Fishing, climate change and north-east Atlantic cod stocks

by Nova Mieszkowska. David Sims and Steve Hawkins May 2007 Marine Biological Association of the UK, Plymouth

This report summarises research on past and present states of north-east Atlantic cod stocks, with particular focus on the North Sea regional stocks. The relative effects of fishing pressure and climate change are examined, and the many ways in which the climate can directly and indirectly affect stock success are highlighted. The interaction between these two stressors on the North Sea cod populations is explained and recommendations made for the future assessment and management of North Sea cod stocks in the light of continued climate change.

NORTH-EAST ATLANTIC COD STOCKS

In the north-east Atlantic, cod occurring south of 62° North are assessed and managed as six separate stocks: East Baltic, West Baltic, West Scotland, Irish Sea, Celtic Sea and North Sea¹. Microsatellite markers also reveal significant genetic differences at the regional scale between cod populations in the North Sea and Baltic Sea², and between populations in the central English Channel, Celtic Sea, Outer Hebrides and southern and northern North Sea³. Genetically distinct sub-populations have also been identified along the Norwegian coast⁴.

Overall, there is a pattern of increasing genetic differences as distance between capture locations increases. This suggests that many stocks should be treated as distinct but interbreeding units. Such spatially separated populations are likely to have different behavioural and life history strategies, including growth and mortality rates, age and size at maturation, and fecundity (potential reproductive capacity)⁴. Body mass at particular ages varies greatly between these stocks, and exhibits year-to-year variation within populations, resulting in direct consequences for stock assessment and catch forecasting¹.

Migration of cod between different fisheries management areas is well established in the literature reviewed. Individuals are known to migrate across large areas of sea between Iceland and Greenland stocks⁵; there is some mixing between the North Sea, Skagerrak and Kattegat stocks⁶ and Arcto-Norwegian and Barents Sea stocks⁷. Transport of larvae between spawning grounds (e.g. the North Sea and Skagerrak^{8,9}) also occurs via currents.

Electronic tagging devices placed on individual cod have shown that migratory behaviour is different for fish from separate stocks. Individuals tagged in the North Sea have been tracked over both long¹⁰ and short distances, despite North Sea cod being considered as several separate stocks¹¹. By contrast, movement of fish between geographically separated populations in the Irish Sea and North Sea is very low^{12,13}. Movement of individuals has been related to temperature differences between feeding and spawning grounds⁷ or current patterns⁷.

Tagging studies have also highlighted the difference in seasonal activity between distinct stocks in the Irish Sea and North Sea, which could be behavioural responses to variations in the distribution and abundance of prey species between the different seas¹⁴. The extent of migration in cod appears highly variable, and may be linked to changes in both climate and fishing pressure. It is estimated that in the 1970s, 50 million fish migrated from Greenland to Iceland each year to spawn^{6,15}. Juvenile survival within the Greenland stock has been very low during the last two decades¹⁵ and resultant return migration to the Icelandic stock appears to have declined significantly as a result⁶.

FISHING PRESSURE

An unexploited fish population will reach a level that reflects the carrying capacity of the environment¹⁷. The structure of such a population in its age profile and sex ratio leads to maximum reproductive potential, enabling sustained recruitment in the face of ecological variation. Removal of large fish from the population via intensive fishing mortality leads to lower recruitment (breeding rates). This in turn leads to fewer, smaller, less mature fish.





(a) (b)

Figure 1. Marine Biological Association trawl in 1963 (a) and 2001 (b) showing fewer larger species of fish such as skate, ray, brill and conger eel.

Over time fish can show evolutionary responses including earlier maturation at smaller sizes, leading to further reductions in fecundity^{18,19}. Thus long-term removal of large quantities of adults can reduce the overall resilience of the stock and reduce stock sustainability. Cod are no exception: from the mid-1960s to the mid-1980s landings of cod in the North Sea increased in response to several strong year classes that occurred during a period of cooler climatic conditions. Since the 1980s, average catches of north-east Atlantic cod have remained at 200,000 tonnes per year²⁰ despite variations in recruitment, and there has been a subsequent decline in abundance ¹⁸. This decline has coincided with the onset of rapid climate warming, and it is possible that climate change will exert additional pressures on already stressed stocks. Causes and mechanisms responsible for fluctuations in fish stock biomass remain poorly identified²¹, so it is imperative that increased research effort is made into the relative effects of overfishing and climate change on fish stocks around the UK.

