Aqua notes 2023:17

Climate effects on fish in Sweden

– Species-Climate Information Sheets for 32 key taxa in marine and coastal waters

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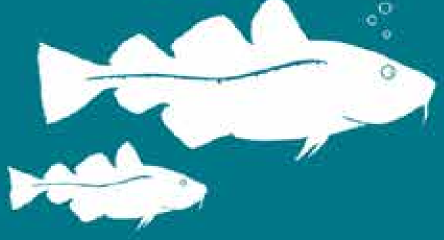

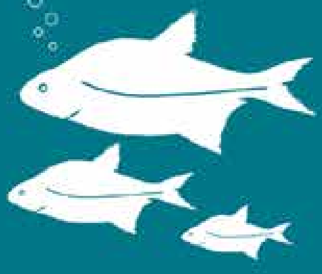

Climate effects on fish in Sweden – Species-Climate Information Sheets for 32 taxa in marine and coastal waters

Klimateffekter på fisk i Sverige – Artfakta för 32 taxa i hav och kust

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Funding: Swedish Agency for Marine and Water Management, Dnr 1638-20

How to cite this report:

Bartolino, V., Koehler, B., Bergström, L. (2023). Climate effects on fish in Sweden – Species Climate Information Sheets for 32 taxa in marine and coastal waters. Aqua notes 2023:17. Uppsala: Department of Aquatic Resources. https://doi.org/10.54612/a.4lmlt1tq5j

How to cite a taxon-specific section in this report (example for chapter 6.1.):

Sundelöf, A. (2023) Atlantic bluefin tuna. In Bartolino, V., Koehler, B., Bergström, L. (2023). Climate effects on fish in Sweden – Species-Climate Information Sheets for 32 taxa in marine and coastal waters. Aqua notes 2023:17. Uppsala: Department of Aquatic Resources. https://doi.org/10.54612/a.4lmlt1tq5j

Responsible for publication series:	Noél Holmgren, Swedish University of Agricultural Sciences (SLU), Department of Aquatic Resources
Editor:	Stefan Larsson, Swedish University of Agricultural Sciences (SLU), Department of Aquatic Resources
Publisher:	Swedish University of Agricultural Sciences (SLU), Department of Aquatic Resources
Year of publication:	2023
Place of publication:	Uppsala
Illustration cover:	Cod (left): Fredrik Saarkoppel; Bream (right): SLU
Copyright:	All images are used with the permission of the author.
Title of series:	Aqua notes
Part number:	2023:17
ISBN:	978-91-8046-896-1
DOI:	https://doi.org/10.54612/a.4lmlt1tq5j
Keywords:	climate change, environment, fish, Baltic Sea, Oresund, Kattegat, Skagerrak, North Sea, review

This report was updated 2023-12-22

- page 2, line 16 read before "Authors: Johan Dannewitz and Stefan Palm", is now changed to "Authors: Stefan Palm and Johan Dannewitz"

- page 2, line 40 read before "Authors: Johan Dannewitz, Stefan Palm and Catarina Magnusson", is now changed to "Author: Katarina Magnusson"

- page 15, line 29 read before "Johan Dannewitz, Stefan Palm, Catarina Magnusson", is now changed to "Katarina Magnusson"

Förord

Föreliggande rapport är en del av ett bredare kunskapsunderlag om förväntad klimatpåverkan på kommersiellt viktiga resurser för svensk fiske. Syftet är att ge en överblick av kunskapsläget för specifika arter och bestånd, baserad på litteraturgenomgångar. En associerad rapport (Aqua reports 2023:9) ger en sammanvägd analys av effekter på fisksamhällen och fiske i Sverige. Underlaget är en del av en beställning från Havs-och vattenmyndigheten till SLU Aqua inom ramen för projektet för GFP-rådgivning (HaV Dnr 1638-20). Rapporten är skriven på engelska.

Summary

The purpose of this publication is to summarize the state of knowledge on the effects of environmental variability and climate change for individual species and stocks based on literature review, giving species-climate information for 32 key taxa in Swedish marine and coastal waters. The report is written in English.

The extent and scale of recent changes in climate due to global warming is unprecedented and causes increasing effects on ecosystems. In oceans, ongoing warming leads to, for example, increased water temperatures, decreased ice cover and effects on hydrology and water circulation patterns that can in turn influence salinity. The environmental alterations affect species distribution, biology, and hence also the delivery of marine ecosystem services and human well-being.

The results of this review on the effects of environmental variability and climate change on marine taxa are presented as species-climate information sheets designed in a user-friendly format aimed to enhance accessibility for professionals spanning different fields and roles, including e.g. scientific experts, NGOs affiliates and managers. The species-climate information sheets presented here cover 32 key taxa selected among the economically and ecologically most important coastal and marine fish and crustacean species in Swedish waters.

The species-wise evaluations show that climate change leads to a wide range of effects on fish, reflecting variations in their biology and physiological tolerances. The review also highlights important data and knowledge gaps for each species and life stage. Despite the high variability and prevailing uncertainties, some general patterns appeared. On a general level, most fish species in Swedish marine and coastal waters are not expected to benefit from climate change, and many risks are identified to their potential for recruitment, growth and development. Boreal, marine and cold-adapted species would be disadvantaged at Swedish latitudes. However, fish of freshwater origin adapted to warmer temperature regimes could benefit to some extent in the Baltic Sea under a warming climate. Freshwater fish could also be benefitted under further decreasing salinity in the surface water in the Baltic Sea.

The resulting effects on species will not only depend on the physiological responses, but also on how the feeding conditions for fish, prey availability, the quality of essential fish habitats and many other factors will develop. A wide range of ecological factors decisive for the development of fish communities are also affected by climate change but have not been explored here, where we focused on the direct effects of warming. The sensitivity and resilience of the fish species to climate change will also depend on their present and future health and biological status. Populations exposed to prolonged and intense fishing exploitation, or affected by environmental deterioration will most likely have a lower capacity to cope with climate change effects over time.

For both the Baltic Sea and the North Sea, it is important to ensure continued work to update and improve the species-climate information sheets as results from new research become available. It can also be expected that new important and relevant biological information and improved climate scenarios will emerge continuously. Continued work is therefore important to update and refine the

species-climate information sheets, help filling in currently identified knowledge gaps, and extend to other species not included here. Moreover, there is need to integrate this type of species-level information into analyses of the effects of climate change at the level of communities and ecosystems to support timely mitigation and adaptation responses to the challenges of the climate change.

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1. Introduction

The extent and scale of recent changes in climate due to global warming are beyond comparison over centuries, as well as are projections for the future (IPCC 2021). As a result, climate-related effects on ecosystems are also increasing. These changes occur globally and include ecosystems in Sweden (e.g. Bergström et al. 2019). As air temperature increases and heat transfers from the surface down into the water column, also sea temperature rises. Oceans store by far the largest amount of heat produced by global warming, and significant further warming of the oceans is expected with highest certainty over the coming century (IPCC 2019). Further, the anthropogenically elevated carbon dioxide emissions result in increased CO2 uptake into the oceans, causing subsequent acidification of the sea. Climate changes also lead to other alterations, such as decreasing ice cover, rising sea levels, increasing oxygen consumption, and effects on nutrient cycling and primary production. All these environmental alterations affect the distribution and biology of species, and, ultimately, the delivery of ecosystem services with effects on human well-being. Mitigation measures to reduce the impacts of climate change include actions both to reduce global warming and the already ongoing and likely future effects on species and ecosystems.

The present report aims to synthesise and improve the accessibility of up-to-date knowledge on the effects of environmental variability and climate change on different fish and invertebrate species and stocks in Swedish marine and coastal waters. The report documents what is known about how fish and invertebrates are currently responding to climate change, at different life stages, and what could happen in the future. By this, it also displays for what species and aspects there are important knowledge gaps that need to be filled. The results are presented with a common format, hereafter referred to as species-climate information sheets, to improve usability and comparability on the current level of understanding for individual species and stocks, based on available scientifically published evidence.

1.1. Effects of climate change on Swedish seas

Sweden is surrounded by the North Sea and the Baltic Sea, which are both affected by climate change, albeit with some different characteristics. A short summary of recent and likely future climate changes in these seas is provided here, and a more detailed summary is given for example by Bartolino et al. (2023).

The North Sea, including the Skagerrak and Kattegat along the west coast of Sweden, is characterised by large variability in temperature both in space and time. However, overriding this, there is evidence of exceptional warming over time, especially during the past three decades (for details, see Huthnance et al. 2016). Variation in salinity along the Swedish west coast is mainly driven by the level of outflow of brackish water from the Baltic Sea, and to some extent by direct local run-off from land. Overall, there has been a freshening of the North Sea in recent time, as well as an increase in sea level and acidification (Schrum et al. 2016). Most studies assume that runoff from the catchment area and outflow from the Baltic Sea will increase further under a future climate (e.g., Wakelin et al. 2012).

In the Baltic Sea, sea surface temperature has increased more than the average increase observed for the global ocean (HELCOM/Baltic Earth 2021; Meier et al. 2022), the rate of increase has accelerated during the past three decades, and the Baltic Sea is expected to be a hot spot for warming also in the future (Gröger et al. 2019). More severe heatwaves have lately been documented in the region (Humborg et al. 2019, Naumann et al. 2019), and the maximum extent of sea ice during winter has decreased by 30% over the last century. The Baltic Sea is heavily affected by eutrophication, which has led to extended areas with anoxic or hypoxic conditions near or close to the deep seabed. Warming further intensifies oxygen depletion, and increases oxygen consumption of organisms, however, models show that future oxygen conditions in the deep waters of the Baltic Sea mainly depend on the future development of nutrient loading (Saraiva et al. 2019a,b). Climate change may also affect salinity levels in the Baltic Sea, although projections on salinity are more uncertain (Meier et al. 2022). The Baltic Sea has a natural gradient where salinity decreases from its opening to the inner areas, driven by a combination of river runoff from land and influence from inflow of marine waters from the North Sea. Linked to changes in the levels of precipitation and runoff from land, the salinity of surface waters in the Baltic Sea shows a decreasing trend that is likely to continue in the future (HELCOM/Baltic Earth 2021). Salinity in the deeper water layers is mainly linked to the occurrence of saltwater inflows from the North Sea, which sporadically renew the deep water with saline, oxygen-rich water (Mohrholz 2018). No long-term trend in the frequency of major inflows has been detected (Meier et al. 2017). Models predict that vertical stratification during summer will increase due to warming, but its contribution to changes in salinity is uncertain (Saraiva et al. 2019a).

1.2. Potential responses of fish to climate change

Fish are ectothermic and may react strongly to changes in water temperature. In well-connected offshore and coastal systems, fish may respond to climate change effects both by altered geographical ranges and depth distribution. Moreover, climate change can cause biological or physiological impacts on their behaviour, recruitment success, growth, and/or fecundity. Typically, the rate of biological processes increases with higher temperature (Brown et al. 2004). Such changes can either result in net positive or negative effects for the animal, where some fish species could be negatively affected by warming temperatures, while others may have higher temperature preferences than current ambient conditions and could benefit from a warming environment in certain areas (Veneranta et al. 2013). Other climate-related effects, such as freshening or reduced oxygen availability, may also affect fish directly, by effects on their behaviour and physiology. In addition, indirect effects on fish may occur through climate-related changes in for example prey availability, competitive relationships, food web productivity, access to suitable habitats, or other ecosystem processes.

The magnitude and type of effects on fish vary not only among species, but also among life stages within one species. Fish have complex life cycles that involve several life stages. These may have distinct ecological niches in relation to habitats occupied, and distinct trophic interactions. Overall, four main stages can be identified, specifically early life stages as eggs and fish larvae, the juvenile stage and the adult stage. Of these, the early life stages are often more sensitive to changes in the external environment, and environmentally driven changes in the mortality of early life stages have strong effects on the recruitment to the adult population. Changes in the spawning environment are expected to be particularly influential in the Baltic Sea (Bartolino et al. 2023). Several marine species reproduce at the lower limit of their salinity tolerance in the Baltic Sea, and further freshening of the Baltic Sea waters is expected to affect them negatively (MacKenzie et al. 2007), while the recruitment success of some freshwater species may increase (Härmä et al. 2008).

For fish larvae, survival also depends on suitable temperatures after hatching, and on food availability when larvae transition from endogenous to exogenous feeding. Growth rates may increase within the thermal windows of the concerned life stage, which may reduce the risk for predation mortality and enhance survival for some species, but only if also supported by sufficient food availability (Kjellman et al. 2001, Pekcan-Hekim et al. 2011, Kokkonen et al. 2011). If such conditions are not fulfilled, increased metabolic energetic cost could become detrimental, as can be seen as more likely for species with narrower thermal windows. Additionally, many fish species have pelagic eggs and larvae, and changes in the strength and patterns of water mass circulations (due to alterations in water temperature, salinity and density, as well as in the intensity and direction of dominant winds) can influence enrichment, concentration and retention processes which affect their early life stage survival (Bakun 1998). This can also affect the connectivity between spawning and nursery habitats (Petitgas et al. 2013).

Juvenile fish are often dependent on specific nursery areas either in pelagic, demersal, or benthic habitats, depending on the species, and for many taxa coastal habitats have a particular relevance as nursery grounds. Therefore, in addition to the direct effects of warming, young fish may also be influenced by climate-related effects on the quality of nursery areas, for example if climate change affects turbidity via changes in the river run-off or nutrient conditions (Bergström et al. 2013, van Dorst et al. 2019). Further factors that affect the survival and growth of young fish are for example habitat quality and food availability, which can also be influenced by climate change (HELCOM 2018, HELCOM/Baltic Earth 2021, Kraufvelin et al. 2018). Weather extremes, such as drought periods during biologically critical seasons, can also have negative effects on recruitment, since coastal tributaries are important spawning and nursery areas for many coastal species (HELCOM 2018).

Adult fish are affected by similar factors as young fish. However, since adult fish generally have higher mobility, and the species may have undergone changes in habitat preference or diet after reaching maturity, the level of sensitivity may differ between juveniles and adults. The effects of water temperature on body growth and metabolism also differ among species and size-classes. A larger body requires more maintenance than a smaller one, and there are examples showing that warming affects large individuals more than small ones (Lindmark et al. 2022). Therefore, rising water temperatures can lead to small individuals growing faster, while large individuals may suffer from heat under corresponding conditions (Lindmark et al. 2023), as shown for instance in experiments on perch in the Baltic Sea (Huss et al. 2019). Moreover, in many fish species, the maturation process is influenced by temperature and food availability, among other factors conditioning the trade-off between growth and maturation. These and other differences in body growth could cause changes in the size distribution within populations as the water gets warmer (Gårdmark and Huss 2020).

Hence, climate change can affect the individual fitness of fish as well as population abundances and, consequently, fish species composition through several pathways. By this, climate-related effects on fish can also lead to changes in the structure and function of marine food webs, with effects on biodiversity, ecosystem resilience, as well as the production of fish as resource for fisheries. Bartolino et al. (2023) give a comprehensive overview of potential future climate effects on Swedish commercially important fish stocks and fisheries on a system-level, and evaluate the vulnerability and distribution of climate-related risk for the Swedish fisheries and coastal regions under future climate scenarios.

2. Methodological background

The species-climate information sheets were designed around the life cycle of a generic fish with the four main life stages egg, larvae, juvenile and adult, as shown in Figure 1. The same format has also been applied for the commercially important crustaceans such as European lobster (*Homarus gammarus*), Norway lobster (*Nephrops norwegicus*) and northern shrimp (*Pandalus borealis*).

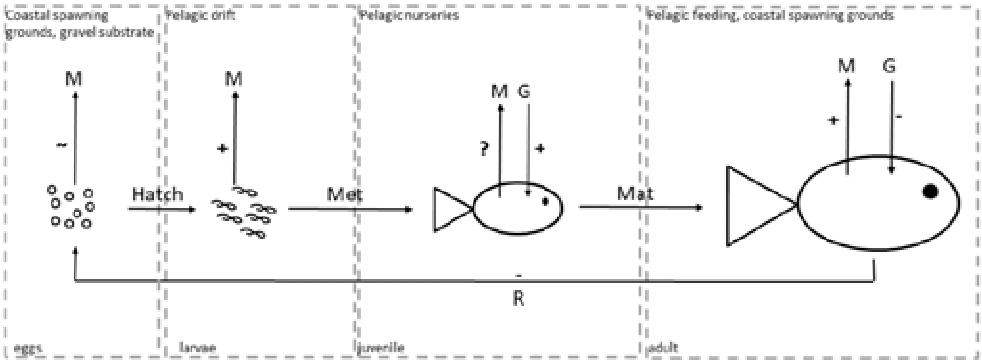

Figure 1. Schematic of expected impact of warming on main life stages and processes, using North Sea autumn-spawning herring as an example. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

Climate change can affect processes internal to each of the stages presented in Figure 1, in the form of effects on survival or growth. It can also affect processes that link the different life stages (i.e., hatching, metamorphosis, settling, maturity, recruitment). In this work, the best available knowledge on the effects of environmental variability and climate change on these aspects was searched by screening the scientific literature for indications and evidence of links between environmental drivers and biological processes regulating the physiology, life cycle and dynamics of the selected key species. The analysed literature included experimental work under controlled conditions, field observations and model-based inference, as well as outcomes from process-oriented and correlative analyses. In many cases, formal validations of results are lacking, which brings a risk of spurious correlations that were considered in the interpretation of the text. When different studies gave contrasting results, this was reported in the form of uncertainty rather than aiming towards a single interpretation.

The evaluations focus on Swedish marine and coastal waters, hence covering the North Sea and Baltic Sea, and are based on available relevant research from these areas as well as from other geographical areas when considered applicable.

Results were presented at the level of species or for separate stocks in the cases of cod, herring and sprat. The included taxa were identified by order of priority based on their commercial interest and ecological importance, in dialogue with representatives of the Swedish Agency for Marine and Water management. In all, species-climate information sheets were prepared for 32 taxa (Table 1). The work is a combined effort from several researchers, and the authorship for each of the species or stocks are presented in association with each species-climate information sheet.

Table 1. Species and stocks included in the present report

Chapter	Species	Author
6.1	Atlantic bluefin tuna	Andreas Sundelöf
6.2	Atlantic halibut	Valerio Bartolino
6.3	Atlantic salmon	Stefan Palm, Johan Dannewitz
6.4	Ballan wrasse	Erika Andersson
6.5	Blue whiting	Johan Lövgren
6.6	Cod	Diana Hammar Perry
6.7	Cyprinids	Matilda Andersson, Frida Sundqvist
6.8	Edible crab	Johanna-Luise Kozák
6.9	European grayling	Matilda Andersson, Frida Sundqvist
6.10	European lobster	Andreas Sundelöf
6.11	European plaice	Francesca Vitale
6.12	European whitefish	Matilda Andersson, Frida Sundqvist
6.13	Flounder	Alessandro Orio
6.14	Hake	Valerio Bartolino
6.15	Herring	Valerio Bartolino, Lena Bergström
6.16	Mackerel	Alessandro Orio
6.17	Northern pike	Matilda Andersson, Frida Sundqvist
6.18	Northern shrimp	Christopher Griffiths
6.19	Norway lobster	Andreas Sundelöf
6.20	Norway pout	Johan Lövgren
6.21	Perch	Matilda Andersson, Frida Sundqvist
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6.30	Thornback ray	Patrik Börjesson
6.31	Turbot	Massimiliano Cardinale
6.32	Whiting	Johan Lövgren

3. Discussion

The species-climate information sheets collated here (sections 6.1-32) review and synthesise scientific evidence of how selected fish and invertebrate species present in the Sweden seas respond to environmental variability and climate change. The species included have been selected to primarily represent fish and crustacean species of commercial interest. In all, 32 species-climate information sheets are made available, covering pelagic, benthic/demersal, coastal and anadromous species.

The combined results give the possibility to make some general conclusions, although they should be interpreted with awareness, as the list is not complete. Also, our review highlights important data and knowledge gaps for each species and life stage that remain to be filled. For comparison, 40 fish or shellfish species or stocks on the Swedish west coast and 20 fish species or stocks in the Baltic Sea are currently identified as being commercially important (Swedish Agency for Marine and Water Management, in preparation), following general advice on the identification of commercial stocks for the purposes of reporting on their environmental status within the EU Marine Strategy Framework Directive (EC 2017, ICES 2022). Further, in total 144 species are currently regularly occurring in Swedish coastal waters shallower than 30 meters depth, according to a comprehensive assessment of monitoring and citizen science data (Koehler et al. 2022). The actual number of fish species in the Swedish marine and coastal waters is probably higher, as some additional species are likely occurring only in deeper waters.

The evaluations show that climate change can lead to a wide range of effects on fish communities, reflecting variation in the biology and physiological tolerance of different species and life stages, as well as species interactions. Despite the high variability and prevailing uncertainties, some patterns appear. On a general level, boreal, marine and cold-adapted species would be disadvantaged at Swedish latitudes, while several temperate species are already showing benefits from a warming environment as reflected by several documented cases of habitat expansion (i.e., hake, seabass). Also, species of freshwater origin adapted to warmer temperature regimes could benefit to some extent in the Baltic Sea under a warming climate. Freshwater fish could also be benefitted if there is a continued freshening in the surface water in the Baltic Sea. However, the resulting effects will not only depend on physiological response, but also on how the feeding conditions for fish, prey availability and the quality of essential fish habitats and many other factors will develop. Most of the fish species in Swedish waters are not expected to benefit from climate change and many risks are identified. Further, a wide range of such ecological factors decisive for the development of fish communities are also affected by changes in climate but have not been explored in this report. In addition, the sensitivity and resilience of species to climate change will depend on their present and future health and biological status. Further, populations exposed to prolonged and intense fishing exploitation or affected by environmental deterioration will most likely have a lower resilience towards climate change effects over time.

The results presented here provide information for species and stocks present in the Swedish seas, most of which are shared with other countries. In the case of coastal populations, the main results could also be applicable to other nearby countries where the same species are present. For the Baltic Sea, an evaluation of past and potential future climate change effects on the Baltic Sea ecosystem was recently provided through a combined effort of HELCOM and Baltic Earth (2021), using a systematic approach to provide a broad regional overview. For fish, the contributors to that report concluded that increasing temperatures and hypoxia have generally resulted in decreasing distributions of marine fish such as flatfish, herring and cod in the Baltic Sea region in recent time, and also contributed to a reduced growth and body condition of cod, while higher sprat recruitment was linked to winters with low ice cover. They also concluded that coastal spring- and summer-spawning fish species such as perch, cyprinids and pike could benefit from a warming climate, via earlier spawning, faster egg- and larval development, and increased larval survival, while for example autumn- and winter-spawning species such as salmonids would be disfavoured. Migratory anadromous species, such as salmon, return to rivers earlier after a warm winter or spring, while warm autumn or winter water temperatures seem to lower the survival of salmon migrating back to sea (HELCOM and BalticEarth 2021). The results presented here generally align with the regional results but provide more detail and specific references at the level of different species and life stages.

In the North Sea, most of the species having their northerly or southerly range margins there have shifted their distribution northward (Perry et al. 2005). Examples of direct and indirect effects of climate change on fish in the North Sea are diverse and include effects on growth and maturation, on behaviour with implications for migration and distribution, on egg and larval dispersal, and on prey phenology and foodweb interactions (for a review of notable examples, see Brander et al. 2016). Strong spatial heterogeneity in climate effects among different parts of the North Sea (see section 1.1), high species richness, and the variety and complexity of processes and interactions all contribute to the variability in observed and potential future responses. A regional overview and synthesis of the effects of climate change in the North Sea, similar to that existing for the Baltic Sea, is missing, but would be highly beneficial for developing a more comprehensive understanding of potential future changes in the ecosystem including fish and fisheries (see also for example ICES 2023). As the level of connectedness among different water masses is higher in the North Sea compared to the Baltic Sea, it could be expected that a more developed understanding of connectivity among populations and geographical areas would provide an important basis for such work.

For both the Baltic Sea and the North Sea, it would be important to ensure future work to regularly update and improve the species-climate information sheets as new knowledge and information becomes available, for example by integrating updated biological information and climate scenarios. It can be foreseen that important and relevant information in these fields will emerge continuously in the near future. This would be important to provide a more refined view, help filling in currently identified knowledge gaps, and include taxa not yet part of this catalogue.

4. Acknowledgements

A special thanks to the colleagues who contributed to review the species-climate information sheets, in alphabetical order: Sara Bergek, Ulf Bergström, Patrik Bohman, Elisabeth Bolund, Massimiliano Cardinale, Maria Eggertsen, Lachlan Fetterplace, Ann-Britt Florin, Kerstin Holmgren, Stefan Larsson, Alessandro Orio, Björn Rogell, Göran Sundblad, Frida Sundqvist, Daniel Valentinsson, Francesca Vitale, Håkan Wennhage, and Karolina Wikström.

This report was initiated by a commission from HaV on the potential climate change effects on Swedish fish and fisheries, as part of the framework contract on the CFP advice (Dnr 1638-20).

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6. Species-climate information sheets

The species-climate information sheets are provided here in alphabetical order. References used for each species are shown in direct connection to each text, for convenience.

6.1. Atlantic bluefin tuna (*Thunnus thynnus*)

Atlantic bluefin tuna (*Thunnus thynnus*) is a warm-blooded, long-lived, long-distance migrating apex predator circumventing the northern Atlantic on a yearly basis (Aarestrup et al., 2022; Block et al., 2001; Fromentin & Powers, 2005). Spawning occurs primarily in the Mediterranean and the Gulf of Mexico and adults migrate throughout the northern Atlantic for foraging. Adult bluefin tuna has a strong resilience to temperature and a wide window of tolerance (3-30 degrees from tag data (Aarestrup et al., 2022; Block et al., 2001). Previous knowledge of tolerance and optimal temperature ranges (Druon et al., 2016) and effects on distribution may have to be revised by expected results from recent tagging in parts of the distribution range that has not been widely tested yet (Aarestrup et al., 2022).

Low temperatures does not seem to have limited even smaller sized bluefin tunas to reach well above 62 degrees N (Ságat.no, 2021) and ocean temperatures below 6-11 degrees (ICCAT, 2007; Jansen et al., 2021). Climate variations on somatic growth has been proposed but not shown (Fromentin & Powers, 2005). A study using tag-recaptures, NAO, AO and PNA climate patterns and a 60-year time series of daily resolved growth increments revealed significant inter-annual effects and highly non-linear effects on somatic growth (Zhou, 2022). Simulated projections showed increased growth in the recent decades (Zhou, 2022) and Atlantic Multidecadal Oscillation has been shown influential in changes of stock distribution of bluefin tuna (Faillettaz et al., 2019).

Following the past 10-year biomass increase of bluefin tuna in the Atlantic (ICCAT, 2017) and the range expansion observed since at least 2017 (Aarestrup et al., 2022) also a range shift to the north may be expected. Bluefin tuna is a visual forager, using sight for hunting prey at depth down to at least 700 meters in the Northern North Sea.

Seasonality in light at northern latitudes has been suggested to curb a poleward range expansion of prey species, by high foraging-related predation mortality (Ljungstrom et al., 2021). A prey species expanding its range poleward may experience such latitudinally elevated predation mortality. However, the predation mortality will be excerted by the increasing appearance of Bluefin tuna in the area, following the rebuilding of the Eastern Bluefin tuna stock. The long-range migrations of bluefin tuna from spawning areas (primarily the Mediterranean) are expected to persist and develop to the north following ocean temperature increase. A poleward expansion by bluefin tuna may instead put increased predation mortality on the southern distribution limits of cold-water species as well as the northern distribution limit of the warmer water species.

Bluefin tuna has the most spatially and temporally constrained larval habitats of all tuna species, and the larvae inhabit waters at sea temperatures above 20-22°C (Reglero et al., 2014). Hatching time is substantially reduced at elevated temperatures (from 20-26°C, (Gordoa & Carreras, 2014)) and elevated temperatures increase spawning area and larval survival in the Mediterranean (Reglero et al., 2019).

Modelled data suggest that bluefin tuna in the Mediterranean spawn during rising temperatures, but at temperatures below what may cause metabolic meltdown in larvae (Fiksen & Reglero, 2022). Larvae may be able to adjust to a changing temperature by shifting their vertical distribution to optimize temperature tolerance (Reglero et al., 2018). Reglero et al (2018) showed that larvae were distributed shallower in strongly stratified waters, potentially limiting vertical displacement. Spawning areas are currently under scrutiny (Richardson et al., 2016; Rodriguez et al., 2021) and potential effects of climatic factors are yet to be described. How spawning behavior and larval survival could be affected by climatic changes in these other areas has not been tested or hypothesized.

It is not clear how bluefin tuna larvae adapt to the narrow temperature preference by vertical movement to keep matching prey items for the larvae. Heatwaves increase survival of larvae, but also increase the metabolic rate and emphasizes the need for matching larval development with available food items (Fiksen & Reglero, 2022). However, for the Gulf of Mexico spawning stock habitat modelling revealed limitations to spawning areas induced by an increase in temperature (Muhling et al., 2015).

Table 6.1. Climate change processes and response, key conclusions.

Atlantic Bluefin tuna		
Process	Response to climate change	Reference
Mortality	Warming increases larval survival	Fiksen & Reglero (2022)
Maturation	Warming increases growth rate, potentially affecting maturation	Zhou, C. (2022)
Growth	Warming increases growth	Zhou, C. (2022)
Spawning	Warming reduces spawning areas Timing of spawning sensitive to temperature	Muhling et al. (2015) Fiksen & Reglero (2022)
Hatching	Warming decreases hatching time, and increases spawning success	Gordoa & Carreras (2014), Reglero et al. 2019

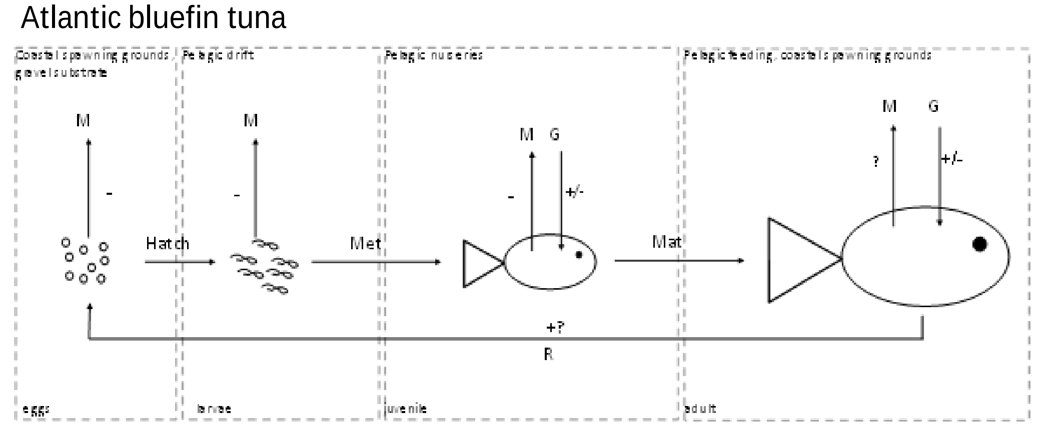

Figure 6.1. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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Authored by Andreas Sundelöf

6.2. Atlantic halibut (*Hippoglossus hippoglossus*)

The Atlantic halibut is a large cold-water flatfish with a wide distribution across the North Atlantic. It spans from Greenland to the Faroe Islands and south along the US coast of Virginia and along the Norwegian coasts, into the North Sea and the Skagerrak. Joensen (1954) and McCracken (1958) were among the first to hypothesize that more than one panmictic population could exist over such a wide distributional area. In the Atlantic US and Canada, a separate stock is assigned for each of the four management areas (NAFO). However, despite several tagging and genetic studies, results have not been conclusive on the population structure of halibut throughout the North Atlantic. To date, its level of connectivity among the offshore North Sea-Skagerrak, the coastal fjords and the Norwegian Sea remains unknown.

Atlantic halibut is found across a broad range of temperatures from -0.9°C to 19°C but shows a preference for temperatures in the range 2-11°C (Kaschner et al. 2019). An increase of the species has been reported in the Northwest Atlantic since early 2000s, possibly in relation to an expansion of suitable habitats for juveniles, but the net effect of climate change on nursery productivity is unclear (Shackell et al. 2021). Negative effects of a warming environment could exist for other stages of the life cycle.

Several traits in the Atlantic halibut (e.g., growth, timing of spawning) show geographical phenotypic variation, and physiological adaptations to different environmental conditions experienced by the species throughout its wide distribution have been reported. However, the relative importance of genetics and environment on these differences remain unclear.

Experimental studies have shown that halibut growth is influenced by temperature and photoperiod, and have also indicated latitudinal adaptations which could compensate for a shorter growing season for sub-populations at higher latitudes (Imsland and Jonassen 2001). Halibut growth capacity has been shown to increase with latitude and its temperature optimum to be related inversely with latitude (Imsland and Jonassen 2001).

Adults are strong swimmers capable of long-distance migrations, moving between summer feeding grounds on the continental shelf and deeper winter spawning areas on the continental slope (Haug, 1990). There are indications of possible feeding and spawning site fidelity but the actual drivers for migrations are unknown, leading to uncertainty on how they could be influenced by climate change (Shackell et al. 2021). In contrast, juveniles are concentrated on nursery grounds, showing a more sedentary behaviour (Haug 1990). Temperature tolerance increases with size, which suggests that juveniles are less resilient to a warming environment, at least close to the upper thermal distribution of the species (Jonassen et al. 1999; Imsland and Jonassen 2001).

Halibut spawning season extends from December to March, showing a peak in January-February. Spawning takes place near the bottom at 300-700 m depth, at temperatures between 5 and 7ºC (Haug, 1990). Variations in the phenology have been observed along a latitudinal gradient, with earlier spawning reported in the northern Norway compared to the southern part (Glover et al. 2006). Eggs and larvae are pelagic for 13-20 days and 90 days, respectively, before settlement to the bottom (Cargnelli et al. 1999). The development of both eggs and larvae requires low water temperatures in winter (approximately three months <6ºC) which may restrict the availability of suitable habitats for spawning in the future (Gubbins et al. 2013). Experiments indicate that the sex ratio is not influenced by temperature (Hughes et al. 2008).

A decline in wild catches of halibut and increased interest in halibut farming has stimulated experimental work using halibut as a model species, to investigate physiological responses of marine fish to a warming environment and increasing CO_2. Grans et al. (2014) found a decreased growth of halibut with increasing temperature, which was not related to reduced oxygen transport capacity but to unclear mechanisms. Their results showed that the decrease in growth was considerably more pronounced under a CO_2-elevated environment, suggesting that acidification, as expected under climate change, may limit the distribution, productivity and general fitness of this species even at typical ambient sea temperatures. Experiments on oxidative stress in halibut connected increased acidity (tested pH range 7.6-8.0, which is compatible with forecasts for the North Atlantic by the end of the 21st century) to increased oxidative damage regardless of the temperature experienced, attributed to an accumulation of protein carbonyls and hence insufficient responses of the antioxidant defense system (Almroth et al. 2019).

