Environmental factors and uncertainty in fisheries management in the northern Baltic Sea

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Academic dissertation

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Interpretation of results	LU	LU	LU, AR, SK	LU, SK, HP	LU
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Contents

List of terms and abbreviations

BN	Bayesian network; a Bayesian statistical method
Chl	Chlorophyll; chlorophyll *a* concentration
FGFRI	Finnish Game and Fisheries Research Institute
IBSFC	International Baltic Sea Fishery Commission
ICES	International Council for the Exploration of the Sea
MDS	Multidimensional scaling; a multivariate statistical method
MCMC	Markov chain Monte Carlo; a computational method for generating samples from a probability distribution
N	Nitrogen; total nitrogen concentration in the water
P	Phosphorus; total phosphorus concentration in the water
parr	Salmon juvenile living in the river
recruitment	Amount of fish in the age group that recruits to the fishery
smolt	Salmon juvenile that leaves its native river and migrates to the sea
SSB	Spawning stock biomass; the total biomass of mature (spawning) fish
SYKE	Finnish Environment Institute
TAC	Total Allowable Catch

1 Introduction

The famous quote from Thomas H. Huxley (1883), “probably all the great sea-fisheries are inexhaustible; that is to say that nothing we do seriously affects the number of fish” (cited in Knauss, 1994; Auster and Shackell, 2000), has, unfortunately, proven wrong (Caddy and Cochraine, 2001; Hilborn *et al.*, 2003), and the need for fisheries management is nowadays widely recognized. The challenge of fisheries management is to be reliable and effective despite inevitable uncertainty about the state and functioning of the fish stocks and the whole ecosystem (Charles, 1998; Myers *et al.*, 2001; Harwood and Stokes, 2003).

The size of any fish stock essentially depends on three things: the size of the stock in the recent past, fishing pressure, and environment. It is a well-established fact in fisheries biology that the size on a new year-class (recruitment) depends on the size of the spawning stock (Hilborn and Walters, 1992, p. 241; Myers and Barrowman, 1996), although some controversy still exists on the topic (Gilbert, 1997). Various stock-recruitment curves have been proposed to describe the dependency of recruitment on the spawning stock size in restricted space and given restricted resources. Generally, they share the idea that on low spawning stock sizes the recruitment must be low, and that when stock size increases, the average recruitment must reach some maximum value that cannot be exceeded. The shape of this curve is dependent on the biology of the species and the environmental conditions surrounding the stock.

The environmental conditions ultimately set the limits within which fish stocks have to thrive or perish, and the role of the environment in fish stocks’ productivity has been widely recognized (Myers, 1998; Werner, 2002). Both biotic factors such as predation, competition, and availability of food items, and abiotic factors such as thermal conditions, salinity, and geographic factors, influence the success of species. While biotic factors can strongly affect the abundance of species, as demonstrated by collapse of the Newfoundland cod (*Gadus morhua* L.) stock and subsequent increase in shellfish abundance (Bundy, 2001; Worm and Myers, 2003) and the decline in cichlid abundance in Lake Victoria after the introduction of Nile perch (*Lates niloticus* (L.)) (Witte *et al.*, 2000), the abiotic factors have been studied longer and more intensively, and are also often seen as more important to the success of populations (Cushing, 1982, pp. 168–172; Myers, 1998; Kupschus and Tremain, 2001). The abiotic factors are especially strong in affecting species abundance in the limits of the distribution range (Myers, 1998), when usually one factor is clearly the limiting factor in the recruitment, and perturbations in it affect the population directly.

Fish need suitable spawning, nursery, and feeding areas to establish natural populations in an area. The egg and larval life stages are often more vulnerable to the perturbations of the environment than adults (Urho, 2002, p. 20; Werner, 2002), and thus the environmental conditions in the egg and larval areas are crucial to the success of species. In cases where reproduction areas have been deteriorated but feeding areas remain, stocking of reared juvenile fish has been used to maintain the population (Cowx, 1994; Jokikokko *et al.*, 2002; Romakkaniemi *et al.*, 2003). Stocking has also been used to introduce species to areas, especially lakes, they have not previously inhabited (Cowx, 1994; Ruuhijärvi *et al.*, 1996; Tammi *et al.*, 2003).

For naturally reproducing stocks, fluctuating environmental factors incur variation to the recruitment and stock size, and fishing often further increases the natural variation (Beddington and May, 1977; May *et al.*, 1978). The status of the fish stocks can often be only inadequately deduced from data, however, and fisheries managers need to cope with uncertainty about the fish stock status.

Several fisheries management strategies have been developed as answers to the inevitable uncertainty about the fish stock status, such as target and limit reference points (Caddy and Mahon, 1995; Caddy, 1999; Collie and Gislason, 2001; ICES, 2006a), spawn-at-least-once policy (Myers and Mertz, 1998a), and marine protected areas (Lauck *et al.*, 1998; Roberts *et al.*, 2001; Halpern, 2003). All of these strategies need to be customized for the particular stock and sea area, however; the reference points, for example, have to be set according to the natural abundance and productivity of the stocks, concretizing the spawn-at-least-once policy needs information on the growth rate and maturity size of the species, and marine protected areas need information on the habitats the fish use.

The use of information from various sources, such as other stocks of the same species (Hilborn and Liermann, 1998; Myers and Mertz, 1998b), ecologically similar species (Punt and Hilborn, 1997; McAllister and Kirkwood, 1998), historical records from the same stock (Jackson *et al.*, 2001), or expert knowledge based on biological insight (Punt and Hilborn, 1997), has been seen as one way of mapping the possible states of fish stocks, and thus facing the uncertainty. This knowledge can be used as a starting point of new analyses, and the results of these analyses again as new starting points. This practice reflects the ideal of science: to build on previous work, to stand on the shoulders of giants (Hilborn and Liermann, 1998). Previous knowledge is used formally in Bayesian analysis, in which prior knowledge is updated with new data to form posterior knowledge, a synthesis of priors and new data (Gelman *et al.*, 1995; Sivia, 1996; Punt and Hilborn, 1997).

In this thesis I examine the commercially exploited fish stocks of the coast of Finland, northern Baltic Sea, their relationship to the environmental factors surrounding them, and uncertainty related to these relationships as well as to the stock status. Improved information about the fish stocks' responses to the environmental factors, combined with realistic estimates of uncertainty, can be useful in many ways. Better knowledge about stocks' reactions to environmental conditions can explain observed variability and hence decrease uncertainty about relevant biological parameters such as growth rate, natural mortality, etc. Environmental requirements of species can also be taken into account in the design of local management strategies so that year-specific reactions to the environmental perturbations will not be needed. Furthermore, better knowledge of fish stocks' environmental requirements can be used to estimate whether improvements in the quality of the environment, such as reduced nutrient loading, can improve the fish stock status.

2 Background: Fisheries in the northern Baltic Sea

2.1 The Baltic Sea, a variable and demanding environment

The northern Baltic Sea (Fig. 1), as defined here, consists of Gulf of Bothnia, Gulf of Finland, and the Archipelago Sea. It is a unique and very demanding area for aquatic life: It is a brackish-water area in which the surface salinity varies

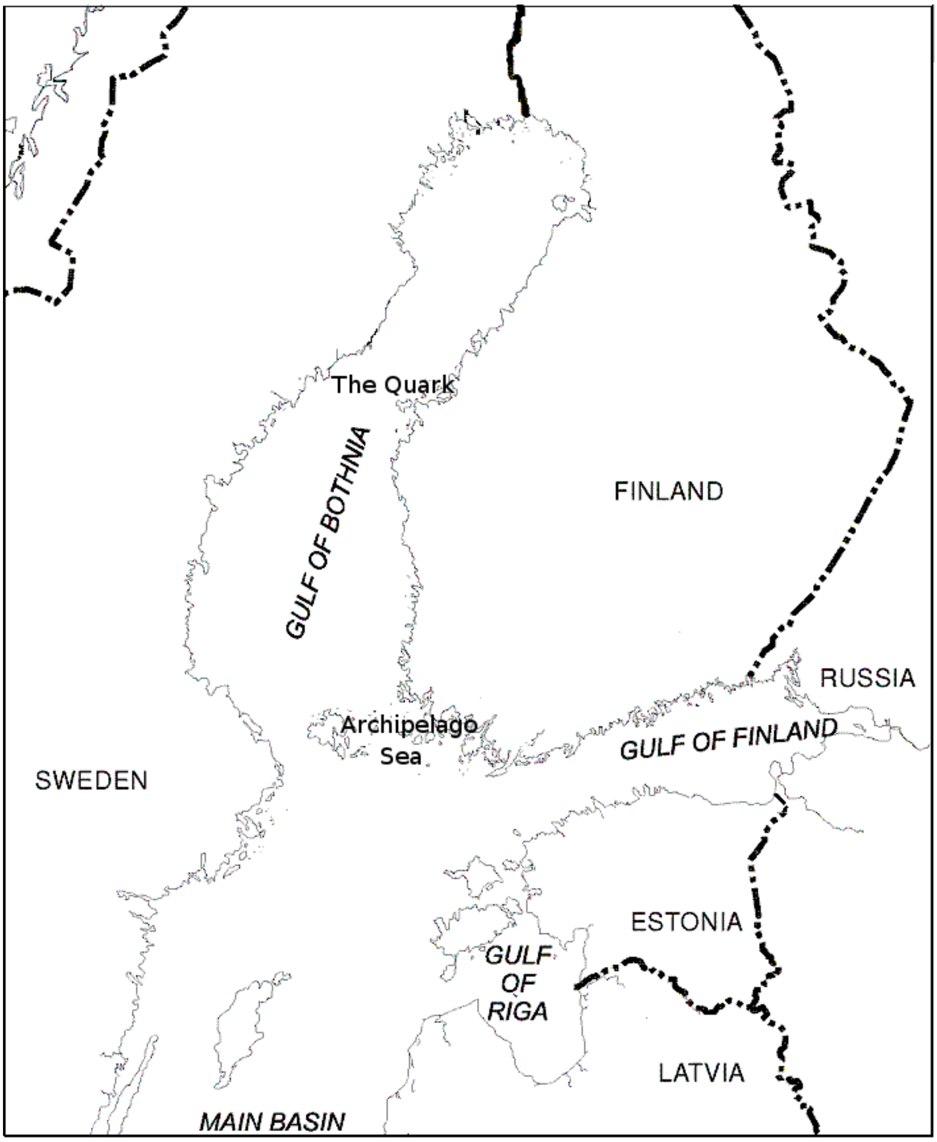

Figure 1: The northern Baltic Sea consists of Gulf of Bothnia and Gulf on Finland.

from zero in river mouths to over 5‰ in the Archipelago Sea (Pitkänen *et al.*, 2001). The average duration of the ice-covered season varies from less than 60 to 194 days (Seinä and Peltola, 1991), and the water temperature range is relatively wide, varying between 0–20°C. There is a permanent halocline in the Gulf of Finland caused by continuous discharge of fresh water from rivers and irregular pulses of saline water from the North Sea, but in the Gulf of Bothnia, no clear halocline can be observed (Kullenberg, 1981).

The glacial erosion of the Ice Age and subsequent land uplift have transformed the coastline to include habitats ranging from rocky shores to gravel, sand, and clay-dominated shores (Winterhalter *et al.*, 1981; Granö *et al.*, 1999). Granö *et al.* (1999) referred to this mosaic-like landscape as an archipelago coast and noted that it has a high geodiversity, a concept similar to biodiversity. The archipelago coast offers a large amount of spawning areas to species spawning in shallow waters, while the high geodiversity accounts for variable environment types.

The Baltic Sea supports both marine and freshwater species in amounts enabling commercial fishery; yet only relatively few species have adapted to its exceptional conditions. 22 marine, 29 freshwater, and 9 holeuryhaline species occur in the coast of Finland (Lehtonen and Rask, 2004) in comparison with 120 species in the North Sea (Ojaveer *et al.*, 1981) and 43 permanent species in Finnish lakes (Lehtonen and Rask, 2004).

The diverse nature of the Baltic Sea has the effect that the species composition varies along the Baltic: the number of marine species in the Baltic reduces towards the east and north, where the proportion of freshwater species is the largest (Ojaveer *et al.*, 1981). Low salinity and cold winters have restricted the dispersion of some marine species to the northern part of the Baltic such as the coast of Finland (Lehtonen and Rask, 2004). The species composition varies even along the coasts of northern Baltic Sea (Ojaveer *et al.*, 1981).

Between the early 1900s and 1980s, phosphorus and nitrogen loading to the Baltic Sea increased by factors of 8 and 4 (Larsson *et al.*, 1985). The anthropogenic nutrient load has affected the Baltic Sea ecosystem; the effects include increasing primary production, decreasing water transparency, and consequent changes in the littoral zone, especially the decrease of *Fucus vesiculosus* L. zones (Cederwall and Elmgren, 1990). The fish stocks have also been affected (Lappalainen, 2002); since the early 1970s, the fish fauna of the coast of Finland has changed to include a larger proportion of cyprinid fishes (Lehtonen and Rask, 2004).

The fish species studied in this thesis present a wide variety of ecological preferences: there are both marine and freshwater species, species preferring cold, oxygen-rich waters and those preferring warm waters, and pelagic and littoral species. Many of the Baltic fish species (both freshwater and marine species) live near the limits of their distribution ranges, where environmental factors are more important in determining the success of reproduction than in the centre of the range (Myers, 1998, 2001). This implies that Baltic fish species are probably susceptible to environmental variability. The meta-analysis by Myers (1998) also shows that correlations between environmental factors and fish abundance at the limits of the species' geographical ranges often stand up to examination; i.e. the environment-population correlations at these limits are strong and persistent enough to be observed in successive tests. This susceptibility should be taken into account in fisheries management for example by increasing the minimum allowed stock size so that the stock will sustain itself even through years with very poor survival.

