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Fish community composition, size structure and interspecific competition in areas open to exploitation and partially protected from recreational fishing: case studies from brackish lagoons of the southern Baltic Sea, with a focus on northern pike (*Esox lucius*)

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III. List of abbreviations

BACI	-	Before-After Control-Impact design
BIC	-	Bayesian information criterion
BPUE	-	Biomass-per-unit-effort
CI	-	Control-Impact study
CPUE	-	Catch-per-unit-effort
GLM	-	Generalized linear model
MPA	-	Marine protected area
N. and S.	-	Neuensiener- and Selliner See
NMDS	-	Non-metric multidimensional scaling
OA	-	Open-access area
PERMANOVA	-	Permutational multivariate analysis of variance
RDA	-	Redundancy analysis
SIMPER	-	Similarity percentage analysis

Abstract

This study examined the impact of fishing/protection on fish communities and populations of four species with varying mobility and commercial value in a Control-Impact study. Three 30-year-old partially protected marine areas (MPAs) with varying protection measures were compared to adjacent open fishing areas (OAs) in the southern Baltic Sea, Eastern Germany, across three seasons in 2022. Species richness, total fish abundance, and targeted vs. non-targeted species abundances within fish communities were assessed. Specific species populations were compared regarding numerical and biomass abundance and size, with a specific focus on the northern pike (*Esox lucius*, L. 1758), including age, somatic growth, physical condition, food composition and specialization. Differences were observed between OAs and MPAs in fish communities, with higher total fish abundances in two MPAs. Factors such as protection status, area, season, temperature, salinity, macrophyte coverage, and reed share significantly influenced fish community composition. Mobile species targeted only by commercial fisheries showed no consistent relationship between their abundance/size and protection status, varying only across areas and seasons. Less mobile species, popular among anglers, were more abundant in MPAs, with their size only influenced by area and season. Age was higher in one MPA compared to its OA for northern pike, and somatic growth was generally lower in MPAs. No clear connections were found between northern pike's physical condition, diet, and protection. Management differences between area-pairs did not account for the magnitude of the outcomes. The studied MPAs were effective in protecting fish communities in the research area, with higher targeted species abundances in MPAs. However, the MPAs offer limited protection for species mainly targeted by commercial fishing, primarily benefiting stationary species with additional angling pressure, while the absence of common indicators of reduced fishing pressure in the MPAs points towards existing fishing pressure hindering full population recovery by preventing natural sizes, ages, and high-density dependence for targeted fish species within these protected areas.

1. Introduction

Human activities resulted in an increasing loss of biodiversity across all marine ecosystems (Dulvy et al. 2003; Magurran et al. 2015). Even though impacts, such as loss of ecosystem services and resilience, have been widely discussed (Worm et al. 2006), local oceanic, coastal and brackish water ecosystem still face strong population declines (Jackson et al. 2001; Lotze et al. 2006; Nikolaou and Katsanevakis 2023; Worm et al. 2005). Overexploitation through marine fisheries is one of the major environmental problems, altering fish population dynamics, through the reduction of abundances and the truncation of sizes and ages of harvested species (Dulvy et al. 2003; Lester et al. 2009). Even though many stocks, especially western stocks, are experiencing recovery, fishing effort still continues to alter local fish communities, but in a more sustainable manner (Hilborn et al. 2020). Commercial- as well as recreational fisheries can affect fish communities through direct and indirect effects (Helfman 2008; Lewin et al. 2006). Immediate effects of exploitation that remove target and bycatch species or induce habitat alterations through destructive gear (e.g. bottom trawling) and therefore cause demographic changes are defined as direct effects in this study (Helfman 2008). Indirect effects of exploitation within this study are defined as inter- and intraspecific interactions and ecosystem processes shaped by fisheries, such as trophic cascades, following the fishing activity (Helfman 2008). Direct impacts of selective fisheries can result in the alteration of the fish community composition by reducing target species abundances. As fisheries are also size selective, typically targeting larger individuals, the population characteristics of single target fish species can be subjected to effects such as decreased size, reproductive output and age in areas targeted by fisheries (Lester et al. 2009).

Indirect effects such as top-down cascades have been observed in both pelagic and coastal marine ecosystems (Östman et al. 2016; Scheffer et al. 2005). Through the selective removal of large predatory fish species, prey species may increase their abundance and share of the fish community caused by a relaxation of predation pressure (Baum and Worm 2009; Östman et al. 2016). But fisheries might not only indirectly effect interactions between different species but also among conspecifics (Lizaso et al. 2000). By lowering target species abundances, fisheries might decrease intraspecific competition and therefore cause compensatory density dependent mechanisms that increase growth, physical condition and lower natural mortality of targeted fish species in fished areas (Evangelista et al. 2020; Lizaso et al. 2000; Lorenzen and Enberg 2002). In species like plaice (*Pleuronectes platessa*, L. 1758) and white seabream (*Diplodus sargus*, L. 1758) these compensation effects have been found by releasing the species from intraspecific competition (Hinz et al. 2017; Lloret and Planes 2003). In fact, the surplus production in fisheries is based on density-dependence, where the population growth rises as the stock is thinned out (Beverton and Holt 1957). The positive effects of fishing pressure on growth and condition might however only be observed, if fishing just remove

conspecifics and other competitors and releases the surviving population from competition (Hinz et al. 2017). When destructive fishing methods, such as bottom trawling, increase the predator/prey ratio by lowering prey species abundances, the condition and therefore potentially also growth of predatory species, that are harvested, may decline (Hinz et al. 2017). Generally, density dependence and the resulting compensatory mechanisms are believed to be the main ecological drivers of observed changes in life-history traits such as growth and physical condition on fished populations (Beverton and Holt 1957; Eikeset et al. 2016).

Yet, growth of commercial species may also be affected by high fishing mortality (unselective or selective) that induce genetic changes, if trait heritability and selection intensity are high and the time of exposure to fishing is long enough (Hutchings and Kuparinen 2020). This evolutionary pressure is often exerted by selective processes of fisheries (fisheries-induced evolution), and may alter adaptive traits of targeted fish species (Heino et al. 2015). Size selective harvesting can favor a fast life history of fishes by increasing the mortality of large individuals of a population, causing faster juvenile growth, earlier maturation, increased reproductive investment and slower adult fish growth (Heino et al. 2015). Faster density-dependent growth through reduced intraspecific competition could counterbalance the possible slower adult growth or foster faster premature growth of fished stocks affected by fisheries-induced evolution (Eikeset et al. 2013; Evangelista et al. 2020). The possible effects of fishing on growth therefore have both a demographic and an evolutionary component (Evangelista et al. 2020). The interaction of these drivers on growth might vary in relation to both selection processes and/or population ecology but the effects of fisheries induced evolution on growth may be diminished when density-dependent growth is present (Arlinghaus et al. 2009; Eikeset et al. 2016; Evangelista et al. 2020; Heino et al. 2008).

Fishing may change the whole fish community composition directly through the removal of commercial and bycatch species (Bianchi et al. 2000; Jennings and Kaiser 1998), be a direct competitor to predatory fish by removing their prey (Kulatska et al. 2021), lower the density-dependent competition for food by removing conspecifics (Hinz et al. 2017) or even alter ecosystems and habitats (Jennings and Kaiser 1998; Lewin et al. 2006). Therefore, it is possible that fishing may indirectly alter the food composition of target and non-target species. As mentioned earlier, the effect partially depends on the influence of fisheries on the ecosystem (Hinz et al. 2017). If fisheries mostly remove conspecifics and competitors, the food choice may change to more optimal feeding conditions, but if fisheries alter the ecosystem in a way that leaves less prey for the individual, feeding conditions may be affected negatively by fisheries (Hiddink et al. 2016; Hinz et al. 2017). The ratio of prey to consumer biomass is thus the variable that will explain whether fishing will cause an increase or a decrease in the food intake and corresponding responses in growth and condition of a predator. To this date research has mainly focused on analyzing the direct and indirect of fishing separately. Direct

fishing pressure effects on the population density combined with indirect effects on food resources remain understudied and research mostly concentrates on the effect of bottom trawling as it is among the most detrimental fishing gears (Badalamenti et al. 2008; Fanelli et al. 2010; Hiddink et al. 2016; Hinz et al. 2017; Johnson et al. 2015; Sinopoli et al. 2012; Van Denderen et al. 2013). Most of these studies do not combine food composition research with growth and condition indices of targeted species. A combination is however necessary to conclude if the change in resources negatively affects population growth/condition or if the lowered intraspecific competition for different food resources in fished areas outweighs any negative effects of altered food resources (Lorenzen and Enberg 2002). Studies on the effect of less destructive passive gears, like gill nets, fyke nets and fishing with rod and reel on this combination of direct and indirect effects could not be found. Hiddink et al. (2016) hypothesized that gears, that affect prey species to a lesser extent, would reduce the possible negative effects of fishing on growth and condition through reduced prey densities.

Because intraspecific competition might increase food specialization (Svanback and Bolnick 2007), it is plausible to assume that fished populations might react to lower abundances of conspecifics by changes in feeding ecology such as a decreased diversity of prey items. Yet, a study on gopher rockfish *Sebastes carnatus* (JORDAN & GILBERT, 1880) found higher prey specialization in one of four areas with fishing pressure and less conspecific densities compared to a reference protected area with higher conspecific densities (Loury et al. 2015). The findings of this study however are most likely attributed to geographical differences of the compared areas. Therefore, density dependent food generalization through exploitation has yet to be proven.

The emergence and severity of the effects of exploitation mostly depend on the management in place, compliance with regulations and characteristics of surrounding ecosystems and of targeted species (Gigliotti and Taylor 1990; Hilborn and Ovando 2014; Lester et al. 2009). That said, ecosystems are diverse and subject to natural fluctuations unrelated to human activities (Magurran 2016). This implies that ecosystem and species characteristics have to be considered when protecting biodiversity and fish populations in different areas and to avoid false interpretations about the local impacts of fisheries.

Protection and sustainability of marine biodiversity is often promoted through the use of indirect management tools, such as size limits and gear restrictions (Pitcher et al. 2012). Yet, the only logical possibility to fully restore or maintain natural biodiversity is to keep or create areas without fishing pressure (Costello and Ballantine 2015). These no-take protected areas are often called marine reserves and have the highest benefits for conservation management but also offer unfished reference areas to study the effects of fishing and therefore also benefit fisheries management (Costello 2014). Less than 1 % of the ocean is covered by reserves, while 94 % of the protected areas still allow fishing. These partially protected areas, from now

on referred to as marine protected areas (MPAs), were created around the world, aiming to partially protect exploited fish communities and habitats while still providing valuable ecosystem services for users in and around these areas (Grorud-Colvert et al. 2021; Jobstvogt et al. 2014; Leenhardt et al. 2015). MPAs can have a wide variety of protection measures, ranging from seasonal closures, gear restrictions, boating bans to permanent fishing bans and encompass marine parks with diverse zoning levels, permitting various activities in distinct regions (Laffoley et al. 2019). The observed benefits of marine reserves and MPAs on the organisms within, can be categorized into effects acting on the fish community itself and the responses of single populations. On a community level, the cessation or reduction of fishing in MPAs can cause an increased diversity (often expressed as species richness) and total biomass of previously exploited fish communities (Edgar et al. 2007; Lester et al. 2009; Micheli et al. 2004a; Sciberras et al. 2013). The fish community composition is further expected to compromise an increased share of previously targeted species, compared to continuously fished areas (Baskett and Barnett 2015; Micheli et al. 2004a; Sciberras et al. 2013). Particularly predatory species are thought to increase their share of the fish community in MPAs as they are often the primary target of fisheries (Baskett and Barnett 2015; Micheli et al. 2004a). Through trophic cascades, however, it is also possible that the elevated predation pressure can decrease abundances of non-harvested prey species in MPAs compared to fished areas (Lester et al. 2009). On a population level, MPAs most often increase the abundances of targeted species by reducing their mortality (Baskett and Barnett 2015). Enhanced survival rates can subsequently result in shifts in the population structure, characterized by the presence of larger and older fish (Baskett and Barnett 2015; Taylor and McIlwain 2010). Indirectly, MPAs may additionally elevate intraspecific competition by increasing densities of conspecifics when populations recover to their carrying capacity (Lizaso et al. 2000). Due to density-dependent feedback mechanisms, populations within these protected areas may experience a decline in their growth and individual fitness, manifesting as reduced physical condition (Lizaso et al. 2000; Lloret and Planes 2003). The higher intraspecific competition inside MPAs might also invert the effects of fishing on food choice and specialization by favoring more specialized individuals, but as mentioned above, the jury is still out whether such effects are prevalent (Lloret and Planes 2003; Lory et al. 2015).

Despite all benefits discussed, the advantages of MPAs for fisheries targeting surrounding areas open to fishing are still highly debated, because there has been conflicting outcome on the spillover of MPAs (net transport of individuals from MPAs to OAs through larvae or adult dispersion and emigration) (Agardy et al. 2011; Di Lorenzo et al. 2016). As the proportion of protected areas in a specific region increases, fishing effort will be displaced and the net outcome may be a decrease in the yield of fishers, which has been shown for the Great Barrier Reef in Australia (Fletcher et al. 2015). While spillover was expected to increase juvenile

recruitment and adult spillover, thereby offsetting the reduction in the fishing area's size, this compensation could not be substantiated (Fletcher et al. 2015). By displacing fishers and other users from MPAs and therefore concentrating the activities into the unprotected area, the creation of MPAs further has the potential to increase competition, conflicts among users and the risk of local overexploitation in open areas (Agardy et al. 2011). Because MPAs do have potential shortcomings, it's crucial to consider the specific design and management features that can greatly influence their effectiveness in preserving marine ecosystems to avoid conflicts and maximize the potential benefits for users and biodiversity.

The effectiveness of MPAs mostly depends on their management, size, age, isolation but also the characteristics of the species that are to be protected (Edgar et al. 2014b; Le Quesne and Codling 2009). MPAs that have a high level of protection from fishing and are well enforced are expected to have the highest benefits for local biodiversity (Edgar et al. 2014b; Grorud-Colvert et al. 2021). If human activities are still allowed inside the MPAs, depending on the specific disturbances, the protection effect can be greatly diminished (Denny and Babcock 2004; Piet and Rijnsdorp 1998). The same applies for increased noncompliance of users and consequent illegal harvest inside MPAs which can potentially diminish targeted species inside MPAs (Kritzer 2004). The benefits of protection were found to increase with MPA size, age and the level of isolation (Edgar et al. 2014b). The mobility of targeted species aimed to protect through area-based conservation management is a key species characteristic that can greatly influence the outcome of protection measures (Le Quesne and Codling 2009; Pilyugin et al. 2016; Watson et al. 2019). Stationary species have the highest potential to profit from MPAs because the chances of individuals crossing MPA borders rise with increasing mobility, which makes mobile species vulnerable to fisheries again (Le Quesne and Codling 2009; Pilyugin et al. 2016). To elaborate on that issue, MPAs might not be the right management tool for fisheries targeting highly mobile species with a minor bycatch probability and rather benefit multi-species fisheries, where other management tool fail due to the complexity of the fisheries, or fisheries targeting sedentary species (Grüss 2014; Hilborn et al. 2004). From a fisheries perspective, however, species must be mobile enough to benefit the fisheries through spillover, otherwise MPAs create wilderness-like areas, while beyond the reserve boundaries fisheries yields and revenue remains unaffected (Di Lorenzo et al. 2020). In conclusion, the implementation of MPAs should not be seen as the ultimate and only tool to protect biodiversity and fished populations, as to small area size, poor design, planning and managing, degradation of surrounding ecosystems, displacement of fishers and species characteristics, such as a high mobility, can create the illusion of protection when, in reality, no effective protection is in place (Agardy et al. 2011). Therefore, it is crucial that the effectiveness of individual MPAs is assessed for example by using a Before-After Control-Impact design (BACI)

or by performing a simpler Control-Impact study (CI), comparing MPAs to comparable areas that are fished, if data before protection are not available.

As MPAs may represent reference areas for unfished conditions their creation can reverse the potential effects of fishing (Hanns et al. 2022). Therefore, it is possible to measure the effect of fishing on local ecosystems and MPA effectiveness by comparing an area-pair that includes a structurally similar open access area (OA) and MPA. This approach further allows for the testing of scientific theories such as density dependence and the resulting intraspecific competition if protection increases abundances of target species inside the MPAs and the target species has a limited mobility. For this CI design to work, however, it is necessary that the analyzed area-pairs also compromise regulations, characteristics and species, that allow for differences between the sites with differing fishing pressures. It is, for example, possible that the effect of protection is undetectable if differences in fishing pressures between OAs and MPAs are low, either due to equally low or high fishing pressures in the area-pairs if MPAs only offer limited protection from fishing (Gorud-Colvert et al. 2021; Kritzer 2004; Zupan et al. 2018). Because MPAs are often not randomly allocated and might have been strategically placed in areas of naturally greater habitat quality (Margules and Pressey 2000), it is very important in this OA-MPA comparison to account for differences in many ecological parameters that could account for demographic changes of fish species. When performed correctly, this comparison method of evaluating the effects of protection/fishing has proven to measure the typical effects of area-based management and has been used to test MPA effectiveness (Davies et al. 2022; Sciberras et al. 2013). A meta-analysis on 51 case-studies around the world that measured the effects of such CI studies between OAs and MPAs found that the total density, abundance and biomass of targeted fish species inside the MPAs was consistently higher than in the OAs (Sciberras et al. 2013). Unexpectedly, the diversity, measured as species richness, as well as the length of targeted species was generally not lower in OAs in the CI comparisons. Yet, multiple CI studies showed varying fish composition between OAs and MPAs, often showing commercially targeted species being more abundant in MPAs and non-targeted species being more abundant in the OAs (Graham et al. 2003; Nelson et al. 2018; Schroeder and Love 2002; Sciberras et al. 2013; Varnes and Olsen 2023; Watson et al. 2007). On the population level, CI studies have shown higher ages of exploited species in MPAs compared to OAs (Halvorsen et al. 2017; Stoner et al. 2012; Taylor and McIlwain 2010). Density dependent smaller growth rate has been observed in some protected areas compared to OAs (Nelson et al. 2018; Taylor and McIlwain 2010; Watson et al. 2022), but other CI studies found either no effect of protection on fish growth (Berggren et al. 2022) or opposite effects as growth increased in MPAs compared to OAs (Carbonara et al. 2022). Research on other density dependent traits such as physical condition and food choice (e.g. specialization) in relation to protection is limited and findings between OAs and MPAs were

often attributed to habitat differences rather than protection/exposure to fishing (Lloret and Planes 2003; Loury et al. 2015). These studies reflect typical drawbacks of all CI studies as habitats cannot be fully described and measured and therefore CI studies have to include a number of MPAs and similar OAs to assure that changes are driven by protection rather than the habitat in a given ecosystem. Spill-over of fishes from MPAs to the compared OAs may further reduce effects and create control sites conditionally affected by the treatment which negates basic assumptions of the CI model (Ferraro et al. 2019; Moffitt et al. 2013). CI models in comparison with BACI models also do not account for ecosystem changes.

Brackish ecosystem research on the influence of protection has, compared to terrestrial, freshwater and marine ecosystems, a rather limited extent (Barnes 1999). Yet, these productive ecosystems offer important habitats for a range of freshwater, saltwater and specially adapted brackish-water fish species (Remane and Schlieper 1958).

The world's second largest brackish sea is the Baltic Sea, a shallow (mean depth: 55 m), productive but highly degraded inland sea which is connected to the Atlantic Ocean through the North Sea (Lotze et al. 2006; Reusch et al. 2018). Resource depletion of the Baltic Sea started around 1000 years B.P. (Lotze et al. 2006). Because of the long history of human activities and high human densities, the Baltic Sea is among the most degraded brackish-water ecosystems (Lotze et al. 2006; Reusch et al. 2018). The alteration of the Baltic Sea ecosystem was even suggested to be used as a time machine to predict future changes in other coastal oceans because the degree of degradation in the Baltic Sea is well-advanced in comparison to most other coastal marine ecosystems and substantial knowledge on the man-made drivers exist (Reusch et al. 2018). All major taxonomic groups, including fishes, faced high abundance declines in the Baltic Sea (HELCOM 2018; Lotze et al. 2006). Pollutants, eutrophication, increasing oxygen-depleted sea beds, acidification, alien species, climate change and overharvest are among the most important drivers of this decline (Reusch et al. 2018; Wennerström et al. 2017). The Baltic Sea is among the most intensely fished marine areas worldwide and even though it only comprise a small area (0.11 % of total ocean area) the fisheries account for 1.2 % of the global capture fisheries (Aps and Lassen 2010; Reusch et al. 2018). Overexploitation is thought to be one of the leading reasons for declining abundances of many commercially exploited fish species (Froese et al. 2022; HELCOM 2018; Möllmann et al. 2021). The integrated biodiversity status for fish is therefore low in the Baltic Sea with most commercial species, except plaice and dab (*Limanda limanda*, L. 1758), suffering major declines in the last decades, being in an overfished status or even faced stock collapses in the case of cod (*Gadus morhua*, L. 1758) and European perch (*Perca fluviatilis*, L. 1758) (Froese et al. 2015; HELCOM 2018; Järv 2002; Möllmann et al. 2021). Even though, successful management has caused an increase in top predator abundances as well as fish

stocks and reduced nutrient input and pollutants, global warming now poses a new threat that may diminish the gains achieved' since 1974 (Reusch et al. 2018).

The Baltic Sea, especially the eastern and northern parts, comprise a multitude of shallow brackish-water coastal lagoons, which are a key spawning, juvenile development, feeding and migration habitat for a number of specially adapted freshwater and saltwater species (Kraufvelin et al. 2018). The fish community composition greatly varies among lagoons and was observed to be driven by habitat availability, temperature, salinity, nutrient levels, vegetation coverage and wave exposure but generally is poor in species (Karas and Hudd 1993; Kautsky and Kautsky 2000; Sandström et al. 2005; Snickars et al. 2009; Winkler 2002). The commercial fishing pressure in the coastal areas is considerably lower when compared to offshore areas in the Baltic Sea, but additional substantial angling pressure may exist. In Swedish coastal areas recreational fisheries were estimated to remove up to 5 – 20 times the amount of the total biomass caught by commercial fishers (Hansson et al. 2018; Karlsson et al. 2015), while in German coastal areas recreational fishing for specific marine and freshwater species can account for more than 50 % of the total landings (Strehlow et al. 2012; Van Gemert et al. 2022). Otherwise, these coastal ecosystems share many comparable anthropogenic pressures with the Baltic Sea itself and fish communities have been changing in response to multiple manmade threats (Kraufvelin et al. 2018; Newton et al. 2014). Such fish community changes include declining trends of predatory fish species and increasing number of cyprinid and gasterosteid species due to eutrophication and commercial and recreational fishing pressure (Bergström et al. 2016a; Eriksson et al. 2009).

Fish community responses to exploitation/protection have been studied in the coastal Baltic Sea habitats, documenting altered fish community composition in protected areas compared to OAs with a higher species richness inside reserves and higher abundances of a targeted species and lower abundances of non-target species inside the protected areas compared to control sites (Bergström et al. 2019; Nelson et al. 2018). Increases of large predatory freshwater species abundances have further been observed in species such as northern pike (*Esox Lucius*, L. 1758) and European perch inside protected areas in Sweden which may have induced a top-down control on prey fish species abundances (e.g. common roach (*Rutilus rutilus*, L. 1758), three-spined stickleback (*Gasterosteus aculeatus*, L. 1758)) in reserves who in turn increased in abundances as predator abundances declined due to exploitation (Bergström et al. 2022a; Byström et al. 2015; Nilsson et al. 2019; Olin et al. 2022). Yet, increased abundances of northern pike did not decrease abundances of prey species in MPAs in other Swedish coastal sites of the Baltic Sea (Eklöf et al. 2023). Nevertheless, top-down effects of MPAs might be important in the face of the rise of a species which poses a threat for coastal Baltic Sea biodiversity: the three-spined stickleback (Eriksson et al. 2009; Olin et al. 2022). Abundances of three-spined sticklebacks are increasing, especially in the central Baltic

Sea, most likely due to a lack of predation pressure from predators such as northern pike, European perch and Atlantic cod, eutrophication and climate change (Olin et al. 2022). Their rising numbers affect coastal Baltic ecosystems negatively by impairing the recruitment of predatory species and enhancing the effects of eutrophication (Bergström et al. 2019; Byström et al. 2015; Eriksson et al. 2009; Nilsson et al. 2019; Olin et al. 2022).

Marine reserves and MPAs in the Baltic Sea lagoons have also shown benefits on a population level for a range of targeted fresh- and saltwater predatory fish species and crustaceans that significantly increased their abundances, sizes and ages inside the protected areas (Berggren et al. 2022; Bergström et al. 2019; Bergström et al. 2022a; Berkström et al. 2021; Eklöf et al. 2023; Florin et al. 2013; Nelson et al. 2018). Positive population responses to coastal Baltic Sea MPAs are especially promising for commercially targeted predatory fish species with a freshwater origin because their home range is comparably small (1 – 20 km), compared to marine species (50 – 200 km and more), which can migrate over large distances (Berkström et al. 2021). Since coastal Baltic reserves and MPAs are typically small in size and not designed to protect fish, their ability to protect mobile marine species from fishing is limited (Bergström et al. 2019; Kriegl et al. 2021; Sundblad et al. 2011). Because local coastal Baltic predatory fish species such as European perch and northern pike currently face strong population declines (Bergström et al. 2022d; Järv 2002; Olsson 2019; Van Gemert et al. 2022), the study of the effectiveness of MPAs in protecting these populations is relevant because of their role as keystone species and their value to both commercial and recreational fisheries (Arlinghaus et al. 2018; Arlinghaus et al. 2023d; Hansson et al. 2018; Koemle et al. 2023).

Indirect effects of protection have also been documented in the Baltic Sea lagoons. Both northern pike and European perch grew slower in MPAs compared to OAs which is attributed to a higher density of conspecifics inside the MPAs (Berggren 2019; Edgren 2005; Nelson et al. 2018). Studies on the effect of fishing/protection on physical condition have found no difference between fished and unfished areas in European perch caught in coastal lagoon ecosystems of the Baltic Sea (Nelson et al. 2018). Research comparing food composition and specialization inside and outside of MPAs does not exist for the Baltic Sea to this date. Gaining insights into the broader repercussions of human pressures on Baltic Sea lagoon ecosystems, however, necessitates a comprehensive understanding of coastal fish communities as well as specific harvested species and how they are affected by protection.

Baltic fish communities are changing due to declining abundances of harvested fish species which can be attributed to their exploitation and other environmental challenges (Bergström et al. 2016a; Froese et al. 2015; Reusch et al. 2018). Therefore, the study of protection from fishing on fish communities, exploited species and their prey species, is ecologically and socially relevant. This research is not only necessary to assess the effectiveness of local MPAs but also to find solutions for recent problems affecting the Baltic Sea biodiversity. In this study,

demographic differences of brackish-water lagoon fish communities in three area-pairs containing a partially protected and an unprotected site, with varying protection measures, were assessed in three seasons in an ecosystem known for its intensive and size-selective commercial and recreational fisheries (Arlinghaus et al. 2023e). An additional focus laid on differences in condition, growth and nutrition of northern pike, a key predatory fish species. Given that the effectiveness of safeguarding fish communities and specific populations within the studied MPAs had not been previously evaluated, the findings obtained from this study were subjected to meticulous analysis and interpretation to formulate relevant management recommendations.

The chosen MPAs are part of a brackish lagoon system, henceforth referred to as Bodden, which is located in the western Baltic Sea on the eastern part of the Germany coast. The Bodden consist out of multiple eutrophic to polytrophic lagoon-type waterbodies which vary in salinity and are weakly connected to the Baltic Sea (Schubert and Telesh 2017; Winkler and Schröder 2003). The Bodden provides many valuable ecosystem services for the residents and tourist because it is a natural heritage, with landscapes and beaches attractive to visitors and it provides local food such fish and seafood (Schubert and Müller 2023). Many marine, freshwater and diadromous fish species share these brackish- and estuary ecosystems (Winkler and Schröder 2003). Species richness is compared to other (coral reef-) coastal marine ecosystems low (40 - 87 total species, depending on the specific Bodden lagoon), with a handful of species accounting for most of the biomass (Thiel et al. 2005; Winkler et al. 1995; Winkler and Schröder 2003). The Bodden provides an important spawning, nursery and feeding habitat for a range of native fish species (Löser 2004; Thiel 1990; Thiel 2004). Some species live permanently in coastal habitats of the Baltic Sea and the Bodden, while others, such as common roach, common bream (*Abramis brama*, L. 1758), European perch and northern pike, have the potential to seasonally migrate to spawn in freshwater or migrate to their feeding grounds in lagoons or even into the Baltic Sea (Aro 2002; Henking 1923; Müller and Berg 1982; Roser et al. 2023; Thiel et al. 2005). Species compositions highly vary among different lagoons and are mostly dependent on factors such as seasons, habitat structure (e.g. macrophyte coverage), trophic status or salinity (Fredrich 1975; Löser 2004; Pribbernow et al. 1985; Rittweg et al. 2023b; Thiel 1990; Winkler et al. 1984). Additionally, a local Bodden juvenile fish community composition can be additionally dependent on environmental parameters such as wind speed, currents, insolation, water transparency, pH, dominant vegetation type, substrate and water depth (Löser 2004; Thiel et al. 2005). Three-spined sticklebacks were related to shallow waters and the dominant species of the fish community, while the fish composition shifted to an Atlantic herring (*Clupea harengus*, L. 1758) dominated state in deeper waters (Löser 2004). Fish communities were dominated by marine species in open areas, exposed to currents and wind, while freshwater species were found more often in

sheltered areas with reduced currents (Fredrich 1975; Löser 2004). In Swedish fish community studies, the wave exposure index was successfully used to account for these current and wind driven effects (Eklöf et al. 2020; Niemi et al. 2023; Wijkmark and Isæus 2010). The juvenile fish composition in the Bodden may also vary daily and even depend on the time of the day (Fredrich 1975). Generally, the oligohaline, nutrient rich lagoons are expected to have a higher share of freshwater species, especially cyprinids, while mesohaline lagoons with lower nutrient levels are expected to include a lower share of cyprinid (Persson et al. 1991; Rittweg et al. 2023b; Thiel 1990; Winkler 1990; Winkler and Debus 2006). These drivers of coastal fish communities in the Baltic Sea could potentially result in a dynamic Bodden fish community that is linked to the specific area characteristics and season. Consequently, the inclusion of these specific parameters into the study of protection effects is necessary to avoid misinterpretation of the differences between area-pairs.

Partial fishing pressure still existed inside the MPAs investigated in this study. Commercial fishing is allowed in all MPAs while recreational fishing is mostly forbidden or restricted. The extent of the fishing pressure in the different areas was unknown at the onset of this study, which necessitated comparative surveys of fishing pressure in research areas to rightfully assign differences between area-pairs to contrasting fishing pressures in OAs and MPAs. All MPAs were created in 1990 without the specific aim to just protect fish populations. They are, compared to oceanic and pelagic MPAs, very small in size (Halpern 2003; Niessner et al. 2023a). Adjacent OAs are targeted by unselective multi-species commercial fisheries which catch fish species of all trophic levels while recreational fishers selectively and almost exclusively target large predatory species and Atlantic herring, which enter the lagoons for spawning in spring and a smaller stock in autumn (Arlinghaus et al. 2023d; Koemle et al. 2023). These fisheries use a variety of gears, including gill nets, fyke nets, eel traps, long lines and angling, while trawling is forbidden (Arlinghaus et al. 2023d; Koemle et al. 2023). Research on the impact of fisheries on fish communities and individual target species is scarce in the Bodden. But at least two freshwater species, pikeperch and northern pike, were studied in past work (Arlinghaus et al. 2023f; Gröger et al. 2007; Winkler 1980; Winkler 1991). While commercial catches of pikeperch only showed a small non-significant negative annual trend from 1972 - 1988, break points of the fishing mortality F in the Bodden were calculated to inform fisheries management and subsequently demonstrated a relationship between fishing pressure and potential declines (Gröger et al. 2007). Northern pike however, faced population declines in recent decades, which can be attributed to overexploitation to some extent, but declines are also environmentally driven (Arlinghaus et al. 2023e; Arlinghaus et al. 2023f). Even though the MPAs of this brackish-water ecosystem have been in place for 30 years their effectiveness in protecting local fish communities and populations as well as possible effects of density dependence inside the protected areas have never been studied. Hence, this

research offers initial insights into how fishing and area-based management shape brackish-water fish communities in the German Baltic.

The main effect of partial or no-take MPA is to control fishing pressure. Therefore, one expects outcomes that are directly or indirectly related to fishing pressure, e.g., fish community composition, fish abundance and size- and age structure that vary among MPAs and OAs (Lester et al. 2009). Hence, it was hypothesized that (1) fish species richness and biomass is increased in MPAs relative to OAs and (2) that the relative abundance and share of harvested fish species is higher in MPAs compared to OAs, (3) they are longer and older in MPAs compared to OAs (direct effects of protection), (4) harvested fish species are better conditioned and grow faster in OAs compared to MPAs, (5) the protection status alters prey choice and individual food specialization of targeted fish is higher in MPAs compared to OAs (indirect effects of protection). The final expectation was that outcomes would scale with local fishing pressure and be undetectable in MPA vs. OA comparisons where the differences in fishing pressure would be small.

2. Methods

2.1. Research area

For this study three areas that included area-pairs of fished and partially protected sites in the Bodden, located at the German coast of the Southern Baltic, were self-defined (Fig. 1). Area-pairs were chosen by a selection procedure that aimed to find areas including a protected and an unprotected site in close proximity to another in order to compare structurally similar areas only vary regarding their protection status. By including three area-pairs specific overarching results of protection could be identified. Further, protection characteristics of individual MPAs could be analyzed. The areas and their pairs chosen were not separated from their surrounding ecosystem throughout the study. Fish could freely migrate in- and outside of these areas.

The Bodden consists of multiple small, sandy lagoons located in and around the island of Rügen. The Grabow-area (Fig. 1) was part of the so called “East Darß-Zingster Bodden”, which consists of a chain of eutrophic, shallow (mean depth: 2.0 m) brackish water lagoon ecosystems in the western part of the Bodden. The area has a comparably high salinity with strong fluctuations in salinity because it is located in close proximity to the Baltic Sea (8.3 ± 1.6 PSU) (Niessner et al. 2023b). The water of the area is characterized by a mean yearly total phosphorus content of 55.9 ± 23.1 µg/l and chlorophyll a content of 27.7 ± 19.6 mg/m³ (Niessner et al. 2023b). In the year 2022, 24 commercial fisher caught 92 tons of fish in this area (Koemle et al. 2023). No data on the removal and effort of anglers in this area is available. The total annual fishing mortality rate (F) of all gears for one large predatory fish species, northern pike, in this area is among the lowest of the Bodden (F: 0.176, 95% CI [0.116, 0.25]) (Radinger and Arlinghaus 2023). Angling mortality rate accounts for about 94 % of the total F of northern pike, but only 5 % of anglers traveling to the Bodden chose this area as their primary fishing location (Radinger and Arlinghaus 2023). Large parts of the “East Darß-Zingster Bodden” are protected by the national park “Nationalpark Vorpommersche Boddenlandschaft” which has been established in 1990 (Fig. 1, Tab. 1). The national park regulations are enforced by water police and local rangers. The area-pair chosen for this study included a site of this national park where angling and fishing was still allowed (hereafter named Grabow-OA) and a partially protected area where angling and boating has been prohibited for 32 years (Grabow-MPA, Tab. 1). The Grabow-MPA was part of the “protection zone I”, in which commercial fishing is only allowed for full time fisher with a special permission (Tab. 1). Angling and boating are forbidden in the MPA (Tab. 1).

The second area chosen was the Ummanz-area, which was located at the eastern-part of the “Westrügener Bodden” (Fig. 1) (Niessner et al. 2023b). The “Westrügener Bodden” is located on the west side of the Rügen island. A mean depth of 1.8 m and a mean salinity of 8.7 ± 1.1 PSU characterizes this area (Niessner et al. 2023b). The “Westrügener Bodden” has the

highest mean salinities auf the Bodden lagoons (Niessner et al. 2023b). Mean yearly phosphorus ($40 \pm 19.6 \mu\text{g/l}$) and chlorophyll a concentration ($7.9 \pm 6.9 \text{ mg/m}^3$) of the meso-eutrophic area is the lowest in the Bodden lagoons (Niessner et al. 2023b). The 37 active commercial fishers caught 64 tons of fish in the year 2022 in this area (Koemle et al. 2023). The extraction volume of anglers and their effort are unknown. Total F of northern pike is higher in the “Westrügener Bodden” when compared to the “East Darß-Zingster Bodden” (F: 0.222, 95% CI [0.155, 0.307]) (Radinger and Arlinghaus 2023). Even though most anglers generally choose this area as their prime fishing destination (23.5 %), angling only account for 32% of F (Arlinghaus et al. 2023d; Radinger and Arlinghaus 2023). The whole area is part of the national park “Nationalpark Vorpommersche Boddenlandschaft” (Niessner et al. 2023a). Unlike in the Grabow-area, the MPA site chosen in the “Westrügener Bodden” (hereafter called Ummanz-MPA) was part of the “protection zone II”, which meant that all full time and part time fisher can target this area without any special permission (Tab. 1). Angling and boating was prohibited (Tab. 1), while angling, commercial fishing and boating was allowed in the chosen OA in the “Westrügener Bodden” (Ummanz-OA).

The last research area-pair was situated in the northern part of the “Greifswalder Bodden”-area (Fig. 1). This is the deepest lagoon in the Bodden-area (mean depth: 5.8 m) (Niessner et al. 2023b). The lagoon is located on the east side of the Rügen island. Due to its geographic location on the eastern part of Rügen and its proximity to the Peene river estuary the mean salinity of this lagoon is comparably low ($7.2 \pm 0.9 \text{ PSU}$) (Niessner et al. 2023b). The logon is eutrophic and has mean total phosphorus values of about $45.8 \pm 21.1 \mu\text{g/l}$ and a mean chlorophyll a concentration of $14.6 \pm 13.6 \text{ mg/m}^3$ (Niessner et al. 2023b). “Greifswalder Bodden” has the highest amount of active commercial fishers with 56 full time and part time fishers, that caught about 98 tons of fish in 2022 (Koemle et al. 2023). Like the other areas, the catch and effort of anglers is unknown. F of northern pike is the highest of all areas in the Greifswalder Bodden (F: 0.327, 95% CI [0.048, 0.685]) (Radinger and Arlinghaus 2023). Angling accounts for about 42 % of the northern pike F (Radinger and Arlinghaus 2023). The two lake-like lagoons (N. and S.-area, Fig. 1) chosen for this study were located at the northern part of the “Greifswalder Bodden” and part of the reserve “Biosphärenreservat Südost-Rügen” established in 1990 (Niessner et al. 2023a). As this area-pair was the only area-pair where OA and MPA were not geographically connected, the likelihood of environmental / fish community differences may have been increased (Soininen et al. 2007). In contrast to the two other area-pairs, angling, commercial fishing and boating was partially allowed in the MPA of the N. and S.-area (Tab. 1), while angling, commercial fishing and boating was fully permitted in the OA of the N. and S.-area.

All three areas have a temporal northern pike spawning closure (Grabow and Ummanz: from 04/01 – 05/01, N. and S.: 04/01 – 06/01) each year. Common roach, common bream and

European perch are not protected by any spawning closure in any of the areas. There is a minimum length limit applied in OAs and MPAs for northern pike and European perch (Northern pike: 500 mm, European perch: 200 mm). Otherwise, there is a bag limit of 3 pike per day in the OAs for anglers and live baiting as well as bait trawling is forbidden for anglers. There is no quota system for any species among freshwater species in the OAs and MPAs for commercial fishing.

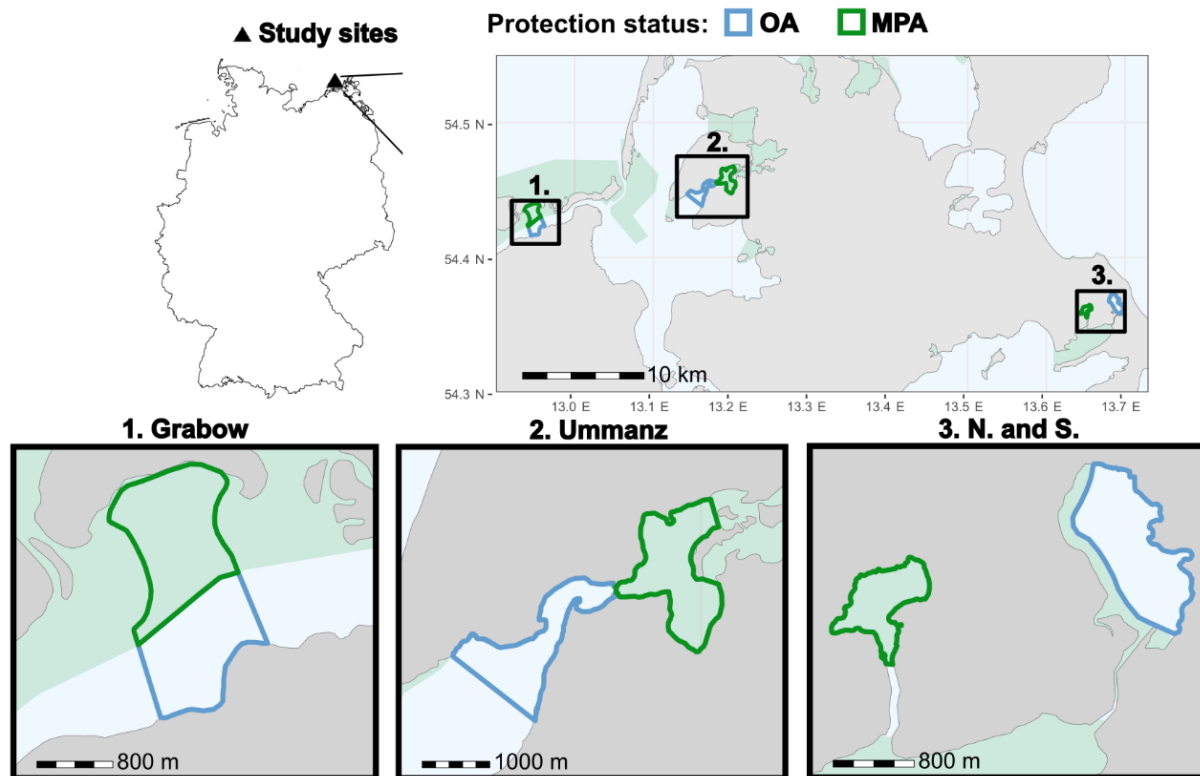


Figure 1. Map of the three area-pairs sampled in this study (N. and S.: Neuensiener-/Selliner See) and their location on the island of Rügen, located in North-East Germany. Green background color marks protected areas. Outlines represent the borders of the areas chosen for this study (OA: open access area (blue outline), MPA: marine protected area (green outline)). Area maps were modified after Roser (2023).