CLIMATE CHANGE

Climate change has many impacts on the seas and the species that live in them. These include increases in sea temperature, changes in salinity, alterations in ocean currents and more extreme storm events^{24,80}. The climate of the north-east Atlantic has been warming since the mid-1980s in response to anthropogenic inputs of greenhouse gases into the atmosphere. The rate and scale of change is greater than any previous natural fluctuations over the last 1,000 years²². Climate is predicted to continue warming throughout the coming century at rates equal to or greater than the current rate of increase^{23,24}. Global climate models have forecast further warming of 0.5°C to 1°C (depending on emissions scenario) in seas around Britain during the 21st century (Figure 2), although regional models predict even greater rises in areas such as the English Channel, which may warm by as much as 4°C.

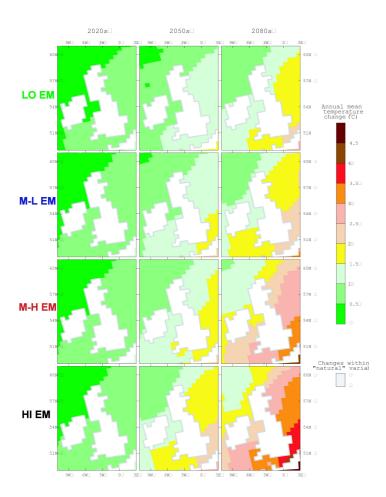


Figure 2. UCKIP annual mean sea surface temperature predictions under low, medium and high scenarios for the 21st century (reproduced from Hulme et al. 2002).

PREVIOUS RESPONSES TO CLIMATE BY NORTH-EAST ATLANTIC FISH STOCKS

The effects of climate change on fish populations are diverse³⁶. There is increasing evidence that global climate change has impacted upon marine fish populations via direct and indirect effects of changes in sea temperature³³. Changes in pelagic species have long been linked to climate; an example being fluctuations between herring and pilchard (sardine) occurring in the western English Channel as long ago as the Middle Ages³⁷⁻⁴⁰. Similarly for demersal fish, the "gadoid outburst" in the North Sea occurred despite increased fishing mortality between the 1960s and 1980s^{15,21} and was driven by an increase in cod recruitment during an episode of cooler climatic conditions.

Cod have been shown to respond to climate change. The North Atlantic warmed during the 1920s and 1930s, and a subsequent increase in abundance of cod was seen in West Greenland stocks at the northern end of their range. Towards the north of their range, increased recruitment also occurred off the coast of Iceland and increases in abundance and a northward expansion of cod were observed in the Barents Sea during this period (Brander et al., 2006). Recruitment of the Arcto-Norwegian cod stock has been shown to have responded positively to higher temperatures in various ways throughout the 20th century: strong year classes occurred in warmer years, particularly at the beginning of warm periods because of increased gonad production⁴¹. Icelandic cod inhabit warmer water masses than the Arcto-Norwegian, Greenland and North Sea stocks, and the positive response in recruitment for this stock to increased temperatures is lower, but still evident⁴². The Icelandic stock showed strong recruitment more frequently in years of strong influence by Atlantic water masses and absence of severe ice conditions in the north⁴². Towards the southern limit in the Bristol Channel, which is a nursery ground for many demersal species, cod have increased in abundance with rising mean annual sea surface temperatures⁴³, demonstrating that climate warming does not always have a detrimental effect on stock size for this species, even towards the south of its range in contrast to the North Sea.

DIRECT EFFECTS OF TEMPERATURE

Temperature impacts directly on all life-stages of fish, from production for sperm and eggs to spawning, growth, metabolism and activity of the larval, juvenile and adult stages. Cod have been shown to have certain temperature preferences within the habitat of a specific stock unit – a relationship that has been apparent for more than 100 years⁷. Some of the clearest signals of environmentally driven stock fluctuations are seen in recruitment data for different fish populations¹⁷.