Johannesson and André (2006) have shown that several of the Baltic fish species have genetically adapted to the Baltic Sea environment. This means that these stocks are unique and could not be replaced with stockings from inland waters or oceans, should they collapse beyond recover. This emphasizes the importance of knowing the relationships with these stocks and the changing environment.

2.2 Fish and fisheries

Despite the demanding nature of the aquatic environment of the northern Baltic Sea, it supports various fish species in a magnitude that enables professional fishery. Most, if not all, of these species live at the edges of their distribution ranges in terms of some environmental factors, such as salinity or temperature.

The commercial fishing fleet of the northern Baltic Sea targets several species such as Atlantic salmon (*Salmo salar* L.), Baltic herring (*Clupea harengus membras* L.), sprat (*Sprattus sprattus* (L.)), cod, European flounder (*Platichthys flesus* L.), northern pike (*Esox lucius* L.), vendace (*Coregonus albula* L.), whitefish (*Coregonus lavaretus* L.), sea-run brown trout (*Salmo trutta* L.), smelt (*Osmerus eperlanus* (L.)), bream (*Abramis brama* (L.)), ide (*Leuciscus idus* (L.)), roach (*Rutilus rutilus* (L.)), burbot (*Lota lota* (L.)), perch (*Perca fluviatilis* L.), pikeperch (*Sander lucioperca* (L.)), European eel (*Anguilla anguilla* (L.)), rainbow trout (*Oncorhynchus mykiss* (Walbaum)), and turbot (*Scophthalmus maximus* (L.)). Eel, rainbow trout and turbot were omitted from the analyses in this thesis, because the data regarding them were quite sparse.

2.2.1 Salmon

The salmon population in the Baltic Sea belongs to the Atlantic salmon species, *Salmo salar* L., but is genetically isolated from the Atlantic populations (Ryman, 1983; Ståhl, 1987). Hydroelectric power production, logging, and pollution that took place during the 19th and 20th centuries have reduced the number of rivers available for salmon reproduction. Presently, significant wild salmon stocks exist in 13 rivers discharging into the Gulf of Bothnia, and some natural reproduction occurs in 12 rivers discharging into the Gulf of Finland and one discharging into the Gulf of Bothnia (ICES, 2001).

Salmon reproduce in the same river in which they were born. Their juveniles have territorial behaviour, and in the northern Baltic Sea they spend 2–4, normally 3, years in the river before migrating to the sea for feeding (Karlsson and Karlström, 1994, and references therein). The finite space available in rivers, combined with territorial behaviour of salmon parr, have the effect that salmon reproduction in any river is limited to certain level (Symons, 1979; Solomon, 1985). This river-specific reproduction capacity generally sets the ultimate upper limit to the stock size.

The main feeding areas of the northern Baltic salmon are the central and southern areas of the main basin of the Baltic Sea where they feed and grow for 1–4 years (Karlsson and Karlström, 1994); tagged Baltic salmon are only very rarely reported outside the Baltic area (Christensen and Larsson, 1979; Christensen *et al.*, 1994).

The salmon fisheries of northern Baltic have heavily relied on reared fish in the recent decades. River channel modifications have weakened the chances of natural salmon reproduction, and hatchery-reared fry, parr, and smolts have been released into the rivers to compensate for the loss of naturally produced offspring. Sweden started releasing fry already in the 1860s, and in 1987 the total rearings in the Baltic Sea exceeded 5.5 million smolts (Ackefors *et al.*, 1991). Most of the wild northern Baltic salmon stocks have been in a poor state for decades (Jutila, 1992; Pruuki, 1993; Karlsson and Karlström, 1994), and hatchery-reared juvenile salmon have been released into 8 northern Baltic rivers with wild salmon stocks. In addition, salmon smolts have been released into 15 rivers without a wild stock (ICES, 2001). About 90% of the smolts entering the Baltic Sea have been hatchery-reared in recent decade (Jutila *et al.*, 2003). High fishing pressure has caused that only few Baltic salmon survive to spawn the second time (Karlsson and Karlström, 1994).

Concern has been raised that stocking of salmonids may be detrimental to the natural population in e.g. increasing competition, affecting the timing of smolt migration, and attracting predators (reviewed by Einum and Fleming, 2001), and also in threatening the genetic diversity of the natural stock due to causing overfishing of the wild component as well as inbreeding and hybridization (reviewed by Laikre *et al.*, 2005).

The suspended International Baltic Sea Fishery Commission (IBSFC) set the goal of “safeguarding of wild salmon stocks” as part of the Salmon Action Plan 1997–2010, and the current European Union’s Common Fisheries Policy seems to support similar goals. The corresponding operational management objective was to increase the natural production of wild Baltic salmon to at least 50% of the natural smolt production capacity of each river by 2010, while keeping the catches as high as possible (IBSFC, 1995).

It is generally accepted that the wild Baltic salmon stocks have not reached the general level of the natural smolt production capacity during the last decades (Karlsson and Karlström, 1994; ICES, 2001); however, there is only weak knowledge about the shape of the stock-recruitment curve and hence about the maximal recruitment. Attempts have been made to estimate the maximum smolt production level of northern Baltic rivers, and the most regularly referred estimates have been used as reference points in the assessment and management of Baltic salmon. The recent increase in Baltic salmon populations (Romakkaniemi *et al.*, 2003) indicates that some of the proposed 'maximum values' are clearly underestimates, however. Due to the Salmon Action Plan goal, the maximum values have a direct effect to needed spawner escapement and thus to the salmon fishing regulations. Since the maximum smolt production estimates are weakly defined, the salmon management as a whole becomes weakly defined.

2.2.2 Baltic herring

Baltic herring is a subspecies of Atlantic herring (*Clupea harengus harengus* L.), and it differs from Atlantic herring in many aspects, most importantly in its smaller size and its ability to reproduce in lower salinities. It is a pelagic species that feeds in the pelagic areas on zooplankton, crustaceans, and fish eggs, juveniles, and even adult fish (Ojaveer *et al.*, 1981). Even though herring is a marine species, it is well adapted to the low salinity of the northern Baltic, occurring even in the northernmost areas where the surface salinity is below 3‰ and spawning in salinities as low as 3–4‰. The adaptation can also be seen in growth rates that are nearly similar in the northernmost part of Gulf of Bothnia and the Archipelago Sea (Parmanne, 1990). Even though herring lives in the pelagic, it spawns in the coastal zone, in sand, gravel, and stony bottoms (Ojaveer *et al.*, 1981) or on vegetation (Aneer and Nellbring, 1982) and its eggs fasten to the substrate. Herring larvae and juveniles remain in near-shore and sheltered areas (Urho and Hildén, 1990). The amount and quality of the coastal reproduction areas hence directly affect the success of herring populations and possibly set the upper limits for the herring year class size.

Herring's main competitor for food resources in the Baltic Sea is sprat and its main predator is cod. The weight-at-age of Baltic herring has decreased since the 1970s and early 1980s (Flinkman *et al.*, 1998; Cardinale and Arrhenius, 2000; ICES, 2005), which has been attributed to decline of zooplankton species preferred by herring (Flinkman *et al.*, 1998; Cardinale and Arrhenius, 2000) and competition induced by low predation by cod (Flinkman *et al.*, 1998).

The Bothnian Sea herring fishery is one of the most important fisheries in Finland (FGFRI, 2006a), the main fishing gear being pelagic trawl (ICES, 2005). The fishery is managed by setting Total Allowable Catches (TACs) based on stock size assessments made by ICES Working Group on the Assessment of Pelagic Stocks in the Baltic (e.g. ICES, 2006a) using Virtual Population Analysis (VPA) and its extension, Extended Survivor Analysis (XSA) (Shepherd, 1999). The stock size of the Bothnian Sea herring has increased simultaneously with the decrease of the weight-at-age (ICES, 2006a; **V**). The herring yields have generally been lower than the TACs, although in recent years they have been nearly equal (ICES, 2005). The management has been based on biomass and fishing mortality based reference points (ICES, 2006a), but no probabilistic models have been used when producing these reference points, and no systematic analyses of uncertainties related to these exist.

2.2.3 Cod and sprat

Cod and sprat are the other major pelagic/benthopelagic species of the Baltic Sea. They are marine species, but have adapted to the brackish conditions of the Baltic Sea, being able to spawn in the Baltic proper (Parmanne *et al.*, 1994; Nissling and Westin, 1997), sprat even in the Archipelago Sea, Gulf of Finland, and Gulf of Riga (Ojaveer *et al.*, 1981). Salinity and oxygen concentration are critical factors to the survival of their eggs, since the eggs are pelagic, and need to float in oxygen-rich water to survive.

The sizes of the sprat and cod stocks are estimated in ICES working groups using VPA and XSA (ICES, 2005), and the fishery is regulated by TACs, determined based on biological reference points for biomass and fishing mortality (ICES, 2005).

2.2.4 Other species

The coast of Finland is home to several fish species that are also subject to commercial fishery, and the diverse nature of the coast of Finland is reflected in the species composition. For example, vendace occurs only in the least saline parts of the Baltic Sea, while pikeperch and flounder are abundant only in the southern or south-western part of the coast of Finland, respectively, and don't occur in the northernmost parts at all (Ojaveer *et al.*, 1981). All of these species have had to adapt to the brackish conditions of the Baltic Sea that differ from their native freshwater or marine environments.

Populations of these species are relatively local; tagging experiments have shown that the migrations of pikeperch in the Archipelago Sea were generally less than 30 km and those of pike less than 10 km even when tags returned less

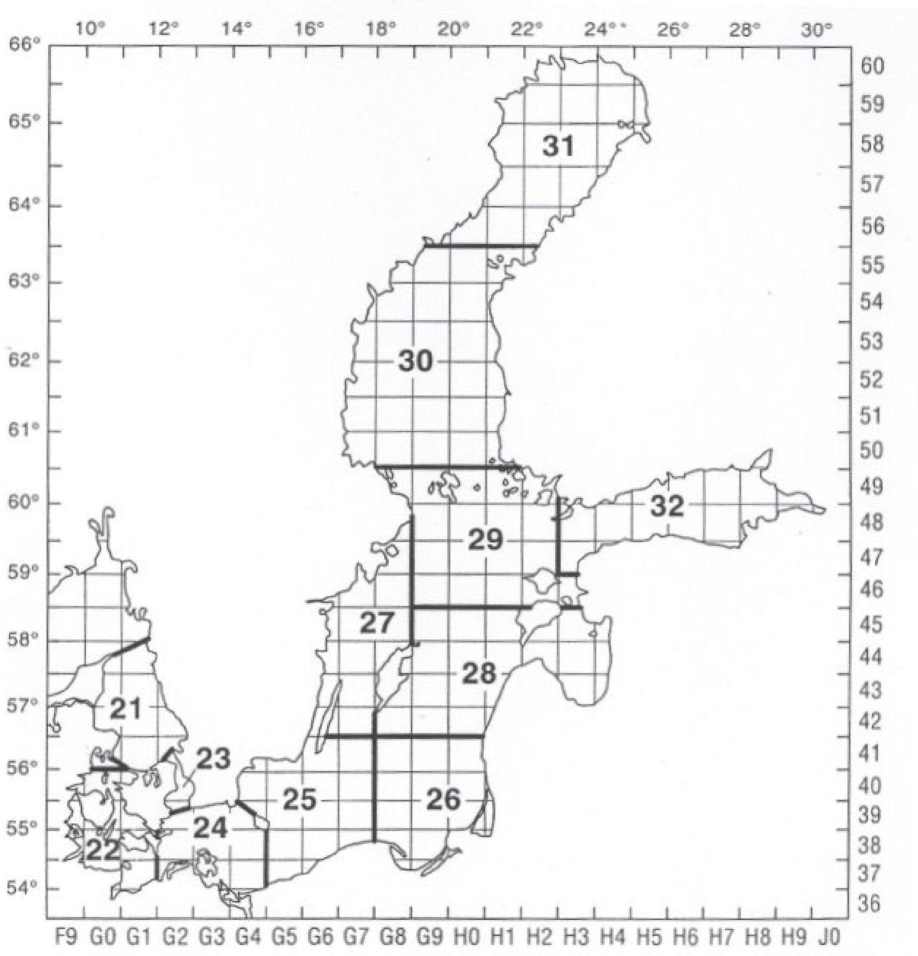

Figure 2: The statistical rectangles. Figure reprinted by the permission of ICES.

than two months after the release were excluded (Lehtonen *et al.*, 1983). Bream and roach generally migrated less than 20 km in the same study. Also the flounder and perch populations are quite local (Aro and Sjöblom, 1982, 1983).

All of these species are dependent on the shallow coastal waters for reproduction. The freshwater species pikeperch, roach, bream, pike, burbot, perch, and ide spawn in river mouths, inlets, and coastal waters, and the salmonid species sea-run brown trout, whitefish, smelt, and vendace spawn in rivers and in the sea area on hard sand or gravel bottoms. The flounder populations of the coast of Finland also spawn on shallow coastal areas despite flounder being a marine species.

Fishing of these species is not restricted by TACs or other international regulations, with the exceptions that there are spring-time closed periods in flounder fishing in the Gulf of Finland and subdivisions 22, 26, 28, and southern part of

29 (Fig. 2), and that same technical measures which apply to salmon apply also to brown trout. Mostly the fisheries are regulated by technical measures such as mesh size restrictions, minimum landing sizes, and area and time closures. In Finland, sea-run brown trout has a general minimum landing size of 40 cm and pikeperch 37 cm, but these can be increased and new minimum landing sizes can be set by local decision. Most technical measures are set and maintained locally.

