

**MANAGEMENT OF PIKEPERCH (*SANDER LUCIOPERCA*)
IN THE COASTAL WATERS OF THE BALTIC SEA**

KARI SAULAMO

Faculty of Biological and Environmental Sciences
University of Helsinki
Finland

Faculty of Biological and Environmental Sciences
University of Helsinki
Finland

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in the coastal waters of the Baltic Sea**

Kari Saulamo

Academic dissertation

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Supervisors: Prof. emer. Hannu Lehtonen
Faculty of Biological and Environmental
Sciences
University of Helsinki
Finland

Univ. lect. Jyrki Lappalainen
Faculty of Biological and Environmental
Sciences
University of Helsinki
Finland

Members of the thesis advisory committee: Adj. prof. Pekka J. Vuorinen
Natural Resources Institute Finland (Luke)
Helsinki
Finland

PhD Antti Lappalainen
Natural Resources Institute Finland (Luke)
Helsinki
Finland

Reviewers: Adj. prof. Jari Raitaniemi
Natural Resources Institute Finland (Luke)
Turku
Finland

Adj. prof. Zeynep Pekam-Hekim
Swedish University of Agricultural Sciences
Öregrund
Sweden

Opponent: PhD Markus Vetemaa
Estonian Marine Institute
University of Tartu
Tallinn
Estonia

Custodian: Prof. Jukka Horppila
Faculty of Biological and Environmental
Sciences
University of Helsinki
Finland

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List of original publications

- I.** Saulamo, K., Lappalainen, J. & H. Lehtonen, 2005. Biological characteristics of pikeperch, *Sander lucioperca*, during spawning migration in a Baltic bay. *Fisheries Management and Ecology* 12: 131–136.
- II.** Saulamo, K. & J. Lappalainen, 2007. Effects of abiotic factors on movements of pikeperch during pre-spawning and spawning season in the Baltic archipelago. *Hydrobiologia* 579: 271–277.
- III.** Saulamo, K. & G. Thoresson, 2005. Management of pikeperch migrating over management areas in a Baltic archipelago area. *Ambio* 34: 118–122.
- IV.** Saulamo, K., Heikinheimo, O. & J. Lappalainen, 2018. Growth and size-selective fishing mortality of exploited pikeperch population in Baltic coastal waters. Submitted manuscript.

Author's contribution

- I.** Mr Saulamo was solely responsible for planning the study, undertaking the field work and performing the statistical analyses and was mainly responsible for writing. Dr Lappalainen and Professor Lehtonen participated in the writing and Dr Lappalainen gave feedback on statistical methods. The original idea to perform a tagging experiment in the Östhammar area to study the dispersal area of the local pikeperch stock came from Dr Erik Neuman (refers also to papers **II** and **III**).
- II.** Mr Saulamo was solely responsible for planning the study, undertaking the field work and performing statistical analyses and mainly responsible for writing. Dr Lappalainen participated in the writing and gave feedback on statistical methods.
- III.** Mr Saulamo was responsible for the planning the tagging study, undertaking the field work and statistical analyses. Mr Thoresson was responsible for planning and conducting the inquiry study included in the paper. Mr Saulamo was solely responsible of writing the article.
- IV.** The planning of the study was undertaken together. Mr Saulamo was solely responsible for the statistical analyses and mainly responsible for writing the manuscript.

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Abstract

Fisheries management needs to address a wide array of biological, economic and social issues in a coherent way to achieve long-term sustainability. It can be argued that economically viable fisheries inevitably require healthy fish stocks. Our knowledge of fish populations, their behaviour and dynamics is still relatively limited, mostly because fish cannot be observed directly and they are typically highly mobile and undertake migrations up to several thousand kilometres. Additionally, fish populations fluctuate temporally and spatially depending on the biophysical characteristics of the environment and interactions in the ecosystem. By increasing our knowledge of the ecology of exploited species and how they respond to the impacts of fishing, we increase the probability of success with the management of the fish populations.

The main contribution of this thesis is improved scientific understanding of the biology of the pikeperch and how this relates to the management of pikeperch fisheries. In the articles included in this thesis, the movements of the pikeperch are studied during the spawning season to gather information on biological characteristics, such as changes in size distribution, sex ratio and maturity between fish ascending to the spawning grounds at different times. Moreover, the effect of how different abiotic factors stimulate the movements of pikeperch during pre-spawning and spawning season is analysed. The interaction between biology and the management of the pikeperch is studied by analysing the challenging situation in which pikeperch are exploited by several management units. The effects of high fishing pressure and selective fishing on growth and the production of pikeperch stock are also studied. These are key issues for pikeperch fisheries across the Baltic Sea.

It is demonstrated that there are differences in the biological characteristics between pikeperch arriving at the spawning ground at different times, and signs that there can be early and late spawners in the populations. It is also shown that in cases where the pikeperch migrates over several management areas, overfishing is inevitable if there is no agreed cooperation between the areas. Furthermore, it is proven that excessive fishing pressure with highly selective fishing gears creates strong phenotypic selection for slower growth in the studied pikeperch population.

Fisheries managers are advised to consider the spatial and temporal dynamics of the pikeperch stocks in order to protect the different stock components. Management should aim for constant escapement, for example, during the spawning season, to protect both early and late spawners. Thus, pikeperch managers should focus on distributing harvesting with caution regarding space, time and also between age groups to avoid adverse ecological effects from fishing, and especially, to avoid the risk of decreasing the long-term productivity of the stock.

To better understand the population dynamics of pikeperch populations and their response to fishing, further studies on genetic variation and the importance of the age and size structure of the spawning population on the population dynamics of the pikeperch are recommended.

1. Introduction

1.1 Background

Fisheries management needs to address a wide array of biological, economic and social issues in a coherent way to achieve long-term sustainability (Ludwig et al., 1993; Charles, 2001; Garcia et al., 2003; Mahon et al., 2008). These factors can be, and usually are, in conflict with each other, especially in the short term. One example of a typical short-term dilemma is maintaining employment and maximization of jobs that requires the highest possible, sustainable fishing effort, whereas the sustainability of the ecosystem might require very low fishing pressure, and even the closure of a fishery (Botsford et al., 1997; Hilborn, 2007). In the longer term, it can be argued that these factors are positively correlated, since economically viable fisheries inevitably require healthy fish stocks. Over a longer time scale, it is impossible to sustain human needs without sustaining ecosystems (Grumbine, 1997). When fish stocks become overfished, rebuilding them to sustainable levels necessitates management actions with substantial short-term social and economic side-effects, such as increased unemployment and decreased revenues, in order to restore the long-term productivity of stocks (Rosenberg et al., 2006; Shertzer & Prager, 2007; Sissenwine & Symes, 2007; Brodziak et al., 2008; Villasante & Sumaila, 2010). Therefore, it is desirable to prevent the problem from occurring (Hall & Mainprize, 2005; Gaines & Costello, 2013). The negative trend of overexploitation is difficult to reverse due to the short-term side-effects, and reducing the fishing effort has been shown to be the most difficult task in fisheries management (Hilborn & Walters, 1992). The costs of overexploitation are enormous. It is estimated that overfished stocks could globally increase fishery production by 16.5 million tonnes and annual rent by \$32 billion, if these were sustainably harvested (FAO, 2016). In 2014, the total yield captured from fisheries was 93.4 million tonnes (FAO, 2016). The Canadian cod (*Gadus morhua*) is the best-known example of the collapse of a fishery with enormous biological, economic and social consequences (Hutchings, 1996; Myers et al., 1997; Rose et al., 2000). The Atlantic cod, which ranges from southern Labrador to the northern half of Newfoundland's Grand Bank, has declined from relative to abundance in the early 1960s to a 90% reduction by the 1990s (Walters & Maquire, 1996; Hutchings & Rangeley, 2011). This collapse has led to thousands of jobs lost and the total cost of billions (Grafton et al., 2000).