North Atlantic cod recruitment correlates with sea temperature at the species' limits of distribution⁴², but stocks show different recruitment responses to changes in temperature depending on their location. Stocks towards the northern limits of the range, which occupy waters of lowest temperature, show a general increase in recruitment in response to warming sea temperatures. An example is the northern North Sea, where recruitment levels have been seen to increase in some years with warmer temperatures⁴². However, more recent studies have shown

¹ The gadoid outburst was a sudden, huge increase in stocks of cod and related species (e.g. haddock) that occurred in response to a switch to cooler climatic conditions in the North Sea between the 1960s and 1980s.

very poor recruitment in warm years during the late 1990s⁴⁴. Stocks near to southern limits that experience higher ambient temperatures show a general decrease in recruitment in response to warming waters. Cod in the Irish and Celtic seas are living close to their upper temperature limits, and recruitment in these areas is lower sea surface temperature (SST) becomes warmer⁴². Mid-range stocks show no significant relationship with temperature^{7,42,45}. Recruitment between 1954 and 1958 was inversely proportional to SST in the mid North Sea⁴⁶. Recruitment is low where the temperature in the first half of the year is high²⁰, whereas cold temperatures can result in both high and low recruitment. It is important to note that such spatial variation in reproductive investment can complicate medium-term stock projections¹⁸.

As fishing pressures have already led to cod maturing when younger and at smaller sizes, increasing sea temperatures may have a doubly negative impact on the species. Temperature rises increase stress during reproduction – an activity that requires more energy⁵² as food limitation causes declines in growth at optimal temperatures⁵³, and resultant declines in survival and recruitment (growth-dependent mortality)⁵⁴.

INDIRECT EFFECTS OF CLIMATE

Temperature rises in the north-east Atlantic are associated with huge changes in the distribution and availability of the main prey species of cod juveniles. The coldwater copepod *Calanus finmarchicus* is a major biomass component of zooplankton within the North Atlantic and is the major prey species for larval and pelagic juvenile fish in the north-east Atlantic^{1,70}. It has moved 1000km north since the 1980s and is replaced in part by a warmer water species *Calanus helgolandicus*. Overall, however, there is half as much *Calanus* productivity than in the cooler years of the 1960s.

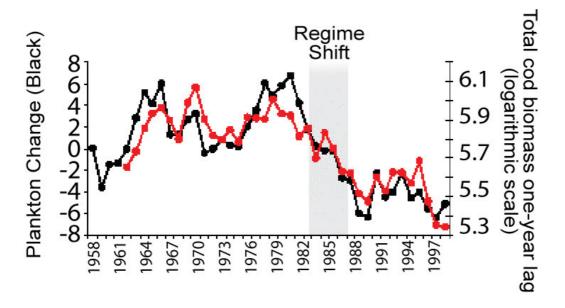


Figure 3. Changes in zooplankton (black line) and cod biomass (red line). Sir Alister Hardy Foundation for Ocean Science.

In the North Sea, long-term changes in cod recruitment vary significantly with changes in zooplankton with a one-year time lag (Figure 3). Survival, as measured by an index of the stock-recruitment relationship, is seen to correlate positively with the plankton index, and both indicate that changes in plankton affect the survival of cod larvae and juveniles²⁶. During the cooler period between 1963 and 1983, there was a high abundance of zooplankton prey for larval cod and the prey had a high mean size. The results showed that high cod recruitment years (1963-1983) coincided with increases in *Calanus finmarchicus*, A shift in dominance from the coldwater copepod *C. finmarchicus* to the warm-water species *C. helgolandicus* over the second half of the 20th century has been linked to subsequent declines in cod recruitment Such fluctuations follow changes in SST in the North Sea²⁶.

When the dynamics of prey species are also incorporated into stock models, further differences in recruitment and SSB are suggested⁷¹. Decreases in recruitment of one-year-old cod and subsequent declines in SSB appear to be associated with both climate warming and the levels of sandeel landings in the central North Sea. Cod recruitment is positively correlated to sandeel recruitment, emphasising the importance of understanding interspecific interactions.

Climate can also act indirectly via large-scale atmosphere/ocean coupling, dispersal of eggs and larvae within current systems, changes in turbulence, the timing and abundance of food supply, and levels of predation^{6,26,55}. The spatial extent of trends in recruitment regulation for cod, haddock and herring stocks across the North Atlantic suggests that the driving force is operating over a large area rather than through local biological interactions⁵⁶. This may be due to the direct effects of climate, or climate-driven changes in biological systems.

The North Atlantic Oscillation (NAO) is the main index of winter atmospheric circulation over the North Atlantic. During positive NAO years, warmer, wetter winters occur and seawater temperatures are warmer around the UK. When the NAO switches to a negative phase, winter SST around the British coastline are colder^{34,37,57}. Over the last 25 years the frequency and magnitude of NAO positive-index events have increased and winter sea surface temperatures have become milder in British coastal waters. The NAO is predicted to remain in a positive phase in coming decades.

