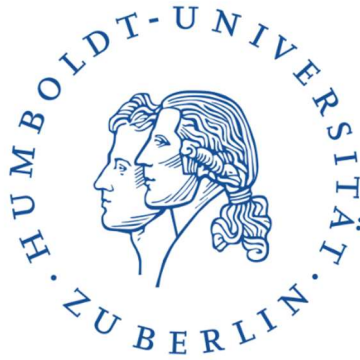




Faculty of Life Sciences

Albrecht Daniel Thaer-Institute for Agricultural and Horticultural Sciences

Examining Evidence for Angling-Induced Timidity in Northern Pike (*Esox lucius* L.): A Case Study from Lagoons in the Southern Baltic Sea

Master's Thesis in the Study Program: Fish Biology, Fisheries & Aquaculture

Submitted by: Phillip Roser
Student ID: 611042
roserphi@hu-berlin.de

1st Examiner: Prof. Dr. Robert Arlinghaus

Division of Integrative Fisheries Management, Albrecht-Daniel-Thaer Institute of Agriculture and Horticulture, Faculty of Life-Sciences, Humboldt-Universität zu Berlin, Germany

Department Fish Biology, Fisheries and Aquaculture, Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB), Berlin, Germany

2nd Examiner: Prof. Dr. Thomas Klefoth

Chair of Ecology and Conservation, Faculty of Nature and Engineering, City University of Applied Sciences, Bremen, Germany

Berlin, 20.10.2023

Contents

List of figures	3
List of tables	8
Glossary and definitions.....	9
Abstract	10
1 Introduction.....	11
2 Methods.....	18
2.1 Description of the study area	18
2.2 Characterization of sampling sites	19
2.3 Fieldwork	26
2.3.1 Monitoring of fishing effort	26
2.3.2 Recording of habitat characteristics.....	27
2.3.3 Angling.....	28
2.3.4 Angling-independent gears	30
2.3.5 Processing of pike.....	33
2.3.6 Aging.....	34
2.3.7 Camera transects.....	34
2.4 Statistical analysis	36
2.4.1 Catch rates of different gears between MPA and OA	36
2.4.2 Evidence for timidity-induced effects on CPUE.....	38
2.4.3 Length and age	40
2.4.4 Growth	41
2.4.5 Proportional stock density	41
2.4.6 Attack rate.....	41
2.4.7 Landing rate	42
2.4.8 Lure-effects on catchability.....	42
2.4.9 Probability of zero catch.....	44
2.4.10 Analysis of recapture data.....	45
3 Results	46

3.1 Descriptives.....	46
3.1.1 Observed fishing effort.....	46
3.1.2 Angling catches.....	46
3.1.3 Gillnet catches	48
3.1.4 eDNA	48
3.1.5 Telemetry.....	50
3.1.6 Camera transects.....	50
3.2 Statistical analysis	51
3.2.1 Catch rates of different gears between MPA and OA	51
3.2.2 Body length, age and growth.....	56
3.2.3 Attack- and landing rate	62
3.2.4 Probability of zero catch	63
3.2.5 Evidence for timidity-induced effects on CPUE.....	65
3.2.6 Lure-effects on catchability.....	67
3.2.7 Analysis of recaptures	71
4 Discussion	73
4.1 Pike abundances between MPA and OA	74
4.2 Body size and growth	76
4.3 Evidence for angling-induced timidity from gear comparisons	79
4.4 Evidence for angling-induced timidity from other metrics	82
4.5 Effects of lure type and color	85
4.6 Recapture probability.....	86
4.7 Overall assessment of angling-induced timidity	87
4.8 Study limitations	88
5 Conclusions and implications for management.....	90
References	92
Acknowledgements.....	108
Appendix	110
Declaration of independence	112

List of figures

FIGURE 1 SCHEMATIC REPRESENTATION OF DIFFERENT RELATIONSHIPS BETWEEN CPUE AND ABUNDANCE, MODIFIED BY CHANGES IN CATCHABILITY.	15
FIGURE 2 EXTENT OF THE BRACKISH LAGOON SYSTEM ON THE BALTIC COAST OF NORTHEAST GERMANY. COLORS VISUALIZE AVERAGE SALINITIES. THE SYSTEM WAS SUBJECT TO PRIOR SAMPLINGS AND THIS DATA IS ALSO USED IN THIS STUDY.	19
FIGURE 3 LOCATIONS AND GEOGRAPHICAL SETTINGS OF THE THREE COMPARISON AREAS SUBJECT TO SAMPLING. PROTECTED SITES (MPA) ARE DISPLAYED AS GREEN POLYGONS, FISHED SITES (OA) AS BLUE POLYGONS. MINT GREEN COLOR DENOTES THE OVERALL EXTENT OF AREAS WITH PROTECTION STATUS.	20
FIGURE 4 BAR PLOTS DISPLAYING THE MACROPHYTE COVERAGES DETERMINED BY VISUAL SURVEYS IN EACH SITE (COLOR) AND ACROSS SEASONS (X-AXIS) IN THE THREE COMPARISON AREAS (HORIZONTAL PANELS).	21
FIGURE 5 LEFT: INTERPOLATED DEPTH MAP OF THE COMPARISON AREA WERDERBUCHT. DEPTH IS DISPLAYED BY A COLOR GRADIENT FROM BLUE (DEEP) TO YELLOW (SHALLOW). OUTLINE COLOR DISPLAYS THE RESPECTIVE SITE. RIGHT: DENSITY PLOT OF DEPTH DATA PER SITE (COLOR). DIAMONDS DISPLAY MEAN DEPTH.	23
FIGURE 6 LEFT: INTERPOLATED DEPTH MAP OF THE COMPARISON AREA UMMANZ. DEPTH IS DISPLAYED BY A COLOR GRADIENT FROM BLUE (DEEP) TO YELLOW (SHALLOW). OUTLINE COLOR DISPLAYS THE RESPECTIVE SITE. RIGHT: RELATIVE FREQUENCY OF INTERPOLATED DEPTH DATA PER SITE (COLOR). MEAN DEPTH IS DISPLAYED BY DIAMONDS.	24
FIGURE 7 LEFT: INTERPOLATED DEPTH MAP OF THE COMPARISON AREA SELLIN WITH THE SMALLER NEUENSIENER SEE (MPA) ON THE LEFT AND THE LARGER SELLINER SEE (OA) ON THE RIGHT. DEPTH IS DISPLAYED BY A COLOR GRADIENT FROM BLUE (DEEP) TO YELLOW (SHALLOW). OUTLINE COLOR DISPLAYS THE RESPECTIVE SITE. RIGHT: RELATIVE FREQUENCY OF INTERPOLATED DEPTH DATA PER SITE (COLOR). MEAN DEPTH IS DISPLAYED BY DIAMONDS.	25
FIGURE 8 ANGLING SAMPLING WITH LURES FROM THE DRIFTING BOAT AT WERDERBUCHT.	28
FIGURE 9 MPA SAMPLING LOCATIONS OF NON-RANDOMIZED ANGLING (RED DOTS). SIZE INDICATES EFFORT, I.E. THE SUM OF INDIVIDUAL ANGLING HOURS. BLACK CIRCLES AROUND THE THREE COMPARISON AREAS WERDERBUCHT, UMMANZ AND NEUENSIENER SEE (MPA OF AREA SELLIN) REPRESENT THE RESPECTIVE SAMPLING EFFORT FROM RANDOMIZED ANGLING TO SET EFFORTS IN RELATION. IN WERDERBUCHT, THE NUMBER OF RANDOM AND NON-RANDOM ANGLING SESSIONS WAS ROUGHLY EQUAL. GREEN POLYGONS DELINEATE AREAS WITH PROTECTION STATUS.	29
FIGURE 10 SETTING OF GILLNETS DURING SUNSET IN THE OA OF WERDERBUCHT IN OCTOBER 2023.	31
FIGURE 11 SAMPLING STEPS OF EDNA SAMPLING. LEFT: TAKING WATER SUBSAMPLE FOR MIXED SAMPLES. RIGHT: FILTERING EDNA FROM MIXED SAMPLE.	32
FIGURE 12 PROCESSING OF A LARGE FEMALE PIKE.	34
FIGURE 13 LURES USED DURING CAMERA TRAWLING: MEPPS GIANT MARABOU BUCKTAIL SPINNER IN BRIGHT YELLOW (LEFT) REPRESENTING A HIGHLY CONSPICUOUS AND UNNATURAL LURE VERSUS	

THE SAVAGE GEAR REAL TROUT IN A NATURAL DESIGN (RIGHT) CONVINCINGLY MIMICKING A REAL PREY.....	35
FIGURE 14 SCHEMATIC DRAWING OF THE SETUP USED FOR LURE TRAWLING.	35
FIGURE 15 CONCEPTUAL DEPICTION OF TIMIDITY AS WITNESSED BY A GEAR*SITE INTERACTION. IF THE DIFFERENCES IN CATCH RATES BETWEEN ANGLING AND ANGLING-INDEPENDENT GEARS ARE PURELY ABUNDANCE DRIVEN, THE SLOPES ARE EXPECTED TO BE SIMILAR BETWEEN GEARS (LEFT PLOT). HOWEVER, IF THERE IS AN ADDITIONAL TIMIDITY EFFECT, THE SLOPE OF ANGLING IS EXPECTED TO BE SIGNIFICANTLY STEEPER THAN THAT OF ANGLING-INDEPENDENT GEARS.....	38
FIGURE 16 LURES FROM STANDARDIZED COLOR COMPARISON. AGGRESSIVE FIRETIGER (LEFT) AND NATURAL RAINBOW TROUT DESIGN (RIGHT).	44
FIGURE 17 OBSERVED FISHING EFFORT IN THE 3 COMPARISON AREAS (HORIZONTAL PANELS) PER SITE (X-AXIS). COLUMNS SHOW THE SUM OF OBSERVATIONS PER CATEGORY ACROSS ALL SAMPLING DAYS. MEAN DAILY VALUES ARE DISPLAYED BY BLACK POINTS. NUMBERS FOR DAILY MEAN $\pm$ SD ARE SHOWN AS TEXT WITHIN EACH FACET. DATA WERE RECORDED BETWEEN APRIL 2022 AND JANUARY 2023.....	46
FIGURE 18 RAW DATA OF eDNA CONCENTRATIONS (COPIES / ML) FOR THE THREE COMPARISON AREAS (COLOR) AND THEIR SITES (X-AXIS) ACROSS THE THREE SEASONS (PANELS). BLACK DOTS REPRESENT MIXED SAMPLES, DISTRIBUTION IS EMPHASIZED BY BOXPLOTS. DIAMONDS DISPLAY MEAN VALUES.....	49
FIGURE 19 FOOTAGE FROM LURE CAMERA TRAWLING. (A) A PIKE FOLLOWING THE BUCKTAIL SPINNER. (B) A LARGE INDIVIDUAL ATTACKING THE RUBBER TROUT. (C) A PIKE WITH GREATER INTEREST IN THE CAMERA THAN IN THE BUCKTAIL SPINNER. (D) SEASONAL DIFFERENCES IN VISIBILITY AND MACROPHYTE ENTANGLEMENT CONTRIBUTED NEGATIVELY TO IDENTIFICATION OF PIKE IN THE VIDEO MATERIAL.	51
FIGURE 20 RAW (TOP ROW) AND PREDICTED (BOTTOM ROW) CPUE (PIKE/H) FROM RANDOMIZED ANGLING SESSIONS FOR EACH AREA (COLOR) AND SITE (X-AXIS) ACROSS THE THREE SAMPLING SEASONS (VERTICAL PANELS). DISTRIBUTION OF RAW DATA IS EMPHASIZED BY VIOLIN PLOTS WITH MEAN VALUES REPRESENTED BY DIAMONDS.	52
FIGURE 21 RAW (TOP ROW) AND PREDICTED (BOTTOM ROW) GILLNET CPUE (PIKE / 100 M NET * 12 H) FROM GILLNET SAMPLING FOR EACH AREA (COLOR) AND SITE (X-AXIS) ACROSS THE THREE SAMPLING SEASONS. DISTRIBUTION OF RAW DATA IS EMPHASIZED BY VIOLIN PLOTS WITH MEAN VALUES REPRESENTED BY DIAMONDS. SHAPE OF RAW DATA POINTS DENOTES THE RESPECTIVE NET-TYPE.	53
FIGURE 22 RAW DATA (TOP ROW) AND PREDICTED VALUES (BOTTOM ROW) FOR TELEMETRY COUNTS. EACH BLACK DOT IN THE RAW DATA REPRESENTS THE NUMBER OF DETECTED PIKE ON ONE SAMPLING DAY. BOXPLOTS (MEDIAN, BOX: 25 AND 75 PERCENTILE, WHISKER: 10 AND 90 PERCENTILE) EMPHASIZE THE DISTRIBUTION OF MEASUREMENTS PER SITE AND AREA, DIAMONDS REPRESENT MEAN VALUES.	54
FIGURE 23 CPUE OF PIKE (PIKE/H) BETWEEN MPA AND OA FROM BOTH RANDOMIZED AND NON-RANDOMIZED ANGLING SAMPLINGS. THE UPPER PANEL DISPLAYS RAW DATA, EACH POINT REPRESENTING ONE INDIVIDUAL ANGLING SESSION FROM ONE SAMPLER. VIOLIN PLOTS	

EMPHASIZE DISTRIBUTION OF RAW DATA, DIAMONDS DISPLAY MEAN VALUES. THE LOWER PANEL DISPLAYS MODEL PREDICTIONS. COLORS REPRESENT SEASONS, SITES ARE SEPARATED ALONG THE X-AXIS.	55
FIGURE 24 DENSITY PLOT OF TOTAL LENGTHS OF PIKE CAPTURED WITH GILLNETS AND DURING RANDOMIZED ANGLING IN THE THREE COMPARISON AREAS (HORIZONTAL PANELS) BETWEEN APRIL 2022 AND JANUARY 2023. COLOR DENOTES THE SITE OF CAPTURE; VERTICAL DOTTED LINES REPRESENT MEAN VALUES.	56
FIGURE 25 DENSITY PLOT OF THE BODY LENGTHS OF PIKE CAPTURED DURING MPA COMPARISON SAMPLING SPLIT UP BY SEASON (Y-AXIS), GEAR (HORIZONTAL PANELS) AND SITE (VERTICAL PANELS). PERCENTAGES ON THE LEFT-HAND SIDES OF EACH PLOT DISPLAY THE SHARE OF FEMALES IN THE CATCH. RESPECTIVE SAMPLE SIZES ARE DENOTED ON THE RIGHT-HAND-SIDE OF EACH PLOT, EMPHASIZED BY SHADE WITH HIGHER SAMPLE SIZES REPRESENTED BY DARKER COLOR. ANGLING DATA CONTAIN FISH FROM BOTH RANDOMIZED AND NON-RANDOMIZED SAMPLINGS CONDUCTED BETWEEN 2021 - 2023.	57
FIGURE 26 RAW (LEFT) AND PREDICTED DATA $\pm$ SE (RIGHT) ON TOTAL BODY LENGTH (MM) OF PIKE CAPTURED WITH DIFFERENT GEARS (COLOR) BETWEEN THE SITES (X-AXIS) IN THE THREE COMPARISON AREAS (HORIZONTAL PANELS). LEFT: BLACK DOTS REPRESENT INDIVIDUALS, BOXPLOTS EMPHASIZE THE DISTRIBUTION. DIAMONDS SHOW MEAN VALUES.	58
FIGURE 27 RAW DATA (LEFT) AND PREDICTIONS (RIGHT) OF PIKE AGE (YEARS) FROM INDIVIDUALS CAPTURED WITH DIFFERENT GEARS (COLOR) IN THE TWO SITES (X-AXIS) IN THE THREE COMPARISON AREAS (HORIZONTAL PANELS). BLACK DOTS IN LEFT PANELS REPRESENT INDIVIDUALS, DISTRIBUTION OF THE DATA IS EMPHASIZED BY BOXPLOTS. DIAMONDS DISPLAY MEAN VALUES. PREDICTED MEANS $\pm$ SE ARE CONNECTED BY LINES TO EMPHASIZE THE SIGNIFICANT ($P < 0.01$) INTERACTION BETWEEN SITE AND GEAR. NOTE THAT AGES BETWEEN MPA AND OA ARE APPROXIMATELY IDENTICAL FOR GILLNETS (BLUE) IN ALL COMPARISON AREAS BUT MARKEDLY LOWER FOR FISH ANGLED IN OA WHEN COMPARED TO THE MPA.	59
FIGURE 28 RAW DATA (LEFT) AND PREDICTIONS (RIGHT) OF SIZE-CORRECTED GROWTH OF PIKE FROM THE THREE DIFFERENT AREAS (HORIZONTAL PANELS). RAW DATA IS DISPLAYED BY BLACK DOTS, SIZE INDICATES AGE AT CAPTURE. BOXPLOTS EMPHASIZE THE DISTRIBUTION OF RAW DATA, DIAMONDS INDICATE MEAN VALUES. PREDICTED MEANS $\pm$ SE ARE CONNECTED BY LINES TO EMPHASIZE THE INTERACTION BETWEEN SITE AND GEAR.	60
FIGURE 29 BAR PLOTS DISPLAYING CALCULATED PROPORTIONAL STOCK DENSITIES FOR THE MPA (GREEN) AND OA (BLUE). COLORED NUMBERS INSIDE THE PANELS SHOW THE CALCULATED PSD FOR EACH BAR, BLACK PERCENTAGES DISPLAY THE RESPECTIVE SHARE OF FEMALE PIKE IN THE SAMPLE. NUMBERS AT THE LOWER MARGINS OF EACH PANEL DENOTE RESPECTIVE SAMPLE SIZES AVAILABLE FOR THE CALCULATIONS. ON THE LEFT (A) DATA IS SPLIT UP BY SEASON (X-AXIS) AND GEAR (HORIZONTAL PANELS), PLOT (B) DISPLAYS POOLED DATA FROM ALL GEARS AND ACROSS SEASONS.	61
FIGURE 30 DIFFERENCES IN ATTACK RATES (LEFT) AND LANDING RATES (RIGHT) OF PIKE BETWEEN MPA AND OA (X-AXIS). RED POINTS DISPLAY THE ESTIMATED MEANS FROM THE MODEL OUTPUT [$\pm$ 95% CONFIDENCE LIMITS]. GREY DOTS DISPLAY THE RAW DATA USED AS MODEL INPUT WHERE	

EACH DOT CORRESPONDS TO ONE FISHING SESSION. SIZE AND SHADE VISUALIZE THE NUMBER OF PIKE ENCOUNTERS IN EACH SESSION, WHICH COMPRISE BITES PLUS FOLLOWERS FOR THE ATTACK RATE (LEFT) AND BITES PLUS LANDED PIKE FOR THE LANDING RATE (RIGHT). LARGE DARK DOTS HAVE A HIGHER WEIGHT IN THE MODEL. DIFFERENCES BETWEEN MPA AND OA WERE SIGNIFICANT FOR BOTH INDICES ($P = 0.034$ AND $P < 0.01$ FOR ATTACK RATE AND LANDING RATE, RESPECTIVELY).	63
FIGURE 31 PROBABILITIES OF OBTAINING NO FISH CONTACT DURING A 1 H ANGLING SESSION FOR EACH SITE (X-AXIS) AND SEASON (Y-AXIS), AS PREDICTED FROM BINOMIAL GLMM. SLOPES BETWEEN MPA AND OA ARE NOT SIGNIFICANTLY DIFFERENT BETWEEN THE SEASONS.....	64
FIGURE 32 SCALED DATA FOR ANGLING AND GILLNET-CATCHES FROM SPRING 2022. COLORED POINTS AND BOXPLOTS SHOW THE DISTRIBUTION OF THE NORMALIZED DATA. BLACK POINTS DISPLAY THE PREDICTED MODEL VALUES FOR EACH GROUP, ERRORBARS SHOW THE 95% CONFIDENCE INTERVALS ESTIMATED FROM BOOTSTRAPPING. SLOPE DIFFERENCES BETWEEN BLACK LINES CONNECTING PREDICTED VALUES FOR EACH GEAR BETWEEN THE SITES VISUALIZE THE INTERACTION EFFECT.....	65
FIGURE 33 COLORED POINTS REPRESENT NORMALIZED RAW DATA FROM ANGLING (YELLOW) AND EDNA SAMPLING (BLUE) FOR EACH SITE (MPA / OA). BOXPLOTS DISPLAY THE DISTRIBUTION OF DATA. BLACK DOTS SHOW MODEL PREDICTIONS WITH ERRORBARS DISPLAYING THE 95% CONFIDENCE INTERVALS FROM BOOTSTRAPPING. THE DIFFERENCE IN SLOPES BETWEEN BLACK LINES VISUALIZES THE INTERACTION EFFECT BETWEEN GEAR AND SITE.	66
FIGURE 34 SCALED CPUE VALUES FROM TELEMETRY AND ANGLING DATA. COLORED POINTS REPRESENT INDIVIDUAL DATA POINTS WITH BOXPLOTS REFLECTING DISTRIBUTION OF THE DATA. BLACK DOTS DISPLAY MODEL ESTIMATES, ERRORBARS SHOW 95% CONFIDENCE INTERVALS FROM BOOTSTRAPPING.....	67
FIGURE 35 DIFFERENCES IN PIKE CPUE (PIKE/H) FOR DIFFERENT LURE TYPES (6 LEVELS) BETWEEN MPA AND OA. RAW DATA (RIGHT Y-AXIS) ARE PLOTTED AS COLORED POINTS WHERE, EACH REPRESENTING ONE FISHING SESSION. PREDICTED MEANS AND STANDARD ERRORS (LEFT Y-AXIS) ARE DISPLAYED IN BLACK. STARS ON THE LOWER PLOT MARGIN INDICATE SIGNIFICANT DIFFERENCES FOR EACH LURE TYPE BETWEEN MPA AND OA (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$) AND N SPECIFIES THE NUMBER OF OBSERVATIONS (NUMBER OF FISHING SESSIONS EACH LURE WAS FISHED). LURE TYPES ALONG THE X-AXIS ARE ORDERED IN DECREASING ORDER OF PROPORTIONAL CHANGE (DIFFERENCE IN PREDICTED CPUE BETWEEN MPA AND OA).	68
FIGURE 36 CPUE (PIKE/H) OF THE SIX DIFFERENT LURE CATEGORIES (6 LEVELS, REPRESENTED BY COLOR) BY SITE (X-AXIS). MODEL PREDICTIONS AND STANDARD ERRORS (LEFT Y-AXIS) ARE PLOTTED ON TOP OF RAW DATA (RIGHT Y-AXIS), REPRESENTED BY SMALL COLORED POINTS. THE SIGNIFICANT INTERACTION IS VISUALIZED BY THE VARIATION IN SLOPES BETWEEN MPA AND OA ALONG THE X-AXIS. LURES ARE ORDERED BY EFFECT SIZE FROM LEFT (STRONGEST) TO RIGHT (LOWEST).....	69
FIGURE 37 CATCH RATES (PIKE/H) FOR SOFT AND HARD LURES (COLOR) IN THE TWO SITES (X-AXIS). RAW DATA POINTS ARE DISPLAYED AS SMALL DOTS (RIGHT Y-AXIS), BLACK POINTS REPRESENT	

MODEL ESTIMATES (LEFT Y-AXIS). STARS ON THE LOWER PLOT MARGIN INDICATE SIGNIFICANCE FOR DIFFERENCES BETWEEN THE LURE TYPES WITHIN EACH RESPECTIVE SITE (N.S. = $P > 0.05$, * = $P < 0.05$). THE LACK OF A SIGNIFICANT INTERACTION EFFECT BETWEEN SITE AND LURE TYPE CAN BE DEDUCTED FROM THE APPROXIMATELY EQUAL SLOPES BETWEEN MPA AND OA BETWEEN THE LURE TYPES.....	69
FIGURE 38 CPUE (PIKE/H) FOR DIFFERENT LURE COLORS BETWEEN THE SITES (X-AXIS). MODEL PREDICTIONS (LEFT Y-AXIS) ARE DISPLAYED ON TOP OF RAW DATA POINTS (RIGHT Y-AXIS). STARS ON THE LOWER PLOT MARGIN INDICATE SIGNIFICANCE FOR DIFFERENCES BETWEEN THE COLORS WITHIN REACH RESPECTIVE SITE (N.S. = $P > 0.05$, * = $P < 0.05$).	70
FIGURE 39 CPUE (PIKE/HOUR) FROM STANDARDIZED LURE ANGLING WITH THE TWO COLOR-PATTERNS. PREDICTED DATA (LEFT Y-AXIS) ARE PLOTTED OVER RAW DATA (RIGHT Y-AXIS). EACH DATA POINT REPRESENTS ONE ANGLING SESSION. STARS ON THE LOWER PLOT MARGIN INDICATE SIGNIFICANCE FOR DIFFERENCES BETWEEN THE COLORS WITHIN REACH RESPECTIVE SITE (N.S. = $P > 0.05$, * = $P < 0.05$).	71
FIGURE 40 COMPARISON OF THE TIME BETWEEN TWO SUBSEQUENT CAPTURES OF INDIVIDUAL PIKE. GROUPS ON THE X-AXIS SEPARATE FISH INTO PIKE WHICH HAVE BEEN CAPTURES WITH LURES BOTH TIMES ("ANGLING-ANGLING") OR WHICH HAVE BEEN CAUGHT WITH LURES THE FIRST TIME AND WHO HAVE BEN RECAPTURED WITH COMMERCIAL GEARS ("ANGLING-COMMERCIAL"). COLORS DENOTE THE CALENDAR MONTH OF THE RESPECTIVE RECAPTURE EVENT, SHAPES DISPLAY SEX. DISTRIBUTION IS EMPHASIZED BY BOXPLOTS (MEDIAN, BOX: 25 AND 75 PERCENTILE, WHISKER: 10 AND 90 PERCENTILE). MEAN VALUES FOR EACH GROUP ARE DISPLAYED BY BLACK DOTS.	72

List of tables

TABLE 1 ABIOTIC CHARACTERISTICS AND MACROPHYTE COVERAGE OF THE SIX SITES OVER THE COURSE OF THE THREE SAMPLING SEASONS.	21
TABLE 2 NON-SEASONAL SITE CHARACTERISTICS AND GEOGRAPHIC INFORMATION. NO INFORMATION ON WAVE EXPOSURE WAS AVAILABLE FOR SELLIN.	22
TABLE 3 SAMPLING PERIODS FOR MONTHLY FIELDWORK BLOCKS FOR THE THREE SEASONS. ALL DATES REFER TO 2022.	26
TABLE 4 DESCRIPTIVE DATA ON OVERALL ANGLING EFFORTS, SEPARATED BY RANDOMIZED AND NON-RANDOMIZED ANGLING.	30
TABLE 5 NUMBERS OF PIKE TAGGED WITH ACOUSTIC TELEMETRY TRANSMITTERS BETWEEN 2020 AND 2022 IN THE COMPARISON AREAS, SPLIT UP BY THE RESPECTIVE SITES. IN WERDERBUCHT AND UMMANZ 100% OF TAGGED PIKE ORIGINATED FROM MPAS.	33
TABLE 6 ANGLING EFFORT AND RESPECTIVE CATCH-RELATED SUMMARIES FROM BOTH RANDOMIZED AND NON-RANDOMIZED SAMPLING EVENTS.	47
TABLE 7 CATCH STATISTICS FROM RANDOMIZED COMPARISON ANGLING FOR EACH COMPARISON AREA.	47
TABLE 8 OVERVIEW OF GILLNET PIKE CATCHES ACROSS ALL SEASONS, AREAS AND SITES.	48
TABLE 9 MEASURED eDNA CONCENTRATIONS ACROSS ALL SEASONS, AREAS AND SITES.	49
TABLE 10 DAILY TELEMETRY COUNTS OF PIKE INDIVIDUALS FROM THE THREE COMPARISON AREAS. ...	50
TABLE 11 TOTAL NUMBERS OF PIKE ATTACKS AND FOLLOWERS FROM LURE CAMERA TRAWLING FOR EACH SITE AND LURE. BS: BUCKTAIL SPINNER; RT: RUBBER TROUT.	50
TABLE 12 PROPORTIONAL STOCK DENSITIES FOR EACH COMPARISON AREA AND SITE. DATA CONTAINS ALL PIKE FROM GILL-NETTING AND RANDOMIZED ANGLING.	62
TABLE 13 POST-HOC COMPARISONS BETWEEN THE PROBABILITY OF NO FISH CONTACTS IN DIFFERENT SEASONS. SIGNIFICANT DIFFERENCES AT THE 5%-LEVEL ARE HIGHLIGHTED IN BOLD.	64

Glossary and definitions

Area	Refers to the three study locations consisting of a MPA and OA pair
CPD	Conditional probability distribution
CPUE	Catch per unit effort
C&R	Catch-and-release
FIE	Fisheries-induced evolution
GLM	Generalized linear model
GLMM	Generalized linear mixed model
MPA	Marine protected area
OA	Open access
PSD	Proportional stock density
Site	Refers to the protection status (MPA and OA)
TL	Total length

Abstract

Pike (*Esox lucius*) constitute an important target species in recreational fisheries across their distributional range and belong to the top three target species of anglers in Germany. Anglers and fishers impact on the abundance of target species, usually reducing biomass and leading to size and age truncation through mortality. Additionally, in angling with artificial lures hook avoidance learning and selection may lead to angling-induced timidity effects, where the reactivity of surviving pike to future capture is reduced. In the present study, catch per unit effort as a measure of abundance as revealed by different gear types were compared between three marine protected areas (MPA) and nearby open access areas (OA) in lagoons of the southern Baltic Sea in Germany. Additionally, pike behavior towards lures was examined using the MPA vs. OA contrast as a natural experiment in differential exposure to past fishing pressure. It was hypothesized that fisheries mortality leads to higher abundances and larger sizes of pike inside MPAs and that timidity is present in exploited parts of the population and manifests in differential angling vulnerability of individuals between MPA and OA sites. In support of the first and second hypothesis, it was found that inside MPAs pike were more abundant and the share of large fish was higher relative to OA sites in two areas. Supporting the third hypothesis, pike inside MPAs exhibited increased levels of aggression towards artificial lures. Moreover, it was found that the fish vulnerable to angling in OA sites encompassed the faster growing phenotypes, suggesting the potential for selection. Comparison of relative abundances between MPAs and OAs assessed by angling and non-angling gears could not quantify the absolute effect of timidity on catch rates, either due to a small effect size or because sampling gear biases prevented an unpolluted measure of true relative abundance differences among sites. In light of the collective evidence in this thesis, it is concluded that differences in pike angling catch rates among MPA and OA sites were mainly driven by the abundance-increasing impact of pike protection in MPAs, with angling-induced timidity having second-order effect. The presented evidence shows that pike in the coastal areas of the German Baltic coast exhibit angling-induced timidity and that pike removals reduce abundance and catch rates. The possible angling-selection on faster-growing pike may reduce the growth potential of the evolving stock in the future. Controls on total fisheries mortality, commercial and recreational, is needed to protect pike abundances and high catch rates. Rotating spatial closures may be one underutilized option that might protect both pike and pike catch rates to anglers, but in order to reap the benefits access to temporarily opened sites must also be allowed to anglers and not just fishers.

1 Introduction

The adverse effects of fishing on fish stocks are commonly associated with commercial fisheries, where failure in management has left many stocks in poor status and sparked a major controversy on the sustainability of wild fish (Pauly et al. 1998; Jackson et al. 2001; Mason 2002; Myers & Worm 2004; Juan-Jordá et al. 2011; Hilborn et al. 2020). In contrast, the impact of recreational fishing on wild fish stocks is discussed less frequently despite its potential for effects of comparable magnitude if poor management is in place (Post et al. 2002; Lewin et al. 2006). Recreational fishing is nowadays the predominant form of fishing in many industrialized countries around the world, particularly in inland waterbodies and coastal environments (Coleman et al. 2004; Arlinghaus et al. 2006, 2015). The number of anglers has long outnumbered that of commercial fishers (Arlinghaus et al. 2019). Similar to commercial fisheries, angling can cause a truncation of the size structure and reduce the density of the target species (Goedde & Coble 1981; Mosindy et al. 1987; Pierce et al. 1995; Arlinghaus et al. 2010; Ahrens et al. 2020) and even the collapse of entire stocks has been documented as a consequence of recreational overfishing (Post et al. 2002; Erisman et al. 2011). In addition, angling has the potential to cause changes in life-history and behavior of the target populations (Arlinghaus et al. 2009; Saura et al. 2010; Claireaux et al. 2018; Monk et al. 2021). Since in angling the fish takes the decision that determines the outcome of an encounter with a hook (Lennox et al. 2017), behaviors that reduce angling vulnerability benefit the target population in the presence angling pressure. Such behaviors could thus become increasingly prominent in fished populations, either due to plastic changes through learning following a hooking experience (Beukema 1970) or due to ongoing selection and resulting evolutionary changes through the removal of the vulnerable stock component (Uusi-Heikkilä et al. 2008).