Fisheries management has been blamed for the depletions and stock collapses, but there is also evidence that when fisheries management has been applied, it has worked both for reducing fishing pressure and rebuilding fish stocks (Mace, 2004; Beddington et al., 2007; Worm et al., 2009; Hilborn & Ovando, 2014). These observations apply especially to assessed stocks, that is to stocks for which there is an adequate amount of reliable data and knowledge about the fishery and the dynamics of the stock (Neubauer et al., 2013; Hilborn & Ovando, 2014). In those fisheries, often small scale fisheries, that lack complete data on stock status, the track record is, however, poorer (Garcia et al., 2008; Costello et al., 2012). It can, therefore, be argued that successful management of fisheries requires good scientific understanding of the dynamics and behaviour of the exploited stocks (Pitcher et al., 1998; Botsford et al., 2006; Beddington et al., 2007). This science has to be mature enough, so that the scientists can communicate the associated costs and benefits of various management actions to the political

decision makers (Rice, 2005). Sustainable fisheries management also need the involvement of stakeholders (Jentoft, 2000; Charles, 2001; Holmes & Lock, 2010), the conversion of scientific advice into policy through a participatory and transparent process (Mora et al., 2009) and competent management authority able to set and enforce regulations and monitor the status of the stock (Noss & Cooperrider, 1994; Hilborn, 2007; Broziak et al., 2008).

Our knowledge of fish populations, their behaviour and dynamics is relatively limited, mostly because fish cannot be observed directly and they are typically highly mobile and undertake migrations up to several thousand kilometres. Further, fish populations fluctuate temporally and spatially, depending on the biophysical characteristics of the environment and complex interactions in the ecosystem (Hilborn & Walters, 1992; Sainsbury et al., 2000; Garcia & Charles, 2007). Scientific knowledge, especially in relation to small-scale fisheries, is limited. Small-scale fisheries are locally and regionally important fishing sectors and in order to secure the sustainable development of the small-scale fisheries, knowledge on biology and population dynamics needs to be improved (FAO, 1995; Pauly et al., 2002; Salas et al., 2007). By increasing our knowledge of the ecology of exploited species and how they respond to the fishing, we increase the probability of success with the management of the fish populations.

1.2 Management of fisheries

Production of fish stocks and fisheries management

The theory behind harvesting and managing of fish resources is based on the density-regulated population regulation (e.g., Gulland, 1970; 1977). Fish populations are capable of net population growth under favourable conditions and compensatory density dependence operates to offset the losses of individuals (Rose et al., 2001). As the abundance of a population is reduced by harvesting, density-regulated mechanisms in the population compensate for this loss by increasing per capita productivity, that is fecundity, maturation, individual growth and survival (Rothschild, 1986; Myers et al., 1997). Compensatory responses may be direct and take place immediately, for example, when an individual fish changes its behaviour or foraging time due to changed predation risk, or indirect and delayed owing to ecosystem-scale changes in predation risk and food production (Walters et al., 2005). When harvesting exceeds the compensatory responses of the fish population, the stock will decline, whereas a harvesting rate that allows the fish population to replace itself and maintain its productivity in variable environmental conditions can be said to be sustainable. Fisheries management try to prevent excessive build up of the fishing effort and limit the rate of exploitation to what can be sustained in the long term (Garcia & Charles, 2007). These actions require regulation, usually restricting the fishing pressure, which can be done with catch quotas, effort limitations, gear restrictions, gear limitations, season lengths, size limits of caught fish and closed areas (Hilborn & Walters, 1992; Murawski et al., 2000; Caddy & Agnew, 2004; Worm et al., 2006).

How the fishing and different management actions affect fish stocks

Different regulations affect fish populations and also how the catches are distributed between fishermen. In order to assess the effects of management measures on the population

and distribution of catches between fishermen, fisheries manager have to have a good understanding of the temporal and spatial dynamics of the fish population, as well as knowledge on the behaviour and dynamics of the fisheries. For example, adjusting the season lengths of mobile species decreases yields in areas where the stock is present during the closure, whereas adjacent areas can benefit from the regulation. Managers should know the dispersal areas and movements of the populations as an integral part of fish resource management (e.g., Murawski, 2000). Many fish stocks have different sub-stock structures showing differences, for example, in spawning behaviour (Frank & Brickman, 2001). Ignoring these differences can lead to erosion of the spatial structure of the entire population and declining production of the population in the long term (Ricker, 1973; Tuck & Possingham, 1994). Different components of the population may vary in productivity; reproductive surplus in one portion of the population may also be essential to recolonization of other areas (Hilborn et al., 1995; Frank & Brickman, 2001). As success of reproduction may be dependent on matching the timing of zooplankton production (Cushing, 1975), protecting the different spawning components can have a crucial role in securing the reproduction success of the stock in the long term. Egg development and larval phases of fish are more sensitive to environmental disturbances than during adult stage and tolerance limits are much narrower (Trippel et al., 1997). Under changing environmental conditions, the significance of single population components can increase from small to crucial for the population as a whole.

Fish populations are often also partially segregated by size in space or time, or both, and spatially or temporally unevenly distributed fishing pressure can create selection pressure for life history traits, especially for growth rate and maturation size (Sinclair, 1992; Swain et al., 2007). Different technical measures, such as minimum mesh-size regulations, commonly used for trawls, seines and gill nets to allow smaller fish to escape, can also exert strong phenotypic selection (Machiels & Wijsman, 1996; Jennings et al., 1998; Law, 2000; Sinclair et al., 2002). Selectively removing larger individuals typically acts for slower growth and reproduction at a smaller size (Law, 2000; Conover & Munch, 2002; Milardi et al., 2011). If the phenotypic variation in these life history traits is genetic, fishing can cause evolutionary change in respective traits (Stokes & Law, 2000; Birkeland & Dayton, 2005; Walsh et al., 2006; Law, 2007). Beyond these traits, it has been suggested that further traits might evolve following fishing, such as morphology (Ricker, 1981), migration distance (Jørgensen et al., 2008), skipping of spawning (Jørgensen et al., 2006) and natural mortality, which can increase due to fishing (Jørgensen & Holt 2013). Selective evolution in fish populations can be rapid; Koskinen et al. (2002) have found that populations of grayling (*Thymallus thymallus*) have evolved in several quantitative life history traits, such as growth, survival and yolk-sac volume, in a timescale of approximately 10 generations.

On a population scale, harvesting destabilizes the abundance of species (Beddington & May, 1977; May et al., 1978; Anderson et al., 2008; Shelton & Mangel, 2011). This instability also leads to oscillations in yields. Increased variability is thought to be related especially to the truncated age/size structure of the populations (Berkeley et al., 2004a, 2004b; Hutchings & Reynolds, 2004; Hutchings & Baum, 2005; Hsieh et al., 2006). Truncated age structure makes fisheries dependent on young, inexperienced spawners that are less fecund and produce eggs and larvae of lower quality (Trippel, 1995; Birkeland & Dayton, 2005). Furthermore, due to

shortening of the reproductive season and a decrease in the chance that some offspring of the population will encounter favourable conditions, truncated populations track environmental fluctuations more directly (Conover & Munch, 2002; Anderson et al., 2008).

To minimize the risks and side-effects of fishing for underlying populations, the ecologically ideal management system would be the one where each individual stock were managed separately (Hilborn & Walters, 1992). The management area would then cover the whole life cycle: the spawning, feeding and wintering areas of the population. Not every single stock can be managed separately in real life, and furthermore, the dispersal areas of the stocks continuously change. Environmental factors such as temperature, light condition, presence of prey species and abundance of predators are constantly changing and affecting the behaviour and movements of the individuals and, to larger extent, the dispersal areas of the populations. Fish constantly balance their physiological requirements and their needs for reproduction, food and shelter by searching for areas with an optimal combination of environmental factors (Fry, 1971; Wootton, 1998; Jørgensen et al., 2008). The suitability and value of various management measures depend on the species, ecosystem, local characteristics of the fisheries and governance system. A combination of tools is usually required (Worm et al., 2009). As a part of the whole management process, boundaries of resources, ecosystems, communities and institutions should be carefully considered (Garcia et al., 2003; Hilborn, 2004). Communities and institutions responsible for the management of the fish resource vary from a single private owner to local communities, fishermen, states and even coalitions of states (e.g., the European Union). In many fisheries, there can be several authorities regulating the fishery, for example, a local management entity can have full authority over effort regulation, whereas minimum size limits might be decided regionally or at the state level by a public fisheries management authority. For example, in the Baltic archipelagos of Finland and Sweden, there are local management systems based on private ownership of the fishing rights with owners organized into associations, mostly corresponding to old administrative units, such as villages and municipalities (Saulamo & Neuman, 2001). These units are usually responsible for managing the total fishing effort and its temporal and spatial distribution, whereas minimum size limits are decided by public fisheries management authorities at the regional or national level. In local communities, different forms of rights-based managements have been implemented on smaller spatial scales for millennia (Costello et al., 2008). These forms of management vary in shape and arrangement from private ownership to co-management arrangements with government or nongovernmental organizations (Pinkerton, 1989; Brown, 2001; Pitcher et al., 2009). Community-based management has been found to be the important element in successful small-scale fisheries (Worm et al., 2009).