Table 6.2. Climate change processes and responses, key conclusions

Atlantic halibut		
Process	Response to climate change	Reference
Mortality	Development of early life stages requires long periods of low winter temperatures	Gubbins et al. 2013
Maturation		
Spawning	Time of spawning is anticipated by warming	Shackell et al. 2021
Growth	Growth may increase with temperature in the coldest part of its distributional range, but not at the southern boundaries. However, as temperature optimum is inversely related to latitude, the potential increase in growth with increasing temperature could be less pronounced. Juvenile growth is likely less resilient to changes in temperature. Growth is negatively affected by acidification	Imsland and Jonassen 2001 Jonassen et al. 1999 Grans et al. 2014
Recruitment		

Atlantic halibut

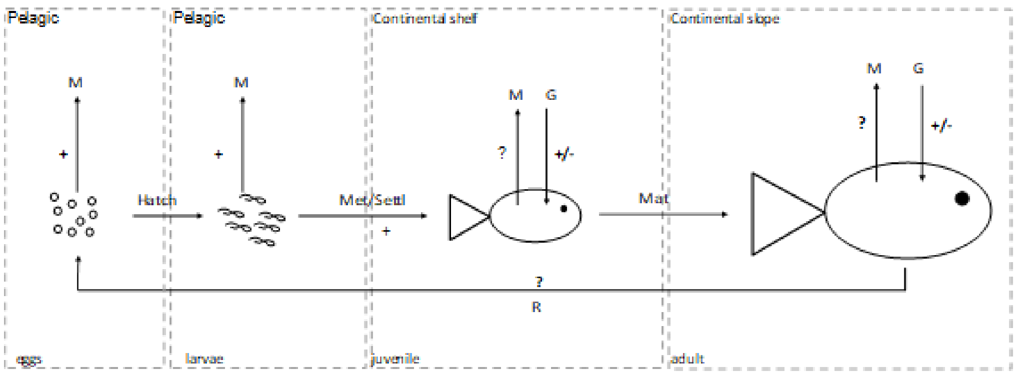

Figure 6.2. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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6.3. Atlantic salmon (*Salmo salar*)

The Atlantic salmon (hereafter salmon) exists in temperate and subarctic regions of the northern Atlantic Ocean and European and North American rivers flowing into this oceanic area. Most salmon populations are anadromous, with a juvenile phase in running freshwater followed by a period at sea, during which the fish feed, grow and undergo extensive migrations before they migrate back to freshwater to breed. There are over 2000 rivers that support salmon populations, about 1500 of which discharge into the Northeast Atlantic distributed from Portugal to Northern Russia, including Iceland (ICES 2021a). In Europe, the species also exist in the Baltic Sea (c. 30 rivers with wild salmon) and as "landlocked" populations in a few large lakes (e.g. Vänern and Ladoga).

Most maturing wild salmon return to reproduce in their river of origin. This precise homing behavior has resulted in genetic differences between salmon from different rivers and tributaries, with local populations being adapted to different environmental conditions. In addition, large-scale genetic differences exist between salmon from the western and eastern sides of the Atlantic (e.g. King et al. 2007), as well as among three major genetic population groups within Europe (Eastern Atlantic, Barents/White Sea, Baltic Sea; Bourret et al. 2013) which are presumed to reflect long-term genetic isolation combined with postglacial recolonization from different ice age refugia.

Considerable life-history variation exists between salmon from different rivers and geographic areas, reflecting both genetic variation and phenotypic plasticity (e.g. Barson et al. 2015). After one to several years in freshwater as a juvenile "parr", the young salmon metamorphoses into a "smolt" that migrates to sea. During the initial "post-smolt" phase, the marine diet changes gradually to being dominated by fish, and growth increases markedly. Adult salmon mature at various ages and sizes, typically returning to spawn after one to three years at sea, but also sometimes at older sea ages. Although spawning is associated with high mortality, some adults may spawn several times.

The salmon is exposed to multiple stressors during its anadromous life cycle. Effects of climate change (CC) in both freshwater and the marine environment, reduced connectivity due to dams and barriers to migration, and freshwater habitat destruction have been identified as the most important stressors, having a high or very high negative impact on salmon populations (ICES 2015). Fisheries exploitation and disease outbreaks have also had negative effects on salmon populations in some areas (e.g. ICES 2021b). At the same time, the relative importance of different stressors varies considerably between regions and even between local populations within restricted areas (ICES 2017). Salmon is also subjected to extensive aquaculture, which for various reasons is considered a considerable threat to many wild populations (e.g. Forseth et al. 2017).

A changing climate has potential to affect salmon feeding, growth, survival and migratory routes. Most anticipated consequences for salmon are negative, although locally some positive development may also be foreseen. Whereas global effects of CC may be predicted with a certain degree of confidence, it is much more difficult to downscale such effects to the local level. Therefore, it may often be possible to predict consequences of CC for salmon in a certain geographic region, or with respect to stocks in southern vs. northern rivers, whereas it is typically hard to predict effects on specific populations (ICES 2017).

Studies on climate effects and drivers of important salmon life history characteristics, which are often used to assess likely impacts of CC, are numerous. Therefore, the aim of this summary is not to give a full list of all studies relevant for assessing the impact of CC on salmon populations, but rather to present selected examples from the scientific literature on factors and processes that may affect the distribution and abundance of this anadromous species. For more comprehensive reviews, see e.g. Jonsson and Jonsson (2009), ICES (2017) and Gillson et al. (2022). Since potential climate effects on salmon tend to differ between freshwater and marine habitats, the below presentation has been divided according to these main environments, followed by some additional topics of a more general nature.

Freshwater environments

Climate change with associated higher temperatures and increased climate variability is predicted to affect virtually all components of the global freshwater system (IPCC 2021). For example, the risk of both floods and droughts will increase, despite increased precipitation predicted on the global scale. Temperature and precipitation constitute major drivers for salmon productivity in freshwater. Further, changes in these drivers are expected to affect other processes, including abiotic factors such as river discharge and water characteristics (pH, dissolved oxygen levels, water colour etc), as well as biotic factors (food availability, predation etc), which will also impact salmon during their freshwater phase (ICES 2017).

Potential impacts of CC on salmon in freshwater include changed growth patterns, increased mortality, younger smolt age and earlier smolt migration, earlier attainment of sexual maturity, and spawning later in the season (Jonsson and Jonsson 2009, ICES 2017). Predicted effects of CC are briefly reviewed in more detail below.

In the northern distribution, where summer temperatures are lower, a warmer climate may not significantly affect natural mortality rates of parr during summer months. However, increased temperature may reduce ice-covered periods in rivers during winter, which may cause negative effects on salmon parr survival in northern areas (e.g. Finstad et al 2004). In contrast, profound effects on the survival of parr can be anticipated when temperature increases in the southern distribution range (Jonsson and Jonsson 2009, ICES 2017), especially during extreme weather events in summer, which are predicted to increase in the future as a result of CC (IPCC 2021). The magnitude of such effects are, however, likely to vary on spatial scales and due to local contexts (ICES 2017). Salmon parr are able to switch rearing habitat and move into cooler habitats when temperature is rising (e.g. Erkinaro and Gibson 1997), and populations in rivers with colder tributaries and/or cold ground water flows are therefore predicted to be more resistant to elevated temperatures (e.g. Kurylyk et al. 2015).

Climate models predict that milder winters will also become wetter (IPCC 2021). Increased egg mortality may result from rain and snow events followed by ice scouring of stream beds (Cunjak et al. 1998), and winter flooding may increase extinction risk for some populations (Battin et al. 2007). Negative effects from warm and wet winters may include washout of eggs and fry from gravels (Jensen and Johnsen 1999) or a mismatch in the timing of hatching of eggs and emergence of fry and the abundance of prey, resulting in insufficient energy reserves for survival (McGinnity et al. 2009, Jonsson and Jonsson 2011). At the same time, density-dependent mortality may decrease because more habitats become available when the wetted area increases (e.g. Linnansaari et al. 2008, Hedger et al. 2013, Hvidsten et al. 2015). In rivers in the intermediate distribution range, milder winters could cause a reduction in ice building and ice scouring, which also may increase opportunities for parr to survive the winter. Effects of milder and weather winters are thus rather difficult to predict, and will likely vary between regions and rivers depending on factors such as latitude, altitude, gradient, groundwater influence and topography (ICES 2017).

Winter, spring and summer droughts are expected to become more frequent, particularly in the southernmost part of the distribution range, which will most likely have negative effects on the productivity of many southern salmon populations. Younger parr are sensitive to low flow because of low mobility and reduced ability to escape (Elliott and Elliott 2006), whereas older parr tend to move to deeper pools, if available, during severe droughts (Armstrong et al. 1998). Droughts and low discharge in southern rivers comes in addition to other climate-induced changes, such as an increase in water temperature, which could be energetically costly and may therefore affect salmon negatively, particularly in the southern part of their distribution (ICES 2017).

The impact of CC on growth of salmon parr is expected to vary considerably depending on latitude and other factors such as e.g. density of conspecifics (Bal et al. 2011). Growth-temperature relationships can be used to predict possible effects for regions and individual populations (e.g. Mallet et al 2009). For populations in the northern distribution area, increased temperatures will likely result in faster growth (Jonsson and Jonsson 2009 and references therein), which will in turn affect other life history characteristics (see below). On the contrary, for populations in intermediate and southern areas, summer temperatures may rise to sub-optimal or even lethal levels and affect salmon productivity negatively (ICES 2017).

Drivers affected by CC are expected to impact both the size and age at smoltification, as well as the timing of the smolt migration in spring and early summer. With increasing temperatures, smolt age and size are expected to decrease in temperate and northern latitudes due to higher expected growth rate (L'Abée-Lund et al. 1989). Earlier studies have found that smolts are adapted to enter the sea when optimal marine environmental conditions prevail (e.g. McCormick et al. 1998, Hvidsten et al. 2009). The smolt run-timing is becoming earlier across the North Atlantic by 2.5 days per decade on average, which is believed to be a result of CC as the shift in phenology matches changes in air, river, and ocean temperatures (Otero et al. 2014). According to model predictions, temperature increases over land due to CC are expected to exceed those over the surface of the oceans, and since smolt migration is partly cued by the water temperature in rivers, mismatches relative to marine conditions might result and affect survival (Kennedy and Crozier 2010).

Spawning date seems to have evolved to allow progeny to emerge when conditions are favorable in spring (Quinn, 2005). The upstream migration of mature salmon can be delayed at low river flow (Solomon and Sambrook 2004, Jonsson et al. 2007), which may delay spawning and increase straying of returning salmon into non-native rivers (Jonsson and Jonsson 2009). Extremely high flow, on the other hand, can also delay the upstream migration of adult salmon (Jonsson et al. 2007) due to elevated migratory costs associated with higher flow (Enders et al. 2005). CC may also decrease the size and age at maturity (e.g. ICES 2017). Large salmon females produce more and larger eggs, compete more effectively for spawning sites and dig deeper redds, while large males have a better competitive ability and are commonly preferred by females as mates (Quinn, 2005). Changing temperature and flow regimes resulting from CC may thus influence spawning success in a variety of ways, including the ability of adult salmon to access suitable spawning areas, the timing of spawning and the size and quality of eggs (ICES 2017).

Marine environments

Projected changes in sea surface temperatures (SST) predict warming at higher latitudes in the Atlantic Ocean where salmon have their primary adult feeding grounds (ICES 2017). Synchronous population declines for salmon in North America and Europe during several decades have been interpreted as evidence of a common response with populations being negatively impacted by warming ocean conditions, although different mechanisms may be governing survival rates for salmon from the two sides of the Northern Atlantic (Friedland et al. 2014). Also for salmon in the Baltic Sea, estimates of survival during the post-smolt phase have been found to be negatively correlated with temperature, indicating that warming conditions have impacted sea survival negatively (Friedland et al. 2017, HELCOM 2021).

Salmon growth at sea is affected by temperature – either directly via physiological processes or indirectly via environmental factors (e.g. food availability) – and marine survival appears to be strongly mediated by growth (Friedland et al. 2000). Up to an optimum level (13°C) salmon growth in the sea increases, whereas at higher temperatures it is inhibited (Handeland et al. 2003). The empirical evidence of effects from increasing SST on salmon is mixed, with reported examples of both reduced (e.g. Todd et al. 2008) and increased (e.g. Friedland et al. 2000) marine growth. For certain populations, reports of declining growth have been linked to anomalous warming in specific marine feeding areas (Todd et al. 2008).

Growth and survival also depend on access to suitable prey. Potentially climate-related changes in the distribution and condition of marine keystone forage species, such as capelin in the NW Atlantic (ICES 2016), may thus have negative consequences for top predators such as salmon. In particular, scarce food resources and reduced growth when smolts have entered salt water may result in increased mortality; in the Atlantic Ocean, significant negative correlations have been demonstrated between SST and salmon post-smolt growth and survival (Friedland et al. 2009). Likewise, annual variation in salmon sea survival has been demonstrated to coincide with variation in the recruitment of herring in the Baltic Sea (Mäntyniemi et al. 2012), known as an important prey species for post-smolts in that area (Salminen et al. 2001).

Age and size at maturation are key life-history traits with strong links to individual fitness and evolutionary trade-offs (Roff 1992). Sea age and maturation rates in salmon are controlled by both genetic and environmental factors (e.g. ICES 2017). The size of salmon spawners is largely dependent on the number of years spent at sea, with a large body size typically associated with many offspring. But many years at sea also increases the risk of dying before having reproduced.

Although altered marine conditions, mediated via effects on salmon growth, survival and maturation, may explain changes in sea age composition, the mechanisms for this are not clear (ICES 2017). For populations migrating into the Atlantic Ocean, widespread changes in sea age composition have been reported, with long-term declines (ICES 2016) in the proportion of multi-sea winter (MSW) salmon returning to many rivers, followed by more recent increases in some areas (ICES 2021c). Past changes in sea age composition seems to have been consistent throughout the geographic range and over time (ICES 2010 and references therein), suggesting that characteristics of the marine environment have been the main drivers of the change in age at maturity (Aprahamian et al. 2008). For salmon in the

Baltic Sea, no evidence of altered growth opportunities at sea or life history changes coupled to CC yet seem to exist (ICES 2021b), although retrospective studies of past changes in growth patterns and age at maturity/repeat spawning are ongoing based on archived scale collections and tagging data.

Climate-driven eco-system changes occurring in the early 1990s in the NW Atlantic have been suggested to affect marine productivity of salmon from both Europe (Beaugrand and Reid 2012) and North America (Mills et al. 2013). For example, the consumption of capelin by salmon feeding at Greenland was lower in 2006-2011 compared to in 1965-1970, which coincides with a drop in mean energy density (c. 34 %) of this important prey species after 1990 (Renkawitz et al. 2015). Similarly, eco-system changes affecting the distribution of marine predators on salmon post-smolts have been suggested to affect sea survival negatively for both North American (Friedland et al. 2012) and Baltic Sea (Friedland et al. 2017) populations. In the brackish Baltic Sea, increased precipitation and lowered salinity may reduce cod populations predating on sprat which may, in turn, result in increased M74 in salmon, a mortality-syndrome positively correlated with the proportion of sprat in the diet of Baltic salmon (Mikkonen et al. 2011, ICES 2018).

Species distribution

A warmer climate will likely result in fragmentation and/or extinction of salmon populations in the southern distribution range, while the species may colonize new rivers in the most northern parts (northern North America and in north-east direction along the continental coast of Russia) (e.g. Jonsson and Jonsson 2009, ICES 2017). This prediction is in agreement with, for example, CC models for eastern Canada, showing an overall loss of juvenile salmon habitats (Minns et al. 1995), and experiments using molecular biomarkers of temperature stress on wild caught salmon parr from Miramichi river in New Brunswick, Canada (Lund et al. 2002).

In the marine environment, continued warming will likely result in ice free summers in the Arctic Ocean. This has potential to make presently inaccessible marine habitats available for salmon - a northern range shift that may already have commenced, and that could especially benefit populations from rivers in Western and Northern Norway (Jensen et al. 2014).

Parasites and diseases

Although few documented examples seem yet to exist, a warmer climate has been suggested to be associated with increased risks for salmon mortality due to parasites and diseases, especially during sensitive times in the life cycle such as transitions between fresh- and saltwater (ICES 2017). For example, increased water temperature yields a shorter generation length in the salmon louse *Lepeophtheirus* *salmonis* (Tully 1992), a natural parasite that is causing significant problems for wild salmon populations in areas of intense aquaculture (Finstad et al. 2011). Populations of pink salmon (*Oncorhynchus gorbusca*) originating from the Pacific Ocean, once introduced to Northern Russia and from there spreading into neighboring rivers in Norway (Sandlund et al. 2019) as well as other north Atlantic countries (e.g. Staveley and Ahlbeck Bergendahl 2022), may benefit from climate warming and extend their distribution to more southern parts of Europe. If so, this may have (largely unknown) consequences for native salmon populations, for example via spread of new parasites and diseases (ICES 2017). Potential effects by a warming climate on salmon populations affected by the freshwater ectoparasite *Gyrodactylus salaris* and proliferative kidney disease PKD (caused by the myxozoan *Tetracapsuloides bryosalmonae*) have also been discussed (Harris et al. 2007).

Genetic diversity

Conserved genetic diversity will be crucial if salmon populations are to be able to respond to changing conditions through evolutionary (adaptive) responses. In the long run, evolution is the only way a population may keep track with long-term directional environmental changes induced by CC, although adjusted phenotypes (phenotypic plasticity) may facilitate fast short-term responses to unpredictable (stochastic) environmental fluctuations (ICES 2017).

Both population losses and reductions in population size are expected to affect the species’ genetic structure. Reduced numbers of individuals in populations stressed by a warmer climate have been predicted (e.g. Lassalle and Rochard 2009), and is expected to result in fewer breeders and a reduced effective population size (N_E). This in turn results in increased random losses of hereditary variation, increased inbreeding and less efficient natural selection, and ultimately reduced chances of population endurance. Population extirpations due to CC also seem likely (Jonsson and Jonsson 2009, Lassalle and Rochard 2009) and will inevitably result in lost intraspecific genetic diversity, in particular if/when regional population groups with unique phylogenetic histories will go extinct. Reductions in genetic diversity may become exaggerated if natural gene flow between remaining local populations becomes reduced, due to population extirpation and fragmentation.

Table 6.3. Climate change processes and responses, key conclusions

Atlantic salmon (NE and NW Atlantic Ocean, Baltic Sea)		
Process	Response to climate change	Reference(s)
Mortality	Increased egg mortality due to changed flow and ice conditions.	Cunjak et al. (1998), Jensen and Johnsen (1999)
	Increased parr mortality due to high water temperature, droughts and/or changed ice cover.	ICES (2017), Finstad et al. (2004)
	Increased post-smolt (and eventually adult) mortality correlated with increased sea surface temperature.	Friedland et al. (2009, 2017), Todd et al. (2008)
Growth	Decreased/increased growth of parr in southern/northern rivers with increased water temperature.	Jonsson and Jonsson (2009), ICES (2017)
	Decreased (or increased) growth of post-smolts depending on variation in sea surface temperature across the distribution range.	Friedland et al. (2000, 2009)
	Decreased growth of adults with increased sea surface temperature.	Todd et al. (2008)
Spawning	Delayed river entry and spawning due to low or high river flow.	Jonsson et al. (2007)
Recruitment	Decreased recruitment caused by increased egg and parr mortality.	See above
	Decreased recruitment caused by reduced egg deposition (and egg size) due to altered size and age distributions among returning spawners.	ICES (2017)
	Increased recruitment due to larger wetted areas in northern rivers.	Hedger et al. 2013, Hvidsten et al. 2015
	Increased smolt production in northern rivers due to increased parr growth and lowered smolt age.	L'Abée-Lund et al. (1989)

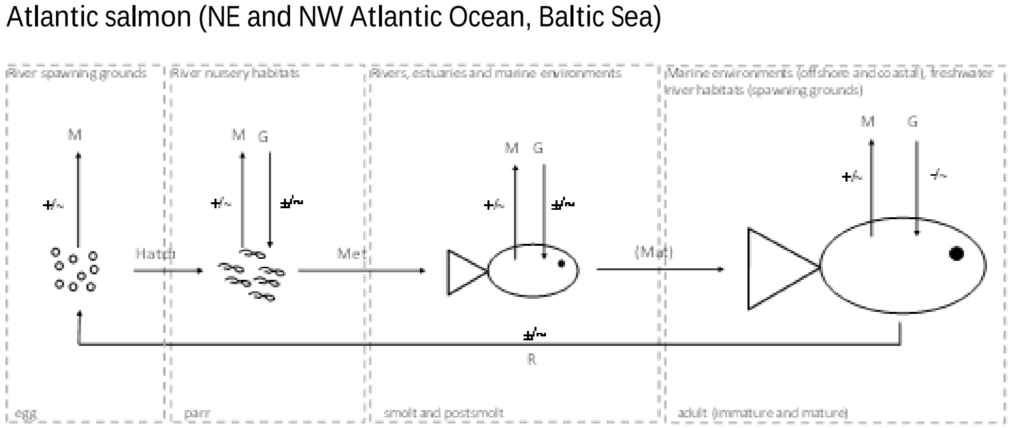
Atlantic salmon (NE and NW Atlantic Ocean, Baltic Sea)

Figure 6.3. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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6.4. Ballan wrasse (*Labrus bergylta*)

The ballan wrasse (*Labrus bergylta*) can reach a body length of up to about 60 cm (Darwall et al. 1992) and is the largest of the wrasse species native to Sweden. It is a protogynous hermaphrodite with benthic eggs and male parental care (Darwall et al. 1992). It spawns multiple times during spring, April-June in western Norway (Muncaster et al. 2020) and the eggs hatch after about 6 days (141 h) at 12°C (D'Arcy et al. 2012), followed by a larval stage lasting around 49 days (Ottesen et al. 2012). The distribution range stretches all the way from Morocco and the Azores to mid Norway (Kullander et al. 2012), where it inhabits vegetated hard substrate, rocky walls, and eelgrass (Freitas et al. 2021). Preferred food sources are especially bivalves and decapods (Deady and Fives 1995).

Hydrographic conditions determine dispersal of juveniles of species with limited adult migration (Sundt & Jørstad 1998). Since adult ballan wrasse are rather sedentary with small home ranges (Morel et al. 2013; Villegas-Ríos et al. 2013) and due to the benthic nature of the eggs, most dispersal of the species is likely done during the pelagic larval stages.

How ballan wrasse larvae is affected by climate change is unknown, however, the pelagic larval stage of the tropical fire clownfish (*Amphiprion melanopus*) is shortened by a higher rearing temperature (28 compared to 25°C) and absolute, but not developmental age has an impact on swimming speed (Green and Fisher 2004). Earlier studies on temperature effects on larvae of Gilthead seabream (*Sparus aurata*; Polo et al. 1991) and bream (*Abramis brama*; Kucharczyk et al. 1997) show that although the growth rate increase within a certain range of temperatures, higher temperatures can also cause higher mortality (Polo et al. 1991; Kucharczyk et al. 1997) and even a decrease in growth rate (Kucharczyk et al. 1997). Shima and Findlay (2002) found, however, that fast growing larvae of kelp bass (*Paralabrax clathratus*) settle sooner and enhance survival of the juvenile fish a few days after settling (Shima and Findlay 2022) and in a study on prey consumption rates and prey concentration of sea beam (*Archosargus rhomboidalis*), bay anchovy (*Anchoa mitchilli*) and lined sole (*Achirus lineatus*) larvae, it was shown that the amount of time it takes for the larvae to find their prey decrease as larvae grow, especially at low prey concentrations (Houde and Schekter 1980). So, it would seem profitable to reach a more developed stage as fast as possible.

While D'Arcy et al. (2012) state that ballan wrasse eggs hatch faster at higher temperatures (96 h at 16.5°C compared to 171 h at 10.5 °C), Rembelski (2014) concludes that the hatching rate and the survival of the eggs are higher at a temperature of 12°C compared to other temperatures between 8-16 °C, in combination with a 12 h light regime (Rembelski 2014). Regarding juvenile fish, ballan wrasse juveniles grow faster at 16°C compared to 13 and 10°C with no significant effect on mortality.Response to higher temperatures is poorly known

(Cavrois-Rogacki et al. 2019). Temperature may also influence gonadal maturity of the female ballan wrasse, but more research is needed (Muncaster et al. 2010).

The depth preference of ballan wrasse is affected by sea temperature as well (Leclercq et al. 2018; Freitas et al. 2021), such that fish inhabit shallower areas during summer when the surface temperature is warmer and deeper areas during winter when the surface temperature is colder than deeper down (Freitas et al. 2021). In the study by Freitas et al. (2021) the temperature range inhabited by ballan wrasse lay between 4.6°C and 19.4°C, equivalent to the warmest available water layers at the time of the year.

Additionally, because not all habitats are present at all depths, habitat use, and availability may change with changing temperature allowing more favourable shallower habitats to be used by ballan wrasse at warmer sea surface temperatures (Freitas et al. 2021). Also, aerobic scope (the difference between minimum uptake of oxygen at rest and maximum oxygen uptake at workout) of ballan wrasse seems to increase with temperatures between 5 and 25°C. It is possible that higher temperatures could improve the aerobic scope even further, but that has yet to be examined (Yuen et al. 2019) as well as whether an increase in the aerobic scope would result in an advantage, like for juvenile brown trout (*Salmo trutta*), only if resources are not a limiting factor (Auer et al. 2015).

Ballan wrasse is expected to do well under expected warming of summer sea water temperatures in Skagerrak (Freitas et al. 2021). However, fish from mid Norway, southern Scandinavia and Galicia in Spain belong to genetically separated populations (Seljestad et al. 2020). The genetic diversity is greater within the populations around the British Isles (D’Arcy et al. 2013) and in Galicia (Seljestad et al. 2020) compared to southern Scandinavia. The genetic difference between Galicia and southern Scandinavia is also greater than between Galicia and western Scandinavia (Seljestad et al. 2020). Whether these differences have an impact on tolerance to climate factors like temperature and pH needs to be determined as well as response to other ecological factors, for example infections and food availability in a changing climate.

Table 6.4. Climate change processes and responses, key conclusions

Ballan wrasse		
Process	Response to climate change	Reference
Mortality	No effect on mortality of juveniles raised at elevated temperatures (16°C). With reservation for potential beneficial temperatures for bacterial infections.	Cavrois-Rogacki et al. 2019
Maturation	Temperature may influence steroid levels, but further studies are needed.	Muncaster et al. 2010
Growth	Faster juvenile growth at higher temperatures.	Cavrois-Rogacki et al. 2019
Overwintering	Possible change of depth range/habitat use	Freitas et al. 2021
Recruitment	Faster hatching of eggs at temperatures of 12.9-16.5°C compared to 10.5 °C.	D'Arcy 2013

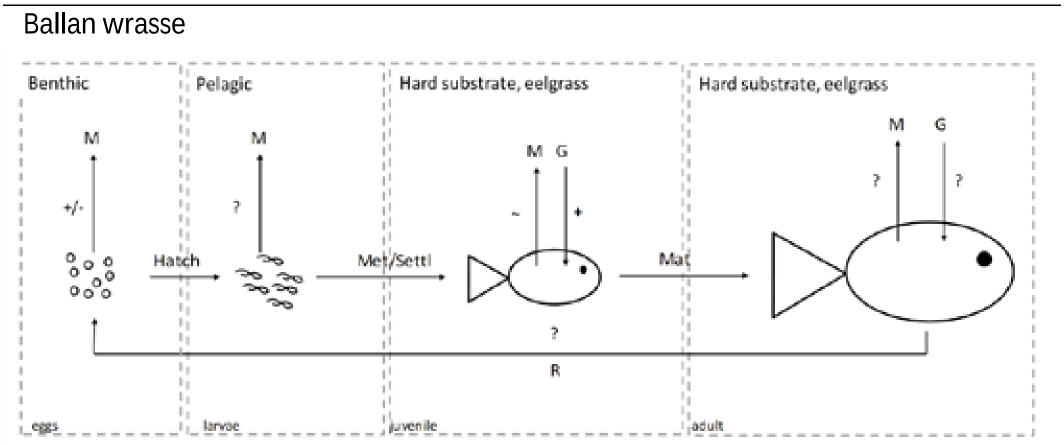

Figure 6.4. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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Authored by Erika Andersson

6.5. Blue whiting (*Micromesistius poutassou*)

The blue whiting (*Micromesistius poutassou*, Risso, 1827) is a commercially important gadoid found throughout the North-East Atlantic. The main summer feeding grounds are to the north and northeast of the British Isles. In the spring there is a southerly migration to the main spawning grounds which are over deep-waters outside the 200 m isobath to the west of the British Isles (Bailey, 1982; Bartsch and Coombs, 1997).

Acoustic surveys of spawning aggregations and vertical distribution sampling of newly spawned eggs have indicated that blue whiting spawning occurs at depths of 300-600 m (Monstad et al. 1996). Larvae are found mostly in the upper 60 m of the water column (Coombs et al. 1981).

The recruitment success and spawning distribution has been seen to be highly correlated with a specific and narrow salinity range (Miesner and Payne 2018). The apparent importance of the salinity range may have a number of explanations. Blue whiting eggs have initially neutralbuoyancy which allow them to maintain their position in the water column (Ådlandsvik et al. 2001). As the eggs develop the density changes and they move towards the surface where after hatching the larvae subsequently feed in food-rich surface waters. This transport is impacted by salinity as it impacts water density, therefore making salinity a critical variable for blue whiting spawning and recruitment (Ådlandsvik et al 2001; Miesner and Payne 2018).

Another explanation to the importance of salinity for recruitment success is that the zooplankton community associated with a higher salinity is more favourable to the growth of the blue whiting larvae (Bailey 1982, Hatun et al. 2009)

Thus, response of blue whiting to climate change will be largely dependent on how large scale water mixing will develop in the future with warmer and more saline conditions in the spawning region expected to have positive effects on recruitment (Miesner and Payne 2018).

Table 6.5. Climate change processes and responses, key conclusions.

Blue whiting		
Process	Response to climate change	Reference
Spawning	Increase in temperature and salinity is expected to increase egg survival.	Ådlandsvik et al. 2001
Growth	Increase in temperature and salinity are expected to influence the zooplankton community structure increasing the abundance of suitable preys for both larvae and juveniles (the effects indicated on survival and growth, respectively).	Bailey 1982, Hatun et al 2009, Payne et al. 2012
Recruitment	Increase in temperature and salinity will make more areas suitable for recruitment of blue whiting.	Miesner and Payne 2018

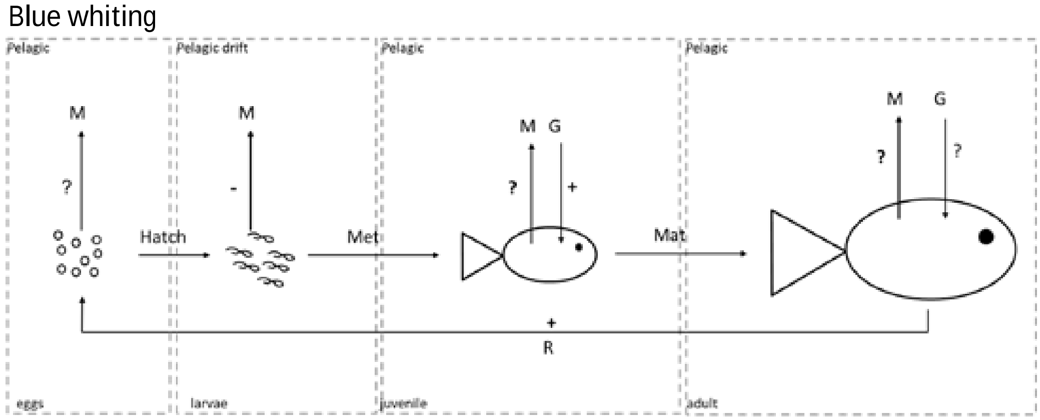

Figure 6.5. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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Authored by Johan Lövgren

6.6. Cod (*Gadus morhua*)

Atlantic cod is a geographically broad ranging species that has adapted to a wide range of environmental conditions from warmer shallow coastal waters to the colder waters of the deep sea, and from oceanic salinities to the brackish waters of the Baltic Sea. Historically, the species has been subject to highly important fisheries over its distributional range, though several stocks have declined rapidly in the last decades.

Given the adaptability of Atlantic cod the species inhabits waters ranging in temperature from below -1°C to above 20°C, however they are typically found in waters between 0-12°C (Drinkwater 2005). While cod inhabit areas with variable temperatures, optimal growth occurs between 10-15°C with larger cod exhibiting peak growth rates at the lower end of that range (Björnsson et al. 2007). Additionally, spawning cod have a narrower temperature preference range from 1-8°C (Righton et al. 2010).

Not only is temperature an important aspect in both juvenile and adult growth rates, it has also shown to account for year-to-year variation in growth rates for many cod stocks (Dutil and Brander 2003), and temperatures at either end of the species thermal range, extreme cold or extreme heat, result in slowed growth as a result of reduced feeding despite the presence of sufficient food (Waiwood et al. 1991). In fact, Rätz and Lloret (2003) found that the bottom temperature of a stocks range had an impact on the populations body condition, with stocks in warmer waters having better condition (Fulton’s condition index, K). The link between temperature and growth and body condition is also exemplified by the fact that larger females tend to arrive and begin spawning earlier, and therefore spawn for a longer duration, than smaller females (Tomkiewicz and Köster 1999).

Additionally, spawning time varies considerably and can be related to geographic location, for instance cod on the west coast of Sweden spawn in winter, while cod in the Baltic are found to spawn in early summer (reviewed by Hüssy 2011). Spawning is also linked to water temperature with cod inhabiting warmer waters spawning earlier, which has been related to the faster development of the gonads in fish leading to earlier readiness to spawn (Hutchings and Myers 1994). While temperature is an important aspect in spawning, egg size and larval development of Atlantic cod have also been shown to have considerable phenotypic plasticity among individual cod eggs and larvae of different sizes (Miller et al. 1995).

The adaptability of the species can be seen, not only in relation to temperature, but salinity as well with cod found in fully oceanic, highly saline areas to the brackish waters of the Baltic (35 psu to 5/6 psu, respectively) (Kijewska et al. 2016) with salinities of 11-15 psu necessary for reproduction for Baltic cod (Nissling and Westin 1997).

Atlantic cod populations vary from migratory, swimming large distances both vertically in the water column and latitudinally, to rather stationary settling in coastal fjord areas (see summary by Neuenfeldt et al. 2013, Kirubakaran et al. 2016). Despite the species wide geographic range and high adaptability there is still concern arising from the fact that the species range falls within areas predicted to experience some of the largest degree of anthropogenic change (Drinkwater 2005). Brander (2010) also points out that cod populations have shown extensive patterns of change in productivity resulting from lower growth and condition due to large-scale climate forcing and some cod populations have already shown significant range shifts due to temperature changes, while a review by Petitgas et al. (2013) indicates that climate change may result in increased habitat availability and stock productivity.

6.6.1. Eastern Baltic cod

Eastern Baltic cod (EBC) is living at some of the extremes of the species tolerances having adapted to the brackish conditions of the Baltic Sea. The genetic adaptation of EBC indicates that the salinity gradient creates a border maintaining genetic and physiological separations between cod stocks with EBC found in salinities as low as 5 psu, and that this adaptation protects this subpopulation from the osmotic stress resulting from the daily vertical migrations between saline deep waters and low salinity shallow-waters, as well as migrations to spawning areas (Kijewska et al. 2016). Additionally, EBC is exposed to hypoxic waters with deteriorated oxygen levels in the deep water layers (Schaber et al. 2012).

As a result of a combination of environmental and anthropogenic causes, including overfishing, EBC has shown considerable deterioration in growth and overall body condition. There has been a substantial reduction in the size distribution of EBC, a decrease in the age at maturity and an indication of reduced growth of juveniles in the last decade (Hüssy et al. 2018) as well as signs of reduced larval survivability as temperature increases (Nissling 2004). Additionally, the parasite load of EBC has increased contributing to a surge in the number of cod in poor condition (Bergenius et al. 2019). As well as an increase in parasites, cod larvae became food limited in the 1990s as a result of a decrease in the population size of the copepod Pseudocalanus sp. (summarized by ICES 2005) and there is evidence of changes in metabolism, possibly related to shifts in environmental conditions (Svedäng et al. 2020).

