Global Change Biology (2007) 13, 1348–1367, doi: 10.1111/j.1365-2486.2007.01369.x

Impact of 21st century climate change on the Baltic Sea fish community and fisheries

BRIAN R. MACKENZIE*, HENRIK GISLASON†, CHRISTIAN MÖLLMANN‡[1] and FRIEDRICH W. KÖSTER‡

*Department of Marine Ecology and Aquaculture, Danish Institute for Fisheries Research, Technical University of Denmark, Kavalergården 6, DK-2920 Charlottenlund, Denmark, †Department of Marine Fisheries, Danish Institute for Fisheries Research, University of Copenhagen, Charlottenlund Castle, DK-2920 Charlottenlund, Denmark, ‡Department of Marine Fisheries, Danish Institute for Fisheries Research, Technical University of Denmark, Charlottenlund Castle, DK-2920 Charlottenlund, Denmark

Abstract

The Baltic Sea is a large brackish semienclosed sea whose species-poor fish community supports important commercial and recreational fisheries. Both the fish species and the fisheries are strongly affected by climate variations. These climatic effects and the underlying mechanisms are briefly reviewed. We then use recent regional – scale climate – ocean modelling results to consider how climate change during this century will affect the fish community of the Baltic and fisheries management. Expected climate changes in northern Europe will likely affect both the temperature and salinity of the Baltic, causing it to become warmer and fresher. As an estuarine ecosystem with large horizontal and vertical salinity gradients, biodiversity will be particularly sensitive to changes in salinity which can be expected as a consequence of altered precipitation patterns. Marine-tolerant species will be disadvantaged and their distributions will partially contract from the Baltic Sea; habitats of freshwater species will likely expand. Although some new species can be expected to immigrate because of an expected increase in sea temperature, only a few of these species will be able to successfully colonize the Baltic because of its low salinity. Fishing fleets which presently target marine species (e.g. cod, herring, sprat, plaice, sole) in the Baltic will likely have to relocate to more marine areas or switch to other species which tolerate decreasing salinities. Fishery management thresholds that trigger reductions in fishing quotas or fishery closures to conserve local populations (e.g. cod, salmon) will have to be reassessed as the ecological basis on which existing thresholds have been established changes, and new thresholds will have to be developed for immigrant species. The Baltic situation illustrates some of the uncertainties and complexities associated with forecasting how fish populations, communities and industries dependent on an estuarine ecosystem might respond to future climate change.

Keywords: Baltic Sea, climate change, ecosystems, estuaries, fish, fishing, management, salinity, temperature

Received 5 April 2006; revised version received 18 December 2006 and accepted 29 January 2007

Introduction

The production and distribution of fish depends strongly on environmental conditions. Changes in hydrographic and meteorological variables such as temperature, salinity, storminess and cloudiness have all been shown to affect fish life history (e.g. success of reproduction, spatial distributions, migration patterns, growth and mortality rates; Bakun, 1996; Stenseth *et al.*, 2004). These influences can sometimes impact overall population dynamics so much that populations will undergo multiyear trends in abundance. If these populations are commercially exploited, the trends in abundance will in turn affect how the populations are managed (e.g. setting of fishing quotas, establishment of closed fishing areas and seasons). Particular examples of populations which undergo or have undergone

Correspondence: Brian R. MacKenzie, tel. +45 3396 3403, fax +45 3396 3434, e-mail: brm@difres.dk

[1] Present address: Institute for Hydrobiology and Fisheries, University of Hamburg, Hamburg, Germany.

such fluctuations are the cod population in the North Sea during the late 1950s–1960s when it increased, and again during the past 10–15 years when it decreased (Beaugrand *et al.*, 2004), and populations of sardine and anchovy in many of the world's major upwelling zones (e.g. near the coasts of southern Africa, Peru and Chile; Bakun, 1996; Chavez *et al.*, 2003; Stenseth *et al.*, 2004).

Fish species and populations in the Baltic Sea (Fig. 1) have also been impacted by climatic variations. These impacts include changes in growth, survival and production rates and will be reviewed briefly below. The changes in fish biology, which are often accompanied by changes in the structure and function of the entire Baltic ecosystem, have occurred as a consequence of changes in climatic and hydrographic forcing at inter- and multiannual time scales (Hänninen *et al.*, 2000; Axenrot & Hansson, 2003; Köster *et al.*, 2005). Recently, some of the multiannual changes have been characterized as regime shifts (Köster *et al.*, 2003b; Alheit *et al.*, 2005; Hagen & Feistel, 2005).

There is now strong evidence that global climate change has had an anthropogenic component in recent decades (Levitus *et al.*, 2001; Barnett *et al.*, 2005) and that climate change will continue during the 21st century (IPCC, 2001). Whether some of these global changes are also affecting hydrographic conditions in the Baltic is presently under investigation, but there is evidence that (1) sea temperatures in both the surface (MacKenzie & Schiedek, 2007) and deeper (halocline) layer (MacKenzie & Köster, 2004) of the Baltic have increased during most of the 1990s and early 2000s (Fig. 2), (2) winters have become milder (Hagen & Feistel, 2005), (3) precipitation over the Baltic watershed has increased (Hänninen *et al.*, 2000) and (4) salinity in the central Baltic has decreased (Alheit *et al.*, 2005; Möllmann *et al.*, 2005) (Fig. 3).

In this study, we address how some of the expected climate changes might influence Baltic fish species and populations. These influences could be particularly important in a brackish coastal sea such as the Baltic where strong horizontal and vertical gradients in salinity, temperature and oxygen concentration limit the reproduction and distribution of most species. We then evaluate how the climate-induced changes in fish ecology will affect Baltic fisheries and suggest potential fishery management actions, which could be implemented to support long-term sustainability of the populations.

Methods

This study combines a qualitative review of Baltic fisheries and ecosystem literature with recent regional climate model outputs for the 21st century climate of northern Europe. The intention is to provide an initial evaluation of how climate change will affect Baltic fish populations and fisheries during the 21st century. Such an evaluation is timely as several countries around the

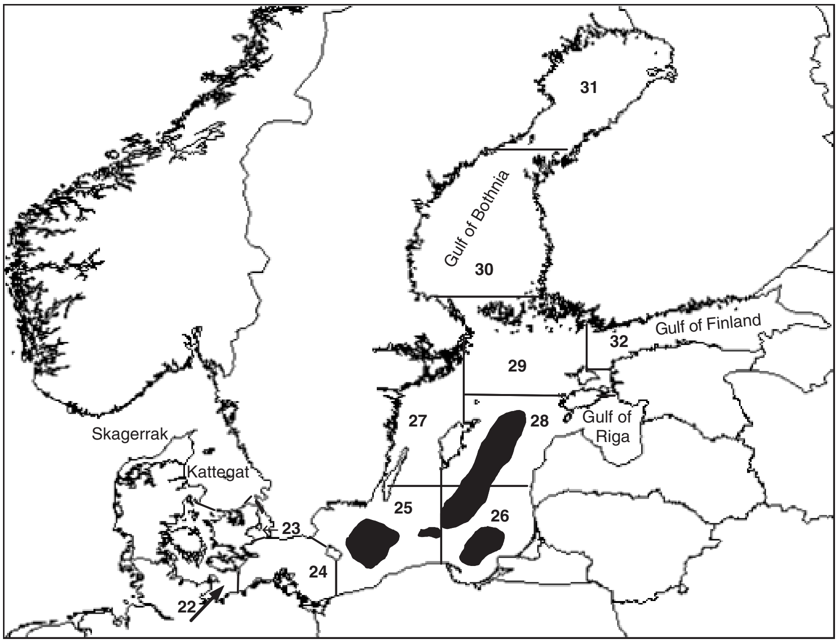

Fig. 1 Map of the Baltic Sea showing the ICES subdivisions. The HELCOM definition for the Baltic Sea includes the Kattegat and subdivisions 22–32. Subdivision 22 contains the Belt Sea. Black areas show deep basins of the eastern Baltic Sea where cod spawning occurs (Bagge *et al.*, 1994).

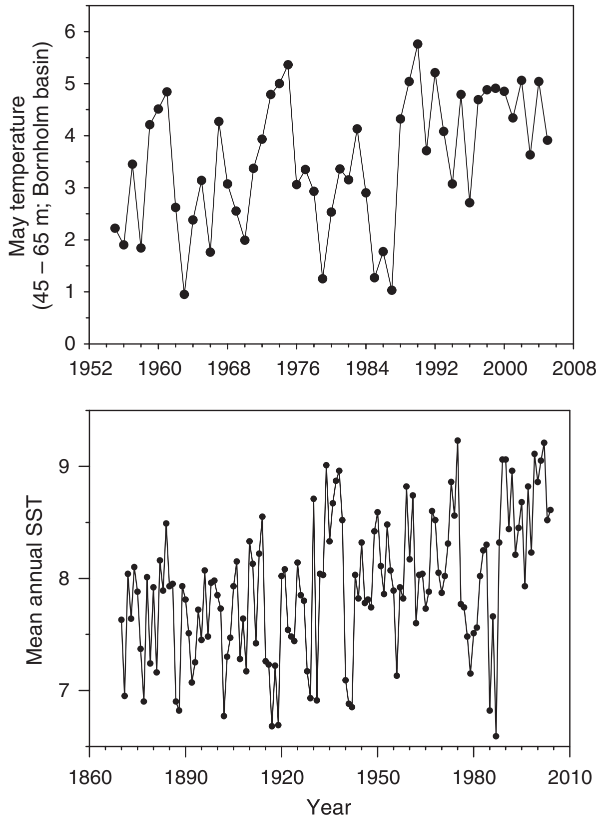

Fig. 2 (a) Time series of temperature in May at depth of 45–65 m in Bornholm Basin, Baltic Sea (ICES Subdivision 25). Data from 1955 to 1999 are from the ICES Hydrographic database (see MacKenzie & Köster, 2004 for details), and data from 2000 to 2005 are kindly provided by Dr Hans-Harald Hinrichsen, GEOMAR, Kiel, Germany. (b) Mean annual sea surface temperature (SST) in the central Baltic Sea (54.0°N–60.5°N; 14.5°E–23.5°E) based on ships-of-opportunity measurements compiled by the Hadley Centre for Climate Prediction, United Kingdom (MacKenzie & Schiedek, 2007). Note the different scaling on both axes in the panels.

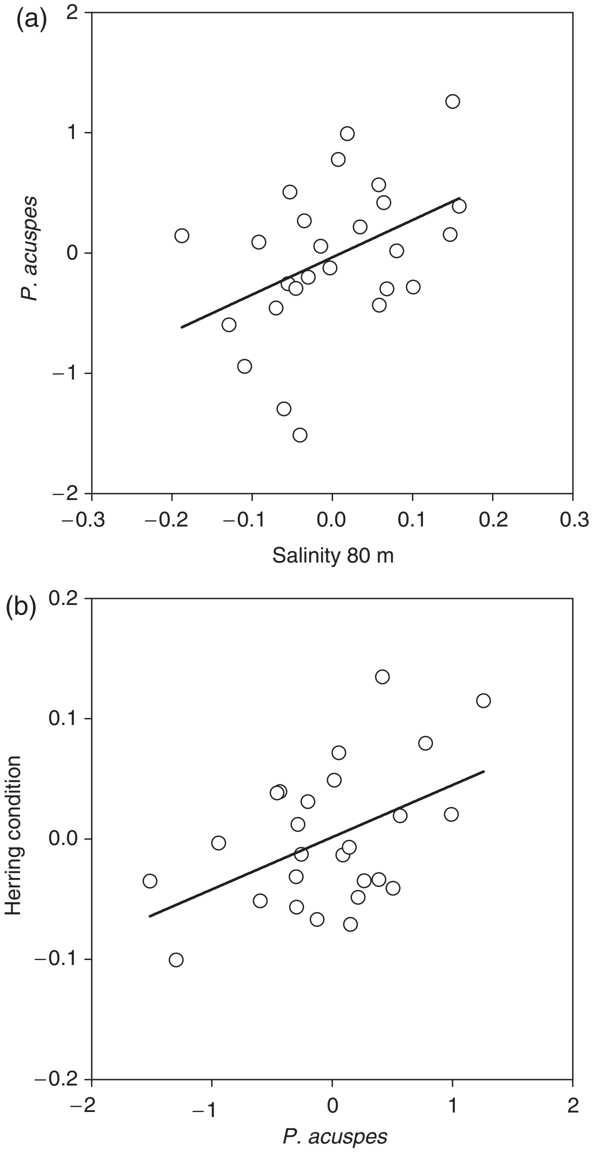

Fig. 3 Relationships between log-anomalies of (a) salinity (psu) and *Pseudocalanus acuspes* ($n \times m^{-3}$), and (b) *P. acuspes* and herring condition (mean weight at 18 cm) for the years 1977–2002 (Möllmann *et al.*, 2005); the relationships are statistically significant (a) $R^2 = 19\%$, $P = 0.025$; (b) $R^2 = 23\%$, $P = 0.014$)

Baltic (e.g. Denmark, Finland) and elsewhere (e.g. Canada, Great Britain) are preparing, planning to prepare, or have prepared, climate adaptation policies and strategies. Governments are therefore requesting advice from government ministries, industries and nongovernmental organizations in various socioeconomic sectors of their countries on what the most important impacts of climate change will be and how those sectors might respond to climate change. The geographic coverage of the study is the Baltic Sea as defined by the Helsinki Convention for the Protection of the Marine Environment of the Baltic Sea, and therefore, includes all waters from the Kattegat and Belt Sea to the Gulfs of Bothnia and Finland (Fig. 1). The Baltic itself is divided into subdivisions for the management of its ecosystem and fisheries. The study focuses on wild populations and, therefore, does not address how aquaculture or sea-ranching in the Baltic will be impacted by climate change.

