Essential Young-of-the-Year Fish Macrophyte Habitats Along the Swedish East Coast

– Evaluation of Representativity of Marine Protected Areas and Pressures on Habitats in the Gulf of Bothnia

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Master's degree project, 60 credits
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Essential Young-of-the-Year Fish Macrophyte Habitats Along the Swedish East Coast – Evaluation of Representativity of Marine Protected Areas and Pressures on Habitats in the Gulf of Bothnia

Essentiella Makrofythabitat för Årsyngel av Fisk längs den Svenska Ostkusten – Utvärdering av Representativiteten hos Marina Skyddade Områden och Påverkansfaktorer på Habitat i Bottniska Viken

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Abstract

Along the coastal zone of the Baltic Sea high productivity habitats form important areas for many organisms, including young-of-the-year (YOY) fish. Habitats consisting of aquatic vegetation provide YOY fish with important services, such as refuge from large predators and food sources. However, relationships between YOY fish abundance/species richness and habitat cover, and environmental variables across multiple scales, remains unclear, as well as the relationship between essential YOY fish habitats and different intensities of recreational boating. Additionally, the amount of essential YOY fish habitats protected by marine protected areas (MPAs) is unknown. To address these questions relationships between YOY fish and habitat/environmental variables were analyzed for a large data set consisting of 4,670 samples along the Swedish Baltic Sea coast using Generalized Additive Models (GAMs). Samples were collected by SLU Aqua between 2007 and 2018 using small underwater detonations and estimation of habitat cover was conducted by snorkeling. Spatial analyses using ArcGIS Pro 2.5.0 were conducted to study the correlation between boating activity and the density of essential YOY fish habitats, and the representativity of YOY fish habitats within the MPA network. Overall, there was a significant relationship between vegetated coastal habitats and YOY fish abundance and species richness, by displaying a higher abundance and species richness of YOY fish in areas with a higher vegetation cover. Significant relationships between individual YOY fish species and different types of vegetation were also found. However, based on the spatial analyses these valuable YOY fish habitats were insufficiently covered by the MPA network, with only 13 % overall cover. A target of 30 % protection is suggested by the European Commission and is a central part of the EU Biodiversity Strategy for 2030. Furthermore, the valuable habitats are highly subjected to boating activity posing a risk for a decrease in the distribution of YOY fish habitats. Therefore, it is strongly encouraged to consider location refinement, expansion, and updated management of the MPA network, and to regulate the average number of boats allowed in ecologically valuable areas.

KEYWORDS

Baltic Sea, fish habitats, vegetation cover, fish species richness, recreational activities, boating, marine protected areas

Populärvetenskaplig sammanfattning

Kustområden i Östersjön är viktiga och produktiva områden för årsyngel av fisk. Grunda vegetationsbottnar bidrar med viktiga tjänster för årsyngel, då dessa habitat ger skydd från rovfiskar samt bidrar med föda. Däremot finns begränsad kunskap om förhållandet mellan mängden och artrikedomen av årsyngel och utbredningen av olika bottentyper samt miljövariabler. Utöver detta saknas även kunskap om relationen mellan viktiga yngelhabitat och olika intensitet av båttrafik samt om dessa habitat skyddas tillräckligt av marina skyddade områden. I denna studie försöker jag fylla ut kunskapsluckan om relationen mellan årsyngel och habitattäckning/miljövariabler genom att analysera data från 4,670 provtagningar längsmed den svenska Östersjökusten med hjälp av regressionsanalyser, Generalized Additive Models (GAMs). Provtagningarna utfördes av SLU Aqua mellan åren 2007 och 2018, genom små undervattens-detonationer för ansamling av fisk data, i samma område uppskattades även habitattäckning via snorkeldyk. Utöver detta mättes även flertalet miljövariabler. Rumsliga analyser av kopplingen mellan antal båtar och habitatutbredning samt representativiteten av viktiga yngelhabitat inom marina skyddade områden, utfördes i ArcGIS Pro 2.5.0. Resultaten visade att de viktigaste habitaten för hög artrikedom och abundans av årsyngel var vegetationsbottnar. Dessutom fanns samband mellan olika vegetations typer och individuella fiskarter. Dock, är dessa viktiga vegetationsbottnar inte tillräckligt skyddade av nätverket av marina skyddade områden, då dessa endast skyddade 13 % av vegetationsbottnar och målet enligt EU:s nya Biodiversitet Strategi för 2030 är att skydda 30 % av viktiga habitat. Utbredningen av vegetationsbottnar var även begränsade i områden med hög båttrafik. Därför uppmanas expansion, ökad representativitet och uppdatering av förvaltningen av MPA nätverket för att kunna skydda dessa viktiga yngelhabitat i större utsträckning, samt att reglera förekomsten av båtar i områden av högt ekologiskt värde.

NYCKELORD

Östersjön, fiskhabitat, vegetationstäckning, fisk diversitet, fritidsaktiviteter, båtaktivitet, marina skyddade områden

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Abbreviations

MPA	Marine Protected Area
YOY	Young-Of-the-Year
PSU	Practical Salinity Unit
GIS	Geographical Information Systems
SLU	Swedish University of Agricultural Sciences

1. Introduction

Coastal waters are highly productive and provide valuable habitats for many organisms (Hansen et al., 2019). Habitats consisting of aquatic vegetation provide many young-of-the-year (YOY) fish with nurseries, including food sources and refuges from predators (Eriksson et al., 2004; Rozas and Odum, 1988). Fish assemblages are highly influenced by the structural complexity of habitats, which provide many niches and thereby enhance species richness (Pihl and Wennhage, 2002). In hard bottom areas, the surface of high rugosity and stable substrate enables settlement of various species like macroalgae, increasing the complexity of the habitat (Gratwicke and Speight, 2005). Softbottom habitats also provide an important substrate for aquatic vegetation growth, for species that are more tolerant to sedimentation but generally sensitive to drag and tear such as angiosperms and charophytes (Eriksson et al., 2004). The geomorphology of each habitat therefore plays an important role for the habitat cover, regulating the occurrence of aquatic vegetation and hence fish species (Snickars et al., 2009). By forming canopies and meadows (Madsen et al., 2001), aquatic vegetation facilitates the settlement of small invertebrates providing fish with a valuable food source (Grenouillet and Pont, 2001; Wikström and Kautsky, 2007). A higher density of aquatic vegetation has also been found to correlate with less predation on fish than in unvegetated areas, due to shelter and reduced efficiency of predation by piscivores (Rozas and Odum, 1988). The condition of habitat is crucial for many fish species, and might be a limiting factor for survival rate (Pihl and Wennhage, 2002).

Both aquatic vegetation and fish depend on environmental conditions, e.g. salinity, temperature, secchi depth, wave exposure and eutrophication, which regulate their distribution (Mackenzie et al., 2007). The Baltic Sea, which is a semi-enclosed basin, has a salinity gradient created by the differences in saltwater inflow, outflow and freshwater runoff between different regions, causing conditions ranging from limnetic (< 1 PSU (Practical Salinity Unit)) in the north and north-east to marine conditions (25 PSU) in the southwest, with a salinity level of 5-8 PSU in the central basin (the Baltic Proper) (Ehlin, 1981; ICES, 2020; Mackenzie et al., 2007). The greater freshwater content of the northern Baltic Sea comes from meltwater from the numerous mountains by river input, precipitation as rain and higher snow accumulation (due to the lower annual temperature). Additional water input from the North Sea through the Danish sounds provide saltwater that blends the water mass into a brackish content, contributing to the higher salinity levels south and south-westwards (Ehlin, 1981). Additionally, the surface water temperature changes throughout the north-south gradient due to differences in climatic conditions, impacting the growth and recruitment of species (Sandström and Karås, 2002; Siegel and Gerth, 2015). This results in a mix of species of both freshwater and marine origin in the Baltic Sea. The distribution of both aquatic vegetation and YOY fish is therefore regulated by the salinity level (Snickars et al., 2009), temperature, secchi depth, which limits the light attenuation of the water mass (Bergström et al., 2013) and wave exposure, that form the physical harshness and disturbance of species and control their distribution (Friedlander et al., 2003; Snickars et al., 2009). Differences in secchi depth is highly connected to the concentration of phytoplankton biomass (Mazumder et al., 1990). An increase in nutrient loads, may result in eutrophicated coastal habitats, affecting ecosystems by the increase of both phytoplankton and epiphytic filamentous algal growth. Aquatic vegetation, in particular, is affected by these changes since a reduced secchi depth and excessive overgrowth of filamentous algae causes reduced photosynthesis and thereby limit growth and recruitment of species (Gagnon et al., 2017).

Anthropogenic stressors including eutrophication, coastal construction, recreational boating and fishing in the coastal zones contribute to habitat degradation that results in species decline (Hansen et al., 2019; Leppäkoski et al., 1999; Sundblad and Bergström, 2014). Some species are more sensitive to stressors such as *Chara spp.*, which has declined during the last part of the twentieth century (Hansen and Snickars, 2014; Havs- och vattenmyndighetens rapport, 2020). Degradation of valuable habitats caused by boating activities has different effects on organisms depending on the species (Sandström et al., 2005). Boats tend to physically damage vegetation, create scares and cuts from motorboat propellers, increase water turbidity, shadow vegetation with docks and enhance eutrophication by fuel emissions (Hansen et al., 2019; Sagerman et al., 2020). Furthermore, other human activities such as fishing may introduce trophic cascades by causing a decrease in the populations of large piscivores, thereby increasing the abundance of meso-predators. This can result in strong predation pressure on small grazers and ultimately increase the coverage of filamentous algae, degrading the function of aquatic vegetation as valuable fish nursery habitat (Donadi et al., 2017; Eklöf et al., 2020; Hansen and Snickars, 2014).

To preserve valuable habitats for functionally important groups, the Swedish national environmental objectives, the Helsinki (HELCOM) convention and the European Commission stated in the EU Biodiversity Strategy for 2030, aim to promote ecologically representative ecosystems through marine protected areas (MPAs). The protected areas consist of nature reserves, national parks and Natura 2000-sites, created with the goal of maintaining or restoring biodiversity, ecological functions and the physical structure of habitats (Naturvårdsverket, 2007; Sala et al., 2021). The MPAs are managed both by direct and indirect measures, where the direct management include regulation of area access, fishing, recreational activities, and restoration efforts, whereas the indirect management include public awareness, management and restoration of the water quality, regulation of nutrient and pollution emissions and inhibition of invasive species (HELCOM, 2007). Selection of sites is determined by the costs of implementing an MPA relative to conservation and management requirements (Leslie, 2005; Possingham et al., 2000). In addition to the ecological perspective, the MPAs enable restoration of ecosystem services like fisheries and tourism (HELCOM, 2010; Sundblad et al., 2011). Based on the MPA plan of integrating nature conservation with fisheries, a larger extent of habitat preservation may enhance the catches of commercially important fish stocks by fish “spill over” into surrounding areas (Sundblad et al., 2011). Today most oceans are protected to some extent although as argued by Berkström et al. (2019), Costello and Ballantine (2015) and Sala et al. (2021), these legislations are insufficient, and the negative impacts on biodiversity and ecosystem functioning proceed.

1.1 AIMS OF STUDY

This study aimed to (1) examine the relationship between young-of-the-year (YOY) fish species abundance/species richness and aquatic vegetation, substrate, and environmental variables such as surface temperature, wave exposure, secchi depth, salinity, and water depth in the Baltic Proper and the Gulf of Bothnia. Considering the stressors that the Baltic Sea experiences mainly due to anthropogenic activities, this study also aimed to (2) examine to what extent valuable habitats are protected by the MPA network in the Gulf of Bothnia to reduce the potentially negative impacts by human activities and (3) examine to what extent these YOY fish habitats are affected by physical impact from recreational boating. It was hypothesized that the percent cover of macrophytes would be of importance for YOY fish species, because vegetated habitats provide important functions, such as food and refuge (Rozas and Odum, 1988), and thereby enhance species richness and abundance. Since evidence suggests that the MPA network insufficiently cover ecologically important habitats (Berkström et al., 2019; Costello and Ballantine, 2015) it was hypothesized that the MPA network does insufficiently cover important habitats for YOY fish. Furthermore, these habitats were hypothesized to be negatively affected by the extent of docks and coastal boating activities, which may degrade these habitats by disturbances and physical damage (e.g. Hansen et al., 2019; Leppäkoski et al., 1999).

2. Material and Methods

2.1 STUDY AREA

The Baltic Sea is a brackish water-system located in northern Europe, ranging from having high freshwater contents in the north to more saline conditions in the south (Figure 1). This variation in salinity levels is mainly due to the drainage basins, that cover an area 4.3 times that of the sea itself, and by the inflow of saltwater through the Danish Straits (Ehlin, 1981; Lass and Matthäus, 1996). The large drainage areas providing the Baltic Sea with freshwater can be found in the northern and western parts of the sea, caused by the climatic conditions (e.g. rain and snow) in combination with the enclosure by mountains (Ehlin, 1981). Because of barotropic – and baroclinic currents the saltwater balance of the Baltic Sea is maintained. However, reduced baroclinic pressure caused by shallow sill depths, create an inconsistent bottom current inflow. Hence, westerly winds are the main driver for the Baltic Sea saltwater inflow (Lass and Matthäus, 1996). The surface water temperatures are affected by the climatic conditions, resulting in the yearly mean surface temperatures being lower in the north compared to the south (Siegel and Gerth, 2015). These variabilities in water properties create natural borders for species occurrences. The present study focus on two main basins in the Baltic Sea; the Gulf of Bothnia (salinity < 6 ppt) in the north and the Baltic Proper (salinity 6-10 ppt) in the south (Figure 1). In the Baltic Sea a mix of angiosperms and macroalgae occur with both freshwater and saltwater origin. Dominant aquatic vegetation with freshwater origin includes, *Chara tomentosa, Najas marina, Myriophyllum spicatum, Stuckenia pectinata* and *Potamogeton perfoliatus. Fucus vesiculosus* with saltwater origin occurs in coastal waters of the Baltic Proper. The highly variable substrate types occurring in the regions affect which of the two vegetation types that dominate, where angiosperms are mostly found on softbottom substrate in contrast to macroalgae that occur on hard substrate (Eriksson et al., 2004). The same variability, caused by water properties e.g. salinity and surface temperature, apply to fish species**,** where the origin of species determines whether it can be found more southward in marine conditions or northward in freshwater conditions (Sparholt, 1994). A network of MPAs can be found throughout the Baltic Sea which aim to protect the species in this region. In the Gulf of Bothnia, the network covers 2,955 km^2 of the coastal zones to ensure ecological functions, and if necessary restore habitat to achieve a favourable conservation status (Figure 1).

