *et al.*, 2002; Jarp *et al.*, 1996 and Stangeland *et al.*, 1996)) so an increased temperature regime may shorten this window as spring warming of water may well be increased reducing the period when infection can take place. Conversely cooling of the aquatic environment in autumn may be slower and the autumn infectious window may well increase in duration. This may result in a change in the seasonal distribution of diseases and it may well allow the pathogens to encounter new hosts as their duration in the aquatic environment is different from today. For example an increased infectious window in the autumn may mean that autumn migrating fish such as the critically endangered smelt may encounter pathogens that it does not normally meet.

Parasitic diseases

As parasites of fish and shellfish often have very complex life cycles involving many intermediate hosts, understanding how climate change would affect parasite abundance and the incidence of infection is more difficult to predict. Some parasites will become rare or disappear from Scottish waters because their physiology is not suitable to the warmer environment or their intermediate and final hosts decline in numbers as the environment changes, migrate further north to cooler waters (Drinkwater 2005; Rose 2005 and Clark *et al.*, 2003) or the parasites thermal limits are exceeded (Boxaspen, 1997 and Boxaspen & Naess, 2000). However other parasites will become more abundant as their definitive host and intermediate hosts colonise the new environment or, as Scottish waters warm up, the environment will be able to support new parasitic organisms, which are currently at or below their thermal minimum, and they would be able to survive and colonise new hosts in the warmer ecosystem. For example *Caligus curtis*, currently rare in Scottish waters, may effectively extend their range further north, especially if susceptible fish hosts can over-winter or establish viable populations.

The biology of parasites with direct life cycles, such as sea lice (*Lepeophtheirus salmonis*) is a little easier to predict potential changes in. It would be expected that a 2°C increase in water temperature will decrease the life cycle by approximately 2 days and permit more generations in a season (Boxaspen 1997; Boxaspen & Naess 2000 and Heuch *et al.*, 1995), potentially increasing the infective pressure of this parasite in Scotland. However, the time the copepodid stage remains infectious will also decrease from about 10 days under current climatic conditions to around 8 days under the warmer regime suggested here (Johnson & Albright 1991a, 1991b). During the over-wintering period more copepodid and mobile stages may survive allowing a more rapid establishment of infection each spring. Currently *L. salmonis* has a population boom in early May and declines in numbers in late October (Pike & Wadsworth 2000). Under a warmer regime with warmer springtime

temperatures the spring lice bloom may occur earlier in the year and the autumn decline push into November or even December. Such an extended season would undoubtedly lead to more clinical interventions to control lice as well as increased lice infective pressure within the environment.

Fungal disease

Like bacteria, as temperature increases the generation time of fungal organisms decreases so that, under higher temperature regimes, most fungal infections would be predicted to progress faster once the host was infected. However, as mentioned above, assuming the animal is not at its thermal limit, the fishes' immune system will be operating more effectively and may well overcome the infection.

Saprolegnia is one disease that could cause concern in a warming environment. Currently this disease occurs each spring and causes major welfare issues with parr and smolts often necessitating clinical intervention and treatment with antifungal drugs. Under warmer conditions it is feasible that *Saprolegnia* would occur earlier in the year and progress faster in infected fish (Gieseke *et al.*, 2006; Udomkusonsri & Noga 2005; Lategan *et al.*, 2004; De Canales *et al.*, 2001; Howe & Stehly 1998, Howe *et al.*, 1998 and Quiniou *et al.*, 1998) and the autumn decline in the disease would occur later in the year.

Fungal diseases exotic to Scotland becoming established is a potential concern especially as the trade in tropical ornamental fish (including goldfish, which are often cultured under warm water regimes in the Middle and Far East, China and USA) may be a source of introduction of the exotic fish fungi into the country.

Storminess. Very low confidence.

