SPATIAL AND TEMPORAL VARIATION IN FISH POPULATIONS AND ASSEMBLAGES IN COASTAL WATERS OF THE NORTHERN BALTIC PROPER

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2015

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PAGE LAYOUT

Nikke Ehrukainen | Tähkä-Design

“Kokemus on hieno asia.
Kokemus on sitä, että tietää
jälkeenpäin miten jokin asia
olisi pitänyt hoitaa.”

–Jyri Erma–

ABSTRACT

The distribution and traits of fish are of interest both ecologically and socio-economically. In this thesis, phenotypic and structural variation in fish populations and assemblages was studied on multiple spatial and temporal scales in shallow coastal areas in the archipelago of the northern Baltic Proper. In Lumparn basin in Åland Islands, the fish assemblage displayed significant seasonal variation in depth zone distribution. The results indicate that investigating both spatial and temporal variation in small scale is crucial for understanding patterns in fish distribution and community structure in large scale. The local population of Eurasian perch *Perca fluviatilis* L displayed habitat-specific morphological and dietary variation. Perch in the pelagic zone were on average deeper in their body shape than the littoral ones and fed on fish and benthic invertebrates. The results differ from previous studies conducted in freshwater habitats, where the pelagic perch typically are streamlined in body shape and zooplanktivorous. Stable isotopes of carbon and nitrogen differed between perch with different stomach contents, suggesting differentiation of individual diet preferences. In the study areas Lumparn and Ivarskärsfjärden in Åland Islands and Galtfjärden in Swedish east coast, the development in fish assemblages during the 2000's indicated a general shift towards higher abundances of small-bodied lower-order consumers, especially cyprinids. For European pikeperch *Sander lucioperca* L., recent declines in adult fish abundances and high mortalities (Z = 1.06–1.16) were observed, which suggests unsustainably high fishing pressure on pikeperch. Based on the results it can be hypothesized that fishing has reduced the abundances of large predatory fish, which together with bottom-up forcing by eutrophication has allowed the lower-order consumer species to increase in abundances. This thesis contributes to the scientific understanding of aquatic ecosystems with new descriptions on morphological and dietary adaptations in perch in brackish water, and on the seasonal variation in small-scale spatial fish distribution. The results also demonstrate anthropogenic effects on coastal fish communities and underline the urgency of further reducing nutrient inputs and regulating fisheries in the Baltic Sea region.

Keywords: Fish assemblage, fisheries, eutrophication, seasonality, trophic level, morphology, stable isotopes, fish diet

SVENSK SAMMANFATTNING (Swedish abstract)

Fiskarnas egenskaper och utbredning har alltid varit av stort ekologiskt och socioekonomiskt intresse. Denna avhandling handlar om fenotypisk och strukturell variation hos fiskpopulationer och -samhällen på olika rumsliga och tidsliga skalor i norra egentliga Östersjöns grunda skärgårdsområden. I Lumparn på Åland visade fisksamhället tydlig säsongsvariation mellan olika djupzoner. Resultaten indikerar också att kunskap om fisksamhällens strukturella variation på små rumsliga och tidsliga skalor är nödvändig för att kunna förstå förändringar i samhällsstrukturen på större skalor. I den lokala abborpopulationen *Perca fluviatilis* L. observerades habitat-specifik variation i morfologi och födoval. De pelagiska abborrarnas föda bestod av fisk och bottenlevande evertebrater, och de var i genomsnitt högre i kroppsform än de litorala abborrarna. Resultaten skiljer sig från tidigare studier utförda i sötvattenhabitat, där pelagiska abborrar oftast är mera strömlinjeformade än litorala abborrar och har djurplankton som huvudsaklig föda. Förhållandet av stabila kol- och fosforisotoper skiljde sig mellan abborrindivider med olika maginnehåll, vilket tyder på differentiering i individuellt födoval. Likartade förändringar noterades i fisksamhällets struktur under 2000-talet i tre olika kustnära studieområden – Lumparn och Ivarskärsfjärden på Åland samt Galtfjärden i Svenska östkusten. I alla tre fisksamhällen ökade abundansen av små fiskar och speciellt mörtfiskar. Abundansen av stora gösar *Sander lucioperca* L. minskade i alla tre studieområden, och mortaliteten hos gös var hög (Z = 1.06–1.16). Detta tyder på ohållbart högt fisketryck och på att fisket har minskat stora rovfiskars proportion i fisksamhället. Tillsammans med övergödning har detta gynnat mindre fiskar på lägre trofinivåer. Den här avhandlingen bidrar till vetenskaplig förståelse om akvatiska ekosystem med nya beskrivningar på morfologi och födoval hos abborre i brackvattenhabitat, och på småskalig variation i fisksamhällens struktur. Resultaten bevisar också antropogeniska effekter på kustnära fisksamhällen och framhäver behovet att skära ned näringsutsläpp och reglera fisketrycket i Östersjöns kustregioner.

Nyckelord: Fisksamhället, fiske, övergödning, säsongsvaration, trofinivå, morfologi, stabila isotoper, födoval

SUOMENKIELINEN TIIVISTELMÄ (Finnish abstract)

Tieto kalojen ominaisuuksista ja levinneisyydestä on aina ollut sekä ekologisesti että sosioekonomisesti tärkeää. Tässä väitöskirjatutkimuksessa tutkittiin pohjoisen Itämeren saaristovyöhykkeen kalapopulaatioita ja -yhteisöjä päällekkäisesti useassa alueellisessa ja ajallisessa mittakaavassa. Ahvenanmaan Lumparnilla kalayhteisön rakenne vaihteli voimakkaasti eri syvyysvyöhykkeiden välillä vuodenajasta riippuen. Tulokset osoittavat, että yhteisörakenteen vaihtelun huolellinen kartoittaminen pienessä mittakaavassa auttaa olennaisesti ymmärtämään kalayhteisöjen rakennetta ja toimintaa suuressa mittakaavassa. Lumparnin ahvenpopulaatiossa *Perca fluviatilis* L. havaittiin elinympäristöjen välisiä eroja sekä kalojen morfologiassa että ruokavaliossa. Ulappavyöhykkeen ahvenet käyttivät ravinnokseen kaloja ja pohjaeläimiä ja olivat ruumiinmuodoltaan korkeampia kuin rantavyöhykkeen ahvenet. Tulokset eroavat aikaisemmista järvissä tehdyistä tutkimuksista, joissa ulappavyöhykkeen ahventen on todettu käyttävän ravinnokseen tyypillisesti eläinplanktonia ja olevan ruumiinmuodoltaan virtaviivaisempia kuin rantavyöhykkeen ahvenet. Yksilöillä joilla oli erilaiset mahansisällöt, oli myös erilainen hiilen ja typen stabiilien isotooppien suhde, mikä viittaa yksilöiden väliseen erilaistumiseen ravinnonvalinnassa. Kalalajien vallintasuhteet muuttuivat 2000-luvun aikana samankaltaisesti kolmella eri rannikkoalueella – Ahvenanmaan Lumparnilla ja Ivarskärsfjärdenillä sekä Ruotsin itärannikon Galtfjärdenillä. Pienikokoisten lajien edustajat, erityisesti särkikalat, yleistyivät, kun taas suuret petokalat, erityisesti suuret kuhat *Sander lucioperca* L., harvinaistuivat kaikilla tutkimusalueilla. Kuhapopulaatioissa havaittiin myös korkeaa kuolevuutta (Z = 1.06–1.16), mikä yhdessä yksilömäärien vähenemisen kanssa viittaa kestämättömän korkeaan kalastuspaineeseen. Tulokset viittaavat myös siihen, että kalastus on vähentänyt suurten petokalojen osuutta kalayhteisöissä, mikä yhdessä rehevöitymisen kanssa on suosinut ravintoverkossa alemmilla tasoilla olevia lajeja edesauttaen niiden edustajien runsastumista. Tämä väitöskirjatutkimus tuottaa uutta tieteellistä tietoa vedenalaisista ekosysteemeistä esittelemällä uusia tuloksia sekä ahvenen morfologiasta ja ravintovalinnasta murtovedessä että rannikoiden kalayhteisöjen rakenteen vuodenaikaisvaihtelusta. Lisäksi tulokset tuovat esille yhteiskunnan haitallisia vaikutuksia rannikkovesien kalayhteisöihin ja korostavat Itämeren rannikkoalueiden ravinnepäästöjen ja kalastuspaineen rajoitusten tarpeellisuutta.

Avainsanat: kalayhteisö, kalastus, rehevöityminen, vuodenaikaisvaihtelu, trofiataso, morfologia, stabiilit isotoopit, kalojen ravintovalinta

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ORIGINAL PUBLICATIONS

ORIGINAL PUBLICATIONS

The thesis is based on four papers, which are referred to in the text by their Roman numerals. The original publications have been reprinted with the kind permission of copyright holders.

I MUSTAMÄKI N, Jokinen H, Scheinin M, Bonsdorff E & Mattila J (2015)

Spatial and seasonal structure of fish community in a brackish water embayment in the Archipelago Sea, Baltic Sea. ICES Journal of Marine Science. DOI: 10.1093/icesjms/fsv068.

II MUSTAMÄKI N, Cederberg T & Mattila J (2014)

Diet, stable isotopes and morphology of Eurasian perch (*Perca fluviatilis*) in littoral and pelagic habitats in the northern Baltic Proper. Environmental Biology of Fishes 97: 675–689.

III MUSTAMÄKI N & Mattila J

Structural changes in three coastal fish assemblages in the northern Baltic Sea archipelago. Manuscript.

IV MUSTAMÄKI N, Bergström U, Ådjers K, Sevastik A & Mattila J (2014)

Pikeperch (*Sander lucioperca* (L.)) in decline: high mortality of three populations in the northern Baltic Sea. Ambio 43: 325–336.

1 INTRODUCTION

Scientists who aim to explore the structure and function of ecosystems have the disadvantage – and the privilege – of having to deal with endless variation in nature. Finding general patterns in the structure and function of a natural system can seem impossible considering the variety of habitats and species assemblages, affected by the seasonally changing environmental conditions, human activities and other factors. Simultaneous synergistic or antagonistic effects of multiple factors on different scales are difficult to identify and even more difficult to quantify, and scientists have only recently begun to grasp the system-wide effects of multiple stressors.

Considering aquatic ecosystems, fish are probably the most familiar ecosystem compartment for the general public. Fish, and especially coastal fish, also provide food, recreation and income for millions of people worldwide. This thesis focuses on the dynamics of coastal fish communities in the archipelago region of the northern Baltic Proper. The seasonal and spatial distribution of fish in shallow coastal waters, diet and morphology of Eurasian perch *Perca fluviatilis* in different habitats, recent trends in European pikeperch *Sander lucioperca* populations and coastal fish assemblages are addressed in particular. The effects of fisheries and eutrophication on coastal fish assemblages are discussed.

1.1 FISH COMMUNITIES: DYNAMIC SYSTEMS OF MOBILE ORGANISMS

The abiotic factors together with the biota create habitats: “a description of a physical place, at a particular scale of space and time, where an organism either actually or potentially lives” (Kearney 2006). Habitat preferences of fish, regular fish movements and seasonal reproduction patterns create complex variation in fish abundances in space and time. Regular movements of some migratory fish (Hobson 1999) and especially of those of special commercial value such as salmon *Salmo salar* (Karlsson & Karlstråm 1994) are rather well studied as the main focus of fish studies has traditionally been on the commercial stocks. The local (within/between-habitat) movements and fine-scale spatial distributions of many fish species are less well studied, and community level studies especially are still today few in number (Letourneur et al. 2001; Methven et al. 2001; Sundblad & Bergström 2014; Snickars et al. 2014).

The scene in the coastal aquatic environment is set by the geographical location and topography of the water body, which has for the northern Baltic Proper archipelago been described by Snickars et al. (2009), Vahteri et al. (2009) and Rosqvist et al. (2010) among others. Because primary production needs daylight, the aquatic communities are typically organised in depth zones, the best known example being the rocky shore zonation (Alongi 1998; Chappuis et al. 2014). The primary production in a system is further regulated by the nutrient availability (Nixon 1995; Alongi 1998; Scheinin & Mattila 2010). In systems with a salinity gradient, such as estuaries (Alongi 1998; Elliot 2007), the biota is distributed according to its salinity tolerance. Also, the fish are typically distributed according to species-specific preferences for depth, substrate and habitat structure (Pihl et al. 2002; Vahteri et al. 2009; Malek et al. 2014; Snickars et al. 2015). Descriptions on the depth zone distribution of coastal fish communities are still few (Pihl & Wennhage 2002), and most studies on littoral fish have been conducted in the easily accessible shallow littoral zone (Allen 1982; Rajasilta et al. 1999; Sandström & Karås 2002). Characterisation of the reproduction habitats, which are often located in the shallow coastal zone (Snickars et al. 2009; Kallasvuo et al. 2011), has recently become an important area of research because the coastal development increasingly threatens spawning sites of many species (Sundblad & Bergström 2014).

The mechanisms of fish movement include at least connectivity of metapopulations and/or habitats withy larval dispersal (Cowen & Sponaugle 2009; Sheaves et al. 2015), diel foraging (Methven et al. 2001; Pihl et al. 2002; Hrabik et al. 2006) and annual spawning migrations (Karlsson & Karlstråm 1994; Pihl et al. 2002; Stockwell et al. 2014). Many species undergo ontogenetic habitat shifts as a part of the normal growth and development (Wang & Eckmann 1994; MacPherson 1998; Byström et al. 2003; Elliot et al. 2007). Biological interactions such as competition (Mehner et al. 1996; Estlander et al. 2010; Kekäläinen et al. 2010) and anti-predator behaviour (Brabrand & Faafeng 1993; Snickars et al. 2004) can also initiate a habitat shift.

Not only are the fish mobile, but also the absolute species abundances change seasonally. In temperate regions such as the Baltic Sea region, majority of the primary production, growth and reproduction occur during the warm summer months resulting in characteristic seasonal cycles in all biota (Axenrot & Hansson 2004; Nordström et al. 2009; Scheinin & Mattila 2010). In the Baltic Sea, spawning of most fish species takes place in springtime (Byström et al. 2003; Snickars et al. 2010; Kallasvuo et al. 2011; Sundblad & Bergström 2014), and as a consequence abundance of young-of-the-year fish is generally high in late summer (Sandström & Karås 2002; Axenrot & Hansson 2004; Kallasvuo et al. 2011). Recruitment success, how many juveniles survive to adulthood, is later reflected in year-class strength, abundance of fish born in a particular year in the catches of adult fish (Pekcan-Hekim et al. 2011; Heikinheimo et al. 2014).

The above-mentioned patterns in habitat preference, fish movement and recruitment have most often been described for single species. Traditionally, the fisheries science has concentrated on following stock sizes of commercially important species (Mace 2001; Möllmann et al. 2014). The fisheries-scientific term fish stock refers to "semi-discrete groups of fish with some definable attributes of interest to managers" (Begg et al. 1999), often practically equalling a population or subpopulation. Currently, there is a trend towards community-level studies (Möllmann & Diekmann 2012; Olsson et al. 2012; Sundblad & Bergström 2014) along with the recent development in multivariate analysis methods (Anderson 2001) and the growing need for ecosystem-based management that sets the focus on the system rather than on single species (Pikitch et al. 2004; Möllmann et al. 2014). As the monitoring interest usually lies in the long-term trends (Mace 2001; Ådjers et al. 2006), the issue of the seasonal changes is often circumvented by conducting the sampling at the same time each year and descriptions on the seasonal variation in fish communities in the Baltic Sea are still few in number (Axenrot & Hansson 2004; Olsson et al. 2012).