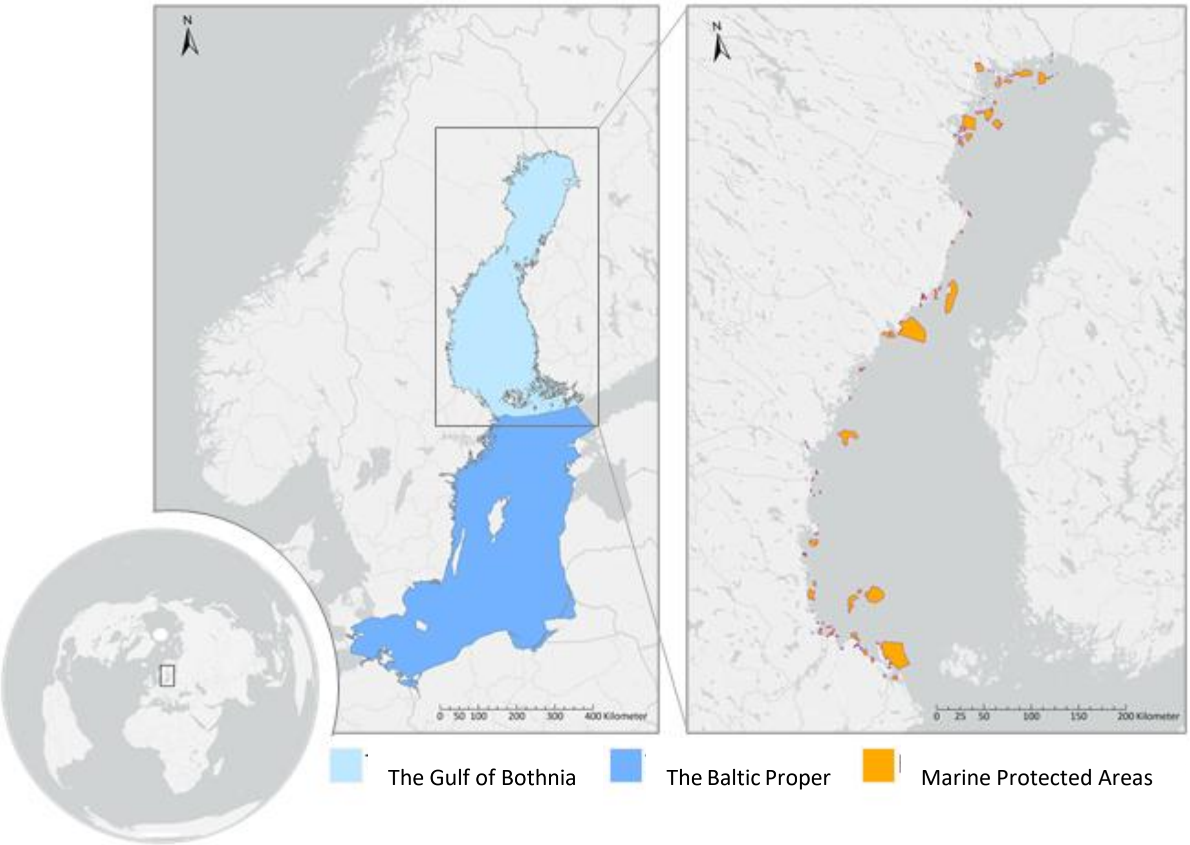

Figure 1: *Maps displaying the Baltic Sea. Map on the left highlights the two Baltic Sea basins examined in this study, in light blue the Gulf of Bothnia and in dark blue the Baltic Proper. On the right, the marine protected areas in the Gulf of Bothnia are displayed in orange.*

2.2 YOUNG OF THE YEAR FISH AND HABITAT INTERACTIONS

2.2.1 Data collection of fish abundance and habitat cover

In this study I used data on young-of-the-year fish, vegetation, substrate, and environmental variables provided by the Swedish University of Agricultural Sciences, Department of Aquatic Resources (SLU Aqua). These data were collected by SLU Aqua in national and local surveys, monitoring programmes and research projects. In total 4,670 samples were collected along the Swedish Baltic Sea coast, covering an approximately 1,150 km north-south extent. All data was collected during mid to late summer (late July to mid-September) between 2007 and 2018. Sampling of YOY fish was conducted by small underwater detonations, using a non-electric system with 10 g primers that target fish of maximum 20 cm in size. Stunned fish within this detonation area, of approximately a five-meter radius (~80 m^2), were collected by surface netting of floating individuals or underwater by snorkelling. Percentage cover of different substrate classes and macrophyte species were estimated within the detonated area by snorkelling. Vegetation cover could override 100 % coverage since vegetation grows in several dense layers on top of each other, resulting in measurements of so-called cumulative vegetation cover. The most common and ecologically important vegetation species were analysed in detail in this study. A total of 32 species of angiosperms and macroalgae were divided into four groups based on functionality/vegetation type. Rooted angiosperms were the most common types, while none-rooted angiosperms were rare with one recorded species only (Table 1). At all sites, the collected fish were identified to species and counted. Considering the annual changes in YOY fish abundance, the numerous and continuous samples included in this data set make up a robust data set to study the effect of environmental variables and habitat type on YOY fish assemblages (Hansen et al., 2019).

***Table 1**: Vegetation divided into four categories based on functionality and its occurrence in the Gulf of Bothnia and the Baltic Proper. The average vegetation cover (AVC) shown in percent (%) and the standard deviation (SD) for the Gulf of Bothnia (GOB) and the Baltic Proper (BP). Based on data of vegetation estimation in percent within a five meters radius from SLU Aqua. * only abundant for the Gulf of Bothnia. ** only abundant for the Baltic Proper.*

Vegetation	Common name	Rooted angiosperm	Non-rooted angiosperm	Rooted macroalgae	Non-rooted macroalgae	AVC GOB (%) +/-SD	AVC BP (%) +/-SD
Callitriche hermaphroditica	Northern water-starwort	X				2.2 +/-8.9	0.4 +/-4.0
Ceratophyllum demersum	Hornwort		X			0.7 +/-5.6	2.1 +/-7.9
Chara aspera	Rough stonewort			X		4.1 +/-15.5	2.6 +/-12.1
Chara baltica	Baltic stonewort			X		0.4 +/-3.3	1.4 +/-8.3
Chara canescens	Bearded stonewort			X		<0.1+/-<0.1	0.2 +/-2.8
Chara connivens	Convergent stonewort			X*		<0.1 +/-0.2	
Chara fragilis/globularis	Fragile stonewort			X*		0.1 +/-1.8	0.1 +/-0.9
Chara horrida				X		<0.1 +/-0.5	0.1 +/-1.3
Chara tomentosa	Coral stonewort			X		3.9 +/-1.5	1.3 +/-8.2
Chara virgata	Delicate stonewort			X		0.1 +/-2.4	<0.1 +/-0.2
Chorda filum	Sea lace				X**		1.4 +/-5.3
Filamentous algae					X**		3.2 +/-14.9
Fucus vesiculosus	Bladder wrack				X	1.5 +/-9.5	10.5 +/-22
Fucus radicans	Narrow wrack				X	0.1 +/-2.5	<0.1 +/-0.8
Furcellaria lumbricalis	Clawed fork weed				X**		0.4 +/-3.9
Lemna trisulca	Star duckweed	X				3.4 +/-16.4	0.4 +/-5.6
Monostroma balticum	Baltic sea lettuce				X**		0.5 +/-4.4
Myriophyllum alterniflorum	Alternateflower watermilfoil	X*				0.5 +/-4.0	
Myriophyllum sibiricum	Siberian watermilfoil	X				3.2 +/-10.9	0.5 +/-4.0
Myriophyllum spicatum	Eurasian watermilfoil	X				0.9 +/-5.3	4.3 +/-11.1
Myriophyllum verticillatum	Whorl-leaf watermilfoil	X*				0.1 +/-0.9	
Najas marina	Spiny naiad	X				7.2 +/-19.9	5.1 +/-16.3
Phragmites australis	Common reed	X				0.8 +/-3.9	1.3 +/-5.1
Polysiphonia					X**		0.4 +/-4.9
Potamogeton perfoliatus	Perfoliate pondweed	X				5.1 +/-12.6	3.4 +/-9.2
Ruppia cirrhosa	Spiral ditchgrass	X**					3.0 +/-9.9
Ruppia sp.	Ditchgrass	X**					0.6 +/-3.9
Stuckenia filiformis	Fineleaf pondweed	X*				0.2 +/-3.1	
Stuckenia pectinate	Sago pondweed	X				9.2 +/-18.7	14.3 +/-22
Vaucheria spp.	Yellow-green algae				X	3.6 +/-16.2	2.3 +/-13.5
Zannichellia palustris	Horned pondweed	X				1.5 +/-7.7	2.0 +/-8.3
Zostera marina	Eelgrass	X**					2.5 +/-10.5

2.2.2 Substrate type

Substrate type may both favour or disfavour vegetation growth depending on vegetation type. The substrate itself may also provide food and shelter for fish depending on complexity (Pihl and Wennhage, 2002) and could therefore be an additional important explanatory variable for YOY fish abundance. Thus, substrate type was included in this study with data provided by SLU Aqua where they classified substrate by seven categories based on the Swedish standard SS-EN ISO 14688-1:2002; *bedrock*, *large boulders* (> 600 mm), *boulders* (200–600 mm), *stones* (20–200 mm), *gravel* (2–20 mm), *sand* (0.2–2 mm) and *finer sediment* (<0.06 mm).

2.2.3 Environmental variables

To analyse various factors that may impact the abundance of YOY fish communities, I used the abiotic variables surface wave exposure, salinity, secchi depth, surface temperature and water depth in addition to the vegetation - and substrate data in the prior analysis. Calculation for wave exposure in the data set by SLU Aqua were produced with the technique established by Isæus (2004), called the simplified wave exposure model (SWM), where a new software called WaveImpact 1.0 was used to improve the grid calculations. This software also considered both wave refraction and diffraction effects, combined with average wind conditions over a five-year period. With measurements from 16 compass directions a surface wave exposure model was produced. The secchi depth data provided by SLU Aqua were measured by a secchi disc with a 10-centimetre precision. The secchi depth was measured prior to the detonation and not directly at the sample site to avoid alarming nearby fish. The salinity data provided by SLU Aqua were measured at 1 meter above the bottom substrate and measured at each sample site. They also measured water depth, where a marked wire was lowered at the detonation site with a 10-centimetre precision. The dataset provided by SLU Aqua contained measurements of secchi depth and wave exposure at each sample site, however I used supplementary data on wave exposure provided by Isæus, (2004) and secchi depth data provided by Erlandsson et al., (2021). The secchi depth models produced by Erlandsson et al. (2021) covered the eastern coastline of the Baltic Sea. They were created by using Generalized Additive Models (GAM) including water transparency field data from April to September 2002-2018, provided by SHARK (Svenskt HavsARKiv), and were used as response variables. The predictors of Erlandsson et al. (2021) models were water depth, landmass within 5 km radius, distance from baseline, distance from large water basin, distance from 10-meter bathymetric contour, average wave exposure within 1 km radius and one coordinate variable, resulting in a comprehensive secchi depth model for the Baltic Sea (Erlandsson et al., 2021).

2.2.4 Data analysis

In order to test the effects of environmental variables, substrate- and vegetation types on YOY fish abundance and species richness, Generalized Additive Models with random effect (GAMs) were conducted. Variability in ecological data creates challenges in the choice of statistical models. Therefore, three different models (Generalized Linear Mixed Models (GLMMs), Negative Binomial Regression Models (NBs) and GAMs) were tested in R (version 1.3.1073) to provide the most parsimonious models. This resulted in the Generalized Additive Models (GAMs) (package *mgcv*) (Hastie, 2020) being used due to overall best fit, although indicating overdispersion, based on a combination of diagnostics plots and the Akaike information criterion (AIC-values), seeking the lowest values (Akaike, 1974). Furthermore, overdispersion was tested using the Pearson's chi-squared test where models with maximum values of 1 were considered the most parsimonious ones. Multicollinearity between predictor variables (wave exposure, salinity, surface temperature, water depth, secchi depth, substrate and vegetation types) was assessed using variance inflation factor (VIF) (package *car*) (Fox and Monette, 1992), with a cut-off of VIF = 2. The latter predictor variable was grouped by four vegetation types and was also analysed by species (Table 1). The variable *finer sediments* was removed since it had a VIF value above 2, proposing that the variable could be linearly predicted from the other predictor variables. The predictor variables were scaled and occasionally log scaled due to high variability in measures. The 3 response variables used were (1) total fish abundance, (2) fish species abundance, and (3) fish species richness (number of species). The analyses were conducted per basin, with one group of analyses focusing on the Gulf of Bothnia and one on the Baltic Proper. This division reflects the differences in salinity levels and hence the changes in species composition. "Area" and "Year" were set as random variables in the GAMs to account for variability within an area and the yearly fluctuations of YOY fish within areas. Based on significance of variables (p-value < 0.05) from the abundance and species richness analyses, valuable YOY fish habitats were identified to be used in the next step of the study.