The spawning time of EBC has shifted from spring to summer in the last few decades as a result of temperature changes, which has also led to a change in food availability, and thus an increase in egg and larval mortality leading to recruitment failure (Köster et al. 2005, 2008). While adult EBC are adapted to lower salinities, reproduction has specific salinity requirements with spawning occurring at a salinity of around 11-12 psu and the cod eggs showing neutral buoyancy from 12-18 psu (Nissling and Westin 1997). In fact, EBC eggs have also adapted to the brackish conditions and are both larger and lighter than eggs from the western Baltic and North Atlantic (Vallin et al. 1999). Given these specific requirements the Bornholm Basin is an important spawning area for EBC meaning that the shift in spawning season of EBC has also lead to increased predation of cod eggs by clupeids as sprat and herring are also found within the Bornholm Basin (Köster and Möllmann 2000). Previously, the Gdansk Deep and the Gotland Basin were also important spawning areas, however deteriorating conditions and oxygen levels have meant that these areas no longer support spawning cod and developing eggs and larvae as they did previously (Vallin et al. 1999).

Cod make both seasonal migrations to spawning grounds as well as daily vertical migrations between deep and shallow waters, moving to cooler deep water when surface temperatures increase. This makes EBC particularly sensitive to projected future changes to temperature, salinity and oxygen. There has been an increase in hypoxic areas within the Baltic Sea over the last 20 years, with oxygen levels below cod tolerance, but despite this cod has been shown to spend an increasing amount of time in these deeper, low-oxygen waters, likely because of a reduction in areas of suitable habitat (Casini et al. 2021).

Eastern Baltic cod are already very limited in geographic range, with few areas meeting the appropriate conditions necessary for them, however due to their unique adaptations this subpopulation is able to live just within the species salinity tolerance levels. Therefore, as predicted global climate alters the Baltic Sea EBC will likely be highly affected, and experience even habitat reduction. Future predictions for the Baltic, while variable, show a likely decrease in salinity, increase in hypoxic areas and an increase in temperature (Vuorinen et al. 2015, Saraiva et al. 2019, Meier et al. 2021), all of which will reduce even further the amount of area with suitable habitat for the EBC.

Table 6.6.1. Climate change processes and responses, key conclusions.

Eastern Baltic cod		
Process	Response to climate change	Reference
Mortality	Low salinity and oxygen conditions decrease egg survival. Egg and larval mortality cause low recruitment. Temperature increase causes lower larval survivability.	Köster et al. 2005, 2008; ICES 2005; Nissling 2004
Maturation	Decreased size at maturity and reduced juv. growth	Hüssy et al. 2018
Growth	Food limited due to decreased copepod *Pseudocalanus* sp population. Shift in spawning season to summer when nauplii copepod supply is low. Growth increases related to temperature show upper limits, above which growth slows or stops. Possible change in metabolism related to increased temperature.	ICES 2005, Köster et al. 2005; Righton et al 2010; Svedäng et al 2020.
Recruitment	Low recruitment due to food limitations & climate variability	Köster et al. 2005

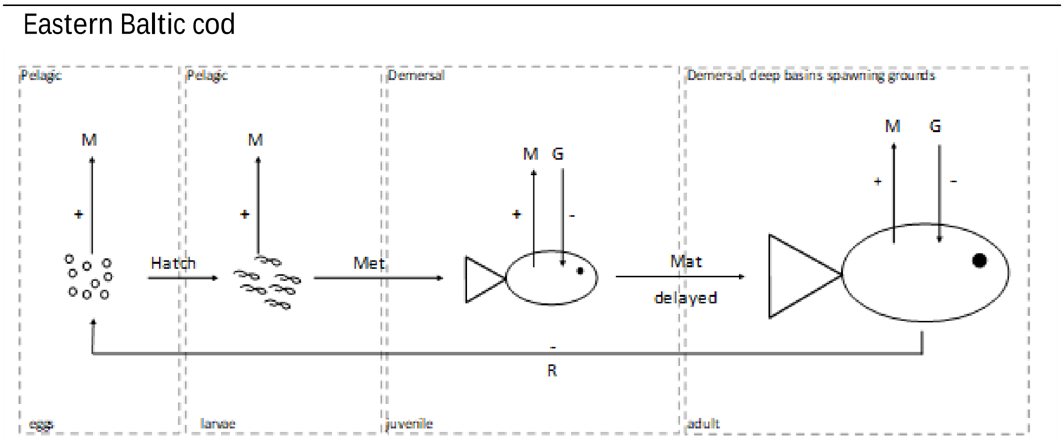

Figure 6.6.1. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

6.6.2. Western Baltic cod

Cod within the western Baltic Sea subpopulation live within the transition zone between the brackish waters of the Baltic and the fully oceanic North Sea. Here, salinities can range from as low as 10 psu at the eastern end of the range to 33 psu with the inflow of well oxygenated water from the North Sea to the west. Until recently the western Baltic cod (WBC) stock was thought to be healthy and well managed, however it has now declined significantly resulting in the International Council for the Exploration of the Sea (ICES) suggesting a serious reduction in the catch advice for 2022 (ICES Advice 2021 - cod.27.22-24).

The age structure of WBC is dominated by few age groups and there is a high contribution of first-time spawners, with the spawning stock biomass and recruitment success fluctuating considerably over the last few decades (Hüssy 2011). For WBC peak spawning time begins in March and ends in April or May in salinities as low as 15 psu in the eastern end of the stocks range, to fully marine salinities found in the Kattegat (Nissling and Westin 1997, Bleil et al. 2009). The timing of spawning is influenced by temperature and in addition temperature and oxygen also play a significant role in fertilization, egg and larval development and survival (Hüssy 2011).

As well as the influence of temperature on egg and yolk-sac larvae survival, buoyancy and transport to suitable versus unsuitable (contact with the bottom) locations play a major role in mortality (Hinrichsen et al. 2012, Petereit et al. 2014). Eggs, larvae and pelagic juvenile dispersal is heavily influenced by current direction and speed and can be driven in part by the prevailing winds, with survival success differing with season. Additionally, individuals transported to the southeast have extremely low survivability due to insufficient salinities disrupting buoyancy (Hinrichsen et al. 2012). Given the high mortality of eggs and larvae transported to the east, and the genetic evidence of adaptation to the low salinity found in the eastern Baltic cod which is not present in the WBC (Kijewska et al. 2016), there is likely very little emigration of WBC to the east from Bornholm (Hinrichsen et al. 2017) and mixing with the EBC is primarily occurring in the Arkona Basin of the western Baltic (McQueen et al. 2019, Funk et al. 2020).

Adult cod undertake highly complex migrations seasonally and at the onset of maturation to spawning grounds. Within the western Baltic the migrations patterns can be highly variable with some cod in the Belt Sea migrating towards the southern Kattegat and Danish Belts, while cod in Mechlenburg Bay have been shown to migrate towards the east along the coasts of Germany and Poland (summarized by Hüssy 2011).

Due to the complexity of the migration patterns and the importance of temperature on the onset of spawning as well as the importance of salinity for egg survival, WBC may face significant habitat changes as a result of predicted future global ocean changes altering salinity and temperature in the Baltic (Meier et al. 2011, 2021, Vuorinen et al. 2015). Of great importance for the western Baltic cod stock is the influence of wind on egg and larval transport, and there have been predictions of increases in wind speed (Meier et al. 2011) and therefore management of WBC must take into account the impact of climate forcing on the recruitment process (Petereit et al. 2014).

Table 6.6.2. Climate change processes and responses, key conclusions.

Western Baltic cod		
Process	Response to climate change	Reference
Mortality	Egg and larval mortality with reduced salinity and potential changes in wind driving transport to unsuitable habitats	Hinrichsen et al. 2012, 2017, Petereit et al. 2014
Maturation	Earlier maturation with increased fishing pressure and temperature	Hüssy 2011
Growth	Faster growth with warmer temperature	Hüssy 2011
Recruitment	Temperature and oxygen have significant effect on fertilization, egg/larval development and survival	Hüssy 2011

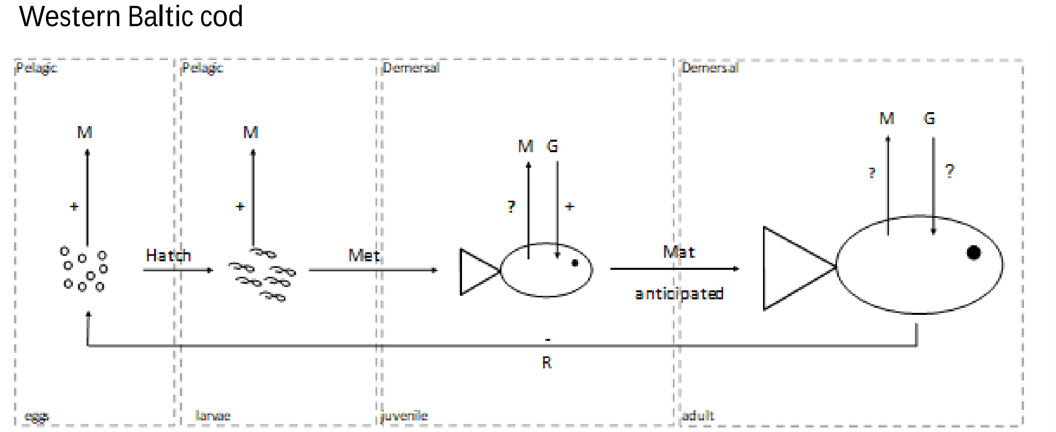

Figure 6.6.2. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

6.6.3. Kattegat cod

Kattegat is characterized by a lower salinity upper layer flowing in from the brackish waters of the Baltic Sea at 18-26 psu, and a strong halocline separating the deeper, high salinity oxygen-rich waters from the North Sea with salinities between 32-34 psu. The climate conditions in the area are mainly influenced by large-scale circulation patterns, resulting in alterations of the temperature regimes within the Kattegat and Baltic Sea (Lindegren and Eero 2013). While oxygen rich water flows in from the North there has been an increase in the last few decades of periods of anoxia and hypoxia within the Kattegat (Karlson et al. 2002). Temperature changes and the seasonal occurrence of hypoxia have been considered as reasons for the lack of recovery of the collapsed stock due to overfishing, despite stricter management regulations (Lindegren and Eero 2013, Sguotti et al. 2019).

The hypoxic/anoxic conditions alter the benthic community composition which can lead to a reduction in food availability and therefore reduced juvenile survival (Karlson et al. 2002). Additionally, temperature effects influencing trophic interactions have also been considered as a reason for reduced growth and survival of early life stages of cod (Beaugrand et al. 2003), and it is therefore proposed as another reason for the lack of stock recovery in the Kattegat (Lindegren and Eero 2013).

The current cod spawning stock biomass in the Kattegat is estimated to have been reduced by 94% since the 1970s, and it is thought that it only provides 34% of the locally retained larvae, whereas in the 1970s 83% of larvae retained in the area was thought to be the contribution of the Kattegat spawning stock (Jonsson et al. 2016) and surveys indicate that there has been an almost total disappearance of aggregations of spawning cod (Svedäng and Bardon 2003). South-eastern Kattegat close to the Sound and off the coast of Falkenberg, however, are considered spawning grounds with cod beginning to aggregate for spawning there in January (Vitale et al. 2008). In fact, the importance of different spawning areas has changed considerably since the 1970s due to serious losses of spawning stock biomass from both the North Sea and the Kattegat, which has resulted in a reduction of larval supply. Larvae flow from North Sea into the Skagerrak and Kattegat can be significant in numbers, however the flow is highly variable related not only to the spawning stock biomass but also likely varies in relation to the North-Atlantic Oscillation index. Therefore, this has also meant that Öresund, or cod from the western Baltic Sea, became a very important supply of larvae to the Kattegat by the mid-2010s providing approximately 50% of larvae to the area (Jonsson et al. 2016), though the overall number of larvae in the area was still drastically reduced compared to the levels in the 1970s. Given the drastic decline of the WBC in the last few years, this has potentially catastrophic consequences for any potential recovery of cod within the Kattegat.

Less than a third of all larvae within Kattegat are thought to originate from spawning cod within the area. This has been proposed as an explanation for the lack of population recovery despite stricter management practices and some years of high juvenile recruitment, because cod originating from outside the area may show natal homing behavior and therefore return to where they were spawned from (Bonanomi et al. 2016). Adult cod within the Kattegat, Skagerrak and Öresund can migrate either to the Baltic and/or the North Sea (Neuenfeldt et al. 2013).

As with other parts of the Swedish coasts, there is predicted to be an increase in ocean surface temperature and a decrease in oxygen concentration within the Kattegat (Meier et al. 2012), having consequences for early development stages of cod (Lindegren and Eero 2013). Additionally, there is new evidence of a potential future freshening of the surface water in the Kattegat, and this together with an increase in surface temperature is predicted to cause an intensification of the pycnocline, potentially shifting the pycnocline up in the water column (Gröger et al. 2019). Since Jonsson et al. (2016) found that larval retention in the Kattegat was highest for larvae floating below the pycnocline, a predicted upward shift of the pycnocline will undoubtedly have consequences for cod larval retention and survivability as a shift upwards would likely mean larvae would be in warmer waters.

Table 6.6.3. Climate change processes and responses, key conclusions.

Kattegat cod		
Process	Response to climate change	Reference
Mortality	Possible changes to larval survivability due to a shift in the pycnocline	Jonsson et al. 2016
Maturation		
Growth	Temp induced changes in trophic interactions reduce growth and survival of early stages	Beaugrand et al. 2003, Karlson et al. 2002
Recruitment	Temp changes and increased hypoxia considered reasons for lack of stock recovery	Lindegren and Eero 2013, Sguotti et al. 2019

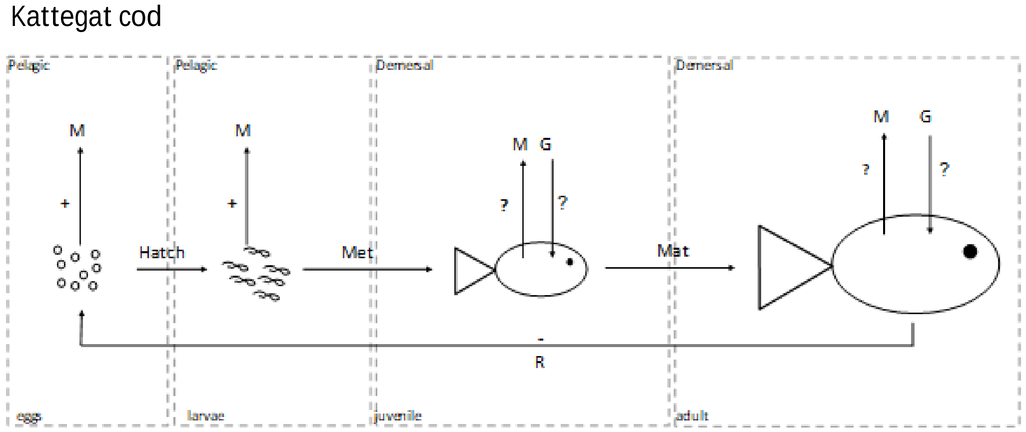

Figure 6.6.3. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

6.6.4. North Sea cod

The North Sea is a region currently experiencing a high degree of ocean change including warming and sea level rise, and future projections predict that these changes will continue and intensify over the next century (O'Brien et al. 2000, Quante and Colijin 2016). The oceanic waters of the North Sea have historically supported a highly productive fishing area though overfishing has depleted cod stocks since the 1970s (Fromentin et al. 1998, Jonsson et al. 2016).

Already in the middle of the 1990s there was a clear shift in age at maturity in cod due to fishing pressure in the North Sea with faster growth and earlier maturity which has led to smaller cod spawning therefore producing fewer, less viable eggs than larger spawning cod (Rochet 2001, Wright et al. 2011). This shift to an earlier age at maturity also means that after maturity these smaller cod devote more energy to post-maturity growth, thus having potentially less energy for reproduction causing a decrease in fecundity (Rochet 2001). Not only has there been a change in growth as a result of fishing pressure but low zooplankton abundance and shifts in plankton ranges are also associated with bad cod recruitment and decreased larval survivability, with spatial overlap of larval cod and zooplankton essential for larval growth (Beaugrand et al. 2003, ICES 2005). Additionally, large-scale climate forcing is also considered responsible for the change in cod productivity because of reduced individual growth and condition (Brander 2010).

Specifically, an increase in temperature has been associated with weak year-classes for North Sea cod, and in combination with the reduced spawning-stock biomass due to a high fishing pressure, a change in temperature might result in the prevention of stock recovery via low production of new recruits (O’Brien et al. 2000). Cod in the North Sea show a preference for spawning in high salinity waters with temperatures of approximately 5-7°C, showing strong site fidelity and continuously returning to many of the historically reported spawning grounds (Lelièvre et al. 2014, González-Irusta and Wright 2016). The predictive spawning ground model by González-Irusta and Wright (2016) also indicated that cod select areas with coarse sand bottoms for laying eggs avoiding places with strong currents. Due to the preference for high salinity waters many of the spawning grounds are located close to salinity transition areas between coastal and shelf water, which leads to good feeding conditions, with the physical processes found at these frontal areas possibly restricting egg and larval dispersal, transporting them to suitable nursery habitats (Munk et al. 2002).

Within the North Sea there are both migratory and resident populations with clear evidence of two separate ecotypes, one found in the deep waters of the northeast and the other in shallower areas. Very little movement between the life stages of these cod populations has been observed and therefore it is likely that they experience very different temperatures and depths (González-Irusta and Wright 2016).

While the two populations might experience different temperatures, the projected future increase in temperature in the North Sea is likely to influence both negatively. Given that there has already been clear evidence that in years of increased temperature at spawning locations cod show avoidance of warmer areas, considerably reducing suitable habitats (González-Irusta and Wright 2016), a continued temperature increase will likely have deleterious effects on all cod populations in the North Sea. If warmer waters result in a shift in spawning location egg and larval survivability will likely be influenced given the specific requirements at frontal locations of high salinity and the change in the plankton community (Beaugrand et al. 2003, González-Irusta and Wright 2016), thus leading to reduced recruitment for an already reduced species.

Table 6.6.4. Climate change processes and responses, key conclusions.

North Sea cod		
Process	Response to climate change	Reference
Mortality	Increased temps modified plankton community leading to reduced cod larvae survivability	Beaugrand et al. 2003
Maturation		
Growth	Lower individual growth and condition caused by large-scale climate forcing	Brander 2010
Recruitment	Change of spawning location due to warmer temperatures	Gonzalez-Irusta & Wright 2016

North Sea cod

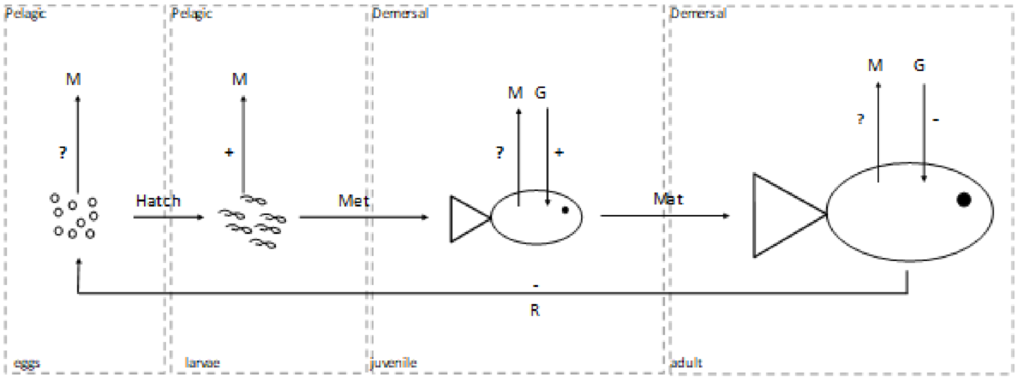

Figure 6.6.4. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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Authored by Diana Hammar Perry

6.7. Cyprinids (Cyprinidae)

Cyprinids refers to fish within the carp family, Cyprinidae, which is a family of mid-trophic level fish species. Cyprinids are not typical target species for fisheries in Sweden, but they are used as a resource in some other countries around the Baltic Sea (Ådjers et al. 2006, Snickars et al. 2015, Olsson et al. 2012). This text focuses on two different cyprinid species, roach (Rutilus rutilus) and common bream (Abramis brama), the latter hereafter referred to as bream. Both roach and bream are freshwater species that inhabit coastal waters of the Baltic Sea. Roach is by far the most dominating of these species, but beam occupies the same habitats (Härmä et al. 2008, Lappalainen et al. 2001, Ådjers 2006).

Coastal fish monitoring shows that there has been an increase in cyprinid catches, often dominated by roach, in recent decades, correlating with an increase in temperature (Helcom 2018, Olsson et al. 2012, Bergström et al. 2016, Peltonen and Weigel 2022). Studies from the Gulf of Bothnia and the Gulf of Finland along the Finnish coast show a positive correlation between roach year-class strength and temperature in June (Lehtonen and Lappalainen 1995).

Since both bream and roach are freshwater species, salinity limits their distribution into coastal and sea areas, but both species can live in the brackish waters of the Baltic Sea and adult roach can be found in salinities up to 14 psu (Jäger et al. 1981; Banarescu and Coad 1991 via Härmä et al. 2008). Low spring salinity, below 4 psu, is one of the most important factors determining the reproduction success of roach in the Gulf of Finland (Härmä et al. 2008). For newly hatched roach larvae, salinity above 3.5 psu in spawning areas has been proven lethal, with up to 100 % mortality (Klinkardt and Winkler 1989 via Härmä et al. 2008). Since the larvae require low salinities to survive, modelling studies indicate that if climate change causes salinity to decrease, the habitat available for roach to spawn could increase (Härmä et al. 2008).

Both roach and beam are spring spawners. They spawn for example in reed belts along the coast of the Baltic Sea (Härmä et al. 2008, Lappalainen et al. 2001, Kennedy and Fitzmaurice 1968). The temperature and timing for spawning of bream shows a wide variation between different areas, and bream has been observed to spawn in temperatures between 12-23 °C (Kennedy and Fitzmaurice 1968). In warmer areas, bream is a batch spawner, suggesting that with a rising temperature, bream might start to spawn multiple times a year (Targońska et al. 2014). Within a freshwater population of beam, one study showed that the optimal temperature for beam embryonic development was 21 °C and that spikes in temperature above 23 °C could be lethal, thereby lowering the reproductive success (Targońska et al. 2014). Another study of a lake population showed that the hatching success (and lowest mortality rate) of bream was highest at a temperature of 21.1 °C, and that mortality rate increased significantly at higher temperatures. The same study also showed that the duration of embryotic development decreased with increasing incubation temperature (Kucharczyk et al. 1997). For roach, experimental studies have shown that a constant temperature of 9 °C is a critical minimum temperature for roach embryo development, and with that in mind, warming could lead to an increased abundance in the Gulf of Bothnia or to earlier hatching (Cerny 1974; Gulidov and Popova 1979 via Härmä et al. 2008).

Several studies have shown that the growth rate of cyprinids is affected by temperature (Hardewig and Van Dijk 2003, Kucharzyk et al. 1997, Lappalainen et al. 2001). Juvenile roach have, in lab studies, shown a maximum growth rate at temperatures between 20-27 °C (Hardewig and Van Dijk 2003). This correlates quite well with a lab study of bream taken from a lake in Poland, which shows that their individual growth rate and biomass production rate increases with temperature within the span of 13.5-29.9 C, if given unlimited resources. The rates were highest at a temperature of 27.9 °C and decreased with higher temperatures thereafter (Kucharzyk et al. 1997). If the temperature in the Baltic Sea continues to increase, cyprinids populations can be expected to have a faster individual growth, at least within the northernmost latitudes of the Baltic Sea (Lappalainen et al. 2001). However, abundance and growth might decrease if the population gets so big that intraspecific competition appears (Lappalainen et al. 2001).

Other factors driving the abundance of cyprinids, such as roach and bream, are eutrophication (Diehl 1988, Lappalainen et al. 2011, Berström et al. 2016) and low water transparency (Bergström et al. 2016, Sandström and Karås 2002, Ådjers et al. 2006), which can benefit Cyprinids. Both bream and roach can successfully forage in conditions with low water transparency and feed on a range of pray items (Diehl 1988, Sundblad et al. 2011). Juvenile bream feeds mainly on zooplankton, intermediate size classes feed on benthic invertebrates, while larger individuals of both bream and roach are generalists. Their food consists mainly of molluscs, but also includes zooplankton, zoobenthos, and plant material (Hoogenboezem 2000, Lappalainen et al. 2001, Wolnomiejski and Grygiel 2002).

Table 6.7. Climate change processes and responses, key conclusions

Cyprinids		
Process	Response to climate change	Reference
Mortality	If salinity decreases, the mortality of young life stages of roach in brackish water could decrease. Temperatures above 23 °C will increase mortality in bream embryos	Härmä et al. 2008 Kucharczyk et al. 1997
Maturation		
Growth	Warming increases the growth rate of bream and juvenile roach.	Kucharczyk et al. 1997, Hardewig and Van Dijk 2003 Lappalainen et al. 2001
Recruitment	Warming might induce batch spawning in bream. Warming will affect the embryonic development and hatching success of bream. Warming (increasing temperature in June) correlates positively with roach year-class strength. A decrease in salinity could benefit the reproduction success of roach by increasing the available spawning area. Increases in temperature may increase roach abundance in northern latitudes of the Baltic Sea, or cause a shift to earlier hatching since the minimum threshold for embryo development is 9°C.	Targońska et al. 2014 Targońska et al. 2014, Kucharczyk et al. 1997 Lehtonen and Lappalainen 1995 Härmä et al. 2008 Cerny 1974; Gulidov and Popova 1979 via. Härmä et al. 2008)

Cyprinids

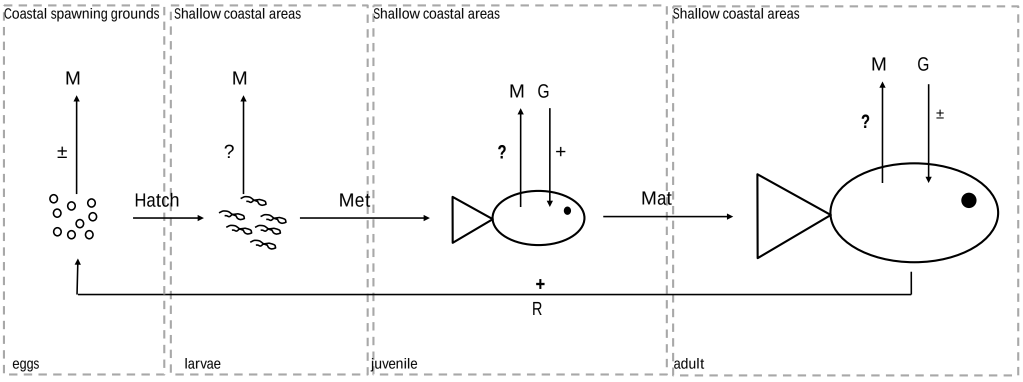

Figure 6.7. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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6.8. Edible crab (*Cancer pagurus*)

The edible crab (*Cancer pagurus)* or brown crab is distributed in Sweden along the whole west coast and down into the Öresund. In the rest of Europe it is found from 71 °N (Troms in Norway) down to the European Atlantic coast including the British Isles and Ireland as well as the Faroe Islands and Shetland, south to the coast of Portugal and into the Mediterranean, east to the Adriatic Sea.

The habitat is described as bedrock, mixed course grounds and offshore in muddy sand. Adult brown crabs occur at depths of 6 to 100 m, but usually between 6 and 40 m depth and tolerate current speeds ranging between 0 and 1.5 m s-1 (Neal & Wilson, 2008). Small crabs, on the other hand, are often numerous in the intertidal zone. The brown crab has a salinity preference of 30-40 psu, whereas juveniles (50-100 mm CW) can tolerate reduced salinities for extended periods (Wanson et al., 1983). Brown crabs predominantly live in the sub-littoral zone where in Swedish waters it experiences a relatively narrow range of temperature, that is consistently below 15^{o}C and usually closer to 5-8^{o}C.

Brown crab has a seasonal reproductive life cycle with mating by copulation during late summer until autumn in Sweden and occurs shortly after the female has moulted (Brown & Bennett, 1980). Females are carrying eggs for 6-9 months after copulation and release the larvae in late spring (Thompson et al., 1995). Incubation and larval development is limited to near-seabed temperatures over 8°C (Lindley, 1987). In a laboratory experiment larval development was only successfully completed between 14 and 15°C (Weiss et al., 2009). The juveniles settle in the intertidal zone and remain there for about three years until they reach a carapace width of 6-7 cm, before moving to the subtidal areas (Bennett, 1995). Due to being intertidal, juveniles are tolerant of low salinities (Wanson et al., 1983).

Effects from temperature change are much depending on the time of the year. Adult brown crabs are not tolerant to temperatures over 31.5°C (Cuculescu et al., 1998). An acute rise of temperature in an already warm summer could lead to mortality. In winter a rise in temperature would lead to an increase of activity associated with a rise in metabolic rate, but nothing is known about the possible impacts (Neal & Wilson, 2008).

Like most invertebrates, brown crabs are osmocomform, which means that the osmotic pressure of the organism´s cells is equal to the osmotic pressure of their surrounding environment (Wanson et al., 1983). An advantage of this ability is that organisms do not need to expend much energy as osmoregulators in order to regulate ion gradients. A disadvantage is that brown crab is affected by the osmolarity of the environment and thereby to changes in salinity and seawater CO2 (Whiteley et al., 2018). Laboratory experiments show that brown crabs are more sensitive to rising temperatures when exposed to very low pH as it may occur under conditions of ocean acidification (Metzger et al., 2007). But since the brown crab is a highly mobile species, it would probably avoid hypersaline water, which might explain why no evidence on this effect has been found in the wild (Neal & Wilson, 2008).

Males are largely described as resident, making more random short movements within small territories. Females were documented in Sweden migrating significantly longer distances up to 100 km southbound against the currents. This is described with the hypothesis that migration is related to reproduction and compensating for the larval dispersal with the currents (Ungfors, 2007).

The brown crab is mainly nocturnal and planktivorous, and a successful and versatile predator, preying at more than one trophic level. One study has shown that the feeding behavior can be negatively influenced by ocean acidification, and that the consequence may be a shift in prey selection towards smaller mussels and increased metabolic costs which lead to reduced food consumption rates (Wang et al., 2018). The effects at a population level and ecosystem implications remain unknown but brown crab together with other decapods is recognized to have an important role in structuring the benthic communities via predator-prey interactions as well as competition with other species for food and habitat (Boudreau & Worm, 2012). In particular, a decrease in feeding pressure of the brown crab as a consequence of elevated pCO2 is expected to result in a decreased predation on mussels of which brown crab is one of the main predator (Wang et al., 2018).

Table 6.8. Climate change processes and responses, key conclusions.

Edible crab		
Process	Response to climate change	Reference
Mortality	Temperatures over 20°C are not tolerated. Higher temperatures provoke a movement to colder and deeper waters. Poorly equipped for changes in salinity and seawater CO_2.	Karlsson & Christiansen 1996, Neal & Wilson, 2008 Whiteley et al., 2018
Maturation		
Growth	No feeding below 5°C. Productivity might be affected but mortality is unlikely. Ocean acidification has negative effects on the foraging behavior and energy metabolism. Feeding performances declines with increased pCO2.	Karlsson & Christiansen 1996, Neal & Wilson 2008 Wang et al., 2018
Overwintering	Rising temperature in winter lead to increased activity associated with rise in metabolic rate.	Karlsson & Christiansen 1996, Neal & Wilson 2008
Recruitment	Larval incubation is limited to near-seabed temperatures over 8°C Larval development is only completed at 14 and 15°C	Lindley 1987; Thompson et al. 1995 Weiss et al., 2009
Ecosystem	Feeding pressure of the brown crab on the abundance of mussels is expected to decrease with elevated pCO2	Wang et al., 2018

Edible crab

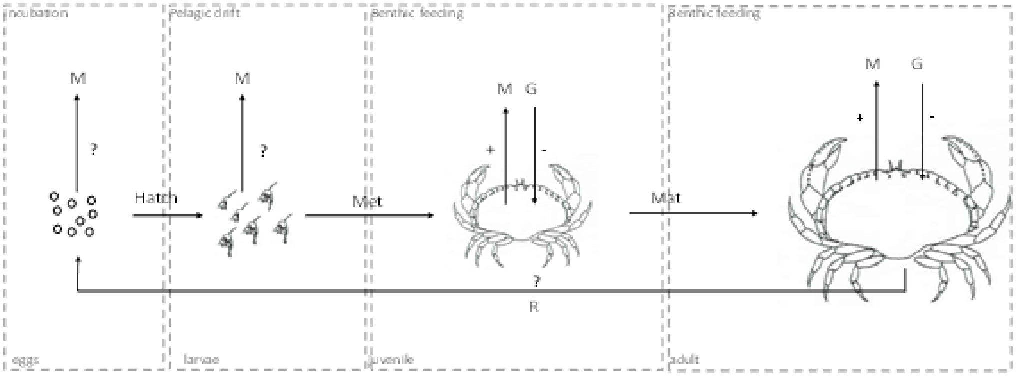

Figure 6.8. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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6.9. European grayling (*Thymallus thymallus*)

European grayling (*Thymallus thymallus*), hereafter grayling, is a salmonid fish that occurs mostly in freshwater habitats, but also occupies brackish water in some areas, like the northern parts of the Baltic Sea (Swatdipong 2009). Grayling is considered a cold-water species, preferring a lower temperature. In the Baltic Sea, grayling is found in the Gulf of Bothnia and Gulf of Finland in cold waters with low salinity (Appelberg et al. 2012). Grayling has a low salinity tolerance and can live in waters with a maximum salinity of 3 psu (Abel and Johnson 1978 via Gum 2007).

The majority of grayling in the Baltic Sea are anadromous, feeding in the Gulf of Bothnia or Gulf of Finland and traveling upstream to spawn. A smaller proportion in the Gulf of Bothnia constitutes an endemic sea-spawning population that lays its eggs in rocky outer archipelago areas (Appelberg et al. 2012, HELCOM 2013). Spawning areas of sea-spawning grayling are limited to two areas in Sweden (Alanärä et al. 2006 via HELCOM 2013). European grayling is listed as critically endangered by HELCOM (2013). The condition of the sea-spawning population is more critical than that of the anadromous one.

Since grayling thrives in colder waters, an increased temperature in the Baltic Sea can be expected to have a negative effect on grayling in its southern range of distribution, but there could be a positive effect in the northern range of its distribution (HELCOM 2013, Hammar and Green 2013 via Björkvik 2014). An increase in temperature could also increase the growth rate of grayling, as indicated by a study by Mallet et al. (2011). This could be true until the temperature exceeds a maximal growth temperature of 21 °C for an extended period of time (Mallet et al. 2011), and at even higher temperatures the growth rate decreases again (Persat and Pattee 1981 via Northcote 1995). If the growth rate increases with higher temperatures, the mean age of the population may decrease, based on results by Northcote (1995) who observed that the mean age of grayling was higher in colder waters.