These fisheries can be considered as data-poor cases that require robust management measures, since they are often composed of several local stocks, and the knowledge of the status of these stocks is often weak. Precautionary management of these stocks would benefit from an "early-warning system" that would utilise all available information about the trends in environmental factors that are relevant to these species, and observations of species that are known to react similarly to environmental pressures. This might give us a warning of potential stock decline before clear signs can be seen in fishing data.

3 The scientific approach and aims of the study

Fisheries data often have qualities that are statistically challenging: sampling performed by fishing vessels is far from random, and randomizing catch samples is also very challenging a task (Hilborn and Walters, 1992, pp. 414–415). Data may also be highly skewed (Maravelias *et al.*, 1996; Syrjala, 2000; Myers, 2001), highly scattered (Hilborn and Walters, 1992, p. 243; Planque and Frédou, 1999), strongly peaking (leptokurtic) (Chen and Fournier, 1999), and they often have relatively short time series (Myers, 2001). The challenge is thus to find information sources, statistical methods, and management strategies that are robust to the undesirable properties of data, and optimally utilise the information included in them.

The fragmented nature of the northern Baltic Sea coast and the sparseness of data available on many of the commercially exploited stocks emphasize the importance of management measures and research that utilise available information optimally and are robust to uncertainties. This information includes observations from the environment, species that live in the same area, and existing knowledge of the biology of these species.

The northern Baltic Sea is an interesting study area since it offers a relatively wide variation of environmental factors as well as spatial variation in the fish assemblage. Majority of the species targeted by professional fishermen are strongly local (Aro and Sjöblom, 1982, 1983; Lehtonen *et al.*, 1983), which creates a link between the fish yields and the reproduction possibilities of any location. Hence, we can assume that yields of a certain area reflect the reproduction and growth opportunities of that species in that particular area. This makes it possible to study the relationship of the environmental conditions and the success of fish stocks using data of exceptional magnitude, the fisheries and environmental data of the whole length of the coast of Finland.

Total fish catch data used in this thesis are somewhat unconventional in the field of ecological research. These data were chosen for two primary reasons: Firstly, they encompass a large geographic area with relatively good spatial resolution, and a long uninterrupted time series. While the responses of several fish species to environmental conditions have been studied in the northern Baltic, these studies mostly have a finer spatial scale as well as shorter or broken time series. The present large-scale study is meant to complement these studies and offer a comparison to their results. Secondly, studying the usefulness and applicability of such data sets that are most often available even in relatively data-poor cases is useful in the wide context of fisheries assessment and management.

Fisheries managers have to make their decisions under large uncertainty, and cost-effective ways to decrease the uncertainty are valuable. Evaluation of the usefulness of various readily available data sources, as well as statistical methods in decreasing this uncertainty is hence the methodological aim of this thesis. These information sources include readily available data bases such as the total catch and environmental data, and expert knowledge. Multivariate and Bayesian statistical methods were utilised to analyse these information.

This thesis is based on 4 research articles and one review article (appendices **I–V**). The articles address the following questions:

I. Do the commercial catch data of the coast of Finland prove informative in relation to biological aspects? What kind of ecological groups can be found in the commercially exploited fish fauna of the northern Baltic Sea?

II. Can large-scale data bases be used to estimate the relationships between environment and fish abundance? Which environmental factors are the most important in affecting the fish abundance in the Baltic Sea and what are the risks associated with trends in these variables?

III. Can a board of experts be efficiently used to gather information on a relevant ecological factor on which no data exist? How large are the salmon smolt production potentials of the Gulf of Bothnia rivers with wild salmon stocks?

IV. What are good model structures for probabilistic age-structured and stock-recruitment models for a pelagic fish stock? What kind of precautionary reference points are useful for management? What are the reference points for the Bothnian Sea Baltic herring stock?

V. What are the benefits and drawbacks of Bayesian networks in environmental science? In what kind of problems are Bayesian networks useful?

4 Materials and methods

4.1 Information sources

4.1.1 Fisheries data

The Finnish Ministry of Agriculture and Forestry maintains registers of fishermen and fishing vessels, and all 3000 fishing units are required to report on their fishing activity to the authorities, using either EU logbooks or monthly coastal reports. At the end of the year, the Finnish Game and Fisheries Research Institute (FGFRI) obtains the data and checks, analyzes, and supplements them. The data are also cross-checked with landing statistics and with data collected from the wholesale buyers of fish. Both the data acquisition and compilation of statistics are controlled by EU regulations, e.g. EC 3880/91 (FGFRI, 2002). The methods of data compilation and the reliability of the statistics are described in the FGFRI quality report of the statistics (FGFRI, 2002, 2004). These data of years 1980–2001, including several fish species (**I**, **II**) were used.

The catch statistics are compiled per statistical rectangle (Fig. 2) as defined within the International Council for the Exploration of the Sea (ICES) fishing areas. The spatial resolution of the statistics is exceptionally fine: each of the ICES statistical rectangles covers an area between half a parallel and one meridian; e.g. 60.0–60.5°N, 21.0–22.0°E.

Total fish yields were used to approximate the fish abundances in different parts of the sea and different years. Professional fishermen's yields were used because, despite their obvious shortcomings, they are the most reliable source of long-term and geographically large-scale fisheries data in regard of many species. Some experimental fishing and echo-sounding data exist, but they are considerably sparser both spatially and temporally than the professional fishing data.

Total yields were aggregated to yearly level to reduce noise, such as random and seasonal variation. Furthermore, the data were transformed from total catches into catches per unit area of water surface, due to the different water surface areas of the rectangles. The final datasets consisted of yearly catches of 16 fish species from 44 (**I**) or 11 species from 40 (**II**) rectangles during 21 years.

Total yield data are not likely to be representative of the relative abundances of species due to different species being targeted with differing intensity, and catchability that varies between species. They can, however, serve as a proxy of the variance of abundance within species across time and geographic area.

4.1.2 Water quality and geographical data

The environmental variable data were compiled for the same ICES statistical rectangles as the fish yields and covered the years 1977–1997 (**II**). The water quality data originated from the database of the Finnish Environment Administration (FEA), including information on salinity, concentrations of total nitrogen (N), total phosphorus (P), and phytoplankton chlorophyll *a* (Chl). The data were obtained from national monitoring programmes of the FEA and monitoring surveys conducted by the regional environmental centres of Finland and coordinated by the Finnish Environment Institute (SYKE). The total number of sampling stations varied from 1086 in 1995–1997 to 1259 in 1983–1991. There was an average of 24 stations per ICES square in 1995–1997. Salinity and nutrient levels were taken from surface layer (0–5 m) and Chl from integrated water samples (surface to 5 m). Salinity and Chl were measured between July and September to avoid the phytoplankton bloom that occurs in May–June, and total nutrients either between February and March. Total N and P were analyzed from unfiltered samples according to standard methods used in Finland (Koroleff, 1976). Chl was analyzed after filtering (Whatman GF/C) according to Lorenzen (1967). Salinity was calculated using the Practical Salinity Scale.

The geographical variables included the average duration of ice cover per year and the length of shore line. The shore density data were obtained from Hildén *et al.* (1982) and are based on a study conducted in the University of Turku. Shore density is defined as the length of the shoreline in the rectangle, measured from the basic water level line from a 1:20 000 map, and divided by the area of water surface in the rectangle (in hectares), and it reflects the availability of coastal areas in the rectangle. The length of the ice-covered season is expressed as the mean number of ice-covered days per year during 1963–1980 (Leppäranta *et al.*, 1988). The shore density and length of the ice-covered season were assumed to be constant throughout the study period.

These environmental variables were chosen because they represented different aspects of the environmental conditions, such as trophic level, availability of sheltered spawning sites, thermal conditions, and salinity. Furthermore, they have been observed continually since the 1970s throughout the sea area of Finland, are representative of the quantity of interest, and are as resistant as possible to short-term variations and errors caused by sampling, etc. For example, the duration of ice cover per year was chosen instead of water temperature measurements, since it is far more reliable in describing the general thermal conditions than occasional measurements of water temperature. Similarly, total nutrient levels were chosen instead of any specific chemical form, because they are more resistant to irrelevant changes and thus better describe the trophic status of the area.

4.1.3 Salmon spawning capacity knowledge

As spawning stock size has been the limiting factor of the salmon reproduction in the Gulf of Bothnia for decades (Karlsson and Karlström, 1994), no data exist that could be used to estimate the maximum smolt production level allowed by the river environments. Estimates of salmon smolt production capacity in the Gulf of Bothnia (**III**) were hence collected from a panel of five experienced salmon biologists working in the area. The marginal utility of information decreases as the number of experts increase, and using 3–5 experts is suggested (Makridakis and Winkler, 1983; Clemen and Winkler, 1985; Ferrell, 1985).

The experts estimated the probability distributions for the river-specific variables that described the characteristics of the river, and conditional probability distributions that determined the juvenile salmon stocks' responses to the river characteristics. For successful combination of the estimates it is vital that experts agree on what is to be estimated and on the definitions regarding the model, and considerable time was used to assure that the experts were familiar with the concept of probability distributions and agreed on all the definitions of the model.

4.1.4 Herring fishery data

Bothnian Sea (ICES subdivision 30, Fig. 2) herring catch data (**IV**) of the years 1973–2005 were obtained from the Finnish Game and Fisheries Research Institute. The data set, similar to that used by ICES Baltic Fisheries Assessment Working Group (ICES, 2006a), consists of catch in tonnes and age-structured catch in numbers, and yearly average weights and ratio of mature fish at age.

4.2 Modelling

The information content of the total yields data were studied by analysing species associations based on these data only using multidimensional scaling (**I**). The sensitivity of 11 of these species to environmental conditions was analyzed using a Bayesian network (**II**). The smolt production potentials of 13 Gulf of Bothnia rivers were estimated by structuring expert knowledge using a Bayesian network (**III**). The Bothnian Sea Baltic herring stock size, its stock-recruitment relationship, and biological reference points were estimated using a hierarchical Bayesian model (**IV**). Detailed descriptions of the methods are presented in the appendices (**I–IV**); an overview of the methods is given here. Paper **V** summarises and reviews the use of Bayesian networks, a useful modelling method used in papers **II** and **III**.

4.2.1 Multidimensional scaling

Ordination methods are widely used in ecology to group species and relate species abundance and environmental data (e.g. Fernández-Aláez *et al.*, 2002; Hoeinghaus *et al.*, 2003; Soininen and Könönen, 2004). In this study (**I**) we used multidimensional scaling (MDS), which is especially well suited to abundance data where it is possible that zeros emerge from both ends of the environmental gradient, such as from there being either too high or too low salinity for the species to occur there (Legendre and Legendre, 1998). Multidimensional scaling was used as the statistical method since the aim was to do an exploratory analysis of the data.

Ordination of the statistical rectangles as well as the fish species was performed. MDS was applied to determine the ordination of the rectangles (Legendre and Legendre, 1998). The rectangles were grouped using cluster analysis that was conducted with the same distance matrix that was used with the MDS, and the final solution was found with the single linkage method. The ordination of the fish species was performed using the complete dataset of 924 observations and 16 fish species. The data were standardized by subtracting the means and dividing by the standard deviations of the catches of each species. To examine the stability of the species associations, the data were divided into 2 sets: the 1980s and the 1990s (the latter included the year 2000).

Groups among the fish species were found by hierarchical clustering. Ward's method, an agglomerative algorithm minimizing the intragroup variance, was applied with the correlation (subtracted from 1) as the dissimilarity measure. The clustering was visualized as a tree graph (dendrogram). The statistical analyses were carried out with SURVO MM software (Mustonen, 2001).

4.2.2 Bayesian networks

Bayesian networks (BNs, **II**, **III**, **V**) are mathematical models that consist of a set of variables with mutually exclusive states, and directed links between these variables. Furthermore, the directed links must not form a cycle (Jensen, 2001, p. 19). The values of the variables need not be known exactly, but a probability distribution describing the probabilities of each of the alternative mutually exclusive states being true must be explicitly stated. If a variable has incoming links ("parents"), it has a conditional probability table defining the probabilities of its states given that each of the (combinations of) values of the parent(s) is true. Bayesian networks are, hence, fully conditional probabilistic models over a discrete domain. (Some attempts at developing Bayesian network methodology to continuous variables exist, but results are still relatively modest; see e.g. Madsen *et al.*, 2005.) Bayesian networks are particularly useful in modelling situations in which knowledge about structural relationships, dependencies and independencies, can

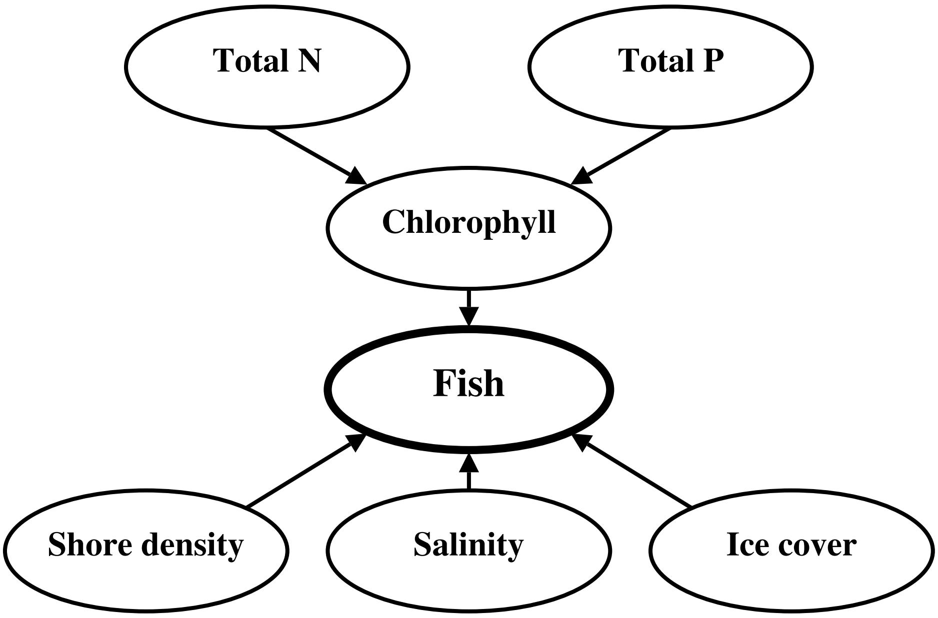

Figure 3: Scheme of the structure of the model used for estimating the roles of environmental variables in fish production. For simplicity, the 11 fish species were in this scheme replaced with the *Fish* variable; in the model there is a variable for each of these species separately.

be utilised (Madsen *et al.*, 2005), which is often the case in environmental research problems.