Quantifying the consequences of climate variability on Baltic fish populations requires both detailed process knowledge of lifehistories and species interactions, as well as long time series of abundance and distribution. The former information is being compiled from field and laboratory studies (Vallin *et al.*, 1999; Jutila *et al.*, 2005; Köster *et al.*, 2005), whereas the latter is being compiled from fisheries institutes, historical archives, tax records and archaeological evidence (Enghoff, 1999; Holm *et al.*, 2001; MacKenzie *et al.*, 2002; Ojaveer & Andrushaitis, 2004). In the Baltic region, both approaches are being used in an interactive and iterative fashion. Eventually, they will provide information about how fish abundances and distributions varied when exploitation was lower and during alternate combinations of environmental conditions (e.g. Little Ice Age, Medieval Warm Period) differing from those observed in the late 20th century, but resembling those conditions that may occur again as a consequence of climate change.

The effects of climate variability on Baltic fish populations are probably best documented for the cod, sprat and herring populations in the eastern part of the Baltic Sea (ICES Subdivisions 25–32). These populations have been the focus of several large international and national research programmes since the early 1990s. Climate-related results from these investigations will be summarized below, and impacts of climate variability on other species (e.g. flatfishes, freshwater species) will be presented subsequently.

Results and discussion

Biodiversity of the Baltic fish community

Compared with similar-sized ecosystems elsewhere the overall species richness and biodiversity of the Baltic fish community is low. For example, the North and Black Seas have ca. 230 and 170 species, respectively, whereas the Baltic has ca. 100 (EEA, 2002). The main reason for the low species richness in the Baltic Sea is its low salinity which imposes a physiological stress to both marine and freshwater species (Voipio, 1981; HELCOM, 2002; Ojaveer & Kalejs, 2005). Marine species such as sole *Solea solea* and plaice *Pleuronectes platessa* are common in the Kattegat (salinity >25‰) but become much less common further south and east-northeastwards into the Baltic. In an analogous manner, freshwater species, such as perch (*Perca fluviatilis* L.), pikeperch (*Stizostedion lucioperca* L.) and whitefish (*Coregonus lavaretus maraenoides* Poljakow), are more common in the northern Baltic and coastal areas than in southern, western and offshore areas of the Baltic (Voipio, 1981; Ojaveer, 2002). Hence, many fish species in this ecosystem are living at the physiological limit of their geographical distribution, and for some this has led to genetic differences among populations living in different parts of the Baltic (Nielsen *et al.*, 2001; Nielsen *et al.*, 2003; Jørgensen *et al.*, 2005).

Effects of climate variability and change on ecology of Baltic fish populations

Hydrographic processes affecting salinity have particularly rapid and dramatic impacts on species distributions and their susceptibility to exploitation in different parts of the Baltic. These processes clearly include major Baltic inflows of saline North Sea water (Schinke & Matthäus, 1998), and changes in precipitation patterns, evaporation rates and runoff (Hänninen *et al.*, 2000). Changes in temperature, especially during winter, as well as wind forcing, will affect fish habitats and geographic distributions.

Cod, sprat and herring in the eastern Baltic Sea (ICES subdivisions 25–32)

Direct effects on cod and sprat recruitment – influences of hydrographic conditions on egg and larval survival. The survival of fish early life stages in the eastern Baltic (ICES Subdivisions 25–32) is sensitive to hydrographic conditions in the spawning areas (Bagge *et al.*, 1994; Parmanne *et al.*, 1994; Wieland *et al.*, 1994). Eggs of Eastern Baltic cod successfully develop only in deep water layers with oxygen concentrations $>2\,\mathrm{mL\,L^{-1}}$ and a salinity >11 psu. These thresholds are the basis for the so-called reproductive volume (RV), i.e. the water volume sustaining cod egg development (Plikshs *et al.*, 1993; MacKenzie *et al.*, 2000). The climate-induced decrease in RV since the 1980s caused high cod egg mortality, especially in the eastern basins, i.e. Gdansk Deep and Gotland Basin (Köster *et al.*, 2003a).

Owing to a different specific gravity, sprat eggs float shallower than cod eggs (Nissling *et al.*, 2003), and consequently their survival is less affected by poor oxygen conditions. However, sprat eggs occur at depths where the water temperature is affected by winter cooling (Wieland & Zuzarte, 1991), and egg and larval development is influenced by extremely low water temperatures. Consequently, weak year classes of Baltic sprat have been associated with severe winters (MacKenzie & Köster, 2004; Nissling, 2004), resulting in temperatures of below 4 °C in the intermediate water layer during spawning time. The absence of severe winters since 1986–1987 and related favourable thermal conditions for sprat egg survival contributed to the generally high reproductive success of Baltic sprat during the 1990s (Köster *et al.*, 2003a; MacKenzie & Köster, 2004) (Fig. 4). Warm summer temperatures also promote sprat recruitment (Baumann *et al.*, 2006).

Behavioural studies demonstrated that cod larvae exposed to oxygen concentrations below $2\,\mathrm{mL\,L^{-1}}$ were mostly inactive or moribund (Rohlf, 1999). Although an impact of the environment on larval survival can therefore be expected, no direct effect of hydrography on

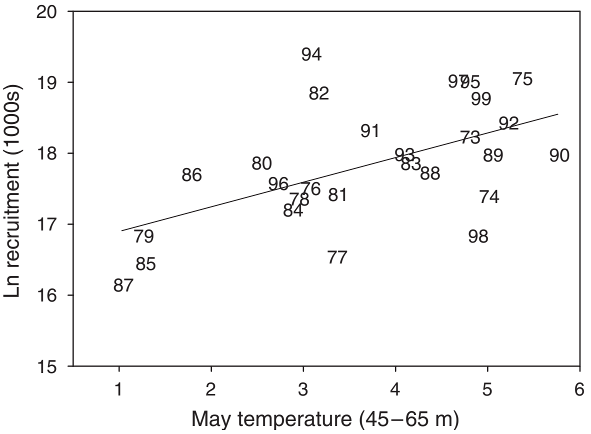

Fig. 4 Relationship between May water temperature at 45–65 m in the Bornholm Basin (ICES Subdivision 25, Fig. 1) and $\log_e$ sprat recruitment for the years 1973–1999 (MacKenzie & Köster, 2004). The relationship is statistically significant ($R^2 = 28\%$; $P = 0.003$). Symbols on panel represent the years when sprat were born and when temperatures were measured in sprat spawning areas.

observed larval abundance has been detected in a statistical analysis (Köster *et al*., 2001). Consequently, other factors such as food availability might be critical for larval survival. The same may be true for sprat, where the relationship between temperature and larval survival during the 1990s is most likely a result of enhanced plankton production at higher temperatures (Köster *et al*., 2003a).

Indirect effects on cod, sprat and herring recruitment – influences of mesozooplankton abundance on larval survival. The effect of food availability on growth and survival of cod larvae has been investigated using a coupled hydro/trophodynamic individual-based model (Hinrichsen *et al*., 2002a). Model results suggest that the co-occurrence of peak prey and larval abundances is critical for high survival rates. The decline of the *Pseudocalanus* sp. stock during the 1980s–1990s, a result of low salinity and oxygen conditions (Möllmann *et al*., 2000, 2003a), caused a food-limitation for early cod larvae. Model simulations including *Pseudocalanus* sp. nauplii as prey resulted in high survival rates, whereas omitting *Pseudocalanus* sp. resulted in low survival (Hinrichsen *et al*., 2002a). Thus, low *Pseudocalanus* sp. availability has contributed to the low recruitment of cod since the late 1980s, and evidence exists that it prevented the stock from recovery despite improved egg survival after the major inflow in 1993.

In contrary to cod, sprat larvae prey mainly on the copepod *Acartia* spp. (Voss *et al*., 2003). Higher water temperatures during the 1990s have resulted in a drastic increase in the standing stock of these copepods (Möllmann *et al*., 2000, 2003b). This enhanced food supply may, thus, have contributed to the high reproductive success of sprat during the 1990s (Köster *et al*., 2003a).

Herring recruitment in some parts of the Baltic is also affected by temperature and zooplankton abundance. In the Gulf of Riga, recruitment is positively correlated with both variables and this is used in fisheries management (Kornilovs, 1995; ICES, 2005a). Larval herring growth rates in the northern Baltic (SW Finland) are positively temperature dependent (Hakala *et al*., 2003), and larger size may allow higher survival rates. Herring recruitment in the central Baltic Sea also increases with sea temperature (Axenrot & Hansson, 2003).

Indirect effects on cod and sprat recruitment – influences of predation by clupeids on egg survival. A substantial predation on cod eggs by clupeids has been observed in the Bornholm Basin (ICES Subdivision 25). Egg predation by sprat is most intense at the beginning of the cod spawning season (Köster & Möllmann, 2000a). After spawning ends in spring, most sprat leave the basin, resulting in a reduced predation pressure on cod eggs. In parallel, herring return from their coastal spawning areas to feed in the Bornholm Basin, which includes predation on cod eggs (Köster & Möllmann, 2000a).

The drastic increase in the sprat stock during the 1990s has increased the potential of cod egg predation mortality. However, the shift in cod peak spawning time from spring to summer (Wieland *et al*., 2000) resulted in a decreasing predation pressure by sprat. Additionally a decline in individual sprat predation on cod eggs was observed from 1993 to 1996, despite relatively high concentrations of cod eggs in the plankton. This is explainable by a reduced vertical overlap between predator and prey. Owing to the increased salinity after the 1993 major Baltic inflow (Schinke & Matthäus, 1998), cod eggs were neutrally buoyant in shallower water layers, while clupeids were deeper, due to enhanced oxygen concentration in the bottom water (Köster & Möllmann, 2000a). As a result, predation on cod eggs is higher in stagnation periods, and contributed to the low reproductive success since the 1980s. Similarly, egg cannibalism was found to be an important source of sprat egg mortality in the Bornholm Basin, thereby representing a self-regulating process for the sprat stock (Köster & Möllmann, 2000b). The intensity of egg cannibalism depends as well on the vertical overlap between predator and prey, which is influenced by the prevailing salinity and oxygen conditions.

Direct and indirect effects on herring and sprat growth – influences of salinity, oxygen concentration and *prey (mesozooplankton, nektobenthos) abundance.* Herring weight-at-age has decreased significantly during the mid-1990s–2000s (ICES, 2005a). Several hypotheses have been proposed and tested to explain the decrease: (i) size-selective predation of cod on herring (Sparholt & Jensen, 1992; Beyer & Lassen, 1994), (ii) mixing of substocks with different growth rates (ICES, 1997) and (iii) a real decrease in growth rates due to changes in the biotic environment (Cardinale & Arrhenius, 2000). Recent evidence support the last hypothesis (Rönkkönen *et al*., 2004; Möllmann *et al*., 2005).

Herring and sprat have similar diets during much of their ontogeny (Möllmann & Köster, 1999; Casini *et al*., 2004). In addition, the feeding areas of herring and sprat in the Central Baltic overlap vertically in winter, as well as spring and early summer when both species feed during daytime in the halocline of the deep basins (Köster & Schnack, 1994). Here, the clupeids compete for the calanoid copepod *Pseudocalanus* sp. dwelling in the high salinity layer (Möllmann *et al*., 2004). The reduced availability of *Pseudocalanus* sp. resulted in a lowered food intake of herring and can be related to the decrease in herring condition (Möllmann *et al*., 2003a, 2005) (Fig. 3). Recently, Rönkkönen *et al*. (2004) supported this finding by showing that growth rates of herring in the northern Baltic depended explicitly on the abundance of the copepod *Pseudocalanus* sp.

As herring grow, their dietary preferences change and larger nektobenthic species such as *Mysis mixta* and amphipods become common prey (Möllmann *et al*., 2004; Casini *et al*., 2006). When the abundance of these prey decreases in deep parts of the Baltic, as occurs during anoxia periods (Välipakka, 1990), large herring are forced to consume zooplankton species (Möllmann *et al*., 2004; Casini *et al*., 2006). As a consequence, consumption of small prey by large herring increases foraging costs. This mechanism is believed to have contributed to the reduced growth in herring during the 1990s and early 2000s (Flinkman *et al*., 1998; Rönkkönen *et al*., 2004).

Food availability, especially *Pseudocalanus* sp. population size, has been hypothesized to have caused a decrease in sprat growth during the 1990s (Cardinale *et al*., 2002; Möllmann *et al*., 2004; Casini *et al*., 2006). However, correlations between the abundance of the copepod and sprat condition in the Central Baltic are weak (Möllmann *et al*., 2005). It is more likely that strong intraspecific competition at high stock size caused the lowered growth in sprat, explaining a significant relationship between sprat condition and sprat stock size (Möllmann *et al*., 2005; Casini *et al*., 2006). Similarly, interspecific competition with the large sprat stock has contributed to the reduced herring growth (Rönkkönen *et al*., 2004; Möllmann *et al*., 2005; Casini *et al*., 2006).