2.3 PROTECTION AND DISTURBANCE OF FISH RECRUITMENT HABITATS

2.3.1 Spatial analyses

For the spatial analyses of important YOY fish habitats I used modelled vegetation maps provided by Florén et al. (2018) with a 250 m^2 resolution, since vegetated habitats were identified by the statistics in section 2.2 as essential habitats for most YOY fish species. I used the most recent updated map from 2019 of marine protected areas (Natura 2000-sites and nature reserves) covering the Gulf of Bothnia provided by SLU Aqua, to see if the essential YOY fish habitats were sufficiently protected. The protection of habitats was derived in percentage (%) to evaluate the efficiency of the network compared with the suggested goal of representativity by the EU Biodiversity Strategy for 2030 suggesting a cover of ≥30 % (European Commission, 2020). Additionally, recreational boating was analysed with an average berth abundance map with 0.25 km^2 resolution provided by Moksnes et al. (2019) with the aim to analyse the possible correlation between vegetation presence/absence and recreational boating. These analyses were conducted in ArcGIS Pro 2.5.0. The spatial analysis was divided into two parts, (I) calculation of percent vegetation included in marine protected areas (MPAs) and (II) percent vegetation related to recreational activities where berth abundance was used as a proxy for anthropogenic pressure on the marine environment. The Europe Albers equal areas conic projection was used to reduce distortion for all data, because of its adjustment for use in temperate zones (Snyder, 1987). Since most aquatic vegetation was found to promote YOY fish abundance and species richness (see results below), only total vegetation cover, and not vegetation types nor vegetation species, was included. Although, to nuance the findings, the partly red listed *Chara spp.* were also analysed based on their important ecological function for fish assemblages, their exposure to human activities as well as their vulnerability to increased nutrient loads (Hansen and Snickars, 2014; Havs- och vattenmyndighetens rapport, 2020).

The spatial predictions in vegetation maps provided by Florén et al. (2018) were generated using statistical modelling of data collected in the field. For the modelling process, environmental variables were correlated to the response variables (e.g., vegetation coverage). Florén et al. (2018) used ensemble modelling conducted by the package *BIOMOD2*. Generalized Additive Models (GAMs), RandomForest (RF), Generalized Boosting Model/Boosting Regression Trees (GBMs), Artificial Neural Network (ANN) and Flexible Discriminant Analysis (FDA) were used to produce the best prediction. Thereafter the model was evaluated for certainty and data variation to produce a map prediction. The prediction was calculated by the environmental variables and the response variable in a raster dataset, resulting in a final spatial prediction. The prediction is a probability-based map with a value between 0 and 1. The quality of the prediction was validated using Map-based area under curve (MapAUC). Lastly, a prediction was made for the combined data set (modelling and validation data) to calculate the sensitivity and specificity, to enable separation of prediction data values between absence and presence. The data output of prediction variables with presence was thereafter divided into sections of probabilities, based on the certainty of the model (“high expectation” - and “low expectation” of vegetation occurrence). For the present study only the high expectation data output from Florén et al. (2018) was used to optimise the certainty of results.

2.3.2 Overlay analysis - MPAs

The MPA network in this study includes nature reserves and Natura 2000-sites, based on the most recent update of the network from 2019 provided by SLU Aqua. To evaluate if the current MPA network offers adequate protection of important vegetation habitats for YOY fish communities, spatial overlay analyses with the “intersect” tool in ArcGIS were performed. The analysis was used to create a new shapefile displaying vegetated areas within the MPAs. By calculating vegetation in the Gulf of Bothnia as well as the area of vegetation within the MPAs, the overlap between MPAs and vegetated habitats could be estimated in square kilometres and percent.

2.3.3 Overlay analysis - boating

To estimate the potential impact of boating activities on vegetation, the “intersect” and “spatial join” tools in ArcGIS Pro 2.5.0 were used. For the prediction, the modelled vegetation distribution map by Florén et al. (2018) and a berth abundance map covering the entire Swedish coast created by Moksnes et al. (2019) were used. Moksnes et al. (2019) calculated the average number of berths per 0.25 km^2 by multiplying the sum of length of all docks within the 0.25 km^2 area with 0.23, which is the average number of moorings found per meter of dock. The data for that analysis originated from maps provided by Metria from Törnqvist et al. (2020).

To standardize the berth abundance data I used discrete values to present a range of average berth abundances (ABAs). The discrete values used were, 5 (ABA ≤ 5), 10 (ABA > 5 & ABA ≤ 10), 20 (ABA > 10 & ABA ≤ 20), 40 (ABA > 20 & ABA ≤ 40), 60 (ABA > 40 & ABA ≤ 60), 80 (ABA > 60 & ABA ≤ 100) and 100 (ABA ≥ 100). To be able to compare ABA with vegetation data, an average vegetation cover for every 0.25 km^2 was calculated for the same area. To investigate if the spatial distribution of vegetation is negatively affected by recreational boating activity, vegetation cover was estimated in square kilometres and in percentage per 0.25 km^2 area. In addition, the same analyses was conducted for *Chara spp.,* which represent the more sensitive species (Eriksson et al., 2004; Hansen and Snickars, 2014).

3. Results

3.1 YOUNG OF THE YEAR FISH AND HABITAT INTERACTIONS

In total 36 species of YOY fish were identified, where some were more abundant than others. Out of the total, 14 species were selected for this study to represent the most common YOY fish (for the Gulf of Bothnia and the Baltic Proper). However, the northern pike in the Gulf of Bothnia was included due to its ecological importance although not being an abundant species (Table 2). The north-south salinity gradient of the Baltic Sea results in different species compositions in the different basins. Common YOY fish species with freshwater origin in the

Table 2: YOY fish species presence (X) and proportion (%) of catch in the Gulf of Bothnia and the Baltic Proper.

Fish species	Common name	Gulf of Bothnia	Abundance Gulf of Bothnia (%)	Baltic Proper	Abundance Baltic Proper (%)
Abramis brama/Blicca bjoerkna	Common/silver bream	X	1.0	X	1.2
Alburnus alburnus	Common bleak	X	6.2	X	9.2
Clupea harrengus	Atlantic herring	X	2.2	X	12
Esox Lucius	Northern pike	X	0.2	X	1.1
Gasterosteus aculeatus	Three spined stickleback	X	68	X	48
Gobiusculus flavescens	Two-spotted goby			X	0.4
Gobius niger	Black goby			X	0.4
Gymnocephalus cernua	Eurasian ruffe	X	0.4		
Osmerus eperlanus	European smelt			X	0.4
Perca fluviatilis	European perch	X	8.5	X	5.3
Pungitius pungitius	Nine spined stickleback	X	1.8	X	1.4
Rutilus rutilus	Common roach	X	8.5	X	19.7
Scardinius erythrophthalmus	Common rudd	X	0.9		
Tinca tinca	Tench	X	0.9		

Gulf of Bothnia found in this data set were Eurasian ruffe (*Gymnocephalus cernua*), tench (*Tinca tinca*) and common rudd (*Scardinius erythrophthalmus*) while saltwater originated species such as black goby (*Gobius niger*) and two spotted goby (*Gobiusculus flavescens*) dominated in the Baltic Proper as well as the European smelt (*Osmerus eperlanus*) despite being of freshwater origin. Regardless of the differences in water properties, species with both freshwater and saltwater origin such as the freshwater originated species European perch (*Perca fluviatilis*), northern pike (*Esox lucius*), common bleak (*Alburnus alburnus*), common roach (*Rutilus rutilus*) common/silver bream (*Abramis brama/Blicca bjoerkna*), and the saltwater originated species Atlantic herring (*Clupea harrengus*), three-spined stickleback (*Gasterosteus aculeatus*) and nine-spined stickleback (*Pungitius pungitius*) occured in both basins (Table 2).

3.1.1 YOY fish abundance analyses

There was a positive relationship between total abundance of YOY fish (no. of fish/m^2) and cumulative vegetation cover (in percent) in both the Gulf of Bothnia and the Baltic Proper (Figure 2). However, not all YOY fish species displayed correlation with total cumulative vegetation cover. These species mostly varied between basins, although common/silver bream showed no evident relationship for either basin. The basin-specific species with no correlation with total cumulative vegetation cover were for the Gulf of Bothnia, common bleak, while for the Baltic Proper it was nine-spined stickleback. Additionally, the Atlantic herring in both basins displayed a negative relationship with total cumulative vegetation cover, while the basin-specific species were for the Gulf of Bothnia, common rudd, Eurasian ruffe and for the Baltic Proper, two-spotted goby, black goby and European smelt (Figure 2 & Appendix 1). A decrease in YOY fish abundance was found around 200% cumulative vegetation cover for the Baltic Proper (Figure 2B) while the Gulf of Bothnia displayed a steady increase (Figure 2A).

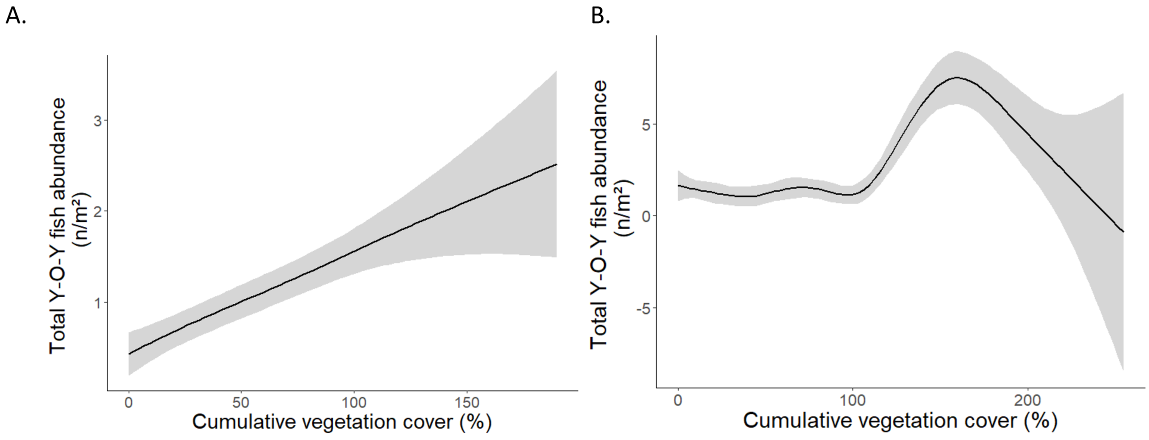

Figure 2: *Regression plots from GAMs displaying positive relationships between fish abundance (number of individuals per m^2) and cumulative vegetation cover in percent (%) in (A) the Gulf of Bothnia and (B) the Baltic Proper. Confidence intervals are displayed with the grey area.*

When separated into vegetation types (Table 1), there were significant positive relationships found between rooted angiosperms and many YOY fish species in both the Gulf of Bothnia and the Baltic Proper, including common roach, European perch, northern pike, tench (only Gulf of Bothnia), common/silver bream and three-spined stickleback (Appendix 1 & 2). However, the Atlantic herring differed between basins, with a positive relationship in the Gulf of Bothnia but a negative relationship in the Baltic Proper (Table 3 & Table 4). There was also a significant positive relationship between non-rooted macroalgae and fish abundance in the Gulf of Bothnia for the common rudd, nine-spined stickleback and three-spined stickleback while this was found for the northern pike, two-spotted goby, black goby, nine-spined stickleback and three-spined stickleback in the Baltic Proper (Table 3 & Table 4). Additionally, there was a significant positive relationship between rooted macroalgae and northern pike, tench, three-spined stickleback, and a negative relationship between rooted angiosperms and Eurasian ruffe in the Gulf of Bothnia. A positive relationship between rooted macroalgae and total fish abundance was found in the Baltic Proper, although a negative relationship was found for the two-spotted goby and Atlantic herring (Table 3 & Table 4).

Table 3*: Relationship between fish abundance and five categories of vegetation types for the Gulf of Bothnia. Significant relationships illustrated by asterisk (*), *** = 0.001, ** = 0.01 and * = 0.05. Symbols within brackets denote positive or negative relationships. Empty cells indicate no relationship found between variables.*

Fish species	Rooted angiosperm	Non-rooted angiosperm	Rooted macroalgae	Non-rooted macroalgae	Total vegetation
Atlantic herring	(+) ***				(-) ***
Tench	(+) ***		(+) ***		(+) ***
Common bleak					
Common/Silver bream	(+) *				
Common roach	(+) ***				(+) ***
Common rudd				(+) ***	(-) *
Eurasian ruffe	(-) **				(-) ***
European perch	(+) ***				(+) ***
Nine spined stickleback				(+) ***	(+) ***
Northern pike	(+) ***		(+) ***		(+) ***
Three spined stickleback	(+) ***	(-) **	(+) ***	(+) ***	(+) ***
Total fish species	(+) ***			(+) ***	(+) ***

Table 4: *Relationship between fish species and five categories of vegetation types for the Baltic Proper. Significant relationships illustrated by asterisk (*), *** = 0.001, ** = 0.01 and * = 0.05. Symbols within brackets denote positive or negative relationships. Empty cells indicate no relationship found between variables.*

Fish species	Rooted angiosperm	Non-rooted angiosperm	Rooted macroalgae	Non-rooted macroalgae	Total vegetation
Atlantic herring	(-) ***		(-) ***		(-) ***
Black goby	(-) ***			(+) ***	(-) *
Common bleak				(-) **	(+) ***
Common/Silver bream	(+) ***				
Common roach	(+) ***				(+) ***
European perch	(+) **				(+) ***
European smelt					(-) ***
Nine spined stickleback				(+) ***	
Northern pike	(+) ***			(+) ***	(+) ***
Three spined stickleback	(+) ***			(+) ***	(+) ***
Two spotted goby			(-) *	(+) *	(-) ***
Total fish species	(+) ***		(+) ***	(+) ***	(+) ***

While looking closer at the individual species of vegetation types positive relationships were found between some plant species and YOY fish species abundance (Appendix 3). However, some plant species tended to have a negative relationship with certain YOY fish. The filamentous algae in the Baltic Proper had a positive relationship with three-spined stickleback and nine-spined stickleback, while displaying a negative relationship with northern pike and black goby. The abundance of total YOY fish species was positively correlated to most individual plant species, except for *Phragmites australis* for the Gulf of Bothnia (Appendix 3A) and *Vaucheria spp., Ruppia sp., Chorda filum, Callitriche hermaphroditica, Chara tomentosa* and *Chara fragilis/globularis* for the Baltic Proper (Appendix 3B). The relationships between fish abundance and variables such as surface temperature and water depth differed for the same species in different basins (Table 5 & Table **6**). In the Gulf of Bothnia finer sediments correlated positively with all YOY fish species and European perch and northern pike in the Baltic Proper, although negatively for the two-spotted goby, black goby, Atlantic herring and three-spined stickleback (Table 5 & Table **6**).