Table 1. The institutions, regulations and knowledge gaps of the open access (OA) and marine protected areas (MPA) in the three study areas (N. and S.: Neuensiner-/Selliner See).

Area	Protection status	Institution	Regulations	Knowledge gaps
Grabow	OA	Nationalpark Vorpommersche Boddenlandschaft	- angling and commercial fishing allowed with licenses	- fishing pressure, gears, and targeted species unknown
	MPA	Nationalpark Vorpommersche Boddenlandschaft	- navigation ban - angling ban - commercial fishing ban with exemption	- exception for an unknown number of commercial fishers - fishing pressure and gears used unknown - targeted species unknown
Ummantz	OA	Nationalpark Vorpommersche Boddenlandschaft	- angling and commercial fishing allowed with licenses	- fishing pressure, gears, and targeted species unknown
	MPA	Nationalpark Vorpommersche Boddenlandschaft	- navigation ban - angling ban - commercial fishing allowed - protected season from April to May	- fishing pressure, gears, and targeted species unknown
N. and S.	OA	Biosphere reserve Südost-Rügen	- angling and commercial fishing allowed with licenses - protected season from April to May	- fishing pressure, gears and targeted species unknown
	MPA	Biosphere reserve Südost-Rügen	- navigation ban - limitation of angling - commercial fishing allowed - protected season from April to May	- fishing pressure, gears and targeted species unknown - angling allowed from shore for a limited number of anglers (unknown fishing pressure)

2.2. Biological characteristics of targeted species

To study the abundance, biomass, length and age differences between OAs and MPAs, four harvested fish species were chosen that varied regarding their ecology, mobility, and importance for commercial- and recreational fisheries. Home ranges and mobility of targeted species are important since they can determine the effectiveness of spatial protection (Grüss et al. 2011; Lizaso et al. 2000). Species with a low mobility generally represent the most suitable research species to observe differences between OAs and adjacent MPAs (Kramer and Chapman 1999). These species are assumed to spend a sufficient time inside the

protected areas to recover from fishing pressure. Therefore, they present better study organisms compared to highly mobile species which can migrate out of the protected areas and experience effects of fisheries (Grüss et al. 2011; Lizaso et al. 2000). For this brief overview of mobility, the focus was laid on observations of the specific species in areas comparable to the Bodden where larger migrations are possible due to large, connected ecosystems. To evaluate the likelihood of density dependent tradeoffs to occur in the studied MPAs, one species (northern pike) was further described in the light of species characteristics that could contribute to intraspecific competition.

The importance of a species to commercial and recreational fisheries is further presented to later discuss if differences between OAs and MPAs regarding demographic traits are to be expected for the specific species. If a species is valuable for a fishery, it will likely show signs of lowered fishing pressure in MPAs, whereas non-target species are either unaffected or positively affected by protection through lowered predation pressure (Lester et al. 2009; Lizaso et al. 2000). All species were crudely divided into low fishing pressure species that were only targeted by commercial fisheries and high fishing pressure species that were targeted by commercial and recreational fisheries.

2.2.1. Low fishing pressure species

Common roach

The common roach (Fig. 2) is found all throughout Europe and generally most abundant in nutrient rich lakes and medium sized rivers and backwaters, but it also populates the brackish-water areas of the Bodden (Kottelat and Freyhof 2007). According to the International Union for Conservation of Nature (IUCN) conservation status, common roach are not threatened (Freyhof and Wright 2011). Common roach have been described as partial migrants, meaning parts of the population perform spawning migrations and subsequent migrations to their feeding grounds and other parts are resident (Brodersen et al. 2008; Kottelat and Freyhof 2007; Skov et al. 2008). In the Bodden common roach are assumed to perform spawning migrations into oligohaline bays of Bodden lagoons (Thiel et al. 2005), which is, according to literature, also to the preferred time of fishers to catch them (Winkler 1989). After spawning common roach may then swim as far as into the open Baltic Sea to reach their feeding habitat (Henking 1923; Thiel et al. 2005).

Common roach in the German river “Spree” have been observed to have a high mobility, traveling up to 12 km daily (Baade and Fredrich 1998). Therefore, this species was expected to have a high mobility inside the Bodden as well. According to a previous study in parts of the Bodden and the Baltic Sea, common roach were observed to be mobile, periodically traversing between the lagoons and the Baltic Sea in both directions and utilizing significant portions of

the Bodden within a specific timeframe (Henking 1923). Nowadays movements of common roach in the specific German Baltic lagoons have yet to be studied.

If Atlantic herring is excluded from the total landings of commercial fisheries in the Bodden, the predominant species in the catches are common roach and common bream (Koemle et al. 2023), implying a high importance for commercial fisheries. Oppositely, less than 1 % of the anglers fish for common roach in the Bodden (Weltersbach et al. 2021). It is reasonable to assume that recreational fisheries exert only a very small fishing pressure on common roach. Due to their high mobility and being only targeted by commercial fishing, which is not excluded from the MPAs studied, common roach were not expected to show differences in abundance, biomass and length in OAs compared to MPAs.

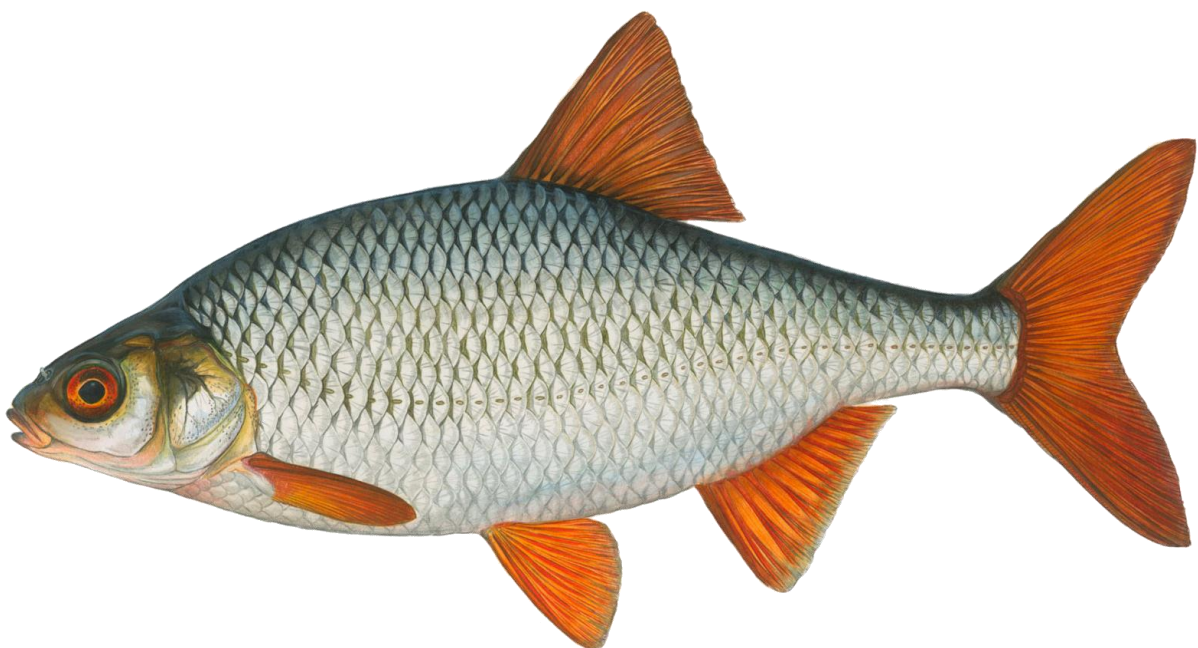


Figure 2. Illustration of a common roach (*Rutilus rutilus*, © Eric Otten, DAFV).

Common bream

The common bream (Fig. 3) inhabits a wide range of European lakes and rivers and is also found in the Bodden lagoons (Kottelat and Freyhof 2007). Common bream are not threatened in Europe according to the IUCN Red list (Freyhof and Wright 2011). Spawning migrations are common and they can start in autumn and end in spring, during which the common bream can travel as far as 100 km (Kottelat and Freyhof 2007). In British connected wetlands common bream were observed to have resident and migratory phenotypes that mixed during spawning season (Winter et al. 2021). Furthermore, common bream migrations were also assigned to size and predation risk (Skov et al. 2011). Migrating to shallow stream habitats, smaller individuals evaded the probability of potential predation (Skov et al. 2011). Common bream were also observed to migrate when somatic condition is low (Brodersen et al. 2019). Similar

to common roach in the Bodden, they are also believed to perform long spawning migrations into oligohaline lagoons in spring and feeding migrations after spawning into the lagoons and the Baltic Sea (Thiel et al. 2005). Old bream were observed to migrate in the Baltic Sea, which is seen as a feeding habitat (Winkler 1989). Henking (1923) found that common bream were mobile in parts of the Bodden and even migrated into the Baltic Sea and back from the Baltic Sea into the lagoons. The drivers of these migrations are unknown. Recent common bream movements in the Bodden have not been studied. Common bream are, after Atlantic herring, the dominating fish species in the catch of commercial fishers in the Bodden (Koemle et al. 2023). Only a very small percentage of recreational fishers (< 1 %) target this species (Weltersbach et al. 2021). The expectations regarding differences between OAs and MPAs in common bream abundance, biomass and length for this study equaled those of common roach.



Figure 3. Illustration of a common bream (*Abramis brama*, © Eric Otten, DAFV).

2.2.2. High fishing pressure species

European perch

European perch (Fig. 4) can be found throughout Europe in almost all waterbodies and ecosystems, including the Bodden and are therefore also not threatened according to the IUCN Red list (Freyhof and Wright 2011). They can undertake small spawning migrations in spring from which they return to their feeding habitats (Freyhof and Wright 2011). European perch populations that inhabit brackish-water ecosystems can have anadromous subpopulations that migrate into freshwater and some subpopulations that reproduce in brackish water (Breian 2022; Hall et al. 2022; Tibblin et al. 2012). Catadromous European perch populations that

perform short trips to brackish lagoons have been studied in Denmark (Skovrind et al. 2013). Regarding their mobility it was found that in Estonian coastal waters European perch were found to migrate up to 160km with an average migration speed of 11 km/day (Järv 2000). Other studies in coastal Baltic Sea lagoons found that European perch have a limited mobility with a home range averaging out at about 10 km for most individuals (Böhling and Lehtonen 1984; Saulamo and Neuman 2002). Yet, the mobility highly varied among different areas. Therefore, it is likely that the European perch's mobility cannot be generalized and depends on the specific lagoon ecosystem. In the Bodden they perform spawning migrations into oligohaline lagoons in spring and feeding migrations afterwards into the lagoons and the Baltic Sea (Thiel et al. 2005). Henking (1923) found that European perch were partially stationary on a monthly basis but would move considerable distances throughout the years, even migrating to the Baltic Sea and back.

Strong declines of local European perch population abundances have been observed in the Baltic Sea which were caused by overexploitation or recruitment failure (Nilsson et al. 2004; Vetemaa et al. 2001). No monitoring data of the European perch populations in the Bodden exists, but they are targeted by both commercial as well as recreational fisheries (Arlinghaus et al. 2023d; Koemle et al. 2023). European perch comprise a low percentage of the total catch of commercial fishers in this region (Koemle et al. 2023), but about 19 % of the anglers chose European perch as their target species in the Bodden (Weltersbach et al. 2021).

Assuming that European perch were partially stationary during the sampling, it was expected that spatial protection would influence the abundance and biomass of European perch, due to recreational fishing being mostly excluded from the MPAs. Sizes of the European perch were not expected to differ between OAs and MPAs as their high mobility should make the whole population vulnerable to fishing annually.



Figure 4. Illustration of a European perch (*Perca fluviatilis*, © Eric Otten, DAFV).

Northern pike

Northern pike (Fig. 5) are found in most waterbodies of Europe and inhabit a wide range of aquatic ecosystems that offer aquatic vegetation, including the coastal areas of the Baltic Sea (Kottelat and Freyhof 2007). Northern pike populations in the Baltic Sea are generally divided into two phenotypes: anadromous northern pike, which spawn in freshwater and stay in the brackish lagoons the rest of the year and those which stay in the brackish water year-round (Dhellemmes et al. 2023c; Larsson et al. 2015; Nolte et al. 2023). They are known to show strong homing behavior (Eklöv 1997; Roser et al. 2023). Northern pike fit the description of an organism with low to intermediate mobility. The average home range size of these top predators in brackish lagoons ranges from 3 - 14 km, with core home ranges lower than 2 km in the Bodden (Berkström et al. 2021; Dhellemmes et al. 2023b; Karaas and Lehtonen 1993; Saulamo and Neuman 2002). The low mobility makes this fish species a prime target for protection studies and density-dependent research in MPAs. Further, northern pike are highly territorial (Anders Nilsson 2006; Eklöv 1992) and have been shown to exhibit density-dependence traits and behaviors (Anders Nilsson 2006; Pierce and Tomcko 2003; Pierce et al. 2003). Large northern pike oust and cannibalize smaller conspecifics (Anders Nilsson 2006). Additionally, northern pike have been shown to maximize their dispersal (Haugen et al. 2006), corresponding to the ideal free distribution theory (Fretwell 1969). Furthermore, intraspecific competition over space and food items has been shown to negatively affect northern pike growth (Anders Nilsson 2006; Eklöv 1992). Northern pike exhibited a slower growth rate in protected areas where densities of conspecifics were higher (Berggren 2019; Berggren et al. 2022; Edgren 2005). Therefore, northern pike represent an ideal study species

because they have been found to be density dependent, and even showed these effects in MPAs. Another benefit of using northern pike as a study species to assess differences between area-pairs, varying in regards to their fishing pressure, is its high commercial and recreational value for many European fisheries (Kuparinen and Lehtonen 2018). In the Bodden northern pike only account for a small share of the catch of commercial fishers (Koemle et al. 2023) but they are the prime target of recreational fishers (Arlinghaus et al. 2023d). These circumstances allow the expectation that northern pike abundances, length and age would differ comparing OAs and MPAs. Increased abundances inside the MPAs were expected to cause density dependent tradeoffs in northern pike. The information provided by this research on how MPAs influence pike populations is particularly valuable in the face of dwindling brackish pike populations in some European fisheries at present (Nilsson et al. 2004; Van Gemert et al. 2022).



Figure 5. Illustration of a northern pike (*Esox lucius*, © Eric Otten, DAFV).

2.3. Fishing effort analysis

Owing to their establishment in the distant past and their exclusion of most anglers and fishers the MPAs chosen represent areas well suited for the study of reserve effects on fish communities. However, no area-pair could be identified that included a no-take MPA. Therefore, a measurement of fishing effort was performed in OAs and MPAs to assign fishing pressure differences between area-pairs to the specific area. Herby, it was ensured that results from the analysis could be discussed in the light of present/absent fishing effort differences between OAs and MPAs. In order to attribute variations in fish community composition and characteristics of fish populations to differences in fishing pressure, the existing information regarding fishing pressures in the Bodden, documented by Arlinghaus et al. (2023a) was integrated with observational data on fishing effort collected during the 2022 fieldwork. The number and type of fishing gears and the number of anglers observed in OAs and MPAs was noted each day, as researchers sampled the specific areas. Following the acquisition of the data, the area-pairs were ranked, depending on fishing pressure differences between OAs and MPAs (low, medium, high). Recreational fishing exerts a high fishing pressure on northern pike and potentially European perch in the Bodden (Arlinghaus et al. 2023d; Arlinghaus et al. 2021). Additional recreational fishing pressure in OAs was therefore expected to be a sufficient driver for changes in fish communities and fish populations dynamics, even if commercial fishing pressures were equal in area-pairs.

2.4. Habitat analysis

Differences in ecological parameters between MPAs and OAs can easily overshadow potential effects of reduced fishing pressure (Lizaso et al. 2000). Therefore, a wide range of important ecological parameters were measured to describe the different area-pairs throughout the three chosen seasons (spring, summer, autumn, Tab. 2). The environmental factors were also used to measure how these variables affected the fish community composition, while also comparing it to the impact of protection status.

Firstly, the surface area of each predefined OA and MPA zone was calculated using the software ArcGIS (Version: 10.8). To measure the average depth of the different protection status a boat with a depth finder (Garmin GPSMAP 923xsv) was maneuvered through the areas in a tight grid while the water depth was recorded. Gathered data for each site were converted from a .sl2 to .csv format (<https://kw-m.github.io/sl2-csv-converter/>). Subsequently, the recorded grid was interpolated by using a kriging algorithm. The average depth of each site was then calculated as the mean depth of the interpolated areas. Macrophyte coverage was measured by randomly allocating six transects containing ten equidistant points in each protection status in all areas/seasons once (transects were conducted in close timely proximity to the pike net sampling in Tab. 3). The transects started at the shore and ended in the

approximate center of each protection status. At each point an underwater camera was hovered approximately 0.3 m above the seabed and the percental macrophyte coverage recorded on an onboard screen was measured visually on-site. Hereafter, strata in 1 m steps were created that summarized the macrophyte percentages for the protection status in the areas for all seasons. Weighted macrophyte coverage means were then calculated by using the percentage of each depth stratum to the total protection status as the weight. The reed share for each area pair was calculated once according to Niemi et al. (2023). Additionally, the wave exposure index of each area-pair was calculated using the Simplified Wave Model (SWM) presented by Wijkmark and Isæus (2010). Regularly, throughout the sampling period water temperature and salinity were measured using a multimeter and the Secchi-depth was measured to account for differences in turbidity.

2.5. Fish community composition analysis

To compare fish communities between the different area-pairs in different seasons, standard water framework directive (European Standard EN 14757, (CEN 2015)) benthic multi-mesh gillnets of 30 m length and 1.5 m height, with mesh sizes of 5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43, 55 mm (panel length of each mesh size was 2.5 m) were utilized. 6 nets were randomly placed in the six sites on each sampling occasion in April (spring), July (summer) and October (autumn, Tab. 2, Fig. 6). Nets were set at sunset and retrieved at sunrise (Fig. 6). Each fish caught was first identified to species level and afterwards total length (mm) as well as weight (mg) were measured (Fig. 6). When fish were damaged due to the handling procedure or predators, such as birds and otters, the length was visually estimated, and the weight was back calculated by using a length-weight relationship of the specific species. For this relationship all fish captured during the research were included. Catch-per-unit-effort (CPUE) was calculated as fish/30 m net and biomass-per-unit-effort (BPUE) was calculated as kg/30 m net. Species richness was calculated as the number of species per 30 m net.

To compare harvest to non-harvest species in regards to their response to protection, the captured species were divided into two groups. One group represented fish species that were targeted by fisheries or due to their large size were more vulnerable to the multi-species gears used in the Bodden (Tab. 7) (Koemle et al. 2023). Whereas, the other group mostly consisted out of species that were too small to be captured in the gears used or not of interest for the local fisheries (Tab. 7). CPUEs and BPUEs were calculated for both species groups separately as fish / 30 m net and kg/30 m net.

As gillnets represent a passive gear in which fish need to entangle, this capture technique is biased towards more active, fast moving and spiny species (Backiel and Welcomme 1980; Hamley 1975; Kurkilahti 1999). These biases need to be considered but as this was a comparison with equal gears, abundance and biomass differences between sites, areas and

seasons are interpretable because these biases apply to all researched fish communities equally. Birds were regularly observed feeding from the nets (Fig. X), but it was assumed that the loss of fish from the net was equally distributed among sites and areas.

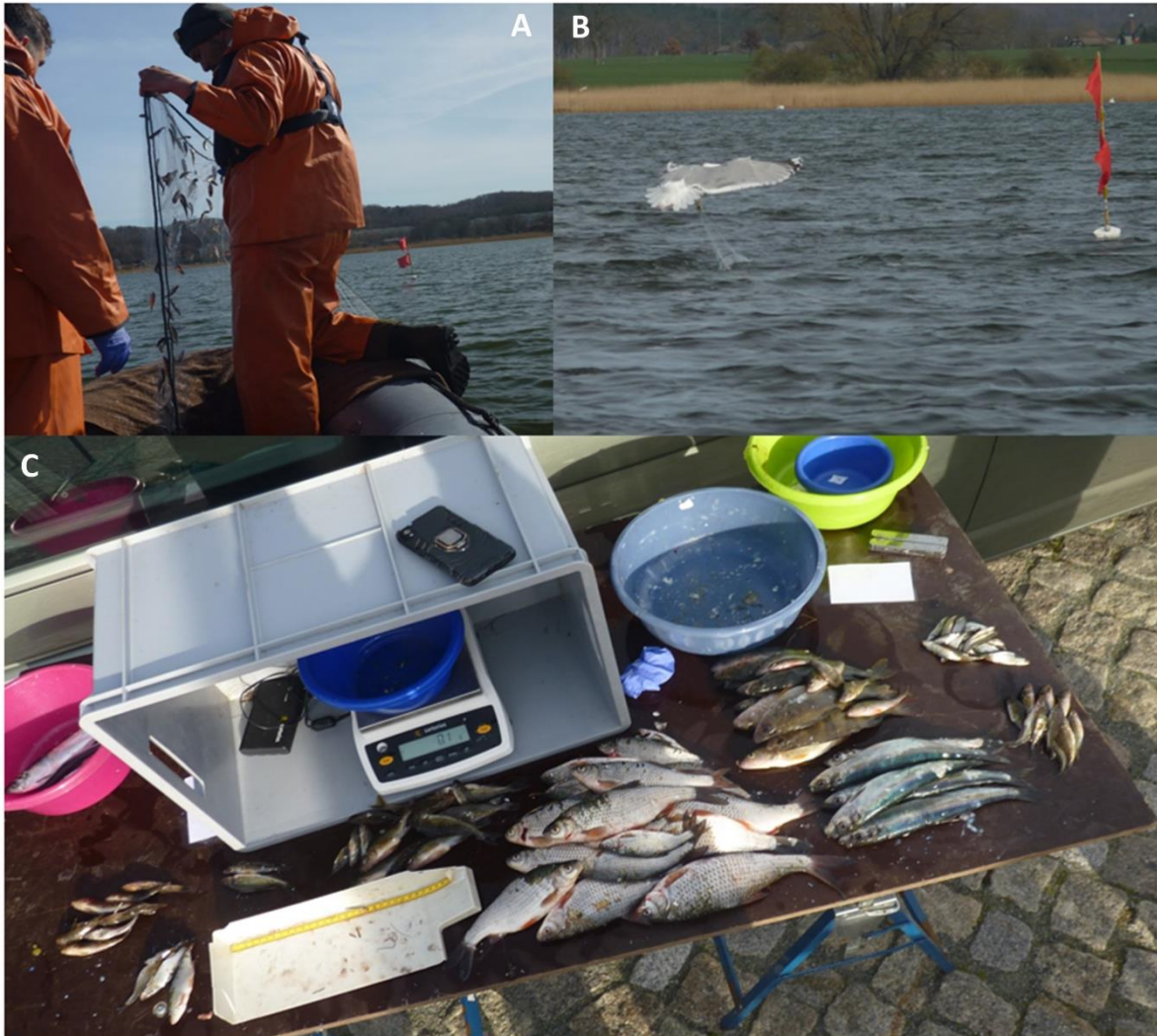


Figure 6. A: retrieving the nets in the OA of the Neuensienner- and Selliner See-area (Picture credit: Phillip Roser). B: seagull trying to rip a fish out of the net in the MPA of the Neuensienner- and Selliner See-area (Picture credit: Phillip Roser). C: length and weight measurement setup in the field.

2.6. Fish abundance, biomass, and length measurements

To measure absolute abundances, biomasses and length of common roach, common bream and European perch the nets used for the fish community composition and benthic multi-mesh nets of 100 m length and 1.5 m height, with mesh sizes of 50, 60, 75, 95 und 110 mm (panel length of each mesh size was 25 m, hereafter referred to as “pike nets”). The additional pike nets assured that larger individuals of all species were captured due to the larger mesh sizes. The sampling design and data collection equaled the fish community sampling, but sampling

days differed (Tab. 2) and CPUEs/BPUEs of the nets were calculated as fish/100 m net and kg/100 m net. As all three species have a moderate to high mobility, gill nets should yield a good approximation of abundances, but the length in all gill net types might be skewed towards larger individuals that are increasingly mobile (Hamley 1975).

2.7. Northern pike abundance and length measurements

To avoid potential shortcomings of northern pike gillnetting (Mueller et al. 2017) and low catch rates in seasons other than spring (Neumann and Willis 1995), angling with artificial lures was applied as a sampling method to measure the abundances of northern pike. Angling was further identified as the most consistent and effective sampling method to predict northern pike abundances in the Bodden (Feldhege et al. 2023). Angling effort varied among areas in each sampling season (Tab. 2) and was performed from drifting boats to cover a large area, to achieve representative abundance data. The starting site (OA/MPA) in each area was chosen at random. Then four 45 to 120 min trials were conducted that alternated between sites (2 OA trials, 2 MPA trials per day, fishing efforts were always equal in the consecutive trials between sites). To randomize the area covered with the boats, random points were chosen on the map, that indicated the starting point for a boat drift. The orientation of the drifts was contingent upon the prevailing wind direction. Drifts ended if the boundary of a site was reached. Subsequently, a new random drift began. Up to three boats with a maximum of 5 anglers per boat sampled the sites, but overall angler numbers on the boats varied. Lures selection was up to the angler, but one lure always had to be fished for two consecutive trials to avoid lure effects between OAs and MPAs. The captured northern pike were measured regarding their total length (mm) and weight (mg). CPUE was calculated as pike per boat. BPUE was calculated as kg per boat. On each angling day the salinity (PSU) and turbidity (Secchi depth (m)) were measured. Angling selectively targets hungry and bold individuals (Keiling et al. 2020; Klefoth et al. 2017; Wilson et al. 2015). Yet, this should not affect the interpretability of the results since the method was equal in all sites, areas and seasons. However, since recreational fisheries in the Bodden are exploiting northern pike stocks while also practicing catch-and-release, their populations could also be affected by the timidity syndrome and acquired hook avoidance (Arlinghaus et al. 2017; Beukemaj 1970; Monk et al. 2021). If northern pike in the OAs would not bite or be less aggressive towards lures because they are timid while individuals in the MPAs, that have not been targeted yet, attack lures, angling as an abundance measure would yield false abundance results. Indications for timidity syndrome and hook avoidance in northern pike in the Bodden were substantiated (Braun et al. 2023). But abundance differences between areas could still be shown because the timidity only partially affected the catch rates (Braun et al. 2023). This study did not control for timidity syndrome. To compare northern pike lengths between OAs and MPAs all individuals captured with the 30 m and 100 m gillnets as well as

the angled fish were measured to the nearest millimeter and the sex was externally determined according to Casselman (1974).

Table 2. Sampling dates and seasons (spring, summer, autumn) for the different gears (angling, benthic multi-mesh gillnets, pike nets) used in the different sampling areas (Grabow, Ummanz, Neusiner – and Selliner See (N. and S.)).

Area	Season	Gear	Date
Grabow	spring	Angling	2022-04-28, 2022-05-04, 2022-05-25, 2022-06-08
		Benthic multi-mesh gillnets	2022-05-03
		Pike nets	2022-05-01
	summer	Angling	2022-07-24, 2022-08-03, 2022-09-20, 2022-09-27
		Benthic multi-mesh gillnets	2022-07-31
		Pike nets	2022-07-30
	autumn	Angling	2022-10-23, 2022-10-27, 2022-11-30, 2022-12-03
		Benthic multi-mesh gillnets	2022-11-01
		Pike nets	2022-10-24
Ummanz	spring	Angling	2022-04-17, 2023-04-22, 2022-04-27, 2022-05-24, 2022-06-10
		Benthic multi-mesh gillnets	2022-04-18
		Pike nets	2022-04-22
	summer	Angling	2022-07-12, 2022-07-14, 2022-07-22, 2022-09-21, 2022-09-28
		Benthic multi-mesh gillnets	2022-07-16
		Pike nets	2022-07-18
	autumn	Angling	2022-10-19, 2022-11-28, 2022-12-01, 2022-12-04
		Benthic multi-mesh gillnets	2022-10-11
		Pike nets	2022-10-20
N. and S.	spring	Angling	2022-04-03, 2022-04-07, 2022-06-07, 2022-06-09
		Benthic multi-mesh gillnets	2022-04-11
		Pike nets	2022-04-06
	summer	Angling	2022-07-03, 2022-07-07, 2022-09-19, 2022-09-26
		Benthic multi-mesh gillnets	2022-07-05
		Pike nets	2022-07-04
	autumn	Angling	2022-10-04, 2022-10-07, 2022-11-29, 2022-12-02
		Benthic multi-mesh gillnets	2022-10-05
		Pike nets	2022-10-08

2.8. Northern pike age

Age was used as an indicator of (reduced-) fishing pressure. As fisheries increase the mortality rate and often target older/longer fish, fished populations are expected to decrease their average age in fished areas when compared to MPAs (Lester et al. 2009).

As northern pike grow slower in cold seasons (Diana 1979) their calcified bone structures and scales form annual growth increment differences (annuli). These structures are visible as uninterrupted rings on the structures and can be used for the determination of the age of a northern pike (Oele et al. 2015). Even though wing bones, opercular bones or otoliths are considered to be more consistent determinants of age in northern pike (Frost and Kipling 1959; Rittweg et al. 2023c), scales were used since their removal still allows the release of analyzed fish, as this study was part of a larger tagging study (BODDENHECHT: www.boddenhecht-forschung.de). Each measured northern pike caught in the 30 and 100 m gillnets as well as the angled individuals were euthanized, and 10-15 scales were removed near the left side of the dorsal fin. The scales were frozen (-20°C) and later analyzed. After thawing the scales, they were cleaned in a detergent solution with precision wipes. Subsequently, three to five scales, that did not show signs of being regrown, were fixated between two glass slides and laid under a stereo microscope (LEICA MZ8, magnification: 0.78 x 10) and the individual scales were photographed with an attached camera (LEICA MC190 HD). The photos were imported to ImageJ2 (Version: 2.14.0) including the processing package Fiji (Version: 2.14.0) and the plugin ObjectJ (Version: 1.05d). Image names and order were randomized to avoid learning bias and knowledge about the site, area, season or length of a specific fish. One trained reader was estimating the age of all scales to avoid a reader bias. Annuli were marked and counted, and the total number of rings indicated the age of a fish (Fig. 7). Age readings of all scales of an individual northern pike were averaged and rounded. This value was then assumed to be the actual age-at-catch of the fish.

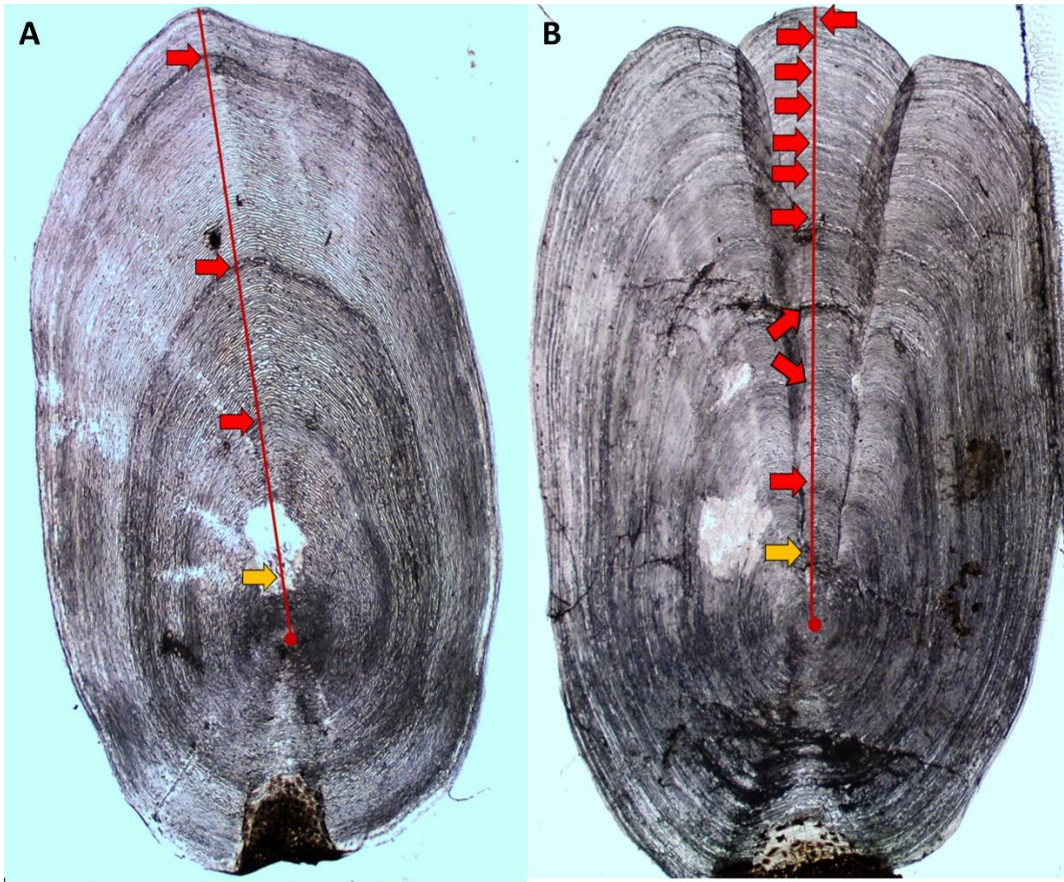


Figure 7. Pictures of a two different pike scales under the microscope (A: 3 years old, B: 10 years old). Yellow arrows indicated the pseudoannulus (transition to piscivory) and red arrows indicate actual annulus (winter ring, picture credit: Timo Rittweg).

2.9. Pike physical condition measurements

To quantify the individual health of an organism a wide range of condition indicators have been established (Stevenson and Woods Jr 2006). These indicators measure the amount of energy stored within an individual (Stevenson and Woods Jr 2006). For several species it has been shown that competition over resources can decrease the condition of individuals of a population (Azour et al. 2015; Casini et al. 2011; Casini et al. 2014). This emphasizes the importance of condition measurements as a tool to study density related competition in MPAs. In this study the focus laid on common and approved measurements of physical condition like the relative condition factor (Le Cren 1951) and the hepatosomatic index (HSI) (Stevenson and Woods Jr 2006).

The relative condition factor was calculated for all northern pike caught with the 30 m and 100 m gillnets as well as the ones caught with rod and reel. The relative condition factor was calculated as follows:

$$Kn = \frac{W_o}{W_E}$$

where W_O is the observed weight and W_E the expected weight calculated from the length-weight regression acquired from Willis (1989).

Liver sampling to measure HSI was performed only if pike died in the gillnets or during angling. Northern pike, caught during the angling trials, that bled out of the gills were dispatched, as bleeding increases the chance of hooking mortality (Arlinghaus et al. 2008). From each dispatched northern pike, the liver was removed, and the wet weight (mg) was measured.

The HSI measures the relative weight of the liver in comparison to the gutted body weight. As the liver is a major energy storage for fish, the relative weight is used as an estimate of the energy status (Alonso-Fernandez and Saborido-Rey 2012; Nunes et al. 2011). The HSI will be calculated using the following formula:

$$HSI = 100 * \frac{W_L}{W_G}$$

With W_L being the weight of the liver [g] and W_G being the somatic weight [g].

2.10. Growth rate

The growth rate of organisms is a well-studied density dependent life-history trait and can be, like all other life-history traits, separated into density independent (environmental factors) and compensatory density dependent growth (Lizaso et al. 2000; Rose et al. 2001). To draw conclusions on the density dependence of the growth in the present study, the growth rate will be discussed in the light of other indicators of intraspecific competition, namely condition and food specialization.

Growth rate was calculated using the size-specific growth rate proposed by Berggren et al. (2022) but instead of wing bones, scales were used as growth determinants. As the length between annual increments of calcified structures and scales of fish has a relationship to the fish growth in a specific year (Cheung et al. 2007), these structures can be used to describe growth throughout an individual's life and can therefore also be used to back calculate the length of an individual at a specific age. The maximum length of the anterior radius of each scale and the distances between growth increments of the analyzed northern pike scales were measured with the software ImageJ2 and the above-mentioned add-ons. The length at age i was back-calculated using the Fraser-Lee equation which is based on the scale-proportional hypothesis (Francis 1990). The size-specific growth for each individual northern pike was then calculated following Berggren et al. (2022).

2.11. Food composition and prey selectivity

To acquire the stomach content of euthanized northern pike captured with all gears, gastric lavage was performed. The stomach content was flushed out of the stomach and then filtered through a fine filter mesh. Stomachs of fish that died during the study either in the net or due

to hooking mortality were not flushed but their stomachs were removed, opened and all prey items were collected. All prey items were frozen and analyzed. To test if gastric lavage consistently removed all prey items, the stomachs of 15 live northern pike were flushed, all prey items were removed and then the individuals were dispatched. Subsequently, the stomachs were removed and checked for leftovers, but all stomachs were empty. This outcome led to the technique being acknowledged as a reliable method for consistently obtaining the entire stomach contents of live northern pike.

All items of the stomachs were identified to the lowest practical taxonomic level (Fig. 8). Hard structures of fish remains were identified with the appropriate identification guides (Bräger and Moritz 2016; Härkönen 1986; März 1987). Subsequently, food items, if possible, were measured to the nearest millimeter to back calculate the weight from the species-specific weight-length regression obtained from the multi-mesh gillnets of the specific season and area. If neither length or weight of a prey item could be assigned, the average length and weight of the species in the specific area and season was assigned to that prey item. Herewith, the prey count and biomass of each prey type in an individual's stomach could be calculated. The individual specialization (Bolnick et al. 2002) was calculated following Svanback and Bolnick (2007).

According to the optimal foraging theory (Pyke et al. 1977) every organism aims to maximize its net energy intake by maintaining the lowest possible benefits-costs ratio when foraging. Competition over food resources can push an organism out of their optimal foraging range (Milinski 1982). The niche variation hypothesis (van Valen 1965) proposes that instead of specializing on their optimal prey, populations which experience food competition are expected to diversify their prey sources. This increase in population diet breadth can arise from the usage of all available resources by the whole population or from increased individual specialization on specific prey items not used by other individuals of the population (van Valen 1965). These behaviors have been observed in several species when competition increased due to higher population densities (Svanbäck and Bolnick 2005; Svanbäck and Bolnick 2007; Svanbäck and Persson 2004; Ward et al. 2006). To our knowledge, only one study exists that measured food specialization as a result of reduced fishing pressure in MPAs (Loury et al. 2015). However, this study only focused on the diet and did not include other measurements of resource limitations, such as condition or growth. Therefore, it is unclear if the population was even affected by competition.

The individual diet specialization (Bolnick et al. 2002), a measurement of mean proportional prey similarity between individuals and their population, was applied as an indicator for density dependent food specialization in this study.