A direct relationship among salinity, and herring and sprat growth was shown by some authors (Cardinale & Arrhenius, 2000; Cardinale *et al*., 2002; Rönkkönen *et al*., 2004). However, this relationship probably reflects the change in mesozooplankton community structure rather than a direct physiological effect of salinity on these euryhaline fish species.

Conceptual model of climate effects on recruitment and growth of cod, sprat and herring populations in the eastern Baltic. Our present understanding of direct and indirect effects of climate variability on cod and sprat recruitment, as well as herring and sprat growth can be summarized schematically (Fig. 5). Climate affects salinity and oxygen (S/O_2) through runoff and inflows of North Sea water, and water temperature (T) through direct air–sea interaction. Changes in S/O_2 directly affect cod recruitment via egg survival, and indirectly via *Pseudocalanus* sp. abundance which influences larval survival. High temperatures directly support sprat recruitment (Fig. 4) via increased egg survival, and indirectly via the role of *Acartia* spp. availability on larval survival. Warm temperature also promotes herring recruitment in the central Baltic and in the Gulf of Riga. Furthermore, hydrographically mediated egg predation regulates cod and sprat recruitment.

Herring growth appears to be affected by the indirect effect of S/O_2 on *Pseudocalanus* sp. and the increased competition with the enlarged sprat stock. In addition, growth of larger herring has probably also been limited by food availability due to the effect of stagnation periods and anoxia on abundance of nektobenthic prey. Reduced growth in turn probably has affected reproduction (e.g. longer time to maturity, lower relative fecundity) and recruitment but these links have not been studied yet. The increase in the sprat stock is mainly a result of reduced predation by cod and high reproductive success during the 1990s and has caused a density-dependent decrease in sprat growth. This intra- and interspecific competition may have been amplified by low availability of *Pseudocalanus* sp. (Fig. 3), mysids and amphipods.

Flatfishes (plaice, dab, flounder and sole). Plaice is an important commercial species in the Kattegat and to a lesser extent in the Belt Sea. Its spatial distribution depends partly on the salinity gradient through the Kattegat-Belt Sea-western Baltic (Fig. 1). In addition, interannual variations in juvenile plaice abundance in the Kattegat is at least partly controlled by wind-driven hydrographic transport of eggs and larvae from the Skagerrak (Pihl, 1990; Nielsen *et al*., 1998).

Plaice was common in the central Baltic (ICES Subdivisions 25–28) in the earlier decades of the 20th century when it supported directed commercial

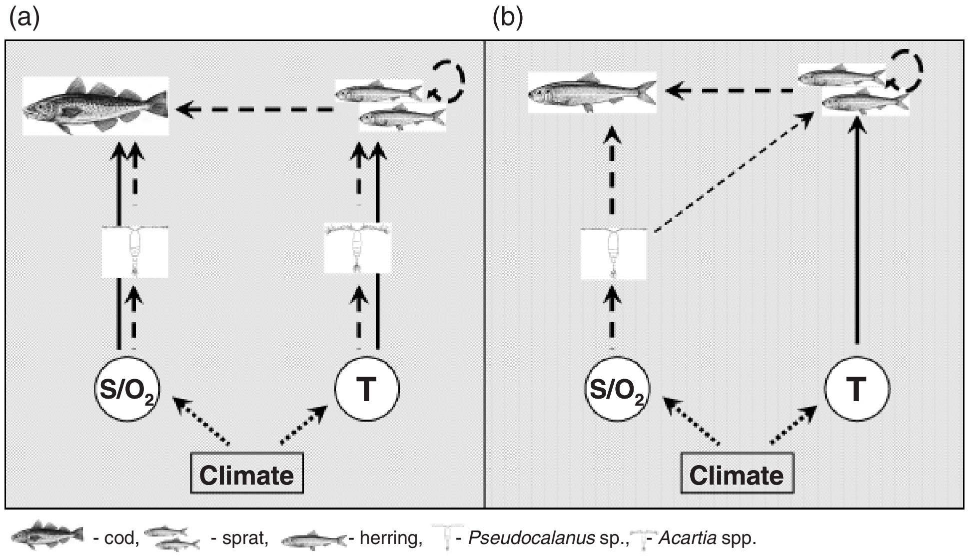

Fig. 5 Conceptual model of major climate effects on recruitment (a) and growth (b) of three fish species (cod, sprat and herring) in the eastern Baltic Sea. Dotted arrows – effect of climate on hydrography, dashed arrows, indirect effects; and solid arrows direct effects; S, salinity; O_2, oxygen; *T*, temperature (explanations, see text).

fisheries (Temming, 1989). The stock declined in the late 1930s–1940s because of recruitment failures associated with recruitment overfishing and unsuitable hydrographic conditions for survival of eggs and larvae (Temming, 1989). The population recovered in the 1950s following several large inflows of saline, oxygen rich water. However, research surveys conducted in the Bornholm Basin during the 1970s and 1980s show that the population declined again (Temming, 1989). The reason for the second stock decline in the central Baltic is hypothesized to be caused by a combination of: (i) high bycatches in trawl fisheries which were targeting cod, (ii) high predation pressure by the large cod stock in the early to mid-1980s and (iii) low plaice recruitment success during the stagnation period in the second half of the 1980s (Temming, 1989; Nissling *et al.*, 2002). Since the mid-1980s, the plaice population has remained small (ICES, 2005a), despite much lower abundances of an important predator (cod) and also lower bycatch mortality in the cod fishery. Presumably, plaice recovery has been delayed because hydrographic conditions (salinity and oxygen levels in deep water) since the early 1980s have generally been unfavourable for fertilization and survival of eggs (Nissling *et al.*, 2002).

Dab (*Limanda limanda*) presently inhabits the Kattegat and the western Baltic. However, historically, dab also existed in the central Baltic and used the Bornholm Basin as its main spawning area. Catch statistics and research surveys indicate that the dab stock in the central Baltic collapsed with the plaice stock during the early 1930s–1940s (Temming, 1989). Unlike the plaice stock, the dab stock has never recovered. Temming (1989) argues that successive recruitment failures due to unfavourable hydrographic conditions during the early 1930s and predation by cod caused the dab stock to decline. Compared with other marine species (e.g. plaice, flounder and cod) in the central Baltic, dab eggs require higher salinities for activation of spermatozoa and successful fertilization of eggs, and to remain buoyant at depths where suitable oxygen concentrations allow egg development (Nissling *et al.*, 2002). Dab eggs are therefore less likely to be fertilized and to survive at low salinities and are more likely to be exposed to deep water with lower oxygen concentrations than other marine species in the Baltic. Moreover, and in comparison with plaice, dab spawns later in the year (Temming, 1989), when oxygen conditions at depths of neutral egg buoyancy are more likely to be lower than earlier in the year (Matthäus, 1978; MacKenzie *et al.*, 1996). The differences in hydrographic requirements and spawning behaviour among the species (Nissling *et al.*, 2002) have probably prevented recovery of the dab stock, even though abundance of a key predator, cod (Temming, 1989), is now very low (ICES, 2005a). Recovery of the central Baltic dab population, assuming a remnant population is still present, will likely require a multiyear period during which subhalocline salinities and oxygen levels are high and predation by cod is low.

Flounder, *Platichthys flesus*, is a third commercially and ecologically important flatfish species in the area. Flounder is able to reproduce (i.e. activation of spermatozoa, fertilization of eggs) at lower salinities than other flatfishes in the Baltic and therefore its habitat and biomass are much larger (Nissling *et al.*, 2002). Its distributional range extends from the Kattegat into the central-northern Baltic, including low salinity coastal areas. Trends in total abundance and biomass are uncertain (ICES, 2005a). However, catch rates in the eastern and northern areas (e.g. Gulf of Finland) rise 3–4 years after increases in bottom salinity caused by major Baltic inflows, and subsequently, fall in the period between inflows (Ojaveer & Kalejs, 2005). The increase in catch rates and landings following inflows is consistent with the beneficial effect of increases in salinity on reproductive parameters (Nissling *et al.*, 2002).

Sole spatial distributions are limited in the Kattegat-Belt Sea area by salinity, and the species is rarely seen in the western or eastern Baltic where salinities are too low (Muus & Nielsen, 1999). In areas where salinities can be tolerated by sole, other factors limit abundance and distribution. In the Kattegat and Skagerrak the species is located near its northerly limit of distribution (Muus & Nielsen, 1999) and temperature is probably an important factor affecting abundance. Sole abundance in the Kattegat as recorded in research vessel surveys and in analytical biomass estimates has risen during the late 1990s and early 2000s (ICES, 2005a). Recent warm temperatures in the Kattegat and Skagerrak during this period (MacKenzie & Schiedek, 2007) may have enabled sole to increase its survival and distributional range during these years. However, the mechanisms responsible for the increase in sole abundance are unknown and require further investigation.

Migratory and freshwater species. Several studies have shown how salmon lifehistory is influenced by variations in water temperature. Both the smolt run and survival of wild Atlantic salmon in the Baltic are temperature dependent (Kallio-Nyberg *et al.*, 2004; Jutila *et al.*, 2005). Entry to the Baltic from rivers is triggered by temperatures >10 °C, and survival of smolts in the open Baltic is highest at intermediate temperatures (9–11 °C; Fig. 6). When in the open Baltic, salmon avoid warm water (>11–12 °C) by moving to deeper, colder layers (Alm, 1958). Spawning migrations to rivers are also temperature dependent, with salmon arriving earlier when spring temperatures are higher than average (Dahl *et al.*, 2004).

The influence of temperature on sea trout (*Salmo trutta*) is less well documented. However, studies of the influence of salinity on survival and growth of sea trout parr showed no differences between parr raised in fresh or brackish (6.7 psu) water (Landergren, 2001). The higher salinity coastal habitat should, therefore, not impose a metabolic barrier to sea trout parr entering the coastal zone from rivers without smolting.

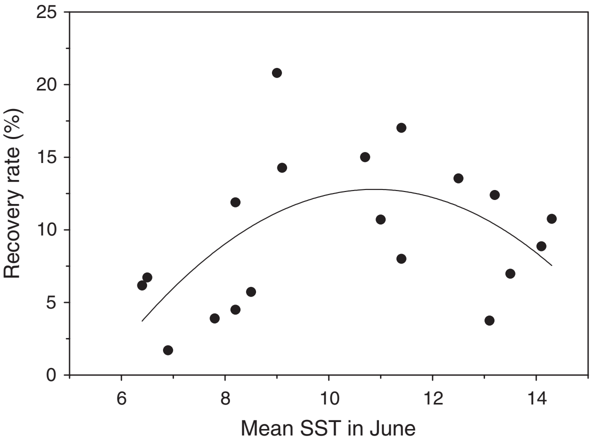

Fig. 6 Relationship between recapture rate (%; as an indicator of survival rate) of Carlin-tagged wild Atlantic salmon smolts and mean sea surface temperature (SST) in June at the islands of Krunnit, northern Baltic Sea for 19 years during 1972–1999. The fitted second order polynomial curve explains 31% of the variation ($P = 0.051$) in survival rate (Jutila *et al.*, 2005).

Variations in salinity also affect whitefish (*Coregonus* sp.) reproduction (Albert *et al.*, 2004). Fertilization of eggs in the laboratory was higher at salinities <3.3 psu than at 4–6.2 psu, and egg survival remained high at salinities 0.2–1.3 psu. Hatching tended to occur earlier at lower salinities.

Temperature variations influence pikeperch and perch biology. Year–class strength for both species at several sites around the Baltic increased with summer and spring temperatures during the first year of life (Bohling *et al.*, 1991; Lappalainen & Lehtonen, 1995; Kjellman *et al.*, 2003). The presumed reason for the beneficial effect of temperature on recruitment in these species is via the positive influence of temperature on growth rates and body size (Lappalainen *et al.*, 2000; Lozys, 2004). Winter mortality rates are size-dependent in some Baltic areas; warm summers, which result in faster growth and larger prewinter body sizes, are, therefore, likely to improve over-winter survival rates (Lappalainen *et al.*, 2000).

Both of these species are sensitive to salinity variations. As a result habitats for eggs, larvae and adults are restricted to salinities generally lower than 10 psu (Lozys, 2004). Distributions of these species are, therefore, confined to coastal areas and rivers but could increase if salinities in the Baltic fall. Growth of 0-group perch in laboratory experiments was higher at 5 psu than in freshwater, presumably because the lower salinity imposes lower metabolic costs for osmoregulation (Lozys, 2004).

Some marine species enter the Baltic seasonally from the Kattegat, North Sea and open northeast Atlantic. These species include garfish *Belone belone* and mackerel *Scomber scombrus*. Other species (e.g. some herring populations) leave the Baltic on a seasonal basis. The timing of migration to and from the Baltic, as well as the residence time within (or outside) the Baltic are determined partly by climatic variables including temperature. For example, the arrival time of garfish and its departure from the Baltic occurred earlier in warm years during 1986–2005 (Jacobsen, 2006). Residence time varied by ca. 6 weeks and was also shorter in warm years (Jacobsen, 2006). These differences in migration behaviour affect not only the ecology of garfish, but also its role in the food web as a predator and competitor with other species. Similar effects of temperature on other migratory behaviour in other Baltic species remain to be documented.