The UKCIP predictions for wind speeds are very uncertain, such that it is not possible to assign even a low confidence value to changes in wind speed. It is predicted that winter depressions will become more frequent, with deeper lows. However it is difficult to clearly predict regional effects. Based on the existing UKCIP forecasts, some areas are predicted to experience an increase (up to 10 percent) in the 20 year return period daily mean speeds in some seasons (e.g. West coast of Scotland in autumn/winter and Orkney/Shetland in summer). This represents an increase in the frequency of stormy conditions, which will have significance for the integrity of aquaculture structures and increase the risk of escapes. Mean daily wind speeds with 2 year return periods are predicted to decline over much of the West coast of Scotland during summer months. These calmer conditions are likely to have effects on planktonic communities (see below).

Harmful algal blooms. Low confidence.

Climate change is having a complex effect on phytoplankton communities. Several studies have associated rising surface temperatures with an increase in the relative abundance of flagellates and dinoflagellates (compared to **diatoms**), e.g. in the NE Atlantic (Edwards *et al.*, 2006), North Sea (Edwards & Richardson 2004), Baltic Sea (Wasmund *et al.*, 1998) and Norwegian coast (Saetre *et al.*, 2003). Both of these groups contain potentially toxic or nuisance species which can be responsible for stress or kills of cultured finfish or result in harvesting closures for shellfish growing waters. There are many complicating factors and for the regions where Scottish aquaculture is concentrated there are no accurate predictions for the future trends in the occurrence of such harmful algal blooms (HABs). Changes in precipitation will affect the salinity of coastal waters as well as the stratification of water columns and the availability of nutrients for phytoplankton growth. In addition the zooplankton communities which graze on **phytoplankton** communities have also been observed to be changing.

It is possible that the future hydrodynamic regime will favour a different planktonic community to the present. It is possible that species currently absent or rare in Scottish waters may become established and new toxic / nuisance species may pose problems for aquaculturists. The phenology (temporal patterns of occurrence) of planktonic species are also likely to be altered (Edwards & Richardson 2004), with effects on the timing and efficacy of shellfish spat fall.

Shellfish Classification. Low confidence.

Precipitation, by influencing run-off from land, has an impact on shellfish classification (determined according to the presence of enteric bacteria in cultured shellfish). Increased run-off from land where livestock faecal material is present can increase the presence of enteric bacteria in shellfish. Shellfish farmers may be prevented from selling or be required to depurate shellfish harvested from areas with a poor classification. Under a regime of reduced precipitation during summer months it is reasonable to expect that this situation will become less frequent.

Confidence assessments

'What is already happening' – Low

'What could happen in the future' - Low

We have reviewed the levels of confidence given in the 2006 report and do not feel that these warrant changing, so overall they remain 'low'. Where confidence levels are provided in the individual sections of the full review (e.g.

for direct effects of temperature increase) they are for 'what could happen in the future', not 'what is happening now'.

Knowledge gaps

Impacts of climate change on the environmental impacts of aquaculture – e.g. assimilative capacity of receiving water bodies.

Commercial impacts

Given the uncertainties associated with the predictions it is not possible to predict the economic impacts on the aquaculture industry at present.

References

Aune, A., Imsland, A.K. and Pittman, K. (1997). Growth of juvenile halibut, *Hippoglossus hippoglossus* (L.), under a constant and switched temperature regime. *Aquaculture Research* **28**(12): p. 931-939.

Benediktsdottir, E., Verdonck, L., Sproer, C., Helgason, S. and Swings, J. (2000). Characterization of *Vibrio viscosus* and *Vibrio wodanis* isolated at different geographical locations: a proposal for reclassification of *Vibrio viscosus* as *Moritella viscosa* comb. nov. *International Journal Of Systematic And Evolutionary Microbiology* **50**: p. 479-488.

Bjornsson, B. and Tryggvadottir, S.V. (1996). Effects of size on optimal temperature for growth and growth efficiency of immature Atlantic halibut (*Hippoglossus hippoglossus* L.). *Aquaculture* **142**(1-2): p. 33-42.