1.2 INTRASPECIFIC VARIATION IN FISH

In community-level studies the diet and traits are often assumed identical in conspecific individuals (Araujo et al. 2011; Bolnick et al. 2011). In most animals, however, fish included, the effect of age and size of the individual on its diet is often evident, which may have crucial importance for trophic interactions (Werner & Gilliam 1984; Quevedo et al. 2009; Rudolf et al. 2014; Svanbäck et al. 2015). A fish may undergo one or several ontogenetic diet shifts from the juvenile diet towards the adult diet as described for perch by Mehner et al. (1996) Sandstöm and Karås (2002) and Estlander et al. (2010). Even individual diet specialisation has been documented in several fish species (reviewed by Araujo et al. 2011), but theories of underlying mechanisms are still under development.

In many fish species, habitat choice and intraspecific diet specialisation seem to be connected to body shape, i.e. morphology (Skulason & Smith 1995). This so called resource polymorphism phenomenon has been extensively studied in perch which is rather sedentary in behaviour (Bergek & Björklund 2009) and displays high morphological plasticity (Svanbäck et al. 2015). Typically, in lake systems juvenile perch feeds on zooplankton and the adult perch population is divided into sub-populations of fish-feeding, deep-bodied littoral perch and plankton-feeding, streamlined pelagic perch (Svanbäck & Eklöv 2003, 2006), although some contradictory results have been reported (Kekäläinen et al. 2010). In the pelagic environment a streamlined body ought to be more beneficial for preying on zooplankton, while in the littoral environment a deeper body would provide higher manoeuvrability for benthic foraging in a structurally complex habitat (Skulason & Smith 1995; Svanbäck & Eklöv 2003).

Although direct comparisons have not been reported, it seems that in the brackish Baltic Sea, the ontogenetic diet shift from zooplankton to invertebrates/fish occurs earlier and cannibalism is less common than in lake habitats (Lappalainen et al. 2001; Sandstöm & Karås 2002; Svanbäck & Eklöv 2003, 2006). Individual diet specialisation in perch has been documented in perch based on stomach contents (Svanbäck et al. 2015), stable isotopes (Quevedo et al. 2009) and gut bacteria (Bolnick et al.

2014). Currently it is not clear how diet, competition, predation, habitat, inherited features and morphology interact and lead to formation of phenotypically diverse sub-populations in perch (Horppila et al. 1999; Svanbäck et al. 2008; Bergek & Björklund 2009; Kekäläinen et al. 2010).

1.3 TROPHIC INTERACTIONS AND AQUATIC FOOD WEBS

Within an ecosystem, the trophic interactions of the species compose a food web, “a map that describes which kinds of organisms in a community eat which other kinds” (Pimm et al. 1991). The trophic level expresses the position of a species in a food web beginning on the primary producers on trophic level 1 (Pimm et al. 1991). The ecosystem is regulated from within by bottom-up and top-down processes (Hunter & Price 1992; Horppila et al. 1998; Möllmann & Diekman 2012) comprised of multi-level trophic interactions. Bottom-up regulation implies that the system is built on and supported by the primary production, and changes in primary production, bottom-up forcing, are reflected to the whole system (Chassot et al. 2007; Viaroli et al. 2008; Burghart et al. 2013). Top-down regulation implies that abundance and biomass of a system are controlled by consumers, and changes in consumer abundances may cause cascading effects, trophic cascades, in the whole system (Casini et al. 2008; Eriksson et al. 2009). The relative importance of the bottom-up and top-down processes in ecosystem regulation has been debated extensively (Hunter & Price 1992; Horppila et al. 1998; Möllmann & Diekmann 2012).

Determining the diets and trophic levels of single species and the construction of food webs based on those largely relies on the stomach content analysis (Ahlbeck et al. 2010; Baker et al. 2014) and stable isotope analysis (Peterson & Fry 1987; Vander Zanden & Rasmussen 1999; Post 2002). Isotopes are naturally occurring variants of the same element with different number of neutrons and therefore different atom masses. Because of metabolic processes, the heavier isotopes enrich in the food chains in relation to the lighter isotopes and therefore the ratio between the heavier and the lighter isotopes in an organism reflects its trophic position (Peterson & Fry 1987).

Using the isotopes of nitrogen (heavier $^{15}\mathrm{N}$ and lighter $^{14}\mathrm{N}$) and carbon (heavier $^{13}\mathrm{C}$ and lighter $^{12}\mathrm{C}$) is well applicable to food web studies (Vander Zanden & Rasmussen 1999; Post 2002; Nordström et al. 2009). The δ-value describes the isotope ratio in the sample related to an international standard ($\delta = \mathrm{R}_{\mathrm{sample}} / (\mathrm{R}_{\mathrm{standard}} - 1) \times 10^3$, where R = heavier isotope : lighter isotope, Peterson & Fry 1987). The $\delta^{15}N$ enriches by 3–5‰ per trophic level, and is often used to estimate the trophic level of an organism. The $\delta^{13}C$ enriches 0–1‰ per trophic level, and it is often used to identify food sources (Peterson & Fry 1987; Post 2002). The isotope signals in the primary producers, the baseline δ-values, and the enrichment per trophic level vary spatially, and therefore the δ-values cannot be directly compared among different sites (Vander Zanden & Rasmussen 1999; Post 2002). In terms of $\delta^{15}N$, the problem can be overcome by calculating the trophic level with the $\delta^{15}N$ of a local organism of a known trophic level (baseline $\delta^{15}N$), and the local enrichment rate of $\delta^{15}N$ (*Trophic level* = (trophic level of baseline organism + $\delta^{15}N_{sample}$ – baseline $\delta^{15}N$) / enrichment of $\delta^{15}N$, Post 2002).

1.4 FISHERIES AND EUTROPHICATION THREATEN THE COASTAL FISH STOCKS

The anthropogenic effects, the (negative) effects of human activity, on coastal sea areas are evident worldwide (Airoldi & Beck 2007; HELCOM 2013; Newton et al. 2014). This thesis mainly addresses the effects of eutrophication and fisheries on coastal fish communities.

Due to blooms of cyanobacteria, eutrophication is probably the most commonly known environmental problem in the Baltic Sea today (Lundberg et al. 2005; Andersen et al. 2011; HELCOM 2013). Eutrophication, the increase of primary production by excess nutrient inputs (Nixon 1995), is characterised by high levels of nitrogen and phosphorus, high chlorophyll a concentration, high turbidity and low Secchi depth (Nixon 1995; Lundberg et al. 2005; Andersen et al. 2011; Carstensen et al. 2014). The increased primary production may benefit especially the lower order consumer fish and increase the total fish abundance (Bonsdorff et al. 1997; Ådjers et al. 2006; Chassot et al. 2007; Lefébure et al. 2013). Eutrophication may lead to oxygen depletion, hypoxia, in bottom waters (Lundberg et al. 2005; Carstensen et al. 2014) which adversely affects the benthic fauna (HELCOM 2013; Carstensen et al. 2014) and demersal fish (Eby et al. 2005). The deteriorated light conditions through turbidity affect the macrophyte- and zooplankton communities (Rosqvist et al. 2010; Scheinin & Mattila 2010; Burghart et al. 2013; Scheinin et al. 2013) changing the environment for fish (Sandström & Karås 2002; Snickars et al. 2009).

Fishing directly affects abundances of the target fish species (Mace 2001; Law 2002; Eero 2004; Birkeland & Dayton 2005) and indirectly the whole ecosystem (Casini et al. 2008; Eriksson et al. 2009; Möllmann & Diekmann 2012). Many commercially targeted fish species are large-bodied predators (FGFRI 2006; SwAM 2012; ICES 2014), and larger individuals are often more desired as catch (Law 2002; Birkeland & Dayton 2005; Pauly & Palomares 2005). Excessive (size-selective) fishing pressure induces changes in the size distribution (Bianchi et al. 2000; Dulvy et al. 2004), growth and maturation (Law 2002) of the target species, and may lead to recruitment overfishing where the harvesting rate exceeds the recruitment rate (Mace 2001; Eero 2004; Shin et al. 2005). Perhaps the most infamous example is the collapse of the North Atlantic cod stock (Mace 2001). Although excessive fishing is generally acknowledged harmful, the fishing quotas are politically sensitive and political and socio-economic interests often make implementation on fishing restrictions complicated (Mace 2001; Lappalainen 2002; Eero 2004; Heikinheimo et al. 2006).

Reduction of certain species and/or size classes by fisheries changes the size spectrum, dominance relationships and trophic structure of the fish community (Bianchi et al. 2000; Pauly & Palomares 2005; Olsson et al. 2012), which remains unnoticed by the traditional single-species approach (Begg 1999; Mace 2001; Möllmann et al. 2014). A decline in the large predators can relax the top-down regulation and induce a trophic cascade, where the relaxed predation allows an increase in lower-level consumer fish, which in turn increases predation on zooplankton and allows an increase in phytoplankton (Eriksson et al. 2009; Möllmann et al. 2015). The increase in phytoplankton increases turbidity which affects macrophytes and changes the visual environment of fish. Previous studies indicate that such trophic cascades already have taken place in the Baltic Sea and other marine systems (Casini et al. 2008; Eriksson et al. 2009; Baden et al. 2012; Möllmann et al. 2015).

As described above, the observed ecosystem-level effects of bottom-up forcing by eutrophication (Chassot et al. 2007; Viaroli et al. 2008; Rosqvist et al. 2010; Burghart et al. 2013; Scheinin et al. 2013) and the top-down induced trophic cascade (Casini et al. 2008; Eriksson et al. 2009; Baden et al. 2012) can be similar in many aspects (Hunter & Price 1992; Horppila et al. 1999; Breitburg et al. 2009; Möllmann et al. 2015), and further shaped by the local conditions (Olsson et al. 2012). Disturbance from eutrophication and/or fisheries and/or other stressors may lead to a regime shift where the whole aquatic system abruptly shifts from a state with clear-water, macrophyte and predatory fish-dominance to a state dominated by turbid water, phytoplankton and plankton feeding fish (Scheffer & Carpenter 2003; Rosqvist et al. 2010; Möllmann et al. 2015). In empirical research it may be impossible to distinguish between causes of such a shift, especially as the same system is often subjected to several stressors and their effects intermix (Scheffer & Carpenter 2003; Viaroli et al. 2008; Breitburg et al. 2009; Lefébure et al. 2013; Möllmann et al. 2015). After a lengthy scientific debate (Hunter & Price 1993; Sheffer & Carpenter 2003), a consensus on multiple stressors causing large-scale ecosystem effects has begun to emerge in the literature (Breitburg et al. 2009; Olsson et al. 2012; Möllmann et al. 2014, 2015). Recent studies report several approaches to multi-species community/system level analyses (Casini et al. 2008; Eriksson et al. 2009; Rosqvist et al. 2010; Olsson et al. 2012) and attempts to applications in ecosystem-based management (Mace 2001; Pikitch 2004; Möllmann et al. 2014).

2 AIMS OF THE THESIS

The overall aim of this thesis was to clarify patterns of seasonal and spatial variation and development over time in coastal fish assemblages in the shallow coastal areas in the archipelago region of the northern Baltic Sea. The main research questions assessed in the studies included in this thesis were:

- Which fish species are present and how abundant are they (papers I, III & IV)?

- How does the presence and distribution of species change among depth zones (paper I), seasonally (paper I) and over longer time periods (papers III & IV)?

- Can the fish species abundances (papers I, III & IV) or intraspecific variation (papers I, II) be linked to habitat characteristics (papers I & II) or anthropogenic stressors (papers I, III & IV)?

- Can the diet, morphology and stable isotope signals in perch be linked to each other and/or to the habitat characteristics (paper II)?

3 MATERIALS AND METHODS

The study was conducted in three coastal basins, namely Lumparn, Ivarskärsfjärden and Galtfjärden, in the northern Baltic Sea (Fig. 1). The material originates from two field projects, one conducted in Lumparn in 2008–2010 (papers I & II) and the other in Lumparn, Ivarskärsfjärden and Galtfjärden (papers III & IV) in 1995–2009. Methods used in this study are summarised in Table 1.

3.1 STUDY AREAS

The study areas Lumparn (60°07′N 20°07′E, papers I, II, III & IV) and Ivarskärsfjärden (60°16′N 19°48′E, papers III & IV) in the Åland Islands, and Galtfjärden (60°10′N 18°34′E, papers III & IV) on the Swedish east coast are brackish coastal basins located in the inner archipelago zone of the archipelago in the northern Baltic Proper (Fig. 1).

The archipelago between Finland and Sweden in the northern Baltic Sea is one of the largest archipelago areas in the world with tens of thousands of islands and skerries. The coastlines of the region are constantly reshaped by the post-glacial land uplift of 4–5 mm/year (Vestøl 2006). Salinity is 3–7, and the water temperature ranges from near-zero and ice cover in wintertime to up to 25°C in late summer (Rosqvist et al. 2010). The islands and shallow water create a mosaic of littoral habitats with rich biota of macrovegetation (Rosqvist et al. 2010; Rinne et al. 2011),

Table 1. Scope and scale of the original papers I–IV.

	Paper I	**Paper II**	**Paper III**	**Paper IV**
Time range	3 years Early summer and late summer	3 years Late summer	10 years Autumn	15 years Autumn
Ecological scale	Assemblage – system n_{fish} = 27 467	Individual – population n_{fish} = 2 299	Assemblage n_{fish} = 37 108	Population n_{fish} = 8 124
Geographical scale	Local 0.5–10 km 1 area 7 study sites	Local 4 km 1 area 2 study sites	Regional 30–100 km 3 areas 18 study sites	Regional 30–100 km 3 areas 18 study sites
Scope	Fish assemblage; spatial and seasonal patterns	Perch; intrapopulation and individual variation	Fish assemblage; long-term development	Pikeperch; long-term development
Data gathering	Gillnet fishing[1]. Water sampling. Zooplankton sampling. Zoobenthos sampling. Macrophyte and substrate survey	Gillnet fishing[1]. Stomach content analysis. Stable isotope analysis	Gillnet fishing[1]. Water sampling. Commercial fishing catches. Air temperature. North Atlantic Oscillation.	Gillnet fishing[1]. Age reading. Water sampling. Bird counts. Commercial fishing catches. Air temperature.
Variables of interest	Fish abundance and biomass. Water measurements. Coverage of substrates and macrophytes. Zooplankton and zoobenthos abundance.	Perch length, weight and body depth. Perch stomach contents and main food item. Perch stable isotope ratio of carbon and nitrogen.	Fish abundance, biomass, mean length, mean trophic level, diversity and number of species. Water measurements. Fishing pressure.	Pikeperch abundance, length, age, year-class strength and mortality. Water measurements. Fishing pressure. Great cormorant abundance.