The Bayesian network model used to estimate the importance of various environmental factors to fish production included 6 environmental variables and 11 fish species (**II**, Fig. 3) from 40 statistical rectangles along the coast of Finland (Fig. 2). The environmental variables were total nitrogen (N) and total phosphorus (P) concentrations, chlorophyll *a* (Chl) concentration, the shore density, average yearly ice cover duration, and salinity, and the 11 fish species included all species within the Finnish catch statistics which don't perform long migrations. These species were pikeperch, northern pike, bream, roach, European flounder, Eurasian perch, Baltic herring, vendace, burbot, smelt, and ide. Together, these species comprised over 77% of the catches in 2005, herring forming large majority (FGFRI, 2006b).

The large variability in the environmental types offered by the coast of Finland was utilised here to infer about the roles of various environmental factors on the success of fish species. Four time slices were taken from each location, as well, to account for changes in the environment during the last decades. To link the environmental conditions at the egg and larval stages with the catches of fish that are caught as adults, the catches and the values of the environmental variables were pooled into 3-year groups and the fish catches were linked with the environmental variables of the preceding 3-year period.

Bayesian network was chosen as the modelling method due to its ability to treat uncertain dependencies explicitly and in a mathematically coherent manner. BNs also allow construction of models with minor amounts of assumptions. Most importantly, they can be used to examine the tails of the probability distributions, i.e. the probability that the value of the interest variable falls below a certain limit, etc.

It was assumed that the total yields reflect the productivity of the species in that location. This assumption is based on the fact that all of the species in this analysis are exploited by commercial fishery, and the exploitation rates are so high that the stocks can be considered fully exploited (Kuikka, 1994). In this situation, the yields can be assumed to reflect the productivities of the stocks. The responses of the fish yields to the various environmental factors were studied especially in terms of the risk that the yields drop to the low end of the observed scale, reflecting relatively weak reproduction success in the prevailing conditions.

The model structure (Fig. 3), based on expert opinion about the causal connections in the northern Baltic Sea ecosystem, was designed so that the effect of each environmental variable could be investigated separately, as well as any combinations of them. The model parameters, i.e. the conditional probabilities, were learned from data using the learning algorithm implemented in Hugin, documented by Laurizen (1995). The modelling approach was to study the probabilistic dependencies between the variables in the data, and to see how the fish abundances are likely to change given changes in the environmental factors in the light of the data.

The salmon production potential model (**III**, Fig. 4) summarizes the current expert knowledge about smolt production capacities (SPCs) of the Gulf of Bothnia rivers with wild salmon stocks. The model was constructed in cooperation with salmon experts and it aims to describe all the noteworthy factors that affect salmon smolt production, while striving to remain as simple as possible. The variables of the model were chosen so that they adhered to concepts familiar to the experts.

The model consists of 10 variables (Fig. 4), 5 of which (solid rectangles in Fig. 4) describe or reflect the external factors, physical and biological, to which salmon are exposed in the reproduction rivers. Three variables (ovals in Fig. 4) describe the juvenile salmon stocks' response to the external factors. The remaining variables (dashed rectangles in Fig. 4) are auxiliary variables that enable handling of all the estimates in the same model.

Five experienced salmon experts from the Gulf of Bothnia estimated the model parameters, i.e. the (conditional) probability tables. Each expert did this alone via a questionnaire form, with the possibility to hold discussions with the analyst,

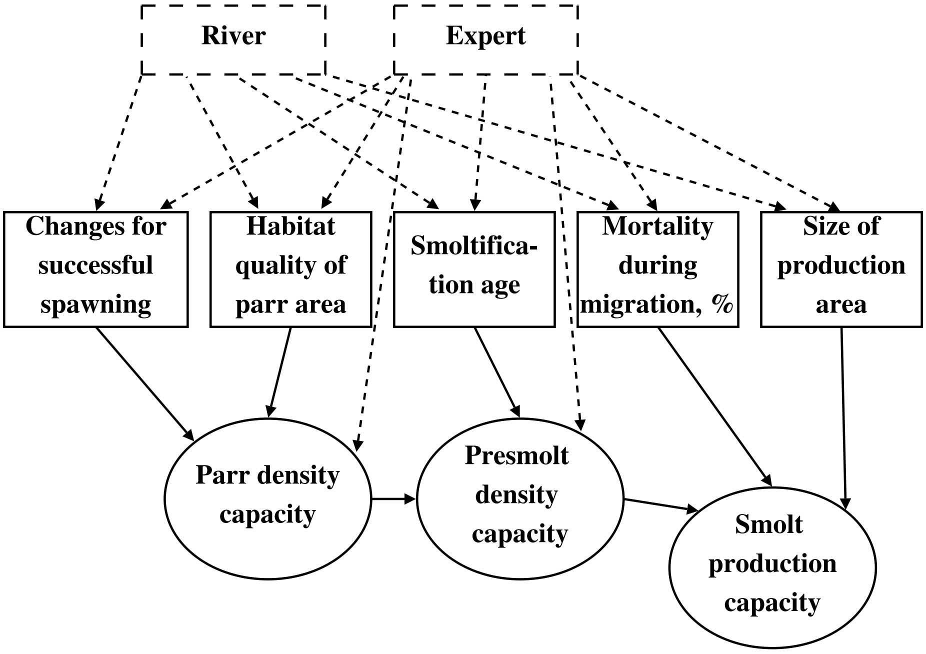

Figure 4: Structure of the salmon smolt production potential model. The solid rectangular nodes denote river-specific characteristics which are estimated for each river separately by each expert; the elliptical nodes denote conditional estimates on related input arcs, e.g. smolt production capacity depends on presmolt density capacity, mortality during migration, and the size of production area. The dashed nodes denote the auxiliary variables. The variables that are children of River are estimated separately for each river; the variables that are children on "expert" include separate estimates from each expert.

since hints exist that interaction between experts at this stage may increase overconfidence and thus produce poorer results (Morgan and Henrion, 1990, p. 165). The probability distributions of the experts were combined by simple average. The probabilities given by the experts were treated equally and symmetrically (Clemen and Winkler, 1999).

The pros and cons of Bayesian networks are reviewed and examples of their use are given in paper **V**. The models in this thesis were built using the Hugin software (Hugin Expert A/S, Aalborg, Denmark; `http://www.hugin.com`; Madsen *et al.*, 2005).

4.2.3 Hierarchical pelagic fish stock model

Two hierarchical models were built to demonstrate the probabilistic estimation of pelagic fish stocks and to study the Bothnian Sea herring stock: A hierarchical, age-structured model for estimating herring stock size and structure, and a separate model for the estimation of stock-recruitment relationship. Biomass and fishing mortality based limit and target reference points were also computed (**IV**). These models were implemented using OpenBUGS software (Thomas *et al.*, 2006).

The age-structured model produces probabilistic estimates for the yearly age structure, the number of eggs spawned each year, recruitment, natural and fisheries-induced mortalities, and fishery selection for each age each year. Beverton-Holt and hockey stick (Barrowman and Myers, 2000) recruitment functions were used in the stock-recruitment model and spawning stock biomass based reference point were computed for both cases.

Spawning potential (number of spawned eggs) or spawning stock biomass based limit reference points (B_{lim}) were defined so that with Beverton-Holt function B_{lim} was the spawning potential that produces 50% of the asymptotic recruitment, and with the hockey stick curve, B_{lim} was defined as the minimum spawning potential that produces the maximum amount of recruits, i.e. the change point of the function. To account for uncertainty, the precautionary approach reference points (B_{pa}) should be defined so that there is a known, small probability of crossing the real but unknown limit reference point. In other words, B_{pa} were defined so that we take a percentile from the upper tail of the probability distribution of B_{lim}, and the corresponding spawning potential is B_{pa}. This approach takes directly into account the uncertainty related to the estimation of stock size and recruitment. Hence, the more uncertainty there is, the larger the distance between the median of B_{lim} and B_{pa}.

Fishing mortality reference points were computed based on the spawning-per-recruit approach (Sissenwine and Shepherd, 1987; Mace and Sissenwine, 1993). Successive fish generations have to replace each other on average, so each recruit has to be able to produce one recruit in average during its lifetime. Fishing naturally diminishes the lifetime spawning potential of the individuals as it removes them from the population. The spawning-per-recruit approach is based on the idea that this decrease in the spawning potential can be computed and compared to the natural reproductive capacity of the stock, and then estimate how large a decrease in the spawning potential, i.e. how heavy fishing pressure, is still sustainable. For every constant fishing mortality level, there is a corresponding straight line going through the origin of the spawner-recruitment plot. This line corresponds to the average survival ratio needed to maintain the fishing mortality level. The steeper the line, the higher survival is needed to maintain that fishing mortality (Sissenwine and Shepherd, 1987; Mace and Sissenwine, 1993).

Sissenwine and Shepherd (1987) also defined the replacement fishing mortality F_{rep}, the fishing mortality that allows each recruit to replace itself on average, and suggested that it could be defined as the fishing mortality with the slope equal to median survival ratio. They also proposed that this F_{rep} could be used as the reference point for overfishing, i.e. the F_{lim}. In this study, the yearly survivals were computed in the stock-recruitment model, and median survival was used to determine F_{rep}=F_{lim}, the fishing mortality that the stock can still sustain if it constantly has the median survival. Precautionary approach reference point for fishing mortality F_{pa} are computed based on the probability distribution of survival similarly to the computation of B_{pa}; we calculate the percentiles of the probability distribution of the survival from the low end of the distribution, i.e. prepare for the fact that the true survival is in the low end of the distribution, and the compute the fishing mortality levels that this survival can sustain.

5 Results

5.1 Multidimensional scaling of fish yields

Hierarchical clustering of the fish species (**I**, Fig. 5) revealed 3 biologically compatible groups: the freshwater species, together with the marine species herring and flounder, formed one group, the salmonid species (smelt, whitefish, vendace, trout, and salmon) formed another, and cod and sprat formed the third group. These associations, revealed by ordination and clustering, correspond closely to fish biologists' views of species similarity.

To study the stability of the species associations, the data were divided into 2 sets: the 1980s and 1990s, the cut-off point being determined by the decrease in cod catches in the study area since the mid-1980s, resulting in the end of the cod fishery 1990. Thus the 2 periods represent different types of ecosystem state — one with cod present both in the ecosystem and fishery and the other with cod virtually absent from both. The results suggest that collapse of the cod stocks did

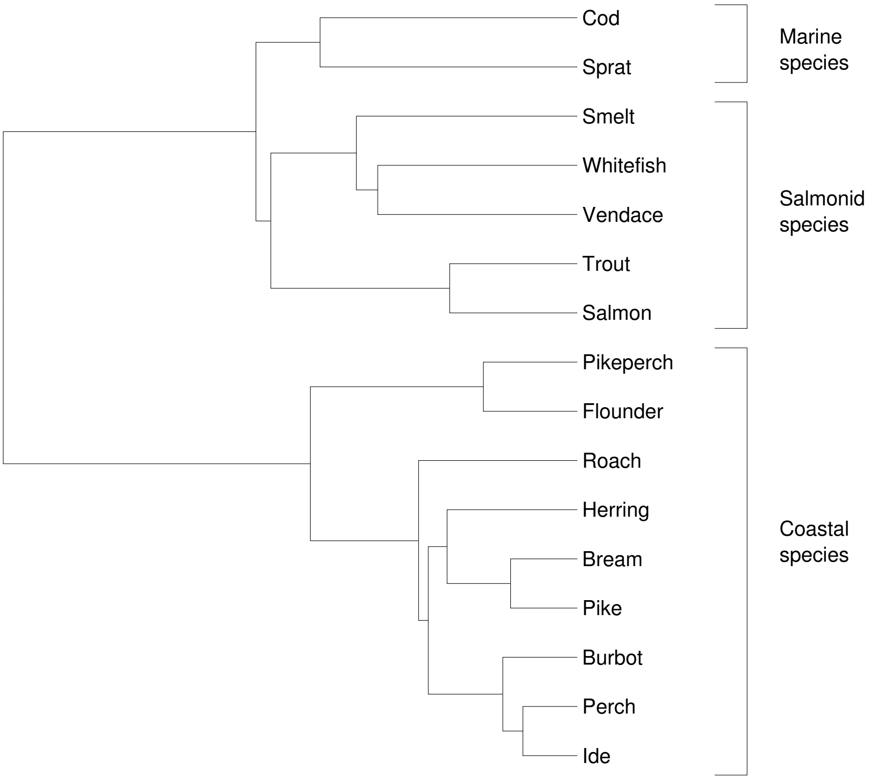

Figure 5: Dendrogram of the species associations based on multivariate analyses of the fish yield data of the coast of Finland.

not alter the ecosystem so much that it would have strongly affected the reciprocal associations of the other species.

