

**The effects of climate induced temperature changes
on cod (*Gadus morhua* L.): Linking ecological and
physiological investigations**

**Die Effekte klimabedingter Temperaturveränderungen
auf den Kabeljau (*Gadus morhua* L.): Eine Verknüpfung
von ökologischen und physiologischen Untersuchungen**

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Zusammenfassung

Der Kabeljau (*Gadus morhua* L.) gehörte während der letzten 500 Jahre zu den wichtigsten Fischarten der nordatlantischen Fischerei. Innerhalb der letzten 10 Jahre ist jedoch ein Großteil der Kabeljaubestände zusammengebrochen. Überfischung mag hierbei der wichtigste Grund für den Rückgang der Bestände sein, aber es wird immer offensichtlicher, dass Klimaveränderungen ebenfalls einen bedeutenden Einfluss auf die Kabeljaubestände ausüben, da sich Temperatur maßgeblich auf die Fruchtbarkeit, die Rekrutierung und auch das Wachstum der Fische auswirkt. Obwohl der Einfluss von Temperatur auf die Ökologie des Kabeljaus bereits seit vielen Jahren untersucht wird, ist noch kein mechanistisches Prinzip von Ursache und Wirkung beschrieben worden.

Das Ziel dieser Arbeit war es, Untersuchungen im Feld und ökologische Experimente mit physiologischen Methoden zu kombinieren, um ein mechanistisches Verständnis dafür zu gewinnen, wie sich klimabedingte Temperaturveränderungen auf den Kabeljau auswirken. Die ökologischen Ansätze konzentrierten sich auf das Wachstum und die Fruchtbarkeit von Individuen aus unterschiedlichen klimatischen Regionen, während sich die physiologischen Untersuchungen sowohl mit Sauerstoffverbrauchsmessungen ganzer Tiere als auch mit dem Stoffwechsel von Mitochondrien beschäftigten. Es wurde Kabeljau aus der südlichen Nordsee, der Ostsee, von der norwegischen Küste, aus der nordöstlichen Arktis und aus dem Weißen Meer untersucht.

Um die Auswirkungen des Temperaturregimes auf das Wachstum des Kabeljaus in der Natur zu ermitteln, wurden Jahresringe von Otolithen aus der südlichen Nordsee, der Ostsee und dem Weißen Meer zur Altersbestimmung von Individuen gelesen. Die gewonnenen Ergebnisse wurden durch Literaturdaten ergänzt und dienten der Berechnung der von Bertalanffy-Wachstums-Raten. Es zeigten sich Unterschiede in der Lebensgeschichte der Tiere: Im Allgemeinen wächst kalt adaptierter Kabeljau langsamer, erreicht dafür allerdings aufgrund seiner höheren Lebenserwartung größere Maxima hinsichtlich Länge und Gewicht. Die Wachstumsparameter des Weißmeer-Kabeljaus unterschieden sich dabei erheblich von denen anderer Populationen.

Diese Population zeigte neben dem geringsten Wachstumsfaktor (k) auch den kleinsten L_{∞} -Wert. Die Werte der Wachstumsbilanz berechnet nach Pauly (1979) waren bei Kabeljau aus warmen Regionen am höchsten.

Um mögliche Effekte auf das Wachstum verschiedener Kabeljau-Populationen durch unterschiedliche Futterverfügbarkeit im Freiland auszuschließen und die optimale Wachstumstemperatur abschätzen zu können, wurden Individuen aus der südlichen Nordsee bei unterschiedlichen Temperaturen gehältert und im Überfluss gefüttert. Die so gewonnenen Daten wurden mit extern durchgeführten Wachstumsstudien an Kabeljau der norwegischen Küste und Exemplaren aus der nordöstlichen Arktis verglichen. Trotz Hälterung über einen Zeitraum von mehreren Monaten wuchsen die Individuen aus der südlichen Nordsee signifikant schneller als Exemplare der norwegischen Küste und der nordöstlichen Arktis. Diese Ergebnisse entsprechen Feldbeobachtungen und deuten auf einen genetischen Unterschied hinsichtlich des Wachstums zwischen den drei Populationen hin, der auch durch Laborakklimation oder Feldakklimatisation nicht überwunden werden kann. Trotz der gezeigten Unterschiede in der spezifischen Wachstumsbilanz wurden die höchsten Wachstumsraten bei allen drei Kabeljau-Populationen in einem Temperaturspektrum von 10 - 11°C festgestellt. Daraus lässt sich schließen, dass dies die optimale Temperatur für das Wachstum des Kabeljaus ist.

Die aus den Wachstumsversuchen ermittelten Modellgleichungen ermöglichten die Entwicklung einer Simulation für das Wachstum des Kabeljaus aus unterschiedlichen klimatischen Regionen in Hinblick auf eine mögliche globale Erwärmung. Im Falle einer erhöhten Umgebungstemperatur würde der südliche Kabeljaubestand seine Verbreitungsgrenze aus der südlichen Nordsee nordwärts verlagern. Das Wachstum des nordost-arktischen Kabeljaus würde positiv beeinflusst und die Verbreitung dieser Population sich nach Norden ausweiten.

Die Fruchtbarkeit verschiedener Individuen aus unterschiedlichen Breiten wurde anhand der Zählung von Eizellen und durch Literaturdaten bestimmt. Tiere aus hohen Breiten wiesen niedrige Fruchtbarkeit sowie geringe Wachstumsraten auf. Daraus lässt sich eine temperaturbedingte Umstellung im Energiebudget schließen, die der Fruchtbarkeit und dem Wachstum in kälteren Zonen abträglich ist. Um eine vermutete Stoffwechselanpassung des Kabeljaus an die

Kälte zu untersuchen, wurden Sauerstoffverbrauchswerte von ganzen Tiere aus der Nordsee, dem Weißen Meer und der nordöstlichen Arktis gemessen. Ein kompensatorischer Anstieg der Standardstoffwechselrate trat bei Kabeljaupopulationen auf, die in der Kälte leben. Diese Kältekompensation steht im Einklang mit der geringeren Wachstumsleistung und der geringeren Fruchtbarkeit von Tieren aus hohen Breiten.

Es stellt sich nun die Frage, welche energiezehrenden Prozesse in der Kälte hervortreten. Neben Anpassungen der Enzymkapazitäten, Veränderungen des Membranaufbaus und weiteren physiologischen Prozessen spielt die mitochondriale Kapazität bei der Temperaturanpassung eine wichtige Rolle. Daher wurden in dieser Arbeit thermische Sensitivitäten der mitochondrialen Atmung und Protonenleckströme in isolierten Lebermitochondrien von Kabeljau der südlichen Nordsee und der Barents-See miteinander verglichen. Die aeroben Kapazitäten der ATP-Gewinnung und die Protonenleckverluste der Lebermitochondrien des nordöstlichen Arktis-Kabeljaus waren generell bedeutend höher als beim Nordsee-Kabeljau. Diese temperaturbedingte Erhöhung deutet ebenso auf eine Kälteadaptation hin wie der erhöhte Sauerstoffverbrauch bei ganzen Tieren. Kaltadaptierte Individuen kompensieren erhöhte Mitochondrienkapazitäten jedoch nicht mit wechselnder Lebergröße oder mitochondrialem Proteingehalt. Auf diese Weise reflektieren kalt adaptierte Lebermitochondrien und erhöhte Protonenleckströme die erhöhten Stoffwechselkosten, die im Einklang mit der Reduzierung der Wachstumsleistung und der Fruchtbarkeit stehen. Im Gegensatz dazu spiegelt sich Kälteakklimation nicht generell in den funktionellen Eigenschaften der Lebermitochondrien des Kabeljaus wider. Steigende Temperaturen können unter Umständen den Wirkungsgrad der ATP-Gewinnung herabsetzen; dennoch ist zu beobachten, dass Mitochondrien der Leber bei höheren Temperaturen intakt bleiben, als sie der Kabeljau in seinem Lebensraum erfährt. Protonenleckströme der Mitochondrien sind bei kaltadaptierten Individuen erhöht. Dies trägt zu einem erhöhten Sauerstoffbedarf bei nordostarktischem Kabeljau bei und könnte die niedrigeren kritischen Temperaturen erklären.

Mitochondrialer Sauerstoff- und Substratbedarf spielen sehr wahrscheinlich eine Rolle bei der Energieverfügbarkeit hinsichtlich Wachstum und

Zusammenfassung

Reproduktion, aber legen auch die thermischen Toleranzbereiche fest, welche durch den Grad der permanenten Kälteanpassung definiert werden.

Summary

Cod (*Gadus morhua* L.) has been one of the most important species for the North Atlantic fisheries for more than 500 years. Over the last decade a number of North Atlantic cod stocks have collapsed. The high fishing pressure may be the most important reason for the collapse of stocks but it becomes more and more obvious that climate changes are also responsible for changes in cod stock size, as temperature influences fecundity, recruitment, and growth. Although the influence of temperature on the ecology of cod has been studied for many years, a mechanistic cause-and-effect-relationship has not been established yet.

The aim of this thesis was to combine field data analyses and ecological experiments with physiological investigations for a mechanistic understanding of the effects of climate change on cod. The ecological approaches focussed on growth and fecundity of specimens from different climatic regions, while the physiological investigations were dealing with respiration measurements of whole animals as well as mitochondrial properties. Investigations were carried out with cod from the Southern North Sea, the Baltic Sea, the Norwegian coast, the North East Arctic, and the White Sea.

To estimate the effects of the climatic regime on growth of cod in nature, yearly rings on otoliths were read for age determination, taken from specimens from the Southern North Sea, the Baltic Sea and the White Sea. Data gained by reading otoliths and obtained from literature were used to calculate the Bertalanffy growth parameters. The observed parameters reflected differences in life histories: in general, cod found at colder temperatures grew more slowly but reached greater maxima in length and mass due to a longer lifespan. The growth parameters of White Sea cod differed considerably from that of the other populations. This population displayed a small growth factor (k) and the smallest L_{∞} - value as well. Nonetheless, values of growth performance according to Pauly (1979) were still highest for cod living in warm waters.

To exclude possible effects of variable food availability on growth of different cod populations and to estimate the optimum temperature for growth, Southern North Sea cod were reared at different temperatures and fed in excess. These data were compared to external growth studies on Norwegian coastal cod and

specimens from the North East Arctic region. Despite long term maintenance at different temperatures, growth in the experimental study was significantly higher in Southern North Sea individuals, followed by lower growth rates in cod from the Norwegian coast and the North East Arctic, respectively. These results coincide with field observations and strongly suggest a genetic difference between these populations that cannot be overcome by lab acclimation or field acclimatization processes. Despite different specific growth performances seen in the present experiments, the highest growth rates in all three cod populations were measured in a temperature range from 10 - 11°C and concluded to be the optimum temperature for growth of cod. Intraspecific differences in thermal optimum do not occur among cod within the same size-range and with unlimited food.

The model - equation obtained in the growth experiments facilitated the development of a simulation for growth of cod from different climatic regions in relation to global warming. During a temperature rise due to global warming, cod living at its southern distribution would shift further North and disappear from the Southern North Sea. Growth of North East Arctic cod would be positively affected, and the distribution of this population would extend northward as well.

Fecundity of cod from different climatic regimes was determined on the basis of oocyte-countings and added literature data. The ecological findings suggest that decreasing fecundity coincides with decreasing growth at higher latitudes. This indicates a change in energy budget unfavourable for fecundity and growth in the cold.

To investigate the putative role of the degree of metabolic cold adaptation in cod, oxygen consumption rates of whole animals were measured in individuals from the North Sea, the White Sea and the North East Arctic maintained at different temperatures. A compensatory rise in standard metabolic rate occurred in cod populations living in colder waters. This cold compensation strongly coincided with lower growth performance and reduced fecundity, as confirmed by field investigations for animals from higher latitudes. Lowest growth performance was found for White Sea cod which relate to high levels of standard metabolic rate.

The question arose which energy consuming processes are elevated in the cold.

Next to adjustments in enzyme capacities, alterations in membrane composition, and other physiological processes, regulation of mitochondrial performance is thought to play an important role in temperature adaptation. Therefore thermal sensitivities of mitochondrial respiration and proton leakage rates were compared in isolated liver mitochondria from Southern North Sea cod and North East Arctic cod acclimated to different temperatures. Aerobic capacities of ATP-formation and proton leakage rates of liver mitochondria from North East Arctic cod were significantly higher than in liver mitochondria from North Sea cod. These temperature-related increments indicated cold adaptation in similar ways as the increased oxygen consumption rates of whole animals. However, cold-adapted cod did not compensate for elevated mitochondrial capacities by changing liver size or mitochondrial protein content. Thus, cold-compensated liver mitochondria and elevated proton leakage reflect enhanced costs, in parallel to the reduction in growth performance and fecundity observed in Northern populations in field and experimental studies. In contrast, cold-acclimation within one population is not generally reflected in liver mitochondria of cod. Mitochondrial oxygen demand may also play a role in thermal tolerance of cod. Rising temperature may reduce the efficiency of ATP-formation. However, cod liver mitochondria maintain function at higher temperatures than cod experience in their environment. Proton leakage rates are higher in cold-adapted cod than in specimens living in the warm. This contributes to an elevated oxygen demand for North East Arctic cod and may lead to a lower critical temperature of this population.

Mitochondrial oxygen and substrate demand likely plays a role in energy availability for growth and reproduction but also in the setting of oxygen dependent thermal tolerance windows defined by the level of permanent cold adaptation.

1 Introduction

Cod (*Gadus morhua* L.) has been one of the most important species for the North Atlantic fisheries for more than 500 years (e.g. Cushing 1986). The total catch of cod rose from the beginning of the 20th century, peaked with 3.9 million tons in 1968 and has declined steadily since then (Brander 1996). In the last decade, a number of North-West Atlantic cod stocks have collapsed (Hutchings & Myers 1994b, Myers et al. 1996). The North Sea cod stock for example, has been below the conventional 'minimum biologically acceptable level' (ICES 1991) of 150 000 t since 1984 (ICES 1997). The high fishing pressure may be the most important reason for the collapse of stocks, but it becomes more and more obvious that climate change is also responsible for changes in cod stock size as temperature regime influences fecundity, recruitment and growth (e.g. Nakken 1994, Brander 1996, O'Brien et al. 2000). Different studies on the impact of climate change and climate variability on invertebrate and fish stocks exist for the Northwest Atlantic (e.g. Frank et al. 1990) and for the west coast of North and South America where the influence of the 1982/1983 El Niño event on marine communities has been investigated intensively (e.g. Avario & Muñoz 1987, Arntz & Tarazona 1990, Lubencho et al. 1993, Peterson et al. 1993). Beside the effects of interannual climate variability, the impact of decadal-scale climate variation on marine communities and populations has been well documented (Cushing 1982, Beamish 1995, Bakun 1996). Recently, Parsons & Lear (2001) reviewed the effects of climate changes on marine ecosystems resulting from changes in the North Atlantic Oscillation (NAO). They reported that changes in the pattern of the NAO have differential impacts on cod varying from region to region: in contrast to North Sea cod, North East Arctic cod exhibits strong recruitment and rapid growth during warm years, which are associated with a positive NAO index.

Although the influence of climate variability and temperature on the ecology of cod (*Gadus morhua*) has been studied for many years, a mechanistic cause and effect relationship has not yet been established.

Brander (1995) examined 17 North Atlantic cod stocks and found out that cod from higher latitudes exhibits lower growth rates. He attributed most of the observed variability in growth to temperature. Brander (1995) pointed out that

more attention should be paid to quantifying the effects of temperature on growth of cod, because it probably has significant effects on stock assessment, catch forecasting and evaluation of the consequences of climate change.

Energy allocation to growth and reproduction is only possible after the requirements for physiological maintenance have been met (Wieser 1994). The question arises which metabolic regulatory processes are elevated in the cold and may lead to decreased energy availability to growth and reproduction (Pörtner et al. 2001). When comparing populations along a latitudinal cline the discussion of metabolic cold adaptation (MCA) plays an important role. MCA can either be observed as a rise in temperature specific metabolism in aquatic ectotherms of temperate zones during winter (e.g. in *Zoarces viviparus*, van Dijk et al. 1999) seen as seasonal acclimatization or as a general rise of metabolism in cold adapted animals in comparison to individuals living in temperate zones (e.g. in the polychaete *Arenicola marina*, Sommer & Pörtner 1999). If a compensatory rise in standard metabolic rate of aquatic animals living in the cold occurs, the question will arise which cellular mechanisms and trade-offs are involved.

Next to adjustments in enzyme capacities (Dahlhoff & Somero 1993, Foster et al. 1993b) and alterations in membrane composition (Prosser 1991, Miranda & Hazel 1996) the regulation of mitochondrial performance is thought to play an important role in defining metabolic demand during temperature adaptation (Pörtner et al. 1998). In contrast to Antarctic species, cold-adapted species of the Arctic displayed a rise in mitochondrial aerobic capacity (Sommer & Pörtner 2002). Elevated aerobic capacities of mitochondria of the cold adapted polychaete *Nereis pelagica* and the bivalve *Arctica islandica* (Tschischka et al. 2000) are indications for cold compensation. To meet energy demands and maintain function in the cold an increase in mitochondrial density (proliferation) was observed in fish (e.g. Guderley & Blier 1988, Archer & Johnston 1991) and also in invertebrates (e.g. Sommer & Pörtner 1999). Species in the Antarctic developed functional properties of permanent cod adaptation over millions of years (Pörtner 2002). To reduce the viscosity of blood, most Antarctic fish hold only low numbers or are completely devoid of red blood cells (Egginton 1997, Davissson et al. 1997). Higher levels of lipid and mitochondrial numbers in Antarctic fish result in improved oxygen diffusion and shorter cytosolic

diffusion distances (Sidell 1991, 1998). Proliferation may lead to a rise in oxygen demand, owing to an elevated proton leakage with any mitochondria present. Proton leakage is defined as the passive influx of protons through the inner mitochondrial membrane which is driven by the proton gradient set up during respiration (Brand 1990, Pörtner et al. 1998). Consequently a baseline mitochondrial oxygen demand without concomitant ATP-production can be observed (Fig. 1).

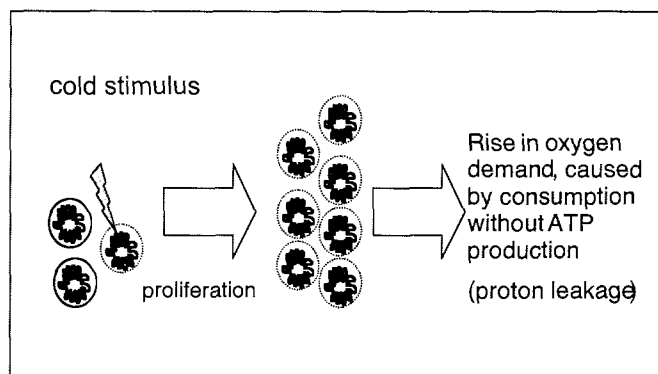


Fig. 1: Schematic overview of mitochondrial compensation at low temperatures.

More than 25% of cellular oxygen uptake at rest may be attributed to mitochondrial proton leakage (e.g. Brookes et al. 1998). As a trade-off mitochondrial proliferation in the cold may reduce the energy available to growth and reproduction owing to elevated costs of mitochondrial maintenance. Furthermore, the increase in mitochondrial density may cause a rise in oxygen demand which becomes detrimental during warming when it cannot be covered by oxygen uptake through ventilation and circulation any longer (see Pörtner et al. 2001).

The aim of this thesis is to combine field data analysis and ecological experiments focussing on growth and fecundity of specimens from different climatic regions (Southern North Sea, Baltic Sea, Norwegian coast, North East Arctic and White Sea), with physiological experiments aiming for a better mechanistic understanding of the effects of climate change on cod (Fig. 2).

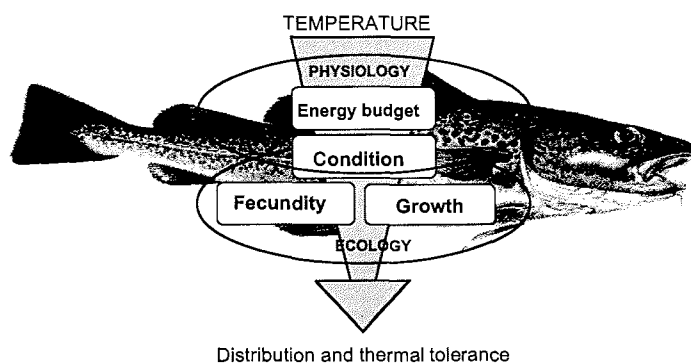


Fig. 2: Overview of the different aspects of this thesis. The combination of ecological and physiological studies should help to explain the effects of temperature on the distribution and thermal tolerance of *Gadus morhua*.

To sum up, in this thesis the following questions regarding the effects of climate change on the ecology and physiology on *Gadus morhua* in a latitudinal cline are addressed:

1. How does temperature affect growth and fecundity of cod from different populations? Are differences in growth of cod just based on different life histories? Or can a clear relation between environmental temperature and productivity of cod be determined?
2. Does the optimum temperature for growth differ between cod populations and what will happen with growth of cod during climate change?
3. Does cold adaptation and acclimation lead to a change in the standard metabolic rate of *Gadus morhua*?
4. Can studies of the thermal sensitivities of maximum respiration and proton leakage in isolated liver mitochondria from cod be used to explain, firstly why energy for growth and fecundity may become limiting in the cold and secondly, which mechanisms are involved in setting the thermal tolerance limits of different cod populations?