[1] All the estimates on fish abundance are based on gillnet catches. The gillnet is a highly selective gear; the catchability is species-specific and dependent on the mesh size and the soak time (Appelberg et al. 1995; Olin et al. 2009). Thus the gillnet catch should never be regarded as a mirror image of the fish community, but a subsample of the fish assemblage recruited to the gear. The whole fish community cannot be sampled representatively with any single method, and therefore several sampling methods must be combined in order to accurately describe the whole community.

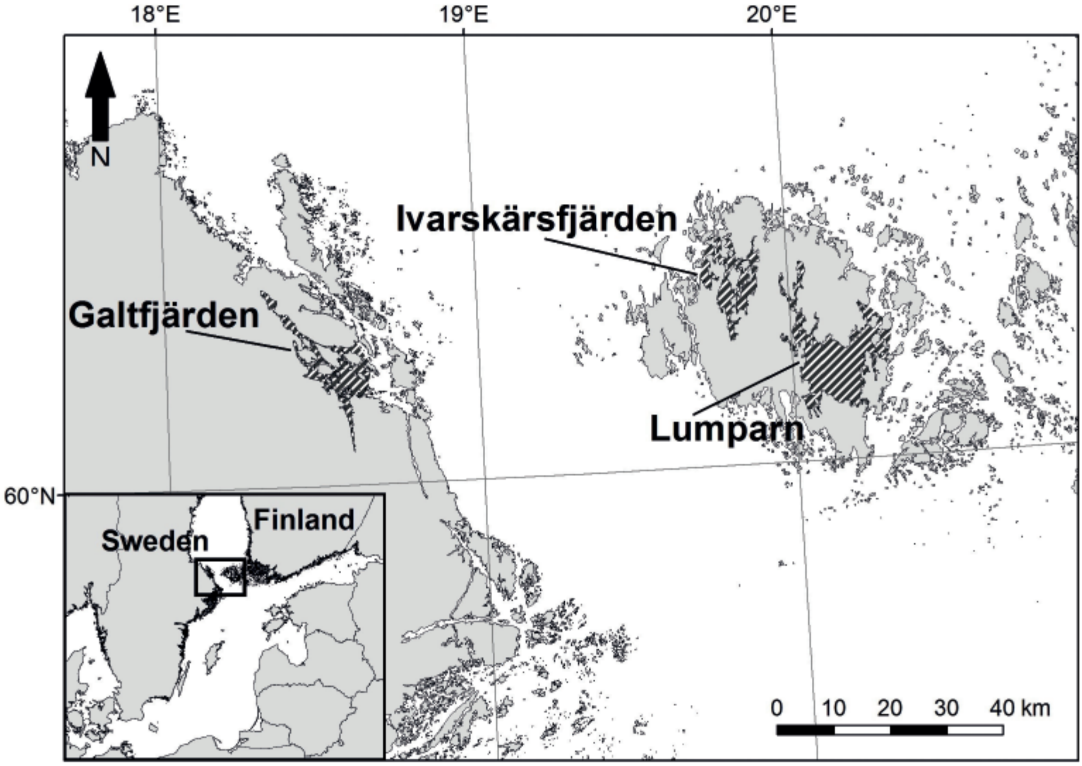

Figure 1. Study areas. The study areas Lumparn and Ivarskärsfjärden in the Åland Islands, and Galtfjärden on the Swedish east coast in the northern Baltic Proper. Map by Ulf Bergström.

plankton (Scheinin & Mattila 2010; Sheinin et al. 2013), macroinvertebrates (Perus & Bonsdorff 2004; Nordström et al. 2009; Törnroos & Bonsdorff 2012; Törnroos et al. 2013), birds (Heinänen 2010) and fish (Ådjers et al. 2006; Vahteri et al. 2009; Snickars et al. 2015).

3.2 STUDIES IN LUMPARN IN 2008–2010 (PAPERS I & II)

The Lumparn basin can be divided into three different habitat zones by depth –'shallow littoral zone' from the shoreline down to approximately 3 m depth, 'deep littoral zone' at 3–8 m depth and the 'bentho-pelagic zone' from approximately 8 m down to the maximum depth of 25 m. In the shallow littoral zone where the daylight reaches is characterised by structurally complex macrophyte vegetation. In the deep littoral zone, there is little or no daylight and macrophyte vegetation, while the bentho-pelagic zone consists of vegetation-free clay substrate and the water column above it. Three littoral locations (northern littoral, NL; western littoral, WL; and southern littoral, SL) were chosen to cover variation within both types of littoral habitats, and

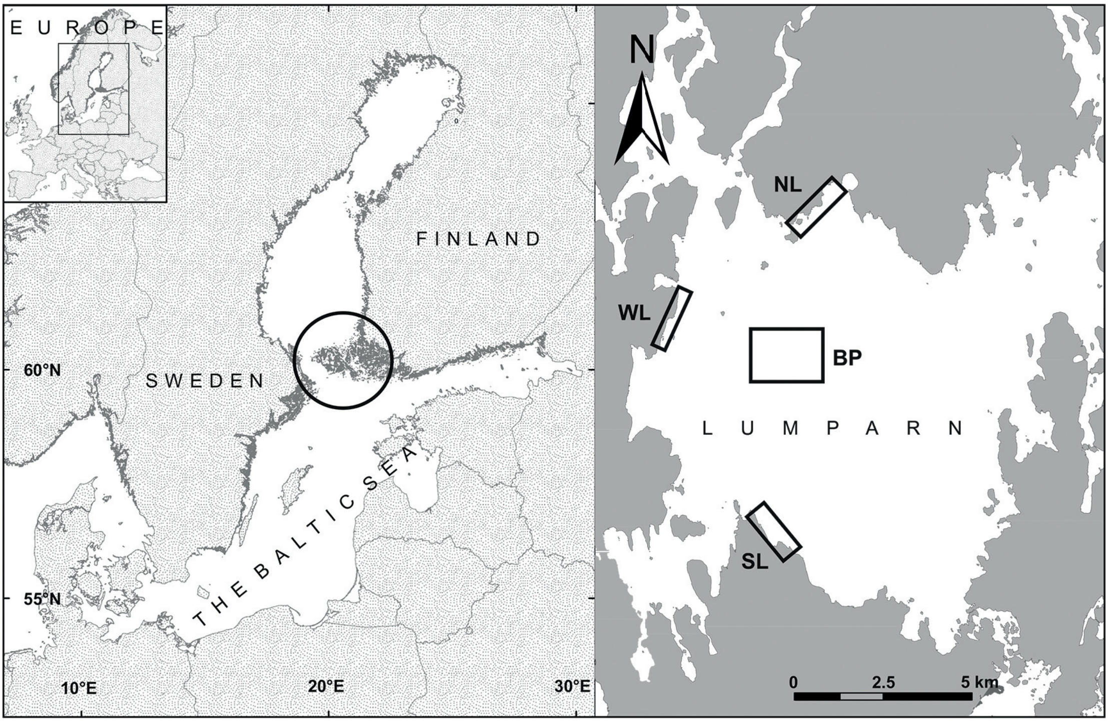

Figure 2. The studied locations in the Lumparn basin (Fig. 1). BP = bentho-pelagic, NL = northern littoral, WL = western littoral, and SL = southern littoral. Each littoral location was further divided into a 'shallow littoral' (s, depth 0–3 m) and a 'deep littoral' (d, depth 5–8 m) study site, resulting in seven study sites in total. Map by Henri Jokinen.

each of them was further divided into a 'shallow littoral' (s) and a 'deep littoral' (d) study site. The bentho-pelagic habitat was represented by a sampling area (BP) in the middle of the Lumparn basin (depth 17–22 m). A sampling point for water and plankton was located in the middle of each of the resulting seven study sites; NL/s, NL/d, WL/s, WL/d, SL/s, SL/d and BP (Fig. 2).

Fishing was conducted in early summer (May–June) and late summer (August–September) with Nordic multimesh gillnets placed overnight (c. 12 h). A Nordic multimesh gillnet is designed to catch the full length distribution of the fish population and is comprised of 12 panels with different mesh sizes (5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43 and 55 mm bar length; Appelberg et al. 1995). The placement and number of the gillnets used was related to the depth of the water column (total 240 Nordic gillnets in the littoral study sites and 210 in the bentho-pelagic study site). Each individual fish was identified for species, measured for *total length* to the nearest 1 mm, and weighed for *total weight* to the nearest 0.1 g.

3.2.1 SEASONAL AND SPATIAL VARIATION IN THE FISH COMMUNITY (PAPER I)

The whole fishing catch caught in 2008–2010 at the seven study sites (Fig. 2) was studied (n = 27 467). The proportion of adult fish ripe for spawning was noted. Catch-per-unit-effort as the average number of individuals per gillnet ($CPUE = n_{\text{fish}} / n_{\text{net nights}}$) was used as a measure of fish species abundances. For the Baltic herring *Clupea harengus var. membras*, separate *CPUE* values were calculated for small/juvenile (< 9 cm *total length*) and large/adult (≥ 9 cm *total length*) individuals.

Macrophyte species coverages and substrate type coverages were mapped in each shallow littoral study site as in Scheinin et al. (2013). The substrate in the deep littoral and BP study sites were studied with an Ekman grab sampler and macrophytes with a Luther rake. Zoobenthos samples were taken with an Ekman grab sampler and sieved through a 500 µm sieve. The fauna was identified to the lowest possible taxa, counted, and weighted wet to the nearest 0.01 g. Water sampling and zooplankton sampling were conducted monthly in each study site. For water, Secchi depth (m), chlorophyll a (µg/l) temperature (°C), salinity, pH, total nitrogen (µg/l), total phosphorus (µg/l), turbidity (NTU) and oxygen contents (%) were measured. For zooplankton, pooled samples from the whole water column were taken and filtered through a 50 µm plankton sieve. The zooplankton species were identified to the lowest possible taxa and counted. The abundances were converted to biomasses (µg/l, wwt) as in Scheinin and Mattila (2010).

Environmental variables used in the multivariate analyses (section 3.2) were *exposure* (Bekkby et al. 2008), *mean coverage* (%) of the substrate types, *mean coverage* (%) of the dominant macrophyte groups of taxa, *mean biomass* (g/m2) of the dominant zoobenthic groups of taxa, *seasonal mean biomass* (µg/l) of the dominant zooplankton groups of taxa, and *seasonal means* of the water measurements.

3.2.2 PERCH DIET, STABLE ISOTOPES AND MORPHOLOGY (PAPER II)

The material consisted of the perch (n = 2 299) caught in the gillnet fishing in the NL/shallow, NL/deep and BP study sites, and beach seining in the NL/shallow study site in August–September in Lumparn in 2008–2010 (Fig. 2). In addition to *total length* (mm) and *total weight* (g), each individual perch was measured for *body depth* to the nearest 1 mm and determined for sex. The *body condition* (Fulton's condition factor $K = total\ weigth\ /\ total\ length^3$, Ricker 1975) and the *relative body depth* ($D_{BR} = body\ depth\ /\ total\ length$, paper II, Cederberg 2011) were calculated. Stomachs were removed and a stomach content analysis was performed, the main food item identified, and the *mean proportion* (wet weight) of each group of stomach contents for each 2.5 cm length category of perch calculated as described in paper II. For the baseline $\delta^{15}N$, Baltic clams

Macoma balthica were collected from the study sites. Muscle samples of the perch and the Baltic clams were taken, prepared, and sent for analysis of $\delta^{15}N$ and $\delta^{13}C$ according to the instructions of the Stable Isotope Facility, University of California (http://stableisotopefacility.ucdavis.edu). The *individual trophic level* of each perch was calculated with the baseline $\delta^{15}N$ and the local enrichment of the $\delta^{15}N$ according to Post (2002).

The Baltic clam displays seasonal variation in δ-values suggesting it may switch between the suspension- and deposit-feeding modes based on resource availability (Nordström et al. 2009). The possible bias to the baseline was minimized by collecting all the Baltic clams at the same time. The choice of the tissue to be analysed and pre-treatment of the samples may result in different δ-values in the stable isotope analysis, but according to Carabel et al. (2006) fish muscle tissue should not need pre-treatment and thus the stable isotope samples were not pre-treated in this study.

3.3 STUDIES IN LUMPARN, IVARSKÄRSFJÄRDEN AND GALTFJÄRDEN IN 1995–2009 (PAPERS III & IV)

The fish sampling in Lumparn, Ivarskärsfjärden and Galtfjärden in 1995–2009 was conducted annually in autumn on six sampling points (Fig. 1) with series of bottom-set gillnets placed overnight (c. 14 h). The gillnet series used in 1995–1998 consisted of four gillnets with mesh sizes of 25, 30, 38 and 50 mm bar length, and in 1999 a gillnet with the mesh size of 45 mm bar length was added to the series. The annual effort was 90 net nights in Lumparn and Ivarskärsfjärden and 135–180 net nights in Galtfjärden. Each individual fish was identified for species and measured for *total length* (mm). Water sampling for salinity, pH, temperature (C°), total phosphorus (µg/l), total nitrogen (µg/l), chlorophyll a (µg/l) and Secchi depth (m) was conducted annually in August in each study area. Data on the commercial fisheries catches were obtained from the official national statistics, and data on air temperatures from the national meteorological institutes.

3.3.1 LONG-TERM TRENDS IN THE FISH ASSEMBLAGES (PAPER III)

The total fish catch (n = 37 108) from 1999–2010 was studied. Total *number of species, mean total length* (± SD), *mean species trophic level* (± SD, species trophic level according to Froese & Pauly 2011) and *Shannon index* (H, Shannon & Claude 1948) were calculated for each year and study area. Annual values of *CPUE* were calculated separately for each species and study area. Annual commercial catches (kg/ha) of each species or group reported were calculated for each study area. Annual values for station-based North Atlantic Oscillation were derived from the National Center for Atmospheric Research (Hurrell et al. 2014).

3.3.2 LONG-TERM TRENDS IN THE PIKEPERCH STOCKS (PAPER IV)

The material consisted of all the pikeperch (n = 8 124) caught in 1995–2009. Age (years) of each individual pikeperch was determined. Annual CPUE values were calculated for each gillnet monitoring point for 'all pikeperch', 'small pikeperch' (< 40 cm in *total length*) and 'large pikeperch' (≥ 40 cm in *total length*). The 'large pikeperch' exceed the minimum landing size of all study areas and ought to represent both the spawning stock and the part of the stock directly affected by fisheries. Annual commercial pikeperch catch (kg/ha) was calculated. Daily mean water temperature was estimated based on daily mean air temperature and the available water temperature data. The *year-class strength* was approximated based on the CPUE values of three-year-old pikeperch, and the *year-class strength* was related to the water temperature. Great cormorants *Phalacrocorax carbo* were counted annually in Galtfjärden, and the annual pikeperch consumption by great cormorants was estimated as in Östman et al. (2013). The pikeperch instantaneous mortality (Z) and annual mortality (A) were estimated with a linear regression model according to Dunn et al. (2002).

3.4 STATISTICAL ANALYSES

The multivariate non-parametric analyses in papers I and III were performed with the PRIMER 6 with PERMANOVA+ program package (www.primer-e.com). The parametric and non-parametric univariate analyses in papers II, III and IV were performed with the GraphPad Prism version 5.04 for Windows (www.graphpad.com), PASW statistics version 18.0 and the IBM SPSS statistics version 21 (www-01.ibm.com/software/analytics/spss).

