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Resolving the effect of climate change on fish populations

Adriaan D. Rijnsdorp, Myron A. Peck, Georg H. Engelhard, Christian Möllmann, and John K. Pinnegar

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This paper develops a framework for the study of climate on fish populations based on first principles of physiology, ecology, and available observations. Environmental variables and oceanographic features that are relevant to fish and that are likely to be affected by climate change are reviewed. Working hypotheses are derived from the differences in the expected response of different species groups. A review of published data on Northeast Atlantic fish species representing different biogeographic affinities, habitats, and body size lends support to the hypothesis that global warming results in a shift in abundance and distribution (in patterns of occurrence with latitude and depth) of fish species. Pelagic species exhibit clear changes in seasonal migration patterns related to climate-induced changes in zooplankton productivity. Lusitanian species have increased in recent decades (sprat, anchovy, and horse mackerel), especially at the northern limit of their distribution areas, while Boreal species decreased at the southern limit of their distribution range (cod and plaice), but increased at the northern limit (cod). Although the underlying mechanisms remain uncertain, available evidence suggests climate-related changes in recruitment success to be the key process, stemming from either higher production or survival in the pelagic egg or larval stage, or owing to changes in the quality/quantity of nursery habitats.

Keywords: climate change, eco-physiology, ecosystem, fish, population dynamics.

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A. D. Rijnsdorp: Wageningen IMARES (Institute for Marine Resources and Ecosystem Studies), PO Box 68, 1970 AB IJmuiden, The Netherlands, and Aquaculture and Fisheries Group, Department of Animal Science, Wageningen University, PO Box 338, 6700 AH, Wageningen, The Netherlands. M. A. Peck and C. Möllmann: Institute of Hydrobiology and Fisheries Science, University of Hamburg, Olbersweg 24, 22767 Hamburg, Germany. G. H. Engelhard and J. K. Pinnegar: Centre for Environment, Fisheries and Aquaculture Science, Pakefield Road, Lowestoft NR33 0HT, England, UK. Correspondence to A. D. Rijnsdorp: tel: +31 317 487191; fax: +31 317 487326; e-mail: adriaan.rijnsdorp@wur.nl.

Introduction

Resolving the effect of climate change on fish populations is complicated, because climate change affects a multitude of environmental factors that may affect various processes at different levels of biological organization (Harley *et al.*, 2006; Lehodey *et al.*, 2006; Tasker, 2008). For example, even if the effect of changes in an environmental factor on the physiology of an organism is known, it will be difficult to evaluate the outcome of this organism-level physiological response at the population or ecosystem level (MacKenzie and Köster, 2004). Statistical analysis of available time-series revealed changes in distribution and abundance of fish species that correlate with environmental variables (Perry *et al.*, 2005; Weijerman *et al.*, 2005; Heath, 2007). However, statistical correlations do not necessarily indicate underlying processes (Köster *et al.*, 2005).

It may be argued that it will be impossible to detect generalities in the response of fish populations to climate change, because the number of influential factors is too large and individual species may differ too widely in their response. Nevertheless, we believe that it is possible to derive common patterns by developing hypotheses about the effect of climatic factors (abiotic variables) on fish populations, based on first principles and by taking account of different levels of biological organization (from cellular- and organism-level eco-physiology to population- and

ecosystem-level responses; Figure 1). In this paper, we (i) review the environmental variables and oceanographic features relevant to fish that are most likely to be affected by climate change, (ii) derive theoretical expectations from first principles and physiological and ecological theory, (iii) derive working hypotheses for future research, and (iv) review the empirical evidence from a selection of well-studied species in the Northeast Atlantic ecosystems against such a theoretical background.

Effects of climate change on the abiotic marine environment

The effects of climate change are expected to differ in both magnitude and direction among geographic areas (IPCC, 2007). Northern high-latitude areas will experience the largest increase in air temperature associated with the melting of sea ice (ACIA, 2004). Intermediate increases in air temperature are expected for the northern Nordic, Barents, and Baltic Seas, and the smallest increases are expected in more southern areas, including the North and Mediterranean Seas. Ocean temperature will follow increases in air temperature, although to a lesser extent, owing to the high heat storage capacity of water masses. Shallow areas will exhibit larger increases in sea temperatures than deeper waters. In western Europe, the frequency of very cold winters and of very hot summers is expected to decrease and increase,

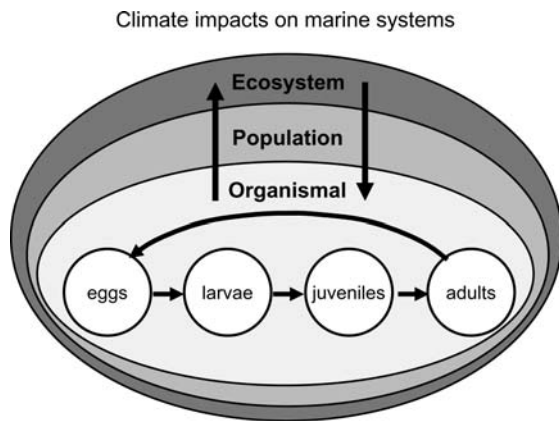


Figure 1. Climate change will affect fish populations on all levels of organization.

respectively (Hulme *et al.*, 2002). Changes in the strength and prevailing direction of wind over European marine areas remain uncertain, although the expectation is that there will be an increase in average and extreme windspeeds over northern Europe (Hulme *et al.*, 2002). Precipitation and river run-off are expected to increase in northern Europe and decrease in southern Europe (Frei *et al.*, 2006). In addition, the seasonality of run-off will change, increasing in winter, but decreasing in spring in northwestern Europe. In warmer regions, such as the Mediterranean, differences in the magnitude of river run-off between winter and summer will increase (IPCC, 2007).

Climate change will affect a range of abiotic factors that are tightly linked to the production and distribution of fish populations, and these climate-driven biotic changes will likely differ between the open ocean, shelf seas, and coastal waters (Walther *et al.*, 2002; Lehodey *et al.*, 2006). Although the importance of the various environmental factors varies regionally, some general conclusions can be reached. Temperature, because of its pervasive effect on organisms, is important in all regions. Stratification (resulting from the interplay between temperature and windforcing) will also be an important factor in all regions, owing to the effect of stratification on the vertical structure of marine ecosystems and on bottom-up processes. Changes in wind strength and direction not only influence mixing and water circulation in the open ocean, but also affect the strength of upwelling within shelf and coastal regions. Sea ice is only of direct relevance in the more northern regions, such as the Barents and Baltic Seas. In general, changes in salinity will have less of a direct effect upon most organisms, although salinity is a very important abiotic factor in the Baltic, where it affects the buoyancy of eggs and early life stages of the prey species of fish (MacKenzie *et al.*, 2007). The increase in carbon dioxide emissions has resulted in an increase in CO₂ concentrations in the oceans (IPCC, 2007), reducing oceanic pH and changing the saturation horizons of aragonite, calcite, and other minerals essential to calcifying organisms (Feely *et al.*, 2004).