Glacial relict species. Some fish species (e.g. sea snail *Liparis liparis*, four-horned sculpin *Triglopsis quadricornis*) living in the Baltic survived the last glaciation (ca. 10–12 000 years ago). These species require cold, oxygen-rich water, tolerate low-brackish salinities (e.g. 5.5–6.5 psu), and are present in low abundances in especially the northern coastal areas of the Baltic Sea (Ojaveer *et al.*, 1999). Their narrow habitat requirements suggest that they will be susceptible to multiple aspects of expected future climate changes. An increase in temperature will cause them to move northwards and/or to deeper water. However, their northward movement could be restricted by low salinity, and their movement to deeper waters could be limited by lower oxygen concentrations associated with eutrophication and the temperature-related decrease in oxygen solubility. As a result the habitats of some of these species will likely become even smaller as a consequence of climate changes.

Baltic fisheries and their management

Commercial fish catches are dominated by only a few species (i.e. sprat *Sprattus sprattus*, herring *Clupea harengus* and cod *Gadus morhua*; Fig. 7). Many other species, including those mentioned in previous sections, are exploited but their catches are much lower and contribute <10% of the total landings (ICES, 2005a). These species include flounder, plaice, salmon, eel (*Anguilla anguilla*) and nearshore coastal species such as whitefish, pikeperch and perch.

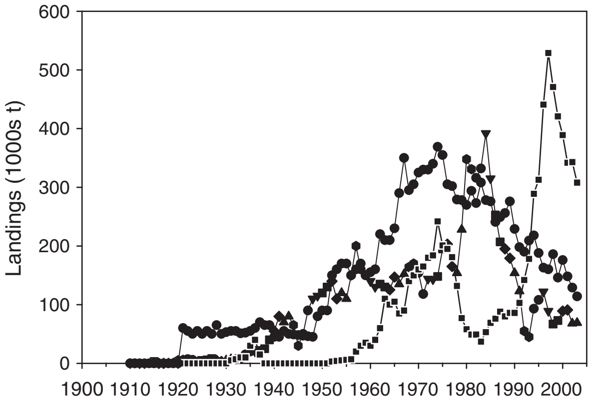

Fig. 7 Total international landings of the three commercially most important fish species (cod, herring, sprat) in the Baltic Sea during the 20th century. Triangles, cod; circles, sprat; diamonds, herring. Data source: (Sparholt, 1994; ICES, 2005a).

Baltic fisheries have been managed by the European Union and the International Baltic Sea Fisheries Commission until the end of 2005. Since 2006, bilateral agreements between the EU and Russia have replaced agreements with the IBSFC. The most important commercial species have quotas and other regulations (e.g. mesh sizes, closed seasons/areas) intended to promote long-term sustainability of their populations. The scientific advice for making management decisions about international fisheries primarily comes from the International Council for the Exploration of the Sea (Daw & Gray, 2005; ICES, 2005a). Management of the fisheries is partly disaggregated spatially to reflect local differences in both the fisheries and species biology (e.g. growth rates, maturity, migration patterns). As a result, independent quotas are assigned for different populations of the same species in the Baltic. The Baltic itself is, therefore, subdivided into subdivisions for administrative purposes (Fig. 1).

The effects of climate and hydrographic variability on early lifehistory stages documented above can have impacts at population levels and therefore how fisheries are managed. For example, cod recruitment in the eastern Baltic Sea decreased during the 1980s because of inadequate salinity and oxygen conditions, and has remained low except for 1–2 years following the major inflows in 1993 and 2003 (ICES, 2005a). The stock has still not recovered to long-term average abundance (ICES, 2005a). This example indicates that fishing closures or major quota reductions will not necessarily ensure population recovery if environmental and other factors have deteriorated from those observed when the stock biomass was increasing or high. An analogous example is the central Baltic dab population which has completely collapsed and will not likely recover unless hydrographic conditions improve substantially in spawning areas (Temming, 1989; Nissling *et al.*, 2002). Other examples of failed population recoveries (due to various causes), despite fishing bans or major reductions, exist in the literature (Caddy & Agnew, 2004). On the other hand, continued exploitation of eastern Baltic cod in the presence of detrimental environmental conditions will accelerate the biomass decline induced by poor recruitment and will delay and possibly prevent a recovery of the Baltic cod population at improved environmental conditions (ICES, 2006a).

Alternatively, when environmental conditions improve, higher catch levels can be sustained because fish production increases. This situation seems to exist presently for Baltic sprat whose recruitment is positively related to sea temperature (Fig. 4). This knowledge has been used to simulate how fishing and environmental variability jointly affect the risk for population decline. For example, assuming current fishing mortalities under warm temperatures typical for the late 1980s–1990s, there is $<0.1\%$ probability that the population during the next 10 years will fall to levels which would require implementation of major quota reductions (Fig. 8). In contrast, if fishing occurred at a precautionary level (i.e. F_{PA}, which would be a 20% increase over current levels) and if temperatures fall to levels observed in the mid-1970s–1980s, then the risk for serious population decline increases to nearly 20% within 10 years. The range of fishing yields, therefore, depends on both a sufficiently large spawner population to ensure high levels of egg production, and an environment that promotes survival of offspring. This result has also been obtained in a similar modelling analysis of the 10-year development of the eastern Baltic cod stock under different environmental (i.e. salinity-oxygen conditions in cod spawning areas) and spawner biomass situations (ICES, 2003b).

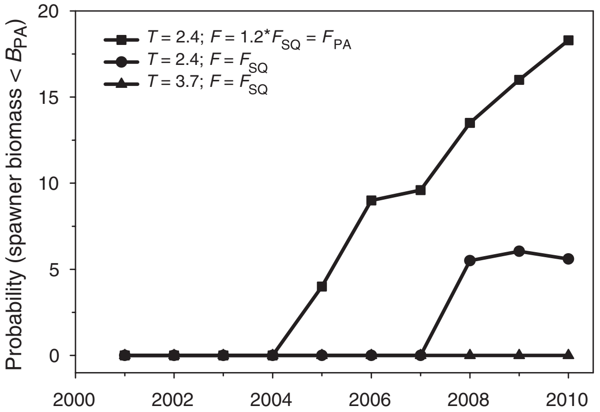

Fig. 8 Probability that simulated sprat spawner biomass falls below the precautionary approach biomass ($B_{PA} = 275\,000$ tonnes) under different temperature and exploitation scenarios. The simulations assume that recruitment depends on both temperature and spawner biomass. ▲, temperature = 3.7° (mean temperature during 1973–1999) and status quo exploitation during 1998–2000 (F_{SQ});. ●, temperature = 2.4° (mean temperature during 1973–1999 − 1 SD) and status quo exploitation during 1998–2000; squares: temperature = 2.4° and 1.2 × status quo exploitation during 1998–2000 ($1.2 \times F_{SQ}$; reference period for F_{SQ} was 1998–2000). See MacKenzie & Köster (2004) for details. PA, precautionary approach; SQ, status quo; F, fishing mortality rate. Reproduced with permission from Ecological Society of America.

A look ahead to 2100 and beyond

Current scientific policy and consensus suggests that there will be at least three major drivers of ecosystem change in the Baltic Sea during the coming decades. One driver will be that associated with climate change (IPCC, 2001; BACC, 2006), including warmer temperatures, increased precipitation (Döscher & Meier, 2004; Räisänen *et al.*, 2004; Meier *et al.*, 2006) and possible changes in wind direction and speed (BACC, 2006; Meier, 2006). The second driver, if fully implemented, will be a reduction in fishing mortality as a part of the EU's obligations to promote long-term sustainable fishing (EU, 1998; Daw & Gray, 2005) and to support international agreements on Precautionary Approach to Fishing (FAO, 1995), the protection of biodiversity (UN, 1992, 2002) and the ecosystem approach to fisheries management (Gislason *et al.*, 2000). The latter driver should lead to changes in the fish community, population structure and food web interactions. The third driver, again if fully implemented, will be an overall reduction in nutrient loading (Gren *et al.*, 2000). In addition, there will likely continue to be introductions of non-native species (Schiedek, 1997; ICES, 2004), including fish (Sapota & Skora, 2005). The occurrence of introductions and their functional consequences for the Baltic ecosystem and food webs are difficult to predict (Leppäkoski *et al.*, 2002).

These driving forces (climate change, fishing, eutrophication, species invasions) will interact with each other, and even in isolation would have major and complex impacts on the Baltic ecosystem. However, forecasting how fish populations will respond to the *combination* of these changes will require much greater understanding of how food webs are structured than is presently available (MacKenzie *et al.*, 2002). A few examples based only (and perhaps naively) on how climate change might affect fish populations will illustrate some of the uncertainties and complexities involved.

Climate change over the next 70–100 years is expected to raise sea levels by 20–50 cm, increase water temperatures and precipitation in northern Europe and change the seasonal distributions of warming, cooling and precipitation (IPCC, 2001; Räisänen *et al.*, 2004; BACC, 2006; Meier, 2006; MacKenzie & Schiedek, 2007). The rise in sea level will submerge some low-lying coastal areas. As a result the area of shallow water habitat for coastal species and size of nursery areas for juvenile fish of offshore species could potentially increase.

Regarding sea temperatures, recent numerical model experiments using a regional coupled ocean–atmosphere model driven by global circulation models show that mean annual surface temperature (SST) in the Baltic can be expected to increase during the 21st century by 2–3 °C under the IPCC A2 and B2 scenarios for future global atmospheric concentrations of CO_2 (Döscher & Meier, 2004; Meier, 2006). Even larger increases in SST using the same models and CO_2 scenarios are likely in parts of the Baltic during some seasons (e.g. a rise of 3–4 °C in spring–summer in the central Baltic; Fig. 9).

Regarding salinity, past observations (Hänninen *et al.*, 2000) and ocean-climate process modelling (Omstedt *et al.*, 2004) show that higher precipitation leads to lower salinity in the Baltic Sea. While future warmer tempera-

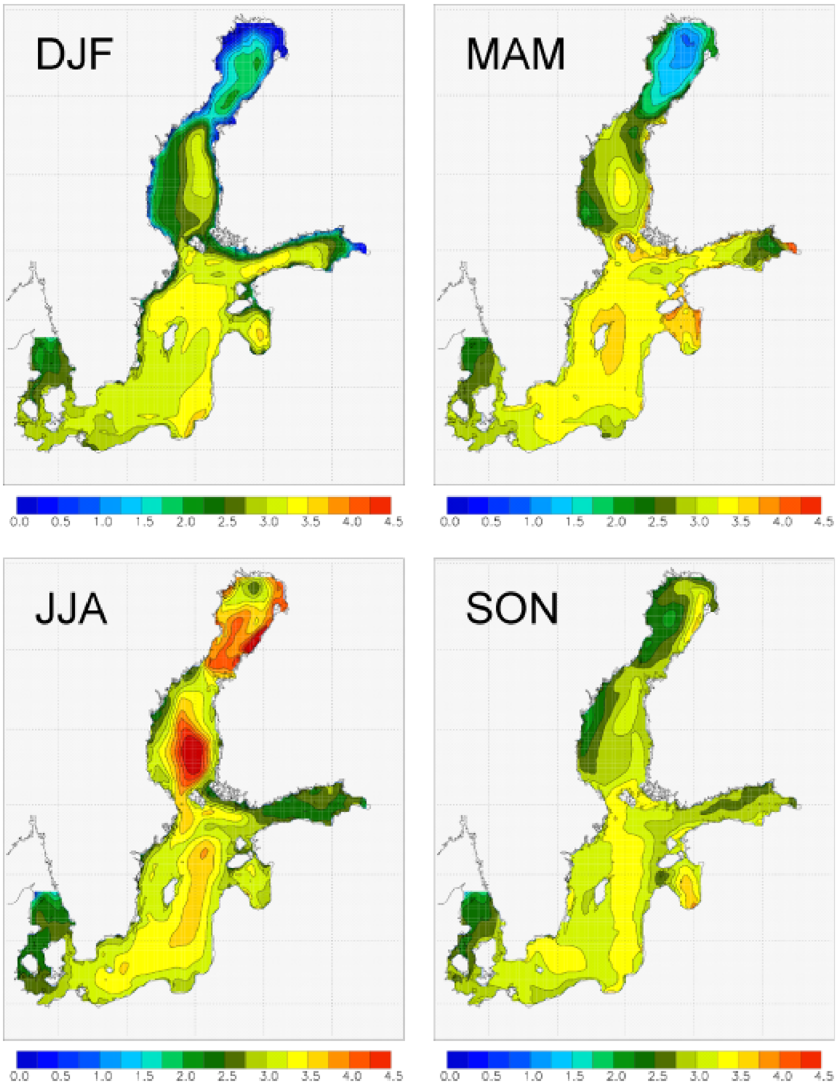

Fig. 9 Average sea surface temperature in the Baltic Sea during 2071–2100 for the four seasons of the year as estimated from a series of numerical model experiments using a regional coupled ocean–atmosphere model driven by global circulation models under the IPCC A2 and B2 scenarios for future global atmospheric concentrations of CO_2 (Meier, 2006). Note that the colour scale differs among the panels. Each panel is an ensemble average based on outputs from six different combinations of models and scenarios (see Döscher & Meier, 2004 for details). Reproduced with permission from Alliance Communications Group, a divisions of Allen Press Inc.

tures will lead to higher rates of evaporation (Meier, 2006) and potentially could in principal balance the increase in precipitation, this situation is not likely for the Baltic region (Meier, 2006; Meier *et al*., 2006). Here, salinity is expected to decrease (Fig. 10) because the increase in precipitation will exceed the increase in evaporation (Meier, 2006). These changes in salinity are evident in a multimodel ensemble approach using seven different regional models, five global models and two different CO_2 scenarios (Meier *et al*., 2006). The magnitude of the expected decrease in salinity (7–47%) will differ spatially and is predicted to be largest in the central Baltic (ICES Subdivisions 25–28) and the Belt Sea (ICES Subdivision 22) (Meier, 2006; Meier *et al*., 2006).