Grayling generally spawns in early spring. Although the reported water temperature at spawning varies between populations, the range is generally from 4 to 18°C (Elliott 1981 via Crisp 1996). In the Baltic Sea, spawning usually occurs between April and June, with an optimal temperature for spawning between 5-7 °C (Gönczi 1989 via Björkvik 2014). In rivers, graylings lay their eggs on gravel surfaces in shallow areas (Northcote 1995, Bašić et al. 2018), while sea-spawning grayling lays eggs in sandy or rocky near shore areas in the outer archipelago (HELCOM 2013). The temperature after spawning affects egg survival with an optimal temperature range of 4.1-7.5 °C for >50 % survival (Crisp 1996). With such a narrow temperature span, compared to other salmonid species (Ibbotson et al. 2001, Jonsson and Jonsson 2009), an increase in temperature could lead to a decrease in recruitment. A long-term study by Wedekind and Kueng (2010), performed on a grayling population in Switzerland, showed that an increasing spring temperature caused spawning to occur 3-4 weeks earlier, potentially decreasing the survival of embryos and larvae, since temperatures may still dip below the approximate lethal limit of 3 °C early in the season (Humpesch 1985 via Crisp 1996).

Since the grayling eggs are not buried, extreme discharge events, related to for example heavy rainfall or snow-melt, could cause them to be washed out, thus decreasing the recruitment success of anadromous grayling (Bašić et al. 2018). For sea-spawning graylings, increased wave action could cause a decrease in the reproductive success (Helcom 2013). Studies have also shown that no, or a decreased, discharge could lead to a decreased survival rate of 0+ graylings (Bašić et al. 2018). Grayling recruitment is also affected by acidity, where an increased acidity has been shown to disrupt reproduction in the pH range of 5.5-5.9 (Degerman and Lingdell 1993 via Björkvik 2014). Short periods of acidity is usual in northern streams during spring floods and since grayling spawns later in spring they are usually not affected, but with warming causing earlier spawning the chance of acidity disrupting reproduction may increase (Berglund and Persson 1995 via Björkvik 2014).

Table 6.9. Climate change processes and responses, key conclusions

European grayling		
Process	Response to climate change	Reference
Mortality	Warming may decrease the mean age of fish in colder waters. Warming may decrease egg and larvae survival as a result of spawning occurring earlier in spring.	Northcote 1995 Wedeking and Kueng 2010
Maturation		
Growth	Warming increases growth rate until temperatures exceed 21°C for extended periods of time, above which growth decreases.	Mallet et al. 2011, Persat and Pattee 1981; Northcote 1995
Recruitment	Warming could cause a decrease in reproductive success, due to a narrow optimal spawning temperature between 5-7 °C. Decreased recruitment due to disrupted reproduction in acidic waters, with a pH in the range 5.5-5.9. Extreme discharge events would decrease anadromous grayling recruitment due to egg wash-out, while low or no discharge would decrease 0+ survival.	Gönczi 1989; Björkvik 2014 Degerman and Lingdell 1993, via Björkvik Bašić et al. 2018

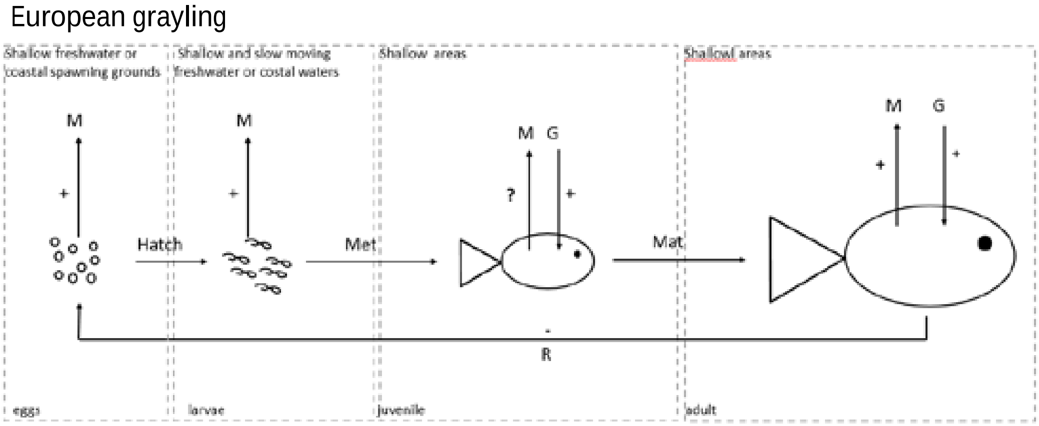

Figure 6.9. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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6.10. European lobster (*Homarus gammarus*)

European lobster, *Homarus gammarus*, is a long-lived decapod crustacean living in rocky subtidal environments in the Mediterranean and Eastern Atlantic primarily down to 40 meters depth. It is a marine species distributed from the Mediterranean to the Northern Norwegian Sea. Adults are sensitive to elevated temperatures (above 22ºC) for physiological excretion of ammonium and larvae are sensitive to low salinity. These limitations result in the curbed distribution of European lobster in Swedish waters to Skagerrak, Kattegat and parts of Öresund and primarily distributed around or below the summer halocline.

European lobster has internal fertilization and a brooding time of 9-10 months, when females after excretion carry the fertilized eggs under the abdomen. Eggs hatch into a pelagic larval stage with 4 moults before it settles to a bottom dwelling life. Average size at sexual maturity is 78 mm carapax length (L50 of females) when the female is around 5-6 years old (Sundelof et al., 2015).

Crustacean biology is strongly temperature dependent. European and American lobsters (*Homarus gammarus*, *H. americanus*) are no exceptions and shifts in temperature may potentially affect several aspects of their biology (Coleman et al., 2021; Goode et al., 2019; Mazur et al., 2022). Although climate related changes in pH and salinity and availability of oxygen may have implications for lobster larvae and adults recent studies have focused on temperature.

Many studies during the past 10-15 years have been performed on American lobster, while fewer have covered the European lobster. Their life histories are very similar and inference on European lobster is assumed relevant from studies also on American lobster.

Increased temperature stress lobster larvae and narrows the settling habitat available at 12-16 degrees Celsius (Steneck & Wahle, 2013). This effect has been more pronounced in the southern distribution range for *H. americanus*, and less so in the more northern, due to colder ocean currents but also depending on the mixing due to large tidal amplitudes in the Gulf of Maine (Goode et al., 2019). Incorporating environmental variability and projections of future change has predicted decadal declines even in the northern range (Oppenheim et al., 2019). This seems to be, at least partly, driven by temperature effects on food items of the larvae (Calanus, (Greenan et al., 2019)).

Strong positive effects of temperature on adult growth rates have been documented on *H. gammarus* (Coleman et al., 2021). Furthermore time to hatching and larval development times were shortened by increased experimental temperatures at least up to 22 degrees Celsius (Schmalenbach & Franke, 2010), in turn leading to an increased survival through the larval phase. What effects such decreased mortality and increased growth rates will have on a harvested stock is not yet predicted. Warmer temperatures enhance growth rates at the expense of physiological stress that may cause loss of genetic variability and adaptability of *H. americanus* through temperature induced genetic erosion (Harrington et al., 2019). It has been suggested that maximum size limits for landing mitigates loss of adaptability through preservation of genetic variability on larger individuals and secured reproduction and recruitment (Le Bris et al., 2018).

More individuals with less genetic variability are thus assumed to reach post larval phase and affect recruitment positively. However, many individuals will by a faster individual growth rate more quickly recruit into the fishery. This may in turn lead to a fishery on fewer year classes and the average age of a reproducing individual to be younger.

Restrictive harvesting regulations may mitigate the effects of climate change. No-take-zones (NTZ) have strong local effects on population abundance (Knutsen et al., 2022) and will help preserve adaptability. Although shellfish diseases are not highly prevalent in lobster populations and temperature effects are uncertain (Rowley et al., 2014) diseases have been hypothesized to increase in NTZ although it has not been quantified (Davies et al., 2015). Lack of quantified increases in incidence of shellfish diseases in NTZ is perhaps due to the higher available genetic variability (Le Bris et al., 2018) that can be expected in the more abundant populations in NTZ.

Increased freshwater runoff may have detrimental effects on suitable settling grounds as the larval development is sensitive to a salinity below 17 ppt (Charmantier et al., 2001) affecting potential settling through a gradient of salinities. Settling at salinities below 17 ppt will be nonexistent and the geographical limit for 17 ppt may shift in the future due to increased runoff.

Table 6.10. Climate change processes and responses, key conclusions

European lobster		
Process	Response to climate change	Reference
Mortality	Temperature provokes early hatching Faster larval growth decreases early life stage mortality	Schmalenbach & Franke (2010)
Maturation	Warming increases growth rate and implicitly early maturation	Coleman et al (2021)
Growth	Faster larval growth and genetic erosion Faster adult growth rates, anticipates recruitment to fishery	Schmalenbach & Franke (2010), Harrington et al. (2019) Coleman et al (2021)
Settling	Warmer water compresses available habitat for settling Reduced salinity below 17 ppt inhibits settling	Steneck & Wahle (2013) Charmantier et al. (2001)

European lobster

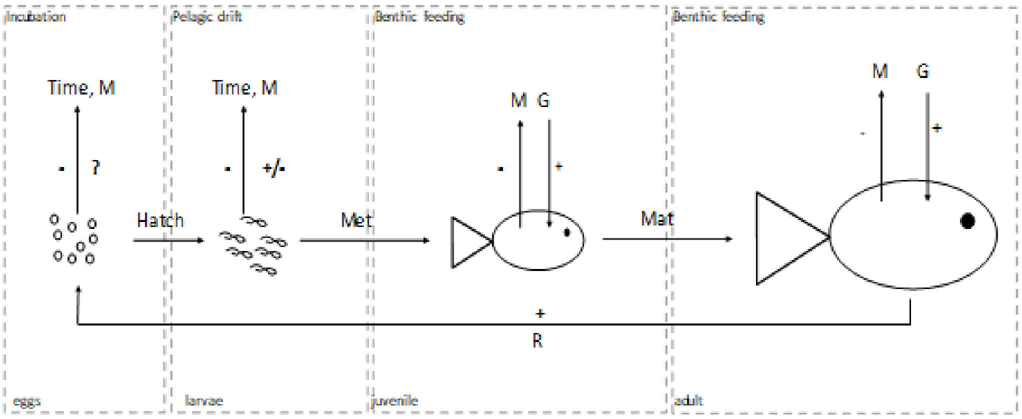

Figure 6.10. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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6.11. European plaice (*Pleuronectes platessa*)

The European plaice (*Pleuronectes platessa*) is one of the most abundant flatfishes in the north-eastern Atlantic region. It is also one of the most dominant species in coastal nursery grounds, residing on relatively shallow sand and mud bottoms with varying depths, from 0-200 (mostly 10 to 50 meters). Plaice is a ‘bottom-dweller’, i.e. lives near the seabed, preying mainly on clams, echinoderms and other benthic animals and uses sand as protection.

The spatial distribution of plaice (Rijnsdorp *et al.* 2009) is seasonal and linked to the migration patterns between spawning and feeding areas (Bolle *et al.* 2005, Hunter *et al.* 2003). Plaice spawns in offshore waters during the winter months (Harding *et al.*, 1978; Rijnsdorp, 1989; Miller *et al.*, 1991). After spawning, planktonic eggs and larvae drift to shallow inshore areas (De Veen, 1978; Fox *et al.*, 2009). Settlement in these nursery grounds occurs at a size of about 13 mm and coincides with completed metamorphosis from a bilaterally symmetrical larva into a laterally compressed juvenile. (Russell, 1976). The juvenile demersal life stage is concentrated in shallow soft bottom coastal areas throughout the summer (Norcross *et al.*, 1995) whereas larger individuals successively move to deeper grounds in autumn (Gibson *et al.*, 2002). At around 2-5 years, depending on sex, plaice attain sexual maturity (Rijnsdorp, 1989) and undergo offshore spawning migrations to join the reproductive population.

The spawning period of plaice is affected by water temperatures were a higher water temperature results in an earlier spawning period (Rijnsdorp,1989, Teal et al, 2008) and a lower recruitment (Van der Veer 1986, Fox *et al.*, 2000). Recruitment rates show high fluctuations between years. Several underlying mechanisms may be involved in maximizing the chances of a successful planktonic phase and in minimizing the mortality of the pelagic stages. According to Cushing’s “match/mismatch” hypothesis, year class strength depends on the synchronicity between the seasonal abundance of larvae and the productivity of the pelagic system, i.e. plankton production (Cushing 1990). Shallow coastal nursery areas are particularly susceptible to increasing temperature, which may impact their productivity (Beukema 1992, Kröncke *et al.* 1998, Phillippart *et al.* 2003). Cold winters often produce strong year classes (van der Veer & Witte, 1999, Fox et al. 2000), and low egg mortality is associated with low seawater temperatures (Harding et al. 1978, Dickey-Collas et al.2003). Low temperatures may also reduce larval mortality due to lower predator activity or to an improved match between the production cycles of larvae and their food (Cushing 1972, Leggett & Deblois 1994). Temperature may also act in combination with other factors such as eutrophication and fisheries (Rijnsdorp & van Leeuwen 1996). Some studies focussing on the Swedish west coast, showed that with increased eutrophication there is also an increase in filamentous algae on the sandy shallow bottoms creates unfavourable conditions for the settling of the plaice larvae (Isaksson and Phil, 1992, Phil et al, 1995, Wennhage, 2002) and reduce the benthic infauna (Troell et al, 2005), which is the main food source for juvenile plaice. Further, exudates produced by algae in combination with low oxygen levels increase mortality rates of plaice larvae during settlement (Larson, 1997).

A decrease in productivity as well as a mismatch with the timing of larval production (i.e. shift in spawning season) will in turn affect larval and juvenile growth. Detailed studies suggested that growth rate of juvenile plaice (age 0-1) is positively affected by increasing temperature conditions (Zijlstra *et al*. 1982, van der Veer & Witte, 1993, Amara, 2003, Teal *et al*, 2008). Growth rate in juvenile plaice in coastal areas was also positively correlated with eutrophication in the form of input of nitrates and phosphate, from the mid-1950s to the 1980s (Rijnsdorp and van Leeuwen, 1996, Colijn *et al*., 2002). For the intermediate sizes (15–30 cm) of plaice, increased growth rate could be attributed to both eutrophication and beam trawling which enhances food availability for this particular size class (Rijnsdorp and van Leeuwen, 1996).

Meteorologically driven variability in the hydrodynamics of the southern North Sea greatly affects the transport patterns of plaice eggs and larvae, suggesting an important role in determining recruitment variability and spatial connectivity (Bolle *et al*., 2009). Wind conditions and currents during larval development play a significant role in year-class strength (Pihl 1990, Nielsen *et al*. 1998) and could also influence recruitment in a specific year (Van der Veer & Witte 1999). Wind patterns and thus water circulation may be atypical in colder years, enhancing settlement (Nielsen et al. 1998, van der Veer *et al*. 1998).

Recent reviews suggest that recruitment variability is highly complex, regulated by trophodynamic and physical processes acting over many temporal and spatial scales and throughout pre-recruit life (Leggett and Deblois, 1994; Houde, 2008).

In addition to spawning time, recruitment and growth, temperature has also been found to have significant effects on the abundance and distribution of plaice. Since early 1990s, there has been substantial changes in the relative distribution of younger age-classes of plaice (age 1–3) in the North Sea (Desaunay *et al*. 2006, Tulp *et al*., 2008; Rijnsdorp *et al*., 2009, Støttrup *et al*, 2017). The abundances have increased in deeper, more offshore areas, while decreasing in coastal areas. Skogen and co-authors (2004) ascribed this shift in distribution of younger plaice, to a lowered freshwater run-off of nitrogen to the coastal areas recorded during the same period. A shift of larger plaice (20–39 cm) towards deeper waters already took place before the 1980s (van Keeken *et al*., 2007).

A decrease and eventually disappearance of age 1 plaice in the coastal nurseries in Southern North Sea (van Keeken *et al*., 2007; Teal *et al*., 2012; Poos *et al*., 2013) have been also attributed to higher temperatures exceeding the upper tolerance limits for growth (20 °C) and limiting food availability. Both high temperature and food scarcity, would trigger fish movement to other areas, colder or with higher food supply, to maximize their growth (van der Veer *et al*., 2009, Teal *et al*, 2012).

Flatfishes are particularly exposed to pollution because they live in close contact with the substratum, where contaminants accumulate, and they often ingest small sediment particles when capturing benthic prey (Moles *et al*. 1994). This way, it is likely that pollution affects survival and life-history traits such as growth rates, fecundity, size at maturity and maximum size (Gibson *et al*, 2015).

Table 6.11. Climate change processes and responses, key conclusions

European plaice		
Process	Response to climate change	Reference
Mortality	Exudates produced by algae in combination with low oxygen levels increase mortality rates of plaice larvae during settlement	Larsson 1997
	Low temperatures may reduce larval mortality due to lower predator activity or to an improved match between the production cycles of larvae and their food.	Cushing 1972, Leggett & Deblois 1994
	Low egg mortality is associated with low seawater temperatures	Harding et al. 1978, Dickey-Collas et al. 2003
Maturation	Onset and end of spawning negatively correlated with the water temperature at beginning and during the spawning period	Rijnsdorp 1989
	Shortened spawning period in warmer years	Teal et al., 2008
Growth	Reduced growth rate during summer when temperature exceed optimal temperature	Rijnsdorp and van Leeuwen 1996, van der Veer *et al.* 2009, Teal et al. 2012
	Growth rate of 0-group and 1-group plaice is positively affected by temperature	Zijlstra *et al.* 1982, van der Veer & Witte 1993, Amara 2003, Teal *et al.* 2008
	Growth rate in juvenile plaice positively correlated to eutrophication (increased input of nitrates and phosphate)	Colijn et al., 2002, Rijnsdorp and van Leeuwen, 1996
Distribution and abundance	Changes in the relative distribution of smaller age-classes of plaice (age 1–3). Abundance increased in deeper offshore areas, while decreased in coastal areas related to a decreased nitrogen input and increased temperature in the coastal areas.	Desaunay *et al*. 2006, Tulp *et al*. 2008; Rijnsdorp *et al*. 2009, Støttrup *et al*. 2017, van Keeken *et al*. 2007; Teal *et al*. 2012; Poos *et al*. 2013
Recruitment	Changes in productivity are at least partly related to a climate-related change in recruitment due to a temperature-induced change in the quality/quantity of the nursery habitat.	Beukema 1992, Kröncke et al. 1998, Phillippart et al. 2003
	Recruitment negatively related to temperature in waters around the UK	Fox et al. (2000)
	Winter temperature on the spawning grounds has an inverse relationship with year-class strength.	Van der Veer 1986
	Wind conditions during larval development showed significant correlations with the 0-group abundance and with year-class strength.	Nielsen et al. 1998; Pihl 1990
	The transport patterns of eggs and larvae is affected by hydrodynamic variability (meteorologically driven).	Bolle et al. (2009)

European plaice

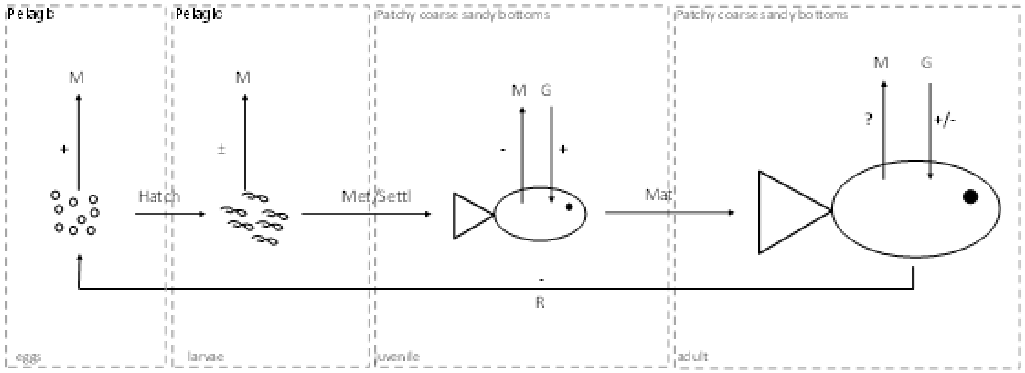

Figure 6.11. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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6.12. European whitefish (*Coregonus lavaretus*)

European whitefish (*Coregonus lavaretus*), hereafter whitefish, is a freshwater species recognized as a cold-water species, preferring relatively lower water temperatures (Olsson et al. 2012). Long term monitoring studies of coastal fish populations in the Baltic Sea show that whitefish increased as salinity decreased in the mid-1990s, but then again decreased in parallel with increasing temperature (Olsson et al. 2021).

Whitefish in the Baltic Sea have both a sea-spawning and an anadromous form. The sea-spawning form spawns in coastal areas on sandy bottoms, whilst the anadromous form moves into rivers and streams to spawn in freshwater (Appelberg, 2012). Both sea-spawning and anadromous whitefish spawn in October to November (Himberg et al. 2015) when the temperature decreases to between 3.5-7.2 °C (Veneranta et al. 2013a). The eggs hatch in spring when the ice-cover subsides, and the temperatures reach around 2-4 °C (Veneranta et al. 2013a).

Studies on anadromous whitefish spawning in rivers in the northern Gulf of Bothnia, performed using otolith chemistry methods, show that a subset of the population undertakes long migrations to feeding grounds further south where salinity is higher, the southernmost being around the Åland islands (Hägerstrand et al. 2017, Himberg et al. 2015). The individuals with feeding grounds in the southern Gulf of Bothnia grow faster than their non-migratory counterparts, which remain close to their home rivers, likely due to more abundant food resources and a longer growth season (Lehtonen and Himberg 1992 via Hägerstrand et al. 2017). The sea-spawning population reproduce along the entire coast within the Gulf of Bothnia, but the individuals are more stationary (Sõrmus and Turovski 2003 via Veneranta et al. 2013b).

The age at maturity of whitefish varies between 2 and 5 years, and age within a spawning stock can vary between 2 and 12 years (Lehtonen 1981 via Veneranta et al. 2021). Studies on anadromous whitefish show that they mature at an earlier age today, compared to in the late 1990's (Veneranta et al. 2021). The earlier maturity correlates with an increased temperature (Veneranta et al. 2021), but it could also reflect responses to fishing pressure (Lehtonen and Jokikokko 2002) or increased predation by seals (Appelberg 2012).

Studies also show that the growth rate in younger individuals of whitefish has increased (Kallio-Nyberg et al. 2019, Veneranta et al. 2021). The increased growth in young individuals is probably related to increased temperature (Veneranta et al. 2021), while a counteractive effect of fisheries could explain why an increased growth rate is not also observed in older age groups (Veneranta et al. 2021)

Whitefish egg survival could be negatively affected by a decreased ice coverage, as a result of increased temperature in the Baltic Sea (HELCOM 2013). Brown et al. (2013) suggested that the ice-cover protects the eggs by reducing effects by wind and waves.

Eutrophication affects whitefish recruitment negatively (Lundberg et al. 2009 via Veneranta et al 2013b). Hence, indirect effects of eutrophication could interact with the effects of climate change on whitefish. Increases of filamentous algae, their increased bottom coverage, and sedimentation (Berglund et al. 2003) decrease the survival of whitefish eggs and impair larval habitats (Veneranta et al. 2013b).

Table 6.12. Climate change processes and responses, key conclusions

European whitefish		
Process	Response to climate change	Reference
Mortality		
Maturation	Earlier maturation with increasing temperatures.	Veneranta et al. 2021
Growth	Warming increases the growth rate in young individuals.	Kallio-Nyberg et al. 2019, Veneranta et al. 2021
Recruitment	Decreased size at maturity might decrease the reproductive capacity* ** Not empirically tested but a conclusion drawn based on the relationship between fish size and reproductive capacity.*	Veneranta et al. 2021

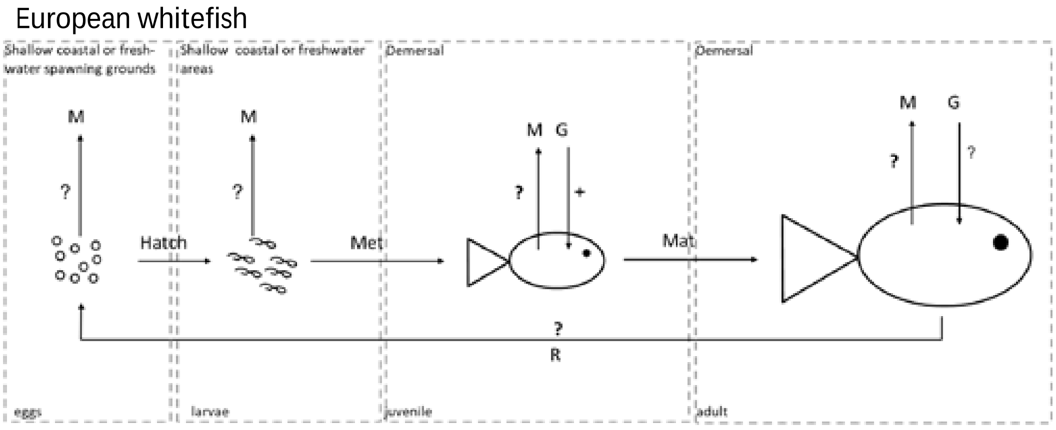

Figure 6.12. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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6.13. Flounder (*Platichthys* spp.)

The European flounder (*Platichthys flesus* Linnaeus, 1758) is a demersal flatfish species distributed along the northeastern Atlantic coast, from the White Sea to the Mediterranean and Black Sea. Its maximum size can reach 60 cm and it can live up to 15 years (Skerritt, 2010; www.fishbase.org).

P. flesus inhabits primarily brackish and coastal waters but can enter estuaries and live for long periods in freshwater habitats although unable to spawn there (Hemmer-Hansen et al., 2007). Although it is found on sandy and muddy substrate from 1 to 100 m depth, it prefers depths shallower than 50 m.

Juvenile flounder feed mostly on meiofauna (animal size between 0.1 and 1 mm), especially on copepods, ostracods and small larvae, while the adult predominantly on benthic macrofauna, especially on bivalves, polychaetes and crustaceans. This shift in the diet composition reduces the competition between different life-stages (Aarnio et al., 1996; Florin, 2005; Skerritt, 2010).

P. flesus has been recorded to migrate over vast distances to reach the spawning grounds but the annual average migration distances are around 30 km (Aro, 1989; Bagge and Steffensen, 1989; Skerritt, 2010; ICES, 2010).

Flounder usually feeds in shallow, coastal areas during summer, migrates to deeper areas in winter and spawns there in spring. It reaches sexual maturity around the second or third year and the spawning season extends between February and June (Skerritt, 2010). The European flounder is a broadcast spawner with floating eggs that sinks as development occurs. The pelagic larvae spawned at sea drift to shallow water nursery areas where they will metamorphose into benthic juvenile flatfish (Florin, 2005). In the Baltic Sea, the “Reproductive Volume” for *P. flesus* is defined by salinity between 10.7 and 12 psu and oxygen concentrations > 1 mg L^{-1} (Ustups, et al 2013).

In the Baltic Sea some flounders have been reported to present different spawning behaviour and reproductive characteristics compared to the more typical one (Solemdal, 1967, 1973; Nissling et al., 2002; Nissling and Dahlman, 2010), as well as differences in their population genetic (Hemmer-Hansen et al., 2007; Florin and Höglund, 2008). These have led to the recognition of a species closely related to the European flounder, endemic to the Baltic Sea (Momigliano et al., 2017, 2018; Jokinen, 2020). The newly described Baltic flounder *P. solemdali* (Momigliano et al., 2018) spawns demersal eggs in shallow coastal waters and banks and can reproduce successfully in salinities as low as 6 psu (Momigliano et al., 2018). This could be an adaptation in order to avoid the anoxic conditions present in the deeper areas of the Baltic (Florin, 2005; Hemmer-Hansen et al., 2007; Florin and Höglund, 2008). These two species are considered parapatric, co-occurring in some areas of the central Baltic Sea (Momigliano et al., 2017, 2018; Jokinen, 2020). However, the distinct reproductive strategies associated with differences in salinity result in spatial segregation during spawning (Solemdal, 1967; Nissling et al., 2002; Nissling and Larsson, 2018).

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6.13.1. Baltic flounder (*Platichthys solemdali*)

Due to the recent description of Baltic flounder *P. solemdali* (Momigliano et al., 2018), potential effects of climate change on this species are not well studied. In this chapter, all the references dating before the description of Baltic flounder could be assumed to be relevant for this species due to the reference to the "demersal spawning flounder" or are referring to areas where Baltic flounder is the dominant species. Climate change is expected to reduce the Baltic Sea salinity (Meier et al., 2012; Saraiva et al., 2019), which will affect fertilization and egg development of flounder (Nissling et al., 2002). Nissling and Wallin (2020) show that the occurrence of weaker and stronger flounder year-classes is related to the variability in spermatozoa motility, fertilization and early egg development at different salinities. In particular, due to the high variability in spermatozoa motility and fertilization rates in the range 6–7 psu, even small changes in salinity conditions could produce severe effects on the reproductive success and consequently on recruitment variability of Baltic flounder (Nissling and Wallin, 2020).

Increased water temperatures will affect larval viability in terms of yolk sac depletion and growth (Wallin, 2016). Moreover, future variability in temperature may affect feeding conditions due to alterations in the zooplankton community (Alheit et al., 2005; Möller et al., 2015) or mismatch between occurrence of larvae and preferred food items (sensu Cushing, 1990), and thus potentially recruitment to the adult stock.

Eutrophication is also expected to impact the habitat quality of Baltic flounder through an increase of filamentous algae and increase occurrence of coastal hypoxia events (Bonsdorff et al., 1997; Conley et al., 2011). These will cause a reduction and loss of important high-quality habitats and an overall reduction of productive habitats for flounder. Berglund et al. (2003) already described how eutrophication related macroalgal blooms and the occurrence of detached drifting filamentous algae have increased in nursery areas for flounder, potentially reducing the nursery value of these areas (Pihl et al., 1999, 2005). Furthermore, drifting macroalgae accumulating at deeper coastal bottoms, also reduce the quality of Baltic flounder adult habitats, through degradation of food resources (Norkko and Bonsdorff, 1996a) and worsened oxygen conditions (Norkko and Bonsdorff, 1996b).

Baltic flounder living in the northernmost margin of its distribution will face lower salinity and elevated temperatures together with eutrophication. Such changes will favour freshwater species associated with warmer water and high productivity, potentially increasing Baltic flounder food competition with roach and other cyprinids (Jokinen 2020).

Though climate change has the potential to negatively affect Baltic flounder, it will also decrease competition with the European flounder in the southern areas of the Baltic and potentially promote an expansion of its distribution as the reproductive strategy of Baltic flounder is less sensitive to lower salinity (Nissling et al., 2017)

Table 6.13.1. Climate change processes and responses, key conclusions.

Baltic flounder		
Process	Response to climate change	Reference
Growth	Potential negative effects on larval viability in terms of yolk sac depletion and growth due to increase in temperature	Wallin, 2016
	Increase in temperature may affect feeding conditions due to alterations in the zooplankton community or mismatch between occurrence of larvae and preferred food items	Alheit et al., 2005; Möller et al., 2015
Spawning	Potential negative effects on spermatozoa motility, fertilization and early egg development due to decrease in salinity	Nissling et al., 2002
	Habitat loss due to increased eutrophication	Jokinen, 2020
Recruitment	Decrease in salinity may affect recruitment success due to unsuccessful spawning	Nissling and Wallin, 2020
	Increase in eutrophication-related macroalgal blooms may potentially reduce the nursery habitats	Pihl et al., 1999, 2005
	Recruitment in the northern areas may be affected due to insufficient salinity for fertilization and egg development	Nissling et al. 2017

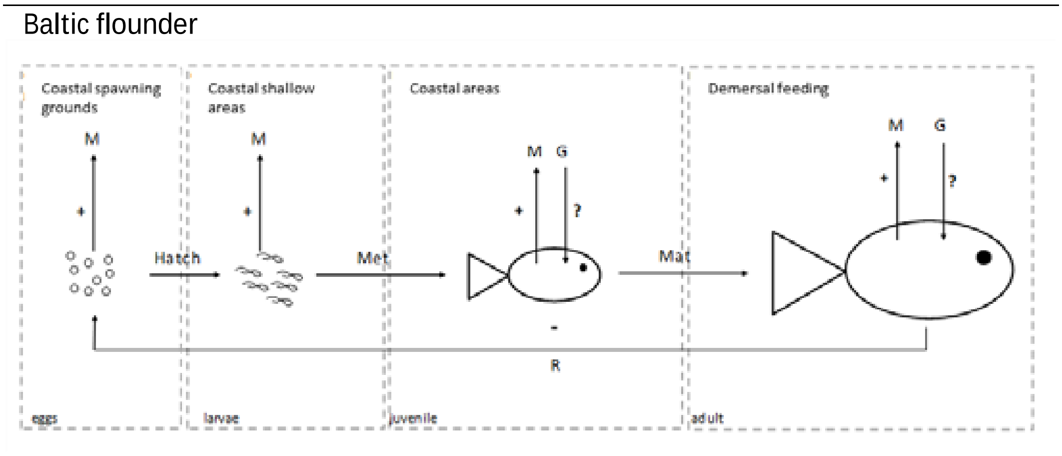

Figure 6.13.1. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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6.13.2. European flounder (*Platichthys flesus*)

Climate change is expected to negatively impact European flounder recruitment in the Baltic Sea. This is due to the combined effects of changes in temperature, salinity, precipitation, and oxygen consumption in the bottom waters (Ustups et al., 2013). The forecasts for the Baltic watershed show an increase in precipitation and runoff (Meier, 2006) as well as a change of its seasonality that could impact the frequency of major Atlantic water inflows (MacKenzie et al., 2007). Moreover, 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 to eastern Baltic deep basins during winter (Hinrichsen et al., 2002). Raise in bottom water temperatures will increase organic matter degradation, accelerating nutrient cycling and the consumption of bottom water oxygen (Meier et al., 2011). All these effects together will reduce the reproductive volume of flounder with negative consequences on flounder abundance, distribution and recruitment, which is likely already impaired due to the deteriorated salinity and oxygen conditions in the deep basins (Temming, 1989; Nissling et al., 2002; MacKenzie et al., 2007; Ustups et al., 2013; Nissling et al., 2017; Hinrichsen et al., 2017, 2018; Momigliano et al., 2019).

Based on salinity and oxygen requirements for egg survival (Hinrichsen et al., 2017) including opportunities to obtain neutral egg buoyancy (Nissling et al., 2017), a contraction towards the southern areas of the Baltic Sea of the distribution of *P. flesus* can be expected. Main factors are ascribed to insufficient salinity for fertilization and egg development affecting recruitment in the northern areas of the distribution (Nissling et al., 2002) and to degradation of suitable habitats in the deep basins, in particular the Gotland Basin (Nissling et al., 2017).

Given that anoxia severity in the southern and western areas of the Baltic Sea is partly temperature dependent (Rasmussen et al., 2003), the higher temperatures associated with climate change will probably cause an increase in the frequency and extent of anoxic events (MacKenzie et al., 2007). Anoxic events cause direct mortalities of fish and their prey (Karlson et al., 2002), and cause fish and prey to redistribute to other less-optimal areas where feeding, growth and survival rates may be lower (Pihl, 1994). As a demersal species largely feeding on benthic preys, flounder is expected to be particularly affected where oxygen deficiency occurs (MacKenzie et al., 2007).