Bond, C.E. (1996). *The Biology of Fishes*. New York: Thomson Learning. 576.

Bowden, T.J. (2003). A study of the susceptibility of Atlantic halibut, *Hippoglossus hippoglossus* (L.), to viral haemorrhagic septicaemia virus isolated from turbot, *Scophthalmus maximus* (L.). *Journal of Fish Diseases* **26**(4): p. 207-212.

Bowden, T.J., Smail, D.A. and Ellis, A.E. (2002). Development of a reproducible infectious pancreatic necrosis virus challenge model for Atlantic salmon, *Salmo salar* L. *Journal of Fish Diseases* **25**(9): p. 555-563.

Bowden, T.J., Thompson, K.D., Morgan, A.L., Gratacap, R.M.L., Nikoskelainen, S. (2007) Seasonal variation and the immune response: a fish perspective. *Fish and Shellfish Immunology* **22**: p: 695-706.

Boxaspen, K. and Naess, T. (2000). Development of eggs and the planktonic

stages of salmon lice (*Lepeophtheirus salmonis*) at low temperatures. *Contributions to Zoology* **69**(1-2): p. 51-55.

Boxaspen, K. (1997). Geographical and temporal variation in abundance of salmon lice (*Lepeophtheirus salmonis*) on salmon (*Salmo salar* L.). *ICES Journal of Marine Science* **54**(6): p. 1144-1147.

Bricknell, I.R., Bron, J. E. and Bowden, T.J. (2006). Diseases of gadoid fish in cultivation: a review. *Ices Journal of Marine Science* **63**(2): p. 253-266.

Bruno, D.W. (2004). Prevalence and diagnosis of bacterial kidney disease (BKD) in Scotland between 1990 and 2002. *Diseases of Aquatic Organisms* **59**(2): p. 125-130.

Cano, J.M. and Nicieza, A.G. (2006). Temperature, metabolic rate, and constraints on locomotor performance in ectotherm vertebrates. *Functional Ecology* **20**(3): p. 464-470.

Claireaux, G., Webber, D.M., Kerr, S.R. and Boutilier, R.G. (1995). Physiology and behavior of free-swimming Atlantic Cod (*Gadus-Morhua*) facing fluctuating temperature conditions. *Journal of Experimental Biology* **198**(1): p. 49-60.

Clark, R.A., Fox, C.J., Viner, D. and Livermore, M. (2003). North Sea cod and climate change - modelling the effects of temperature on population dynamics. *Global Change Biology* **9**(11): p. 1669-1680.

Coyne, R., Smith, P., Dalsgaard, I., Nilsen, H., Kongshaug, H., Bergh, O. and Samuelsen, (2006). Winter ulcer disease of post-smolt Atlantic salmon: An unsuitable case for treatment? *Aquaculture* **253**(1-4): p. 171-178.

De Canales, M.L.G., Ortiz, J.B., Del Valle, M.G. and Sarasquete, C. (2001). Saprolegniasis in wild fish populations. *Ciencias Marinas* **27**(1): p. 125-137.

Drinkwater, K.F. (2005). The response of Atlantic cod (*Gadus morhua*) to future climate change. *Ices Journal of Marine Science* **62**(7): p. 1327-1337.

Duguid, J.P., Marmion, B.P. and Swain, R.H.A. (1978). *Medical Microbiology*. 13 ed. Vol. 1. Edinburgh, London and New York: Churchill Livingstone. 666.

Edwards, M. and Richardson A.J. (2004). Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* **430**, 881-884.