In general, parametrical statistical tests were used if the data - either original or transformed values - met the requirements of normality by Kolmogorov-Smirnov test ($p > 0.05$) and homogeneity by Levenes test ($p > 0.05$). In case the data did not meet the requirements of normality and homogeneity, non-parametric analyses were used instead. One-way approaches were chosen for the univariate tests, as the data, even after transformations, was not suitable for two-way parametrical tests. In all analysis of variance, ANOVA, Bonferroni post hoc test was used. In the Kruskall-Wallis tests either the Dunn's post hoc test was used, or pairwise comparisons were performed with the Mann–Whitney U test and the significance levels were Bonferroni-corrected (5 % significance level = $0.05/n_{\text{comparisons}}$). In case the variables were continuous and normally distributed, the parametric Pearson's correlation analysis was used. Otherwise, the non-parametric Spearman's rank correlation analysis was used.

In paper I, a Principal Component Ordination PCO (Clarke 1993) was constructed for the normalised environmental variables in order to detect patterns in the environmental variables in the Lumparn basin. A Bray-Curtis dissimilarity matrix was constructed with the square root transformed fish CPUE data. To visualise seasonal and spatial patterns in the fish assemblages, the matrix was subjected to a non-metric Multidimensional Scaling nMDS (Clarke 1993). Differences among the study sites and depth zones were analysed with a Permutational Multivariate Analysis of Variance, PERMANOVA (a nonparametric equivalent of multivariate analysis of variance, Anderson 2001). The environmental variables which best explained the variation in the fish species abundances were identified with the non-parametric multivariate regression method Distance-based Linear Modelling, DistLM (Anderson et al. 2008).

In paper II, the *relative body depth, body condition* and $\delta^{13}C$ between the littoral and bentho-pelagic study sites were compared with the analysis of covariance, ANCOVA, with total length as covariate. The stomach contents between the study sites were compared with Mann–Whitney U-test. Relationships among $\delta^{15}N$, $\delta^{13}C$, *relative body depth, body condition, total length* and *mean proportions* of stomach contents were analysed with the Pearson and Spearman correlation analyses. The differences in $\delta^{15}N$, $\delta^{13}C$, *individual trophic level, relative body depth* and *body condition* among perch with different main food source were tested with ANOVA.

In paper III, trend over time was identified with Linear regression analysis or Spearman correlation analysis for *mean total length, mean species trophic level, number of species, Shannon index, CPUE* and environmental variables. For the multivariate analyses of the whole fish assemblage, a Bray-Curtis dissimilarity matrix was constructed with the square-root transformed fish species (*CPUE*) data. To analyse patterns in the fish assemblages, the matrix was subjected to nMDS (Clarke 1993). Differences among the study areas were analysed with PERMANOVA (Anderson et al. 2008). The environmental variables which best explained the variation in the fish species abundances were identified with DistLM (Anderson et al. 2008).

In paper IV, differences among the study sites in hydrography and pikeperch abundance were analysed with either ANOVA or Kruskall–Wallis test. Trends in the abovementioned parameters within study sites over time were analysed with the Spearman correlation analysis. Relationship between log-transformed *year-class strength* and water temperature was studied with LR analysis.

4 RESULTS AND DISCUSSION

4.1 DESCRIPTION OF THE FISH HABITATS IN LUMPARN

Within the Lumparn basin (paper I), the shallow littoral habitat type was characterised by high variety of substrate types, mainly gravel, boulders, silt and sand. The dense macrophyte vegetation consisted mainly of common reed *Phragmites australis*, pondweeds *Potamogeton* spp. and *Stuckenia pectinata* and bladderwrack *Fucus vesiculosus*. All macrophyte species encountered were common and the species composition typical for the archipelago region (Munsterhjelm 2005; Rinne et al. 2011). The southern littoral location was sandier and the macrophyte vegetation there was sparser than in the northern and western littoral locations. In the deep littoral habitat type, the substrate consisted mainly of clay and no macrophyte vegetation was encountered, although according to Scheinin and Söderström (2004) the macrophyte vegetation in the basin reaches to the depth of 8 m. In the bentho-pelagic habitat type the substrate consisted invariably of clay and there was no vegetation.

The zoobenthic community in the Lumparn basin (paper I) was dominated by mudsnails *Hydrobia* spp. in numbers, and the Baltic clam in biomass. Also for zoobenthos, the species composition was similar as in previous descriptions from the nearby areas (Perus & Bonsdorff 2004; Törnroos et al. 2013). Due to high abundances of Baltic clam, the zoobenthos biomass was highest in the bentho-pelagic area and western deep littoral study site. Due to high abundances of mudsnails, the zoobenthos abundance was highest in the western and southern deep littoral study sites (paper I).

Water temperature, total nitrogen content, total phosphorus content and total zooplankton biomass peaked in late summer. The surface water quality and zooplankton community were very similar in all study sites in the Lumparn basin (paper I). Also for the zooplankton, the species encountered were common and the community structure and seasonal variation similar as in previous descriptions from the archipelago region (Scheinin & Mattila 2010; Scheinin et al. 2013). Near bottom in the bentho-pelagic area the water was colder, total phosphorus higher and oxygen content lower than in the other study sites. However, the water mass in the Lumparn basin seems to have been effectively mixed as neither temperature stratification nor hypoxia was observed during this study. Hypoxia has been occasionally observed in late summer in Lumparn (unpublished, Environmental Laboratory of Åland).

4.2 SPATIAL AND SEASONAL VARIATION IN FISH ASSEMBLAGE IN THE LUMPARN BASIN

The Lumparn fish assemblage was dominated by Baltic herring, perch, roach *Rutilus rutilus*, bleak Alburnus alburnus, three-spined stickleback *Gasterosteus aculeatus* and ruffe *Gymnocephalus cernua*, and in total 26 species were encountered (paper I). In early summer, perch was aggregated to the shallow littoral zone, ruffe into the deep littoral zone, three-spined and ten-spined stickleback *Pungitius pungitius* to the vegetation-rich western and northern shore, and greater sandeel *Hyperoplus lanceolatus* and lesser sandeel *Ammodytes tobianus* to the sandy southern shore. In late summer, perch and ruffe declined in abundance and both species were more evenly distributed among the depth zones, while the stickleback and sandeel species were nearly absent. Small Baltic herring was encountered in high abundances in all

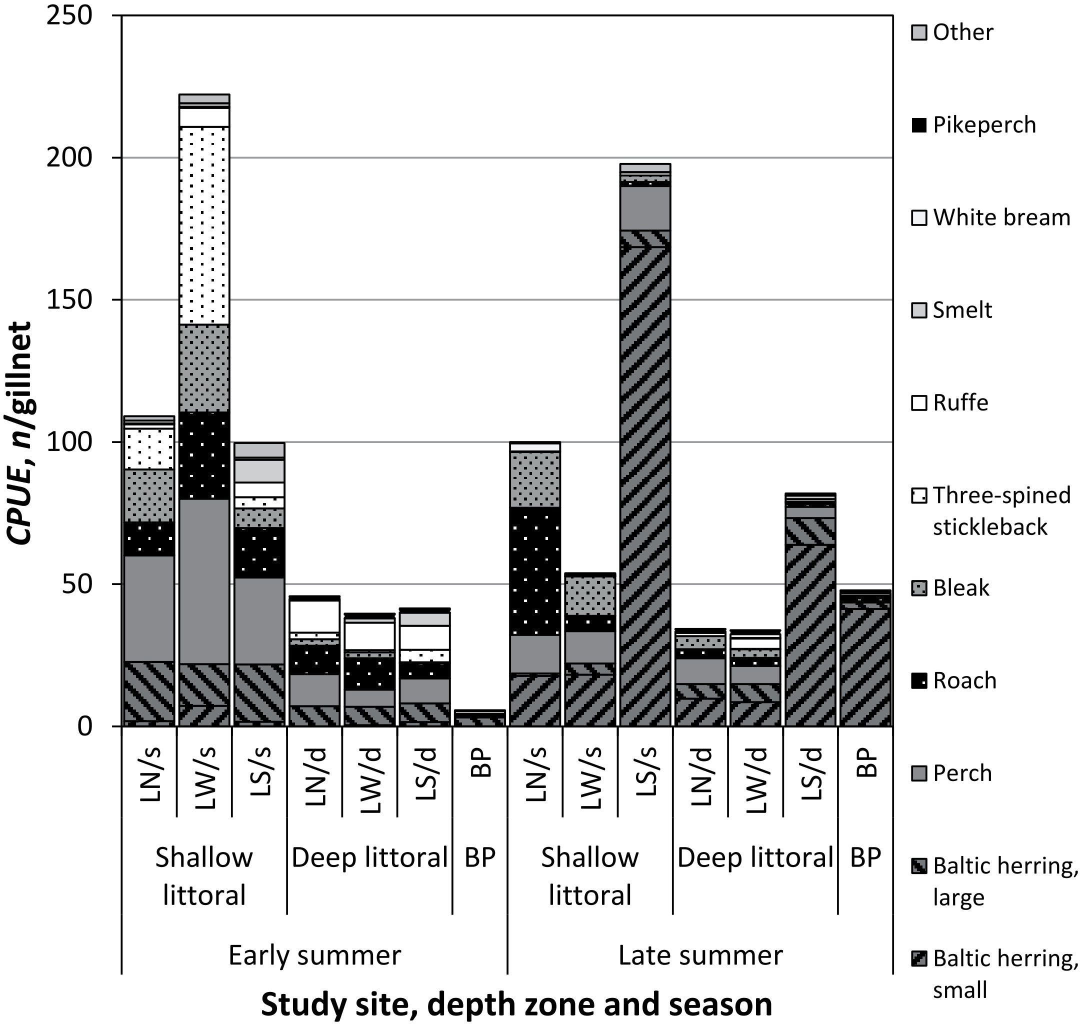

Figure 3. The species abundances ($CPUE = n_{fish} / n_{nets}$) in the seven study sites in Lumparn basin in early summer (May–June) and late summer.

study sites in late summer, but it especially seemed to favour the sandy southern shore and the surface waters of the bentho-pelagic location (Fig. 3). The study site-season interaction was statistically significant in PERMANOVA ($p < 0.001$, paper I). The above-described site and depth-specific seasonal patterns, and the higher aggregation to specific depth zones in early summer were also illustrated in nMDS (paper I). Depth, season and the 3D macrophyte coverage were identified as the most significant environmental variables affecting the fish species abundances in the DistLM procedure (paper I). The results indicate that depth was the most important spatial character, and both the fish assemblage and the biotic environmental characteristics were further affected by local conditions and seasonal variation in the abiotic factors.

The fish in the Lumparn basin (paper I) seemed to display both spawning migration (Deegan 1993; Able 2005; Elliot et al. 2007) and ontogenetic habitat shifts (MacPherson 1998). The ripe adult fish were aggregated to certain depth-zones or specific sites in early summer, presumably for spawning as most fish species in the region – for instance Baltic herring (Kääriä et al. 1997), three-spined stickleback (Snickars et al. 2009; Björkblom et al. 2010), perch (Byström et al. 2003; Snickars et al. 2010; Sundblad & Bergström 2014), smelt *Osmerus eperlanus* (Shpilev et al. 2005), roach (Sundblad & Bergström 2014) and lesser sandeel (Bonislawska et al. 2014) – spawn in the littoral zone in springtime, and juveniles were encountered in late summer. In addition to the gillnet catches, in August 2008–2010, young-of-the-year individuals of three-spined stickleback, ten-spined stickleback, common goby *Pomatoschistus microps* and sand goby *Pomatoschistus minutus*, were numerous in the shallow littoral study sites (unpublished, Noora Mustamäki; Jokinen 2010) and in perch stomach contents (paper II; Cederberg 2011). It seems apparent that the Lumparn basin serves as a nursery area for the above-mentioned species and Baltic herring (Kääriä et al. 1997). In late summer, the adult fish were more evenly dispersed throughout the basin; ten-spined stickleback, three-spined stickleback, greater sandeel and lesser sandeel practically disappeared, and the abundances of perch and adult Baltic herring were generally lower in the late summer, suggesting post-spawning migration out of the Lumparn basin (Fig. 3). Baltic herring was the only species in which individuals ripe for spawning were encountered in the late summer, and in which individuals that were too small to be juveniles of the previous spring were encountered in early summer catches. This suggests the existence of autumn spawning Baltic herring (McQuinn 1997) in the area, but further studies on age distribution and spawning of Baltic herring would be needed to confirm this.

It appears that perch spawned and resided as juveniles in the shallow littoral zone (papers I & II), as previously described by Snickars et al. (2004). Possibly the juveniles and small/young adults generally preferred the littoral food sources (paper II) and/or the shelter provided by the habitat structure in the shallow littoral zone

(Brabrand & Faafeng 1993; Snickars et al. 2004). The possible habitat shifts in perch larvae previously observed in lakes (Wang & Eckmann 1994; Byström et al. 2003), which should also be clarified for Baltic Sea perch, were not observable with the sampling methods used in this study. When perch reached the size of 12–15 cm in *total length*, it seems that some of them displayed an ontogenetic habitat shift and migrated to deeper water, while others stayed in the littoral zone. It cannot be concluded from this material whether the bentho-pelagic perch performed diel feeding migrations to the deeper areas (Hrabik et al. 2006) or if they resided there more permanently, but the observed statistically significant differences in morphology and stable isotope composition between the littoral and the bentho-pelagic individuals suggest sedentary behaviour (paper II). However, the observations of littoral invertebrates in the stomach contents of some bentho-pelagic perch, and benthic invertebrates in the stomach contents of some littoral perch indicate that at least some adult individuals did forage in both habitats, as previously reported by (Svanbäck et al. 2015) for lake habitats.

In addition to perch, also roach and white bream *Blicca bjoerkna* displayed size-specific distributions with increasing adult fish *total length* towards deeper areas ($p < 0.05$, paper I). In fact, similar trend was observed for several species, but the differences were not statistically significant. As the size of the individual fish is an important factor determining its diet and trophic position (Werner & Gilliam 1984; Svanbäck et al. 2015), this intraspecific variation indicates that the fish assemblages can be structurally and functionally different among depth zones even with similar species abundances. Size distribution of the adult fish and differences in abundance may indicate habitat shifts, but the pattern may also be a result of differences in growth, competition, predation and survival in the different habitat types (Lappalainen et al. 2001; Snickars et al. 2002; Kekäläinen 2010; Hixon et al. 2012). For firm conclusions on mechanisms, the age and growth of the fish species in the different habitat types should be determined.

Paper I illustrates that within a relatively small (max distance 10 km) coastal area with no internal physical barriers, the structure of the fish assemblage can vary significantly over a distance of a few hundred meters corresponding to 5–20 meter variation in total depth, depending on the time of the season. The findings support earlier ones indicating high complexity in the small-scale distribution of coastal fish (Letourneur et al. 2001; Methven et al. 2001; Pihl and Wennhage 2002), and provide the first description of the seasonality of such patterns for a coastal Baltic Sea environment.