Animals can alter their behavior in response to predation and angling can be thought of as a form of predation (Ahrens et al. 2012; Klefoth et al. 2012). Hook avoidance in response to hooking experiences has been found in different species and can be attributed to learning, i.e. behavioral plasticity (Beukema 1996, 1970; Raat 1985; Young & Hayes 2004; Klefoth et al. 2013). There are indications that not only a direct capture event is necessary for the acquisition of hook avoidance but the ingestion of a bait without a successful landing may be sufficient to render individuals invulnerable to fishing gear (Beukema 1970; Fernö & Huse 1983). Also, social learning has been put forth as a mechanism leading to reduced angling vulnerability in individuals witnessing the hooking of a conspecific but the majority of studies fails to find such effect and private hooking experiences seem to be the main mechanism for hook avoidance (Wegener et al. 2018;

Louison et al. 2019; Lovén Wallerius et al. 2019; Chen & Zeng 2020; Lovén Wallerius et al. 2020; Czapla et al. 2023). A number of studies have found rapidly declining catch rates within relatively short time periods despite only minor or no changes in overall fish abundance, likely driven by learned hook avoidance (Van Poorten & Post 2005; Askey et al. 2006; Blackwell et al. 2023; Wegener et al. 2018; Koeck et al. 2020). Particularly fisheries with a high proportion of catch-and-release (C&R) angling, a practice that is increasingly common and even mandatory in some localities, bear the potential for learned hook avoidance (Bartholomew & Bohnsack 2005). Individuals released after a hooking event have been found to exhibit short-term alterations in behaviors such as activity and habitat preferences but recover to normal values within weeks after the capture (Hoolihan et al. 2011; Baktoft et al. 2013; Ferter et al. 2015; Klefoth et al. 2008; Klefoth et al. 2011). Many studies show that hook avoidance is retained only for a limited time as witnessed by a significant boost in catch rates after the reopening of the fishery following fishing closures (Wegener et al. 2018; Koeck et al. 2020). The duration for which individuals retain learned lure avoidance ranges from less than seven months up to one year according to different studies conducted with common carp *Cyprinus carpio* L. (Beukema 1969; Raat 1985; Czapala et al. 2023). Interestingly, catch rates also increase when fish with learned avoidance towards a certain lure type are exposed to a novel, previously unknown lure, which further suggests the capacity for associative learning in fish with respect to fishing gear (Louison et al. 2019). In line with these findings, the fly-fishing success in a trout stream subject to high angling efforts was increasing with smaller, more subtle flies and angler skill which was deemed necessary to “outsmart” fish (Young & Hayes 2004). The scope for learning may be more pronounced in lure fishing as compared to fishing with natural bait due to the distinct and often unnatural characteristics of lures such as color, movement, size and sound (Beukema 1970; Arlinghaus et al. 2017a).

Besides individual learning experiences, angling can also alter the behavior and life-history traits of targeted fish stocks through fisheries-induced evolution (FIE), i.e. genetic changes caused by fishery-related alterations in the traits that maximize fitness (Law 2000; Uusi-Heikkilä et al. 2008). Even when harvested unselectively, fish evolve faster life-histories and associated changes in behavior and metabolic rate are possible due to correlations between these traits (Heino et al. 2015). Angling, however, is highly selective towards various attributes of fish. Body size (Keiling et al. 2020; Bieber et al. 2023a) and stomach content (Bryan 1974; van Densen & Vijverberg 1982; Raat 1991; Pope et al. 2005) were both repeatedly found to significantly predict angling vulnerability. If selection favors small body size through the removal of large fish, a short life-history is likely to emerge where juvenile growth increases, fish mature early and the investment in gonads

hampers adult growth rates (Heino et al. 2015). Fisheries-induced effects on growth were indeed observed both under laboratory conditions and in the wild (Saura et al. 2010; Alós et al. 2014; Uusi-Heikilä et al. 2015). In addition, personality traits (i.e. consistent individual differences in behavior) (Conrad et al. 2011) were found to affect angling catchability. For example, a number of studies successfully linked boldness (i.e. the willingness to feed in the presence of a predator) to angling vulnerability (Klefoth et al. 2013, 2017; Wilson et al. 2015; Tsuboi et al. 2016). However, the relationship seems to be context dependent given that various studies were unable to find this effect (Kekaäläinen et al. 2014; Vainikka et al. 2015; Härkönen et al. 2016; Keiling et al. 2020; Bieber et al. 2023a) and Wilson et al. 2011 even found timid fish to be more vulnerable. Also, exploration (i.e. the willingness to explore novel environments) was associated with increased angling vulnerability (Alós et al. 2012, 2016; Härkönen et al. 2014, 2016). Since personality traits were found to have a genetic basis in fish (Dochtermann et al. 2014), there is a risk that angling leads to the genetic manifestation of timid and avoidant fish (Monk et al. 2021). The genetic basis of factors determining angling vulnerability in fish was impressively demonstrated in a selective breeding experiment in black bass (*Micropterus salmoides* Lacépède) where fish vulnerable and invulnerable to angling were bred in separation and the magnitude of the trait increased in each generation, leaving a highly vulnerable and a highly invulnerable selection line (Philipp et al. 2009). In line with this, field studies found a correlation between angling pressure and gear avoidance (Alós et al. 2015a, Colefax et al. 2016) and studies from spear-fishing environments have termed fish wariness “the most sensitive indicator of fishing pressure” (Goetze et al. 2017). While the evolutionary response to fishing may be purely seen as an adaptive mechanism increasing overall survival, there are concerns that it has the potential to favor traits that may be detrimental for the overall fitness of the stock (Sutter et al. 2012) and changes in yield-determining traits are a threat to sustainable fisheries management (Heino & Godø 2002). The combined effect of plastic and genetic changes affecting behavior were hypothesized to lead to the emergence of an increasingly timid population where fish are avoidant and harder to catch was thus termed “timidity syndrome” (Arlinghaus et al. 2016a, 2017b).

Northern pike (*Esox lucius* L., hereafter pike) are large-bodied predatory fish that are commonly found in most freshwater bodies and brackish coastal areas of the temperate zones in the northern hemisphere with a key role for ecosystem functioning (Crossman 1996; Eriksson et al. 2009). Pike are a popular target species for anglers due to their large size and wide distribution (Mann 1996). Despite their popularity among recreational fishers, there is limited literature on the occurrence of timidity. Beukema (1970) found that pike previously unexposed to angling showed initially high and subsequently rapidly

declining catch rates for artificial lures (spinners) while catch rates with life bait remained high throughout all sampling days. This indicates that pike are able to recognize and actively avoid spinners but fail to do so with life bait which was explained by the greater variability of stimuli emanating from life bait when compared to the spinner. Pike were moreover found to show distinct declines in catch rates when fishing pressure was maintained for extended periods under C&R, indicative for learning (Kuparinen et al. 2010; Arlinghaus 2017a). Arlinghaus (2017a) moreover observed higher catch rates with soft plastic lures when compared to spoons which was attributed to the more natural appearance of the former. However, the authors found no indications for differential learning between the two lure types. A recent study from Lucas et al. (2023) investigating the response of naïve pike towards artificial lures and dead bait under laboratory conditions found that differences in boldness of individuals explained angling vulnerability in a way that bolder pike exhibited a greater likelihood to attack both dead bait and lures. Boldness, however, was unrelated to the likelihood of hunting living prey. The investigated pike were moreover found to avoid fishing lures and dead bait over time, indicating learned avoidance even in the absence of hooks. Pike therefore should be a suitable species to investigate lure timidity as they fulfill the conditions necessary to exhibit angling-induced lure avoidance: the potential for behavioral selection and learning.

Management in small scale fisheries is typically data poor due to financial constraints and the lack of feasibility for providing fishery-independent data (Post et al. 2002). As a substitute, fishery-dependent data (such as catch per unit effort, CPUE) are commonly used to infer stock status as this is often the only available source of data and also its use as proxy for abundance in scientific surveys is omnipresent due to the good feasibility of sampling efforts (Jansen et al. 2013; van Gemert et al. 2022; Eklöf et al. 2023; Tibblin et al. 2023). However, this implies major limitations as it assumes a directly proportional relationship between catch rates and the underlying abundance. Since the catchability q modifies the relationship between CPUE and abundance, inferences on stock status drawn from CPUE only apply if q is constant.

$$\frac{C}{E} = A * q$$

Equation 1: Relationship between catch (C), effort (E), abundance (A) and catchability (q) (Hilborn & Walters 1992)

If the catchability changes with variations in abundance or fishing pressure, however, the relationship between CPUE and abundance becomes nonlinear. Either catch rates may

remain high despite a decline in abundance (“hyperstability”) or drop disproportionately faster than the underlying abundance (“hyperdepletion”) (Figure 1).

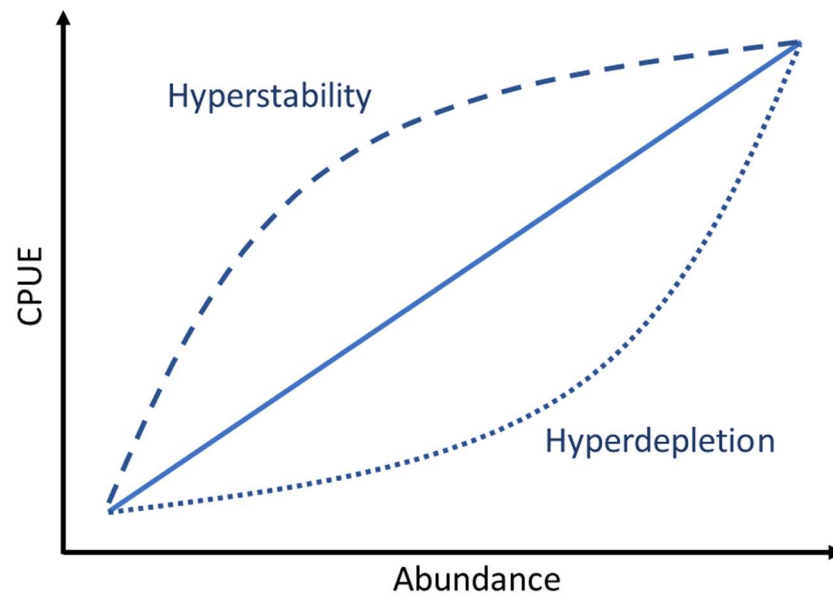


Figure 1 Schematic representation of different relationships between CPUE and abundance, modified by changes in catchability.

Under hyperstability, catch rates (perceived stock size) can be high even when the stock is already severely depleted. It typically occurs if fish are aggregating or bound to certain structures which facilitates capture and bears the risk of critical depensation (Post et al. 2002; Lewin et al. 2006; Erisman et al. 2011). Under hyperdepletion, on the other hand, catch rates can be low despite relatively high abundances. This phenomenon is often behavior mediated where a vulnerable component of the stock is harvested while the remaining individuals are invulnerable to the gear and is thus a common symptom of gear avoidance (Hilborn & Walters 1992; Ahrens et al. 2012; Alós et al. 2019). While the catchability is also modified by other factors, such as angler skill, food availability and seasonal variations (Bryan 1974; Baccante 1995; Mann 1996; Seekell et al. 2011), angling pressure was found to have the strongest effect on catchability and the importance of this relationship has been stressed repeatedly (Walters & Bonfil 1999; Pauly et al. 2002; Kuparinen et al. 2010).

When confronted with low catch rates, which are a main driver of angler satisfaction (Arlinghaus 2006; Hunt et al. 2019), managers are bound to implement measures to improve the status. One prominent management tool is stocking of additional fish, which satisfies anglers and may seem appropriate from a manager’s perspective given that data suggest declines in abundance (Arlinghaus & Mehner 2005). However, this approach fails to achieve long term integrity of the system and is unlikely meet the

management goals from a conservation perspective as it bears ecological risks. While catch rates may temporarily increase if catch-size, naïve fish are stocked, the initial conditions are likely to quickly recur when hook avoidance is acquired also in the newly stocked fish (Blackwell et al. 2023). In such case, other measures, such as rotating closures, could be more appropriate and less risk prone (Feary et al. 2011; Januchowski-Hartley et al. 2014; Camp et al 2015; Wegener et al. 2015; Koeck et al 2020).

Systems to study hook avoidance need to allow for the comparison of fish behavior in both, the presence- and absence of angling pressure. This may be either temporally or spatially. If spatial sites are ought to be compared, such system could be thought of as different lakes where some are fished while others are unfished. However, lake specific variation could blur the effect of interest and can only be compensated through a large number of replicates. One way to circumvent this is by studying the effect within one system, when areas with and without angling pressure can be neatly delineated. Marine protected areas (MPA) offer this opportunity and can be used as reference areas to study the effects of fishing (Agardy 1994; Januchowski-Hartley et al. 2011, 2014; Alós et al. 2015a, b). A prerequisite for such comparison, however, is that the species of interest has a sufficiently small home range in order to assure that the majority of individuals lives within the respective site and does not frequently travel between the sites so that strong differences in the exposure to fishing gear can be expected. A second prerequisite for such study is that the species of interest must be actively targeted by anglers in the open access (OA) sites, so that hook avoidance can be assumed to occur.

A suitable species for such study is the northern pike. Pike are ambush predators that commonly do not travel large distances and apart from spawning migrations in early spring, pike display small home ranges and have been found to be inactive most of the time (Diana 1980; Berkström et al. 2021; Dhellemmes et al. 2023b). While generally being considered to have a low salinity tolerance, pike can be found across the coastal areas of the Baltic Sea where they constitute an important fisheries resource for both anglers and fishers (Olsson et al. 2023). Differences in catch rates between fished and unfished sites have been observed previously for pike in Swedish coastal waters of the system and concomitant differences in food web functioning indicate that such differences are indeed due to higher predator abundance in unfished sites (Edgren 2005; Bergström et al. 2022a, b; Eklöf et al. 2023). This confirms the presence of fisheries induced effects in the broader system and also suggests that the desired effects may be present and observable in such setup. In the brackish lagoons around the German island or Rügen, in the southern Baltic Sea, pike are a popular game fish for anglers from the region and beyond due to their fast growth and the high proportion of trophy fish in the stock (Koemle et al. 2021; Arlinghaus et al. 2023a, b; Riepe et al. 2023; Rittweg et al.

2023). Traditionally, pike are also exploited by commercial fishers and conflicts have arisen between the groups, particularly in the light of a recent noticeable decline in catch rates (Vogt 2020; Arlinghaus et al. 2021; van Gemert et al. 2022). About 74% of the pike captured by anglers are released (Arlinghaus et al. 2023b), which offers the potential for pike to exhibit both evolutionarily based wariness of but also learned hook avoidance.

The aim of the study was to evaluate the presence of hook avoidance and its contribution to low angling catch rates in a mixed coastal pike-fishery co-exploited by both anglers and fishers. The hypotheses were that

- H1* Pike abundance is reduced in OAs compared to MPAs.
- H2* Pike size structure is truncated in OA compared to MPAs.
- H3* Timidity leads to more cautious behavior of pike towards lures, negatively impacting angling CPUE.
- H4* More aggressive and faster growing pike are selectively captured with angling.
- H5* More realistic (1) lure types and (2) lure colors show higher catch rates in the OA than in the MPA while naïve fish in the MPA strike unnatural lure types and colors equally well or better.
- H6* Pike recaptured using the same gear will exhibit a longer time interval between their first and second capture compared to pike recaptured using different gear, due to learned avoidance behavior.
- H7* The probability to recapture a pike by angling is higher in the MPA due to the lack of ongoing reinforcement of lure timidity.

The study contributes to a better understanding of the relevance of lure avoidance in pike angling, a desired target species of many recreational fishers in the northern hemisphere, and moreover give managers an indication about the reliability of pike angling catch rates as a proxy for abundance.

2 Methods

2.1 Description of the study area

The Baltic Sea is a brackish water body located in northern Europe. It is characterized by strong salinity gradients (decreasing salinity from southwest to northeast) which result from riverine freshwater inflow and seawater exchange with the North Sea through narrow straits near Denmark. Given the oligo- to mesohaline conditions it is inhabited by both marine and freshwater species. Changes in water levels occur frequently and are mainly driven by Baltic-wide prevailing wind-directions. The study was conducted in the southern Baltic Sea around the German Island of Rügen (Figure 2). The region is characterized by complex, shallow lagoon systems which significantly influence the salinity dynamics by retaining freshwater stemming from several larger river systems (e.g. Recknitz, Peene, Ryck & Barthe) (Arlinghaus et al. 2023a; Niessner et al. 2023a). While the entire system ranges about 100 km from west to east and covers a surface area of about 2000 km² (Arlinghaus et al. 2023a), the abiotic and biotic characteristics vary between the different lagoons and differences in the level of exposures to the open Baltic Sea cause gradients not only in salinity but also in nutrient loads and visibility, thereby also affecting species composition (Niessner et al. 2023a). Average water depths of the lagoons range between 1.8 - 5.8 m and mean phosphorus contents lie between 40 - 100 µg/l (Niessner et al. 2023a). Consequently, secchi-depths range from 0.4 m for the lagoons more exposed to Baltic waters and 1.9 m for more sheltered lagoons affected by agricultural runoff (Niessner et al. 2023a). Within the lagoons, many freshwater species are commonly found, such as bream (*Abramis brama* L.), roach (*Rutilus rutilus* L.), perch (*Perca fluviatilis* L.), pikeperch (*Sander lucioperca* L.) and pike (Winkler 1989).

Between 2019 and 2023, an inter- and transdisciplinary research project called BODDENHECHT (www.boddenhecht-forschung.de) was carried out, focusing on various aspects of the pike stock inhabiting the brackish lagoons around the Islands of Hiddensee, Rügen and Usedom and the Peninsula of Fischland-Darß-Zingst (Figure 2). The project was funded by the EU-Maritime Fisheries Fund (EMFF) and the federal state of Mecklenburg-Vorpommern. This thesis is embedded in the broader context of the project and takes advantage of previous works conducted within the project. These include previous tagging procedures of pike with n = 389 acoustic telemetry tags and n = 4,685 external floy-tags (Dhellemmes et al. 2023a, b). Tagging took place in various locations across the lagoon system and was aided by anglers, guides and fishers

involved in the project. Recaptures of marked fish could be reported via an online platform and a lottery chance was given for recaptures to incentivize reporting.

While some of the data used in this thesis derive from samplings dating back to 2019 and were gathered in different parts of the system, the main body of data was collected during a systematic sampling of the three comparison areas described in the following section.

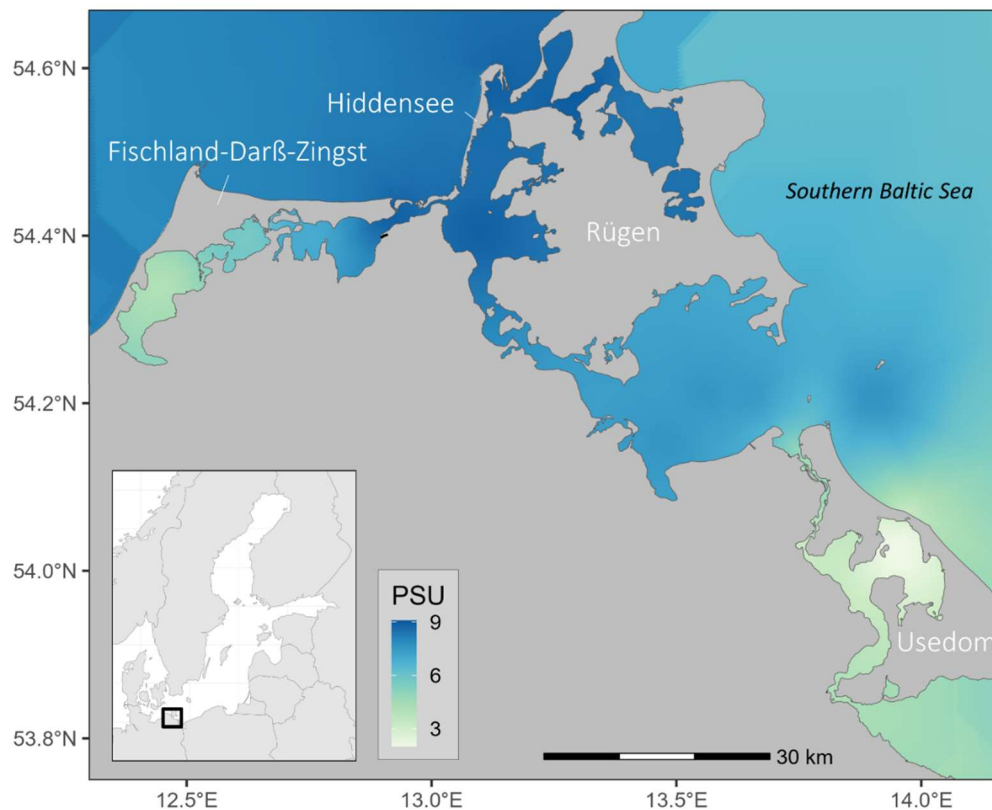


Figure 2 Extent of the brackish lagoon system on the Baltic coast of northeast Germany. Colors visualize average salinities. The system was subject to prior samplings and this data is also used in this study.

2.2 Characterization of sampling sites

To be able to make inferences beyond a single location, three comparison areas were chosen for sampling, each consisting of a protected (MPA) and an unprotected (OA) site. An initial set of potentially suitable study locations was identified via GIS. Following a pre-selection process, considering e.g. the proximity to previous tagging locations of pike with hydroacoustic transmitters, five locations were scouted to assess the situation on-site under different aspects such as (1) structural similarity between the sites and (2) the presence of infrastructure (accessibility, nearest boat slip). Finally, three areas were chosen as best compromising these aspects. The three pairs will be referred to as ‘areas’ hereafter while the protection status (MPA / OA) is referred to as ‘site’. Within each area,

the extend of the investigated sites was defined to an approximately equal dimension where possible (Figure 3, Table 2).

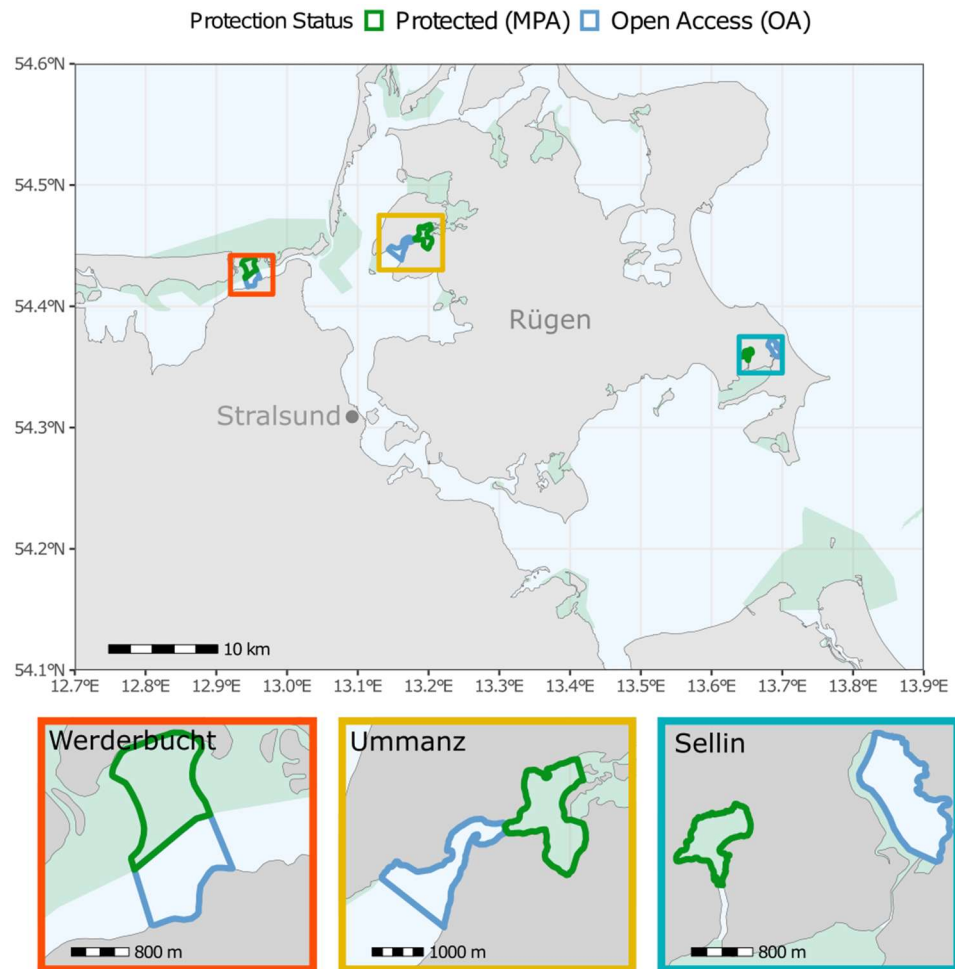


Figure 3 Locations and geographical settings of the three comparison areas subject to sampling. Protected sites (MPA) are displayed as green polygons, fished sites (OA) as blue polygons. Mint green color denotes the overall extent of areas with protection status.

Abiotic parameters of the sampling sites are displayed in Table 1. No significant differences in salinity, visibility and temperature were found for between MPA and OA in any of the comparison areas (Appendix 1). Recorded mean macrophyte coverages were at comparable levels between the sites for most areas and seasons. Obvious differences in macrophyte coverage between MPA and OA were only evident in spring in Werderbucht and in autumn in Sellin, where the mean coverage was lower in the MPAs (Table 1, Figure 4). Since values for mean macrophyte coverage were calculated using weighted means (see section 2.3.2.II), no statistical testing was conducted. Mean water depth was shallower in the MPAs of Ummanz and Sellin when compared to the OA sites, while there was no difference in Werderbucht (Table 2). Wave exposure was lower in the MPAs for both Werderbucht and Ummanz, indicating a higher shelteredness of these sites (Table 2).

Table 1 Abiotic characteristics and macrophyte coverage of the six sites over the course of the three sampling seasons.

Area	Season	Site	Macrophyte Cover [%]	Water Temp [°C ± SD]	Salinity [PSU ± SD]	Visibility [m ± SD]
Werderbucht	Spring	OA	34.6	15.9 ± 3.3	8.7 ± 0.2	0.6 ± 0.2
		MPA	20.4	15.7 ± 3.5	8.9 ± 0.3	0.6 ± 0.2
	Summer	OA	62.2	18.5 ± 3.8	9.6 ± 0.5	2.8 ± 1.5
		MPA	65.3	18.3 ± 4	9.6 ± 0.6	2.8 ± 1.5
	Autumn	OA	45.9	7.4 ± 4.7	8.7 ± 0.2	3.7 ± 0.7
		MPA	47.6	6.6 ± 3.9	8.8 ± 0.8	3.1 ± 1.2
Ummanz	Spring	OA	22.5	14.3 ± 3.5	8.9 ± 0.2	1.3 ± 0.6
		MPA	24.5	14.2 ± 3.5	9.0 ± 0.1	1.3 ± 0.6
	Summer	OA	29.7	19.5 ± 3.2	9.6 ± 0.7	1.4 ± 0.6
		MPA	24.9	19.4 ± 3	9.7 ± 0.7	1.3 ± 0.6
	Autumn	OA	54.0	9.4 ± 3.8	8.7 ± 0.5	3.9 ± 0.2
		MPA	66.9	9.4 ± 3.9	8.7 ± 0.5	3.9 ± 0.2
Sellin	Spring	OA	14.5	11.1 ± 7.5	7.5 ± 0.1	1.5 ± 0.8
		MPA	12.3	11.0 ± 7	7.3 ± 0.2	1.3 ± 0.6
	Summer	OA	39.6	19.7 ± 3.9	8.0 ± 0.5	1.4 ± 0.7
		MPA	44.6	19.5 ± 4.1	7.9 ± 0.6	1.1 ± 0.1
	Autumn	OA	44.6	7.6 ± 5.1	7.5 ± 0.5	2.5 ± 0.4
		MPA	6.38	7.5 ± 5.1	7.4 ± 0.5	2.4 ± 1.4

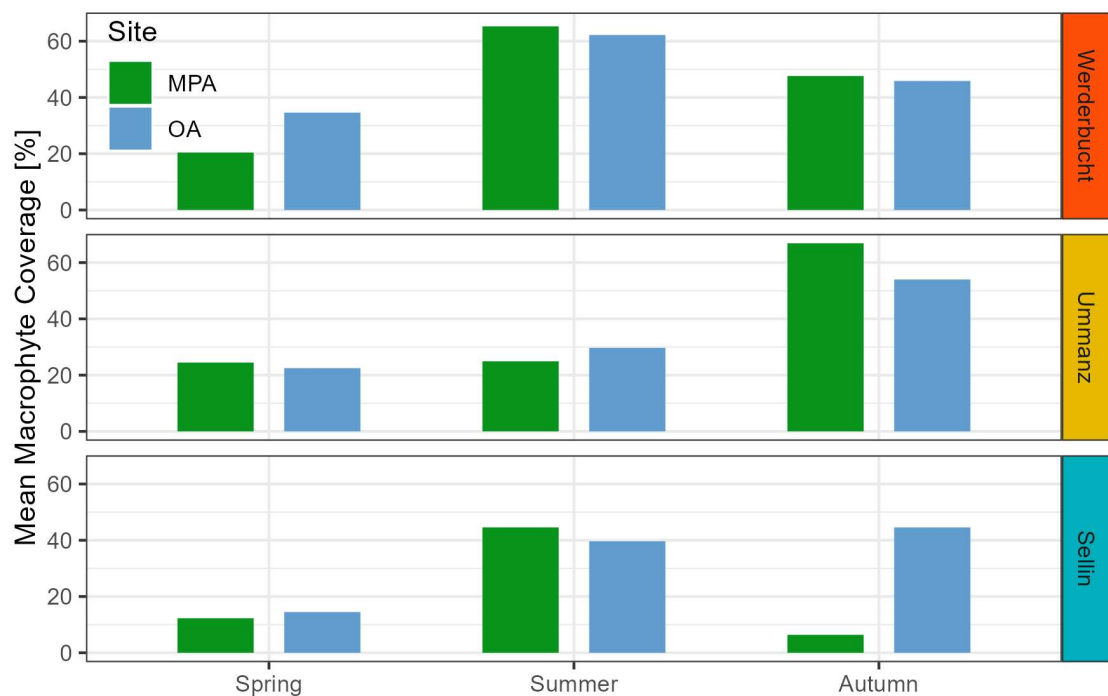


Figure 4 Bar plots displaying the macrophyte coverages determined by visual surveys in each site (color) and across seasons (x-axis) in the three comparison areas (horizontal panels).

Table 2 Non-seasonal site characteristics and geographic information. No information on wave exposure was available for Sellin.

Area	Site	Latitude [°N]	Longitude [°E]	Surface [km ² / ha]	Mean Depth [m]	Max. Depth [m]	Wave Exposure [SWM]
Werderbucht	OA	54.4237	12.9501	1.1 / 110	0.9 ± 0.7	3.9	18538.1
	MPA	54.4344	12.9461	1.4 / 140	0.9 ± 0.4	3.7	11793.3
Ummanz	OA	54.4460	13.1602	1.5 / 150	0.9 ± 0.7	5.9	10890.8
	MPA	54.4600	13.1939	1.8 / 180	0.6 ± 0.4	3.9	3105.6
Sellin	OA	54.3645	13.6885	1.0 / 100	1.3 ± 0.4	2.6	NA
	MPA	54.3610	13.6500	0.4 / 40	1.0 ± 0.4	4.2	NA

Werderbucht

This area is located in the “Grabow”, a Bodden lagoon with highly variable conditions. It is situated in a channel between the main land and the easternmost extensions of the Darß-Zingst Peninsula, which constitutes the barrier between the Darß-Zingst Boddenchain and the Baltic Sea. The northern parts of the area, in which the MPA is situated, are less strongly exposed to the currents due a basin character and water masses are therefore retained longer here than it is the case in the more exposed southern part of the area (location of the OA site). Average salinity was 9 PSU (Table 1) but maximum values of 14 PSU have been recorded at rising Baltic water levels and can drop to values around 5 PSU when Baltic waters fall and turbid, low-salinity waters from the Darß-Zingst lagoon follow. The pike fishery in the Darß-Zingst lagoon is strongly dominated by anglers while the commercial fishery is comparatively small (Radinger & Arlinghaus et al. 2023). The MPA site at Werderbucht is located inside *Nationalpark Vorpommernsche Boddenlandschaft Kernzone 1*, an zone with strict exclusion of boating traffic and fishing activities since the implementation of the national park in the 1990s (Niessner et al. 2023b). However, few commercial fishers are excluded from these regulations for historical reasons and are in theory allowed to pursue commercial fishing inside the MPA. Other gears than eel traps could not be observed during the sampling period (see section 3.1.1), indicating that pike are not the primary focus of existing fishing activities in this site. Besides previous samplings for scientific purposes from within the project BODDENHECHT, the MPA has not experienced angling pressure for three decades. Depth was about 0.9 ± 0.7 m for the MPA and 0.9 m ± 0.4 [mean ± SD] for the OA (Table 2). However, the OA overall exhibited a larger portion of shallow areas which were compensated in the mean by the presence of a fairway channel (deep blue line in the OA in Figure 5, left). The latter was excluded from sampling due to boat traffic.

Overall, 69% and 65% of the area were shallower than 1 m in the OA and MPA, respectively.