Table 5: *Significant relationships between fish abundance and environmental variables for the Baltic Proper. Significant relationships illustrated by asterisk (*), *** = 0.001, ** = 0.01 and * = 0.05. Symbols within brackets denote positive or negative relationships. Empty cells indicate no relationship found between variables.*

Fish species	Substrate	Water properties	Environmental variables
Atlantic herring	(-) * Finer sediments	(+) *** Salinity (+) *** Surface temperature	(+) *** Water depth
Black goby	(-) *** Finer sediments	(+) * Salinity	
Common bleak	(-) ** Bedrock	(+) ** Surface temperature (-) ** Secchi depth	(-) *** Wave exposure
Common/Silver bream		(+) ** Surface temperature	(-) *** Wave exposure
Common roach	(-) *** Gravel	(-) *** Salinity (-) ** Secchi depth	
European perch	(+) ** Finer sediments	(-) * Salinity (+) ** Surface temperature (-) *** Secchi depth	(-) *** Wave exposure
European smelt			
Nine spined stickleback		(+) *** Salinity (-) *** Surface temperature	
Northern pike	(-) *** Bedrock (+) *** Finer sediments	(-) *** Salinity	(+) *** Water depth
Three spined stickleback	(-) *** Finer sediments	(+) *** Salinity (+) *** Surface temperature (+) * Secchi depth	(+) *** Water depth
Two spotted goby	(+) *** Bedrock (-) *** Finer sediments		(+) *** Wave exposure

***Table 6:** Significant relationships between fish abundance and environmental variables for the Gulf of Bothnia. Significant relationships illustrated by asterisk (*), *** = 0.001, ** = 0.01 and * = 0.05. Symbols within brackets denote positive or negative relationships. Empty cells indicate no relationship found between variables.*

Fish species	Substrate	Water properties	Environmental variables
Atlantic herring	(-) ** Large stones (+) *** Sand (+) *** Finer sediments	(+) *** Salinity (-)** Surface temperature (-) *** Secchi depth	(+) *** Water depth
Common bleak	(+) *** Finer sediments	(-) *** Secchi depth	(-) *** Water depth
Common/Silver bream	(+) *** Finer sediments	(-) *** Secchi depth	(-) *** Wave exposure
Common roach	(+) *** Finer sediments	(-) *** Salinity (+)***Surface temperature (-) *** Secchi depth	(-) *** Wave exposure
Common rudd	(+) *** Finer sediments		
Eurasian ruffe	(-) ** Large stones (+) *** Finer sediments	(-) ** Salinity (-) *** Secchi depth	
European perch	(+) *** Finer sediments	(-) *** Salinity (+)** Surface temperature (-) *** Secchi depth	(-)***Wave exposure (-) *** Water depth
Nine-spined stickleback	(+) *** Finer sediments	(+) * Salinity	(-) ** Water depth
Northern pike	(+) *** Finer sediments	(-) *** Salinity (-) ** Secchi depth	
Tench	(+) *** Finer sediments		(-)***Wave exposure (-) ** Water depth
Three-spined stickleback	(+) *** Large stones (+) *** Finer sediments	(+) *** Salinity (-)** Surface temperature (+) *** Secchi depth	(-) *** Water depth

3.1.2 YOY fish species richness analyses

In the Gulf of Bothnia fish species richness positively correlated with all vegetation types. However, a positive relationship was only found between the rooted angiosperms and non-rooted macroalgae and fish species richness in the Baltic Proper (Table 7 & Appendix 4).

Table 7: *Relationship between fish species richness and five categories of vegetation types in the Gulf of Bothnia/ the Baltic Proper. Significant relationships illustrated by asterisk (*), *** = 0.001, ** = 0.01 and * = 0.05. Symbols within brackets denote positive or negative relationships. Empty cells indicate no relationship found between variables.*

Fish species richness	Rooted angiosperm	Non-rooted angiosperm	Rooted macroalgae	Non-rooted macroalgae	Total vegetation
The Gulf of Bothnia	(+)***	(+)**	(+)**	(+)***	(+)***
The Baltic Proper	(+)***			(+)***	(+)***

At around 150 % cumulative vegetation cover, an initiated decline in YOY fish species richness was found in the Baltic Proper (Figure 3B). However, this decline was not found in the Gulf of Bothnia, where a relatively steady increase in fish species richness with cumulative vegetation cover was found (Figure 3A). Additionally, YOY fish species richness in all basins positively correlated with most plant species, with exceptions of *Zannichellia palustris, Polysiphonia* and *Ruppia sp.* for the Baltic Proper (Table 8). A significantly negative relationship was also found between YOY fish species richness and secchi depth for both basins, but a positive relationship between species richness and finer sediments in both basins. Fish species richness also positively correlated with surface temperature for the Gulf of Bothnia (Table 9).

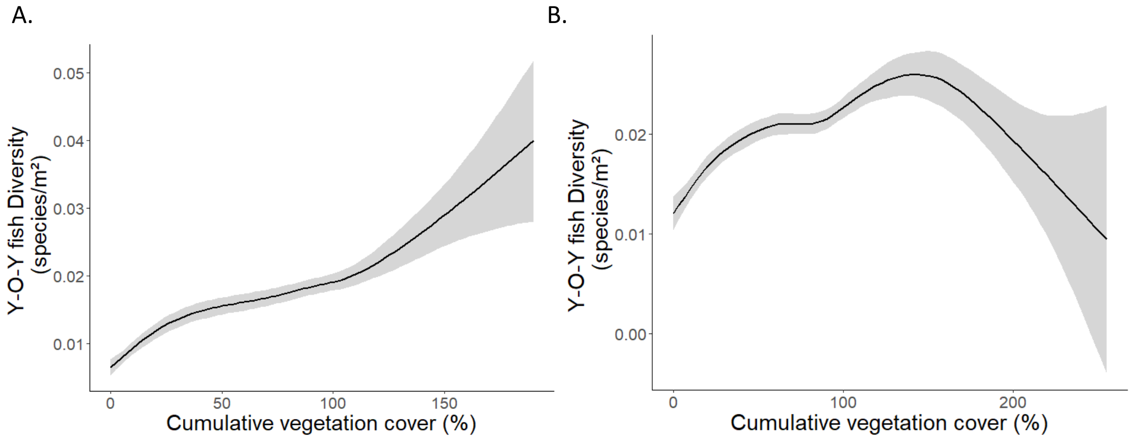

Figure 3: *Regression plots from GAMs displaying relationships between fish species richness (number of fish species per m^2) and percent vegetation cover in (A) the Gulf of Bothnia and (B) the Baltic Proper. Confident interval displayed by grey area.*

Table 8: *Significant relationships between species richness and vegetation species in the Gulf of Bothnia and the Baltic Proper. Positive or negative relationships between species richness and vegetation species displayed by +/- sign. Empty cells indicate no relationship found between variables.*

Vegetation species	Common name	Fish species richness	
		The Gulf of Bothnia	The Baltic Proper
Callitriche hermaphroditica	Northern water-starwort	(+)***	
Ceratophyllum demersum	Hornwort	(+)***	
Chara spp.	Stonewort		
Fucus vesiculosus	Bladder wrack	(+)*	(+)***
Lemna trisulca	Star duckweed	(+)***	
Myriophyllum alterniflorum	Alternate flower watermilfoil		
Myriophyllum sibiricum	Siberian watermilfoil	(+)**	(+)**
Myriophyllum spicatum	Eurasian watermilfoil	(+)***	
Najas marina	Spiny naiad	(+)***	(+)***
Phragmites australis	Common reed	(+)***	(+)***
Polysiphonia			(-)*
Potamogeton perfoliatus	Perfoliate pondweed	(+)***	
Ruppia sp.	Widgeon grass		(-)*
Stuckenia pectinata	Sago pondweed	(+)***	(+)***
Vaucheria spp.	Yellow-green algae	(+)***	(+)***
Zannichella palustris	Horned pondweed		(-)*

Table 9: *Significant relationships between fish species richness and habitat variables in the Gulf of Bothnia/the Baltic Proper. Significant relationships illustrated by asterisk (*), *** = 0.001, ** = 0.01 and * = 0.05. Symbols within brackets denote positive or negative relationships. Empty cells indicate no relationship found between variables.*

Fish species richness	Substrate	Water properties	Environmental variables
The Gulf of Bothnia	(+) *** Finer sediments	(+)* Surface temperature (-)*** Secchi depth	
The Baltic Proper	(+) * Finer sediments	(-)* Secchi depth	

3.2 PROTECTION AND DISTURBANCE OF FISH RECRUITMENT HABITATS

3.2.1 Protection by MPAs

The MPA network with an area of 2,955 km^2 in the Gulf of Bothnia covers 13 % of essential YOY fish habitats, identified in section 3.1.1 as vegetated areas along the eastern coastline of Sweden (covering a total of 1,960 km^2). 87 % of key habitats remains without protection by direct or indirect management (Table 10). *Chara spp.* had an MPA coverage of 20 % (Table 10).

Table 10: *Calculated percentage coverage of (coastal) vegetation and marine protected areas (MPA) for Gulf of Bothnia in square kilometers (km^2) and percentage (%).*

	Square kilometers (km^2)	Percentage (%)
Total vegetation within MPA	254	13
Chara spp. within MPA	37	20

3.2.2 Disturbance by recreational boating

The highest average vegetation cover (40 %) was found when the average number of berths was the lowest (5 berths). An increase in the average number of berths correlates with a general decrease in average vegetation cover (Table 11). However, this trend was not found for *Chara spp.,* which generally had a low abundance under 23 % cover irrespective of the average number of berths (Table 12).

Table 11*: Calculated average vegetation cover in both square kilometres (km^2) and percentage (%) with different densities of docks corresponding to a maximum of average 5, 10, 20, 40, 60, 80 and 100 berth per 0.25 km^2 .*

Average number of berths per site (0.25 km^2)	Average vegetation cover per site (km^2)	Average vegetation cover per site (%)
5	0.101	40
10	0.072	29
20	0.069	28
40	0.049	20
60	0.028	11
80	0.048	19
100	0.057	23

Table 12: *Calculated average Chara spp. cover in both square kilometres (km^2) and percentage (%) with different densities of docks corresponding to a maximum of average 5, 10, 20, 40, 60, 80 and 100 berths per 0.25 km^2.*

Average number of berths per site (0.25 km^2)	Average *Chara spp.* cover per site (km^2)	Average *Chara spp.* cover per site (%)
5	0.043	17
10	0.034	14
20	0.031	12
40	0.010	4
60	0.031	12
80	0.003	1
100	0.057	23

4. Discussion

As hypothesized, aquatic coastal vegetated habitats are important for several YOY fish species. The results of the Generalized Additive Models (GAMs) displayed that a higher cumulative vegetation cover increased both total YOY fish abundance and species richness. In line with the hypotheses, the MPA network had an insufficient protection of YOY fish habitats as spatial analysis showed that only 13 % of coastal vegetation is currently protected whereas the suggested target by the European Commission for habitat protection is 30 % cover (European Commission, 2020). Additionally, a relationship was found between a decrease in vegetation cover and increased number of berths. However, no relationship was found between the cover of the vulnerable species *Chara spp.* and boating activity, *Chara spp.* occurred in relatively low densities, which could be an effect of adaptation and habitat competition (Hansen et al., 2019; Van den Berg et al., 1999).

4.1 VEGETATION ENHANCES FISH ABUNDANCE AND SPECIES RICHNESS

The positive correlation between total YOY fish abundance/species richness, and vegetation cover, indicates that vegetation plays an important role for YOY fish. This relationship relies on several functions which aquatic vegetation provide, such as refuge and food availability (Eriksson et al., 2004; Grenouillet and Pont, 2001). Prey of larger YOY fish usually occur in densely vegetated habitats, enhancing foraging profitability and fish growth (Rozas and Odum, 1988). However, not all YOY fish species in my study were correlated with these habitats, possibly because of the different preferences in habitat structures (e.g., open water or bare substrate), habitat competition and tolerance to different environmental conditions (e.g., turbidity), which may result in wider distributions of YOY fish species (Sandström and Karås, 2002; Snickars et al., 2009; Winfield, 1986).

Of all four vegetation types (rooted/non-rooted angiosperms and rooted/non-rooted macroalgae), the rooted angiosperms correlated most frequently with the abundance and species richness of YOY fish. These plant species usually occur in softbottom habitats (Eriksson et al., 2004), and may explain the positive relationship between finer sediments and many YOY fish species. The positive relationship between rooted angiosperms and YOY fish is likely due to the larger plant size of rooted angiosperms compared to the other vegetation types, hence offering the most habitat for YOY fish. Other vegetation types also influenced the abundance of YOY fish but differed between basins. Differences in YOY fish habitat preferences may be an effect of habitat suitability, quality and types (Fulton et al., 2020; Snickars et al., 2009). The structural complexity of habitats is also suggested to play an important role for YOY fish, since more complex habitat provides more food and shelter (Gratwicke and Speight, 2005). Changes in habitat quality, i.e. alterations of vegetated habitat, might affect the fish assemblage and species richness (Pihl et al., 1994). A common alteration in the Baltic Sea is increased filamentous algal growth, that has been found to impact the quality of habitats by filamentous algae smothering and impeding the growth of large macrophytes and hence decreasing their potential as nursery and feeding grounds for many fish (Sandström and Karås, 2002). Because of their small body sizes, YOY and juvenile fish are exposed to high predation risk and may therefore be tightly linked to more complex habitat, such as vegetation, that offers adequate protection from predators (Gratwicke and Speight, 2005; Ismail et al., 2018).

Correlations to specific plant and algal species also differed between YOY fish species. The abundances of total YOY fish, European perch and common/silver bream negatively correlated with increasing coverage of common reed (*Phragmites australis*) in the Gulf of Bothnia whereas total YOY fish and common/silver bream in the Baltic Proper displayed a positive relationship. Additionally, for both basins the common roach had a negative correlation with common reed. As the vegetation serves as a spawning habitat for both the common roach and the European perch (Čech et al., 2009; Härmä et al., 2008), the negative relationships found in the Gulf of Bothnia are surprising. Changes in the distribution of common reed has, however, shown to affects the overall biodiversity in these habitats (e.g. Chambers et al., 1999; Hellings and Gallagher, 1992). Common reed has in recent years increased in abundance and distribution due to change in coastal management and eutrophication (Härmä et al., 2008), which has formed a more homogenous reed belt, reducing the biodiversity and possibly food availability for YOY fish (Chambers et al., 1999; Hellings and Gallagher, 1992; Pitkänen et al., 2013). This may explain the negative relationship between YOY fish abundance and common reed in the Gulf of Bothnia. It could possibly also be an effect of sampling bias, where the chosen sampling method is not well adapted to densely vegetated reed belts. As these areas are inaccessible by boat, this may affect the sampling and indirectly the relationship between fish species and common reed in this study.