Climate change and effects on fish populations and exploited ecosystems: theoretical expectations

Fish have complex life cycles, comprising several distinct life-history stages (egg, larva, juvenile, and adult; Figure 1), each of which may be affected in different ways by climate change. Over

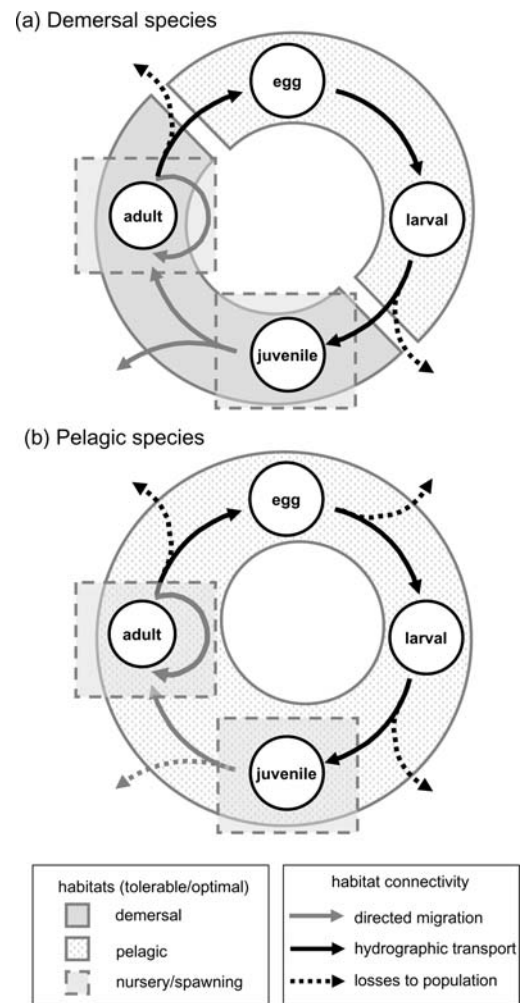


Figure 2. Complex life cycle and life-cycle closure of (a) demersal and (b) pelagic fish species. Fish life-history stages inhabit different habitats and demonstrate ontogenetic niche shifts. Pelagic fish remain in the pelagic habitat throughout their life cycle, but stages may inhabit different water masses. Demersal fish are characterized by a pelagic egg and/or larval stage and a demersal juvenile and adult stage. At major habitat shifts, individuals may be lost (vagrants, dashed arrows). Relative habitat size may differ among the stages and may form a bottleneck in determining population abundance.

their lifespan, fish typically increase in body size by a factor of 10^5 (Rothschild, 1986), and successive life-history stages may require spatially separated habitats. A prerequisite for population persistence is connectivity among habitats required by successive life stages, allowing the survivors to mature and return to the spawning grounds to reproduce successfully (Figure 2; life-cycle closure: Sinclair, 1988). Within these stage-specific habitats, fish must experience suitable abiotic conditions, find food for growth, and find shelter to escape from predation or disease. Demersal and pelagic species differ in their habitat requirements. Pelagic species remain within the three-dimensional pelagic habitat (although some species, such as herring, require specific demersal habitats for spawning), whereas demersal species display a distinct transition from the three-dimensional pelagic realm of (eggs and) larvae to the two-dimensional habitat of the demersal stages. During their life-history transitions, augmented

through hydrographic transport or directed migration, animals may be lost from the population (dashed arrows in Figure 2). Because the life cycle is embedded in a geographical setting, the size of the various habitats differs, which could result in bottlenecks at specific life-history stages (dashed squares in Figure 2).

Climate-driven changes in fish populations may result from four, often interlinked, mechanisms: (i) a physiological response to changes in environmental parameters, such as temperature, (ii) a behavioural response, such as avoiding unfavourable conditions and moving into new suitable areas, (iii) population dynamics, through changes in the balance between rates of mortality, growth, and reproduction in combination with dispersal, which could result in the establishment of new populations in new areas, or abandonment of traditional sites, (iv) ecosystem-level changes in productivity and/or trophic interactions. In addition, (v) commercial exploitation greatly affects the abundance and distribution of fish and may interact with the effects of climate change. In the following sections, we expand upon each of these five themes with regard to potential climate effects to derive a suite of testable hypotheses.

Physiological response

At the individual level, direct changes in the environmental factors (such as local temperatures) will invoke changes in physiological rates. Insight regarding such eco-physiological responses will be crucial to interpret the mechanisms underlying observed changes in distribution or patterns of behaviour. Species can only tolerate a specific range of environmental conditions that, among other factors, places constraints upon their range of distribution. Fry (1971) proposed how different environmental factors can load metabolic costs and affect the metabolic scope. Recently, Pörtner and Knust (2007) demonstrated that the partial oxygen pressure (PO_2) within blood provided a direct measure of metabolic scope (Figure 3). Low levels of blood PO_2 outside of pejus temperatures (pejus = getting worse) reflect the reduction in aerobic scope, limiting the energy available for activity, growth, reproduction, and other vital rates. Pejus temperatures are not fixed, but can be modified to some extent by population-specific adaptation to local environmental conditions (arrows in Figure 3). Differences

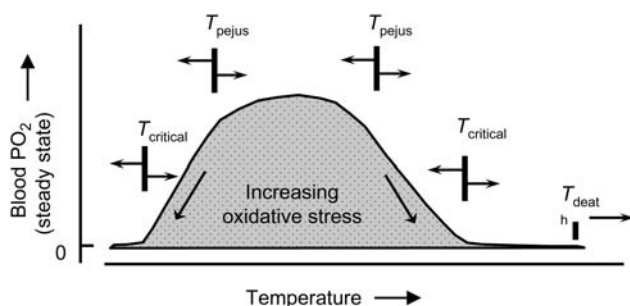


Figure 3. At the cellular level, optimal and suboptimal temperatures are reflected by changes in the rates of aerobic and anaerobic metabolism. Optimal temperatures coincide with the highest levels of PO_2 . Pejus temperatures (T_{pejus}) denote the onset of limits in aerobic scope and increased energy demands. Critical temperatures are those where aerobic scope is zero, anaerobic metabolism is measurable and, at the upper $T_{critical}$, cellular-level stress proteins are produced. At higher temperatures (T_{death}), denaturation and death occur. Arrows denote population-specific adaptation (after Pörtner and Knust, 2007).

exist in the tolerance of extreme temperatures within species (e.g. related to differences in acclimation) and/or between species (differences in thermal physiology). For example, a review of the upper and lower lethal temperatures of various marine fish species indicated that thermal tolerance changed markedly with latitude (MAP, unpublished data). The range of tolerable temperatures was narrower in fish inhabiting high and low latitudes and wider for fish inhabiting intermediate latitudes (MAP, unpublished data). Although caution must be taken not to oversimplify the estimates of thermal preference gauged from fish in the field (because other environmental factors can modify preferred temperatures), patterns of change in tolerance may give a first approximation of the relative effects of climate-driven temperature changes (Figure 4a). The relationship also allows us to use the geographical distributions of species (Arctic, Boreal, Lusitanian, Tropical, Atlantic) as a classification scheme to evaluate the expected response.