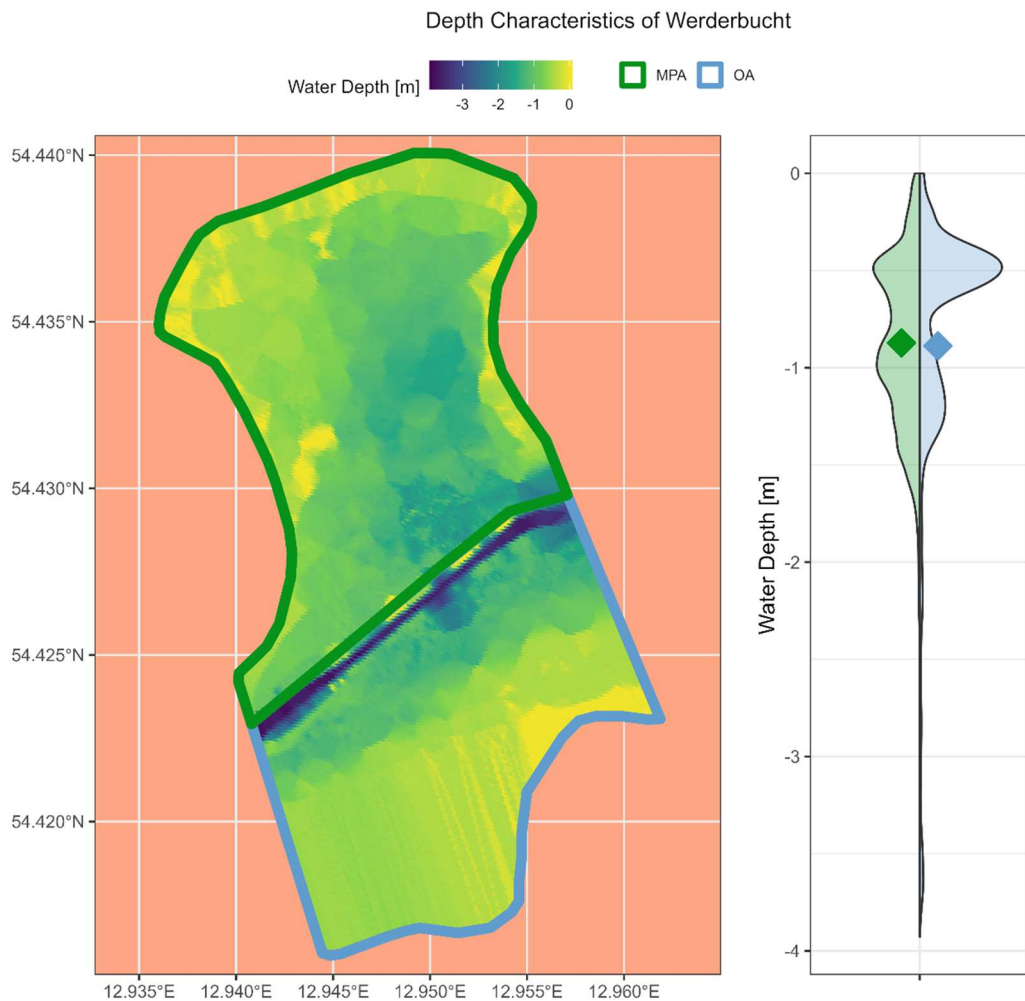


Figure 5 Left: Interpolated depth map of the comparison area Werderbucht. Depth is displayed by a color gradient from blue (deep) to yellow (shallow). Outline color displays the respective site. Right: Density plot of depth data per site (color). Diamonds display mean depth.

Ummanz

The area is part of the Bodden lagoon Kubitzer Bodden, located west of the Island of Rügen. In the system, pike landings from commercial and recreational fishers were recently found to be at comparable levels (Radinger & Arlinghaus 2023). The study area is semi-enclosed between the Island of Rügen to the east and the smaller Island of Ummanz to the west (Figure 3). Given the protection from wind on both sides through the land masses, the area has a sheltered character, which is more pronounced in the MPA part of the area while the OA experiences high waves more frequently (Table 2). The entire study area is part of the *Nationalpark Vorpommernsche Boddenlandschaft – Pflege und Entwicklungszone* in which angling and fishing is permitted. However, the

section considered MPA for this study underlies a boating prohibition and access from land is not allowed, therefore fishing and angling are indirectly prohibited. As with Werderbucht, exclusions from the boating prohibition exist for some fishers and therefore commercial fishing on pike takes place inside the MPA while angling does not. In addition, the MPA site is a spawning protection zone, rendering the intended fishing for pike illegal in April and May and thus effectively prolonging the pike spawning closure for one month. In Ummanz, the MPA was clearly shallower with water depths of 0.6 ± 0.4 m and $0.9 \text{ m} \pm 0.7$ m [mean $\pm$ SD] for MPA and OA, respectively (Table 2). The OA exhibited a greater share of depths > 1 m which were not found in the MPA (Figure 6, right). While 86% of the MPA were shallower than 1 m, the respective figure for the OA was only 57%. Across all seasons, salinity was 9.2 ± 0.6 PSU [mean $\pm$ SD] and ranged from 8 - 10 PSU for both sites.

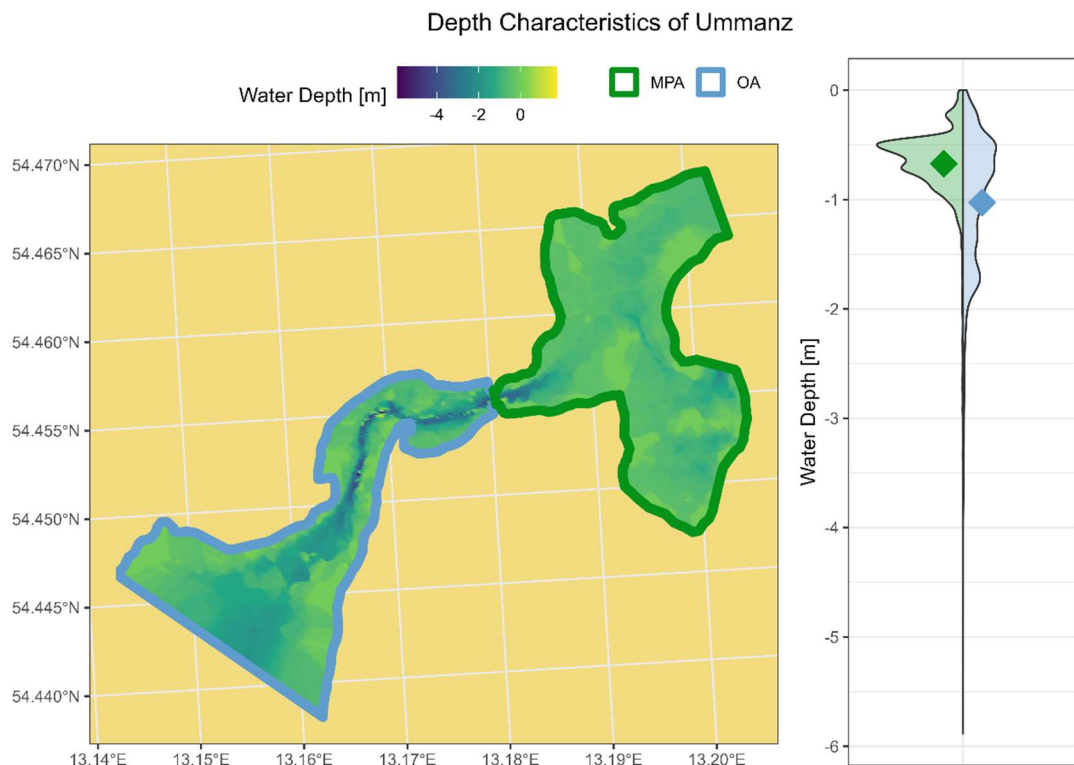


Figure 6 Left: Interpolated depth map of the comparison area Ummanz. Depth is displayed by a color gradient from blue (deep) to yellow (shallow). Outline color displays the respective site. Right: Relative frequency of interpolated depth data per site (color). Mean depth is displayed by diamonds.

Sellin

The lake pair of Sellin (Neuensiener See [MPA] and Selliner See [OA]) is located on the easternmost tip of the Island of Rügen. The two lakes are enclosed by land but are connected to the Greifswalder Bodden lagoon via a channel and are therefore affected by regular changes in water levels and salinity. On the larger Bodden-level, fisheries

landings of pike were recently found to be roughly equal between commercial and recreational fishers (Radinger & Arlinghaus 2023). Both lakes lie within the jurisdiction of the “Biosphärenreservat Südostrügen”. In lake Selliner See (OA) both fishing and angling is permitted across most of the lake, except for a coastal strip along the south-western shore which underlies additional protection as “Naturschutzgebiet” (NSG; translates to “nature protection zone”) and where fishing is not permitted. These zones were excluded from sampling. The smaller lake Neuensiener See additionally is entirely declared NSG and fishing is more strictly limited here. While both angling and fishing are permitted, the delineation between the two lakes into MPA and OA was informed by stronger regulations in Neuensiener See where a maximum of 50 recreational fishing licenses are issued per year. Additionally, only very few spots are accessible from land due to dense reed belts along the lake shore and boating is only permitted to a handful of anglers, which effectively limits angling pressure for large parts of the lake. Mean depths were $1.0 \text{ m} \pm 0.4 \text{ m}$ and $1.3 \text{ m} \pm 0.4 \text{ m}$ [mean $\pm$ SD] for MPA and OA, respectively (Table 2). Similar to Werderbucht, there was a fairway across the OA in which sampling was not pursued due to boat traffic (Figure 7). Overall, 60 % of the MPA were shallower than 1 m while this figure was only 18% for the OA.

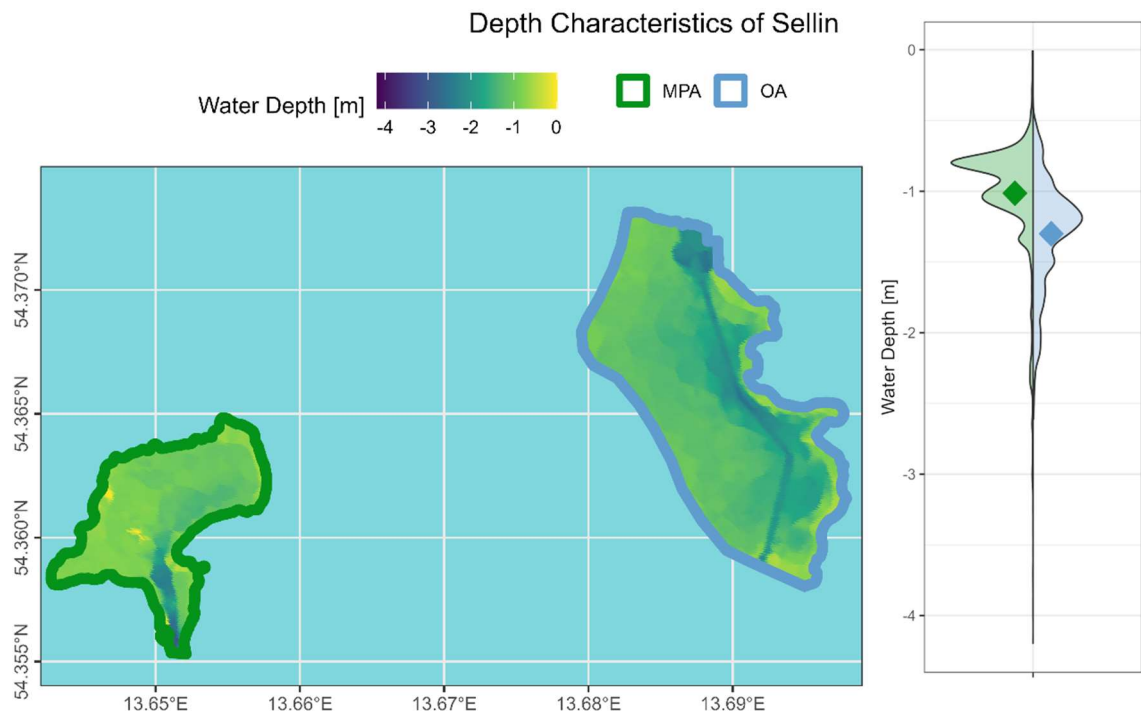


Figure 7 Left: Interpolated depth map of the comparison area Sellin with the smaller Neuensiener See (MPA) on the left and the larger Selliner See (OA) on the right. Depth is displayed by a color gradient from blue (deep) to yellow (shallow). Outline color displays the respective site. Right: Relative frequency of interpolated depth data per site (color). Mean depth is displayed by diamonds.

Across all seasons, salinity was 7.6 ± 0.6 PSU [mean $\pm$ SD] for the MPA and 7.7 ± 0.5 PSU [mean $\pm$ SD] for the OA. Values ranged from 6.4 to 9.1 PSU in both sites.

2.3 Fieldwork

Main fieldwork efforts in the three comparison areas were conducted across three seasons (spring, summer, autumn) to capture seasonal variation in the data. Monthly fieldwork blocks were undertaken throughout the months April, July and October 2022. In each of these monthly blocks, each of the three areas were sampled over an approximately 10-day period within which a standardized sampling protocol took place (Table 3). This protocol comprised two randomized angling days, pike gillnetting, preyfish gillnetting, eDNA sampling, macrophyte sampling and setting of longlines which are further elaborated in the following sections.

Table 3 Sampling periods for monthly fieldwork blocks for the three seasons. All dates refer to 2022.

Area	Spring	Summer	Autumn
Werderbucht	22.04 - 04.05	24.07 - 03.08	23.10 - 02.11
Ummanz	16.04 - 21.04	11.07 - 22.07	11.10 - 21.10
Sellin	02.04 - 14.04	03.07 - 10.07	02.10 - 09.10

After each monthly fieldwork block, additional randomized angling days (for the definition of the term randomized angling see section 2.3.3) were conducted in each area to increase the number of observations since angling catches are known to be highly affected by daily variation. The additional angling days for each season took place after the monthly fieldwork block of the respective season. In some instances, angling days were temporally closer to the next monthly sampling block but were nonetheless assigned the season of the previous monthly fieldwork block in order to obtain balanced data with regards to season. The term season therefore does not strictly correspond to the meteorological term when it is referred to in the context of randomized angling data.

It was distinguished between randomized and non-randomized angling days as sampling efforts for comparison angling between MPA and OA sites already took place starting in 2020, however, the design and locations differed (see section 2.3.3).

2.3.1 Monitoring of fishing effort

To obtain data on the presence of both commercial and recreational fishing effort in all sites, observed fishing effort (gear type and quantity) was recorded throughout all samplings in the three comparison areas.

2.3.2 Recording of habitat characteristics

2.3.2.I Depth

In each area echosounder surveys were conducted to gather data on the depth structure. For this, parallel gridlines were projected on the area and followed at low speeds while recording depth profiles using an echosounder (Garmin GPS Map 923xsv). Data were subsequently converted from .sl2 to .csv format (<https://kw-m.github.io/sl2-csv-converter/>) and a kriging algorithm was used to interpolate the grid in R and derive summary statistics such as average depth. Values were corrected for deviations from normal water levels at the day of sampling by using official measurements from nearby measuring stations.

2.3.2.II Macrophyte coverage

To capture differences in habitat quality for pike, the macrophyte coverage was recoded in each season during the main fieldwork blocks (April, July, October). In each area 12 transects were followed from shore to the central parts of a waterbody (6 per site). At 10 equally distanced points along each transect, the water depth and estimated macrophyte coverage were recorded. Where visibility was sufficient, the coverage was estimated by direct visual observations. At greater depths or increased turbidity an underwater camera-system was employed. This system consisted of a 2 m metal bar at which and a camera was attached facing downwards. The camera was connected to a screen via a cable, videos could thus be assessed in real time. To assess mean macrophyte coverages, mean coverage was calculated for each 1-m depth stratum per site and season. Subsequently, weighted means were determined from summarized data by using the share of each depth stratum (determined from echosounder survey) to the entire site as a weight.

2.3.2.III Wave Exposure Index

As a measure for the shelteredness of bays, the wave exposure index (Isaeus 2004) was used. For this, all raster points lying within the sampling areas were extracted from a SWM raster layer and mean values were calculated for each site. No values were specified in the raster file for the lake pair of Sellin.

2.3.3 Angling

Angling data were collected by performing rod-and-reel fishing with artificial lures from a drifting boat as this best represents the local fishery and effectively allows to cover large surfaces (Figure 8). On each sampling day, the starting site (MPA / OA) of the first session was randomized to control for an effect of daytime. After termination of each session, sites were alternated. Session duration varied between 45 minutes and 2 hours but the duration of two consecutive sessions was equal to standardize effort between sites. A total of 4 sessions was fished on each fishing day (2 sessions in each site). On each fishing day, between one and three boats were employed with up to five people fishing on each boat. For each fishing session and angler, metrics potentially containing information on lure timidity were recorded such as the (1) lure specific information (lure type, - color & length), (2) the number of followers (i.e. pike following the lure without attacking it), (3) the number of bites (i.e. pike biting the lure but not being landed) and (4) the number of pike landed. In addition, water parameters (salinity [PSU], oxygen [mg/L] and Secchi depth [cm]) were measured in each site on each sampling day. Two slightly different sampling designs were followed, which are described in the following sections. Details on sampling efforts can be found in Table 6.



Figure 8 Angling sampling with lures from the drifting boat at Werderbucht.

Randomized angling

Randomized angling took place between April 2022 and January 2023. Fishing was conducted within predefined polygons (Figure 3). To ensure that the data collected were representative of the overall sampling site rather than resulting from aggregated effort at certain spots deemed to be good fishing spots, the starting points of drifts were randomly chosen along the shore in accordance with the prevailing wind direction. Since the water

levels varied between days, at low levels some parts of the areas were excluded for sampling when water depth was too shallow for boating (~ 0.5 m). Lure choice was free but a lure had to be fished for two consecutive sessions (MPA and OA) to control for a possible lure effect confounding the site effect. Captured pike were tagged with external floy-tags upon capture and kept in sling bags until processing. Overall, 13 fishing days were conducted in Werderbucht and Sellin, each, and 14 days in Ummanz.

Non-randomized angling

Alternating angling between the sites took place on additional 19 days with a slightly less restrictive design where site choice was up to the boat captain and lures could be changed at any time. This type of fishing took also place in a greater variety of MPAs (Figure 9) and adjacent OAs but fishing was not strictly spatially confined within certain polygons as it was the case in randomized angling. Pike from non-randomized comparison angling were measured, sexed and tagged with external floy-tags on board immediately after capture and released on-site.

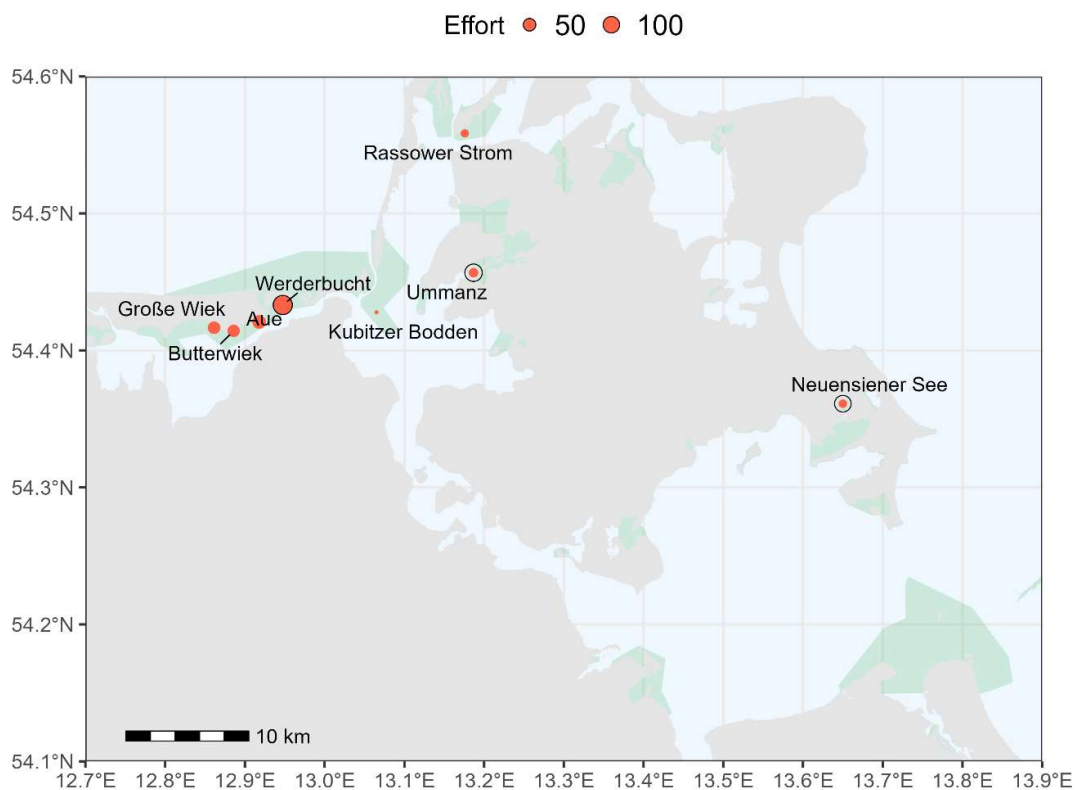


Figure 9 MPA sampling locations of non-randomized angling (red dots). Size indicates effort, i.e. the sum of individual angling hours. Black circles around the three comparison areas Werderbucht, Ummanz and Neuensier See (MPA of area Sellin) represent the respective sampling effort from randomized angling to set efforts in relation. In Werderbucht, the number of random and non-random angling sessions was roughly equal. Green polygons delineate areas with protection status.

Table 4 Descriptive data on overall angling efforts, separated by randomized and non-randomized angling.

	Randomized Angling	Non-Randomized Angling
Number of fishing days	40	19
Accumulated effort (h)	964	800
Number of areas fished	3	8
Date range	2022-04-03 - 2023-01-19	2020-12-03 - 2023-03-04

2.3.4 Angling-independent gears

To provide alternative metrics of pike abundance to the angling catches, a number of angling independent gears were employed. These gears provided estimates of relative abundance (CPUE) potentially unbiased by timidity and were used to identify to what extent differences in angling catches between the sites were attributable to differences in abundance and/or catchability. Furthermore, the invasive gears (gillnets, longlines) functioned as reference gears to sample pike, as timid individuals were expected to be invulnerable to lures. Fish captured with these gears thus provided data on the invulnerable stock component for the analysis of length and growth.

2.3.4.1 Gillnets

Two types of gillnets were used for sampling: (1) pike gillnets which were specifically designed with mesh sizes suitable for pike (50, 60, 75, 95- and 110-mm knot to knot, with each mesh size found within 20-m panels) and (2) preyfish gillnets to sample preyfish communities containing the mesh sizes 5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43, 55, 70, 90, 110 and 135 mm (knot to knot) with each mesh size represented by a 2.5 m panel in accordance with European Standard EN 14757. Pike- and preyfish-gillnets were 100 m and 40 m long, respectively and 1.5 m high. Both gillnet types were employed on one occasion within each season and area. For each netting event, the same procedure described below was followed. A total of 12 nets (6 per site) was randomly set around sunset. Positioning of nets was randomized in QGIS within the polygons of each site (command *"Random points inside polygons"*). Random net positions were adjusted to the nearest possible location if water depth was too shallow or locations were in boat fairways. Anker and flagged buoys were attached to each end and nets were set in accordance with the wind direction from the drifting boat. Setting of nets started approximately 1-2 h before sunset and lifting was initiated soon after sunrise (Figure 10). Employment time for nets was 15 h on average but ranged between 9-20 h. High values were due to logistic constraints preventing an earlier lifting of the nets when high catches of bream occurred since large bream were released in-situ. Effort was later on calculated under consideration of the employment time. Captured pike were tagged

with external floy-tags directly after capture to assign individuals to net-ID and the respective mesh size captured in and stored in life wells on the boat. Further processing took place on land. Pike mortality in the nets was temperature dependent with higher mortalities in summer.



Figure 10 Setting of gillnets during sunset in the OA of Werderbucht in October 2023.

2.3.4.II Longlines

Six longlines were employed overnight (three in each site). Longlines consisted of a 30 m main line with five hooks on 50 cm steel leaders in equal distance to each other. Hooks were baited with live bait between 10 and 25 cm length. Longlines were attached to anchors on each end and marked with black flags. Locations were randomly chosen (see section 2.3.4.I Gillnets). No pike were caught with longlines at any point in time, hence longlines are not presented in the results section.

2.3.4.III eDNA

As an alternative metric reflecting pike abundance, 10 eDNA mixed samples were taken from each area (5 per site) and season. Mixed samples were created from 5 subsamples collected at ~ 20 m distance from each other. Three of the five mixed samples from each site were chosen adjacent to gillnet-locations while the remaining two were chosen according to the wind direction (1 sample along the upwind and downwind shore,

respectively). This design was chosen to be able to test for correlations between eDNA abundance and pike catches in gillnets but also identify potential relationships between wind direction and eDNA concentrations as eDNA accumulates at the surface and may thus accumulate at downwind shores (Rourke et al. 2021). On each occasion, eDNA sampling was conducted prior to setting of gillnets. For all working steps, disposable gloves were used by the sampler to avoid unintended contamination with pike DNA from other sources. Subsamples containers (200 ml) were slowly filled with water by dipping them just below the water surface, thereby maximizing the amount of water from the surface layer where eDNA accumulates (Figure 11). Creation of mixed samples took place on land by dispensing the five sub-samples from one sampling point into a 5 L container, previously rinsed with demineralized water. In accordance with the manufacturer's instructions of eDNA kits (Sinsoma GmbH, Austria), water was drawn through the filters from mixed samples with a syringe until the filter's permeability limit was reached due to clogging with particles and no more water could be drawn (Figure 11). This limit was reached after 350 to 1000 ml. Within 48 h after sampling, filters were sent to Sinsoma GmbH, Austria for analysis. The samples were analyzed for pike-specific DNA using ddPCR (droplet digital PCR) at 57°C to determine concentrations. The following primer-probe combinations were used (Olsen et al. 2015, 2016):

Forward Primer: 5'-CCTTCCCCCGCATAAATAATATAA-3',
 Reverse Primer: 5'-GTACCAGCACCAGCTTCAACAC-3',
 Probe: 5'-FAM-CTTCTGACTTCTCCCC-BHQ-1-3'.

Because initial analysis revealed a high share (29%) of samples with no detectable level of pike DNA, a second analysis was carried out to determine the presence of DNA from other species and assess the validity of samples. In three samples no DNA was found and these observations were thus removed from the dataset.



Figure 11 Sampling steps of eDNA sampling. Left: Taking water subsample for mixed samples. Right: Filtering eDNA from mixed sample.

2.3.4.IV Telemetry

As another metric potentially reflecting pike abundance between the sites, telemetry detections were recorded. Pike were tagged with acoustic transmitters (MM-R-16 50 HP & MM-R-16 33 HP, Lotek Wireless Inc., ON, Canada) between 2020 and 2022 within the project BODDENHECHT for the analysis of exchange movements and abundances. Details can be found in Dhellemmes et al. (2023a, b). The subset of pike tagged with acoustic transmitters and released within the comparison areas investigated in this study were unbalanced between the sites in two of the areas, total numbers per area and site are displayed in Table 5.

Table 5 Numbers of pike tagged with acoustic telemetry transmitters between 2020 and 2022 in the comparison areas, split up by the respective sites. In Werderbucht and Ummanz 100% of tagged pike originated from MPAs.

	MPA	OA
Werderbucht	50	0
Ummanz	28	0
Sellin	4	4

To record pike tagged pike, a hydrophone (VR-100, Oceans Research) was employed during drift angling to detect tagged fish in the study areas. Counts of individuals during one day were eventually summarized for each site to yield a telemetry abundance estimate for each site and fishing day. Since there was no systematic sampling of the sites but drifts were random (see section 2.3.3), not all fish might not have detected on each sampling day. However, given the random patterns of drift and the relatively large distance covered during most days (when wind was sufficient) it can be assumed that the number of unique detections was close to the number of tagged fish actually present. The minimum distance between transmitter and receiver necessary to successfully detect a fish is reduced at low water depth, high turbidity and high macrophyte cover which may have caused differences in detectability between sampling days.

2.3.5 Processing of pike

For both, pike from random angling and gillnetting, the following metrics were recorded: total length [mm], weight [g], sex (external determination, Casselmann 1974). In addition, tissue samples were taken from pectoral fins for genetic analysis, scale probes for aging and stomach contents using a stomach pump (this data is not part of the present thesis). For the gentle treatment of the animals, the sample collection took place in a designated measuring tray (Figure 12). After the handling procedure, pike were returned to the site of capture and released.



Figure 12 Processing of a large female pike.

2.3.6 Aging

To see whether growth differed between individuals as a function of site and gear, the size-corrected growth (Berggren et al. 2022) was calculated from scales. Scale samples were collected with pincers from a spot a few centimeters below the dorsal fin. Approximately 5-10 scales were gently removed from each fish during the handling procedure. From each fish, three scale were mounted onto a glass microscopic slide and a high-resolution photo was taken under a stereo-microscope (Leica MZ8). Images were subsequently imported into the software ImageJ2 (Version: 2.14.0) and transition points between yearly growth rings (annuli) from the core were identified visually and marked. To avoid sampling bias (e.g. as a result of increasing reader experience) the sequence of scales was randomized. Also, only one person was age reading the scales for consistency. After the software provided the data for absolute increment for each scale (i.e. the distance between the growth rings) the size-corrected growth was calculated from mean values of the three scales investigated.

2.3.7 Camera transects

To record pike behavior towards artificial lures of different kinds, camera-based lure trawling was conducted for 2 hours in each site and area per season. Two rods were employed simultaneously during trawling, each equipped with a Water Wolf - UW 2.0 underwater camera and one of two lures (Figure 13, Figure 14). On one rod, a 20 cm Savage Gear Real Trout (hereafter termed rubber trout) in natural design was fished, which is a highly realistic representation of sea trout, a potential prey of pike. On the

other rod a bright yellow bucktail spinner (Mepps Giant Marabou) of the same length was fished, which is a rather unrealistic lure as it doesn't imitate a specific prey but is highly conspicuous due to its distinct color and the emission of light reflexes, sound and the creation of acoustic vibrations.



Figure 13 Lures used during camera trawling: Mepps Giant Marabou Bucktail Spinner in bright yellow (left) representing a highly conspicuous and unnatural lure versus the Savage Gear Real Trout in a natural design (right) convincingly mimicking a real prey.

Lures were attached behind the cameras on a 30 cm steel leader. Since pike were expected to be startled when passed by a motorized boat in close proximity in the shallow waters, side planners were rigged on the line at approximately 3 m distance to make sure lures were kept at a distance from the boat (Figure 14).

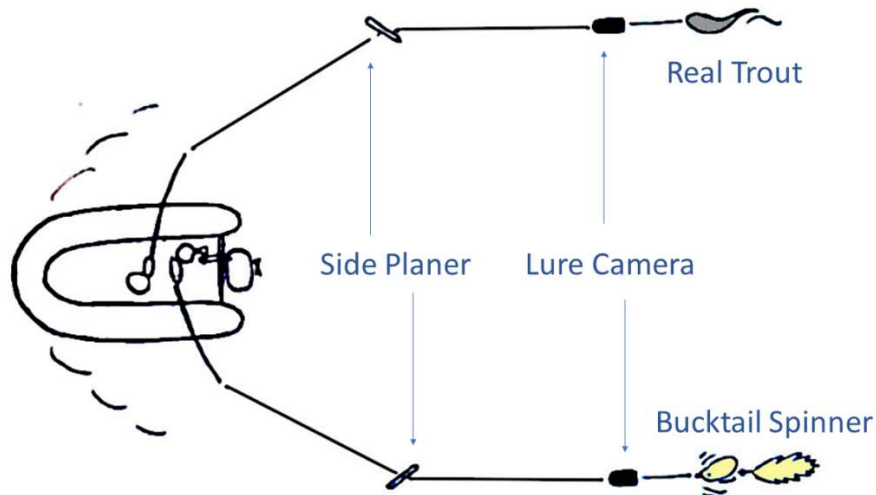


Figure 14 Schematic drawing of the setup used for lure trawling.

Hooks were removed from lures to avoid entanglements with macrophytes. Pike encounters were categorized into the behavior "attack" and "follower". An individual was only counted once, either as bite or as follower. If the same individual attacked a lure repeatedly, only one attack was considered. Analysis aimed at finding differences in behavioral responses of pike from each site towards the two lure types used.

2.4 Statistical analysis

Plotting of results and statistical analysis was performed in R studio version 4.2.2. (R Core Team 2022). The packages involved in data analysis were dplyr (Wickham 20216), lme4 (Bates et al. 2015), glmmTMB (Mollie et al. 2017), ggplot2 (Wickham et al. 2016). Fixed model terms were reported via the *Anova* function of the car package which uses likelihood ratio tests to determine overall significance of individual variables (Fox & Weisberg 2019). The type argument specifying the sum of squares to be used in the Wald chi-square tests was set to 2 for models without (significant) interaction and to 3 for models where the interaction was significant. Estimated marginal means and pairwise comparisons (Tukey HSD) were calculated using the emmeans package (Lenth et al. 2023). To display estimated differences between levels of categorical variables, ratios are reported. These represent the proportional change.