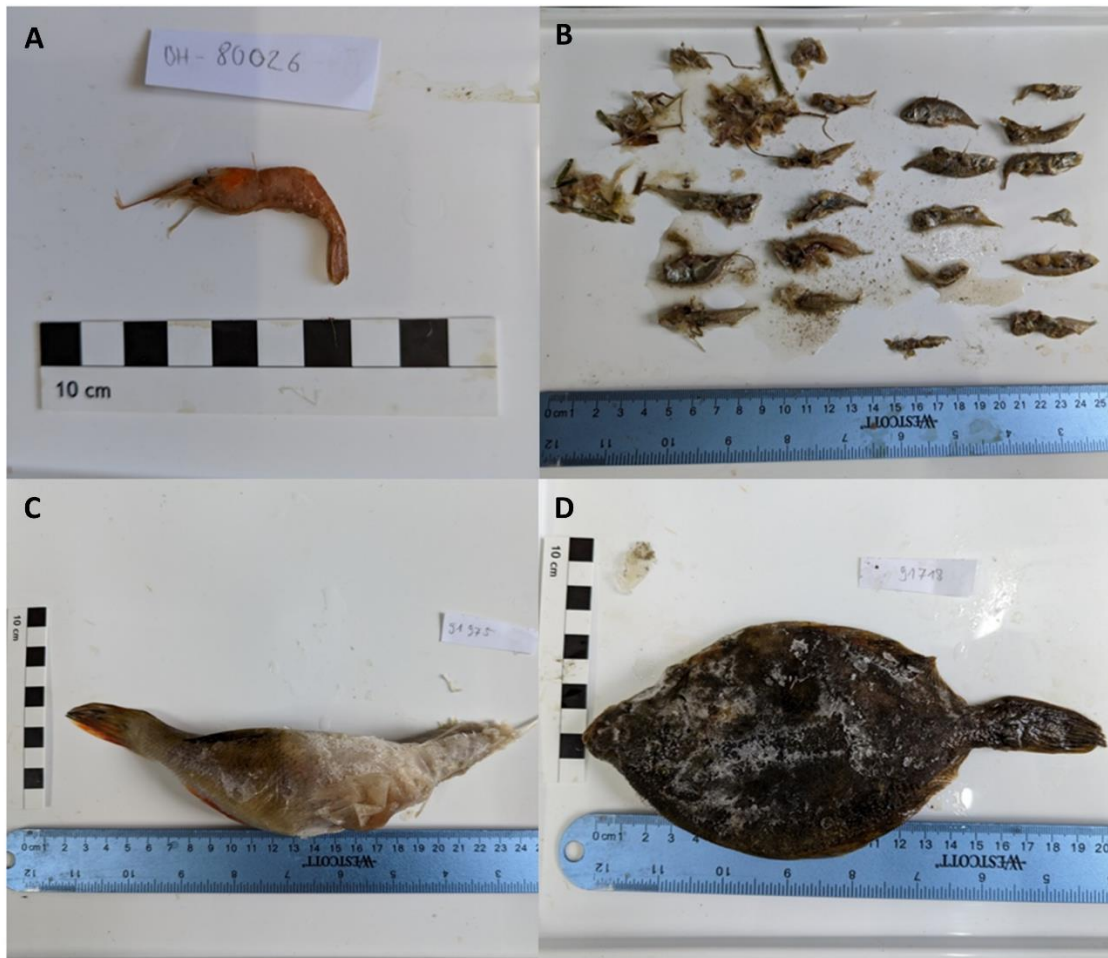


Figure 8. Different prey items found in exemplary northern pike stomachs in this study (A: Baltic shrimp (*Palaemon adspersus*), B: 23 nine-spined and three-spined sticklebacks (*Gasterosteus aculeatus*) found in one individual pike, C: European perch (*Perca fluviatilis*), bottom D: European flounder (*Platichthys flesus*)).

2.12. Statistical analysis

All MPAs analyzed where established 30 years ago and therefore time scale effects could be ruled out and were not included in any statistical model.

2.12.1. Species richness and fish community composition

To measure if the species richness of the individual 30 m gillnets differed between OAs and MPAs a linear model was created, including a three-way interaction between protection status (OA, MPA), area (Grabow, Ummanz, N. and S.) and season (spring, summer, autumn) to predict the species richness. The model fit was visually assessed by plotting a Q-Q plot and a plot of the residuals against the predicted values for the chosen model. These plots were computed with the R package 'DHARMa' (Hartig 2017). Model fit was analyzed visually. Overparameterized models were reduced to fit the data. To test whether the main effects and

the interaction terms of the model influenced the species richness a type III Wald chisquare test from the R package 'car' (Fox and Weisberg 2019) was used. If an interaction term of two or three of the categorical variables was significant, post-hoc 'mvt'-adjusted pairwise comparisons of estimated marginal means was performed with the R package 'emmeans' (Russell 2017) to compare differences between the groups. This model fit assessment, the interpretation of main effects and interactions, as well as the post-hoc tests were performed for all following linear, generalized and generalized mixed models. Individual deviations from this procedure are noted for the specific models.

To account for a possible zero inflation or overdispersion in all following abundance and biomass models, a comparison of the Bayesian information criterion (BIC) for four models (Poisson distributed GLM(M), zero-inflated GLM(M), negative binominal GLM(M), zero-inflated negative binominal GLM(M)) was conducted. The model with the lowest BIC was chosen to fit the data most accurately. To fit biomass data into these count models all biomass values were rounded up. Generalized linear CPUE and BPUE models were computed using the R package 'glmmTMB' (Brooks et al. 2017). To explore the influence of protection in relation to areal and seasonal effects on the biomass of all fish species combined caught in the 30 m gillnets, a negative binominal generalized linear model was chosen, including the interaction between protection status, area and season.

The relation between the protection status and the numerical abundances of harvested and non-harvested fish species caught in the 30 m gillnets was analyzed using a Poisson-distributed generalized linear mixed model including the protection status as a predictor variable and area and season as random variables. The influence of area and season on these CPUEs was not analyzed because the harvest-related categorization of the fish species only allowed to answer fisheries related questions. As there were no interactions in this model, a type II Wald chi-square test was used to analyze predictor effects.

To explore the variations of the fish community compositions (numerical and biomass composition) in relation to protection status, area, season, total surface area, depth, macrophyte coverage, reed share, wave exposure, temperature, salinity and visibility, multivariate canonical ordination was performed using a redundancy analysis (RDA). It modelled the effects of a matrix containing the explanatory variables on a response matrix containing the CPUE or BPUE for all species caught in the specific 30m gillnets. Since the units of the explanatory variables differed all variables were scaled and the response variables were Hellinger-transformed to give low weights to variables with low count and many zeros (Borcard et al. 2011). Significance of the RDA and its axis was performed using a permutation test (999 permutations). Explanatory variables with strong collinearities were removed from the model (Variance inflation factors > 2 between variables indicated collinearity). Subsequently, forward selection was applied on the model that included only variables free

from collinearity among themselves, aiming to retain only those variables that exhibited the strongest associations with the fish community composition. Global RDA significance, axis significance, and significance of the explanatory variables of the final numerical and biomass RDA models were again tested with a permutation test (999 permutations). An additional similarity percentage analysis (SIMPER, 999 permutations) was performed testing species-specific abundance and biomass effects that contributed to the Bray-Curtis dissimilarities between OAs and MPAs (Clarke 1993). Both analysis were computed using the R package 'vegan' (Oksanen et al. 2019)

2.12.2. Abundance, biomass, lengths and age analysis of specific species

Common roach

Both CPUEs (fish/30 m gillnet, fish/100 m gillnet) of the individual gears for the next three species were combined without harmonizing their units. A zero-inflated negative binominal generalized linear mixed model had the lowest BIC concerning the abundance data of common roach. Included in this model was the response variable CPUE and the interacting predictor variables protection status, area and season. Additionally, the gear type was included as random variable and an offset of the logarithmized gillnet length was included into the model to account for the different net types and lengths. The analysis of the rounded BPUE of common roach equaled that of the CPUE. To explore the influence of protection on common roach length a linear mixed model was created using the total lengths of common roach caught with both gear types. The model included the interactions between protection status, area and season as predictor variables and the gear type as a random variable. The rest of the analysis equaled that of the CPUE.

Common bream

The common bream CPUE analysis matched the common roach CPUE analysis. To predict the rounded common bream BPUE in relation to the three-way interaction between protection status, area and season a Poisson distributed generalized linear mixed model, including the gear type as a random variable and the logarithmized net length as an offset fitted best. The length analysis of common bream equaled that of common roach.

European perch

The dependencies of the numerical abundance of European perch were computed using a negative binominal generalized linear mixed model that included the CPUE of European perch in the two gillnet types as a response variable and the same predictor-, random- and offset variables as the common roach CPUE model did. The analysis of rounded BPUE of European

perch was identical to the BPUE approach used for common roach. The length model of European perch equaled that of the common roach model.

Northern pike

The effect of protection on the angling CPUE/BPUE for the individual boats was analyzed using a zero-inflated Poisson distributed generalized linear model, which had the best fit. The model included the interaction between protection status, area and season as well as an offset for the summarized angling effort (min) of all anglers on a specific boat in a specific trial, to account for the different duration of the trials and the different number of anglers on a given boat.

To explore the influence of protection in relation to areal and seasonal effect on the total length of northern pike caught in all gears a linear mixed model was computed including the interaction between protection status, area and season as well as the random variable, gear type, to account for the gear differences. Further, the sex of the northern pike was included as a random variable to account for sex dependencies on the length as northern pike exhibit strong sexual dimorphism regarding length-at-age, with females growing much larger (Craig 1995; Frost and Kipling 1967; Neumann et al. 1994).

The model analyzing the age of northern pike in relation to protection, areal and seasonal effects was overparameterized when including an interaction between the predictors protection status, area and season. Therefore, only the interactions between protection status and area, as well as protection status and season were included in a linear mixed model with the gear type as a random variable.

2.12.3. Condition indices and growth in northern pike

The influence of protection on the relative condition of northern pike caught with all gears was assessed using a linear mixed model including the interaction of protection status, area and season as predictor variables. Gear type and sex were included as random variables to adjust the model for the possible influence of these variables on the relative condition. Due to the low mortality of northern pike during the fieldwork, the HSI observations lacked the quantity required to incorporate any interactions into the HSI model (42 northern pike (OA: 7, MPA: 35)). Therefore, a linear mixed model was computed that only included protection status, area and season as main predictors and gear type and sex as random factors. As there were no interactions in this model, a type II Wald chisquare test was performed to detect any influences of the predictors on the response variable.

To explore the factors contributing to the size-specific growth only the predictors protection status, area and season as main predictors without interactions were included to prevent overfitting of the model. Unlike Berggren et al. (2022) no sex-specific models were computed, as sex was included as a random variable alongside the identification number of the fish, since

multiple measurements were included if a fish was older than one year, and the specific start age of each growth increment, to correct for the declining growth with older age. As with the HSI, a type II Wald chi-square test was performed to test the significance of the predictors, as there were no interactions in the model.

2.12.4. Prey choice and specialization in northern pike

As the number of northern pikes with food in their stomach was low in different sites and areas during specific seasons, no interactions were included in any of the prey analyses (Tab. 3). Gear type was included as a random variable in the prey composition and specialization model since the choice of gear can affect the amount of food and the food composition found in the stomach (Hayward et al. 1989; Jurajda et al. 2013).

A non-metric multidimensional scaling (NMDS) approach was chosen to compare the general food composition (counts, biomass) of northern pike in the two protection status, areas and season. The prey counts and prey biomasses were transformed using the Hellinger distance measure to relativize the influence of the response variables (Rao 1995). The NMDS was computed with the transformed data using the Bray-Curtis distance measure and nine starting dimensions (Legendre and Gallagher 2001). Afterwards, permutational multivariate analysis of variance (PERMANOVA) were used to indicate the drivers of food composition in the stomachs of northern pike (999 permutations). NMDS analysis was performed using the R package 'vegan' (Oksanen et al. 2019). Post-hoc comparison between different levels of the predictor variables was performed by using sequential test for contrasts with the R package 'cluster' (Kaufman and Rousseeuw 2009).

Relations between individual specialization and the protection status, area and seasons were explored computing a linear mixed model without interactions but including the gear type and sex as random variables. A type II Wald chi-square test was used to find significant predictors driving the individual specialization of northern pike.

Table 3. Number of northern pike (N) with prey contents in their stomach for the specific area (N. and S.: Neuensierer- und Selliner See) and season (spring, summer, autumn) for the open access areas (OA) and marine protected areas (MPA).

Area	Season	N (OA)	N (MPA)
Grabow	spring	9	26
Grabow	summer	3	7
Grabow	autumn	0	9
Ummanz	spring	5	9
Ummanz	summer	2	5
Ummanz	autumn	1	4
N. and S.	spring	10	14
N. and S.	summer	1	1
N. and S.	autumn	1	2

All statistical analyses were performed in RStudio Version: 2023.09.0+463 "Desert Sunflower" for windows at a type-1 error probability α of 0.05. All graphs were created using the R package "ggplot2" (Wickham 2016).

3. Results

3.1. Comparison of ecological parameters between area-pairs

All three main areas were shallow, mesohaline, had high reed shares and a low macrophyte coverage (Tab. 4). The area-pairs generally had a similar habitat structure and environmental conditions in most seasons (Tab. 4). But differences were found in the Ummanz-area-pair which differed regarding the reed share and the wave exposure (Tab. 4). Additionally, the N. and S.-OA had more than twice the size of the MPA (Tab. 4). Macrophyte coverage differed in the N. and S.-area in autumn (Tab. 4). In total, the Ummanz-area had the highest surface area and the N. and S. area the smallest (Tab. 4). Regarding the wave exposure the N. and S.-area was the most sheltered area, followed by the Ummanz-area (Tab. 4). Generally, the areas showed lowest macrophyte coverage in spring and the highest macrophyte coverage in autumn. Another seasonal trend detected in all areas was that higher turbidities were observed in spring compared to autumn (Tab. 4).

Table 4. Eight environmental variables characterizing the protection status within the areas and season. Means $\pm$ standard deviations are given if multiple measurements were carried out in the respective season (OA: open access area, MPA: marine protected area, N. and S.: Neuensierer- and Selliner See).

Area	Season	Protection status	Total surface area (km ²)	Mean depth (m)	Macrophyte coverage (%)	Reed share (%)	Wave exposure	Temperature (°C)	Salinity (PSU)	Visibility (m)
Grabow	spring	OA	1.1	0.9 $\pm$ 0.7	34.6	90.8	18538.1	15.9 $\pm$ 3.3	8.7 $\pm$ 0.2	0.6 $\pm$ 0.2
	spring	MPA	1.4	1.2 $\pm$ 0.4	20.4	93.9	11793.3	15.7 $\pm$ 3.5	8.9 $\pm$ 0.3	0.6 $\pm$ 0.2
	summer	OA	1.1	0.9 $\pm$ 0.7	62.2	90.8	18538.1	18.5 $\pm$ 3.8	9.6 $\pm$ 0.5	2.8 $\pm$ 1.5
	summer	MPA	1.4	1.2 $\pm$ 0.4	65.3	93.9	11793.3	18.3 $\pm$ 4	9.6 $\pm$ 0.5	2.8 $\pm$ 1.5
	autumn	OA	1.1	0.9 $\pm$ 0.7	45.9	90.8	18538.1	7.4 $\pm$ 4.7	8.7 $\pm$ 0.2	3.7 $\pm$ 0.7
	autumn	MPA	1.4	1.2 $\pm$ 0.4	47.6	93.9	11793.3	6.6 $\pm$ 3.9	8.8 $\pm$ 0.8	3.1 $\pm$ 1.2
Ummanz	spring	OA	1.5	0.9 $\pm$ 0.7	22.5	94.8	10890.8	14.3 $\pm$ 3.5	8.9 $\pm$ 0.2	1.3 $\pm$ 0.6
	spring	MPA	1.8	0.6 $\pm$ 0.4	24.5	59.4	3105.6	14.2 $\pm$ 3.5	9 $\pm$ 0.1	1.3 $\pm$ 0.6
	summer	OA	1.5	0.9 $\pm$ 0.7	29.7	94.8	10890.8	19.5 $\pm$ 3.2	9.6 $\pm$ 0.7	1.4 $\pm$ 0.6
	summer	MPA	1.8	0.6 $\pm$ 0.4	24.9	59.4	3105.6	19.4 $\pm$ 3	9.7 $\pm$ 0.7	1.3 $\pm$ 0.6
	autumn	OA	1.5	0.9 $\pm$ 0.7	54	94.8	10890.8	9.4 $\pm$ 3.8	8.7 $\pm$ 0.5	3.9 $\pm$ 0.2
	autumn	MPA	1.8	0.6 $\pm$ 0.4	66.9	59.4	3105.6	9.4 $\pm$ 3.9	8.7 $\pm$ 0.5	3.9 $\pm$ 0.2
N. and S.	spring	OA	1	1.3 $\pm$ 0.4	14.5	94.8	1948	11.1 $\pm$ 7.5	7.5 $\pm$ 0.1	1.5 $\pm$ 0.8
	spring	MPA	0.4	1 $\pm$ 0.4	12.3	99.7	1948	11 $\pm$ 7	7.3 $\pm$ 0.2	1.3 $\pm$ 0.6
	summer	OA	1.	1.3 $\pm$ 0.4	39.6	94.8	1948	19.7 $\pm$ 3.9	8 $\pm$ 0.5	1.4 $\pm$ 0.7
	summer	MPA	0.4	1 $\pm$ 0.4	44.6	99.7	1948	19.5 $\pm$ 4.1	7.9 $\pm$ 0.6	1.1 $\pm$ 0.1
	autumn	OA	1.	1.3 $\pm$ 0.4	44.6	94.8	1948	7.6 $\pm$ 5.1	7.5 $\pm$ 0.5	2.5 $\pm$ 0.4
	autumn	MPA	0.4	1 $\pm$ 0.4	6.3	99.7	1948	7.5 $\pm$ 5.1	7.4 $\pm$ 0.5	2.4 $\pm$ 1.4

3.2. Fishing effort analysis

There was no angling pressure observed in the Grabow- and Ummanz-MPA (Fig. 9), but in the N. and S.- MPA anglers were counted. However, the mean number of anglers was lower compared to the OA (Fig. 9). Gill nets were not observed in the Grabow- area (Fig. 9), whereas in the Ummanz-area the mean number of nets was higher in the MPA compared to the OA (Fig. 9). In the N. and S. area the number of gillnets observed was higher in the OA (Fig. 9). Eel traps were observed in all areas and their numbers were on average higher in the MPAs, except in the Grabow-area (Fig. 9). Fyke nets were only observed in the Ummanz-OA (Fig. 9). Generally, the MPAs were characterized by a low to absent angling pressure but experienced commercial fishing pressure. OAs generally had a high count of anglers but sometimes had an even lower or equal amount of commercial fishing pressure compared to the MPAs (Fig. 9). By combining the general characterization of the area-pairs in the methods part (Tab. 2) and the results shown here, it was concluded that the Grabow-area had the highest fishing pressure contrast between OA and MPA of all area-pairs. Both literature and internal observations suggest a high angling pressure in the OA, absence of angling in the MPA and an equally low amount of commercial fishing pressure in the OAs and MPAs (Fig. 9). The Ummanz-area allowed commercial fishing without restrictions inside the MPA but excluded angling. It was therefore seen as an area with intermediate fishing pressure contrast since the MPA was even fished more intensively with some gears than the OA (Fig. 9). Because neither angling or commercial fishing were excluded in the N. and S.-MPA and all fishing gears, except fyke nets, were observed in the MPA, it was seen as an area-pair with a low fishing pressure contrast (Fig. 9).

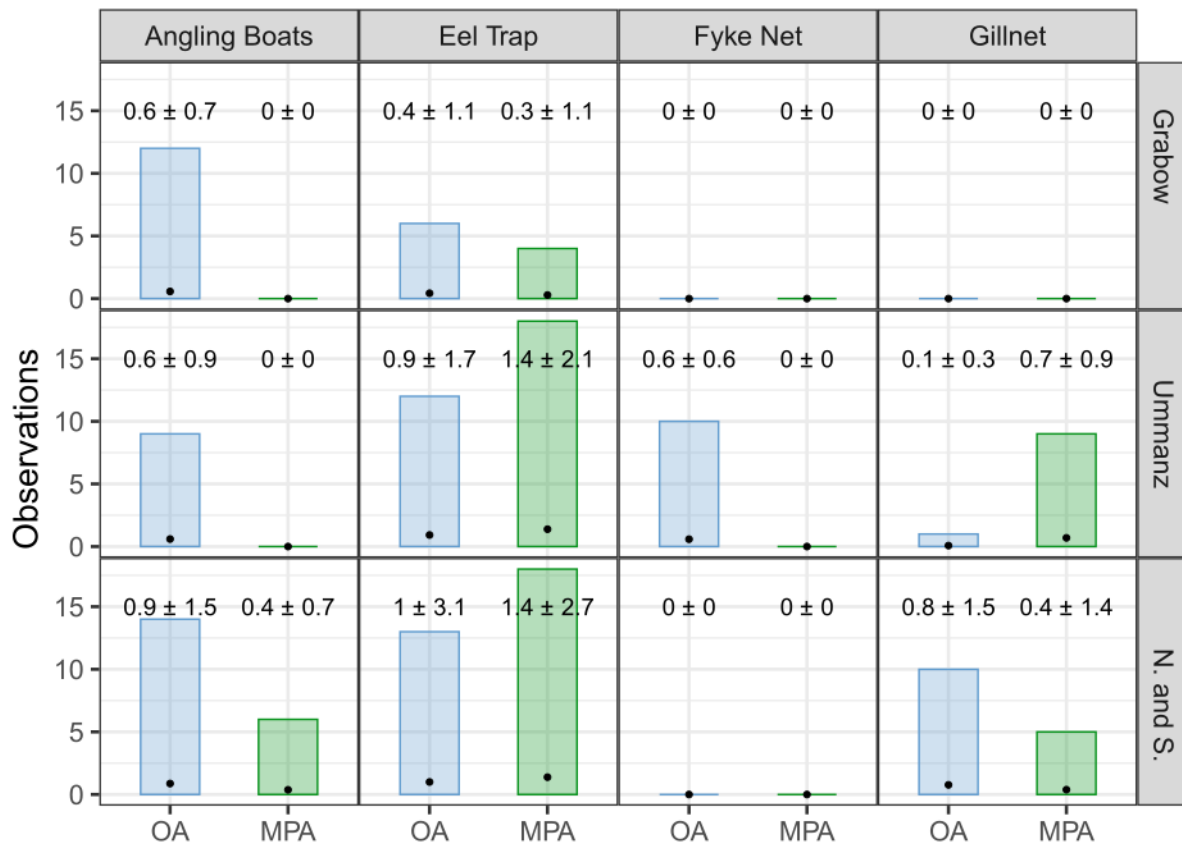


Figure 9. Box plots (black dot: mean, box: 25 and 75 percentile) that show how many anglers, gill nets, eel traps and fyke nets were observed on each sampling day in the open access areas (OA) and marine protected areas (MPA) of three areas (N. and S.: Neuensienner- and Selliner See). Graph modified after Roser (2023).

3.3. Species richness/abundances of all species and (non-) harvested species in OAs and MPAs

3.3.1. Species richness in OAs and MPAs

The species richness in the benthic multi-mesh gillnets ranged from 2 – 11 species (mean: 6 ± 2). No differences in species richness between OAs and MPAs could be found (Tab. 5, Fig. 10). Even though no significant species richness differences between the protection status were observed, the species richness was on average higher in MPAs (mean: 7 ± 2) compared to OAs (mean: 6 ± 2). Area, season and the interaction effect between both were significant correlates of the species richness (Tab. 10). Species richness differences between areas in the different seasons were rare and only occurred in summer with lower diversity in the Grabow-area (mean: 5 ± 2) compared to the Ummanz-area (8 ± 2 , EMMs: $t(89) = -2.8$, $p < 0.05$) and in autumn, when lower species richness was observed in the Grabow-area (mean: 4 ± 2) compared to the N. and S.-area (mean: 6 ± 2 , EMMs: $t(89) = -2.9$, $p < 0.05$). The species richness was higher in the Grabow-area in spring (mean: 7 ± 2) compared to summer (EMMs:

$t(89) = 2.6$, $p < 0.05$) and higher in spring compared to autumn (EMMs: $t(89) = -4.5$, $p < 0.001$). In the Ummanz-area species richness was also higher in spring (mean: 7 ± 2) when compared to autumn (mean: 5 ± 2 , EMMs: $t(89) = -3.2$, $p < 0.01$). No seasonal differences in species richness were found in the N. and S.-area.

Table 5 Wald-test outcome showing if a predictor was a significant correlate of the species richness per 30 m net, as estimated through a linear model. The outcome of the ANOVA for the predictor variables includes the F-value, the degrees of freedom (Df) and the p-value. Significant values are highlighted in bold characters.

Linear model	F-value	Df	p-value
ANOVA results			
Fixed effects / interactions			
Protection status	1.024	1	0.314
Area	3.28	2	< 0.05
Season	5.709	2	< 0.01
Protection status : Area	2.004	2	0.141
Protection status : Season	0.265	2	0.767
Area : Season	3.412	4	< 0.05
Protection status : Area : Season	1.331	4	0.264

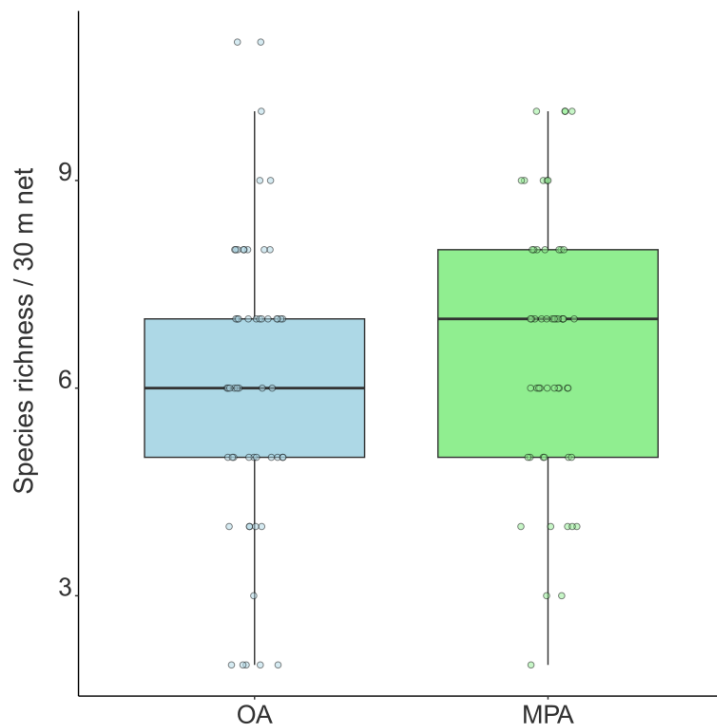


Figure 10. Boxplot (median, black dot: mean, box: 25 and 75 percentile, whisker: 10 and 90 percentile) that shows how the species richness per 30 m net (y-axis) is related to the protection status (OA: open access area, MPA: marine protected area, x- axis). Significant differences between groups (boxplots) are marked as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

3.3.2. Abundances (numerical, biomass) of all species in OAs and MPAs

A total of 9104 fish (1208.32 kg) were caught on benthic (8431 fish, 373.7 kg) and pike (673 fish, 834.6 kg) multi-mesh gillnets. The catch consisted out of 32 species (Tab. 8). Four species accounted for 82 % of the total numerical catch (bleak, common roach, European perch, three-spined stickleback). Of sea trout (*Salmo trutta*, L. 1758), gibel carp (*Carassius gibelio*, BLOCH 1782), tench and sand goby only single individuals were captured (first two species not in Table 3 because they were captured in the pike multi-mesh gillnets). Round gobies were the only invasive species observed (Kvach and Winkler 2011).

Of the 8431 fish caught with the benthic multi-mesh gillnets 4900 fish (58 %) were caught in MPAs. Protection status was a significant correlate of the abundance of the entire fish community (Tab. 6). Abundances caught in the MPAs averaged out at 92.4 ± 81.6 fish/100 m net and OAs averaged out at 65.3 ± 83.2 fish/100 m net (Fig. 11). The differences in abundances were explained by the significant two-way interaction term between protection status and area (Tab. 6). Significant all-species CPUE differences between OAs and MPAs were only observed in the Grabow-area (EMMs: $t(88) = -3.92$, $p < 0.01$) and the N. and S.-area (EMMs: $t(88) = -1.8$, $p < 0.05$). Both times abundances were higher in the MPAs (Grabow = mean: 70.2 ± 61.8 fish / 100 m net, N. and S. = mean: 151.4 ± 103.9 fish/100 m net) compared

to OAs (Grabow = mean: 28 ± 24 fish / 100 m net, N. and S. = mean: 112.9 ± 125.1 fish/100 m net, Fig. 11).

Table 6. Wald-test outcome showing if a predictor correlated with the abundance (catch per-unit-effort, fish/100 m net) of all fish species caught per 30 m benthic multi-mesh gillnet, as estimated through a generalized linear model. The outcome of the Wald-test for the predictor variables includes the Wald chi-square statistics, the degrees of freedom (Df) and the p-value. Significant values are highlighted in bold characters.

Generalized linear model Wald-test results	Wald chi-square	Df	p-value
Fixed effects / interactions			
Protection status	8.157	1	< 0.001
Area	7.582	2	< 0.05
Season	31.363	2	< 0.001
Protection status : Area	6.987	2	< 0.05
Protection status : Season	2.988	2	0.224
Area : Season	7.325	4	0.119
Protection status : Area : Season	8.095	4	0.088

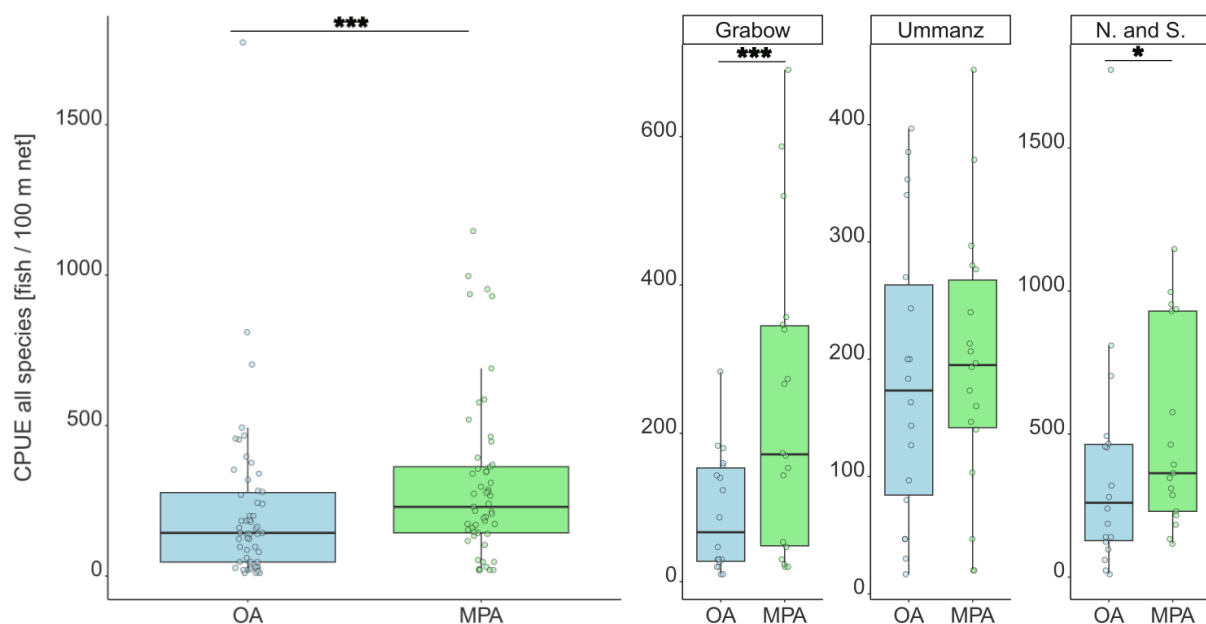


Figure 11. Boxplots (median, box: 25 and 75 percentile, whisker: 10 and 90 percentile) that show how the catch per-unit-effort (CPUE, fish/100 m net, y-axis) for the entire fish community caught in benthic multi-mesh gillnets is correlated with the protection status (OA: open access area, MPA: marine protected area, x- axis, left figure) and how the CPUE is correlated with the interaction of protection status (x-axis) and area (upper labels, N. and S.: Neuensien- and Seliner See, right figure). Significant differences between groups (boxplots) are marked as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

The 373.7 kg caught with the benthic multi-mesh gillnets consisted out of 145.9 kg (39 %) fish caught in the OAs and 217.1 kg (61 %) caught in the MPAs. Protection status was a significant correlate of the biomass abundance of the entire fish community (Tab. 7). Biomasses caught in the OAs averaged out at 2.7 ± 2.4 kg/100 m net and MPAs averaged out at 4.1 ± 2.7 kg/100m net (Fig. 12). The differences in abundances were explained by the significant three-way interaction term between protection status, area and season (Tab. 7). Significant all-species BPUE differences between OAs and MPAs were observed in the Grabow-area in summer (EMMs: $t(89) = -3.02$, $p < 0.001$), the Ummanz-area in autumn (EMMs: $t(89) = -1.01$, $p < 0.05$) and the N. and S.-area in summer (EMMs: $t(89) = -3.97$, $p < 0.001$) and autumn (EMMs: $t(89) = -5.4$, $p < 0.001$). All biomass abundances were higher in the MPAs (Grabow, summer = mean: 3.1 ± 1.3 kg/100 m net; Ummanz, autumn = mean: 1.7 ± 1.4 kg/100 m net; N. and S., summer = mean: 6.6 ± 1.3 kg/100 m net; N. and S., autumn = mean: 7.7 ± 1.8 kg/100 m net) compared to OAs (Grabow, summer = mean: 1.1 ± 1.1 kg / 100 m net; Ummanz, autumn = mean: 0.7 ± 0.8 kg / 100 m net; N. and S., summer = mean: 2.5 ± 1.7 kg/100 m net; N. and S., autumn = mean: 1.9 ± 0.8 kg/100 m net, Fig. 12).

Table 7. Wald-test outcome showing if a predictor correlated with the biomass abundance (biomass-per-unit-effort, kg/30 m net) of all fish species caught with 30 m benthic multi-mesh gillnet, as estimated through a generalized linear model. The outcome of the Wald-test for the predictor variables includes the Wald chi-square statistics, the degrees of freedom (Df) and the p-value. Significant values are highlighted in bold characters.

Generalized linear model Wald-test results	Wald chi-square	Df	p-value
Fixed effects / interactions			
Protection status	11.745	1	< 0.001
Area	7.511	2	< 0.05
Season	8.22	2	< 0.05
Protection status : Area	3.924	2	0.613
Protection status : Season	2.121	2	0.209
Area : Season	4.998	4	0.642
Protection status : Area : Season	10.791	4	< 0.01

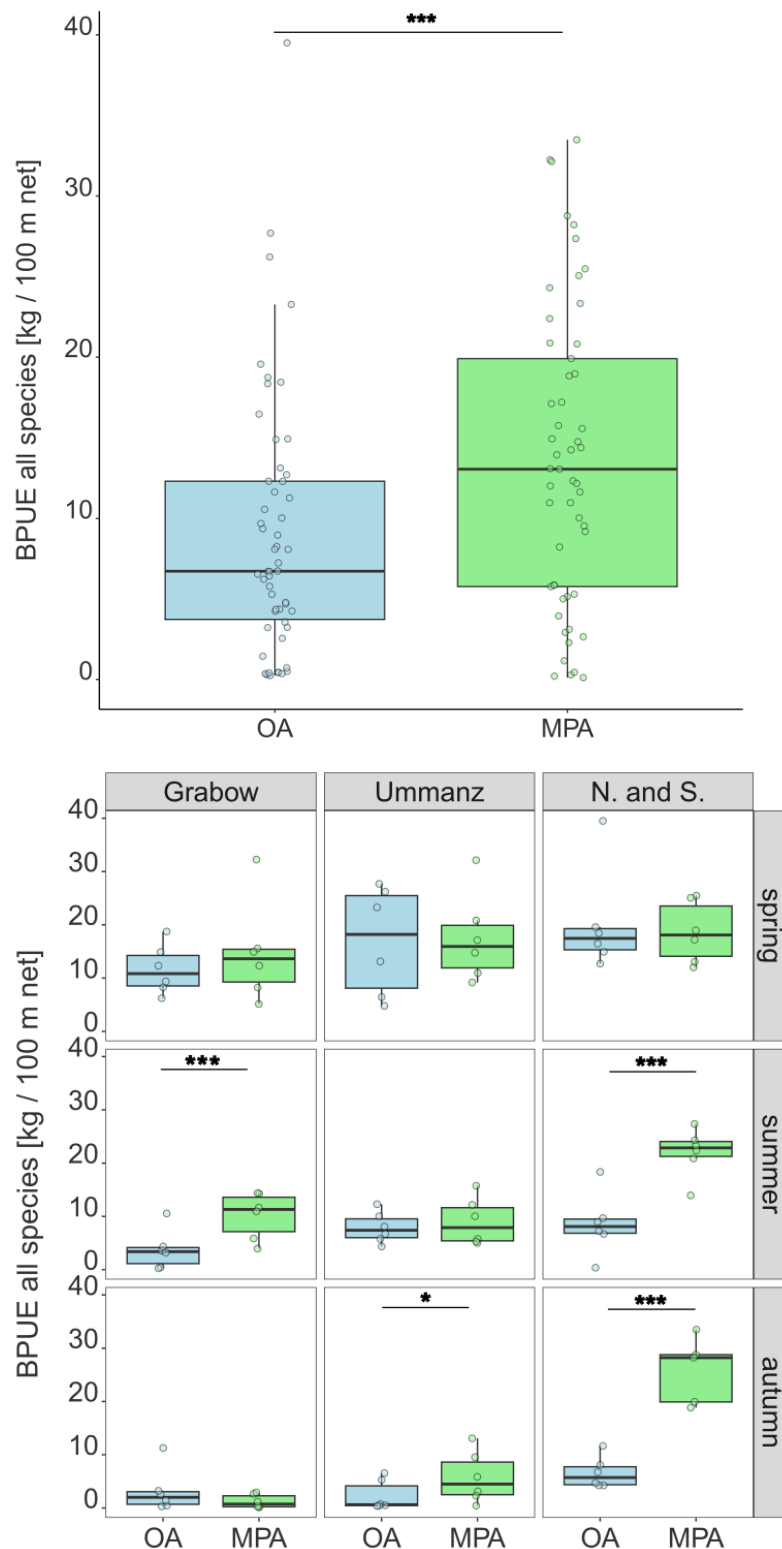


Figure 12. Boxplots (median, box: 25 and 75 percentile, whisker: 10 and 90 percentile) that show how the biomass-per-unit-effort (BPUE, kg / 100 m net, y-axis) for the entire fish community caught in benthic multi-mesh gillnets is correlated with the protection status (OA: open access area, MPA: marine protected area, x- axis, top figure) and how the BPUE is correlated with the interaction of protection status (x-axis), area (upper labels, N. and S.: Neuensienner- and Seliner See) and season (right labels, bottom figure). Significant differences between groups (boxplots) are marked as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

3.3.3. Abundances and sizes of (non-) harvested species in OAs and MPAs

The average numerical abundance of harvested fish species in MPAs was 48.2 ± 34.9 fish / 30 m net and a mean of 32.6 ± 30.7 fish/30 m net was observed in OAs. However, the abundance of harvested fish species did not vary among the protection status (χ^2 : 1.21, df:1, $p = 0.27$). The analysis of CPUE of non-harvested fish species yielded similar results. Their abundance did not significantly differ among protection status (χ^2 : 0.01, df:1, $p = 0.99$). While abundance in MPAs averaged out at 44.2 ± 76.1 fish/30 m net, OAs had a mean of 32.7 ± 77.3 fish/30 m net.

Biomass abundances of harvested species did not differ between MPAs (mean: 3.2 ± 2.9 kg/30 m) and OAs (mean: 2.8 ± 2.5 kg/30 m, χ^2 : 1.3, df:1, $p = 0.12$). Similarly, the biomass abundance of non-harvested species did not differ between MPAs (mean: 0.4 ± 0.8 kg/30 m) and OAs (mean: 0.3 ± 0.7 kg/30 m, χ^2 : 0.3, df:1, $p = 0.18$).

3.4. Fish community composition in OAs and MPAs

3.4.1. Numerical fish community composition

Regarding abundances, the overall fish community composition was dominated by bleaks, followed by common roach and European perch (Tab. 8, Fig.13). Generally, this distribution could be observed in both OAs and MPAs, but only in OAs three-spined stickleback were the third most common species (Tab. 8, Fig.13).

After forward model selection protection status and all other predictors, except SWM wave exposure and surface area, were identified as significant correlates of the numerical fish community composition (Tab. 9). The chosen predictors explained a high amount of variance (37 %, adjusted R^2). SIMPER analysis indicated that only four species explained 58 % of the Bray-Curtis dissimilarities between the two protection status regarding their abundance (Tab. 10). Common roach had the highest contribution to the between protection status dissimilarity, followed by bleak, European perch and three-spined stickleback (Tab. 10). Common roach and three-spined stickleback made up a higher proportion in the catches of the OA compared to the MPA (Tab. 8). European perch and bleaks were more dominant in the MPAs fish composition compared to the OAs (Tab. 8). This can also be seen in Figure 14 as common roach and three-spined stickleback have a positive relationship with the protection status variable and European perch and bleak a more negative relationship. This indicated that these species are differently related to protection status. 22 of the 28 species tested (79 %, Tab. 9), including common roach, bleak, European perch and three-spined stickleback, had a lower CPUE in the OA compared to the MPA (Tab. 10). Except for European sprat, all species that had a higher CPUE in the OA had a weak effect on the dissimilarities between the protection status (Tab. 10).

Compared to the strength of the effect of almost all other predictors on the fish community (numerical) the protection status explained little variation in the fish community composition (0.6 %, Fig. 14). Salinity (7.6 %), season (3.7 %), temperature (3.2 %), area (2.3 %), reed share (1.9 %) and macrophyte coverage (1.5 %) explained more variance of differences in fish species abundances (Fig. 14).

3.4.2. Biomass-based fish community composition

Biomass of the fish community was dominated by common roach, European perch and northern pike (Tab. 8, Fig. 13). This overall pattern could also be observed in the OAs as well as in the MPAs (Tab. 8, Fig. 13). After forward model selection protection status as well as all other predictors, except SWM wave exposure and surface area, were identified as significant correlates of the biomass-based fish community composition regarding abundance according to RDA (Tab. 9). The chosen predictors explained a high amount of variance (36 %, adjusted R^2).

Common roach, European perch, northern pike, bleak, white bream and common bream explained most of the dissimilarities in biomass-based fish community composition between protection status (69 % variance, Tab. 10). The biomass share of common roach to the relative fish composition was much higher in the OA compared to MPAs, while the opposite was found for European perch (Tab. 8). The proportion of northern pike to the fish composition was almost equal but higher in OAs (Tab. 8). High biomasses of the 17 northern pike caught with benthic multi-mesh gillnets can be attributed to the overall large sized individuals caught in this study (Tab. 8, Fig. 13, mean: 717 ± 91 mm). Comparing OAs and MPAs, common bream made up a higher proportion of the fish composition in OAs, while bleaks and white bream made up a higher proportion of the catch in MPAs (Tab. 8). Common roach and northern pike were most positively related to the protection status while European was the most negatively related species to protection status (Fig. 15). 20 species (71 %) had higher BPUEs in the MPAs compared to OAs (Tab. 10). Common roach, the most impactful fish species on the BPUE dissimilarities between protection status, had a higher BPUE in the OA (Tab. 10). Otherwise, all species, including bleak, European perch, common bream, northern pike and white bream had higher BPUEs in the MPAs (Tab. 10).