There is evidence of an ontogenetic shift in temperature tolerance of a species (Figure 4b), such that optimum temperatures for growth decrease with increasing body size of juveniles and adults (Fonds *et al.*, 1992; Imsland *et al.*, 1996; Yamashita *et al.*, 2001;

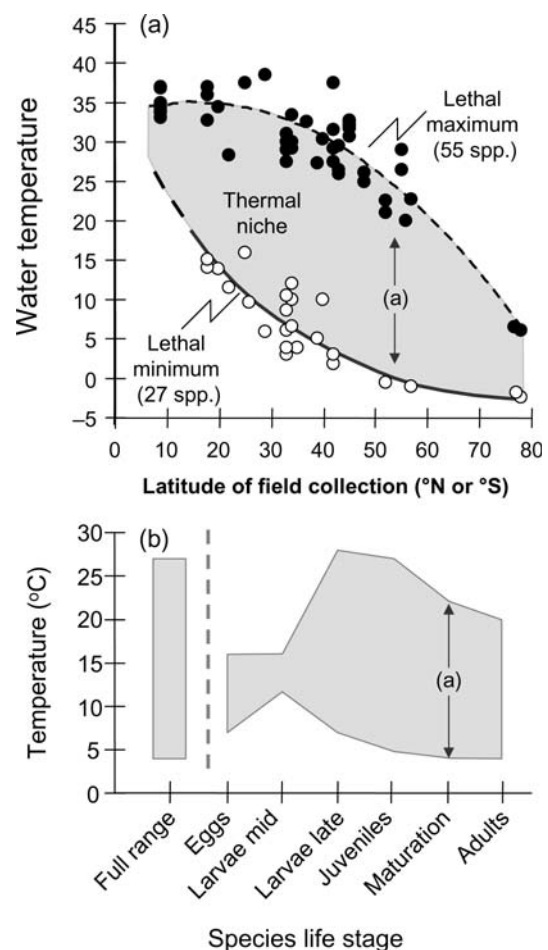


Figure 4. Conceptual diagram of the changes in suitable habitats (based on water temperature) with (a) latitude of the species and/or population and (b) by life stage. The arrow (a) denotes a range of tolerable temperatures measured for adults during maturation and spawning. Data in a and b are from MAP (unpublished data) and Irvin (1974).

Peck *et al.*, 2003; Pörtner and Farrel, 2008). This mechanism can explain the ontogenetic shift in habitats observed in several fish species where young stages occur in shallower waters than older, larger stages (Heincke's Law; Heincke, 1913). In some species, eggs and larvae have been observed to have a narrower range of tolerable temperatures than other life-history stages (specifically juveniles) making these early life stages more vulnerable to changes in temperature (Irvin, 1974; Pörtner and Farrel, 2008). If this is a general phenomenon, it may provide a powerful basis for predicting the potential response of a species to changes in temperature, but further research is needed to test its generality. The sensitivity of larval stages to climate change may be further increased, because of their small body size, which will make them less capable of selecting and migrating towards a suitable habitat, and because of their reasonably high (mass-specific) metabolic rates and lower energy reserves. This will make them more vulnerable to mortality during periods of adverse environmental condition, such as periods of food shortage.

Several authors have stated that marine fish are likely to be less affected by an increase in oceanic CO₂ and a corresponding decrease in pH compared with invertebrate groups, such as molluscs and corals (Feely *et al.*, 2004; Orr *et al.*, 2005; Fabry *et al.*, 2008). However, laboratory studies have revealed that manipulation of pH and CO₂ can have dramatic consequences on the physiology, metabolism, and reproductive biology of fish, with egg fertilization and survival of early developmental phases being primarily affected (Ishimatsu *et al.*, 2005).

It is worth noting that responses at higher levels of organization (population, community, and ecosystem) to climate change are ultimately driven via differences in physiological responses that affect trophodynamic relationships. For example, physiological responses to a change in temperature can differ between primary, secondary, and tertiary consumers, thereby influencing trophic coupling (Freitas *et al.*, 2007) via changes in productivity or phenological shifts and match–mismatch dynamics (Cushing, 1990).

Behavioural response

Organism-level responses, such as changes in behaviour, can result from changes in key abiotic factors, such as temperature or O₂, but the presence (and/or strength) of the response will depend on the ability of the animal to detect environmental gradients and navigate accordingly. In contrast to early feeding larvae of tropical marine fish, which can exhibit reasonably strong swimming capacity (Leis, 2006), larvae of most temperate marine fish species have no, or very limited, swimming ability. Temperate marine fish larvae can respond to reasonably intense environmental signals (e.g. turbulence avoidance; Franks, 2001), but have little capacity to avoid unfavourable environments that requires swimming over large (km) distances.

In later (juvenile and adult) life stages, individual fish can clearly respond to a change in temperature (Woodhead, 1964; Berghahn, 2000) and often exhibit active temperature preference (Tsuchida, 1995). Some elasmobranchs are extremely sensitive to temperature variation (e.g. they can respond to changes of <0.001°C; Brown, 2003) and some sharks move to deeper water before the onset of severe storms (Heupel *et al.*, 2003). Naturally, even for individuals in these later life stages that have strong swimming capacity, knowledge of the location of optimal habitats will not be perfect. Field studies on thermal habitats revealed that fish may inhabit and occupy areas with suboptimal

temperatures even if areas with more optimal temperatures are within reach (Neat and Righton, 2007), but optimal habitats will also be determined by other factors such as food. Behavioural changes can have unexpected consequences. For example, because of an increase in temperature, fish swimming speed increases (Peck *et al.*, 2006). In addition, fish can behave differently in response to oncoming fishing gear making them more (or less) vulnerable to capture (Winger, 2005). Finally, at longer temporal scales, climate-driven changes in temperature can modify the phenology of annual migrations to feeding and/or spawning grounds, as already observed (Carscadden *et al.*, 1997; Sims *et al.*, 2004), and predicted (Huse and Ellingsen, 2008), for temperate marine species. It can be inferred that the behavioural response to changes in environmental conditions will depend on the rate of change and/or the spatial scale over which conditions change relative to fish body size or developmental stage because the capacity for avoidance responses increases with increasing body size.