2.4.1 Catch rates of different gears between MPA and OA

To assess potential differences in pike abundance between MPAs and OAs, the CPUE was analyzed for each of the gear types (angling, gillnets, telemetry) using generalized linear mixed effect models (GLMM) where the catch was used as response variable and site (MPA/OA) as main effect. Since it was expected, that the abundance differences between MPA and OA were a function of fishing pressure, which differed between the three comparison areas (see section 3.1.1), an interaction term between site and area was included to calculate the differences separately for each of the three areas.

2.4.1.1 Randomized angling

Raw data from randomized angling sessions was used, where each observation ($n = 726$) corresponded to one fishing session (mean fishing effort per session = 1.3 h) of one sampler. The model formula was specified as:

$$\begin{aligned} \text{captured fish} \sim & \text{offset}(\log(\text{effort})) + \text{site} * \text{area} + \text{season} + (1|\text{sampler}) + (1|\text{date}) \\ & + (1|\text{area:site}) \end{aligned}$$

The interaction between site and area was included in the model to test whether the effect of protection was significantly moderated by the area. The season (factor, 3 levels, for a definition see section 2.3) was included as a fixed effect. The random terms for sampler and date were used to account for variation due to day and different skill among samplers while the random term “(1|area:site)” was incorporated in the model to account for the hierarchical spatial nesting structure of sites within areas and thereby avoid pseudoreplication. A poisson-conditional probability distribution (CPD) with a log-link

was deemed appropriate as the response data were counts. Model validation showed no significant violation of homoscedasticity and normally distributed residuals.

2.4.1.II Gillnets

To derive statistical measures for differences in gillnet catches between MPA and OA, a GLMM was used to explore the influence of the protection status on gillnet CPUE (pike/h*m_{net length}). The model formula was specified as

$$\begin{aligned} \text{captured fish} \sim & \text{offset}(\log(\text{effort})) + \text{offset}(\log(\text{net} - \text{length})) + \text{site} * \text{area} \\ & + \text{season} + \text{net} - \text{type} + (1|\text{date}) + (1|\text{area: site}) \end{aligned}$$

In contrast to the equivalent model for angling, an offset term for the net length was included since the two net-types used differed in length. Net-type was included as a fixed variable in the model to be able to make separate predictions for each of the two since pike catchability differed between the two net-types. All other aspects of model specification and validation resembled the ones described in the previous section.

2.4.1.III eDNA

Modelling of eDNA data was intended but the data required the inclusion of a three-way interaction between site, season and area for correct predictions given the variability across seasons, sites and areas in the raw data. However, as the amount of data was insufficient for the required model complexity, the resulting model was strongly overfitted with infinitesimal confidence intervals high significance of all model terms. It was therefore opted against a modelling approach and instead only the raw data is presented.

2.4.1.IV Telemetry

To determine abundance estimates derived from telemetry records, telemetry counts per day were modelled using a generalized linear model (GLM). Since a three-way interaction between site, season and area was found to be not meaningful and the only significant two-way interaction was found between site and area, the following formula was applied:

$$\text{count} \sim \text{site} * \text{area} + \text{season}$$

For model specification, a gaussian distribution with an identity link was chosen as response data were approximately normally distributed. Model verification confirmed a good fit of the CPD.

2.4.1.V Full comparison angling dataset

The analysis of catch rates in relation to the site was also performed with the larger dataset of both randomized and non-randomized angling events, where the total number

of observations (i.e. fishing sessions of individual anglers) was $n = 1368$. The model function was specified as:

$$\begin{aligned} \text{captured fish} \sim & \text{offset}(\log(\text{effort})) + \text{site} + \text{season} + \text{site} * \text{season} \\ & + (1|\text{area}) + (1|\text{area}:\text{site}) + (1|\text{date}) + (1|\text{sampler}) \end{aligned}$$

The variables of interest were the site and the season (meteorological scale) but also a possible interaction effect between the two, since an increase of magnitude in the effect of site across the seasons could be an indication for timidity due to ongoing fishing pressure in the OA areas leading to decreasing catches across the year while catches in the MPA might be more stable. The random effects structure controlled for variation in the response variable due to different samplers, dates and areas with the random interaction term between area and site accounting for spatial nestedness. The specific comparison area was not considered as fixed effect, since the number of comparison areas was rather high ($n = 9$) and the dataset was unbalanced with some areas being subject to only very little sampling effort. The model was specified with a poisson CPD and a log-link.

2.4.2 Evidence for timidity-induced effects on CPUE

To determine whether beta estimates for the effect of site were significantly different between angling and angling-independent gears (hypothesis = greater decrease of slope in OA with angling when compared to other gears which potentially better reflect underlying abundance), three different gears were looked at which could explain pike abundance: Gillnet catches, eDNA concentrations and telemetry counts. Each of the three gears were compared with angling catches by building models including an interaction term between gears and site (Figure 15).

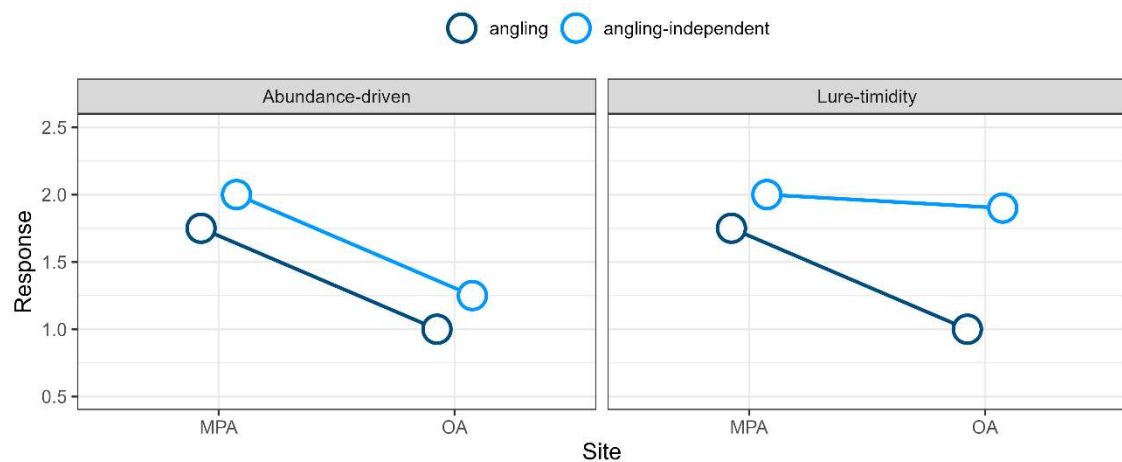


Figure 15 Conceptual depiction of timidity as witnessed by a gear*site interaction. If the differences in catch rates between angling and angling-independent gears are purely

abundance driven, the slopes are expected to be similar between gears (left plot). However, if there is an additional timidity effect, the slope of angling is expected to be significantly steeper than that of angling-independent gears.

Data preparation included appending the long-format data frames from angling and the respective angling-independent gear via the *rbind()* command. The response-variables of both gears were aligned in one column, as were all other variables relevant for the model. The column “gear” was created to differentiate between the two gears. For angling data, raw data were grouped by date, site and boat, yielding one summarized observation for each site and boat employed on the respective sampling day. This was necessary to avoid pseudoreplication as the data structure did not allow to include random effects for variables which were only contained in one of the gears (i.e. “sampler” was contained in angling data but not in gillnet data).

To bring the ranges of the response variable of the two gears to the same scale, response data were normalized within each gear to obtain values between 0 and 1 by the following function:

$$\frac{Y_i - \min(Y)}{\max(Y) - \min(Y)}$$

To account for differences in effort, CPUE (catch/h) was used for angling- and gillnet data and concentration (µg/l) for eDNA. For telemetry, effort was not specifically recorded but lasted over the entire day for all data and was therefore not considered an important metric. GLMMs were then built using the *glmmTMB* package (Mollie et al. 2017). Following the residual analysis for model validation, parametric bootstrapping was applied on eDNA data to validate significances using confidence intervals.

2.4.2.1 Angling * Gillnets:

Because gillnet catches of pike were extremely low in summer and autumn and were thus not deemed representative, only data from spring sampling was used for analysis. Data thus consisted of $n = 32$ observations (each observation representing one individual gillnet) for gillnets and $n = 32$ observations from angling (each observation representing a summarized angling day per boat and site). In accordance with the distribution of normalized data, a GLMM with a gaussian CPD was used and the following formula was specified:

$$\text{count} \sim \text{site} * \text{method} + (1|\text{date}) + (1|\text{area}) + (1|\text{area}:\text{site})$$

The random structure in the model accounts for variation between days and nesting in the data.

2.4.2.II Angling * eDNA:

Because in 31 out of 108 eDNA mixed samples no pike DNA could be detected, these observations were removed from the data for the following analysis. Consequently, eDNA and angling data consisted of $n = 67$ observations (one observation per mixed sample) and of $n = 110$ observations (summarized by boat, day and site), respectively. A tweedie-CPD was deemed a good fit given that response data contained decimals numbers and 18% zeros. The following formula was specified:

$$\begin{aligned} \text{count} \sim & \text{site} * \text{method} + (1|\text{date}) + (1|\text{area}) + (1|\text{season}) + (1|\text{area: site}) \\ & + (1|\text{area: season}) + (1|\text{area: season: site}) \end{aligned}$$

The random structure in the model accounts for variation among days and nesting in the data as well as a crossed structure between season and area where each season is contained in each area and vice versa.

2.4.2.III Angling * Telemetry:

On a total of 19 sampling dates, telemetry counts (individual fish) were recorded during angling from both sites of each area ($n = 38$ observations). These data were appended to the angling data of the respective sampling dates ($n = 380$ observations). Data were modelled with a GLMM with a gaussian CPD. The following formula was used for applied:

$$\text{count} \sim \text{site} * \text{method} + (1|\text{date}) + (1|\text{area}) + (1|\text{area: site})$$

2.4.3 Length and age

To determine whether (1) larger or (2) older pike tended to be underrepresented in the OA angling sample but were found in OA gillnet catches, indicating active lure avoidance of these more experienced fish, the (1) length and (2) age of pike was assessed as a function of an interaction effect between site and gear. As in previous models, the nesting between site and area was used as random terms to avoid pseudoreplication of the variable site. Since data were approximately normally distributed, a gaussian CPD with an identity link function was used in the GLMM. The formula was specified as:

$$(1) \text{ length} \sim \text{site} * \text{gear} + \text{area} + (1|\text{sex}) + (1|\text{area: site})$$

$$(2) \text{ age} \sim \text{site} * \text{gear} + \text{area} + (1|\text{sex}) + (1|\text{area: site})$$

Since the dataset was not large enough to account for a potential three-way interaction between site, gear and season, the model was tested with the inclusion of a second interaction term between season with (a) gear and (b) site but found no significant indications that there was a relationship between them.

2.4.4 Growth

To see whether growth differed between the pike captured with different gears between the sites, size-corrected growth data (where each individual contained one observation for the sum of life years -1) were analyzed. Differences in growth due to sex or age were accounted for by the inclusion of the random variables sex and lifeyear. To statistically account for the repeated measures within individuals, also the individual was used as a random effect in the model with the following formula:

$$growth \sim site * gear + area + (1|individual) + (1|lifeyear) + (1|sex) + (1|area:site)$$

The model was built with a gaussian CPD and an identity link function.

2.4.5 Proportional stock density

In order to evaluate how the protection status affected the size structure, the dataset from all comparison angling events (randomized and non-randomized) as well as the comparison gillnet fishing events where each row corresponded to one observation of a pike captured were analyzed. The concept of the proportional stock density (PSD), proposed by Wege & Anderson (1978) which is an index used to inform about the size structure of a population, was used. It is defined as:

$$PSD = \frac{\text{number of fish} \geq \text{quality length}}{\text{number of fish} \geq \text{stock length}} * 100$$

Suggestions for the two length measures contained in the formula were published by Gabelhouse (1984), where 53 cm was originally proposed as quality length for northern pike. However, since the pike stock of inference is known to be fast growing and 97% of all fish contained in the sample exceeded 53 cm, a threshold of 85 cm was defined for quality fish and 50 cm for stock length as this is the official minimum size limit and thus represents fish entering the fishery.

Additionally, the probability of a fish being larger than quality length, i.e. 85 cm was modelled as a function of site while controlling for other variables potentially explaining this. The model formula was:

$$quality\ fish\ [1 - 0] \sim site + season + sex + (1|area) + (1|area:site)$$

The model was specified with a binomial CPD since the response variable was binary. For this calculation only pike sampled with angling gear were used since data from gillnet fishing were highly unbalanced with respect to seasons.

2.4.6 Attack rate

To determine the probability of a pike following the lure vs. a pike attacking the lure between the sites, the number of followers and the number of attacks (bites + captured

fish) was summarized per day, boat and site from all angling data, yielding a total of 196 observations. A logistic regression was applied to estimate the odds of an individual following the lure without attack vs. the individual attacking the lure.

$$c(\text{follower}, \text{attacks}) \sim \text{site} + (1|\text{date}) + (1|\text{area}) + (1|\text{area: site})$$

By using `cbind(follower, attacks)` as the response term, the model takes into account absolute numbers of the two variables which allows for increased statistical power over a ratio which does no longer contain information on absolute occurrences of the two events. Site was the only fixed variable in the model, as it was the only variable of interest. A random term for date was added to account for temporal autocorrelation. The two random effect terms area and area:site were incorporated in the model to account for spatial nestedness of the data where site was nested within each of the three comparison areas. For modelling, the `glmer()` function from the R-package lme4 package (Bates et al. 2015) was chosen which can handle the `cbind()` command in the response term. A binomial CPD was chosen to model the probability of one event occurring over the other.

2.4.7 Landing rate

To determine the probability of a fish being retained on the hook until capture upon attacking the lure, the number of fail bites (bites where pike were not successfully landed) and the number of landed pike was summarized per day, boat and site from all angling data. The same logistic regression as described in “Attack rate” was used, however, the random term for area was removed since the model showed singular fit when keeping all random terms from model 1. Using the likelihood-ratio test it was found that “(1|area:site)” was a significant improvement over the reduced model containing only the random date term, while (1|area) was not. The final model was:

$$c(\text{bites}, \text{captured fish}) \sim \text{site} + (1|\text{date}) + (1|\text{area: site})$$

All other steps were identical to the ones described in the previous section.

2.4.8 Lure-effects on catchability

2.4.8.1 Lure Type (Observational)

To compare the catchability of different lure types and assess the lure specific differences in catchability inside and outside of MPAs as a potential indicator of timidity (i.e. via lure specific attributes affecting the strength of stimuli emitted from each lure) the effect of lure type * site on the number of captured pike per session was modelled. The dataset used to explore lure effects consisted of n = 1483 observations, where each observation corresponded to one fishing session of one angler with a specific lure type.

Lure types were aggregated in two ways: In a first analysis lures were categorized according to their commercial differentiation into 6 levels (metal lures [spoons and spinners], crankbaits, jerkbaits, swimbaits, rubber lures and flies). In a second analysis lures were categorized into 2 levels using the categories “soft lures” (rubber lures, swimbaits and flies) and “hard lures” (metal lures, jerkbaits and crankbaits). In both analyses, data were unbalanced with regards to lure type. An interaction between lure type and site (categorical, 2 levels) was used as fixed effects since the main interest were differences in catch rates for each lure type depending on site. Raw data of fishing sessions were used as model input, where rows were individual fishing sessions per angler. A GLMM with a poisson CPD and a log-link was used to account for the nature of the response variable (count data). Fishing duration was used as an offset term in the model to account for differences in fishing effort between the sessions. To account for variation caused by sampler, fishing day, season or the comparison area these terms were used as random effects in the model and a random intercept was used for the interaction between area and site to account for spatial nestedness of the sites within areas.

$$\begin{aligned} \text{captured fish} \sim & \text{offset}(\log(\text{effort})) + \text{luretype} * \text{site} + (1|\text{sampler}) + (1|\text{date}) \\ & + (1|\text{season}) + (1|\text{area}) + (1|\text{area: site}) \end{aligned}$$

The model was checked for normality of residuals, homogeneity and overdispersion and was validated in all of these aspects. To minimize the risk of type-1 errors, a Benjamini & Hochberg correction of p-values was used when assessing individual differences between catch rates for each lure between MPA and OA.

2.4.8.II Lure Color (Observational)

To see whether lure color was affecting CPUE, lure color was assigned one of two categories by judging the color profile of the lure, where bright and colorful lures were assigned “shock” and more natural color profiles were assigned “natural”. The same dataset as described in the previous section was used. The effect of lure color on catch rate was then tested in the same GLMM as described in the previous section (1| Lure Type), but where lure type was replaced by lure color while all other terms were held constant. Also, for model validation and derivation of statistical significance the same steps as described previously were undertaken.

2.4.8.III Lure Color (Experimental)

To find whether bright (unnatural) colors were a disadvantage when fishing for pike in OA areas as a further indication for timidity, an experimental fishing design was pursued during randomized comparison angling. For this, standardized lures (Savage Gear Real

Trout, 20 cm) were fished in two distinct color patterns (rainbow trout vs. firetiger, Figure 16). It was expected that the natural design would catch more fish in the OA due to fish potentially being more cautious towards unnatural colors while there would be no such difference or even the reversed trend in the MPA. Each color was fished at least once in each site per fishing day. The sequence was randomized to control for daytime effects. On a total of 23 sampling days at least one angler fished this according to this design. If two anglers followed the design on the same day, both colors were fished simultaneously. The data consisted of 156 observations (i.e. individual angling sessions). To analyze whether the catch rates of the two colors differed systematically between the sites, the same GLMM as in the previous section was applied (interaction effect between color and site).



Figure 16 Lures from standardized color comparison. Aggressive firetiger (left) and natural rainbow trout design (right).

2.4.9 Probability of zero catch

To model the probability of a fishing session without fish contact (i.e. where pike are neither captured, nor registered as bites), raw data from all comparison angling sessions (randomized & non-randomized) were used, where each observation ($n = 1368$) represented one fishing session of an angler. A binary column categorizing fishing sessions into one of two groups (0 = fish contact; 1 = fish contact) was modelled as the response variable in a GLMM (glmer function of the lme4 package). Site (categorical, 2 levels), season (categorical; 4 levels, according to astronomical cycle) and the interaction effect between them were used as the fixed model terms. A potential interaction effect between site and area was not accounted for since data for different areas were highly unbalanced with some areas only having very few observations. Random terms included the date, the combination of date and boat (since it was expected that fishing success varied between the boats on each fishing day), the area and the area:site to account for spatial nestedness, yielding the formula:

$$\text{no contact} [1 - 0] \sim \text{offset}(\log(\text{effort})) + \text{site} + \text{season} + \text{site:season} + (1|\text{sampler}) \\ + (1|\text{date}) + (1|\text{date:boat}) + (1|\text{area}) + (1|\text{area:site})$$

Given the binomial nature of the response variable, a binomial CPD was used in the model.

2.4.10 Analysis of recapture data

In addition to the data collected during fieldwork, a dataset of recaptured pike from the BODDENHECHT project was analyzed. A total of 672 fish were recaptured with angling- or commercial gear, which provided an opportunity to investigate recapture specific patterns that may reveal indications for lure timidity.

2.4.10.I Recapture gear

To test whether pike with a prior lure experience were more likely to be recaptured with commercial gears than angling as a potential indication for lure avoidance, a binary response variable was created indicating whether a fish with a recapture history was recaptured with commercial gears. Similarly, a binary explanatory variable was created, indicating whether a fish was caught with lures at the first capture. The effect of the gear at first capture on the gear at the recapture event was tested. Due to the binary nature of the response variable a binomial CPD was used.

$$\text{recapture_commercial}[1 - 0] \sim \text{firstcatch_lure}[1 - 0]$$

2.4.10.II Time to recapture

It was tested whether the duration between the first and the second capture event of recaptured pike was gear specific in a way that fish which had a prior experience with lures were potentially unavailable for a second capture with lures for extended periods while a recapture with commercial gears (e.g. gillnets / fyke-nets) was more likely within shorter timespans upon their first capture for these individuals. For this analysis all recaptures were categorized with the gear sequence they were captured with (i.e. Angling-Angling; Commercial-Angling and so forth) with respect to their previous and their current capture event. In addition, the duration (number of days) between the two capture events was calculated. Statistical inference was drawn with a Kruskal-Wallis test to see whether the median duration between capture events differed between the gear sequences assigned to each recapture, because data followed no specific distribution.

2.4.10.III Recapture Probability between Sites

To test whether the probability of recapturing an individual was lower in areas subject to regular fishing pressure (OA) than in sites that experienced extended periods without exposure to angling gear (i.e. the MPAs sampled throughout the MPA comparison angling events), data from both comparison angling events as well as capture data from guides who marked fish as part of the project in OA sites were used. The dataset comprised 1672 pike. A binomial model with the formula was used:

$$\text{recapture}[1 - 0] \sim \text{site}$$

3 Results

3.1 Descriptives

3.1.1 Observed fishing effort

Angling pressure was observed in all OA sites, averaging 0.6 boats per day for Werderbucht and Ummanz and 0.9 boats per day in Sellin. In the MPAs of Werderbucht and Ummanz, no anglers were observed on any of the sampling days while mean angling effort was 0.4 angling boats per day in the MPA of Sellin (Figure 17). Commercial gears were found in all MPAs. Lowest commercial fishing effort was found in Werderbucht where only eel traps were observed. In Ummanz, higher levels of commercial fishing pressure were observed inside the MPA (eel traps and gill nets), even exceeding levels in the OA. In Sellin, there was higher commercial fishing effort with eel traps inside the MPA while gillnet effort was twice as high in the OA. Results are shown in Figure 17.

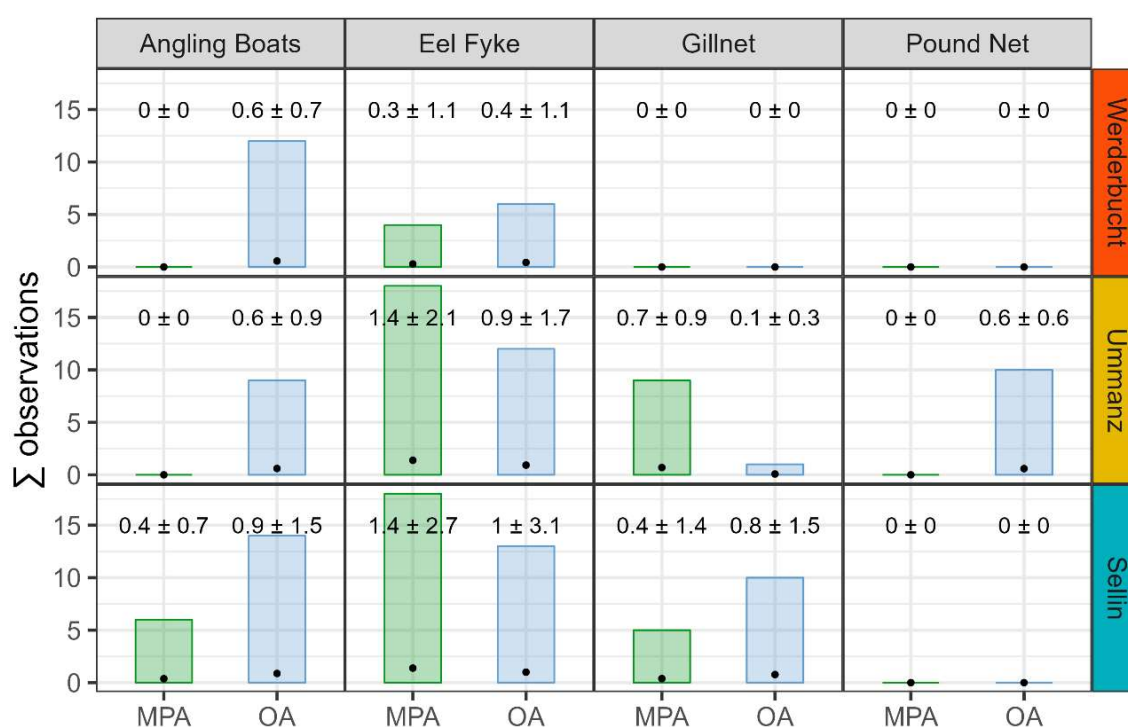


Figure 17 Observed fishing effort in the 3 comparison areas (horizontal panels) per site (x-axis). Columns show the sum of observations per category across all sampling days. Mean daily values are displayed by black points. Numbers for daily mean $\pm$ SD are shown as text within each facet. Data were recorded between April 2022 and January 2023.

3.1.2 Angling catches

During 59 days of comparison angling between MPA and OA, a total of 464 pike were captured. 80% of pike were captured within MPAs. Mean CPUE was around 4 times

higher inside MPAs compared to OAs (Table 6). Fishing effort required to capture a large pike > 1 m total length (TL) was 7-fold higher in the OA than in the MPA during randomized angling and 20-fold higher during non-randomized angling (Table 6). A full summary is provided in Table 6.

Table 6 Angling effort and respective catch-related summaries from both randomized and non-randomized sampling events.

Angling type	Randomized angling		Non-randomized angling	
No. of sampling days	40		19	
No. of samplers / day	4.6 ± 1.4 [mean ± SD]		6.0 ± 3.0 [mean ± SD]	
No. of boats / sampl. day	1.4 ± 0.5 [mean ± SD]		1.6 ± 0.9 [mean ± SD]	
No. of anglers per boat	3.5 ± 0.6 [mean ± SD]		3.9 ± 1.0 [mean ± SD]	
Σ effort (h * sampler)	964		800	
No. of comparison areas	3		8	
Site	MPA	OA	MPA	OA
Pike [n / share]	212 / 80%	54 / 20%	160 / 81%	38 / 19%
Pike > 1 m TL [n]	7	1	21	1
Mean CPUE (pike / h) ± SD	0.439 ± 0.306	0.112 ± 0.132	0.388 ± 0.384	0.098 ± 0.210
Mean CPUE (pike > 1 m TL / h) ± SD	0.015 ± 0.038	0.002 ± 0.013	0.051 ± 0.100	0.003 ± 0.001
Effort (h) per pike > 1 m TL	68.6	481.3	19.6	387.9

During randomized angling, a total of 266 pike were captured. Highest mean CPUE was found in Werderbucht (MPA), followed by Ummanz (MPA) and Sellin (MPA). Differences in mean CPUE between the sites were most pronounced in Ummanz, where mean CPUE was about 6.5 time higher inside the MPA compared to the OA, while this figure was 4.2 in Werderbucht and only 2.1 in Sellin. A summary can be found in Table 7.

Table 7 Catch statistics from randomized comparison angling for each comparison area.

Area	Site	Pike [n / share within area]	Mean CPUE (pike / h) ± SD	Mean CPUE ratio	n pike TL > 1 m
Werderbucht	MPA	96 / 81%	0.478 ± 0.691	4.2	2
	OA	22 / 19%	0.113 ± 0.318		1
Ummanz	MPA	64 / 88%	0.423 ± 0.652	6.5	5
	OA	9 / 12%	0.065 ± 0.232		0
Sellin	MPA	52 / 69%	0.383 ± 0.648	2.1	0
	OA	23 / 31%	0.182 ± 0.416		0

3.1.3 Gillnet catches

Overall, 126 pike were captured during gillnet samplings, 106 (84%) thereof with specific pike gillnets and 20 (16%) with gillnets used to sample the preyfish communities. Strong seasonality was evident in catch rates with 90.5% (n = 114) of all pike captured during spring samplings. Across all seasons, the number of pike captured in Sellin, Ummanz and Werderbucht was 36, 45 and 45, respectively. The ratios of mean gillnet CPUE between MPA and OA sites were 2.5 for Werderbucht and 1.5 for Ummanz and Sellin across seasons. Across all areas and seasons, gillnet CPUE was 1.68 times higher inside MPAs. An enumeration of gillnet catches is provided in Table 8.

Table 8 Overview of gillnet pike catches across all seasons, areas and sites.

Season	Area	Site	n pike from pike gillnets	n pike from preyfish gillnets	n pike total	share from MPA [%] (mean ratio)
Spring	Werderbucht	MPA	26	5	31	74 (2.81)
		OA	10	1	11	
	Ummanz	MPA	22	2	24	60 (1.5)
		OA	14	2	16	
	Sellin	MPA	14	4	18	56 (1.29)
		OA	9	5	14	
Σ Spring					114	64 (1.78)
Summer	Werderbucht	MPA	0	0	0	0 (-)
		OA	1	0	1	
	Ummanz	MPA	0	1	1	50 (1)
		OA	1	0	1	
	Sellin	MPA	0	0	0	-
		OA	0	0	0	
Σ Summer					3	33 (0.5)
Autumn	Werderbucht	MPA	1	0	1	50 (1)
		OA	1	0	1	
	Ummanz	MPA	2	0	2	66 (2)
		OA	1	0	1	
	Sellin	MPA	2	0	2	50 (1)
		OA	2	0	2	
Σ Autumn					9	56 (1.25)
Σ Total					126	63 (1.68)

3.1.4 eDNA

Summarized across seasons and areas, eDNA concentrations were 4.21 ± 7.43 copies / μL (mean $\pm$ SD) for MPAs and 2.92 ± 3.64 copies / μL (mean $\pm$ SD) for OAs, indicating 1.4 times higher concentrations in MPAs. However, there was pronounced

season variation in eDNA concentrations with highest values measured in spring while for most sites the levels were low throughout summer and autumn (Figure 18, Table 9). When looking at the different comparison areas, the seasonal trend was particularly pronounced in Ummanz while in Sellin higher values were detected also in summer and autumn (Figure 18). No area showed consistently higher concentrations in one of the sites across seasons. The share of samples with no detectable levels of pike DNA was highest in summer (Table 9).

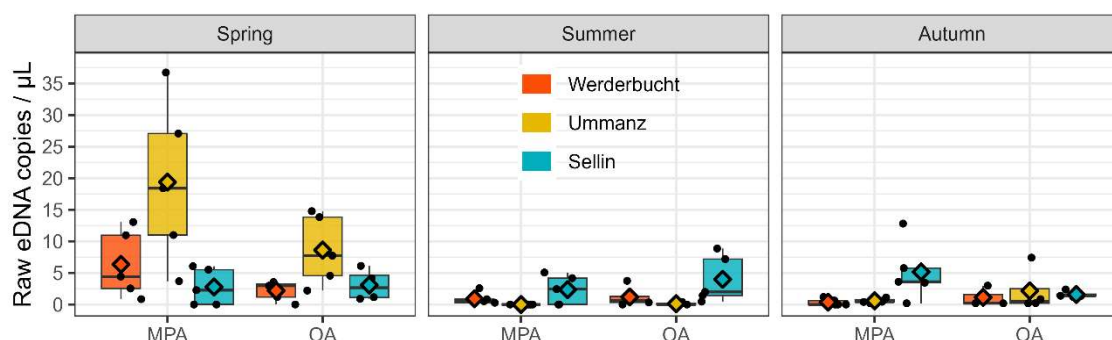


Figure 18 Raw data of eDNA concentrations (copies / μL) for the three comparison areas (color) and their sites (x-axis) across the three seasons (panels). Black dots represent mixed samples, distribution is emphasized by boxplots. Diamonds display mean values.

Table 9 Measured eDNA concentrations across all seasons, areas and sites.

Season	Area	Site	Mean $\pm$ SD [copies / μL]	Range [copies / μL]	Share zeros [%]
Spring	Werderbucht	MPA	6.36 ± 5.35	0.8 - 13.1	0
		OA	2.19 ± 1.53	0 - 3.6	20
	Ummanz	MPA	19.38 ± 13.01	3.7 - 36.7	0
		OA	8.62 ± 5.56	2.2 - 14.8	0
	Sellin	MPA	2.77 ± 2.91	0 - 6.1	40
		OA	3.08 ± 2.5	0.9 - 6.1	0
Summer	Werderbucht	MPA	0.9 ± 0.97	0.3 - 2.6	0
		OA	1.2 ± 1.5	0 - 3.7	20
	Ummanz	MPA	0 ± 0	0 - 0	100
		OA	0.13 ± 0.23	0 - 0.4	66
	Sellin	MPA	2.33 ± 2.33	0 - 5.1	40
		OA	3.98 ± 3.77	0.5 - 8.9	0
Autumn	Werderbucht	MPA	0.36 ± 0.54	0 - 1.2	60
		OA	1.12 ± 1.61	0.2 - 3	0
	Ummanz	MPA	0.58 ± 0.36	0.2 - 1.1	0
		OA	2.16 ± 3.52	0.2 - 7.4	0
	Sellin	MPA	5.16 ± 4.71	0.2 - 12.8	0
		OA	1.58 ± 0.54	1.2 - 2.4	0

3.1.5 Telemetry

In all areas, the number of pike detected per day was higher in the MPA sites. The difference between MPA and OA was most pronounced in Werderbucht, where 87% of mean daily counts were detected inside MPAs while his figure was 74% and 70% for Ummanz and Sellin, respectively. Details are provided in Table 10.

Table 10 Daily telemetry counts of pike individuals from the three comparison areas.