Protection status was again a weak correlate of the fish community composition (0.8 % variance, Fig. 15). Variances in biomass-based fish community were mostly explained by salinity (5.3 %), temperature (4.5 %), seasonality (4 %), reed share (2.2 %) and macrophyte coverage (2 %, Fig. 15). Areal effects only explained less than 1 % (0.7 %) of the fish community composition variance (Fig. 15).

Table 8. The abundance of individuals (N) and biomass (kg) of the 27 species caught with benthic multi- mesh gillnets in total and separated by protection status (OA: open access area, MPA: marine protected area). Additionally, the species-specific share of the total catch in the specific protection status is included (%). The name of the families, the Latin names, abbreviations used in the text / graphs and the common English name for the species are provided. The *-symbol behind the Latin name marks species that were categorized as a harvested species.

Family	Species (lat. Name)	Species (abbr.)	Species (English name)	N (Total)	Biomass (total) [kg]	N (OA)	% (OA)	N (MPA)	% (MPA)	Biomass (OA) [kg]	% (OA)	Biomass (MPA) [kg]	% (MPA)
Clupeidae	<i>Clupea harengus</i> (L. 1758) *	<i>C. harengus</i>	Atlantic herring	64	4.9	32	< 1	32	< 1	1.9	1.3	3	1.3
	<i>Sprattus sprattus</i> (L. 1758) *	<i>S. sprattus</i>	European sprat	384	2.4	249	7.1	135	2.7	1.8	< 1	0.6	< 1
Engraulidae	<i>Engraulis encrasicolus</i> (L. 1758) *	<i>E. encrasicolus</i>	European anchovy	3	0.05	0	0	3	< 1	0	0	< 0.1	< 1
Osmeridae	<i>Osmerus eperlanus</i> (L. 1758)	<i>O. eperlanus</i>	European smelt	5	0.02	5	< 1	0	0	0.2	< 1	0	0
Esocidae	<i>Esox lucius</i> (L. 1758) *	<i>E. lucius</i>	Northern pike	17	47.8	7	< 1	10	< 1	18.8	12.8	29	12.7
Cypriniformes	<i>Rutilus rutilus</i> (L. 1758) *	<i>R. rutilus</i>	Common roach	2401	126	1081	30.6	1320	26.9	65.7	45	60.3	26.4
	<i>Leuciscus idus</i> (L. 1758) *	<i>L. idus</i>	Ide	4	2.4	1	< 1	3	< 1	0.3	< 1	2.1	1.8
	<i>Scardinius erythrophthalmus</i> (L. 1758)	<i>S. erythrophthalmus</i>	Rudd	109	11.5	42	1.1	67	1.3	3.1	2.1	8.4	3.6
	<i>Tinca tinca</i> (L. 1758) *	<i>T. tinca</i>	Tench	1	2.5	0	0	1	< 1	0	0	2.5	1.9
	<i>Abramis brama</i> (L. 1758) *	<i>A. brama</i>	Common bream	17	26.4	7	< 1	10	< 1	12.1	8.2	14.3	6.3
	<i>Blicca bjoerkna</i> (L. 1758)	<i>B. bjoerkna</i>	White bream	298	25.7	75	2.1	223	4.5	5.2	3.5	20.5	9
	<i>Alburnus alburnus</i> (L. 1758)	<i>A. alburnus</i>	Bleak	2940	29.8	1199	33.9	1741	35.5	11.4	7.7	18.4	8.1
Belonidae	<i>Belone belone</i> (L. 1760) *	<i>B. belone</i>	Garfish	2	0.8	2	< 1	0	0	0.8	< 1	0	0
Gadidae	<i>Gadus morrhua</i> (L. 1758) *	<i>G. morrhua</i>	Atlantic cod	3	0.5	1	< 1	2	< 1	< 0.1	< 1	0.5	< 1
Percidae	<i>Perca fluviatilis</i> (L. 1758) *	<i>P. fluviatilis</i>	European perch	916	79.1	237	6.7	679	13.8	17	11.6	62.1	27.2
	<i>Gymnocephalus cernua</i> (L. 1758)	<i>G. cernua</i>	Ruffe	208	6.9	103	3.3	105	3.4	4.2	2.9	2.7	2.1
	<i>Sander lucioperca</i> (L. 1758) *	<i>S. lucioperca</i>	Pike-perch	92	1.8	22	< 1	70	1.4	0.4	< 1	1.4	< 1
Ammodytidae	<i>Ammodytes tobianus</i> (L. 1758)	<i>A. tobianus</i>	Lesser sand eel	7	<0.01	3	< 1	4	< 1	< 0.1	< 1	< 0.1	< 1
Gobiidae	<i>Gobius niger</i> (L. 1758)	<i>G. niger</i>	Black goby	25	0.1	17	< 1	8	< 1	< 0.1	< 1	< 0.1	< 1
	<i>Pomatoschistus microps</i> (KØYER 1838)	<i>P. microps</i>	Common goby	37	<0.01	28	< 1	9	< 1	< 0.01	< 1	< 0.01	< 1
	<i>Pomatoschistus minutus</i> (PALLAS 1770)	<i>P. minutus</i>	Sand goby	1	<0.01	0	0	1	< 1	< 0.01	< 1	< 0.01	< 1
	<i>Neogobius melanostomus</i> (PALLAS 1814)	<i>N. melanostomus</i>	Round goby	133	1.6	62	1.7	71	1.4	1	< 1	0.6	< 1
Cottidae	<i>Myoxocephalus scorpius</i> (L. 1758)	<i>M. scorpius</i>	Shorthorn sculpin	3	0.1	2		1	< 1	< 0.1	< 1	< 0.1	< 1
Gasterosteidae	<i>Gasterosteus aculeatus</i> (L. 1758)	<i>G. aculeatus</i>	Three-spined stickleback	701	1.2	339	9.6	362	7.3	0.6	< 1	0.6	< 1
	<i>Pungitius pungitius</i> (L. 1758)	<i>P. pungitius</i>	Nine-spined stickleback	43	<0.1	8	< 1	35	< 1	< 0.01	< 1	< 0.1	< 1
	<i>Spinachia spinachia</i> (CUVIER 1816)	<i>S. spinachia</i>	Sea stickleback	4	<0.01	0	0	4	< 1	0	0	< 0.01	< 1
Syngnathidae	<i>Syngnathus typhle</i> (L. 1758)	<i>S. typhle</i>	Broadnosed pipefish	3	<0.01	1	< 1	2	< 1	< 0.01	< 1	< 0.01	< 1
Pleuronectidae	<i>Platichthys flesus</i> (L. 1758) *	<i>P. flesus</i>	European flounder	10	1.6	8	< 1	2	< 1	1.4	< 1	0.2	< 1

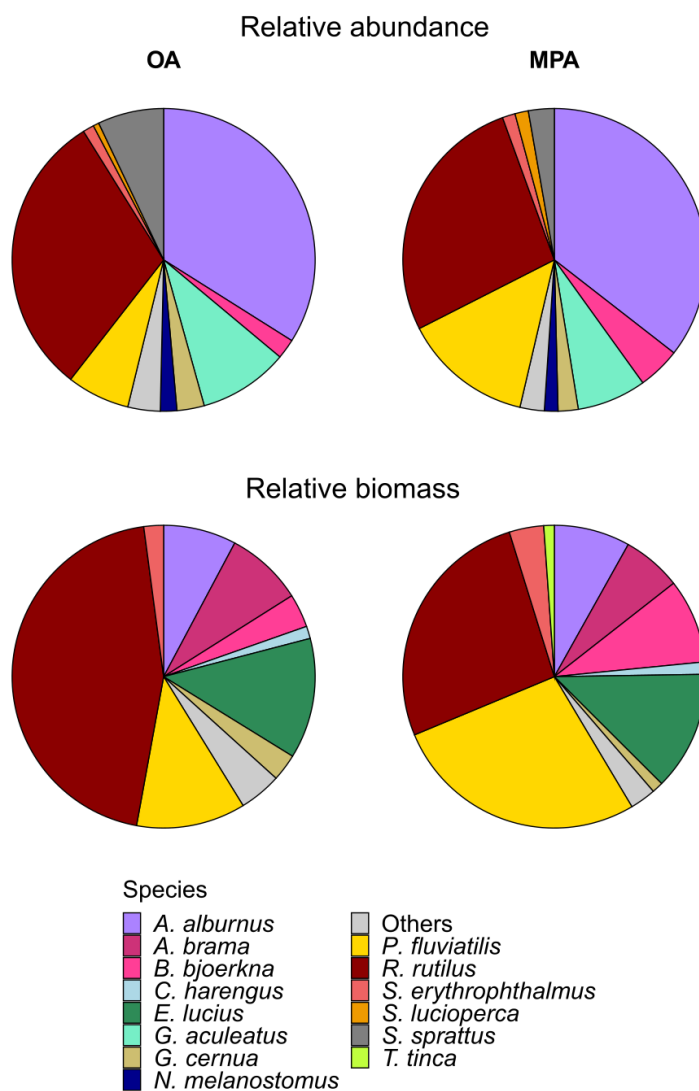


Figure 13. Pie charts representing the relative abundance and biomass of 14 species that were the most abundant within the captured fish communities. All other species were labeled as “Others”. Pie charts show the difference in relative abundance and biomass for the protection status (OA: open access area, MPA: marine protected area, upper four pie charts).

Table 9. Permutation test outcome of two RDAs showing if the scaled environmental predictors are correlated with the fish community composition in regard to the abundance of fish (top) and biomass (kg, bottom). Only fish caught with benthic multi-mesh gillnet were analyzed. The outcome of the Permutation test for the predictor variables includes the F-statistic, the degrees of freedom (Df) and the p-value. All predictors had one degree of freedom because they were scaled prior to the analysis. Significant values are highlighted in bold characters.

Redundancy analysis (RDA)	F	Df	p-value
Permutation test			
Fixed effects			
<u>Numerical:</u>			
Protection status	5.042	1	< 0.001
Area	7.864	1	< 0.001
Season	5.786	1	< 0.001
Temperature	6.122	1	< 0.001
Salinity	22.263	1	< 0.001
Macrophyte coverage	6.711	1	< 0.001
Reed share	6.699	1	< 0.001
<u>Biomass:</u>			
Protection status	5.731	1	< 0.001
Area	3.888	1	< 0.01
Season	4.761	1	< 0.001
Temperature	6.976	1	< 0.001
Salinity	14.969	1	< 0.001
Macrophyte coverage	7.365	1	< 0.001
Reed share	6.511	1	< 0.001

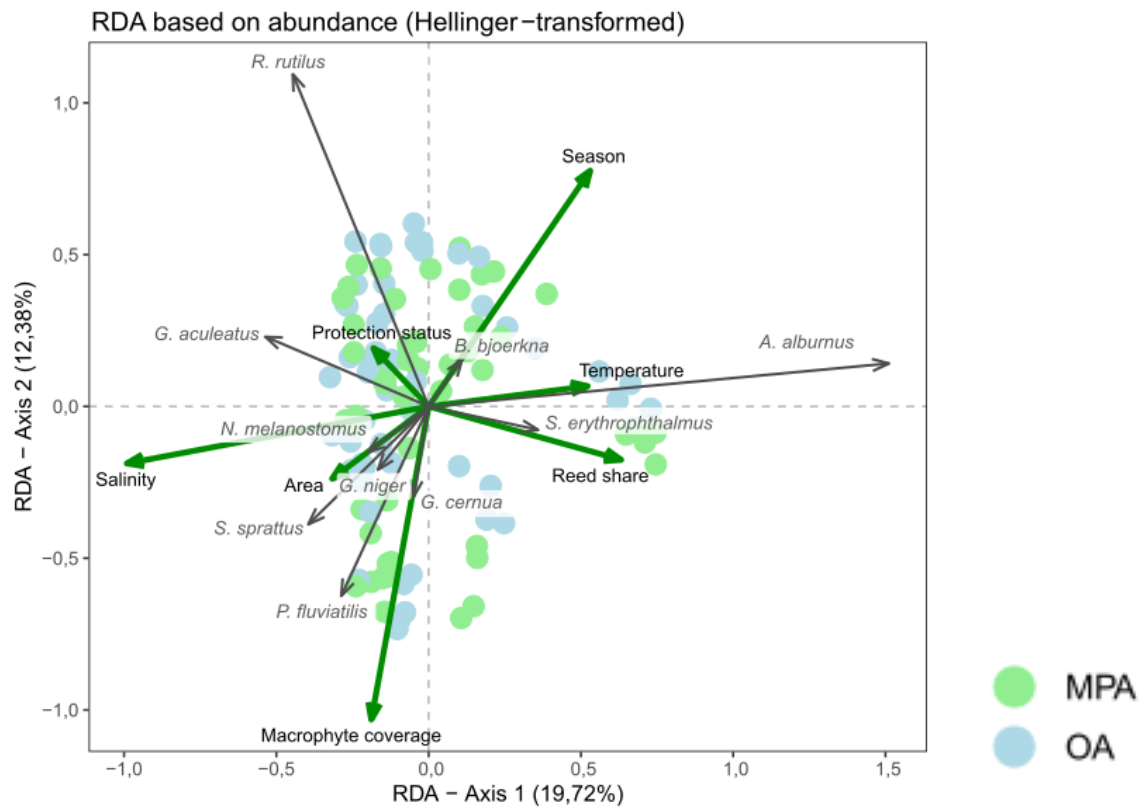


Figure 14. Two-dimensional redundancy analysis (RDA) plot (numerical abundance of fish). Green arrows represent the variables retained by forward modelling and that are significant correlates of the fish community composition. Black arrows represent ten fish species (abbreviations explained in Tab. 2) which had the highest contribution to the between protection status dissimilarity. The strength of correlation of each variable with an individual axis is expressed by the length of an arrow. If Arrows point in different directions the associated variables are negatively correlated. Points represent individual nets and their location in the two-dimensional space of the graph. The points are colored according to protection status. Blue points represent nets placed in open access areas (OA) and green points marine protected areas (MPA). RDA percentages of variation are shown on the appendant axes.

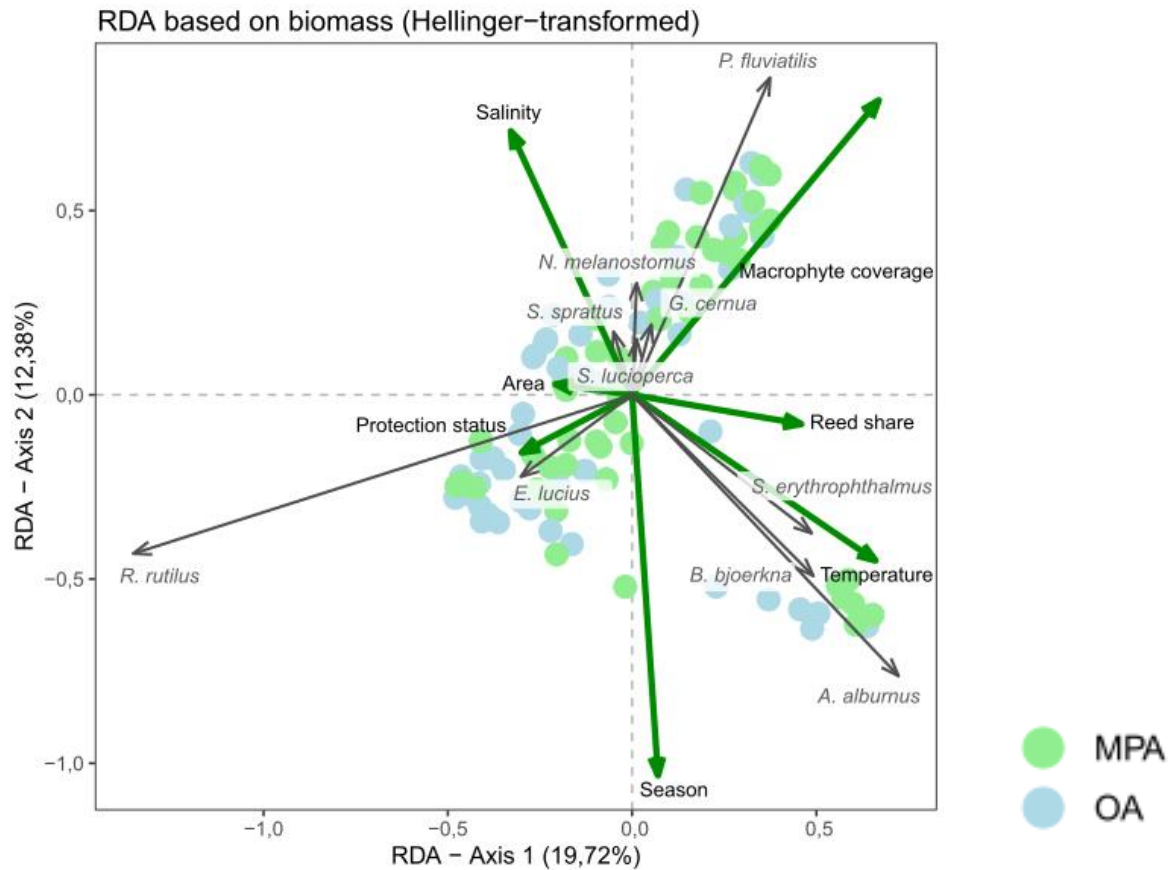


Figure 15. Two-dimensional redundancy analysis (RDA) plot (biomass abundance of fish (kg)). Green arrows represent the variables retained by forward modelling and that are significant correlates of the fish community composition. Black arrows represent ten fish species (abbreviations explained in Tab. 2) which had the highest contribution to the between protection status dissimilarity. The strength of correlation of each variable with an individual axis is expressed by the length of an arrow. If Arrows point in different directions the associated variables are negatively correlated. Points represent individual nets and their location in the two-dimensional space of the graph. The points are colored according to protection status. Blue points represent nets placed in open access areas (OA) and green points marine protected areas (MPA). RDA percentages of variation are shown on the appendant axes.

Table 10. SIMPER analysis results showing species-specific abundance and biomass correlates that contribute to the Bray-Curtis dissimilarity between the two protection status (OA: open access area, MPA: marine protected area) fish community compositions for appendant average catch-per-unit-effort (fish / 30 m benthic multi-mesh net, CPUE $\pm$ SD) and biomass-per-unit-effort (g / 30 m benthic multi-mesh net, BPUE $\pm$ SD). The coloration of the effects shows whether a species contributed to the dissimilarities by being more abundant in the OA (blue) or the MPA (red). The tone of color is proportional to the strength of the effect.

	Species	Mean CPUE $\pm$ SD	Mean CPUE $\pm$ SD	Contribution to	Mean BPUE $\pm$ SD	Mean BPUE $\pm$ SD	Contribution to
OA vs. MPA		OA	MPA	between-group dissimilarity (CPUE)	OA	MPA	between-group dissimilarity (BPUE)
Clupeidae	<i>C. harengus</i>	0.59 $\pm$ 1.42	0.6 $\pm$ 1.48	<0.01	35.69 $\pm$ 91.38	56.56 $\pm$ 186.88	0.02
	<i>S. sprattus</i>	4.61 $\pm$ 10.48	2.55 $\pm$ 6.74	0.05	32.79 $\pm$ 77.85	11.05 $\pm$ 24.88	<0.01
Engraulidae	<i>E. encrasicolus</i>	0 $\pm$ 0	0.06 $\pm$ 0.23	<0.01	0 $\pm$ 0	0.95 $\pm$ 3.91	<0.01
Osmeridae	<i>O. eperlanus</i>	0.09 $\pm$ 0.41	0 $\pm$ 0	<0.01	0.38 $\pm$ 1.66	0 $\pm$ 0	<0.01
Esocidae	<i>E. lucius</i>	0.13 $\pm$ 0.39	0.19 $\pm$ 0.52	<0.01	348.14 $\pm$ 1072.91	546.78 $\pm$ 1811.22	0.08
Cypriniformes	<i>R. rutilus</i>	20.02 $\pm$ 25.37	24.91 $\pm$ 27.82	0.21	1217.4 $\pm$ 1586.76	1137.22 $\pm$ 1345.52	0.24
	<i>L. idus</i>	0.02 $\pm$ 0.13	0.06 $\pm$ 0.23	<0.01	4.87 $\pm$ 35.78	40.77 $\pm$ 248.49	<0.01
	<i>S. erythrophthalmus</i>	0.77 $\pm$ 2.02	1.26 $\pm$ 3.56	<0.01	56.83 $\pm$ 158.1	158.15 $\pm$ 523.83	0.03
	<i>T. tinca</i>	0 $\pm$ 0	0.02 $\pm$ 0.13	<0.01	0 $\pm$ 0	48.07 $\pm$ 349.99	<0.01
	<i>A. brama</i>	0.13 $\pm$ 0.39	0.19 $\pm$ 0.48	<0.01	223.07 $\pm$ 678.95	271.01 $\pm$ 729.33	0.06
	<i>B. bjoerkna</i>	1.38 $\pm$ 2.83	4.21 $\pm$ 5.78	0.03	96.83 $\pm$ 229.64	387.17 $\pm$ 875.68	0.06
	<i>A. alburnus</i>	22.2 $\pm$ 76.58	32.85 $\pm$ 76.93	0.18	210.26 $\pm$ 725.93	348.18 $\pm$ 833.58	0.07
Belonidae	<i>B. belone</i>	0.04 $\pm$ 0.27	0 $\pm$ 0	<0.01	15.26 $\pm$ 112.13	0 $\pm$ 0	<0.01
Gadidae	<i>G. morrhua</i>	0.02 $\pm$ 0.13	0.04 $\pm$ 0.27	<0.01	0.67 $\pm$ 4.93	9.05 $\pm$ 65.85	<0.01
Percidae	<i>P. fluviatilis</i>	4.38 $\pm$ 7.18	12.81 $\pm$ 14.31	0.11	314.99 $\pm$ 525.69	1171.22 $\pm$ 1959.74	0.18
	<i>G. cernua</i>	1.91 $\pm$ 3.71	1.98 $\pm$ 4.95	0.03	78.33 $\pm$ 158.16	51.28 $\pm$ 106.14	0.02
	<i>S. lucioperca</i>	0.41 $\pm$ 1.09	1.32 $\pm$ 4.11	0.01	7.21 $\pm$ 23.01	26.66 $\pm$ 88.82	0.01
Ammodytidae	<i>A. tobianus</i>	0.05 $\pm$ 0.31	0.08 $\pm$ 0.33	<0.01	0.65 $\pm$ 3.78	0.81 $\pm$ 4.41	<0.01
Gobiidae	<i>G. niger</i>	0.31 $\pm$ 0.96	0.15 $\pm$ 0.41	<0.01	1.66 $\pm$ 4.82	0.63 $\pm$ 2.33	<0.01
	<i>P. microps</i>	0.52 $\pm$ 1.12	0.17 $\pm$ 0.37	<0.01	0.78 $\pm$ 1.71	0.25 $\pm$ 0.56	<0.01
	<i>P. minutus</i>	0 $\pm$ 0	0.02 $\pm$ 0.13	<0.01	0 $\pm$ 0	0.03 $\pm$ 0.19	<0.01
	<i>N. melanostomus</i>	1.15 $\pm$ 1.49	1.34 $\pm$ 1.74	0.02	18.17 $\pm$ 31.3	12.59 $\pm$ 22.01	<0.01
Cottidae	<i>M. scorpius</i>	0.04 $\pm$ 0.19	0.02 $\pm$ 0.13	<0.01	1.64 $\pm$ 8.52	0.51 $\pm$ 3.69	<0.01
Gasterosteidae	<i>G. aculeatus</i>	6.28 $\pm$ 15.35	6.83 $\pm$ 18.44	0.08	10.53 $\pm$ 23.97	11.49 $\pm$ 29.76	<0.01
	<i>P. pungitius</i>	0.15 $\pm$ 0.52	0.66 $\pm$ 3.19	<0.01	0.13 $\pm$ 0.45	0.54 $\pm$ 2.48	<0.01
	<i>S. spinachia</i>	0 $\pm$ 0	0.08 $\pm$ 0.33	<0.01	0 $\pm$ 0	0.42 $\pm$ 1.81	<0.01
Syngnathidae	<i>S. typhle</i>	0 $\pm$ 0	0.02 $\pm$ 0.13	<0.01	0 $\pm$ 0	0.04 $\pm$ 0.24	<0.01
Pleuronectidae	<i>P. flesus</i>	0.15 $\pm$ 0.45	0.04 $\pm$ 0.19	<0.01	27.11 $\pm$ 85.38	3.16 $\pm$ 18.71	<0.01

3.5. Abundance (numerical, biomass), length and age differences between OAs and MPAs

3.5.1. Low fishing pressure species

3.5.1.1 Impact of protection on common roach (abundance (numerical, biomass), length)

A total of 2424 common roach were caught. 2401 common roach were caught with the benthic multi-mesh gillnets and 23 with the pike nets. 55 % of the entire common roach catch were caught in the MPAs. Neither was protection status as a main effect correlated with CPUE of common roach nor was any interaction between protection status and area or season a significant correlate of common roach abundance (Tab. 11, Fig. 16). CPUE of common roach averaged out at 33.76 ± 68.51 fish/100 m net in OAs compared to 43.27 ± 78.46 fish/100 m net in MPAs. Instead, the predictor variable area and season were significant correlates of the numerical abundance of common roach, both as a main effect and combined as an interaction (Tab. 11). The abundance of common roach was lower in summer in the N. and S.-area (11.66 ± 18.39 fish/100 m net) compared to the Grabow-area (mean: 46.05 ± 71.03 fish/100 m net, EMMs: $t(\text{Inf}) = -4.14$, $p < 0.001$) and compare to the Ummanz-area (mean: 39.69 ± 47.81 fish / 100 m net, EMMs: $t(\text{Inf}) = -4.15$, $p < 0.001$). The CPUE was higher in the Ummanz-area (mean: 7.22 ± 17.41 fish / 100 m net) compared to the Grabow-area (mean: 1.66 ± 3.26 fish / 100 m net) in autumn (EMMs: $t(\text{Inf}) = 3.27$, $p < 0.01$). When observing the abundance of roach throughout the seasons in the areas, it became evident that in the Grabow-area the catch rate was higher in spring (mean: 93 ± 121.57 fish/100 m net) than in autumn (EMMs: $t(\text{Inf}) = -7.19$, $p < 0.001$) and higher in summer compared to autumn (EMMs: $t(\text{Inf}) = -6.11$, $p < 0.001$). A similar trend could be observed in the Ummanz-area because the abundance of common roach was higher in spring (mean: 52.78 ± 55.48 fish/100 m net) compared to autumn (EMMs: $t(\text{Inf}) = -6.46$, $p < 0.001$) and higher in summer compared to autumn (EMMs: $t(\text{Inf}) = -4.69$, $p < 0.001$). In the N. and S.-area the abundances were higher in spring (mean: 93.36 ± 117.56 fish/100 m net) compared to summer (EMMs: $t(\text{Inf}) = 6.14$, $p < 0.001$) and autumn (mean: 3.21 ± 5.95 fish/100 m net, EMMs: $t(\text{Inf}) = -5.89$, $p < 0.001$). A graph of these findings can be found in the Appendix 1.

Table 11. Wald-test outcome showing if a predictor was related to the catch per unit effort (CPUE, fish/100 m benthic and pike multi-nesh gillnet) of common roach, as estimated through zero-inflated negative binominal generalized linear mixed model. The outcome of the Wald-test for the predictor variables includes the Wald chi-square statistic, the degrees of freedom (Df) and the p-value. Significant values are highlighted in bold characters.

Zero-inflated negative binominal GLMM Wald-test results	Wald chi-square	Df	p-value
Fixed effects / interactions			
Protection status	0.017	1	0.894
Area	9.191	2	< 0.05
Season	45.097	2	< 0.001
Protection status : Area	4.051	2	0.131
Protection status : Season	2.341	2	0.311
Area : Season	24.521	4	< 0.001
Protection status : Area : Season	8.344	4	0.079

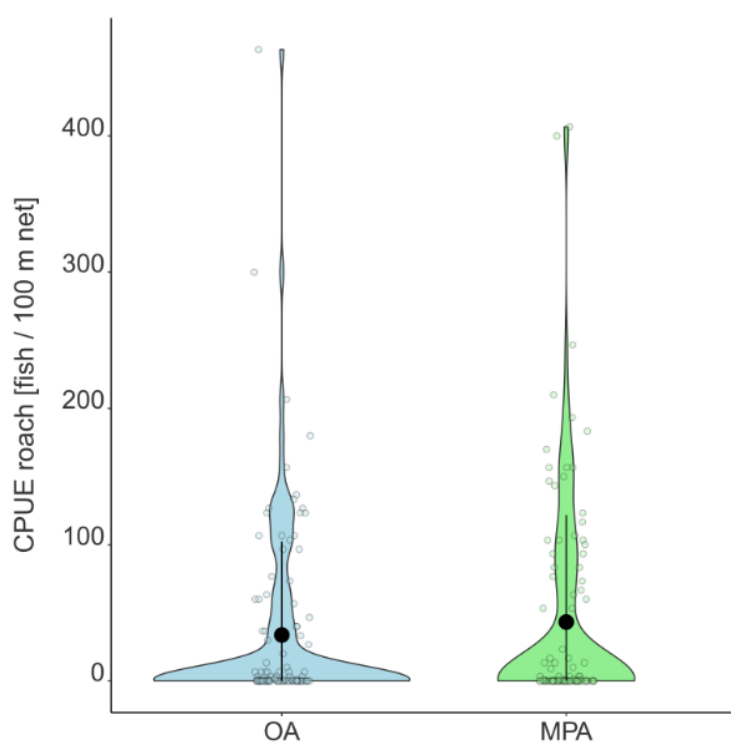


Figure 16. Violin plots (black dot: mean, whisker: standard deviation) that show how the catch-per-unit-effort (CPUE, fish/100 m benthic and pike multi-nesh gillnet) of common roach is related to the protection status (OA: open access area, MPA: marine protected area, x- axis). Significant differences between groups are marked as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

A total of 137 kg of common roach were caught throughout the experiment on the two net types. OAs accounted for a share of 52 % of the total common roach weight (Tab. 8). The biomass of common roach did not vary between OAs and MPAs (Tab. 12). The MPA-BPUE mean was 2.04 ± 3.73 kg/100 m net and the OA-BPUE 2.08 ± 4.24 kg/100 m net (Fig. 17). Two two-way interaction terms between protection status and area and protection status and season and a significant three-way interaction term between protection status, area and season significantly correlated with the common roach BPUE (Tab. 12). The only significant difference between area-pairs was found in the Grabow-area in autumn (Fig. 17). The biomass of common roach was higher in the OA than in the MPA (EMMs: $t(188) = -5.56$, $p < 0.001$, Fig. 17). More areal and seasonal differences between individual protection status are found in appendix 2 and 3. Biomass of common roach were highest in spring in all area-pairs (App. 3).

Table 12. Wald-test outcome showing if a predictor was related to the biomass-per-unit-effort (BPUE, kg / 100 m benthic and pike multi-nesh gillnet) of common roach, as estimated through zero-inflated negative binominal generalized linear mixed model. The outcome of the Wald-test for the predictor variables includes the Wald chi-square statistic, the degrees of freedom (Df) and the p-value. Significant values are highlighted in bold characters.

Zero-inflated negative binominal GLMM Wald-test results	Wald chi-square	Df	p-value
Fixed effects / interactions			
Protection status	0.001	1	0.999
Area	3.269	2	0.195
Season	54.596	2	< 0.001
Protection status : Area	0.651	2	0.722
Protection status : Season	30.495	2	< 0.001
Area : Season	51.831	4	< 0.001
Protection status : Area : Season	22.906	4	< 0.001

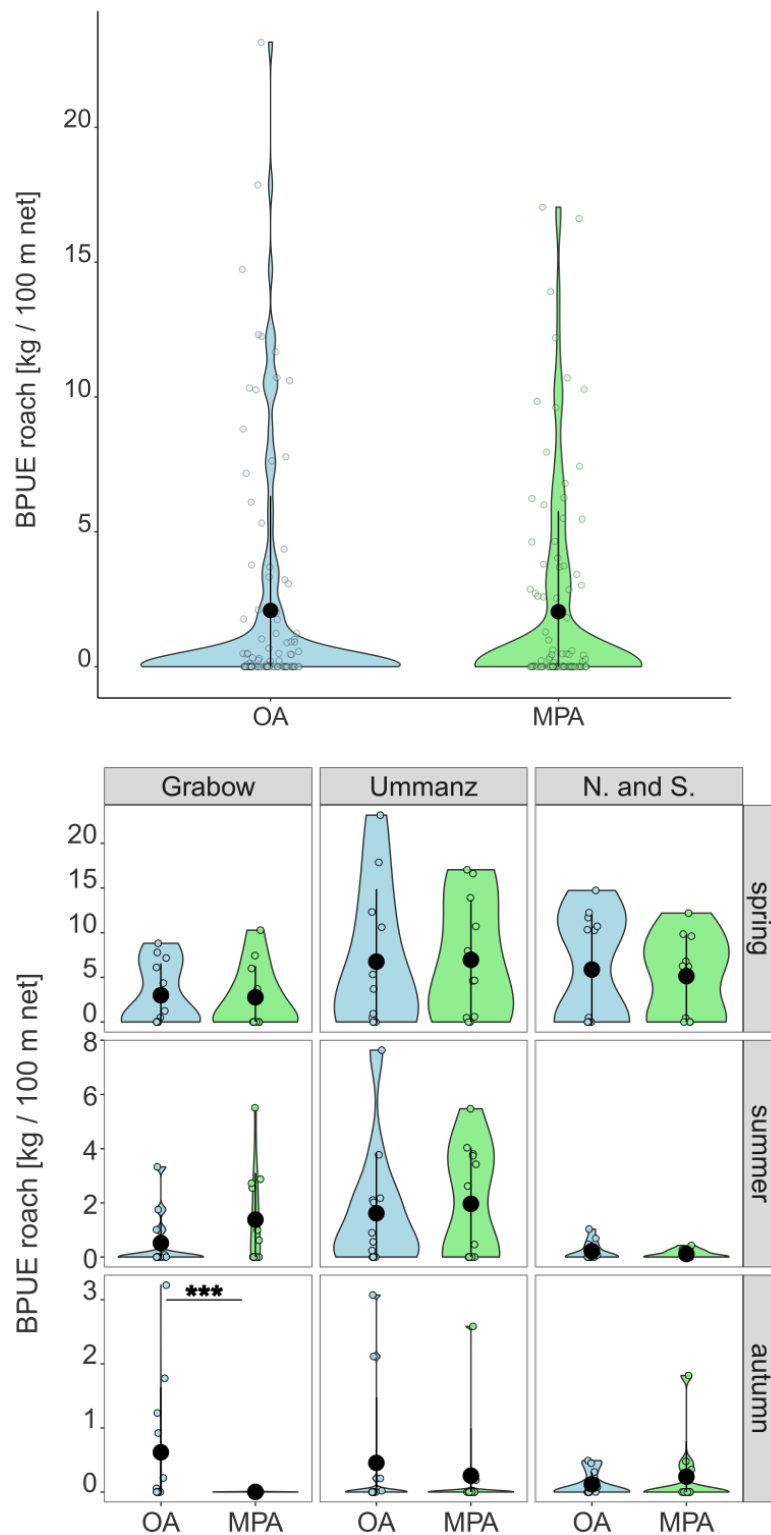


Figure 17. Violin plots (black dot: mean, whisker: standard deviation) that show how the biomass-per-unit-effort (BPUE, fish / 100 m benthic and pike multi-nesh gillnet) of common roach is related to the protection status (OA: open access area, MPA: marine protected area, x- axis, left figure) and how the CPUE is correlated with the interaction of protection status, area (upper labels, N. and S.: Neuensien- and Seliner See) and season (right labels, right figure). Significant differences between groups are marked as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

The total length of common roach reached from 49 to 380 mm (mean: 141 ± 65 mm, Tab. 13). Common roach in the OAs were on average 145.62 ± 69.69 mm large, whereas in MPAs they averaged out at 137.52 ± 61.3 mm (Fig. 18). Additionally, three significant interaction terms between the predictors caused significant variation in the total length of common roach (Tab. 13). Two-way interaction terms between protection status and season as well as area and season, plus the three-way interaction term of protection status, area and season were correlated with the length of common roach (Tab. 13). Common roach in spring were significantly larger in the Grabow-OA compared to the Grabow-MPA (EMMs: $t(2405) = -28.43$, $p < 0.001$, Fig. 18). In the N. and S.- area in spring the common roach in the MPA had a significantly higher total length compared to the OA (EMMs: $t(2405) = 13.88$, $p < 0.05$, Fig. 18). More areal and seasonal differences between individual protection status are found in appendix X. It became evident that in most areas experienced the lowest catch rates in summer compared to spring and autumn (App. 4, 5).

Table 13. Wald-test outcome showing if a predictor related to the length of common roach (mm) as estimated through a generalized linear mixed model. The outcome of the Wald-test for the predictor variables includes the Wald chi-square statistic, the degrees of freedom (Df) and the p-value. Significant values are highlighted in bold characters.

Generalized linear mixed model	Wald chi-square	Df	p-value
Wald-test results			
Fixed effects / interactions			
Protection status	3.854	1	< 0.05
Area	0.342	2	0.842
Season	3.011	2	0.221
Protection status : Area	5.327	2	0.069
Protection status : Season	19.933	2	< 0.001
Area : Season	80.912	4	< 0.001
Protection status : Area : Season	15.464	4	< 0.01

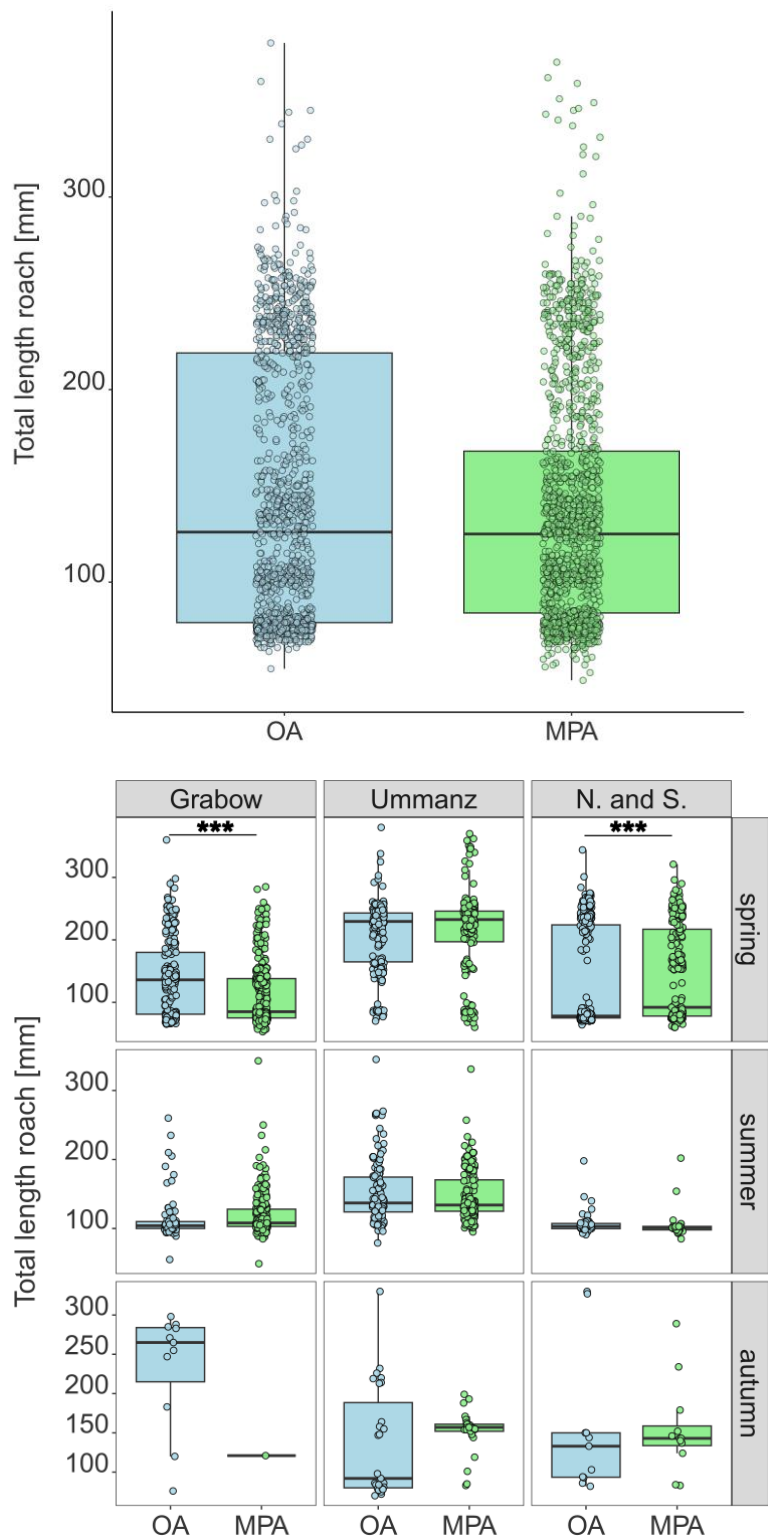


Figure 18. Boxplots (median, box: 25 and 75 percentile, whisker: 10 and 90 percentile) that show how the total length of common roach (mm, y-axis) is related to the protection status (OA: open access area, MPA: marine protected area, x- axis, left figure) and how the total length is related to the interaction of protection status (x-axis), area (upper labels, N. and S.: Neuensien- and Seliner See) and season (right labels, right figure). Significant differences between groups (boxplots) are marked as follows: * = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$.