To estimate the effects of the temperature regime on growth of cod in nature, yearly rings on otoliths were read for age determination, taken from specimens from the Southern North Sea, the Baltic Sea and the White Sea. Southern North Sea cod were reared at different temperatures to exclude the possible effects of variable food availability on growth of different cod populations and to estimate the optimum temperature for growth. Based on the analysis of optimum temperature a simulation was created to examine the growth of cod in nature under a scenario of global warming. To investigate a putative role of MCA in *Gadus morhua*, standard metabolic rates of whole animals were determined in cod from the North Sea, the White Sea and the North East Arctic acclimated at different temperatures. Additionally, thermal sensitivities of mitochondrial respiration were compared in isolated liver mitochondria from North Sea cod and Norwegian coastal cod acclimated to different temperatures.

2 Biology of North East Atlantic cod (*Gadus morhua* L.)

The Atlantic cod belongs to the family of Gadidae which are medium to large size marine fish. They are found in cool waters in the northern hemisphere. This family includes such fish as haddock, hake, saithe etc. (Scott & Scott 1988). Although they are usually bottom dwellers, cod can be found anywhere from the surface to 600 m and from inshore waters to the edge of the continental shelf (Cohen et al. 1990). In the North East Atlantic they are found from Iceland to the Norwegian Sea and south to the Baltic Sea and the Bay of Biscay (Cohen et al. 1990) (Fig. 3).



Fig. 3: Overview of the distribution of North East Atlantic cod

The temperature range in which cod are living is between -0.5°C and 10°C but can vary, depending on the time of year, location, and the size of the fish (Scott & Scott 1988). Cod can be found in waters up to about 20°C (Brander 1996). Food preferences are age dependent: young cod tend to eat small crustaceans such as copepods and amphipods, but as they mature they eat a larger proportion of fish and even show cannibalism (e.g. Arntz 1973, Scott & Scott 1988, Palsson 1994). Growth and reproduction parameters vary among cod populations (Brander 1994a).

Studies of various cod populations have shown that most populations tend to concentrate spawning in terms of time and space. These patterns differ between stocks and often seem to be related to phytoplankton production in a particular area (Brander 1996). Cod time their spawning to coincide with the peak in phytoplankton production so food will be plentiful when their larvae hatch (Cushing 1984). Fecundity ranges from hundreds of thousands to millions of eggs (Chambers & Waiwood 1996, Kjesbu et al. 1996). Once the eggs are released, they will begin to rise to the surface and drift with the currents. Incubation time varies with temperature, but generally they will hatch after 30 or 40 days, when the embryos are 3 - 4 mm (Scott & Scott 1988). After several weeks of living in the upper water column, they will begin to move to the bottom when they are approximately 4 cm in size (Scott & Scott 1988).

The cod populations studied in this work - cod from the Southern North Sea, the Baltic Sea, the Norwegian coast, the North East Arctic and the White Sea - and their corresponding environment are briefly described in the following paragraphs.

North Sea - Cod from the Southern North Sea and the Norwegian coast

The North Sea is a relatively shallow basin, with a surface area of about 575.300 km² and a volume of 42.300km³. The mean depth ranges from about 30 metres in the southeast to 200 metres in the northwest. The North Sea is influenced by the Atlantic Ocean, mainly by input from the north, but also, to a lesser extent, via the English Channel (Knijn et al. 1993). In the German Bight the average bottom temperature in winter (January - March) is 4.5°C, during summer (July - September) it climbs up to 16°C. The Norwegian waters are slightly warmer in winter (mean bottom water temperatures: 7°C), but with a mean temperature of 8.5°C colder in summer than the Southern North Sea.

The growth rate of North Sea cod differs by area and year of survey. The average length of two-year-old cod caught on International Young Fish Surveys in the years 1970 - 1980, for example, varied between 32 cm and 44 cm (van Alphen & Heessen 1984). Cod in the Southern North Sea grow faster than those in the North but reach a smaller maximum length (Daan 1974).

Spawning of cod occurs from the beginning of January to April, but this depends also on latitude. In the German Bight peak spawning occurs in February,

whereas in the more northerly regions, maximum spawning activity shifts to March.

Some North Sea cod become mature in their second year, but it is not before they are 6 years old that all individuals reach maturity (Daan 1974). There is a tendency that cod in the Southern North Sea become mature at a slightly younger age than in the Northern North Sea. As reported by Brander (1994b), fecundity estimates for southern North Sea cod are only available for a small number of years (Schopka 1971, Oosthuizen & Daan 1974, Rijnsdorp et al. 1991). In the Southern North Sea an average mature female with a length of 100 cm carries about five million eggs (Rijnsdorp et al. 1991).

Baltic Sea - Baltic cod

The Baltic Sea is by far the largest body of brackish water of the world extending over an area of about 420 000 km² with a volume of 21 600 km³ and a mean depth of 52 meters (Lozán et al. 1996). The salinity decreases from 20 – 26 ‰ at the Kattegat to 6 – 12 ‰ in the Bornholm areas and to more or less fresh water conditions in the Gulf of Finland and the Gulf of Bothnia. In August the surface layers are warmed up to 16 - 17°C. In February in the Gulf of Bothnia, the Gulf of Finland, Riga Bay, and locally even farther southwards the freezing point is reached, while Atlantic waters of corresponding latitudes are still at 8° - 10°C (Segerstråle 1957). Baltic cod are regarded as two well separated stocks: a small stock southwest and west of Bornholm (the western stock) and a large one inhabiting almost all the rest of the Baltic Sea (the eastern stock). The reproduction period of the western stock stretches from February to April, with variability between years and between areas, probably depending on temperature, salinity and oxygen conditions. All of the Baltic cod mature at an age of 3 years, but in the northern part they mature somewhat later (Brander 1994b).

Barents Sea - North East Arctic cod

The Arcto-Norwegian cod stock is the largest cod stock in the North Atlantic (Brander 1994b). This cod stock is distributed along the Northern Norwegian coast and in the oceanic regions of the Barents Sea - Svalbard area, which spans an area of about 0.6 - 0.7 million km². The mean depth of the Barents Sea is 230 m.

The southernmost distribution is reached during spawning in Norwegian coastal areas south towards Sørøya and Møre, where the bottom temperatures never exceed 7°C (Brander 1994b). Large amounts of age data about this cod population are available (Brander 1994b). The North East Arctic cod matures at about 7 - 8 years. Latest information on the fecundity of Arcto-Norwegian cod can be found in a study by Kjesbu et al. (1998). It was calculated that in 1991 a female of a length of 70 cm produces between 325 - 450 oocytes per gram body weight.

White Sea - White Sea cod

The White Sea is a semi-enclosed Arctic sea and covers approximately 95 000km². The central basin (maximum depth 350 meter) and Kandalaksha Bay (maximum depth 300 meter) are the deepest parts of the White Sea. Compared with the Barents, the White Sea has a more continental climate - a warmer summer and a harsher winter. Surface water temperatures in the White Sea vary seasonally by about 20°C but the bottom temperatures display a constant temperature of about -1.5°C (Klenova 1966). Average water temperature in the Kandalaksha Bay in summer is 14 - 15°C with a salinity of 23 - 24‰. During long winters (October - April) the bays of the White Sea are covered by ice (Klenova 1966). White Sea cod (*Gadus morhua maris albi* Dorujigin) is a subspecies of the Atlantic cod and inhabits mainly shallow waters of the White Sea (Brander 1994b). This subspecies is distributed in the Kandalaksha Bay and around the Solovetsky Islands and does not migrate for long distances. Spawning of this cod occurs in the coastal zone at depths between 15 and 100 meters and starts in the middle of March under ice cover (see Brander 1994b). The White Sea cod attains maturity at an age of 3 - 5 years at a body length of 25 - 35 cm (Brander 1994b). Data about von Bertalanffy growth parameters and fecundity are not available.

3 Material & Methods

3.1 Field cruises and animals

Cod were caught for ecological and physiological studies from different climatic zones (Fig. 4 & Tab. 1). Southern North Sea cod, Baltic cod, and White Sea cod were caught in cooperation with the Alfred-Wegener-Institute for Polar and Marine Research, Bremerhaven (AWI) at different locations as summarized in Tab. 1. North East Arctic cod and Norwegian coastal cod were provided by the University of Bergen.

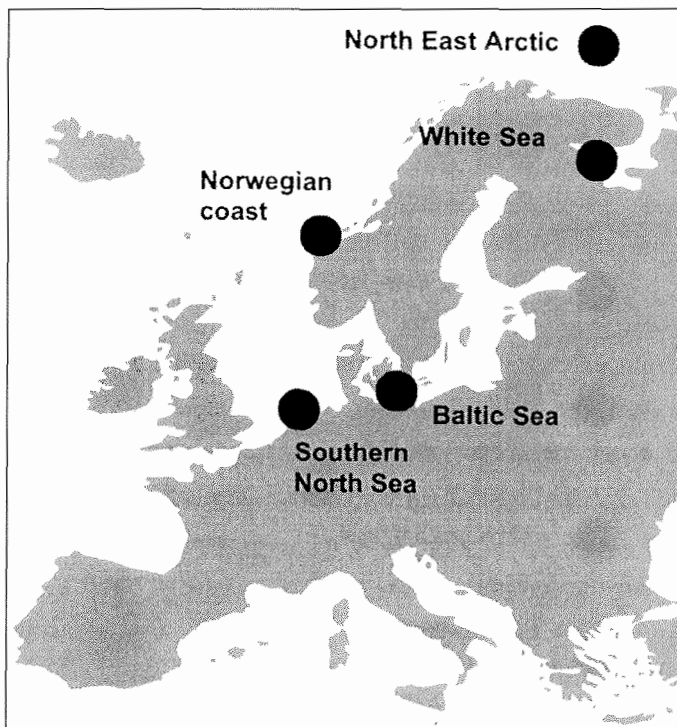


Fig. 4: Schematic overview of the investigation areas for studies on *Gadus morhua*.

Material & Methods

Tab.1: Overview of the areas where cod were taken and for which tasks.

area and position	date	sampling gear	task
White Sea , Russia Kandalashka Bay, Cape Kartesh 66°17'N 33°05'E	July – September 1998	Traps & hook and line	-ecological data collection* -physiological experiments > whole animal respiration
North Sea Bruine Bank 53°45'N – 53°13'N 004°16'E – 03°05'E Tiefe Rinne 54°10'N 007°54'E White Bank 55°27'N – 55°00'N 006°31'E – 006°05'E	February 1999	RV „HEINCKE“ ➤ bottom trawl	- fecundity studies and ecological data - transport of live fish to the AWI for further physiological studies > whole animal respiration > mitochondrial studies
Baltic Sea Kiel Bay 54°32'N 10°48'E Bornholm Bay 54°40'N 15°20'E Gotland-Gdansk Deep 55°30'N 17°40'E North Sea White Bank 55°27'N 006°31'E	April 1999	RV „HEINCKE“ ➤ bottom trawl	- fecundity studies and ecological data collection* - transport of live fish to Helgoland island for growth experiments

*The ecological data include the following parameters:

- total length (cm)
- total weight (g)
- weight of gonads (g)
- sex
- state of maturation according the index scale of Maier (1908)
- weight of the liver (g)
- weight of stomach, full and empty (g)
- organ weight (g)
- otoliths were taken for further age determination

3.2 Growth in nature - Age determination by reading otoliths

To estimate the effects of the climatic regime on growth of cod, yearly rings on otoliths were read in fish from different regions for age determination.

3.2.1 Analysed fish and work in the laboratory

Otoliths (sagittae) of cod were removed from 354 specimens during different expeditions in the Southern North Sea, the Baltic Sea and the White Sea (Tab. 2).

Tab. 2: Overview of the analysed material used for growth studies of *Gadus morhua* from different climatic regions.

	Southern North Sea			Baltic Sea	White Sea
Area	Tiefe Rinne	Weisse Bank	Bruine Bank	Kiel Bay	Cape Kartesh
Position	54°10'N 007°54'E	55°27'N 006°31'E	53°45'N 004°16'E	54°32'N 10°48'E	66°20'N 33°40'E
Time	February 1999			April 1999	August 1998
Number of fish	32	81	65	102	71

For a proper distinction of yearly growth rings, the material was handled according to the following method developed by the "Bundesforschungsanstalt für Fischerei" – Hamburg. Otoliths were embedded in blocks of epoxy resin. After hardening of the resin, blocks were sectioned by a double bladed saw to obtain a transverse section through the otolith core. It was possible to obtain discs of 0.3 mm thickness from the otoliths at the level of the nucleus. These discs were glued on glass plates, and the rings were read with a dissecting microscope according to Bingel (1981).

3.2.2 Data analysis

Data obtained by reading otoliths were used to calculate the parameters of the von Bertalanffy growth equation (von Bertalanffy, 1938):

$$L_t = L_{00} \{1 - e^{-k(t-t_0)}\}$$

where

L_t : length (cm) at given age (years)

L_{00} : asymptotic standard length (i.e. maximum reachable length in cm)

k : body growth coefficient

t_0 : age (years) at length 0

t : age (years)

Growth performance

The estimation of growth performance according to Pauly (1979) was chosen for a comprehensive latitudinal comparison of growth of cod independent from size and age.

$$\emptyset' = \log_{10}k + 2\log_{10}L_{00}$$

where

\emptyset' : growth performance by Pauly (1979)

L_{00} : asymptotic standard length (i.e. maximum reachable length in cm)

k : body growth coefficient

\emptyset' -values for North Sea cod, Baltic cod and White Sea cod were calculated by using the Bertalanffy growth parameters k and L_{∞} obtained in this study (see above). Literature data of growth performance of cod from different regions (Barents Sea, Greenland waters, Northern Norway, Icelandic waters, Norwegian Coast, Southern North Sea, Western Baltic, Gulf of Biscaya) were added. The \emptyset' -values were plotted versus the latitude of the origin of cod.

To test the dependence between latitude and growth performance among all populations a regression analysis was carried out. Testing the significance of the regression was calculated by using t-statistics (Zar 1996) (H_0 : No dependence). The result was considered significant at the $\alpha = 0.05$ level.

3.3 Experimental growth studies

3.3.1 Animals and experimental procedure

A growth experiment with cod from the Southern North Sea was carried out in the AWI laboratories on Helgoland Island between April 27, 1999 and September 10, 1999. Most fish (size: 20 - 33cm, weight: 84 - 378g) were caught with a bottom trawl of RV "Heincke" in April 1999 in the North Sea at the "Tiefe Rinne" (54°08N; 07°55E). Additionally, a number of specimens were taken with hook and line near Helgoland. The animals were kept in four tanks supplied continuously with fresh seawater (salinity 31‰) at four different temperatures (4°C, 8°C, 12°C, 15°C). Under slight narcosis with MS-222 (0.05g/l) the fish were individually tagged with floy tags which were fixed under the second dorsal fin. They were fed daily with an excess of sprats (*Sprattus sprattus*), because the wild cod did not feed on commercial food pellets. After one hour, the remaining sprats were removed from the tank and weighed in order to calculate the amount of food consumed by cod. After an acclimation period of about one month total body length (cm) and body wet weight (g) of each individual fish was determined once every three weeks under slight anaesthesia MS-222 (0.05g/l). Feeding was stopped two days prior to taking measurements.

The experimental growth data collected for the North Sea population were compared to data for Norwegian coastal cod (NCC) and North East Arctic cod (NEAC) obtained by CLICOFI-project partners from the University of Bergen (Johansen & Navdal 2000 – unpublished data). They carried out two growth experiments in which the experimental design differed slightly from the Helgoland experiment. In the first experiment (Bergen 1) offspring of brood stocks from Norwegian Coastal cod (25 – 38cm, 228 – 614g) and North East Arctic cod (29 - 38cm, 159 - 596g) hatched in spring 1997. It was raised under laboratory conditions between spring 1998 and March 1999 (Tab. 3). Fish of both strains were individually tagged with Passive Integrated Transponder (PIT) tags. They were inserted through a 3-mm long incision made with a scalpel on the linea alba, ca. 2-3mm anterior to the papilla. The cod were kept under natural light conditions and at three different water temperatures: 8°C, 12°C and 15°C. They were fed in surplus with commercial dry food (NOR/AQUA). The dry food dissolved in water after a while, making a calculation of the consumption

rates impossible. Fish were measured and weighed once every six weeks. A second growth experiment (Bergen 2) started in Bergen in January 1999 and ended in March 2000. Norwegian coastal cod were raised at 4°C and 12°C using the same experimental design as described above. At the end of the three experiments the fish were killed and sex-determined.

Only the spring/summer periods were selected for growth comparisons between the three populations due to preliminary results, showing the highest growth rates of cod in late spring and summer (Svåsand et al. 1996).

Tab. 3: Overview of the growth experiments analysed in this thesis: Time period, experimental temperatures, size (cm) and weight (g) ranges of cod from the Southern North Sea, the Norwegian coast and the North East Arctic.

HELGOLAND (own investigations)	Southern North Sea cod
Period of the whole experiment	27.04.1999 – 10.09.1999
Analysed period	08.06.1999 – 09.09.1999
Range of lengths (cm) of cod at the start of the experiment	20 – 33cm
Range of weights (cm) of cod at the start of the experiment	84 – 378g

BERGEN 1 (Johansen & Navedal 2000- unpublished data)	Norwegian coastal cod	North East Arctic cod
Period of the whole experiment	27.05.1998 – 05.03.1999	27.05.1998 – 05.03.1999
Analysed period	27.05.1999 – 18.09.1999	27.05.1999 – 18.09.1999
Range of lengths (cm) of cod at the start of the experiment	25 – 38cm	29 – 38cm
Range of weights (cm) of cod at the start of the experiment	228 – 614g	159 – 596g

BERGEN 2 (Johansen & Navedal 2000- unpublished data)	Norwegian coastal cod
Period of the whole experiment	27.05.1998 – 05.03.1999
Analysed period	09.06.1999 – 13.10.1999
Range of lengths (cm) of cod at the start of the experiment	27 – 42cm
Range of weights (cm) of cod at the start of the experiment	109 – 940g

3.3.2 Data analysis

Individual growth rates

To calculate and compare the daily individual growth rates at different experimental temperatures of cod from the Southern North Sea, the Norwegian coast, and the North East Arctic, the following growth equations by Ricker (1979) were chosen:

$$\text{Growth rate (\% *d}^{-1}\text{)} = \frac{((W2 - W1)/W1)}{t} * 100$$

(Daily weight increment (g))

where

W1: initial weight (g)

W2: final weight (g)

t: time in days

$$\text{Growth rate (\%*d}^{-1}\text{)} = \frac{((L2 - L1)/L1)}{t} * 100$$

(Daily length increment (cm))

where

L1: initial length (cm)

L2: final length (cm)

t: time in days

Only fish with positive growth and without obvious injuries were analysed.

Optimum temperature for growth

The optimum temperature for growth of the different cod populations was calculated using the following model equation:

$$dL(T) = dL_{max} * e^{(-k * (T - T_{max}))}$$

where

dL (T): daily length increment (cm)

dL max: maximum length increment (cm)

k: body growth coefficient

T: temperature (°C)

T_{max}: temperature (°C) at which maximum length increments occur (optimal temperature)

Daily length increment (dL) was calculated using the following equation:

$$dL = \frac{(L_{end} - L_{start})}{t}$$

where

dL: daily length increment (cm)

L end: length (cm) at the end of the growing period

L start: length (cm) at the start of the growing period

In the case of North East Arctic cod (NEAC) no growth experiment was carried out at 4°C by Johansen & Naevdal (2000 – unpublished data). Thus, this value was calculated for the determination of optimum temperature for growth of cod.

The difference between the calculated mean growth rates of Norwegian cod and North East Arctic were similar at 8°C, 12°C, and 15°C (0.013 ± 0.001).

Therefore, the mean daily length increment of North East Arctic cod at 4°C could be calculated by combining the differences of the determined mean growth rates as follows:

$$NEAC4^{\circ}C-dL_{mean} = (NCC4^{\circ}C dL_{mean} - ((NCC8^{\circ}C dL_{mean} - NEAC8^{\circ}C dL_{mean}) + (NCC12^{\circ}C dL_{mean} - NEAC12^{\circ}C dL_{mean}) + (NCC15^{\circ}C dL_{mean} - NEAC15^{\circ}C dL_{mean}))/3)$$

NCC..°C-dL_{mean}: mean daily length increment (cm/day) of Norwegian Coastal cod at maintaining temperature

NEAC..°C-dL_{mean}: mean length increment (cm/day) of North East Arctic cod at maintaining temperature

Simulated growth in respect to climate change

To estimate the effects of a climate induced temperature change on growth of cod the data obtained from the experimental growth studies was combined in a scenario in the following way:

1. Daily growth in nature for each month was calculated by using the model equation described above.

$$dL(T) = dL_{max} * e^{(-k * (T - T_{max}))}$$

where

dL (T): daily length increment (cm) at a given temperature (°C)

dL_{max}: daily maximum length increment (cm)

k: body growth coefficient

T: temperature (°C) in nature

T_{max}: temperature (°C) at which maximum length increment occurs (optimal temperature)

dL_{max}, k and T_{max} of cod from the Southern North Sea, the Norwegian coast and the North East Arctic were taken from the data gained in the growth experiments.

Monthly mean water temperatures (T) of the North Sea, the Norwegian coast and the Barents sea were taken from Dippner (1999).

2. Monthly growth rates were calculated by multiplying daily growth rates with the number of days of the corresponding month:

$$ML(T) = dL(T) * \text{number of days of the corresponding month}$$

where

ML (T): monthly growth rate (cm) at a given temperature (°C)

dL (T): daily length increment (cm) at a given temperature (°C)

3. By changing the mean water temperatures in the formula written above, it is possible to simulate the effects of climate change on growth of cod from different populations.