Area	MPA [mean $\pm$ SD / range]	OA [mean $\pm$ SD / range]	Mean ratio
Werderbucht	7.2 $\pm$ 1.6 / 5 - 9	1.1 $\pm$ 1.1 / 0 - 3	6.5
Ummanz	2.8 $\pm$ 0.8 / 2 - 4	1 $\pm$ 1.2 / 0 - 3	2.8
Sellin	2.8 $\pm$ 1.4 / 1 - 5	1.2 $\pm$ 0.7 / 0 - 2	2.3

3.1.6 Camera transects

From over 40 hours of video material, 7 lure attacks of pike were identified, thereof 4 on the bucktail spinner and 3 on the rubber trout (Table 11, Figure 19). In addition, 5 individuals were found to only follow the lures without an attack (bucktail spinner: $n = 4$, rubber trout: $n = 1$). Moreover, several pike were mainly interested in the lure camera (attacks: $n = 5$, follower: $n = 1$). The overall low numbers of pike interactions did not allow for statistical tests. However, the bucktail spinner yielded an equal number of followers and attacks in both sites (MPA: $n = 3$, OA: $n = 1$) while the rubber trout was attacked more vigorously in the MPA (attack rate = 100%, $n = 2$) compared to the OA (attack rate = 50%, $n = 2$). However, if all pike interactions (including interactions with the camera) were considered, the bucktail spinner yielded markedly higher attention in the MPAs ($n = 12$) compared to the trout ($n = 2$), while there was no such difference in the OAs ($n = 2$ for each lure). All interactions with the lure camera were found in the setup with the bucktail spinner within the MPA. The overall number pike individuals detected in the camera footage was 3.5 times higher in MPAs compared to OAs. Results are displayed in Table 11.

Table 11 Total numbers of pike attacks and followers from lure camera trawling for each site and lure. BS: Bucktail Spinner; RT: Rubber Trout.

Site	Lure	Σ Lure attack	Σ Lure follower	Σ Camera attack	Σ Camera follower	Σ Interactions	Attack Rate
MPA	BS	3	3	5	1	12	25%
MPA	RT	2	0	0	0	2	100%
OA	BS	1	1	0	0	2	50%
OA	RT	1	1	0	0	2	50%

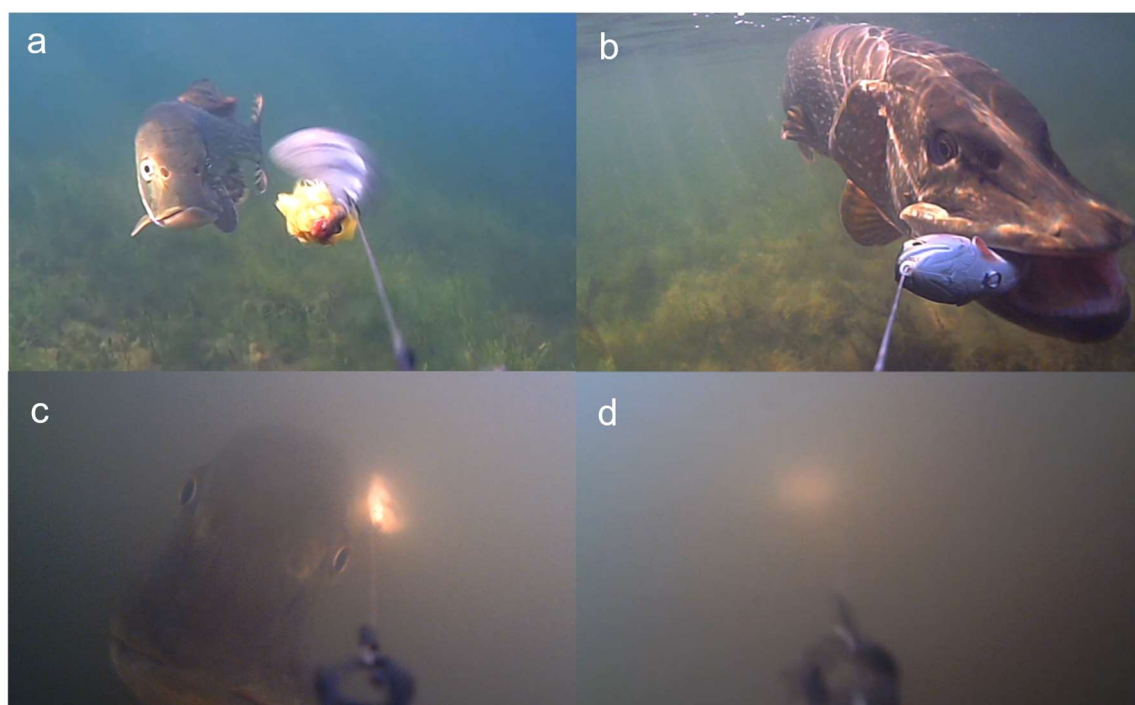


Figure 19 Footage from lure camera trawling. (a) A pike following the bucktail spinner. (b) A large individual attacking the rubber trout. (c) A pike with greater interest in the camera than in the bucktail spinner. (d) Seasonal differences in visibility and macrophyte entanglement contributed negatively to identification of pike in the video material.

3.2 Statistical analysis

3.2.1 Catch rates of different gears between MPA and OA

3.2.1.1 Randomized Angling

Pike angling CPUE (pike / h * angler) differed significantly between the sites ($\chi^2 = 11.3$, $df = 1$, $p < 0.001$), where mean values were 0.434 ± 0.666 (mean $\pm$ SD) for the MPA and 0.117 ± 0.329 for the OA. Similarly, the season had a significant effect on catch rates ($\chi^2 = 7.45$, $df = 2$, $p = 0.024$). Values were 0.261 ± 0.479 (mean $\pm$ SD) for spring, 0.383 ± 0.654 for summer and 0.198 ± 0.488 for autumn. A post-hoc test revealed that the significance of the variable season was driven by the significantly higher catches in summer when compared to autumn (emmeans, ratio = 1.978 ± 0.496 SE, $p = 0.018$), while the other seasons did not differ significantly from each other. There was no significant difference in CPUE between the three areas ($\chi^2 = 1.53$, $df = 2$, $p = 0.465$), however, the interaction effect between site and area was significant ($\chi^2 = 7.31$, $df = 2$, $p = 0.026$). This indicates that the differences in catches between OA and MPA had different magnitudes across the areas. This difference was lowest in Sellin where catches were over two-fold higher in the MPA (emmeans, ratio = 2.319 ± 0.581 SE, $p < 0.001$) but more than 4-fold higher in Ummanz (emmeans, ratio = 4.364 ± 1.031 SE,

$p < 0.001$) and over 7-fold higher in Werderbucht (emmeans, ratio = 7.103 ± 2.529 SE, $p < 0.001$). The model R^2 was 0.26, indicating that the fixed model components explained 26% of the variation in catches. Model results and raw data are displayed in Figure 20.

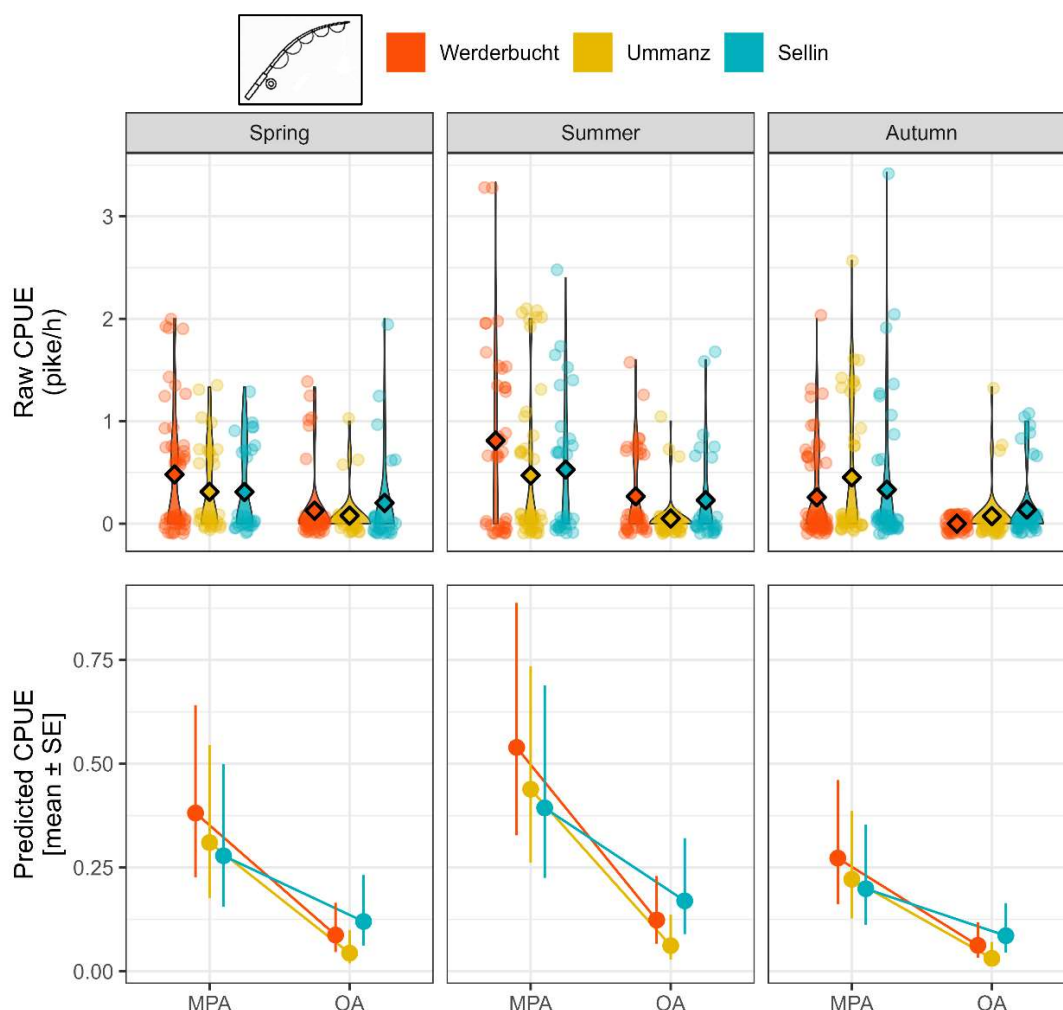


Figure 20 Raw (top row) and predicted (bottom row) CPUE (pike/h) from randomized angling sessions for each area (color) and site (x-axis) across the three sampling seasons (vertical panels). Distribution of raw data is emphasized by violin plots with mean values represented by diamonds.

3.2.1.II Gillnets

Gillnet CPUE (pike / 100 m net * 12 h) was on average (mean $\pm$ SD) 0.591 ± 1.384 in the MPA and 0.313 ± 0.694 in the OA sites when averaging over areas, seasons and net types and this effect was significant ($\chi^2 = 12.5$, $df = 1$, $p < 0.001$). Catches did not significantly differ between the areas ($\chi^2 = 2.88$, $df = 2$, $p = 0.237$) and neither was the interaction effect between site and area significant ($\chi^2 = 0.39$, $df = 2$, $p = 0.821$), indicating that the magnitude of CPUE differences between MPA and OA was not strongly modified by the area. There was a pronounced seasonal effect on gillnet CPUE ($\chi^2 = 91.8$, $df = 2$, $p < 0.001$) with significantly higher CPUE (mean $\pm$ SD) in spring

(1.242 ± 1.632) when compared to summer (0.042 ± 0.2) (emmeans, ratio = 31.678 ± 18.536 SE, $p < 0.001$) and autumn (0.089 ± 0.237) (emmeans, ratio = 14.951 ± 5.186 SE, $p < 0.001$), Figure 21. However, CPUE did not significantly differ between summer and autumn (emmeans, ratio = 0.472 ± 0.315 SE, $p = 0.498$).

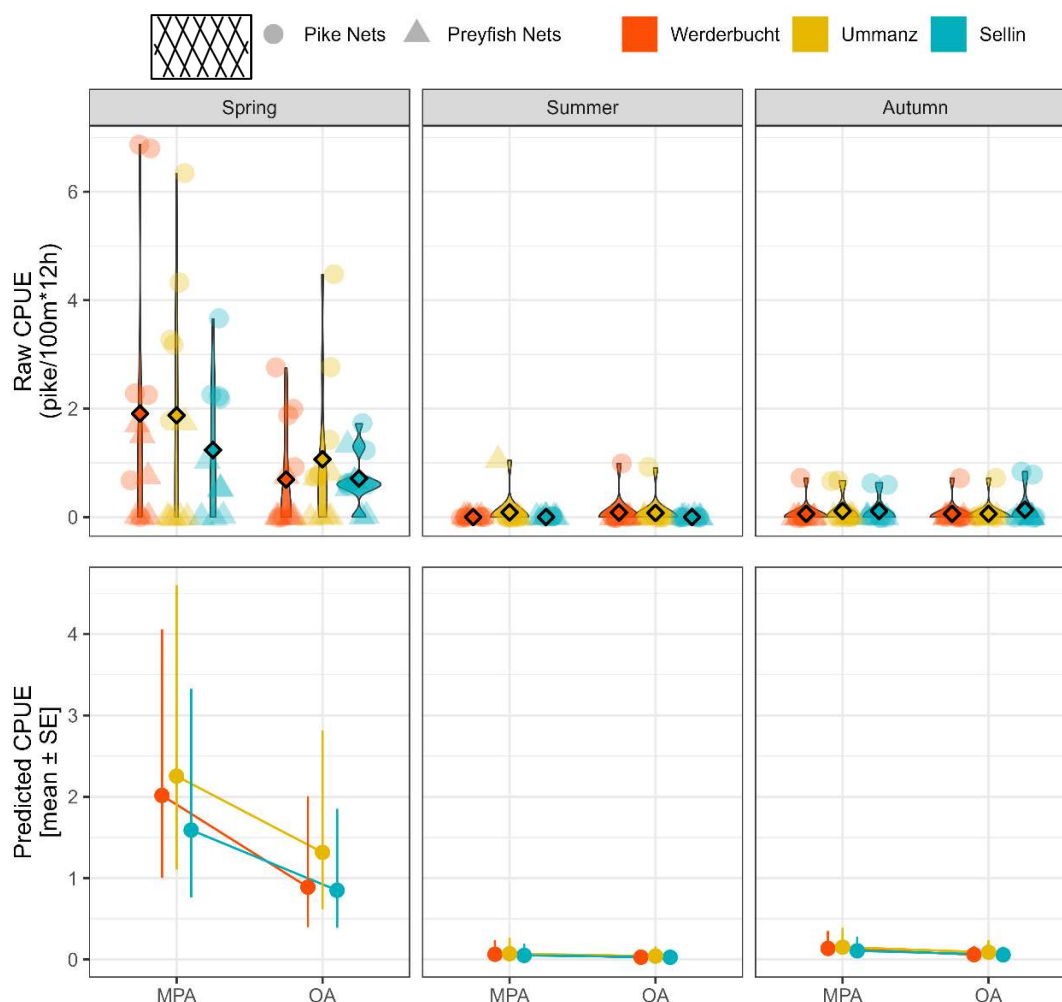


Figure 21 Raw (top row) and predicted (bottom row) gillnet CPUE (pike / 100 m net * 12 h) from gillnet sampling for each area (color) and site (x-axis) across the three sampling seasons. Distribution of raw data is emphasized by violin plots with mean values represented by diamonds. Shape of raw data points denotes the respective net-type.

In spring, when gillnet catches were highest, CPUE (mean $\pm$ SD) was 1.694 ± 2.025 in the MPA and 0.817 ± 1.002 in the OA. As expected, CPUE was significantly affected by the net type ($\chi^2 = 13.3$, $df = 1$, $p < 0.001$) where mean CPUE $\pm$ SD was 0.779 ± 1.451 for the pike nets and 0.134 ± 0.369 for the preyfish nets. The fixed model components explained 29% of the variation in gillnet catches (marginal $R^2 = 0.29$). Raw data and model predictions are displayed in Figure 21.

3.2.1.III Telemetry

The number of detected pike per day was on average (mean $\pm$ SD) 4.5 ± 2.6 individuals for the MPA and 1.1 ± 1 for the OA and the site effect was significant in predicting the number of detected pike ($\chi^2 = 107$, $df = 1$, $p < 0.001$). The season did not significantly affect the number of detections ($\chi^2 = 6.05$, $df = 3$, $p = 0.109$). The effect of area was significant ($\chi^2 = 41.8$, $df = 2$, $p < 0.001$) but must be interpreted with caution due to the significant interaction effect between site and area ($\chi^2 = 46.5$, $df = 2$, $p < 0.001$), indicating that the difference in measured abundances between OA and MPA varied with the area. In Werderbucht this difference was most pronounced with over 6-fold higher detections in the MPA compared to the OA (emmeans, ratio = 6.125 ± 0.521 SE, $p < 0.001$) while this difference was less pronounced for Ummanz (emmeans, ratio = 1.8 ± 0.659 SE, $p = 0.01$) and Sellin (emmeans, ratio = 1.5 ± 0.521 SE, $p = 0.007$). Trends are also displayed in Figure 22.

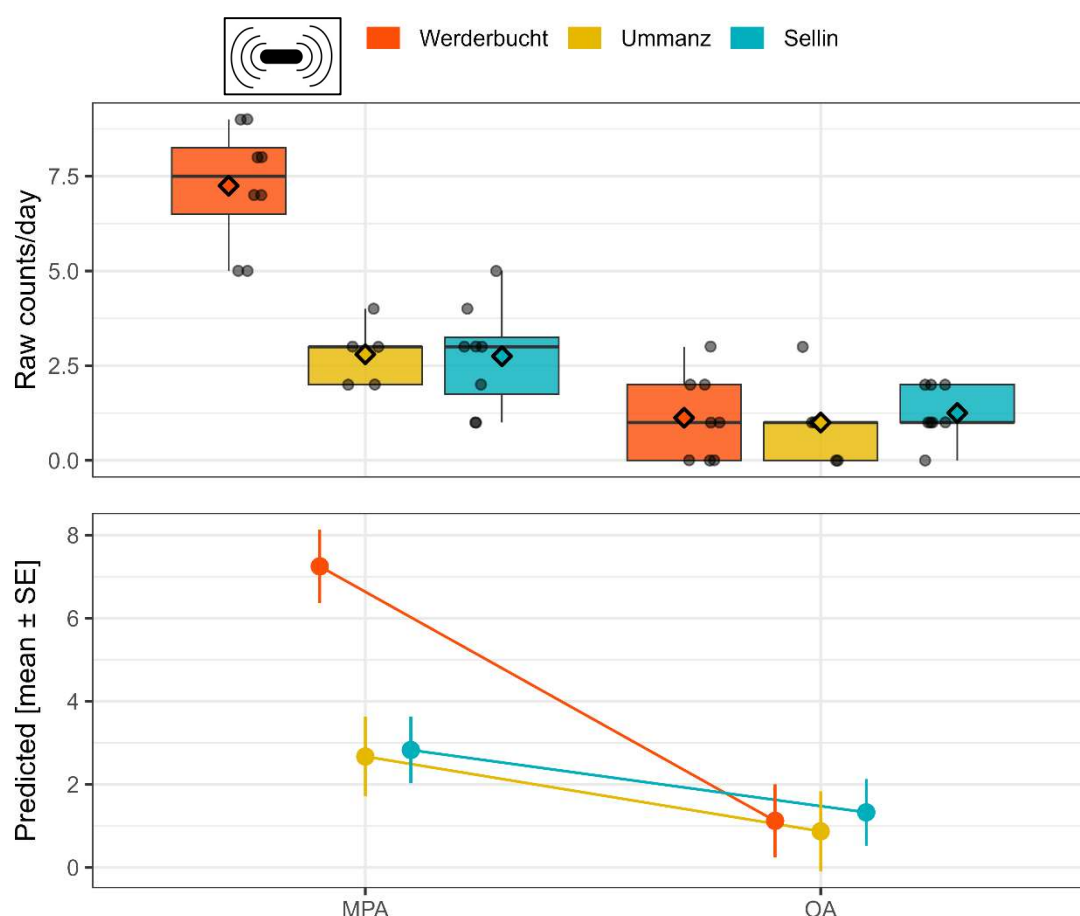


Figure 22 Raw data (top row) and predicted values (bottom row) for telemetry counts. Each black dot in the raw data represents the number of detected pike on one sampling day. Boxplots (median, box: 25 and 75 percentile, whisker: 10 and 90 percentile) emphasize the distribution of measurements per site and area, diamonds represent mean values.

3.2.1.IV Full Comparison Angling Dataset

The model suggested that there was no significant interaction between the site and the season ($\chi^2 = 4.15$, $df = 3$, $p = 0.246$), meaning that the difference in catch rates between OA and MPA was unrelated to the season. The differences in catch rates between the sites were significant ($\chi^2 = 39.9$, $df = 1$, $p < 0.001$), where CPUE (pike / h) per angler was 0.409 ± 0.655 (mean $\pm$ SD) for the MPA and 0.102 ± 0.304 (mean $\pm$ SD) for the OA. Likewise, the season was significantly affecting catch rates ($\chi^2 = 12.3$, $df = 3$, $p = 0.007$). Overall CPUE (pike / h * sampler) [mean $\pm$ SD] was highest in summer (0.374 ± 0.639) followed by spring (0.322 ± 0.61) and autumn (0.189 ± 0.456) while the lowest mean CPUE was found in winter (0.222 ± 0.461). A post-hoc comparison revealed that significant differences existed between spring and winter (emmeans, ratio = 3.239 ± 1.217 SE, $p = 0.009$), summer and winter (emmeans, ratio = 3.748 ± 1.423 SE, $p = 0.003$) and summer and autumn (emmeans, ratio = 1.877 ± 0.455 SE, $p = 0.047$). Raw data and predictions of CPUE per site and season are shown in Figure 23.

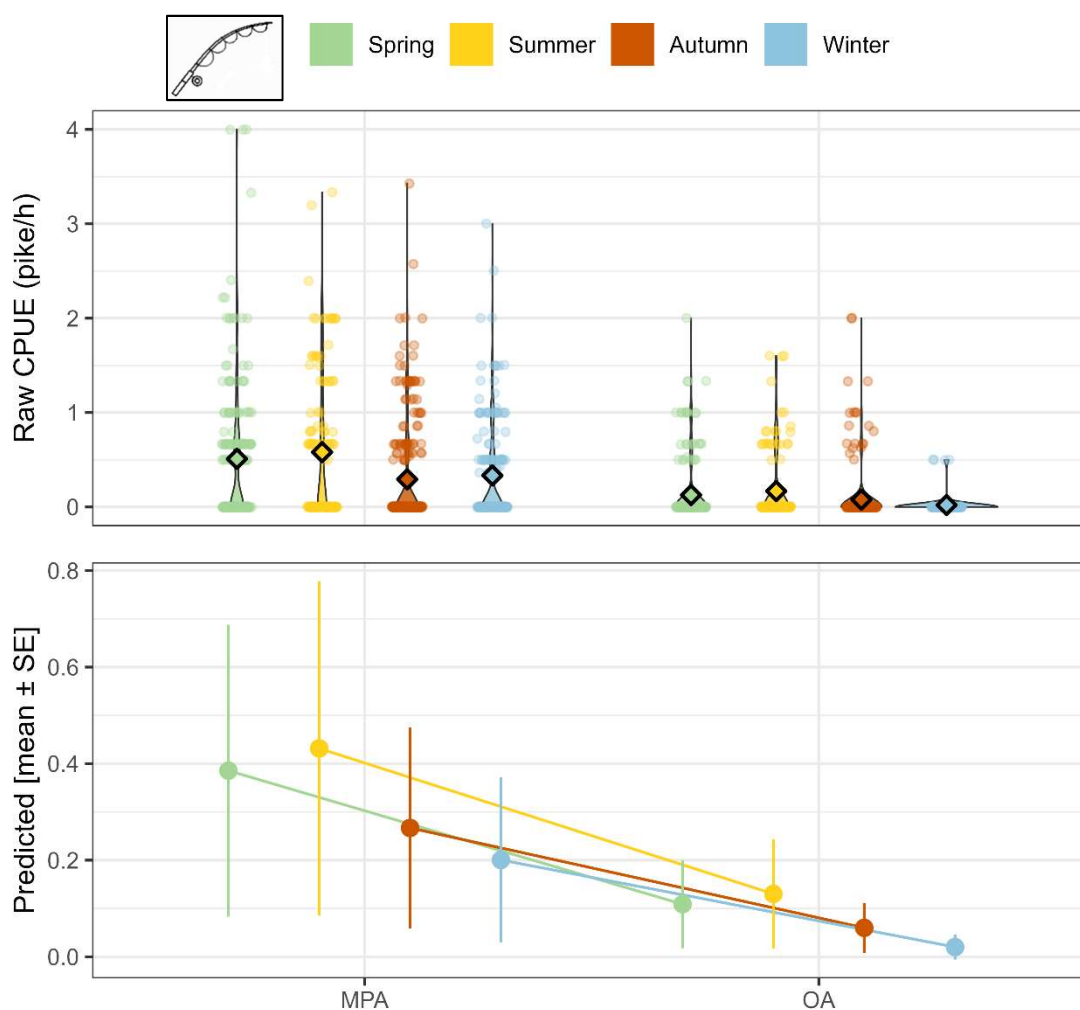


Figure 23 CPUE of pike (pike/h) between MPA and OA from both randomized and non-randomized angling samplings. The upper panel displays raw data, each point

representing one individual angling session from one sampler. Violin plots emphasize distribution of raw data, diamonds display mean values. The lower panel displays model predictions. Colors represent seasons, sites are separated along the x-axis.

3.2.2 Body length, age and growth

In pooled data from all comparison samplings (randomized-, non-randomized angling and gillnets) total length (TL) ranged from 35 to 121 cm (mean $\pm$ SD = 80.8 ± 12.7 cm) in the MPA and from 50 to 109.6 cm (mean $\pm$ SD = 76.6 ± 11 cm) in the OA. During all angling samplings, 30 pike with TL > 1 m were captured, 28 (93%) thereof in the MPA. Size distributions of pike from randomized angling and gill-netting in the three comparison areas are presented in Figure 24. Seasonal and gear-related differences in length distributions of pike from all comparison samplings are presented in Figure 25.

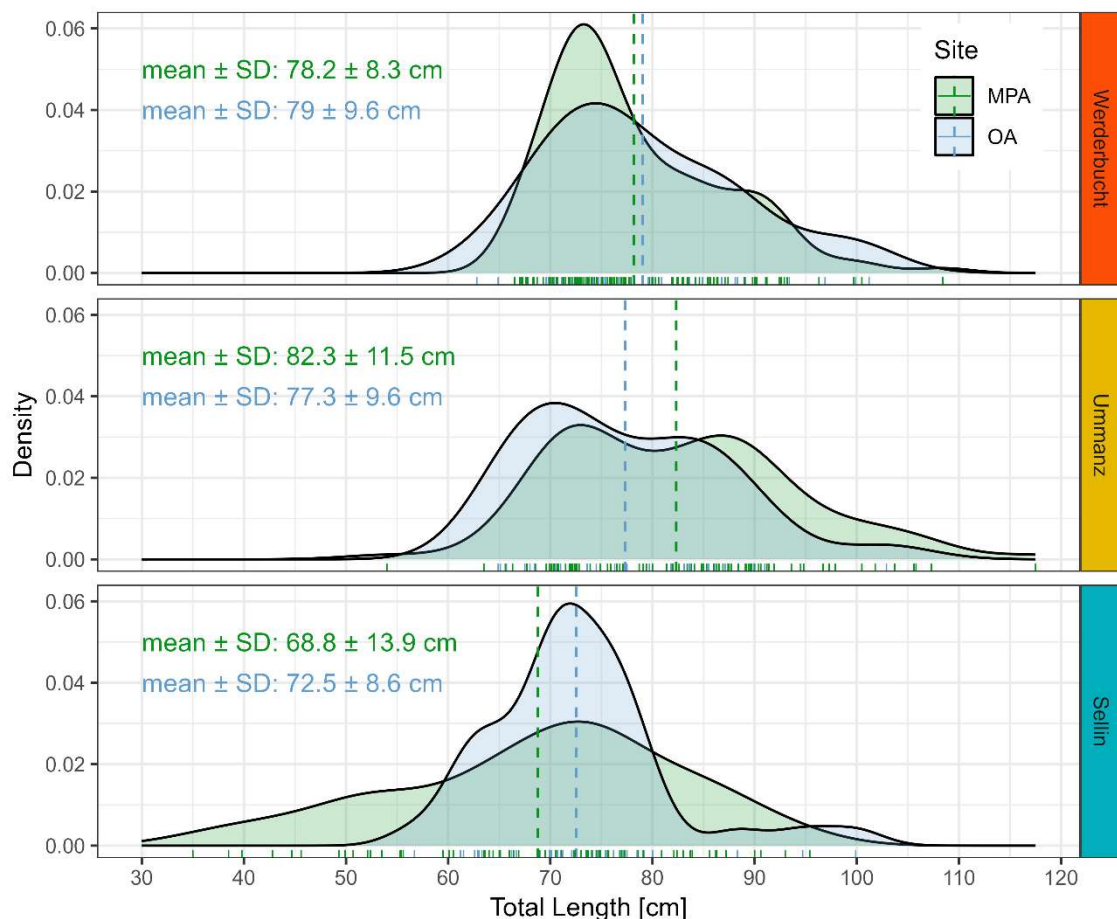


Figure 24 Density plot of total lengths of pike captured with gillnets and during randomized angling in the three comparison areas (horizontal panels) between April 2022 and January 2023. Color denotes the site of capture; vertical dotted lines represent mean values.

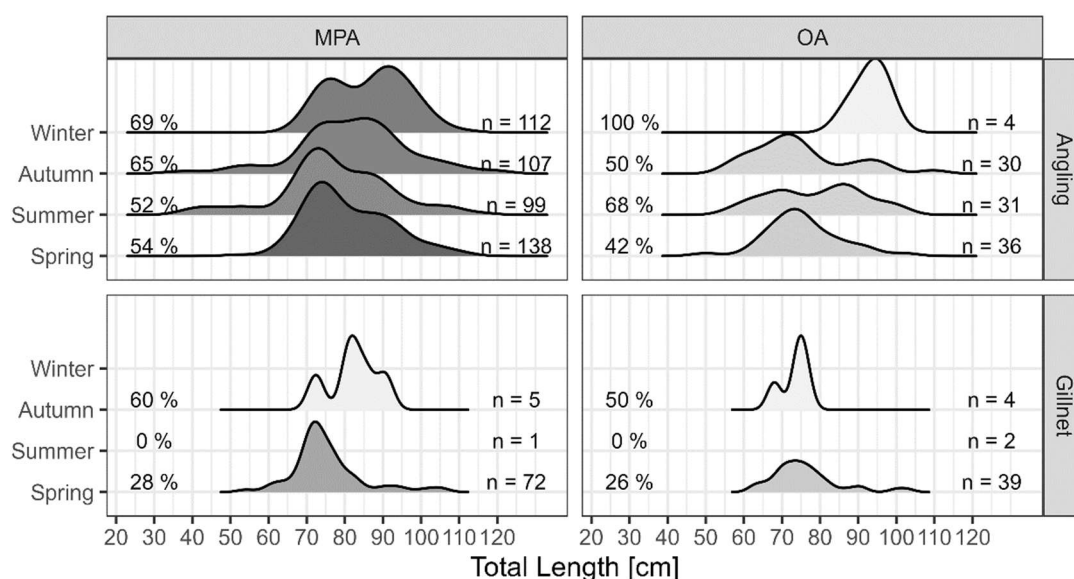


Figure 25 Density plot of the body lengths of pike captured during MPA comparison sampling split up by season (y-axis), gear (horizontal panels) and site (vertical panels). Percentages on the left-hand sides of each plot display the share of females in the catch. Respective sample sizes are denoted on the right-hand-side of each plot, emphasized by shade with higher sample sizes represented by darker color. Angling data contain fish from both randomized and non-randomized samplings conducted between 2021 - 2023.

3.2.2.1 Modelling length

The average body length of pike captured during randomized angling and gill-netting did not differ significantly ($\chi^2 = 0.1$, $df = 1$, $p = 0.748$) between the sites (mean TL $\pm$ SD: MPA = 771.1 ± 120.7 mm, OA = 760.8 ± 95.8 mm). Similarly, there were no significant differences in pike body length between pike captured with different gears individuals captured with different gears ($\chi^2 = 0.88$, $df = 1$, $p = 0.348$) (mean TL $\pm$ SD: gillnets = 755.8 ± 89.5 mm, angling = 774.3 ± 124.4 mm). The interaction effect between site and gear was not significant ($\chi^2 = 0.23$, $df = 1$, $p = 0.631$), indicating that neither of the gear types captured differently sized individuals in any of the sites (Figure 26). However, pike length differed significantly between the areas ($\chi^2 = 18.4$, $df = 2$, $p < 0.001$). Pike from Sellin were on average 701.1 ± 123.6 mm (mean $\pm$ SD) long and were significantly smaller than pike from Ummanz ($p = 0.003$) with an average length of 811.9 ± 112.7 mm but also significantly smaller than pike from Werderbucht ($p < 0.001$), which had an average length of 783.5 ± 86.0 mm. Raw data and model predictions for the three comparison areas are displayed in Figure 26. Means of raw data for each area, site and gear can be found in Appendix 2.