Information on temperature effects on early life stage development of European flounder in the Baltic Sea are scarce. Ustups et al. (2013) did not find any significant statistical effect of temperature on egg and larvae distribution of flounder. However, as for the Baltic flounder, increased water temperatures will possibly affect larval viability in terms of yolk sac depletion and growth (Wallin, 2016). Moreover, future variability in temperature may affect feeding conditions due to alterations in the zooplankton community (Alheit et al., 2005; Möller et al., 2015) or mismatch between occurrence of larvae and preferred food items (sensu Cushing, 1990), and thus potentially recruitment to the adult stock.

Table 6.13.2. Climate change processes and responses, key conclusions.

European flounder		
Process	Response to climate change	Reference
Mortality	Increased mortality due to increased frequency and extent of anoxic events	MacKenzie et al., 2007
Growth	Potential negative effects on larval viability in terms of yolk sac depletion and growth due to increase in temperature	Wallin, 2016
	Increase in temperature may affect feeding conditions due to alterations in the zooplankton community or mismatch between occurrence of larvae and preferred food items	Alheit et al., 2005; Möller et al., 2015
Spawning	Potential negative effects on spermatozoa motility, fertilization and early egg development due to decrease in salinity	Nissling et al., 2002
Recruitment	Combined effects of changes in temperature, precipitation and bottom water oxygen consumption will decrease the reproductive volume and thus recruitment	Ustups et al., 2013
	Recruitment in the northern areas may be affected due to insufficient salinity for fertilization and egg development	Nissling et al. 2017

European flounder

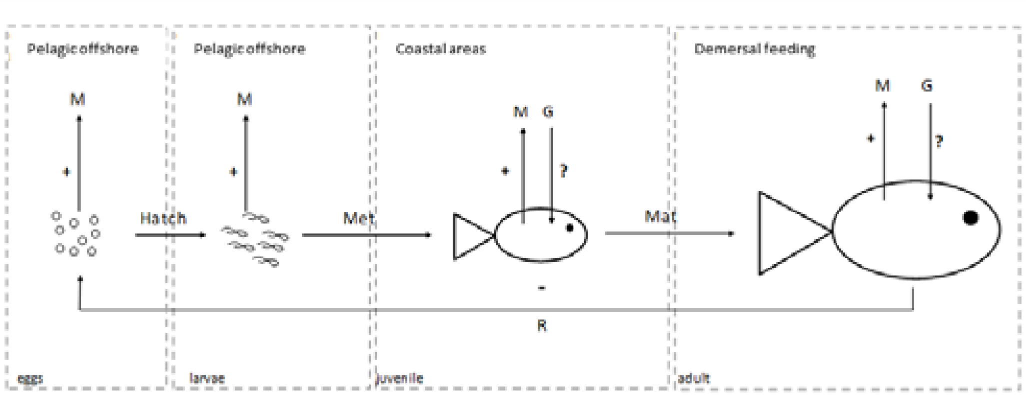

Figure 6.13.2. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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Authored by Alessandro Orio

6.14. Hake (*Merluccius merluccius*)

European hake (*Merluccius merluccius*) is widely distributed over the Northeast Atlantic shelf, from Norway to Mauritania and throughout the whole Mediterranean (Casey and Pereiro 1995). Otolith chemistry and genetics confirm a main differentiation between the Mediterranean and Atlantic populations (Tanner et al. 2012; Leone et al. 2019). Population structure remains largely unclear within these two geographical domains (Lundy et al. 1999, Castillo et al. 2005, Pita et al. 2014), although recent DNA sequencing suggest separation of hake from the Norwegian Sea (Leone et al. 2019). In the Atlantic, hake is assessed and managed as two stocks (i.e., the northern and southern stocks) separated at the Capbreton Canyon in the Bay of Biscay (ICES, 2021). The northern stock core habitat extends along the French coast, the waters west of the British Isles and Irish Sea, and the southern North Sea (hereafter we refer to this stock if not specified). The hake stock expands throughout the North Sea and the Skagerrak-Kattegat (Baudron and Fernandes 2015) where it may show inverse pattern with other gadoids (cod, haddock, whiting, saithe) over multidecadal variations, although there is no evidence that this directly is a result of competition. A recent expansion of hake, as well as one reported during the 1920s-1950s, is interpreted as the result of density-dependent processes and favourable large-scale climatic conditions, following the current warm phase of the Atlantic Multidecadal Oscillation (Werner et al. 2016, Staby et al. 2018, Gullestad et al. 2020).

Major spawning areas are the shelf edge at around 200 m depth in the Bay of Biscay, and the shelf in the Celtic Sea (Ibaibarriaga et al. 2007, Alvarez et al. 2004). After the recent expansion, spawning activity is also reported along the western slope of the Norwegian Trench in the North Sea (Werner et al. 2016). It is unclear if there is a seasonal displacement between the spawning activity at the continental shelf and the shelf edge. Hake is a batch spawner that reproduces all year-round in the southern and Mediterranean part of its range, which is likely a successful reproductive strategy under increasing variability associated to climate change (Murua 2010). Spawning of the northern stock is protracted over a long period of time from January to August with a progressively delayed peak with higher latitude, i.e. January-May in the Bay of Biscay, April-July west of Ireland, May-August in the west of Scotland (Alvarez et al. 2001). Spawning activity in the central and northern North Sea takes place around July. Early life stages are planktonic. The highest abundances of eggs are seen at temperatures of 10.5-12.5ºC in the Northeast Atlantic (Coombs and Mitchell 1982, Alvarez et al. 2004), but high concentrations of larvae have also been found at higher temperatures in some areas (i.e., southern stock larvae off Galician shelf show peak abundance at 13.4ºC, García-Fernández et al. (2021)). The recruits settle in inshore waters approximately 40 days after hatching. The coastward transport and coastal retention of early life stage of hake (from spawning areas to nursery areas) represent critical mechanisms influencing survival rates and ultimately recruitment success (Goikoetxea, 2011). Field observations suggest that geostrophic and tidal currents likely have a stronger role than wind-induced current for the northern hake stock (Alvarez et al. 2004).

Correlative analyses suggest that the hydro-climatic regime shift reported in the Northeast Atlantic during the late 1980s, characterized by warmer water temperatures and moderate eastward transport, have favoured hake recruitment success (Goikoetxea and Irigoien, 2013). Early life stages of the northern hake stock were found to benefit from a warming environment either through the widening of the optimal environmental window or/and higher growth rates (Goikoetxea, 2011). In the Mediterranean, hake recruitment was found to be negatively affected by summer heat waves coupled to water stagnation (Bartolino et al. 2008) but the potential extent of warming in the northeast Atlantic and North Sea is unlikely to represent a limit for the recruitment success of the northern stock.

Using otolith increment width-based growth chronology, Vieira et al. (2020) found evidence that the growth of the southern stock of European hake is affected by water temperature, with different responses in fish of different ages. More specifically, increasing ocean temperature appears detrimental for growth in the first years (2-5 years) after which the effect progressively changes to become positive in older individuals (6-10 years). For age2 fish, Vieira et al. (2020) estimated that a 1°C increase in sea surface temperature during winter and in water column temperature during spring reduced growth by 11% and 32%, respectively, which appear dramatic in the light of existing climate change projections. The actual processes involved in this response remain unknown.

Table 6.14. Climate change processes and responses, key conclusions.

Hake		
Process	Response to climate change	Reference
Mortality	Coastward transport and retention of early life stages from spawning areas to nursery grounds positively affect survival of eggs and larvae Warming may benefit early life stages via faster larval growth and/or widening of the optimal environmental window	Alvarez et al. 2004; Goikoetxea and Irigoien, 2013 Goikoetxea, 2011
Maturation		
Growth	Warming has shown negative effect on the growth of younger fish (age 2-5) and positive effect on growth of adults (correlation with both sea surface temperature and bottom temperature)	Vieira et al. 2020
Recruitment	Positive NAO (i.e., warmer temperatures and stronger westerly winds) increase recruitment success	Goikoetxea and Irigoien, 2013
Habitat expansion	Expansion of stock distribution, including spawning habitats in the North Sea	Baudron and Fernandes 2015, Staby et al. 2018

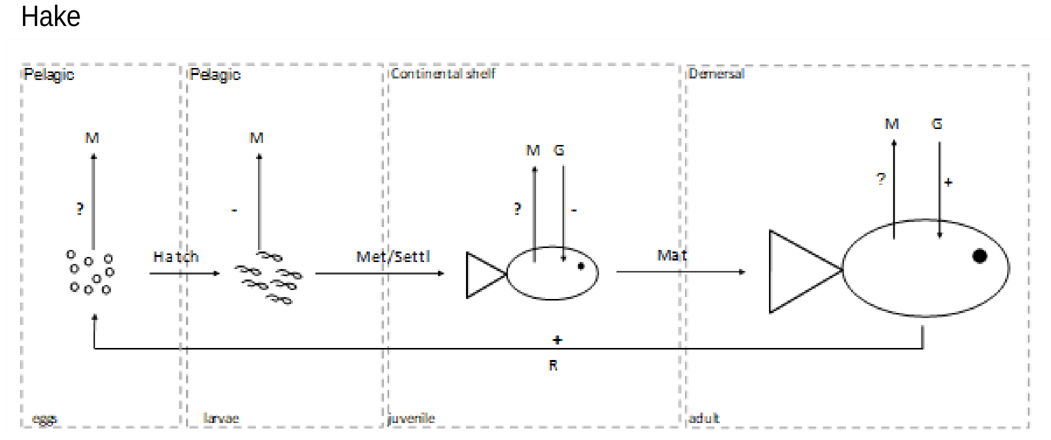

Figure 6.14. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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Authored by Valerio Bartolino

6.15. Herring (*Clupea harengus*)

Atlantic herring has high phenotypic plasticity, which is considered to be one of the main explanations to the success of this species, its adaptation to a wide range of environmental conditions encountered throughout its wide distribution and its exceptional resilience to fisheries exploitation (Geffen 2009).

Herring appears quite unique among marine fish in having a wide range of discrete spawning seasons while using specific spawning locations. These two aspects represent the major characteristics used to identify the various populations and stocks.

Differently from most other pelagic fish, herring eggs are laid and retained in high densities on benthic substrates before hatching. Spawning grounds are primarily coastal or on offshore banks. Spawning substrate varies from gravel to rocks and in the Baltic it is also constituted of seaweeds in the littoral or sublittoral zones.

Due to the flexible life-history strategy of herring, different populations can lay viable eggs at variable times throughout the year, enabling the species to reproduce successfully throughout almost every season. Hatching occurs in a wide range of temperatures. For example, Peck et al. (2012) noted optimal hatching between 7 and 13°C, with hatching rates still >50% between 5 and 19°C. The embryonic metabolism shows little dependency between egg size and temperature, with possibly a lower impact of temperature on the fitness of the early life stages compared to other fish species (Geffen 2009).

Throughout its wide distribution, different herring populations have adapted to the most diverse environmental conditions. For instance, it is one of the few marine fish species able to reproduce across a salinity range spanning from 35 psu in the North Sea to 3 psu in the Bothnian Bay. Given the diversity of conditions experienced in different regions, responses to temperature, salinity and a changing environment are variable among the stocks and often stock specific.

Growth of herring larvae is sensitive to both temperature and feeding conditions, but unlike many other marine species, they can survive long periods of little or no growth which could partly explain their relatively high survival when spawning takes place in seasons of low productivity (Johannessen et al. 2000). However, as for other species, slow growth and low individual condition have negative effects on vulnerability to predation (Skajaa et al. 2004).

Fields experiments have shown that distributions of herring larvae are influenced by water-mass features (Heath et al. 1991), as well as food concentrations and light intensity (Munk et al. 1989).

Larvae and juveniles can perform important ontogenetic migrations from spawning locations to nursery grounds resulting in extensive mixing of juveniles from different spawning components/populations (Clausen et al. 2007). As part of the adaptive life-history strategy of the species, this could favour colonization and response to variations in population abundance (Geffen 2009).

Many herring populations are characterised by extensive annual migrations between feeding and spawning grounds. Larger herring seem to spawn earlier than smaller fish, resulting in so-called "spawning waves", and tend to perform longer migrations into their feeding grounds (Lambert 1987). The Baltic Sea hosts both populations which are permanently resident and others performing long migrations to the North Sea (ICES 2020a,b).

Genetic research on Atlantic herring is providing new insights on the population structure (Lamichhaney et al. 2012), showing genetic differentiations among spawning types (Han et al. 2020) and in the adaptations to cope with the brackish environment of the Baltic Sea (Barrio et al. 2016). While on-going research on genetics is expected to contribute to possible redefinition of some of the stock boundaries in the near future, such as in the complex transition zone of the Kattegat-Skagerrak and Western Baltic, and in the Gulf of Bothnia, the present stock classification should be considered largely valid.

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6.15.1. North Sea Autumn Spawning herring

Warming waters have been associated with strong biogeographical shifts and a reorganization in the copepod assemblage in the North Sea (Beaugrand et al. 2002), in turn reducing the herring survival rates through the winter larval development phase (Payne et al. 2009). The 2000 planktonic regime shift in the North Sea shows close relationship with the decreasing productivity of the stock and it is considered one of the leading mechanisms for the recruitment regime shift (Payne et al. 2009, ICES 2018). Recruitment, in particular the abundance of post yolk-sac larvae, has also been correlated with the Atlantic multidecadal oscillation (Gröger et al. 2010).

Herring larval transport, from spawning areas along the eastern UK coasts to nursery areas in the north-eastern North Sea, are predominantly driven by wind during winter. Reduction in cyclonic circulation related to climate change can induce disruption in the advection of herring larvae with consequences for the recruitment (Bartsch et al. 1989).

The link between climate change and biological parameters is less understood. Hunter et al. (2019) did not find a clear relationship between herring growth and temperature, but Clausen et al. (2018) identified a negative effect of climate change on both herring growth and recruitment via reduction in the abundance of the important prey *Calanus finmarchicus*. Brunel and Dickey-Collas (2010) tested the changes in von Bertalanffy growth parameters as a response to a warming environment across a range of herring stocks. They found that temperature correlates negatively with W_{inf} and positively with k in the North Sea stock, implying that temperature increase would lead to higher body weight for young ages, but to smaller body weight for older fish and shorter life expectancy. A significant negative relationship between length at first maturity (L50) and temperature was also detected with similar influence on the maturation schedule in the northern and southern North Sea despite spatial differences in the temperature regimes across the region (Hunter et al. 2019).

Table 6.15.1. Climate change processes and responses, key conclusions

North Sea Autumn Spawning herring		
Process	Response to climate change	Reference
Mortality	Reduced larval survival linked to changes in zooplankton community Alteration of winter wind patterns and circulation can affect advection of early life stages from spawning to nursery areas	Payne et al. 2009 Bartsch et al. 1989
Maturation	Earlier maturation with increased temperature	Hunter et al. 2019
Growth	Warming environment associated with higher body weight for young ages, but smaller body weight for older fish and shorter life expectancy Negative effect of warming via reduced abundance of zooplankton	Brunel and Dickey-Collas 2010 Clausen et al. 2018
Recruitment	Negative effect of warming via reduced abundance of zooplankton 3-year lag correlation with AMO	Clausen et al. 2018, Gröger et al. 2010

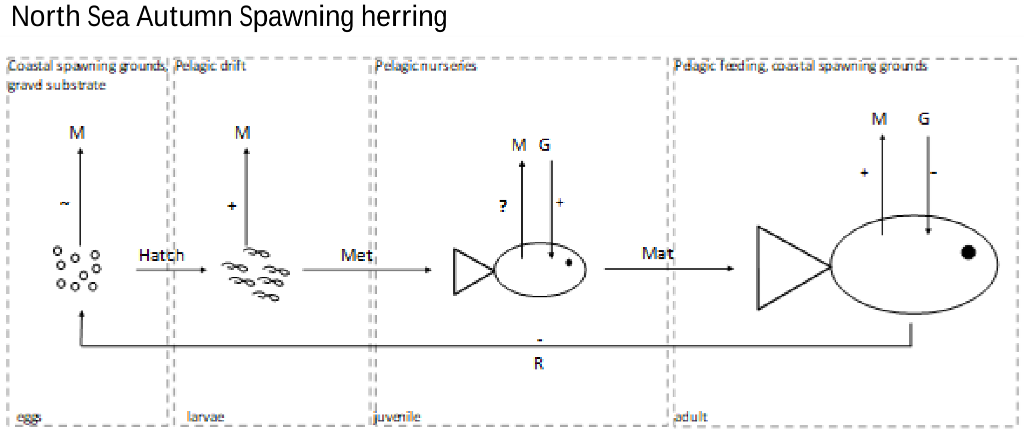

Figure 6.15.1. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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6.15.2. Western Baltic Spring Spawning herring

The Western Baltic Spring Spawning herring stock is a typical example of a meta-population (i.e., a complex of separated spawning components within a population). The majority of the stock performs extensive migrations between coastal spawning grounds in the western Baltic and feeding grounds in the Kattegat-Skagerrak and eastern North Sea. Current knowledge suggests that recruitment in this herring stock is affected by complex interactions of factors, mainly warming, eutrophication and habitat degradation. These factors affect spawners, eggs and larvae in different ways.

All spawning sites are characterized by low salinity (<12 psu), shallow waters and spawning substrate of macrophytes (Kanstinger et al. 2018). These habitats warm quickly in Spring and are rich in nutrients, supporting the development of large abundance of mesozooplankton, especially calanoid copepods such as *Eurytemora affinis* and *Acartia* spp., which are the main preys of the herring larvae (Paulsen et al. 2016).

The onset of Spring spawning in Greifswald Bay, which is considered one of the main spawning grounds, is temperature-dependent at a threshold of approximately 4°C (Polte et al. 2021). As a consequence of average milder Winter temperatures this threshold is reached earlier in recent years with consequent anticipation of the spawning (Polte et al. 2021). Moreover, herring eggs hatch at a wide range of temperatures, but their developmental time is strongly driven by temperature potentially leading to early hatching and shorter length-at-hatch as temperature increases impacting larval survival (Peck et al. 2012). Overall, the consequences of the shift in phenology (i.e., anticipation of spawning and early hatching) are still under study. It is hypothesized that a mismatch with the prey of herring or unfavorable thermal environments affecting larval growth and survival could arise. Paulsen et al. (2016) found that larval growth was best explained by the abundance of the preferred prey, the copepod *Eurytemora affinis*, which decreases rapidly at temperatures exceeding 15°C late in the season.

Polte et al. (2017) found patterns of small scale habitat selection during larval ontogeny, with medium size larvae distributed in the pelagic area of Greifswald Bay as opposed to larger larvae that returned to shallow littoral areas where they remained until after their metamorphosis. Experimental work showed that temperature-dependent differences in larval morphology influence swimming performance, suggesting a trade-off between growth rate and locomotor activity (Moyano et al. 2016). The implications for the habitat selection of larvae in the wild remain unknown.

Eutrophication and increased turbidity are among the main factors contributing to deterioration and shrinking of macrophyte coverage, which is essential spawning habitat for this herring (Kanstinger et al. 2018). von Nordheim et al. (2018) found that complex, healthy macrophyte substrates reduce egg mortality and that this effect is possibly more pronounced at higher temperatures, such as towards the end of the spawning season. Moreover, increase in herring egg mortality has been locally related to blooms of filamentous algae which have become more common in coastal waters due to eutrophication (von Nordheim et al. 2020). Reduction in macrophyte coverage has also reduced the suitable herring spawning habitats toward the most shallow areas, making them more vulnerable to extreme weather events. Stormy weather, which is expected to increase in intensity and frequency with climate change, can have considerable impact on the survival rate of herring eggs especially in the littoral and sub-littoral lower depths (Moll et al. 2018).

Studies from the Kiel Fjord, southwestern Baltic, suggested that jellyfish predators such as *Aurelia aurita* can have an important top-down control on the plankton community in the area, representing both a potential competitor and predator on herring larvae (Moller 1984, Ramirez-Romero et al. 2018).

Table 6.15.2. Climate change processes and responses, key conclusions

Western Baltic Spring Spawning herring		
Process	Response to climate change	Reference
Mortality	Increased egg mortality due to eutrophication and increased frequency of storm events	von Nordheim et al. 2018, 2020; Moll et al. 2017
	Effect of increased temperature on anticipated hatching with the result of shorter length-at-hatch which impacts larval survival	Peck et al. 2012
	Warming induced shift towards a jellyfish-dominated foodweb is expected to increase mortality of larvae via food competition and direct predation	Moller 1984, Ramirez-Romero et al. 2018
Spawning	Time of spawning is anticipated in time by warming	Polte et al. 2021
Growth	Temperature driven anticipation of spawning and early hatching increase the risk of mismatch with peak in prey abundance	Peck et al. 2012

Western Baltic Spring Spawning herring

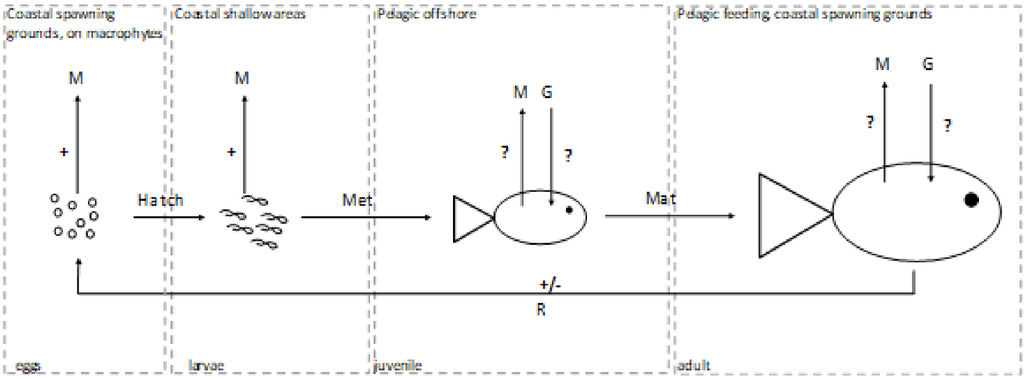

Figure 6.15.2. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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6.15.3. Central Baltic herring

Compared to other regions within the distribution of herring, the central Baltic Sea represents an environment at the limit, characterized by extreme levels and high variability of key hydrographic parameters, such as salinity and temperature. Food availability is also more variable than in other regions, as reflected by the generally lower growth and poorer conditions of herring populations inhabiting the Baltic Sea. Hence, there are multiple implications for the productivity and dynamics of the Baltic herring populations, especially in the light of the profound ecosystem changes observed in the Baltic Proper during the last few decades (Alheit et al. 2005, Casini et al. 2009), and also in the perspective of climate change which is expected to exacerbate some of those boundary conditions (MacKenzie et al. 2007).

Growth and condition of herring in the central Baltic have been progressively deteriorating throughout the 1980s and 1990s. Since the early 2000s, weight-at-age (used as a proxy for condition) has been fluctuating at levels 30-50 % lower compared to the values observed in the 1970s. Analyses of herring stomachs have shown that since the late 1970s, the total stomach fullness has decreased and the fraction of empty stomachs increased caused by a decrease in the availability of the copepod *Pseudocalanus* sp., the dominant food item during the feeding seasons in Spring and Summer (Möllman et al. 2004). Several correlation studies from different areas of the stock distribution found that salinity (linked to precipitation and inflow of Atlantic water) is an important predictor of herring condition, probably via regulation of the mesozooplankton dynamics in the offshore areas (Cardinale and Arrhenius 2000, Rönkkönen et al. 2004). However, this bottom-up control becomes of secondary importance under increasing clupeid densities, especially due to competition with sprat (Casini et al. 2006, Casini et al. 2011, Smoliński, 2019). Such interacting effect of hydrological forcing and density dependent mechanisms has a pronounced spatio-temporal pattern within the stock distribution (i.e, lost in condition has been more pronounced in areas with lower salinity and larger sprat densities; Casini et al. 2011) and it has been suggested to follow a threshold dynamic (i.e., sprat abundances above a certain level decouple herring growth from hydro-climatic factors and become the main driver; Casini et al. 2010).

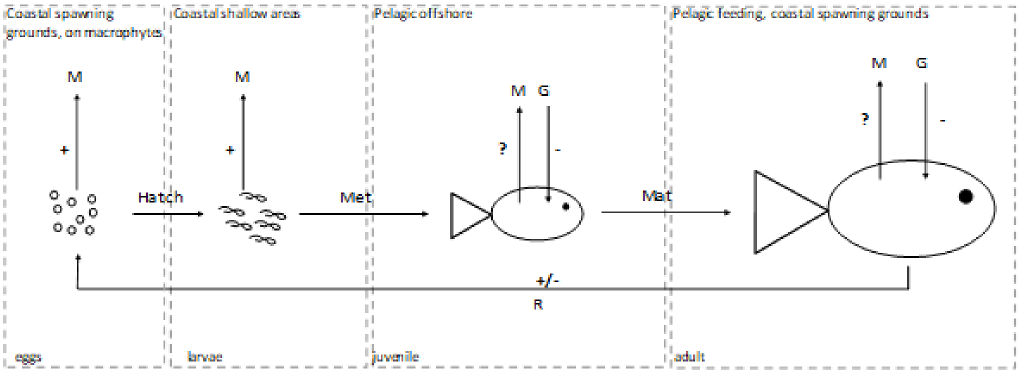
Numerous studies have attempted to correlate the central Baltic herring recruitment with several environmental variables, including temperature (i.e., Bartolino et al. 2014), wind stress and salinity (Pecuchet et al. 2015) as well as larger scale climate indices such as the North Atlantic Oscillation (Axenrot and Hansson 2003) and the Baltic Sea Index (Cardinale et al. 2009). However, correlations found in one study are supported by others only in a limited number of cases, which makes difficult to draw inference on potential causative relationships and conclusions on drivers of herring recruitment. Among all, the thermal environment during Summer (often approximated by sea surface temperature during the month of August) and the abundance of zooplankton (in particular *Pseudocalanus* sp.) have been found positively correlated with the strength of recruitment across several studies (Cardinale et al. 2009, Margonski et al. 2010, Bartolino et al. 2014, Pécuchet et al. 2015). The condition of spawners has been found to correlate with population recruitment (Cardinale et al. 2009), which is supported also by a histological study where poor individual condition during the maturation process was linked to a heavy down-regulation of fecundity through atresia and in some cases skipped spawning (Bucholtz et al. 2013).

Like for other herring populations, spawning grounds of the central Baltic herring are primarily located in coastal habitats in depths less than 10 m, although deeper spawning grounds have been observed (Aneer 1989). Macrophyte substrates are preferred but other substrates are used as well with the exception of soft bottoms. Therefore, like for other herring populations, successful spawning is highly dependent on the quality of the spawning habitats which are particularly exposed to anthropogenic influence as well as local and site-specific physical changes in light conditions, wave exposure, storminess and temperature.

Rajasilta et al. (2011) found that juvenile herring reared in controlled conditions has an optimal accumulation of fat reserves, somatic condition and growth rate at salinities of 8-12 psu, which is somewhat higher than the salinity in most of the nursery grounds in the Baltic Sea. Experimental work by Illing et al. (2016) showed that larval tolerance to low salinity is not significantly different among herring populations within the Baltic Sea and also in comparison with herring from the North Sea. These short-term tolerance tests suggested that herring larvae in the length range of 10-15 mm cannot tolerate salinities <2 psu. This means that climate-driven changes in rainfall patterns (both intensity and timing) and the decreasing salinity in the Baltic Sea could represent an important bottleneck to the persistence of some of the herring spawning components (central Baltic herring, Gulf of Bothnian herring), especially in the eastern and northern spawning grounds where freshening is expected to exceed physiological limits. Other factors which have been found to influence herring larval growth rate are temperature, zooplankton abundance, and wind speed and direction (Hakala et al. 2003).

Table 6.15.3. Climate change processes and responses, key conclusions

Central Baltic herring		
Process	Response to climate change	Reference
Mortality	Decreasing salinity is likely to exceed larval physiological limits in areas part of the distribution	Illing et al. 2016
Spawning	Atresia and skipped spawning linked to poor conditions	Bucholtz et al. 2013
Growth	Decreasing salinity negatively affects the availability of main zooplankton preys (i.e., *Pseudocalanus* sp.) during Spring and Summer (feeding season) Intra-specific competition has a small but detectable negative effect on condition Inter-specific competition with sprat has pronounced negative effect on condition Growth rate of juveniles has an optimum at salinities of 8-12 psu Larval growth rate increases of 0.043 mm/day per 1° C increase in the average water temperature	Cardinale and Arrhenius 2000, Möllman et al. 2004, Rönkkönen et al. 2004 Casini et al. 2011 Casini et al. 2010 Rajasilta et al. 2011 Hakala et al. 2003
Recruitment	Positively correlated with Summer temperature	Cardinale et al. 2009, Margonski et al. 2010, Bartolino et al. 2014



Central Baltic herring

Figure 6.15.3. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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6.15.4. Gulf of Bothnian herring

Herring is the only marine pelagic species using the Gulf of Bothnia for spawning (Aro 1989). Both Spring and Autumn spawning populations occur and can utilise the same spawning grounds concurrently at different times of the year. The Spring spawning type is the dominant today, though autumn spawners may historically have been more dominant in some areas (Lundmark 2010). Local knowledge reported from interviews suggests that changes in dominance between Spring and Autumn spawners has occurred several times in living memory (Gunnartz et al. 2011), suggesting that there is some level of flexibility to interannual climate variability at species level. However, there is as yet no systematic assessment of herring population structure along different parts of the Gulf of Bothnia (Appelberg et al. 2019).

Compared to other geographical areas, herring in the Gulf of Bothnia is clearly smaller in size. In general, herring develops more quickly in the lower salinity of the Baltic Sea, reaching sexual maturity at 2–3 years age, though individual fish escaping mortality factors can live up to 25 years. Herring in the Gulf of Bothnia generally shows a broad preference for relatively shallow spawning sites with hard substrata and submerged vegetation, though they will also spawn on other shallow substrates such as sand (Bergström et al. 2021). Potentially suitable herring nursery occur in many places along the coastline (Erlandsson et al. 2021), although it has not yet been validated to which extent these are functional.

Herring can perform vertical migrations which may increase the tolerance of adult stages to unsuitable temperatures. During the day, herring often move closer to the bottom, while during the night they rise closer to the surface following the movements of the zooplankton. Herring also have seasonal inshore/offshore movements from deep water in winter into shallow water to spawn and feed in spring, where they remain until most herring move back into deeper water for the winter. At the end of Winter, most Bothnian Sea herring can be found in deep offshore waters, with roughly 75 % in water deeper than 50 m and less than 10 % in water shallower than 30 m, while in the Autumn, a larger proportion of the fish are in water less than 20 m deep (Appelberg 2019).

The main natural mortality factors of herring in the Gulf of Bothnia are seals and seabirds, which may show range shifts under climate change, but effects on their population sizes, and hence foraging rates, are uncertain (HELCOM/Baltic Earth 2021).

Cardinale et al. (2009) found that the recruitment success of herring in the Bothnian Sea correlated positively with summer temperature. Herring, being of marine origin, may however be affected by climate-related effects on salinity (Pekcan-Hekim et al. 2016, see also references under “Central Baltic Herring”). In the Bothnian Sea, where main part of the Gulf of Bothnian herring stock is present, no trend in surface or bottom seawater temperature has been seen in the recent past (1965-2019), but there has been a decrease in salinity coupled to increased runoff from land (Wesslander et al. 2020). For example, climate-driven changes in rainfall patterns (both intensity and timing) and decreasing salinity in the Gulf of Bothnia could reduce the availability of herring spawning grounds , as freshening may exceed physiological limits.

Herring may also be affected indirectly by changes in the food web, as the condition of herring is coupled to the condition of its prey (Karlson et al. 2020). Faithfull et al. (2021) highlighted effects of climate and eutrophication on pelagic productivity and food web efficiency as main knowledge gaps for the region. Based on studies from the Finnish part of the Bothnian Sea (Parmanne et al. 2004) the diet of herring can be varied in the coastal zone, including copepods, fish larvae, fish eggs, cladocerans, amphipods and mysids, with fish making up nearly half the volume of the diet. Herring in the open ocean zone is understood to feed mainly on copepods (Rajasilta et al. 2014). Since the young life stages are dependent on zooplankton for growth and development, effects of climate change on the seasonal succession patterns of zooplankton leading to temporal mismatches between prey availability and prey demand, or decreased zooplankton productivity, are likely risks (Flinkman et al. 1998, Karlson et al. 2020).

Table 6.15.4. Climate change processes and responses, key conclusions

Gulf of Bothnian herring		
Process	Response to climate change	Reference
Mortality	Not studied in the Gulf of Bothnia, but references for Central Baltic herring may partly apply. For larvae, climate-related changes in temperature and salinity can decrease food availability and induce temporal mismatches which may reduce the early survival of herring.	
Maturation	Not studied in the Gulf of Bothnia, but references for Central Baltic herring may partly apply	
Growth	Not studied in the Gulf of Bothnia, but references for Central Baltic herring may partly apply Decrease in food availability and lowered food web productivity induced by climate-related changes, may decrease growth.	
Recruitment	Not studied in the Gulf of Bothnia, but references for Central Baltic herring may partly apply	

Gulf of Bothnian herring

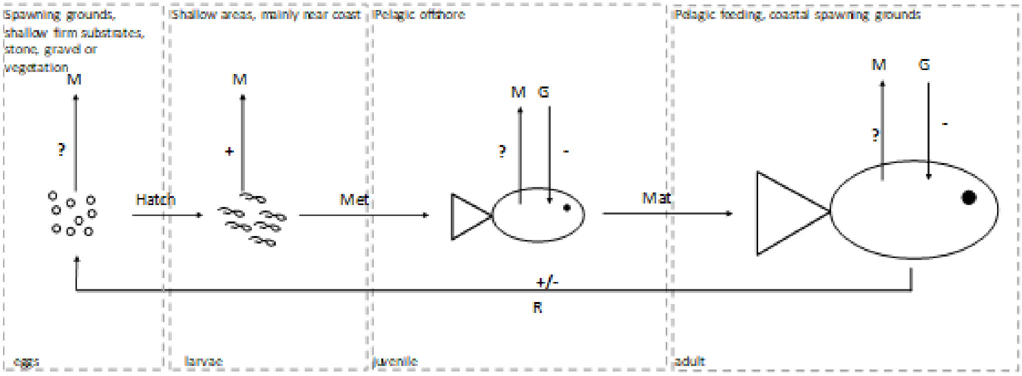

Figure 6.15.4. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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6.16. Mackerel (*Scomber scombrus*)

Atlantic mackerel (*Scomber scombrus* Linnaeus, 1758) is a small pelagic, schooling migratory species of great commercial importance (Trenkel et al., 2014). Atlantic mackerel occupies an important ecological niche, feeding on a variety of zooplankton, phytoplankton, and the pelagic larval and juvenile stages of several commercially important fish species (Engelhard et al., 2014; Trenkel et al., 2014; Pinnegar et al., 2015; Skaret et al., 2015). They are also an important food source for marine mammals and other fish and are a commercially important species (ICES, 2022). Atlantic mackerel occurs on both the east and west sides of the north Atlantic and is traditionally classified into five spawning components (Gíslason et al., 2020).

In the Northeast Atlantic, mackerel spawn from Hatton Bank in the west to Kattegat in the east, and from Portugal in the south to the Faroe Islands in the north (with an additional, isolated spawning population in the Mediterranean Sea). Spawning starts in early February off the Portuguese coast and ends in July north of Scotland and in the North Sea (ICES, 2021). The spawning appears to be a single large spatiotemporal continuum, although there are local variations in spawning (Bakken, 1977; Iversen, 1981; Jansen, 2014).