3.5.1.2. Impact of protection on common bream (abundance (numerical, biomass), length)

A total of 393 common bream were caught with both net types (benthic multi-mesh gillnets: 17, pike nets: 376). Abundance of common bream differed between OAs and MPAs (Tab. 14). Common bream abundance averaged out at 2.19 ± 3.88 fish/100 m net in the MPAs and in the OAs at 1.92 ± 3.77 fish/100 m net (Fig. 19). The abundance of common bream differed among seasons (Tab. 14). Common bream were more abundant in the spring (mean: 2.81 ± 5.27 fish/100 m net) compared to the summer (mean: 0.78 ± 1.23 fish/100 m net, EMMs: $t(\text{Inf}) = 6.22$, $p < 0.001$, App. 6). Additionally, significant differences between area-pairs of different main areas were found (Tab. 14). However, post-hoc testing did not yield any differing catch rates between the three area-pairs (Grabow: EMMs: $t(189) = -0.004$, $p = 1$, Ummanz: EMMs: $t(189) = -0.22$, $p = 0.99$, N. and S.: EMMs: $t(189) = 0.89$, $p = 0.75$, Fig. 19).

Table 14. Wald-test outcome showing if a predictor is related to the catch per unit effort (CPUE, fish/100 m benthic and pike multi-mesh gillnet) of common bream, as estimated through zero-inflated negative binominal generalized linear mixed model. The outcome of the Wald-test for the predictor variables includes the Wald chi-square statistic, the degrees of freedom (Df) and the p-value. Significant values are highlighted in bold characters.

Zero-inflated GLMM	negative	binominal	Wald chi-square	Df	p-value
Wald-test results					
Fixed effects / interactions					
Protection status			7.699	1	< 0.01
Area			2.995	2	0.223
Season			14.864	2	< 0.001
Protection status : Area			6.232	2	< 0.05
Protection status : Season			5.018	2	0.081
Area : Season			5.706	4	0.222
Protection status : Area : Season			5.947	4	0.203

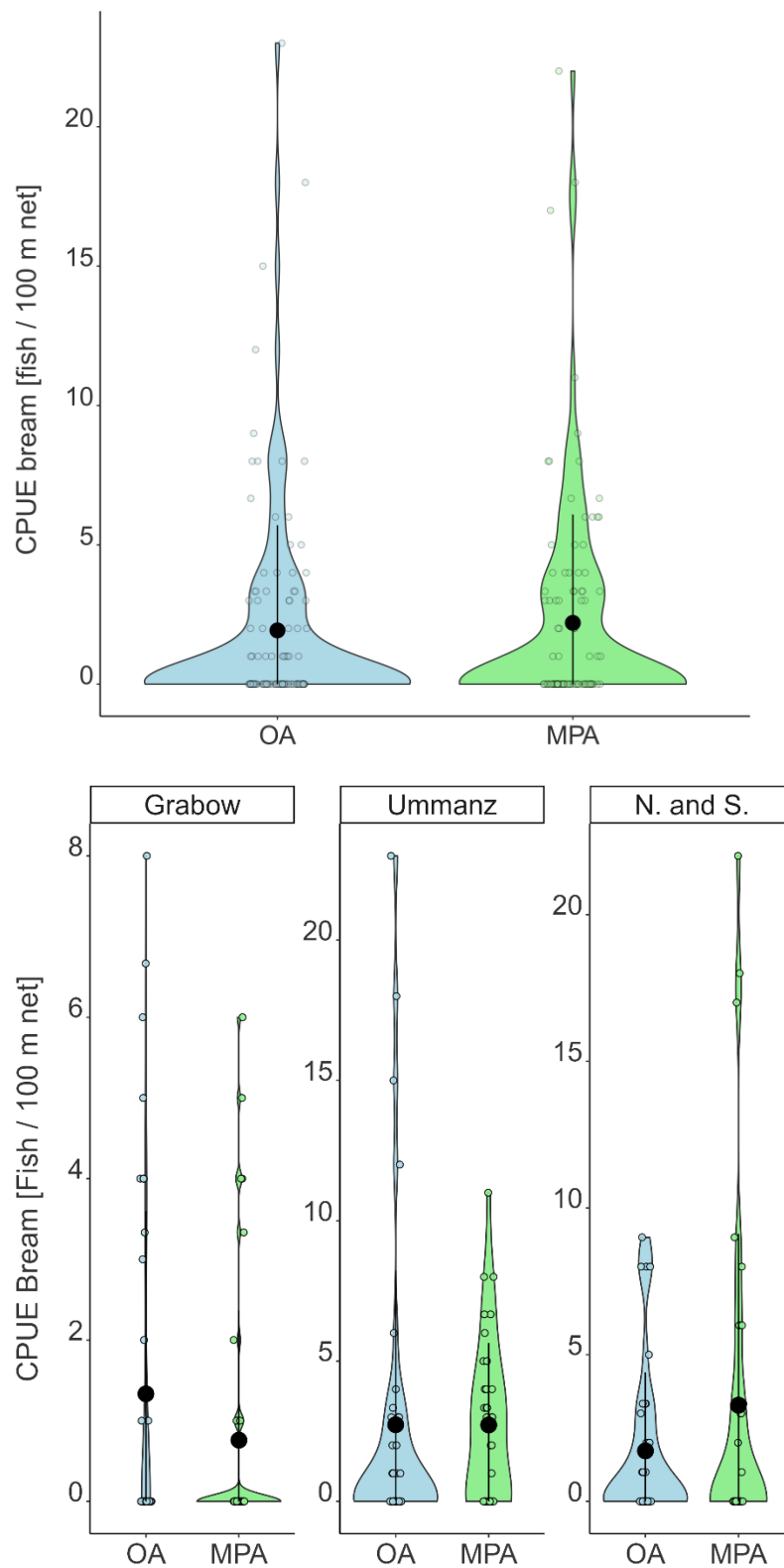


Figure 19. Violin plots (black dot: mean, whisker: standard deviation) that show how the catch-per-unit-effort (CPUE, fish/100 m benthic and pike multi-nesh gillnet) of common bream is related to the protection status (OA: open access area, MPA: marine protected area, x- axis, left figure and the interaction of protection status and area (top labels, N. and S.: Neuensienner- and Seliner See, right figure). Significant differences between groups are marked as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

The total weight of all common bream caught added up to 662 kg. Protection status was a significant correlate of common bream biomass (Tab. 15). BPUE in MPAs averaged out at 3.61 ± 6.64 kg/100 m net, while OAs had a mean of 3.29 ± 6.28 kg/100 m net (Fig. 20). Significant areal and seasonal effects on the common bream BPUE, as well as a two-way interaction term between protection status and area were observed (Tab. 15). The biomass abundance of common bream was higher in spring (mean: 4.43 ± 5.93 kg/100 m net) compared to summer (mean: 1.34 ± 2.18 kg/100 m net, EMMs: $t(197) = 4.01$, $p < 0.001$) and higher in autumn (mean: 4.61 ± 8.87 kg/100 m net) compared to summer (EMMs: $t(197) = 5.09$, $p < 0.001$, App. 7). No significant variation between the protection status in the different areas were observed via post-hoc testing, but in the Grabow- and N. and S.-area trends could be found that indicated a potential difference in catch rate between OAs and MPAs (Grabow: EMMs: $t(197) = -0.65$, $p = 0.08$, Ummanz: EMMs: $t(197) = -0.12$, $p = 0.91$, N. and S.: EMMs: $t(197) = 0.57$, $p = 0.06$, Fig. 20). In the Grabow-area BPUEs were marginally higher in the OA (mean: 2.23 ± 3.66 kg/100 m net) compared to the MPA (mean: 0.72 ± 1.54 kg/100 m net, Fig. 20). In the N. and S.-area the BPUE was marginally higher in the MPA (mean: 5.62 ± 9.95 kg/100 m net) compared to the OA (mean: 3.19 ± 5.02 kg/100 m net, Fig. 20). The biomass of common bream was lowest in the Grabow-MPA when compared to the Ummanz- (EMMs: $t(\text{Inf}) = 3.3$, $p < 0.01$) and N. and S.-MPA (EMMs: $t(\text{Inf}) = 3.65$, $p < 0.01$, Fig. 20).

Table 15. Wald-test outcome showing if a predictor is a significant correlate of the biomass-per-unit-effort (BPUE, kg/100 m benthic and pike multi-nesh gillnet) of common bream, as estimated through zero-inflated negative binominal generalized linear mixed model. The outcome of the Wald-test for the predictor variables includes the Wald chi-square statistic, the degrees of freedom (Df) and the p-value. Significant values are highlighted in bold characters.

Zero-inflated negative binominal GLMM	Wald chi-square	Df	p-value
Wald-test results			
Fixed effects / interactions			
Protection status	4.815	1	< 0.05
Area	14.414	2	< 0.001
Season	8.774	2	< 0.01
Protection status : Area	4.618	2	< 0.01
Protection status : Season	9.889	2	0.099
Protection status : Area : Season	8.432	4	0.122

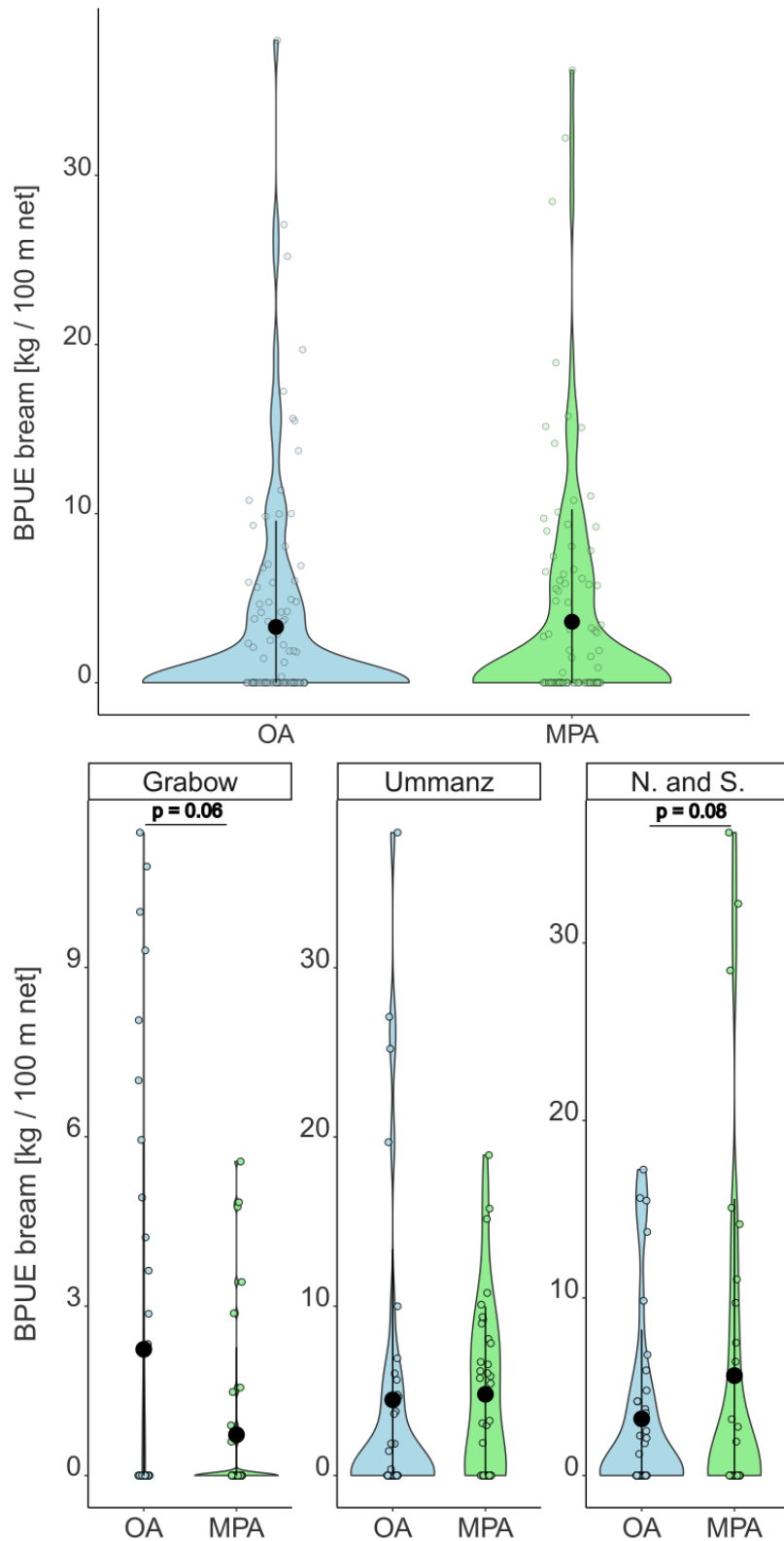


Figure 20. Violin plots (black dot: mean, whisker: standard deviation) that show how the biomass-per-unit-effort (BPUE, fish/100 m benthic and pike multi-nesh gillnet) of common bream is related to the protection status (OA: open access area, MPA: marine protected area, x- axis, left figure) and the interaction of protection status and area (top labels, N. and S.: Neuensien- and Seliner See, right figure). Significant differences between groups are marked as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Common bream total length was high and ranged from 303 to 616 mm (mean: 505 ± 55 mm) since juveniles were not capture. Protection status was a significant correlate of the length of common bream (Tab. 16). Common bream in the OAs were on average 505.94 ± 52.76 mm large and in the MPAs 503.94 ± 57.29 mm (Fig. 21). Area-pairs significantly varied among main areas in regards to the size of common bream (Tab. 16). Common bream in the OA of the Grabow-area were significantly larger than in the MPA (EMMs: $t(373) = -5.83$, $p < 0.001$, Fig. 21). In the Ummanz-area common bream were larger in the MPA than in the OA (EMMs: $t(373) = 4.56$, $p < 0.001$, Fig. 21). Common bream in the MPA of the Grabow-area were smaller than the common bream caught in the MPAs of the Ummanz- (EMMs: $t(746) = 5.09$, $p < 0.001$) and the N. and S-area (EMMs: $t(746) = 5.16$, $p < 0.001$, Fig. 21).

Table 16. Wald-test outcome showing if a predictor is a significant correlate of the total length of common bream (mm) as estimated through a generalized linear mixed model. The outcome of the Wald-test for the predictor variables includes the Wald chi-square statistic, the degrees of freedom (Df) and the p-value. Significant values are highlighted in bold characters.

Generalized linear mixed model	Wald chi-square	Df	p-value
Wald-test results			
Fixed effects / interactions			
Protection status	10.616	1	< 0.01
Area	5.163	2	0.075
Season	4.071	2	0.131
Protection status : Area	28.389	2	< 0.001
Protection status : Season	5.195	2	0.074
Area : Season	4.431	4	0.351
Protection status : Area : Season	3.673	4	0.298

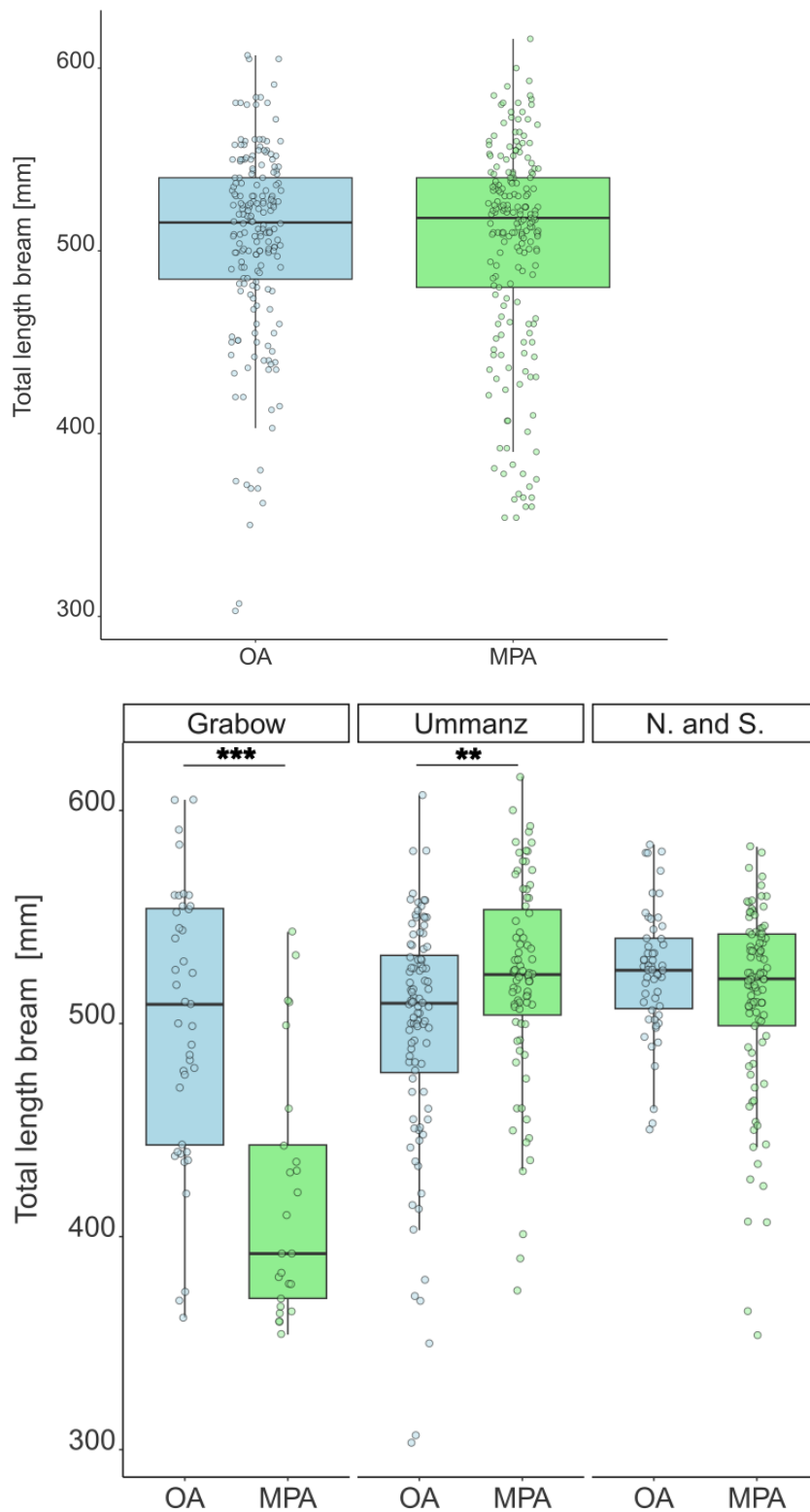


Figure 21. Boxplots (median, black dot: mean, box: 25 and 75 percentile, whisker: 10 and 90 percentile) that show how the total length of common bream (mm, y-axis) is related to the protection status (OA: open access area, MPA: marine protected area, x- axis, left figure) and how the total length is related to the interaction of protection status (x-axis) and area (upper labels, N. and S.: Neuensienner- and Seliner See, right figure). Significant differences between groups (boxplots) are marked as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

3.5.2. High fishing pressure species

3.5.2.1. Impact of protection on European perch (abundance (numerical, biomass), length)

1031 European perch were caught throughout the study with the two net types. Benthic multi-mesh gillnets caught 916 (89 %) of the European perch. 261 (25 %) were caught in the OAs and 770 (75 %) in the MPAs. Abundances of European perch varied significantly among OAs and MPAs (Tab. 17). Catch rates were significantly higher (≈ 4 times higher) in MPAs (mean: 23.08 ± 39.93 fish / 100 m net) than in OAs (mean: 7.61 ± 18.38 fish/100 m net, EMMs: $t(190) = 10.17$, $p < 0.001$, Fig. 22). Area and season as single predictors and the two-way interaction of these two predictors were significant correlates of the CPUE (Tab. 17). The abundance of European perch was higher in the N. and S. area (mean: 18.22 ± 25.11 fish/100 m net) compared to the Grabow-area (mean: 4.22 ± 7.53 fish/100 m net, EMMs: $t(\text{Inf}) = 4.11$, $p < 0.001$) and higher compared to the Ummanz-area (mean: 1.72 ± 2.38 fish/100 m net, EMMs: $t(\text{Inf}) = 5.31$, $p < 0.001$) in spring. In summer the abundances of European perch were lower in the N. and S.-area (mean: 8.33 ± 14.28 fish/100 m net) compared to the Grabow- (mean: 23.13 ± 34.11 fish/100 m net, EMMs: $t(\text{Inf}) = -6.08$, $p < 0.001$) and Ummanz-area (mean: 24.37 ± 37.77 fish/100 m net, EMMs: $t(\text{Inf}) = -7.21$, $p < 0.001$). In autumn the Grabow- (mean: 3.77 ± 4.51 fish/100 m) net, Ummanz- (mean: 12.25 ± 21.59 fish/100 m) and N. and S.-area (mean: 39.98 ± 64.14 fish/100 m) all differed between each other regarding the CPUE. European perch were more abundant in the N. and S.-area compared to both the Grabow-area (EMMs: $t(\text{Inf}) = 9.72$, $p < 0.001$) and the Ummanz-area (EMMs: $t(\text{Inf}) = 7.41$, $p < 0.001$).

In the Grabow-area European perch CPUE was significantly higher in summer compared to spring (EMMs: $t(190) = -5.56$, $p < 0.001$) and autumn (EMMs: $t(190) = -7.16$, $p < 0.001$). European perch CPUE in the Ummanz-area was significantly higher in summer compared to spring (EMMs: $t(190) = -8.99$, $p < 0.001$) and autumn (EMMs: $t(190) = -5.56$, $p < 0.001$) and autumn CPUE was higher than spring CPUE (EMMs: $t(190) = 5.12$, $p < 0.001$). In the N. and S.-area the CPUE of European perch was significantly higher in autumn compared to spring (EMMs: $t(190) = 6.49$, $p < 0.001$) and summer (EMMs: $t(190) = 8.42$, $p < 0.001$). A graph of these findings can be found in the Appendix 8.

Table 17. Wald-test outcome showing if a predictor was a significant correlate of the catch per unit effort (CPUE, fish/100 m benthic and pike multi-nesh gillnet) of European perch, as estimated through a negative binominal generalized linear mixed model. The outcome of the Wald-test for the predictor variables includes the Wald chi-square statistic, the degrees of freedom (Df) and the p-value. Significant values are highlighted in bold characters.

Negative binominal GLMM Wald-test results	Wald chi-square	Df	p-value
Fixed effects / interactions			
Protection status	21.841	1	< 0.001
Area	21.971	2	< 0.001
Season	18.706	2	< 0.001
Protection status : Area	5.322	2	0.069
Protection status : Season	0	2	0.841
Area : Season	120.2	4	< 0.001
Protection status : Area : Season	2.804	4	0.159

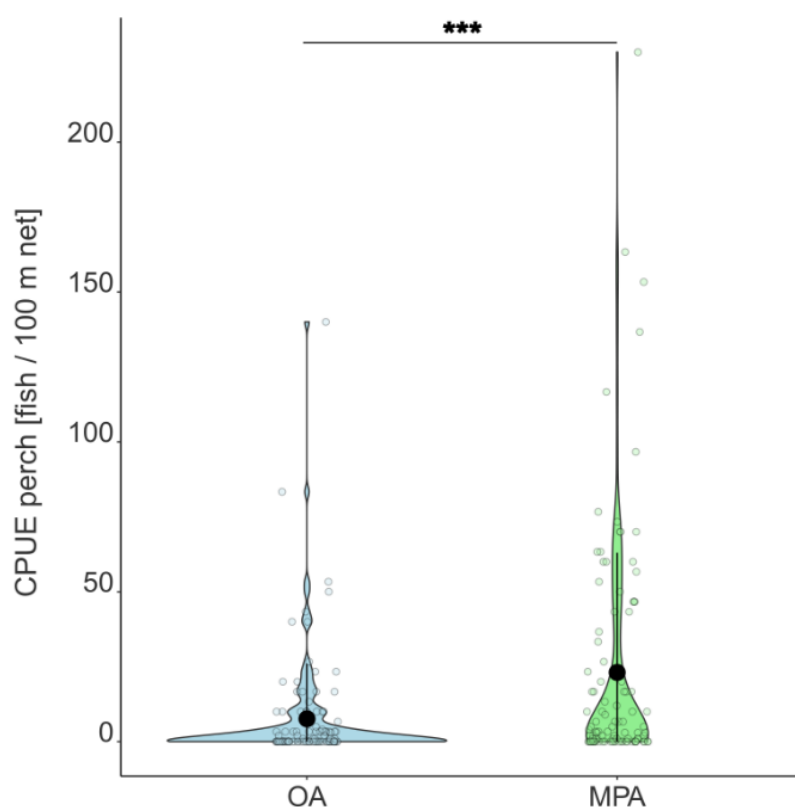


Figure 22. Violin plots (black dot: mean, whisker: standard deviation) that show how the catch-per-unit-effort (CPUE, fish/100 m benthic and pike multi-nesh gillnet) of European perch is related to the protection status (OA: open access area, MPA: marine protected area, x- axis). Significant differences between groups are marked as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

A total European perch weight of 162 kg was caught with both net types (pike nets: 51 % of the biomass catch). 33 kg European perch were caught in the OAs (20 %) and 129 kg (80 %) in the MPAs. biomass of European perch varied significantly among protection status (Tab. 18). The BPUE was about four times higher in the MPAs (mean: 23.08 ± 39.93 kg/100 m net) than in the OAs (mean: 7.61 ± 18.38 kg/100 m net, Fig. 23). All predictors, except area, were significantly correlated with the biomass of European perch (Tab. 18). There were no significant differences found between the Ummanz-area-pair in all seasons (Fig. 23). In the Grabow-area the biomass in the MPA was higher in spring (EMMs: $t(188) = 5.51$, $p < 0.001$) and summer (EMMs: $t(188) = 2.31$, $p < 0.05$, Fig. 23) compared to the OA. In the N. and S.-area European perch BPUE was higher in the MPA in spring (EMMs: $t(188) = 4.73$, $p < 0.001$) and in autumn (EMMs: $t(188) = 2.17$, $p < 0.05$, Fig. 23). Further differences between areas and season for the individual protection status can be seen in the Appendix 9 ad 10.

Table 18. Wald-test outcome showing if a predictor is a significant correlate of the biomass per unit effort (BPUE, kg/100 m benthic and pike multi-nesh gillnet) of European perch, as estimated through zero-inflated negative binominal generalized linear mixed model. The outcome of the Wald-test for the predictor variables includes the Wald chi-square statistic, the degrees of freedom (Df) and the p-value. Significant values are highlighted in bold characters.

Zero-inflated negative binominal GLMM	Wald chi-square	Df	p-value
Wald-test results			
Fixed effects / interactions			
Protection status	30.815	1	< 0.001
Area	2.881	2	0.236
Season	7.638	2	< 0.05
Protection status : Area	20.571	2	< 0.001
Protection status : Season	13.091	2	< 0.01
Area : Season	45.877	4	< 0.001
Protection status : Area : Season	11.578	4	< 0.05

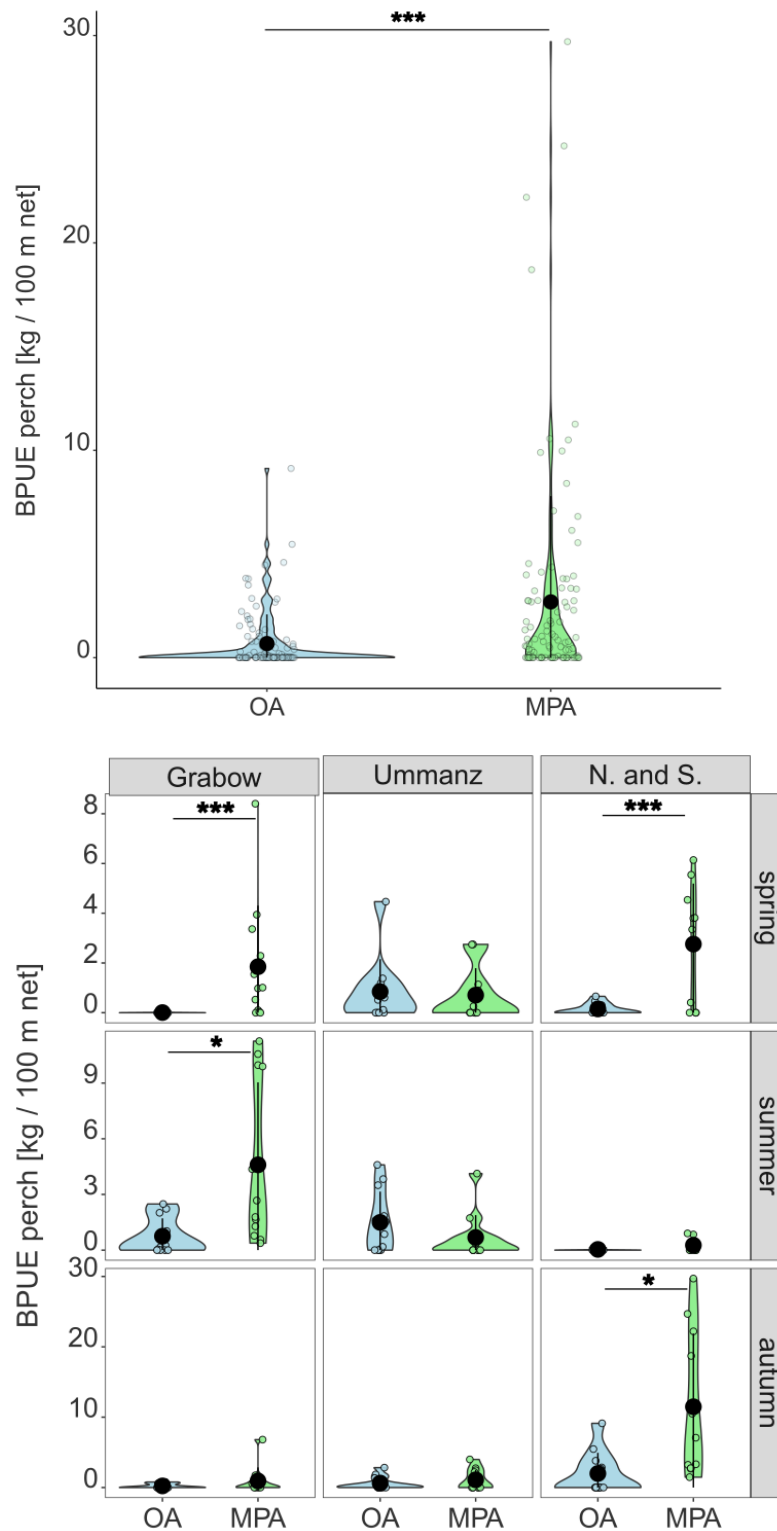


Figure 23. Violin plots (black dot: mean, whisker: standard deviation) that show how the biomass-per-unit-effort (BPUE, fish/100 m benthic and pike multi-nesh gillnet) of European perch is related to the protection status (OA: open access area, MPA: marine protected area, x- axis, left figure) and the interaction of protection status, area (top labels, N. and S.: Neuensien- and Seliner See) and season (right labels, right figure). Significant differences between groups are marked as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

The total length of European perch reached from 47 to 501 mm (mean: 179 ± 94 mm). The length of European perch did not vary between OAs and MPAs (Tab. 19). European perch size in MPAs averaged out at 186 ± 94 mm and in OAs at 161 ± 92 mm (Fig. 24). Only areal effects and a two-way interaction of area and season caused significant differences in total length (Tab. 19). European perch were larger in the Grabow area (mean: 173 ± 104 mm) compared to the Ummanz area (mean: 110 ± 73 mm, EMMs: $t(1012) = 7.25$, $p < 0.001$) and larger compared to the N. and S. area (mean: 85 ± 46 mm, EMMs: $t(1012) = 5.16$, $p < 0.001$) in summer. European perch in the N. and S. area (mean: 224 ± 62 mm) were however larger compared to the Grabow-area (mean: 219 ± 125 mm, EMMs: $t(1012) = -4.91$, $p < 0.001$) and the Ummanz area (mean: 155 ± 67 mm) in autumn (EMMs: $t(1012) = 6.53$, $p < 0.001$). No significant differences between seasons could be found in the Grabow-area between the seasons. In the Ummanz-area (mean: 246 ± 125 mm) European perch were larger in spring when compared to summer (EMMs: $t(1012) = 6.89$, $p < 0.001$) and autumn (EMMs: $t(188) = 5.97$, $p < 0.001$). Total length significantly varied among all seasons in the N. and S.-area (spring mean: 176 ± 44 mm, spring > summer = EMMs: $t(188) = 6.99$, $p < 0.001$, spring < autumn = EMMs: $t(188) = 4.51$, $p < 0.001$, summer < autumn = EMMs: $t(188) = 10.81$, $p < 0.001$). A graph showing this interaction can be found in the appendix 11.

Table 19. Wald-test outcome showing if a predictor is a significant correlate of the total length of European perch (mm) as estimated through a generalized linear mixed model. The outcome of the Wald-test for the predictor variables includes the Wald chi-square statistic, the degrees of freedom (Df) and the p-value. Significant values are highlighted in bold characters.

Generalized linear mixed model	Wald chi-square	Df	p-value
Wald-test results			
Fixed effects / interactions			
Protection status	0.166	1	0.684
Area	60.648	2	< 0.001
Season	3.855	2	0.145
Protection status : Area	0.013	2	0.993
Protection status : Season	2.289	2	0.318
Area : Season	120.2	4	< 0.001
Protection status : Area : Season	2.804	4	0.591

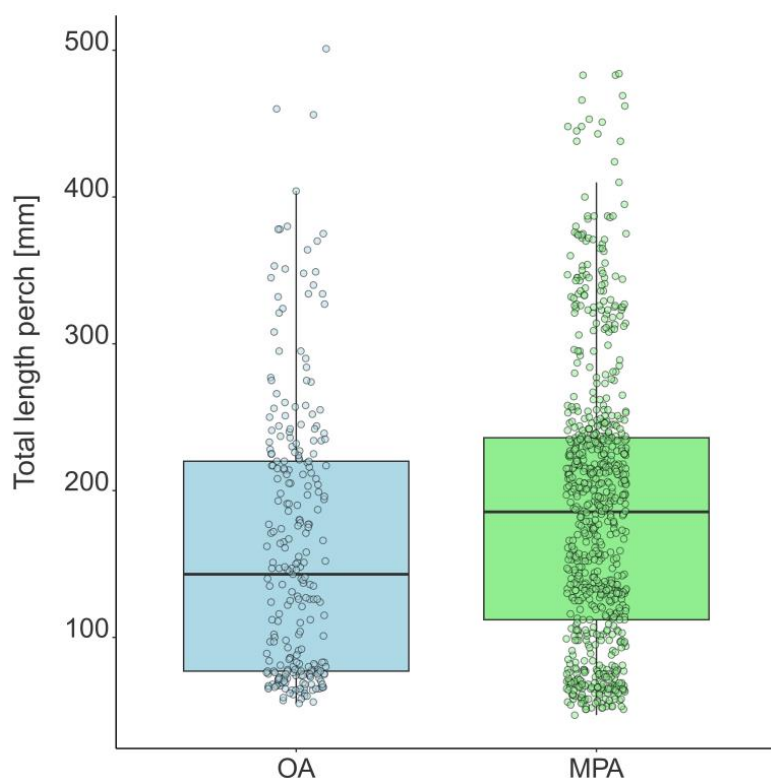


Figure 24. Boxplots (median, box: 25 and 75 percentile, whisker: 10 and 90 percentile) that show how the total length of European perch (mm, y-axis) is related to the protection status (OA: open access area, MPA: marine protected area, x- axis). Significant differences between groups (boxplots) are marked as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

3.5.2.2. Impact of protection on northern pike (abundance (numerical, biomass), length, age)
A total of 389 northern pike were caught, of which 266 (69 %) were caught angling, 106 (27 %) were caught with pike nets and 17 were caught with the benthic multi-mesh gillnets (4 %). During the angling trials 212 (80 %) northern pike were caught in MPAs and 54 (20 %) in OAs. The abundance of northern pike varied significantly among protection status (Tab. 20). Similarly, to European perch, abundances of angled northern pike were in total about four times higher in MPAs (mean: 0.43 ± 0.66 fish/hour) when compared to OAs (mean: 0.12 ± 0.32 fish/hour, Fig. 25). Catch rates were significantly higher in the MPA (EMMs: $t(707) = 11.07$, $p < 0.001$, Fig. 25). CPUE also significantly varied seasonally (Tab. 20). The CPUE was significantly higher in summer (mean: 0.38 ± 0.65 fish/hour) when compared to autumn (mean: 0.19 ± 0.48 fish / hour, EMMs: $t(360) = -2.69$, $p < 0.05$, App. 12).

Table 20. Wald-test outcome showing if a predictor is a significant correlate of the catch per unit effort (CPUE, fish/hour) of northern pike caught by angling as estimated through a zero-inflated Poisson generalized linear mixed model. The outcome of the Wald-test for the predictor variables includes the Wald chi-square statistic, the degrees of freedom (Df) and the p-value. Significant values are highlighted in bold characters.

Zero-inflated Poisson GLMM	Wald chi-square	Df	p-value
Wald-test results			
Fixed effects / interactions			
Protection status	51.112	1	< 0.001
Area	3.885	2	0.421
Season	11.836	2	< 0.01
Protection status : Area	7.234	2	0.064
Protection status : Season	1.927	2	0.587
Area : Season	9.205	4	0.101
Protection status : Area : Season	1.304	4	0.861

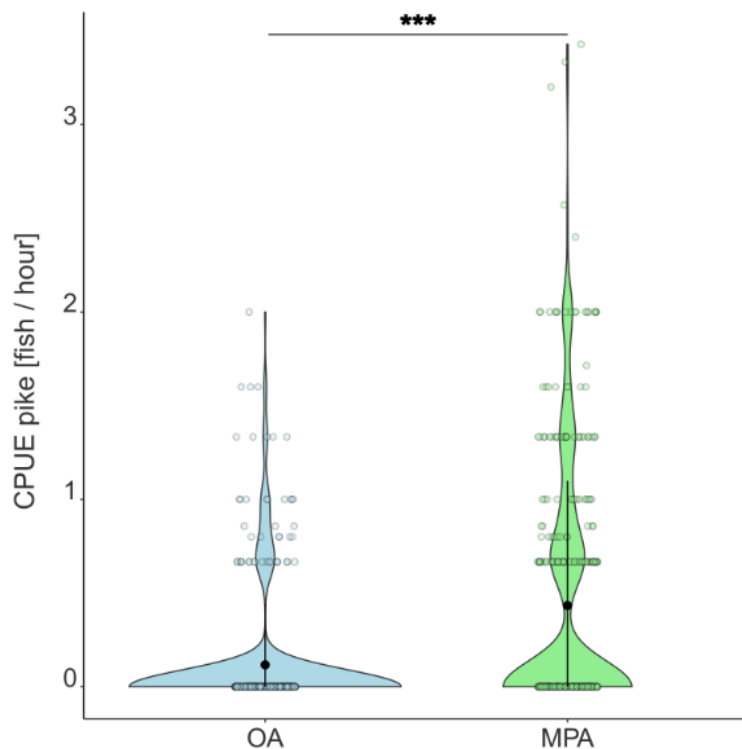


Figure 25. Violin plots (black dot: mean, whisker: standard deviation) that show how the catch-per-unit-effort (CPUE, fish/hour) of northern pike caught by angling is related to the protection status (OA: open access area, MPA: marine protected area, x- axis). Significant differences between groups are marked as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

The total northern pike biomass caught during the angling trials was 665.5 kg, of which 141.8 kg (21 %) were caught in OAs and 523.6 kg (79 %) were caught in MPAs. The biomass abundance of northern pike varied significantly between OAs and MPAs (Tab. 21). Northern pike biomass catch rates were in more than three times higher in MPAs (mean: 1.44 ± 2.39 kg / hour) when compared to OAs (mean: 0.39 ± 1.12 kg / hour, EMMs: $t(707) = 69.74$, $p < 0.001$, Fig. 26). BPUE also significantly varied among areas (Tab. 15). The northern pike biomass was significantly higher in the Grabow-area (mean: 0.99 ± 2.01 kg / hour) when compared to the N. and S.-area (mean: 0.69 ± 1.36 fish / hour, EMMs: $t(707) = -77.95$, $p < 0.001$, App. 13) and higher in the Ummanz-area (mean: 1.08 ± 2.25 fish / hour) compared to the N. and S.-area (EMMs: $t(360) = -59.26$, $p < 0.001$, App. 13).

Table 21. Wald-test outcome showing if a predictor is a significant correlate of the biomass-per-unit-effort (BPUE, kg/hour) of northern pike caught by angling as estimated through a zero-inflated Poisson generalized linear mixed model. The outcome of the Wald-test for the predictor variables includes the Wald chi-square statistic, the degrees of freedom (Df) and the p-value. Significant values are highlighted in bold characters.