5.2 Environmental factors and fish productivity

The responses of the fish yields to various environmental factors (**II**) are reported by giving the probabilities that the fish yields lie in the lowest class given different states of environmental variables (Figs. 6–8). The differences between the columns show the relative sensitivity of the species to a given environmental factor.

The environmental factors were divided into three groups based on their controllability: Nutrient (total P and total N) concentrations and chlorophyll *a* concentration can be controlled through water quality management to some extent. Ice cover duration and salinity of the Baltic Sea are factors that are predicted to change with climate change and hence could, in principle, be controlled through climate policy, although this control is very weak and slow. Shore density cannot be controlled at all in a large scale.

The responses of the fish yields to the water quality variables are illustrated in Fig. 6. Chl has slightly stronger impact than N and P, which don't affect the fish abundance directly but through the chlorophyll concentrations (Fig. 3). Generally, all of the species except vendace benefit from the higher eutrophic status — the risk of falling to the lowest class of fish production is higher if the Chl concentrations are low. Vendace is the only studied species which suffers from the levels of eutrophication present in the northern Baltic Sea at the moment.

Shore density and ice winter duration (Fig. 7) were the most important environmental factors in relation to the risk of stock collapse. Species that spawn in shallow areas (bream, burbot, herring, ide, perch, pike, pikeperch, smelt) are very dependent on the overall amount of shore line. Ice winter duration seems to be the most important factor for most of the species (Fig. 7): a shorter yearly ice cover seems to strongly increase the risk for a decrease in fish yields, with the exception of flounder whose risk of stock collapse is lower with shorter ice cover period. The importance of salinity is small, and the increase in salinity seems to slightly drop the risk of stock collapse with all species except smelt and vendace (Fig. 7).

Current climate change models predict that if climatic change starts to impact the coastal waters of Baltic, there will be decrease in both salinity and the duration of ice cover (Omstedt *et al.*, 2000; Meier *et al.*, 2004). We studied the effect of this concurrent change (Fig. 8). According to the present model, if both salinity and ice coverage drop to the low end of the observed range, the probability that fish productivity falls to the lowest class is 1 for most of the species. With vendace the probability was close to 1, and with herring only 0.546. Flounder is the only species benefiting from this change.

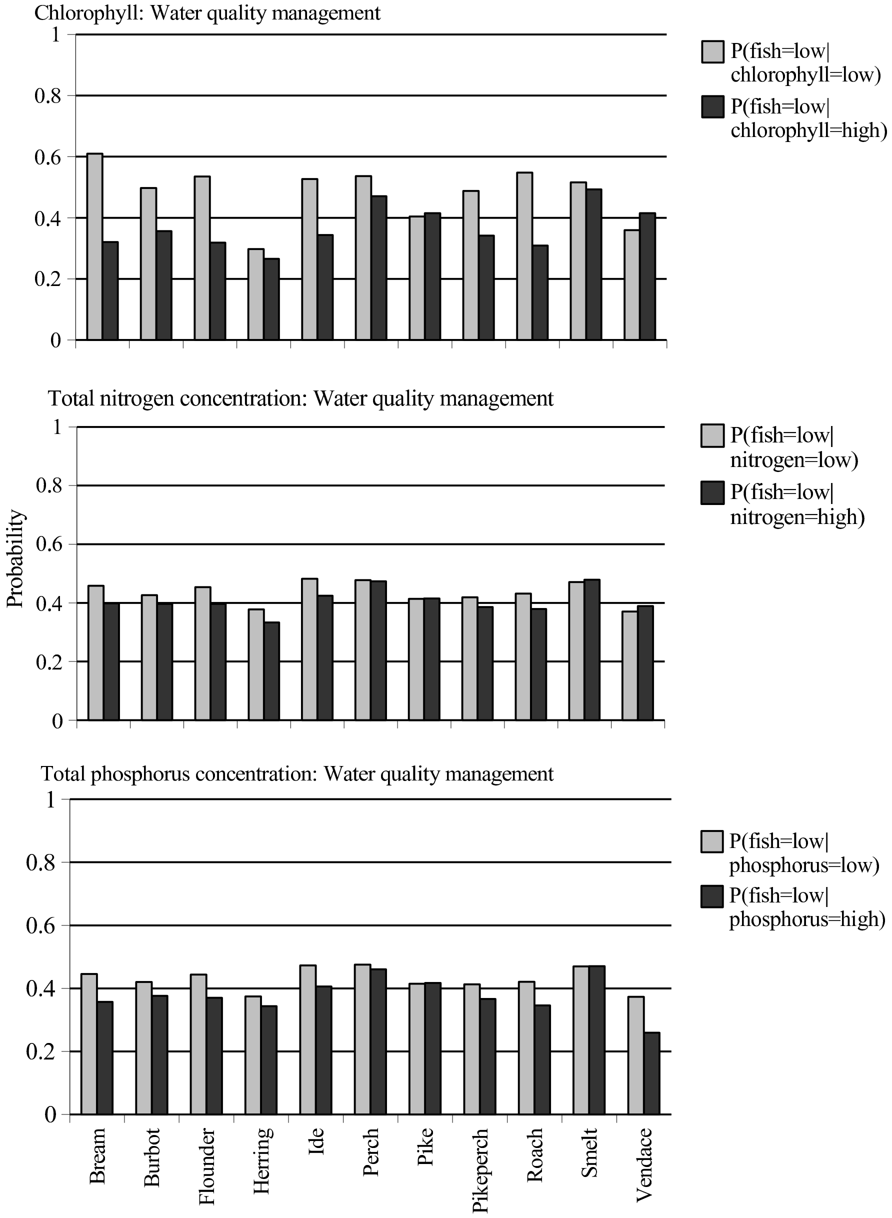

Figure 6: Impacts of partly controllable water quality variables (chlorophyll, nitrogen, phosphorus) on fish productivity. The probabilities that the fish yields lie in the lowest class, if the environmental variables are in the lowest (left, light grey) or highest (right, black) class. For example, when nitrogen is assumed to be low, the probability that bream catch is in lowest class is 0.459 and when nitrogen is high, probability is 0.399. The bigger is the difference between the columns, the more sensitive species is to the changes of that environmental variable.

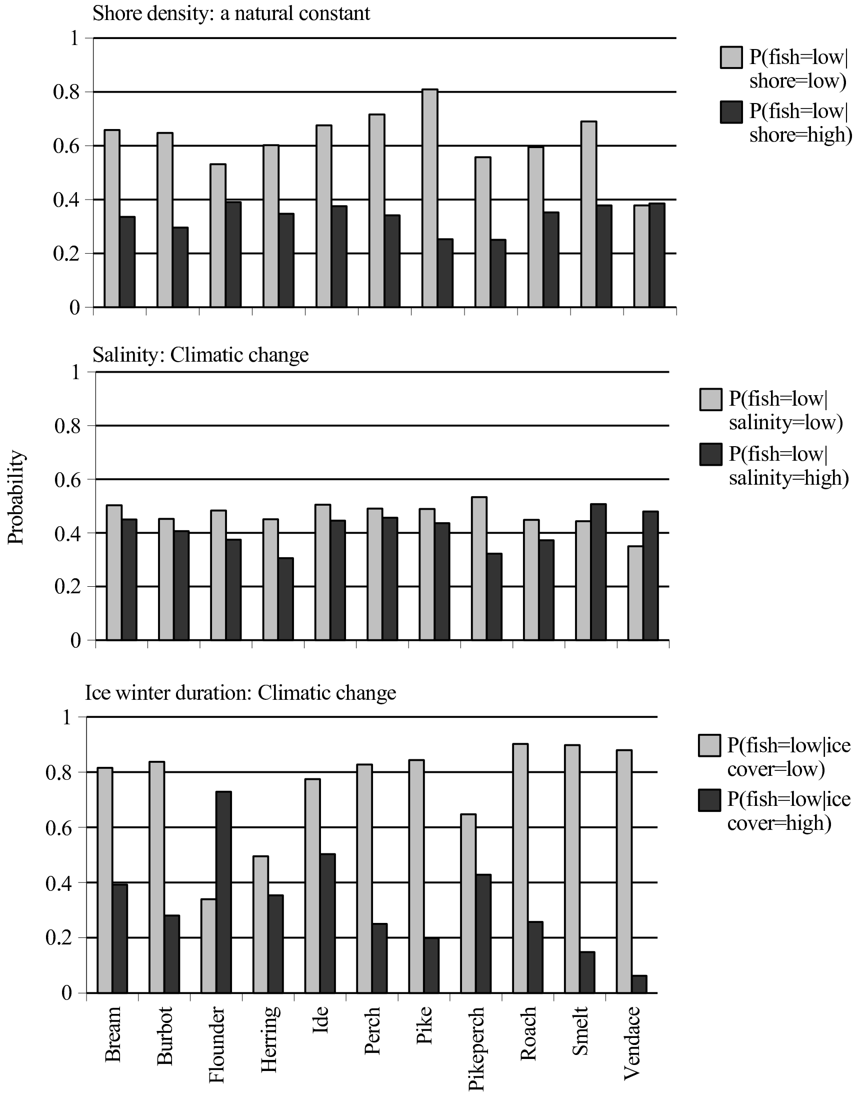

Figure 7: Impacts of uncontrollable (shore density) or poorly controlled (climatic change related) variables on fish productivity. The probabilities that the fish yields are in the lowest class as the environmental variables are in the lowest (left, light grey) or highest (right, black) class. For example, when ice winter duration is low, the probability that vendace productivity is low is 0.880, whereas high ice winter duration lowers this probability to 0.062.

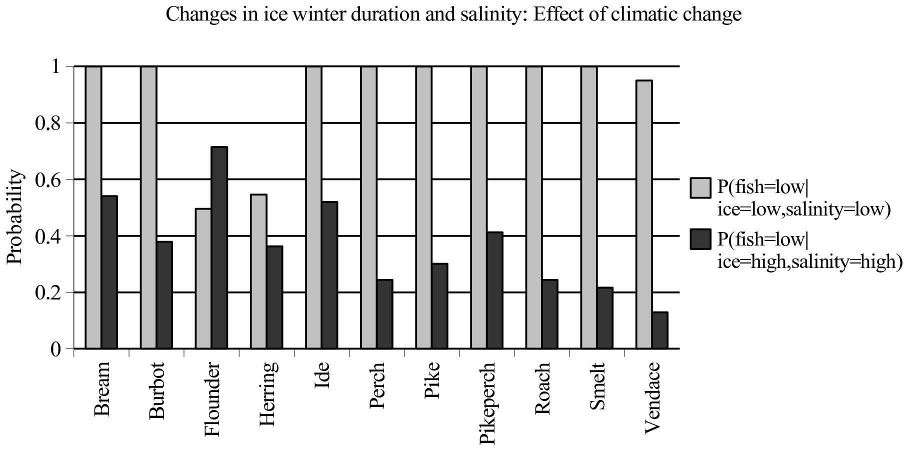

Figure 8: Indicated consequences of climatic change in the Baltic Sea. The light grey columns (left) indicate the probabilities that the fish production would fall to the lowest class if ice winter duration and salinity are both low, as would be the likely result of climatic change. The black columns (right) indicate the probabilities that the fish production would be low if ice winter duration and salinity are high, the opposite scenario of climatic change. With most of the species, the probability that the fish productivity drops to the lowest class in the climatic change scenario is 1.

Table 1: Comparison between the present model, previous estimates of smolt production potential (ICES, 2001), and present smolt production rates, with probabilities of attaining the new target.

River	Previous estimate of smolt production capacity	Probability mass above the previous estimate	Smolt production in 2001	Probability mass above the 2001 production value
Tornio	500 000	0.82	620 000	0.77
Simo	75 000	0.51	47 300	0.72
Kalix	250 000	0.85	287 000	0.81
Öre	20 000	0.49	900	0.98
Vindel	200 000	0.6	75 000	0.93
Ljungan	20 000	0.11	10 000	0.28
Lögde	20 000	0.71	4 100	0.97
Sävar	4 000	0.52	1 500	0.84
Rickle	5 000	0.66	900	0.97
Byske	80 000	0.8	106 000	0.74
Åby	16 000	0.59	16 300	0.58
Pite	33 000	0.71	18 000	0.87
Råne	20 000	0.82	8 800	0.96
Average	95 615	0.63	91 985	0.80

5.3 Salmon smolt production capacity model

The results of the expert knowledge model (**III**) showed clearly that the best available knowledge about the smolt production capacity levels in the Gulf of Bothnia rivers is still vague: the probability distributions were very wide, indicating large uncertainty (Fig. 9). These distributions showed, however, higher estimates of the potential smolt production than the previous point estimates, given by ICES (2001). In most cases, 40–80% of the probability mass was assigned to higher values than those estimates (Fig. 8, Table 1). Only in the case of River Ljungan, the probabilistic estimate gave lower figures that the previous estimates: almost 90% of the probability mass was assigned to values lower than the point estimate proposed earlier (Table 1).

The greatest smolt production capacity was estimated to occur in the Tornio River, the probability distribution peaking strongly at 1–5 million smolts per year (Fig. 9). The Kalix River also had high smolt run values, having the highest probability density in 1–5 million smolts, as well. These two are also the two largest rivers in terms of the size of salmon production areas. Examination of the presmolt density capacities in each river (Fig. 10) reveals, however, that the experts think that there are also relatively large differences in the amounts of smolts produced per a fixed area, result of different environmental conditions in the rivers.