Other vegetation species which were found to be of importance for the ecological system was the cover of filamentous algae. The algae were found to correlate negatively with the northern pike but positively with the three-spined stickleback (hereafter "stickleback") in the Baltic Proper. There has been a steady increase of the meso-predatory stickleback during the last century (Eklöf et al., 2020), and sticklebacks was also found in this study to have the highest abundance among YOY fish species in both basins. Eklöf et al. (2020) suggested that the increase is connected to climate change, eutrophication and the decrease of predatory fish (e.g. European perch and northern pike) due to e.g., overfishing and habitat destruction. Through trophic cascades, caused by the reduction of large predators, the increased meso-predator abundance suppress invertebrate grazers, which benefit filamentous algal growth (Donadi et al., 2018). The increase of filamentous algae, overfishing and the potential meso-predation on northern pike larvae by sticklebacks (Eklöf et al., 2020) may result in a negative feedback loop which would further suppress the abundance of larger predatory fish and cause a potential regime shift driven by the increase of stickleback (Eklöf et al., 2020).

Furthermore, the abundance of some YOY fish species were correlated with secchi depth in this study which is in line with a previous study that have found that fish species are adapted to either decreased or increased secchi depth (Sandström and Karås, 2002). As water transparency is highly connected to eutrophicated states, a high nutrient load will shift the benthic production to pelagic by the increase in phytoplankton biomass, which is associated with low secchi depth (Hilton et al., 2006; Sandström and Karås, 2002). The stickleback showed a positive correlation with secchi depth, which may be explained by the species being a visual predator and thus adapted to clear water habitats (Quesenberry et al., 2007). However, the common roach, European perch, northern pike, Eurasian ruffe, common bleak, common/silver bream and Atlantic herring in the Gulf of Bothnia and common roach, European perch, northern pike, and common bleak in the Baltic Proper were negatively correlated with secchi depth. For the northern pike and European perch this may be explained by the high presence of sticklebacks in areas of increased secchi depth, potentially suppressing the two species distribution as discussed above (Eklöf et al., 2020). Whereas, other species occurrence within habitats of low secchi depth may reflect species adaptations to different water properties i.e. common roach which is adapted to turbid waters (Sandström and Karås, 2002).

4.2 ESSENTIAL YOY FISH HABITATS ARE UNDER PRESSURE AND ONLY PARTLY COVERED BY THE MPA NETWORK

The coverage of the MPA network was found to extend 2,955 km^2 along the Swedish Gulf of Bothnia coast, whereas the vegetated coastal areas covered 1,960 km^2, why the MPA network could potentially cover a large proportion of the vegetated habitats. However, the current network only covers 13 % of the vegetated habitats, leaving 1,706 km^2 of potential YOY fish habitats unprotected. The main goal of MPAs is to protect valuable habitats by designing networks to maintain ecologically representative systems (HELCOM, 2016; Naturvårdsverket, 2007; Sala et al., 2021). Yet, the vegetated habitats that YOY fish depend on and which are crucial for maintaining strong adult fish stocks are weakly represented, and, in turn may affect the commercial fisheries. This suggests that the integration between human usage of ecosystems and nature conservation has not been successful (Sundblad et al., 2011). Furthermore, results showed that 20 % of the sensitive *Chara spp.* were covered by the MPA network. The goal for protection of ecologically valuable habitats by the European Commission was until recently 10 % (Convention on Biological Diversity, 2010) which would consider the MPA cover of 13 % of vegetated habitats adequate. However, the new EU Biodiversity Strategy for 2030 suggests an MPA coverage of minimum 30 % (European Commission, 2020), proposing that the 13 % cover of vegetation habitats and 20 % by *Chara spp.* by the current MPA network is insufficient.

A higher density of berths was found to be negatively associated with aquatic vegetation, likely by having a negative impact on the coverage of plants by shadowing, physical disturbance and increased turbidity (Hansen et al., 2019; Sagerman et al., 2020). At a density of maximum 5 berths (per 0.25 km^2) mean vegetation cover was 40 % (per 0.25 km^2), whereas a higher density of berths decreased vegetation cover to 10-30 %. This corresponds to the pattern found in a previous study by Hansen et al. (2019). Despite declines in total vegetation cover with increasing berth abundance, the cover of the vulnerable (and partly red-listed) species *Chara spp.* did not decrease with an increase in the number of berths. Instead, it remained at a generally low coverage under 23 %. Generally, *Chara spp.* is adapted to clear water conditions that allows light penetration, but dense stands of *Chara spp*. may also retain in areas affected by boating due to its reduction-efficiency of turbidity, locally improving the environmental conditions for the plant species (Eriksson et al., 2004; Hansen et al., 2019; Van den Berg et al., 1999). Angiosperms, however, have also adapted to turbid waters by elongated shoots in habitats of low transparency, which is a competitive advantage in areas affected by boating (Eriksson et al., 2004). *Chara spp.* occurring with a generally low average density of under 23 % (per 0.25 km^2) in areas with boating, may be due to a combination of increased turbidity caused by boating activity and competition for space with angiosperms, suppressing the density of *Chara spp.* Although *Chara spp.* occur in a relatively low density, the species may persist in areas of lower competition and boating due to its ability to reduce turbidity locally and may explain the lack of a negative relationship between *Chara spp.* cover and the number of berths. However, since vegetation has overall shown to be of great importance for many YOY fish species establishment of MPAs in sites with essential YOY fish habitats and stricter regulations within MPAs should be of high interest, since boating has shown negative impacts on total vegetation cover by possibly sediment disturbance and physical scarring (Asplund and Cook, 1997; Hansen et al., 2019). Shading by docks has also been found to impact the growth and establishment of plants species. Eriander et al. (2017) revealed that the coverage of eelgrass (*Zostera marina*) on the Swedish west coast was reduced by 42-64 % within areas under or adjacent to shoreline construction (docks and marinas). Furthermore, they present that floating docks compared to docks elevated on poles has a stronger decreasing effect on eelgrass. It is suggested that this relationship relies on the shading effect, where elevated docks enable more sunlight to reach the water surface due to the docks standing further away from the water surface than the floating docks (Burdick and Short, 1999; Eriander et al., 2017; Shafer, 1999). Since the vegetated habitats usually rely on shallow and sun exposed areas shading by dock construction and dredging, that physically harm vegetated habitats, may have further degrading impacts. Stricter regulations could include reduced boat speed limits within MPAs to prevent sediment resuspension and increased water-turbidity that would enhance the light availability and promote increased growth for plant species.

In general the analyses provided reliable information on the importance of macrophyte habitats for YOY fish abundance and species richness and results correspond well to previous studies (e.g., de Nie and European Inland Fisheries Advisory Commission, 1987; Hansen et al., 2019; Ismail et al., 2018; Sundblad et al., 2011), although some limitations are worth mentioning. The GAMs did indicate overdispersion for some analysis, yet they were the most parsimonious models tested. The spatial analyses were conducted over large areas, and hence could be improved by a higher resolution to provide a more detailed result. Furthermore, the modelled vegetation maps did not correspond with all plant species presented in the statistical analyses due to limitations in data availability and could therefore underestimate the vegetation cover in the MPAs and boat activity impact analyses. Still, the presented results provide a good basis for describing the importance of certain habitats for YOY fish, their protection and potential impact by boating.

4.3 CONCLUSIONS

In conclusion, the present study found a strong positive relationship between vegetated coastal habitats and fish abundance and species richness. 13 % of these habitats in the Gulf of Bothnia are currently covered by the MPA network, whereas 20 % of vulnerable species such as *Chara spp.* are protected. The coverage by MPAs does insufficiently support the EU Biodiversity Strategy for 2030 where 30 % of marine habitats should be protected. These habitats are highly subjected to boating activity, and results show a negative impact on macrophyte cover by increasing number of berths. In order to spare habitats from disturbances and physical destruction, adjustments including location refinement and updated management of MPAs, as well as regulation of the average number of berths allowed in highly valuable areas, are highly encouraged.

5. References

Akaike, H., 1974. A New Look at the Statistical Model Identification.

Asplund, T.R., Cook, C.M., 1997. Effects of Motor Boats on Submerged Aquatic Macrophytes. Lake Reserv. Manag. 13, 1–12. https://doi.org/10.1080/07438149709354290

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. https://doi.org/10.1111/1365-2664.12083

Berkström, C., Wennerström, L., Bergström, U., 2019. Ekologisk konnektivitet i svenska kust-och havsområden. Sver. Lantbruksuniversitet Institutionen För Akvat. Resur.

Burdick, D.M., Short, F.T., 1999. The Effects of Boat Docks on Eelgrass Beds in Coastal Waters of Massachusetts. Environ. Manage. 23, 231–240. https://doi.org/10.1007/s002679900182

Čech, M., Peterka, J., Říha, M., Jůza, T., Kubečka, J., 2009. Distribution of egg strands of perch (Perca fluviatilis L.) with respect to depth and spawning substrate. Hydrobiologia 630, 105–114. https://doi.org/10.1007/s10750-009-9783-z

Chambers, R.M., Meyerson, L.A., Saltonstall, K., 1999. Expansion of Phragmites australis into tidal wetlands of North America. Aquat. Bot. 64, 261–273. https://doi.org/10.1016/S0304-3770(99)00055-8

Convention on Biological Diversity, 2010. DECISION ADOPTED BY THE CONFERENCE OF THE PARTIES TO THE CONVENTION ON BIOLOGICAL DIVERSITY AT ITS TENTH MEETING X/2. The Strategic Plan for Biodiversity 2011-2020 and the Aichi Biodiversity Targets.

Costello, M.J., Ballantine, B., 2015. Biodiversity conservation should focus on no-take Marine Reserves: 94% of Marine Protected Areas allow fishing. Trends Ecol. Evol. 30, 507–509. https://doi.org/10.1016/j.tree.2015.06.011

de Nie, H.W., European Inland Fisheries Advisory Commission, 1987. The decrease in aquatic vegetation in Europe and its consequences for fish populations 57.

Donadi, S., Austin, Å.N., Bergström, U., Eriksson, B.K., Hansen, J.P., Jacobson, P., Sundblad, G., van Regteren, M., Eklöf, J.S., 2017. A cross-scale trophic cascade from large predatory fish to algae in coastal ecosystems. Proc. R. Soc. B Biol. Sci. 284, 20170045. https://doi.org/10.1098/rspb.2017.0045

Donadi, S., Austin, Å.N., Svartgren, E., Eriksson, B.K., Hansen, J.P., Eklöf, J.S., 2018. Density-dependent positive feedbacks buffer aquatic plants from interactive effects of eutrophication and predator loss. Ecology 99, 2515–2524. https://doi.org/10.1002/ecy.2501

Ehlin, U., 1981. Chapter 2 Hydrology of the Baltic Sea [WWW Document]. https://doi.org/10.1016/S0422-9894(08)70139-9

Eklöf, J.S., Sundblad, G., Erlandsson, M., Donadi, S., Hansen, J.P., Eriksson, B.K., Bergström, U., 2020. A spatial regime shift from predator to prey dominance in a large coastal ecosystem. Commun. Biol. 3, 459. https://doi.org/10.1038/s42003-020-01180-0

Eriander, L., Laas, K., Bergström, P., Gipperth, L., Moksnes, P.-O., 2017. The effects of small-scale coastal development on the eelgrass (Zostera marina L.) distribution along the Swedish west coast – Ecological impact and legal challenges. Ocean Coast. Manag. 148, 182–194. https://doi.org/10.1016/j.ocecoaman.2017.08.005

Eriksson, B.K., Sandström, A., Isæus, M., Schreiber, H., Karås, P., 2004. Effects of boating activities on aquatic vegetation in the Stockholm archipelago, Baltic Sea. Estuar. Coast. Shelf Sci. 61, 339–349. https://doi.org/10.1016/j.ecss.2004.05.009

Erlandsson, M., Fredriksson, R., Bergström, U., 2021. Kartläggning av viktiga uppväxtområden för fisk i grunda kustområden i Östersjön. Aqua Rep. Sver. Lantbruksuniversitet.

European Commission, 2020. COMMUNICATION FROM THE COMMISSION TO THE EUROPEAN PARLIAMENT, THE COUNCIL, THE EUROPEAN ECONOMIC AND SOCIAL COMMITTEE AND THE COMMITTEE OF THE REGIONS EU Biodiversity Strategy for 2030 Bringing nature back into our lives.

Florén, K., Wijkmark, N., Fyhr, F., Tano, S., Beltrán, J., 2018. Kartering av bentiska naturvärden i Bottniska viken. Hav Och Vattenmyndigheten.