Relationships between the NAO index with the physical environment and biological responses of the ocean's ecosystems have been well established^{33,57-60}. The index has been linked to changes in recruitment success of most cod stocks in this region³², particularly via the direct effects of environmental temperature on larval and juvenile growth and survival⁶¹⁻⁶³. When all north-east Atlantic cod stocks are combined within a single recruitment model, a significant geographic pattern between the strength of the NAO and recruitment is evident, with stock-specific trends emerging⁶⁴.

Several studies show that environmental conditions during a positive NAO index have a mostly negative influence on southern stocks and positively influences northern stocks on both seaboards of the Atlantic^{64,65}. These studies draw contrasting conclusions from the stock-recruitment model results published by Brander⁶⁶. Brander's model indicates that recruitment within European shelf-sea stocks is more strongly affected by environmental fluctuations when their spawning stock biomass is low⁶⁶. The confounding results may be due to differences in methodology used by Stige et al.⁶⁴, or they may reflect true biological changes. If the findings of

Brander et al.⁶⁶ are an accurate reflection of the north-east Atlantic ecosystem, climate warming is likely to hamper stock recovery from heavy fishing pressure, but is not the driving force behind the recent decline in North Sea cod stocks. Comparisons of such studies highlight the difficulty in predicting the effects of climatic variability on SSB and recruitment success.

Many responses of marine ecosystems to ocean climate variability are complex and not fully understood because of interactions between different levels of the food chain⁶⁹. Long-term changes in cod recruitment may be controlled by plankton fluctuations because of matches or mismatches in relationships between predators and prey²⁶. Indirect effects via the timing, location, magnitude and size of zooplankton production²⁶ may therefore exert a controlling influence on stock size and success.

Given the underlying positive mode trend of the NAO since the 1970s, the long-term prognosis is poor for recruitment success in north-east Atlantic populations¹. However, the strength of positive NAO events has been declining since the 1990s⁶⁷. A weakening of the connection between the NAO and spring stratification in the northern North Sea has been observed since 1990, influencing the timing of the spring phytoplankton bloom and having a knock-on effect for the survival of juvenile fish⁶⁸. The relationship between the strength and phase of the NAO and SST has begun to decouple since 2000 due to an eastward shift in the Icelandic low-pressure and Azores high-pressure centres. If this pattern continues, the NAO index may not be the most suitable proxy for examining the future effects of climatic variables on marine fish.

INTERACTIONS BETWEEN CLIMATE CHANGE AND FISHING

Sustainability of harvesting is largely determined by relating SSB and survival of recruits on entering the fishery⁵¹. Although climate change is likely to enhance the decline in recruitment success of fish stocks, the underlying reduction in spawning stock biomass in UK coastal waters is being driven by fishing pressure⁴⁵. Changes in environmental temperature may, however, prevent recruitment reaching levels as high as recorded in the cooler 1960s and 1970s, even if spawning stock biomass were to rebuild to the high levels of those periods²⁰.

North Sea cod now mature at a smaller size and at a younger age than in 1970 and are more reproductively active earlier. Inshore cod are also more reproductively active at a given size or age in comparison with offshore cod – a spatial trend not apparent in 1970^{18,19}. This has not been consistent with changes in growth conditions; therefore there may have been genetic changes in life history traits because of intense periods of size-selected mortality, most likely due to fishing pressure¹⁸. However, it is not possible to make a quantitative assessment of the relative contribution of fishing and climate to most previous fisheries collapses, as the factors interact and insufficient data on both drivers is available from this period⁷².

The complex behaviour of fish and the interactions between fishing pressure and climate change are highlighted in a study carried out on potential changes in the latitudinal distribution of a suite of commercial species in the North Sea. The study concluded that the ranges of most fish were shifting north in response to a warming climate⁷³. The findings were taken from fisheries landings data and were based on the assumption that greatest numbers of fish occur in the central area of a species' geographical distribution^{29,74}. Brown's rule has recently been questioned^{75,76} as many species are not in fact found in greatest abundances at the centre of their

geographic distribution. With regard to fish, there are complex patterns of aggregation in spawning, feeding or nursery grounds in many areas throughout their geographic range that are thus likely to invalidate Brown's rule.