The results demonstrate that patterns observed in one depth zone or season cannot be directly extrapolated to larger areas, and that drawing meaningful conclusions on the small-scale distribution in the fish assemblage structure requires sufficient replication of sampling in space and time. It should be noted here that also the catchability of fish with gillnet, which is a passive gear, varies according to fish size and species (Appelberg et al. 1995; Olin et al. 2009) and may also change seasonally. Therefore it may be advisable to combine a gillnet fishing survey with active fishing gears suitable for the study site such as seining, trawling (Olin et al. 2009), detonations (Snickars et al. 2009) or echo-sounding (Axenrot & Hansson 2004). The whole range of habitats that each species uses throughout its lifecycle and seasonally should be clarified in order to plan effective management in the coastal marine environment (Able 2005; Elliot et al. 2007). Combining the effects of the multiple gradients affecting seasonally changing habitats for a better understanding of spatial distribution of fish is an important future prospective for studies on ecology and ecosystem-based management of shallow coastal areas.

Seasonality in the small-scale and depth-zone distribution of fish within the Lumparn basin and between the Lumparn basin and adjacent areas and the entire archipelago region is far from thoroughly investigated, and this study can serve as a starting point for future research in this field. As the baseline $\delta^{15}N$ values were found to be statistically significantly different between the littoral and the pelagic zones in the Lumparn basin (paper II), it may be possible to further analyse the possible habitat shifts in fish with a stable isotope analysis from fish otoliths. The isotope signal in the annual growth rings of the fish otoliths is similar to the isotopic composition of the water the fish has resided in, and can therefore be used to track fish movements (Hobson 1999).

4.3 RESOURCE POLYMORPHISM IN PERCH IN THE LUMPARN BASIN

Two thirds of the perch caught were female and no difference was observed in the sex distribution between the littoral and bentho-pelagic habitats (χ_{21} = 0.14, p = 0.71). The females grew faster (unpublished, Noora Mustamäki) than the males and therefore the largest individuals tended to be females. However, when the *body condition, relative body depth*, stable isotopes and stomach contents were analysed for difference between sexes with *total length* as covariate, no statistically significant differences were observed. It was concluded that even though the sex does affect the growth, the driving factor for these parameters was the body size of the fish and not the sex *per se*, and therefore the sexes were pooled for further analyses.

Juvenile perch was encountered only in the littoral areas, where it fed on zooplankton and shifted to a diet of invertebrates and fish at the length of 3–7 cm. The larger littoral perch fed on littoral invertebrates and fish, while the bentho-pelagic perch fed on benthic invertebrates and fish (Fig. 4). In both habitats, the isopod *Saduria entomon* comprised a considerable part of the invertebrate diet of large individuals (paper II). The littoral perch had significantly higher *body condition*, $\delta^{13}C$ and *individual trophic level*, but lower *relative body depth* and $\delta^{15}N$ than the bentho-pelagic perch (Table 2).

In the littoral study site, the diet of perch (paper II; Cederberg 2011) was rather

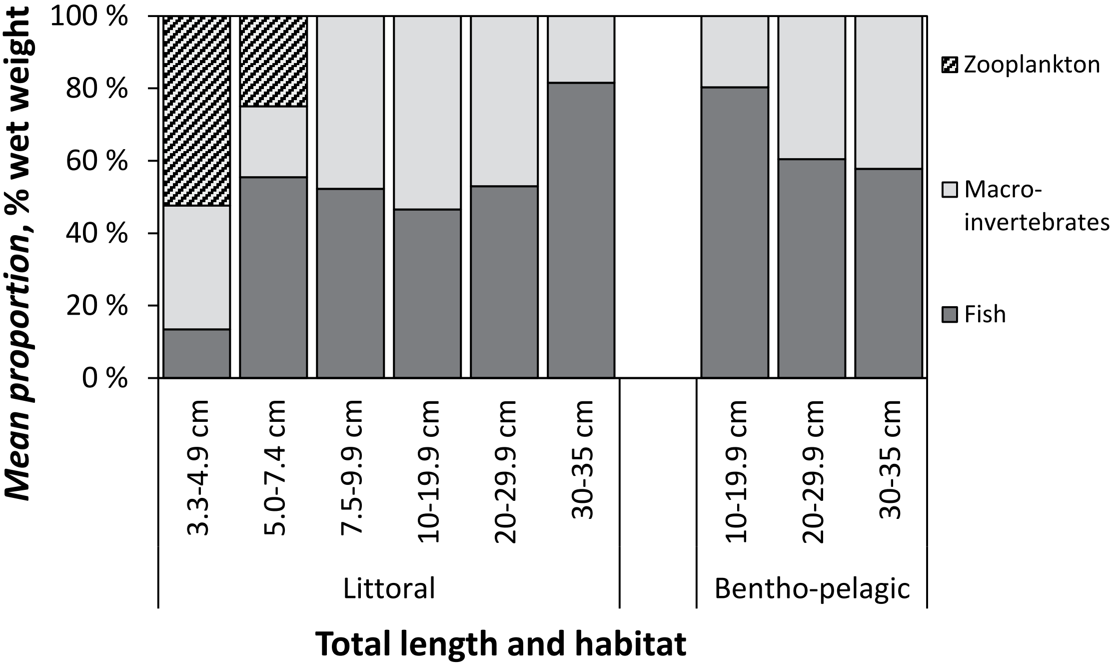

Figure 4. Diet of perch in the littoral and bentho-pelagic locations in the Lumparn basin. The littoral perch consumed mainly littoral macroinvertebrates and bento-pelagic perch benthic macroinvertebrates. Cannibalism was observed in less than 1 % of cases.

Table 2. Comparison of perch isotope ratios of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$), *individual trophic level* (trophic level based on individual $\delta^{15}N$ and baseline $\delta^{15}N$), r*elative body depth* (*body depth / total length*) and body condition (Fulton's condition factor K = *total weight / total length*^{3}) in the littoral and bentho-pelagic habitats in the Lumparn basin. *Relative body depth*, *body condition* and $\delta^{13}C$ were positively correlated with *total length*.

Habitat	**Littoral**	**Bentho-pelagic**
Depth	1–8 m	17–22 m
Baseline $\delta^{15}N$	Higher	Lower ***
Perch *relative body depth* [1]	Lower	Higher ***
Perch *body condition* [1]	Higher	Lower ***
Perch $\delta^{15}N$	Lower	Higher **
Perch $\delta^{13}C$	Higher	Lower ***
Perch *individual trophic level*	Higher	Lower ***

** = $p < 0.01$, *** = $p < 0.001$, see paper II for the statistical analyses.

[1] Fig. 2 in paper II.

similar to the diet of littoral perch in lakes (Mehner et al. 1996; Horppila et al. 1999; Svanbäck & Eklöv 2003, 2006; Estlander et al. 2010), although the juveniles displayed an ontogenetic shift from zooplankton diet to invertebrates and fish earlier than in lakes, and cannibalism was rare (4 cases in total). One reason for these discrepancies could be the high late-summer abundance of small-bodied young-of-the-year fish in the Lumparn basin that the juvenile perch could start feeding on during their first summer (Mehner et al. 1996). Although performed for different purpose, previous studies on perch diet in the northern Baltic Proper by Lappalainen et al. (2001) and Sandström and Karås (2002) are in line with these results. In the bentho-pelagic zone, however, the perch had deeper bodies than in the littoral zone and fed on benthic invertebrates and fish, which clearly differed from previous descriptions on the streamlined zooplanktivorous pelagic perch in lakes (Svanbäck & Eklöv 2003, 2006). In fact, rather than pelagic, the perch in the deeper areas in Lumparn could be characterised as benthic feeders also feeding on fish. In Lumparn, the Baltic herring – not encountered in lakes – was the dominant planktivore and the benthic fauna was abundant. Possibly it was more beneficial for the perch in the bentho-pelagic zone to feed on zoobenthos and abundant young-of-the-year fish, instead of competing on zooplankton with the Baltic herring. Based on previous studies, the presence of other species affects perch behaviour and morphology in lakes; predation risk affects habitat shifts in perch larvae (Byström et al. 2003), and competition and predation affect perch morphology (Kekäläinen et al. 2010). The effect of presence of other zooplanktivores on the zooplanktivory of perch could be further clarified.

The morphological differences between littoral and bentho-pelagic perch, although statistically significant, were small and not observable with a naked eye. Using several morphometric measurements, as in Svanbäck and Eklöv (2003, 2006) and Bergek and Björklund (2009), rather than only the *relative body depth* used in paper II, could possibly have revealed more patterns in the body shape of perch. Previously, Bergek and Björklund (2009) reported fine-scale differences in both genetics and morphology of perch in the Baltic Sea. Cederberg (2011) observed no difference in either perch diet or morphology among the northern, western and southern littoral locations in Lumparn, indicating that the variation within the littoral habitats of the Lumparn basin was small. Svanbäck and Eklöv (2003, 2006) and Svanbäck et al. (2015) have previously concluded that the perch body depth is connected to diet, habitat and inherited features, signifying resource polymorphism. Kekäläinen et al. (2010) did not observe any habitat-specific differences in the body depth of perch, but showed instead a connection to the abundances of other species suggesting that predation and/or competition may also affect the perch morphology. The choice of the feeding habitat within a water body could possibly be the result of diet specialisation (shaped by genotype, predation, competition and resource availability) and the morphology would develop thereafter. This would explain why the results of this study and previous studies conducted in brackish habitats (Lappalainen et al. 2001; Sandström & Karås 2002) are different from the results of lake studies (Svanbäck et al. 2015): the perch in brackish water occupies a different ecological niche than the perch in freshwater lakes, and the local conditions and interactions affect the diet and habitat choice which then shape the morphology accordingly. Taken together, the results indicate high plasticity and dietary and morphological adaptability in perch. It seems plausible to assume that this is one central reason why perch is such a common species in a wide range of freshwater and brackish habitats. Further studies should include comparisons of diet, stable isotopes and morphology of perch from different Baltic Sea coastal areas in order to clarify if the patterns observed in this study apply to the Baltic Sea perch more generally.

The stable isotope signals differed among perch with different main food item in the stomach contents, suggesting that the stomach contents at the moment the individual perch happened to get caught might not be a random event but represent a more consistent diet (Fig. 5). Developing a distinct stable isotope signal and body shape in combination with a certain diet suggests that perch has individual diet preferences that are consistent over longer periods of time (Vander Zanden & Rasmussen 1999; Post 2002; Araujo et al. 2011; Bolnick et

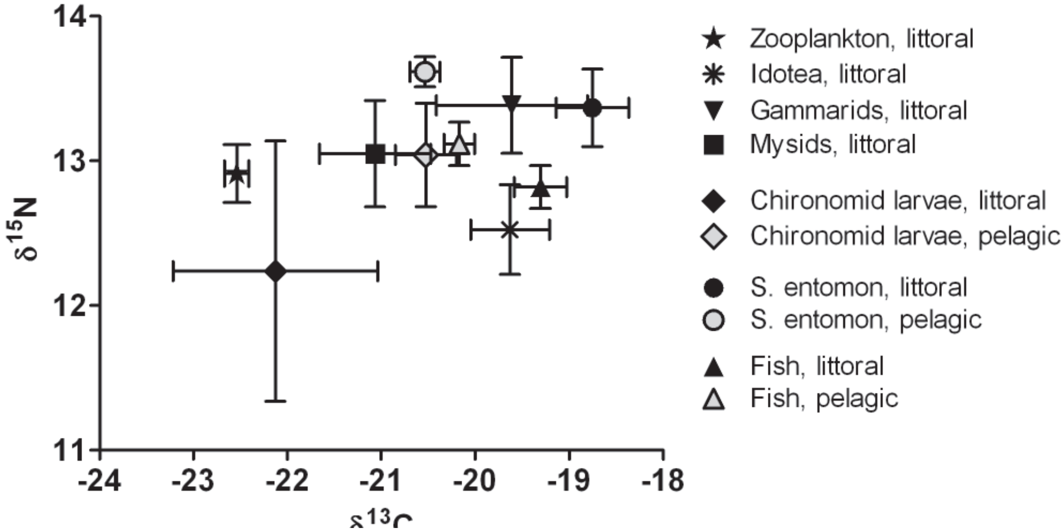

Figure 5. δ-values (mean ± SE) of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) in perch from the northern littoral location and bentho-pelagic location (Fig. 1) with different main food item in the stomach contents.

al. 2011). However, the small differences in $\delta^{15}N$ indicate that although preferring certain type of prey, the perch still fed on several trophic levels. Also, $\delta^{13}C$ was, but $\delta^{15}N$ was not correlated with the *total length* of the individual perch indicating that even though the diet changed with individual growth, the average trophic level of the diet did not change. This is consistent with the stomach content data showing that perch of all sizes fed on several trophic levels (paper II). Previously, Svanbäck et al. (2014) and Quevedo et al. (2009) reported individual diet choice in perch by estimating niche widths, but paper II is the first report in which the stable isotope signals were directly related to specific stomach contents. Individual diet choice in perch and how the seasonal variation in the diet (Cederberg 2011) is reflected in the isotope signals could be studied further with a more extensive isotope study in the Lumparn basin and also other Baltic Sea coastal areas for which this study can serve as a pilot.

To my knowledge, paper II is the first published study where the diet, stable isotopes and morphology of perch between littoral and pelagic habitats have been compared in a brackish water environment. The seasonal and spatial patterns in diet, stable isotopes, morphology and distribution of perch, and their connections to habitat characteristics, genotypic variation and interactions with other species in brackish habitats should be addressed in future studies.

4.4 LONG-TERM TRENDS IN THREE COASTAL FISH ASSEMBLAGES

The study areas Lumparn, Ivarskärsfjärden and Galtfjärden were highly eutrophic (Lundberg et al. 2005) and especially the pikeperch stocks were under considerable fishing pressure (paper IV). Due to the geographical location and topography, Galtfjärden had lower temperature and salinity than Lumparn and Ivarskärsfjärden (paper IV). Predation pressure by a great cormorant breeding colony and frequently observed grey seals *Halichoerus grypus* was highest in Galtfjärden (Table 3).

Over the study period, the fish assemblages of Lumparn, Ivarskärsfjärden and Galtfjärden shifted towards higher dominance of small-bodied lower order consumer fish (PERMANOVA; Study area: $p < 0.01$, Year: $p < 0.01$, Fig 6 ; Paper III). Especially the pikeperch stocks were found to be depleted (Table 3; paper IV). Also perch and smelt declined both in total abundance and proportion in Galtfjärden, while in Lumparn and Ivarskärsfjärden the abundance of perch increased but its proportion in both assemblages remained stable (Table 3; paper III). Fisheries and eutrophication were identified as plausible causes of the observed adverse changes (papers III & IV). A decline in both mean length and mean trophic level was observed in the fish assemblages of all three study areas due to the declining proportion of the large-bodied predatory fish, especially pikeperch, and increasing proportion of secondary consumers, especially roach and other cyprinid species (Fig. 6).

Table 3. Environmental stressors and changes over time in the fish assemblages and pikeperch populations in Lumparn, Ivarskärsfjärden and Galtfjärden. Fish assemblage parameters: species abundances ($CPUE = n_{fish} / n_{gillnets}$), *mean total length* (the mean total length of all fish), *mean trophic level* (the mean of the trophic levels of all fish; species trophic levels according to Froese & Pauly 2010), *number of species* and *Shannon index* (Shannon & Claude 1948). Pikeperch population parameters: abundance (*CPUE*) of small (< 40 cm in *total length*) and large (≥ 40 cm in *total length*) individuals, *year-class strength* (based on 3-year old individuals), and mortality (instantaneous mortality, Z, and annual mortality, *A*, based on linear regression as in Dunn et al. 2002). All parameters were recorded annually. The commercial fisheries catches, chlorophyll a level and salinity were the most important factors affecting the variation in the fish species abundances in the fish assemblages (based on DistLM; paper III).