Northeast Atlantic mackerel becomes mature at age 2–3 years old, spawn annually, and most of the stock is less than 12 years old (ICES, 2022). Mature individuals undertake a seasonal migration along a south-to-north axis currently ranging from Gibraltar to Svalbard, approximately from latitude 36°N to 78°N (ICES, 2013; Nøttestad et al., 2016). Their migration cycle is characterized by over-wintering, followed by spawning in the south from January to July, whereas they feed in the north during summer and fall (Belikov et al., 1998; Uriarte and Lucio, 2001; Iversen, 2002; Jansen et al., 2012; Utne et al., 2012; Nøttestad et al., 2016).

In the northeast Atlantic, several studies have described temperature’s influence on adult (Astthorsson et al., 2012) and egg (Beare and Reid, 2002; Bruge et al., 2016) distributions, and seasonality of occurrence. Beare and Reid (2002) showed a correlation between the increase in egg production of Northeast Atlantic mackerel and the increase in water temperature. However, Bruge et al. (2016) hypothesize a potential increase mortality in mackerel eggs with increased temperature if the mackerel is not able to spawn in deeper cooler waters. Over recent years, the spawning distribution has shifted gradually northwards, likely in response to increasing temperature (Hughes et al., 2014; Bruge et al., 2016). The most extreme change in the Northeast Atlantic mackerel distribution, however, has occurred in the feeding period over summer. Historically, the summer feeding distribution was largely restricted to the Norwegian Sea, but in recent years it has expanded northwards as far as Svalbard, and westwards as far as Greenland (Berge et al., 2015; Jansen et al., 2016).

Table 6.16. Climate change processes and responses, key conclusions

Mackerel		
Process	Response to climate change	Reference
Mortality	Potential increase in egg mortality with increase in temperature	Bruge et al., 2016
Habitat expansion	Already observed in the Northeast Atlantic because of increasing temperature.	Asthorsson et al., 2012; Hughes et al., 2014; Berge et al., 2015; Bruge et al., 2016; Jansen et al., 2016
Spawning	Increased egg production with increase in temperature.	Beare and Reid, 2002

Mackerel

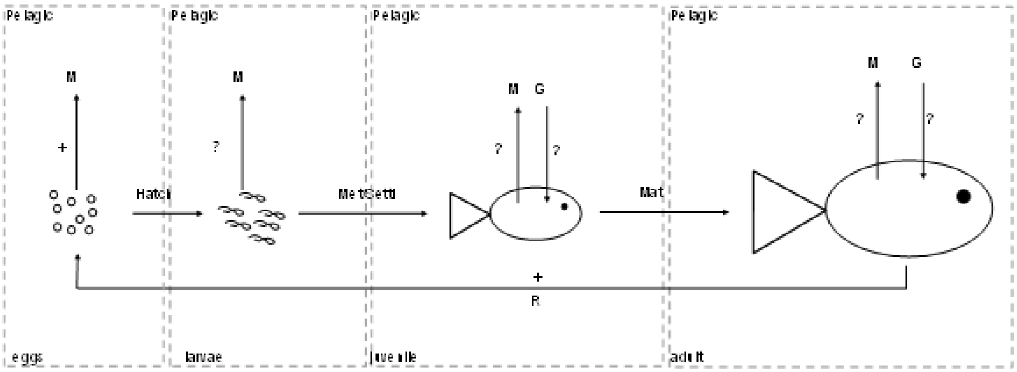

Figure 6.16. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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6.17. Northern pike (*Esox lucius*)

Northern pike (*Esox lucius*), hereafter pike, is an important predator in coastal Baltic Sea ecosystems, but the pike populations have shown marked decreases in recent years (Olsson 2019, Bergström et al 2022). Suggested explanations for the decreases include overfishing, decreased availability of spawning grounds, increased predation, and eutrophication (Olsson 2019, Bergström et al 2022, Winkler 2002, Sundblad and Bergström 2014).

Pike is one of many species in the Baltic Sea with a freshwater origin. Pike depends on low-salinity habitats for spawning, but different reproductive strategies have been observed. Studies along the Swedish coast of the Baltic Sea have shown that one subset of the population uses low-salinity wetlands along the coast for spawning, while another one, approximately 50 %, have an anadromous life-history strategy, migrating to freshwater streams to spawn (Larsson et al. 2015, Westin and Limburg 2002, Engstedt et al. 2010).

Salinity tolerance differs markedly between fish in varying stages of development and with different life history strategies. In coastal spawning pike, eggs can hatch at salinities up to 8.5 psu, fry grow normally at salinities up to 13 psu, and adults can be found (if only for short periods of time) at salinities up to 15 psu (Jørgensen et al. 2010, Jacobsen et al. 2017). Eggs from freshwater-spawning pike, however, showed drastically lower hatching success at salinities of only 4 psu (16.7%) compared to 89.7% success in freshwater (Greszkiewicz et al. 2022). Salinity does not seem to affect the larval density of pike but warmer temperatures on the other hand seem to correspond well with higher larval densities (Donadi et al. 2020). A change in salinity could have an effect on pike distribution. If, for example, salinity in the Baltic Sea were to decrease, due to an increase in runoff or decrease in saltwater inflow, the pike distribution might extend (Neumann 2010 and Wake 2012 via Larsson et al 2015).

Pike requires warm, shallow and well-oxygenated areas with suitable vegetation as nursery areas (Casselman and Lewis 1996, Larsson et al. 2015). After approximately one month, juveniles migrate to extend their distribution (Nilsson et al. 2014). Pike year class strength is positively correlated with temperature (Peat et al. 2016), and the growth of young individuals (but not older individuals) has been shown to increase with temperature. There may be an upper limit to the increase in recruitment with temperature since fast-growing individuals have been shown to be more active and show a more risk-taking behavior (Berggren et al. 2022). Thus, making them more susceptible to predation from top predators, such as grey seals or great cormorants, which have increased along the Swedish coastline (Hansson et al. 2018). Pike recruitment could be affected if the intensity of river runoff changes, since it could change the suitability and availability of coastal wetlands for spawning and nurseries (Larsson et al. 2015).

Pike optimal recruitment occurs at a temperature of 23-24 °C. The optimal growth for young individuals differs with age but is only slightly lower than the maximal recruitment temperature. Pike optimal growth during the first year is between 22-23 °C and for 2-3 years old pike it is between 19-21 °C. Thus, the optimal temperature for growth decreases with age (Casselman and Lewis 1996). A further increase in temperature, above optimal growth, becomes negative, and temperatures above 30 °C are lethal to pike (Ridenhour 1957 via Casselman and Lewis 1996).

Pike is a visual predator depending on sight to catch prey and therefore an increased water turbidity reduces the pike's ability to feed. A positive relation has been observed between Secchi depth (measure of water transparency) and pike weight (Craig and Babaluk, 1989 via Casselman and Lewis 1996).

Table 6.17. Climate change processes and responses, key conclusions

Northern pike		
Process	Response to climate change	Reference
Mortality	Warming increases mortality for fast-growing individuals. Temperatures over 30°C in the natural environment are lethal	Berggren et al. 2022 Ridenhour 1957; Casselman and Lewis 1996
Maturation		
Growth	Warming increases growth of small pike in the Baltic Sea, no change in the growth of large pike. Lower growth when oxygen decreases Optimum temperature for growth of northern pike decreases with age.	Berggren et al. 2022 Adelman and Smith 1977; Casselman and Lewis 1996 Casselman and Lewis 1996
Recruitment	Higher larval densities in warmer waters. Maximum recruitment occurs at 23–24°C Year class strength is positively correlated with temperature	Donadi et al. 2020 Casselman and Lewis 1996 Peat et al. 2016

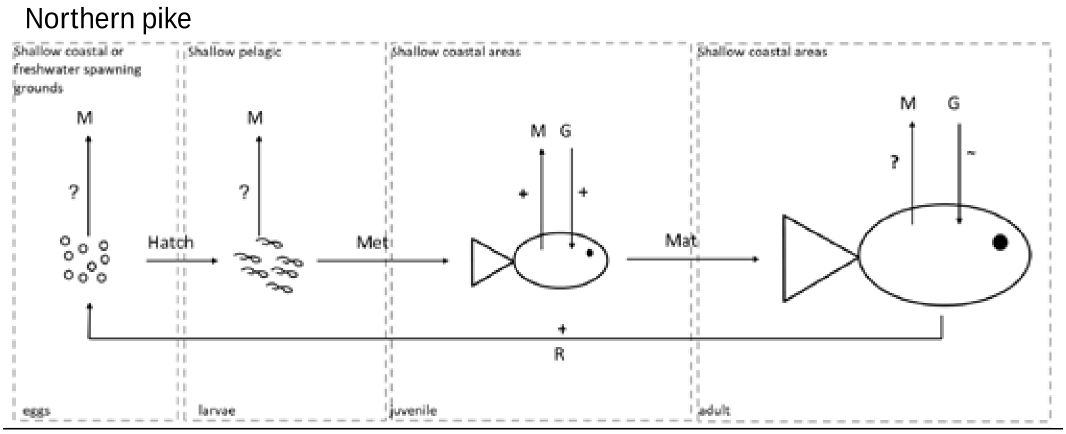

Figure 6.17. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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6.18. Northern shrimp (*Pandalus borealis*)

Pandalus play a central role in the ecosystem of the North Sea and surrounding areas (Skagerrak and northernmost part of the Kattegat) and are eaten by numerous fish species including Atlantic cod, haddock, and saithe (Jørgensen *et al*., 2014; ICES 2022a). *Pandalus* also support a large commercial fishery with landings often exceeding 10,000 tonnes annually (ICES, 2022b).

The populations of *Pandalus* in the North Sea are split into three main stocks based on geographical separation, hydrographical conditions, and investigations on genetic stock structure (Knutsen et al. 2015):

- The Skagerrak and Norwegian Deep stock
- The Fladen Ground stock
- The Farn Deeps stock.

Currently, only *Pandalus* in the Skagerrak and the Norwegian Deep are exploited and landings from the Fladen Ground and the Farn Deeps have been negligible for many years (ICES 2021). Spawning stock size is low in all three areas compared to historic levels (ICES, 2022a, b). Sweden has fishing interests only on the Skagerrak and Norwegian Deep stock.

Pandalus are opportunistic foragers and scavengers, and consume a varied diet including plankton, polychaetes, small crustaceans, and bottom microfauna (Shumway et al. 1985). The species is predominantly a benthic feeder but is known to exhibit vertical migrations during the night in the pursuit of food (Barr 1970). Cannibalism has also been noted (Allen 1959; Shumway et al. 1985).

In the Skagerrak and Norwegian Deep, *Pandalus* are found at depths of 100-500m, at temperatures ranging from 6-9°C, and on sandy/muddy substrata (Shunway et al. 1985; Bergstrom 2000). It is suggested in Knutsen et al. (2015) that juvenile shrimp drift on strong oceanic currents, however, the potential for this North Sea stock to redistribute or adapt to changing hydrographical conditions remains understudied. That said, information on the probable effects of changing temperature and pH can be gained from laboratory work or work done in other areas (e.g., Gulf of Maine) and these are discussed below.

Pandalus are protandric hermaphrodites, meaning that individuals are born as males and become females later in life. In the North Sea and the Skagerrak, sex change normally takes place at age 2 as a gradual process throughout late winter and early spring (ICES, 2022b). Primary females, who never exhibit male characteristics, are sometimes observed in low proportions in the population (Shunway et al. 1985). Typically, individuals mature and reproduce first as males, and then as females.

In the Skagerrak and the North Sea, spawning and mating takes place in October-November and females carry the fertilised eggs under their abdomens until hatching occurs in March the following year (Knutsen et al. 2015). The species has five pelagic larval stages (Ouellet & Allard 2006), with larvae drifting with ocean currents for approx. 2-3 months prior to settlement (Shunway et al. 1985). Once settled on the bottom, growth is relatively rapid and there are clear differences in size distributions between year-classes (Shunway et al. 1985). Differences in size distributions are also observed between areas and stocks (ICES 2022b).

Recruitment of *Pandalus* is thought to be temperature dependent, with higher recruitment being historically correlated with colder sea temperatures (Richards et al. 1996; 2012). Paradoxically, exceptionally strong year-classes have been produced in recent years despite an overall warming trend (e.g., Hunter et al. 2011). In fact, the 2021-year class in the Skagerrak is estimated to be large (ICES, 2022a). Spatial differences in recruitment are also present in the North Sea, with studies suggesting that the Skagerrak acts as a nursery ground for the Skagerrak and Norwegian Deep stock (Knutsen et al. 2015).

Temperature has both positive (growth) and negative (physiological condition) effects on *Pandalus*. As temperature increases, the growth rate of *Pandalus* also increases, however, due to trade-offs between consumption and metabolism, individuals are expected to have a reduced body condition and change sex at earlier ages (Stickney and Perkins 1977; Bergstrom 2000; Daoud et al. 2007). Fecundity will also respond to temperature, with egg loss being greater when ovigerous females experience higher temperatures (Nunes 1984). Moreover, egg development rates and yolk conversion efficiencies have both been shown to be faster at higher temperatures (8°C compared to 5°C or 2°C), resulting in earlier hatch times, and larvae that are both smaller and have poorer overall physiological condition (Brillon et al. 2005). *Pandalus* larvae, as in many marine species, need to feed rapidly after hatching to avoid starvation (Stickney and Perkins 1977; Wienberg 1982). Consequently, any phenological shifts in the timing of hatching that are not matched by shifts in the timing of the spring phytoplankton bloom could have important consequences for population dynamics and the survival of new recruits.

In a wider ecosystem context, warmer conditions might also shift the distribution and phenology of *Pandalus* predators causing increases in natural mortality. In fact, such trends have already been observed in the Gulf of Maine, whereby a temperature mediated expansion of the distribution of longfin squid has been linked to the 2012 collapse of the *Pandalus* stock (Richards & Hunter 2021). Equally, temperature mediated range shifts might also decrease natural mortality rates as *Pandalus* predators may redistribute to colder waters.

In addition to temperature effects, decreasing pH is also expected to impact the survival and development time of *Pandalus*. Experimental work by Bechmann et al. (2011) and Arnberg et al. (2012), both found that *Pandalus* larvae reared at pH levels predicted for the year 2100 (IPCC, 2007) had significantly longer development times. Moreover, survival of both adult and larval life stages was significantly lower (68% and 70%, respectively) when low pH conditions were coupled with warmer temperatures (Dupont et al. 2014; Arnberg et al. 2018). Such findings confirm a synergistic interaction between pH and temperature, meaning that their combined negative effects on *Pandalus* in the North Sea might be greater than their individual effects.

Anthropogenic warming has also been linked to an increased susceptibility of crustaceans to disease (including *Pandalus*), especially when pathogens have optimal temperatures that are higher than their host's (Shields 2019). Two pathogenic parasites, one causing egg mortality (Chang et al. 2020) and the other causing black spot gill syndrome (Lee et al. 2019), are known to cause mortality in *Pandalus* and infection rates have been shown to be higher under warmer conditions (Apollonio et al. 1986).

Table 6.18. Climate change processes and responses, key conclusions

Northern shrimp in the North Sea and surroundings areas		
Process	Response to climate change	Reference
Mortality	Reduced adult survival when exposed to increased temperature and reduced pH – tested conditions match those predicted for the North Sea in 2100	Dupont et al. 2014; Arnberg et al. 2018; Bechmann et al. 2011; IPCC 2007
	Warming results in earlier hatch times - larvae are smaller and have a poorer physiological condition, therefore the likelihood of starvation is increased. Earlier hatch times might also cause a phenological mismatch between larvae and their prey causing even greater starvation rates.	Brillon et al. 2005
	Parasite infection rates have been shown to increase in higher temperatures	Apollonion et al. 1986
Sex change	Age at sex change is reduced at higher temperatures	Shunway et al. 1985; Bergstrom 2000
Maturation	Warming speeds up egg development and increases egg loss	Nunes 1984
Growth	Faster growth of all life-stages as temperature increases	Stickney and Perkins 1977; Daoud et al. 2007
	Decreased pH shown to reduce larval development rates	Bechmann et al. 2011; Arnberg et al. 2012
Recruitment	Inverse relationship between temperature and recruitment, albeit outliers have been observed	Richards et al. 1996; 2012

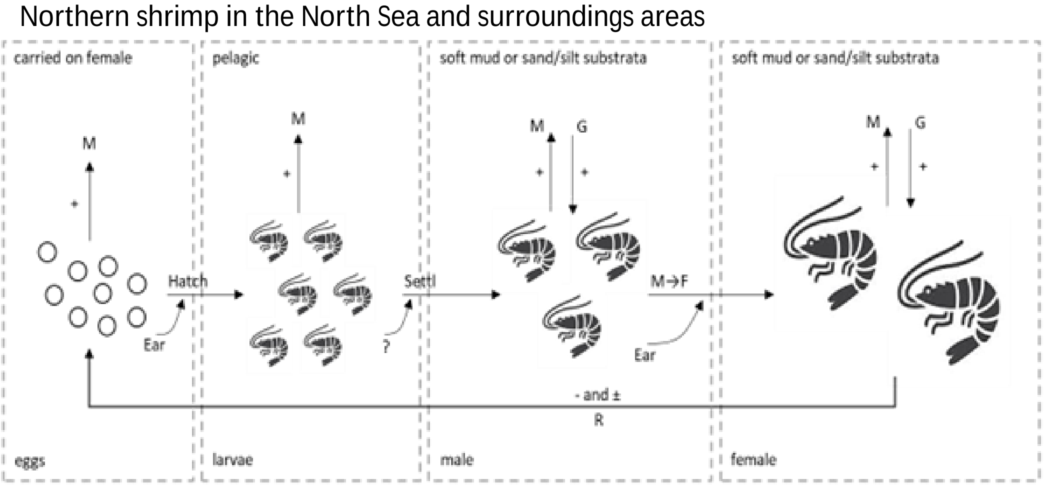

Figure 6.18. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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6.19. Norway lobster (*Nephrops norvegicus*)

Norway lobster (*Nephrops norvegicus,* nephrops) is long-lived decapod crustacean sustaining an economically important fishery in the Mediterranean and NE Atlantic. Nephrops are predominantly associated with muddy sea floor from 20 to 800 meters. They reside in oceanic water of 33-34 psu and are generally described as stenohaline (intolerant to reduced salinity).

Nephrops spawning (extrusion of eggs to the underside of the female abdomen) takes place during a prolonged period in late summer/autumn and embryo incubation is 7-9 months in NE Atlantic (Farmer, 1973), but shorter in the Mediterranean (Mori et al., 1998). Incubation time is highly influenced by temperature and warming significantly shortens incubation times (increase from 8 to 20 degrees shortens incubation duration from 300 to 140 days (McGeady et al., 2021)). In the NE Atlantic, larvae are hatched into the water column during March to June and spend 50-60 days in a pelagic phase with several instars and metamorphoses (Hill, 1990) before settling onto muddy seabeds. North Atlantic Oscillation pattern has been shown to influence abundance of nephrops over large scales (Vasilakopoulos & Maravelias, 2016). Positive NAO phases (warmer temperatures, winter storms etc.) have been suggested to provoke a general decrease in the lower trophic levels, which constitute prey for juvenile and adult Nephrops (Herraiz et al., 2009).

Marine crustaceans appear to be capable of building solid shells at decreased pH levels in the ocean (Kroeker et al., 2010; Ries et al., 2009). However, larval phases are sensitive to more general stress responses. Nephrops larvae have been demonstrated to be sensitive to stress by both decreased salinity and pH (Wood et al., 2015) although embryonic development may be insensitive to decreases in pH (Styf et al., 2013). Sensitivity to climate driven changes in pH and salinity may be a future bottleneck for stocks of nephrops. Decreased pH, comparable to levels expected by the end of the century, had lethal effects with high variability between broods with survival probabilities ranging 30-65% (Wood et al., 2015).

The immune response of adult nephrops was increased by exposure to ocean acidification (Hernroth et al., 2012). Such energy demanding responses are assumed to result in lower fitness, survival and/or reproductive output. Responses are projected to be more pronounced at higher temperatures, adding to the potential detrimental effects to individuals and stocks.

As for lobster, shifts in incubation time and larval development times are expected for nephrops from a change in ocean temperatures. Between 1982 and 2010 peak larval release date was shifted approximately 17 days earlier (McGeady et al., 2021). Extending such logic into the realm of larval transport and settling may greatly affect dispersal and distribution of larvae. Potentially larval distribution may mismatch with both food items as well as grounds for successful settling.

Spatial management practices of important fishing and settling grounds may be warranted to mitigate such effects.

Nephrops populations seem to have rather high prevalence of Pink crab disease. Effects of climate change, such as increased ocean temperature, may impact spread and response but has not been predicted as strong (Rowley et al., 2014).

Table 6.19. Climate change processes and responses, key conclusions

Norway lobster		
Process	Response to climate change	Reference
Development	Warmer water shortens egg incubation Decreased pH (to levels expected by 2100) has lethal effects on pelagic larvae	McGeady et al. (2021) Wood et al. (2015)
Growth	Warming reduces abundance levels through trophic interactions Warming induced increased immune response Suggesting lower fitness, survival or growth	Herraiz et al. (2009) Hernroth et al. (2012)
Diseases	Inconclusive	

Norway lobster

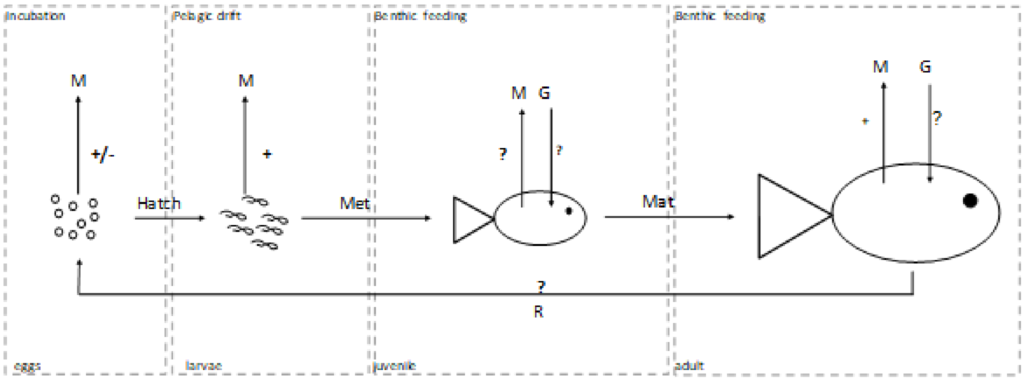

Figure 6.19. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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Authored by Andreas Sundelöf

6.20. Norway pout (*Trisopterus esmarkii*)

Norway pout *(Trisopterus esmarkii*) is a small (approx. 20 cm length), short-lived, boreal gadoid species (Hislop et al. 2015). It is widely distributed in the Northeast Atlantic, from the southwest Barents Sea, sometimes at Bear Island, south to the English Channel and the Bay of Biscay, around Iceland and Faroe Islands (Mikkelsen 2014; Raitt & Adams 1965).

Norway pout tends to stay relatively deep in the water column, in the depth range 80-250 m. The prey types consist of small organisms, mainly zooplankton (Albert 1994; Raitt & Adams 1965). The pelagic age 0 group stays in the upper 50 m of the water column and feeds mainly on copepods while larger specimens (10-20 cm) prefer mysids, in addition to small fishes, such as gobies (Hislop et al. 2015). Feeding activity peaks during night (Raitt & Adams, 1965).

Similarly, to other gadoids found in the North Sea (i.e., cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) and saithe (*Pollachius virens*)), Norway pout shows: (i) distributional center of gravity in the northern North Sea (Hislop et al. 2015), (ii) the most important spawning areas at the shelf region between Shetland and Norway (Sundby et al. 2017), (iii) drifting of early life stages farther south into the North Sea and partly into the Skagerrak, (iv)similar long-term changes in stock abundances during the 1960s and 1970s followed by a decline (Hislop, 1996) most probably due to the increasing temperature in the North Sea.

The decline in the stock of Norway pout occurred somewhat later than for the other three gadoid species. This could be related to that Norway pout is the only one that inhabits the deepest and coldest part of the North Sea (the deep Skagerrak and the Norwegian Trench). But it can also relate to that the abundance is lagged due to the predation from the other gadoids on the Norway pout (Cormon et al. 2016).

Little is known about the recruitment processes of Norway pout, although warming temperatures appear to be associated with a decrease in the stock (Engelhard et al. 2011). The Norway pout stock dynamics are influenced by strong predation especially by saithe, grey gurnard (*Eutrigla gurnardus*), whiting (*Merlangius merlangius*) and in the most recent period hake (*Merluccius merluccius*). The response of Norway pout to warming conditions in the North Sea will ultimately depend on the relative effects of warming on the recruitment of the stock, on the abundance and distribution of its main predators and the overall status of the North Sea food web (Engelhard et al. 2014).

Empirical evidence suggest that this small, short-lived gadoid allocates a disproportionate amount of energy to the first time reproduction, resulting in high spawning stress and associated mortality (Lambert et al. 2009; Bailey and Kunzlik 1984; Ursin 1963). Nielsen et al. (2012) shows that density-dependence processes, but we argue also environmentally driven processes, can influence growth rates and maturity ratios and could lead to increases in mortality rates.

Table 6.20. Climate change processes and responses, key conclusions

Norway pout		
Process	Response to climate change	Reference
Mortality	Predation mortality will depend on the response of the main North Sea predatory fish (i.e. cod, hake, saithe)	Engelhardt et al. 2014 Cormon et al. 2016
Maturation	Increased mortality at spawning due to energetic stress due to climate change	Lambert et al. 2009; Nielsen et al. 2012
Recruitment	Increase in temperature will potentially decrease recruitment success	Engelhard et al. 2011

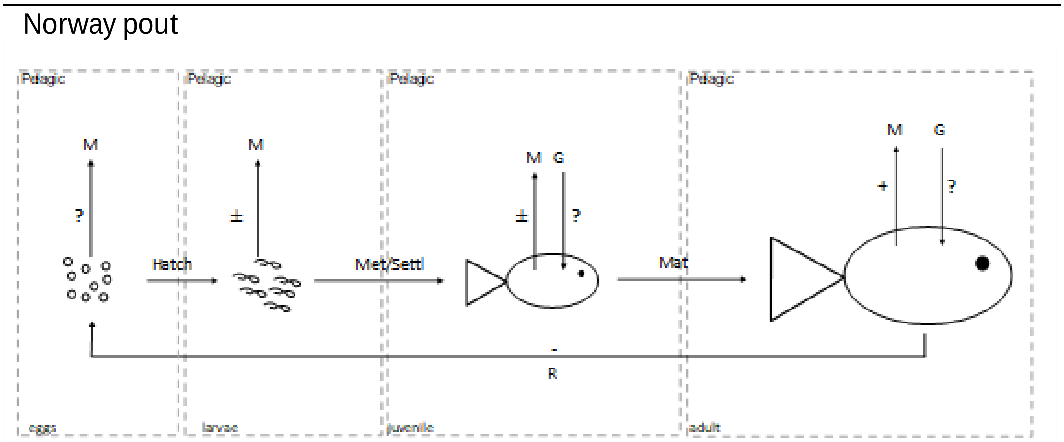

Figure 6.20. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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Authored by Johan Lövgren

6.21. Perch (*Perca fluviatilis*)

Eurasian perch (*Perca fluviatilis*) is an abundant and widely distributed species along the low-salinity coastal zones of the Baltic Sea. Perch is a freshwater fish and its distribution encompasses the entire Baltic Sea, but are in some regions, like Öresund, limited by its salinity tolerance, to the less saline estuaries. Perch has an upper salinity tolerance between 10-15 psu (Lutz, 1972 via Overton et al. 2008), although some adult perch have been shown to tolerate salinities up to around 18 psu (Olsen, 2002, via. Overton et al. 2008). However, the growth rate of juvenile perch has been shown to decrease with increasing salinity (Overton et al. 2008). Studies also show that the survival of perch fry in brackish waters (around 7 psu) is significantly lower than in freshwater environments (Tibblin et al, 2012). A change in salinity could have an effect on perch distribution. If for example, salinity in the Baltic Sea where to decrease, due to an increase in runoff or decrease in saltwater inflow, the perch distribution and spawning habitats may extend (Mackenzie et al. 2007).

Perch are spring spawners. Like many other freshwater species in the Baltic Sea, they can have both a migratory and resident form. The migratory form moves into streams and rivers to spawn in freshwater, whilst the resident form spawns in coastal water. Spawning in freshwater has been shown to be a life-history strategy that can increase juvenile survival (Tibblin et al. 2012). As adults, both forms mix within coastal foraging habitats, and show limited foraging ranges (Ahlbeck et al. 2017 and Hansson et al. 2019).

The abundance, distribution and growth of perch are influenced by temperature. Monitoring of coastal fish communities in the Baltic Sea shows that there has been a shift in the mid-1990s towards a higher proportion of species that prefer higher temperatures, such as perch (Olsson et al. 2012). There is also a positive correlation between perch year-class strength and temperature (Koli et al. 1985, Böhling et al. 1991). Temperature also influences the local distribution of perch, with an earlier outward migration, from the shallow coastal spawning grounds towards deeper waters, of age-0 perch during warmer years (Kjellman et al. 2001). With a continued increase in temperature in the Baltic Sea, perch populations in the northern end of the distribution could increase (Olsson et al. 2012).

Experimental studies also confirm that perch growth depends on temperature, with a higher growth rate for one-year-old perch in warmer waters. However, the mean length of the population has shown to be lower in areas with warmer waters than in colder waters (van Dorst et al. 2019, Huss et al. 2019). This is in line with the theoretical expectations that warmer temperatures should lead to a faster growth but smaller adult body size (Atkinson 1994 via Lindmark et al. 2018). Besides all factors listed above, temperature also influences age at maturity, with maturity occurring at a lower age in warmer waters (Heibo et al. 2005).

Perch are visual predators and therefore dependent on vision for finding food (Diehl 1988). During its lifetime, perch undergoes onthogetic niche shifts. Early in life, perch forages on zooplankton. They then switch to benthic invertebrates, and eventually, when large enough, to fish (Persson 1988). Large piscivorous perch are important predators along the coast of the Baltic Sea, consuming for example gobies, herring and three-spined stickleback (Lappalainen et al. 2001), and are aso themselves important prey for birds and seals, as well as being a valuable part of coastal fisheries (Hansson et al. 2018).

Perch growth can be negatively impacted by increased turbidity due to effects on its foraging efficiency (Diehl 1988, van Dorst et al. 2020). However, a larger threat from increased turbidity is reduced habitat availability, as high turbidity decreases macrophyte growth in the littoral zone, and prey availability, as turbidity shifts systems from benthic to pelagic production, hence reducing the density of macroinvertebrate prey (Lappalainen et al. 2000, Sandström and Karås 2002, Bergström et al 2013).

Table 6.21. Climate change processes and responses, key conclusions

Perch		
Process	Response to climate change	Reference
Mortality	Warming increases mortality of both juvenile and adult perch. A decrease in salinity may increase the survival of free-swimming perch fry.	Heibo et al 2005, Overton et al. 2008, Tibblin et al. 2012
Maturation	Lower age-at-maturity in warmer waters.	Heibo et al 2005
Growth	Warming increases growth in small-bodied perch. Optimum growth at low salinities (0-4 ppt)	Overton et al. 2008, Tibblin et al. 2012, Van Dorst et al. 2019, Huss et al. 2019
Recruitment	The year-class strength of perch is positively correlated with temperature	Böhling et al. 1991, Lappalainen et al 2001.

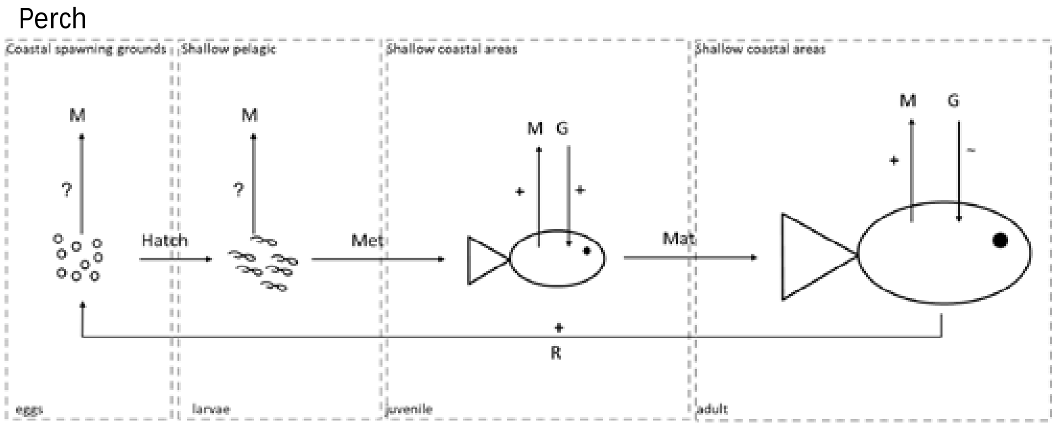

Figure 6.21. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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Authored by Matilda Andersson and Frida Sundqvist

6.22. Pikeperch (*Sander lucioperca*)

Pikeperch (*Sander lucioperca*) is a freshwater species that lives along the coast of the Baltic Sea with its northern range extending into the southern Bothnian Bay (Pekcan-Hekim et al. 2011, Lehtonen et al. 1996). The general distribution of pikeperch along the coast is limited by its tolerance of salinity. Although adult pikeperch can occasionally be found at salinities up to 12 psu, early life stages have a lower salinity tolerance (Deelder and Willemsen 1964, via Lehtonen et al 1996). Because of this low salinity tolerance, spawning is restricted to shallow inlets, estuaries and bays where salinity is low and temperatures are comparatively high (HELCOM 2021, Lehtonen et al. 1996).

Long-term monitoring of the coastal fish communities in the Baltic Proper and Bothnian Sea shows that freshwater species that prefer warmer temperatures have increased over time, correlating with an increase in temperature over time during the warm season on both a regional and local scale (Olsson et al. 2012). Such trends could also affect pikeperch positively. In the Baltic Sea, pikeperch reaches maturity at between 4-6 years age and at a length of 35-44 centimeters, with the males maturing at a younger and smaller size than females (Kosior and Wandzel 2001, Lappalainen et al. 2003, Ozyurt et al. 2011). Studies show that maturity occurs at an earlier age in the southern populations of the Baltic Sea, attributed to higher temperatures causing faster growth (Lappalainen et al. 2003).

Spawning starts when water temperature reaches 10-14 °C, which usually occurs in late-May to early-June (Colby and Lehtonen 1994 via Lappalainen et al. 2003). The year-class strength of pikeperch varies between years but depends on water temperature, with stronger year-classes at higher temperatures (Lappalainen et al. 2009, Pekcan-Hekim et al. 2011, Veneranta et al. 2011, Heikinheimo et al. 2014).

Higher temperatures during its first summer benefits the growth rate and body size of pikeperch, which in turn is usually attributed to a lower mortality (Pepin and Myers 1991 via Pekcan-Hekim et al. 2011), because larger juveniles typically have a better ability to find food and escape predators (Pepin 1991). Higher temperatures continue to increase growth even beyond the first year, provided sufficient food resources, even though the benefit diminishes as pikeperch length increases)(Lappalainen et al. 2009, Heikinheimo et al. 2014).