CONCLUSIONS

Cod stocks in the north-east Atlantic, especially the North Sea, have been impacted upon heavily owing to sustained overfishing by modern fleets. It seems unlikely that global climate warming is the primary factor causing the decline in fish numbers, but evidence suggests that this phenomenon may be exerting additional pressures on already overexploited stocks by further reducing recruitment rates that are already low due to reduced SSB. Indirect effects of climate change on the availability of prey for juvenile fish are predicted to be detrimental to the recovery of fish stocks, and current climate conditions are likely to drive this decline in suitable prey supply for the foreseeable future. Temperature effects on cod growth, reproduction and recruitment will cause significant effects that require consideration when making stock assessments and catch forecasts, and predicting the future responses of fish to climate change. Knowledge of the basic biological and physical processes alone limit our ability to understand how cod stocks respond to pressures from overfishing and climate change. This data must be combined with accurate fisheries landing data in a holistic approach in order to fully understand the synergistic effects of climate and fishing on the ecosystem^{1,7}.

There is a need to take precautionary measures to give stocks a chance to rebuild⁷⁷⁻⁷⁹. Although climate change appears to be one of the factors responsible for non-recovery of cod in the North Sea, fisheries are no longer sustainable at the present level of fishing effort. Future policy must take both factors into account when deciding upon sustainable stock quotas⁷⁹. It is also imperative that we act to reduce greenhouse gas emissions to prevent further acceleration in the rate of global warming and reduce the future impacts of climate change and subsequent effects on fish stocks.

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REFERENCES

- 1. Brander, K.M., 1995. The effect of temperature on growth of Atlantic cod (*Gadus morhua* L.). ICES Journal of Marine Science 52: 1-10.
- 2. Nielsen, E.E., Hansen, M.M., Schmidt, C., Meldrup, D. & Grønkjær, P., 2001. Population origin of Atlantic cod. Nature 413: 272.
- 3. Hutchinson, W.F., Carvalho, G.R. & Rogers, S.I., 2001. Marked genetic structuring in localized spawning populations of cod Gadus morhua in the North Sea and adjoining waters, as revealed by microsatellites. Marine Ecology Progress Series 223: 251-260.

- 4. Salvanes, A.G.V., Skjæraasen, J.E. & Nilsen, T., 2004. Sub-populations of coastal cod with different behaviour and life-history strategies. Marine Ecology Progress Series 267: 241-251.
- 5. ICES Cooperative Research Report 2000. Report of the ICES Advisory Committee on Fishery Management (ICES Copenhagen). www.ices.dk/
- 6. Chen, Q., Chan, K.S., Lekve, K., Torstensen, E., Gjøsæter, Ottersen, G. & Stenseth, N.C., 2005. Population dynamics of cod *Gadus morhua* in the North Sea region: biological density-dependent and climatic density-independent effects. Marine Ecology Progress Series 302: 219-232.
- 7. Sundby, S., 2000. Recruitment of Atlantic cod stocks in relation to temperature and advection of copeopod populations. Sarsia 85: 277-298.
- 8. Munk, P., Larsson, P.O., Danielsen, D. & Moksness, E., 1995. Larval and small juvenile cod Gadus morhua concentrated in the highly productive areas of a shelf break front. Marine Ecology Progress Series 125: 21-30.
- 9. Munk, P., Larsson, P.O., Danielsen, D. & Moksness, E., 1999. Variability in frontal zone formation and distribution of gadoid fish larvae at the shelf break in the northeastern North Sea. Marine Ecology Progress Series 177: 221-233.
- 10. Gulland, J.A. & Williamson, G.R., 1962. Transatlantic Journey of a Tagged Cod. Nature 195: 921.
- 11. Bedford, B.C., 1966. English cod tagging experiments in the North Sea. ICES CM 1966/G:9.
- 12. Robichaud D. & Rose G.A., 2002. The return of cod transplanted from a spawning ground in southern Newfoundland. ICES Journal of Marine Science 59: 1285-1293.
- 13. Knutsen, H., Jorde, P. E., André, C., Stenseth, N. CHR., 2003. Fine-scaled geographical population structuring in a highly mobile marine species: the Atlantic cod. Molecular Ecology 12: 385-394.
- 14. Righton, D., Metcalfe, J. & Connolly, P., 2001. Different behaviour of North and Irish Sea cod. Nature 411: 156-158.
- 15. ICES 2002. Workshop on the transport of cod larvae. ICES CM C:13:45.
- 16. Davies, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B., & Wood, S., 1998. Making mistakes when predicting shifts in species range in response to global warming. Nature 391: 783-786.
- 17. Cushing, D., 1995. Population production and regulation in the sea: a fisheries perspective. 1-354. Cambridge University Press.
- 18. Yoneda, M. & Wright, P.J., 2004. Temporal and spatial variation in reproductive investment of Atlantic cod *Gadus morhua* in the northern North Sea and Scottish west coast. Marine Ecology Progress Series 276: 237-248.
- 19. Barot, S., Heino, M., O'Brien, L. & Dieckmann, U., 2004. Long-term trend in the maturation reaction norm of two cod stocks. Ecological Applications 14: 1257-1271.
- 20. O'Brien, C.M., Fox, X.J., Planque, B. & Casey, J., 2000. Climate variability and North Sea cod. Nature 404: 142.
- 21. Pope J.G. & Macer C.T., 1996. An evaluation of the stock structure of North Sea cod, haddock, and whiting since 1920, together with a consideration of the impacts of fisheries and predation effects on their biomass and recruitment. ICES Journal of Marine Science 53:1157-1169.
- 22. Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J., Dai, X., Maskell, K. & Johnson, C.A, ed., 2001. Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change, 1 edn, pp 873. Cambridge University Press, Cambridge, New York.
- 23. Hulme, M., Jenkins, G.J., Lu, X., Turnpenny, J.R., Mitchel, I.T.D., Jones, R.G., Lowe, J., Murphey, J.M., Hassel, I.D., Boorman, P., McDonald, R., & Ed, H.S., 2002. Climate Change Scenarios for the United Kingdom: The UKCIP02 Scientific Report. Tyndall Centre for Climate Change Research, School of Environmental Sciences, University of East Anglia, Norwich.
- 24. IPCC, 2007. Climate Change 2007: The Physical Science Basis. Summary for Policymakers: 1-21.
- 25. Beaugrand, G., Reid, P.C., Ibanez, F., Lindley, J.A., & Edwards, M., 2002. Reorganization of North Atlantic Marine Copepod Biodiversity and Climate. Science 296: 1692-1694.