- Edwards, M., Johns D.G., Leterme S.C., Svendsen E. and Richardson A.J. (2006). Regional climate change and harmful algal blooms in the NE Atlantic. *Limnol. Oceanogr* **51**(2), 820-829.
- Eggset, G., Mortensen, A., Johansen, L.H. and Sommer, A.I. (1997a). Susceptibility to furunculosis, cold water vibriosis, and infectious pancreatic necrosis (IPN) in post-smolt Atlantic salmon (*Salmo salar* L.) as a function of smolt status by seawater transfer. *Aquaculture* **158**(3-4): p. 179-191.
- Eggset, G., Mikkelsen, H. and Killie, J.E.A. (1997b). Immunocompetence and duration of immunity against *Vibrio salmonicida* and *Aeromonas salmonicida* after vaccination of Atlantic salmon (*Salmo salar* L.) at low and high temperatures. *Fish and Shellfish Immunology* **7**(4): p. 247-260.
- Einer-jensen, K., Ahrens, P., Forsberg, R. and Lorenzen, N. (2004). Evolution of the fish rhabdovirus viral haemorrhagic septicaemia virus. *Journal Of General Virology* **85**: p. 1167-1179.
- Galbreath, P.F., Adams, N.D., Sherrill, L.W. and Martin, T.H. (2006). Thermal tolerance of diploid versus triploid rainbow trout and brook trout assessed by time to chronic lethal maximum. *Environmental Biology of Fishes* **75**(2): p. 183-193.
- Gieseke, C.M., Serfling, S.G. and Reimschuessel, R. (2006). Formalin treatment to reduce mortality associated with *Saprolegnia parasitica* in rainbow trout, *Oncorhynchus mykiss*. *Aquaculture* **253**(1-4): p. 120-129.
- Goniaea, T.M., Keefer, M.L., Bjornn, T.C., Peery, C.A., Bennett D.H. and Stuehrenberg, L.C. (2006). Behavioral thermoregulation and slowed migration by adult fall Chinook salmon in response to high Columbia River water temperatures. *Transactions of The American Fisheries Society* **135**(2): p. 408-419.
- Heuch, P.A., Parsons, A. and Boxaspen, K. (1995). Diel vertical migration: a possible host-finding mechanism in salmon louse (*Lepeophtheirus salmonis*) copepodids? *Canadian Journal of Fisheries and Aquatic Sciences* **52**(4): p. 681-689.
- Hirvela-Koski, V., Pohjanvirta, T., Koski, P. and Sukura, A. (2006). Atypical growth of *Renibacterium salmoninarum* in subclinical infections. *Journal of Fish Diseases* **29**(1): p. 21-29.
- Howe, G.E. and Stehly, G.R. (1998). Experimental infection of rainbow trout with *Saprolegnia parasitica*. *Journal of Aquatic Animal Health* **10**(4): p. 397-404.

- Howe, G.E., Rach, J.J. and Olson, J.J. (1998). Method for inducing saprolegniasis in channel catfish. *Journal of Aquatic Animal Health* **10**(1): p. 62-68.
- Hurst, T.P., Spencer, M.L., Sogard, S.M. and Stoner, A.W. (2005). Compensatory growth, energy storage and behaviour of juvenile Pacific halibut *Hippoglossus stenolepis* following thermally induced growth reduction. *Marine Ecology-Progress Series* **293**: p. 233-240.
- Imsland, A.K., Jonassen, T.M., Stefansson, S.O., Kadowaki, S. and Berntssen, M.H.G. (2000). Intraspecific differences in physiological efficiency of Juvenile Atlantic halibut *Hippoglossus hippoglossus* L. *Journal of the World Aquaculture Society* **31**(3): p. 285-296.
- Jacobson, K.C., Arkoosh, M.R., Kagley, A.N., Clemons, E.R., Collier, T.K. and Casillas, E. (2003). Cumulative effects of natural and anthropogenic stress on immune function and disease resistance in juvenile chinook salmon. *Journal Of Aquatic Animal Health* **15**(1): p. 1-12.
- Jarp, J., Taksdal, T. and Torud, B. (1996). Infectious pancreatic necrosis in Atlantic salmon *Salmo salar* in relation to specific antibodies, smoltification, and infection with erythrocytic inclusion body syndrome (EIBS). *Diseases of Aquatic Organisms* **27**(2): p. 81-88.
- Johnson, S.C. and Albright, L.J. (1991a). The developmental stages of *Lepeophtheirus salmonis* (Krøyer, 1837) (Copepoda, Caligidae). *Canadian Journal of Zoology* **69**(4): p. 929-950.
- Johnson, S.C. and Albright, L.J. (1991b). Development, growth, and survival of *Lepeophtheirus salmonis* (Copepoda, Caligidae) under laboratory conditions. *Journal of the Marine Biological Association of the United Kingdom* **71**(2): p. 425-436.
- Jonsdottir, H., Malmquist, H.J., Snorrason, S.S., Gudbergsson, G. and Gudmundsdottir, S. (1998). Epidemiology of *Renibacterium salmoninarum* in wild Arctic charr and brown trout in Iceland. *Journal of Fish Biology* **53**(2): p. 322-339.
- Kollner, B., Wasserrab, B., Kotterba, G. and Fischer, U. (2002). Evaluation of immune functions of rainbow trout (*Oncorhynchus mykiss*) - how can environmental influences be detected? *Toxicology Letters* **131**(1-2): p. 83-95.
- Larsson, S. and Berglund, I. (2006). Thermal performance of juvenile Atlantic salmon (*Salmo salar* L.) of Baltic Sea origin. *Journal of Thermal Biology* **31**(3): p. 243-246.