The combined effects of changes in temperature, precipitation and salinity, and possibly wind will influence circulation in the Baltic. In the past, reduced river runoff has been shown to promote inflows by reducing Baltic sea level and by intensifying deep currents flowing into the Baltic (Schinke & Matthäus, 1998). An increase in precipitation and runoff during the 21st century, as is forecasted for the Baltic watershed (Meier, 2006; Meier *et al*., 2006), and a change in the seasonality of runoff, could, therefore, have opposite effects and reduce the frequency of major Baltic inflows. The increase in precipitation will enhance the surface outflow of freshwater from the Baltic to the Kattegat and North Sea. Moreover, the recent occurrence of strong inflows during warm summers (2002 and 2003) may also be a Baltic response to global warming (Feistel *et al*., 2004).

Wind conditions directly and indirectly affect Baltic fish populations. These effects include for example, impacts on transport of fish larvae (Hinrichsen *et al*., 2005a, b) and on food production for fish larvae via variations in coastal upwelling (Gidhagen, 1986). If future climate change leads to changes in wind-induced circulation, or if the expected changes in temperature and salinity increase the sensitivity of Baltic circulation to wind conditions, then larval fish ecology could be impacted. However, the projections of future wind conditions in the Baltic regions are very uncertain and differ widely among models (BACC, 2006; Meier *et al*., 2006). As a result, we cannot specify whether future wind conditions will have beneficial or detrimental effects on fish ecology.

Considered in isolation, the consequences of the changes in temperature (warmer) and salinity (lower) on the major fish populations may be *relatively* easy to forecast. For example, warm temperatures improve reproductive success in fish species near their northern limits of distribution, including some northern Baltic herring populations (Kornilovs, 1995; Axenrot & Hansson, 2003), the Baltic sprat population (MacKenzie & Köster, 2004; Baumann *et al*., 2006) and possibly the Kattegat sole population. However, an expected reduction in average salinity (Meier, 2006) will restrict spawning habitats of these and other marine-brackish water species (Nissling *et al*., 2002; Ojaveer & Kalejs, 2005). As a result the beneficial effects of higher temperature on the reproduction of some species and populations will

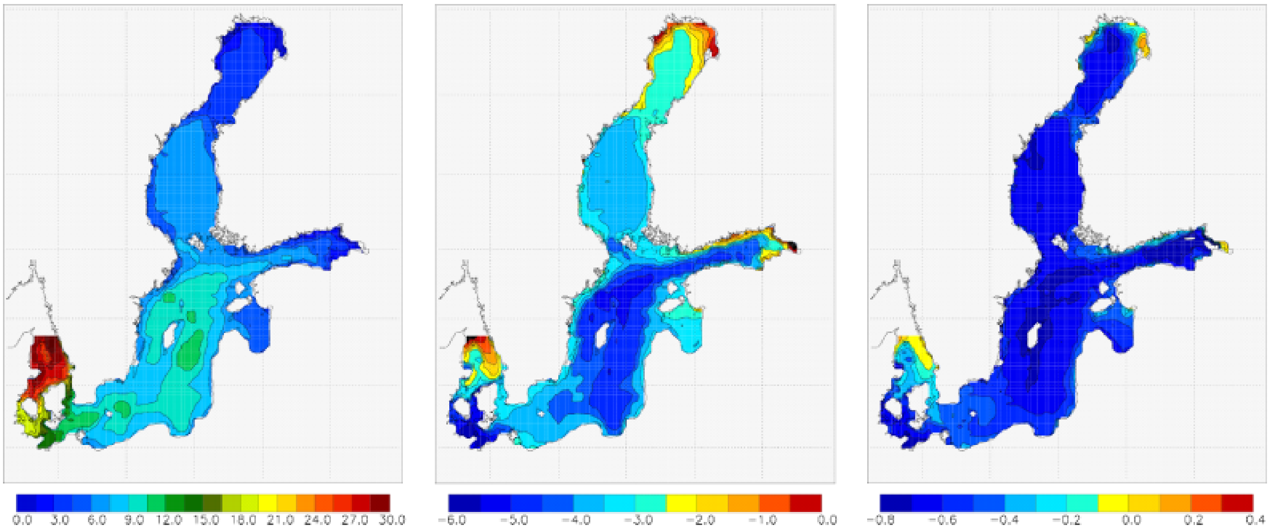

Fig. 10 Vertically averaged salinity (‰) in the Baltic Sea (Meier, 2006). The left panel shows the spatial distribution of salinity for the control period 1961–1990, as derived from the Rossby Centre Regional Climate – Ocean model (colour scale is from 0‰ to 30‰ in intervals of 1.5‰). The middle and right panels show the difference in salinity between the control period and the scenario period (2071–2100) as estimated by two different models for the IPCC A2 CO_2 scenario (middle panel, global forcing of the Rossby regional model was provided by the ECHAM4/OPYC3 model; right panel, global forcing of the Rossby regional model was provided by the HadAM3H model). See Meier (2006) for details. Reproduced with permsission from Springer-Verlag Heidelberg.

be partly counteracted by the reduction in salinity. The relative importance of these two effects is not presently clear, partly because at the temporal and spatial scales relevant for fish life-history it is not known by how much temperatures will rise, by how much salinities might fall, nor how some of the various fish species would react physiologically and genetically (ICES, 2005b) to these changes. These concepts are summarized schematically in Fig. 11 and require further investigation.

Similarly, it is difficult to forecast how the eastern Baltic cod population will react to future climate change. Cod egg survival and recruitment is improved when salinities and oxygen concentrations in deep water are both high (Plikshs *et al*., 1993; Vallin *et al*., 1999; Köster *et al*., 2003a). The anticipated reduction in salinity (Meier, 2006; Meier *et al*., 2006) will further constrain cod spawning habitats (Plikshs *et al*., 1993; Vallin *et al*., 1999; MacKenzie *et al*., 2000). Moreover higher water temperatures will increase oxygen consumption rates in the deep parts of the Baltic where cod eggs live, thereby further reducing the size of cod spawning habitats (MacKenzie *et al*., 1996). Higher water temperatures in winter in the western Baltic will also reduce oxygen concentrations because of the lower solubility of oxygen in warmer water flowing from the western Baltic to eastern Baltic deep basins during winter (Hinrichsen *et al*., 2002b). Although nutrient loading is expected to decrease over the coming decades (Gren *et al*., 2000), large pools of nutrients and organic matter in the deep water and sediments of the Baltic (Conley *et al*., 2002) and its watershed will persist for many years (HELCOM, 1996). As a result, oxygen conditions in the deep layers will only slowly improve as nutrient loading rates decrease. Lastly, if predators of cod eggs (e.g. herring, sprat; Köster & Möllmann, 2000a) benefit more from climate change than cod itself, then predator–prey interactions among the fish species will also suppress the cod population.

Consequently, the present clupeid-dominated regime in the Central Baltic fish community (Köster *et al*., 2003b; Alheit *et al*., 2005) could become stabilized. However, changes in exploitation have a strong potential to alter food web structure and thus to modify the outcome of climate-induced changes. For example, a lower exploitation of cod would increase the chance of high reproductive success despite a generally low carrying capacity. Surviving cod offspring would increase predation pressure on sprat, whose biomass would fall, thereby lowering also the predation by sprat on cod eggs and *Pseudocalanus* sp. This interaction would have a feedback because the reduced sprat biomass would lead to higher reproductive success of cod and enhanced feeding conditions for cod larvae, as well as juvenile and adult herring and sprat. Clupeid growth rates would also increase (Fig. 5). However, the earlier considerations on the reproductive biology of cod suggest that the eastern Baltic cod stock will suffer under future climate change and could collapse completely, as has happened previously for dab and plaice in the central Baltic (Temming, 1989; Nissling *et al*., 2002), unless some of these negative effects are counteracted by both lower cod fishing mortality rates and an increase in inflow intensity and frequency.

The interaction between climate change and eutrophication will also affect benthic fish in shallow and coastal areas of the Baltic, including much of the western Baltic, Belt Sea and Kattegat. These areas have in the past been subjected to frequent episodes of anoxia in the late summer and early autumn (Karlson *et al*., 2002).

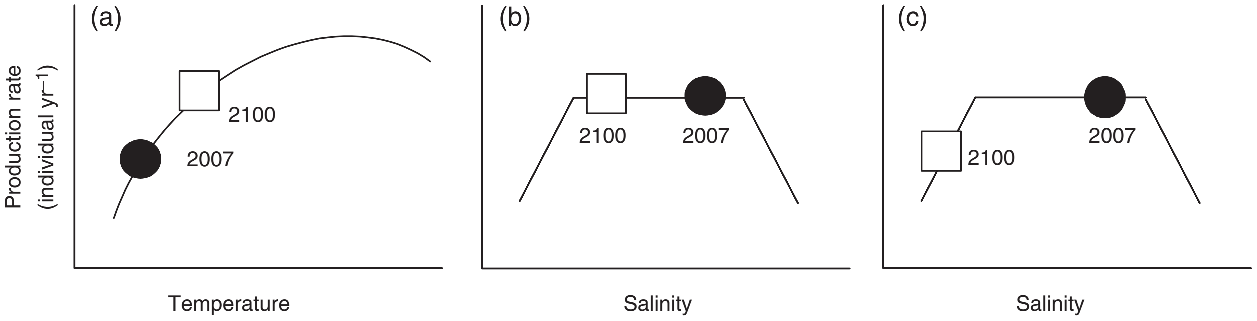

Fig. 11 Schematic representation of how changes in temperature and salinity could affect recruitment (the annual rate of production of new individuals, $n\,\mathrm{yr}^{-1}$) of a species throughout its entire geographic range (solid lines on each panel), and specifically in the Baltic Sea. Circles shown on panels represent average contemporary (2007) temperature (a) or salinity (b, c) experienced by a Baltic population relative to the ranges experienced by this species throughout its entire geographical range. The squares in each panel depict future (2100) conditions experienced by the species in the Baltic Sea. (a) Depicts a species whose geographical distribution in the Baltic Sea is at the cold end of its thermal range. (b and c) show the present and expected salinity ranges experienced by the species in the Baltic and how recruitment is affected by these salinity ranges (e.g. via direct physiological effects on eggs or larvae). (c) is similar to (b), except that the expected salinity range is instead assumed to be sufficiently low to affect recruitment.

Given that anoxia severity in these areas is partly temperature dependent (Rasmussen *et al.*, 2003), the frequency and extent of anoxic events will likely increase with higher temperatures associated with climate change. These events cause direct mortalities of fish and their prey (Karlson *et al.*, 2002), and cause fish and prey to relocate to other areas where feeding, growth and survival rates may be lower (Pihl, 1994). Hence, benthic fish species such as cod, plaice, sole and flounder in these areas may experience higher frequencies of anoxia-related declines than in other areas; these impacts are, however, less likely to affect pelagic species such as herring, sprat and possible immigrants such as anchovy or sardine.

Despite the uncertainties and contrasting effects of how climate change might affect the fish community in the Baltic region, two general predictions are possible at the present time. First, a systematic change in the hydrographic environment, for example towards warmer, fresher conditions (Räisänen *et al.*, 2004; BACC, 2006; Meier *et al.*, 2006), will lead to relative changes in the existing species composition and their distribution within the Baltic. For example, the ranges of marine species can be expected to contract, and the habitats of cold-adapted species whose habitats are presently restricted by warm temperatures, such as salmon (Alm, 1958), can also be expected to shrink.

Second, a decrease in salinity will inhibit invasion by new species unless they are tolerant to these conditions (Elmgren & Hill, 1997; Schiedek, 1997; Leppäkoski *et al.*, 2002). Hence, among those temperate marine fish species which have recently been expanding their geographic ranges northwards (Brander *et al.*, 2003; Genner *et al.*, 2004; Beare *et al.*, 2005; Perry *et al.*, 2005), only a small number will successfully colonize the Baltic because few will be able to reproduce successfully in its low salinity (Ojaveer & Kalejs, 2005). A reduction in salinity, particularly in the Belt Sea (Meier, 2006) where the horizontal salinity gradient in the Baltic is largest (Voipio, 1981; HELCOM, 2002), will, therefore, lead to further restrictions in range and biomass of existing 'marine' fish species such as plaice, cod, sole and sprat, which may not be compensated by immigration of new species. Moreover, recovery of other marine species which have already collapsed (e.g. dab) will be inhibited or perhaps prevented by further reduction in salinity. These processes could lead to a decrease in the overall species richness and biodiversity of the Baltic fish community. Whether the decrease in production and biomass of marine species will be offset completely by increases by freshwater species (thereby maintaining a similar overall level of fish production), is unclear because of uncertainties in how individual species will respond to climate change, interactions among species within the foodweb and rates of adaptation by species living in the Baltic Sea and also by those which will immigrate and invade.