Zero-inflated Poisson GLMM	Wald chi-square	Df	p-value
Wald-test results			
Fixed effects / interactions			
Protection status	3.661	1	< 0.05
Area	26.956	2	< 0.001
Season	2.109	2	0.062
Protection status : Area	4.975	2	0.083
Protection status : Season	5.137	2	0.076
Area : Season	7.341	4	0.118
Protection status : Area : Season	4.546	4	0.337

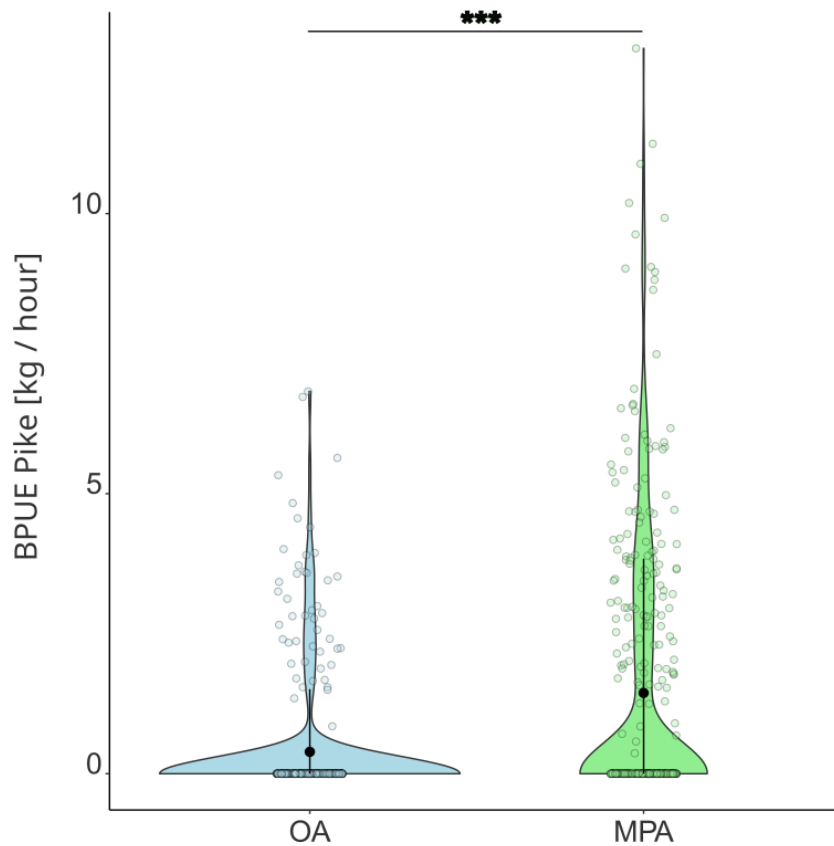


Figure 26. Violin plots (black dot: mean, whisker: standard deviation) that show how the biomass-per-unit-effort (BPUE, kg/hour) of northern pike caught by angling is related to the protection status (OA: open access area, MPA: marine protected area, x- axis). Significant differences between groups are marked as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Total length of the 386 measurable northern pike caught with all sampling methods ranged from 350 to 1175 mm (mean: 768 ± 114 mm). The size of northern pike did not differ between OAs and MPAs (Tab. 22, Fig. 27). Northern pike in MPAs had a mean length of 771 ± 141 mm, while OA northern pike had an average length of 760 ± 95 mm (Fig. 27). Size of northern pike was however affected by a two-way interaction between area and season (Tab. 22). Northern pike were larger in the N. and S. area in spring (mean: 734 ± 87 mm) compared to summer (mean: 648 ± 151 mm, EMMs: $t(63) = 3.92$, $p < 0.01$, App. 14). Additionally, larger pike were observed in the Ummanz- (mean: 833 ± 111 mm) compared to the N. and S.-area in summer (EMMs: $t(361) = -4.59$, $p < 0.001$) and larger in the Grabow-area (mean: 808 ± 102 mm) compared to the N. and S. area in summer (EMMs: $t(360) = -6.99$, $p < 0.001$, App. 14).

Table 22. Wald-test outcome showing if a predictor is a significant correlate of the total length of northern pike (mm) caught by all gears as estimated through a generalized linear mixed model. The outcome of the Wald-test for the predictor variables includes the Wald chi-square statistic, the degrees of freedom (Df) and the p-value. Significant values are highlighted in bold characters.

Generalized linear mixed model	Wald chi-square	Df	p-value
Wald-test results			
Fixed effects / interactions			
Protection status	2.021	1	0.155
Area	35.579	2	< 0.001
Season	31.291	2	< 0.001
Protection status : Area	4.883	2	0.087
Protection status : Season	3.415	2	0.181
Area : Season	32.636	4	< 0.001
Protection status : Area : Season	4.066	4	0.397

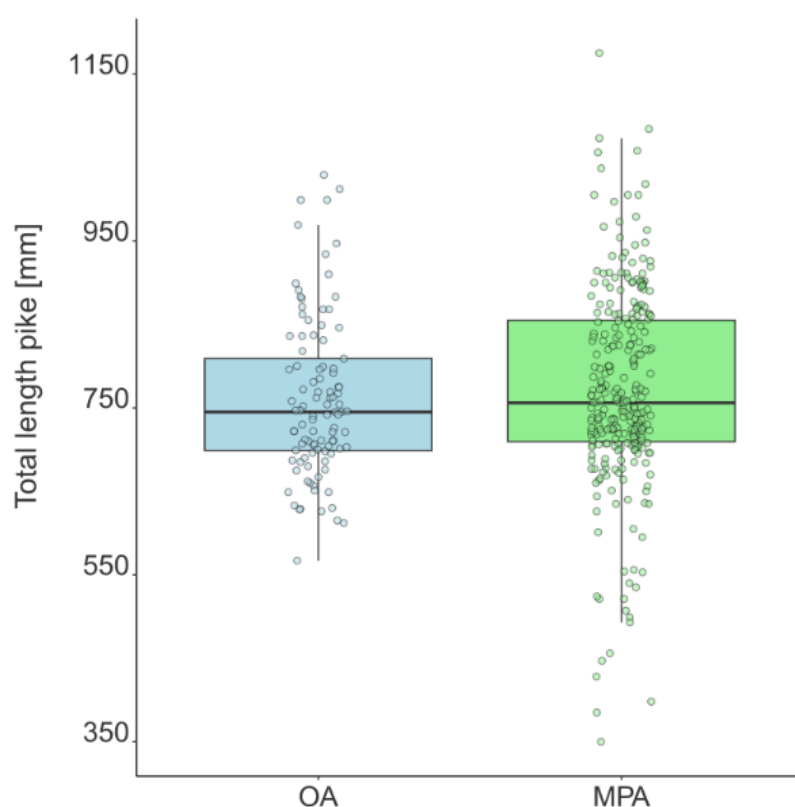


Figure 27. Boxplots (median, box: 25 and 75 percentile, whisker: 10 and 90 percentile) that show how the length of northern pike (mm, y-axis) caught by all gears is related to the protection status (OA: open access area, MPA: marine protected area, x- axis). Significant differences between groups (boxplots) are marked as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Age-at-catch of 297 Northern pike analyzed ranged from 1 to 12 years (mean: 5 ± 2 years). The age of northern pike differed significantly between the protection status (Tab. 23). Northern pike caught in MPAs had a mean age of 5 ± 2 years and northern pike caught in OAs had a mean age of 4 ± 2 years (Fig. 28). Northern pike age additionally showed seasonal trends (Tab. 23), as older fish were captured in spring (mean: 4 ± 2 years) compared to summer (mean: 3 ± 2 years, EMMs: $t(286) = -5.34$, $p < 0.01$). Age was further correlated with the interaction term between protection status and area (Tab. 23). Northern pike were only significantly older in the Ummanz-MPA (mean: 6 ± 2 years) compared to the Ummanz-OA (mean: 4 ± 2 years, EMMs: $t(265) = -4.68$, $p < 0.001$, Fig. 28).

Table 23. Wald-test outcome showing if a predictor is a significant correlate of the age of northern pike (years) caught by all gears as estimated through a generalized linear mixed model. The outcome of the Wald-test for the predictor variables includes the Wald chi-square statistic, the degrees of freedom (Df) and the p-value. Significant values are highlighted in bold characters.

Generalized linear mixed model	Wald chi-square	Df	p-value
Wald-test results			
Fixed effects / interactions			
Protection status	0.249	1	< 0.001
Area	5.877	1	0.052
Season	4.982	2	0.12
Protection status : Area	18.278	2	< 0.001
Protection status : Season	7.661	2	0.075

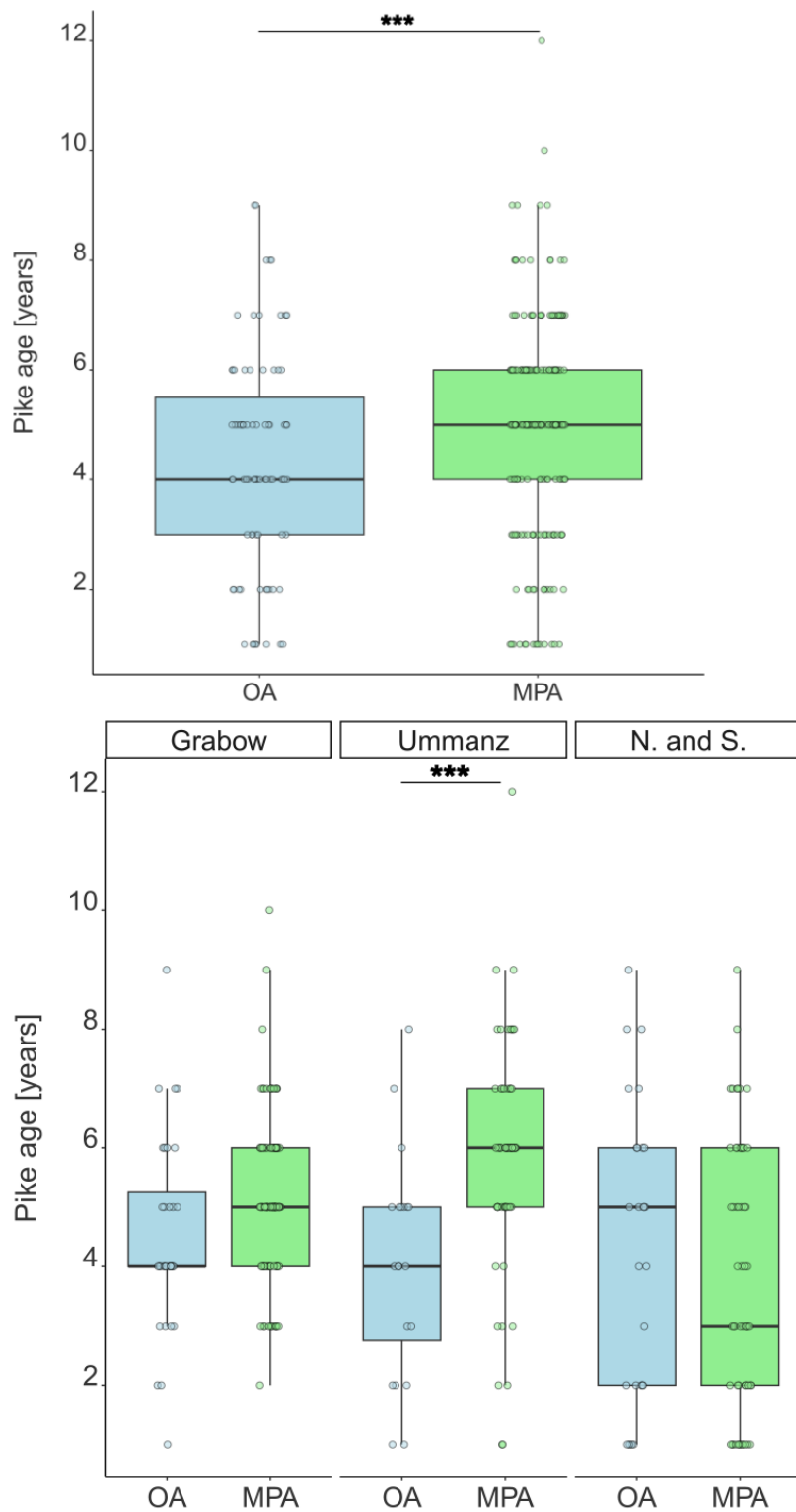


Figure 28. Boxplots (median, box: 25 and 75 percentile, whisker: 10 and 90 percentile) that show how the age of northern pike (years, y-axis) caught by all gears is related to the protection status (OA: open access area, MPA: marine protected area, x- axis, left figure) and how the age is related to the interaction of protection status (x-axis) and area (upper labels, N. and S.: Neuensienner- and Seliner See, right figure). Significant differences between groups (boxplots) are marked as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

3.6. Impact of protection on condition and growth in northern pike

3.6.1. Relative condition

Relative condition of 378 northern pike caught with all sampling methods ranged from 0.69 to 1.47 (mean: 1 ± 0.16). Neither was protection status as a single predictor a significant correlate of the relative condition nor was any interaction with protection status and area and / or season (Tab. 24). Relative condition in OAs averaged out at 1 ± 0.11 while it had a mean of 1.01 ± 0.11 in MPAs (Fig. 29). Relative condition only significantly varied seasonally (Tab. 24). Northern pike had a higher relative condition in spring (mean: 1.02 ± 0.12) compared to autumn (mean: 0.98 ± 0.09 , EMMs: $t(11) = -2.46$, $p < 0.05$, App. 15).

Table 24. Wald-test outcome showing if a predictor is a significant correlate of the relative condition of northern pike caught by all gears as estimated through a generalized linear mixed model. The outcome of the Wald-test for the predictor variables includes the Wald chi-square statistic, the degrees of freedom (Df) and the p-value. Significant values are highlighted in bold characters.

Generalized linear mixed model	Wald chi-square	Df	p-value
Wald-test results			
Fixed effects / interactions			
Protection status	0.757	1	0.384
Area	1.158	1	0.561
Season	13.028	2	< 0.01
Protection status : Area	2.039	2	0.361
Protection status : Season	0.235	2	0.889
Area : Season	4.573	4	0.333
Protection status : Area : Season	5.166	4	0.271

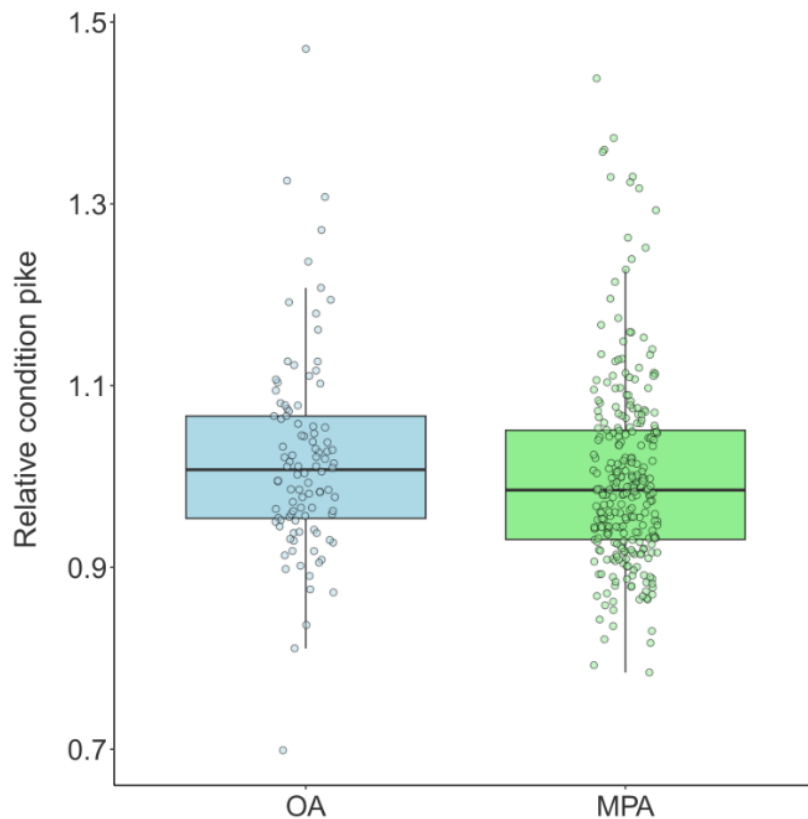


Figure 29. Boxplots (median, box: 25 and 75 percentile, whisker: 10 and 90 percentile) that show how the relative condition of northern pike (y-axis) caught by all gears is related to the protection status (OA: open access area, MPA: marine protected area, x- axis). Significant differences between groups (boxplots) are marked as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

3.6.2. Hepatosomatic index

42 northern pike (OA: 7, MPA: 35) were dispatched during this study and used for liver analysis. The HSI of northern pike caught with all gears ranged from 0.7 to 2.45 % (mean: 1.42 ± 0.41 %). HSI did not significantly vary between OAs and MPAs (Tab. 25). Northern pike had a mean HSI of 1.43 ± 0.44 % in the MPAs and a mean of 1.38 ± 0.21 % in the OAs (Fig. 30). Areal and seasonal differences in HSI could not be observed (Tab. 25).

Table 25. Wald-test outcome showing if a predictor is a significant correlate of the hepatosomatic index (%) of northern pike caught by all gears as estimated through a generalized linear mixed model. The outcome of the Wald-test for the predictor variables includes the Wald chi-square statistic, the degrees of freedom (Df) and the p-value. Significant values are highlighted in bold characters.

Generalized linear mixed model	Wald chi-square	Df	p-value
Wald-test results			
Fixed effects			
Protection status	0.237	1	0.625
Area	0.825	2	0.661
Season	2.177	2	0.336

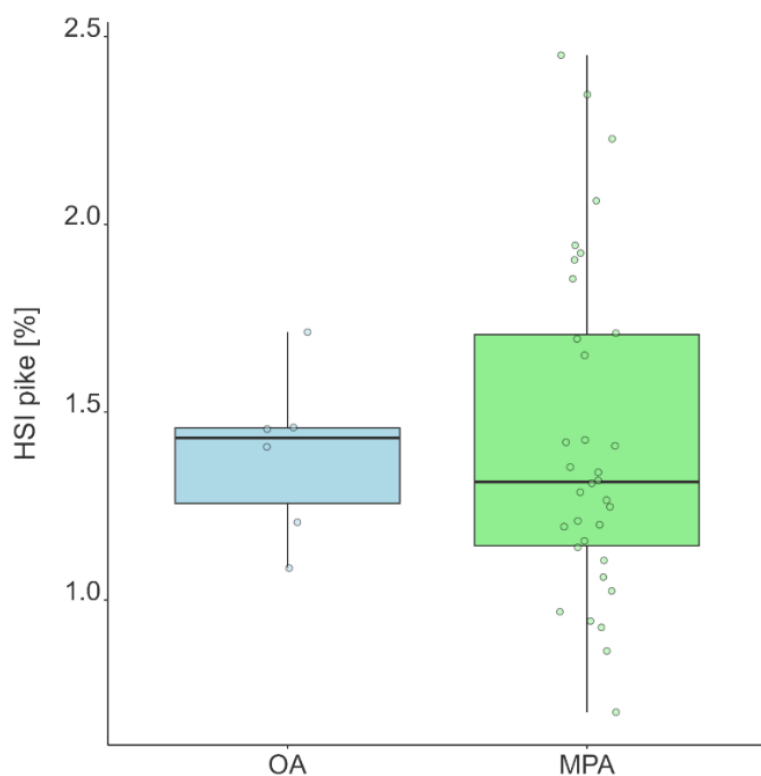


Figure 30. Boxplots (median, box: 25 and 75 percentile, whisker: 10 and 90 percentile) that show how the hepatosomatic index of northern pike (HSI, %, y-axis) caught by all gears is related to the protection status (OA: open access area, MPA: marine protected area, x- axis). Significant differences between groups (boxplots) are marked as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

3.6.3. Size-specific growth

Size-specific growth of northern pike analyzed ranged from 225 to 591 mm (mean: 430 ± 48 mm). Protection status was significantly correlated with the size-specific growth (Tab. 20). Northern pike caught in OAs (mean: 434 ± 43 mm) grew faster than those caught in MPAs (mean: 428 ± 50 mm, EMMs: $t(272) = 2.02$, $p < 0.05$, Fig. 19). Significant areal differences were further observed in regards to the size-specific growth (Tab. 20). Northern pike grew significantly slower in the N. and S.-area (mean: 421 ± 48 mm) compared to the Ummanz-area (mean: 434 ± 53 mm, EMMs: $t(268) = 3.78$, $p < 0.001$, App. 16).

Table 26. Wald-test outcome showing if a predictor a significant correlate of the size-specific growth (mm) of northern pike caught by all gears as estimated through a generalized linear mixed model. The outcome of the Wald-test for the predictor variables includes the Wald chi-square statistic, the degrees of freedom (Df) and the p-value. Significant values are highlighted in bold characters.

Generalized linear mixed model	Wald chi-square	Df	p-value
Wald-test results			
Fixed effects			
Protection status	4.098	1	< 0.05
Area	17.563	1	< 0.001
Season	0.167	2	0.919

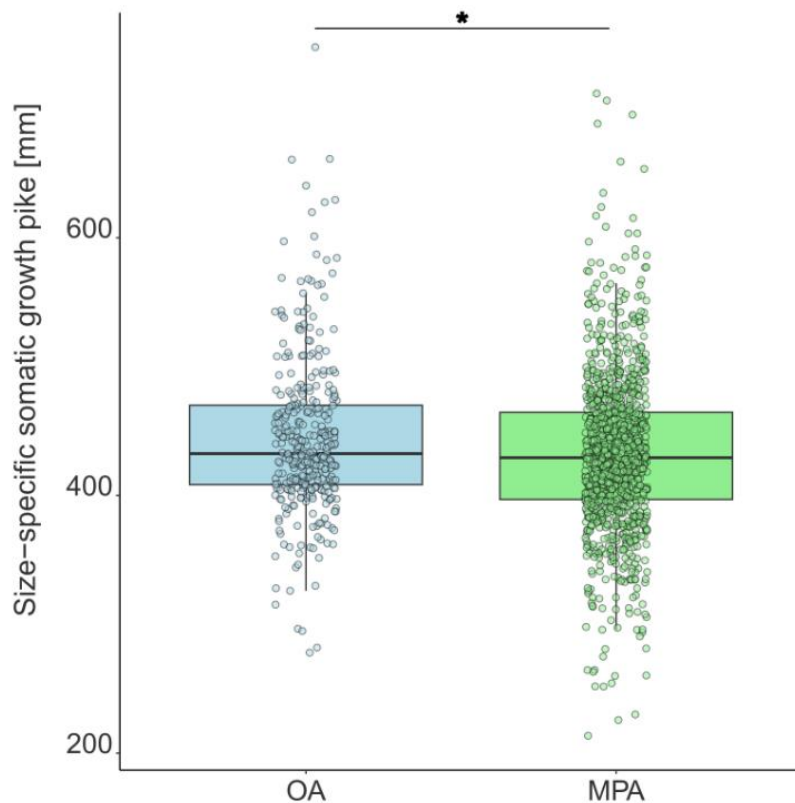


Figure 31. Boxplots (median, box: 25 and 75 percentile, whisker: 10 and 90 percentile) that show how the size-specific growth of northern pike (mm, y-axis) caught with all gears is related to the protection status (OA: open access area, MPA: marine protected area, x- axis). Significant differences between groups (boxplots) are marked as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

3.7. Impact of protection on prey choice/-specialization in northern pike

3.7.1. Food composition

A total of 113 northern pike (29 % of total catch) had prey remains in their stomach after the catch, while 276 northern pike (71 %) had empty stomachs. 15 crustacean- and fish species could be identified as food particles (Tab. 27). The food particle found most often in stomachs of northern pike were three-spined sticklebacks and round goby (Tab. 27). Common roach and European perch made up the highest biomass of all stomachs sampled (Tab. 27).

Numerical percentages of different prey species in northern pike stomachs were mostly equal for northern pike caught in OAs and MPAs (Fig. 32, Tab. 27). Three-spined sticklebacks and round goby made up the highest percentages in both protection status (Fig. 32, Tab. 27). OAs and MPAs differed regarding their third highest numerical percentage, which in the case of OAs was Atlantic herring and in the case of MPAs nine-spined stickleback (Fig. 32, Tab. 27). Permutational MANOVA revealed that stomach content composition of northern pike did not

vary between OAs and MPAs regarding prey counts of individual species (Tab. 28). The 95 % confidence intervals of both protection status prey count NMDSs highly overlapped which illustrated their similarity (Fig. 33). Significant differences in prey composition were however observed among areas and seasons (Tab. 28). The prey composition differed between the Grabow- and the Ummanz area (STC: $F(1) = 4.24$, $p < 0.001$, Fig. 33), the Grabow- and N. and S. area (STC: $F(1) = 4.27$, $p < 0.01$, Fig. 33) and between the Ummanz- and the N. and S. area (STC: $F(1) = 5.11$, $p < 0.001$, Fig. 33). Regarding seasonal trends, the prey composition did only differ in summer and spring (STC: $F(1) = 3.35$, $p < 0.01$, Fig. 33).

The biomass of the different prey species visually differed in OAs and MPAs (Fig. 32). While prey biomass composition in OAs mostly consisted out of Atlantic herring, European eel ($n = 1$) and round goby, MPA prey biomass composition mostly consisted out of common roach, European perch and Atlantic herring (Fig. 32, Tab. 27). Yet, a permutational MANOVA revealed that protection status was not a significant correlate of prey biomass composition of northern pike (Tab. 28). 95 % confidence interval ellipses highly overlapped in the NMDS plot, indicating that the stomachs analyzed did not differ regarding their prey biomass composition between protection status (Fig. 33). Significant differences in prey composition were observed among areas and seasons (Tab. 28). The prey composition differed between the Grabow- and the Ummanz area (STC: $F(1) = 1.61$, $p < 0.001$, Fig. 28), the Grabow- and N. and S. area (STC: $F(1) = 1.25$, $p < 0.01$, Fig. 28) and between the Ummanz- and the N. and S. area (STC: $F(1) = 1.75$, $p < 0.001$, Fig. 28). Regarding seasonal trends, the prey composition did only differ when comparing summer and spring (STC: $F(1) = 3.6$, $p < 0.01$, Fig. 28).

Table 27. The count of prey items (N) and accumulated biomass of the 16 taxa found within the pike stomachs caught by all gears in total and divided by protection status (OA: open access area, MPA: marine protected area). The name of the families, the Latin names, abbreviations used in the text and graphs and the common English name for the taxa are included in the table. The number of stomachs examined for each group is noted below the group name.

Family	Species (lat. Name)	Abbr.	Species (English name)	N (Total) 109 stomachs	Biomass (total) [g] 109 stomachs	N (OA) 32 stomachs	% (OA)	N (MPA) 77 stomachs	% (MPA)	Biomass (OA) [g] 32 stomachs	% (OA)	Biomass (MPA) [g] 77 stomachs	% (MPA)
Gammaridae	<i>Gammarus sp.</i>	<i>Gammarus sp.</i>	Gammarid	6	4.2	1	1.6	5	2.8	3.5	< 1	0.7	< 1
Crangonidae	<i>Crangon crangon</i>	<i>C. crangon</i>	Brown shrimp	1	1.2	0	0	1	< 1	0	0	1.2	< 1
Palaemonidae	<i>Palaemon adspersus</i>	<i>P. adspersus</i>	Baltic shrimp	5	7	1	1.6	4	2.4	1.4	< 1	5.6	< 1
Clupeidae	<i>Clupea harengus</i>	<i>C. harengus</i>	Atlantic herring	19	1130.4	9	15	10	5.6	582.3	38.2	548.1	15.3
Cypriniformes	<i>Rutilus rutilus</i>	<i>R. rutilus</i>	Common roach	13	1370.7	3	5	10	5.6	148.9	9.7	1221.8	34.2
	<i>Alburnus alburnus</i>	<i>A. alburnus</i>	Bleak	1	15.1	0	0	1	< 1	0	0	15.1	< 1
Anguillidae	<i>Anguilla anguilla</i>	<i>A. anguilla</i>	European eel	1	240	1	1.6	0	0	240	15.7	0	0
Percidae	<i>Perca fluviatilis</i>	<i>P. fluviatilis</i>	European perch	16	1157.9	2	3.3	14	7.9	75	4.9	1082.9	30.6
	<i>Gymnocephalus cernua</i>	<i>G. cernua</i>	Ruffe	3	57.1	1	1.6	2	1.1	26.1	1.7	31	< 1
Gobiidae	<i>Gobius niger</i>	<i>G. niger</i>	Black goby	5	31.8	2	3.3	3	1.7	11.4	< 1	20.4	< 1
	<i>Neogobius melanostomus</i>	<i>N. melanostomus</i>	Round goby	51	556.1	16	26.6	35	19.8	227.1	14.8	329	9.2
Gasterosteidae	<i>Gasterosteus aculeatus</i>	<i>G. aculeatus</i>	Three-spined stickleback	73	90.1	20	33.3	53	30.1	28.7	1.8	61.3	1.7
	<i>Pungitius pungitius</i>	<i>P. pungitius</i>	Nine-spined stickleback	31	19.4	8	3.3	35	16.4	<0.01	< 1	17.7	< 1
	<i>Spinachia spinachia</i>	<i>S. spinachia</i>	Sea stickleback	3	17.3	0	0	3	1.7	0	0	17.3	< 1
Pleuronectidae	<i>Platichthys flesus</i>	<i>P. flesus</i>	European flounder	8	392.1	2	3.3	6	3.4	181.2	11.8	210.8	5.9
unidentified fish				3		1	1.6	2	1.1				

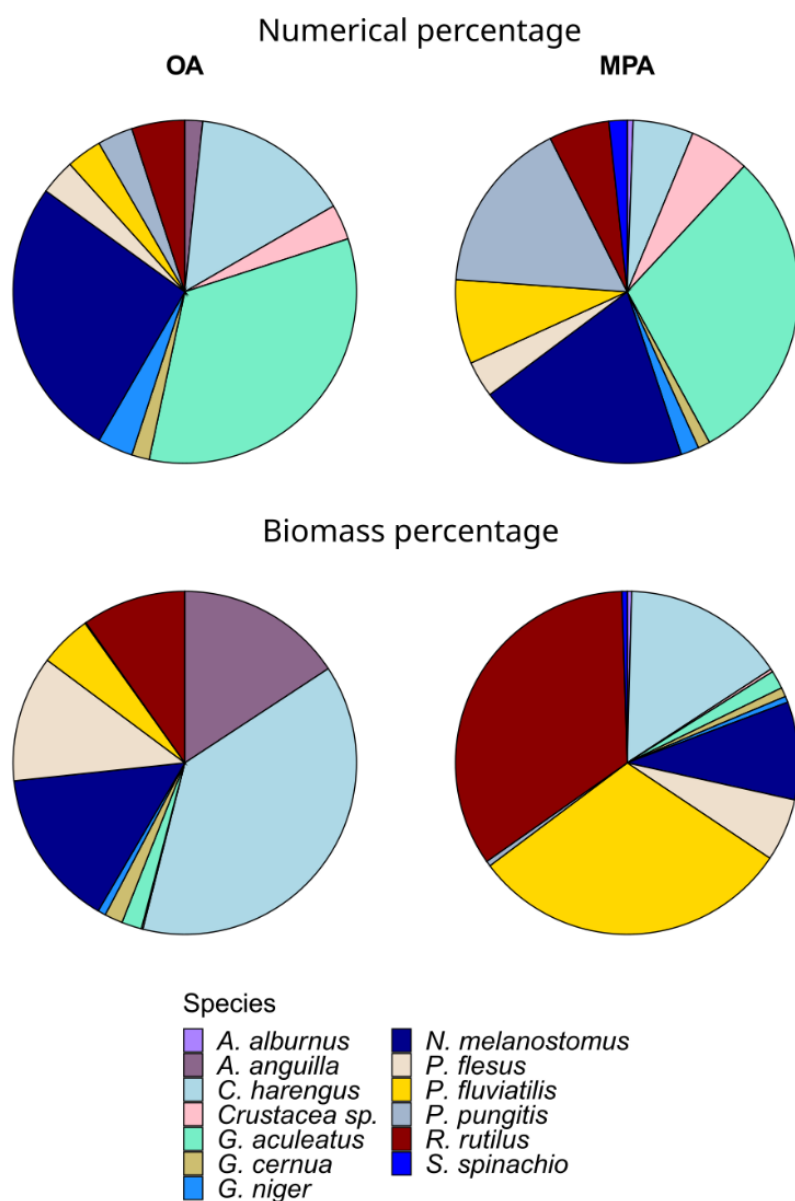


Figure 32. Pie charts representing the numerical and biomass percentages of all prey taxa except unidentified items that were found in the stomachs of northern pike caught by all gears in two protection status (OA: open access area, MPA: marine protected area).

Table 28. Permutation test (999 permutations) outcome showing if a predictor is a significant correlate of the prey species composition (counts: top table, biomass: bottom table) of northern pike caught by all gears as estimated through a permutational MANOVA. The outcome of the permutation test for the predictor variables includes the F-statistic, the degrees of freedom (Df) and the p-value. Significant values are highlighted in bold characters.

Permutational MANOVA	F	Df	p-value
Permutation test: 999 permutations			
Fixed effects			
<u>Counts:</u>			
Protection status	1.289	1	0.255
Area	4.38	2	< 0.001
Season	2.629	2	< 0.01
<u>Biomass:</u>			
Protection status	1.266	1	0.26
Area	3.867	2	< 0.001
Season	2.671	2	< 0.01

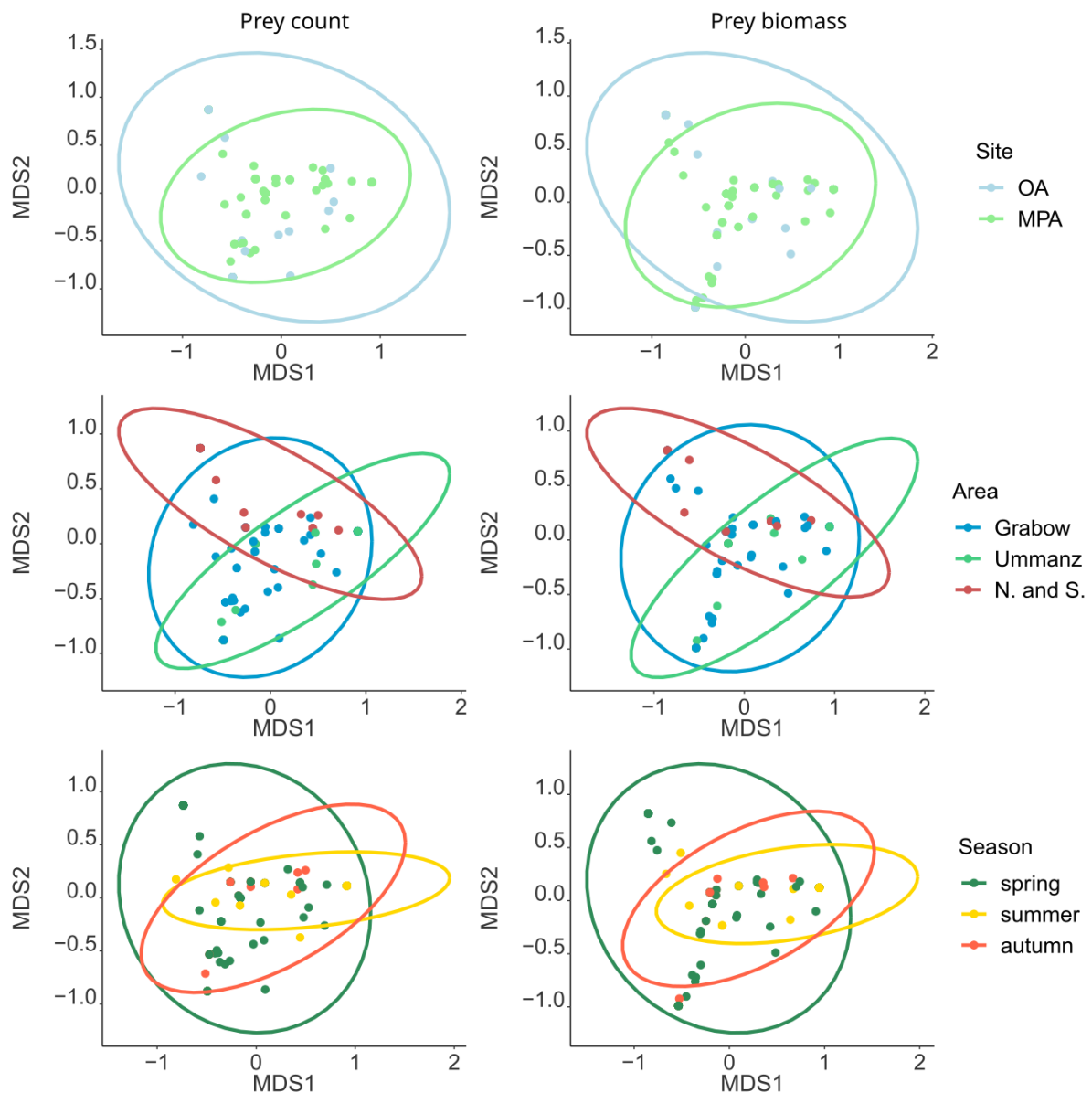


Figure 33. Non-metric multidimensional scaling plots of the digestive tract content composition (prey counts (left) and biomass (right)) of northern pike (points indicate individual fish) caught by all gears. Plots are shown for the protection status (upper graph, OA: open access area, MPA: marine protected area), area (middle graph, N. and S.: Neuensienner- and Selliner See) and season (lower graph). Ellipses represent the 95 % confidence interval. Axis MDS1 and MDS2 represent non-metric Euclidean distances.

3.7.2. Individual specialization

Individual food specialization of 113 northern pike analyzed ranged from 0.004 to 0.69 (mean: 0.19 ± 0.14). None of the predictors was a significant correlate of individual specialization of northern pike (Tab. 29). Rounded means of individual specialization were equal between OAs (mean: 0.19 ± 0.14) and MPAs (mean: 0.19 ± 0.15 , Fig. 34).

Table 29. Wald-test outcome showing if a predictor is a significant correlate of the individual food specialization of northern pike caught by all gears as estimated through a generalized linear mixed model. The outcome of the Wald-test for the predictor variables includes the Wald chi-square statistic, the degrees of freedom (Df) and the p-value. Significant values are highlighted in bold characters.

Generalized linear mixed model	Wald chi-square	Df	p-value
Wald-test results			
Fixed effects / interactions			
Protection status	0.009	1	0.922
Area	2.124	2	0.345
Season	1.641	2	0.441
Protection status : Area	1.325	2	0.515
Protection status : Season	2.491	2	0.287
Area : Season	2.516	4	0.641

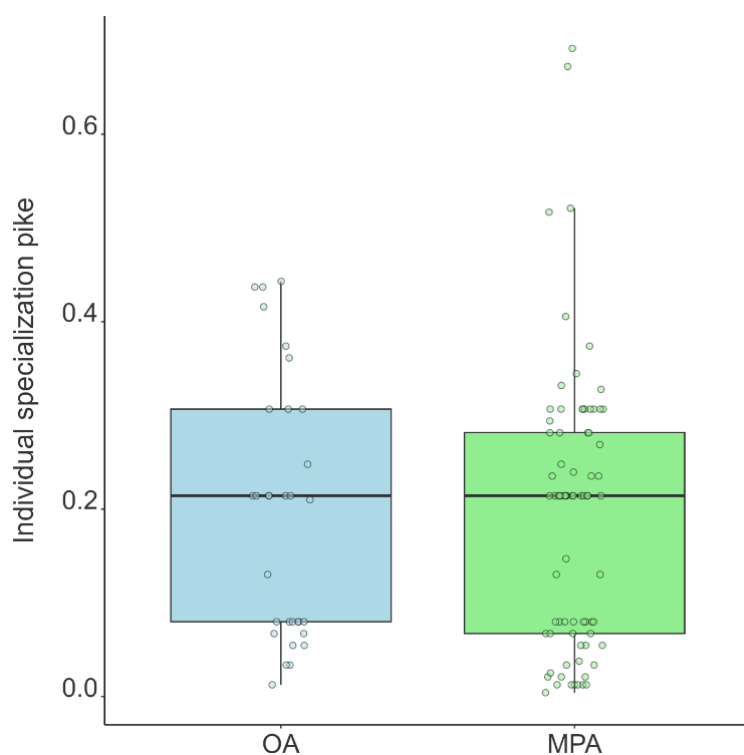


Figure 34. Boxplots (median, box: 25 and 75 percentile, whisker: 10 and 90 percentile) that show how the individual food specialization of northern pike (y-axis) caught by all gears is related to the protection status (OA: open access area, MPA: marine protected area, x- axis). Significant differences between groups (boxplots) are marked as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

4. Discussion

Partially protected areas are the predominant spatial management strategy employed in marine ecosystems globally (Costello and Ballantine 2015). However, the effectiveness of many local MPAs in protecting fish communities and populations from the direct and indirect effects of fishing remains largely unknown. This study assessed the impact of three partially protected areas in German Baltic lagoons on the coastal fish community and four targeted species with varying mobility and value for commercial- and recreational fisheries. Specifically, MPAs, still allowing commercial fishing, were compared to control sites where both commercial- as well as recreational fishing was allowed with respect to composition of fishes, abundances and sizes of targeted fishes and age, growth, physical condition and food composition of one targeted species. Applying this CI design to three seasons within one year, no clear relation between protection and species richness, abundances of mobile species not targeted by recreational fishers, lengths of all four targeted species, age, condition, and food composition could be found. However, fish community composition and total abundance were related to protection. Specifically, less mobile species targeted by recreational fishing showed increased abundances in MPAs compared to the recreationally fished reference sites, a sign of decreased fishing pressure, and northern pike exhibited decreased growth inside the MPAs when compared to OAs. In the following paragraphs these findings will be discussed.