Population dynamic response

Productivity of fish populations, in terms of biomass, is determined by recruitment, growth, and mortality. Most commercial species are broadcast spawners producing millions of eggs (Rothschild, 1986). Mortality rates of early life-history stages are very high and variable, generating large fluctuations in annual recruitment. Relatively small changes in growth and mortality rates during the egg and larval phases can have a large effect on the recruitment success of populations (Figure 5; Houde, 1987). Because the early life-history stages are likely to be more sensitive

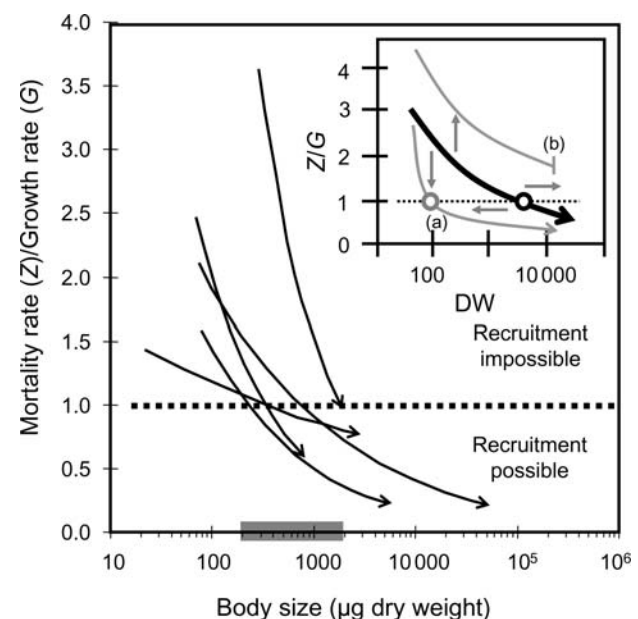


Figure 5. Population-level effects of climate: relationship between the ratio of individual growth rate (G , % d^{-1}) and mortality rate (Z , % d^{-1}). Increase in the biomass of cohorts and successful recruitment is only possible when $Z/G < 1.0$. Body sizes at which this occurs differ among species. The grey area denotes the range of trajectories calculated for early life stages of five marine fish species by Houde (1987). A variety of responses to climate change is possible. The critical body size (size at $Z/G = 1.0$) (a) may shift or (b) recruitment may fail, represented when Z/G is always > 1 .

to climate change (see the section on “Behavioural response”), we expect that climate change will have a major effect on the distribution and abundance of fish through its influence on recruitment. The mechanism will be either the match–mismatch between the timing of reproduction relative to the production of larval food and/or predators (Cushing, 1990; van der Veer *et al.*, 2000; Platt *et al.*, 2003; Temming *et al.*, 2007), or the connectivity (retention or transport) between spawning and nursery areas (Sinclair, 1988; Wilderbuer *et al.*, 2002).

Interstock comparisons indicated a dome-shaped pattern in the relationship between recruitment strength and spawning temperature experienced during the spawning season, with maximum recruitment at an intermediate temperature in cod and sprat (Brander, 2000; MacKenzie and Köster, 2004). In cod, this temperature was close to the optimal temperature for larval growth (Brander, 2000). However, the effects of climate on recruitment are not limited to processes acting during the egg and larval stages, but may extend to later (juvenile and adult) life stages. For example, year-class strength in sprat appears to be established during the post-larval or juvenile period (Köster *et al.*, 2003), and low growth rates and poor condition of juvenile sprat can result from top-down control of their zooplankton prey resources (Baumann *et al.*, 2007).

Productivity will also be influenced by the effect of temperature on growth rate (Brander, 1995; Teal *et al.*, 2008). In a comparative study of 15 cod stocks, sevenfold differences in the productivity among stocks corresponded to the differences in the temperature of the environment (Dutil and Brander, 2003). Fish species are generally plastic in their age and size at sexual maturity. An increase in juvenile growth, as well as an increase in temperature, may result in a decrease in the length and/or age of first maturation, affecting growth of adults as surplus energy is channelled into reproduction at an earlier age and/or smaller size (Heino *et al.*, 2002).

Mortality may be high when temperature conditions reach extreme values. Low temperatures during winter may increase mortality, especially of smaller fish that have reasonably fewer energy reserves compared with larger conspecifics (Post and Evans, 1989; Sogard, 1997). During severe winters in the North Sea, high mortality has been reported for Lusitanian species, such as sole and conger eel, but only rarely for Boreal species, such as cod, plaice, and dab (Woodhead, 1964). Mortality may also be high during hypoxic (or anoxic) conditions, as has been reported for the Kattegat (Diaz, 2001). Although mass mortalities during summer in relation to harmful algal blooms (Yin *et al.*, 1999; Heil *et al.*, 2001) have been reported elsewhere, no records are known for the Northeast Atlantic. Climate change may have the most dramatic (negative) effects on the productivity of fish populations by increasing the frequency of these “episodic” extreme events.

For some broadcast spawning fish species, there is evidence that the size of populations is determined by the size and availability of spawning and/or nursery habitats (Rijnsdorp *et al.*, 1992; Gibson, 1994; Sparholt, 1996; MacKenzie *et al.*, 2000). Limits on the availability of these habitats may act as a bottleneck for population size (and/or productivity). In these cases, the focus should be on the effect of climate change on the critical life-history stage(s). Whether this relationship is applicable will depend on the relative size of the habitat in relation to that of other life-history stages and is determined by the specific geographic setting.

Life-cycle closure may be affected if climate change influences the connectivity between the habitats of successive life-history

stages (Sinclair, 1988). For instance, changes in ocean climate may affect the transport of eggs and larvae between the spawning grounds and the nursery areas (Corten, 1986; van der Veer *et al.*, 2000; Wilderbuer *et al.*, 2002), or the climate effect on the timing of spawning migrations may influence the arrival of the adults at the spawning grounds (Sims *et al.*, 2004).

Ecosystem response

Climate change can affect all trophic levels of marine ecosystems, eventually resulting in changes in the productivity and distribution of fish stocks. On the lower trophic levels, climate is expected to affect primary and secondary productivity through its effect on physiological rates of species, the availability of nutrients (upwelling or stratification), and the advection of water into shelf areas and enclosed basins. On a qualitative level, the increase in average and extreme winds over European marine areas may increase upwelling, enhance primary production, and eventually increase fish productivity (Dickson *et al.*, 1988; Jahncke *et al.*, 2004; Rykaczewski and Checkley, 2008). A further effect will be the translocation of deep-water species into shelf seas (Blanchard and Vandermeersch, 2005). Within shelf areas, increased warming will result in earlier water mass stratification (if not balanced by increased wind-mixing), which will affect the timing of the spring bloom and the level and composition of primary production. Primary productivity may also be influenced by changes in precipitation and river run-off. In areas where coastal production is enhanced by nutrient input (from either organic matter or nutrients through rivers), changes in precipitation will likely affect coastal fish production. Hence, an increase in river run-off into the Bay of Biscay may enhance the productivity of sole, whereas a decrease in run-off into the Mediterranean Sea could result in a decrease in the productivity of sole in that region (Salen-Pickard *et al.*, 2002; Le Pape *et al.*, 2003; Darnaude *et al.*, 2004).