- 26. Beaugrand, G., Brander, K.M., Lindley, J.A., Souissi, S. and Reid, P.C., 2003. Plankton effect on cod recruitment in the North Sea. Nature 426: 661-664.
- 27. Edwards M. & Richardson, A.J., 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature 430: 881-884.
- 28. Mieszkowska, N., M.A. Kendall, S.J. Hawkins, R. Leaper, P. Williamson N.J. Hardman-Mountford & A.J. Southward, 2006. Changes in the range of some common rocky shore species in Britain a response to climate change? Hydrobiologia 555: 241-251.
- 29. Brown, J.H., Stevens, G.C., & Kaufman, D.M., 1996. The geographic range: size, shape, boundaries and internal structure. Annual Review of Ecology and Systematics 27: 597-623.
- 30. Pearson, R.G. & Dawson, T.P., 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography 12: 361-371.
- 31. Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Guldberg, O.H. & Bairlein, F., 2002. Ecological responses to recent climate change. Nature 416: 389-395.
- 32. Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P.C. & Stenseth, N.C., 2001. Ecological effects of the North Atlantic Oscillation. Oecologia 128: 1-14.
- 33. Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K.S. & Lima, M., 2002. Ecological effects of climate fluctuations. Science 297: 1292-1296.
- 34. Walker, G.T. & E.W. Bliss, 1932. World Weather V, Memoirs of the Royal Meteorological Society 4:53-84.
- 35. Bertness, M.D., Leonard, G.H., Levine, J.M., & Bruno, J.F., 1999. Climate-driven interactions among rocky intertidal organisms caught between a rock and a hot place. Oecologia 120: 446-450.
- 36. FSBI, 2007. Climate change and the fishes of Britain and Ireland: Briefing Paper 4. Fisheries Society of the British Isles, Granta Information Systems, Cambridge, UK.
- 37. Van Loon, H. & J.C. Rogers, 1978. The Seesaw in Winter Temperatures between Greenland and Northern Europe. Part I: General Description. Monthly Weather Review 106: 296–310.
- 38. Southward, A.J., Boalch, G.T. & Maddock, L., 1988. Fluctuations in the herring and pilchard fisheries of Devon and Cornwall linked to change in climate since the 16th Century. Journal of the Marine Biological Association of the United Kingdom 68: 423-445.
- 39. Southward, A.J., Langmead, O., Hardman-Mountford, N.J., Aitken, J., Boalch, G.T., Dando, P.R., Genner, M.J., Joint, I., Kendall, M.A., Halliday, N.C., Harris, R.P., Leaper, R., Mieszkowska, N., Pingree, R.D., Richardson, A.J., Sims, D.W., Smith, T., Walne, A.A., & Hawkins, S.J., 2005. Long-term oceanographic and ecological research in the western English Channel. Advances in Marine Biology 47: 1-105.
- 40. Hawkins, S.J., Southward, A.J. & Genner, M.J., 2003. Detection of environmental change in a marine ecosystem evidence from the Western English Channel. Science of the Total Environment 310: 245-256.
- 41. Sætersdal, G. & Loeng, H., 1987. Ecological adaptation of reproduction in Northeast Arctic cod. Fisheries Research 5: 253-270.
- 42. Planque, B. & Fredou, T., 1999. Temperature and the recruitment of Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 56: 2069-2077.
- 43. Genner, M.J., Sims, D.W., Wearmouth, V.J., Southall, E.J., Southward, A.J., Henderson, P.A., & Hawkins, S.J., 2004. Regional climatic warming drives long-term community changes of British marine fish. Proceedings of the Royal Society London, Series B 271: 655-661.
- 44. Turrell, B., 2006. Climate change and Scottish fisheries. Fisheries Research Services Collaborative Report No 12/06: 1-28.
- 45. Ottersen, G. & Sundby, S., 1995. Effects of temperature, wind and spawning stock biomass on recruitment of Arcto-Norwegian cod. Fisheries Oceanography 4: 278-292.
- 46. Dickson, R.R., Pope, J.G. & Holden, M.J., 1974. Environmental influences on the survival of North Sea cod. In: Blaxter, J.H.S., (editor). The early life history of fish: proceedings of an international symposium held at the