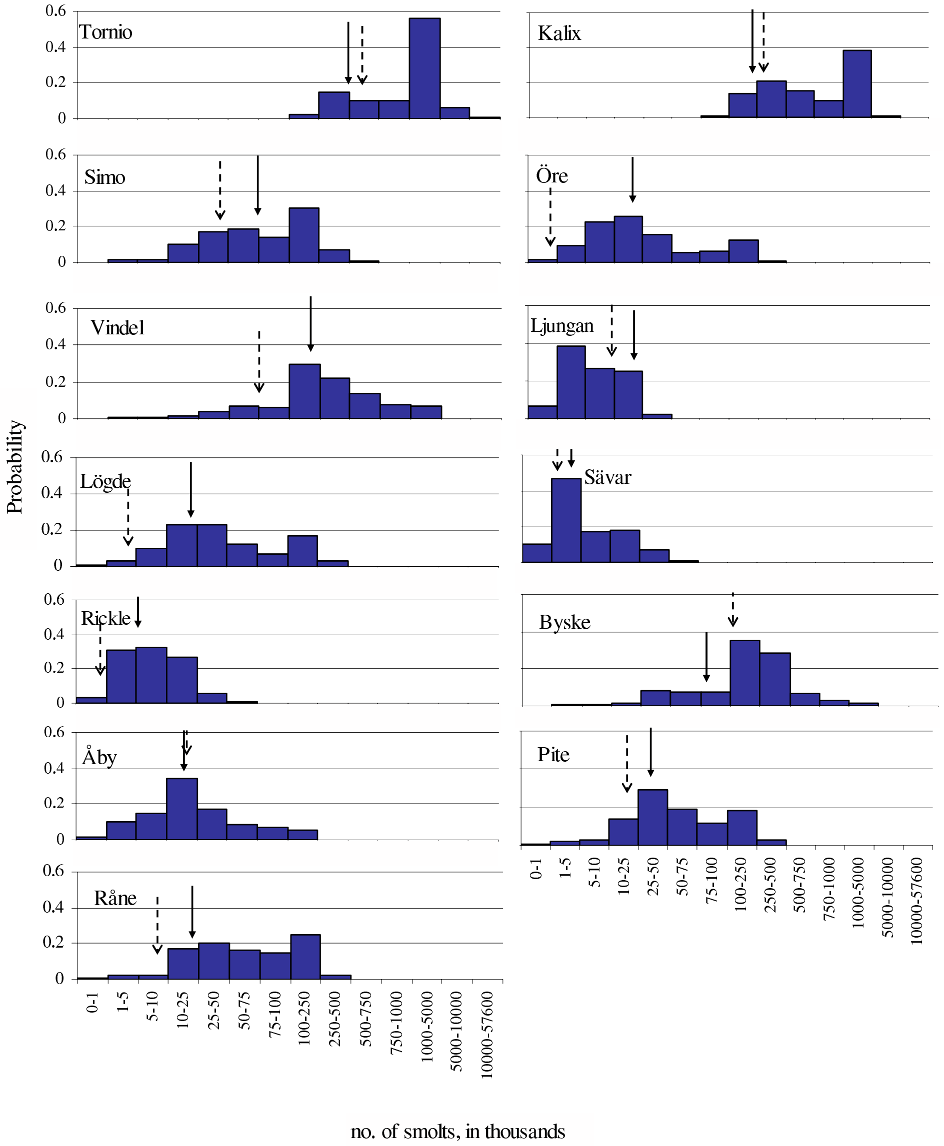

Figure 9: Probability distributions for smolt production capacities in northern Gulf of Bothnia wild salmon rivers. Numbers of smolts in thousands. Solid arrows indicate the previously given point estimates of smolt production capacity (ICES, 2001), and dashed arrows indicate the smolt production in 2001. Note that the x-axis is not linear.

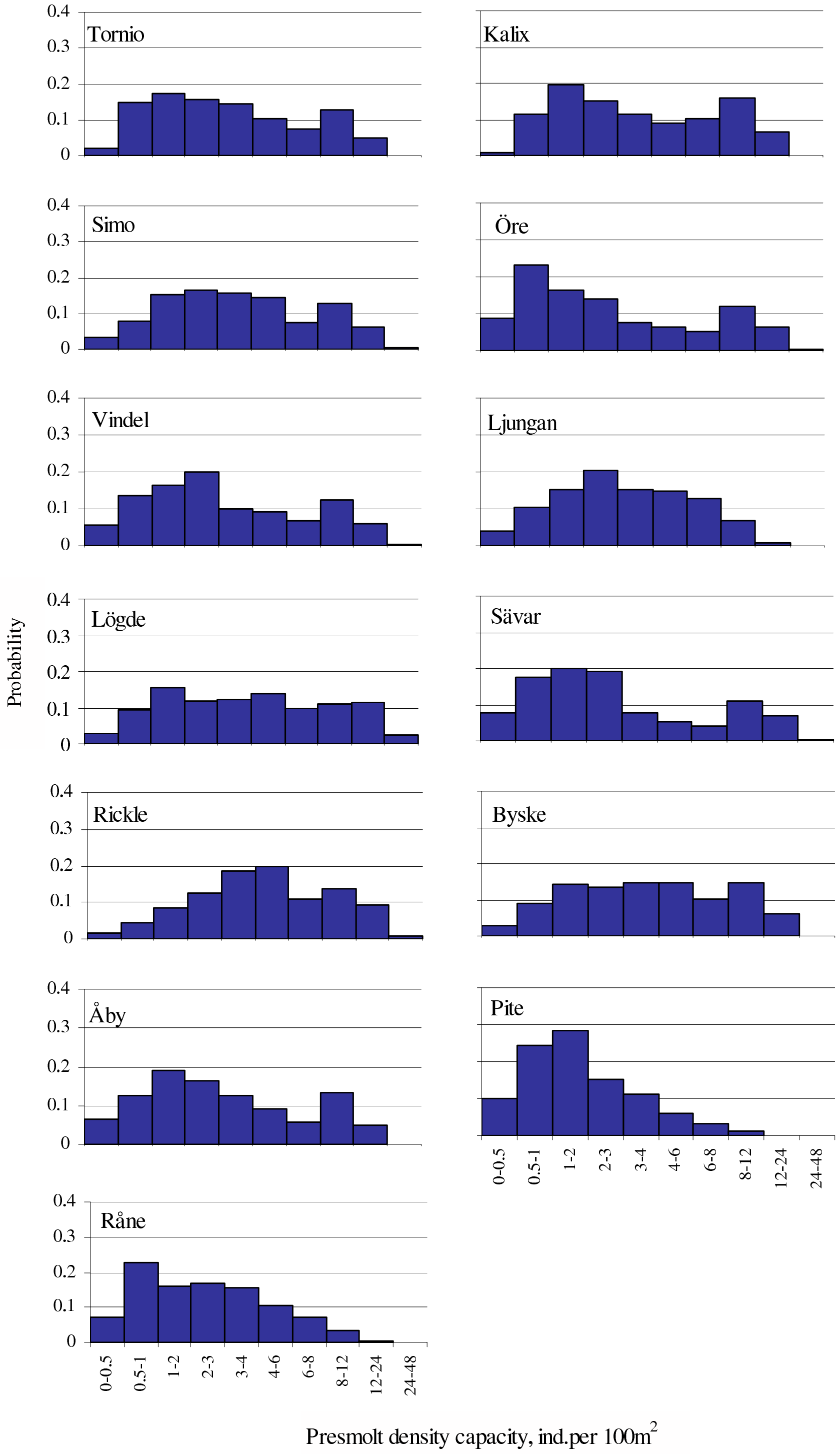

Figure 10: Probability distributions for pre-smolt density capacity for each river. Note that the x-axis is not linear.

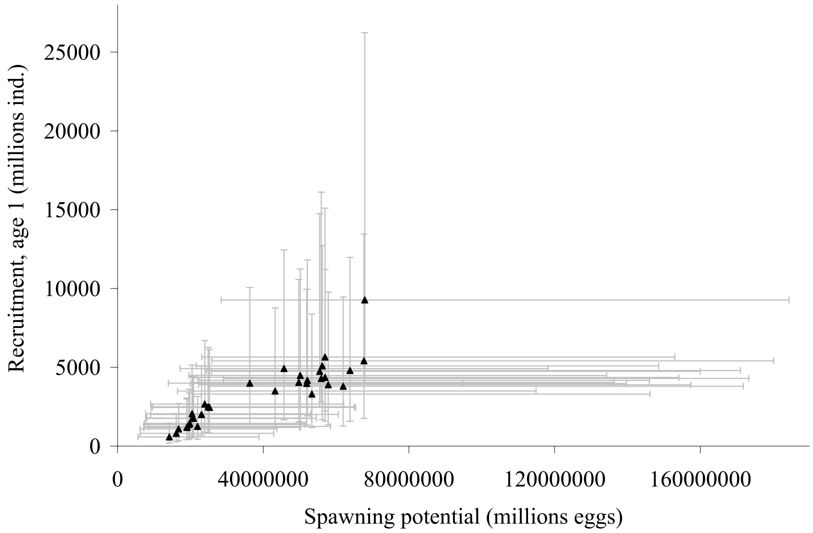

Figure 11: The stock-recruitment observations with the associated 95% credible intervals.

5.4 Herring model

The Bothnian Sea herring model (**IV**) revealed high uncertainty about the stock size and recruitment (Fig. 11). The 95% credible intervals show the range within which the true value lies with 95% probability, while the dots represent the median.

The data included considerable amount of information about the stock-recruitment parameter α, the slope at the origin (Fig. 12). This variable translates to the survival of eggs in very low egg densities, or in the case of the hockey stick curve, the survival below which the density-dependence starts to affect. The upper limits of recruitment, i.e. the asymptote of the Beverton-Holt curve and the maximum value of the hockey stick curve, were updated only very slightly by the data, implying that the data set included only very little information about this quantity (Fig. 13a). This was further examined by running the model with a very vague prior (Fig. 13b). The data updates the prior only very weakly, demonstrating that there's very little information in the data that can be used to estimate the carrying capacity.

The uncertainty about the spawning biomass based biological reference point B_{lim} was very large (Fig. 14). 90th and 95th percentiles of the B_{lim} distribution were computed to illustrate the values of egg production at which there is 90% and 95% probability that this value is at or above the uncertain B_{lim} value; in other words, there is 10% or 5% risk of crossing the unknown biological limit reference point. These values are good candidates for B_{pa}.

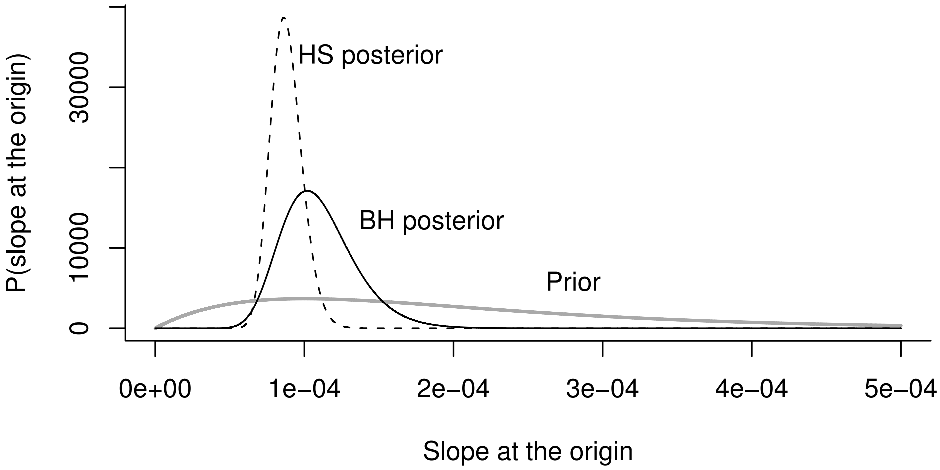

Figure 12: The prior (grey line) and posteriors for the slope at the origin of the Beverton-Holt (solid line) and hockey stick (dashed line) stock-recruitment functions.

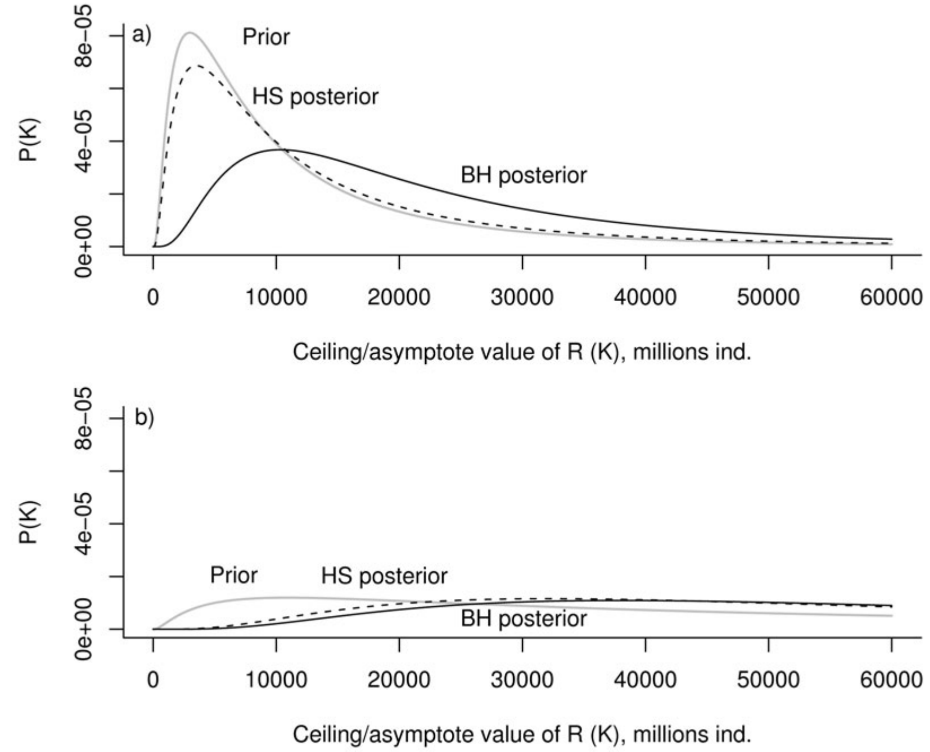

Figure 13: The prior (grey line) and posteriors for the ceiling/asymptote value of recruitment (K) of the Beverton-Holt (solid line) and hockey stick (dashed line) stock-recruitment functions. In a), the informative prior, and in b) the vague prior of the alternative model run.