The abundance of juvenile pikeperch is positively correlated with turbidity, although the specific mechanism explaining this relationship is unclear (Veneranta et al. 2011). Possible explanations include lower predation risk in turbid environments due to decreased reaction distance of predators (Veneranta et al. 2011), higher zooplankton biomass (Winkler et al. 1994, via Lehtonen et al. 1996), and visual adaptations in pikeperch that allow them to forage effectively in low-light conditions (Sandström and Karås 2002, Sandström 1999).

Pikeperch often thrive in more eutrophic areas, and the abundance of pikeperch could increase or decrease depending on the level of eutrophication (Letonen et al. 1996, Bergström et al. 2013). A study along the Finnish coast of the Baltic Sea shows that eutrophication has favored pikeperch during recent decades, resulting in an extended distribution further out in the archipelago, and further north along the coastline (Pekcan-Hekim et al. 2011).

Table 6.22. Climate change processes and responses, key conclusions

Pikeperch		
Process	Response to climate change	Reference
Mortality	Warming decreases mortality for juvenile perch but there can be increased mortality due to intraspecific competition in strong year-classes.	Pepin and Myers 1991; Pekcan-Hekim et al. 2011, Heikinheimo et al. 2014
Maturation	Warming can cause earlier maturation in fast growing pikeperch.	Lappalainen et al. 2003
Growth	Warming increases pikeperch growth but the positive effect on growth decreases as the pikeperch grows.	Lappalainen et al. 2009
Recruitment	The year-class strength of pikeperch correlates positively with temperature. Higher turbidity is associated with higher recruitment.	Pekcan-Hekim et al. 2011, Veneranta et al. 2011, Lappalainen et al. 2009, Heikinheimo et al. 2014. Veneranta et al. 2011

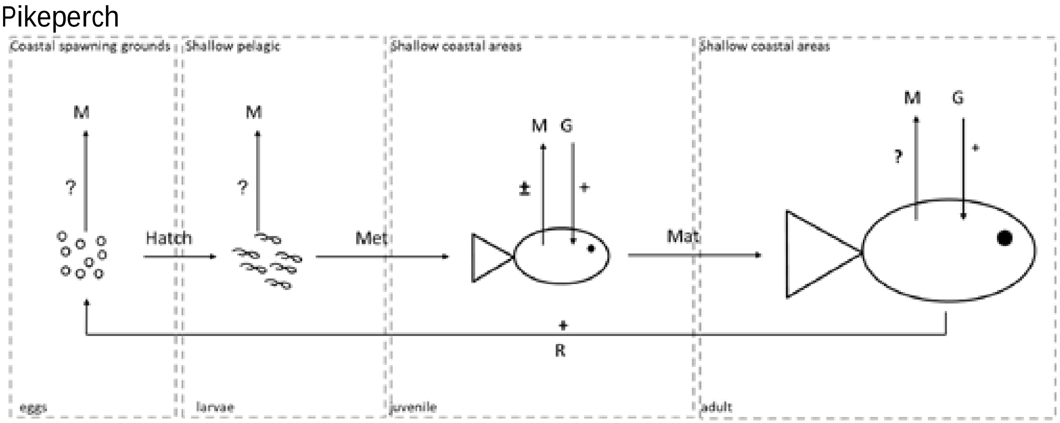

Figure 6.22. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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6.23. Round goby (*Neogobius melanostomus*)

Round goby (*Neogobius melanostomus*) is a non-indigenous species in the Baltic Sea, native to the Caspian and Black seas and acclimated to a range of different salinity levels (Corkum et al. 2004). The introduction to the Baltic Sea presumably occurred via ballast water in the 1980's to the Gulf of Gdansk, where it was first observed in 1990 (Corkum et al. 2004). Now, round goby is expanding its distribution range and has been found in all sub-regions of the Baltic Sea (Puntila et al. 2018). Round goby is considered to have a limited daily mobility and a strong resident behavior (Christoffersen et al. 2019). The long-distance spread throughout the Baltic Sea is, most likely, caused by transport via ballast water of cargo ships (Corkum et al. 2004). Their ability to spread locally is in all probability due to their wide tolerance to a range of conditions.

Temperature is one of the conditions for which round goby has a wide tolerance. The species thrives in warm waters but has been found in waters ranging in temperature from -1 to 30 °C (Moskalkova 1996 via Cross and Rawding 2009). Depth is another key variable. In the Polish zone of the Baltic Sea, a study observed round goby from the coastal zone and down to depths of 40-60 m. Round goby can tolerate hypoxic conditions for at least a few days (Cross and Rawding 2009) but may attempt to escape areas with low oxygen conditions (Kornis et al. 2012). A study by Kotta et al. (2016), modeling the distribution of round goby in relation to different environmental variables, shows that one of the primary local environmental conditions related to round goby distribution is wave exposure, with higher abundances in sheltered areas.

Round goby is an aggressive and territorial species competing for food resources and habitat with native species (Bergstrom and Mensinger 2009). When feeding, round goby is an insatiable generalist, feeding on a variety of food sources including zooplankton (juveniles), benthic invertebrates, small fishes and eggs and larvae of large fishes. However, they seem to prefer bivalves as adults (Kornis et al. 2012). Due to its abundance in the Baltic Sea, round goby has become an important prey for other fish species such as perch (*Perca fluviatilis*) and cod (*Gadus morhua*), and in some areas it has become a main food source (Almqvist et al. 2010).

Studies have shown that the growth rate of round goby is higher in relatively warmer waters but that round goby in colder waters continues to grow at an older age, resulting in a larger maximum size in relatively colder waters (Sokołowska and Fey 2011). In the southern Baltic Sea, round goby can live up to 6 years and reaches a larger size than in most other populations (Sokołowska and Fey 2011), including freshwater populations and populations within its natural home range (Sokołowska and Fey 2011, Kornis et al. 2012). The larger size could partly be due to a higher growth rate in areas with a higher salinity, as the salinity in the southern Baltic Sea is higher than in most other areas round goby has invaded (Sokolowska and Fay

2011). Heavy fishing in its natural home range, the Caspian and Black Sea, have also led to a reduced size spectrum there (Apanasenko 1973 and Moskalkova 1996, via Sokołowska and Fey 2011).

Round goby matures early, with onset of maturity at ages between 1 and 4, depending on sex, location and temperature (Wandzel 2000, Almqvist et al. 2010). Round goby has an earlier onset of maturity in warmer waters (Sokolowska and Fey 2011). Round goby is able to spawn multiple times per season (Wandzel 2000, Almqvist et al. 2010). The spawning season starts when temperatures increase in spring. Within its native range, round goby can spawn as often as every 3-4 weeks (Charlebois et al. 1997 via Kornis et al 2012). In its native environment, spawning of round goby starts at a temperature of 12 °C (Tomczak and Sapota 2006), and spawning has been observed at water temperatures between 9-26 °C (Kornis et al. 2012). An increase in temperature in the Baltic Sea could thus prolong the spawning season and increase the number of spawning occasions for round goby (Kornis et al. 2012). After spawning, the males guard the nest. A single nest can contain up to 10 000 eggs from multiple females, and the fertilization and hatching rate can be as high as 95 % (Charlebois et al. 1997 via Kornis et al. 2012).

Table 6.23. Climate change processes and responses, key conclusions

Round goby		
Process	Response to climate change	Reference
Mortality	Warming may lead to a shorter lifespan, since the maximum age is lower in warmer waters.	Sokołowska and Fey 2011
Maturation	Earlier maturation in warmer waters.	Sokołowska and Fey 2011
Growth	Higher growth rates in areas with higher salinity. Growth rate is higher in warm water, but maximum size is larger in colder water.	Sokołowska and Fey 2011, Corkum 2004 Sokołowska and Fey 2011
Recruitment	Increased temperatures can increase the number of spawning occasions per year.	Kornis et al. 2012

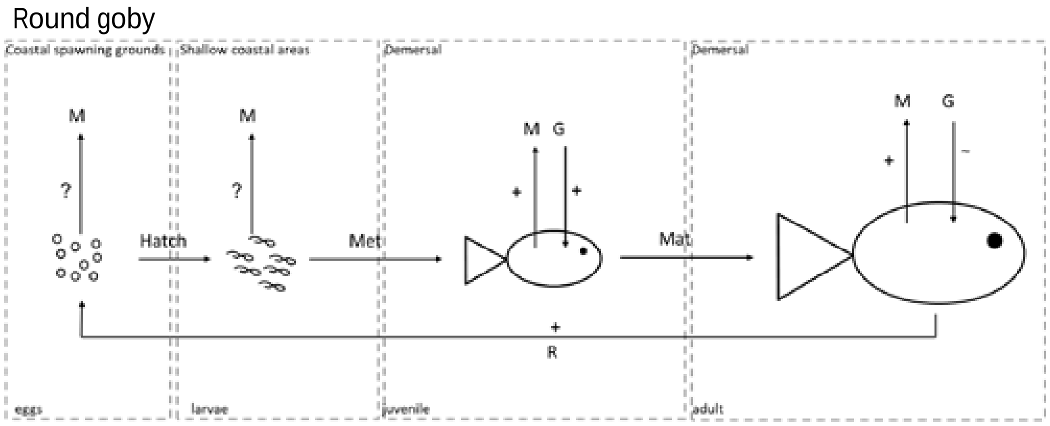

Figure 6.23. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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6.24. Saithe (*Pollachius virens*)

Saithe (*Pollachius virens*) is major top predator fish species in the North Sea, and supports the fishery economy of several European countries (Cormon et al. 2016). Saithe is a semi-pelagic, strongly schooling fish living on both sides of the North Atlantic Ocean. Spawning takes place at bottom depths of 100-200m (Homrum et al. 2012).

Saithe may reach a total length of 130 cm, a whole-body weight of more than 20 kg, and live up to 30 years (Coehen et al. 1990). Age at first maturity varies, starting at 4–5 years, but most individuals reach maturity around 7–8 years (Olsen et al. 2010).

Saithe spawn during wintertime, with peak activity in February, at depths of about 200m on the banks along the coast of western and northern Norway (Olsen et al. 2010).

Eggs and larvae drift from the spawning grounds and the fry settle in the littoral zone, but move to coastal banks as juveniles (Sande et al. 2019). At sexual maturation, saithe perform winter migrations to the spawning areas, which are located even further offshore (Homrum et al. 2012).

Saithe is an important predator; young specimens feed mainly on copepods, krill and other pelagic crustaceans, while herring (*Clupea harengus*), sprat (*Sprattus sprattus*), blue whiting (*Micromesistius poutassou*), Norway pout (*Trisopterus esmarkii*), and small haddock (*Melanogrammus aeglefinus*) become more important as prey later in life (Sande et al. 2019, Homrum et al. 2012).

Saithe is a poorly studied species and very little is known about the life history of the species (Sande et al. 2019). However, mesocosm experiments has showed that saithe growth is highly positively related to an increased temperature (Sande et al. 2019), suggesting that the growth of juvenile and adult saithe potentially will increase as ocean temperature will increase (Andersen and Riis-Vestergard 2003, Sande et al. 2019). Cook and Heat (2005) looked at the relationship between temperature and recruitment and spawning stock biomass and found a positive effect on saithe and whiting (*Merlangius merlangus*) compared to cod (*Gadus morhua*), plaice (*Pleuronectes platessa*) and sole (*Solea solea*).

During the last 20 years, Northern European hake (*Merluccius merluccius*) has expanded its spatial distribution in the North Sea region as an effect of the increased temperature in the ocean. A modelling study show that the expansion of hake could have a large impact on the abundance and distribution of saithe, since the species are competing for the same prey species (Cormon et al. 2016).

Table 6.24. Climate change processes and responses, key conclusions

Saithe		
Process	Response to climate change	Reference
Growth	Saithe showed a positive response in growth with an increased temperature	Sande et al. 2019
	Increased competition from hake as the distribution of hake is increasing with warming water	Cormon et al. 2014, 2016
Recruitment	Increasing temperature showed a positive effect on the SSB-Recruitment relationship	Cook and Heat 2005

Saithe

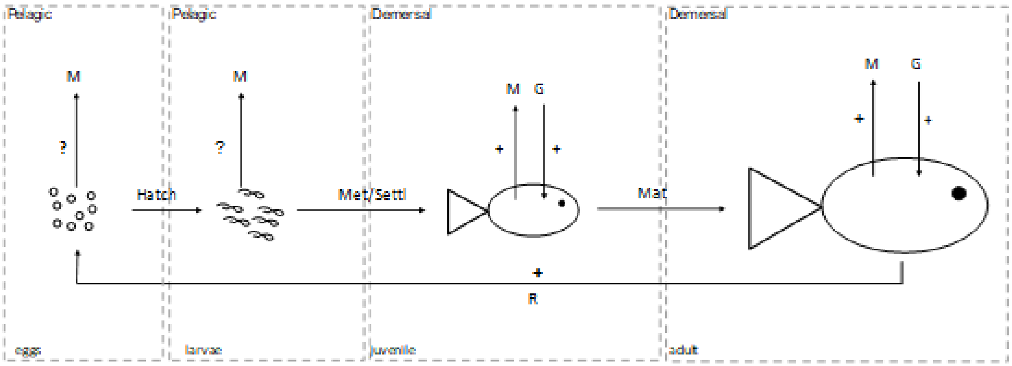

Figure 6.24. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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6.25. Sandeel (*Ammodytes* spp.)

Sandeel plays a central role in the North Sea ecosystem, being an important prey for seabirds, marine mammals and predatory fish, and supporting one of the largest single species fisheries in the area (Furness 2002, Engelhard et al. 2014).

The life cycle of sandeel is characterized by a specialized overwintering burying strategy, with the result of a strong preference for fine gravel and coarse sand habitats, high site-fidelity and a patchy distribution. Patches of suitable sandeel habitats have different degrees of larval connectivity which has supported the division of sandeel in the North Sea into a number of management units (san.sa.1r-7r).

The diet of sandeel is very flexible (Malzahn and Boersma 2009), based on stomach content analyses of both larvae and adults with preys ranging from phytoplankton (e.g. diatoms) and protozoans (e.g. dinoflagellates) to larger mobile zooplankton (e.g. copepods).

The recruitment of sandeel has dramatic interannual fluctuations, with a large year-class typically being followed by a small one. Unusually strong year-classes can sustain large biomasses for several years (ICES, 2020). As for other short-lived fish, recruitment is poorly correlated with the spawning stock biomass and variability in recruitment is highly influenced by other drivers including environmental forcing.

Timing of metamorphosis in sandeel is size-dependent. Hence, higher growth rates leading to shorter larval phases are expected to increase the survival (Eliasen et al., 2011; Gurkan et al., 2012). Further, energetic costs and survival during the first overwintering period by post-settled juveniles are dependent on reaching a critical threshold size (van Deurs 2011). Energy budget models predict that mortality from starvation due to insufficient food availability is an important factor influencing the abundances of sandeel (MacDonald et al., 2018).

Dispersal is primarily the result of larval drift while adult movement is limited. Hence, successful settlement depends largely on oceanic current patterns, and access and distribution of suitable sandy habitats. Sandeel has strong preference for fine gravel and coarse sand substrates and tends to avoid fine silt (Wright et al., 2000; Holland et al., 2005). While sediment composition can be assumed quite stable from one year to another, it has shown considerable changes on a decadal time-scale in the North Sea primarily driven by broad-scale climate fluctuations (Wieking and Kröncke 2001).

Oceanographic fronts have been reported to support early life-stages of sandeel in high abundances (Munk et al., 2002) and years with strong recruitment in the Dogger Bank have been associated with current flow regimes moving north during February (Henriksen et al. 2018). Relationship of recruitment with the large-scale climate described by the NAO and AMO remains unclear, with contrasting findings by different authors (Arnott and Ruxton, 2002; van Deurs et al., 2009; Lynam et al., 2013, Lindegren et al., 2018).

Conditions for growth are heterogenous throughout the North Sea as reflected by higher growth in the central and northeastern areas (Boulcott et al., 2007; Rindorf et al. 2016). Adult sandeel have a limited time window of feeding to build up energy reserves for a non-feeding overwintering period (Bergstad et al., 2002). Therefore, conditions before the onset of overwintering affect the time extent sandeel can stay buried in the sand (Henriksen et al. 2021a). Moreover, reserve depletion during the overwintering is also function of temperature and earlier emergence has been observed in warmer years (Henriksen et al. 2021a).

Temperature has been found to have both positive and negative effects. At present, empirical evidence on temperature-mediated larval growth is missing (MacDonald et al., 2019b), but bioenergetics models specific for sandeel predict a positive relationship between temperature and growth (Gurkan et al. 2012, 2013, van Deurs et al. 2013). Rindorf et al. (2016) showed that growth rate and condition of adult sandeel are positively related to temperature. However, warming has been shown to delay and inhibit gonad development of adult sandeel (Wright et al. 2017a, b). Moreover, the spawned eggs develop faster under higher temperatures provoking earlier hatching and smaller sizes-at-hatching (Régnier et al., 2018), with expected increase in predation mortality and increased risk of trophic mismatch between sandeel larvae and important prey (Régnier et al., 2019). Henriksen et al. 2021b) found a negative correlation between the second year of life and the autumn bottom temperature, suggesting higher mortality in warm years and with a more pronounced effect in the southern North Sea.

Table 6.25. Climate change processes and responses, key conclusions

Sandeel (North Sea)		
Process	Response to climate change	Reference
Mortality	Higher temperature provokes early hatching and smaller size-at-hatching with increased risk of mortality Faster larval growth anticipates metamorphosis increasing survival	Régnier et al., 2018, 2019 Eliasen et al., 2011; Gurkan et al., 2012
Maturation	Warming delays and inhibits gonad development	Wright et al., 2017a,b
Growth	Faster larval growth anticipates metamorphosis Adult growth and condition positively affected by temperature increase	Eliasen et al., 2011; Gurkan et al., 2012 Rindorf et al. 2016
Overwintering	Shorter overwintering period during warmer years increases risk of both higher exposure to predation and mismatch with suitable preys	Henriksen et al. 2021a,b
Recruitment	Negative effects of warming on maturation may impact the reproductive output	Wright et al. 2017a,b

Sandeel (North Sea)

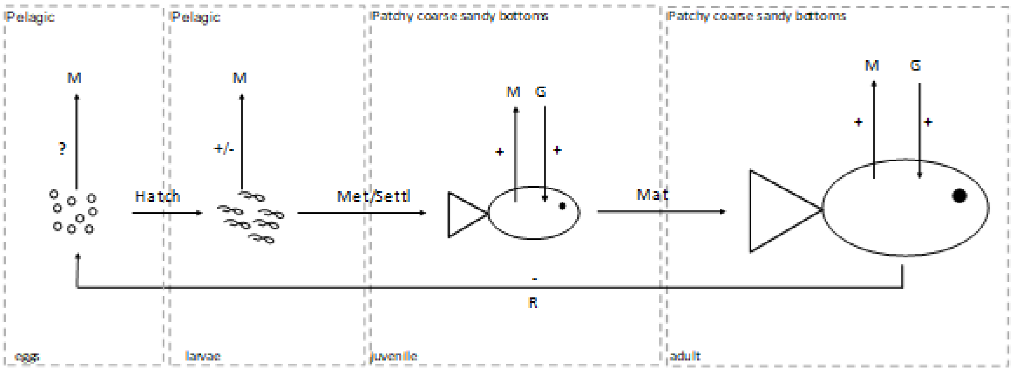

Figure 6.25. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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6.26. Seabass (*Dicentrarchus labrax*)

Seabass (*Dicentrarchus labrax*) is a widely distributed demersal species found subtidally down to 100 m around the Northeast Atlantic to the Mediterranean Sea and west coast of Africa (Freyhof and Kottelat, 2008). In the Northeast Atlantic, ICES (https://www.ices.dk/) recognizes at least four separate stocks of seabass, the largest being the stock distributed in northern and central Bay of Biscay and that inhabiting the central and southern North Sea, Irish Sea, English Channel, Bristol Channel, and Celtic Sea. Seabass can tolerate a wide range of salinities as they occupy shallow waters, estuaries and out into deeper waters. Adults spend the winter in deeper water, shoal in early summer and move into coastal waters and estuaries. Young fish are known to school in shallow waters for at least one year before joining the adults and moving offshore in the winter (Sánchez Vázquez and Muoz-Cueto 2019).

This wide geographical and ecological range of distribution is related to the physiological adaptations of the species, mainly due to its tolerance to low and high temperature and its ability to regulate osmotic stress (Sánchez Vázquez and Muoz-Cueto, 2019). The species inhabit at temperatures between 8-24°C (Froese and Pauly, 2016) but in the Mediterranean coastal lagoons it has been reported to tolerate temperatures from 5°C to 32°C (Barnabe, 1990). In recent years seabass has been recorded further north, and this northward extension to their range is thought to be related to changes in sea temperature as distribution of seabass is thought to be highly affected by water temperature (Sánchez Vázquez and Muoz-Cueto 2019).

European seabass is a slow-growing species with a lifespan of up to 25 years (Sánchez Vázquez and Muoz-Cueto, 2019). Sexual maturity in Atlantic fish is reached at around 4-7 years (30-40 cm) in males, and 5-8 years (36-46 cm) in females (Pawson and Pickett 1996; www.fishbase.org). Adults move closer inshore into warmer waters to spawn from March to mid-June. Spawning occurs in batches, and eggs are pelagic (Murua and Saborido-Rey 2003).

Despite its generally high tolerance for a wide range of temperatures and salinities, basic functions essential for juvenile seabass surviving and well performing in the wild, such as predation, predator avoidance, neurofunction and ability to face chemical stress may be compromised by a too large increase in water temperature (Almeida et al., 2015). This may be of particular concern if recruitment phase in northwest European estuaries and coastal areas happens gradually in warmer environments because of global warming (Almeida et al., 2015). Maturation of the gonads on the other hand is triggered by relative high temperature. The complete gonadal maturation and spawning for female seabass living in waters around Britain is not occurring until they grow up to 42 cm and remain in water with temperature over 10°C during the main period of gonad development (Pawson et al., 2000). The temperature experienced during the early life stages affects the sex ratio. In the specific, exposure to temperatures below 16°C until 56 days post hatching increases the proportion of seabass that develop as females but decreases the proportion of females if exposure to cold waters occurs after that period, with the proportion of males reaching 90% after 230 days at 16°C (Vandeputte et al., 2020). Observations from nursery areas along the Portuguese coast suggest that lower salinities within estuarine nurseries have a positive effect on juvenile abundance (Bento et al. 2016). Experiments in tanks indicated limited acclimation capacity for seabass exposed to extreme warm temperature (33°C) (Islam Md et al., 2020). However, overall results indicate that European seabass acclimatized to low salinities (experiments conducted at 12 psu and 6 psu) can cope better during extreme warm exposure (33 °C). This indicates that seabass might be able to colonise the Baltic Sea with global warming as first record of the species in the southern Baltic Sea might also indicate (Bagdonas 2011).

The growth of the juvenile sea bass from a Mediterranean population was estimated to be maximum at 26 °C with growth peaking within a narrow range of temperatures and declining thereafter (Person-Le Ruyet et al., 2004). These findings agree with those of Barnabé (1990) who reported an optimal temperature range of 23 to 27 °C for the growth of the species. Russell et al. (1996) reported that growth of juvenile seabass in British waters (at the northern limit of the species range) did not occur at 7 °C and was high at 18 °C. However, the analysis did not include temperature over 18 °C so that even larger growth can be expected with a further increase in temperature.

Table 6.26. Climate change processes and responses, key conclusions

Seabass		
Process	Response to climate change	Reference
Mortality	Warming will decrease survival of juveniles in the northwest European estuaries and coastal areas but would increase at the northern boundaries of the distribution	Almeida et al., 2015
Maturation	Maturation will be favored by increasing temperature. Sex ratio will be affected by increasing temperature	Pawson et al., 2000 Vandeputte et al., 2020
Growth	Growth increases in juvenile seabass with increasing temperature with a maximum around 26 °C	Person-Le Ruyet et al., 2004; Russell 1996; Person-Le Ruyet et al., 2004.
Recruitment	See mortality	
Habitat expansion	Already observed in the northern part of the Northeast Atlantic because of increasing temperature. The species might colonise the Baltic Sea with increasing temperature due to its high tolerance for low salinity.	Sánchez Vázquez and Muoz-Cueto 2019; Bagdonas 2011

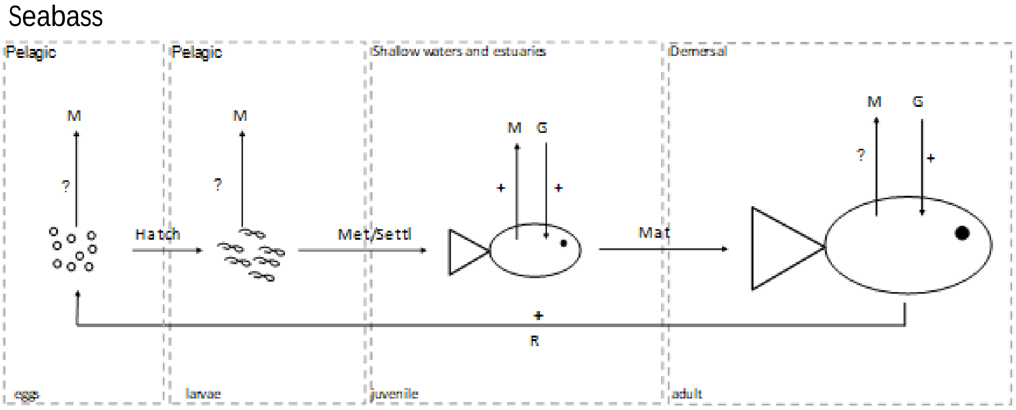

Figure 6.26. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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6.27. Sea trout (*Salmo trutta*)

Sea trout, here referring to anadromous forms of brown trout, is native to Europe and wild forms mainly occur along the western coasts from Portugal to the White Sea (Elliott 1994). Anadromous populations also occur elsewhere due to stocking (Klemetsen et al. 2003). Brown trout is a plastic species, and has a partially migratory life history. If they do not have access to the sea, they stay their whole life in the freshwater, sometimes migrating to nearby lakes or pools. If the trout have access to the sea, they often form anadromous populations where parts of the population enter adjacent marine habitats, primarily estuaries or coastal waters to feed for a summer or longer periods of time (Knutsen et al. 2001, Klemetsen et al. 2003).

The migration to the sea is normally concentrated in spring and sometimes in fall (Jonsson and Jonsson 2009a, b), but trout may also utilize the streams during winters. Once ready for spawning, sea trout return in autumn or winter to the native river to lay their eggs on stony/gravel substrate. The eggs hatch the following spring, and the larvae (alevins) stay in the gravel for weeks feeding on their yolk. Once the fry emerge from the gravel, they start feeding in or near the spawning area, preferring moderately fast flowing water in shallow areas. At this stage, the fish are territorial and compete for the resources. As the fish grow larger they disperse to deeper more slowly flowing parts of the stream preferring stony bottoms or finer substrates.

Temperature optimum for trout increases with size, and is 7-10°C for eggs, 14-17°C for juveniles, and 17-19°C for adults (references in Table S3 in Kärcher et al. 2021). Climate change leads to increasing temperatures, but is also predicted to cause milder weather and more stormy winters in Northern Europe, as well as more severe and frequent extreme weather events like floods and drought (IPCC 2021, HELCOM 2021). A changing climate will have impacts on both the freshwater and the marine phase of the sea trout, affecting growth and survival, migration, distribution, and life history characteristics (Jonsson and Jonsson 2009a, Graham and Harrod 2009, ICES 2018).

Species distribution

Sea trout recruitment often takes place in small, shallow streams, which are particularly prone to dry out in a warming climate. Temperatures may rise to levels outside the range of thermal tolerance, and/or oxygen to drop to low or lethal levels, leading to further loss of suitable habitats and impair stream connectivity. Trout has already declined in lower latitudes (Almodóvar et al. 2012). Depending on different future climatic scenarios, further reduction (64-100%) is predicted in the southern and central European basins and redistribution of suitable habitats will push trout distribution to high altitude areas (Wenger et al. 2011, Almodóvar et al. 2012, Filipe et al. 2013, Muñoz-Mas et al. 2016, Santiago et al. 2020, Kärcher et al. 2021, Basen et al. 2022). Habitat loss may be less severe in the northern basins (Lassalle and Rochard 2009), where brown trout may benefit from higher temperatures (Donadi et al. 2021). Small shaded streams can buffer against temperature increases (Broadmeadow et al. 2011, Borgwardt et al. 2020, Spanjer et al. 2022) and trout escape to deep-water refugia. In intensively regulated rivers, however, an increase in mean summer air temperature of 3-6°C can result in a 57-78% decrease in trout density (Donadi et al. 2021). Increasing temperatures may also lead to species displacement or invasion of introduced species, which threatens the native trout (Öhlund et al. 2008, Wenger et al. 2011).

Recruitment

Successful recruitment depends on the availability of suitable spawning and nursing habitats accessible to spawners. Water loss, low oxygen levels and changed runoff patterns threaten many shallow habitats in a warming climate and increased erosion can impair reproductive performance in alpine countries due to bed clogging (Scheurer et al. 2009, Junker et al. 2015). Increasing temperatures lead to shorter developmental time for eggs and fry (Crisp 1988, Elliott and Hurley 1998, Hari et al. 2006, Santiago et al. 2020), and increase survival at emergence in cold years (Jensen and Johnsen 1999). However, the egg stage is particularly vulnerable to increasing temperatures in a warming climate, and few egg hatch at the upper limit of the thermal range for trout egg survival of 1-8°C (review in Elliott and Elliott 2010).

Growth

Sea trout exhibits strong phenotypic plasticity to temperature variability (Forseth et al. 2009, Lejk et al. 2021). For example, anadromous individuals tend to mature later and grow to larger size than individuals that stay all their life in freshwaters. Some studies suggest that trout growth is adapted to thermal conditions (e.g., Archer et al. 2021). Growth generally increases southwards along a latitudinal gradient (L’Abée-Lund et al. 1989, Berg and Jonsson 1990, Kallio-Nyberg et al. 2015) due to increasing productivity and longer growth season (Bærum et al. 2021). The effects of increasing temperature can be particularly strong for small and young fish in temperate and northern areas (Elliott and Elliott 2010, Bærum et al. 2021) owing to stronger effects of increasing food rations (Forseth and Jonsson 1994). Whereas small increases in water temperature in winter and spring (<2.5°C) often have positive effects on trout growth, larger increases (3-4°C) can have negative effects (Elliott and Elliott 2010). The effect can only be positive as long as there is sufficient food available to support growth (Ries and Perry 1995). Increasing temperatures can change the growth trajectory in trout: faster growth and early maturation in young fish ends up with smaller body size at an older age (Bærum et al. 2021).

Mortality

Summer drought cause habitat deterioration and mortality in young trout, especially for 1+ year fish (Elliott and Elliott 2010), and cause problems for migrating individuals that gets a longer and more difficult journey to the sea (Berg and Jonsson 1990). In snow-fed streams and rivers, increasing flows in spring can cause increased mortality in alevins due to scouring of the habitat (Jensen and Johnsen 1999). Increasing winter temperature can result in decreased survival during the sea phase due to early arrival to sea (at a small size) where the small smolt is exposed to high levels of predation (Jonsson and Jonsson 2009b). In addition, increasing temperature may result in physiological stress leading to increased vulnerability to disease, such as proliferative kidney disease (PKD) (Borgwardt et al. 2020) and ulcerative dermal necrosis (Casas-Mulet et al. 2021).

Dispersal

Trout undergo dispersal at several stages throughout its life cycle. In a warming climate, cold-water fish will need to disperse to more suitable habitats (Comte et al. 2013). Low oxygen levels in pools and small water levels may reduce activity and migration, affecting the migration within the system as well as migration between the freshwater and the sea (Armstrong et al. 2003). Temperatures during the embryo stage can influence later behavioral decisions such as migratory behavior (Jonsson and Greenberg 2022). Increasing temperature may trigger earlier smolt migration (Hembrel et al. 2001, Jonsson and Jonsson 2009b, Harvey et al. 2020) and also advance migration from sea to the spawning river (Legrand et al. 2021, de Eyto et al. 2022), resulting in a wider migratory period (Larios-López et al. 2015).

Life history

Increasing temperature is linked to earlier smolt age (L’Abée-Lund et al. 1989, Elliott and Elliott 2010, Birzaks 2020), shorter longevity (Jonsson et al. 1991), prolonged spawning period (Berg and Jonsson 1990), and changes in life strategy (Jonsson and Jonsson 2009a). The prevalence of anadromy in trout populations tends to increase with latitude, in order to optimize the trade-off between feeding opportunities against increased costs of migration and risk of predation in marine waters versus freshwaters. Increasing temperatures can cause trout to shift from anadromy to more resident forms (Jonsson and Jonsson 2009a, b) in response to increased productivity in the freshwater habitat and reduced connectivity to the sea.

In conclusion, a warming climate may affect trout distribution, abundance, growth, maturity, survival, and migration pattern. However, the direction of effects can vary with climate and geographic area. At high altitudes and in northern latitudes, increasing temperatures can benefit trout due to increasing productivity and habitat availability. At intermediate and lower latitudes, especially towards the southern edge of its distribution, effects are generally negative due to reduced quality, availability and accessibility of suitable habitats and increased susceptibility to parasites and diseases. Negative effects also occur at all latitudes when habitats become less stable, and when temperature exceeds the thermal optimum for the various life stages of trout.