Fish community responses

The hypothesis that species richness would increase in the MPAs compared to OAs was not supported by the results of this study, which is consistent with meta-analysis data analyzing 50 datasets (Soykan and Lewison 2015) and 51 datasets (Sciberras et al. 2013) respectively, where species richness, as well as other indicators of diversity, did not consistently differ between OAs and MPAs. These findings, however, diverge from the consistent trend of higher species richness typically observed in reserves compared to OAs in other meta-analysis studies and studies on reserves in the Baltic Sea (Claudet et al. 2008; Lester et al. 2009; Nelson et al. 2018). However, Nelson et al. (2018) did not statistically test their results and could therefore not reach a strong conclusion. The observed similarity in species richness between OAs and MPAs in the study at hand could have arisen from the lack of complete protection from exploitation (Lester and Halpern 2008). However, even though species richness is commonly used and easy to interpret, it may have limited ability to detect fish community composition changes (Lyashevskaya and Farnsworth 2012; Pillans et al. 2007; Russ 1985). Effects of protection, following the intermediate disturbance hypothesis and community succession theory of Connell (1978), can both increase species richness, if fisheries extensively remove target species in OAs, by promoting coexistence of otherwise competing species or decrease species richness if fishing pressure in the OAs is light to medium (Lester

et al. 2009). Additionally, species richness may also decline in MPAs due to complex trophic interactions following increased predator abundances, consequently reducing abundances of prey species (Graham et al. 2003; Micheli et al. 2004b; Takashina et al. 2012). Therefore, studies have suggested that species richness itself is not a clear indicator for ecosystem or MPA health, condition or effectiveness (Sandin et al. 2008; Soykan and Lewison 2015). The influence of protection on the diversity inside the OAs and MPAs greatly depends on the prior history of exploitation and the local fish communities (Lester et al. 2009). In the research areas of this study the observed similarity of species richness in OAs and MPAs is likely a combined result of ecosystem characteristics and fisheries management. Firstly, as the species richness in the Baltic Sea (Kautsky and Kautsky 2000) as well as in the Bodden (Rittweg et al. 2023b) and the research areas is generally low, differences in species richness are less likely to be detected since the probability of catching different species is lower (Lyashevskaya and Farnsworth 2012). Secondly, all MPAs experienced fishing pressure from a multispecies fishery, which, in theory, should reduce species richness in both areas equally (Lester and Halpern 2008; Sciberras et al. 2013). Lastly, active gears, that may destroy habitats (Auster and Langton 1999) are prohibited, and only non-destructive passive gears are being used. Therefore, species losses in OAs due to habitat destruction as observed by Buhl-Mortensen (2017) are highly unlikely in the Bodden. The species richness of the ecosystem was driven mostly by seasonal changes, with highest values measured in spring for two areas. This can likely be attributed to seasonal spawning migrations of marine species, like Atlantic herring, European smelt and garfish (Thiel et al. 2005; Winkler 1996) into the lagoons in spring, thereby increasing the diversity temporally, while larvae of these species were too small to be captured in the gill nets (Löser 2004). However, as there were only three sporadic samplings conducted in each area throughout the year, these observations may also represent daily variations in species richness within the surveyed areas, because sampled Bodden fish community compositions in the catch may change daily (Fredrich 1975; Pribbernow et al. 1985). This deficiency becomes further evident in relation to the high dependency of the fish community composition on environmental variables, both in this study and in different studies in the Bodden testing dependencies of the fish community composition (Löser 2004; Rittweg et al. 2023b). Fisheries/protection in this study do not explain much of the fish community composition and small differences are likely to be explained by environmental differences inside and outside the protected areas.

In alignment with the suggested hypothesis, the fish community abundance was higher in most MPAs (Grabow, N. and S.) when compared to their related OAs. In a meta-analysis examining the impacts of partially protected areas, this trend emerged as a consistent observation across 51 individual case studies (Sciberras et al. 2013). This total abundance increase and change in fish community composition has also been observed in Baltic Sea reserves and MPAs, for

coastal lagoons and an exclusively marine fish community close to the North Sea (Nelson et al. 2018; Sköld et al. 2022), while the study at hand dominantly captured freshwater species. Even though commercial fishing pressure existed inside the two MPAs, they are therefore effective in protecting the fish community biomass. This finding is in contrast to the results obtained by Lester and Halpern (2008), who observed no discernible impact of MPAs on total biomass in a meta-analysis. Lester and Halpern attributed this lack of effect to the comparison of paired areas reporting data on species that were targeted in both OAs and MPAs. Notably, these abundance results were predominantly observed within the Grabow-area with the highest fishing pressure differences between area-pairs, as well as in the N. and S.-area with the lowest fishing pressure differences due to additional angling pressure inside the MPA. As increased fishing pressure inside MPAs should diminish possible positive effects of protection on the abundances (Zupan et al. 2018), the strong abundance differences between OA and MPA in the N. and S.-area were unexpected. One potential rationale for these disparities may be that the evaluation of fishing pressure may have generated erroneous perceptions regarding the intensity of fishing on particular species within the sites, concealed habitat distinctions that might underlie the variations in species abundances in the areas or the low number of observations and the short time span of the research.

Fish community composition, both in regard to numerical and biomass abundances, was related to protection which was found in a number of other studies in coastal Baltic ecosystems (Bergström et al. 2019; Bergström et al. 2022a; Bergström et al. 2022b; Nelson et al. 2018). This study, however, is the first indication that fishing alters fish communities in the Bodden. As only the recreational fishing pressure differed between OAs and MPAs, the study at hand further indicates that angling can change the fish community composition in the lagoons, which has been concluded in earlier studies in kelp forests and tropical reefs (Colefax et al. 2016; Rhoades et al. 2019). Yet, abundances of the groups categorized as targeted- and non-targeted species did not differ between OAs and MPAs, which contradicted the proposed hypothesis, as increased abundances of target species through lowered mortality and declines of non-target species through trophic feedbacks in MPAs, such as increased predation pressure, are described to be key aspects of protected areas worldwide (Lester et al. 2009; Sciberras et al. 2013). Research in coastal Baltic lagoons in Sweden, resembling the Bodden lagoons, found similar effects in reserves, as proportions of predatory species were not higher in the reserve when compared to a fished area as well as higher prey species abundances in reserves compared to fished areas (Bergström et al. 2022b; Nelson et al. 2018). However, the proportion of predatory fish species sharply declined when the reserves were reopened for fishing. Oppositely, other studies performed in coastal Baltic ecosystems showed higher shares of targeted predatory species in reserves compared to the fished areas (Bergström et al. 2019; Bergström et al. 2022c). Regarding the results presented for harvested species, the

findings are likely caused by a combination of multispecies exploitation in both protection status, removing species relatively unselective in OAs and MPAs alike (Lester and Halpern 2008) and the categorization chosen, which does not separate predatory and non-predatory species. Anglers in the Bodden, however, mostly target predatory species (Weltersbach et al. 2021) and the fishing pressure exerted by this fishery represents the only difference between most area-pairs. Therefore, predatory and prey species, both subject to commercial fisheries in OAs and MPAs, are amalgamated, concealing the variations in predatory species abundance between paired areas. The abundances of the two most significant predatory species in the Bodden, the northern pike and European perch (Weltersbach et al. 2021), were however greatly affected by protection in the study at hand. Notably, each of these predatory species exhibited increased abundances within MPAs compared to OAs, which aligns with prior findings in the Baltic Sea (Bergström et al. 2019; Bergström et al. 2022b). As this study did not categorize species into recreationally and commercially targeted species, no conclusion can be drawn on the effect of additional angling pressure in the OAs, as target species highly overlap for the two groups.

The similar abundances of non-harvested species in MPAs and OAs are seemingly conflicting in the face of increased densities of predatory fish species in MPAs compared to OAs. These findings oppose the assumption that removal of predators through fishing may increase abundances of prey species, due to relaxed predation pressure in OAs (Baum and Worm 2009; Östman et al. 2016) and the adverse effect in MPAs, where increased predator densities may consequently lower prey species abundances (Lester et al. 2009). Yet, equal or even increased abundances of non-harvested species are a common finding in CI studies concentrating on the effect of protection (Micheli et al. 2004b; Sciberras et al. 2013). Higher abundances of non-target species in MPAs compared to OAs can often be attributed to harmful effects of destructive fishing methods (Micheli et al. 2004b). Micheli et al. (2004b) suggested that equal abundances between area-pairs may occur because whole trophic levels/species groups are typically not affected by protection and indirect effects of protection are therefore easily missed because the responses are mostly species specific. As this study did not specifically test the abundances of specific non-targeted species, it cannot be concluded if single species responses may be overshadowed by the categorization, if the non-harvested species were not affected by the observed abundances of only partially protected predators or if environmental variation outweighed any predator-prey effects (Mehner 2010; Noakes et al. 2012). Additionally, Bodden fisheries target many prey species of the opportunistic predators European perch and northern pike (e.g. common roach, Atlantic herring (Couture and Pyle 2015; Jacobson et al. 2019; Koemle et al. 2023; Skov and Nilsson 2018)), which is why some prey species were categorized as harvested species. Therefore, some variation may be covered by the categorization chosen. However, as especially common roach individually did

not show any response to protection, it is likely that prey species generally are not affected by trophic cascades induced by protection in the studied areas. It is further important to name the short-comings of any CI study, in that it cannot be excluded that the effect attributed to protection could be confounded with environmental variables differing between area-pairs not accounted for in this study.

Regardless of the difficult nature of the study of trophic cascades, positive impacts of protection on trophic cascades, such as increasing predator abundances causing declines in planktivorous fish species (mainly three-spined stickleback in the Baltic Sea) consequently decreasing algal blooms which can finally resulted in increased growth of macrophytes or corals were still found in other studies on coral reefs and coastal and open areas of the Baltic Sea (Babcock et al. 2010; Bergström et al. 2019; Casini et al. 2008; Donadi et al. 2017; Eriksson et al. 2009). Turbidity, macrophyte coverage and abundances of three-spined stickleback did not differ between area-pairs in the presented study, even though Baltic European perch and northern pike abundances were higher in MPAs compared to OAs, and northern pike in this study and in earlier studies in the Bodden preyed on three-spined sticklebacks (Jacobson et al. 2019; Winkler 1987). Similar results to partial protection could be observed in another partially protected area in the Baltic Sea, as no definite evidence for trophic cascades in and out of MPAs could be shown (Eklöf et al. 2023). Eklöf et al. (2023) suggested that this may stem from the missing abundance differences of European perch between the area-pairs. As the study at hand found increased European perch abundances in MPAs compared to OAs, partial protected areas in the Baltic Sea may not generate ecosystem-level effects that reduce negative indirect impacts of fishing on eutrophication or even decreased recruitment of predatory species observed coastal Swedish reserves of the Baltic Sea through three-spined stickleback predation on fish larvae (Bergström et al. 2019; Byström et al. 2015; Donadi et al. 2017; Nilsson et al. 2019). It is important to notice, that the negative effects of trophic cascades such as observed in Sweden have not been studied in the Bodden. Therefore, it is unknown whether the studied Bodden food webs are unaffected by partial protection either due to the existing fishing pressure in MPAs or the absence of such trophic cascades in general, as such top-down cascades induced by predator enhancement have been shown to rarely affect lower trophic levels in field studies (Bernes et al. 2015; Mehner 2010).

The environmental variables included in this study explained considerably more variance than protection and it is therefore concluded that they are the prevailing drivers of the fish community with protection only causing small differences. The environmental variables related to fish community composition matched with earlier research studying fish communities in the Bodden and comparable costal parts of the Baltic Sea, specifically areal and seasonal dependencies, as well as changes in relation temperature, salinity and macrophyte coverage

(Fredrich 1975; Löser 2004; Pribbernow et al. 1985; Rittweg et al. 2023b; Snickars et al. 2009; Thiel 1990; Uspenskiy et al. 2022; Winkler et al. 1984). Additionally, the presented study is the first indicator that the reed share is a determinant of fish communities in the Baltic Sea and the Bodden, which so far only has been shown to affect northern pike abundances in Swedish coastal lagoons (Niemi et al. 2023). Unlike Snickars et al. (2009) and Eklöf et al. (2020), this study could not find any relation between the fish community composition and the wave exposure index, which might be attributed to the generally low values measured as all areas were at least to some degree sheltered and no highly exposed area was studied. Additionally, the low number of sites compared might also explain why no influence of the wave exposure on fish communities was found. For the same reason, the general outcome of the fish community composition analysis must be interpreted cautiously because the environmental measurements often had low numbers of observations. If new marine protected areas are planned in the Bodden, future studies should analyze the importance of these variables on the fish community in promoting higher abundances for specific vulnerable species to prioritize areas with important features to maximize the potential benefit of spatial management (Berglund et al. 2012; Hilborn et al. 2022; Kriegl et al. 2021).

It is concluded that the MPAs in the Bodden may positively affect fish community abundances in specific areas and seasons. As differences between areas and seasons always pointed towards higher abundances in the MPAs, it is likely that the additional recreational angling pressure causes a greater depletion of predatory species populations outside the MPAs. However, this research found that the MPAs studied likely have a low effectiveness in protecting the entire fish community and trophic levels themselves, because multi-species fisheries are allowed inside the MPAs, possibly altering fish communities by unselectively removing a range of species. Trophic cascades were not observed, as mostly predatory species increased their abundances within the MPAs while non-harvested and harvested prey species did not increase their abundances in OAs, but their presence cannot be refuted.

The whole fish community assessment only occurred 3 times in one year in each area and the results therefore have to be carefully interpreted since the fish community composition in the Bodden is highly plastic and can fluctuate seasonally and even daily (Fredrich 1975; Löser 2004; Pribbernow et al. 1985). Additionally, the results presented here just reflect the fish community responses for one year. As fishing pressure and gears used by the fisheries as well as the environment could change in the OAs and MPAs over time, the effectiveness of the studied MPAs could vary substantially (Babcock et al. 2010). Further, gillnets are a selective gear, mostly targeting active, fast moving and spiny species (Backiel and Welcomme 1980; Hamley 1975; Kurkilahti 1999). The observed fish community composition may therefore not represent the actual composition because sedentary species, like round gobies (Ray and Corkum 2001), are underrepresented when compared to beach seine hauls in the studied

areas in the same year (Rittweg et al. 2023b). All fish community responses could be biased by environmental differences between OAs and MPAs that were not accounted for and represent the typical drawback of CI studies, even if three area-pairs were included. Additionally, this study only tried to account for fishing mortality between the area-pairs by including a fishing effort measurement. However, decreased boat traffic and increased abundances of fishes inside reserves and MPAs may attract natural predators such as grey seals (*Halichoerus grypus*, FABRICUS 1791) and great cormorants (*Phalacrocorax carbo*, L. 1758) which can diminish the benefits of the exclusion of fishing mortality (Arlinghaus et al. 2021; Bergström et al. 2022b; Bergström et al. 2022c; Bergström et al. 2022d). Seals and cormorants have been observed in most of the areas studied, but as no measurements of potential predation pressure were conducted, this study is not able to derive inferences on whether natural mortality affected the results of this study. Future studies in the Bodden should increase the amounts of observations with additional sampling gears and consider continuous samplings efforts throughout several years, to not only increase the resolution of the fish community responses to protection but also to study the effects on future problems such as climate change on the effectiveness of the MPAs (Babcock et al. 2010; Reusch et al. 2018). Further, it is recommended to measure the effects of natural mortality by predators on the fish communities inside Bodden-MPAs to ensure the long term effectivity of these sites in the face of rising numbers of avian and mammalian predators (Hansson et al. 2018).

Fish population responses

This study demonstrates the effectiveness of the partial protection provided by the Bodden-MPAs in safeguarding fish species characterized by low to moderate mobility and subject to added angling pressure in OAs, which elevates their mortality due to recreational fishing, as indicated by Lewin et al. 2006. This is evident in the observed higher numerical and biomass abundances of European perch and northern pike within MPAs, suggesting a mortality reduction within these protected areas. This is in alignment with the hypothesis proposed as the increase of abundances of targeted species in MPAs is one of the major predictions of MPA literature (Alós and Arlinghaus 2013; Lester and Halpern 2008; Lewin et al. 2006; Sciberras et al. 2013; Westera et al. 2003). Earlier studies on European perch (Bergström et al. 2019; Bergström et al. 2022c; de Moraes et al. 2023) and northern pike (Bergström et al. 2022b; Bergström et al. 2022c; Bergström et al. 2016b; Edgren 2005) in Swedish lagoons and a Czech reservoir comparing reserves with fished reference areas found 3 – 7 times higher abundances of European perch and 2 – 4 times higher abundances of northern pike in reserves compared to references areas. One Swedish study found opposite result for European perch in reserves with higher abundances in the OA, but these abundances differences are most likely linked to differences between the compared areas other than fishing pressure differences (Nelson et al.

2018). The only MPA CI comparison on European perch and northern pike in the Baltic Sea found 2.5 times higher catch rates of northern pike in the MPA, partially protected by seasonal closures, compared to the OA (Eklöf et al. 2023). European perch catch rates in that previous study were not affected by the partial protection. Even though the MPAs of the Bodden presented in this study mostly only controlled for recreational fishing pressure the relative abundance differences between OAs and MPAs for these predatory species were equal or even higher compared to reserves in freshwater and brackish-water ecosystems, which strengthens the conclusion that these MPAs are contributing to the recovery of recreationally targeted species. It is however important to notice that the actual fishing pressure in the OAs of this study and the literature cited did not measure the total mortality in the OAs and in the case of partial protection, in the MPAs. Consequently, it's challenging to make direct comparisons between different studies when assessing the relative differences in species abundance between reserves/MPAs and OAs. This difficulty arises because of the lack of comprehensive understanding of the extent of the direct fishing-related impacts in these reference sites. As recreational fisheries accounts for about half of the total catch of northern pike in the Bodden (Van Gemert et al. 2022), the fishing pressure on this species is considerable and protection from it showed to improve the abundances. For European perch no fishing mortality data are available, but as they are among the main target species of anglers in the Bodden (Weltersbach et al. 2021), equal effects of recreational fishing on this species can be hypothesized which seems to be corroborated by higher abundances found in MPAs compared to OAs.

The defined fishing effort differences among area-pairs did not explain the extent of the abundance differences between OA and MPAs for European perch and northern pike. Except for European perch biomass, the trends of increased abundances were similar in the area-pairs. Only the Ummanz-area did not show higher biomass abundances in the MPA compared to the OA. As it was classified as an area with medium fishing pressure and recreational fishing was banned, this result was unexpected (Lewin et al. 2006; Zupan et al. 2018). It cannot be concluded if the findings were driven by unaccounted fishing pressure or habitat differences between the OA and MPA. As the N. and S.-area did not exclude recreational fishing and was hypothesized to have the smallest fishing pressure differences between OA and MPA of all studied area-pairs, the increased biomass abundances in this area-pair were also unexpected (Zupan et al. 2018). Higher biomass abundances of European perch in the N. and S.-MPA could therefore just reflect habitat preferences of this species. As European perch were shown to exhibit a high mobility and comparably large seasonal migrations in the Bodden and other Baltic ecosystems (Henking 1923; Järv 2000) biomass differences between the two OAs and MPAs in certain seasons may be linked to migration. The MPAs could potentially present primary migration targets. Yet, the findings could have also been linked to seasonal changes

in fishing pressure (Harmelin et al. 1995; Seytre and Francour 2009) and could indicate that the migrating populations are quickly diminished in the OAs upon arrival. Yet, higher European perch abundances were found in two different and unrelated MPAs compared to their OAs in most of the seasons studied and northern pike abundances were almost exclusively related to protection. Therefore, this study still is a strong indicator for the effective protection offered by the spatial protection.

Neither European perch nor northern pike size was higher in MPAs compared to OAs, which opposed the suggested hypothesis. Larger sizes of harvested species are a typical finding in marine reserves compared to OAs (Baskett and Barnett 2015; Lester et al. 2009). Oppositely, larger sizes of targeted species in MPAs compared to OAs are less common (Lester and Halpern 2008; Sciberras et al. 2013; Zupan et al. 2018). Similar effects were observed in European perch and northern pike populations in Baltic lagoons in Sweden, as they were larger in reserves compared to OAs (Berggren et al. 2022; Bergström et al. 2019) but no such findings could be observed in MPAs, partially regulating recreational fishing effort, compared to OAs (Eklöf et al. 2023). Given the increased fishing effort outside the MPAs measured in the study at hand, the presented results oppose the general effect of size selective marine fishing reducing the lengths of target species (Jennings and Kaiser 1998). However, as mostly only recreational fishing pressure varied between the area-pairs these results may relate to the specific characteristics of angling in the Bodden. Anglers targeting trophy fishes typically release larger fishes (Sutton 2003) and a high share of anglers targeting predatory species in the Bodden is considered a trophy angler type (Koemle et al. 2021; Koemle et al. 2022) resulting in release rates higher than 50 % for European perch and about 60 - 73 % for northern pike (Arlinghaus et al. 2023d; Arlinghaus et al. 2021). As the release of large northern pike may maintain a natural size structure of targeted populations (Ahrens et al. 2020; Gwinn et al. 2015), northern pike sizes could potentially be unaffected by the additional recreational fishing pressure in the OAs due to the release of large individuals, while densities are still affected due to the harvest of medium sized individuals. Another explanation for the observed size equality between OAs and MPAs could be related to the potential mobility of the studied species. The predatory species studied were at least partially mobile (Dhellemmes et al. 2023b; Henking 1923; Saulamo and Neuman 2002), which potentially is also reflected by the observed seasonality of the sizes of the predatory species in the study at hand. Space use of many freshwater species, such as northern pike is expected to allometrically scale (Minns 1995; Rosten et al. 2016). It is therefore possible that larger individuals within the MPAs are more vulnerable to passive fishing gear and cross MPA borders more often, therefore increasing the risk of capture and consequently causing equal sizes in OAs and MPAs. Generally, northern pike tagged in the MPAs of this study have been recaptured in the OAs (Arlinghaus et al. 2023c), which supports this hypothesis. However, in the Bodden, body size

only scaled positive on a between lagoon level, meaning larger individuals traversed more between lagoons, while in a given lagoons only larger males use more space (Dhellemmes et al. 2023a). Additionally, larger northern pike were found to be more sedentary in the Grabow-area and therefore more likely to be protected by areal protection, while no such relation was found in the Ummanz-area (Arlinghaus et al. 2023c). No studies on size-specific space use of European perch in the Bodden are available. The influence of size-dependent mobility of northern pike and European perch to diminish higher body sizes in MPAs therefore needs further research to reach definite conclusions. An alternative explanation for the undetected size differences between OAs and MPAs could be related to increased compensatory growth rate of individuals in OAs due to reduced intraspecific competition (Hilborn and Walters 2013; Lizaso et al. 2000; Rose et al. 2001), possibly resulting in fast growing individuals, which may compensate for the increased size selective mortality in the fished areas. As the study at hand showed that northern pike grew faster in the OAs compared to the MPAs, compensatory growth could be a plausible explanation for the absence of size differences between OAs and MPAs. It is also possible that one or more of the proposed interpretations are interacting to cause similar sized predatory fish in OAs and MPAs.

As the age of northern pike was only significantly higher in the Ummanz-MPA compared to the OA, the hypothesis, that this targeted species would generally show higher ages in the MPAs due to decreased mortality (Baskett and Barnett 2015; Taylor and McIlwain 2010), could only be partially supported by the results. The findings in the Ummanz-area are in alignment with earlier research on northern pike, showing higher ages in reserves compared to OAs (Berggren et al. 2022). However, since the ages did only differ between one area-pair, the relation between protection and higher ages does not commonly show in the Bodden MPAs and therefore might be only related to environmental or fisheries specific characteristics of the Ummanz-MPA. As size and age are generally correlated (Morgan 1987; Von Bertalanffy 1938), the practice of catch-and-release of larger / older northern pike could prevent the populations decline in age in response to increased recreational fishing pressure. Additionally, migrations of fish from the MPAs into OAs may hinder the formation of natural age structures in the MPAs due to a lack of protection for mobile species (Pilyugin et al. 2016). As the Ummanz-MPA provides a large, partially isolated area, it is possible that the effectivity in protecting northern pikes was highest (Edgar et al. 2014a), even though fishing pressure differences between the OA and MPA were only moderate. Higher ages but absent size differences in the Ummanz-MPA compared to the OA, could be explained by the slower growth of northern pike inside the MPAs.

The general areal and seasonal differences in the size of European perch as well as the size and age of northern pike, which were mostly higher in spring, hints towards the migration of larger and older individuals into the lagoons during spawning. These spawning migrations for

European perch and northern pike have been observed in many coastal Baltic Sea lagoons (Jacobsen et al. 2017; Karaas and Lehtonen 1993; Karas 1996; Skovrind et al. 2013; Westerborn et al. 2023) and for northern pikes in the Bodden (Dhellemmes et al. 2023b).

Regarding the mobile and mostly commercially targeted species common roach and common bream, the abundance as well as size analysis indicate that the MPAs are not effective in protecting these species from the direct effects of commercial fishing. No consistent patterns that showed higher abundances or sizes in MPAs compared to OAs existed. While in particular areas or seasons some differences between OAs and MPAs were observed, in other areas or seasons opposite or no differences in abundances and sizes could be shown. It is likely that these differences were therefore driven by site specific characteristics rather than fishing pressure. These findings coincide with popular MPA literature since the MPAs studied only create the illusion of protecting these species (Agardy et al. 2011). The MPAs are still being targeted by commercial fisheries inside and outside the MPAs equally, diminishing possible effects of protection (Denny and Babcock 2004; Piet and Rijnsdorp 1998). Additionally, the high mobility of these cyprinid species and the small size and connectivity of the MPAs may result in individuals regularly crossing the borders of the MPAs (Baade and Fredrich 1998; Brodersen et al. 2008; Henking 1923; Skov et al. 2011; Skov et al. 2008; Winter et al. 2021). Yet, as there is no additional fishing pressure observed in the OAs for these cyprinid species, it is unlikely that mobility caused the presented results. The high value of cyprinids for commercial fishers and consequent high mortality makes it very likely that direct effects of fishing could be observed if commercial fishing was excluded from large areas of the Bodden (Koemle et al. 2023; Repecka 1999). However, studies in reserves and MPAs mostly find no effect or negative effects of protection on these cyprinids (Bergström et al. 2019; de Moraes et al. 2023; Nelson et al. 2018), which is often attributed to increased piscivorous fish abundances inside the MPAs. Therefore, another possible explanation for equal abundances and sizes in the studied OAs and MPAs might be the increased predation pressure of European perch and northern pike on the cyprinids. These predatory species can greatly reduce abundances of cyprinids in lakes and potentially the Baltic Sea (Bergström et al. 2019; Jeppesen et al. 2012). However, only common roach were found in the stomachs of northern pike and common bream mean size captured in the Bodden is too large to be eaten by European perch and smaller individuals of northern pike. Therefore, only predation on common roach may have decreased the abundances potentially gained due to protection.

Seasonal fluctuations in the different areas of the abundances and lengths of the common roach and bream were the prominent drivers in this study, with the highest abundances and lengths mostly occurring in spring. As adults of both species perform spawning migrations during spring into shallow lagoons (Aro 2002; Hansson et al. 2019; Thiel et al. 2005; Winkler 1996), the pattern observed can be attributed to seasonal migrations inside the lagoons.

This study could not reach definite conclusions on whether the mobility or the value to commercial- or recreational fisheries of a species did determine the outcome of protection / fishing on the four species tested. However, European perch also represent a potentially mobile species (Saulamo and Neuman 2002) and abundance increases of this species have been found in the MPAs compared to the OAs. Hence, one might infer that the absence of discernible protection effects on the sizes of predatory species and the abundances and sizes of cyprinid species could be attributed to the uniformity of commercial fishing pressure on all four species between OAs and MPAs. It can therefore be concluded that protection from recreational fishing regularly increases the abundances of European perch and northern pike in many reserves and even in MPAs in the Baltic Sea lagoons (Bergström et al. 2019; Bergström et al. 2022b; Bergström et al. 2022c; Eklöf et al. 2023) and that the investigated MPAs mostly are effective in protecting abundances of these predatory species. As previous studies found similar effects, especially northern pike and to some extent also European perch may present suitable research species to study the effect of protection on population recovery from direct effects of fishing, as they are both targeted by angling and/or show low – moderate mobility. In the face of declining stocks of northern pike and local stocks of European perch in the Baltic Sea (Bergström et al. 2022d; Järv 2002; Olsson 2019; Olsson et al. 2023; Van Gemert et al. 2022; Winkler and Debus 2006), the MPAs in the Bodden present an effective management tool in protecting these keystone species, even if open for commercial fishing. However, as there is currently no quota for these low – moderate mobility species for commercial fishers, there is a high risk of local overfishing in the Bodden MPAs (Dhellemmes et al. 2023b; Koemle et al. 2023). The MPAs must therefore not be seen as the ultimate solution to the declines of these species as the effect of commercial fishing pressure inside the MPAs could not be assessed in this study due to the lack of no-take reserves in the Bodden. Common roach and bream are only theoretically protected in these MPAs, if recreational fishers would start to target these species more frequently. Under current conditions, the MPAs cannot generate the effects associated with protection for cyprinids because fishing pressures are equal between OAs and MPAs. As this may be coupled with their mobility, it can be assumed that many other mobile species, especially migratory marine species, like Atlantic herring, sea trout or Atlantic cod (Berkström et al. 2021), should not benefit from these small MPAs. Yet, the current stock of cyprinid species is not assessed but earlier studies in the Bodden found stable commercial catches over several decades (Winkler 1989; Winkler 2002) and even tendencies of increasing population numbers in Swedish Baltic ecosystems (Bergström et al. 2016a). Hence, there is probably no need to protect these species with spatial management at present, but it is important to assess the current local stocks to fully justify this statement. The shortcomings of the fish population analysis were the limited sampling days for European perch, the CI design shortcomings discussed in the fish community section of this discussion,

the unknown real fishing effort in the areas and the biased sampling methods. The scientific angling trials to estimate northern pike abundances may have produced biases, because angling induced timidity or reduced activity in OAs could have caused lower angling catch rates in these sites (Arlinghaus et al. 2018; Arlinghaus et al. 2017), therefore creating the illusion of low abundances. As this hook-avoidance behavior has been observed in northern pike experimentally (Lucas et al. 2023), in field studies (Monk et al. 2021) and in the Bodden (Braun et al. 2023), the catch rates were likely affected by the timidity syndrome to some extent and do not represent actual abundances.

Life-history responses

Indirect effects of fisheries or protection have been observed to be just as common and of similar magnitude as direct effects (Babcock et al. 2010). However, these indirect changes only occur if direct effects cause an absolute increase in abundance or biomass of targeted species. Northern pike showed direct decreases of abundances in relation to additional recreational fishing pressure in the OAs when compared to MPAs. Therefore, it was unexpected to find no differences in physical condition, prey choice and specialization between OAs and MPAs, because the increased northern pike densities in MPAs should experience higher intraspecific competition over resources (Lizaso et al. 2000). The observations were further not affected by the differing fishing pressures among areas. The available literature on physical condition and food choice is scarce and mostly inconclusive, even in reserves (Fagín 2015; Lloret and Planes 2003; Loury et al. 2015; Nelson et al. 2018), where highest densities of conspecifics are expected (Lester and Halpern 2008). Lizaso et al. (2000) concluded that due to the plasticity of life-history traits, CI study designs fail to detect density-dependence because geographically separated areas may differ regarding their environmental conditions. The question further remains if mobile adult fishes living in marine ecosystems are resource limited. The area studied is open and northern pike can easily migrate to other feeding areas if food sources become limiting. Even though their mobility is generally low in the Bodden (Dhellemmes et al. 2023b) and therefore expected to experience higher intraspecific competition in MPAs (Kramer and Chapman 1999), the OAs and MPAs were generally only a couple of hundred meters apart from each other. The movement of northern pike from MPAs into OAs was observed in a recent acoustic telemetry and catch-recapture experiment (Dhellemmes et al. 2023b; Dhellemmes et al. 2023c; Radinger and Arlinghaus 2023). Consequently, no density-dependent changes in the measured parameters between OAs and MPAs could be explained by northern pike reacting to resource limitations by small scale migrations (Andersen et al. 2008; Kobler et al. 2009). However, also opposite migrations from OAs into MPAs were also observed and prey abundances (fish community abundances) were generally higher in MPAs compared to OAs,

which suggests that food is not a limiting factor in the MPAs. Consequently, it is questionable whether density-dependence is the main reason for the observed results.

In contrast to the findings regarding physical condition and food choice, somatic growth rates were higher in OAs and MPAs, which is in line with the hypothesis proposed, that decreased intraspecific competition in OAs due to the increased removal of conspecifics, would increase this life-history trait. There are many studies pointing towards increased growth rates after the removal of conspecifics due to fishing (Hinz et al. 2017; Lizaso et al. 2000; Lorenzen and Enberg 2002), as the whole surplus production of fishes is based on this assumption (Beverton and Holt 1957). The majority of studies, comparing somatic growth in marine reserves to fished reference areas found increased somatic growth of targeted species inside the reserves (Carbonara et al. 2022; Nelson et al. 2018; Taylor and McIlwain 2010). However, the only published study available on northern pike found no effect of no-take reserves on the growth rate when compared to fished areas (Berggren 2019), attributing this effect to counteractions between increased natural selection in MPAs favoring fast growing fish, while increased intraspecific competition induces slower growth in northern pike (Carlson et al. 2007; Pierce et al. 2003). As four times higher densities of northern pike were found in the MPAs compared to the OAs in the study at hand, it is likely that the growth depression in MPAs is caused by density-dependence and not by selective processes (e.g. fisheries-induced evolution), because density-dependence, if present, is predicted to overshadow the effects of fisheries-induced evolution (Arlinghaus et al. 2009; Eikeset et al. 2016; Evangelista et al. 2020; Heino et al. 2008). As somatic growth is the only life-history trait that measured differences between OAs and MPAs regarding possible increased density dependence and therefore worsened conditions in MPAs, it cannot be concluded with certainty that density-dependence plays a significant role in the MPAs of the Bodden. Discrepancies between findings of condition, diet and growth measurements are a common result of studies on juvenile and adult fish species (Fonseca and Cabral 2007; Hoey and McCormick 2004; Koizumi et al. 2018; Molony and Sheaves 1998; Suthers 1998) and the indices therefore have to be interpreted separately in the light of their individual characteristics. As physical condition, HSI, prey choice and food specialization represent “snapshots” of an individual’s daily, weekly or seasonal changes in energy allocation or food choice (Amundsen and Sánchez-Hernández 2019; Miller et al. 2015; Wuenschel et al. 2019), the study at hand showed that during the experiment there were no density-dependent changes between OAs and MPAs. These conclusions find support in the observation that seasonal effects, such as the allocation of energy into gonads during spring for relative condition and the seasonal variations in the composition of prey fish in the study areas, play a significant role in determining both relative condition and prey selection. Since the size-specific somatic growth represents a measurement showing a life-long energy investment (Berggren et al. 2022), the study at hand showed that protection can result in

northern pike populations inside MPAs experiencing increased intraspecific competition and consequent lower somatic growth over a longer time period even in only partially protected areas. Oppositely, the removal of conspecifics in areas open to recreational exploitation lowered the intraspecific competition over limited resources and increased the somatic growth of northern pike.

Yet, these results must be interpreted cautiously because of the individual drawbacks of each index. Relative condition, HSI and stomach content analysis itself have been criticized to be misleading and produce incorrect conclusion: in the case of relative condition regarding its assumption that the slopes of all samples being compared are equivalent to a particular predetermined value (Cone 1989), in the case of HSI because it mostly relates to seasonal changes in energy allocation (Wuenschel et al. 2019) and for stomach content analysis itself because it only represents a “snapshot” of an individual’s recent diet and overestimation of slowly digested prey being a common bias (Amundsen and Sánchez-Hernández 2019). Additionally, the low observations in HSI and high numbers of terms in the size-specific growth model did not allow testing interactions which could have explained underlying variance. Lastly, the values and means of the size-specific growth values should not be taken as the actual growth rates of the observed areas, as the results showed unrealistically high somatic growth values, even if the somatic growth of northern pike in the Bodden is generally higher compared to other habitats worldwide (Rittweg et al. 2023a). The values are inconsistent with previous research on the growth of northern pike (Berggren et al. 2022; Diana 1983; Rypel 2012). While there is a likelihood of bias in the scale readings, the uniformity of this bias's impact on both OAs and MPAs lends support to the validity of the conclusion pertaining to the influence of protection measures on somatic growth. Future studies should test targeted fish populations between OAs and MPAs mostly regarding methods describing longer time frames of energy allocation and food choice, because all short-term methods did not find any suspected evidence of density-dependence in this study and earlier studies (Fagín 2015; Lloret and Planes 2003; Loury et al. 2015; Nelson et al. 2018). Such measurements should include the somatic growth and possible stable isotope analysis of muscle tissue or hard structures of fish for food choice to depict a longer time period (Church 2012; Wainright et al. 1993).

5. Conclusion and management implications

The present study shows the high relevance of protection from recreational angling on sedentary predatory species targeted by anglers in the Bodden, while mobile cyprinid species mostly targeted by commercial fishing do not benefit from the protection from recreational fishing. Given that population declines within the investigated species have exclusively manifested in the predatory species northern pike and European perch (Bergström et al. 2022d; Järv 2002; Olsson 2019; Olsson et al. 2023; Van Gemert et al. 2022; Winkler and

Debus 2006), it can be deduced that the Bodden-MPAs, irrespective of their particular management strategies, exhibit effectiveness in safeguarding the abundance of the most vulnerable species within the fish community. Recreational fishing can present a threat to targeted species, significantly reducing their abundances (Lewin et al. 2006) and is believed to be an anthropogenic pressure altering fish populations in many, especially Scandinavian, coastal Baltic ecosystems (Bergström et al. 2022d; Hyder et al. 2018; Olsson et al. 2023; Van Gemert et al. 2022). Therefore, the current management provides conservation benefits for recreationally targeted species and fisheries management benefits by not displacing commercial fishers (Agardy et al. 2011).

Density-dependent spill-over of adults from the Bodden-MPAs into the OAs (Abesamis and Russ 2005; Di Lorenzo et al. 2020) was observed for northern pike, but so was the opposite migration from OAs into MPAs (Arlinghaus et al. 2023c). The commercial exploitation inside the MPAs hinders northern pike and probably also other species affected by the commercial fisheries, from reaching their carrying capacity (Lizaso et al. 2000). Further, the study at hand provided only limited support for increased intra-specific competition inside the MPAs. Therefore, while spill-over was observed in the Bodden, the reasons might not be density related and rather reflect the insufficient size and connection of the MPAs (Arlinghaus et al. 2023c).

The present study is constrained in its capacity to draw definitive conclusions regarding the sufficiency of Bodden-MPAs in halting the ongoing declines of the northern pike in the Bodden (Olsson et al. 2023; Van Gemert et al. 2022) and any potential future declines of fish species influenced by exploitation. This limitation arises from the uncertainty surrounding actual fisheries-induced mortality in both OAs and MPAs, as well as the recognition that relative differences in abundances between OAs and MPAs do not necessarily provide a definitive measure of the health of the population sizes in these locations. BACI studies are necessary to reach a more precise conclusion on the effectiveness of the MPAs in protecting the whole fish community and targeted species, because they rule out environmental baseline differences between the compared OAs and MPAs. This approach holds particular promise when considering the establishment of reserves within the Bodden, as it is only within such reserves that an unexploited community and populations of targeted species can be observed, allowing for the definition of the baseline characteristics of an unexploited community/population and to also measure the effect of commercial fishing on the fish communities. Currently only less than 1 % of the Bodden surface area is protected from all forms of fishing and around 30 % of the area is partially protected, while there is little connectivity between the often small protected areas (Niessner et al. 2023a). The home ranges of many endemic species targeted by Bodden-fisheries are too large to be totally protected by the size of the current MPAs (Arlinghaus et al. 2023c; Berkström et al. 2021). Generally,

increased size and connectivity and decreased or absent fishing pressure in the MPAs would generate higher potential conservation benefits for the fish community, completely protecting their populations even during migrations to spawning or feeding habitats (Berkström et al. 2021; Lester and Halpern 2008; Sciberras et al. 2013), that could have potentially caused the observed ineffectiveness of the MPAs in protecting the sizes and ages of the targeted species in the study at hand. Therefore, the institutions managing the MPAs must define their aims regarding the protection of fishes. If the aim is mainly conservation related, the optimal solution would be the creation of large, connected no-take reserves. If the aim is to support the commercial and recreational fishing sector, while still providing smaller conservation benefits, different strategies could be chosen. As the current management provides benefits for both conservation and commercial fisheries, the status quo is a reasonable option. Yet, it has to be stated that the exclusion of only recreational fishing from the MPAs has the potential to cause conflicts among commercial and recreational fishers, as it is perceived as unfair by anglers (Arlinghaus et al. 2022b; Slaton et al. 2023). This phenomenon becomes apparent in light of the majority of recreational fishers expressing their disapproval of permitting fishing activities from artisanal sector within the Bodden MPAs, as indicated in a recent survey (Arlinghaus et al. 2023b). Further, most anglers fish the Bodden in the hopes of catching large trophy northern pike (Arlinghaus et al. 2023d). As the current stock is growth overfished (Van Gemert et al. 2022), northern pike may not reach the desired sizes anymore. It may therefore be recommended to not only create or manage MPAs that prohibit angling, but to design a connected web of MPAs that include no-take MPAs and MPAs excluding either commercial- or recreational fisheries to provide environmentally as well as socially sustainable spatial protection. As both commercial as well as recreational fishers in a recent survey voted for 18 – 20 % of the Bodden to be covered by no-take reserves and generally agree with the benefits of these areas (Arlinghaus et al. 2023b), there is a high potential for the management institutions to develop new protected areas or connections between areas. But as there are tensions among Bodden fisheries and conservation (Arlinghaus et al. 2022a), this process has to include adaptive management to include the local user groups in the management process to reach a sustainable design (Cánovas-Molina and García-Frapolli 2020; de Oliveira Júnior et al. 2021; Pomeroy et al. 2007).