3.4 Fecundity studies

3.4.1 Field and laboratory analysis

For fecundity studies cod were caught with a bottom trawl during two expeditions in the Southern North Sea and the Baltic Sea (Tab. 4).

Tab. 4: Overview of the analysed material used for fecundity studies on *Gadus morhua*.

	Southern North Sea		Baltic Sea		
area	White Bank	Bruine Bank	Kiel Bay	Bornholm Basin	Gotland Deep
position	55°27'N 006°31'E	53°45'N 004°16'E	54°32'N 10°48'E	54°40'N 15°20'E	55°30'N 17°40'E
time	February 1999		April 1999	April 1999	April 1999
number of fish	13	9	7	53	25

Only gonads that could be classed to maturity stages III and IV according to Maier (1908) were used. The handling of the samples followed the method of Bleil & Oberst (1993): The ovaries were broken up and fixed in 4% formalin. The material was shaken by hand to support the fixing process and a better separation of the eggs from the tissue. When the fixation process was finished (after 48 hours minimum) the gonads were washed, and a cascade of different sieves with mesh sizes of 1000µm, 500µm and 125µm was used for the separation of eggs and tissue. Nine sub-samples of 50 eggs each were sorted out. All eggs and tissue were dried, weighed and calculated to the 'absolute fecundity'.

3.4.2 Data analysis

The mathematical relationship between the absolute fecundity and either age or length (L) of cod was tested for the best fit (i.e. maximum value for r^2) by using the following formulae (Schopka 1971):

1. $F_{abs} = a * L^b + b$
2. $F_{abs} = a * L^b$

where

F_{abs} : Absolute fecundity (total number of eggs per fish spawned per season)

L: total length of the fish (cm)

a, b: constants

3.5 Design of physiological experiments

The effects of acclimation and adaptation on oxygen uptake and mitochondrial functions for Southern North Sea cod, North East Arctic cod, and White Sea cod were studied using the following experimental design (Tab. 5): Cod from the Southern North Sea and the North East Arctic were acclimated to 4°C and 12°C. White Sea cod was kept at 12°C. The whole animal respiration rates of individuals from these acclimated populations were measured at different temperatures. Additionally, respiration rates of isolated liver mitochondria from North Sea cod and North East Arctic cod were studied in the temperature range from 4°C to 20°C.

Tab. 5: Overview of the different acclimation temperatures and physiological experiments with different cod populations.

	acclimation temperature	Respiration of whole animals (temperature of analysis)	Respiration of liver mitochondria (temperature of analysis)
North Sea cod	4°C	4°C	4°C
	12°C	12°C 15°C 18°C 20°C	12°C 15°C 18°C 20°C
North East Arctic cod	4°C	4°C	4°C
	12°C	12°C	12°C 15°C 18°C 20°C
White Sea cod	12°C	12°C 14°C 16°C 18°C	

3.6 Respiration of whole animals

3.6.1 Animals and experimental set-up

White Sea cod were caught with hook and line in summer 1998 (for details see Tab. 1). Animals were kept in cages for 2 weeks in the Chupa Bay near the Russian station at an ambient temperature of $12^{\circ}\text{C} \pm 2^{\circ}\text{C}$. Cod (*Gadus morhua*) from the German Bight and North East Arctic were caught with a bottom trawl net and transported to the AWI. Two groups of animals from the North Sea and the North East Arctic were acclimated for six weeks at 4°C and 12°C and fed ad libitum with blue mussel (*Mytilus edulis*) twice a week. Feeding was stopped five days prior to the respiration experiments.

The respiration rates of cod from the White Sea were measured at 12°C , 15°C , 18°C and 20°C . Those of German Bight cod and North East Arctic cod were determined at 4°C , 8°C , 12°C , 15°C , 18°C and 20°C . All measurements were carried out with a flow through respirometer (Fig. 5).

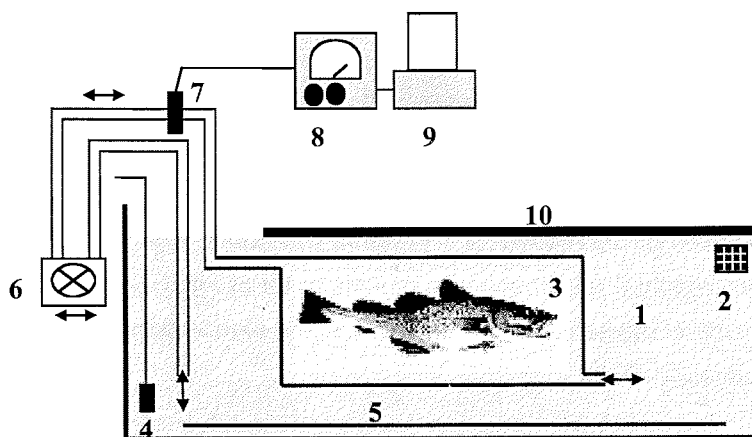


Fig. 5: The flow through respirometer. 1 water bath, 2 filter, 3 respirometer chamber, 4 aerator, 5 heating coil, 6 water pump, 7 Clark oxygen electrode, 8 oxygen monitor, 9 chart recorder, 10 lid

3.6.2 Experimental procedure

In order to avoid handling stress, cod were anaesthetized with 0.05 g/l MS-222, gently placed into the chamber (volume: 12 litre) (Fig. 5), and left undisturbed for at least 24 hours. The chamber was kept in a water bath with a sea water volume of about 100 litres. The salinity was kept at 32‰. The water was constantly aerated and recirculated over a filter. A heater coil in combination with a thermostat allowed to set the desired water temperature to within $\pm 0.2^\circ\text{C}$.

The flow rate was set, according to the size of the fish and the water temperature, between 300 and 700 ml/min. It was regulated in a way that the out-flowing water displayed about 20% less oxygen content than the in-flowing water. The oxygen (O_2) concentration was monitored with a Clarke-type oxygen electrode (Eschweiler, Kiel) and recorded permanently by a chart recorder. The electrode was calibrated to zero oxygen in a saturated solution of sodium sulphite normoxic oxygen levels in air saturated sea water. At the beginning and at the end of each measurement the water flow was reversed so that the oxygen content of the aerated water could repeatedly be used for calibration prior to passing through the respirometer chamber. In order to monitor recovery from handling stress, measurements began as soon as the fish was placed into the respirometer. After a stable reading was obtained (Fig. 6) the temperature was either increased or decreased by 1°C within two hours. After the desired temperature was reached respiration was measured for at least 12 hours. The lowest stable value of oxygen uptake was taken as the standard metabolic rate (Pörtner & Grieshaber 1993).

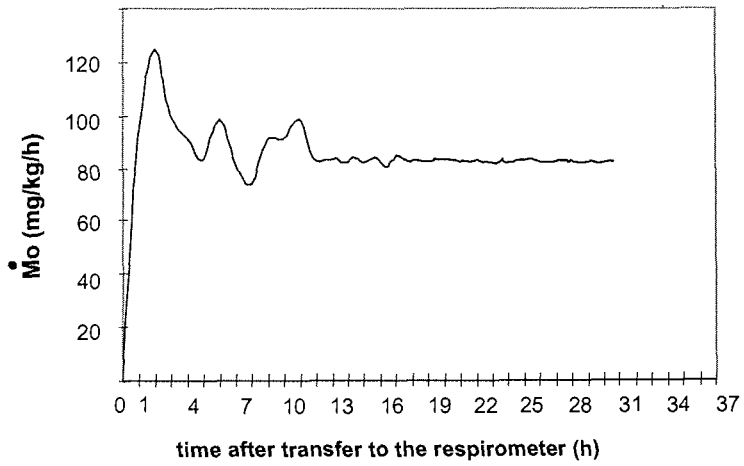


Fig. 6: Plot of oxygen consumption rate of a single specimen of White Sea cod at 12°C. After transfer to the respirometer chamber, oxygen consumption was elevated due to handling stress. After 12 hours the $\dot{M}o_2$ stabilized and indicating standard metabolic rate.

3.6.3 Data analysis

Oxygen consumption

The rate of oxygen consumption was calculated using the formulae:

$$\dot{M}O_2 = \frac{(P_{O_2(in)} - P_{O_2(out)}) * \beta_{O_2} * fr}{w}$$

where

- $\dot{M}O_2$: oxygen consumption ($\mu\text{mol} * \text{min}^{-1} * \text{g}^{-1}$)
- $P_{O_2(in)}$: partial oxygen pressure of inflowing water (Torr)
- $P_{O_2(out)}$: partial oxygen pressure of outflowing water (Torr)
- β_{O_2} : solubility of oxygen in water (Boutilier et al. 1984)
- fr: flow rate ($\text{l} * \text{min}^{-1}$)
- w: weight of cod (g)

Due to variations in body mass, $\dot{M}O_2$ was adjusted to a standard body weight (1 kg) according to Saunders (1963):

Standardized value = $(1/\text{body weight})^{0.8} * \text{measured value}$.

The P_{O_2} values were calculated as follows:

$$P_{O_2} = (P_b - P_{H_2O}) * 0.209$$

where

- P_{O_2} : partial pressure of oxygen (Torr)
- P_b : barometric pressure (Torr)
- P_{H_2O} : water vapor pressure at a given temperature taken from tables (Boutilier et al. 1984)
- 0.209: fraction of oxygen in dry air

3.7 Respiration of isolated liver mitochondria

3.7.1 Animals and preparation of mitochondria

The functions of mitochondria were studied in cod from the German Bight and the North East Arctic acclimated to 4°C and 12°C.

Cod were anaesthetized with MS-222 (0.05 g/l), transported to the lab, and killed by a blow to the head. The liver was quickly removed and 2-3 g were cut into small pieces by using a pair of scissors. The tissue was sampled in a petri dish containing 30 ml isolation buffer (50 mM Hepes, 85 mM KCl, 80 mM sucrose, 5 mM EDTA, 5 mM EGTA, 1% BSA, 1 µg/ml aprotinin, pH 7.1 at 20°C). Extraction and homogenisation occurred in the same buffer by use of a motor-driven glass/Teflon homogeniser (Heidolph, Kehlheim, Germany) and application of 3 – 5 passes. After centrifugation of the resulting homogenate (12 min at 300G) the pellet was rehomogenised in 30 ml isolation buffer and centrifuged again. The combined supernatants were spun for 8 min at 10000G. The mitochondrial pellet was resuspended in 1 – 3 ml of assay medium (50 mM Hepes, 85 mM KCl, 80 mM Sucrose, 5 mM KH₂PO₄, 1% BSA, 1 µg/ml aprotinin, pH 7.1 at 20°C).

3.7.2 Analysis of mitochondrial respiration

Oxygen consumption of isolate liver mitochondria was measured at five different temperatures (4°C, 8°C, 12°C, 15°C, 20°C), using a Clarke-type oxygen electrode in a thermostatted respiration chamber. The electrode was calibrated to zero oxygen in a saturated solution of sodium sulphite and to 100 % air saturation in aerated medium of the respective temperature. 100 – 200 µl of the mitochondrial suspension were combined with assay medium to a total volume of 1 ml containing 5 µM AP5A (diadenosine pentaphosphate) and 3.3 mM succinate. After the addition of 0.3 mM ADP state-III respiration was recorded. State IV respiration was determined after all ADP had been phosphorylated. Finally, the respiration rate induced by proton leakage was recorded after adding 25 µl oligomycin (state-IV + ol.) which is an inhibitor of mitochondrial F₀F₁ – ATPase. After the experiment the protein concentration of the mitochondrial pellet was determined by the Biuret method (Gornall et al. 1949), after adding 5% deoxycholate to the mitochondrial suspension to solubilize

membrane proteins, TCA to precipitate the proteins and diethyl ether and ethanol to separate the membrane lipid.

3.7.3 Data analysis

State-III (Aerobic capacity of ATP-formation) and state-IV_{ol.} (proton leakage rate) respiration and ADP/O ratio were defined according to Chance & Williams (1955). The respiratory control ratio (RCR) was determined according to Estabrook (1967) by dividing state-III respiration rate by state-IV_{ol.} respiration rate.

Arrhenius break temperature were determined by a method of continuous two-phase regression (Dahlhoff & Somero 1993).

The following formulae were used to estimate the relationship between total liver of cod and mitochondrial capacities:

Calculation of hepatosomatic index (HSI) to compare liver sizes:

HSI: liver mass (g)/body mass (g) *100

Calculation of aerobic capacity of ATP-formation in total liver of cod (state-III respiration_{whole liver}):

state-III respiration_{whole liver} = state-III respiration * total liver weight * protein content

where state-III respiration of isolated liver mitochondria (nmolO/min*mg protein), total liver weight of cod (g) and mitochondrial protein content (mg) per g of total liver were multiplied.

Calculation of proton leakage rates in total liver of cod (state-IV_{ol.} respiration_{whole liver}):

state-IV_{ol.} respiration_{whole liver} = state-IV_{ol.} respiration * total liver weight * protein content

where state-IV_{ol.} respiration of isolated liver mitochondria (nmolO/min*mg protein), total liver weight of cod (g) and mitochondrial protein content (mg) per g of total liver were multiplied.

3.8 Statistics

Analyses of variance (ANOVA) (Backhaus et al. 1990; Underwood 1997) were carried out for the following comparisons:

- Food consumption of Southern North Sea cod in growth experiments.
- Daily growth rates of Southern North Sea cod, Norwegian Coastal cod, North East Arctic cod in growth experiments.
- Hepatosomatic Index of Southern North Sea cod and North East Arctic cod acclimated to different temperatures in laboratory.
- Mitochondrial capacities in whole liver of cod acclimated to different temperatures at a temperature of analysis of 12 °C.

Analyses of covariance (ANCOVA) (Backhaus et al. 1990; Underwood 1997) were calculated for the following comparisons:

- Length and weight of cod from different populations at specific ages.
- Oxygen uptake of Southern North Sea cod and White Sea cod acclimated to different temperatures at different temperatures of analysis.
- Mitochondrial properties of isolated liver in North Sea and North East Arctic cod acclimated to different temperatures at different temperatures of analysis.

Prior to ANOVA/ANCOVA data were tested for normality and homogeneity of variances. The Bartlett's test on homogeneity of variances was applied since this test takes account of heterogenous sample sizes (Zar 1996). Results were considered significant at the $\alpha = 0.05$ level.

To determine differences between only two treatments the unpaired two way t-test was carried out. Data following non-parametric distribution were compared by using Man Whitney U-test (Zar 1996).

4 Results

4.1 Growth in nature

The analysis of growth in nature was based on age-length and age-weight relations. Age was determined by reading otoliths of cod from the North Sea, the Baltic Sea and the White Sea. Age-length data for Norwegian cod were adopted from Godø & Haug (1999) and for North East Arctic cod from Jørgensen (1992) and Ozhigin et al. (1995). Age-weight relationships for cod from the Norwegian coast and the North East Arctic were taken from ICES (2001a). Von Bertalanffy growth curves and von Bertalanffy growth parameters were determined for age-length relationships.

4.1.1 Age-length relation

In Fig. 7 Bertalanffy growth curves based on age-length relations are shown for different cod populations: in general, growth of cod increased with decreasing latitude, whereas Baltic cod grew slower than cod from the Norwegian coast.

The detailed Bertalanffy growth parameters are summarized in Tab. 6. The largest growth factor (k) was found for Baltic Sea cod (0.347), followed by Southern North Sea cod (0.221) and Norwegian coastal cod (0.218), but these animals revealed a smaller final length than North East Arctic cod which displayed the largest final length i.e. 129 cm (Tab. 6).

Tab. 6: Bertalanffy growth curve parameters for cod from different geographical areas. Data for the Norwegian coast by Godø & Haug (1999) and for the North East Arctic region by Jørgensen (1992) and Ozhigin et al. (1995). L_{00} values were taken from Lundbeck (1953), Trout (1954), Daan (1974), Bagge et al. (1994), Brander (1994b).

Region	Sample size	Bertalanffy growth equation: $L_t = L_{00} \{1 - e^{-k(t-t_0)}\}$	fit (r^2)
North East Arctic	77	$L_t = 129 (1 - \exp(-((0.133)) (t-(0,395))))$	0,977
White Sea	63	$L_t = 63 (1 - \exp(-((0,151)) (t-(-1,060))))$	0,921
Baltic Sea	96	$L_t = 67.7 (1 - \exp(-((0,347)) (t-(0,305))))$	0,865
Norwegian coast	117	$L_t = 105 (1 - \exp(-((0,218)) (t-(0,245))))$	0,9591
Southern North Sea	113	$L_t = 111 (1 - \exp(-((0,221)) (t-(-0,052))))$	0,852

Results

White Sea cod differed totally from the other populations. White Sea specimens displayed a small growth factor (k : 0.151) and the smallest L_{∞} -value (63 cm). Due to the mathematical process involved in the Bertalanffy equation (von Bertalanffy 1938) positive t_0 -values result for North East Arctic cod, Baltic cod and Norwegian coastal cod. Thus, the corresponding curves pass through the y-axis intercept below zero (Fig. 7). This is just a mathematical phenomenon, which will be neglected in further discussions (see Pitcher & Hart 1982).

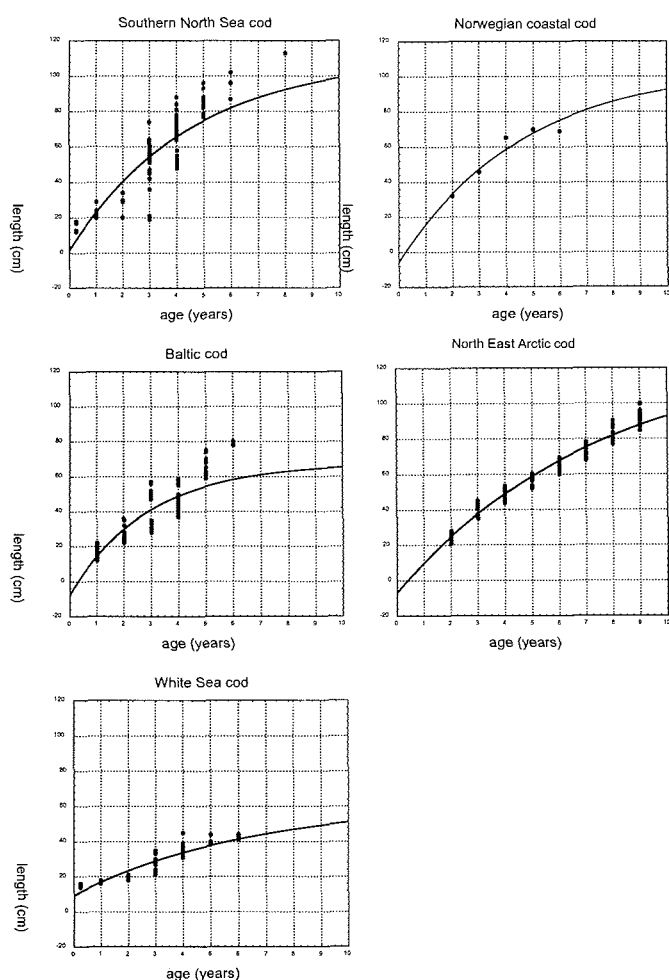


Fig. 7: Relationship between age (years) and length (cm) in cod from different regions (Southern North Sea, Norwegian coast, Baltic Sea, White Sea, North East Arctic). Data for the Norwegian coast by Godø & Haug (1999) and for the North East Arctic region by Jørgensen (1992) and Ozhigin et al. (1995).

Results

For a statistical analysis of growth of cod from different climatic regimes the length data were grouped in age classes (Tab. 7). Only mean values and sample sizes for Norwegian cod were given in the dataset by Godø & Haug (1999). Thus the age-length data for Norwegian cod were shown in Tab. 7, but could not be included in the statistical analysis (Tab. 8).

Tab. 7: Mean lengths (cm) of cod at different age classes (years) from different geographical areas. Data for the Norwegian coast by Godø & Haug (1999) and for the North East Arctic region by Jørgensen (1992) and Ozhigin et al. (1995).

Area	Age (years)	1	2	3	4	5	6
White Sea	Mean lengths (cm)	16.9	19.8	28.0	35.9	39.6	42.3
	Standard deviation	0.71	0.98	4.18	4.19	2.1	1.5
	Sample sizes	12	10	20	10	7	4
North East Arctic	Mean lengths (cm)	-	24.1	40.5	48.9	56.9	64.7
	Standard deviation	-	2.7	3.4	3.2	3.2	3.2
	Sample sizes	-	7	10	10	10	10
Baltic Sea (Kiel Bay)	Mean lengths (cm)	16.8	27.7	38.9	45.4	65.8	79
	Standard deviation	3.15	4.70	10.4	6.6	5.4	1.1
	Sample sizes	18	17	19	28	12	2
Norwegian Coast	Mean lengths (cm)	-	-	45.6	65.1	69.9	68.8
	Standard deviation	-	-	7.6	7.2	7.6	6.8
	Sample sizes	-	-	19	23	61	14
Southern North Sea	Mean lengths (cm)	22.5	28.3	51.3	65	85.6	97
	Standard deviation	2.72	4.60	12.85	11.83	6.60	11.0
	Sample sizes	10	10	32	31	8	5

Up to the age of two years the mean lengths of cod from the investigated populations were quite similar and no significant differences based on otolith readings were found (Tab. 7 & 8). From 3 to 6 years, White Sea cod were significantly smaller than specimens from the Southern North Sea and the North East Arctic. At the age of 3, 4 and 6 years. White Sea cod were also significantly smaller than cod from the Baltic Sea. The Southern North Sea population revealed significantly larger mean length values than cod from the Baltic Sea between 3 and 5 years old and between 4 and 6 years North Sea cod were longer than North East Arctic cod. 6 years old, Southern North Sea cod reached a body length of 97 cm, whereas for comparison, North East Arctic cod were just 64 cm long.