Table 6.27. Climate change processes and responses, key conclusions

Sea trout		
Process	Response to climate change	Reference
Distribution	Loss and redistribution of suitable trout habitats (particularly in the southern and the central European basins); gain of habitats at high altitudes Increased abundance in northern basins	Lasalle and Rochard 2009, Wenger et al. 2011, Almodóvar et al. 2012, Filipe et al. 2013, Muñoz-Mas et al. 2016, Basen et al. 2022 Donadi et al. 2021
Recruitment	Reduction of suitable summer habitat due to drought Decrease in successful hatching of eggs with increasing temperature Shorter duration of egg incubation period and alevin stage; increase survival at emergence in cold years Impairment of reproductive performance of gravel-spawning fish due to river bed clogging in alpine countries (increased erosion)	Muñoz-Mas et al. 2016, Santiago et al. 2020 Elliott and Elliott 2010 Crisp 1988, Elliott and Hurley 1998, Hari et al. 2006, Santiago et al. 2020; Jensen and Johnsen 1999 Scheurer et al. 2009
Growth	Increased growth with increasing temperature; decreased growth with higher increases in temperature	L'Abée-Lund et al. 1989, Berg and Jonsson 1990, Forseth and Jonsson 1994, Ries and Perry 1995, Elliott and Elliott 2010, Kallio-Nyberg et al. 2015, Lejk et al. 2021, Bærum et al. 2021
Mortality	Increased survival at emergence with increasing temperature and increased alevin mortality with increasing flow Increased mortality in young trout (especially in 1+ year fish) with increasing droughts Increased smolt mortality and decreased homing precision with increasing temperatures as seaward migration are pushed earlier in the year Increased mortality in trout with increasing temperature due to higher emergence of and susceptibility to profilerative Kidney disease (PKD) and ulcerative dermal necrosis due to *Saprolegnia parasitica*	Jensen and Johnsen 1999 Elliott and Elliott 2010 Jonsson and Jonsson 2009b Borgwardt et al. 2020, Casas-Mulet et al. 2021
Dispersal / migration	Early onset of downstream migration and delayed entry and spawning with changing flow; increased duration of spawning period	Hembrel et al. 2001, Jonsson and Jonsson 2009b, Elliott and Elliott 2010, Larios-López et al. 2015, Birzaks 2020, Harvey et al. 2020, Legrand et al. 2021, de Eyto et al. 2022, Jonsson and Greenberg 2022
Life-history	Increased residency and decreased occurrence of anadromy with increasing temperature Delayed river entry and spawning due to low or high river flow Lower smolt age with increasing temperature	Jonsson and Jonsson 2009b Berg and Jonsson 1990 Elliott and Elliott 2010

Sea trout

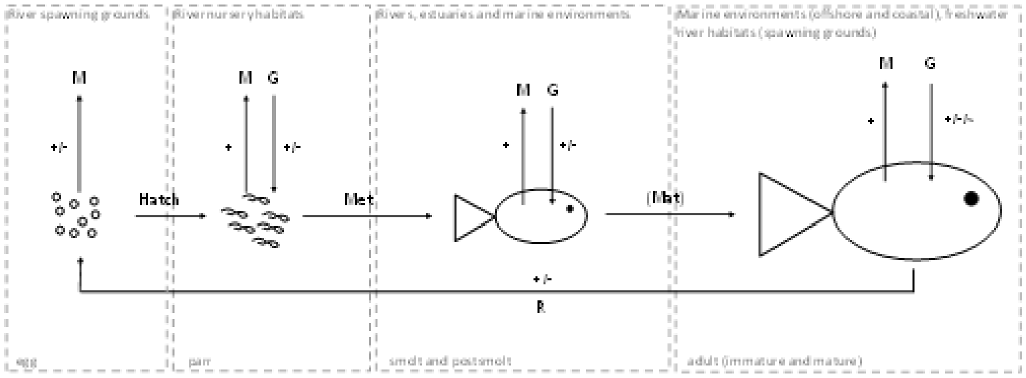

Figure 6.27. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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Authored by Katarina Magnusson

6.28. Sprat (*Sprattus sprattus*)

European sprat (*Sprattus sprattus*) is a short-lived and fast-growing pelagic fish species. It forms large schools, often inshore and also in a mixture with other clupeids such as herring, throughout the European continental shelf seas extending its distribution into the Mediterranean where it occurs with distinct populations in the Adriatic Sea and in the Black Sea. The distribution throughout the Greater North Sea ecoregion has two main centers of aggregation in the shallow, coastal waters of the southern North Sea and in the Kattegat which are recognized part of a single large population (ICES 2018). A distinct population is distributed throughout the south and central Baltic Sea. The broad geographical distribution of the species is supported by its tolerance for a wide range of temperatures and salinities, and a certain plasticity as suggested by differences in the scheduling of life-history events (i.e., spawning occurs in Spring-Summer in the North Sea and Baltic Sea while it happens during Winter in the Mediterranean; Wahl and Alheit 1988, Dulĉić 1998).

Sprat is a batch spawner, similar to other clupeids, with eggs released over a prolonged period of time and a broad range of temperatures (6-15ºC). Sprat spawns pelagic eggs which remain in the surface layers in the North Sea while sink to intermediate depth of 30-60 m in the Baltic Sea due to the surface layers low salinity (Wieland and Zuzarte 1991). Overall, the development and survival of eggs and yolk sac larvae are viable over a broad temperature range (4.5-18ºC), but there are evidences that these thermal boundaries narrow down rapidly for first feeding larvae (Thompson et al. 1981, Nissling 2004, Petereit 2008) to expand again for late larvae and juveniles. In the northern latitudes (North Sea and Baltic Sea), the first feeding season after the metamorphosis into juveniles (35-55 mm standard length) is crucial for the storage of energy necessary for the first overwintering (Peck et al. 2012).

Sprat plays an important ecological role in the ecosystem by exerting a strong grazing pressure on zooplankton communities and acting as a key prey for a wide range of predators, including marine birds, mammals, and predatory fish. Sprat is an obligate particulate plankton feeder (i.e., preys are eaten almost individually by rapid opening and closing of the mouth) schooling in high densities which likely contribute of strong intra-specific and inter-specific density-dependency as reported by several studies both in the North Sea and in the Baltic Sea (Casini et al. 2011, Hunter et al. 2019, Lindegren et al. 2020). Under low productivity and disruptive environmental perturbations, as expected in numerous climate change scenarios, more flexible feeding mode as found in other small pelagic fishes (herring, sardine and anchovy) and invertebrates (e.g. jellyfish and ctenophores) could represent a competitive advantage over sprat (Pech et al. 2012).

The physiology of the early life stages of the North Sea and the Baltic Sea populations is similar in many aspects (e.g., development rates of eggs and different stage larvae) and differences in life history scheduling likely reflect to large extent differences in seasonality in water temperature, productivity and prey availability. However, sprat has a short-life span in the North Sea where individuals rarely exceed age4-5 (e.g., age3+ is used in the assessment, ICES 2021a), but not in the Baltic Sea where the population is characterized by a more complex demographic structure made of numerous age groups (e.g., age8+ is used in the assessment, ICES 2021b).

Many studies and analyses on the relationship between sprat productivity (i.e., recruitment and growth) and environmental variability have been published for the Baltic Sea, while relatively little has been presented for the North Sea.

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6.28.1. North Sea and Kattegat-Skagerrak sprat

Little research on the relationship between North Sea and Kattegat-Skagerrak sprat (hereafter referred as North Sea sprat) productivity and environmental variability has been published. There are indications that recruitment success and growth have been on average low after the mid-1990s which has been suggested as a possible shift in the productivity of the stock (Clausen et al. 2018). However, in the early 1980s recruitment success was also relatively low, indicating likely a temporary peak in productivity in the late 1980s rather than an actual regime shift.

North Sea sprat recruitment shows a positive relationship with salinity (Pecuchet et al. 2014; Akimova et al. 2016) that in the southern and central North Sea is mainly influenced by inflow of oceanic waters from the north and the river run-off from the south. Considering the tolerance of the specie for a wide salinity range, it is likely that the relationship with recruitment is mainly an indirect effect plausibly via alteration of the amount and composition of the zooplankton in the North Sea (Akimova et al. 2016). Another recent correlative analysis (ICES 2018) suggested that sprat recruitment could also be negatively affected by sea-surface temperature (SST in the same period of the year) as a consequence of increasing metabolic costs during a period of low zooplankton availability which may result in increased larvae/juvenile mortality during winter. However, it is noted that this analysis was only peer-reviewed within a recent benchmark and would require further validation before could be accepted.

Using statistical modelling and long-term observational data from the southern North Sea, Lindegren et al. (2020) found a dome-shaped relationship between the growth of sprat and temperature with a peak in the response at approx. 9ºC. They also found a positive relationship between growth and zooplankton abundance, in particular with *Temora longicornis* which represents one of the sprat main preys in the North Sea (Raab et al. 2012, Van Ginderdeuren et al. 2014). Sprat diet partially overlap with that of herring and even more with the diet of sardine and anchovy (Raab et al. 2012, Voss et al. 2009) which are shifting their distributions northwards and increasing their abundance in the North Sea also as a consequence of a warming environment (McLean et al. 2019). The ability of these other species to switch between filter and particulate feeding mode, but not in sprat which is limited to particulate feeding, has been hypothesized to represent a disadvantage for sprat especially under low zooplankton concentrations as induced by poor ocean productivity or by disruptive environmental perturbations (Peck et al. 2012).

In the southern North Sea spawning occurs in spring until early summer (Alheit 1987). Sea water temperature is an important determinant for the time and length of the spawning season of sprat, with spawning occurring in the southern North Sea in the temperature range of 6-12ºC (Wahl and Alheit 1988). A negative relationship was found between the size at maturity (length corresponding to a 50% probability of first maturation) and temperature (Hunter et al. 2019).

Eggs and larval sprat development is temperature dependent which results in differential growth rates in deep cold off-shore areas compared to warm near-shore shallow areas. Coupled hydrographic and individual-based models show that concentration of larvae is highest at the frontal zones in the southern North Sea where both relatively low and high growth rate larvae co-occur (Daewel et al. 2008). In addition to temperature and prey biomass, water turbulence above a certain threshold significantly affects larval survival under low food conditions (Daewel et al. 2008).

Experimental work on sprat eggs from the southern North Sea and English Channel by Thompson et al. (1981) showed similar egg survival in the temperate range 4.5 and 18 ºC but suggested that temperatures on the highest spectrum of this range would compromise the survival in the wild due to early developmental stage-at-hatch.

Table 6.28.1. Climate change processes and responses, key conclusions

North Sea and Kattegat-Skagerrak sprat		
Process	Response to climate change	Reference
Mortality	Water turbulence above a certain threshold promotes survival of larvae under low food conditions	Daewel et al. 2008
Maturation	Time of spawning is affected by water temperature, with viable temperature range of 6-12ºC. Increasing temperature results in smaller size at maturity	Wahl and Alheit 1988 Hunter et al. 2019
Growth	Growth has a dome-shaped relationship with temperature with maximum growth around 9ºC Increasing abundance of competitors such as anchovy and sardine in the North Sea is expected to affect growth (no empirical evidence of direct competition yet, but strong diet overlap and co-occurrence of eggs and larvae)	Lindegren et al. 2020 Lindegren et al. 2020
Recruitment	Positive effect of salinity on recruitment likely via foodweb interaction Increase water temperate in Q4 negatively correlate with recruitment	Pecuchet et al. 2014; Akimova et al. 2016 WKSPRAT 2018

North Sea and Kattegat-Skagerrak sprat

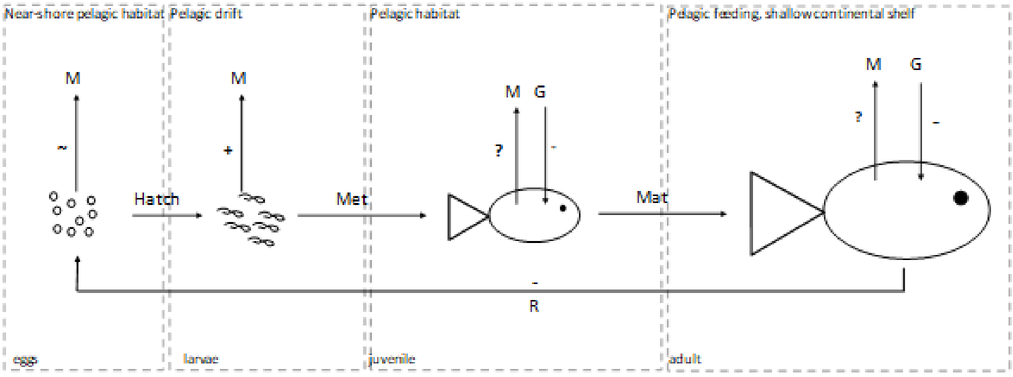

Figure 6.28.1. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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6.28.2. Baltic Sea sprat

Recent investigations about the abiotic factors affecting Baltic sprat recruitment are quite few but studies covering the field have been published back in time. The variability of recruitment has increased during the 1990 indicating that many factors interplay, to a larger degree, in the recruitment process from spawning and during the subsequent egg and larval development phases.

Using time-series and correlative analyses, MacKenzie and Köster (2004) showed that recruitment at age 1 was mainly related to mid-water (45-65 m depth) temperature in May the year before. Moreover, both May temperature and recruitment were correlated to ice cover and North Atlantic Oscillation winter index, suggesting that Baltic sprat recruitment is originally driven by large-scale climate factors (MacKenzie and Köster, 2004). The importance of temperature was also evidenced by the correlative analyses by Margoński et al. (2010) who found a close correlation between recruitment at age 1 and summer temperature the year before. Both studies also indicated that the spawning stock biomass had a minor role in determining recruitment at age 1 for Baltic sprat (MacKenzie and Köster 2004; Margoński et al. 2010).

Also using correlative analyses, Baumann et al. (2006) found that sprat recruitment at age 0 was related to the spawning biomass and to temperature at different degrees in winter, spring and summer the same year. Although other factors (e.g. wind speed) might play a role, temperature seems therefore to be the main factor affecting the early life stages of Baltic sprat, acting on gonad maturation, egg survival, size at hatching, larval swimming capability and growth and zooplankton abundance and composition (Kalejs and Ojaveer, 1989; Köster et al. 2003; Nissling et al. 2003; Baumann et al. 2006). Especially August surface temperature correlated with recruitment at age 0. Accordingly to Nissling et al. (2003) in the northern reproduction area, i.e. in the Gdansk Deep and especially Gotland Basin, salinity conditions are also important, probably because in these areas the salinity is lower and a part of the eggs may not obtain neutral buoyancy and sink to the bottom where they encounter low-oxygen conditions (Nissling et al. 2003). This underlines also the importance of saline water inflows from the North Sea for egg survival. Baumann et al. (2008) using advection modelling also found a positive relation between the retention of egg and larvae in the deep spawning basins and recruitment, while pronounced transport to coastal areas is detrimental for year-class strength (Baumann et al. 2008; Voss et al. 2012).

Nissling (2004) showed experimentally that sprat viable hatch (i.e. number of larvae with normal swimming functions) was constant in the range 5-13 ºC, but it was lower at temperature between 1-4 ºC, with a considerably decrease between 4 and 3 ºC. Larval size at hatching was also lower at lower temperatures. Larval survival and size at yolk sac completion were lower at 5 ºC than at 7-13 ºC. These experimental findings confirm experimentally the sprat nature of a warm water species (Nissling, 2004). Experimental work by Petereit et al. (2008) showed a relation between egg development and hatching. No hatching was observed above 14.7ºC and hatching success was significantly reduced below 3.4 ºC. Larval yolk sac phase was shortened from 20 to 10 days at 3.8 and 10ºC respectively (Petereit et al. 2008).

Egg production is mostly related to spawning biomass, however, temperature and adult size prior spawning (autumn/winter) play also a role (Köster et al. 2003). Temperature may affect egg production either via regulating spawner feeding condition, batch fecundity as well as batch number, or the onset of spawning (Köster et al. 2003).

A positive effect of temperature have been also suggested for adult Baltic sprat condition. Higher temperature can directly affect the physiology of sprat and favour the main planktonic prey species for sprat with a positive effect on its condition. However, density-dependence competition for prey seems to be the key factor driving Baltic sprat condition (Cardinale et al. 2022; Casini et al. 2011).

Table 6.28.2. Climate change processes and responses, key conclusions

Baltic Sea sprat		
Process	Response to climate change	Reference
Mortality	Higher temperatures favor egg and larval survival as well as the productivity of zooplankton prey of sprat larvae. In the northern spawning areas salinity increases the buoyancy of the eggs and thus enhances the survival of eggs which do not sink to low-oxygen deep layers	Kalejs and Ojaveer, 1989; Köster et al. 2003; Nissling et al. 2003; Baumann et al. 2006; Nissling et al. 2003: Nissling, 2004; Voss et al. 2012
Maturation	Higher temperature anticipates gonadal maturation	Köster et al. 2003
Growth/Condition	Larval yolk sac phase is shortened, and larval size at yolk sac completion is higher, at higher temperature. Adult condition is positively correlated to temperature.	Cardinale et al. 2002; Nissling, 2004; Petereit et al. 2008; Casini et al. 2011
Recruitment	There is a positive relation between temperature in spring and summer and recruitment at age 0 the same year and at age 1 next year.	MacKenzie and Köster, 2004; Baumann et al. 2006; Margoński et al. 2010

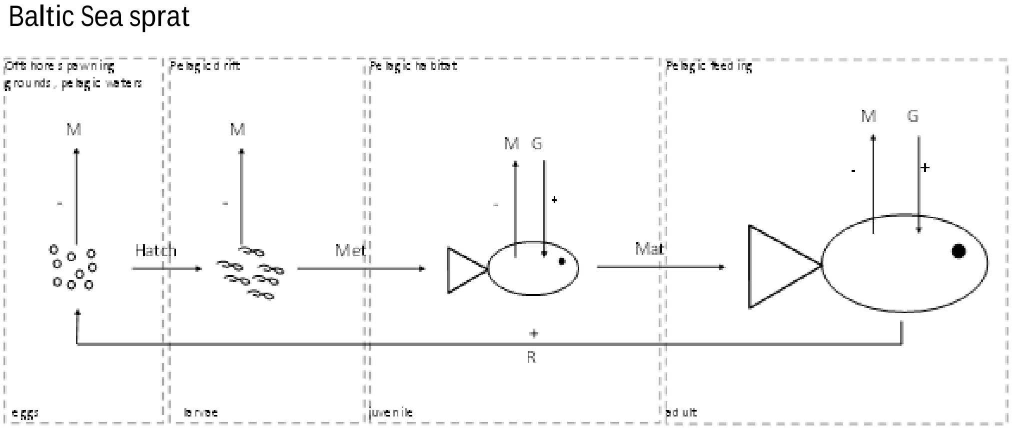

Figure 6.28.2. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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6.29. Starry ray (*Amblyraja radiata*)

The starry ray (*Amblyraja radiata*) is widely distributed throughout the North Atlantic. Based on genetics, the species may be divided into three major clusters represented by the NW Atlantic, Greenland and the NE Atlantic, including the North Sea (Chevolot et al. 2007, Lynghammar et al. 2016).

It is arguably the most abundant skate species in the North Sea, and mainly distributed in the central and northern parts. The population was increasing from the early 1970’s to the 1990’s, representing ~90% of the total skate biomass (Skjæraasen and Bergstad 2000). From 2000 and onwards the NE Atlantic population has been decreasing (ICES 2021a, b). There has not been a directed fishery for starry ray in the North Sea, and since 2015, it falls under the EU regulation for prohibited species (Art. 20 of Council Regulation (EU) 2021/92). Large numbers are however still by-caught and discarded in demersal trawl fisheries.

It is a benthic, largely resident species, inhabiting sandy and muddy bottoms. Although it can be found in shallow waters in the southern North Sea and the Kattegat it prefers cool, deeper waters and both juveniles and adults are mainly found in 60 – 300 m depth. It is an opportunistic feeder, juveniles (< 40 cm) feeding mainly on polychaetes and amphipods, whereas adults feed on decapods and fish. The proportion of fish in the diet increase with size (Skjæraasen and Bergstad 2000, Packer et al. 2003). Tagging experiments in the North Sea and in the western Atlantic suggest that migration is limited and with few exceptions, individual rays moved less than 60 Nm from where they were caught (Walker et al. 1997, Kneebone et al. 2020).

The starry ray is a relatively early maturing species for a chondrocyte, females and males attaining sexually maturity at 5-6 years of age and lengths around 40 – 50 cm (Walker 1998, Skjæraasen and Bergstad 2000, McCully et al. 2012). It is reproductively active year round, producing 20-40 eggs per female each year (Walker 1998, Parent et al 2008). Development time in oviparous elasmobranchs is correlated to water temperature (Wheeler et al. 2020) and for starry ray incubation times from 1.1 to 2.5 years (Berestovskii 1994, Parent et al. 2008).

Halibut and Greenland shark have been reported to prey on eggs of starry ray but also gastropods are believed to impose mortality. Cox et al. (1999) estimated that between 4 and 18% of egg capsules had been predated by predatory gastropods suggesting that egg predation may be a major factor influencing the abundance of skate populations.

Modelling exercise show that distribution and abundance of starry ray in the North Sea is closely associated with lower sea surface temperatures (SST), deeper waters and soft bottom substrates. Warming due to climate change will likely result in a contracted distributional range, shifting northwards and or/ into deeper areas, and may be part of the explanation for the decreasing trend in recent years (Sguotti et al. 2016). Starry ray in the northwestern Atlantic is considered a climate-sensitive species for similar reasons. However, the impact of climate change on the population level is confounded by fishing effects, which adds complexity to the situation (Hare et al 2016).

Table 6.29. Climate change processes and responses, key conclusions

Starry ray		
Process	Response to climate change	Reference
Mortality	Higher temperatures lead to faster development and shorter incubation time, shortening the period when the egg is exposed to predation and possibly reducing egg mortality.	Wheeler et al 2020
Growth	Experimental warming has been shown to enhance metabolism, feeding, and digestion in various species. A rise in temperature could potentially have a positive impact on growth and condition. However, the outcome remains uncertain as increased energetic requirements might also impede growth.	Santos et al 2021
Maturation	Increased growth and condition can lead to earlier maturation, but potentially also to less fecund females if the advanced maturation results in smaller individuals, as the number of offspring produced tends to correlate with size.	Santos et al 2021, Hume 2019
Recruitment	Effect of warming on hatching and neonate survival may have positive impact on recruitment output	Wheeler et al 2020, Santos et al 2021.

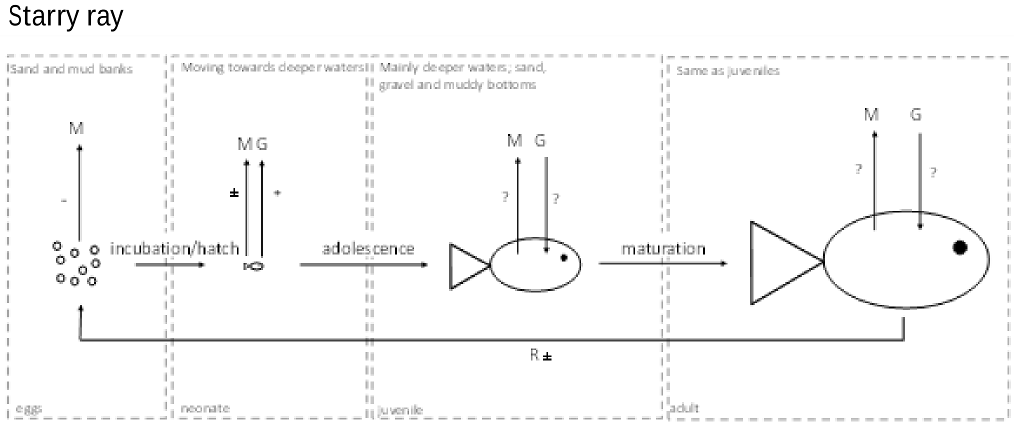

Figure 6.29. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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6.30. Thornback ray (*Raja clavata*)

The thornback ray (*Raja clavata*) is distributed throughout the Northeast Atlantic with distinct regional groups in the Mediterranean basin and Black Sea, the Azores and in the European continental shelf, including the Skagerrak and Kattegat (Chevolot et al. 2006a). Tagging studies have suggested limited migration rates within the North Sea (Walker et al. 1997, Hunter at al. 2005), but relatively high levels of gene flow between the North Sea, English Channel and Irish Sea indicate that long distance movements take place (Chevolot et al. 2006b).

Before the 1950's, thornback ray was common throughout the North Sea, but the range and abundance have decreased over the past century, with the stock concentrated in the southwestern North Sea where it is the main commercial skate species. Since 2009, survey catches have increased in the southern North Sea and the English Channel but the status of thornback ray in the central/northern North Sea is still uncertain (ICES 2021). The species occurs year-round in Swedish water, albeit in low numbers. In the Skagerrak and Kattegat, it is protected under both the EU regulation for prohibited species (Art. 20 of Council Regulation (EU) 2021/92) and national regulations (FIFS 2004:36).

The thornback ray is a medium sized, sexually dimorphic species, females attaining a larger size (L_{max} 120 cm) than males (100 cm). Thornback rays mature between 9 and 12 years of age and at lengths around 77 cm and 66 cm for females and males, respectively (Walker 1998, McCully et al. 2012). At this stage, adults show seasonal movements, from deeper waters (10-30 m) in winter, to shallower waters (<10 m) in spring to mate and spawn (Walker et al. 1997, Hunter 2005). Egg capsules are deposited on the seabed, and hatch after 4-5 months depending on the temperature (Ellis and Shackley 1995). As for other oviparous species, developmental time is correlated to temperature and earlier hatching can be expected under warming environment (Wheeler et al. 2020). In *Raja microocellata*, a related species, a 2-4 C increase during incubation resulted in significantly faster development and smaller size at hatching, suggesting that climate change can lead to an increased reproductive rate in oviparous species (Hume 2019).

Modelling exercise show that distribution and abundance of thornback ray in the North Sea is closely associated with higher sea surface temperatures (SST), shallow waters (5-40 m) and coarser (sand, gravel), or mixed bottom substrates (Sguotti et al. 2016). Warming due to climate change may support an expansion of the present distribution area, but it is doubtful if the historic range can be re-occupied unless current levels of fishing induced mortality is reduced.

Table 6.30. Climate change processes and responses, key conclusions

Thornback ray		
Process	Response to climate change	Reference
Mortality	Higher temperatures lead to faster development and shorter incubation time, shortening the period when the egg is exposed to predation and possibly reducing egg mortality.	Wheeler et al 2020
Growth	Experimental warming has been shown to enhance metabolism, feeding, and digestion in various species. A rise in temperature could potentially have a positive impact on growth and condition. However, the outcome remains uncertain as increased energetic requirements might also impede growth.	Santos et al 2021
Maturation	Increased growth and condition can lead to earlier maturation, but potentially also to less fecund females if the advanced maturation results in smaller individuals, as the number of offspring produced tends to correlate with size.	Santos et al 2021, Hume 2019
Recruitment	Effect of warming on hatching and neonate survival may have positive impact on recruitment output	Wheeler et al 2020, Santos et al 2021.

Thornback ray

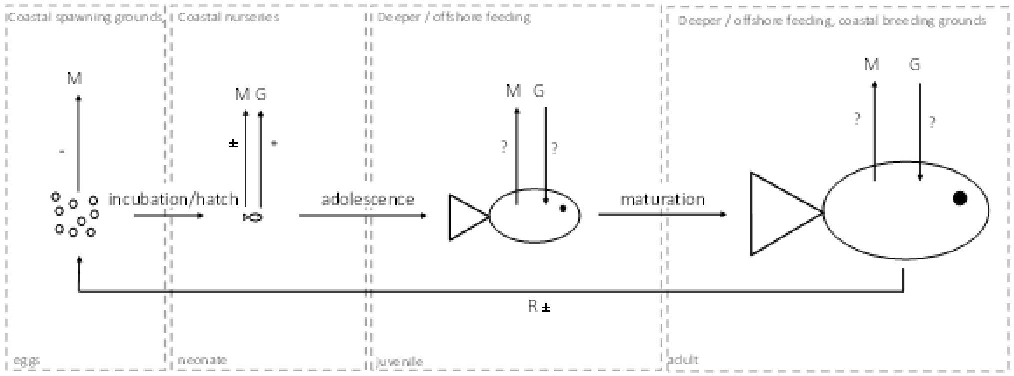

Figure 6.30. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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6.31. Turbot (*Scophthalmus maximus*)

Turbot, *Scophthalmus maximus L.*, is a large left eyed marine flatfish of the family Scophthalmidae, Order Pleuronectiformes, which lives in the Northeast Atlantic Ocean (from Morocco to the Arctic Circle) and in the Mediterranean Sea as well as in the Black Sea (Froese & Pauly, 2016). The species is found primarily close to shore in sandy shallow waters.

ICES (https://www.ices.dk/) identifies at least four stocks in the Atlantic: The North Sea, the Skagerrak/Kattegat, the Baltic Sea, and the Iberian Peninsula-Bay of Biscay stock. Florin and Höglund (2007) found low genetic differentiation and no evidence of isolation by distance in the Baltic Sea and Kattegat. In contrast, Nielsen et al. (2004) reported a sharp cline in genetic differentiation going from the low saline Baltic Sea to the high saline North Sea. The data were explained best by two divergent populations connected by a hybrid zone (Nielsen et al., 2004). The low genetic differentiation between the Atlantic subpopulations indicates relatively high gene flow (do Prado et al. 2018). The North Sea stock has the highest abundance and represents the center of global abundance for this species (Cardinale et al., 2021). On the other hand, the biomass in the Kattegat-Skagerrak stock has declined by about 86% since 1920s and the northern component of the Kattegat-Skagerrak stock population has virtually vanished (Cardinale et al., 2009).

Turbot experiences a diverse physical and biological environment across its range. The Atlantic Ocean has a subtle salinity gradient running roughly from north to south, while sharp differences are found between the Northern Atlantic Ocean (approx. 35 PSU—practical salinity units) and the Baltic Sea (up to 2 PSU in the northern area). In the Mediterranean Sea, the salinity is even higher than in the Atlantic Ocean (approx. 38 PSU) but drops abruptly in the transition to the Black Sea, where salinity levels resemble the Baltic Sea (approx. 11 PSU). Contrasting patterns of surface temperature also occur across latitude and between seasons. A north–south cline exists in the Atlantic area (annual average from 7°C in Norway up to 16°C off the Spanish coast), which increases further in the transition to the Mediterranean Sea (approx. 21°C), especially during summer.

Temperature is one of the most important factors influencing the growth rate of turbot. The typical dome-shaped effect of temperature on the growth rate of this species has been well documented in laboratory experiments (e.g., Burel et al., 1996, Imsland et al., 2000, Imsland et al., 2007). Maximum growth rates span across a wide range of temperatures, documented between 18 and 22°C for juveniles from different locations of the Northeast Atlantic, as a result of geographical adaptation (Imsland and Jonassen 2001). The optimal temperature for growth and feed conversion has been found to decrease with size (Imsland et al., 1996). Experiments in hatcheries have shown that the optimal temperature for growth is predicted to decline with increasing body weight, 22.5, 20.8, 19.1 and

17.5°C for 1, 10, 100 and 1000 g fish, respectively (Árnason et al., 2009). However, adults show a higher thermal tolerance as the growth response to temperature is more pronounced in juveniles than adults (Imsland and Jonassen 2001).

Optimum conditions for juvenile turbot survival were observed to be between 12 and 18°C with salinities between 20 and 35 PSU for North Sea turbot. This contrasted with corresponding data for turbot from the southern Baltic proper, according to which survival sharply decreased in temperatures below 14 °C and was high in salinities of 10 to 15 PSU (Karås and Klingsheim 1997).

ICES does not identify any key ecosystem drivers that has a significant impact on the dynamic of turbot in the North Sea and Kattegat-Skagerrak (ICES 2020).

Table 6.31. Climate change processes and responses, key conclusions

Turbot		
Process	Response to climate change	Reference
Mortality	Warming will decrease survival of juveniles in the North Sea and increase in the Baltic Sea. Decline in salinity would negatively affects turbot in the Baltic Sea	Karås and Klingsheim 1997
Growth	Warming has shown to have positive effects on the growth of younger fish and negative effect on growth of adults (correlation with temperature in tank experiments)	Burel et al., 1996, Imsland et al., 2000, Imsland et al., 2007, Árnason et al. 2009

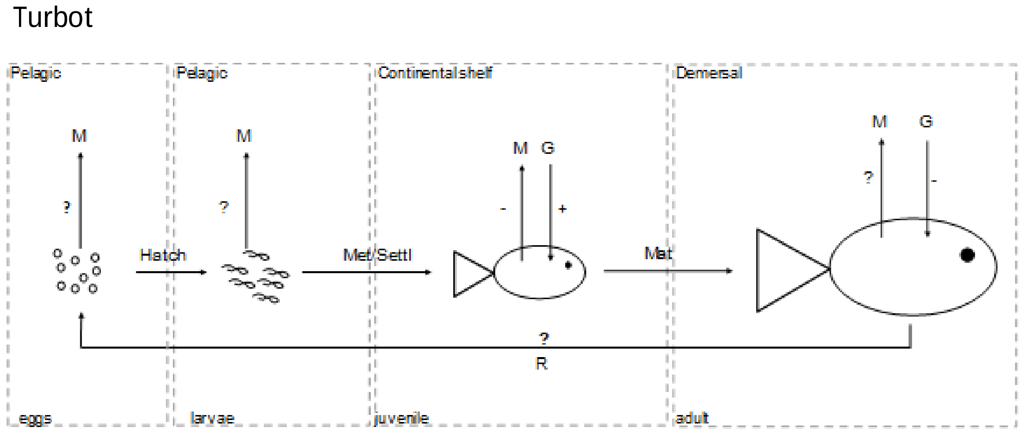

Figure 6.31. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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6.32. Whiting (*Merlangius merlangius*)

Whiting (*Merlangius merlangius*) are one of the most common species in demersal fish communities and their eggs and larvae are among the dominant species recorded from plankton hauls (Hislop, 1996). Whiting is widely distributed throughout north-eastern Atlantic coastal waters, extending from the southeastern Barents Sea to Iceland and Portugal, and occurring also in the Mediterranean and Black Sea (Greenstreet and Hall, 1996).

Whiting has a longer pelagic phase than most other common gadoids in the North Sea thus spending a longer time in a relatively less stable environment. At around 2 years of age, most whiting are mature and able to spawn (Hislop, 1996).

There are few direct studies of the expected response of whiting to an increase in water temperature, due to global warming. Dulvy et al. (2008) classified North Sea whiting as a species with cold thermal preference. From the analysis of survey data they found that whiting has marginally but significantly deepen its distribution between the early 1980s and mid-2000s possibly as a consequence of increasing surface water temperature. On the other hand, Kerby et al. (2012) did not find any evidence of a shift in distribution of whiting related to climate change.

There are also a few studies that points to the fact that whiting would be favoured by an increase in water temperature. Cook and Heat (2005) looked at the relationship between temperature, recruitment and spawning stock biomass and found a positive effect on saithe (*Pollachius virens*) and whiting compared to cod (*Gadus morhua*), plaice (*Pleuronectes platessa*) and sole (*Solea solea*). In addition, Serpetti et al. (2017) simulated potential North Sea food web effects under different temperature regimes and found that the whiting would be favoured by an increase in temperature. However, mostly because this increase in temperature would cause the decline of whiting's main predators, seals and cod, and not due to the increase in temperature *per se*.

Table 6.32. Climate change processes and responses, key conclusions

Whiting		
Process	Response to climate change	Reference
Recruitment	Increasing temperature showed a positive effect on the SSB-Recruitment relationship	Cook and Heat 2005
Mortality	Decrease in predation mortality due to a potential decrease in main predators' density (i.e., cod and seal)	Serpetti et al 2017

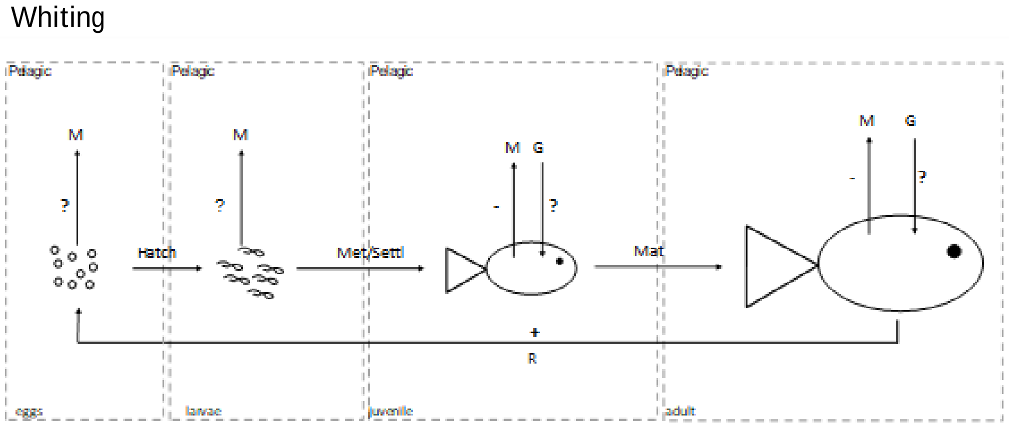

Figure 6.32. Schematic of expected impact of warming on main life stages and processes. The elements included are hatching (Hatch), metamorphosis (Met), maturity (Mat), natural mortality (M), growth (G) and recruitment (R). A plus sign (+) refers to an expected increase in the rate of the process as a consequence of climate change, a minus sign (-) to an expected decrease, (~) to no expected change, (±) to contrasting effects with uncertain net effect, and (?) to an unknown effect.

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