Study area		**Lumparn**	**Ivarskärsfjärden**	**Galtfjärden**
Time period		1999–2009	1999–2009	1995/1998–2008
Environmental stressors	Eutrophication status	High [1]	High [1]	Very high [1]
		Lowest [2]	Intermediate [2]	Highest [2]
	Commercial fishing catch	Intermediate [2]	Lowest [2]	Highest [2]
	Predator abundance [3]	Lowest [2]	Intermediate [2]	Highest [2]
Fish assemblage, paper III	Total catch, *CPUE*	↑	↑	→
	Mean total length	↓	↓	↓
	Mean species trophic level	↓	↓	↓
	Number of species	→	→	→
	Shannon index	→	→	→
	Pikeperch, *CPUE*	→	→	↓
	Cyprinids, *CPUE*	↑	↑	↑
	Perch, *CPUE*	↑	↑	↓
Pikeperch, paper IV	Large pikeperch, *CPUE*	↓	↓	↓
	Small pikeperch, *CPUE*	→	→	↓
	Year-class strength	→	→	↓
	Z / A	1.15 / 68%	1.16 / 69%	1.06 / 65%
		High [3]	High [3]	High [3]

Predators; grey seal *Halicoerus grypus* and great cormorant *Phalacrocorax carbo*.

Cyprinids; mainly roach *Rutilus rutilus* and white bream *Blicca bjoerkna*, single individuals of bream *Abramis brama*, vimba *Vimba vimba* and ide *Leuciscus idus*.

↑ = increasing, ↓ = decreasing, → = no trend over time (papers III and IV)

[1] According to Lundberg et al. (2005)

[2] Study areas compared to each other

[3] Related to Eero (2004), Heikinheimo et al. (2006), and Vainikka & Hyvärinen (2012)

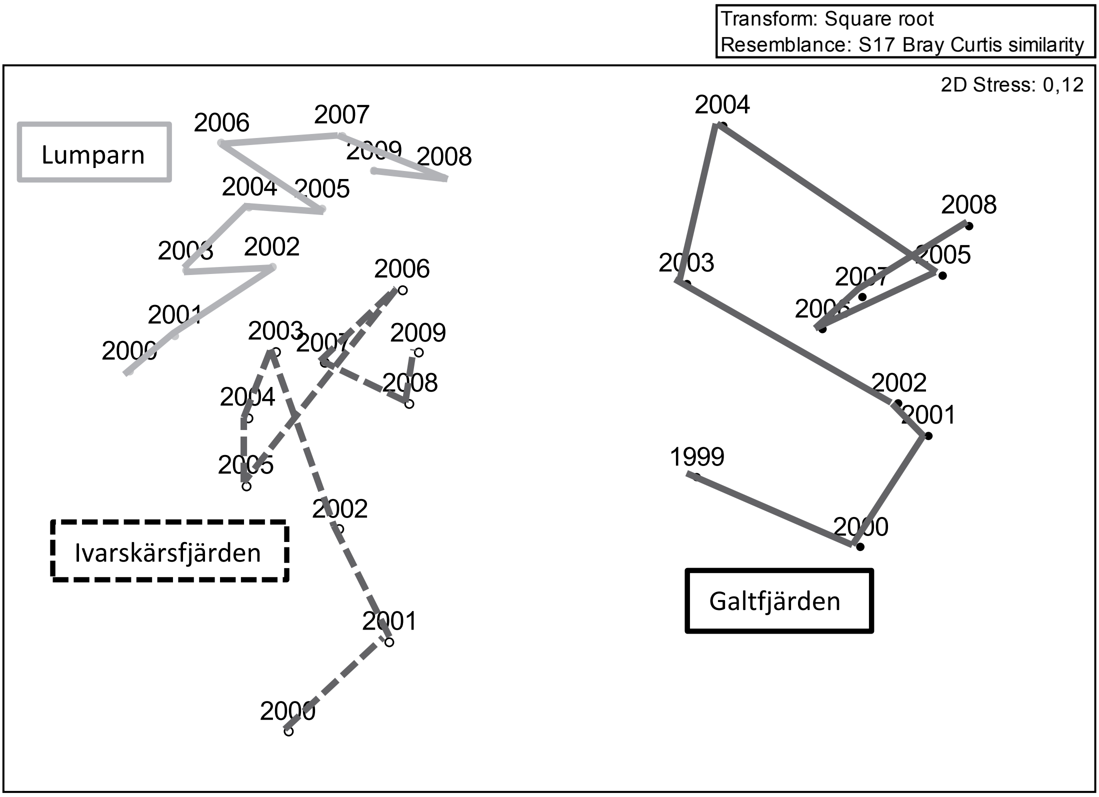

Figure 6. Non-parametric multidimensional scaling (nMDS) of the annual species abundances (square rooted *CPUE*, *CPUE* = $n_{\text{fish}}/n_{gillnets}$ annually) in Lumparn, Ivarskärsfjärden and Galtfjärden.

The magnitude of changes seemed to be related to the general level of the multiple stressors; initially the lowest predatory fish abundance and the most drastic changes during the sampling period were observed in Galtfjärden that was the most eutrophic (Lundberg et al. 2005) area and where also the commercial fisheries catches (kg/ha) were highest (papers III & IV). In addition, the predation pressure by great cormorants and grey seals was considered to be highest in Galtfjärden (paper IV). On the other hand, despite the eutrophic conditions, the observed changes were least dramatic in Ivarskärsfjärden where the pressures of fisheries and predation were the lowest. Pikeperch has been expected to benefit from eutrophication as it prefers turbid water, but it seems clear that any positive effect has been counteracted by the high fishing pressure (paper IV; Eero 2004; Heikinheimo et al. 2006), and in Galtfjärden also predation (paper IV; Östman et al. 2013; Salmi et al. 2015) and possibly also other factors.

High pikeperch mortalities (instantaneous mortality Z = 1.06–1.16, annual mortality A = 65–69%) were observed in all study areas (Table 3; Eero 2004; Heikinheimo et al. 2006; Vainikka & Hyvärinen 2012). In Galtfjärden, where the great cormorant predation seemed to add to the pressure on the heavily fished pikeperch and perch populations (Paper IV; Östman et al. 2013; Salmi et al. 2015), the declining abundances and declining *year-class strength* indicate recruitment overfishing (Bianchi et al. 2000; Shin et al. 2005). As expected based on previous studies by Pekcan-Hekim et al. (2011) and Heikinheimo et al. (2014), a positive relationship between summer temperatures and pikeperch *year-class strength* was found (paper IV). During the study period there were several warm summers yielding to strong year-classes in the northern Baltic Sea region (Heikinheimo et al. 2014), which was observed also in paper IV. Most likely the warm summers have affected also other species, and the summer temperature is a plausible explanatory factor to the increased total fish abundances in Lumparn and Ivarskärsfjärden (paper III). However, a declining trend in the pikeperch year-class strength was observed in Galtfjärden. In all study areas, all the pikeperch encountered were relatively young and small, and it is thus probable that many individuals only live to spawn once (Lappalainen et al. 2003; Birkeland & Dayton 2005). During the studies conducted in the Lumparn basin in 2008–2010 (papers I & II; Jokinen 2010), only a couple of pikeperch individuals larger than the minimum landing size of 37 cm were encountered.

Although eutrophication has been considered harmful to benthic fish species due to increased hypoxia (Eby et al. 2005; Snickars et al. 2015), in this study no adverse changes were observed in the benthic fish species. On the contrary, fourhorn sculpin *Myoxocephalus quadricornis* was abundant and in Galtfjärden (Fig. 6; paper III). However, the large fluctuations and increasing trend in abundance in Galtfjärden could partly be due to increased hypoxia in deeper areas (Carstensen et al. 2014). Hypoxia could force the benthic sculpin to move to depths/places that coincide with the sampling stations and thus increase its proportion in the catches (Eby et al. 2005; Snickars et al. 2015), but the theory could not be verified based on this material. The proportion of benthic species in the fish assemblages of Lumparn and Ivarskärsfjärden was clearly lower compared to Galtfjärden, and consisted mainly of ruffe, gobids and eelpout (papers I, II & III; unpublished, Noora Mustamäki). No effect of air temperature or NAO was observed in this study either, although previous studies indicate that global climate change may be an important driver of changes in coastal fish communities (Pekcan-Hekim et al. 2011; Olsson et al. 2012; Heikinheimo et al. 2014; Möllmann et al. 2014). Possibly some other temperature/climatic variable should have been used instead, or the time series was simply too short to reveal changes caused by large-scale climatic trends. In any case, the effects of global warming on fish assemblages cannot be ruled out based on these results.

I hypothesize that the overall changes in the fish assemblages observed in the study areas were caused by simultaneous bottom-up forcing and relaxing of top-down control and competition (Hunter & Price

1993; Breitburg et al. 2009). The removal of pikeperch (paper IV) and in Galtfjärden possibly also perch (paper III) by fisheries has reduced the predation pressure and competition, allowing an increase in the abundance of secondary consumers (Casini et al. 2008; Eriksson et al. 2009), in these areas especially cyprinids and fourhorn sculpin. The development has been further enhanced by eutrophication and possibly also warm summers increasing the total fish abundance (Bonsdorff et al. 1997; Ådjers et al. 2006; Chassot et al. 2007; Heikinheimo et al. 2014). The parallel increase of lower order consumers and decrease of higher order consumers was reflected in declining *mean total length and mean species trophic level* (Bianchi et al. 2000; Dulvy et al. 2004; Pauly & Palomares 2004) of fish in the communities. These changes are most likely reflected in other parts of the ecosystem, changing the structure of the system and the energy flows, and thus potentially leading to overall ecosystem changes (Airoldi & Beck 2007; Viaroli et al. 2008; Eriksson et al. 2009; Burghart et al. 2013; Newton 2014).

Casini et al. (2008) and Eriksson et al. (2009) have described recent similar overall community changes in the aquatic ecosystems of the same region, and Baden et al. (2012) for the Swedish west coast. The removal of predatory fish by fisheries has induced trophic cascades leading to increases the secondary consumer fish abundance and further to phytoplankton blooms in the pelagic zone (Casini et al. 2009) and overgrowth of filamentous algae in the littoral zone (Eriksson et al. 2009; Baden et al. 2012). The development observed in the three coastal fish assemblages in paper III therefore seems to be a part of large-scale changes in the state of coastal aquatic environments in northern Europe (Chassot et al. 2007; Möllmann et al. 2015; HELCOM 2013).

The declines in pikeperch abundance (papers III & IV) and high mortalities (paper IV) observed in this study and previous studies by Lappalainen et al. (2002), Eero (2004) and Heikinheimo et al. (2006) are a clear call for management actions on Baltic Sea pikeperch. Increasing the minimum landing size and the mesh size, and restrictions and bans on fishing should be implemented (paper IV; Heikinheimo et al. 2006; Vainikka & Hyvärinen 2012). Pikeperch fishing already is more strictly regulated in Åland Islands than in the Swedish east coast, which together with the on average higher water temperature may be one reason to the generally higher abundances in Lumparn and Ivarskärsfjärden compared to Galtfjärden.

The adverse impacts of eutrophication and excessive fishing pressure on aquatic ecosystems has already been acknowledged in several previous studies (Casini et al. 2008; Eriksson et al. 2009; Andersen et al. 2011; Möllmann et al. 2014; Snickars et al. 2015), and although the management and conservation of the Baltic Sea has been a political issue for decades (HELCOM 2013), the results achieved appear unsatisfactory as demonstrated in this thesis (papers III & IV). Due to buffering and compensatory mechanisms, an ecosystem can tolerate a small or short-term disruption, but long-term disruptions may lead to reorganization of the trophic structure and result in a new stable state in the whole system, such as a shift in a fish community from a predatory fish dominated state to a lower order consumer dominated one (paper III; Scheffer & Carpenter 2003; Casini et al. 2008; Eriksson et al. 2009; Möllmann et al. 2015). Even though the actual shift may occur within a relative short period of time (paper III), these are typically long-term events driven by years or decades of anthropogenic pressure (papers III & IV; Breitburg et al. 2009; Möllmann et al. 2015). Even in the unlikely case of discontinuing all anthropogenic pressure, reversing such large-scale events may prove difficult as the compensatory mechanisms may have changed in favour of the new state (Möllmann et al. 2015).

4.5 JUVENILE FISH IN THE SHALLOW ARCHIPELAGO WATERS IN THE NORTHERN BALTIC SEA

Studies on juvenile fish, spawning grounds, recruitment or year-class strengths are usually conducted in regard of management of the adult fish population (paper IV; Snickars et al. 2010; Kallasvuo et al. 2011; Sundblad & Bergström 2014). Several previous studies have established a link between zooplankton abundances and juvenile fish (reviewed by Daewel et al. 2014), but it has not been thoroughly investigated how the juvenile fish abundance and the zooplankton-juvenile fish-interaction are controlled by higher order consumers. In the Lumparn basin, zooplankton was a main component in the diet of young-of-the-year perch, and the young-of-the-year fish were the prey of choice for many perch (paper II; Cederberg 2011) and pikeperch (Jokinen 2010) in the late summer. As stated above, high abundances of the small-bodied gobid and stickleback juveniles in late summer may trigger an early ontogenetic diet shift (Mehner et al. 1996) observed in perch in paper II and previously by Sandström and Karås (2002). It seems that the young-of-the-year fish were either specifically preferred by perch and pikeperch, or simply very easily available. These findings suggest that not only the young-of-the-year fish were potential recruits to their respective adult stocks, but that they also comprised a temporary food web compartment of their own by feeding on the zooplankton on its peak abundance and by comprising a central part of the late summer diet of the higher order consumer fish. Future studies should further clarify the trophic role and interactions of young-of-the-year/juvenile fish.

4.6 VARIATION IN FISH COMMUNITIES

Spatial and temporal variation on fish community level is still today poorly understood, as it is rather impossible to include measures of all sources of variation in a single study or analysis. Growth and species-specific or even individual ontogenetic shifts in diet and habitat preferences of a single fish shape the population structure and create variation within population (paper II; Bergek & Björklund 2009; Araujo et al.

2011; Bolnick et al. 2013). The number of offspring produced by a fish population is not only affected by the absolute size of the spawning stock, but also the spawning stock structure is important as larger individuals tend to produce more offspring (Birkeland & Dayton 2005). Reproduction and fish health in general can also be adversely affected by chemical pollution, parasites (Björkblom et al. 2013) and infections (Ström-Bestor et al. 2010). The survival of the offspring is affected by temperature and therefore global warming ought to increase the abundances and growth of juvenile fish in the future (paper IV; Lefébure et al. 2013; Heikinheimo et al. 2014). Also food availability and competition (Mehner et al. 1996) and predation on eggs, fry and juveniles (papers II & IV) affect the recruitment. Eutrophication may increase the survival by increasing primary production and thereby abundance of zooplankton (Bonsdorff et al. 1997; Lefébure et al. 2013) that many juvenile fish feed on (Mehner et al. 1996; Sandström & Karås 2002). Increased turbidity by eutrophication may benefit some species, for instance roach in competition with perch (Lappalainen et al. 2001). Variation in the number of offspring produced and its survival creates the long-term variation in the species year-class strengths (paper IV; Heikinheimo et al. 2014).