1.3 Pikeperch and its fisheries in the Baltic Sea

Pikeperch *Sander lucioperca* (L.) and its fisheries in the Baltic archipelago areas of Finland and Sweden offer a many-sided subject to study both the biology of the species and its exploitation. Pikeperch is a valuable species both for commercial and recreational fisheries in the coastal areas of the Baltic Sea (Lehtonen, 1983; Lehtonen et al., 1996; Heikinheimo et al., 2006; Pekcan-Hekim et al., 2011). Pikeperch is a warm water species and prefers to live in open

waters (Deelder & Willemsen, 1964). It is a mobile species showing migrations from shallow spawning areas to feeding areas located typically in outer areas and towards deeper wintering areas (Lehtonen, 1979; Segerstrale, 1983; Lehtonen & Toivonen, 1987). Migrations depend on the morphometry of the coast and especially the location and quality of spawning areas (Lehtonen & Toivonen, 1987; Saulamo & Neuman, 2002). Typically, migrations of pikeperch extend approximately 10 km (Lehtonen & Toivonen, 1987; Saulamo & Neuman, 2002) but it can migrate up to 300 km (Lehtonen, 1979). Migrations to the spawning areas begin around one month prior to the actual spawning (**I-II**; Lehtonen & Toivonen, 1987; Koed et al., 2002). Tagging experiments have shown that pikeperch home to the same spawning inlet or bay for reproduction (**III**; Lehtonen & Toivonen, 1987). Spawning areas are located in sheltered inlets and bays (Lappalainen & Lehtonen, 1995; Lappalainen et al., 1995) where water warms up fastest in spring, and salinity is low enough to assure normal development of the egg and larval stages (Klinkhardt & Winkler, 1989). As an adult, pikeperch can, at least periodically, tolerate salinities of up to 29–33 ‰ (Brown et al., 2001), but the fertilization, egg development and larval phase of fish are usually more sensitive and have much narrower tolerance limits (Wootton, 1998). Optimal salinity for the pikeperch is around 6 ‰ (Craig, 2000). After spawning, pikeperch move to the feeding areas, which are typically located close to the spawning areas.

Large, natural fluctuations in year-class strengths are characteristic for the pikeperch (Lappalainen & Lehtonen, 1995; Lappalainen et al., 1995; Heikinheimo et al., 2006, 2014; Pekcan-Hekim et al., 2011). Pikeperch live on the edge of the distribution range in the Baltic Sea and even minor changes in environmental factors can have a large impact on the survival and distribution of the species (Colby & Lehtonen, 1994). The size and structure of the pikeperch population is strongly influenced by their success at the juvenile stage (Ginter et al., 2011). The juvenile stage success, measured as a strength of a year class, has been observed in a number of studies in the Baltic Sea to be positively correlated with temperature during the first growing season (Lappalainen & Lehtonen, 1995; Kjellman et al., 2003; Pekcan-Hekim et al., 2011).

As a valuable species both in commercial and recreational fisheries, many pikeperch stocks are subject to excessive fishing pressure (**III**; Lehtonen, 1983; Eero, 2004; Heikinheimo et al., 2006). Excessive fishing pressure can lead to recruitment overfishing of the pikeperch (Van Densen, 1987; Turunen, 1996). This overfishing occurred with the collapse and closure of the pikeperch fishery in the Estonian Pärnu Bay in 2000, subsequent to a shift from the Soviet planned economy with low market demand and a fixed low price for fish, to the free market conditions of high demand and high prices for fish (Eero, 2004). A more common occurrence is growth overfishing, where pikeperch are caught well before their growth potential is fully utilised (Lehtonen, 1983; Heikinheimo et al., 2006). Management of pikeperch fisheries consists, typically, of gear restrictions, minimum mesh sizes, size limits and prohibiting fishing during the spawning season and in spawning areas (Lehtonen, 1983).

2. Aims of the study

The overall aim of this thesis is to produce scientific information on the biology of pikeperch and its relationship to fisheries management.

Aim I: Spring is an important season for many pikeperch fisheries in the Baltic Sea area and fishing pressure on fish migrating to spawn is high. To be able to impose reasonable regulations, information on size distribution and sex ratio are required from the whole spawning season, especially if particular sized fish or sexes are to be protected. The aim I is to determine trends in the biological characteristics, such as size distribution, sex ratio and maturity of the pikeperch during the spawning migration in a narrow sound, just outside an important spawning area, as a basis for setting regulations more precisely.

Aim II is to study the effects of temperature, water level and moon phase on the movements of pikeperch during the pre-spawning and spawning season in a coastal area in the Baltic Sea. Detailed information about the factors stimulating the actual fish movements, especially from northern populations of pikeperch in brackish waters, is still lacking.

Aim III of this study is the analysis of management implications of migrations for a situation in which several, small, independent management units exploit the same pikeperch stock. This is carried out by comparing the spatial distribution of recaptures from a tagging experiment with that of the total catches as derived from an inquiry. Furthermore, a modified yield and recruit model analysis is performed to find the most rational fishing strategy for a single management unit with regard to pikeperch being stationary to various degrees. The existence of possible individual spawning behaviour is also studied, comparing tagging day with recapture day in subsequent years.

Aim IV is to study the effects of temperature and year-class strength on pikeperch growth. A further aim is to analyse the possible phenotypic selection for smaller growth in heavily exploited pikeperch population by comparing back-calculated lengths of fish at a given age within a year class, with fish caught at two subsequent times.

3. Material and methods

3.1 Study areas

The Baltic Sea

The Baltic Sea is an enclosed sea of the Atlantic Ocean. Water exchange between the two bodies is limited and the water in the Baltic Sea is brackish with a strong salinity gradient. In the southern parts, the surface salinity is 10–13 ‰; in the Gulf of Finland, it is 5–9 ‰; and in the Gulf of Bothnia, it is 3–7 ‰ (Kullenberg, 1981). In river mouths, salinity can be zero. Seasonal variations in temperature are large compared with those in oceans. The difference between summer and winter surface temperature in the Baltic is typically 14 °C, and in the archipelagos it can be up to 20 °C. In the northern parts and in the archipelagos, winter temperature is normally around 0 °C, and summer temperatures in archipelago areas are over 20 °C (Kullenberg, 1981). Changes in temperature, together with salinity conditions, are important factors that affect the fish species composition in the Baltic Sea. Due to the salinity gradient, marine species are more abundant in the south and the number of fresh water fish increase towards the north. For example, the neutral egg buoyancy of the cod in the Baltic is about 13–15.5 ‰, which effectively limits the successful spawning of cod (Nissling & Westin, 1991). The Baltic Sea is thus a challenging environment for both the marine species and fresh water species and, especially, for fertilization, egg development and the larval phases of fish, which are more sensitive and have much narrower tolerance limits, which restrict the dispersal of fish in the Baltic Sea (Urho, 2002). As adults, fish species in the Baltic can tolerate differences in hydrographic conditions, for example, salinity, relatively well.