Climate-driven changes in the level of primary productivity will likely be accompanied by phenological changes that affect lower trophic level coupling and eventually the recruitment success of marine fish (Cushing, 1990). Changes in phenology and a resulting trophic mismatch have been reported for the North Atlantic plankton community where the level of response differs throughout the community and the seasonal cycle, resulting in a mismatch between trophic levels and functional groups (Beaugrand *et al.*, 2003; Platt *et al.*, 2003; Edwards and Richardson, 2004). This trophic mismatch can finally affect fish stock recruitment, as reported for the North Sea cod/*Calanus finmarchicus* interaction (Durant *et al.*, 2005). To some extent, biophysical modelling approaches can be used to identify “mediator chains” (Dippner, 2006) describing how climate-induced changes in physical factors (e.g. stratification) are propagated up the foodweb to affect processes (e.g. match–mismatch dynamics) important to the survival of marine fish (Daewel *et al.*, 2008a, b).

Beyond a strict bottom-up control, a number of different control patterns exists within foodwebs (i.e. top-down and wasp-waist controls) and climate-induced changes will depend on the prevailing control pattern, illustrated in Figure 6, making it challenging to predict how climate change will affect marine fish stocks within those foodwebs (Stenseth *et al.*, 2002; Jennings *et al.*, 2008). There is a continuing discussion on whether ecosystems are primarily regulated by bottom-up or top-down processes (Frank *et al.*, 2007). The traditional view in marine ecology of a bottom-up control (Strong, 1992) is supported by a number of

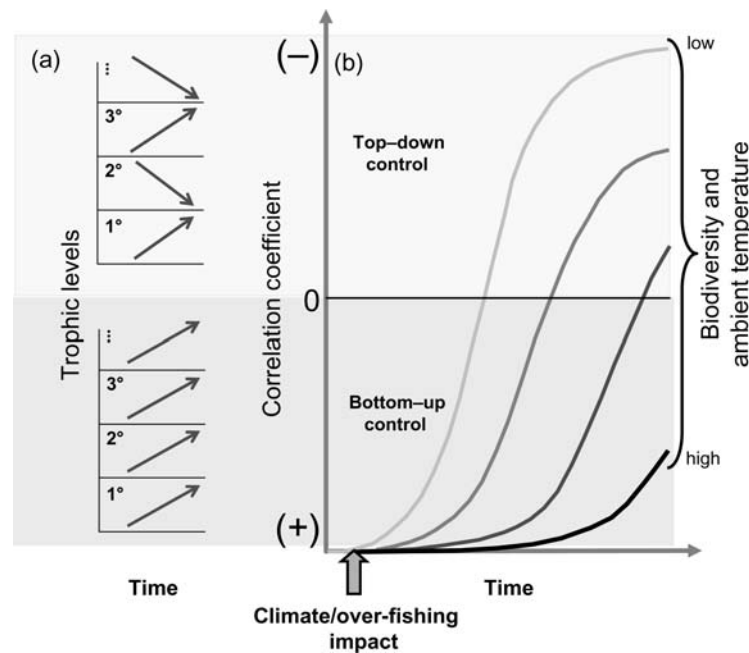


Figure 6. (a) Propagation of climate-induced changes at the bottom of the foodweb depends on dominance of bottom-up control (lower panel) or a top-down-induced cascade pattern (upper panel); (b) schematic on a potential control change in the upper trophic levels of marine ecosystems (y-axis: moving correlation between two trophic levels, positive correlation coefficients indicating bottom-up control, negative coefficients indicating top-down control). Overfishing and/or climate change (arrow) may induce a change from the original state, i.e. bottom-up control (Strong, 1992) to top-down control, potentially inducing multilevel trophic cascades. The velocity and strength of the change, i.e. the vulnerability of an ecosystem for a control change, depends on the level of biodiversity and the ambient temperature (Frank *et al.*, 2007; Litzow and Ciannelli, 2007).

recent studies (Ware and Thomson, 2005; Greene and Pershing, 2007). Other studies, however, suggest that the dominance of bottom-up control can switch to top-down control, resulting in trophic cascades initiated by overfishing (Worm and Myers, 2003; Frank *et al.*, 2005; Daskalov *et al.*, 2007; Möllmann *et al.*, 2008). Moreover, recent studies emphasize the simultaneous importance of both climate- (bottom-up) and fisheries-induced (top-down) effects in marine ecosystem reorganizations (Möllmann *et al.*, 2008, 2009). The strength of these processes also appears to depend on foodweb complexity and thermal conditions (Frank *et al.*, 2007), and may oscillate between bottom-up and top-down controls (Hunt *et al.*, 2002; Hunt and McKinnell, 2006). The control change can be triggered by both climate changes and overfishing (Litzow and Ciannelli, 2007; Casini *et al.*, 2008a, b). Therefore, predicting the effect of climate changes on marine ecosystem development, and hence the productivity of different fish stocks, particularly in light of the additional (interacting) pressure of exploitation, will be a grand challenge for the future (Greene and Pershing, 2007).

Effects of fishing

Fisheries might interact with climate change in causing changes in fish populations, through various mechanisms. Climate change could affect the distribution of particular species and hence their susceptibility to particular fishing fleets, becoming more or less “catchable” as a result. Similarly, climate-related distribution shifts may affect the protective capabilities of closed-areas, because species or life stages may shift outside the boundaries of the protected area and hence become vulnerable to fishing (e.g. the North Sea Plaice Box—Van Keeken *et al.*, 2007).

Extensive fishing may cause fish populations to become more vulnerable to short-term natural climate variability (O’Brien *et al.*, 2000; Walther *et al.*, 2002; Beaugrand *et al.*, 2003; Anderson *et al.*, 2008), by making such populations less able to “buffer” against the effects of the occasional poor year classes. During recent decades, there has been a clear, positive correlation between temperature and recruitment in Northeast Arctic cod; however, this link was weak or non-existent in earlier periods (Ottersen and Stenseth, 2001). A major implication is that fishery-induced impoverishment of stock structure (reduced and fewer ages and smaller sizes) can increase the sensitivity of a previously “robust” stock to climate change (Ottersen *et al.*, 2006). Conversely, long-term climate change may make stocks more vulnerable to fishing, by reducing the overall carrying capacity of the stock, such that it might not be sustained at, or expected to recover to, levels observed in the past (Jennings and Blanchard, 2004).