Fox, J., Monette, G., 1992. Generalized Collinearity Diagnostics. J. Am. Stat. Assoc. 87, 178–183. https://doi.org/10.2307/2290467

Friedlander, A.M., Brown, E.K., Jokiel, P.L., Smith, W.R., Rodgers, K.S., 2003. Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. Coral Reefs 22, 291–305. https://doi.org/10.1007/s00338-003-0317-2

Fulton, C.J., Berkström, C., Wilson, S.K., Abesamis, R.A., Bradley, M., Åkerlund, C., Barrett, L.T., Bucol, A.A., Chacin, D.H., Chong-Seng, K.M., Coker, D.J., Depczynski, M., Eggertsen, L., Eggertsen, M., Ellis, D., Evans, R.D., Graham, N.A.J., Hoey, A.S., Holmes, T.H., Kulbicki, M., Leung, P.T.Y., Lam, P.K.S., Lier, J. van, Matis, P.A., Noble, M.M., Pérez-Matus, A., Piggott, C., Radford, B.T., Tano, S., Tinkler, P., 2020. Macroalgal meadow habitats support fish and fisheries in diverse tropical seascapes. Fish Fish. 21, 700–717. https://doi.org/10.1111/faf.12455

Gagnon, K., Gräfnings, M., Boström, C., 2017. Shifts in coastal fish communities: Is eutrophication always beneficial for sticklebacks? Estuar. Coast. Shelf Sci. 198, 193–203. https://doi.org/10.1016/j.ecss.2017.08.047

Gratwicke, B., Speight, M., 2005. Effects of habitat complexity on Caribbean marine fish assemblages. Mar. Ecol. Prog. Ser. 292, 301–310. https://doi.org/10.3354/meps292301

Grenouillet, G., Pont, D., 2001. Juvenile fishes in macrophyte beds: influence of food resources, habitat structure and body size. J. Fish Biol. 59, 939–959. https://doi.org/10.1111/j.1095-8649.2001.tb00163.x

Hansen, J.P., Snickars, M., 2014. Applying macrophyte community indicators to assess anthropogenic pressures on shallow soft bottoms. Hydrobiologia 738, 171–189. https://doi.org/10.1007/s10750-014-1928-z

Hansen, J.P., Sundblad, G., Bergström, U., Austin, Å.N., Donadi, S., Eriksson, B.K., Eklöf, J.S., 2019. Recreational boating degrades vegetation important for fish recruitment. Ambio 48, 539–551. https://doi.org/10.1007/s13280-018-1088-x

Härmä, M., Lappalainen, A., Urho, L., 2008. Reproduction areas of roach (Rutilus rutilus) in the northern Baltic Sea: potential effects of climate change. Can. J. Fish. Aquat. Sci. 65, 2678–2688. https://doi.org/10.1139/F08-167

Hastie, T., 2020. Generalized Additive Models.

Havs- och vattenmyndighetens rapport, 2020. Åtgärdsprogram för sällsynta kransalger längs kusten.

HELCOM, 2016. Ecological coherence assessment of the Marine Protected Area network in the Baltic. Balt Sea Env. Proc No 148.

HELCOM, 2010. Towards an ecologically coherent network of well-managed Marine Protected Areas – Implementation report on the status and ecological coherence of the HELCOM BSPA network. Balt Sea Env. Proc No 124B.

HELCOM, 2007. Planning and management of Baltic Sea Protected Areas: guidelines and tools. Balt Sea Env. Proc No 105.

Hellings, S.E., Gallagher, J.L., 1992. The Effects of Salinity and Flooding on Phragmites australis. J. Appl. Ecol. 29, 41–49. https://doi.org/10.2307/2404345

Hilton, J., O'Hare, M., Bowes, M.J., Jones, J.I., 2006. How green is my river? A new paradigm of eutrophication in rivers. Sci. Total Environ., Monitoring and modelling the impacts of global change on European freshwater ecosystems 365, 66–83. https://doi.org/10.1016/j.scitotenv.2006.02.055

Hulisz, P., Piernik, A., Mantilla-Contreras, J., Elvisto, T., 2016. Main Driving Factors for Seacoast Vegetation in the Southern and Eastern Baltic. Wetlands 36, 909–919. https://doi.org/10.1007/s13157-016-0803-2

ICES, 2020. Baltic Sea Ecoregion ? Ecosystem overview. https://doi.org/10.17895/ICES.ADVICE.7635

Isæus, M., 2004. Factors structuring Fucus communities at open and complex coastlines in the Baltic Sea. Dep. Bot. Stockh. Univ.

Ismail, S.N., Hamid, M.A., Mansor, M., 2018. Ecological correlation between aquatic vegetation and freshwater fish populations in Perak River, Malaysia. Biodiversitas J. Biol. Divers. 19, 279–284. https://doi.org/10.13057/biodiv/d190138

Lass, H.U., Matthäus, W., 1996. On temporal wind variations forcing salt water inflows into the Baltic Sea. Tellus A 48, 663–671. https://doi.org/10.1034/j.1600-0870.1996.t01-4-00005.x

Leppäkoski, E., Helminen, H., Häninen, J., Tallqvist, M., 1999. Aquatic biodiversity under anthropogenic stress: an insight from the Archipelago Sea (SW Finland) 16.

Leslie, H.M., 2005. A Synthesis of Marine Conservation Planning Approaches. Conserv. Biol. 19, 1701–1713. https://doi.org/10.1111/j.1523-1739.2005.00268.x

Mackenzie, B.R., Gislason, H., Möllmann, C., Köster, F.W., 2007. Impact of 21st century climate change on the Baltic Sea fish community and fisheries. Glob. Change Biol. 13, 1348–1367. https://doi.org/10.1111/j.1365-2486.2007.01369.x

Madsen, J.D., Chambers, P.A., James, W.F., Koch, E.W., Westlake, D.F., 2001. The interaction between water movement, sediment dynamics and submersed macrophytes. Hydrobiologia 444, 71–84. https://doi.org/10.1023/A:1017520800568

Mazumder, A., Taylor, W.D., McQueen, D.J., Lean, D.R.S., 1990. Effects of Fish and Plankton and Lake Temperature and Mixing Depth. Science 247, 312–315. https://doi.org/10.1126/science.247.4940.312

Moksnes, P.-O., Eriander, L., Hansen, J., Albertsson, J., Andersson, M., Carlström, J., Egardt, J., Fredriksson, R., Granhag, L., Lindgren, F., Nordberg, K., Wendt, I., Wikström, S., Ytreberg, E., 2019. FRITIDSBÅTARS PÅVERKAN PÅ GRUNDA KUSTEKOSYSTEM I SVERIGE 158.

Naturvårdsverket, 2007. Skydd av marina miljöer med höga naturvärden: vägledning. Naturvårdsverket, Stockholm.

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. https://doi.org/10.1111/j.1095-8649.2002.tb01768.x

Pihl, L., Wennhage, H., Nilsson, S., 1994. Fish assemblage structure in relation to macrophytes and filamentous epiphytes in shallow non-tidal rocky- and soft-bottom habitats. Environ. Biol. Fishes 39, 271–288. https://doi.org/10.1007/BF00005129

Pitkänen, H., Peuraniemi, M., Westerbom, M., Kilpi, M., von Numers, M., 2013. Long-term changes in distribution and frequency of aquatic vascular plants and charophytes in an estuary in the Baltic Sea. Ann. Bot. Fenn. 50, 1–54.

Possingham, H., Ball, I., Andelman, S., 2000. Mathematical Methods for Identifying Representative Reserve Networks, in: Quantitative Methods for Conservation Biology. Springer-Verlag, New York, pp. 291–306. https://doi.org/10.1007/0-387-22648-6_17

Quesenberry, N.J., Allen, P.J., Cech, J.J., 2007. The influence of turbidity on three-spined stickleback foraging. J. Fish Biol. 70, 965–972. https://doi.org/10.1111/j.1095-8649.2007.01350.x

Rozas, L.P., Odum, W.E., 1988. Occupation of submerged aquatic vegetation by fishes: testing the roles of food and refuge. Oecologia 77, 101–106. https://doi.org/10.1007/BF00380932

Sagerman, J., Hansen, J.P., Wikström, S.A., 2020. Effects of boat traffic and mooring infrastructure on aquatic vegetation: A systematic review and meta-analysis. Ambio 49, 517–530. https://doi.org/10.1007/s13280-019-01215-9

Sala, E., Mayorga, J., Bradley, D., Cabral, R.B., Atwood, T.B., Auber, A., Cheung, W., Costello, C., Ferretti, F., Friedlander, A.M., Gaines, S.D., Garilao, C., Goodell, W., Halpern, B.S., Hinson, A., Kaschner, K., Kesner-Reyes, K., Leprieur, F., McGowan, J., Morgan, L.E., Mouillot, D., Palacios-Abrantes, J., Possingham, H.P., Rechberger, K.D., Worm, B., Lubchenco, J., 2021. Protecting the global ocean for biodiversity, food and climate. Nature 592, 397–402. https://doi.org/10.1038/s41586-021-03371-z

Sandström, A., Eriksson, B.K., Karås, P., Isæus, M., Schreiber, H., 2005. Boating and Navigation Activities Influence the Recruitment of Fish in a Baltic Sea Archipelago Area. AMBIO J. Hum. Environ. 34, 125–130. https://doi.org/10.1579/0044-7447-34.2.125

Sandström, A., Karås, P., 2002. Effects of Eutrophication on Young-of-the-year Freshwater Fish Communities in Coastal Areas of the Baltic. Environ. Biol. Fishes 63, 89–101. https://doi.org/10.1023/A:1013828304074

Shafer, D.J., 1999. The Effects of Dock Shading on the Seagrass Halodule wrightii in Perdido Bay, Alabama. Estuaries 22, 936. https://doi.org/10.2307/1353073

Siegel, H., Gerth, M., 2015. Development of Sea Surface Temperature (SST) in the Baltic Sea 2014 8.

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. Estuar. Coast. Shelf Sci. 81, 247–256. https://doi.org/10.1016/j.ecss.2008.10.021

Snyder, J.P., 1987. Map Projections--a Working Manual. U.S. Government Printing Office.

Sparholt, H., 1994. Fish species interactions in the Baltic Sea 33.

Sundblad, G., Bergström, U., 2014. Shoreline development and degradation of coastal fish reproduction habitats. AMBIO 43, 1020–1028. https://doi.org/10.1007/s13280-014-0522-y

Sundblad, G., Bergström, U., Sandström, A., 2011. Ecological coherence of marine protected area networks: a spatial assessment using species distribution models. J. Appl. Ecol. 48, 112–120. https://doi.org/10.1111/j.1365-2664.2010.01892.x

Törnqvist, O., Klein, J., Vidisson, B., Häljestig, S., Katif, S., Nazerian, S., 2020. Fysisk störning i grunda havsområden – Kartläggning och analys av potentiell påverkanszon samt regional och nationell statistik angående störda områden 125.

Van den Berg, M.S., Scheffer, M., Van Nes, E., Coops, H., 1999. Dynamics and stability of Chara sp. and Potamogeton pectinatus in a shallow lake changing in eutrophication level, in: Walz, N., Nixdorf, B. (Eds.), Shallow Lakes ’98. Springer Netherlands, Dordrecht, pp. 335–342. https://doi.org/10.1007/978-94-017-2986-4_37

Wikström, S.A., Kautsky, L., 2007. Structure and diversity of invertebrate communities in the presence and absence of canopy-forming Fucus vesiculosus in the Baltic Sea. Estuar. Coast. Shelf Sci. 72, 168–176. https://doi.org/10.1016/j.ecss.2006.10.009

Winfield, I.J., 1986. The influence of simulated aquatic macrophytes on the zooplankton consumption rate of juvenile roach, Rutilus rutilus, rudd, Scardinius erythrophthalmus, and perch, Perca fluviatilis. J. Fish Biol. 29, 37–48. https://doi.org/10.1111/j.1095-8649.1986.tb04997.x

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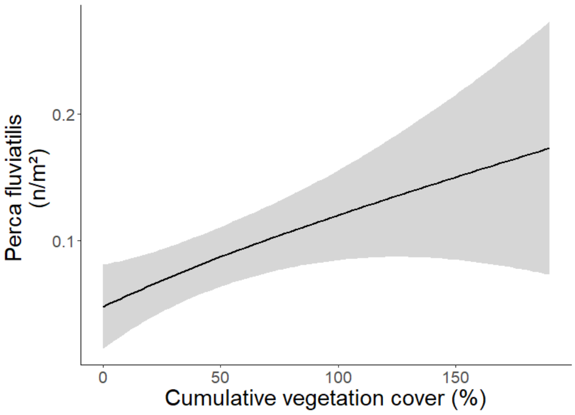
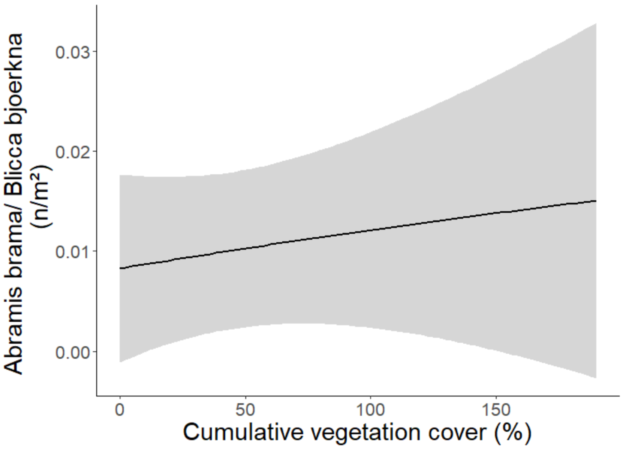
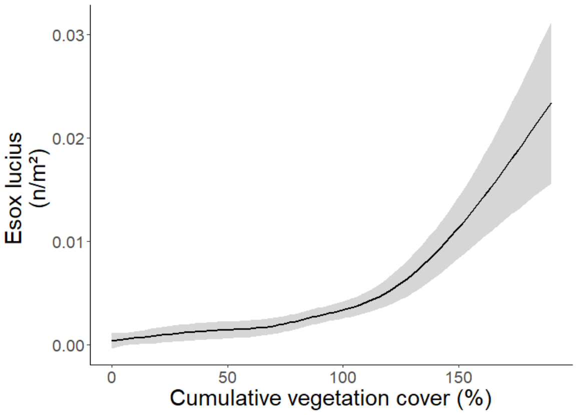
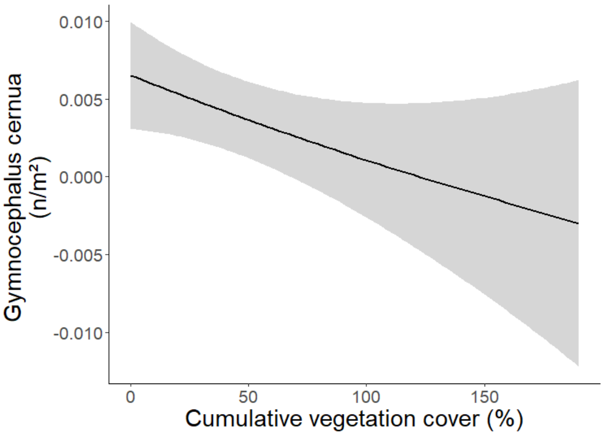
Appendices