The MPAs in the Bodden only protect the analyzed fish communities and populations from the direct and indirect effects of exploitation. Yet, many declines of specific species, such as northern pike, are currently also driven by problems such as climate change, loss of spawning and juvenile habitats, predation from seals, cormorants and three-spined stickleback as well as decreased abundances of prey species (Arlinghaus and Ehrlich 2023; Olin et al. 2022; Reusch et al. 2018). Therefore, spatial management should only be seen as a complementary

management tool, while habitat and predator management should be included to aid the recovery of fish communities and populations.

The intricate interplay between fisheries and environmental factors, as they impact fish communities, demographic traits, and individual life-history traits, continues to challenge researchers. While disentangling these effects remains a complex endeavor, the present study aligns with previous research in its ability to observe the direct demographic changes induced by fisheries. Yet, the complex nature of the indirect effects of fishing persists, yielding results that are less unequivocal. Nevertheless, this study underscores the value of spatial management as a practical and effective tool for safeguarding fish communities and populations. By shedding light on these multifaceted interactions, this study contributes to the ongoing effort to balance the exploitation of the oceans with the conservation of their biodiversity. Moving forward, this research could guide and inform sustainable practices that benefit both the environment and the livelihoods of those dependent on aquatic ecosystems.

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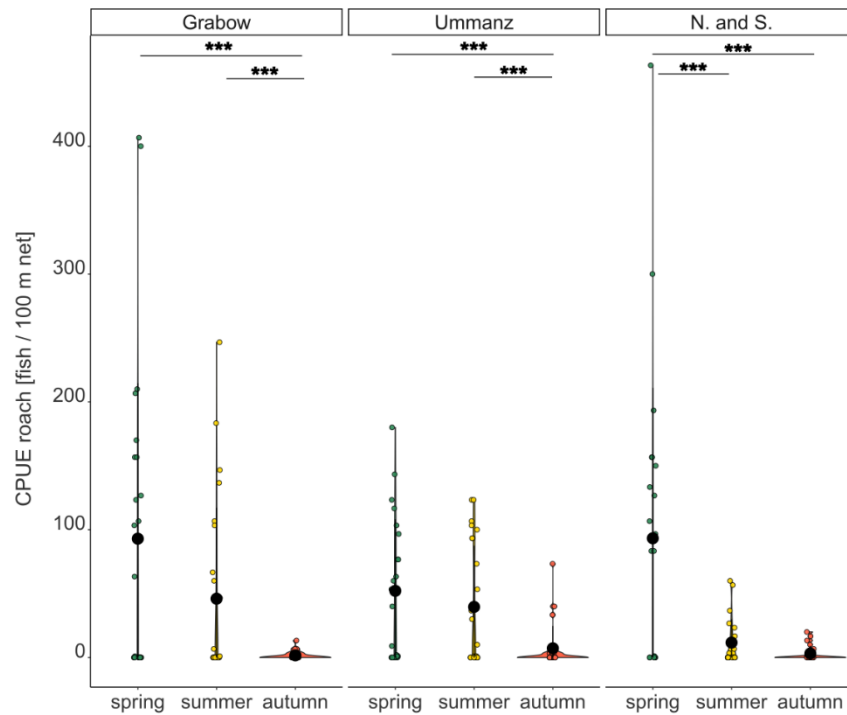
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Appendix



Appendix 1. Violin plots (black dot: mean, whisker: standard deviation) that show how the catch-per-unit-effort (CPUE, fish / 100 m benthic and pike multi-nesh gillnet) of common roach is related to the interaction of area (N. and S. = Neuensiener and Selliner See, upper labels) and season (x- axis). Significant differences between groups are marked as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Appendix 2. Pairwise test results calculated by estimated marginal means for the relative biomass of common roach. The table includes the contrast, which in this case is the comparison between areas, the site, season, estimate, standard error (SE), degrees of freedom (DF, Inf: number > 10000), z-ratio and the p-value (green color indicates that the first name of the contrast-pair has the significantly higher values, red color indicates that the second name of the contrast-pair has the significantly higher values).

Contrast	Season	Site	Estimate	SE	DF	z-ratio	p-value
N. and S. - Ummanz	autumn	MPA	0.14140984	0.62239185	Inf	0.22720388	1
N. and S. - Grabow	autumn	MPA	4.0237412	1.10153487	Inf	3.65284958	< 0.01
Ummanz - Grabow	autumn	MPA	3.88233136	1.07621487	Inf	3.60739427	< 0.01
N. and S. - Ummanz	autumn	OA	0.14005108	0.59903605	Inf	0.23379408	1
N. and S. - Grabow	autumn	OA	0.01351817	0.58021396	Inf	0.02329859	1
Ummanz - Grabow	autumn	OA	-0.12653291	0.49293875	Inf	-0.2566909	1
N. and S. - Ummanz	spring	MPA	-0.42759538	0.41996201	Inf	-1.0181763	0.9929391
N. and S. - Grabow	spring	MPA	0.32357312	0.45237961	Inf	0.71526902	0.99976757
Ummanz - Grabow	spring	MPA	0.7511685	0.44230984	Inf	1.69828576	0.74434453
N. and S. - Ummanz	spring	OA	0.02368034	0.42098863	Inf	0.05624935	1
N. and S. - Grabow	spring	OA	0.63996121	0.43447603	Inf	1.4729494	0.88322044
Ummanz - Grabow	spring	OA	0.61628087	0.42060153	Inf	1.46523688	0.88695232
N. and S. - Ummanz	summer	MPA	-2.81018946	0.48053625	Inf	-5.8480278	< 0.001
N. and S. - Grabow	summer	MPA	-2.53695473	0.48354299	Inf	-5.2465960	< 0.001
Ummanz - Grabow	summer	MPA	0.27323473	0.43537925	Inf	0.62757867	0.99994144
N. and S. - Ummanz	summer	OA	-1.73614046	0.46997185	Inf	-3.6941375	< 0.01
N. and S. - Grabow	summer	OA	-1.09199947	0.54663151	Inf	-1.9976884	0.5069641
Ummanz - Grabow	summer	OA	0.64414099	0.50298687	Inf	1.28063182	0.95457963

Appendix 3. Pairwise test results calculated by estimated marginal means for the relative biomass of common roaches. The table includes the contrast, which in this case is the comparison between seasons, the site, area, estimate, standard error (SE), degrees of freedom (DF, Inf: number > 10000), z-ratio and the p-value (green color indicates that the first name of the contrast-pair has the significantly higher values, red color indicates that the second name of the contrast-pair has the significantly higher values).

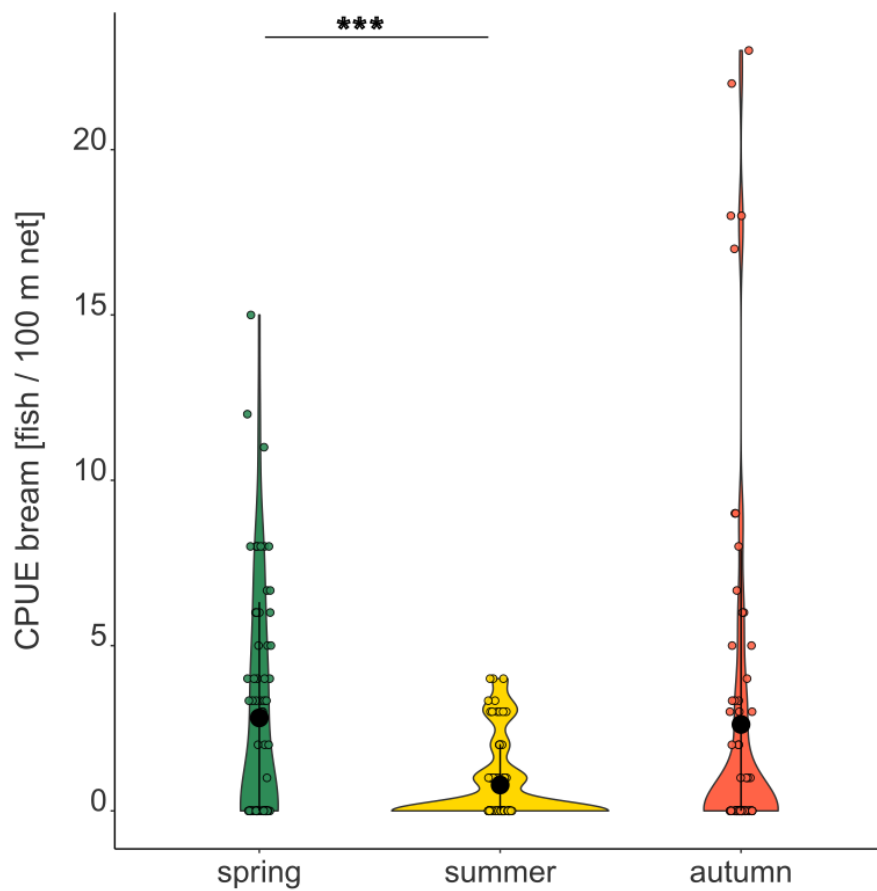
contrast	Area	Site	estimate	SE	df	z-ratio	p-value
autumn - spring	N. and S.	MPA	-2.16338347	0.56203717	Inf	-3.84918221	< 0.01
autumn - summer	N. and S.	MPA	1.37581599	0.59700133	Inf	2.30454428	0.28234648
spring - summer	N. and S.	MPA	3.53919946	0.47934678	Inf	7.38338007	< 0.001
autumn - spring	N. and S.	OA	-2.11747816	0.5586499	Inf	-3.79034912	< 0.01
autumn - summer	N. and S.	OA	0.8859922	0.59982102	Inf	1.47709429	0.87948777
spring - summer	N. and S.	OA	3.00347036	0.47729666	Inf	6.29266992	< 0.001
autumn - spring	Ummanz	MPA	-2.73238869	0.50175493	Inf	-5.44566383	< 0.001
autumn - summer	Ummanz	MPA	-1.57578331	0.51168042	Inf	-3.07962401	< 0.05
spring - summer	Ummanz	MPA	1.15660538	0.41620194	Inf	2.77895242	0.08483458
autumn - spring	Ummanz	OA	-2.2338489	0.46509871	Inf	-4.8029566	< 0.001
autumn - summer	Ummanz	OA	-0.99019934	0.46913545	Inf	-2.11068965	0.41548114
spring - summer	Ummanz	OA	1.24364957	0.40782784	Inf	3.04944747	< 0.05
autumn - spring	Grabow	MPA	-5.86355154	1.05003288	Inf	-5.58415996	< 0.001
autumn - summer	Grabow	MPA	-5.18487993	1.05531558	Inf	-4.91310847	< 0.001
spring - summer	Grabow	MPA	0.67867161	0.45670893	Inf	1.4860047	0.87500002
autumn - spring	Grabow	OA	-1.49103512	0.45325866	Inf	-3.28958993	< 0.05
autumn - summer	Grabow	OA	-0.21952543	0.52526381	Inf	-0.4179337	0.99999934
spring - summer	Grabow	OA	1.27150969	0.51041399	Inf	2.49113406	0.18319101

Appendix 4. Pairwise test results calculated by estimated marginal means for the total length of common roach. The table includes the contrast, which in this case is the comparison between areas, the site, season, estimate, standard error (SE), degrees of freedom (DF, Inf: number > 10000), z-ratio and the p-value (green color indicates that the first name of the contrast-pair has the significantly higher values, red color indicates that the second name of the contrast-pair has the significantly higher values).

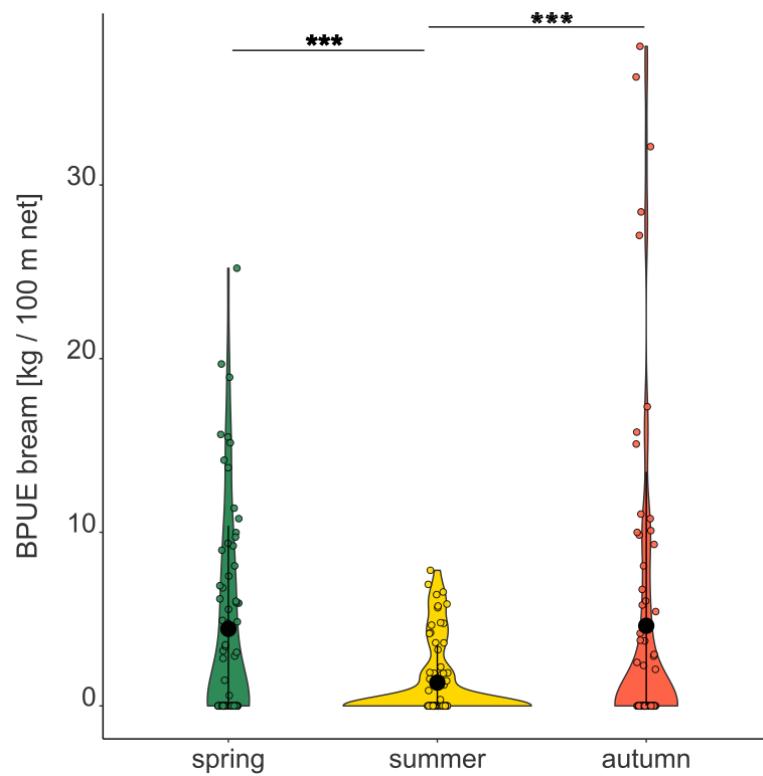
Contrast	Season	Site	estimate	SE	DF	t-ratio	p-value
Grabow - N. and S.	autumn	MPA	-33.5	57.0794061	2428	-0.5869016	0.99996924
Grabow - Ummanz	autumn	MPA	-30.88	55.9261679	2428	-0.5521565	0.99998419
N. and S. - Ummanz	autumn	MPA	2.62	19.259217	2428	0.13603876	1
Grabow - N. and S.	spring	MPA	-31.413368	4.35848634	2428	-7.2074031	< 0.001
Grabow - Ummanz	spring	MPA	-89.769792	4.8795207	2428	-18.397256	< 0.001
N. and S. - Ummanz	spring	MPA	-58.356422	5.37057394	2428	-10.865956	< 0.001
Grabow - N. and S.	summer	MPA	11.3959523	12.4716404	2428	0.91374927	0.99719087
Grabow - Ummanz	summer	MPA	-27.438172	5.45999377	2428	-5.0253120	< 0.001
N. and S. - Ummanz	summer	MPA	-38.834121	12.6769985	2428	-3.0633538	< 0.05
Grabow - N. and S.	autumn	OA	101.160535	22.6189825	2428	4.47237335	< 0.001
Grabow - Ummanz	autumn	OA	98.5050505	19.6160684	2428	5.02165106	< 0.001
N. and S. - Ummanz	autumn	OA	-2.6554848	18.6976328	2428	-0.1420229	1
Grabow - N. and S.	spring	OA	11.1073137	4.56861915	2428	2.43121899	0.20881886
Grabow - Ummanz	spring	OA	-65.415634	5.4396927	2428	-12.025612	< 0.001
N. and S. - Ummanz	spring	OA	-76.522952	4.99869284	2428	-15.308596	< 0.001
Grabow - N. and S.	summer	OA	6.70886838	9.35391409	2428	0.71722578	0.99974241
Grabow - Ummanz	summer	OA	-36.549392	7.70465052	2428	-4.7438092	< 0.001
N. and S. - Ummanz	summer	OA	-43.258260	8.9036204	2428	-4.8585023	< 0.001

Appendix 5. Pairwise test results calculated by estimated marginal means for the total length of common roach. The table includes the contrast, which in this case is the comparison between seasons, the site, area, estimate, standard error (SE), degrees of freedom (Inf: number > 10000), z-ratio and the p-value (green color indicates that the first name of the contrast-pair has the significantly higher values, red color indicates that the second name of the contrast-pair has the significantly higher values).

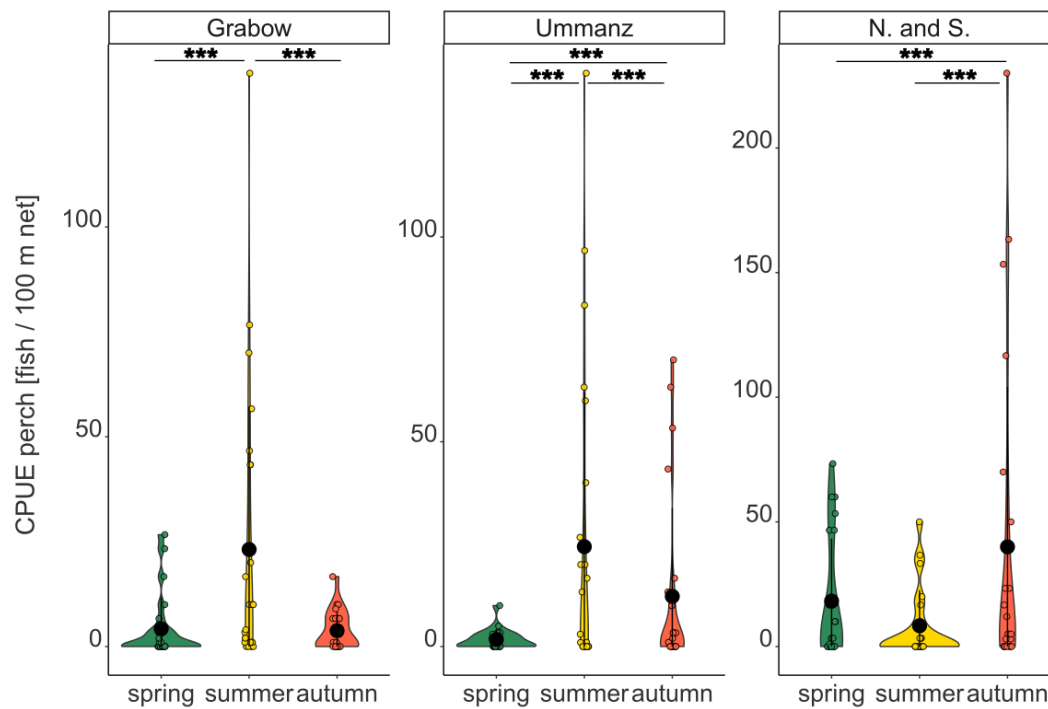
Contrast	Area	Site	Estimate	SE	DF	t-ratio	p-value
autumn - spring	Grabow	MPA	10.0712644	54.903118	2428	0.18343702	1
autumn - summer	Grabow	MPA	2.17547624	54.9524263	2428.00002	0.03958836	1
spring - summer	Grabow	MPA	-7.8957881	4.3868096	2428.00357	-1.7998935	0.64047
autumn - spring	N. and S.	MPA	12.1578964	16.2081043	2428.00025	0.75011218	0.99951644
autumn - summer	N. and S.	MPA	47.0714286	19.8451823	2428	2.37193229	0.22679479
spring - summer	N. and S.	MPA	34.9135322	12.4617061	2428.00042	2.80166552	0.0732276
autumn - spring	Ummanz	MPA	-48.818527	11.712968	2428.09841	-4.1679041	< 0.001
autumn - summer	Ummanz	MPA	5.61730351	11.7385039	2428.001	0.47853658	0.99999608
spring - summer	Ummanz	MPA	54.4358314	5.84760325	2428.30132	9.30908425	< 0.001
autumn - spring	Grabow	OA	94.095138	16.9160314	2428.00026	5.56248306	< 0.001
autumn - summer	Grabow	OA	120.536261	17.5269782	2428	6.87718442	< 0.001
spring - summer	Grabow	OA	26.4411235	6.82202643	2428.00158	3.87584595	< 0.001
autumn - spring	N. and S.	OA	4.04191687	15.6876922	2428.34363	0.25764891	1
autumn - summer	N. and S.	OA	26.0845951	17.0856406	2428.30412	1.52669693	0.83752362
spring - summer	N. and S.	OA	22.0426782	7.86349774	2428.00048	2.80316456	0.07289055
autumn - spring	Ummanz	OA	-69.825550	11.3256136	2428.00893	-6.1652775	< 0.001
autumn - summer	Ummanz	OA	-14.518181	11.7028549	2428.00856	-1.2405677	0.95780632
spring - summer	Ummanz	OA	55.3073698	6.50293109	2428	8.50499091	< 0.001



Appendix 6. Violin plots (black dot: mean, whisker: standard deviation) that show how the catch-per-unit-effort (CPUE, fish / 100 m benthic and pike multi-mesh gillnet) of common bream is related to the season (x- axis). Significant differences between groups are marked as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.



Appendix 7. Violin plots (black dot: mean, whisker: standard deviation) that show how the biomass-per-unit-effort (BPUE, kg / 100 m benthic and pike multi-nesh gillnet) of common bream is related to the season (x- axis). Significant differences between groups are marked as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.



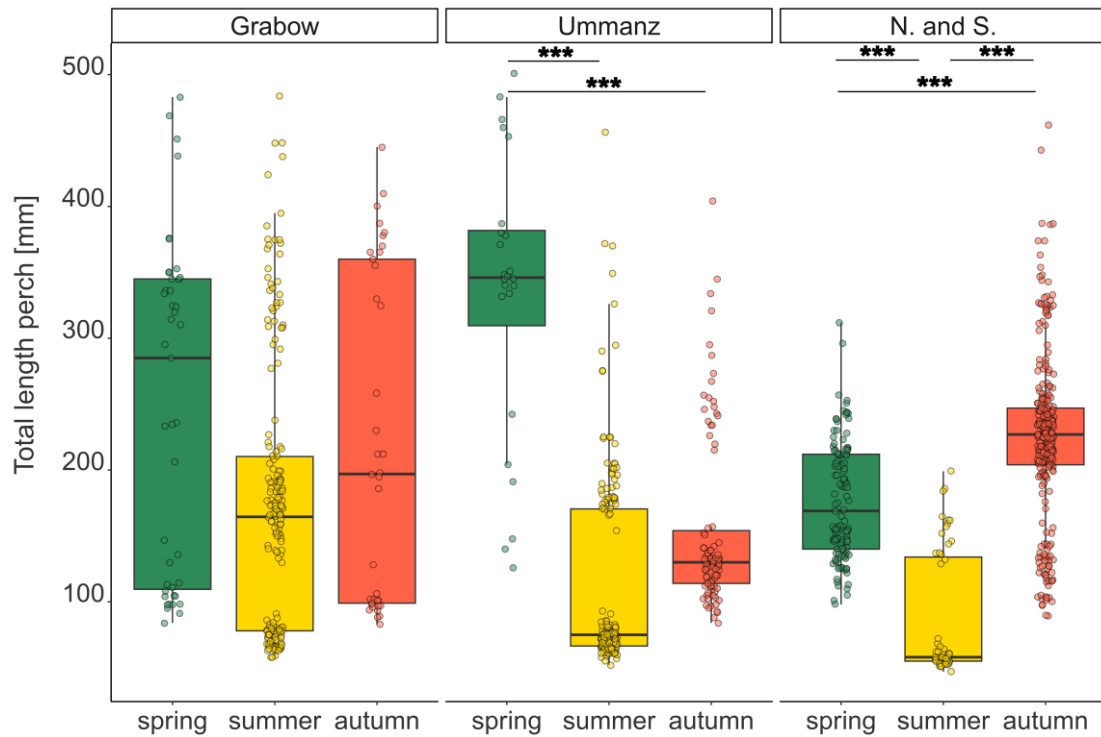
Appendix 8. Violin plots (black dot: mean, whisker: standard deviation) that show how the catch-per-unit-effort (CPUE, fish / 100 m benthic and pike multi-nesh gillnet) of European perch is related to the interaction of area (N. and S. = Neuensiener and Selliner See, upper labels) and season (x- axis). Significant differences between groups are marked as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Appendix 9. Pairwise test results calculated by estimated marginal means for the relative biomass of European perch. The table includes the contrast, which in this case is the comparison between areas, the site, season, estimate, standard error (SE), degrees of freedom (Inf: number > 10000), z-ratio and the p-value (green color indicates that the first name of the contrast-pair has the significantly higher values, red color indicates that the second name of the contrast-pair has the significantly higher values).

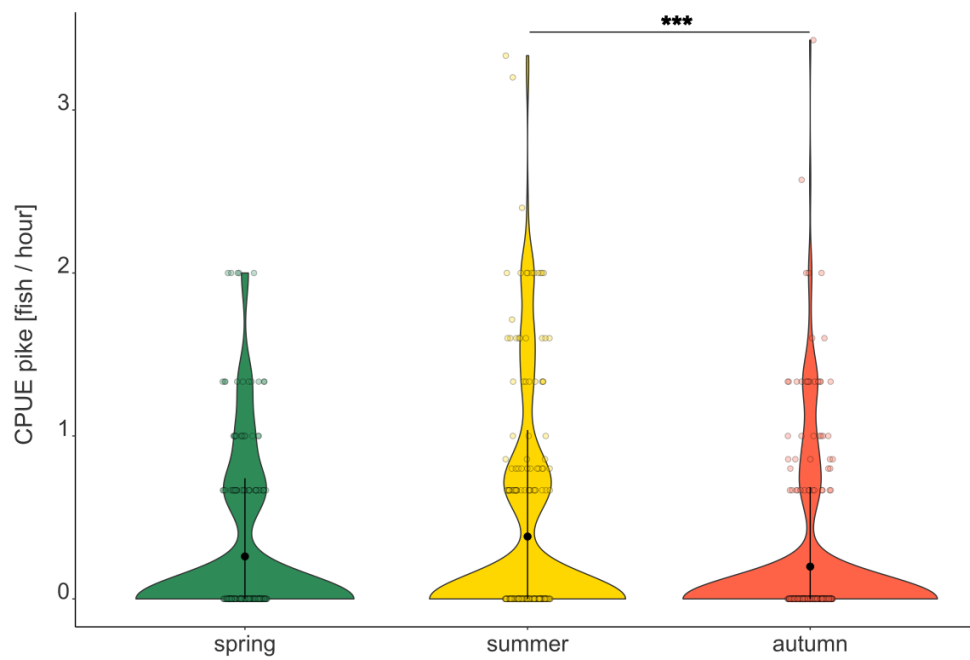
Contrast	Season	Site	Estimate	SE	DF	z-ratio	p-value
N. and S. - Ummanz	autumn	MPA	1.65560442	0.49322038	Inf	3.35672349	< 0.05
N. and S. - Grabow	autumn	MPA	2.1048465	0.45147134	Inf	4.66219294	< 0.001
Ummanz - Grabow	autumn	MPA	0.44924208	0.52490611	Inf	0.85585226	0.99861911
N. and S. - Ummanz	autumn	OA	1.61702969	0.55415014	Inf	2.91803533	0.05697589
N. and S. - Grabow	autumn	OA	2.34418919	0.58910132	Inf	3.97926317	< 0.001
Ummanz - Grabow	autumn	OA	0.72715949	0.52582651	Inf	1.38288861	0.9229198
N. and S. - Ummanz	spring	MPA	0.93145036	0.56896738	Inf	1.63708921	0.7885565
N. and S. - Grabow	spring	MPA	0.57439585	0.4788603	Inf	1.19950611	0.97266164
Ummanz - Grabow	spring	MPA	-0.3570545	0.53222114	Inf	-0.67087622	0.99988365
N. and S. - Ummanz	spring	OA	-1.4791788	0.54223121	Inf	-2.72794848	0.09935423
N. and S. - Grabow	spring	OA	2.35446717	0.82300979	Inf	2.86080094	0.06768602
Ummanz - Grabow	spring	OA	3.83364597	0.80832957	Inf	4.7426769	< 0.001
N. and S. - Ummanz	summer	MPA	-1.1282544	0.56224444	Inf	-2.00669735	0.50098837
N. and S. - Grabow	summer	MPA	-2.3439327	0.48699621	Inf	-4.81304095	< 0.001
Ummanz - Grabow	summer	MPA	-1.2156782	0.48608617	Inf	-2.50095221	0.18103699
N. and S. - Ummanz	summer	OA	-3.0045621	0.60152042	Inf	-4.99494618	< 0.001
N. and S. - Grabow	summer	OA	-2.3140766	0.60160257	Inf	-3.8465206	< 0.01
Ummanz - Grabow	summer	OA	0.69048543	0.48610016	Inf	1.42045918	0.90798005

Appendix 10. Pairwise test results calculated by estimated marginal means for the relative biomass of European perch. The table includes the contrast, which in this case is the comparison between seasons, the site, area, estimate, standard error (SE), degrees of freedom (Inf: number > 10000), z-ratio and the p-value (green color indicates that the first name of the contrast-pair has the significantly higher values, red color indicates that the second name of the contrast-pair has the significantly higher values).

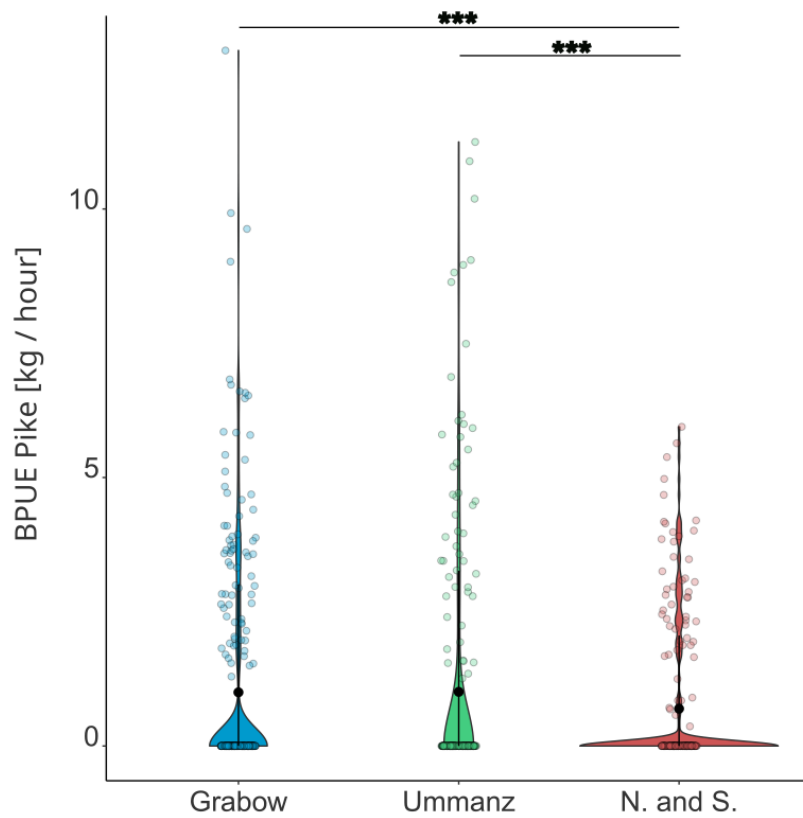
Contrast	Area	Site	Estimate	SE	DF	z-ratio	p-value
autumn - spring	N. and S.	MPA	1.06940762	0.46975382	Inf	2.27652778	0.30406279
autumn - summer	N. and S.	MPA	3.25970905	0.49425298	Inf	6.59522388	6.9361E-10
spring - summer	N. and S.	MPA	2.19030144	0.54165358	Inf	4.04373114	0.00092477
autumn - spring	N. and S.	OA	2.76031712	0.58984349	Inf	4.67974498	5.0421E-05
autumn - summer	N. and S.	OA	3.76240277	0.6576792	Inf	5.72072643	1.8497E-07
spring - summer	N. and S.	OA	1.00208565	0.63464482	Inf	1.57897081	0.82672388
autumn - spring	Ummanz	MPA	0.34525355	0.58849	Inf	0.58667701	0.9999727
autumn - summer	Ummanz	MPA	0.4758502	0.56133796	Inf	0.84770715	0.99875453
spring - summer	Ummanz	MPA	0.13059665	0.58860277	Inf	0.2218757	1
autumn - spring	Ummanz	OA	-0.3358913	0.50317366	Inf	-0.66754562	0.99989085
autumn - summer	Ummanz	OA	-0.8591890	0.48617132	Inf	-1.7672557	0.69494246
spring - summer	Ummanz	OA	-0.5232976	0.50300124	Inf	-1.04035065	0.99167685
autumn - spring	Grabow	MPA	-0.46104304	0.46093898	Inf	-1.00022576	0.99412437
autumn - summer	Grabow	MPA	-1.18907015	0.44351513	Inf	-2.68101375	0.11355487
spring - summer	Grabow	MPA	-0.7280271	0.41603329	Inf	-1.74992517	0.70824751
autumn - spring	Grabow	OA	2.7705951	0.82249525	Inf	3.36852412	0.01289847
autumn - summer	Grabow	OA	-0.8958631	0.52576151	Inf	-1.70393437	0.74258489
spring - summer	Grabow	OA	-3.6664581	0.79797933	Inf	-4.59467816	7.6849E-05



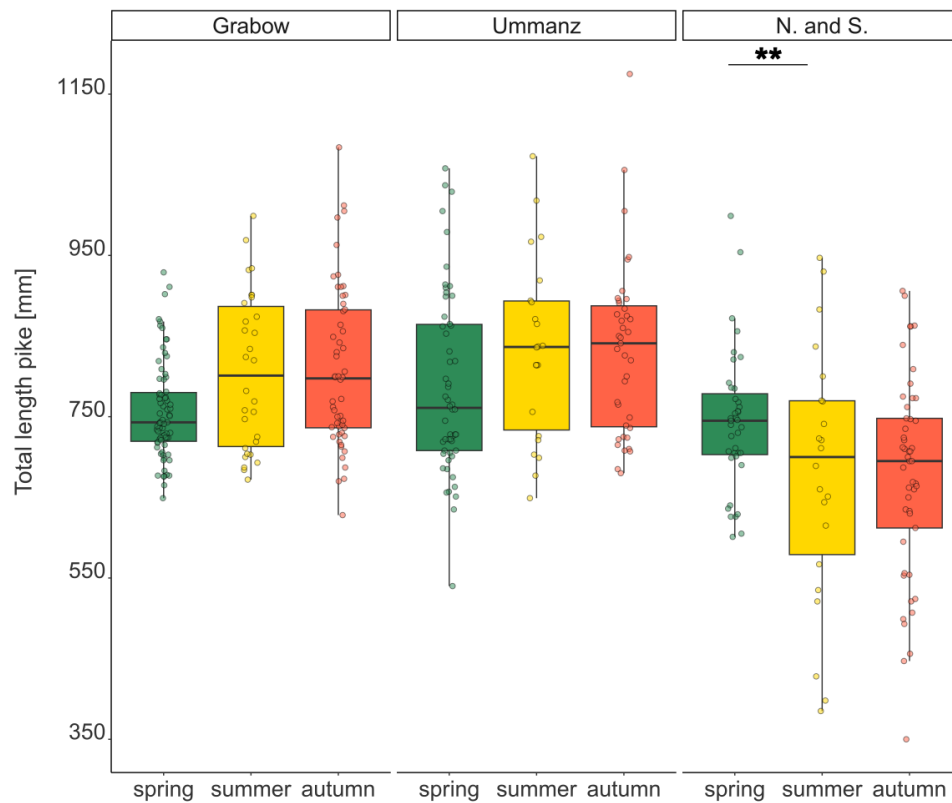
Appendix 11. Boxplots (median, box: 25 and 75 percentile, whisker: 10 and 90 percentile) that show how the total length of European perch (mm, y-axis) is related to the interaction of area (upper labels, N. and S.: Neuensiener- and Seliner See) and season (x-axis). Significant differences between groups (boxplots) are marked as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.



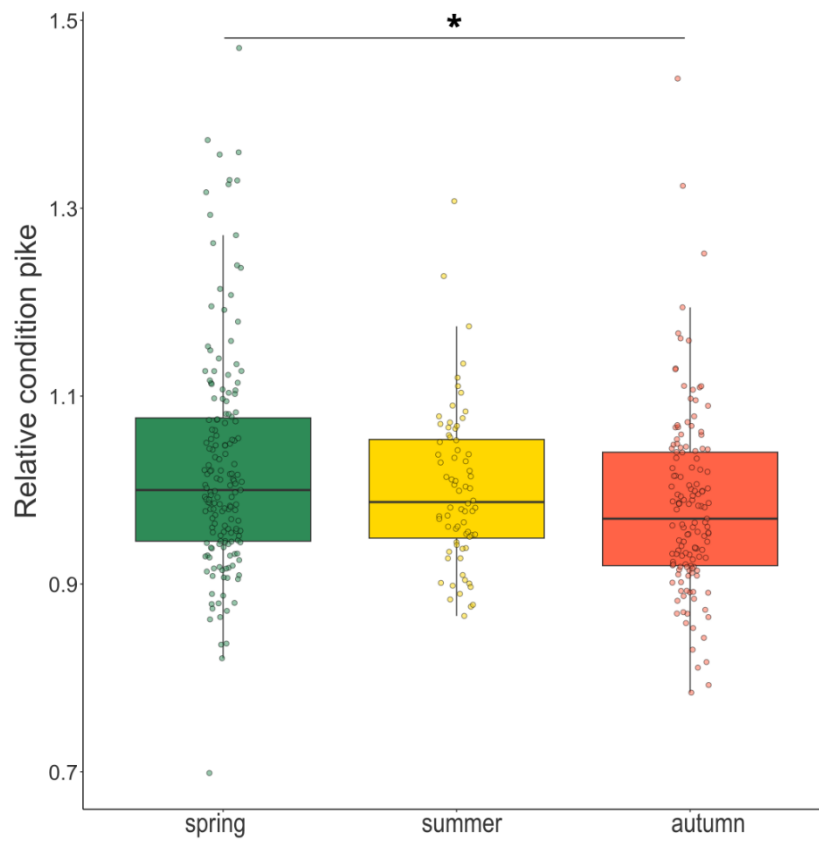
Appendix 12. Violin plots (black dot: mean, whisker: standard deviation) that show how the catch-per-unit-effort (CPUE, fish / hour) of northern pike is related to the season (x- axis). Significant differences between groups are marked as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.



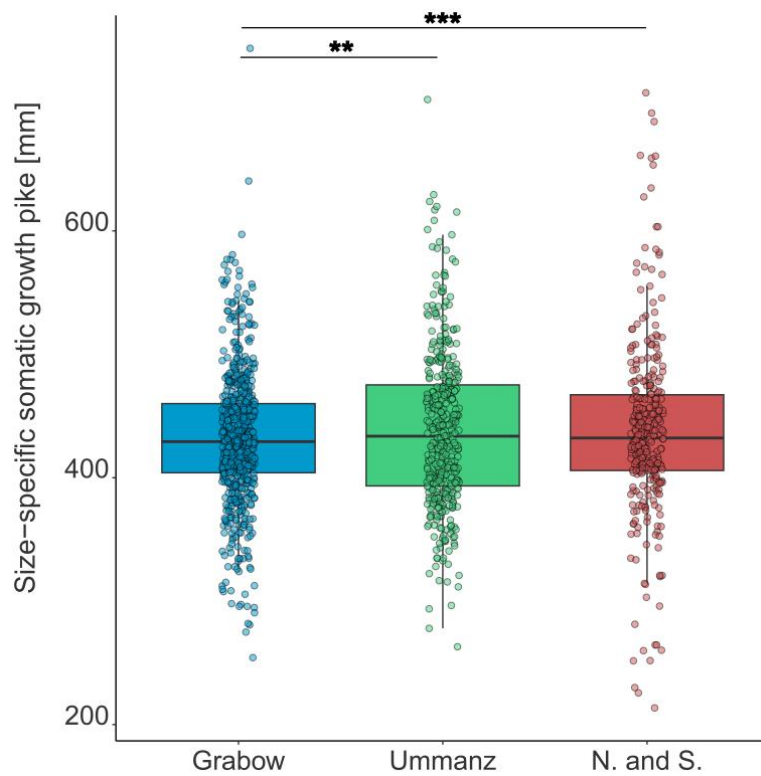
Appendix 13. Violin plots (black dot: mean, whisker: standard deviation) that show how the biomass-per-unit-effort (BPUE, kg / hour) of northern pike is related to the area (N. and S. = Neuensiener and Selliner See, x- axis). Significant differences between groups are marked as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.



Appendix 14. Boxplots (median, box: 25 and 75 percentile, whisker: 10 and 90 percentile) that show how the total length of northern pike (mm, y-axis) is related to the interaction of area (upper labels, N. and S.: Neuensien- and Seliner See) and season (x-axis). Significant differences between groups (boxplots) are marked as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.



Appendix 15. Boxplots (median, box: 25 and 75 percentile, whisker: 10 and 90 percentile) that show how the relative condition of northern pike (y-axis) is related to the seasons (x-axis). Significant differences between groups (boxplots) are marked as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.



Appendix 16. Boxplots (median, box: 25 and 75 percentile, whisker: 10 and 90 percentile) that show how the size-specific somatic growth of northern pike (mm, y-axis) is related to area (N. and S. = Neuensienner and Selliner See, x-axis). Significant differences between groups (boxplots) are marked as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Declaration of originality

I hereby declare that this thesis with the title:

“Fish community composition, size structure and interspecific competition in areas open to exploitation and partially protected from recreational fishing: case studies from brackish lagoons of the southern Baltic Sea, with a focus on northern pike (*Esox lucius*)”

is the result of my own work and that I have indicated all sources including online sources, which have been cited without changes or in modified form especially sources of texts graphics, tables, and pictures.

I confirm that I have not submitted this thesis for any other examination.

I am aware that in case of any breach of these rules procedures concerning plagiarism or attempted plagiarism will be taken in accordance with the subject-specific examination regulations and/or the Allgemeine Satzung zur Regelung von Zulassung. Studium und Prüfung der Humboldt-Universität zu Berlin (ZSP-HU).



Wiederherstellbare Signatur

X 

Marlon Braun

Signiert von: 7056bdce-4919-4718-b02e-b93147b5e614

Berlin, 03.11.2023

Place/Date

Full signature