Results

Tab. 8: Overview of the statistical differences of the mean body lengths (cm) in 2 to 6 years old cod from the White Sea (WSC), Baltic Sea (BSC), North East Arctic (NEAC) and North Sea (NSC). Data for the North East Arctic region by Jørgensen (1992) and Ozhigin et al. (1995). ANCOVA/multiple-Tukey Kramer test: *p<0.05, **p<0.01, ***p<0.001. Only those comparisons are shown where significant differences have been found. Norwegian Coastal cod was not included due to insufficient data.

Age (years) and level of significant differences				
2	3	4	5	6
No significant differences	WSC < BSC: **		WSC < BSC: **	WSC < BSC: **
	WSC < NEAC: *	WSC < NEAC: *	WSC < NEAC: ***	WSC < NEAC: **
	WSC < NSC: ***	WSC < NSC: ***	WSC < NSC: ***	WSC < NSC: ***
	BSC < NSC: ***	BSC < NSC: ***	BSC < NSC: ***	
		NEAC < NSC: ***	NEAC < NSC: ***	NEAC < NSC: **
				NEAC < BSC : ***

4.1.2 Age-weight relationships

In contrast to the age-length relationships, significant differences between the age-weight relation of cod from different populations became evident at an age of two years (Tab. 8 & 9). At this age the animals from the White Sea were significantly smaller than cod from the Norwegian coast, the Baltic Sea and the North Sea. North East Arctic cod were also smaller than North Sea cod and Norwegian coastal cod. From 3 to 6 years, North Sea cod are significantly larger than cod from all the other investigated populations. At the age of 5 and 6 years the slowest growing fish – White Sea cod – were also significantly smaller than specimens from the North East Arctic, the Norwegian coast and the Baltic Sea.

Results

Tab. 8: Mean weights (kg) of cod at different age classes (years) from different geographical areas. Data for the Norwegian Coast and for the North East Arctic region were adopted from ICES (2001b).

Area	Age (years)	1	2	3	4	5	6
White Sea	Mean weight (kg)	0.048	0.071	0.251	0.531	0.694	0.912
	Standard deviation	0.003	0.009	0.126	0.218	0.124	0.088
	Sample sizes	12	10	20	10	7	4
North East Arctic	Mean weight (kg)	-	0.114	0.374	0.820	1.438	2.284
	Standard deviation	-	0.027	0.176	0.274	0.365	0.518
	Sample sizes	-	18	18	18	18	18
Baltic Sea (Kiel Bay)	Mean weight (kg)	0.050	0.211	0.629	0.910	2.666	4.100
	Standard deviation	0.021	0.112	0.481	0.384	0.764	0.141
	Sample sizes	18	17	19	28	12	2
Norwegian Coast	Mean weight (kg)	-	0.344	0.841	1.774	2.309	3.051
	Standard deviation	-	0.099	0.100	0.283	0.327	0.689
	Sample sizes	-	5	5	5	5	5
Southern North Sea	Mean weight (kg)	0.130	0.292	1.789	2.857	5.217	9.036
	Standard deviation	0.71	0.115	0.777	1.690	0.306	1.819
	Sample sizes	10	10	32	31	8	5

Tab. 9: Overview of the statistical differences between mean weights (kg) of 2 to 6 years old cod from the White Sea (WSC), Baltic Sea (BSC), North East Arctic (NEAC), the Norwegian coast (NCC) and North Sea (NSC). ANCOVA - Multiple Tukey Kramer test: *p<0.05, **p<0.01, ***p<0.001. Only those comparisons are shown where significant differences have been found. Norwegian Coastal cod was not included due to insufficient data

Age (years) and level of significant differences				
2	3	4	5	6
			WSC < NEAC : **	WSC < NEAC : ***
WSC < NCC: ***		WSC < NCC: ***	WSC < NCC: ***	WSC < NCC: ***
WSC < BSC: **			WSC < BSC: ***	WSC < BSC: ***
WSC < NSC: **	WSC < NSC: ***	WSC < NSC: ***	WSC < NSC : ***	WSC < NSC : ***
NEAC < NSC: **	NEAC < NSC: ***	NEAC < NSC: ***	NEAC < NSC: ***	NEAC < NSC: ***
			NEAC < BSC: ***	NEAC < BSC: ***
NEAC < NCC: ***		NEAC < NCC: ***	NEAC < NCC: ***	
	NCC < NSC: *	NCC < NSC: ***	NCC < NSC: ***	NCC < NSC: ***
	BSC < NSC: **	BSC < NSC: ***	BSC < NSC: ***	BSC < NSC: ***
BSC < NCC: *		BSC < NCC: ***		

4.2 Experimental growth studies

The following results are based on a comparison of growth rates which were determined in experiments with cod from the North Sea (this study), from the Norwegian coast and from the North East Arctic (Johansen & Naevdal 2000 - unpublished raw data). For details see Material & Methods.

4.2.1 Cod size and growth rates

Cod of the three populations used at the start of the growth experiments covered similar size and weight ranges (Tab. 3). Johansen & Naevdal (2000 - unpublished raw data) carried out two experiments (Bergen 1 and Bergen 2) with Norwegian coastal cod in which the mean sizes of these animals differed by up to 10 cm. The effects of these differences in size were analysed here to check whether they influence daily growth rates (Fig. 9). Despite the differences in mean length of Norwegian cod at the start of the experiments, no different daily growth rates were found at 12°C (Fig. 9).

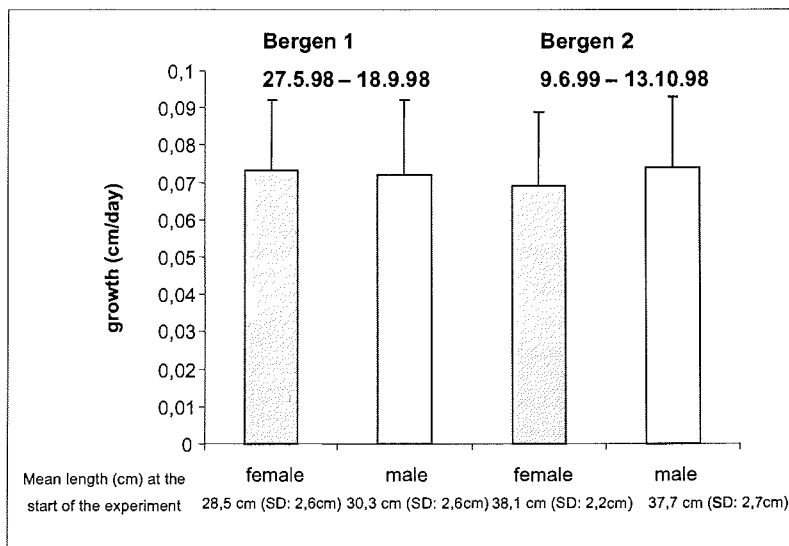


Fig. 9: Experimental growth rates (cm/day) of males and females of Norwegian coastal cod with different lengths at the start of the experiments reared at 12°C in two experiments (Bergen 1 and Bergen 2). No significant differences (ANOVA, $p = 0.9909$) in growth were found. Values are means \pm standard deviation. Raw data by Johansen & Naevdal (2000 - unpublished data).

4.2.2 Mortality

During the three growth experiments some fish died. To evaluate whether this was influenced by temperature or population origin, the mortality rates in relation to temperature have been shown in Fig. 10. Mortality increased with increasing temperature for all investigated populations and the highest values (48%) were detected at 12°C and 15°C for North East Arctic cod. At 4°C mortality was higher in Norwegian coastal cod than in North Sea cod.

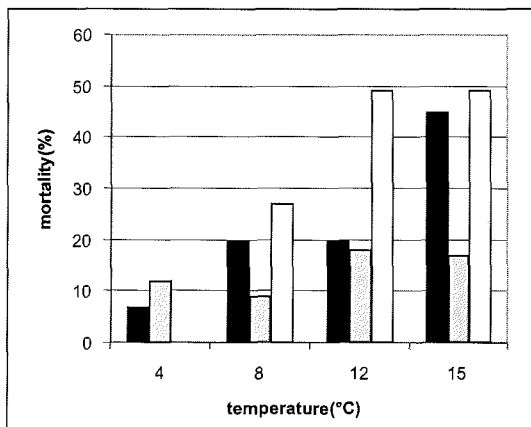


Fig. 10: Mortality (%) of cod from the Southern North Sea (black column), the Norwegian coast (grey column) and the North East Arctic (white column) region at different temperatures during the growth experiments. Raw data for Norwegian coastal cod and North East Arctic cod by Johansen & Naevdal (2000 – unpublished data).

4.2.3 Food consumption

A calculation of food consumption of the Norwegian coastal cod and the North East Arctic cod (Johansen & Naevdal 2000 – unpublished data) was not possible because their commercial dry food dissolved in water.

The food consumption of North Sea cod increased slightly with increasing temperature, whereas animals held at 15°C fed significantly more (37g/day) (Fig. 11).

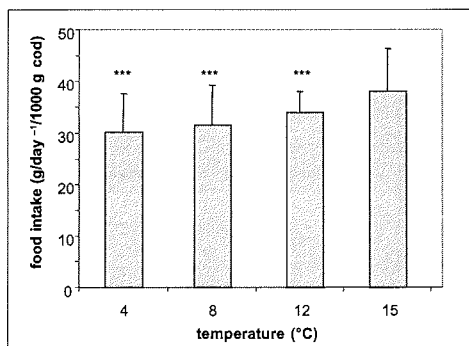


Fig. 11: Daily food intake (g/day) standardized on 1000g of North Sea cod captured during the Helgoland growth experiment at four different temperatures. Black asterisks indicate significant differences from values of cod kept at 15°C. $p^{***} < 0.001$ calculated with ANOVA/Tukey-Kramer multiple comparison test. n: 50 - 54

4.2.4 Growth rates

Daily length increments (%/d)

All cod, independent of their origin and sex, showed the highest individual length increments at 12°C (Fig. 12). Growth was significantly highest in the North Sea animals with values up to 0.458 %/day at 12°C. Lowest mean length increment were calculated for North East Arctic cod at 15°C but these values were not significantly different from those found in Norwegian coastal cod.

Daily weight increments (%/d)

Weight increments also increased with decreasing latitude (Fig. 12). Female specimens of North East Arctic cod grew significantly slower at all temperatures than those from the North Sea, which showed maximum values of 2.3 %/day at 12°C. Significant differences between Norwegian cod and North Sea cod were seen only at 4°C and 8°C. The weight increments of the males were

Results

significantly lower in North East Arctic than in North Sea and Norwegian coastal cod measured at 8°C and also lower than in North Sea cod kept at 12°C.

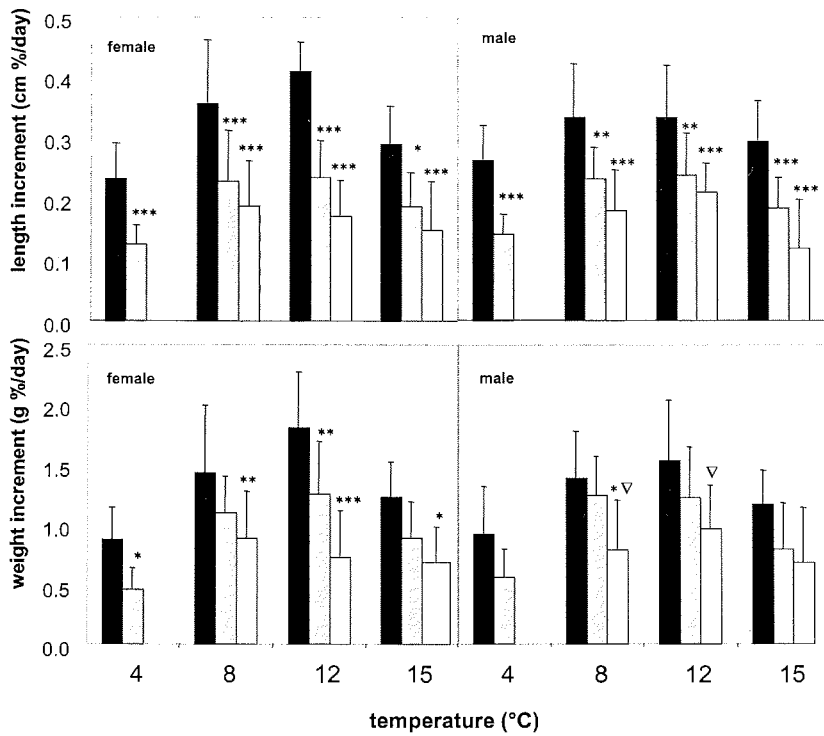
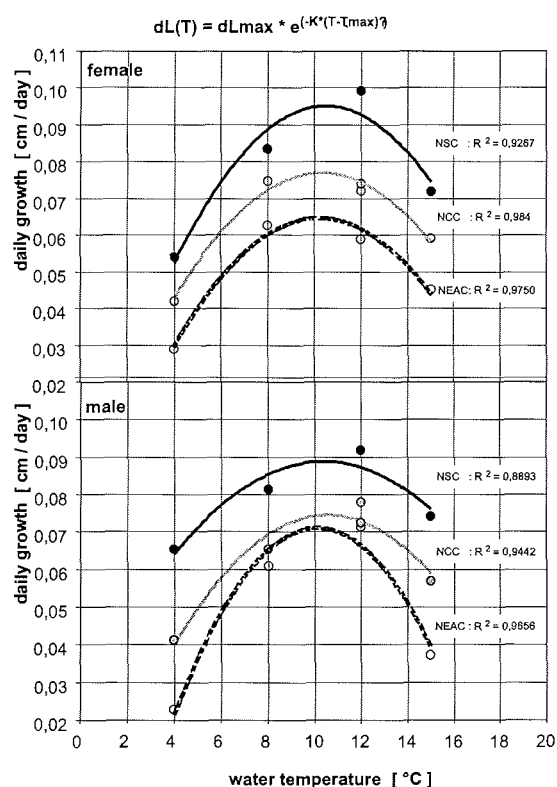


Fig. 12: Experimental growth rates (percent length (cm) and weight (g) increments per day) of males and females of **North Sea cod**, *Norwegian coastal cod* and North East Arctic (white column) cod at different temperatures. Values are means ± standard deviation. Asterisks indicate a significant difference from values of North Sea cod. Triangle indicate a significant difference between Norwegian Coastal cod and North East Arctic cod: ANOVA/Tukey Kramer multiple comparison test: *p<0.05, **p<0.01, ***p<0.001, n: 7-21. Raw data for Norwegian coastal cod and North East Arctic cod by Johansen & Naevdal (2000 – unpublished data).

4.2.5 Optimum temperature for growth

The calculations for the optimum temperature for growth of cod from different populations were based on the raw length increment data of the growth experiments. The analysis revealed the highest growth rates for females and males of cod from the North Sea followed by the animals from the Norwegian coast and the North East Arctic region (Fig. 13). The highest growth rates in all three populations were measured between a water temperature of 10 - 11°C which can be seen as the optimum temperature for growth.



The values for North East Arctic cod kept at 4°C were estimated.

$$NEAC4^{\circ}C-dL_{mean} = (NCC4^{\circ}C dL_{mean} - ((NCC8^{\circ}C dL_{mean} - NEAC8^{\circ}C dL_{mean}) + (NCC12^{\circ}C dL_{mean} - NEAC12^{\circ}C dL_{mean}) + (NCC15^{\circ}C dL_{mean} - NEAC15^{\circ}C dL_{mean}))/3)$$

parameter	North Sea cod (NSC)		Norwegian coastal cod (NCC)		Northeast Arctic cod (NEAC)	
	female	male	female	male	female	male
DL max	0.099	0.933	0.075	0.075	0.067	0.075
K	0.013	0.009	0.013	0.013	0.019	0.030
T max	10.737	10.565	10.490	10.460	10.286	10.457
r ²	0.977	0.958	0.973	0.998	0.972	0.996

Fig.13: Modelled growth curves and parameters of the model equation of cod from the North Sea, the Norwegian coast and the North East Arctic region as derived from the experimental growth studies. Values are mean. n: 7-21. Raw data for Norwegian coastal cod and North East Arctic cod from Johansen & Naevdal (2000 – unpublished data).

4.2.6 Growth of cod and climate change

To evaluate the influence of a global warming in Europe with an associated rise in water temperatures on growth of cod from the North Sea, the Norwegian coast and the North East Arctic a scenario was developed based on the model equation gained from the growth experiments in this thesis. It has to be mentioned that this scenario should function as a basis for a comprehensive discussion focussing on the effect of temperature on growth. Therefore, food limitation or migration due to temperature were neglected in this scenario. However, these aspects will be discussed in chapter 5.

Fig. 14 (A) illustrates the monthly mean water temperatures at a depth between 0 -100 metres for the period 1900-1998 as calculated by Dippner (1999) from ICES data. The corresponding water temperatures in the case of a water temperature rise of 1.5°C have been shown in Fig. 14 (B).

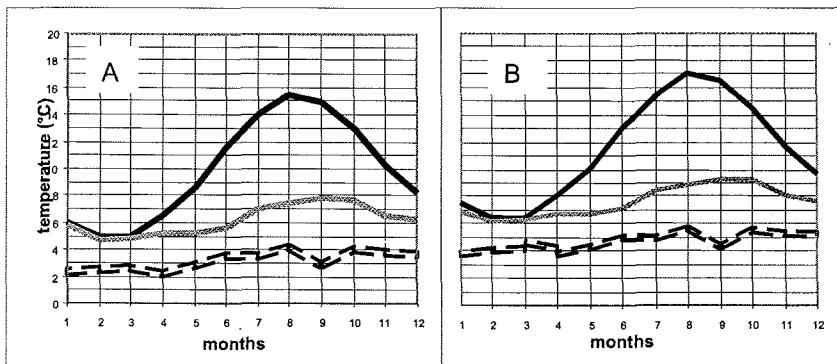


Fig. 14: Monthly mean water temperatures at a depth between 0-100 metres for the period 1900-1998 as calculated by Dippner 1999 (A) from ICES Data and during a scenario of a 1.5°C rise in temperature (B) from the Southern North Sea (black line), Norwegian coastal waters (grey line) and the Barents Sea (dotted line).

Fig. 15 (A) illustrates the higher water temperatures and seasonality of the Southern North Sea between spring and winter with a peak of 15°C in summer, followed by lower temperatures of the Norwegian coastal waters and the Barents Sea.

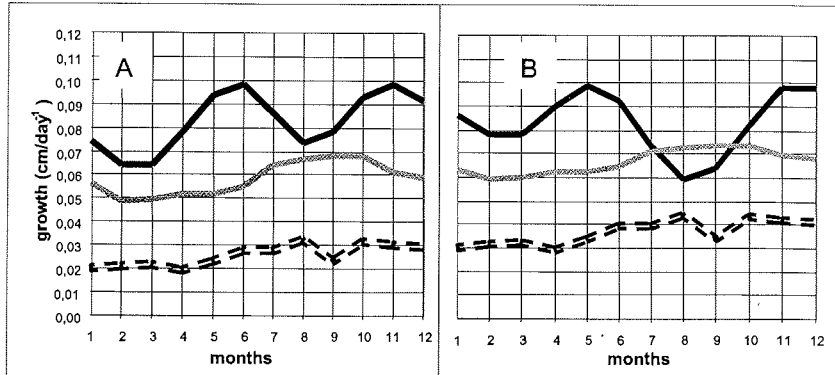


Fig.15: Daily growth rates in a yearly cycle of female cod from the Southern North Sea (black line), Norwegian coastal waters (grey line) and the Barents Sea (dotted line) calculated by the model growth equation $dL(T) = dL_{max} * e^{(-K * (T - T_{max}))}$. Temperatures based on the data from Dippner (1999) (A) and of a scenario of a 1.5°C rise (B), see fig. 14.

The actual water temperatures (Fig. 15 A) of the North Sea led to the highest length increment values and a strong seasonal variability for growth of cod living in this region. Here, two high peaks for growth existed: one in June and one in November, when the environmental temperatures for North Sea cod corresponds to the optimum temperature of 10.7 °C as found out in the growth experiments. Low peaks of growth for North Sea cod also resulted in winter when the water temperature of the Southern North Sea drops to 5°C and in summer when the temperatures can reach 15°C between July and September. So growth is negatively affected by water temperatures below or beyond the optimal range.

The winter temperatures of Norwegian coastal waters are the same as in the Southern North Sea, but throughout the yearly cycle the northern waters are colder and the temperature fluctuations are not so high. Here, a maximum of 8°C occurs in summer. So growth of Norwegian cod is more or less constant from February to June and increases to 0.07 cm/day in September. The environmental temperatures for cod from the Barents Sea never exceed 4°C and are more constant compared to the other regions. Growth of cod living in

Results

this region does not fluctuate very much and length increments (between 0.02 and 0.03 cm/day) are much smaller than of specimens inhabiting the Southern North Sea and Norwegian coastal waters. In the case of a temperature rise by 1.5°C individuals growth would increase in three populations in winter and spring. Changes are highest for Arctic fish and length increments would be doubled. With increasing summer temperatures growth of North Sea cod would decrease and in August the length increment of these individuals would drop down to a theoretical value of 0.048 cm per day. In this case, growth of North Sea specimens would be lower than of cod from the more northerly and colder areas.

4.3 Fecundity studies

On the basis of oocyte countings of North Sea and Baltic cod and literature data for North East Arctic cod (Kjesbu 1988) and Norwegian coastal cod (Botros 1962), absolute fecundity was calculated for each individual. High variability of fecundity of North Sea and Baltic cod was observed.