The changes in species composition and distribution will differ spatially, depending on each species' physiological tolerance for low salinity and the existence of saline water masses having sufficient oxygen concentrations to sustain life stage development. For example, sprat will still be able to spawn successfully in the southern and central Baltic, but its spawning habitat will likely become further restricted in northern and eastern areas; in contrast the spawning habitats of some coastal freshwater and brackish species such as perch and pikeperch could expand. The salinity and temperature-mediated changes in spatial distribution will affect fishing opportunities and catches in the Baltic: fishing fleets whose target species are the more marine species will have to relocate to different (i.e. higher salinity) fishing areas, or remain in present locations and target the existing and any immigrating species which tolerate brackish conditions.

Climate change will not only alter the abiotic conditions in the Baltic, and therefore only the physiological suitability of existing fish habitats. Changes in salinity and temperature, as well as seasonal heat and water budgets, will also lead to changes in stratification and, therefore, the characteristics of food webs (e.g. species composition of the plankton and benthic communities, timing and duration of spring blooms). For example, the predicted reduction in ice cover (and therefore improved underwater light conditions) should lead to an earlier onset of stratification and the spring phytoplankton bloom (BACC, 2006). However, the warmer temperatures will also lead to an intensification of stratification, and therefore, less vertical mixing of nutrients into the photic zone during the postbloom period. In the open ocean, increased stratification in the recent (post-1999) warm period has reduced primary production (Behrenfeld *et al.*, 2006). As primary production rates are positively related to fish production and yield in marine ecosystems (Nixon, 1988; Nielsen & Richardson, 1996; Ware & Thomson, 2005), overall fish production might decrease if stratification increases. These effects might be relatively more pronounced in the southern Baltic, which is less frequently covered by ice.

Future climate change will interact with eutrophication in the Baltic Sea. The projected increase in annual and winter precipitation will lead to increased runoff of nutrients (nitrogen and phosphorous) stored in the Baltic watershed (BACC, 2006). This supply could offset the negative effects of increased stratification on primary (and probably fish) production. It is, therefore, uncertain how the combined effects of climate change and eutrophication will affect lower trophic levels and overall fish production, These topics are, therefore, active areas of Baltic research (BACC, 2006; Dippner, 2006; ICES, 2006b).

Changes in (past) climate clearly do affect Baltic plankton and benthic communities. Analyses of long-term monitoring data demonstrate how the species composition and biomass of the zooplankton (Viitasalo *et al.*, 1995; Dippner *et al.*, 2000; Möllmann *et al.*, 2000) and benthic (HELCOM, 2002) communities in the Baltic covaries with salinity and temperature. Changes in these communities affect feeding and growth of herring and cod larvae, juveniles and adults (Uzars, 1994; Casini *et al.*, 2004). Recent analysis of Continuous Plankton Recorder data shows that climate variability is decoupling links between trophic levels in plankton food webs in the North Sea and wider northeast Atlantic (Edwards & Richardson, 2004). The decoupling is due to species-specific differences in phenological responses to increased temperature (Edwards & Richardson, 2004). Similar studies have not yet been conducted in the Baltic Sea. Decoupling between plankton trophic levels could be detrimental for fish production, particularly if the decouplings include the match between larval fish feeding and production of preferred zooplankton species (Platt *et al.*, 2003; Edwards & Richardson, 2004).

These changes in food web structure and functioning at lower trophic levels have so far not been investigated in detail in the Baltic Sea but will likely have important impacts on the fish community and deserve further study. These effects of climate change, and possible effects of lowered pH (Orr *et al.*, 2005), on lower trophic levels require more investigation.

Fisheries management during 21st century climate change

There are still many uncertainties associated with predicting how climate change will affect fish production and fishing activities in estuarine ecosystems like the Baltic Sea. These uncertainties relate to physiological and ecological responses to the expected abiotic changes in local habitats, the specific functional role of local regions of the Baltic in the lifehistories (e.g. as spawning, nursery or adult feeding areas) of individual fish species and the uncertainty associated with regional models of future climate change (Meier, 2006). The implications of climate change for the management of Baltic fisheries are, therefore, difficult to assess at the present time.

As a first step, however, it can be recognized that many exploited populations and ecosystems are now (or are becoming) regulated according to benchmark (reference) criteria. These criteria are sometimes known as Ecological Quality Objectives (Whitfield & Elliott, 2002; ICES, 2003a) or biological reference points (Collie & Gislason, 2001), and can be values of indicator variables (e.g. biomass of spawning fish of a given species in a local ecosystem, or area of benthic habitat exposed to anoxia in summer) for elements of an ecosystem which society wishes to protect or promote. Many of these benchmarks are typically defined from past observations. If future climate change erodes the ecological basis for the definition of these criteria (e.g. by significantly changing species' habitats or the functionality of ecosystems), then new criteria will have to be developed which will be relevant under future climatic conditions.

The sensitivity of many existing reference criteria to climate change is presently unknown and will need to be investigated (Kell *et al.*, 2005). This could be done in ways similar to those used to explore how biological reference points for cod, herring and sprat in the Baltic are affected by multispecies interactions (Collie & Gislason, 2001). Revisions will require an increase in process knowledge of both the climate–ocean system and the biota, and incorporation of this knowledge into climatically driven ecological scenario models and management perspectives (Kuikka *et al.*, 1999; Eide & Heen, 2002; Cook & Heath, 2005; Sissener & Bjørndal, 2005). Until this has happened the added uncertainty from climate change will either require additional precaution to be incorporated in existing management plans or more robust reference criteria to be developed and applied. In the case of exploited fish populations, reference levels could be based on levels of fishing mortality ensuring that local populations have a high probability of being sustainably exploited, rather than being based on historically defined levels of spawner biomass (Kell *et al.*, 2005). This approach is being attempted for the eastern Baltic cod stock (ICES, 2005a). Hence, fish populations whose biomasses fall, partly due to climate-related changes in spatial distribution, would become exposed to much lower, including zero, fishing mortality. Actions such as these could be components of long-term management strategies for adapting to the effects of future climate change on fisheries.

As an example of how climate change and fishing might affect Baltic fish populations, it is useful to consider cod, and in particular how its intraspecific genetic diversity might change in future. The eastern Baltic cod population (ICES Subdivisions 25–32) is genetically distinct from other cod populations in the Atlantic (Nielsen *et al.*, 2001) and physiologically adapted for reproduction in the brackish salinity of the Baltic (Nissling & Westin, 1997). However, in some years even these adaptations are insufficient to ensure reproductive success (Köster *et al*., 2005). Continued high fishing pressure in combination with frequent periods of detrimental environmental conditions for egg survival suggests that this population may collapse (Jonzen *et al*., 2002; ICES, 2005a), as happened to the central Baltic dab and plaice stocks during the 20th century (Temming, 1989). If the eastern Baltic cod population were to collapse, then recovery would be very slow or perhaps impossible even under low or no fishing mortality. Long recovery time is expected because the local genotypes (Nielsen *et al*., 2001) would be eliminated and because cod immigrating from more saline areas (e.g. Belt Sea, Kattegat) are not adapted to reproduce in brackish environments (Vallin *et al*., 1999). Moreover, evolutionary rates of genetic change by fish populations are generally likely to be slower than the rates of environmental change expected in the 21st century (ICES, 2005b). It is likely that reproduction by the eastern Baltic cod population will become increasingly stressed during the 21st century if salinities fall and temperatures rise. As a consequence, fishing mortality rates should be reduced to low levels, e.g. a target fishing mortality of 0.3 or less as suggested by ICES (2006a), to help conserve this local population.

Conclusions

We have identified some of the main consequences of climate change for the Baltic Sea fish community and its fisheries. The expected combination of a rise in temperature and a decrease in salinity will result in a decrease in abundance and habitat occupied by marine species in the Baltic. In contrast, habitats of freshwater species, particularly those whose growth or survival are enhanced by warmer temperatures, will increase. These changes in the fish community will affect fisheries and may require modifications to existing fisheries management policies. The specific hydrographic features of the Baltic Sea, and how these will change in the future as a result of climate change, make longer-term predictions of fish stock development uncertain. The uncertainty arises because at least *two* key abiotic factors (i.e. salinity and temperature) will change simultaneously and because these changes will have *counteracting* effects on biological phenomena. The relative sensitivity of fish ecology including species interactions to concurrent changes in both variables is not yet precisely known. Furthermore, climate change will directly via atmospheric forcing and indirectly via the changed salinity balance affect other key hydrographic characteristics, such as hydrodynamics (e.g. inflows into the Baltic and thus oxygen concentrations in deeper water areas). New process knowledge of how fish production and food webs are affected by both fishing and climate variability, together with historical information about fishing practices and yields under different combinations of environmental variables, will improve evaluations of how fish stocks and fisheries might develop and can be managed under climate changes.

Acknowledgements

This work has been conducted as part of a Danish project on climate change and aquatic ecosystems (CONWOY; Danish National Science Foundation: www.conwoy.ku.dk), the Census of Marine Life History of Marine Animal Populations project (www.hmap.org), European Union 6th Framework Programme Networks of Excellence on Marine Biodiversity and Ecosystem Functioning (MARBEF; www.marbef.org, contract no. GOCE-CT-2003-505446) and Ocean Ecosystem Analysis (Eur-oceans; www.eur-oceans.org), and GLOBEC. This publication is contribution number MPS-07012 of MarBEF. A preliminary version of this manuscript was produced for the 2006 BALTEX Assessment of Climate Change for the Baltic Sea Basin (BACC). We thank Einar Eg Nielsen (DIFRES, Silkeborg, Denmark), Markus Meier (Rossby Centre, Norrkjöping, Sweden), Henn Ojaveer (Estonian Marine Institute, University of Tartu) and Doris Schiedek (Institute for Baltic Sea Research, Warnemuende, Germany) for discussions and assistance.

References

Albert A, Vetemaa M, Saat T (2004) Effects of salinity on the development of Peipsi whitefish *Coregonus lavaretus maraenoides* Poljakow embryos. *Annales Zoologica Fennica*, **41**, 85–88.

Alheit J, Möllmann C, Dütz J, Kornilovs G, Loewe P, Mohrholz V, Wasmund N (2005) Synchronous ecological regime shifts in the central Baltic and the North Sea in the late 1980s. *ICES Journal of Marine Science*, **62**, 1205–1215.

Alm G (1958) Seasonal fluctuations in the catches of salmon in the Baltic. *Journal du Conseil*, **23**, 399–433.

Axenrot T, Hansson S (2003) Predicting herring recruitment from young-of-the-year densitites, spawning stock biomass, and climate. *Limnology and Oceanography*, **48**, 1716–1720.

BACC. (2006) *Assessment of climate change for the Baltic Sea Basin – the BACC Project (International Conference, Gothenberg, Sweden, May 22–23, 2006)*. IKSS, Gestacht, Germany.

Bagge O, Thurow F, Steffensen E, Bay J (1994) The Baltic cod. *Dana*, **10**, 1–28.

Bakun A (1996) *Patterns in the Ocean: Ocean Processes and Marine Population Dynamics*. Cal. Sea Grant System, NOAA and Centro de Investigaciones Biologicas del Noroeste, La Paz, BCS, Mexico.

Barnett TP, Pierce DW, AchutaRao KM, Gleckler PJ, Santer BD, Gregory JM, Washington WM (2005) Penetration of human-induced warming into the world's oceans. *Science*, **309**, 284–287.

Baumann H, Hinrichsen HH, Mollmann C, Koster FW, Malzahn AM, Temming A (2006) Recruitment variability in Baltic Sea sprat (*Sprattus sprattus*) is tightly coupled to temperature and transport patterns affecting the larval and early juvenile stages. *Canadian Journal of Fisheries and Aquatic Sciences*, **63**, 2191–2201, ISI:000241585400006.

Beare D, Burns F, Jones E, Peach K, Reid D (2005) Red mullet migration into the northern North Sea during late winter. *Journal of Sea Research*, **53**, 205–212.

Beaugrand G, Brander KM, Lindley JA, Souissi S, Reid PC (2004) Plankton effect on cod recruitment in the North Sea. *Nature*, **426**, 661–664.

Behrenfeld MJ, OMalley RT, Siegel DA *et al*. (2006) Climate-driven trends in contemporary ocean productivity. *Nature*, **444**, 752–755.

Beyer JE, Lassen H (1994) The effect of size-selective mortality on the size-at-age of Baltic herring. *Dana*, **10**, 203–234.

Bohling P, Hudd R, Lehtonen H, Karas P, Neuman E, Thoresson G (1991) Variations in year-class strength of different perch (*Perca fluviatilus*) populations in the Baltic Sea with special reference to temperature and pollution. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 1181–1187.

Brander KM, Blom G, Borges MF *et al*. (2003) Changes in fish distribution in the eastern North Atlantic: are we seeing a coherent response to changing temperature? *ICES Marine Science Symposia*, **219**, 260–273.