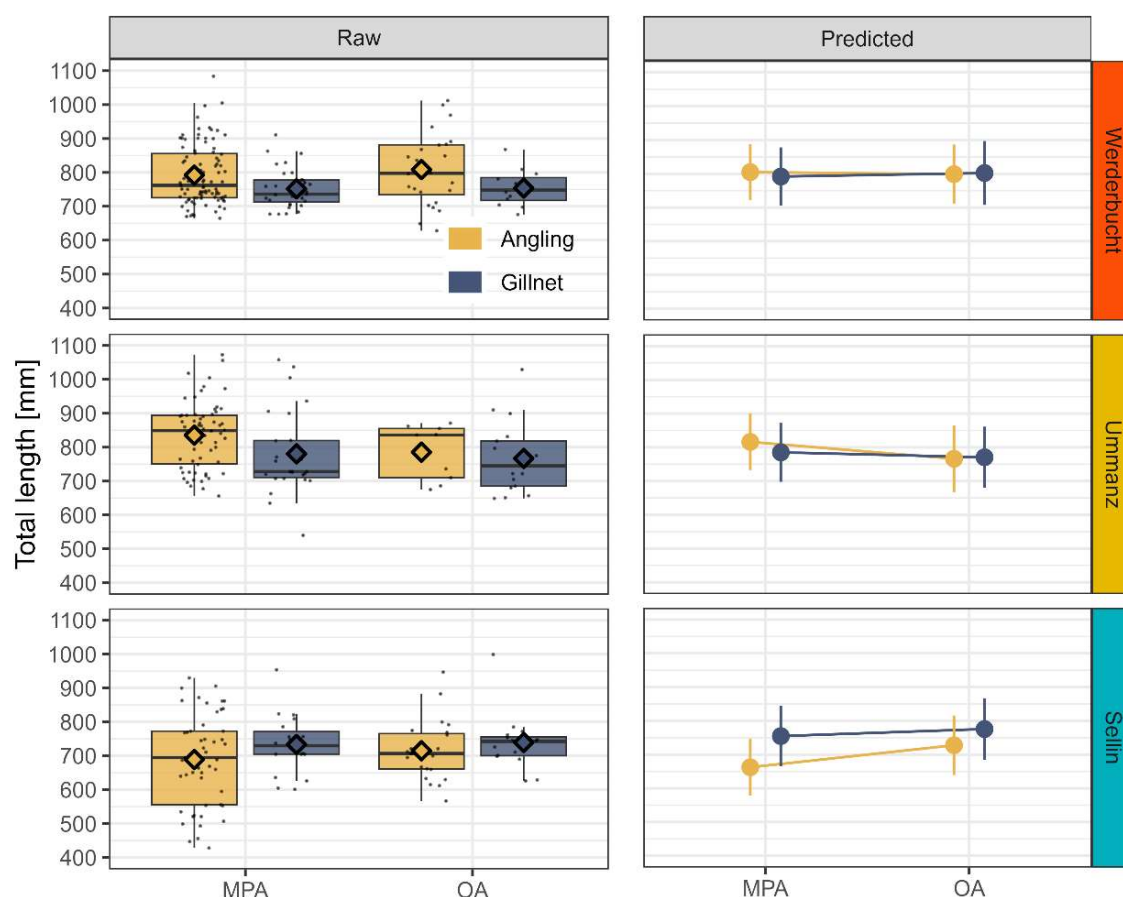


Figure 26 Raw (left) and predicted data $\pm$ SE (right) on total body length (mm) of pike captured with different gears (color) between the sites (x-axis) in the three comparison areas (horizontal panels). Left: black dots represent individuals, boxplots emphasize the distribution. Diamonds show mean values.

3.2.2.II Modelling age

Pike age was significantly related to the site ($\chi^2 = 9.4$, $df = 1$, $p = 0.002$). Pike from the MPA had an average age of 4.98 ± 1.92 (mean $\pm$ SD) years, pike from the OA 4.29 ± 2.01 years. There was no significant relationship between individuals captured with different gears ($\chi^2 = 0.19$, $df = 1$, $p = 0.66$). Mean age $\pm$ SD was 4.63 ± 1.96 years for pike captured with angling and 5.04 ± 1.96 years for pike captured with gillnets. The interaction effect between site and gear was significant ($\chi^2 = 6.96$, $df = 1$, $p = 0.008$) in a way that pike age between the sites did not significantly differ (emmeans, estimate = 0.111 ± 0.465 SE, $p = 0.811$) when comparing pike captured with gillnets (mean age $\pm$ SD: MPA = 5.1 ± 1.9 years, OA = 4.9 ± 2.1 years) while pike captured with angling were significantly younger in the OA (mean age $\pm$ SD: OA = 3.6 ± 1.7 years, MPA = 4.9 ± 1.9 years) (emmeans, ratio = 1.462 ± 0.477 SE, $p = 0.002$), Figure 27. There was variation in the average age of pike from the three areas (mean age $\pm$ SD: Werderbucht = 5.0 ± 1.4 years, Ummanz = 5.4 ± 2.1 years, Sellin = 4.0 ± 2.3 years) but the area effect was not significant ($\chi^2 = 4.8$, $df = 2$, $p = 0.091$). Raw data and predictions

are displayed in Figure 27, means of raw data per area, site and gear can be found in Appendix 3.

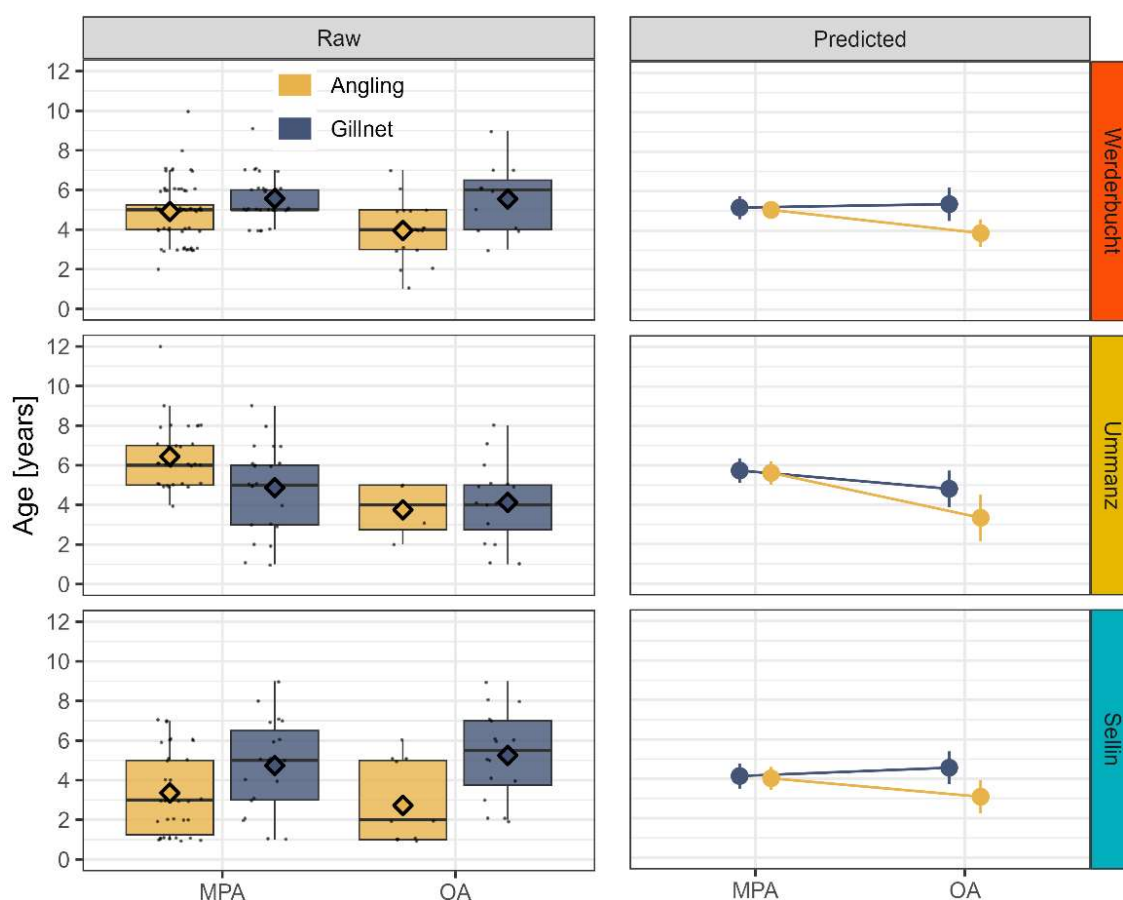


Figure 27 Raw data (left) and predictions (right) of pike age (years) from individuals captured with different gears (color) in the two sites (x-axis) in the three comparison areas (horizontal panels). Black dots in left panels represent individuals, distribution of the data is emphasized by boxplots. Diamonds display mean values. Predicted means $\pm$ SE are connected by lines to emphasize the significant ($p < 0.01$) interaction between site and gear. Note that ages between MPA and OA are approximately identical for gillnets (blue) in all comparison areas but markedly lower for fish angled in OA when compared to the MPA.

3.2.2.III Modelling growth

Size corrected growth was significantly associated with the site ($\chi^2 = 10.7$, $df = 1$, $p = 0.001$). Pike from the MPA were found to have an average size corrected growth of 434.7 ± 57.1 mm (mean $\pm$ SD) while the same figure was 453.6 ± 56.1 mm for pike from the OA. The gear was not significantly related to size corrected growth ($\chi^2 = 0.38$, $df = 1$, $p = 0.538$). Mean values were 442.8 ± 61 mm for pike captured with angling and 435.5 ± 51.2 mm for pike captured with gillnets. There was a significant interaction effect between the site and gear ($\chi^2 = 3.81$, $df = 1$, $p = 0.051$), suggesting that differences in

growth between the sites were gear-dependent. While pike growth did not significantly differ between the sites for individuals captured with gillnets (emmeans, estimate = -4.563 ± 9.012 SE, $p = 0.613$) where average growth (mean $\pm$ SD) was 434.7 ± 53.7 mm for the MPA and 436.9 ± 47.4 mm for the OA, fish captured with angling were significantly faster growing in the OA (473.5 ± 59.8 mm) than in the MPA (434.8 ± 59 mm), (emmeans, estimate = 29.605 ± 9.052 SE, $p = 0.001$), Figure 28. Pike growth did not significantly differ between the areas ($\chi^2 = 1.02$, $df = 2$, $p = 0.601$). Average values were 445.5 ± 78.2 mm for Sellin, 441.7 ± 51.7 mm for Ummanz and 435.5 ± 44.6 mm for Werderbucht (mean $\pm$ SD). Raw data and predictions are displayed Figure 28, means of raw data per area, site and gear can be found in Appendix 4.

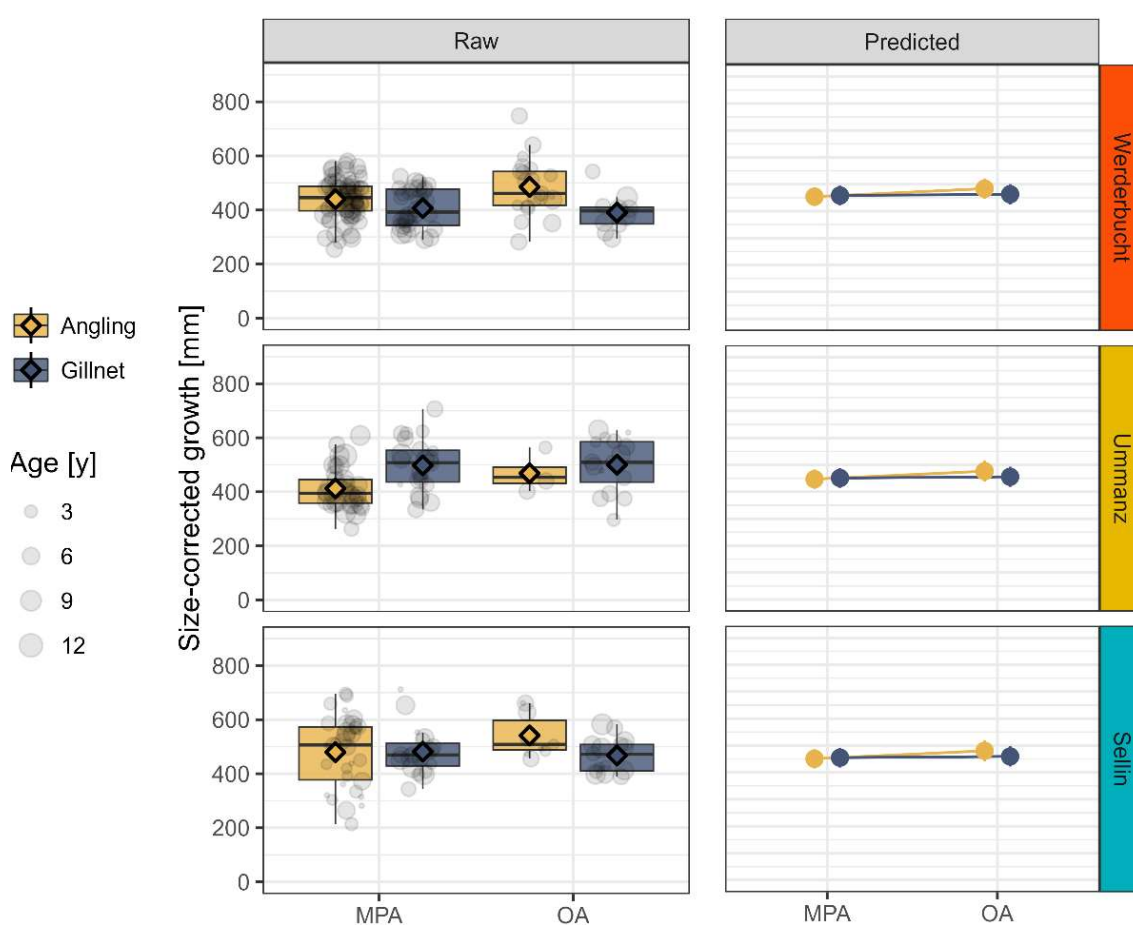


Figure 28 Raw data (left) and predictions (right) of size-corrected growth of pike from the three different areas (horizontal panels). Raw data is displayed by black dots, size indicates age at capture. Boxplots emphasize the distribution of raw data, diamonds indicate mean values. Predicted means $\pm$ SE are connected by lines to emphasize the interaction between site and gear.

3.2.2.IV Proportional Stock Density

When pooling pike from all sampling gears, the proportional stock density index was 1.5 times higher in the MPA (PSD [n]: MPA = 37 [534], OA = 22 [146]), indicating a higher

proportion of “quality fish” (> 85 cm total length) compared to the OA (Figure 29). As expected, there was also a higher share of female pike in the catch from the MPA as females grow to larger sizes (share females: MPA = 55%, OA = 46%; Figure 29). In addition, the PSD was found to vary with gear, with higher values found for angling (PSD = 31, n = 174, share females = 52%) than for gillnets (PSD = 12, n = 111, share females = 27%) when only catches from spring were compared in order to control for seasonal variation given the imbalance in the data with respect to sampling gear. There were also indications for seasonal trends in the share of quality fish with higher values found in winter (Figure 29).

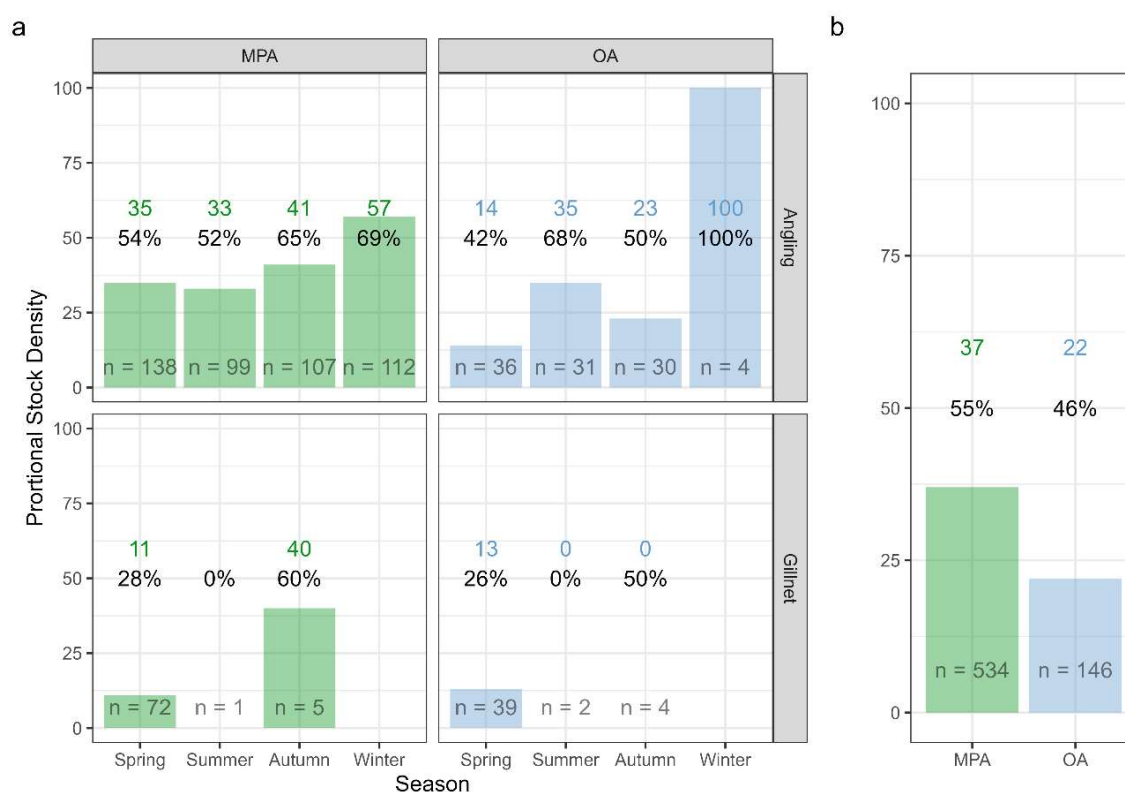


Figure 29 Bar plots displaying calculated proportional stock densities for the MPA (green) and OA (blue). Colored numbers inside the panels show the calculated PSD for each bar, black percentages display the respective share of female pike in the sample. Numbers at the lower margins of each panel denote respective sample sizes available for the calculations. On the left (a) data is split up by season (x-axis) and gear (horizontal panels), plot (b) displays pooled data from all gears and across seasons.

When only considering pike from randomized angling and gill-netting efforts in the three comparison areas, PSD was found to be almost two times higher in the MPAs of Ummanz and Sellin compared to OA sites while in Werderbucht the share of quality fish was slightly higher in the OA (Table 12).

Table 12 Proportional stock densities for each comparison area and site. Data contains all pike from gill-netting and randomized angling.

Area	MPA	OA	Mean ratio
	PSD (n) / share females	PSD (n) / share females	
Werderbucht	22 (123) / 32%	25 (36) / 36%	0.88
Ummanz	42 (91) / 63%	23 (26) / 54%	1.82
Sellin	14 (71) / 52%	8 (39) / 31%	1.75

The results of the binomial model showed that the probability of capturing a quality fish was not significantly influenced by the site ($\chi^2 = 2.39$, $df = 1$, $p = 0.122$) when controlling for area, seasonal and sex effects. Despite the lack of statistical significance, the probability of a female pike being a quality fish (i.e. > 85 cm) was estimated with 73% in the MPA and 61% in the OA. Similarly, for male pike the probability of having a total length > 85 cm was almost doubled for individuals from the MPA despite overall low probabilities (1% and 0.6% for fish from the MPA and OA, respectively). Sex was a highly significant predictor of quality fish ($\chi^2 = 56.5$, $df = 1$, $p < 0.001$) as could be expected given the sexual dimorphism of the species. While predicted probabilities of a female pike being a quality fish were increasing from spring (55%) throughout Summer and autumn (68% and 67%, respectively) to Winter (78%), the effect of season was not statistically significant at the 5%-level ($\chi^2 = 5.78$, $df = 3$, $p = 0.123$).

3.2.3 Attack- and landing rate

The total numbers of attacks present in the dataset were 1032 (MPA) and 299 (OA), while the numbers of followers were 351 (MPA) and 119 (OA). Accordingly, in the MPA 74.6% of all observed pike interactions were attacks while this figure was only 71.5% in the OA. The binomial model suggested that site was a significant predictor of the chance of a pike attacking the lure ($\chi^2 = 4.51$, $df = 1$, $p = 0.034$). It was found that pike in the MPA were 1.84 [1.05 - 3.23; 95% CL] times more likely to attack a lure that caught their attention (as judged by either following or biting the lure) compared to their conspecifics in the open access areas. Expressed in probabilities, pike in the open access had a 73.5% probability of attacking the lure while this number was at 83.6% for pike from the MPA (Figure 30). The overall model explained 23% of the variation in attack rates (conditional $R^2 = 0.23$), however, considering only the fixed model part (site), the explained variation was only 2% (marginal $R^2 = 0.02$).

Data used to model the landing rate contained a total of 457 and 93 landed pike from the MPA and OA, respectively. The sum of bites without a successful landing event from both sites were 575 and 206 for the MPA and OA, respectively. Consequently, the

percentages of bites upon which pike could successfully be landed were 44% and 31% for the MPA and OA, respectively. The model suggested, that the protection status had a significant effect on the probability of landing a fish ($\chi^2 = 7.23$, $df = 1$, $p = 0.007$). Pike from the MPA were 1.75 [1.16-2.63; 95% CL] more likely to be landed upon striking the lure when compared to pike from the OA areas. Expressed in probabilities, pike from the OA had a landing probability of only 29.8% while this number was 42.6% for pike from the MPA (Figure X). The overall model explained 6% of the variation in landing rate (conditional $R^2 = 0.06$) while the fixed part alone could only explain 2% of the variation in the data (marginal $R^2 = 0.02$).

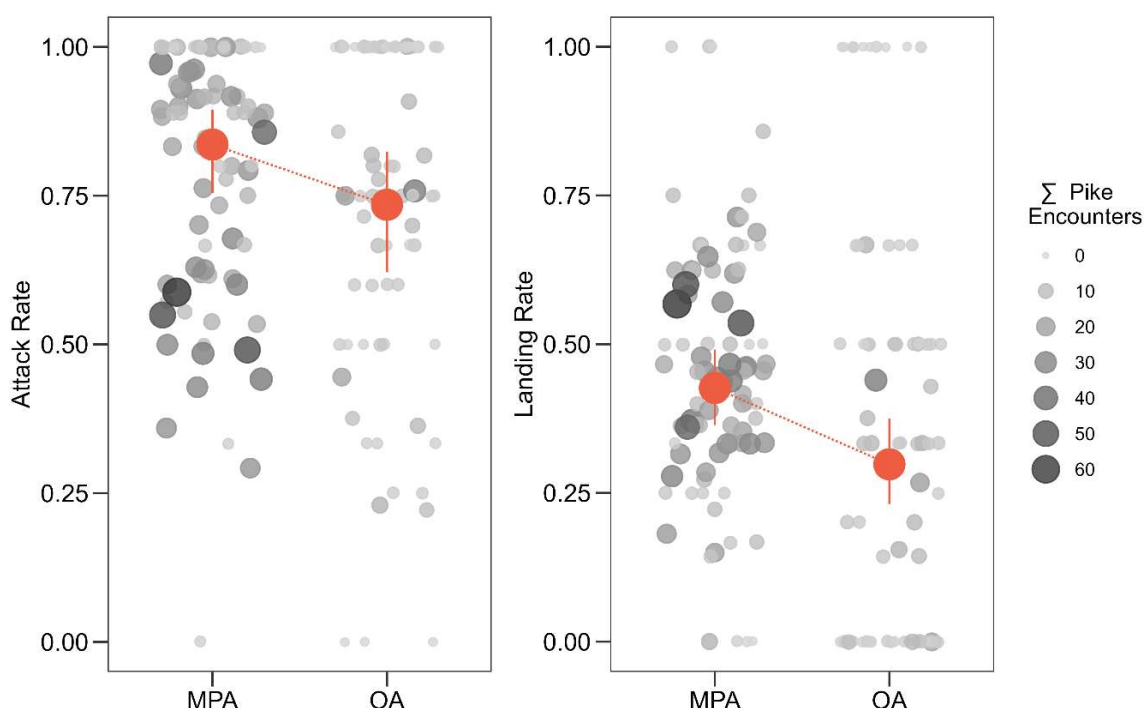


Figure 30 Differences in attack rates (left) and landing rates (right) of pike between MPA and OA (x-axis). Red points display the estimated means from the model output [$\pm$ 95% Confidence limits]. Grey dots display the raw data used as model input where each dot corresponds to one fishing session. Size and shade visualize the number of pike encounters in each session, which comprise bites plus followers for the attack rate (left) and bites plus landed pike for the landing rate (right). Large dark dots have a higher weight in the model. Differences between MPA and OA were significant for both indices ($p = 0.034$ and $p < 0.01$ for attack rate and landing rate, respectively).

3.2.4 Probability of zero catch

The site was a significant predictor for the probability of not getting fish contacts within a 1 h angling session ($\chi^2 = 13.6$, $df = 1$, $p < 0.001$). Predicted probabilities were 41% [0.275 - 0.568; 95% CL] for the MPA and 73% [0.595 - 0.835; 95% CL] for the OA, when

not accounting for seasonal differences. The season was significantly affecting the probability of no fish contacts ($\chi^2 = 18.5$, $df = 3$, $p < 0.001$) with highest predicted probabilities found in autumn with 74% [0.603 - 0.849; 95% CL], followed by winter with 69% [0.497 - 0.828; 95% CL] and summer with 47% [0.297 - 0.657; 95% CL], while the lowest probability was predicted for spring with 39% [0.25 - 0.56; 95% CL], independent of the site. Predictions are displayed in Figure 31. Results from post-hoc comparisons can be found in Table 13. The interaction effect between season and site was not significant ($\chi^2 = 2.93$, $df = 3$, $p = 0.403$), indicating that differences in the probability of no contacts between the sites were not related to seasons. The model explained 21% of the variation contained in the data ($R^2 = 0.208$).

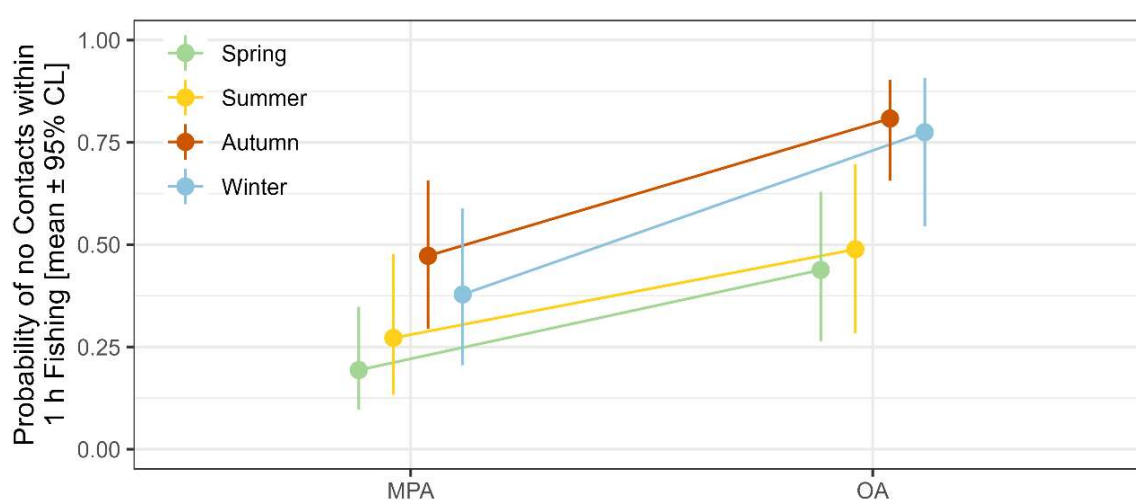


Figure 31 Probabilities of obtaining no fish contact during a 1 h angling session for each site (x-axis) and season (y-axis), as predicted from binomial GLMM. Slopes between MPA and OA are not significantly different between the seasons.

Table 13 Post-hoc comparisons between the probability of no fish contacts in different seasons. Significant differences at the 5%-level are highlighted in bold.

Contrast	Odds ratio	SE	p-value
Spring / Summer	0.7238	0.2989	0.8623
Spring / Autumn	0.2233	0.0839	0.0004
Spring / Winter	0.2985	0.1365	0.0409
Summer / Autumn	0.3085	0.1234	0.0173
Summer / Winter	0.4124	0.1993	0.2577
Autumn / Winter	1.3369	0.5852	0.9109

3.2.5 Evidence for timidity-induced effects on CPUE

3.2.5.1 Angling*Gillnets

In the model comparing catches from angling and gillnets in spring, the interaction between site and gear was found to be not significant ($\chi^2 = 0.07$, $df = 1$, $p = 0.788$), meaning that the differences in relative abundance between MPA and OA were similar between the CPUEs of both gears as can be seen by the nearly parallel lines between the predicted values of the two gears between the sites in Figure 32. This result is in contrast the hypothesis, as angling catches were expected to exhibit a steeper slope between the sites than did gillnets. Looking at the individual effects, normalized catches were not significantly different between the methods ($\chi^2 = 2.27$, $df = 1$, $p = 0.132$) but were highly dependent on the site with significantly higher catches inside the MPA ($\chi^2 = 22$, $df = 1$, $p < 0.001$). The model explained 27.7% of the variance in the data ($R^2 = 0.277$).

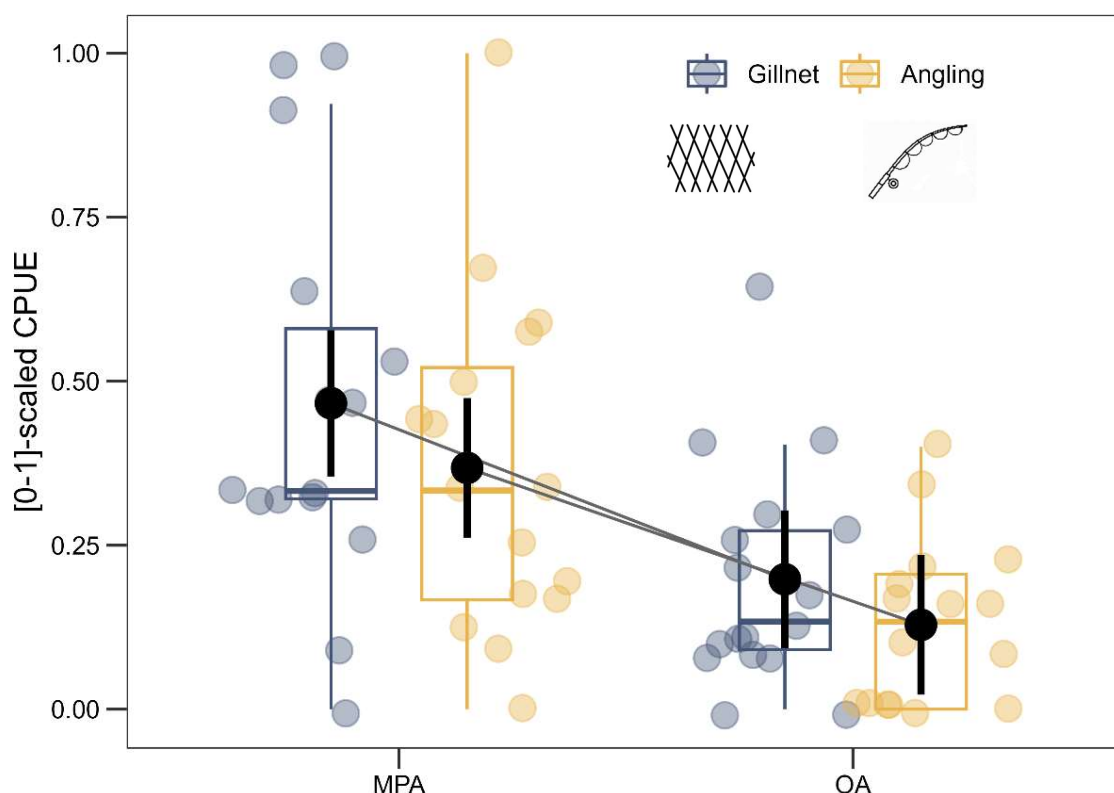


Figure 32 Scaled data for angling and gillnet-catches from spring 2022. Colored points and boxplots show the distribution of the normalized data. Black points display the predicted model values for each group, errorbars show the 95% confidence intervals estimated from bootstrapping. Slope differences between black lines connecting predicted values for each gear between the sites visualize the interaction effect.

3.2.5.II Angling*eDNA

The interaction effect between site and gear was significantly improving the model ($\chi^2 = 6.66$, $df = 1$, $p = 0.01$). Accordingly, there were obvious differences in the slopes between MPA and OA between the two gears (Figure 33) which were in line with the hypothesis, since scaled CPUE exhibited a stronger decrease between sites for angling than for eDNA. The individual effect of method was significant at the 5%-level ($\chi^2 = 4.79$, $df = 1$, $p = 0.029$) as was the effect of site ($\chi^2 = 34.1$, $df = 1$, $p < 0.001$) but both must be interpreted in the light of the presence of the significant interaction effect between them. The proportion of variance explained by the model was 35.2%.