Modelling the abiotic environmental factors, such as depth, substrate type and exposure, in order to identify biotopes and potential habitats is a current trend in marine environmental monitoring (Andersen et al. 2009; Gogina & Zettler 2010; Rinne 2011). The results of this study illustrate that because of the seasonal variation, developing such models for the fish assemblage of the Baltic Sea (Vahteri et al. 2009; Bergström et al. 2013; Snickars 2014) is challenging.

In order to decrease variation in data, fish sampling is most often conducted either once a year or within one depth zone, but this is not sufficient to determine which habitats or geographical areas are inhabited or needed by a specific species of fish, or for construction of general large-scale models. The whole range of habitats that each species uses seasonally and throughout its lifecycle should be clarified in order to understand the structure of the aquatic ecosystems, and to be able to plan effective management in environments where the fish movements are not restricted by physical barriers (Able 2005; Bergström et al. 2013). Thus creating useful small-scale fish distribution models requires considerable sampling effort with sufficient spatial and temporal replication.

Variation in fish communities is highly complex and may appear to be random, as the sources and mechanisms of variation are numerous. Some sources of variation, such as small scale seasonal variation (paper I) are hardly described at all, while others, such as perch resource polymorphism (paper II) are well studied at least in some habitats, but their mechanisms are still poorly understood. The negative effects of high fishing pressure and eutrophication and other habitat degradation are today taken as a fact, but still the mechanisms of their adverse impacts are under debate. In this thesis, several sources of spatial, temporal and biological variation in fish assemblages on different scales were addressed. Together they add to the knowledge of structure and function of Baltic Sea coastal fish communities, and create a complex picture of a dynamic system changing in space and time.

ACKNOWLEDGEMENTS

First I would like to thank my supervisor Docent Johanna Mattila, who has given me good advice during the whole project from fieldwork to manuscript preparation. Professor Erik Bonsdorff has always had time to answer my questions and has also co-authored one of the original papers.

Probably the greatest fieldwork team ever, “Team Gös”: Henri Jokinen, Tony Cederberg and Dr Matias Scheinin, thank you for your never-ending team spirit and your invaluable contribution to the project in fieldwork, in laboratory and in manuscript preparation. Especially Henkka deserves a price for enduring me those three long field periods.

For co-authorship and letting me use your excellent data material I want to thank Dr Ulf Bergström from the Swedish University of Agricultural Sciences, fisheries biologist Kaj Ådjers from the Fisheries Division of the Åland Government and ornithologist Alf Sevastik.

I very much appreciate the contributions of Satu Zwerver, Sara Bystedt and Laura Kauppi, and the colleagues in Stockholm University: Professor Sture Hansson, Dr Ida Ahlbeck Bergendahl and Dr Per Holliland. I also want to thank all my fellow PhD Students in Åbo Akademi University for good company, especially my long-term roommate Dr Camilla Gustafsson.

During this project, I left a piece of my heart on the beautiful Åland Islands. Every summer the magic of the Husö biological station draws in an awesome bunch of people that together with some ghosts and other oddities create a unique working atmosphere. Thank you for the unforgettable summers.

For reviewing the thesis I want to thank Dr Outi Heikinheimo and Dr Leena Nurminen. Dr Richard Svanbäck, Anna Wiksten, Dr Jari Raitaniemi, Dr Rafael Perez-Dominguez and the anonymous reviewers have provided valuable comments on the original papers.

Of the instances that have been of great help during the project I would like to mention Environmental Laboratory and Fisheries Division of the Åland Government, Ålands Sjöräddningssällskap and Finnish Meteorological Institute. I also greatly appreciate the friendly co-operation of the Lumparn water owners and fisherman Ben Holmberg.

This project would not have been possible without financial support from Baltic Sea 2020 Foundation, Finnish Foundation for Nature Conservation, Åbo Akademi University Endowment, Maa- ja Vesitekniikan tuki ry and Swedish Cultural Foundation in Finland.

Last but not least, I am forever in debt to my family for always supporting me. Especially Jani, thanks for understanding. Kikka, the loyal companion sleeping under my chair at the moment, thanks for not understanding.

REFERENCES

Able KW (2005) A re-examination of fish estuarine dependence: Evidence for connectivity between estuarine and ocean habitats. Est Coast Shelf Sci 64: 5–17.

Ahlbeck I, Hansson S & Hjerne O (2012) Evaluation of diet analysis methods by individual based modelling. Can J Fish Aquat Sci 69: 1184–1201.

Airoldi L & Beck MW (2007) Loss, status and trends for coastal marine habitats of Europe. Annu Rev Oceanogr Mar Biol 45: 345–405.

Allen LG (1982) Seasonal abundance, compostition, and productivity of the littoral fish assemblage in Upper Newport Bay, California. Fishery Bulletin 80: 769–790.

Alongi D (1998) Coastal ecosystem processes. CRC Press LCC, USA. 419 pp.

Andersen JH, Axe P, Backer H, Carstensen J, Claussen U, Fleming-Lehtinen V, Järvinen M, Kaartokallio H, Knuuttila S, Korpinen S, Kubiliute A, Laamanen M, Lysiak-Pastuszak E, Martin G, Murray C, Møhlenberg F, Nausch G, Norkko A & Villnäs A (2011) Getting the measure of eutrophication in the Baltic Sea: towards improved assessment principles and methods. Biogeochemistry 106: 137–156.

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Aust Ecol 26: 32–46.

Anderson MJ, Gorley RN & Clarke RK (2008) Permanova+ for Primer: Guide to software and statistical methods.

Appelberg M, Berger HM, Hestghagen T, Kleiven E, Kurkilahti M, Raitaniemi J & Rask M (1995) Development and intercalibration of methods in Nordic freshwater fish monitoring. Water Air Soil Pollut 85: 401–406.

Araujo MS, Bolnick DI & Layman GA (2011) The ecological causes of individual specialization. Ecol Lett 14: 948–958.

Axenrot T & Hansson S (2004) Seasonal dynamics in pelagic fish abundance in a Baltic Sea coastal area. Est Coast Shelf Sci 60: 541–547.

Baden S, Emanuelsson A, Pihl L, Svensson KJ, Åberg P (2012) Shift in seagrass food web structure over decades is linked to overfishing. Mar Ecol Prog Ser 451: 61–73.

Baker R, Buckland A & Sheaves M (2014) Fish gut content analysis: robust measures of diet composition. Fish Fish 15: 170–177.

Begg GA, Friedland KD & Pearce JB (1999) Stock identification and its role in stock assessment and fisheries management: an overview. Fish Res 43: 1–8.

Bekkby T, Isachsen PE, Isaeus M, & Bakkestuen V (2008) GIS modeling of wave exposure at the seabed: A depth-attenuated wave exposure model. Marine Geodesy 31, 117–127.

Bergek S & Björklund M (2009) Genetic and morphological divergence reveals local subdivision of perch (*Perca fluviatilis* L.). Biol J Linn Soc 96: 746–758.

Bergström U, Sundblad G, Downie A-L, Snickars M, Boström C & Lindegarth M (2013) Evaluating eutrophication management scenarios in the Baltic Sea using species distribution modelling. J Appl Ecol 50: 680–690.

Bianchi G, Gislason H, Graham K, Hill L, Jin X, Koranteng K, Manickchand-Heileman S, Paya I, Sainsbury K, Sanchez F & Zwanenburg K (2000) Impact of fishing on size composition and diversity of demersal fish communities. ICES J Mar Sci 57: 558–571.

Birkeland C & Dayton PK (2005) The importance in fishery management of leaving the big ones. TREE 20: 356–358.

Björkblom C, Mustamäki N, Olsson PE, Katsiadaki I & Wiklund T (2013) Assessment of reproductive biomarkers in three-spined stickleback (*Gasterosteus aculeatus*) from sewage effluent recipients. Env Tox 28: 229–237.

Bolnick D, Amarasekare P, Araújo MS, Bürger R, Levine JM, Novak M, Rudolf VHW, Schreiber SJ, Urban MC & Vasseur D (2011) Why intraspecific trait variation matters in community ecology. TREE 26: 183–192.

Bolnick DI, Snowberg LK, Hirsch PE, Lauber CL, Knigth R, Caporaso JG & Svanbäck R (2014) Individuals’ diet diversity influences gut microbial diversity in two freshwater fish (threespine stickleback and Eurasian perch). Ecol Lett 17: 979–987.

Bonsdorff E, Blomqvist E, Mattila J & Norkko A (1997) Long-term changes and coastal eutrophication. Examples from the Aland Islands and the Archipelago Sea, northern Baltic Sea. Oceanol Acta 20: 319–329.

Brabrand Å & Faafeng B (1993) Habitat shift in roach (Rutilus rutilus) induced by pikeperch (*Stizostedion lucioperca*) introduction: predation risk versus pelagic behavior. Oecologia 95: 38–46.

Breitburg DL, Craig JK, Fulford RS, Rose KA, Boynton WR, Brady DC, Ciotti BJ, Diaz RJ, Friedland KD, Hagy JD, Hart DR, Hines AH. Houde ED, Kolesar SE, Nixon SW, Rice JA, Secor DH & Targett TE (2009) Nutrient enrichment and fisheries exploitation: interactive effects on estuarine living resources and their management. Hydrobiologia 629: 31–47.

Burghart SE, Jones DL & Peebles EB (2013) Variation in estuarine consumer communities along an assembled eutrophication gradient: Implications for trophic instability. Est Coast 36: 951–965.

Carabel S, Godínez-Domínguez E, Verísimo P, Fernández L & Freire J (2006) An assessment of sample processing methods for stable isotope analyses of marine food webs. J Exp Mar Biol Ecol 336: 254–261.

Carstensen J, Conley DJ, Bonsdorff E, Gustafsson BG, Hietanen S, Janas U, Jilbert T, Maximov A, Norkko A, Norkko J, Reed DC, Slomp CP, Timmermann K & Voss M (2014) Hypoxia in the Baltic Sea: biogeochemical cycles, benthic fauna and management. Ambio 43: 26–36.

Casini M, Lövgren J, Hjelm J, Cardinale M, Molinero J-C & Kornilovs G (2008) Multi-level trophic cascades in a heavily exploited open marine ecosystem. Proc R Soc B 275: 1793–1801.

Chassot E, Mélin F, Le Pape O & Gascuel D (2007) Bottom-up control regulates fisheries production at the scale of eco-regions in European seas. Mar Ecol Prog Ser 343: 45–55.

Cederberg T (2011) The connection between feeding habits, body depth and environment in Eurasian perch (*Perca fluviatilis* L.). MSc thesis, Åbo Akademi Univ. In Swedish.

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Aust J Ecol 18: 117–143.

Cowen RK & Sponaugle S (2009) Larval dispersal and marine population connectivity. Ann Rev Mar Sci 1: 443–466.

Daewel U, Hjøllo SS, Huret M, Ji R, Maar M, Niiranen S, Travers-Trolet M, Peck MA & van de Wolfshaar KE (2014) Predation control of zooplankton dynamics: a review of observations and models. ICES J Mar Sci 71: 254–271.

Deegan LA (1993) Nutrient and energy transport between estuaries and coastal marine ecosystems by fish migration. Can J Fish Aquat Sci 50: 74–79.

Dulvy NK, Polunin NVC, Mill AC & Graham NAJ (2004) Size structural change in lightly exploited coral reef fish communities: evidence for weak indirect effects. Can J Fish Aquat Sci 61: 466–475.

Dunn A, Francis RICC & Doonan IJ (2002) Comparison of the Chapman-Robson and regression estimators of Z from catch-curve data when non-sampling stochastic error is present. Fish Res 59: 149–159.

Eby LA, Crowder LB, McClellan CM, Peterson CH & Powers MJ (2005) Habitat degradation from intermittent hypoxia: impacts on demersal fishes. Mar Ecol Prog Ser 291: 249–262.

Eero M (2004) Consequences of management of pikeperch (*Stizostedion lucioperca* L.) stock in Pärnu Bay (Baltic Sea) under two different economic regimes, 1960–1999. Fish Res 68: 1–7.

Elliott M, Whitfield AK, Potter IC, Blaber SJM, Cyrus DP, Nordlie FG & Harrison TD (2007) The guild approach to categorizing estuarine fish assemblages: a global review. Fish Fish 8: 241–268.

Eriksson BK, Ljunggren L, Sandström A, Johansson G, Mattila J, Rubach A, Råberd S & Snickars M (2009) Declines in predatory fish promote bloom-forming macroalgae. Ecol Appl 19: 1975–1988.

Estlander S, Nurminen L, Olin M, Vinni M, Immonen S, Rask M, Ruuhijärvi J, Horppila J & Lehtonen H (2010) Diet shifts and food selection of perch *Perca fluviatilis* and roach *Rutilus rutilus* in humid lakes of varying water colour. J Fish Biol 77: 241–256.

FGFR (2006) Finnish Game and Fisheries Research Institute. Kalavarat 2006. Publications of Finnish Game and Fisheries Research Institute, Helsinki, Finland. 79 pp. In Finnish.

Froese R & Pauly D (Eds.) (2013) FishBase. World Wide Web electronic publication. www.fishbase.org, version 10/2013. [Accessed 10th January 2014]

Gogina M & Zettler ML (2010) Diversity and distribution of benthic macrofauna in the Baltic Sea: Data inventory and its use for species distribution modelling and prediction. J Sea Res 64: 313–321.

Heikinheimo O, Setälä J, Saarni K & Raitaniemi J (2006) Impacts of mesh size regulation of gillnets on the pikeperch fisheries in the Archipelago Sea, Finland. Fish Res 77: 192–199.

Heinänen S (2010) From individual species to communities – modelling spatial patterns of breeding bird species in a complex and changing coastal landscape. Dissertation. Åbo Akademi University.

HELCOM (2013) Red List of Baltic Sea underwater biotopes, habitats and biotope complexes. Balt Sea Env Proc No. 138.

Hixon MA, Anderson TW, Buch KL, Johnson DW, McLeod JB & Stallings CD (2012) Density dependence and population regulation in marine fish: a large-scale, long-term field manipulation. Ecol Mon 82: 467–489.

Hobson KA (1999) Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia 120: 314–326.

Horppila J, Peltonen H, Malinen T, Luokkanen E & Kairesalo T (1998) Top-down or bottom-up effects by fish: issues of concern in biomanipulation of lakes. Rest Ecol 6: 20–28.

Horppila J, Ruuhijärvi J, Rask M, Karppinen C, Nyberg K & Olin M (1999) Seasonal changes in the diets and relative abundances of perch and roach in the littoral and pelagic zones of a large lake. J Fish Biol 56: 51–72.

Hrabik TR, Jensen OP, Martell SJD, Malters CJ & Kitchell JF (2006) Diel vertical migration in the Lake Superior pelagic community. I. Changes in vertical migration of coregonids in response to varying predation risk. Can J Fish Aquat Sci 63: 2286–2295.