In Fig. 16 and Fig. 17 the estimated fecundities were plotted versus age (years) and body lengths (cm). The fecundity-age plots revealed an exponential relationship for Baltic Sea, Norwegian coastal and North East Arctic cod (Tab. 10). However, a linear formula appears to fit the North Sea cod data best. Fecundity at age was highest for North Sea cod, followed by the lowest values in North East Arctic cod with intermediate results for animals from the Norwegian coast and the Baltic Sea (Fig. 16). For example, North Sea cod at four years produce more than two million eggs per season whereas cod from the Baltic produce less than about one million eggs per season at the same age.

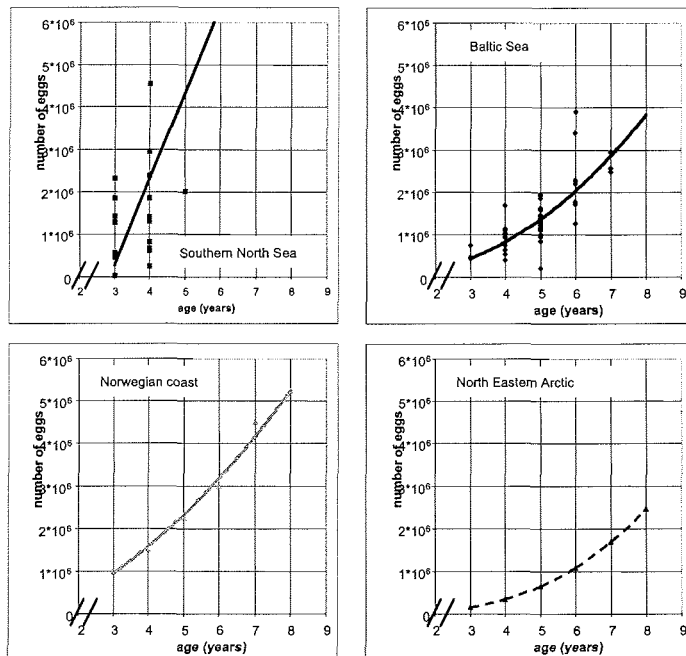


Fig. 16: Relationship between absolute fecundity and age (years) in cod of various regions (Southern North Sea, Norwegian coast, Baltic Sea, North East Arctic). Data for the North East Arctic by Kjesbu (1988) and or the Norwegian Coast by Botros (1962).

Results

Regression analysis showed higher coefficients of determination (r^2) for fecundity at length compared to fecundity at age. The fecundity-length plots revealed an exponential relationship for Norwegian coastal cod and North East Arctic cod (Tab. 10). Linear formulae fit the data of North Sea cod and Baltic cod best. In contrast to the age-fecundity plots, the length-fecundity plots revealed a higher absolute fecundity for Baltic Sea cod than for North Sea cod: 60 cm long cod from the North Sea produced about one million eggs, but about three million eggs were found for Baltic cod at the same length.

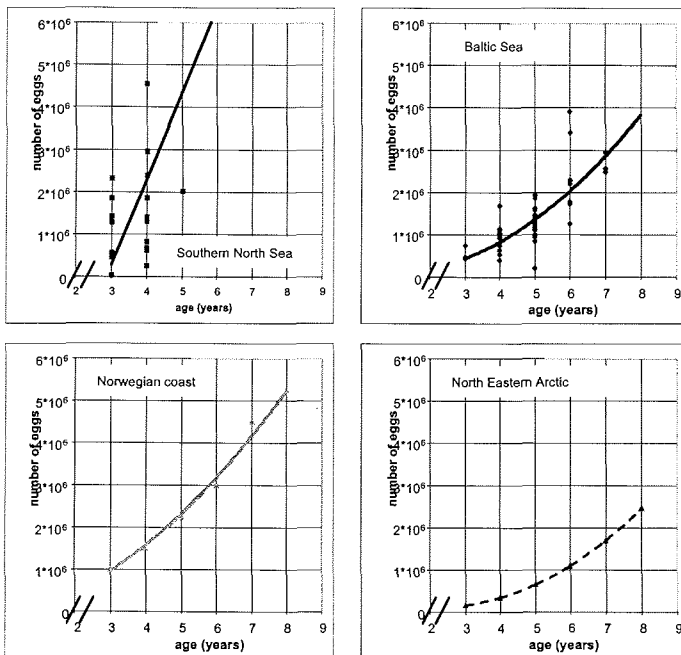


Fig. 17: Relationship between absolute fecundity and length (cm) in cod from various regions (Southern North Sea, Norwegian coast, Baltic Sea, North East Arctic). Data for the Arctic by Kjesbu (1988), for the Norwegian coast by Botros (1962).

Results

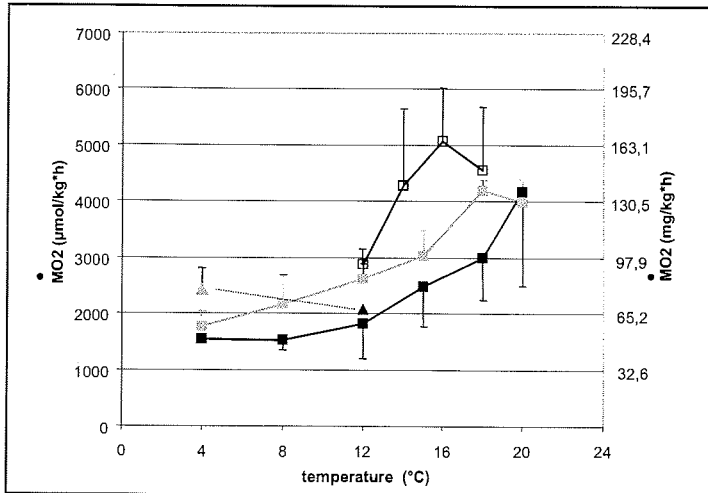
Table. 10: Regression formulae for absolute fecundity of different cod populations
 F_{abs} = absolute fecundity, L = total body length (cm), A = age (years)

Fecundity versus age			
Region	Regression	n	r ²
Baltic Sea	$F_{abs} = 37870 * A^{2.2}$	59	0.554
Norwegian Coast	$F_{abs} = 140101 * A^{1.7}$	-	No data available (Botros 1962)
Southern North Sea	$F_{abs} = 2 * 10^6 * A - 6 * 10^6$	22	0.589
North East Arctic	$F_{abs} = 6.84 * 10^3 * A^{2.8}$	111	0.84 (Kjesbu 1988)
Fecundity versus total body length			
Region	Regression	n	r ²
Baltic Sea	$F_{abs} = 172308 * L - 7 * 10^6$	59	0.710
Norwegian Coast	$F_{abs} = 139400 * (L - 50.4)$	-	No data available (Botros 1962)
Southern North Sea	$F_{abs} = 131648 * L - 7 * 10^6$	22	0.583
North East Arctic	$F_{abs} = 0.804 * L^{3.4}$	111	0.922 (Kjesbu et al. 1988)

4.4 Respiration of whole animals

Oxygen uptake increased with rising temperature in cod from all investigated populations. The highest respiration rates were found in White Sea cod in the range between 12°C and 20°C (Fig. 18). It reached a maximum value of about 5000 mmol/kg*h at 16°C and differed significantly from the corresponding value for North Sea cod acclimated to 12°C. Above 16°C a decrease of aerobic metabolic rate was found in White Sea cod and above 18°C in North Sea cod acclimated to 4°C such a drop in metabolic rate also occurred. The acclimation to 4°C of Southern North Sea cod caused an elevation of oxygen consumption in comparison to the respiration rates of North Sea cod maintained at 12°C. These differences were significant at 15°C and 18°C. Analysis of covariance (ANCOVA) revealed significant differences between all treatments of the three groups (WSC-12°C, NSC-4°C, NSC-12°C) (Tab. 11) Oxygen consumption rates of the North East Arctic fish acclimated to 4°C and measured at this temperature were significantly higher than North Sea animals acclimated to 4°C and 12°C (Tab. 12). This difference between North East Arctic cod and North Sea cod was no longer evident in specimens acclimated to 12°C.

Results



Gadus morhua from the White Sea (WSC) □ 12°C (body length: 26 – 32cm, body weight: 162 – 325g)
Gadus morhua from the Southern North Sea (NSC) △ 4 °C ■ 12 °C (body length:26 – 38cm; body weight: 207 – 559g)
Gadus morhua from the North Eastern Arctic (NEAC) ▲ 4 °C ▲ 12 °C (body length: 33 – 40cm; body weight: 169 – 325g)

Fig. 18: Temperature dependent oxygen consumption (mean ± SD) of White Sea cod (WSC) acclimated to 12°C, and of Southern North Sea cod (NSC) and North East Arctic cod (NEAC) acclimated to 4°C and 12°C. n: 3 – 6.

Tab. 11: Overview of sample sizes and statistical differences (ANCOVA/Tukey-Kramer multiple comparison test) between oxygen uptake curves of North Sea cod acclimated to 4°C or 12°C and White Sea cod acclimated to 12°C (see Fig.18). Data were ln-transformed prior to analysis.

comparison	level of significance
NSC-12°C < NSC-4°C	p < 0.05
NSC-4°C < WSC-12°C	p < 0.05
NSC-12°C < WSC-12°C	p < 0.05

Tab. 12: Overview of calculated statistical differences between oxygen uptake values of different populations and acclimation temperatures. Data were compared at the same measurement temperatures. Comparisons based on the Mann-Whitney test using raw data.

comparison	measuring temperature (°C)	level of significance
NSC-12°C < WSC-12°C	15°C/16°C	p < 0.01
NSC-4°C < WSC-12°C	15°C/16°C	p < 0.05
NSC-12°C < NSC-4°C	15°C	p < 0.05
NSC-12°C < NSC-4°C	18°C	p < 0.001
NSC-12°C < WSC-12°C	18°C	p < 0.05
NSC-4°C < NEAC-4°C	4°C	p < 0.05
NSC-12°C < NEAC-4°C	4°C	p < 0.05

4.5 Respiration of isolated liver mitochondria

The capacity of mitochondrial energy production, as well as mitochondrial proton leakage, mitochondrial respiratory coupling ratios ($R_{CR_{ol}}$), and ADP/O-ratios, were investigated in isolated liver mitochondria of *Gadus morhua* in relation to temperature and two cod populations (NSC, NEAC) chosen from the latitudinal cline. Arrhenius-Break temperatures and activation energy characterized the thermal sensitivity of mitochondrial respiration.

4.5.1 Capacity of ATP-formation

Aerobic capacity (state-III respiration of isolated cod liver mitochondria calculated per mg mitochondrial protein) was higher in North East Arctic cod than in North Sea cod (Fig. 19). This difference was maintained at all temperatures of analysis. A maximum rate of 106 nmol O/min * mg protein was reached at 18°C for Arctic cod acclimated to 12°C. The capacity of mitochondrial state-III respiration was about 2 -3 times lower in animals from the North Sea than in specimens from the North East Arctic region. At 4°C the differences between the mean values were too small to be significant between the two acclimated populations. From 8°C to 20°C the mitochondrial oxygen uptake values per mg protein of North Sea cod acclimated to 4°C and 12°C were significantly lower than the corresponding data from Arctic animals (Tab. 13 & 14).

Within the populations acclimation temperature did not have a general effect on state-III rates. There were no significant differences between the state III rates of North Sea cod acclimated to 4°C and 12°C. Only for North Sea cod acclimated to 15°C a higher mitochondrial oxygen consumption was found above 15°C compared to the rates of North Sea cod acclimated to 4°C and 12°C and measured at 15°C. No significant acclimation effect was found for North East Arctic cod.

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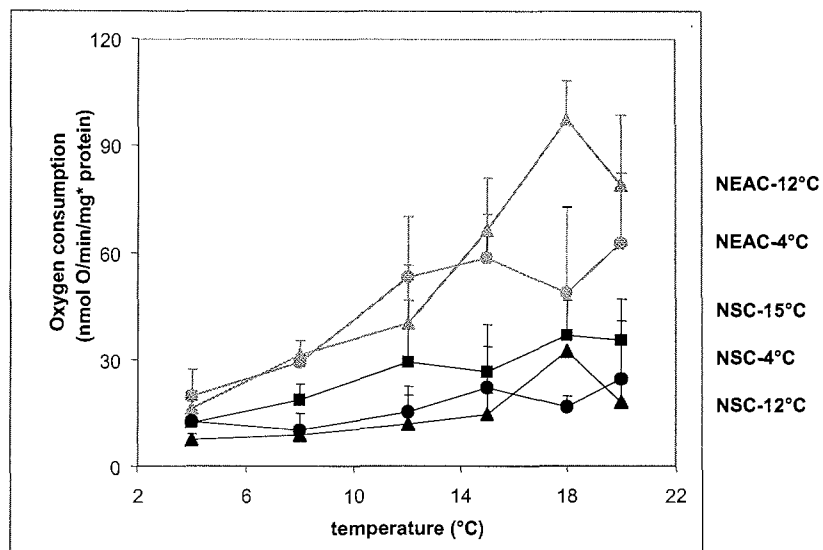


Fig.19: Temperature dependent capacity of ATP formation (state-III respiration: mean±SD) in isolated liver mitochondria of North Sea cod (**NSC**) (body length:26 – 45cm, body weight: 152 - 450g) and Arctic cod (**NEAC**) (body length: 33 – 40cm, body weight: 169 - 325g) acclimated to 4°C (○), 12°C (△) and 15°C (□). n: 2-8, n: 2 for NSC-12°C and NSC-15°C analysed at 18°C.

Tab. 13: Significance of statistical differences (ANCOVA/Tukey-Kramer multiple comparison Test) between state III-respiration rates of isolated liver mitochondria in North Sea cod (NSC) and Arctic cod (NEAC) acclimated to 4°C, 12°C and 15°C. The data were ln-transformed prior to analysis.

comparison	level of significance
NSC-4°C < NSC-15°C	p < 0.05
NSC-4°C < NEAC-4°C	p < 0.001
NSC-4°C < NEAC-12°C	p < 0.001
NSC-12°C < NSC-15°C	p < 0.001
NSC-12°C < NEAC-4°C	p < 0.001
NSC-12°C < NEAC-12°C	p < 0.001
NSC-15°C < NEAC-4°C	p < 0.001
NSC-15°C < NEAC-12°C	p < 0.001

Results

Tab. 14: Overview of calculated statistical differences between mitochondrial oxygen uptake values (state III-respiration) of different populations and acclimation temperatures compared at the same temperatures of analysis. Data availability at 18°C was insufficient for statistical analyses. Comparison based on the Mann-Whitney test using raw data.

comparison	temperature (°C) of analysis	significance
NSC-4°C < NEAC-4°C	8	p<0.05
NSC-4°C < NEAC-12°C		p<0.05
NSC-12°C < NEAC-4°C		p<0.01
NSC-12°C < NEAC-12°C		p<0.01
NSC-15°C < NEAC-4°C		p<0.05
NSC-15°C < NEAC-12°C		p<0.05
NSC-4°C < NEAC-4°C	12	p<0.05
NSC-4°C < NEAC-12°C		p<0.05
NSC-12°C < NEAC-4°C		p<0.05
NSC-12°C < NEAC-12°C		p<0.05
NSC-4°C < NEAC-4°C	15	p<0.05
NSC-4°C < NEAC-12°C		p<0.05
NSC-12°C < NEAC-4°C		p<0.05
NSC-12°C < NEAC-12°C		p<0.05
NSC-15°C < NEAC-4°C		p<0.05
NSC-15°C > NSC-12°C		p<0.05
NSC-12°C < NEAC-4°C	18	not possible
NSC-12°C < NEAC-12°C		
NSC-12°C < NSC-4°C		
NSC-15°C > NSC-12°C		
NSC-4°C < NEAC-4°C	20	p<0.05
NSC-4°C < NEAC-12°C		p<0.05
NSC-12°C < NEAC-4°C		p<0.05
NSC-12°C < NEAC-12°C		p<0.01
NSC-15°C > NSC-12°C		p<0.05

4.5.2 Proton leakage

Mitochondrial proton leakage rates (state-IV + oligomycin respiration per mg mitochondrial protein) depended on acclimation temperature and population in a similar way as state III-respiration did (Fig. 20). The maximum mean value ($18.8 \text{ nmol/min} \cdot \text{mg protein}^{-1}$) was determined for Arctic cod acclimated to 12°C and measured at 18°C . Mitochondria from Arctic cod acclimated to 4°C displayed significant higher proton leakage values than cold acclimated North Sea animals (Tab. 15 & 16). No acclimation effect on mitochondria from North East Arctic cod was found. Just in the case of North Sea cod acclimated to 15°C an acclimation effect could be observed. These animals displayed a significantly higher level of proton leakage than cold acclimated North Sea individuals.

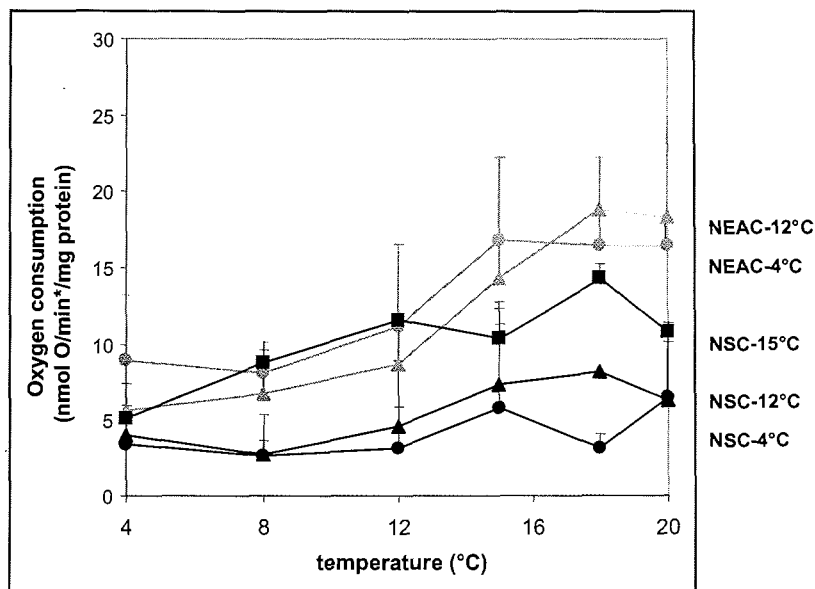


Fig. 20: Mitochondrial proton leakage rates reflected by temperature dependent oxygen consumption (state IV + oligomycin: mean values \pm SD) in North Sea cod (NSC) (body length: 26 – 45cm, body weight: 152 – 450g) and Arctic cod (NEAC) (body length: 33–40cm, body weight: 169 – 325g) acclimated to 4°C (O), 12°C (Δ) and 15°C (\square). n: 2-8, n: 2 for NSC- 12°C and NSC- 15°C analysed at 18°C .

Results

Tab.15: Significance of statistical differences (ANCOVA/ Tukey-Kramer multiple comparison Test) between proton leakage rates (state IV + oligomycin) of isolated liver mitochondria in North Sea cod (NSC) and Arctic cod (NEAC) acclimated to 4°C, 12°C and 15°C. The data were ln-transformed prior to analysis.

comparison	level of significance
NSC-4°C < NSC-15°C	p < 0.001
NSC-4°C < NEAC-4°C	p < 0.001
NSC-4°C < NEAC-12°C	p < 0.001
NSC-12°C < NSC-15°C	p < 0.01
NSC-12°C < NEAC-4°C	p < 0.001
NSC-12°C < NEAC-12°C	p < 0.001

Tab.16: Overview of calculated statistical differences between mitochondrial proton leakage rates (state IV + oligomycin) of different populations and acclimation temperatures compared at the same temperature of analysis. comparison based on the Mann-Whitney test using raw data. Data availability at 18°C was insufficient for statistical analyses.

comparison	temperature (°C) of analysis	significance
NSC-4°C < NEAC-4°C	8	p<0.05
NSC-4°C < NEAC-4°C	12	p<0.05
NSC-4°C < NEAC-12°C		p<0.05
NSC-4°C < NSC-15°C		p<0.05
NSC-4°C < NEAC-4°C	15	p<0.05
NSC-4°C < NEAC-12°C		p<0.01
NSC-4°C < NSC-15°C		p<0.05
NSC-12°C NEAC-4°C	18	not possible
NSC-12°C NEAC-12°C		
NSC-12°C NSC-4°C		
NSC-15°C NSC-12°C		
NSC-4°C < NEAC-4°C	20	p<0.05
NSC-4°C < NEAC-12°C		p<0.01
NSC-12°C < NEAC-4°C		p<0.05
NSC-12°C < NEAC-12°C		p<0.01
NSC-15°C < NEAC-12°C		p<0.05
NSC-15°C < NSC-12°C		p<0.05

4.5.3 Respiratory control ratio (RCR_{ol})

Liver mitochondria of *Gadus morhua* displayed a mean respiratory control ratio (RCR) between 2 and 6 and no significant temperature dependent trend was observed. Liver mitochondria from North Sea cod acclimated to 4°C displayed significantly higher RCR values than those from North Sea animals kept at 15°C when compared at 4°C (Fig. 21). The RCR-values of the two populations acclimated to the same temperatures only differed in one case (Tab. 17). Mitochondria from North Sea cod acclimated to 4°C and measured at 4°C displayed significantly higher respiratory control ratios than the corresponding North East Arctic cod mitochondria.