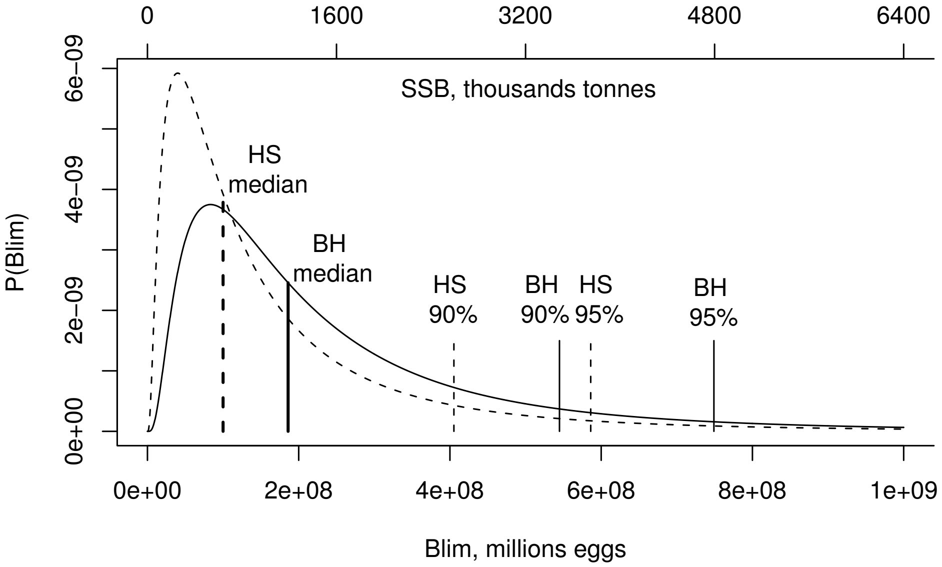

Figure 14: The probability distributions for biological reference point B_{lim}. In hockey stick model (dashed line), this is the break point of the double linear curve, in Beverton-Holt model (solid line) the amount of eggs that produces 50% of the asymptote recruitment. Median, 90, and 95 percentile values of these distributions are marked in the plot. The corresponding SSBs on the alternative x axis (above).

The straight lines in the spawning-recruitment plot (Fig. 15) show the suggested F_{lim}=0.21, computed based on average survival, and various candidates for F_{pa} with varying risk levels. The slope at the origin of the spawner-recruitment relationship curve (α) can be used to approximate a very high fishing mortality level likely to lead to stock collapse (Sissenwine and Shepherd, 1987), and the corresponding fishing mortality should not be exceeded. These values, computed from hockey stick and Beverton-Holt curves using median values, were 0.230 and 0.276, respectively.

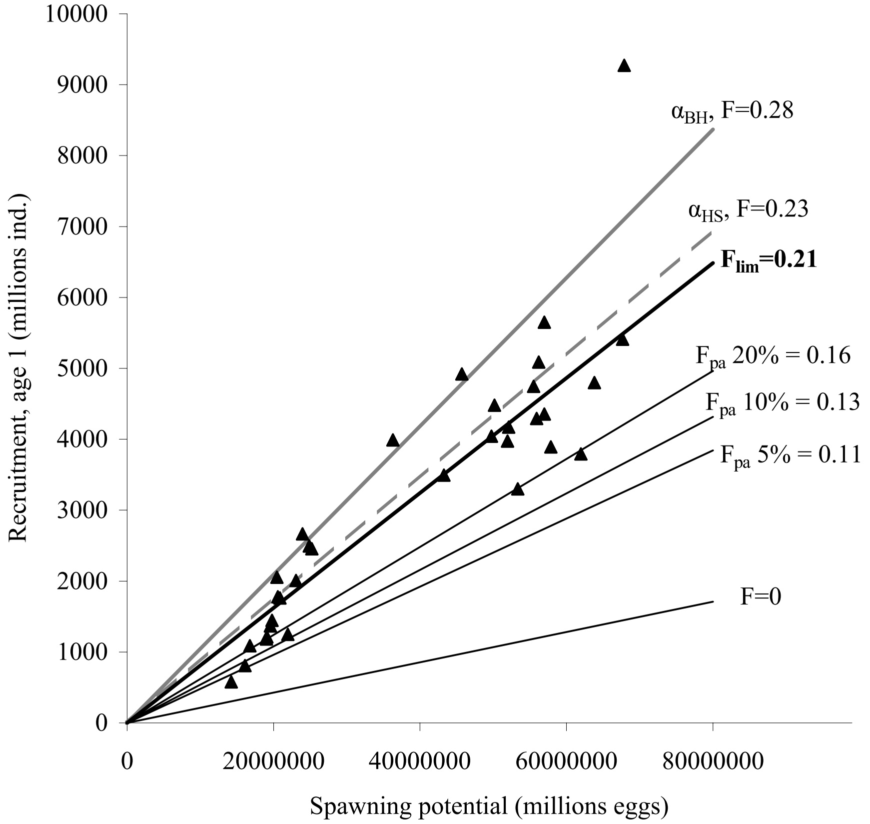

Figure 15: Spawning-per-recruit plot with suggested limit and precautionary approach fishing mortality levels. The fishing mortalities corresponding to the slopes at the origin of the S-R curve are dangerously high and likely to lead to stock collapse. Limit and proposed precautionary approach fishing mortalities are computed based on the probability distribution of survival. Median values of S-R data, natural mortality, and slope at the origin were used in this figure.

6 Discussion

6.1 Fisheries

The effect of the availability and extent of suitable spawning sites on fish stocks' success has been studied only a little so far. The effect of physico-chemical environment on the spawning success of many species has been studied in the Baltic Sea (e.g. Lappalainen *et al.*, 1995; Nissling and Westin, 1997; Lappalainen *et al.*, 2000; Kjellman *et al.*, 2001; MacKenzie and Köster, 2004) but the approach has often been to examine the effect of some environmental variables such as salinity, temperature, or eutrophic status, on the spawning success on known spawning sites. The effect of the availability of suitable spawning sites in determining the fish production in large scale has received only little attention in the study of the preconditions of fish production. Some counterexamples exist: Hildén *et al.* (1982) have studied the importance of availability of spawning sites in the coast of Finland for fish production, and found the destruction of spawning and nursery areas to be the main cause for the negative changes in fish stocks.

The results of this thesis support Werner's (2002) findings that the fish stock sizes are mainly determined by the environmental conditions the fish encounter in egg and juvenile stages. The groups that emerged from the multivariate analysis of the fish yield data (**I**, Fig. 5) are consistently explained by shared features in reproduction and juvenile stage biology even though there are differences in the habits of adult individuals within the groups.

Cod and sprat, which together form one group (Fig. 5), are pelagic / benthopelagic species that also spawn pelagically in salinities higher than those found in the coastal waters. The second group consisted of salmonid species smelt, whitefish, vendace, sea-run brown trout, and salmon. These species reproduce in fresh or low-salinity waters on sand or gravel bottoms (Ojaveer *et al.*, 1981). The third group included the rest of the species, all of which spawn on shallow coastal waters, where their larvae and juveniles also feed and grow (Ojaveer *et al.*, 1981). Flounder and herring, which are marine species, belonged to the third group together with the non-salmonid freshwater species. Despite their marine origin, they too spawn in the littoral zone (Sandman, 1906; Haegele and Schweigert, 1985), and their juveniles are also found there. Urho and Hildén (1990) demonstrated that herring productivity is very dependent on the presence of shallow areas.

Analysis of the effects of environmental factors on fish productivity (**II**) bears the same message (Figs. 6–8). The most important environmental factors affecting the fish abundance and the risk of stock collapse were shore density and the yearly ice cover duration. Shore density corresponds closely to the availability of suitable spawning and feeding areas, and it was an important factor for all species except vendace. This suggests that the availability of suitable spawning grounds is probably the most important factor restricting dispersion of these species despite the fact that they are essentially freshwater species and could also be limited by salinity.

The length of the ice covered season was very important for many of the species (Fig. 7). Several studies exist on the importance on thermal conditions, and they have often been found to be important in determining success of fish species in the northern Baltic Sea (Lappalainen *et al.*, 1995; Kjellman *et al.*, 2001, 2003). The present analysis implies that warmer conditions, implying shortening yearly ice covers, would be a risk for the studied species: a shorter ice cover seemed to increase rather than decrease the risk of collapse for stocks other than flounder.

The effect of shortened ice covered season combined with decrease of salinity predicted by climate change models (Omstedt *et al.*, 2000; Meier *et al.*, 2004) is a major risk to the coastal fish stocks (Fig. 8). The marine species flounder and herring seemed to be less sensitive to the expected changes in the climate. This result is in good accordance with several studies which have shown that climatic change affects aquatic ecosystems and fish production in several areas (e.g. Hare and Francis, 1995; Lin *et al.*, 1995; Megrey *et al.*, 1995; Tang, 1995; Stakhiv and Major, 1997; Klyashtorin, 1998; O'Reilly *et al.*, 2003).

Eutrophic status didn't have a strong impact on the fish abundance, and the small effect was mostly to decrease the risk of stock collapse (Fig. 6). This suggests that the Baltic eutrophication has not deteriorated the environment to the extent that it would markedly affect the studied fish stocks. This implies that water quality improvements may not serve to strengthen the fish stocks in a large scale.

The present study (**I**, **II**) is among the first to examine the ecological interactions of the commercially exploited fish stocks of the coast of Finland in the current scale. The total catch data naturally have their shortcomings compared to experimental fishing data etc., but on the other hand, it facilitates research in geographical and temporal ranges which would otherwise be impossible to cover. The studies in this thesis are meant to complement more detailed, smaller-scale ecological research, and, on the other hand, offer hypotheses for the purposes of further research.

Estimates of the salmon smolt production capacities (**III**), as well as potential parr densities in the rivers, indicated much higher values than what were previously estimated (Figs. 9–10). These results are supported by the fact that the observed parr densities in the Gulf of Bothnia rivers have been higher than what has previously been considered realistic (Romakkaniemi *et al.*, 2003). This implies that the Salmon Action Plan goals are yet to be achieved, and that also the catch potentials might be markedly higher than the traditional estimates. The pre-smolt densities obtained in this study were higher than previous estimates for the Baltic

Sea area, but still lower than the values estimated for Atlantic Canadian rivers. These facts support the assumption that the smolt production capacities, though unknown, are likely to be higher than the previous estimates.

In the salmon smolt production capacity model, the effect of and uncertainty about the total reproduction area in the rivers were taken into account explicitly. In the River Tornio, for example, the experts estimated the reproductive area to be between 4000–7000 hectares, and between 5000–6000 hectares with 54% certainty. Uncertainty about the reproductive area naturally contributes to the overall uncertainty.

The results included a large uncertainty partly due to the fact that there is an unresolved scientific discrepancy about the realistic maximal level of salmon smolt production (Lars Karlsson, National Board of Fisheries, Sweden, pers. comm.). The traditional estimates of maximal smolt production have varied between 1–3.5 smolts per 100 m^2 of nursery area (Karlström, 1977; Jutila and Pruuki, 1988; Kemppainen *et al.*, 1995), corresponding to 0.3–1.5 smolts per 100 m^2 of total fluvial habitat accessible to salmon (Romakkaniemi *et al.*, 1995). In Atlantic Canadian rivers the estimates are considerably higher, as 3 smolts per 100 m^2 of total fluvial habitat is considered average, and in Atlantic European rivers the estimates are even higher (ICES, 1994). Some Baltic salmon experts think that the Baltic estimates should be closer to these levels, while others maintain the more traditional view.

The estimates produced in this study have been used in Baltic salmon life-cycle modelling (Michielsens and McAllister, 2004) as priors for the carrying capacity in the stock-recruitment curve, and used in determining the reference point in ICES Baltic Salmon and Trout Assessment Working Group (ICES, 2006b). They have raised critique and discussion among the ICES scientists (Lars Karlsson, National Board of Fisheries, Sweden, and Atso Romakkaniemi, Finnish Game and Fisheries Research Institute, Finland, pers. comm.), but so far, they continue to be used as they are the only rigorously produced estimates about the quantity.

The age-structured Bothnian Sea herring model (**IV**) shows considerable uncertainty about the stock size (Fig. 11) as well as parameters such as natural and fisheries-induced mortality. The natural mortality was, however, estimated to be close to the value 0.1 in contrast to 0.2 used in the ICES assessments (ICES, 2006a). Fishing mortality estimate peaked around 0.13, which corresponds to fishing mortality values estimated by ICES (2006a).