Fishing will have a major influence on the size structure and species composition of fish assemblages and thus will affect predator–prey relationships (Rice and Gislason, 1996; Daan *et al.*, 2005). Fishing will interact with global warming, because body size generally increases with latitude (Belk and Houston, 2002) and small fish species may take advantage of the removal of the larger predatory fish (Daan *et al.*, 2005). Fishing may also affect ecosystem control causing bottom-up systems to become top-down controlled systems (see the section “Ecosystem response”). How climate change will interact with fishing will depend on the species affected and eventually on the prevailing patterns of ecosystem structure and function (Heath, 2005). Hence, the response of ecosystems under climate and fishing pressure is currently difficult to predict.

Working hypotheses

The response of fish populations to climate change will differ between species. The difference may be related to their adaptations to the environmental conditions in their respective habitats. As such, the biogeographic affinities of the species may be used as a proxy for the expected response to a change in temperature [see Yang (1982) on biogeographic affinities of North Sea fish species]. Populations living at the border of the distribution range are expected to live close to the limits of their range of physiological tolerance, so will be more vulnerable to changes in abiotic conditions than populations living in the centre of the distribution area (Miller *et al.*, 1991). Because water temperature is correlated with water depth, fish may move into deeper water during summer to avoid the warmer water in shallow areas (Dulvy *et al.*, 2008). This leads to the first set of working hypotheses:

H1a: Populations at the limits of their latitudinal range will exhibit stronger responses than those occurring within habitats in the centre of their latitudinal distribution;

H1b: Northerly species at the southern limits of their distribution will decrease in abundance and southerly species will increase at their northern limit;

H1c: Northerly species are expected to retreat into deeper, cooler waters, in response to an increase in surface water temperature.

We expect that the response of species to climate change will be influenced by their habitat requirements (pelagic, demersal, and deep-water species), life-history characteristics (short- or long-lived; specialist or generalist), and trophic position within the ecosystem (apex predators or forage fish). Although many “pelagic” fish species have early life stages residing in the “demersal” habitats and vice versa, fish that are strictly pelagic (all life stages) inhabit water masses with certain abiotic conditions that may change in their spatial distribution, due to climate change, whereas strictly demersal fish may have specific habitat requirements that are geographically fixed owing to seabed characteristics. Environmental conditions tend to be more unvarying at greater depths, although deep-water fish may be influenced indirectly by changes in productivity above them (food availability) and by changes in deep-water currents. Generalists can adapt to the prevailing patterns of food availability, whereas specialists are strongly dependent on the prospects of particular prey organisms. Short-lived species characterized by high reproductive rates (so-called *r*-strategists) are likely to track the changes in their environment relatively rapidly, whereas the responses of long-lived species (*K*-strategists) will be slower (Perry *et al.*, 2005). The ability to track the changes in their environment will apply to an improvement and a deterioration of the environmental conditions. This leads to the following hypotheses:

H2a: Pelagic and demersal species will differ in their responses, because the former can more easily follow changes in water masses than the latter, which have more geographically fixed habitat requirements;

H2b: Deep-water fish species may be less affected by climate change than shelf or coastal species;

H2c: Fish species with narrow dietary preferences will be more sensitive to climate change, than generalists;

H2d: Short-lived species will exhibit stronger responses and will be better equipped to adapt to changes in their environment than long-lived species.

Populations can survive in systems where suitable habitats for the different life-history stages are available and are connected, allowing life-cycle closure (Sinclair, 1988). If the habitat for a certain life-history stage is spatially restricted, a change in habitat suitability of this stage will make the species more sensitive to climate change than those that do not have spatially restricted habitat requirements. Populations living in areas with a large heterogeneity in environmental conditions, or that migrate over large distances, will more likely be able to survive by selecting the appropriate environments than those living in large areas with a more homogeneous environment. This leads to the following hypotheses:

H3a: Species with spatially restricted habitat requirements during part of their life history will be more sensitive to climate change than those without specific habitat requirements;

H3b: Fish populations in oceanographic systems with a high variety of mesoscale features will display less influence of climate change.

Fishing will reduce the size and age structure of a population and reduce its bet-hedging capabilities that would allow it to track conditions suitable for the survival of eggs and larvae (Rothschild, 1986; Ottersen *et al.*, 2006). In addition, fishing may result in a reduction in genetic variability, which would negatively affect the possibilities of an evolutionary response to climate change and the ability of depleted stocks to recover (Anderson *et al.*, 2008).

H4: Fish stocks under intense exploitation will be more vulnerable to climate change than those experiencing low fishing pressure.

The ecosystem response to climate change will depend on the response of the individual species and the resulting effect on trophodynamic interactions among species. Different species within a foodweb will not all respond in the same way to climate change. Species-rich systems, characterized by many weak, readily interchangeable feeding links, rather than a few strong links, are likely to be more stable, because different species may take over vacant ecological functions (Link, 2002) and may be more resilient (Frank *et al.*, 2007) in the face of climate change. Climate change will not necessarily result in gradual and predictable changes in fish populations and ecosystem state. Ecosystems may exhibit multiple stable equilibria and climate change may push systems into a new equilibrium (Scheffer and Carpenter, 2003). Once a “regime shift” has occurred, it may be disproportionately difficult to return to the original state (Beauprand, 2004; Daskalov *et al.*, 2007; Möllmann *et al.*, 2008).

H5a: Ecosystems with simple trophic structure will exhibit more rapid responses to climate change than ecosystems with more complex trophic structure;

H5b: Changes in ecosystem structure caused by climate change may be abrupt.

The introduction of non-native species to a marine ecosystem, and their subsequent establishment, may cause effects that range from almost undetectable to catastrophic (e.g. the complete domination and displacement of native communities; Eno *et al.*, 1997). Improved environmental conditions, as well as new shipping routes, will facilitate the spread of warm-water fish species and pathogens. New species may be introduced to the Arctic, because of ice-free shipping routes (ACIA, 2004), and further colonization of the Mediterranean Sea by tropical species might be anticipated, because of the Suez Canal.

H6: Because of improved local conditions, an increased number of exotic warm-water fish species (and fish pathogens) will become established in European waters.

Observed changes in distribution and abundance

In this section, changes in distribution, abundance, and growth of a selection of fish species in the northeastern Atlantic are reviewed (Table 1) against the background of the above working hypotheses. Species were selected for which sufficient data were available (commercial species) and that represented different “ecotypes” combining the biogeographic affinity (Lusitanian, Boreal, Atlantic), habitats (pelagic or demersal; Atlantic or shelf), and longevity (short, medium, long).

Changes in abundance and distribution of northeastern Atlantic marine species support hypothesis 1. Lusitanian species have increased in recent decades (sprat, anchovy, and horse mackerel), especially at the northern limit of their distribution areas, while Boreal species generally decreased at the southern limit of their distribution range (cod and plaice), but increased at the northern limit (cod). A shift in distribution to deeper waters was recorded in the Boreal species cod and plaice (Hedger *et al.*, 2004; Perry *et al.*, 2005; van Keeken *et al.*, 2007; Dulvy *et al.*, 2008).