Östhammar

The study area (**I–III**), a large inlet close to the town of Östhammar, on the eastern coast of Sweden (60°17N, 18°21E) in the Baltic Sea, is characterized by a sheltered archipelago with three basins connected by narrow straits. The two inner basins (Granfjärden and Östhammarsfjärden) are important spawning areas of pikeperch (**III**). Both are eutrophic and turbid with chlorophyll-a concentrations of about 70 µg L⁻¹ and Secchi-depths of 0.3–1.2 m. (Sandström & Karås, 2001). The outer archipelago acts as a feeding and overwintering area for pikeperch. The primary production decreases towards the outer archipelago and the Secchi-depth there is 1.8–3.5 m (Sandström & Karås, 2001).

In the inner, western parts, littoral areas are typically edged with dense reed (*Phragmites australis*) belts. The underwater vegetation is dominated by *Potamogeton* sp., *Myriophyllum* sp., *Chara* sp., and *Najas marina* (Sandström & Karås, 2001). The average depth ranges from 2–4 m in the west (Granfjärden) to 10–20 m in the central basin (Galtfjärden).

Common fish species are roach *Rutilus rutilus* (L.), bream *Abramis brama* (L.), white bream *Abramis bjoerkna* (L.), bleak *Alburnus alburnus* (L.), ruffe *Gymnocephalus cernuus* (L.), pike *Esox lucius* L., perch *Perca fluviatilis* L., smelt *Osmerus eperlanus* (L.), herring *Clupea harengus* L. and pikeperch (Sandström & Karås 2001). The salinity in the area is approximately 3 ‰. Pikeperch is the most valued species in the fisheries, and gill netting is the dominant fishing method. In 2001, at the time when the field studies began, the pikeperch yield

was ca. 30 tonnes. Households (mostly using subsistence gill nets) caught 18 tonnes, recreational rod fishing 4 tonnes, and professional fishing (five fishermen) 8 tonnes (G. Thoresson, unpublished data). The management of the fishery is executed by 10 independent management areas, of which the westernmost covers the main spawning grounds of the pikeperch (III).

Archipelago Sea

The Archipelago Sea is part of the Baltic Sea between the Gulf of Bothnia, the Gulf of Finland and the Sea of Åland (IV). The Archipelago Sea has a mosaic structure and is characterized by topographic complexity, including some 30,500 islands and over 20,000 km of shoreline (Bonsdorff et al., 1997). Such a structure creates a plethora of habitats and complicated ecological webs (Bonsdorff & Blomqvist, 1993). The average water depth in the Archipelago Sea is 23 m and the maximum depth is 146 m (Leppäkoski et al., 1999). The salinity is 6–7 ‰ (Kullenberg, 1981). In areas close to river mouths, the salinity is remarkably lower, and may even be zero (Pitkänen, 2001). The length of the ice season varies and is 130 to 200 days in the Bothnian Bay (north from the Archipelago Sea), 80 to 100 days in the Gulf of Finland, which is east of the Archipelago Sea (HELCOM, 2007). Water temperatures range from 0 to 20 °C, while the temperature in surface waters can range up to 25 °C (HELCOM, 2007).

In the innermost bays, *Phragmites australis* is a common helophyte. The underwater vegetation varies between biotopes. *Fucus vesiculosus* is a key species providing a canopy and shelter for a variety of organisms. Other typical taxa and species are *Potamogeton* sp., *Myriophyllum* sp., *Cladophora* sp., *Pylaiella littoralis*, *Ectocarpus siliculosus*, *Enteromorpha* spp, *Dictyosiphon* sp., *Ceramium* sp., *Furcellaria lumbricalis*, *Zannichellia major* (Vahteri et al., 1997).

Common fish species in the Archipelago Sea are flounder *Platichthys flesus*, bream, white bream, roach, bleak, ruffe, pike, perch, smelt, herring, sprat *Sprattus sprattus* L., burbot *Lota lota* L. and pikeperch.

3.2 Experimental studies and data used

Statistical analyses were performed using S-PLUS, SPSS and EXCEL. Table 1 summarizes the statistical analyses used in articles **I-IV**. Simulation (**III**) was undertaken using VISUAL BASIC (EXCEL). More details on the collection and analyses of the data can be found in the respective papers.

Table 1. Summary of statistical methods used in original articles (I-IV)

Article	Estimation	Statistical methods	Variables
I	Changes in mean lengths of pikeperch during the pre-spawning period	Kruskal–Wallis rank sum test Tukey test (multiple comparisons)	Length, catches
	Changes in sex ratio of pikeperch ascending to spawning areas in different time periods	Chi-square test Bonferonni (pairwise comparisons)	Sex, catches
II	The effects of temperature, water level and moon phase on activity of pikeperch	Cross-correlation	Temperature (with lag), water level (with lag), moon phase, catch per unit effort
III	Tagging dates and recapture dates in subsequent years	Spearman correlation	Tagging date, recapture date
	Correlation between recaptures and total catches from inquiry	Pearson correlation	Area of recapture, total catch in area
IV	The effects of temperature, age and density on growth of pikeperch	Repeated MIXED model	Back-calculated length increment, temperature sum (June-September), age of fish, stock size
	Possible phenotypic effects of selective fishing on the growth of the pikeperch	Analysis of variance (ANOVA)	Mean back-calculated lengths, year, year class

Östhammar

Fishings

Pikeperch were caught with one-directional trap nets and gill nets in 2001 and 2002 (I-III). In 2001, also small two directional fyke nets were located in innermost Granfjärden (III). In 2001, one large trap net was placed in a sound outside the Östhammarsfjärden basin and was set to only catch fish swimming inward. Gill netting in 2001 took place both in Granfjärden and Östhammarsfjärden. In 2001, taggings began on 9 May and ended on 1 July.

In 2002, the fishing was performed with two one-directional fyke nets, one catching fish swimming inward and the other catching outward-going fish. The fyke nets were placed in a narrow sound connecting the Granfjärden and Östhammarsfjärden basins. Fishing in 2002 began on 3 April, when the study area was still partly ice covered, and ended on 20 June.

The total number of tagged pikeperch was 212 in 2001 and 253 in 2002. The average length of the tagged pikeperch was 43.8 cm in 2001 (range 22–79 cm) and 46.7 cm (range 21–85 cm) in 2002. Tagged fish were marked with nylon dart tags. When tagged, the fish were measured for length (total length), tagged and released immediately at the place of capture. Tags from recaptured pikeperch were sent to the Swedish Institute of Coastal Research with date, gear and catch location information. A reward was paid for returned tags.

Gill net fishing was also performed in 2001 and 2002 to collect gonad samples. In 2001, 22 fish were also tagged from gill net fishings (III) carried out with nets with mesh bar lengths of 45 and 50 mm (net length 30 m, height 1.8 m). In 2002, gill net fishings were performed, mainly with a multimesh gill net consisting of nine different panels (panel length 5 m, total net length 45 m, height 1.8 m) (I). Mesh bar lengths of the panels were 10, 12, 15, 19, 24, 30, 38, 48, and 60 mm. Gill net fishing was carried out in the sound close to the trap net on three occasions with nets with mesh bar lengths of 45 and 50 mm (net length 30 m, height 1.8 m). Fishing time was the same as in the multimesh gill net fishing.

Mean daily water temperature was calculated in 2002 from water temperature measured every other hour with a logger located at the trap net at a depth of 2.5 m (0.5 m from the bottom).

Inquiry

In 2002, a total of 1,995 inquiries were posted to the target group of households or individuals connected with the survey area and living in the municipalities of Östhammar and Norrtälje (III). Of these, 1,443 (72%) were returned. The inquiry was sent to water owners, other estate owners, holders of boat mooring places, fishing club members and occasional visitors to the area. The respondents were assumed to represent the total population of 13,000 households for fishery behaviour and catch rate (G. Thoresson, unpublished data). The total catch estimates describe the fishery in the year 2001.

Archipelago Sea

Fishings

The data used in the study were based on annual samples from the commercial gill net and trap net catches and obtained from the Archipelago Sea, ICES statistical squares 49H1, 49H2, 50H1 of the Baltic Sea in Finland covering the years 1990–2014 (IV, Natural Resources Institute Finland). The age composition data are collected annually by the Institute from the fishermen's catches mostly caught with gill nets and trap nets.