The ceiling/asymptote value of the curve was very uncertain in both of the S-R functions (Fig. 13a). This means that there is only minutely information about the maximum values of recruitment, as demonstrated also by the model run with the vague prior (Fig. 13b). The main difference between the priors and the posteriors was that in the posteriors, the lowest values of K had a very low

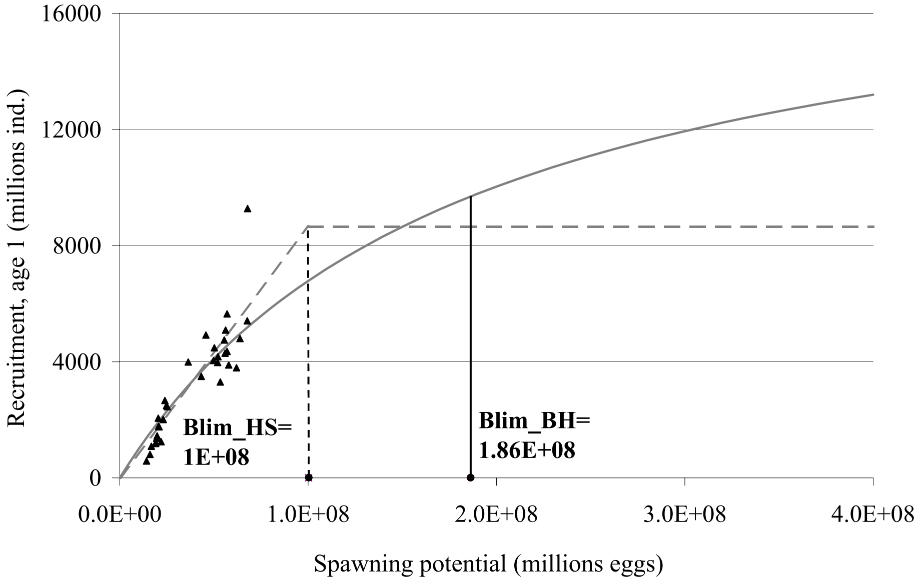

Figure 16: Beverton-Holt and hockey stick stock-recruitment curves fitted to the data. Median values used in the plot.

probability, indicating that the carrying capacity cannot be lower than a majority of the observed values. Apart from that, the data included very little information about the carrying capacity.

The Beverton-Holt and hockey stick models gave very similar model fit in the range where data were available, but quite dissimilar above the range of observed values (Fig. 16). This dissimilarity is also reflected in the biological limit reference points (B_{lim}) determined based on these curves. Due to the large uncertainty associated with the ceiling/asymptote values of the curves, these biological limit reference points were also highly uncertain (Fig. 14). This means that if the target reference points, B_{pa}, are defined so that there is only small probability of being below B_{lim} (Mace, 1994; Caddy and McGarvey, 1996), the B_{pa} will necessarily be very large compared to medians of B_{lim}, as is demonstrated also by the present results (Fig. 14). These figures demonstrate the effect of large uncertainty in practical fisheries management — the larger the uncertainty, the higher buffer is needed between the estimated limit and target reference points.

It is important to note that the two sets of reference points use somewhat different criteria: In the biomass reference point estimation (Fig. 14), the reference level is the natural maximum size of the fish stock in that environment, i.e. the maximum of the stock-recruitment curve, whereas the fishing mortality reference points (Fig. 15) are estimated so that the fish stock in question can support that level of fishing mortality without declining recruitment on average. In this case, the stock can be well below the natural, non-exploited size; the sustainable fishing mortality rate just means that the stock size will not further decrease with the sustainable fishing pressure. Hence, the results are not contradictory as such even though the biomass reference points imply that the current state is well below these points, and the current fishing mortality levels are sustainable with high probability.

The professional catch statistics (**I**, **II**) naturally have some drawbacks as primary data. Many coastal species were left out of the analysis because they are not included in the catches and/or catch statistics. Also, a large part of the catches of species like pike, perch, and pikeperch are taken in recreational fishing, and this proportion doesn't show in our data. The professional catches do have, however, some distinct advantages: they have a long, uninterrupted data series, and they cover the whole length of the coast of Finland and the data collection procedure is standardised. These facts justify the use of professional catch statistics. It was assumed that even though the proportions of species in the catch do not necessarily reflect the proportions of abundances, the fishing pressure on each of the species in different parts of the coast can be assumed to be spatially sufficiently constant. The results obtained in the study support this assumption.

The result that eutrophic status has only a minor importance to the fish abundances may be surprising, taking into account the studies that attribute changes in the Baltic fish assemblage to eutrophication (Hansson and Rudstam, 1990; Lappalainen *et al.*, 2001). It has to be remembered, however, that the geographic scale that was used doesn't take into account local eutrophication hotspots. This means that eutrophication may well have weakened the fish stocks in a local scale without it being seen in the present data. Also, it is important to note that the results cannot be extrapolated to higher eutrophic level than what was found in the data. These results do show, however, that coastal-wide water quality improvement is not likely to result in increased fish production.

Walters and Collie (1988) criticize the study of the effects of environmental factors on fish stocks that is justified by the claim that management will benefit from the results. They argue that while it is a truism that fish production ultimately depends on environmental factors, the research of environmental factors has rarely brought any additional value to fisheries management. The present results about the eutrophic status are an example of a situation where controllable environmental factors have only a minor effect on the strength of the fish stocks. In the Baltic Sea, however, many of the fish stocks live in the limits of their distribution range, and are thus more susceptible to environmental variation (Myers, 1998, 2001). When taking into account that many of these stocks have genetically adapted to the brackish water environment of the Baltic Sea (Johannesson and André, 2006), and are thus unique, the research of the necessary conditions for the survival of these populations is well justified. Precautionary management of these stocks is essential, and Bayesian approach is very useful in providing useful risk and uncertainty estimates for that purpose.

The large uncertainty in the smolt production estimates and the diverging views of the experts have raised criticism towards the study. It has to be remembered, however, that the expert knowledge is all the information we have regarding the smolt production capacities of these rivers. No data exist or is likely to be produced in the near future, since the spawning stocks are not large enough to produce maximal numbers of smolts. This analysis examined openly these expert opinions, revealing the thought processes behind the estimates. The resulting probability distributions include the best available knowledge regarding the maximal smolt production; the large uncertainty demonstrates that that knowledge is still rather vague.

The probabilistic herring model assumes that parameters such as weight-at-age, maturity-at-age, sex ratio, and length-weight relationship are known exactly, without uncertainty. In reality, these estimates are uncertain and ideally should be modelled as such. Allowing uncertainty in these variables might increase the overall uncertainty of the model. On the other hand, it might also reduce uncertainty in some other variables, if the observed variability could be explained by these variables. Also, more realistic priors could be developed for variables such as uncertainty about the real catches, overdispersion, and catchability. This might require considerable effort, but might well be worth it in terms of the information value of modelling results.

6.2 Suitability of methodology

The present study (**I**, **II**) suggests that total catch data can be used as the basis of broad-brush ecological fisheries research. Catch data are often available even when there is no scientifically sampled data. It is possible, though, that contrasts in the environmental conditions along the study area are necessary for the fisheries data to be informative about the associations between the fish and their environment. Such contrasts exist along the coast of Finland in several environmental variables. Explorative statistical analyses such as multidimensional scaling (**I**) can reveal interesting ecological associations for further study or reveal large-scale patterns that can’t be seen in smaller-scale data sets. Knowledge of species associations may also help in determining the early warning signs of population depletion in species that are less intensively monitored. If the unit catches of an evenly exploited stock decrease, the change may be due to environmental factors that probably also affect species having similar critical biological requirements in that specific environment, and precautionary management measures may be called for here.

Bayesian networks were applied in a data-rich case with small amounts of auxiliary information (**II**) and in a case where no data exist (**III**). Bayesian networks offer a flexible tool for a wide range of data availability: they can be used in data-rich situations or to encode expert knowledge in cases where no hard data are available. They are also capable of simultaneously handling numerical and nominal data, as well as correlated explanatory factors and missing data. Paper **V** presents and discusses the features of Bayesian networks as well as aspects that need to be taken into account when applying them to environmental problems.

Bayesian networks account for uncertainties along the causal chain. In the environmental effects model (**II**, Fig. 3) the causal chain is longer from nutrient concentrations than from chlorophyll to the fish. Naturally, even the link between chlorophyll and fish abundance has several elements; the current model is a simplification, and the omitted relationships add noise to the probability distribution. However, the nutrient concentrations don't affect the fish directly but through their ecosystem effects on lower trophic levels. These interactions add unaccounted variability and thus decrease the predictability of the system. This can be also seen in the model results (Fig. 6): the changes in nutrient concentrations have a much smaller effect on fish than changes in chlorophyll concentration, which have a shorter causal chain in between them.

Accounting for uncertainties along the causal chain prevents overconfidence in the strength of responses obtained by manipulating certain parts of the ecosystem, such as reducing nutrient concentrations. This is an important improvement compared to deterministic models that, despite working well in theoretical examinations, are fraught with uncertainty when applied to problems with real data (Wikle, 2003). In this way we can avoid overestimation of management success in cases where there are several uncertain causal links between management and target variables.

The present study (**II**) is among the first to apply Bayesian networks to study the effect of climate change on fisheries. Baran *et al.* (2003) studied the driving forces of fish productivity in the Mekong River using Bayesian networks. Their model included a large number of hydrological, biological, and floodplain-related environmental factors. Contrary to the present analysis, the Mekong River study was based entirely on expert knowledge. Kuikka and Varis (1996) studied the effect of climate change on watersheds based on expert opinion. Their work was focused on the different hypotheses about the cause-effect chains.

This research also includes a case study in which the only source of knowledge is expert knowledge (**III**). To guarantee the validity of the results, it is important that the experts agree on what is being estimated and on the structure and definitions of the model (Morgan and Henrion, 1990). If they don't interpret the variables in the same way, they actually estimate different things, and the resulting estimates are not comparable. The salmon smolt production model presented in this thesis (**III**) was intuitive to the experts, who were used to thinking about the salmon juvenile production in similar terms. Each of our experts applied the same model structure. The current model could be seen as an expert knowledge based model of the effects of environmental variables on the survival of juvenile salmon, hence comparable to the data-based model (**II**).

The results showed considerable uncertainty that included both the difference of opinion between the experts about the general maximal level of smolt production and the uncertainty related to each model component. Keith (1996) criticises the approach of combining expert judgments especially in the case of divergent opinions among experts, based on the argument that the fraction of experts with a certain opinion is most likely not proportional to the probability that this opinion is true. Keith's notion seems to assume, however, that there is a true, objective probability that a certain point of view is true. It is important to notice that as long as there are no better ways to estimate the state of the nature, taking into account various well-justified views yields the best estimate we can obtain. If evidence of the true state of nature accumulates, we can update the estimate by giving more and more weight to the opinions of the experts who seemed to be closer to the truth to begin with. Clemen and Winkler (1999) noted that experts who are very similar in philosophy and modelling style tend to provide redundant information in terms of cost-effectiveness of the knowledge collection, and heterogeneity among experts is thus desirable. In the salmon reproduction model, there is no basis to judge which of the views is closest to the unknown truth, so it is justified to take both of them into account. Bayesian networks provide an excellent tool of combining the conflicting hypotheses in a constructive way in a situation where an estimate is needed despite the lack of hard data.

Bayesian hierarchical modelling (**IV**) is an increasingly popular way of accounting for uncertainty in fisheries management (Walters and Punt, 1994; McAllister *et al.*, 1994; Liermann and Hilborn, 1997; Meyer and Millar, 1999; Mäntyniemi and Romakkaniemi, 2002; Michielsens and McAllister, 2004; Michielsens *et al.*, 2006). The main benefit of Bayesian hierarchical models is that they account for uncertainty in all components of the model and are capable of handling continuous distributions all through the model. On the other hand, they are computationally demanding, and even with modern desktop computers, the models need to be specified carefully to ensure smooth computation. They cannot be used interactively like Bayesian networks since they are generally not solved analytically, but results are obtained through simulation.

Bayesian hierarchical models are well suited to cases in which uncertainty plays a major role, but there is knowledge about the biological and environmental processes related to the problem so that construction of the model structure as well as reasonable priors is possible. This is often the case in temperate fisheries.

Bayesian models provide the user (such as fisheries manager) with a probabilistic estimate. The user might not be familiar with this type of output and might only get confused. At their best, results presented as probability distributions may give much more information than traditional point estimates and confidence intervals, serve as an excellent starting point for discussions, and provide much of information to support decision-making. At their worst, however, they may only serve to confuse the users of the information. Proper discussions should accompany the debut of probabilistic methods into any new realm.

7 Concluding remarks

In the Baltic Sea, many species live on the edge of their distribution range in terms of one or more environmental factors, most commonly salinity or temperature. This empasizes the importance of environmental factors in the survival of these populations. Especially if the populations are under heavy stress due to other factors such as exploitation by man, additional stress from the environment may prove critical. In this situation knowledge about the environmental requirements of the populations may aid substantially in maintaining biodiversity and a healthy ecosystem.

This information is always incomplete, however, and uncertainty about causes and effects as well as the likely magnitude of changes remains. Our knowledge about even the most intensively studied fish stocks such as salmon and herring is limited, and therefore robust integrated management measures are needed to ensure the survival of all populations also in the future.

Bayesian methods provide good tools for doing science and making decisions in the face of the inevitable uncertainty. They are capable of taking explicitly into account the variability in the nature, as well as our insufficient knowledge about nature and its processes, hence helping us understand how the world works and make wise decisions regarding the use of natural resources.

Communicating the uncertainty related to any research result, especially those that are to be used as basis of decision-making, is crucial in avoiding misunderstandings and mismanagement. Although the uncertainty is consistently presented in the output of Bayesian models, these results and their meaning could often be communicated more efficiently, as well as the reasoning behind the methodology and models. Even though Bayesian methods are steadily gaining popularity in fisheries science, they also face considerable amount of opposition. This opposition stems partly from philosophical reasons, but also partly from misunderstanding of the philosophical basis and practical application of the methods. Open discussion of the disagreements would benefit the whole field of fisheries science.

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[1] Sir Elwoodin hiljaiset värit

[2] Claes Andersson

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