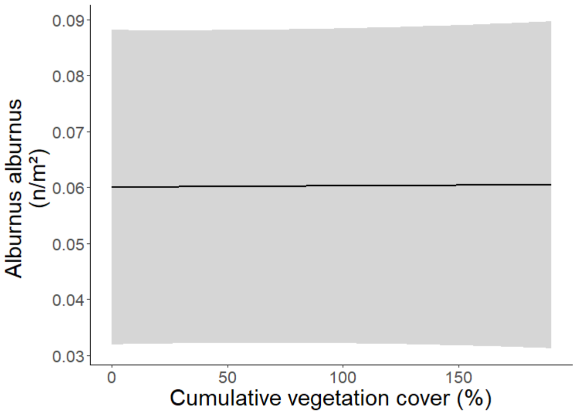
APPENDIX 1

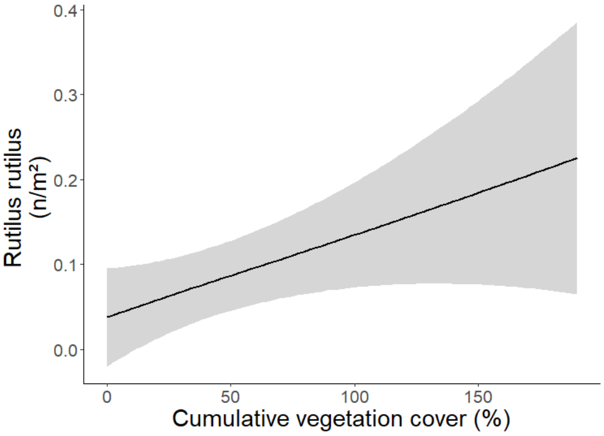


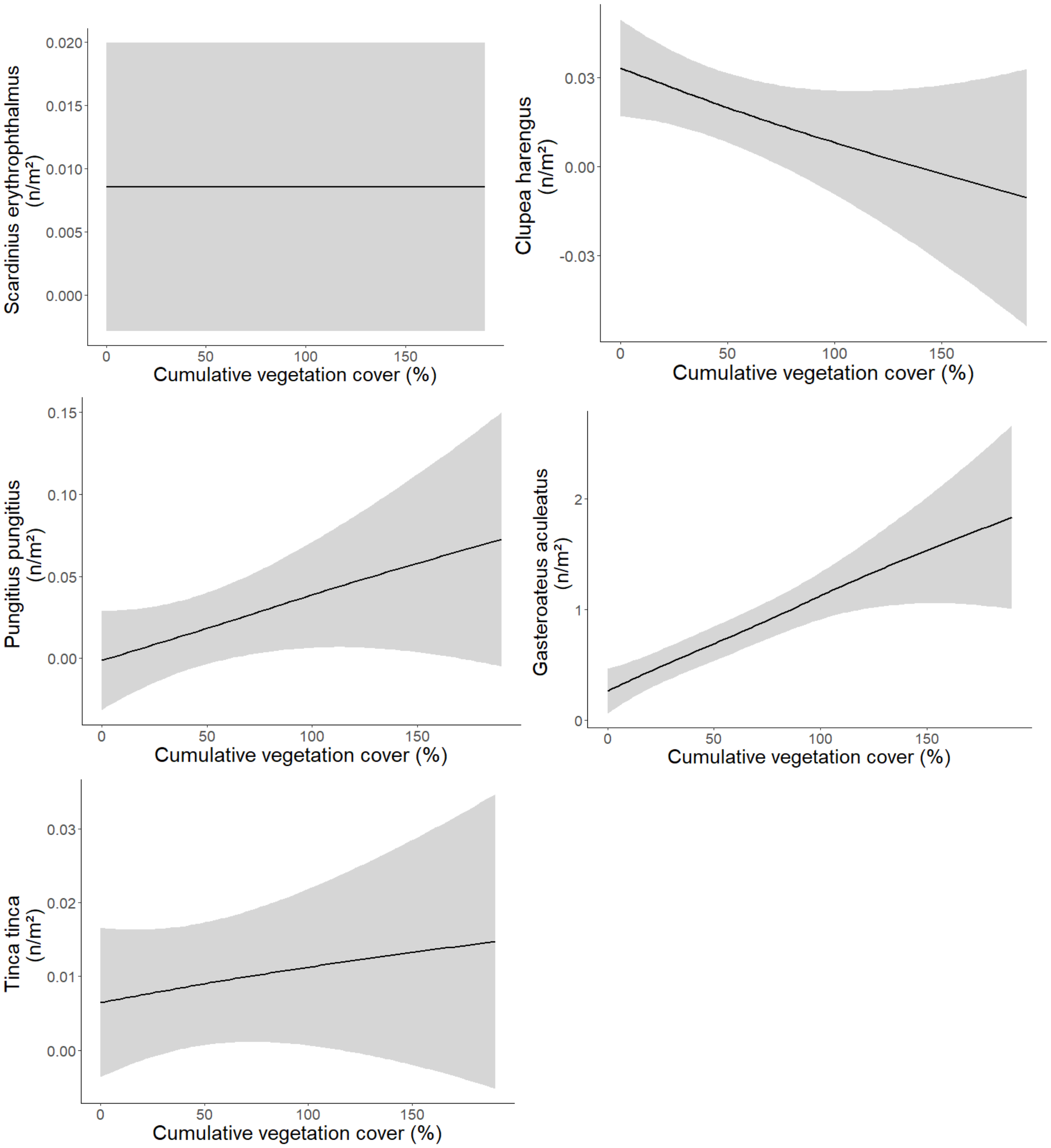




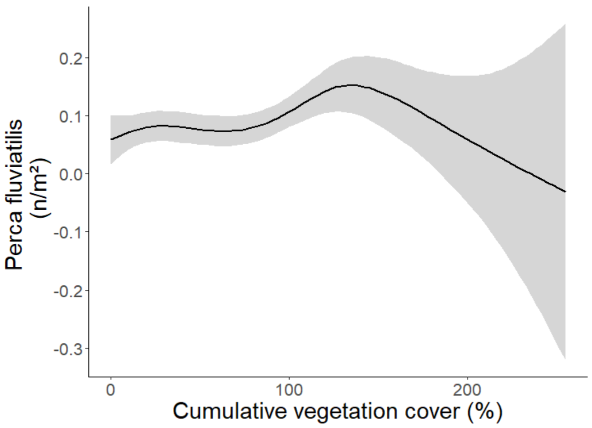


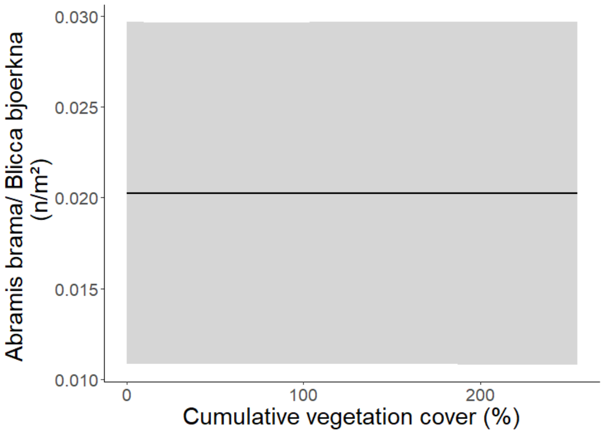


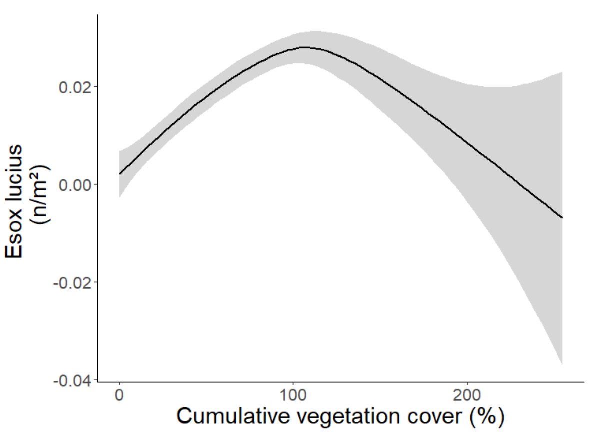


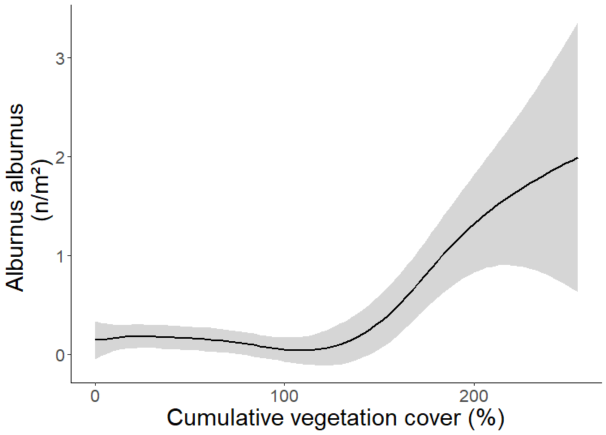


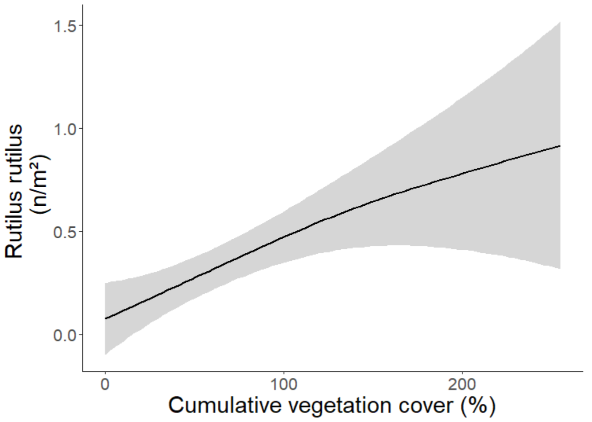
***Appendix 1A**: Regression plots displaying positive or negative relationships between fish abundance (number of individuals per m^2) and cumulative vegetation cover in percent. Confident interval displayed by grey area. The Gulf of Bothnia.*

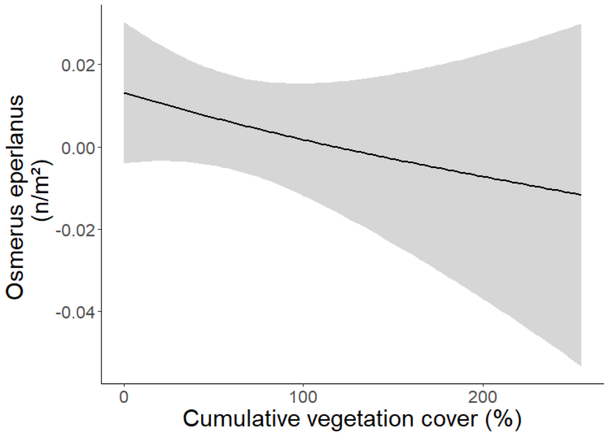

Perca fluviatilis
(n/m²)
0.2
0.1
0.0
-0.1
-0.2
-0.3
0
100
200
Cumulative vegetation cover (%)

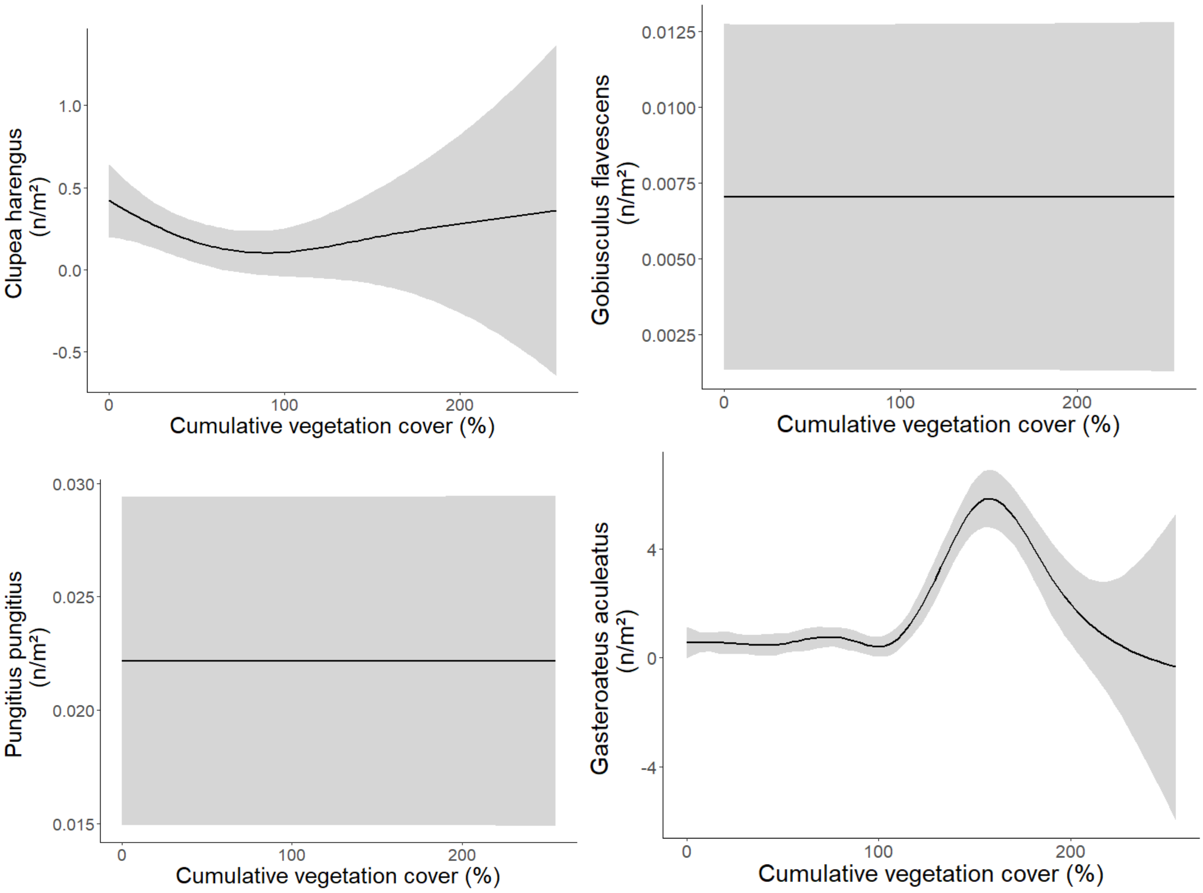

Abramis brama/ Blicca bjoerkna
(n/m²)
0.030
0.025
0.020
0.015
0.010
0
100
200
Cumulative vegetation cover (%)