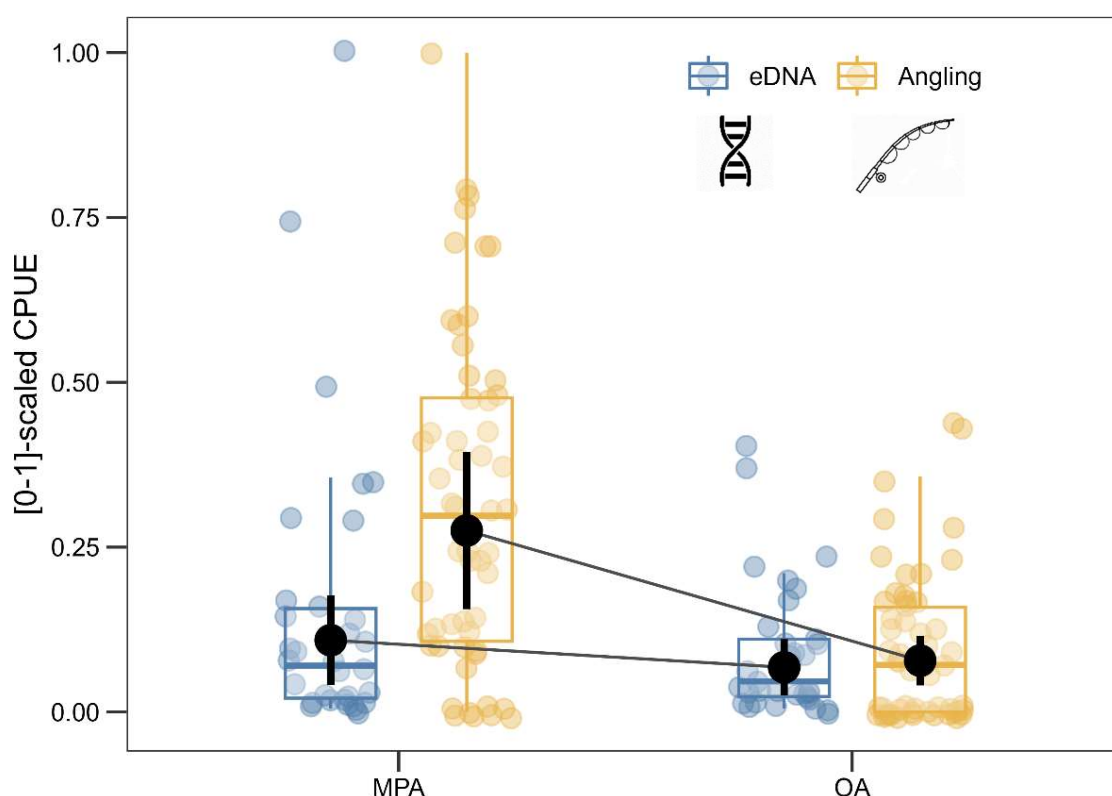


Figure 33 Colored points represent normalized raw data from angling (yellow) and eDNA sampling (blue) for each site (MPA / OA). Boxplots display the distribution of data. Black dots show model predictions with errorbars displaying the 95% confidence intervals from bootstrapping. The difference in slopes between black lines visualizes the interaction effect between gear and site.

3.2.5.III Angling*Telemetry

The interaction term between site and gear was found to be non-significant ($\chi^2 = 2.02$, $df = 1$, $p = 0.156$), indicating that there was no significant difference in slopes between MPA and OA between the two gears, contrasting the hypothesis that angling catches exhibited steeper slopes between the sites. While not significant, normalized telemetry counts even showed a more pronounced difference in slopes between the sites than did

normalized angling data (Figure 34). The site was highly significantly explaining differences in normalized CPUE ($\chi^2 = 14.9$, $df = 1$, $p < 0.001$) with higher values found in the MPA. Differences between the two gears were borderline significant where response values tended to be higher in normalized telemetry data ($\chi^2 = 3.66$, $df = 1$, $p = 0.056$). The model explained 36.9% ($R^2 = 0.369$) of variance contained in the data.

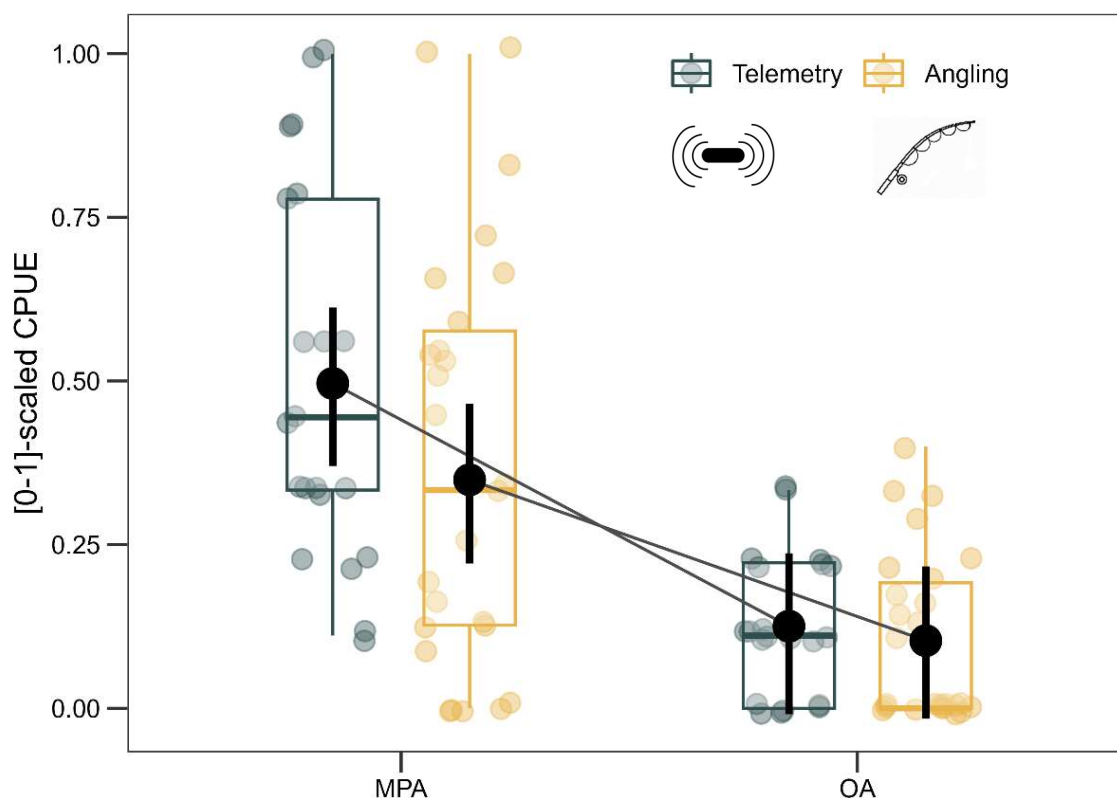


Figure 34 scaled CPUE values from telemetry and angling data. Colored points represent individual data points with boxplots reflecting distribution of the data. Black dots display model estimates, errorbars show 95% confidence intervals from bootstrapping.

3.2.6 Lure-effects on catchability

3.2.6.1 Lure type (observational)

When distinguishing between 6 levels in the variable lure type, the individual main effect of lure type had a marginally significant effect ($\chi^2 = 10.8$, $df = 5$, $p = 0.055$) on the CPUE while the site was highly significant ($\chi^2 = 32.7$, $df = 1$, $p < 0.001$). However, the interaction effect between site and lure type was significant too ($\chi^2 = 12.1$, $df = 5$, $p = 0.033$), indicating that the difference in catch rates between MPA and OA had different magnitudes depending on the lure type. Strongest proportional changes in catch rates between the sites were observed with metal lures where the number of pike captured in the MPA was more than 9-fold higher in the MPA than in the OA (emmeans, ratio = 9.6 ± 6.4 SE, $p < 0.001$), followed by rubber lures where the difference was more

than 7-fold (emmeans, ratio = 7.3 ± 2.3 SE, $p < 0.001$). Values were lower for swimbaits (emmeans, ratio = 4.4 ± 1.5 SE, $p < 0.001$), crankbaits (emmeans, ratio = 4.2 ± 2.9 SE, $p = 0.034$), flies (emmeans, ratio = 3.6 ± 1.5 SE, $p = 0.002$) and jerkbaits (emmeans, ratio = 2.4 ± 0.9 SE, $p = 0.024$). The differences in the slopes between MPA and OA among different lure types (Figure 35, Figure 36) were significant at the 5%-level only between metal lures and jerkbaits ($p < 0.05$) and between rubber lures and jerkbaits ($p < 0.01$).

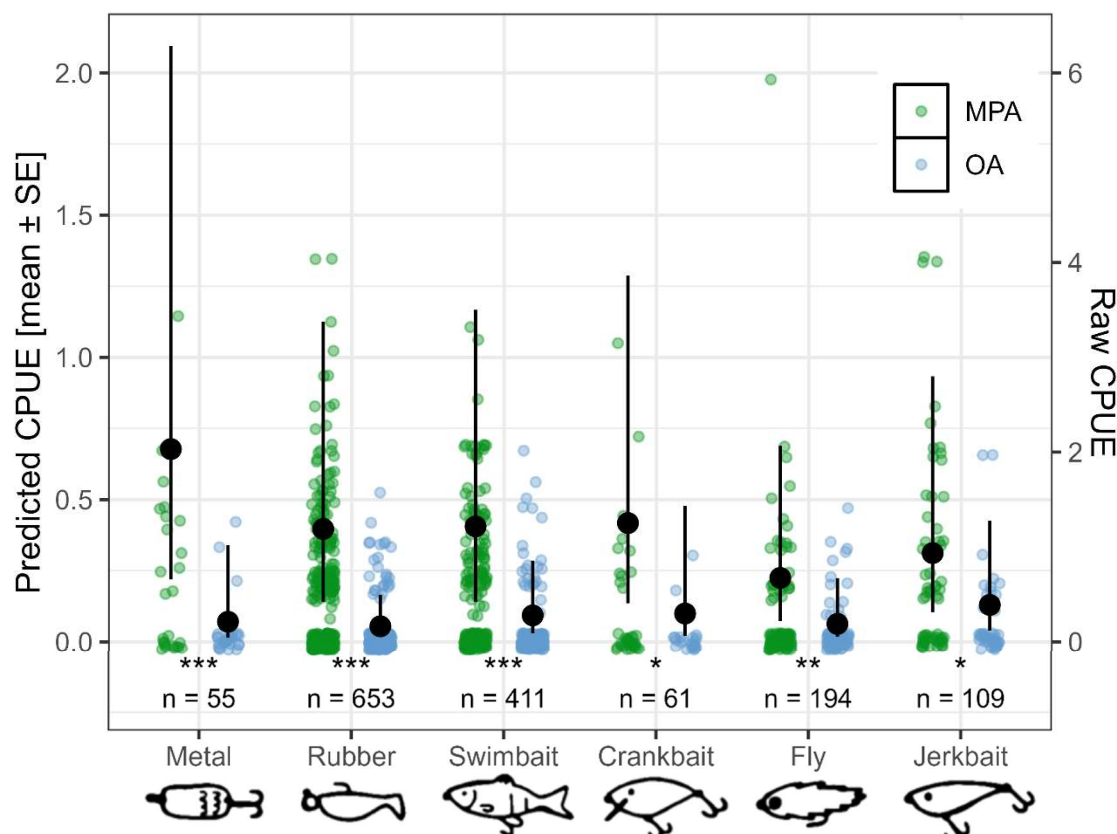


Figure 35 Differences in pike CPUE (pike/h) for different lure types (6 levels) between MPA and OA. Raw data (right y-axis) are plotted as colored points where, each representing one fishing session. Predicted means and standard errors (left y-axis) are displayed in black. Stars on the lower plot margin indicate significant differences for each lure type between MPA and OA (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$) and n specifies the number of observations (number of fishing sessions each lure was fished). Lure types along the x-axis are ordered in decreasing order of proportional change (difference in predicted CPUE between MPA and OA).

In the model with lure type consisting of only 2 levels (hard vs. soft lures), the main effect site was significant ($\chi^2 = 33.5$, $df = 1$, $p < 0.001$) while the lure type was not ($\chi^2 = 2.02$, $df = 1$, $p = 0.155$), indicating that the categorization of lures into hard and soft lures did not explain overall differences in catch rates. The interaction effect between lure type and site was not significant ($\chi^2 = 2.19$, $df = 1$, $p = 0.138$) as can be seen by the parallel

slopes for both categories between MPA and OA in Figure 36. Hence, there was no differential pattern in catch rates between the sites potentially indicative of timidity.

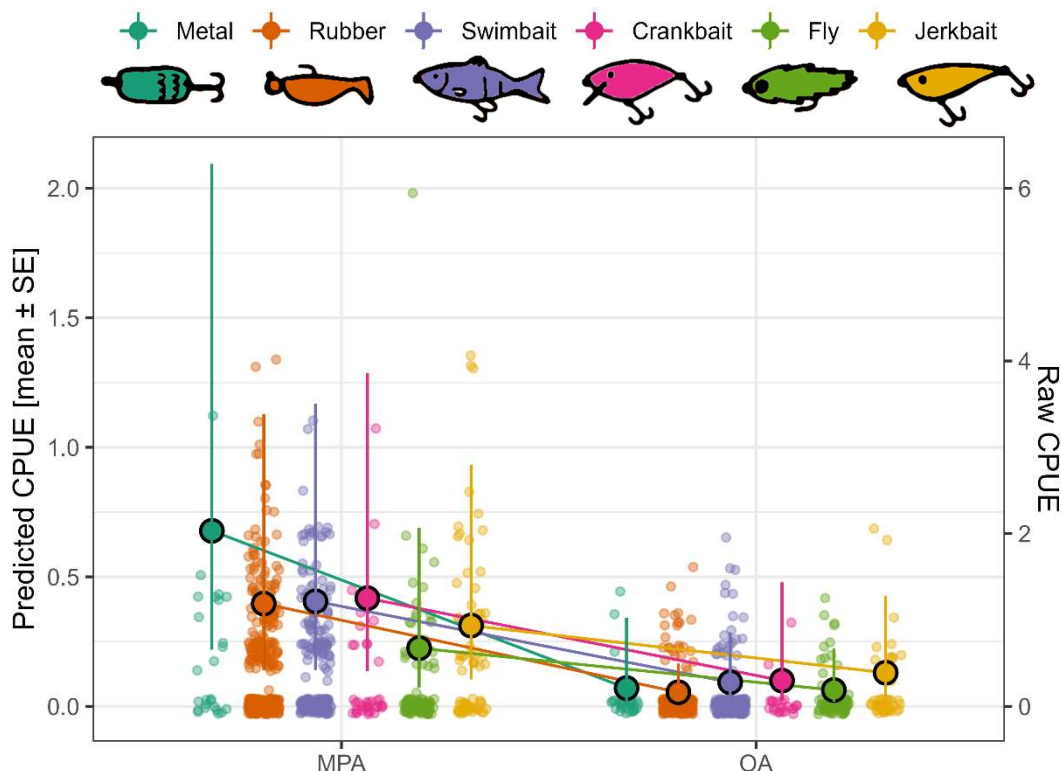


Figure 36 CPUE (pike/h) of the six different lure categories (6 levels, represented by color) by site (x-axis). Model predictions and standard errors (left y-axis) are plotted on top of raw data (right y-axis), represented by small colored points. The significant interaction is visualized by the variation in slopes between MPA and OA along the x-axis. Lures are ordered by effect size from left (strongest) to right (lowest).

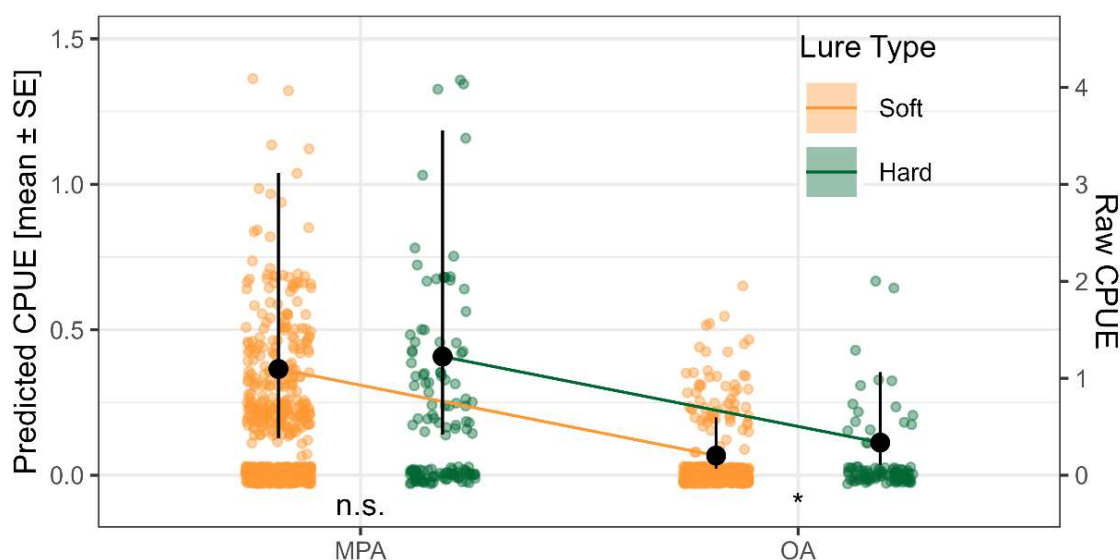


Figure 37 Catch rates (pike/h) for soft and hard lures (color) in the two sites (x-axis). Raw data points are displayed as small dots (right y-axis), black points represent model

estimates (left y-axis). Stars on the lower plot margin indicate significance for differences between the lure types within each respective site (n.s. = $p > 0.05$, * = $p < 0.05$). The lack of a significant interaction effect between site and lure type can be deduced from the approximately equal slopes between MPA and OA between the lure types.

3.2.6.II Lure color (observational)

In the model assessing the interaction effect between lure color and site, only site was found to be statistically significant ($\chi^2 = 53.9$, $df = 1$, $p < 0.001$) while the effect of lure color was not ($\chi^2 = 2.14$, $df = 1$, $p = 0.144$). For the interaction term, the model results indicated no statistical significance ($\chi^2 = 3.1$, $df = 1$, $p = 0.078$). Interestingly, however, moderate statistical significance was found in the difference of the two colors on CPUE within the MPA ($p < 0.05$). However, the effect was contrary to the hypothesis H5 that shock colors may generate higher catch rates in unfished areas. At the same time, predicted catch rates in open access areas were slightly higher for shock colors than for natural colors but this difference was not statistically significant. The model predictions are displayed in Figure 38.

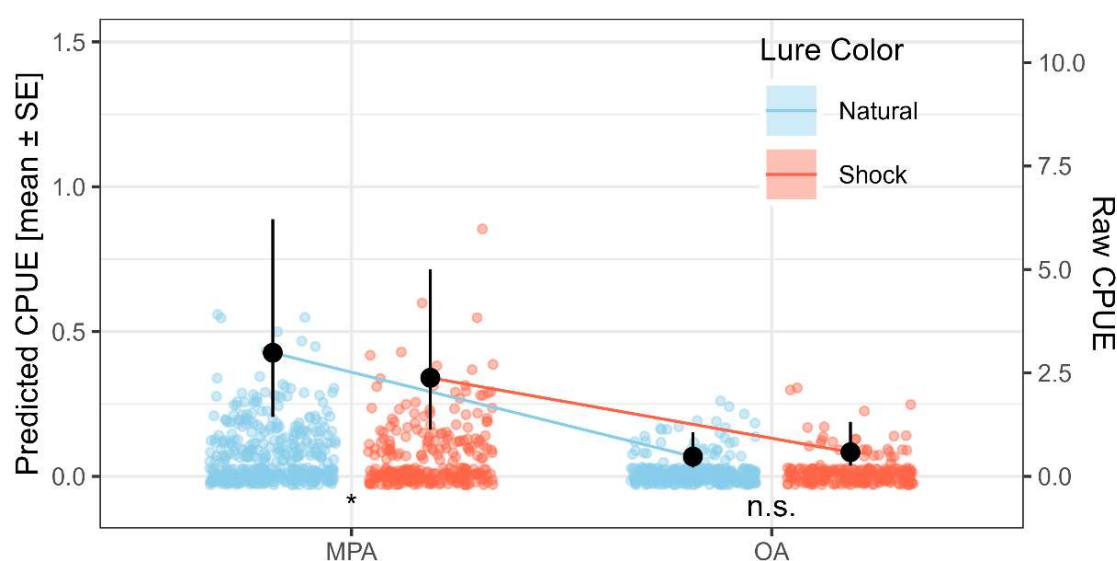


Figure 38 CPUE (pike/h) for different lure colors between the sites (x-axis). Model predictions (left y-axis) are displayed on top of raw data points (right y-axis). Stars on the lower plot margin indicate significance for differences between the colors within reach respective site (n.s. = $p > 0.05$, * = $p < 0.05$).

3.2.6.III Lure Color (Experimental)

In the color experiment with standardized lures, the site was a significant predictor of catch rates ($\chi^2 = 18.6$, $df = 1$, $p < 0.001$). There was no significant effect of lure color on catch rates, indicating that overall CPUE was comparable between the bright colored and the naturally colored rubber trout ($\chi^2 = 1$, $df = 1$, $p = 0.316$). No significant interaction

effect was found between lure color and site ($\chi^2 = 0.14$, $df = 1$, $p = 0.705$), indicating that the catch rates of the two colors were independent of the site.

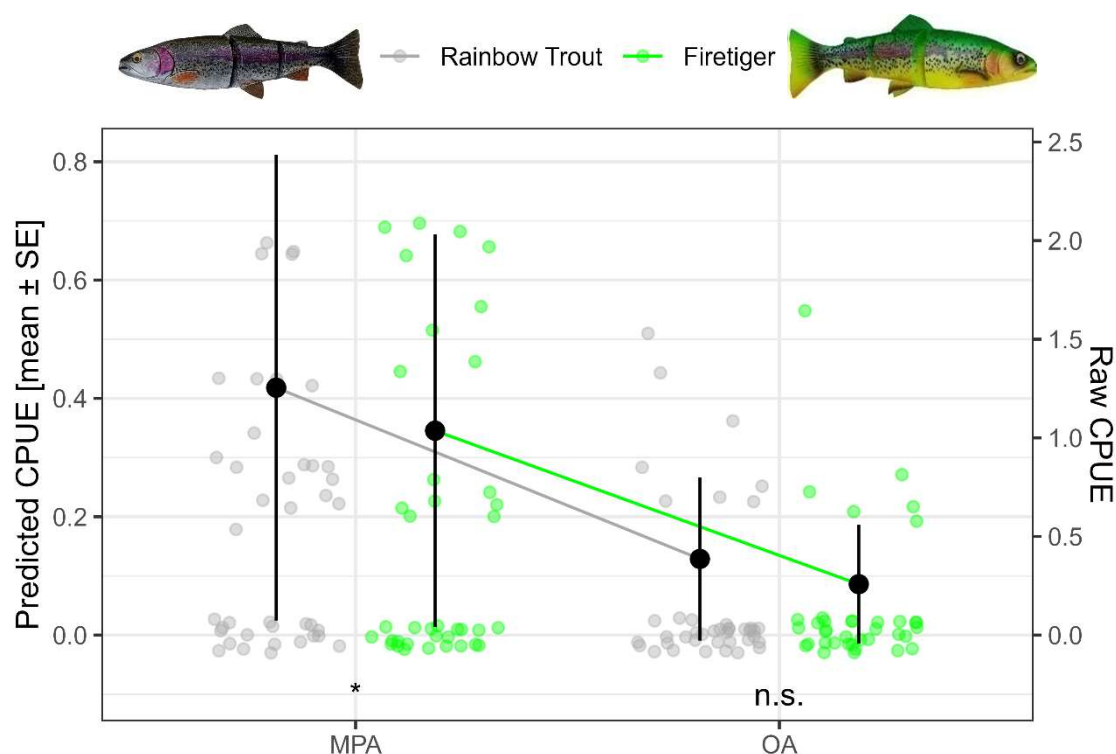


Figure 39 CPUE (pike/hour) from standardized lure angling with the two color-patterns. Predicted data (left y-axis) are plotted over raw data (right y-axis). Each data point represents one angling session. Stars on the lower plot margin indicate significance for differences between the colors within reach respective site (n.s. = $p > 0.05$, * = $p < 0.05$).

3.2.7 Analysis of recaptures

3.2.7.I Recapture Gear

For pike which were recaptured, the gear at first capture was highly significantly related to the gear at second capture ($p < 0.0001$, $df = 1$, $\text{chisq} = 104.8$). However, this relationship was contrary to the hypothesis. Indeed, pike that were first captured with lures had a 20% [0.169 - 0.245; 95% CL] probability of being recaptured with commercial gear while this figure was at 63% [0.563 - 0.691; 95% CL] for fish whose first capture event took place with commercial gear.

3.2.7.II Time to recapture

The durations between the first and second capture of recaptured pike were higher for the group of fish recaptured with commercial fishing gear (291.3 ± 222.8 days [mean $\pm$ SD]; median = 247) than for those fish which were recaptures with lures (253.2 ± 206 [mean $\pm$ SD]; median = 207) and this difference was significant ($p < 0.05$). This finding

was contrary to the hypothesis, as pike were expected to exhibit longer timespans between to angling captures due to lure avoidant behavior.

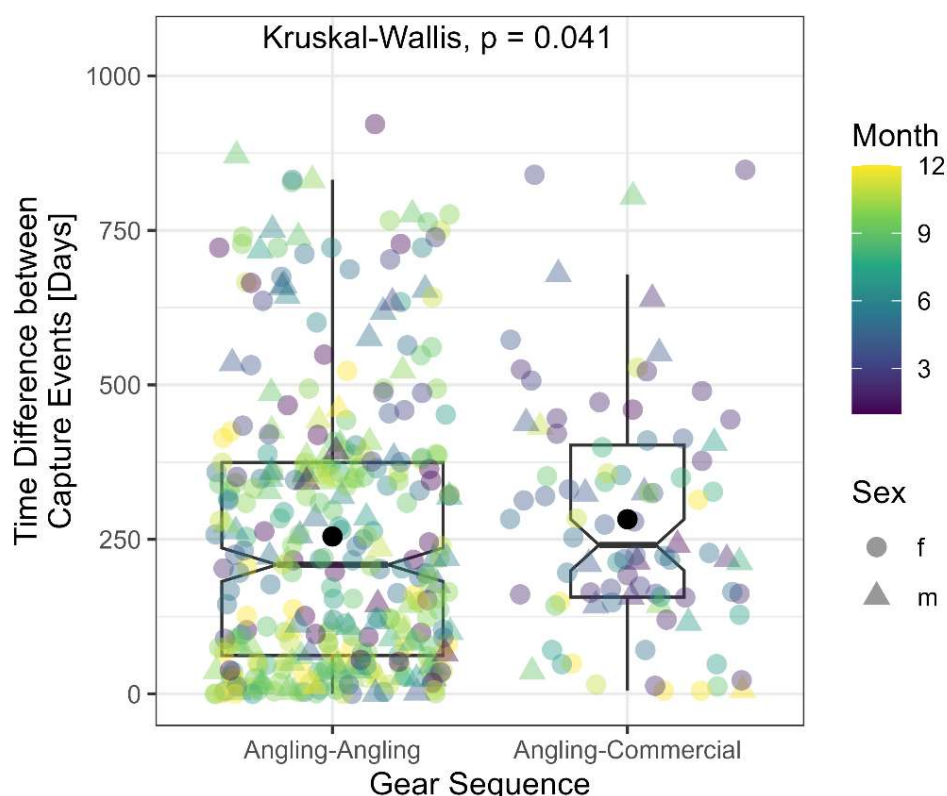


Figure 40 Comparison of the time between two subsequent captures of individual pike. Groups on the x-axis separate fish into pike which have been captures with lures both times (“Angling-Angling”) or which have been caught with Lures the first time and who have ben recaptured with commercial gears (“Angling-Commercial”). Colors denote the calendar month of the respective recapture event, shapes display sex. Distribution is emphasized by boxplots (median, box: 25 and 75 percentile, whisker: 10 and 90 percentile). Mean values for each group are displayed by black dots.

3.2.7.III Recapture Probability between Sites

Site was not a significant predictor of the probability of a recapture ($\chi^2 = 0.02$, $p = 0.8782$, $df = 1$). The estimated probabilities of a recapture were 6.3% [4.7 - 8.4; 95% CL] for the MPA and 6.1% [4.8 – 7.8; 95% CL] for the OA.

4 Discussion

In the present study, the effect of lure timidity was investigated in a coastal Baltic pike population exposed to angling and commercial fishing by comparing pike catch rates, behavior and life-history traits between MPAs and OAs. In support of H1, data from different sampling gears suggested that pike abundance was lower in the OA sites compared to MPAs, likely due to commercial and recreational fisheries removals (Goedde & Coble 1981; Mosindy et al. 1987; Pierce et al. 1995; Edgren 2005; Arlinghaus et al. 2010; Gwinn et al. 2015; Ahrens et al. 2020; Bergström et al. 2022a, b; Eklöf et al. 2023). A higher share of large pike was captured inside the MPAs compared to OAs with angling, suggesting that recreational and commercial fishing caused truncation of the size structure in OA sites through fishing mortality and selective removal of large fish (Goedde & Coble 1981; Olson & Cunningham 1989; Jolley et al. 2008; Sharma & Borgström 2008; Pierce et al. 2010; Olele et al. 2016; Tiainen et al. 2017), thus supporting H2. The contribution of lure timidity to lower angling catches in OA sites could not be clearly documented using gear-specific catch-rate data, but the behavioral metrics attack-rate and landing-rate in angling were significantly lower in OA sites, indicating that pike are harder to catch with artificial lures in sites exposed to angling pressure and thus timidity was present to some degree, supporting H3. When controlled for sex, pike captured with angling in OA sites were equal in size but younger and exhibited faster growth compared to pike angled in MPAs and compared to pike sampled with gillnets in both sites, partially supporting H4. This suggested that the fastest growing fish were more vulnerable to fishing in OA sites, or alternatively that the smaller growing fish were less vulnerable, which could be an adaptive response to past fishing pressure or a result of learning to avoid lures. In disagreement with H5, there was no evidence of lure color amplifying a timidity effect. However, differences in catch rates between MPA and OA varied with lure type, potentially associated with differences in lure avoidance towards specific lures such as spoons. Recapture data revealed no support for lure-timidity and did thus not align with H6 and H7. In conclusion, while several lines of evidence suggested lure timidity was present in the coastal pike stock, its magnitude was not strong enough to be revealed in the gear-specific catch-rate comparisons. Yet, all of the non-angling gear was found to have limitations and therefore, the gear-specific comparisons of angling and non-angling gear types shall not be overinterpreted. It is concluded that timidity exerts impacts on catchability, but this effect is perhaps less important to the abundance-reducing effect of fishing leading to reduced catch rates in OA sites.

4.1 Pike abundances between MPA and OA

Significantly higher pike catch rates inside MPAs when compared to OAs were evident from all sampling methods employed in this study, however, clear seasonal patterns were found for most gears such that differences in pike catch rates among sites were not evident in all time periods and for all MPA vs. OA comparisons.

Angling catch rates were consistently higher in MPAs across seasons and areas. The same trend was found for spring gillnet catches; however, due to strong seasonal variation in catchability as found in other studies on pike (Neumann et al. 1995; Grant et al. 2004) inferential power on site specific differences in CPUE was strongly limited during summer and autumn. While gillnets were found to produce reliable estimates of pike abundance in lake studies where angling data revealed no apparent relationship to abundance (Pierce & Tomcko 2003), opposing views were expressed for sampling of pike in the Baltic Sea where gillnets constitute a poor sampling method for pike due to the low catchability during warmer months (Holmgren 1999; Donadi et al. 2017; Olsson 2019). Pierce (2012) reported greater stochasticity in spring catches and thus advocated overnight gillnet sampling in summer for representative results of abundance, which contrasts the present findings. Given that gillnet catchability not only depends on temperature but can also greatly vary across waterbodies with different basin characteristics (Pierce et al. 2010; Grant et al. 2004), it seems that the applicability of gillnets as a method to estimate relative abundances is highly context dependent. In contrast to Pierce & Tomcko (2003), many authors have argued that angling tracks abundances relatively well (Arlinghaus et al. 2016b; Eklöf et al. 2023; Niemi et al. 2023; Tibblin et al. 2023) despite concerns that results might underrepresent abundances in sites with fishing pressure due to lure timidity (Beukema 1970; Eklöf et al. 2023). Notwithstanding the aforementioned biases, both gillnets and angling are commonly used to infer relative pike abundance and the results strongly suggest that pike were more abundant in the MPA sites of all three areas investigated in this study compared to the respective OA sites.

For the other two methods employed, larger uncertainty remains. While telemetry counts were likewise consistently higher in MPAs, it must be considered that tagging was unbalanced between the sites with the majority of pike tagged inside the MPAs and the results therefore have to be interpreted with caution. Similar preservation applies to eDNA concentrations, where the strong variation across seasons, sites and areas could be due to abiotic factors influencing both excretion rate and decay of DNA (Lacoursière-Roussel et al. 2016; Rourke et al. 2022; Ogonowski et al. 2023) and reliable correlations with

abundance in pike have so far only been produced under controlled conditions (Rourke et al. 2022; Ogonowski et al. 2023).