Hunter MD & Price PW (1992) Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology 73:724–732.

Hurrell J & National Center for Atmospheric Research Staff (Eds). Last modified 05 Sep 2014. “The Climate Data Guide: Hurrell North Atlantic Oscillation (NAO) Index (station-based).” Retrieved from https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based. [Accessed 9th February 2015]

ICES (2014) ICES catch statistics. http://www.ices.dk/marine-data/dataset-collections/Pages/Fish-catch-and-stock-assessment.aspx. [Accessed 10th June 2014]

Jokinen H (2010) The pelagic coastal fish community and its seasonal dynamics, with special consideration for pikeperch: a fishing survey in the Lumparn-area, Åland Islands. MSc Thesis, Åbo Akademi Univ.

Karlsson L & Karlstråm Ö (1994) The Baltic salmon (*Salmo salar* L.): its history, present situation and future. Dana 10: 61–85.

Kearney M (2006) Habitat, environment and niche: what are we modelling? Oikos 115: 186–191.

Kekäläinen J, Kähkönen J, Kiviniemi V & Huuskonen H (2010) Morphological variation of perch Perca fluviatilis in humid lakes: the effect of predator density, competition and prey abundance. J Fish Biol 76: 787–799.

Kääriä J, Rajasilta M, Kurkilahti M & Soikkeli M (1997) Spawning bed selection by the Baltic herring (*Clupea harengus membras*) in the Archipelago of SW Finland. ICES J Mar Sci 54: 917–923.

Lappalainen A, Rask M, Koponen H & Vesala S (2001) Relative abundance, diet and growth of perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) at Tvärminne, Northern Baltic Sea, in 1975 and 1997: responses to eutrophication? Bor Env Res 6: 107–118.

Lappalainen A, Söderkultalahti P & Wiik T (2002) Changes in the commercial fishery for pikeperch (*Stizostedion lucioperca*) on the Finnish coast from 1980 to 1999 – Consequences of environmental and economic factors. Arc Fish Mar Res 49: 199–212.

Lappalainen J, Dörner H & Wysujack K (2003) Reproduction biology of pikeperch (*Sander lucioperca* (L.)) – a review. Ecol Fresh Fish 12: 95–106.

Law R (2000) Fishing, selection, and phenotypic evolution. ICES J Mar Sci 57: 659–668.

Letourneur Y, Darnaude A, Salen-Picard C & Harmelin-Vivien M (2001) Spatial and temporal variations of fish assemblages in a shallow Mediterranean soft-bottom area (Gulf of Fos, France). Ocea Acta 24: 273–285.

Lundberg C, Lönnroth M, von Numers M & Bonsdorff E (2005) A multivariate assessment of coastal eutrophication. Examples from the Gulf of Finland, northern Baltic Sea. Mar Pol Bul 50: 1185–1196.

Mace P (2001) A new role for MSY in single-species and ecosystem approaches to fisheries stock assessment and management. Fish Fish 2: 2–32.

MacPherson E (1998) Ontogenetic shifts in habitat use and aggregation in juvenile sparid fishes. J Exp Mar Biol Ecol 220: 127–150.

Malek AJ, Collie JS & Gartland J (2014) Fine-scale spatial patterns in the demersal fish and invertebrate community in a northwest Atlantic ecosystem. Est Coast Shelf Sci 147: 1–10.

McQuinn IH (1997) Metapopulations and the Atlantic herring. Rev Fish Biol Fish 7: 297–329.

Mehner T, Schultz H, Bauer D, Herbst R, Voigt H & Benndorf J (1996) Intraguild predation and cannibalism in age-0 perch (*Perca fluviatilis*) and age-0 zander (*Stizostedion lucioperca*): Interactions with zooplankton succession, prey fish availability and cannibalism. Ann Zool Fenn 33: 353–361.

Methven DA, Haedrich RL & Rosea GA (2001) The fish assemblage of a Newfoundland estuary: Diel, monthly and annual variation. Est Coast Shelf Sci 52: 669–687.

Möllmann C, Folke C, Edwards M & Conversi A (2015) Marine regime shifts around the globe: theory, drivers and impacts. Philos Trans R Soc Lond B Biol Sci. 2015 Jan 5; 370(1659): 20130260. DOI: 10.1098/rstb.2013.0260.

Möllmann C, Lindegren M, Blenckner T, Bergström L, Casini M, Diekmann R, Flinkman J, Müller-Karulis B, Neuenfeldt S, Schmidt JO, Tomczak M, Voss R & Gårdmark A (2014) Implementing ecosystem-based fisheries management: from single-species to integrated ecosystem assessment and advice for Baltic Sea fish stocks. ICES J Mar Sci 71 (5): 1187-1197.

Newton A, Icely J, Cristina S, Brito A, Cardoso AC, Colijn F, Dalla Riva S, Gertz F, Würgler Hansen J, Holmer H, Ivanova K, Leppäkoski E, Canu DM, Mocenni C, Mudge S, Murray N, Pejrup M, Razinkovas A, Reizopoulou S, Pérez-Ruzafa A, Schernewski G, Schubert H, Carr L, Solidoro C, Viaroli P & Zaldívar JM (2014) An overview of ecological status, vulnerability and future perspectives of European large shallow, semi-enclosed coastal systems, lagoons and transitional waters. Est Coast Shelf Sci 140: 95–122.

Nixon SW (1995) Coastal marine eutrophication: a definition, social causes, and future concerns. Ophelia 41: 199–219.

Nordström M, Aarnio K & Bonsdorff E (2009) Temporal variability of a benthic food web: patterns and processes in a low-diversity system. Mac Ecol Prog Ser 378: 13–26.

Olsson J Bergström L & Gårdmark A (2012) Abiotic drivers of coastal fish community change during four decades in the Baltic Sea. ICES J Mar Sci 69: 961–970.

Pauly D & Palomares ML (2005) Fishing down marine food webs: it is far more pervasive than we thought. Bul Mar Sci 76: 197–211.

Perus J & Bonsdorff E (2004) Long-term changes in macrozoobenthos in the Åland archipelago, northern Baltic Sea. J Sea Res 52: 45–56.

Peterson BJ & Fry B (1987) Stable isotopes in ecosystem studies. Annu Rev Ecol Systemat 18: 293–320.

Pihl L, Cattrijsse A, Codling I, Mathieson S, McLusky DS & Roberts C (2002) Habitat use by fishes in estuaries and other brackish areas. In: Elliot M & Hemingway K (Eds.) Fishes in estuaries. Blackwell Publishing Ltd. Oxford, pp. 10–53.

Pihl L, Wennhage H (2002) Structure and diversity of fish assemblages on rocky and soft bottom shores on the Swedish west coast. J Fish Biol 61: 148–166.

Pikitch EK, Santora C, Babcock EA, Bakun A, Bonfil R, Conover DO, Dayton P, Doukakis P, Fluharty D, Heneman B, Houde ED, Link J, Livingston PA, Mangel M, McAllister MK & Sainsbury KJ (2004) Ecosystem-based fishery management. Science 305: 346–347.

Pimm SL, Lawton JH & Cohen JE (1991) Food web patterns and their consequences. Nature 350: 669–674.

Post DM (2002) Using stable isotopes to estimate trophic position: models, methods and assumptions. Ecology 83: 703–718.

Rajasilta M, Mankki J, Ranta-Aho K & Vuorinen I (1999) Littoral fish communities in the Archipelago Sea, SW Finland: a preliminary study of changes over 20 years. Hydrobiologia 393: 253–259.

Ricker WE (1975) Computation and interpretation of biological statistics of fish populations. Bull Fish Res Board Can 191: 1–382.

Rinne H, Salovius-Laurén S & Mattila J (2011) The occurrence and depth penetration of macroalgae along environmental gradients in the northern Baltic Sea. Est Coast Shelf Sci 94: 182–191.

Rosqvist K, Mattila J, Sandstöm A, Snickars M & Westerblom M (2010) Regime shifts in vegetation composition of Baltic Sea coastal lagoons. Aquat Bot 93: 39–46.

Rudolf VHW, Rasmussen NL, Dibble CJ & Van Allen BG (2014) Resolving the roles of body size and species identity in driving functional diversity. Proc Ryal Soc B 281: 20133203.

Salmi JA, Auvinen H, Raitaniemi J, Kurkilahti M, Lilja J & Maikola R (2015) Perch (*Perca fluviatilis*) and pikeperch (*Sander lucioperca*) in the diet of the great cormorant (*Phalacrocorax carbo*) and effects on catches in the Archipelago Sea, Southwest coast of Finland. Fish Res 164: 26–34.

Sandstöm A & Karås P (2002) Effects of eutrophication on young-of-the-year freshwater fish communities in coastal areas of the Baltic Sea. Env Biol Fish 63: 89–101.

Sheaves M, Baker R, Nagelkerken I & Connolly RM (2015) True value of estuarine and coastal nurseries for fish: Incorporating complexity and dynamics. Est Coast 38: 401–414.

Scheffer M & Carpenter SR (2003) Catastrophic shifts in ecosystems: linking theory to observation. TREE 18: 648–656.

Scheinin M & Mattila J (2010) The structure and dynamics of zooplankton communities in shallow bays in the northern Baltic Sea during a single growing season. Bor Env Res 15: 397–412.

Scheinin M, Sjöqvist C & Mattila J (2013) Microalgal plankton composition in shallow coastal inlets in contrasting trophic and alternative community states. Hydrobiologia 701: 253–271.

Scheinin M & Söderström S (2005) A mapping of aquatic macrophytes along two inner-outer-archipelago gradients in the North-Western and South-Eastern Åland. Research reports from Husö Biological Station. No 112. 61 pp. (In Swedish).

Shannon CE & Claude E (1948) A mathematical theory of communication. Bell Syst Tech J 27: 379–423.

Shin Y-J, Rochet M-J, Jennings S, Field JG & Gislason H (2005) Using size-based indicators to evaluate the ecosystem effects of fishing. ICES J Mar Sci 62: 384–396.

Skúlason S & Smith TB (1995) Resource polymorphism in vertebrates. TREE 10: 366–370.

Snickars M, Sandström A, Lappalainen A, Mattila J, Rosqvist K & Urho L (2009) Fish assemblages in coastal lagoons in land-uplift succession: the relative importance of local and regional environmental gradients. Est Coast Shelf Sci 81: 247–256.

Snickars M, Sandström A & Mattila J (2004) Antipredator behavior of 0+ year *Perca fluviatilis* effect of vegetation density and turbidity. J Fish Biol 65: 1604–1613.

Snickars M, Sundblad G, Sandström A, Ljunggren L, Bergström U, Johansson G & Mattila J (2010) Habitat selectivity of substrate spawning fish - modelling requirements of the Eurasian perch, *Perca fluviatilis*. Mar Ecol Prog Ser 398: 235–243.

Snickars M, Gullström M, Sundblad G, Bergström U, Downie A-L, Lindegarth M & Mattila J (2014) Species–environment relationships and potential for distribution modelling in coastal waters. J Sea Res 85: 116–125.

Snickars M, Weigel B & Bonsdorff E (2015) Impact of eutrophication and climate change on fish and zoobenthos in coastal waters of the Baltic Sea. Mar Biol 162: 141–151.

Stockwell JD, Yule DL, Hrabik TH, Sierszen ME & Isaac EJ (2014) Habitat coupling in a large lake system: delivery of an energy subsidy by an offshore planktivore to the nearshore zone of Lake Superior. Fresh Biol 59: 1197–1212.

Ström-Bestor M, Mustamäki N, Heinikainen S, Hirvelä-Koski V, Verner-Jeffreys D & Wiklund T (2010) Introduction of Yersinia ruckeri biotype 2 into Finnish fish farms. Aquaculture 308: 1–5.

Sundblad G & Bergström U (2014) Shoreline development and degradation of coastal fish reproduction habitats. Ambio 43: 1020–1028.

Svanbäck R & Eklöv P (2003) Morphology dependent foraging efficiency in perch: a trade-off for ecological specialization? Oikos 102: 273–284.

Svanbäck R & Eklöv P (2006) Genetic variation and phenotypic plasticity: causes of morphological and dietary variation in Eurasian perch. Evol Ecol Res 8: 37–49.

Svanbäck R, Eklöv P, Fransson R & Holmgren K (2008) Intraspecific competition drives multiple species resource polymorphism in fish communities. Oikos 117: 114–124.

Svanbäck R, Quevedo M, Olsson J & Eklöv P (2015) Individuals in food webs: the relationships between trophic position, omnivory and among-individual diet variation. Oecologia DOI 10.1007/s00442-014-3203-4.

Quevedo M, Svanbäck R & Eklöv P (2009) Intrapopulation niche partitioning in a generalist predator limits food web connectivity. Ecology 90: 2263-2274.

SwAM (2012) Fiskbestånd och miljö i hav och sötvatten. Resurs- och miljööversikt 2012. The Swedish Agency for Marine and Water Management. Elanders Sverige AB, 234 pp.

Törnroos A & Bonsdorff E (2012) Developing the multitrait concept for functional diversity: lessons from a system rich in functions but poor in species. Ecol Appl 22: 2221–2236.

Törnroos A, Nordström MC, Bonsdorff E (2013) Coastal habitats as surrogates for taxonomic, functional and trophic structures of benthic faunal communities. PLoS ONE 8, e78910.

Vahteri P, O'Brien K & Vuorinen I (2009) Zonation and spatial distribution of littoral fish communities from the southwestern Finnish coast (Archipelago and Bothnian Sea, Northern Baltic Sea). Est Coast Shelf Sci 82: 35–40.

Vainikka A & Hyvärinen P (2012) Ecologically and evolutionarily sustainable fishing of the pikeperch *Sander lucioperca*: Lake Oulujärvi as an example. Fish Res 113: 8–20.

Vander Zanden MJ & Rasmussen JB (1999) Primary consumer $\delta^{13}C$ and $\delta^{15}N$ and the trophic position of aquatic consumers. Ecology 80: 1395–1404.

Vestøl O (2006) Determination of postglacial land uplift in Fennoscandia from leveling, tide-gauges and continuous GPS stations using least squares collocation. J Geodesy 80: 248–258.

Viaroli P, Bartoli M, Giordani G, Naldi M, Orfanidis S & Zaldivar JM (2008) Community shifts, alternative stable states, biogeochemical controls and feedbacks in eutrophic coastal lagoons: a brief overview. Aquatic Conserv Freshw Mar Ecosyst 18: 105–117.

Wang N & Eckmann R (1994) Distribution of perch (Perca fluviatilis L.) during their first year of life in Lake Constance. Hydrobiologia 277: 135–143.

Werner EE & Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. Annu Rev Eco Syst 15: 393–425.

Ådjers K, Appelberg M, Eschbaum R, Lappalainen A, Minde A, Repečka R & Thoresson G (2006) Trends in coastal fish stocks of the Baltic Sea. Bor Env Res 11: 13–25.

Östman Ö, Boström MK, Bergström U, Andersson J & Lunneryd S-G (2013) Estimating competition between wildlife and humans – a case of cormorants and coastal fisheries in the Baltic Sea. PLoS ONE 8(12): e83763.

ISBN 978-952-12-3231-2

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ENVIRONMENTAL AND MARINE BIOLOGY - ÅBO AKADEMI UNIVERSITY 2015