Esox lucius
(n/m²)
0.02
0.00
-0.02
-0.04
0
100
200
Cumulative vegetation cover (%)


Alburnus alburnus
(n/m²)
3
2
1
0
0
100
200
Cumulative vegetation cover (%)


Rutilus rutilus
(n/m²)
1.5
1.0
0.5
0.0
0
100
200
Cumulative vegetation cover (%)


Osmerus eperlanus
(n/m²)
0.02
0.00
-0.02
-0.04
0
100
200
Cumulative vegetation cover (%)



***Appendix 1B**: Regression plots displaying positive or negative relationships between fish abundance (number of individuals per m^2) and cumulative vegetation cover in percent. Confident interval displayed by grey area. The Baltic Proper.*

APPENDIX 2

***Appendix 2A**: Generalized Additive Models of YOY fish abundance and different habitat and environmental variables in the Gulf of Bothnia. Finer sediment was analysed in separate model. In **bold** significant variables (P < 0.05). R A – rooted angiosperms. NR A – non rooted angiosperms, R M – rooted macroalgae, NR M – non rooted macroalgae, Sal – salinity, S T – surface temperature, S D – secchi depth, WD – water depth.*

Effective degrees of freedom
Reference degrees of freedom
F – values
P – values

Fish specie	*R A*	*NR A*	*R M*	*NR M*	*Boulders*	*Stones*	*Sand*	*F S*	*SWM*	*Sal*	*S T*	*S D*	*W D*	*Finer sediment*
Perca fluviatilis	4.989 6.105 7.682 **< 2e-16**								5.149 5.923 4.435 **0.000194**	5.029 6.104 3.877 **0.000638**	5.496 6.581 3.335 **0.002273**	1.001 1.002 35.136 **< 2e-16**	6.476 7.011 14.553 **< 2e-16**	5.206 6.229 46.49 **<2e-16**
Esox lucius	2.759 3.462 8.014 **1.22e-05**		1.000 1.000 23.243 **2.14e-06**							7.259 8.198 6.789 **< 2e-16**	1.001 1.001 1.867 0.17188	2.655 3.346 4.017 **0.00619**		1.381 1.65 61.7 **<2e-16**
Alburnus alburnus				1.485 1.806 1.468 0.17508			2.027 2.474 0.810 0.36788			5.226 6.344 1.965 0.07599	1.000 1.000 0.271 0.60278	1.000 1.000 14.740 **0.00013**	1.001 1.001 23.491 **1.91e-06**	7.681 8.517 18.62 **<2e-16**
Gymnocephalus cernua	1.000 1.000 9.516 **0.00207**		2.246 2.569 0.479 0.56980	1.000 1.000 3.845 0.05004	1.000 1.000 6.684 **0.00981**					5.746 6.822 2.948 **0.00595**		1.000 1.000 22.263 **2.64e-06**		2.07 2.49 25.09 **<2e-16**

Abramis bjoerkna /Blicca brama	1.246 1.455 4.442 **0.0172**								1.000 1.000 17.584 **2.99e-05**		1.594 2.029 1.171 0.3060	1.000 1.000 23.219 **1.64e-06**		7.921 8.616 8.305 **<2e-16**
Gasterosteus aculeatus	3.983 4.965 14.057 **< 2e-16**	3.085 3.850 4.310 **0.002135**	2.984 3.700 7.278 **2.08e-05**	1.397 1.679 53.283 **< 2e-16**	2.348 2.952 8.453 **1.85e-05**					7.458 8.367 10.632 **< 2e-16**	4.777 5.717 5.301 **4.57e-05**	6.127 7.269 4.618 **5.15e-05**	3.241 4.120 5.048 **0.000466**	7.571 8.445 76.12 **<2e-16**
Scardinius erythrophthalmus	3.693 4.636 2.029 0.1040			1.010 1.019 3003.677 **<2e-16**		1.061 1.118 0.892 0.3382			3.728 4.566 2.143 0.0856		2.928 3.815 0.730 0.5667			3.284 3.988 8.005 **2.98e-06**
Tinca tinca	4.857 5.876 5.004 **7.26e-05**		2.723 3.374 10.795 **7.85e-07**						1.000 1.000 15.453 **8.79e-05**			1.001 1.003 1.199 0.27335	3.045 3.685 4.692 **0.00287**	3.676 4.455 8.895 **<2e-16**
Pungitius pungitius				1.468 1.781 16.182 **4.37e-06**						4.059 5.009 2.419 **0.03411**	4.636 5.297 2.279 0.07552		1.000 1.000 8.035 **0.00466**	1.739 2.11 48.38 **<2e-16**
Clupea harrengus	1.135 1.256 12.653 **0.000277**				1.000 1.000 10.042 **0.001569**		1.000 1.000 14.628 **0.000138**			1.004 1.007 16.370 **5.49e-05**	4.317 5.119 3.205 **0.004523**	5.866 6.368 6.466 **4.49e-05**	5.168 6.255 4.984 **3.64e-05**	2.576 3.119 9.084 **5.24e-06**
Rutilus rutilus	4.223 5.200 19.590 **< 2e-16**								4.364 4.993 5.897 **1.86e-05**	7.826 8.605 11.416 **< 2e-16**	6.282 7.291 6.088 **8.29e-07**	2.860 3.592 10.435 **3.60e-07**		7.838 8.602 33.61 **<2e-16**
Total fish species	4.639 5.701 18.272 **< 2e-16**		2.193 2.723 1.348 0.207	1.535 1.873 44.779 **< 2e-16**	5.074 6.012 6.347 **1.25e-06**				6.687 7.815 7.815 **< 2e-16**	4.460 5.476 7.325 **5.51e-07**				6.456 7.536 11.12 **<2e-16**

Appendix 2B**: Generalized Additive Models of YOY fish abundance and different habitat and environmental variables in the Baltic Proper. Finer sediment was analysed in separate model. In* ***bold *significant variables (P < 0.05). R A – rooted angiosperms. NR A – non rooted angiosperms, R M – rooted macroalgae, NR M – non rooted macroalgae, Sal – salinity, S T – surface temperature, S D – secchi depth, WD – water depth.*

Effective degrees of freedom
Reference degrees of freedom
F – values
P – values

Fish specie	*R A*	*NR A*	*R M*	*NR M*	*Bedrock*	*Gravel*	*Sand*	*F S*	*SWM*	*Sal*	*S T*	*S D*	*W D*	*Finer sediment*
Perca fluviatilis	3.470 4.328 4.292 **0.001459**								3.573 4.444 8.353 **1.76e-06**	4.997 6.088 2.547 **0.019650**	5.600 6.718 3.436 **0.001265**	1.002 1.004 15.166 **0.000103**		2.334 2.814 5.332 **0.00241**
Esox lucius	1.002 1.003 73.717 **< 2e-16**			2.736 3.427 14.843 **<2e-16**	1.513 1.853 7.419 **0.00074**					5.439 6.509 13.834 **< 2e-16**			3.423 4.286 9.736 **< 2e-16**	7.041 8.073 6.226 **<2e-16**
Alburnus alburnus				6.174 6.669 3.195 **0.00162**	2.925 3.603 4.545 **0.00250**				4.331 4.996 6.716 **4.51e-06**	3.769 4.761 2.172 0.06775	3.717 4.605 3.339 **0.00688**	3.806 4.803 3.284 **0.00667**		1.001 1.002 0.069 0.796
Gobius flavescens	3.731 4.558 1.685 0.1177	1.000 1.000 0.661 0.4165	3.422 3.836 3.203 **0.0125**	2.664 3.340 3.456 **0.0155**	1.000 1.000 16.439 **5.36e-05**				3.691 4.486 18.630 **< 2e-16**	1.000 1.000 0.721 0.3959	1.000 1.000 2.580 0.1085			1.959 2.359 25.63 **<2e-16**
Abramis bjoerkna /Blicca brama	5.620 6.787 7.108 **< 2e-16**								4.041 5.016 6.743 **4.2e-06**	1.000 1.001 1.420 0.23359	5.569 6.204 2.808 **0.00573**			1.003 1.006 0.941 0.331

Gasterosteus aculeatus	1.220 1.406 33.964 **< 2e-16**			4.006 4.900 12.888 **< 2e-16**						7.815 8.540 12.165 **< 2e-16**	6.304 7.470 6.355 **3.47e-07**	1.163 1.308 4.544 **0.018718**	2.894 3.639 6.602 **0.000108**	5.446 6.515 13.27 **<2e-16**
Osmerus eperlanus	1.001 1.002 0.516 0.473								4.638 5.629 0.448 0.826	1.000 1.000 0.022 0.883	3.897 4.783 0.623 0.671		2.151 2.738 0.122 0.948	3.612 4.448 1.84 0.118
Gobius niger	4.315 5.299 6.984 **2.07e-06**	2.125 2.686 0.436 0.751833	2.129 2.619 1.993 0.117042	3.469 4.301 5.488 **0.000157**	1.000 1.001 1.053 0.304947					1.778 2.280 3.104 **0.040916**		3.543 4.447 1.806 0.119028		2.779 3.369 8.24 **9.51e-06**
Pungitius pungitius			2.458 3.038 1.000 0.412127	2.482 3.082 6.686 **0.000145**						3.762 4.743 4.432 **0.000728**	5.526 6.688 7.564 **< 2e-16**			4.517 5.449 1.898 0.106
Clupea harrengus	2.852 3.572 6.084 **0.000217**		2.440 2.999 9.903 **2.00e-06**							6.695 7.517 5.783 **1.10e-06**	5.935 7.006 4.938 **1.63e-05**		4.262 5.273 12.902 **<2e-16**	3.254 3.947 2.613 **0.03**
Rutilus rutilus	1.209 1.389 22.041 **4.00e-07**					6.813 7.773 4.909 **1.12e-05**				6.172 7.220 7.549 **< 2e-16**		5.677 6.802 3.277 **0.0025**		4.523 5.46 1.924 0.0944
Total fish species	5.146 6.265 9.216 **< 2e-16**	2.172 2.682 1.024 0.528911	6.960 7.965 4.614 **1.75e-05**	3.638 4.488 9.475 **< 2e-16**	1.011 1.023 10.685 **0.001019**	3.129 3.850 4.157 **0.002893**					6.486 7.474 3.961 **0.000241**			6.9 7.947 11.78 **<2e-16**

APPENDIX 3

***Appendix 3A**: Significant relationships between fish abundance and vegetation species in the Gulf of Bothnia. Positive or negative relationships between fish abundance and vegetation species displayed by +/- sign. Empty cells indicate no relationship found between variables.*

Vegetation	Eurasian perch	Common roach	Three spined stickleback	Nine spined stickleback	Atlantic herring	Northern pike	Common /Silver bream	Tench	Common rudd	Total fish species
Stuckenia pectinata	–	+	+			+				+
Potamogeton perfoliatus	+	+	+		+	–		–		+
Lemna trisulca	+	+	+			+		–		
Najas marina	+	+	+		–		+			+
Myriophyllum sibiricum	+									
Myriophyllum alterniflorum	–							–		
Myriophyllum spicatum						–	+			
Myriophyllum verticillatum					–			–		
Zannichella palustris		–			–	–		–		–
Callitriche hermaphroditica	+	+	+					–		+
Ceratophyllum demersum										
Chara spp.			–			+		+		
Zostera marina						+				
Fucus vesiculosus			+						–	+
Fucus radicans									–	
Ruppia sp.						–				
Ruppia cirrhosa						–				
Vaucheria spp.			+	+						+
Phragmites australis	–	–					–			–

***Appendix 3B:** Significant relationships between fish abundance and vegetation species in the Baltic Proper. Positive or negative relationships between fish abundance and vegetation species displayed by +/- sign. Empty cells indicate no relationship found between variables.*

Vegetation	Eurasian perch	Common roach	Three spined stickleback	Nine spined stickleback	Northern pike	Black goby	Two spotted goby	Common/Silver bream	Total fish species
Stuckenia pectinata	+	–	+		+				
Potamogeton perfoliatus	+	+	+		–			–	+
Lemna trisulca			–		+				
Najas marina	+	+	+					+	+
Myriophyllum sibiricum		+							+
Myriophyllum spicatum		–			–				
Zannichellia palustris	–	–			–			–	
Fucus vesiculosus			+	–	+	+	+		+
Fucus radicans				–					
Vaucheria spp.			–	+	+				–
Phragmites australis		–						+	+
Ruppia cirrhosa	–	–	+		+			–	+
Ruppia sp.		–	–		–			–	–
Chorda filum			+			–			–
Zostera marina	–	–			+			–	
Monostroma balticum					+				+
Furcellaria lumbricalis			–		+		+		
Filamentous algae			+	+	–	–			+
Callitriche hermaphroditica	–	+							–
Polysiphonia					–		+		
Chara spp.									–

APPENDIX 4

***Appendix 4**: Generalized Additive Models of YOY fish abundance and different habitat and environmental variables in the Gulf of Bothnia and the Baltic Proper. Finer sediment was analysed in separate model. In **bold** significant variables (P < 0.05). R A – rooted angiosperms. NR A – non rooted angiosperms, R M – rooted macroalgae, NR M – non rooted macroalgae, Sal – salinity, S T – surface temperature, S D – secchi depth.*

	Effective degrees of freedom Reference degrees of freedom F – values P – values									
Species richness	*R A*	*NR A*	*R M*	*NR M*	*Large boulder*	*Boulder*	*Sal*	*S T*	*S D*	*Finer sediments*
The Gulf of Bothnia	4.415 5.439 24.740 **< 2e-16**	1.000 1.000 7.971 **0.00483**	2.747 3.404 4.067 **0.00555**	1.000 1.000 26.911 **6.39e-07**				1.000 1.000 5.355 **0.02083**	2.931 3.683 16.515 **< 2e-16**	2.093 2.547 17.04 **<2e-16**
The Baltic Proper	2.986 3.749 8.790 **2.42e-06**	1.000 1.000 0.230 0.6319	1.104 1.199 0.012 0.9477	1.000 1.000 41.241 **< 2e-16**	1.085 1.165 0.071 0.8186	1.000 1.000 0.026 0.8725	1.089 1.173 0.091 0.9032		1.828 2.318 2.979 **0.0393**	3.236 3.926 2.985 **0.0245**