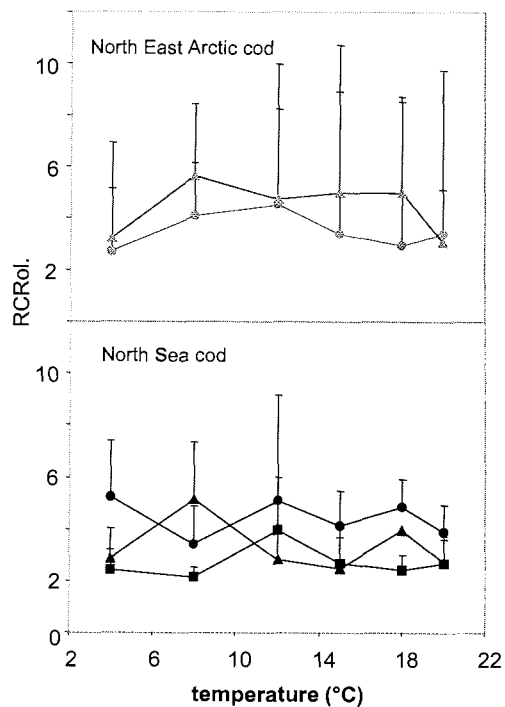


Fig. 21: Respiratory coupling ratios of isolated liver mitochondria from North Sea cod (NSC) and Arctic cod (NEAC) acclimated to 4°C (O), 12°C (Δ) and 15°C (□). n: 2-8.

Results

Tab. 17: Overview of calculated statistical differences between mitochondrial respiratory coupling ratios of different populations and acclimation temperatures compared at the same temperatures of analysis.

comparison		temperature (°C) of analysis	significance
NSC-4°C > NEAC-4°C		4	p<0.05
NSC-15°C < NSC-4°C			p<0.05
NSC-15°C < NSC-12°C		8	p<0.05
NSC-12°C	NEAC-4°C	18	not possible
NSC-12°C	NEAC-12°C		
NSC-12°C	NSC-4°C		
NSC-15°C	NSC-12°C		
NSC-12°C < NSC-4°C		20	p<0.05

Comparison based on the Mann-Whitney test using raw data.
Data availability at 18°C was insufficient for statistical analyses.

4.5.4 ADP/O ratio

The phosphorylation efficiency measured as the ADP/O ratio decreased with increasing temperatures in North East Arctic cod and North Sea cod (Fig. 22). Liver mitochondria from North Sea cod acclimated to 12°C displayed significantly higher values than North Sea cod acclimated to 15°C and than North East Arctic cod acclimated to 4°C and 12°C (Tab. 18 & 19).

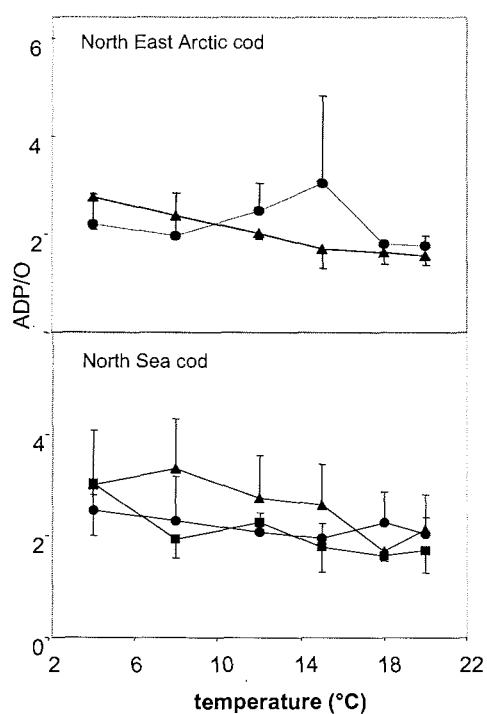


Fig. 22: Phosphorylation efficiency (ADP/O ratio) of isolated liver mitochondria in North Sea cod (NSC) and North East Arctic cod (NEAC) acclimated to 4°C (O), 12°C (Δ) and 15°C (□). n: 2 – 8.

Tab. 18: Significance of differences (ANCOVA) between phosphorylation efficiencies (ADP/O ratio) in isolated liver mitochondria of North Sea cod (NSC) and Arctic cod (NEAC) acclimated to 4°C, 12°C or 15°C. The data were ln-transformed prior to analysis. NSC-4°C had to be excluded from the ANCOVA-test because of non-homogenous variances.

comparison	level of significance
NSC-12°C > NSC-15°C	p < 0.01
NSC-12°C > NEAC-4°C	p < 0.01
NSC-12°C > NEAC-12°C	p < 0.01

Results

Tab. 19: Overview of calculated statistical differences between the phosphorylation efficiencies (ADP/O ratio) of different populations and acclimation temperatures compared at the same temperature of analysis. Comparison based on the Mann-Whitney test. One test was not possible because of non-homogeneous variances. Data availability at 18°C was insufficient for statistical analyses.

comparison	temperature (°C) of analysis	significance
NSC-12°C > NEAC-4°C	8	p<0.05
NSC-12°C > NSC-4°C		p<0.05
NSC-12°C > NEAC-12°C	15	p<0.05

4.5.5 Arrhenius break-temperature (ABT) and activation energy

Neither in North Sea cod nor in North East Arctic cod an Arrhenius discontinuity (ABT) for state-III-respiration rates and state-IV_{ol.}-respiration rates respectively of isolated liver mitochondria was detected (Fig. 23 & 24). Higher acclimation temperatures led to a somewhat higher level of Arrhenius activation energy. In North Sea and North East Arctic cod mitochondria, however, no significant differences were seen between populations and acclimation temperatures (Tab. 20 & 21).

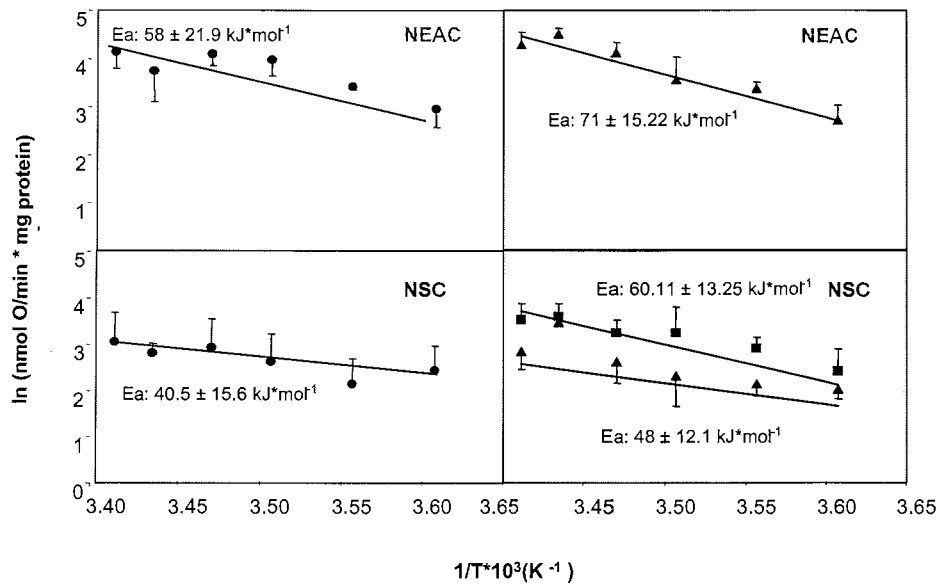


Fig. 23: Arrhenius plots of state-III respiration and Arrhenius activation energies (E_a) of isolated liver mitochondria in North Sea cod (NSC) and North East Arctic cod (NEAC) acclimated to 4°C (O), 12°C (Δ) and 15°C (□). n: 1-8.

Results

Tab. 20: Regression formulae of the different Arrhenius plots of state-III-respiration rates.

NSC-4°C f(4°C – 20°C) = -3.2302x + 12.70 (r ² : 0.7922, p: 0.0175)
NSC-12°C f(4°C – 20°C) = -4.4009x + 17.12 (r ² : 0.7595, p: 0.0237)
NSC-15°C f(4°C – 20°C) = -6.78x + 25.61 (r ² : 0.8745, p: 0.0283)
NEAC-4°C f(4°C – 20°C) = -4.1838x + 17.119 (r ² : 0.8783, p: 0.0057)
NEAC-12°C f(4°C – 20°C) = -6.4638x + 24.884 (r ² : 0.9043, p: 0.0036)

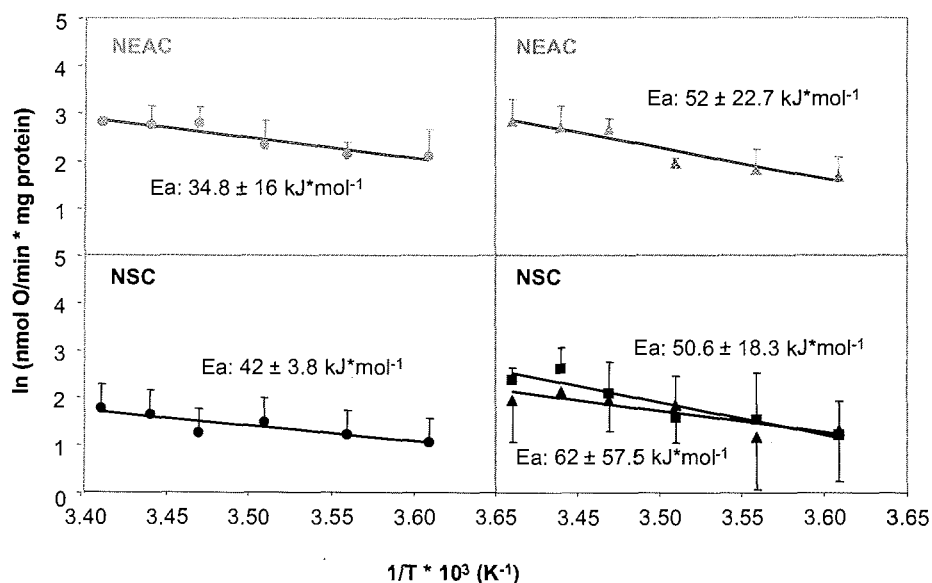


Fig. 24: Arrhenius plots of state-IV_{o1}-respiration and Arrhenius activation energies (E_a) of isolated liver mitochondria in North Sea cod (NSC) and North East Arctic cod (NEAC) acclimated to 4°C (O), 12°C (Δ) and 15°C (□). n: 2-8.

Tab. 21: Regression formulae of the different Arrhenius plots of state-IV-respiration rates.

NSC-4°C f(4°C – 20°C) = -4.1884x + 17.296 (r ² : 0.2062, p: 0.0025)
NSC-12°C f(4°C – 20°C) = -3.6928x + 15.315 (r ² : 0.2387, p: 0.0067)
NSC-15°C f(4°C – 20°C) = -6.8268x + 26.983 (r ² : 0.5105, p: 0.0001)
NEAC-4°C f(4°C – 20°C) = -8.8047x + 34.711 (r ² : 0.4585, p: 0.0014)
NEAC-12°C f(4°C – 20°C) = -8.4711x + 33.421 (r ² : 0.7580, p: 0.0992)

In summary, oxygen consumption was higher in White Sea cod and North East Arctic cod than in North Sea animals at the same temperature. Within a population acclimation to cold temperatures led to an elevated metabolic rate. The latitudinal differences between populations could also be seen in the capacities of liver mitochondria. Aerobic capacity (state-III respiration) and proton leakage (state-IV_{oi} respiration) of isolated cod liver mitochondria were higher in North East Arctic cod than in North Sea cod.

The acclimation effect on liver mitochondria of cod was not obvious compared to the differences in oxygen uptake values of the whole animals. No effect of acclimation on state III respiration and proton leakage was found for North East Arctic cod. A higher mitochondrial oxygen consumption rate (state-III) and proton leakage was only found for North Sea cod acclimated to 15°C when compared to the rates for North Sea cod acclimated to 4°C and 12°C.

Liver mitochondria of *Gadus morhua* were coupled with a mean respiratory control ratio (RCR) between 2 and 6 and no temperature dependent trend was observed.

In North Sea cod higher acclimation temperature led to lower RCR_{oi} values, but no latitudinal trend was observed. The phosphorylation efficiency (ADP/O ratio) decreased with increasing temperatures in North East Arctic cod and North Sea cod and the highest values were found in liver mitochondria from North Sea cod acclimated to 12°C. Neither in North Sea cod nor in North East Arctic cod an Arrhenius break point was detected for state-III respiration rates of isolated liver mitochondria. No significant differences in Arrhenius activation energy were seen between populations and acclimation temperatures.

4.6 Relationship between whole liver and mitochondrial capacities

4.6.1 Liver size of laboratory maintained cod

To estimate whether acclimation temperature affected the liver sizes of laboratory maintained cod from different populations, the HSI of North Sea cod reared at 4°C, 12°C and 15°C were compared to the HSI of North East Arctic cod kept at 4°C and 12°C (Fig. 25). Acclimation to cold temperatures led to a higher HSI. Within the populations, acclimation temperature did have a significant effect on the HSI of North East Arctic cod. A significant lower mean HSI of 0.7 was found for North East Arctic cod acclimated to 12°C in comparison to a mean value of 0.9 in North East Arctic cod maintained at 4°C (Tab. 22). The HSI of North Sea cod displayed a mean value of 1.2 for animals acclimated to 12°C and 15°C and reached a mean value of 2 for North Sea cod acclimated to 4°C. A Tukey-Kramer multiple comparison test revealed a significantly higher mean HSI for NSC-4°C than for NEAC-12°C (Tab. 23).

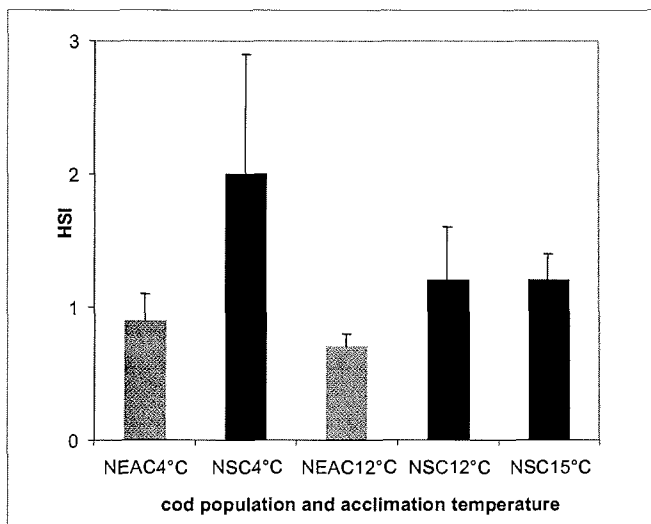


Fig.25: Hepatosomatic Index (HSI) (means \pm standard deviation) of North Sea cod acclimated to 4°C (NSC-4°C), 12°C (NSC-12°C) and to 15°C (NSC-15°C) and of North East Arctic cod acclimated to 4°C (NEAC-4°C) and to 12°C (NEAC12°C). n: 3-7.

Ranges of body weight (g) and liver sizes (g):
 NEAC4°C (body weight: 251g - 325g, liver weight: 2.2g - 2.8g)
 NEAC12°C (body weight: 164g - 268g, liver weight: 1.1g - 1.8g)
 NSC4°C (body weight: 224g - 502g, liver weight: 2.7g - 10.4g)
 NSC12°C (body weight: 185g - 497g, liver weight: 1.9 - 7.5g)
 NSC15°C (body weight: 126g - 274g, liver weight: 1.6g - 5.3g)

Tab. 22: Significance of statistical differences (ANOVA/Tukey-Kramer multiple comparison Test) between HSI of North Sea cod acclimated to 4°C, 12°C and 15°C and North East Arctic cod acclimated to 4°C and 12°C (see Fig. 24)

comparison	level of significance
NEAC-12°C < NSC- 4°C	p< 0.05

Tab. 23: Overview of calculated statistical differences between HSI of different populations and acclimation temperatures. Comparison based on the unpaired two way t-test using raw data.

comparison	level of significance
NSC-4°C = NSC-12°C	-
NSC-4°C = NSC-15°C	-
NSC-12°C = NSC-15°C	-
NSC- 4°C = NEAC-4°C	-
NSC-12°C = NEAC-12°C	-
NEAC-12°C < NEAC-4°C	p<0.05

4.6.2 Aerobic capacity of ATP-formation (state-III respiration) in whole liver

According to the capacities of ATP-formation (state-III respiration) in isolated liver mitochondria (Fig. 26) the mitochondrial oxygen consumption of whole liver of cod from the North East Arctic was higher than in North Sea cod when compared at the same acclimation temperature (Fig. 26). This latitudinal difference was significant between NSC-12°C and NEAC-12°C. Within the populations higher mitochondrial aerobic capacities were determined for North Sea cod and North East Arctic cod acclimated to 4°C than in animals of the same population kept at 12°C, however these differences were not significant. Nonetheless, acclimation of North Sea cod to 15°C led to a significantly higher level of oxygen consumption of whole liver than in North Sea cod acclimated to 12°C (Tab. 24).

Results

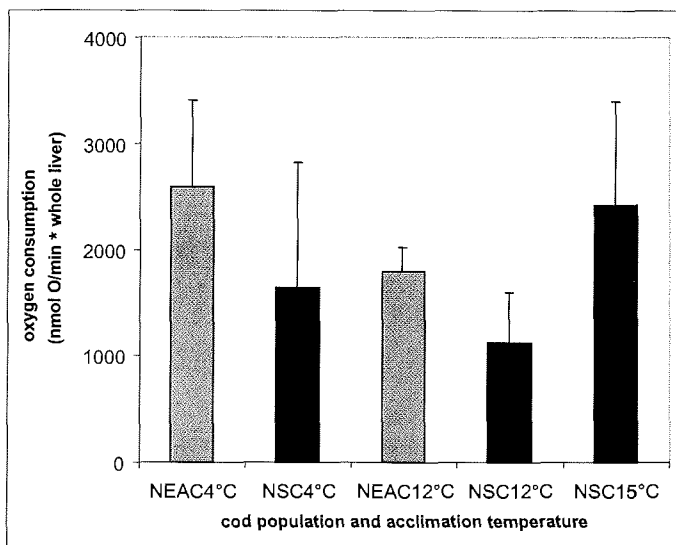


Fig. 26: Capacity of ATP-formation (state-III respiration: mean \pm standard deviation) at 12°C in total livers of North Sea cod (NSC) and North East Arctic cod (NEAC) acclimated to 4°C, 12°C and 15°C. n: 3- 7.

Tab. 24: Overview of calculated statistical differences between mitochondrial oxygen uptake values (state III-respiration) of different populations and acclimation temperatures compared at a temperature of analysis of 12°C. Comparison based on the unpaired two way t-test using raw data.

comparison	level of significance
NSC-4°C = NSC-12°C	-
NSC-4°C = NSC-15°C	-
NSC-12°C < NSC-15°C	p<0.05
NSC- 4°C = NEAC-4°C	-
NSC-12°C < NEAC-12°C	p<0.05
NEAC-12°C = NEAC-4°C	-

4.6.3 Proton leakage in whole liver

The proton leakage calculated to the whole liver of North East Arctic cod acclimated to 4°C and 12°C was slightly enhanced in comparison to the values of North Sea cod acclimated to the same temperatures (Fig. 27). However, these differences were not significant. Within the populations a significant higher proton leakage of the whole liver was found for North Sea cod acclimated to 15°C than for North Sea animals maintained at 4°C or 12°C (Tab. 25 & Tab. 26).

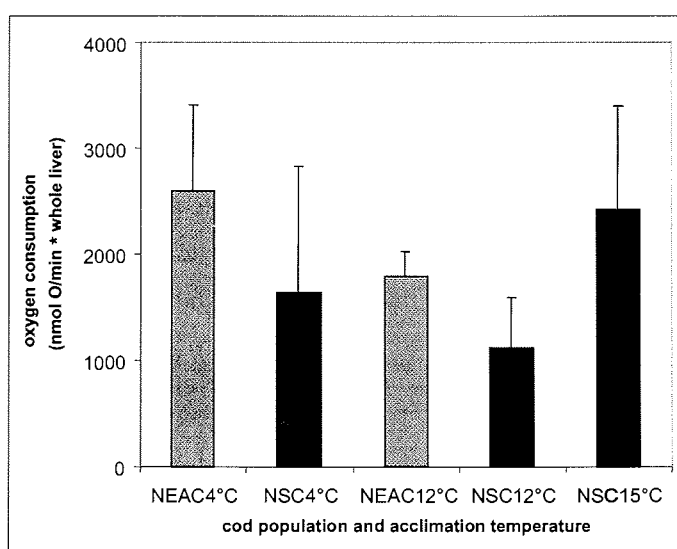


Fig. 27: Mitochondrial proton leakage rates (state-IV + oligomycin) at 12°C in liver mitochondria calculated to the whole liver of North Sea cod (NSC) and North East Arctic cod (NEAC) acclimated to 4°C, 12°C and 15°C. n: 3-7.

Tab. 25: Significance of statistical differences (ANOVA/Tukey-Kramer multiple comparison test) between proton leakage rates (state-IV + Oligomycin) of North Sea cod acclimated to 4°C, 12°C and 15°C and North East Arctic cod acclimated to 4°C. The different population and treatments were compared at a temperature of analysis of 12°C.

comparison	level of significance
NSC- 4°C < NSC- 15°C	p < 0.05
NSC- 12°C < NSC- 15°C	p < 0.05

Results

Tab. 26: Overview of calculated statistical differences between mitochondrial oxygen uptake values (state-III-respiration) of different cod populations and acclimation temperatures compared at a temperature of analysis of 12°C. Comparison based on the unpaired two way t-test using raw data.

comparison	level of significance
NSC-4°C = NSC-12°C	-
NSC-4°C < NSC-15°C	p<0.05
NSC-12°C < NSC-15°C	p<0.05
NSC- 4°C = NEAC-4°C	-
NSC-12°C = NEAC-12°C	-
NEAC-12°C = NEAC-4°C	-

5 Discussion

This study combined different aspects of ecology and physiology studies as a first step to develop a mechanistic understanding of the effects on climate change on cod. To improve the comprehensibility I divided the following discussion into two main chapters. Chapter 5.1 focuses on the ecology of growth and fecundity of cod particularly with respect to climate change and its consequences for the different populations. Chapter 5.2 links the ecological approaches with physiological studies, dealing with the effect of temperature on standard and mitochondrial metabolism of cod.