Caddy JF, Agnew DJ (2004) An overview of recent global experience with recovery plans for depleted marine resources and suggested guidelines for recovery planning. *Reviews in Fish Biology and Fisheries*, **14**, 43–112.

Cardinale M, Arrhenius F (2000) Decreasing weight-at-age of Atlantic herring (*Clupea harengus*) from the Baltic Sea between 1986 and 1996: a statistical analysis. *ICES Journal of Marine Science*, **57**, 882–893.

Cardinale M, Casini M, Arrhenius F (2002) The influence of biotic and abiotic factors on the growth of sprat (*Sprattus sprattus*) in the Baltic Sea. *Aquatic Living Resources*, **15**, 273–281.

Casini M, Cardinale M, Arrhenius F (2004) Feeding preferences of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) in the southern Baltic Sea. *ICES Journal of Marine Science*, **61**, 1267–1277.

Casini M, Cardinale M, Hjelm J (2006) Inter-annual variation in herring, *Clupea harengus*, and sprat, *Sprattus sprattus*, condition in the central Baltic Sea: what gives the tune? *Oikos*, **112**, 638–650.

Chavez FP, Ryan J, Lluch-Cota SE, Ñiquen M (2003) From anchovies to sardines and back: multidecadal changes in the Pacific Ocean. *Science*, **299**, 217–221.

Collie JS, Gislason H (2001) Biological reference points for fish stocks in a multispecies context. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 2167–2176.

Conley DJ, Humborg C, Rahm L, Savchuk OP, Wulff F (2002) Hypoxia in the Baltic Sea and basin-scale changes in phosphorus biogeochemistry. *Environmental Science and Technology*, **36**, 5315–5320.

Cook RM, Heath MR (2005) The implications of warming climate for the management of North Sea fisheries. *ICES Journal of Marine Science*, **62**, 1322–1326.

Dahl J, Dannewitz J, Karlsson L, Petersson E, Löf A, Ragnarsson B (2004) The timing of spawning migration: implications of environmental variation, life history and sex. *Canadian Journal of Zoology*, **82**, 1864–1870, doi: 10.1139/Z04-184.

Daw T, Gray T (2005) Fisheries science and sustainability in international policy: a study of failure in the European union's common fisheries policy. *Marine Pollution*, **29**, 189–197.

Dippner JW (2006) Future aspects in marine ecosystem modelling. *Journal of Marine Systems*, **61**, 246–267, ISI:000239868000009.

Dippner JW, Kornilovs G, Sidrevics L (2000) Long-term variability of mesozooplankton in the Central Baltic Sea. *Journal of Marine Systems*, **25**, 23–31.

Döscher R, Meier HEM (2004) Simulated sea surface temperature and heat fluxes in different climates of the Baltic Sea. *Ambio*, **33**, 242–248.

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

EEA. (2002) *Biodiversity indicators for European seas*. European Environment Agency, Copenhagen http://www.eea.org

Eide A, Heen K (2002) Economic aspects of global warming – a study of the fishing industry in North Norway. *Fisheries Research*, **56**, 261–274.

Elmgren R, Hill C (1997) Ecosystem function at low biodiversity – the Baltic example. In: *Marine Biodiversity – Patterns and Processes* (eds Ormond RG, Gage JD, Angel MV), pp. 319–336. Cambridge University Press, Cambridge.

Enghoff IB (1999) Fishing in the Baltic region from the 5th century BC to the 16th century AD: evidence from fish bones. *Archaeofauna*, **8**, 1–52.

EU (1998) *The common fisheries policy*. European Commission, The official EU website http://europa.eu.int/comm/fisheries/doc_et_publ/cfp_en.htm

FAO (1995) Precautionary approaches to fisheries. Part 1: guidelines on the precautionary approach to capture fisheries and species introductions. *FAO Fisheries Technical Paper*, **350**, 1–52.

Feistel R, Nausch G, Heene T, Piechura J, Hagen E (2004) Evidence for a warm water inflow into the Baltic Proper in summer 2003. *Oceanologia*, **46**, 581–598.

Flinkman J, Aro E, Vuorien I, Viitasalo M (1998) Changes in northern Baltic zooplankton and herring nutrition from 1980s to 1990s: top-down and bottom-up processes at work. *Marine Ecology Progress Series*, **165**, 127–136.

Genner MJ, Sims DW, Wearmouth VJ, Southall EJ, Southward AJ, Henderson PA, Hawkins SJ (2004) Regional climatic warming drives long-term community changes of British marine fish. *Proceedings of the Royal Society of London, Series B*, **271**, 655–661.

Gidhagen L (1986) Coastal upwelling in the Baltic Sea – satellite and in situ measurements of sea-surface temperatures indicating coastal upwelling. *Estuarine, Coastal and Shelf Science*, **24**, 449–462.

Gislason H, Sinclair M, Sainsbury K, O'Boyle R (2000) Symposium overview: incorporating ecosystem objectives within fisheries management. *ICES Journal of Marine Science*, **57**, 468–475.

Gren IM, Turner RK, Wulff F (2000) *Managing a Sea: The Ecological Economics of the Baltic*. Earthscan, London.

Hagen E, Feistel R (2005) Climatic turning points and regime shifts in the Baltic Sea region: the Baltic winter index (WIBIX) 1659–2002. *Boreal Environmental Research*, **10**, 211–224.

Hakala T, Viitasalo M, Rita H, Aro E, Flinkman J, Vuorinen I (2003) Temporal and spatial variation in the growth rates of

Baltic herring (*Clupea harengus membras* L.) larvae during summer. *Marine Biology*, **142**, 25–53.

Hänninen J, Vuorinen I, Hjelt P (2000) Climatic factors in the Atlantic control the oceanographic and ecological changes in the Baltic Sea. *Limnology and Oceanography*, **45**, 703–710.

HELCOM (1996) Third periodic assessment of the state of the marine environment of the Baltic Sea, 1989–1993, Background document. *Baltic Sea Environment Proceedings*, **64**, 1–252.

HELCOM (2002) *Environment of the Baltic Sea area 1994–1998 (Background Document)*. Helsinki Commission Baltic Marine Environment Protection Commission, Helsinki, Finland.

Hinrichsen H-H, John MS, Lehmann A, MacKenzie BR, Koster FW (2002b) Resolving the impact of short-term variations in physical processes impacting on the spawning environment of eastern Baltic cod: application of a 3-D hydrodynamic model. *Journal of Marine Systems*, **32**, 281–294, ISI:000176143600002.

Hinrichsen H-H, Kraus G, Voss R, Stepputtis D, Baumann H (2005a) The general distribution pattern and mixing probability of Baltic sprat juvenile populations. *Journal of Marine Systems*, **58**, 52–66, ISI:000233320200004.

Hinrichsen H-H, Möllmann C, Voss R, Köster FW, Kornilovs G (2002a) Biophysical modeling of larval Baltic cod (*Gadus morhua*) growth and survival. *Canadian Journal of Fisheries and Aquatic Sciences*, **59**, 1858–1873.

Hinrichsen H-H, Schmidt JO, Petereit C, Mollmann C (2005b) Survival probability of Baltic larval cod in relation to spatial overlap patterns with their prey obtained from drift model studies. *ICES Journal of Marine Science*, **62**, 878–885, ISI:000230998900005.

Holm P, Smith TD, Starkey DJ (2001) *The Exploited Seas: New Directions for Marine Environmental History.* Int. Maritime Econ. Hist. Assoc., Maritime Studies Research Unit, Memorial University of Newfoundland, St. John's, Newfoundland, Canada.

ICES (1997) *Report of the working group on the assessment of pelagic stocks in the Baltic*. ICES Conference Meeting 1997/Assess:12.

ICES (2003a) *Report of the ICES Advisory Committee on Ecosystems*. ICES, Copenhagen.

ICES (2003b) *Report of the study group on multispecies assessment in the Baltic*. ICES Conference Meeting 2003/H: 03.

ICES (2004) *Report of the working group on introductions and transfers of marine organisms*. ICES, Conference Meeting 2004/ACME:05.

ICES (2005a) *Report of the Baltic Fisheries Assessment Working Group*. ICES Conference Meeting 2005/ACFM:19.

ICES (2005b) *Report of the ICES working group on genetics in aquaculture and fisheries*, ICES Conference Meeting/F:01, 1–51.

ICES (2006a) *Report of the ICES Advisory Committee on Fisheries Management, Advisory Committee on the Marine Environment, and Advisory Committee on Ecosystems*. ICES Advice 2006 Books 1–10 (http://www.ices.dk/products/icesadvice.asp)

ICES (2006b) Report of the ICES Study Group on Baltic ecosystem model issues in support of the BSRP. *ICES Conference Meeting 2006/BCC:05*, 1–19.

IPCC (2001) Technical summary of the Working Group I report. In: *Climate Change 2001: The Scientific Basis* (eds Houghton JT, Ding Y, Griggs DJ *et al*.), pp. 21–83. Cambridge University Press, Cambridge, UK.

Jacobsen B (2006) *The influence of climate variability on the migration of two pelagic fish species, garfish (Belone belone Linné 1761) and Atlantic mackerel (Scomber scombrus Linné 1758) in Danish waters*, Master's thesis, Department of Marine Ecology, Biology Institute, University of Århus, Denmark.

Jonzen N, Cardinale M, Gardmark A, Arrhenius F, Lundberg P (2002) Risk of collapse in the eastern Baltic cod fishery. *Marine Ecology Progress Series*, **240**, 225–233.

Jørgensen HBH, Hansen MM, Bekkevold D, Ruzzante DE, Loeschcke V (2005) Marine landscapes and population genetic structure of herring (*Clupea harengus* L.) in the Baltic Sea. *Molecular Ecology*, **14**, 3219–3234.

Jutila E, Jokikokko E, Julkunen M (2005) The smolt run and postsmolt survival of Atlantic salmon, Salmo salar L., in relation to early summer water temperatures in the northern Baltic. *Ecology of Freshwater Fish*, **14**, 69–78.

Kallio-Nyberg I, Jutila E, Saloniemi I, Jokikokko E (2004) Association between environmental factors, smolt size and the survival of wild and reared Atlantic salmon from the Simojoki River in the Baltic Sea. *Journal of Fish Biology*, **65**, 122–134.

Karlson K, Rosenberg R, Bonsdorff E (2002) Temporal and spatial large-scale effects of eutrophication and oxygen deficiency on benthic fauna in Scandinavian and Baltic waters – a review. *Oceanography and Marine Biology. Annual Review*, **40**, 427–489.

Kell LT, Pilling GM, O'Brien CM (2005) Implications of climate change for the management of North Sea cod (*Gadus morhua*). *ICES Journal of Marine Science*, **62**, 1483–1491.

Kjellman J, Lappalainen J, Urho L, Hudd R (2003) Early determination of perch and pikeperch recruitment in the northern Baltic Sea. *Hydrobiologia*, **495**, 181–191.

Kornilovs G (1995) *Analysis of Baltic herring year–class strength in the Gulf of Riga*. ICES Conference Meeting 1995/J: 10.

Köster FW, Hinrichsen H-H, Schnack D *et al*. (2003a) Recruitment of Baltic cod and sprat stocks: identification of critical life stages and incorporation of environmental variability into stock-recruitment relationships. *Scientia Marina*, **67** (Suppl. 1), 129–154.

Köster FW, Möllmann C (2000a) Trophodynamic control by clupeid predators on recruitment success in Baltic cod? *ICES Journal of Marine Science*, **57**, 310–323.

Köster FW, Möllmann C (2000b) Egg cannibalism in Baltic sprat (*Sprattus sprattus* L.). *Marine Ecology Progress Series*, **196**, 269–277.

Köster FW, Schnack D (1994) The role of predation on early life stages of cod in the Baltic. *Dana*, **10**, 179–201.

Köster FW, Möllmann C, Hinrichsen H-H *et al*. (2005) Baltic cod recruitment – the impact of climate variability on key processes. *ICES Journal of Marine Science*, **62**, 1408–1425.

Köster FW, Möllmann C, Neuenfeldt S, St.John MA, Plikshs M, Voss R (2001) Developing Baltic cod recruitment models. I. Resolving spatial and temporal dynamics of spawning stock and recruitment for cod, herring and sprat. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 1516–1533.

Köster FW, Möllmann C, Neuenfeldt S *et al*. (2003b) Fish stock development in the central Baltic Sea (1976–2000) in relation to variability in the physical environment. *ICES Marine Science Symposia*, **219**, 294–306.

Kuikka S, Hilden M, Gislason H, Hansson S, Sparholt H, Varis O (1999) Modeling environmentally driven uncertainties in Baltic cod (*Gadus morhua*) management by Bayesian influence diagrams. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 629–641.

Landergren P (2001) Survival and growth rates of sea trout parr in fresh and brackish water. *Journal of Fish Biology*, **58**, 591–593.

Lappalainen J, Erm V, Kjellman J, Lehtonen H (2000) Size-dependent winter mortality of age-0 pikeperch (*Stizostedion lucioperca*) in Pernu Bay, the Baltic Sea. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 451–458.