- Lategan, M.J., Torpy, F.R. and Gibson, L.F. (2004). Control of saprolegniosis in the eel *Anguilla australis* Richardson, by *Aeromonas media* strain A199. *Aquaculture* **240**(1-4): p. 19-27.
- Le Morvan, C., Deschaux, P. and Troutaud, D. (1996). Effects and mechanisms of environmental temperature on carp (*Cyprinus carpio*) anti-DNP antibody response and non-specific cytotoxic cell activity: a kinetic study. *Developmental and Comparative Immunology* **20**(5): p. 331-40.
- Levesque, H.M., Bondy, J., Short, C., Ballantyne, J.S., Driedzic, W.R. and Moon, T.W. (2005). Effects of seasonal temperature and photoperiod on Atlantic cod (*Gadus morhua*). II. Enzymes of intermediary metabolism. *Canadian Journal of Fisheries And Aquatic Sciences* **62**(12): p. 2864-2873.
- Lillehaug, A. (1997). Vaccination strategies in seawater cage culture of salmonids. *Developmental Biological Standards* **90**: p. 401-8.
- Lillehaug, A., Lunestad, B.T. and Grave, K. (2000). Epidemiology of bacterial diseases in Norwegian aquaculture - a description based on antibiotic prescription data for the ten-year period 1991 to 2000. *Diseases of Aquatic Organisms* **53**(2): p. 115-125.
- Marine Fisheries Agency (2006). UK statutory FAO aquaculture report.
- Nagai, T. and Lida, I. (2002). Occurrence of bacterial kidney disease in cultured ayu. *Fish Pathology* **37**(2): p. 77-81.
- Neat, F. and Righton, D. (2006). Warm water occupancy by North Sea cod. *Proc. Roy. Soc. B*. Submitted.
- Nordmo, R. and Ramstad, A. (1999). Variables affecting the challenge pressure of *Aeromonas salmonicida* and *Vibrio salmonicida* in Atlantic salmon (*Salmo salar* L.). *Aquaculture* **171**(1-2): p. 1-12.
- Nordmo, R., Sevattal, S. and Ramstad, A. (1997). Experimental infection with *Vibrio salmonicida* in Atlantic salmon (*Salmo salar* L.): an evaluation of three different challenge methods. *Aquaculture* **158**(1-2): p. 23-32.
- Park, K.C. and Reno, P.W. (2005). Molecular size, pH, temperature stability, and ontogeny of inhibitor(s) of infectious pancreatic necrosis virus (IPNV) in normal rainbow trout serum. *Journal of Aquatic Animal Health* **17**(2): p. 177-190.
- Piganelli, J.D., Wiens, G.D. and Kaattari, S.L. (1999). Elevated temperature treatment as a novel method for decreasing p57 on the cell surface of *Renibacterium salmoninarum*. *Diseases of Aquatic Organisms* **36**(1): p.