In the annual routine sampling, the total length and weight of the fish are measured, sex is determined and scales for age determination are taken from the abdomen, from the standard area for pikeperch: the side of the fish below the front part of the latter dorsal fin, below the lateral line. The pikeperch are aged and the radius of scales and the distances of the annuli are measured with a microfilm viewer from polycarbonate impressions of scales.

The lengths of individual fish at earlier ages were back-calculated on the basis of the distances of annual rings using Fraser and Lee's method (Bagenal & Tesch, 1978). The value of 44 (mm) was used as an intercept term (Ruuhijärvi et al., 1996). The N was 24 855, of which 6 506 were trap net samples and 18 349 were caught with gill nets.

Stock data

Stock size by age group used in the study were estimated using annual fisheries catch data (Official Fisheries Statistics, Natural Resources Institute Finland) and virtual population analysis (VPA) (Pope's cohort analysis, Hilborn & Walters 1992; Heikinheimo et al., 2014). Natural mortality (M) was assumed to be 0.1 in the age groups ≥ 6 , 0.2 at ages 3–5, 0.3 at age 2 and 0.5 at age 1. The natural mortality was assumed to be constant over time. See Heikinheimo et al. (2014) for a detailed description of the VPA.

Temperature data

Daily water temperature measurements from the Archipelago Sea between 1997 and 2008 were obtained from the Finnish Environmental Research Institute. The water temperature was measured from 1 m depth in Ruissalo Island, which is located off the south western coast of Finland, near the city of Turku. For the periods when daily water measurements were not available (1980–1996 and 2009–2013), a dynamic water model (Kjellman et al., 2003) was used to estimate the daily water temperature based on air temperature (see Kjellman et al., 2003 and Pekcan-Hekim et al., 2011 for closer description of the model). The water temperatures were estimated for the period from 1 May to 1 October. In growth estimations, used temperatures were water temperature sums from 1 June to the end of September in each year.

4. Results

Spawning migrations

The pikeperch started to arrive at the spawning areas at a time when the spawning inlet was still partly ice covered (fig. 1, **I, II**). The highest frequencies of incoming fish were observed at the beginning of the spawning season, matching the final break of the ice-cover (**I, II**). After this early peak, catches fluctuated and started to decrease slowly without any clear trend (**I, II**). The migrating pikeperch were in the same maturity stage, based on gonadosomatic index (GSI), in early April as those ascending in late May, suggesting that the spawning season lasts approximately two months (**I**).

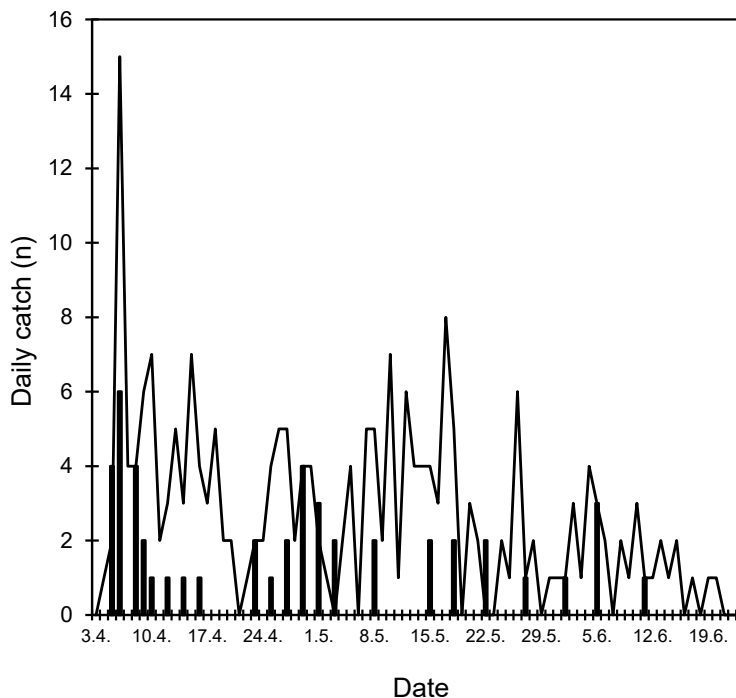


Figure 1. Daily number of pikeperch caught by the fyke net (line) and multimesh gill net (bars) during the spawning migration in 2002 (>35 cm TL) (**I**).

Daily mean lengths of pikeperch moving towards spawning inlet decreased from early April to late May and then increased rapidly in early June to decrease again towards the end of June (**I**, fig. 3). To test the differences in mean lengths of pikeperch arriving at different times at the spawning grounds, the data were divided into three time periods, representing fish arriving at the spawning grounds in the beginning (T1), in the middle (T2), and at the end (T3) of the spawning season. Mean lengths were similar in periods T1 (47.2 cm, SD 12.7 cm, n = 75) and T2 (43.9 cm, SD 9.4 cm, n = 74), but both were significantly lower ($P < 0.002$) than in T3 (60.9 cm, SD 15.3 cm, n 31) (**I**). Even though the sharp increase in mean length during early June suggests that the largest fish move to the spawning grounds later than the smaller

individuals, the increase in mean length was actually because smaller individuals were no longer present in the catches (**I**, fig. 4). Consequently, the actual number of larger fish in June was not higher than during the two earlier periods. Males and females were equally abundant in the catches at the beginning of the spawning season, but male dominance increased thereafter (**I**).

Temperature changes best explained the movements of the pikeperch during the pre-spawning and spawning seasons (fig. 2, **II**). The strongest correlations between CPUE and temperature was one and two days prior to the catches (**II**). This suggests that relative changes in temperature may be more important in stimulating the movements rather than the actual temperature.

The recaptures indicated strong homing behaviour in the Östhammar area (**III**). Homing is known to be well developed in pikeperch (Lehtonen, 1979, 1983; Willemsen, 1977, Colby & Lehtonen, 1994; Nyberg et al., 1996; Jepsen et al., 1999; Lappalainen, 2001). The comparison of tagging and recapture dates also demonstrated that the individual pikeperch migrated to the spawning areas at the same time in two subsequent years (**III**). The dates of recaptures in 2003 correlated positively with the tagging dates in 2002 (Spearman correlation $r = 0.66$; $p = 0.0237$; $n = 13$; **III**, fig. 3). Pikeperch tagged earlier were also recaptured earlier indicating that there are early spawners and those arriving later to the spawning grounds.

The moon phases seemed to affect the activity of pikeperch in the present study, even though the effect was weaker than for temperature (fig. 2, **II**). Day-length could also stimulate spawning migrations of pikeperch, thus explaining the large catches in early April (**I**, **II**). Changes in the water level do not seem to have any effect on the activity of the pikeperch (fig. 2).