Comparison of the changes in distribution between pelagic and demersal species provides support for hypothesis 2. For the pelagic species, changes in distribution patterns have been observed that are related to climate-induced changes in the distribution of their food (herring: Toresen and Østvedt, 2000; Corten, 2001a, b; horse mackerel: Borges *et al.*, 1996; Iversen *et al.*, 2002; mackerel: Reid *et al.*, 2001; ICES, 2007). Changes in plankton have been linked to changes in climate (Beaugrand *et al.*, 2002; Richardson and Schoeman, 2004). A comparison between demersal and pelagic species tentatively suggests that changes in the distribution of the former are smaller than those of the latter. The northward shifts in cod have been related to the transport of eggs and larvae, but not to a northward movement of the demersal stages (Rindorf and Lewy, 2006).

With regard to the underlying mechanisms, the available evidence suggests that the observed changes in productivity are at least in part related to a climate-related change in recruitment (herring, anchovy, sprat, cod, plaice, and sole), either owing to higher production or survival in the egg or larval stage (herring, anchovy, sprat, cod) or to a change in the quality/quantity of the nursery habitat (plaice and sole). In sole and plaice, there is evidence that the timing of spawning is influenced by the temperature during the spawning period (Teal *et al.*, 2008). In the western Atlantic, such an effect is also reported for cod (Hutchings and Myers, 1994). The negative relationship between recruitment and temperature in sole in the North Sea contrasts with the expected positive relationship in this Lusitanian species.

Temperature-related changes in growth have been reported for cod (Brander, 1995; Dutil and Brander, 2003) and 0-group sole and plaice (Teal *et al.*, 2008). The mean length of sole, a Lusitanian species, has increased in autumn, because of an increase in growth rate, and there has also been an increase in the length of the growing season. However, no change in mean length was observed in plaice, a Boreal species that exhibited an increased growth rate early in the season, but reduced growth rate during summer when temperature exceeded their optimal temperature. Growth rate of older age groups of sole and plaice exhibited a dome-shaped pattern since the late 1950s, with relatively high growth rates between the mid-1960s and the mid-1980s, which were not correlated with changes in temperature (Millner and Whiting, 1996; Rijnsdorp and van Leeuwen, 1996). The available data do not allow a quantitative comparison of the relative effects of the climate-induced changes in recruitment and in juvenile and adult growth rates on productivity. The results of the selected species did not allow hypotheses 3–5 to be tested.

With regard to the hypothesis about invasive species (H6), there is strong evidence that increasing connectivity between geographically distinct areas may result in major changes in ecosystems. The opening of the Suez Canal in 1869 allowed entry of Indo-Pacific and Red Sea biota into the southeastern Mediterranean Sea, where these so-called lessepsian migrants now dominate the fish community (50–90% of fish biomass). For many decades, this migration was very limited, partly because of extremely high salinity within the Suez Canal, where dry salt valleys had existed previously. With a warming trend of the seawater and a significant drop in the Canal's salinity to “normal” marine levels (Mavruk and Avsar, 2007), record numbers of newly established non-native fish species have been observed recently in the southeastern Mediterranean Sea, resulting in the creation of a human-assisted Erythrean (Red Sea) biotic province (Goren and Galil, 2005). Trans-located fish species, such as the round goby, have also become established in the Baltic Sea (Karlson *et al.*, 2007).

Discussion

We propose a framework for the study of the effect of climate change on fish populations (Figure 1) and derive a set of testable hypotheses based on first principles. Similar to Harley *et al.* (2006), the framework recognizes that climatic factors will affect successive life-history stages (eggs, larvae, juveniles, and adults) in different ways and via processes acting at all levels of biological organization (from physiological responses of individual organisms to population-level disturbances and to ecosystem-level/trophodynamic effects). The different levels of organization can be viewed as a mechanistic chain. Population-level processes will only operate within the appropriate physiological envelope of abiotic conditions. Equally, ecosystem-level processes will only be relevant when life-cycle closure is possible within the specific geographic location providing interconnection among suitable habitats of successive life-history stages. This framework structures the analysis of the published data and provides the basis for modelling studies to test hypotheses. In our analysis, we have mainly focused on the effects of temperature, although other factors may be incorporated.

Knowledge of the eco-physiology of different life stages will provide a strong basis to infer the response of a species to a change in temperature (and other climate-driven changes in abiotic factors). It will allow us to define the bioclimate envelope

Table 1. Review of the observed changes in distribution, abundance, and production related to climate change in a selection of commercially exploited species of contrasting ecotypes.

Change	Comments	Source
Pelagic species		
1. Atlantic herring, <i>Clupea harengus</i> : Shelf, Boreal, Medium		
Herring populations exhibit multidecadal variations	Multidecadal variations related to climate variations (Russel cycle) and fisheries. Great salinity anomaly affected larval transport in North Sea. Recruitment related to temperature; positive relationship in northern population (Norwegian spring-spawning herring)	Corten (1986, 2001b), Alheit and Hagen (1997), Toresen and Østvedt (2000), and MacKenzie et al. (2007)
Norwegian spring spawners: changes in overwintering, feeding, and spawning areas; more northerly distribution in North Sea with warmer temperatures	Distribution changes related to changes in food distribution	Toresen and Østvedt (2000), Corten (2001a, b), and Holst et al. (2002)
2. Anchovy, <i>Engraulis encrasicolus</i> : Shelf, Lusitanian, Short		
Increase in abundance in northern areas (North Sea). Decrease in Bay of Biscay	Increase in North Sea may be temperature-related. Change in Bay of Biscay related to fishing. Role of climate is uncertain	Boddeke and Vingerhoed (1996) and MacKenzie et al. (2007)
3. Sprat, <i>Sprattus sprattus</i> : Shelf, Lusitanian, Short		
Increase in abundance and production in Baltic; stock collapse in Black Sea	Increased recruitment at higher temperature (and reduced cod predation) at northern limit and decrease at higher temperature at southern limit (Black Sea)	Köster et al. (2003), MacKenzie and Köster (2004), Daskalov et al. (2007), and Möllman et al. (2008)
4. Mackerel, <i>Scomber scombrus</i> : Atlantic, Atlantic, Long		
Northward shift in spawning and feeding areas. Earlier spawning. Increased variation in recruitment	–	Reid et al. (2001) and ICES (2007)
5. Horse mackerel, <i>Trachurus trachurus</i> : Atlantic, Atlantic–Lusitanian, Long		
Increase in northern areas resulting from change in migration to feeding areas	–	Borges et al. (1996) and Iverson et al. (2002)
Demersal species		
6. Atlantic cod, <i>Gadus morhua</i> : Shelf, Boreal, Long		
Increase in abundance in northern areas at higher water temperatures	Arcto-Norwegian cod: increase in recruitment at higher temperatures (overfishing increased sensitivity of the relationship). Temperature-related shifts in spawning sites	Planque and Frédou (1999), Ottersen et al. (2006), and Heath (2007)
Growth	Body growth is strongly temperature-related	Brander (1995)
Productivity changes in Baltic related to inflow of saline Atlantic water	Volume of spawning habitat where eggs and larvae can survive depends on inflow of saline water from North Sea	Sparholt (1996) and MacKenzie et al. (2000)
Decrease in abundance in southern areas (and also North Sea)	Recruitment related to climate effects on zooplankton production and to temperature	O'Brien et al. (2000) and Beaugrand et al. (2003)
Northward shift in distribution within North Sea	Likely resulting from different fishing pressure and local survival of eggs/larvae	Hedger et al. (2004), Perry et al. (2005), and Rindorf and Lewy (2006)
Shift to deeper waters in North Sea	No evidence of cod actively swimming north or to deeper water	Hedger et al. (2004) and Neat and Righton (2007)
7. Plaice, <i>Pleuronectes platessa</i> : Shelf, Boreal, Long		
Distribution shifted to deeper waters (North Sea)	Temperature is a likely cause, although other factors may have contributed	Perry et al. (2005) and Van Keeken et al. (2007)
Decrease in abundance in southern nursery grounds (Bay of Biscay)	–	Desaunay et al. (2006)
Recruitment negatively related to temperature in waters around the UK	–	Fox et al. (2000)
Timing of spawning advanced in warm years (North Sea)	–	Teal et al. (2008)
Changes in growth do not correlate with temperature, except in 0-groups	Growth related to population abundance, eutrophication, and bottom trawling. Growth of 0-groups determined by temperature	Rijnsdorp and van Leeuwen (1996) and Teal et al. (2008)
8. Sole, <i>Solea solea</i> : Shelf, Lusitanian, Long		
Recruitment related to river run-off (Bay of Biscay, Mediterranean Sea)	Nursery habitat quality/quantity increases	Salen-Picard et al. (2002), Le Pape et al. (2003), and Darnaude et al. (2004)