Lappalainen J, Lehtonen H (1995) Year-class strength of pikeperch (*Stizostedion lucioperca* L.) in relation to environmental factors in a shallow Baltic bay. *Annales Zoologica Fennica*, **32**, 411–419.

Leppäkoski E, Gollasch S, Gruszka P, Ojaveer H, Olenin S, Panov V (2002) The Baltic Sea – a sea of invaders? *Canadian Journal of Fisheries and Aquatic Sciences*, **59**, 1175–1188.

Levitus S, Antonov JI, Wang J, Delworth TL, Dixon KW, Broccoli AJ (2001) Anthropogenic warming of earth's climate system. *Science*, **292**, 267–270.

Lozys L (2004) The growth of pikeperch (*Sander lucioperca* L.) and perch (*Perca fluviatilis* L.) under different water temperature and salinity conditions in the Curonian Lagoon and Lithuanian coastal waters of the Baltic Sea. *Hydrobiologia*, **514**, 105–113.

MacKenzie BR, Alheit J, Conley DJ, Holm P, Kinze CC (2002) Ecological hypotheses for a historical reconstruction of upper trophic level biomass in the Baltic Sea and Skagerrak. *Canadian Journal of Fisheries and Aquatic Sciences*, **59**, 173–190.

MacKenzie BR, Hinrichsen H-H, Plikshs M, Wieland K, Zezera A (2000) Quantifying environmental heterogeneity: habitat size necessary for successful development of cod (*Gadus morhua* L.) eggs in the Baltic Sea. *Marine Ecology Progress Series*, **193**, 143–156.

MacKenzie BR, Köster FW (2004) Fish production and climate: sprat in the Baltic Sea. *Ecology*, **85**, 784–794.

MacKenzie BR, Schiedek D (2007) Daily ocean monitoring since the 1860s shows unprecedented warming of northern European seas. *Global Change Biology*, doi: 10.1111/j.1365-2486.2007.01369.x.

MacKenzie BR, St.John MA, Plikshs M, Hinrichsen H-H, Wieland K (1996) *Oceanographic processes influencing seasonal and interannual variability in cod spawning habitat in the eastern Baltic Sea*. ICES Conference Meeting 1996/C + J:4.

Matthäus W (1978) Phytoplankton spring bloom and maximum oxygen content in the Baltic proper. *Kieler Meeresforschungen*, **4**, 147–152.

Meier HEM (2006) Baltic Sea climate in the late 21st century: a dynamical downscaling approach using two global models and two emission scenarios. *Climate Dynamics*, **27**, 39–68.

Meier HEM, Kjellström E, Graham LP (2006) Estimating uncertainties of projected Baltic Sea salinity in the late 21st century. *Geophysical Research Letters*, **33**, L15705, doi 10.1029/2006GL026488.

Möllmann C, Kornilovs G, Fetter M, Köster FW (2004) Feeding ecology of central Baltic Sea herring and sprat. *Journal of Fish Biology*, **65**, 1563–1581.

Möllmann C, Kornilovs G, Fetter M, Köster FW, Hinrichsen H-H (2003a) The marine copepod, *Pseudocalanus elongatus*, as a mediator between climate variability and fisheries in the Central Baltic Sea. *Fisheries Oceanography*, **12**, 360–368.

Möllmann C, Kornilovs G, Fetter M, Köster FW (2005) Climate, zooplankton and pelagic fish growth in the Central Baltic Sea. *ICES Journal of Marine Science*, **62**, 1270–1280.

Möllmann C, Kornilovs G, Sidrevics L (2000) Long-term dynamics of main mesozooplankton in the Central Baltic Sea. *Journal of Plankton Research*, **22**, 2015–2038.

Möllmann C, Köster FW (1999) Food consumption by clupeids in the Central Baltic: evidence for top-down control? *ICES Journal of Marine Science*, **56** (Suppl.), 100–113.

Möllmann C, Köster FW, Kornilovs G, Sidrevics L (2003b) Interannual variability in population dynamics of calanoid copepods in the Central Baltic Sea. *ICES Marine Science Symposium*, **219**, 220–230.

Muus BJ, Nielsen JG (1999) *Sea Fish*. Scandinavian Fishing Year Book, Hedehusene, Denmark.

Nielsen E, Bagge O, MacKenzie BR (1998) Wind-induced transport of plaice (*Pleuronectes platessa*) early life-history stages in the Skagerrak-Kattegat. *Journal of Sea Research*, **39**, 11–28.

Nielsen E, Richardson K (1996) Can changes in fisheries yield in the Kattegat (1950–1992) be linked to changes in primary production? *ICES Journal of Marine Science*, **53**, 988–994.

Nielsen EE, Møller Hansen M, Schmidt C, Meldrup D, Grønkjær P (2001) Genetic differences among cod populations. *Nature*, **413**, 272.

Nielsen EE, Hansen MM, Ruzzante DE, Meldrup D, Grønkjær P (2003) Evidence of a hybrid-zone in Atlantic cod (*Gadus morhua*) in the Baltic and the Danish Belt Sea revealed by individual admixture analysis. *Molecular Ecology*, **12**, 1497–1508.

Nissling A (2004) Effects of temperature on egg and larval survival of cod (*Gadus morhua*) and sprat (*Sprattus sprattus*) in the Baltic Sea – implications for stock development. *Hydrobiologia*, **514**, 115–123.

Nissling A, Müller A, Hinrichsen H-H (2003) Specific gravity and vertical distribution of sprat (*Sprattus sprattus*) eggs in the Baltic Sea. *Journal of Fish Biology*, **63**, 280–299.

Nissling A, Westin L (1997) Salinity requirements for successful spawning of Baltic and Belt Sea cod and the potential for cod stock interactions in the Baltic Sea. *Marine Ecology Progress Series*, **152**, 261–271.

Nissling A, Westin L, Hjerne O (2002) Reproductive success in relation to salinity for three flatfish species, dab (*Limanda limanda*), plaice (*Pleuronectes platessa*), and flounder (*Pleuronectes flesus*), in the brackish water Baltic Sea. *ICES Journal of Marine Science*, **59**, 93–108.

Nixon SW (1988) Physical energy inputs and the comparative ecology of lake and marine ecosystems. *Limnology and Oceanography*, **33**, 1005–1025.

Ojaveer H (2002) Environmental impacts on fish and ecosystem effects on fishing in the Baltic Sea. *Estonian Marine Institute Report Series*, **11**, 1–52.

Ojaveer H, Andrushaitis A (2004) History of ecosystem studies of the Gulf of Riga (Baltic Sea). *Proceedings of the Estonian Academy of Sciences, Ecology*, **53**, 116–143.

Ojaveer E, Kalejs M (2005) The impact of climate change on the adaptation of marine fish in the Baltic Sea. *ICES Journal of Marine Science*, **62**, 1492–1500.

Ojaveer H, Lankov A, Eero M, Kotta J, Kotta I, Lumberg A (1999) Changes in the ecosystem of the Gulf of Riga from the 1970s to the 1990s. *ICES Journal of Marine Science*, **56**, 33–40, ISI:000088024600005.

Omstedt A, Elken J, Lehmann A, Piechura J (2004) Knowledge of the Baltic Sea physics gained during the BALTEX and related programmes. *Progress in Oceanography*, **63**, 1–28.

Orr JC, Pantoja S, Portner HO (2005) Introduction to special section: the ocean in a high-CO_2 world. *Journal of Geophysical Research-Oceans*, **110**: ISI:000232111200004.

Parmanne R, Rechlin O, Sjöstrand B (1994) Status and future of herring and sprat stocks in the Baltic Sea. *Dana*, **10**, 29–59.

Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. *Science*, **308**, 1912–1915.

Pihl L (1990) Year-class strength regulation in plaice (*Pleuronectes platessa* L.) on the Swedish west coast. *Hydrobiologia*, **195**, 79–88.

Pihl L (1994) Changes in the diet of demersal fish due to eutrophication – induced hypoxia in the Kattegat, Sweden. *Canadian Journal of Fisheries and Aquatic Sciences*, **51**, 321–336.

Platt T, Fuentes-Yaco C, Frank KT (2003) Spring algal bloom and larval fish survival. *Nature*, **423**, 398–399.

Plikshs M, Kalejs M, Grauman G (1993) *The influence of environmental conditions and spawning stock size on the year–class strength of the eastern Baltic cod*. ICES Conference Meeting 1993/J:22.

Räisänen J, Hansson U, Ullerstig A *et al*. (2004) European climate in the late twenty-first century: regional simulations with two driving global models and two forcing scenarios. *Climate Dynamics*, **22**, 13–31.

Rasmussen B, Gustafsson BG, Ærtebjerg G, Lundsgaard C (2003) Oxygen concentration and consumption at the entrance to the Baltic Sea from 1975–2000. *Journal of Marine Systems*, **42**, 13–30.

Rohlf N (1999) *Verhaltensänderungen der larven des Ostseedorsches (Gadus morhua callarias) während der Dottersackphase*. Institute of Marine Sciences, University of Kiel, Germany.

Rönkkönen S, Ojaveer E, Raid T, Viitasalo M (2004) Long-term changes in Baltic herring (*Clupea harengus membras*) growth in the Gulf of Finland. *Canadian Journal of Fisheries and Aquatic Sciences*, **61**, 219–229.

Sapota MR, Skora KE (2005) Spread of alien (non-indigenous) fish species *Neogobius melanostomus* in the Gulf of Gdansk (south Baltic). *Biological Invasions*, **7**, 157–164, 10.1007/s10530-004-9035-0.

Schiedek D (1997) *Marenzellaria* cf.*viridis* (Polychaeta: Spionidae) – ecophysiological adaptations to a life in the coastal waters of the Baltic. *Aquatic Ecology*, **31**, 199–210.

Schinke H, Matthäus W (1998) On the causes of major Baltic inflows – an analysis of long time series. *Continental Shelf Research*, **18**, 67–97.

Sissener EH, Bjørndal T (2005) Climate change and the migratory pattern for Norwegian spring-spawning herring – implications for management. *Marine Pollution*, **29**, 299–309.

Sparholt H (1994) Fish species interactions in the Baltic Sea. *Dana*, **10**, 131–162.

Sparholt H, Jensen IB (1992) The effect of cod predation on the weight-at-age of herring in the Baltic. *ICES Marine Science Symposia*, **195**, 448–491.

Stenseth NC, Ottersen G, Hurrell JW, Belgrano A (2004) *Marine Ecosystems and Climate Variation*. Oxford University Press, Oxford.

Temming A (1989) Long-term changes in stock abundance of the common dab (*Limanda limanda* L.) in the Baltic Proper. *Rapports et Procés.-verbaux des Reunions du Conseil Internationale pour l'.Exploration de la Mer*, **190**, 39–50.

UN (1992) *UN convention on biological diversity, Rio de Janeiro, Brazil*. pp. 1–31. United Nations, New York, New York, USA http://www.biodiv.org/doc/legal/cbd-en.pdf

UN (2002) *UN report of the world summit on sustainable development*, Johannesburg, South Africa. pp. 1–173. United Nations, New York, New York, USA http://www.johannesburgsummit.org/html/documents/summit_docs/131302_wssd_report_reissued.pdf

Uzars D (1994) Feeding of cod (*Gadus morhua callarias* L.) in the central Baltic in relation to environmental changes. *ICES Marine Science Symposia*, **198**, 612–623.

Välipakka T (1990) *Zur Verbreitung, Biologieund Ökologievon Mysidacea (Crustacea, Malacosraca) in der Mecklenburger Bucht und in den küstenfernen Gewässern der eigentlichen Ostsee (1985–1988)*. Diss. Thesis. Wilhelm-Pieck-Univ. Rostock.

Vallin L, Nissling A, Westin L (1999) Potential factors influencing reproductive success of Baltic cod, *Gadus morhua*: a review. *Ambio*, **28**, 92–99.

Viitasalo MI, Vuorinen I, Saesmaa S (1995) Mesozooplankton dynamics in the northern Baltic Sea: implications of variations in hydrography and climate. *Journal of Plankton Research*, **17**, 1857–1878.

Voipio A (1981) *The Baltic Sea*. Elsevier, Amsterdam.

Voss R, Köster FW, Dickmann M (2003) Comparing the feeding habits of co-occurring sprat (*Sprattus sprattus*) and cod (*Gadus morhua*) larvae in the Bornholm Basin, Baltic Sea. *Fisheries Research*, **63**, 97–111.

Ware DM, Thomson RE (2005) Bottom-up ecosystem trophic dynamics determine fish production in the northeast Pacific. *Science*, **308**, 1280–1284.

Whitfield AK, Elliott J (2002) Fishes as indicators of environmental and ecological changes within estuaries: a review of progress and some suggestions for the future. *Journal of Fish Biology*, **61** (Suppl. A), 229–250.

Wieland K, Jarre-Teichmann A, Horbowa K (2000) Changes in the timing of spawning of Baltic cod: possible causes and implications for recruitment. *ICES Journal of Marine Science*, **56**, 452–464.

Wieland K, Waller U, Schnack D (1994) Development of Baltic cod eggs at different levels of temperature and oxygen content. *Dana*, **10**, 163–177.

Wieland K, Zuzarte F (1991) *Vertical distribution of cod and sprat eggs and larvae in the Bornholm Basin (Baltic Sea) 1987–1990*. ICES Conference Meeting 1991/J:37.