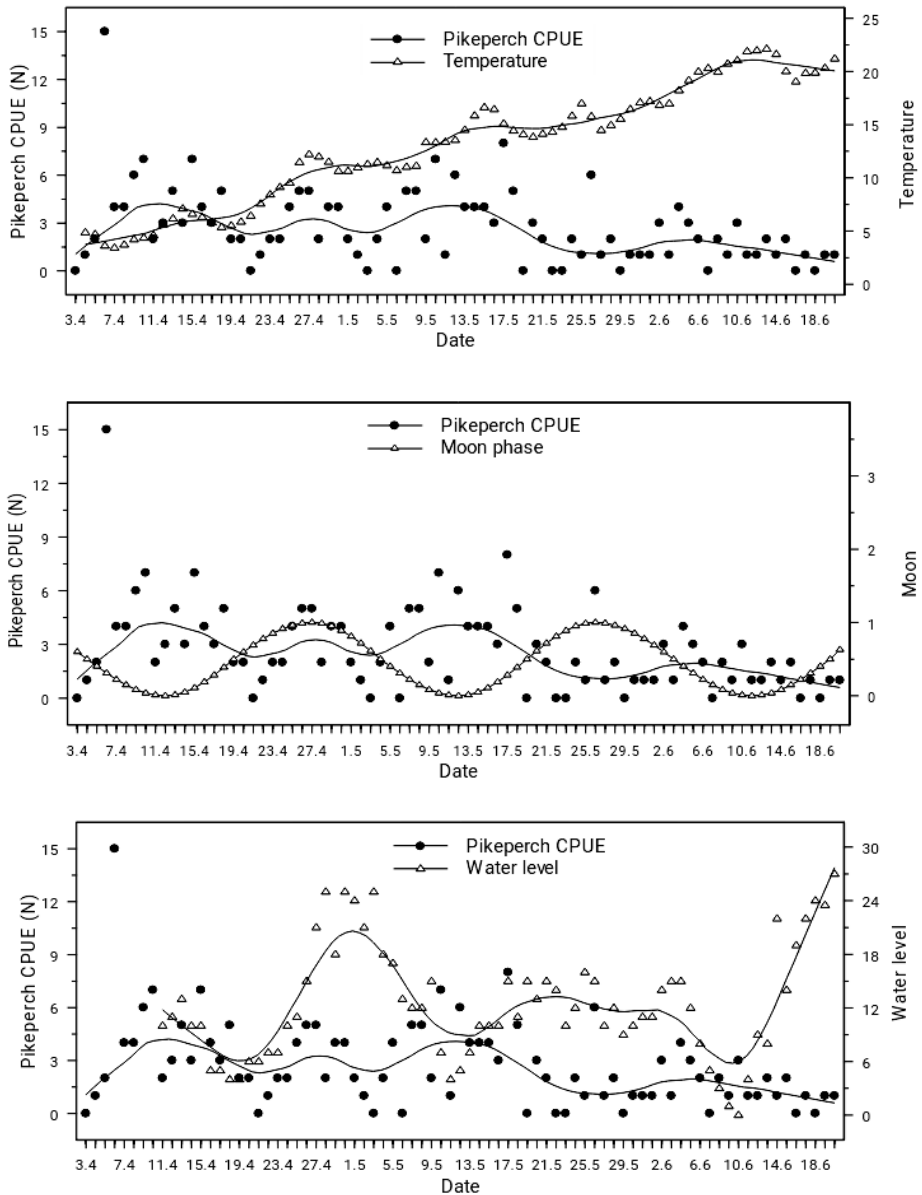


Figure 2. Daily fyke net catches of pikeperch (CPUE) in 2002 with temperature (a), moon phases (b) and water level (c). Lines are smoothed (LOESS) values (II).

Movements and management

The recaptures from the taggings in Östhammar were distributed over 10 management areas (fig. 3, III). The management areas are quite small in this coastal part of eastern Sweden and they are based on the old administrative units of the villages. The yield/recruit (Y/R) model used demonstrated that in the situation in which the pikeperch migrates over several management areas, overfishing is inevitable if there is not cooperation between the areas (III). In the areas where fish are present only for a short period of time (three months), for example, the spawning areas, the short-term exploitation optimum is achieved with relatively high fishing pressure ($F = 0.8$). In the area, where the fish is present nine months, the largest yield is achieved with much lower fishing pressure ($F = 0.25$) (III, fig. 4).

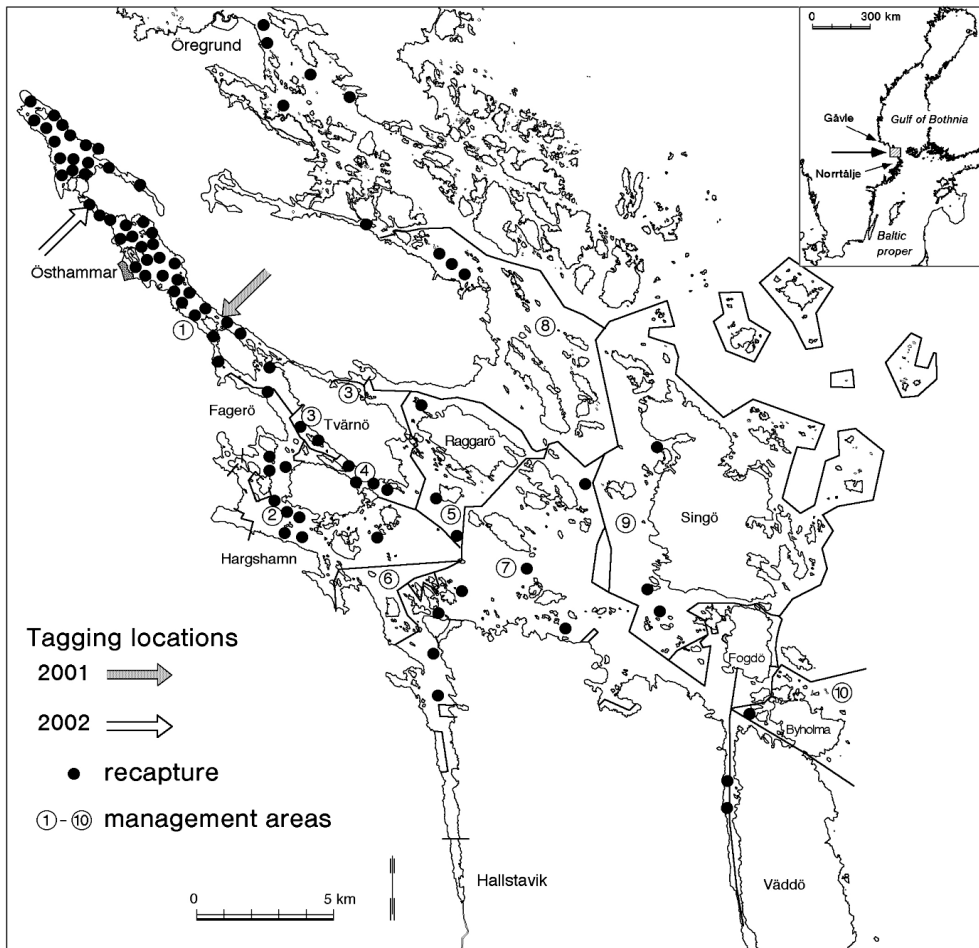


Figure 3. The tagging locations in 2001 and 2002 and the distribution of recaptures in the management areas. Recaptures were also made outside the area shown, the furthest ones in the proximity of the city of Gävle (~100 km from the tagging place, small map).

Growth of pikeperch and effects of fishing

The growth of the pikeperch in the Archipelago Sea was observed to be relatively slow based on the back-calculated lengths (IV). As there was a significant selection for smaller size, the observed growths are biased towards slower growth, especially in those age groups that are subject to the most intensive exploitation (Table 2). The estimated differences in back-calculated lengths at the most common pairs of ages were approximately 6 cm. In the pairs of pikeperch at six and nine years, and at seven and 10 years, the younger group have already been subject to selective fishing, which explains why the differences between these pairs becomes smaller.

Table 2. ANOVA statistics and average differences in mean back-calculated lengths (mm) at age *i* between pikeperch caught at age *i* or *i*+3. R² is the adjusted R squared; * indicates significance P<0.05; ** P<0.01 (IV).

Gear	Age of		Year classes	N	R ²	Year class df and F	Age df and F	Average difference in length at age (mm)
	Age	capture						
Both	2	2 and 5	1997–1998, 2000–2009	5123	0.39	11; 292.51**	1; 38.67**	-5.18
Both	3	3 and 6	1996–2008	5941	0.11	12; 54.17**	1; 75.79**	8.40
Both	4	4 and 7	1995–2007	5725	0.44	12; 57.70**	1; 2511.47**	44.73
Both	5	5 and 8	1994–2006	7556	0.39	12; 26.65**	1; 3870.32**	57.68
Both	6	6 and 9	1993–2005	6091	0.24	12; 11.46 **	1; 1674.83**	58.24
Both	7	7 and 10	1991–1992, 1995, 1997–2004	3441	0.18	10; 27.15**	1; 369.59**	47.45
Gill net	2	2 and 5	1997–1998, 2000–2009	3746	0.43	11; 251.07**	1; 49.67**	-7.13
Gill net	3	3 and 6	1996–2008	4712	0.12	12; 49.58**	1; 45.49**	7.47
Gill net	4	4 and 7	1995–2007	4448	0.43	12; 47.49**	1; 1961.92**	45.27
Gill net	5	5 and 8	1994–2006	5124	0.42	12; 23.62**	1; 3315.35**	59.49
Gill net	6	6 and 9	1993–2005	4636	0.33	12; 10.07**	1; 1924.80**	63.43
Gill net	7	7 and 10	1991–1992, 1995, 1997–2004	2748	0.24	10; 22.98**	1; 494.64**	54.11
Trap net	2	2 and 5	1997–1998, 2000–2009	1377	0.26	11; 43.39**	1; 0.20	-0.63
Trap net	3	3 and 6	1996–2008	1229	0.15	12; 11.67**	1; 46.53**	13.34
Trap net	4	4 and 7	1995–2007	1277	0.53	12; 11,07**	1; 690.25**	49.92
Trap net	5	5 and 8	1994–2006	2432	0.37	12; 18.76**	1; 572.81**	58.60
Trap net	6	6 and 9	1993–2005	1455	0.17	12; 13.08**	1; 74.22**	34.20
Trap net	7	7 and 10	1997, 1999–2002, 2004	438	0.14	5; 11.45**	1; 3.55*	14.38