5.1 The effects of climate change on growth, fecundity, and distribution of cod

5.1.1 Growth in nature

Growth is the integration of a series of processes (feeding, assimilation, metabolism, transformation, and excretion) where all rates are influenced by temperature (Michalsen et al. 1998). The study of the effects of temperature on growth of cod can be used as an effective tool for catch forecasting and evaluation of the consequences of climate changes for this species (Brander 1995).

In many fish species, for example in plaice *Pleuronectes platessa* (L.) and dab *Limanda limanda* (L.) (Déniel 1990), growth is higher in populations living at lower latitudes than in those inhabiting waters closer to the pole. Many authors have shown that cod also grow faster in warmer waters (e.g. Daan 1974, Brander 1994). In accordance with these earlier findings, the von Bertalanffy growth curves of cod from different populations revealed decreased growth of cod from higher latitude. These growth analyses were based on otoliths readings – a reliable tool in growth research (Daan 1974).

The observed von Bertalanffy growth parameters reflect differences in life histories: Cod adapted to cold temperatures grow more slowly but reach greater maxima in length and mass due to a longer lifespan. The largest growth factor (k) was found in Baltic cod, followed by Southern North Sea cod and Norwegian

coastal cod, but these fast growing individuals reached a smaller maximum length than North East Arctic cod and White Sea cod. Due to similar environmental temperatures of Baltic cod and Southern North Sea cod, the differences in growth rates should be discussed under the light of the influence of salinity on growth of cod. Accordingly, Lambert et al. (1994) found higher growth rates in Atlantic cod maintained at lower salinities. The energetic cost of ion regulation is lowest in an isosmotic environment, and it can be argued that enough energy will be spared to increase growth rate in reduced salinity (reviewed by Morgan & Iwama 1999). Later Dutil et al. (1997) found that higher growth rates at low salinity in cod must be attributable to factors such as spontaneous activity and swimming performance rather than to changes in standard metabolic rates or in protein digestibility.

Additionally to von Bertalanffy growth rates, highest values of growth performance, expressed as Φ' , were found for cod from the lowest latitude and underline the influence of the temperature regime on growth of cod.

The growth data obtained by otolith reading and literature studies show a high variability between years, which is consistent with other investigations. Jørgensen (1992) also found differences in the growth increment of North East Arctic cod between different years. Variations in growth rates of early life stages may have a strong influence on size at subsequent age. Brander (2000) reported that 26% of the variability in weight at age three of cod appears to be due to bottom temperature experienced during their first years of life.

Growth dependent on population density has been shown for many heavily exploited marine fish stocks including cod, e.g. in the North Sea (Houghton & Flatman 1981, Daan et al. 1990) and the North-West Atlantic (Ross & Almeida, 1986, Marshall & Frank 1999). The average length of 1 - 3 year old Arcto-Norwegian cod tends to be small when the density of the cohort is high. Cod growth appears to be inversely related to population density, due to the reduced food availability for single individuals (Yaragina & Marshall 2000).

In nature, growth parameters determined by the von Bertalanffy growth equation revealed different life histories for cod from different populations. Nonetheless, values of growth performances after Pauly (1979) are still highest for cod living in the warm.

5.1.2 Experimental growth rates

To exclude the possible effects of variable food availability on growth of different cod populations and to estimate the optimum temperature for growth, Southern North Sea cod were reared at different temperatures and were fed in excess. These data were compared to growth studies on Norwegian coastal cod and specimens from North East Arctic region (Johansen & Naevdal 2000 - unpublished data).

Mortality of North Sea cod increased with increasing temperature. Johansen & Naevdal (2000 - unpublished data) reported the highest mortality rates (48%) for North East Arctic cod at 12°C and 15°C. These results correspond with the low ambient temperature for North East Arctic cod. The Arcto-Norwegian cod stock is distributed along the Northern Norwegian coast and in the oceanic regions of the Barents Sea – Svålbard area, where bottom temperatures never exceed 7°C (see Brander 1994b). Therefore, 12°C to 15°C can be considered close to the critical thermal maximum for North East Arctic cod.

In the present study, cod were fed in excess and like in other studies (e.g. Kohler 1964, Jobling 1988), food consumption of North Sea cod increased with increasing temperature. Reinitz et al. (1978) reported significant differences in food conversion among different populations of rainbow trout (*Oncorhynchus mykiss*). Unfortunately, Johansen & Naevdal (2000 - unpublished data) did not quantify the food consumed neither for Norwegian cod nor for North East Arctic cod in their growth experiment. Therefore, a comparison between food consumption rates of North Sea cod and North East Arctic cod or Norwegian coastal cod was not possible in these experiments.

No significant differences concerning growth were found between males and females neither for length nor for weight increments. Correspondingly, Pedersen & Jobling (1989) found only slight differences in growth performance of cod between sexes except during the short period associated with reproduction.

During long-term maintenance at different temperatures, growth in the present experimental study was significantly higher in Southern North Sea individuals, followed by lower growth rates in cod from the Norwegian coast and the North East Arctic (Johansen & Naevdal 2000 - unpublished data), respectively.

This corresponds with a study by Svåsand et al. (1996). They kept Arcto-Norwegian cod and Norwegian coastal cod under ambient environmental conditions in a Norwegian fjord. In accordance with the present study, Norwegian coastal cod also displayed significantly higher growth rates than Arcto-Norwegian cod.

These results coincide with field observations and strongly suggest a genetic difference that cannot be overcome by the lab acclimation or field acclimatization processes. Genetic studies have shown differences between cod in Norwegian waters and the Arcto-Norwegian cod (Jørstad & Naevdal 1989, Fevolden & Pogson 1996). Recently, Nielsen et al. (2001) found that analysis of nine microsatellite markers revealed major genetic differences between North Sea cod, Baltic cod and North East Arctic cod.

The observed elevated growth of cod living in the warm can be discussed in the light of latitudinal compensation in metabolic rate. Cossins & Bowler (1987) reported that individuals from higher latitudes usually have higher metabolic rates than specimens from low latitudes when compared at the same temperatures. The present study tests the hypothesis that elevated metabolic rate does not reflect high energy availability, but even more so, that elevated metabolic costs due to cold adaptation may result in lower energy availability for growth (see introduction). Details concerning the different physiological processes in different cod populations will be discussed in chapter 5.2 regarding oxygen consumption and mitochondrial capacities.

In contrast to the effects of thermal adaptation there is a model of counter gradient variation as reviewed in Jobling (1996): some high latitude fish have higher capacity for growth than low latitude individuals in order to compensate for a shorter growing season (e.g. for Atlantic silversides – *Menidia menidia*, Conover & Present 1990). A possible explanation for elevated growth of cold adapted species may be an increased food consumption and food conversion efficiency (e.g. Present & Conover 1992). Due to elevated growth rates for cod from low latitudes (Southern North Sea cod), counter gradient variation could not be shown in this study, which is in accordance with the observations by Otterlei et al. (1999): a comparison of Norwegian coastal cod and North East Arctic cod revealed stock-specific differences in mean weight at age, but no

countergradient latitudinal compensation in growth capacity of the two larval cod stocks.

The environmental temperatures for cod from the North East Arctic never exceed 4°C (Dippner 1999). In the study of Johansen & Naevdal (2000 - unpublished data) growth of North East Arctic cod was not studied at 4°C or below. Higher growth performance of North Sea cod and Norwegian cod in comparison to Arctic cod could reflect adjustment to the specific temperature regime used in the present growth experiment. No data about growth of North East Arctic cod below 4°C are available in the literature. In the future, further experiments should be undertaken with temperature regimes from 4°C down to sub-zero temperatures, characterizing the natural environment of the Arcto Norwegian cod.

It has to be mentioned that the hierarchical status of cod reared in tanks may also play a role. Observed growth differences under farming conditions might, therefore not necessarily reflect growth performance in nature (Svåsand et al. 1996). This problem was minimized in the present study by analysing only individuals without any obvious injuries which show positive growth.

Permanently different growth rates in North Sea cod, Norwegian coastal cod, and North East Arctic cod are in line with genetical difference between populations. Differences persist during lab acclimation and field acclimatization.
Countergradient compensation does not occur in cod.

5.1.3 Optimum temperature for growth of cod

The optimum temperature for growth of different fish species as observed in growth experiments varied between populations (e.g. in Atlantic halibut – *Hippoglossus hippoglossus*, Jonassen et al. 2000). Björnsson et al. (2001) assumed that optimum temperature may also differ to some extent between different cod stocks. These assumptions are not confirmed by the findings reported in the present study. Despite differences seen in specific growth performance, the highest growth rates in all three cod populations were found close to 10 - 11°C. This is in accordance with the suggestion, that life in warm waters is likely to reflect the original evolutionary situation (Arntz et al. 1994).

As mentioned for the differences in growth rates, temperature preferences may also be discussed in the light of thermal adaptation: various authors have shown that intraspecific differences in thermal preferences and tolerance windows between populations from different thermal environments are usually found to be small (reviewed in Jobling 1996).

Wild cod are usually found at temperatures lower than the optimal values determined in laboratory experiments, probably due to lower food availability in nature than in laboratory experiments (Björnsson et al. 2001). According to the optimal foraging theory, fish should maximize their surplus energy i. e. their somatic growth and their reproductive effort (e.g. Ware 1982). With an unlimited food availability cod would consequently be expected to move from cold to warmer areas to increase growth rate and reproductive effort.

Although no size-specific differences in growth performance existed in the present work, the relation between size and temperature preferences are mentioned here. It has often been reported that large fish have lower temperature preferences than small fish. Björnsson et al. (2001) found that the optimal temperature for growth decreases with increasing size of Icelandic cod, from 17°C for 2 g fish to 7°C for 2000 g fish. Pedersen and Jobling (1989) found the optimal temperature of large Norwegian cod (1500 – 2500 g) at 9 – 12°C, whereas it was 11 – 15°C for small cod (50 – 1000g). This temperature range matches with the findings of the present study. For larval Norwegian cod (< 1 g) and North East Arctic (< 1 g) cod fed in excess, the optimum temperature for growth was found to be at 14 -16°C (Otterlei et al. 1999). The higher optimum

temperature for larval cod in the study by Ottelei et al. (1999) in comparison to a lower optimum temperature revealed for juvenile cod in this study may, therefore, be explained by the effects of different size ranges as mentioned above.

Optimum temperature for growth of cod from the North Sea, the Norwegian coast, and the North East Arctic is between 10 – 11°C. Thus, North East Arctic cod is living below its thermal optimum for growth.

Intraspecific differences in thermal optima do not occur among cod within the same size range and with unlimited food availability.

5.1.4 Climate change and the effects on growth and distribution of cod

On the basis of a comprehensive comparison of different published models, the Intergovernmental Panel on Climate Change (IPCC) has predicted a climate scenario for Europe (Kundzewicz & Parry 2001). The committee predicted that winter in Europe currently classified as 'cold' will become much more rarer by the 2020s and disappear almost entirely by the 2080s. In contrast, hot summers become more frequent. All observed model simulations show warming in the future across the whole of Europe and in all seasons. Annual mean temperatures over Europe warm at a rate of 0.1 and 0.4°C per decade.

The associated rise of water temperature will dramatically influence marine life. The model equation obtained in the growth experiments facilitates the development of a scenario for growth of cod from different climatic regions in relation to temperature. It may serve as a basis for discussing the possible effects of a temperature rise on the population dynamics of cod.

The influences of food and migration of cod on growth in the light of global warming have also been considered. Present water temperatures of the North Sea lead to the highest length increment values and a strong seasonal variability of growth for cod in this region. With increasing summer temperatures, growth of North Sea cod would decrease dramatically. In August, for example, the length increment of North Sea cod would drop down to a

modelled value of 0.048 cm per day. Instead of decreasing the growth performance, North Sea cod would most likely escape from this critical temperature range. The southern stock will either shift further north (von Westernhagen 1993) or will, alternatively, be exterminated. In the case of warming by 1.5°C, Norwegian cod and the North East Arctic cod population may profit from this water temperature change by an increase in growth performance associated with higher levels of feeding activity (ICES 2000).

However, interactions between temperature and food availability complicate any causes of growth variation in the wild (ICES 2000). An increase in temperature would accelerate growth in case food is not limited; if, however, food is limited, growth would be reduced. There is an optimum temperature for growth at any particular ration. When temperature is below this optimum, food will not be limited and an increase in temperature will accelerate growth. If, however, the temperature is above this optimum, food is limited, resulting in a reduction in growth. Accordingly, whether food is limited or not may depend on temperature. Temperature and salinity affect the timing of spring bloom of phytoplankton, on which the hatched cod depend during their first days (Conover et al. 1995). A large amount of the cod larvae might starve if the phytoplankton bloom occurs before or after the hatching.

Ottersen & Loeng (2000) postulated that high temperature may cause a high production of prey items for larvae, leading to higher growth rates and higher survival through the vulnerable larval and juvenile stages. Furthermore, Brander (1994a) found out that over the first four years of life, each 1°C increase in water temperature resulted in a 29% increase in weight.

Normally, temperatures in the Barents Sea never exceed 4°C (see Brander 1994b). Therefore, a temperature increase would mostly affect the Arctic cod. The positive effect of a temperature rise on North East Arctic cod growth is supported by field studies and laboratory experiments (e.g. Waiwood 1978, Jørgensen 1992). Michalsen et al. (1998) related mean length and mass at age of 2-6 year old Arcto-Norwegian cod to their ambient winter temperatures. Mean individual growth rate was highest for year classes experiencing high winter temperatures.

Apart from the effects of warmer temperature on an increased growth of North East Arctic cod, I suggest that distribution patterns of North East Arctic cod may

also change after warming. Accordingly, Ottersen et al. (1998) reported that in periods of warm water temperatures the distribution of North East Arctic cod extended further East and further North.

In the case of increasing water temperatures due to global warming, cod living at its southern distribution limits would shift further North and disappear from the Southern North Sea. Such a shift may heavily affect fishing activities in the North Sea.

A temperature rise would positively affect the growth of North East Arctic cod, and the distribution of this population will extend North.

In contrast to a possible increase of water temperatures of the North Atlantic due to global warming, some authors suspected that global warming may lead to a European cooling driven by a diversion of the Gulf Stream (Wood et al. 1999, Joos et al. 1999). Generally, heat transported northwards by the Gulf Stream, warms the climate of western Europe (Hall & Bryden 1992, Manabe & Stouffer 1994).

Down-welling of highly saline cold water is an important process driving the Gulf Stream. Rapid sinking occurs principally in two small areas of the North Atlantic, one near Labrador and one in the Greenland Sea, where the warm waters are cooled down by icy winds from nearby glaciers. New models developed by Wood et al. (1999) and Joos et al. (1999) illustrate that global warming could dramatically increase North Atlantic freshwater inflows due to elevated precipitation and ice melt and thus slow down the thermohaline circulation and eventually lead to a diversion of the Gulf Stream.

Accordingly, a cooling of the North East Atlantic would positively affect the dynamics of cod population living at its southern distribution limit. Correspondingly, Dickson et al. (1973) reported that colder years, have been associated with an increase on year-class sizes of North Sea cod. Beside growth, the recruitment success of North Sea cod is positively connected with cold temperatures as well (e.g. Dickson et al. 1973, Svendsen et al. 1995, Dippner 1997). At the other end of the temperature spectrum, populations in colder regions like the Barents Sea appear to suffer from decreasing water temperatures and the distribution limits would shift further south, which is in line

with a study by Castonguay et al. (1999). They found that Atlantic cod in the northern Gulf of St Lawrence have been distributed further south in response to ocean cooling.

5.1.5 Fecundity with respect to temperature

Data concerning fecundity can be used to predict the strength of offspring year classes and give a useful tool to investigate the impact of egg production on the variability of recruitment (Bagge et al. 1994). Experimental work and field observations have demonstrated that temperature clearly affects reproductive potential (Van Der Kraak & Pankhurst 1996), timing of spawning (e.g. Kjesbu 1994, Hutchings & Myers 1994a) as well as embryonic and larval development (Rombough 1997) of cod.

Generally, small fish have a lower fecundity than bigger individuals, and fecundity is a function of body length rather than age (Kjesbu 1988). In the present study, regression analysis showed higher coefficients of determination (r^2) for fecundity-at-length compared with fecundity-at-age relationships. Analogous to growth performances in the field and in experimental studies, fecundity at length was higher for warm adapted cod. Within the present study the highest values were found in populations from the Baltic Sea, followed by the North Sea and Norwegian coastal animals. These results are comparable to other studies (e. g. Botros 1962, Oosthuizen & Daan 1974, Kjesbu 1988) where Baltic cod is reported to have a very high fecundity potential (up to 100% higher) in comparison to cod stocks in the North Sea or the North Atlantic. Even though cod of the Southern North Sea and the Baltic Sea are exposed to similar temperature regimes, fecundity of Baltic cod is markedly higher than that of cod in the North Sea. According to the observed differences in growth rates between Baltic cod and North Sea cod, less salinity may lead to changes in energy budget favourable for fecundity as already discussed in chapter 5.1.1.

The drop in the number of eggs in cod from colder waters does not appear to be compensated by an increase in egg size since a clear effect of ambient temperature on egg size is not apparent (Brander 1994a). The high variability of the fecundity values of cod revealed in this study has also been found in other studies. Kjesbu et al. (1988) reported that the relative fecundity in prespawning

Arcto-Norwegian cod varied between years (1986-1989 and 1991) by as much as 40%. Rijnsdorp et al. (1991) also found that the relative fecundity is quite variable. One reason could be that individual fecundity is influenced by the availability of food (Karlsen et al. 1995, Kjesbu et al. 1998). Feeding in excess results in an increase in the total number of eggs (Kjesbu 1989). Further experimental comparisons of the fecundity of different cod populations under identical conditions would be necessary to analyse the latitudinal differences in more detail.

The direct influence of temperature on fecundity within a species was demonstrated by Kjesbu et al. (1998). They showed that for North East Arctic cod females, standardized to a body length of 90cm, the number of eggs was significantly and positively correlated with environmental temperature and the amount of available food. However, differences in fecundity are intimately linked to growth processes and should be discussed under the aspect of different life histories of cod. Consequently, if the fecundity-size relationship is constant, an increase in growth rate will result in a higher egg production (Rijnsdorp et al. 1991). Therefore the effects of global warming on fecundity for different cod populations follows temperature-dependent mechanisms as already discussed. An elevated growth rate of North East Arctic cod may also lead to higher fecundity. Additionally, age at first maturity differs between the various populations (Brander 1994b). Animals from low latitudes reach their first maturity earlier. Thus, cod in western Norway, in the North Sea, and in the Baltic Sea mature early (2 - 4 years) at relatively small sizes (<40cm) (Svåsand et al. 1990, Brander 1994), whereas the Arctic cod mature later (6 - 14 years) at larger sizes (70 - 90 cm) (Bergstad et al. 1987). On the one hand the fish from higher latitudes mature later, on the other hand they compensate this delay by reaching a higher reachable maximum length and a longer lifespan.

To complete the discussion of the possible effects of global warming on the population dynamics of cod, the relationship between recruitment and temperature has to be taken into account here as well. There is a high correlation between temperature and recruitment of cod. (e.g. Templeman 1972, Ottersen 1996, Planque & Frédou 1999, Pörtner et al. 2001). However, cod populations react differently. Planque & Frédou (1999) analysed the effect of temperature on recruitment for nine different Atlantic cod stocks and reported

that the relationship between temperature and recruitment follows a gradual change. They found that there is a positive relationship in cold waters and no relationship in temperate waters, while a negative relationship exists in warm waters.

Ecological findings on cod from different populations in various climate regimes revealed that decreasing fecundity coincides with decreasing growth (at the same temperature) at higher latitudes indicating a change in energy budget unfavourable for fecundity and growth in the cold.

5.2 Standard metabolic rates and mitochondrial function

- Linking ecological and physiological approaches !

In this chapter the specific tradeoffs involved in cod performance in a latitudinal cline and its physiological mechanisms will be discussed in the light of studies of metabolic rates at the whole animal and at mitochondrial levels.

5.2.1 Respiration of whole animals – Standard metabolic rate

Measured oxygen consumption rates in the present study can be considered to be standard metabolic rates, since the measurements were carried out by use of a dark respiration chamber. The online recording allowed to identify the lowest rates of respiration of cod during the whole time of the experiments (cf. Pörtner & Grieshaber 1993). Saunders (1963) reported that after handling stress, oxygen uptake rates of Atlantic cod return to normal levels within 3 - 5 hours. In the present study cod from both populations recovered completely from handling stress within 12 hours and oxygen uptake remained stable and low thereafter. When animals are fed before measuring oxygen consumption, respiration rates are usually increased due to additional metabolic costs of digestion and of the biochemical processing of food (specific dynamic action – SDA) (Holeton 1973,1974; Johnston & Battram 1993). In the present thesis, feeding was stopped five days prior to respiration analyses to guarantee that SDA was not involved. As seen in Tab. 26 oxygen consumption values determined in the present study are in the lower range of values for cod

measured by other authors, thereby confirming the conclusion that standard metabolism has been analysed.