Dunstaffnage Marine Research Laboratory of the Scottish Marine Biological Association at Oban, Scotland, from May 17-23, 1973. p.69-80. Springer-Verlag.

- 47. Reznick, D.A., Bryga, H. & Endler, J.A., 1990. Experimentally induced life-history evolution in a natural population. Nature 346: 357-359.
- 48. Law, R., 1979. Optimal Life Histories Under Age-Specific Predation. The American Naturalist 114: 399-417.
- 49. Graham, M., 1923. The annual cycle in the life of the mature cod in the North Sea. Fishery Investigations Series II. Marine Fisheries GB, Ministry of Agriculture Fisheries and Food 6. HMSO London.
- 50. Rijnsdorp, A.D., Daan, N., van Beek, F.A. & Heessen, H.J.L., 1991. Reproductive variability in North Sea plaice, sole, and cod. Journale du Conservation et Internationalle Exploration de Mar 47(3): 352-375.
- 51. Cook, R.M., Sinclair, A. & Stefánsson, G., 1997. Potential collapse of North Sea cod stocks. Nature 385: 521-522.
- 52. Otterleigh, E., Nyhammer, G., Folkvord, A. & Stefansson, S.O., 1999. Temperature- and size-dependent growth of larval and early juvenile Atlantic cod (*Gadus morhua*): a comparative study of Norwegian coastal cod and northeast Arctic cod. Canadian Journal of Fisheries and Aquatic Sciences. 56: 2099-2111.
- 53. Swain, D.P., Sinclair, A.F., Castonguay, M., Chouinard, G.A., 2003. Density versus temperature-dependent growth of Atlantic cod (*Gadus morhua*) in the Gulf of St Lawrence and on the Scotian Shelf. Fisheries Research 59: 327–341.
- 54. Gallego, A. & Heath, M., 1997. The effect of growth-dependent mortality, external environment and internal dynamics on larval fish otolith growth: an individual-based modelling approach. Journal of Fish Biology 51: 121–134.
- 55. Sundby, S. & Fossum, P., 1990. Feeding conditions of Arcto-norwegian cod larvae compared with the Rothschild-Osborn theory on small-scale turbulence and plankton contact rates. Journal of Plankton Research 12: 1153-1162.
- 56. Koslow, J.A., 1984. Recruitment patterns in northwest Atlantic fish stocks. Canadian Journal of Fisheries and Aquatic Sciences 41: 1722-1729.
- 57. Hurrell, J.W., & van Loon H., 1997. Decadal variations in climate associated with the North Atlantic Oscillation. Climatic Change 36: 301-326.
- 58. Reid, D.G., 2001. SEFOS-shelf edge fisheries and oceanography studies: an overview. Fisheries Research 50:1-
- 59. Sims, D.W., Genner, M.J., Southward, A.J., Hawkins, S.J., 2001. Timing of squid migration reflects North Atlantic climate variability. Proceedings of the Royal Society B 268: 2607-2611.
- Southward, A.J., 1980. The Western English Channel an inconstant ecosystem? Nature 285: 361-366.
- 60. Pingree, R. D., 2002. Ocean structure and climate (Eastern North Atlantic): in situ measurement and remote sensing (altimeter). Journal of the Marine Biological Association of the UK 82:681-707.
- 61. Ottersen, G., Loeng, H. & Raknes, A., 1994. Influence of temperature variability on recruitment of cod in the Barents Sea. ICES marine science symposia. Copenhagen 1994.
- 62. Dippner, J.W., 1997. Recruitment success of different fish stocks in the North Sea in relation to climate variability. Deutsche Hydrographich Zeitschrifte 49: 277-293.
- 63. Attrill, M.J. & Power, M., 2002. Climatic influence on a marine fish assemblage. Nature 417: 275-278.
- 64. Stige, L.C., Ottersen, G., Brander, K., Chan, K.S. & Stenseth, N.C., 2006. Cod and climate: effect of the North Atlantic Oscillation on recruitment in the North Atlantic. Marine Ecology Progress Series 325: 227-241.
- 65. Brander, K. & Mohn, R., 2004. Effect of the North Atlantic Oscillation on recruitment of Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 61: 1558-1564.
- 66. Brander, K.M., 2005. Cod recruitment is strongly affected by climate when stock biomass is low. ICES Journal of Marine Science 62: 339-343.
- 67. National Oceanographic and Atmospheric Administration, National Weather Service Climate Prediction Centre. www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml

- 68. Sharples, J., Ross, O.N., Scott, B.E., Greenstreet, S.P.R. & Fraser, H., 2006. Inter-annual variability in the timing of stratification and the spring bloom in the North-western North Sea. Continental Shelf Research 26: 733-751.
- 69. Cushing, D. & Dixon, R.R., 1976. Biological and hydrographic changes in British waters during the last 30 years. Biological Reviews 42: 221-258.
- 70. Sysoeva, T.K. & Degtereva, A.A., 1965. The relation between feeding of cod larvae and pelagic fry and the distribution and abundance of their principal food organisms. ICED Special Publication 6: 411-416.
- 71. Bromley, P.J., 2004. The use of ecosystem indices to investigate the decline of recruitment and spawning stock biomass in North Sea cod (*Gadus morhua* L.). ICES ASR, Vigo, Spain 2004.
- 72. Brander, K., Ottersen, G., Wieland, K. & Lilly, G., 2006. Decline and recovery of North Atlantic cod stocks. GLOBEC international newsletter October 2006: 10-13.
- 73. Perry, A., Low, P.J., Ellis, J.R., & Reynolds, J.D., 2005. Climate change and distribution shifts in marine fishes. Science 308: 1912-1915.
- 74. Brown, J.H., 1984. On the relationship between abundance and distribution of species. American Naturalist 124: 255-279.
- 75. Sagarin, R.D., Gaines, S.D. & Gaylord, B., 2006. Moving beyond assumptions to understand abundance distributions across the ranges of species. Trends in Ecology and Evolution 21: 524-30.
- 76. Gilman, S., 2005. A test of Brown's principle in the intertidal limpet *Collisella scabra* (Gould,1846). Journal of Biogeography 32: 1583-1589.
- 77. Longhurst, A., 1998. Ecological geography of the sea. xiii, 398p. Academic Press.
- 78. ICES Cooperative Research Report 1999. Report of the ICES Advisory Committee on Fishery Management (ICES Copenhagen). www.ices.dk/
- 79. ICES 2006. Cooperative Research Report 2006. Incorporation of Process Information into Stock-Recruitment Models. CRR 282. www.ices.dk/
- 80. Baker, T. 2005. Vulnerability Assessment of the North East Atlantic Shelf Marine Ecoregion to Climate Change. Pp 1-77. www.wwf.org.uk/filelibrary/pdf/climatechangeandseas01.pdf