5. Discussion

Temperature best explained the movements and activity of pikeperch during the pre-spawning and spawning season (I). Pikeperch is a warm water species and the strong relationship between catches and temperature is not surprising. Temperature stimulates the activity of the pikeperch and the activity is highest during summer and lowest during winter (Jepsen et al., 1999). Based on the results, the change of the temperature was the trigger for stimulating activity (II).

Day-length can also affect the movements of pikeperch. Neuman et al. (1996) found that the activity of perch in spring was best explained by day-length; periods of high activity took place around the same time in different years, even though temperature varied between years, whereas, the onset of spawning was influenced by temperature.

The phase of the moon also affected the activity of pikeperch, even though this effect was weaker than the temperature (II). Koed et al. (2000) similarly found that the moon phases and the distance moved by pikeperch were significantly correlated, but the correlation coefficient was also relatively low in their study. Moonlight has been found to affect the activity of pelagic fish species, with catches decreasing close to the full moon, which is explained by predator avoidance (Luecke & Wurtsbaugh, 1993; Contor & Griffith, 1995; Gaudreau & Boisclair, 2000). In the Baltic, only seals are large enough to predate on mature pikeperch and, since the findings were similar to the findings of Koed et al. (2000) whose study was carried out in an area where there are no seals, predator avoidance might not explain this behaviour for pikeperch. DeVries et al. (2004) have found that the saltwater entry of different species of Pacific salmon smolts (*Oncorhynchus* sp.) were coordinated with the apogee, at the time when the moon is farthest from the Earth and the gravitational force is low. They considered that a gravitational cue could be the factor behind this behaviour, even though they could not show how or why. At the time of the study (II), the apogee occurred three to four days before the new moon.

The spawning season of pikeperch extended for two months during the year of experimental study (I). The long spawning season secures reproductive success, both because of optimal temperature for larval development and for matching the timing of hatching in relation to available food (Ljunggren, 2002). The year-class strength of the pikeperch is strongly dependent on the temperature during the first year. As with higher temperatures during the growing season, Y-O-Y pikeperch can reach the size that enables them to start to feed on fish early in their first summer and, thus, reach lengths that increase the probability of surviving their first winter (Lappalainen et al., 2000) The inter-annual variability of the natural population size of pikeperch is, thus, usually high, based on large variation in year classes (Colby & Lehtonen, 1994; Lappalainen et al., 1995; Lehtonen et al., 1996).

The recaptures illustrated a strong homing behaviour in pikeperch (III). Homing is known to be well developed in pikeperch (Willemsen, 1977; Lehtonen, 1979; Colby & Lehtonen, 1994; Nyberg et al., 1996; Jepsen et al., 1999). The comparison of tagging and recapture dates also demonstrated that the individual pikeperch migrated to the spawning areas at the same time in two subsequent years. This observation was based on a small number of recaptures, but if the reproduction time is heritable, rather than individually flexible, variation in selection through

the reproductive season may lead to adaptive temporal adaptation to environmental conditions typically experienced at the reproductive time (Hendry & Day, 2005). Such adaptation could be possible for the pikeperch due to the long spawning season. Oomen and Hutchings (2015) found that for Atlantic cod populations the variation in the timing of reproduction had the potential to promote genetic variability in populations as a response to environmental changes. Environmental changes, such as climate change, can impact ecosystems and food webs in unknown ways and adaptations and traits that exist in some part of the populations can be important in the future for the whole population. The results suggest that an adequate escapement should be ensured during the whole period of spawning migration and spawning to avoid possible losses of important population components. Moreover, it is logical to assume that the current migratory patterns of populations are already critical in supporting current productivity (MacCall, 2012) whereas reduced spatial heterogeneity can cause exploited populations to become more vulnerable to, for example, adverse climatic effects (Oomen & Hutchings, 2015). However, mixing and overlapping also take place in the coastal pikeperch stocks and these can receive immigrants from adjacent stocks (Lappalainen et al., 2016).

It was demonstrated that in the situation in which the pikeperch migrates over several management areas, overfishing is inevitable without cooperation between the areas (III). The yields were maximized with relatively high fishing mortality in areas where the fish are present only a short period of the year, for example, the spawning areas and migration routes. This outcome is a consequence of the short fishing season. The rational strategy in these areas is to fish aggressively over the short season, in order to 'catch up with the others'. If the fishing pressure is low in other areas, then it is reasonable for these to also decrease their efforts. On the other hand, if the fishing mortality in the other areas is low, the rational strategy is to fish less aggressively. When fish become more stationary, the optimal strategy changes so that the recommended strategy is to decrease effort if neighbouring areas increase theirs, presuming that the fishing mortality is already relatively high. By acting in this way, the area minimizes its catch losses. These are challenging situations for the managers, since managers seldom have the data from adjacent areas to estimate whether it is profitable to increase or decrease the fishing effort. Several game theoretic research studies have come to the same solution; the competitive exploitation of fish stocks migrating over several management units leads to overfishing of the stock and competitive exclusion (e.g., Clark, 1980; Hannesson, 2011; but see, also, McKelvey, 1999). Studies have also shown that coalitions, which are created to prevent this competition, are unstable (Kwon, 2006; Pintassilgo & Lindroos, 2008; Hannesson, 2011, 2013). The reason for this instability is similar to that situation described above: a single member of a larger coalition gains from breaking out of the coalition. Additionally, stocks that range over several management areas are vulnerable to the lowest standard of management at some part of the season (Mace & Reynolds, 2001). To successfully manage fisheries that range over management areas, cooperation between units is necessary. Cooperation among a limited and clearly defined number of players may be maintained by strong rules even though the overall expectation of the stability of the coalitions has been found to be pessimistic (Hannesson, 2011). The game theory studies have been undertaken mostly in cases where the actors are states or high sea fishing fleets and the studies have not taken into account existing socio-cultural networks, which exist in small communities and can bind the actors tighter together. In local communities, a personal sense of stewardship among fishermen, as well as

the fact that fishermen cannot run away from overfishing and have to live with the consequences of their actions, can lead to sustainable fisheries governance (Wilson et al., 2007). In this case, the expected benefits of managing a resource with long-term sustainability can exceed the costs (Ostrom, 2009) (with ‘costs’ also referring here to non-monetary costs, such as reputation). Thus, in local communities the coalitions can be much stronger than on the international playing field (Berkes et al., 2006).

The general growth pattern of pikeperch was similar to that found in freshwaters and Baltic coastal waters. Temperature had a significant effect on growth (Lehtonen et al., 1996; Ruuhijärvi et al., 1996; Lappalainen, 2001; Lappalainen et al., 2005, 2009). The size of the age group had a small negative effect on growth, indicating density-dependent growth in the population (IV). This finding is similar to that made by Lappalainen et al. (2009) in the eastern Gulf of Finland.