Beyond 16°C a decrease of aerobic metabolic rate was found in White Sea cod and above 18°C in North Sea cod acclimated to 4°C such a drop in metabolic rate also occurred. This could be seen as a first hint for high critical temperatures for the different cod populations.

Tab. 26: Overview of oxygen consumption (standard metabolic rate) of cod from different populations as determined by other authors in comparison to the values revealed in this study.

Species and origin	Oxygen consumption rate (mgO ₂ * kg ⁻¹ * hr ⁻¹)	Ranges of body weight (g)	Measuring temperature (°C)	References
Atlantic cod (Greenland)	61.0 ± 5.6	111 - 186g	4.5°C	Steffensen et al. (1994)
Polar cod (Greenland)	95.6 ± 13.9	143 - 223g	4.5°C	Steffensen et al. (1994)
North Sea cod (acclimated to 4°C)	57.5 ± 10.6	229 - 559g	4.0°C	this study
North Sea cod (acclimated to 12°C)	50.4 ± 2.6	223 - 433g	4.0°C	this study
North East Arctic cod (acclimated to 4°C)	79.3 ± 12.3	251 - 325g	4.0°C	this study
Atlantic cod (Northwest Atlantic)	74.0	190 - 390g	10.0°C	Saunders (1963)
Atlantic cod (Scotland)	131.0 ± 15.5	29 - 82g	10.0°C	Soofiani & Hawkins (1982)
Atlantic cod	85.0	218g	11.5°C	Johnstone & Hawkins (1980)
Atlantic cod (Scotland)	106.0	518g	12.0°C	Edwards et al. (1972)
North Sea cod (acclimated to 4°C)	85.2 ± 9.0	229 - 559g	12.0°C	this study
North Sea cod (acclimated to 12°C)	59.5 ± 20.6	223 - 433g	12.0°C	this study
North East Arctic cod (acclimated to 12°C)	65.5 ± 3.9	169 - 333g	12.0°C	this study
White Sea cod (acclimated to 12°C)	93.7 ± 8.9	162 - 228g	12.0°C	this study

5.2.1.1 Cold adaptation and acclimation of standard metabolic rate

The concept of metabolic cold adaptation (MCA) is one of the most controversially discussed topics in fish physiology, and the debate is still going on (Steffensen 2002). Krogh (1914) predicted that the metabolic rate of cold adapted polar fish would be higher than the rates exhibited by temperate fish cooled to polar temperatures. Others (Scholander et al. 1953,

Wohlschlag 1960, 1963) confirmed these findings, and this process of cold compensation was named *metabolic cold adaptation*. Later Holeyton (1974) criticized the concept of MCA and he argued that previous estimates were too high due to stress induced by the measurement protocol. Recent discussion is still highly controversial. Some authors supported the concept of MCA (e.g. Brett & Groves 1979, Forster et al. 1987, MacDonald et al. 1988) whereas others rejected it (Clarke 1980, 1983, 1991; Bushnell et al. 1994, Clarke & Johnston 1999). Pörtner et al. (2000) and Pörtner (2002) distinguished between cold adapted eurytherms (mostly sub-Arctic to Arctic) displaying MCA and cold adapted stenotherms (mostly Antarctic) which do not or only to a small extent. The cod populations studied here clearly match the criteria of eurythermal animals.

In the traditional sense metabolic cold adaptation would lead to predict a standard metabolic rate that is 2 - 4 times higher for Arctic fish than for temperate species (see Steffensen et al. 1994). However, compensation is likely to occur to various degrees and this consideration suggests that compensation does not have to fully match Wohlschlags (1960) definition to be called MCA. Accordingly, it is more important to determine whether there are significant differences in temperature specific standard metabolic rates of fish from different climatic regimes and to explain its mechanisms than to concentrate on the question of traditional quantification of compensation.

In the present study, the oxygen consumption rates of White Sea cod and North East Arctic cod were higher than in North Sea animals when compared at the same temperatures. The difference between oxygen uptake of White Sea cod and North Sea cod reached up to 50%, and a compensatory rise in metabolic rates in cold-adapted animals definitely occurred. Similar results were obtained by Steffensen et al. (1994) who found elevated standard metabolic rates (10% - 26% higher) for two Arctic species, Greenland cod and Arctic cod, in comparison to Atlantic cod. They were kept in tanks with fluctuating temperatures (between 4 and 7°) and it is not obvious how long the fish were acclimated to these temperatures. Studies by Forster et al. (1987) and Torres & Somero (1988) have shown an elevation (by a factor of 2) of resting metabolic rate in polar fish, which, again, show that some cold adapted fish species compensate for cold temperatures.

In the present thesis, data show that not only cold adaptation but also acclimation to cold temperatures leads to an elevated metabolic rate. North Sea individuals acclimated to 4°C displayed a rise of their oxygen uptake by up to 40% in comparison to North Sea cod acclimated to 12°C. As discussed in the literature, the rise in aerobic capacity to compensate for low temperatures is associated with the following processes:

Enhanced enzyme activities in cold-acclimated as well as in cold-adapted animals were found (Torres & Somero 1988, Crocket & Sidell 1990, Sokolova & Pörtner 2001, Kawall et al. 2002). Lannig et al. (2002 - unpublished data) have shown elevated activities of aerobic enzymes after cold acclimation and in permanently cold adapted white muscle of cod from the North Sea, the Norwegian coast, and the Barents Sea. These adjustments in enzyme capacities of white muscle are in line with elevated rates of oxygen consumption for cold-adapted and cold-acclimated cod in this study and can help to explain their elevated standard metabolic rates in cod living in the cold.

Alterations in membrane compositions have also been found to play a role in cold compensation (Prosser 1991, Miranda & Hazel 1996). Recently, Pörtner (2002) has reviewed the tradeoffs in muscle design and performance in polar ectotherms. Reaching less muscular performance with maximized aerobic design characterizes the trade-offs and constraints involved in adaptation to the permanent cold. An increase in mitochondrial density was found for different fish species (Egginton & Sidell 1989, Johnston et al. 1998, St-Pierre et al. 1998). Although studies of mitochondrial proliferation in cod are not available at the moment, it seems to be an unifying principle for animals in the cold and was even found in invertebrates, for example by Sommer & Pörtner (1999). They showed proliferation of mitochondria in the polychaete worm *Arenicola marina* as an adaptation to lower temperatures. Pörtner et al. (2000) argued that with any mitochondria present, the maintenance cost of ionic and proton gradients across the mitochondrial membrane has to be met. Consequently, an increase in mitochondrial density leads to a rise in aerobic capacity at low temperatures and explains the elevated standard metabolism found for cold-adapted cod in this study.

Compared with the Barents Sea, the White Sea has a more continental climate - a warmer summer and a colder winter. Surface water temperatures in the

White Sea vary seasonally by about 20°C (Klenova 1966). Cod from the White Sea therefore, can be described as to be more eurythermal than the other cod populations. The present findings of metabolic rate being higher in White Sea cod than in North East Arctic cod (despite higher summer temperatures experienced by White Sea cod) supports the conclusion that eurythermal cold adaptation is more costly than stenothermal cold adaptation. Accordingly, metabolic cold adaptation is minor or even absent in polar stenotherms (Clarke & Jonston 1999). Pörtner et al. (2000) concluded that the level of metabolic cold adaptation depends upon the extent of diurnal and seasonal temperature fluctuations leading to higher cost of mitochondrial maintenance in eurythermal than in stenothermal animals.

The observed differences in metabolic rates of cod analysed in this study help to explain why cod from higher latitudes, adapted to cold temperature, exhibit a lower growth potential and lower fecundity than those from southern regions. There is often an inverse correlation between resting metabolic rate and growth rate (Hawkins 1999). The present findings correspond with the contention that resting metabolism does represent a cost to the organism to the effect that energy utilized in maintenance must be met from food or reserves. This energy cannot be used in processes like growth or reproduction (Clarke & Johnston 1999).

A compensatory rise in standard metabolic rate occurred in cod populations living in the cold, especially for the eurythermal White sea cod. This cold compensation strongly coincides with lower growth performance and reduced fecundity, as confirmed by field investigations for cod from higher latitudes.

Lowest growth performance was found for White Sea cod which is in accordance with high costs of eurythermal vs. stenothermal cold adaptation (Pörtner et al. 2000, 2001).

5.2.2 Functions of isolated liver mitochondria

5.2.2.1 Respiratory properties and RCR

If we keep in mind that red muscle mitochondria generally respire faster than mitochondria from liver tissue when using the same substrate (van den Thillart & Modderkolk 1978, Suarez & Hochachka, 1981) and that, in addition, cod is a more active species than fish from Antarctica, mitochondrial oxygen uptake values (state III-respiration) measured for cod in this study are consistent with data obtained by other authors as shown in Tab. 27.

Tab. 27: Overview of oxygen consumption (state-III-respiration) of isolated mitochondria of fish from different populations as determined by other authors in comparison to the values revealed in this study.

Species and origin	Oxygen consumption rate (state III) (nmol O x min ⁻¹ x mg ⁻¹ mitochondrial protein), mean values	Body size (g)	Measuring temperature (°C)	References
<i>Lepidonotothen nudifrons</i> - Antarctica	2.34 ± 0.06 (succinate/liver)	Mean: 24.3 ± 8.4g	0°C	Hardewig et al. (1999)
<i>Lepidonotothen nudifrons</i> - Antarctica	28.6 (pyruvate/red muscle)	29.5 – 50.1g	0°C	Johnston et al. (1998)
<i>Trematomus newnesi</i> - Antarctica	31.2 (pyruvate/red muscle)	5.4 – 24.1g	-1°C	Johnston et al. (1998)
<i>Zoarces viviparus</i> – North Sea	14.27 ± 1.28 (pyruvate + malate/liver)	unknown	15°C	Lannig (2000 – unpubl.)
<i>Oncorhynchus mykiss</i> - Canada	50.8 (succinate/liver)	150 – 300g	15°C	Suarez & Hochachka (1981)
<i>Myoxocephalus scorpius</i> – North Sea	25 – 80 (pyruvate/red muscle)	Mean: 350 ± 224g	3° - 12.5°C	Johnston et al. (1994)
<i>Gadus morhua</i> - North East Arctic acclimated to 4°C	19.6 ± 7.5 (succinate/liver)	169 – 325g	4°C	This study
	53.1 ± 16.8 (succinate/liver)		12°C	
	58.5 ± 12.4 (succinate/liver)		15°C	
<i>Gadus morhua</i> - North East Arctic acclimated to 12°C	16.4 ± 4.6 (succinate/liver)	169 – 325g	4°C	This study
	40.1 ± 16.3 (succinate/liver)		12°C	
	66.3 ± 14.8 (succinate/liver)		15°C	
<i>Gadus morhua</i> - North Sea acclimated to 4°C	12.5 ± 7.2 (succinate/liver)	152 – 450g	4°C	This study
	15.3 ± 7.2 (succinate/liver)		12°C	
	22.1 ± 17.8 (succinate/liver)		15°C	
<i>Gadus morhua</i> - North Sea acclimated to 12°C	7.6 ± 1.4 (succinate/liver)	152 – 450g	4°C	This study
	11.9 ± 8.2 (succinate/liver)		12°C	
	14.7 ± 6.0 (succinate/liver)		15°C	
<i>Gadus morhua</i> - North Sea acclimated to 15°C	12.2 ± 6.4 (succinate/liver)	152 – 450g	4°C	This study
	29.4 ± 17.3 (succinate/liver)		12°C	
	26.4 ± 7.3 (succinate/liver)		15°C	

In the present study, cod liver mitochondria displayed RCR_{ol} -values between 2 and 6, which are comparable to results obtained in other studies provided that the differences between state-IV respiration and state-IV respiration under oligomycin are small in all these cases. Suarez & Hochachka (1981) reported values of 3.7 for rainbow trout using succinate as a substrate. In *Zoarces viviparus* from the North Sea coupling ratios of 3.16 were measured by G. Lannig (unpublished data). In the present study, the RCR_{ol} -values of cod mitochondria were stable and independent of the temperature of analysis. In other fish species like trout, carp or goldfish (van den Thillart & Modderkolk 1978, Moyes et al. 1988, Blier & Guderley, 1993), RCR values were also fairly insensitive to temperature. In contrast, Hardewig et al. (1999) observed a progressive uncoupling of mitochondria at elevated temperatures in the Antarctic fish *Lepidonotothen nudifrons*. Therefore, a general pattern of temperature dependent uncoupling of mitochondria in different organisms does not seem to exist. Probably eurythermal mitochondria are more resistant to uncoupling than mitochondria from stenothermal animals.

5.2.2.2 Do cold adaptation and acclimation also occur in liver mitochondria?

Aerobic capacities (state-III-respiration) of liver mitochondria from North East Arctic cod were significantly higher than in liver mitochondria from North Sea cod. These temperature-induced elevations reflect cold adaptation in the same way as oxygen consumption of whole animals does. Tschischka et al. (2000) also found elevated aerobic capacities in mitochondria from cold-adapted polychaetes and bivalves. For comparison, Johnston et al. (1994, 1998) reported that mitochondria of Antarctic fish show only modest or even no temperature compensation at all of their oxidative capacity when compared to temperate or tropical fish mitochondria. Again, this apparent contradiction can be explained by the different costs of cold adaptation between stenothermal Antarctic fish and eurythermal Arctic animals: in contrast to Antarctic species, cold adapted Arctic eurytherms display a rise in mitochondrial aerobic capacity, which compensates for the temperature-dependent decrement in aerobic capacity (Sommer & Pörtner 2002). The evolutionary background may be that some species in the Arctic may still be found in transition to life in permanent

cold waters while those in the Antarctic already developed functional properties of permanent cold adaptation over millions of years (Pörtner 2002).

The elevated aerobic capacities of liver mitochondria of North East Arctic cod observed in the present study are in line with elevated liver mass specific activities especially of citrate synthase (CS), of cytochrome c oxidase (CCO), and of the electron transport system (ETS) in Northern cod populations (Lannig et al. 2002 – unpublished data).

In contrast to cold adaptation, cold acclimation does not generally lead to functional changes in liver mitochondria of cod. In the present study, no effect of acclimation on state-III-respiration and proton leakage was found for North East Arctic cod, and an even higher mitochondrial oxygen consumption rate (state-III) and proton leakage was found for North Sea cod acclimated to 15°C when compared to the rates for North Sea cod acclimated to 4°C and 12°C. These results are again in accordance with enzyme studies of liver mitochondria by Lannig et al. (2002-unpublished data), where activities of CCO and ETS failed to show a clear pattern of cold acclimation. In North Sea cod the investigated aerobic enzymes show even lower specific activities at 4°C compared to 8°, 12°C and 15°C, whereas enzyme activities in total liver remained similar during acclimation, due to the rise in liver weight. The total CS activities were found to be enhanced after cold acclimation in North East Arctic cod, but CCO and ETS activities decreased with decreasing acclimation temperature. These findings are in line with other studies (Hardewig et al. 1999, van den Thillart & Modderkolk 1978, Rafael & Braunbeck 1988) in which cold acclimation results in unchanged or even falling specific CCO activities in liver mitochondria of different fish species. Suarez & Hochachka (1981) argued that the liver is probably the most metabolically versatile organ in the vertebrate body. Accordingly, temperature-dependent shifts may occur between metabolic functions which may influence the relative change of mitochondrial enzyme capacities (e. g. catabolism versus anabolism).

In the present study, the relationships between liver size, mitochondrial protein content, and mitochondrial capacities of laboratory maintained cod was analysed to estimate whether cod in nature may compensate for differences in observed mitochondrial properties by changing organ size or mitochondrial protein content.

The mitochondrial protein content for all treatments and populations was quite similar (mean: 25 mg/g liver – data not shown) (Lannig 2002-unpublished data). Although acclimation to cold temperatures led to higher HSI, no differences of HSI values were detected between the populations. Thus, aerobic capacity of ATP-formation and proton leakage rates calculated to whole liver size were still elevated for Northern populations, and it becomes evident that the increased capacities of individual liver mitochondria are related to the elevated oxygen consumption rates of whole animals from high latitude.

Cod mitochondria are resistant to temperature dependent uncoupling.

The capacity of ATP-formation and of proton leakage of liver mitochondria from cold adapted cod were elevated, which reflects cold adaptation. Cold-adapted cod do not compensate mitochondrial capacities for temperature by changing liver size.

Thus, cold compensated mitochondria ATP-synthesis capacities and elevated proton leakage rates reflect enhanced cost, in line with the reduction in growth performance and fecundity observed in Northern populations in field and experimental studies.

Cold acclimation is not generally reflected in changing functions of liver mitochondria from cod.

5.2.2.3 Mitochondrial oxygen demand and the oxygen limitation of thermal tolerance

No significant change occurred in the E_a -values of state-III-respiration and of proton leakage rates in cod liver, neither during temperature acclimation nor during cold adaptation. These findings are in accordance with a study by Pörtner et al. (1999) who compared the Arrhenius activation energy of state-III respiration of the Antarctic bivalve *Laterna elliptica* with various literature data for fish (Hardewig et al. 1999, Weinstein & Somero 1998, Guderley 1988) and found that it is largely unaffected by polar cold adaptation. In the present study unchanged E_a -values of state-III and state-IV_{ol} respiration coincide with the observed thermal insensitivity of mitochondrial coupling ratios. Furthermore, no Arrhenius Break points (ABT) were detected, neither for state-III respiration rates nor for proton leakage rates of isolated liver mitochondria in North Sea cod and in North East Arctic cod. Weinstein & Somero (1998) summarised Arrhenius break temperatures in mitochondria from various fish and invertebrate species and found most of the ABT's occur above maximum habitat temperatures and also above critical temperatures of the whole animal. In the present study, capacities of liver mitochondria were analysed in a temperature range between 4°C and 20°C, which could be a thermal range too narrow to detect an ABT. This indicates that the performance characteristics of individual cod liver mitochondria are maintained up to 20°C and this may therefore not help to explain the thermal intolerance of cod beyond 18°C. Nevertheless, the phosphorylation efficiency (ADP/O ratio) of cod liver mitochondria decreased with increasing temperatures in North East Arctic and North Sea cod similar to findings by Hardewig et al. (1999) who investigated mitochondrial capacities in the Antarctic fish *Lepidonothoten nudifrons*. These results lead to the assumption that rising temperature may reduce the efficiency of ATP-formation, although no mitochondrial break-down was seen.

The question arises which physiological processes are responsible for setting the limits of thermal tolerance of cod.

A general model of thermal limitations was proposed for animals in that, insufficient oxygen levels in the body fluids and the transition to an anaerobic mode of mitochondrial metabolism characterize the oxygen limitation of thermal tolerance at both low and high temperature extremes (Pörtner 2001, 2002).

Critical temperatures differ between species and are usually lower for marine animals which are adapted to cold, compared to their warm adapted-counterparts (e.g. Sommer et al. 1997, van Dijk et. al. 1999). If this holds true for cod, then it might relate to the higher mortality rates for North East Arctic in comparison to North Sea cod at 12°C and 15°C rates which were determined in the growth experiments in this study. Farrel (1997) summarised that the limits of aerobic scope in the heart of temperate salmonid fish may cause insufficient blood circulation at extreme temperatures, tallying with the drop in venous oxygen tension observed during warming in cod (cf. Pörtner et al. 2000, 2001). Higher proton leakage rates at the same temperature of analysis were found in this study for liver mitochondria of cod living in the cold. Mitochondrial proton leakage generally correlates with the standard metabolic rate (SMR) of an animal (Brookes et al. 1998). It has been reported that proton leakage comprises 20-30% of SMR in the whole animal in ectotherms and endotherms (Brand 1990, Brand et al. 1994, Brookes et al. 1998). Consequently, the elevated proton leakage rates of North East Arctic cod in comparison to Southern North Sea cod contribute to the increased oxygen consumption of these cold-adapted cod. However, a higher oxygen consumption may enhance the discrepancy between oxygen demand and oxygen uptake, especially at higher temperatures.

In conclusion, the mitochondrial data obtained in this study are in line with the hypothesis (Pörtner et al. 2001) that the insufficient increase of ventilation and circulation and the possible discrepancy between oxygen demand and supply may lead to a drop in aerobic scope for cod, transition to mitochondrial anaerobiosis, and finally a collapse of higher physiological functions in the warm.

Rising temperature may reduce the efficiency of ATP-formation in cod.
Single cod liver mitochondria maintain function at higher temperatures than individual cod.
Elevated proton leakage rates are higher in mitochondria of cold- adapted cod than in temperate specimens. This contributes to an elevated oxygen demand for cold adapted sub-Arctic cod, thereby causing the critical temperature to be lower in this than in the other populations.

5.3 Future perspectives

In this thesis, the combination of ecological and physiological studies on cod from different populations revealed that trade-offs in energy budget are unfavourable for growth and fecundity of specimens living in the cold.

Higher growth performance in North Sea cod and Norwegian cod than in Arctic cod could reflect adjustment to the specific temperature regime used in the present growth experiment. Therefore, further experiments with temperature regimes from 4°C down to sub-zero temperatures which characterize the natural environment of the Arcto Norwegian cod should be undertaken in the future. Additionally, experimental comparisons of the fecundity of different cod populations under identical food conditions would be necessary to exclude the possible effects of variable food availability in nature.

It is assumed that the thermal limits of cod are set by insufficient oxygen levels in the body fluids, due to the discrepancy between oxygen demand and supply via circulation and ventilation. Correspondingly, investigations by magnetic resonance imaging (MRI) and spectroscopy (³¹p-MRS) are ongoing.

In the long run an integrated unitary model of the temperature-sensitive response of cod from the molecular to the population level should be worked out. This could be used to forecast the effects of global warming on stock sizes of cod and provide an effective tool in successful fishery management.

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