29-35.

Pike, A.W. and Wadsworth, S. (2000). Sealice on salmonids: their biology and control. *Advances in Parasitology* **44**: p. 233-337.

Quiniou, S.M.A., Bigler, S., Clem, L.W. and Bly, J.E. (1998). Effects of water temperature on mucous cell distribution in channel catfish epidermis: a factor in winter saprolegniasis. *Fish and Shellfish Immunology* **8**(1): p. 1-11.

Reddin, D.G., Downton, P., and Friedland, K.D. (2006). Diurnal and nocturnal temperatures for Atlantic salmon postsmolts (*Salmo solar* L.) during their early marine life. *Fishery Bulletin* **104**(3): p. 415-427.

Roberts, R.J. (1976). Bacterial diseases of farmed fishes. *Soc Appl Bacteriol Symp Ser* **4**: p. 55-62.

Rose, A.S., Ellis, A.E. and Munro, A.L.S. (1989). The infectivity by different routes of exposure and shedding rates of *Aeromonas salmonicida* subsp. *salmonicida* in Atlantic salmon, *Salmo salar* L., held in sea water. *Journal of Fish Diseases* **12**(6): p. 573-578.

Rose, G.A. (2005). On distributional responses of North Atlantic fish to climate change. *Ices Journal of Marine Science* **62**(7): p. 1360-1374.

Saetre, R., Aure, J. and Danielssen, D.S. (2003). Long-term hydrographic variability patterns off the Norwegian coast and in the Skagerrak. *ICES Marine Science Symposium* **219**, 150-159.

Skall, H.F., Olesen, N.J. and Møllergaard, S. (2005a). Prevalence of viral haemorrhagic septicaemia virus in Danish marine fishes and its occurrence in new host species. *Diseases of Aquatic Organisms* **66**(2): p. 145-151.

Skall, H.F., Olesen, N.J. and Møllergaard, S. (2005b). Viral haemorrhagic septicaemia virus in marine fish and its implications for fish farming - a review. *Journal Of Fish Diseases* **28**(9): p. 509-529.

Stangeland, K., Hoie, S. and Taksdal, T. (1996). Experimental induction of infectious pancreatic necrosis in Atlantic salmon, *Salmo salar* L, post-smolts. *Journal of Fish Diseases* **19**(4): p. 323-327.

Steine, N.O., Melingen, G.O. and Wergeland, H.I. (2001). Antibodies against *Vibrio salmonicida* lipopolysaccharide (LPS) and whole bacteria in sera from Atlantic salmon (*Salmo salar* L.) vaccinated during the smolting and

early post-smolt period. *Fish and Shellfish Immunology* **11**(1): p. 39-52.

Tackle, H., McLeod, A. and Andersen, O. (2006). Cloning and characterization of the executioner caspases 3, 6, 7 and Hsp70 in hyperthermic Atlantic salmon (*Salmo salar*) embryos. *Comparative Biochemistry and Physiology B-Biochemistry and Molecular Biology* **144**(2): p. 188-198.

Udomkusonsri, P. and Noga, E.J. (2005). The acute ulceration response (AUR): A potentially widespread and serious cause of skin infection in fish. *Aquaculture* **246**(1-4): p. 63-77.

Van Muiswinkel, W.B. and Wiegertjes, G.F. (1997). Immune responses after injection vaccination of fish. *Developmental Biological Standards* **90**: p. 55-7.

Wasmund, N, Nausch, G. and Matthaus, W. (1998). Phytoplankton spring blooms in the Southern North Sea. Spatio-temporal development and long term trends. *J. Plankton Res* **20** 1099-1117.