A strong phenotypic selection for slow growth in the Archipelago Sea was observed (IV). The difference in back-calculated lengths at a given age between pikeperch caught three years apart was up to 60 mm in fully recruited age groups, indicating very strong size selection (Table 2, IV). This result also shed light on earlier observations on the slow growth in the Archipelago Sea (Heikinheimo et al., 2006; Raitaniemi & Manninen, 2016). High fishing pressure, with up to 80% of the age group annually removed by fishing (Heikinheimo et al., 2014), combined with selective gill net fishing, effectively removes the fast-growing individuals from the population as they reach the size of ~350 mm and become vulnerable to fishing. So, the proportion of the fast-growing individuals in the population decreases rapidly after that, and to the same degree the proportion of slow-growing individuals increases. In the older age groups the slow growers are thereby dominant. This is reflected in a picture of slow growth in the area if only the observed lengths at age or back-calculated lengths are looked at (IV). High fishing effort and selective fishing is demonstrated to select for slower growth and earlier maturation (Law, 2000; Heikinheimo et al., 2006; Kokkonen et al., 2015; Olin et al., 2018). Selective fishing alters the composition of a population or community and, consequently, in the long term, the ecosystem structure and biodiversity (Garcia et al., 2012). Selective fishing gears and the use of minimum size limits can result in size selectivity in many fisheries that preferentially harvest large fish (Heino & Gødo, 2002; Sinclair et al., 2002; Neuheimer & Taggart, 2010). Excessive fishing imposes strong selection for earlier maturation even when it is non-selective (Law & Grey, 1989; de Roos et al., 2006; Andersen et al., 2007; Jørgensen et al., 2007). Evaluating these effects empirically is difficult (Hard et al., 2008) and whether phenotypic changes in harvested populations are due to evolution, rather than phenotypic plasticity or environmental variation, has been difficult to prove directly (Allendorf & Hard, 2009; Hard et al., 2008). The collective evidence across species and environmental conditions highlights trends in size, age and other traits that are consistent with evolutionary responses to size-selective fishing (Jørgensen et al., 2007; Law, 2007; Fenberg & Roy, 2008). Studies have shown that there have been genetic changes in populations in response to size-selective fishing in laboratory conditions (e.g., Atlantic silverside, *Menidia menidia*, Conover & Munch, 2002; Conover et al., 2005; zebrafish, *Danio rerio*; Uusi-Heikkilä et al., 2017), and support for genetic changes in population in the wild is very strong (e.g., Atlantic cod) (Swain et al., 2007).

High fishing mortality also truncates the age structure of the population, which especially threatens the sustainability of stocks of long-lived species (Venturelli et al., 2009). A typical precautionary standpoint is to delay the beginning of the harvest until after the fish have spawned at least once (Myers & Mertz, 1998). Hallicay and Pinhorn (2002) and Venturelli et al. (2009) have argued that this is not enough—that forcing iteroparous species to spawn as if it was semelparous is not sustainable. Iteroparous species have developed an evolutionary strategy to spread reproductive output across many years and over temporally and spatially variable environmental conditions. In this way, they are able to reduce recruitment variability, as some reproductive success can be ensured, despite potentially long periods of unfavourable environmental conditions for offspring survival (Marteinsdottir & Thorarinsson, 1998; Secor, 2000a, 2000b; Hsieh et al., 2006). There are an increasing number of observations that larger and older females produce more viable offspring compared to smaller and younger individuals. Laboratory experiments on, for example, Atlantic cod suggest that first-time spawners perform very poorly compared to more experienced individuals, and are breeding for a shorter period, producing fewer egg batches, exhibiting lower fecundity and producing smaller eggs with lower fertilization and hatching rates (Solemdal et al., 1995; Trippel, 1998). Trippel (1998) has found that 13% of eggs hatched from first-time spawners of Atlantic cod compared to 62% from a second-time spawners. Berkeley et al. (2004a) have studied black rockfish (*Sebastes melanops*) and found that the larvae from the older spawners of female had growth rates more than three times as fast and survived starvation more than twice as long as larvae from the youngest females. The maternal influence on the quality of the offspring has been reported for several percids, as well as for pikeperch. Olin et al. (2018) have found that both relative fecundity and egg dry weight significantly increased with pikeperch female size and age. Walleye (*Sander vitreum*) juvenile survival was related to the age or size of a female to a degree that could be observed to affect the population dynamics of the species (Venturelli et al., 2010). Larger females of yellow perch (*Perca flavescens*, Mitchill) produce larger eggs and larvae of higher quality (e.g. Huss et al., 2007) and the same has been reported for Eurasian perch as well (Olin et al., 2012). Current management paradigms do not usually count on these effects and assume that parental age and size have no effect on larval survival (Murawski et al., 2001; Venturelli et al., 2009). But selectively removing larger, older individuals can lead to unfavourable effects on populations (Berkeley et al., 2004a; Bobko & Berkeley, 2004; Hsieh et al., 2006). Using both minimum and maximum size limits have been offered as one solution for minimizing these effects. Vainikka et al. (2017) have simulated the effect of such a management strategy on inland pikeperch populations. For heavily exploited populations, this strategy was found not to be enough to ensure stability of yields and minimal evolutionary effect, and their results suggested that fishing mortality rates should be restricted to relatively low levels to minimize the risks of undesirable evolutionary effects of fishing. The manager's rule of thumb (Alverson & Pereyra, 1969; Gulland, 1970) suggests that fishing mortality should be approximately the same as natural mortality, so that $F_{MSY} = M$. This rule has been confirmed by, for example, Zhou et al. (2012) who have carried out a meta-analysis on 245 fish species, including *perciformes*, worldwide. For *perciformes*, the sustainable F_{MSY}/M relation was 0.922 suggesting that the F should be slightly less than the M . This is clearly less than those observed in the study areas (III, IV). Typical M assumptions in age groups that have passed the juvenile years varies between 0.1 and 0.2 (III; Lehtonen, 1983; Heikinheimo et al., 2014). Increased

seal and cormorant populations in the Baltic Sea can be assumed to increase these estimates, but it is unclear how much this predation has increased the natural mortality at the population level, even though a number of studies have come to the conclusion that locally, for example, the predation by cormorants, can have an effect and especially on perch populations (Saulamo et al., 2001; Vetemaa et al., 2010; Östman et al., 2012; Gagnon et al., 2015). Heikinheimo et al. (2016) has studied the cormorant-induced mortality of pikeperch in the Archipelago Sea and estimated that 5–34% (M 0.04–0.13) of the total mortality in age groups 2 to 4 was induced by the cormorants. The damages to catches and economic losses to the fishermen caused by seals and cormorants can, of course, be considerable, even if this additional mortality would not be significant at the population level.

Management approaches should further consider the evolutionary effects of fishing (Law & Grey, 1989; Conover & Munch, 2002; Jørgensen et al., 2007). Distributing harvesting with moderate mortality across the species, stocks and sizes in an ecosystem in proportion to their natural productivity, is recommended to more effectively prevent adverse ecological effects of fishing, while simultaneously supporting sustainable fisheries (Garcia et al., 2012). Such an approach would also improve the sustainability of pikeperch fisheries. Management should also have a precautionary approach in relation to the different components of the pikeperch populations. Pikeperch managers should consider the spatial dynamics of the stock in order to protect the stock and its components from overfishing and also to distribute the yield fairly between fishermen fishing in different parts of the dispersal area of the stock. Since there were also indications that the individual pikeperch migrated to the spawning areas at the same time in subsequent years (III), it is advisable to ensure constant escapement during the spawning season. Olin et al. (2018) have also advised for more stock-specific management of pikeperch fisheries due to differences in the size-dependent maternal influences among pikeperch populations. Management of the pikeperch should thus consider several factors in order to achieve long-term sustainability.

6. Conclusions

It was demonstrated that there are differences in biological characteristics between pikeperch arriving at the spawning ground at different times and signs that there can be early and late spawners in the populations. It was also demonstrated that in cases where the pikeperch migrates over several management areas, overfishing is inevitable if there is no agreed cooperation between the areas. Furthermore, it was proven that excessive fishing pressure with highly selective gears creates strong phenotypic selection for slower growth in the studied pikeperch population.

To better understand the population dynamics of pikeperch populations and their response to fishing, further studies on growth, genetic variation and the importance of the age and size structure of the spawning population to the population dynamics of the pikeperch is recommended. Moreover, the effects of the management actions should be followed and monitored in a way that enables the assessment of the performance of the actions and adapting the management to changes in the ecosystems and in the population dynamics of the pikeperch.

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