Continued

Table 1. Continued

Change	Comments	Source
Recruitment negatively related to temperature in North Sea and positively in the Bristol Channel	–	Rijnsdorp <i>et al.</i> (1992) and Henderson and Seaby (2005)
Timing of spawning advanced in warm years (North Sea)	–	Teal <i>et al.</i> (2008)
Length at end of first year increases with temperature. Changes in growth of older fish do not correlate with temperature	Growth of 0-group determined by temperature and length of growing season. Growth of older age groups related to population abundance, eutrophication, and bottom trawling	Millner and Whiting (1996) and Teal <i>et al.</i> (2008)

Ecotypes were defined as a combination of the following characteristics: habitat (pelagic or demersal; Atlantic or Shelf); biogeographic affinity (Atlantic, Lusitanian, or Boreal); and longevity (long, medium, or short).

and evaluate the change in habitat suitability for the different life stages (Pearson and Dawson, 2003), or evaluate whether observed temperature changes may be responsible for the change in the population abundance, such as for the eelpout in the Wadden Sea (Pörtner and Knust, 2007). Although we have mainly dealt with temperature, climate change may also affect oxygen, salinity, and ocean pH. These factors may load the metabolic scope and decrease the tolerance range of the organism (Fry, 1971), subsequently making it more vulnerable to climate change.

Eco-physiological data can also indicate whether species or species-groups may differ in sensitivity to change in temperature affecting trophic relationships. A review of experimental data on the optimum temperature and temperature tolerance ranges of a number of fish and (epi-)benthic species revealed clear species differences, suggesting that an increase in temperature would result in a shift in the predation pressure from cod and gobies to brown shrimps (Freitas *et al.*, 2007). If the temperature sensitivity of species groups (e.g. autotrophs and heterotrophs; ectotherms and endotherms; and taxonomic groups of different complexity) differ in a systematic manner, this will provide a basis for predicting how a temperature change may affect species and species interactions. Research into differences in sensitivity among species (groups), as well as the underlying mechanism, is needed.

Although climate change may influence the vital rates/productivity of a fish stock (growth, mortality, and recruitment), we suggest that early life-history stages will be most sensitive to the effects of climate change. The underlying mechanisms may differ among species or stocks and will depend on the trophic position (Frank *et al.*, 2007). The importance of processes affecting early life-history stages in determining the productivity of a fish stock is corroborated by a literature review of a selected number of well-studied species in the Northeast Atlantic indicating the importance of temperature effects on the level of recruitment (Table 1). Moreover, (multi-)decadal changes in ocean climate have been driving changes in recruitment and productivity in the North Atlantic and Pacific Ocean (Lehodey *et al.*, 2006). Climate-related changes in growth of recruited life-history stages may influence fish productivity (Dutil and Brander, 2003; Lehodey *et al.*, 2006), although this effect may be confounded by a change in the intra- or interspecific competition for food. Global warming will reduce the probability of low winter temperatures, resulting in a better survival of both southern species and fish of small body size (Post and Evans, 1989). A critical test of whether this inference holds true remains to be done. Most studies in the literature have focused on a specific part of the life cycle and have not attempted to study all processes in an integrated

manner. Dutil and Brander (2003) distinguished between temperature effects on growth and recruitment, but were not able to measure recruitment independent of the growth rate before the recruitment to the fisheries.

Given the complexity of the problem, where climate change is a multifaceted driver and the response of affected fish population too is multifaceted, we believe that scientific progress will benefit from an approach where *a priori* hypotheses are formulated based on first principles of the relevant levels of organization. The hypotheses proposed here are by no means complete. They should rather be regarded as a first set of hypotheses. These hypotheses seek to compare species and species-groups that have contrasting ecological characteristics and are thus likely to differ in their sensitivity to climate change. The classification of species into ecotypes based on biogeographic affinity, habitat requirement, and life-history characteristics may be an important starting point. The review of a number of well-studied fish species in the Northeast Atlantic did not allow us to test all working hypotheses, but supported the hypothesis that species exhibited distributional shifts (latitude and depth) in response to a temperature increase and that the response of pelagic species is stronger than that of demersal species, corroborating a number of recent studies of changes in fish assemblages (Attrill and Power, 2002; Borja *et al.*, 2002; Beare *et al.*, 2004; Genner *et al.*, 2004).

We argue that understanding the complex effects of climate on a species will require an integrated life-cycle approach that examines the importance of different mechanisms acting on all life stages and identifies those developmental stages and mechanisms most critical for life-cycle closure and recruitment. Examples of this type of approach include the body of work performed on Baltic cod and sprat (Köster *et al.*, 2003, 2005; Möllmann *et al.*, 2008), which highlights the possible complex feedbacks among elements of our framework (i.e. effects of physiology on behaviour, behaviour on top-down processes, and climate-driven physical forcing on bottom-up processes).

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