The results are consistent with other studies showing increased abundances of target species in MPAs that reduce fishing pressure (McCormick et al. 1987; Côté et al. 2001; Ojeda-Martínez et al. 2007; Lester et al. 2009; García-Rubies et al. 2013). Importantly, MPAs that limit or reduce fishing pressure have been found to increase pike abundance and evidence for this comes from lakes (de Moraes et al. 2023) but also from other areas of the coastal Baltic Sea (Edgren 2005; Bergström et al. 2007; Bergström et al. 2022a, b), where pike catch rates were found to be two to six times higher inside MPAs when compared to reference sites. Eklöf et al. (2023) found that even seasonally closed areas along the Swedish Baltic coast provided 2.35 times higher pike angling CPUE compared to reference sites and discussed lure timidity as potentially enhancing the pronounced differences in catch rates between the sites. Indeed, higher angling CPUE inside MPAs compared to adjacent OA sites can not necessarily be translated into equally strong differences in abundance. For example, Alós & Arlinghaus (2013) and a follow-up study by Alós et al. (2015a) found that angling catch rates in a Mediterranean MPA were significantly higher compared to reference sites while no difference in fish abundance was found. However, given that studies in pike included different sampling gears and effects were consistent across studies, the exclusion or reduction of fishing effort in MPAs is very likely to have abundance-increasing effects.

Angling can significantly reduce pike biomass and abundance and removal rates of up to 50% of annual production have been found in extreme cases (Mosindy et al. 1987; Goedde & Coble 1981; Pierce et al. 1995; Edgren 2005; Bergström et al. 2023a; Eklöf et al. 2023). The observed higher pike abundances in MPAs of the Swedish coastal waters were likewise found in systems where angling constitutes the dominant or only form of exploitation in the investigated reference sites (Edgren 2005; Bergström et al. 2022b; Eklöf et al. 2023), indicating that anglers are capable of reducing pike abundances significantly in these systems. However, also commercial exploitation of pike can reduce abundances significantly (Edgren 2005; Bergström et al. 2007; Jansen et al. 2013). In the study system, recreational and commercial fishers currently catch roughly equal amounts of pike (Radinger & Arlinghaus 2023) and overall removals through commercial fishers are expected to be higher because 74% of pike captured by recreational fishers are nowadays released (Arlinghaus et al. 2023b). However, removals through anglers were found to be exceeding commercial fisheries landings until recently (Arlinghaus et al. 2023b) and the current situation may thus be caused by higher removals from anglers in the past. Overall removals are currently too high and the pike stock is size and growth overfished (van Gemert et al. 2022; Arlinghaus et al. 2023c,

Fitzgerald et al. 2023). Among the areas investigated in this study, no commercial fishing for pike was observed in Werderbucht and differences in abundance are therefore likely attributable to removals from commercial fishers, while in Ummanz, commercial fishing for pike took place in both sites but was mainly conducted by one fisher inside the MPA and the factor most strongly differentiating the MPA vs. OA contrast was the lack of angling inside the MPA. In Sellin, commercial and recreational fishing for pike was present in both sites but to a lesser degree in the MPA and it seems reasonable to assume that both user groups contribute to the lower abundances in the OA site. In line with the observed differences in fishing effort between MPA and OA across areas, the lowest mean angling CPUE from all three MPA sites was found in Sellin, indicating that the joined exploitation from both user groups decreased pike abundances while the highest CPUE was found in the MPA of Werderbucht where pike were not targeted by fisheries. It therefore seems very likely that differences in overall fishing mortality between the sites were responsible for the observed differences in relative abundance and that the lack or reduction of fishing mortality inside MPAs allowed for a recovery of densities (García-Rubies et al. 2013). This is particularly likely for pike, who has been found to have a rather sedentary behavior in coastal lagoons (Karås & Lehtonen 1993; Dhellemmes et al. 2023a, b). This increases the protection value of even small MPAs as the pike therein are exposed to lower fishing mortality, even if some pike roam outside the protection boundaries as shown for the lagoon pike (Arlinghaus et al. 2023d).

There may be other factors related to habitat quality differences among the sites that might have contributed to abundance differences unrelated to past and current fishing pressure. Many MPAs are historically placed in locations with high ecological value (Agardy 1994) and this was the case in the current system, too. While macrophyte coverages, known to correlate strongly with pike abundance (Casselman & Lewis 1996; Grimm & Klinge 1996), were comparable between the sites, two of the MPA sites were shallower and more sheltered than their OA counterparts which may affect pike abundance independent of differences in fishing pressure (Pursiainen et al. 2021; Flink et al. 2023; Niemi et al. 2023; Roser et al. 2023). Yet, the consistency of the response across all three areas and the collective body of work in the published record strongly suggests that pike fishing has strong abundance reducing effects on the harvestable pike in the system.

4.2 Body size and growth

While mean sizes were not significantly different between MPA and OA sites, a higher proportional stock density index was found in the MPAs of Ummanz and Sellin compared to the OA sites. As pike were targeted by recreational and commercial fishers in both

areas, the observed reduction of large pike in OA sites likely constitutes demographic truncation through fisheries mortality as commonly observed in commercial (Jansen et al. 2013) and recreational fisheries (Goedde & Coble 1981; Olson & Cunningham 1989; Edgren 2005; Arlinghaus et al. 2010; Pierce et al. 2010; Gwinn et al. 2015; Olele et al. 2016; Ahrens et al. 2020). In both areas commercial fishing effort was not only observed in the OA sites but to a limited extent also inside the MPAs and some angling was present in the MPA of Sellin. Therefore, demographic effects through fishing mortality were likely present in both sites, perhaps contributing to the lack of observed differences in mean sizes. In Werderbucht, no commercial fishing gear targeting pike could be observed in any of the sites and pike seem to be predominantly targeted by recreational fishers who nowadays have high release rates of 74% (Arlinghaus et al. 2023b). Therefore, overall fishing mortality is likely lower compared to other areas and relatedly demographic effects were not found in this area.

Pike from OA sites were significantly younger compared to fish from the MPAs, which may be another indication for elevated mortality in sites with higher levels of recreational and commercial fishing pressure (Edgren 2005; Berggren et al. 2022). The higher share of larger and older pike in MPAs could possibly be amplified by active avoidance of areas with fishing pressure by the larger, vulnerable fish or be alternatively explained by high residency behavior and the fact that coastal pike are able to navigate back to MPAs upon translocation (Dhellemmes et al. 2023c). If pike have a high residency, the larger fish may simply accumulate in abundance in MPAs where they are less exposed to mortality, elevating size structure and the mean age of fish in the stock, as shown in this study and in Swedish MPA studies with pike (Edgren 2005; Berggren et al. 2022).

Importantly, however, differences in age and also growth between the sites were modified by the gear in a way that there was no age or growth difference between the sites for pike captured with gillnets while angling selectively captured younger and faster growing pike in OA sites. This gear-specific selectivity on fish with different growth strongly suggests that the angling gear preferentially captured one growth-phenotype. Either the faster growing fish present in OA sites showed higher vulnerability to angling or past selection and possibly evolutionary responses have reduced the reactivity of the slower growing phenotypes in the OA sites to rod-and-reel fishing, or both.

The differential vulnerability towards the different gear types among growth-phenotypes in OA sites indicated that there are differences in behavioral attributes associated with angling vulnerability. The pace of life hypothesis posits that repeatable individual behaviors (“personality”) are predictably associated with life-history-traits (Réale et al. 2007). For example, growth rate and boldness are assumed to correlate across taxa

(Stamps 2007). In fish, this relationship was found both between genotypes but also between individuals exhibiting natural variation in boldness (Biro et al. 2004; Mas-Muñoz et al. 2011; Klefoth et al. 2017). As boldness is often (Klefoth et al. 2017) but not always (Härkönen et al. 2015; Vainikka et al. 2015; Keiling et al. 2020; Bieber et al. 2023a) associated with increased angling vulnerability (summarized in Monk 2017), angling may select for slow growth via the removal of bold and fast-growing individuals (Biro & Post 2008; Sutter et al. 2012; Klefoth et al. 2017). In pike, growth rate was not found to correlate with boldness when assessed in standardized assays (Laskowski et al. 2016; Nyqvist et al. 2012). Instead, a relationship between growth rate and activity was confirmed in this species (Kobler et al. 2009; Nyqvist et al. 2017), a behavior that is also associated with a high angling vulnerability (Røste 2020; Monk et al. 2021). In line with this, Pieterek (2014) found that individuals with a high juvenile growth rate and increased swimming activity were also preferentially captured by angling. A positive relationship between growth rate and vulnerability to capture by passive gears (gill nets) has moreover previously been found in lake pike populations (Carlson et al. 2007; Edeline et al. 2007). Alternatively, also differences in aggression and/or space use may explain differential angling vulnerability, which has been shown to be related to attack rates in muskellunge (Bieber et al. 2023a). In addition, faster growing fish might require more energy and consequently exhibit greater hunger levels, which has been shown to increase vulnerability in muskellunge (Bieber et al. 2023b) and other predatory species (Bryan 1974; van Densen & Vijverberg 1982; Raat 1991). It is very likely that faster growing pike are more active feeders or more aggressive, which can both increase their vulnerability to angling through increased encounter rates with gear or increased readiness to attack (Lennox et al. 2017).

Under ongoing angling selection, it can be expected that vulnerability-determining traits such as activity of aggression become increasingly scarce in exploited populations, potentially even accommodated by evolutionary responses (Arlinghaus et al. 2016a, 2017b; Diaz Pauli & Sih 2017). The observed pattern may therefore (in part) be the result of past angling-selection on the stock in OA sites, leaving behind a large pool of less vulnerable, slower growing individuals in OA sites. Assuming that the possible selection has not occurred to the same degree in MPAs and exposure to lures was lower, keeping reactivity of all fishes high, overall angling vulnerability may be higher in these sites and this includes slower-growing individuals too. In line with the present findings, modelling approaches for pike have predicted that angling-induced selection on length increases reproductive investment and reduces somatic growth of adults (Arlinghaus et al. 2009). Relatedly, negative selection differentials on growth were estimated for pike under minimum length-limit exploitation, which readily captures the longer fish (Matsumura et

al. 2011; see also Monk et al. 2021 for empirical support). Studies from salmonids similarly suggest that exploited populations exhibit slower growth as adults as a result of continuous removal of fast-growing individuals (Nuhfer & Alexander 1994; Saura et al. 2010).

Interestingly, two selection lines of black bass exhibiting genetically based differences in angling vulnerability showed differences in metabolic rates but not in growth (Cooke et al. 2007; Redpath et al. 2010), while a different study investigating the same selection lines even found that the highly vulnerable line exhibited slower growth, likely due to increased energy consumption as a result of a higher metabolic cost (Redpath et al. 2009; Sutter et al. 2012). Hence, there is considerable inconsistency between different studies and complex correlations between different behavioral and metabolic traits and outcomes on growth rate exist, making the mechanistic interpretation of the observed relationship found in this study challenging. It seems most likely however, that a behavioral trait is involved in lure avoidance or space behavior (with faster growing pike moving more) and a metabolic reason, such as elevated hunger levels, positively affects growth rate, which in turn affects vulnerability to angling. If there is heritable variation underlying the growth rate, angling-selection may lead to evolution of low-vulnerable pike, which would contribute to the reduced catch rates offered by heavily exploited OA sites.

4.3 Evidence for angling-induced timidity from gear comparisons

No clear evidence for timidity could be revealed by the gear comparisons, which rely on the assumption that non-angling gear tracks pike abundance in an unbiased way. There are no unbiased fish sampling gears and every method possesses inherent limitations (Pierce & Tomcko 2003; Pierce et al. 2010; Kuparinen et al. 2012; Hangsleben et al. 2013; Fischer & Quist 2014; Allen et al. 2020). Obtaining estimates of pike abundance is particularly challenging as most sampling methods available to date are passive gears where the behavior of the fish determines a capture. Therefore, a solid quantification of the effect size was not possible in the present study.

The comparison between normalized spring data for angling and gillnet showed no difference in normalized CPUE between the sites for gillnets and angling, which contrasted the hypothesized lower angling catchability in OA sites due to timidity. A possible explanation for this pattern is that the MPAs were subject to higher levels of spawning activity. Directed spawning migrations of pike into shallow bays were found in many areas of the Baltic, including this system, seasonally increasing abundance inside these sites (Pursiainen et al. 2021; Flink et al. 2023; Roser et al. 2023). As gillnet catchability is highly dependent on movement and pike activity peaks during spawning

(Casselman 1978; Mann 1996; Grant et al. 2004; Dhellemmes et al. 2023a), higher gillnet catch rates inside MPAs could be attributable to an increased use of the MPAs as spawning sites and associated swimming peaks prior and during spawning, thus constituting an additive effect on catch rates. This causes an artificially high catchability of gill nets which in turn leads to a steepening of the slope when comparing CPUE within and outside MPAs for gill nets. A steepening of the gill net slopes in turn erodes the possibility to detect timidity by angling, which would be suggested if the angling CPUE drops more strongly from MPA to OA than the CPUE of the other gear. In summer and autumn gillnet catchability was low and did not allow for statistical comparisons, however, the general trend suggested no markedly higher CPUE in MPAs during these seasons with 1 out of 3 and 5 out of 9 pike captured in MPAs in summer and autumn, respectively. Seasonal spawning aggregations inside MPAs may not equally increase angling CPUE in these sites as pike might focus primarily on reproduction rather than food intake. In line with this, overall angling catches were comparatively low during spring sampling. While most previous studies on seasonality in pike angling CPUE did not cover the spawning months (Margenau et al. 2003; Kuparinen et al. 2010; Jansen et al. 2013), Eklöf et al. (2023) indeed found a significant positive effect of temperature on pike angling CPUE in Swedish bays in April but suggested that increased physical activity of the poikilotherm pike was driving this effect. In summary, there are indications that gillnet CPUE was disproportionately high in MPAs in spring, potentially obscuring the effect of interest.

Using eDNA concentrations as a baseline for abundance, the results suggest that overall pike abundances were comparable between the sites while angling catch rates were markedly higher in MPAs and this effect could be attributable to timidity. The majority of studies from freshwater systems found a positive relationship between eDNA concentrations and other measures of abundance for a number of species, generally supporting its use as a substitute measure of abundance (reviewed in Rourke et al. 2021). Karlsson et al. (2022) found a strong correlation between pike biomass and eDNA concentrations under controlled conditions, but under natural conditions a relationship between angling CPUE and eDNA concentrations could only be established at high temperatures, likely due to a temporal overlap with spawning activity which boosts eDNA concentrations through the release of eggs and milt to the water (Ogonowski et al. 2023). This effect likely also explains the high concentrations detected in spring samples and measurements therefore presumably depict a seasonally biased picture of abundance, similar to the gillnet data. Outside of spring, low concentrations and a high share of unexplained zero values rendered the reliability of the measurements questionable. eDNA is relatively short-lived and abiotic variables such as salinity, temperature and

sunlight affect the decay rates, which may have contributed to the relatively high share of zeros in the data (Rourke et al. 2021). Moreover, in Werderbucht and Ummanz water masses between MPA and OA change frequently with the tides, generally favoring more similar concentrations between the sites. Consequently, while the hypothesis was supported in the postulated way, uncertainty about the applicability of eDNA as a fine scaled tool to compare fish abundances between two adjacent sites remain.

Contrasting the hypothesis, no difference was found in the relative abundance derived from telemetry when compared to differences in angling CPUE between the sites. Telemetry has been used successfully as a tool to determine abundances in fish (Dudgeon et al. 2015). However, the numbers of tagged fish were unbalanced between the sites in the present study with the majority of pike tagged in the MPAs. Also sample size was low. Thus, the reliability of the positional data as a measure of relative abundance between the sites is limited and only holds true if individuals frequently change between the sites. Pike are usually quite sedentary (Diana 1980; Eklöv 1997; Berkström et al. 2021) and observations from the study system confirm that the majority of fish exhibit high site fidelity (Dhellemmes et al. 2023a, b). Mean home ranges were found to be 160 ha (50% monthly utilization) and 1.330 ha (95% monthly utilization) and these values well exceed the size of most sites in this thesis, indicating that some pike regularly change between the sites (Dhellemmes et al. 2023b). In agreement with this, telemetry data revealed that about 30% of pike from the system are fully resident within MPAs and the vast majority of individuals is found in OA sites at least occasionally (Arlinghaus et al. 2023d). Mark-recapture data on the other hand suggest that individuals tagged inside MPAs were usually recaptured in these sites and the same was true for OAs, indicating that pike are rather resident most of the time (Karås & Lehtonen 1993; Arlinghaus et al. 2023d). Consequently, while there is evidence that dispersal of fish from MPAs takes place in the study system, pike tagged inside the MPA will still have an increased likelihood to be detected within that same MPA as the majority of individuals is rather stationary, rendering telemetry detections in this study unreliable as a proxy for relative abundance.

Overall, the analysis of normalized catch rates between contrasting gears showed varying results and provided only limited indications for timidity, mainly due to uncertainties about sampling biases and strong seasonal variation in the data. All gear types have their own set of biases, and the unbiased estimation of pike abundance is a continued challenge (Kuparinen et al. 2012). In addition, there are statistical limitations to the comparison of datasets with different underlying distributions as it was the case. The overall contribution of timidity could not be quantified but given the approximately equal slopes between gears in the comparison of angling data with gillnets and telemetry,

it seems that lower angling catches in OA sites were mainly driven by differences in underlying abundance.

4.4 Evidence for angling-induced timidity from other metrics

Significantly lower attack rates on artificial lures were evident for pike in the OA sites compared to MPAs as judged by the number of followers relative to the number of attacks (73.5% and 83.6% attack probability in OA and MPA, respectively). A similar approach was used to quantify hook avoidance in brown trout (*Salmo trutta* L.) between two streams with and without fishing pressure by Young & Hayes (2004) who compared the share of individuals vulnerable to fly-fishing after spotting them visually. In line with the present findings, the ratio of captured to observed fish was significantly higher in the unfished stream. The behavior termed “follower” in the present study resembles predator inspection, commonly known from shoaling fish, where individuals approach potential predators to assess the associated risk (Pitcher et al. 1985; Pitcher et al. 1991; Csányi & Dóka 1993). The ability to distinguish artificial lures from prey is known from different predatory species (Andersen & LeRoy Heman 1969; Young & Hayes 2004; van Poorten et al. 2005; Askey et al. 2006; Lennox et al. 2016; Louison et al. 2019; Wegener et al. 2018) and this includes pike (Beukema 1970; Lucas et al. 2023) but also the congeneric muskellunge (*Esox masquinongy*, Mitchill) (Bieber et al. 2023a). Even differentiation between different lure types was shown in black bass (Louison et al. 2019) and trout (Young & Hayes 2004). The stimuli involved in decision making are not yet understood, but vision seems to play a role for assessing risks (Young & Hayes; Sbragaglia et al. 2018). Pike are visual predators (Raaf 1988; Craig & Babaluk 1989) which benefit from high water clarity (Winkler 1991) and lure inspection seems constitute a mechanism by which individuals verify the risk of a lure visually. Because pike can also successfully hunt in turbid water using the lateral line (Raaf 1988; Skov et al. 2002; Skov et al. 2007), however, lure inspection could also include decision making via acoustic vibrations. Given that the frequency of lure avoidance is correlated with exposure to local fishing effort in pike, the behavior seems to represent hook shyness (as shown in lake studies, Kuparinen et al. 2010; Arlinghaus et al. 2017), which can explain why pike in OA sites were indeed more cautious and harder to catch. While differences in turbidity between the sites may bias detection frequency of followers, no statistically meaningful differences in water clarity were present in the current study.

Lower landing rates were found for pike in OA sites, meaning that a lower share of pike was captured relative to the number of registered bites when compared to the MPAs (29.8% and 42.6% landing probability in OA and MPA, respectively). The difference can be explained by fish more cautiously approaching lures (i.e. lower aggression) in OA

sites while pike in MPAs ingested lures more vigorously and deeper, thereby increasing their hooking probability. Arlinghaus et al. (2008) found that pike ingested natural baits deeper than artificial lures and suggested that this was because pike recognized natural baits as a food source. Furthermore, differences in hooking depth among different types of artificial lures were attributed to their resemblance with natural prey with more naturally appearing lures being ingested deeper (Arlinghaus et al. 2008). It may therefore be argued that the reduced landing rates in OA sites could indicate timidity by pike more frequently testing whether lures are actual prey, not ingesting them fully or striking less aggressively to reduce the hooking probability. In a laboratory experiment, bold pike were found to exhibit a higher probability to attack lures compared to shy individuals, showing that intrinsic differences in angling vulnerability exist among individuals in pike (Lucas et al. 2023). However, while the pike in the experiment were found to expel soft baits more quickly than dead baits, no differences in handling were found between shy and bold individuals (Lucas et al. 2023), which may suggest that the differences in landing rates between MPA and OA likewise could be unrelated to underlying differences in personality traits, which would suggest a stronger effect of learning (Beukema et al. 1970). It is important to consider, however, that behaviors were found to be context dependent and vary with the environment, therefore behaviors determined in experimental setups may deviate from those under natural conditions (Klefoth et al. 2012).

Beukema (1970) found that spinners were quickly avoided in a catch and release fishery while catch rates with life bait remained stable over time. This suggests the ability for associative learning in these fish and the lower attack- and landing rates in OA sites may consequently have been observed because a higher proportion of individuals in these sites has had history of prior hooking experiences, rendering them invulnerable or more cautious to artificial lures. A recent laboratory study by Lucas et al. (2023) demonstrated that in pike the probability of attacking a rubber lure or dead bait decreased with the number of encounters even in the absence of hooks. Given that lure avoidance can even be induced through attacks on lures when not resulting in a capture event (Beukema 1970; Lucas et al. 2023) this immensely increases the scope for learning opportunities. In the present study, only one third of all pike from the OA sites could be landed following an attack, meaning that the number of pike which may have gained lure experiences through unsuccessful attacks is two times higher than the actual catch. Based on mark-recapture studies, anglers were estimated to annually capture 10.2% of all pike in the lagoons (Radinger & Arlinghaus 2023). This suggests that 30% of the population may attempt an attack annually, but only one third of these fish are landed. Of the landed catch, 74% are released (Arlinghaus et al. 2023b). It can thus be estimated that a

substantial share of about one quarter of individuals in the stock could gain learning experiences in lure encounters, annually.

An important consideration in hook shyness, however, is the question how persistent the effect is. Fish are known to retain learned lure avoidance only for limited amounts of time (Czapla et al. 2023), indicating that the knowledge about lures can be forgotten as shown by a boost in catch rates following extended fishing closures in coral reefs and pond studies with trout and bass (Feary et al. 2011; Januchowski-Hartley 2013; Koeck et al. 2020; Wegener et al. 2018). The duration for which hook avoidance can be retained was said to be up to one year in carp (Beukema 1969), but more recent work challenges this assumption (Czapla et al. 2023). As learning ability is substantially lower in pike and other predatory fish relative to carp (Coble et al. 1985), it can be expected that lure memory is substantially less in pike than in carp. To date, no studies have yet evaluated the duration of retention of hook avoidance in any predatory fish consistently. Based on time series of CPUE data, Kuparinen et al (2010) and Arlinghaus (2017a) argued that pike have a rather poor capacity for learning and might retain knowledge only for a few days but this assumption has not yet been corroborated by a more systematic approach.

The more cautious behavior of pike from OA sites might also and additionally be a result of angling selection. The removal of vulnerable individuals from a population can result in evolution of traits in a population that reduce their overall vulnerability to angling, such as reduced boldness (Suski & Philipp 2004; Philipp 2009; Klefoth et al. 2017), aggression (Suski & Philipp 2004; Cooke et al. 2007) or exploration, activity and space use (Árnason et al. 2009; Alós et al. 2012, 2016; Härkönen et al. 2014, 2015; Monk et al. 2021). Pike are known to exhibit natural variation in behaviors and personality (Kobler et al. 2009; Tibblin et al. 2016; Lucas et al. 2023). These traits maybe directly selected upon or change in response to correlated selection on life-history traits (Arlinghaus et al. 2017b; Biro and Post 2008). The classical assumption is that selection through angling favors the occurrence of shy, inactive or low aggressive individuals that become increasingly hard to capture (Phillip et al. 2009; Sutter et al. 2012; Arlinghaus et al. 2017b; Tsuboi et al. 2016; Monk et al. 2021), which can occur even with purely size-selective exploitation (Andersen et al. 2017). A shift in behavioral traits due to genetic changes induced by angling selection was found in other predatory species including salmonids (Tsuboi et al. 2016) and black bass (Philipp et al. 2009; Sutter et al. 2012) and selection on behavior is also known to act upon pike in recreational fisheries as more active individuals were found to exhibit higher angling vulnerability (Monk et al. 2021). Given the supposedly low capacity for learning in pike in combination with the previously discussed growth-phenotypes selectively captured with angling gear, it seems that selection is an important component of lure timidity in pike that acts as an additional force.

4.5 Effects of lure type and color

In the experimental approach comparing two identical lures with different color patterns, no evidence for differential catch rates between the sites was found, suggesting that lure avoidance in pike could be unrelated to lure color. Neither were overall catch rates different between the two colors. Likewise, there was no effect of lure color when grouping colors into “natural” and “shock” colors in a larger dataset. The effects of lure color differ between studies and species. In black bass, Moroga et al. (2015) found no effect of lure color on catch rates, while Wilde (2003) reported higher catch rates with firetiger when compared to more natural colors. Braun (2022) tested the effect of UV-reactive colors in perch and found no effect on catch rates. Lure color affected catch rates in mackerel (Hsieh et al. 2001) and catch rates of different lure colors were found to shift with alterations in turbidity in walleye (Nieman et al. 2020). Lucas et al. (2023) tested the effect of lure color by presenting two differently colored soft baits to naïve pike in an experimental setting. The individuals were previously tested for boldness and no differences in the reaction towards the two lures were found between the behavioral types, indicating that lure color alone is not an influential factor of lure avoidance in pike and this observation is corroborated by the present findings. The lack of consistent findings with respect to lure color moreover suggests that color does not play a crucial role in angling catch rates (Lennox et al. 2017)

No effects of lure type were found when using the categories “hard” and “soft” lures, however, there were differences among lures when a higher number of levels was maintained with metal lures and rubber lures showing significantly stronger differences between the sites than did jerkbaits. Arlinghaus et al. (2017a) previously found higher catch rates in pike using soft plastic lures over spoons and the finding was attributed to a higher level of realism of the former, rendering them more enticing for pike due to their greater resemblance with natural prey. A high frequency of deep hooking locations in pike when using soft-plastic lures was discussed to be due to the same mechanism (Arlinghaus et al. 2008), however, this finding was not consistent with another study and other factors such as water temperature, fishing style or the lure material were identified as potentially contributing to differences in hooking depth among different lure types (Arlinghaus et al. 2008; Stålhammar et al. 2014). In the current study there were no differences in the CPUE between rubber lures and metal lures in the OA sites while metal lures clearly outperformed rubber lures in MPA sites. Wilson et al. (2015) demonstrated that more conspicuous lures captured individuals with generally more bold behavior in two bass species. Likewise, larger and therefore more conspicuous fly patterns were less likely to attract trout from a river with high fishing pressure (Young & Hayes 2004).

It may thus be argued that the stimuli emitted from metal lures, especially the conspicuous reflection of light and acoustic stimuli, generate significant attention underwater which attracts naïve pike from greater distances or result in more aggressive attacks while more cautious pike from OA sites are less prone to be overly attracted by these stimuli.

The results from lure trawling tentatively suggested, albeit at low sample size, that the bright and distinct bucktail spinner received markedly more attention inside the MPA compared to the rather natural and inconspicuous rubber trout. This may suggest that the vigorous stimuli (acoustic vibrations, color, sound and reflections) emitted from the bucktail spinner indeed create greater interest in pike from MPAs which may have experienced reduced or no exposure to lures. In contrast, pike in the OA showed seemingly lower susceptibility to these stimuli. However, the attack rate was low for the bucktail spinner inside the MPA suggesting that the attention may not actually be related to the pike's willingness to feed or attack but rather represent curiosity to novel objects, termed neophilia (Bols 1977; Franks et al. 2023). In contrast, the relatively naturally moving rubber trout yielded a much lower number of interactions but higher attack rates, indicating that pike perceive the rubber trout as real prey.

Differences in the slopes of different lure types between MPA and OA could be due to differential learning. However, Arlinghaus et al. (2017a) found no evidence for differential learning between spoons and rubber lures as catch rates of both lure types dropped at the same pace when fishing pressure was maintained for several days, indicating that both lure types were equally successfully and increasingly avoided by the pike. Lucas et al. (2023) likewise found no evidence for differential learning in pike where attack rates dropped equally fast for different rubber lures and dead bait. However, pike were found to be unable to discriminate life bait from natural prey (Beukema 1970).

It is generally challenging to identify factors responsible for differential catch rates among lures due to the variety of stimuli emitted from different lure types and the complexity of factors influencing vulnerability (Lennox et al. 2017). It remains unclear why crankbaits showed no such differential pattern in catch rates between the sites as it would be expected that the noise and acoustic vibrations emitted from these lures create a similar effect as observed for metal lures. As lures were not fished systematically on all sampling days, result should be interpreted with caution.

4.6 Recapture probability

It was found that the amount of time between two captures of the same individual was higher for pike who were first captured with angling and recaptured with gillnets than for

fish captured with lures twice. This was contrary to the hypothesis as an angling capture was expected to reduce individual vulnerability towards angling for extended periods but not affect gillnet vulnerability. Gear avoidance is common in fisheries and the catchability of a gear type commonly decreases for individuals after a capture event (Waters 1960; Ricker 1958; Pierce 1997), including recapture on the same lure in angling (e.g., in salmon, Lennnox et al. 2016 and pike, Beukema 1970). This, together with the potential of fish rapidly recaptured on lures constituting the more vulnerable pools of fish, might explain the longer time of recapture shown by fish first captured on lures and recaptured with gill nets. However, it cannot be ruled out that the relationship in the present data is spurious and caused by uncontrolled spatial and temporal variability in different gear types used by anglers or fishers not present in the experiment or lack of reporting of recaptures. Commercial fishing pressure for pike is low in summer and autumn (Radinger et al. 2023). Therefore, pike are at risk for angling capture for longer periods of the year, which could also explain the observed trend. In addition, differences in the dominant form of exploitation exist between different lagoons (Arlinghaus et al. 2023c). Pike tagged in areas with high angling pressure but few commercial fishers therefore have a lower chance to encounter commercial gears and vice versa. This also could explain why the gear at first capture was significantly related to the gear at second capture.

4.7 Overall assessment of angling-induced timidity

Several indications of angling-induced timidity as well as the potential for growth-phenotype selective angling were revealed in this study, but this effect was not shown when comparing catch rate differences of different gear types among MPA and OA sites. The latter does not rule out the presence of timidity but suggests that the abundance-declining impact of angling and fishing combined might overrule in effect size any additional impact on catch rate by angling-induced timidity. This finding is expected as the abundance reduction of fishing should have stronger impacts than learning or evolutionary adaptations that affect catch rate (Eikeset et al. 2016). The clearest evidence for angling-induced timidity was found when comparing the attack- and landing rates, which were about an absolute 10% lower in OA sites. This figure, however, potentially underestimates the true effect size as both metrics only account for fish following the lure and being observed by the samplers, while those individuals indifferent to lures or not visible due to turbidity or other factors were not detected. This work, however, underscores the reflections by Eklöf et al. (2023) that timidity might increase the catch rates of pike in protected areas in the Baltic, but based on the data it is not possible to express the impact in relative terms and relative to the abundance-declining effect of fishing. The negative effect of angling pressure on catchability and catch rates has been

demonstrated repeatedly through decreasing catch rates in both non-predatory (Beukema 1969; Blackwell et al. 2023) and predatory species (Andersen & LeRoy Heman 1969; van Poorten et al. 2005; Askey et al. 2006; Louison et al. 2019; Wegener et al. 2018) including pike (Beukema 1970; Kuparinen et al. 2010; Arlinghaus et al. 2017a), and this work underscores the effect in a field study.

4.8 Study limitations

There is a number of limitations to this work. Firstly, and most importantly, there were practical limitations to deriving precise abundance estimates of pike. While mark-recapture methods may have yielded better estimates of abundance, there are additional limitations to such approach (Kuparinen et al. 2012). More importantly, the study took place in an open system where immigration and emigration were possible, violating basic assumptions of mark-recapture based abundance estimates (Ricker 1958). Consequently, relative abundance derived from angling-independent gears were used by employing multiple non-angling gears, which came with additional challenges and uncertainties as available fisheries sampling gears yield biased results (Pierce et al. 2010; Hangsleben et al. 2013; Fischer & Quist 2004). In eDNA data, substantial uncertainties about the applicability for abundances in field studies in pike were present while gillnet effort was not sufficient for low catchabilities during summer and autumn. Similarly, sampling effort with long-lines was apparently insufficient as no catches were made in any of the seasons. For future studies, better insights could be gained when system-dependent gear-specific and seasonal variations in catchability are determined beforehand through pilot studies and sampling effort is adapted accordingly. It is hoped that visual tools or echosounders improve in quality so that those may be used as unbiased abundance estimators in the future.

Second, all MPAs investigated in the present study experienced some current and past level of fishing pressure. While fishing effort was monitored on all sampling days, no data of actual pike removals in the study sites could be obtained, neither for present landings nor for long-term harvesting patterns which would affect fisheries-induced effects in the long term. Under strict exclusion of all fishing activities, effects likely would have been more pronounced than revealed in the present study.

A third limitation refers to the observational dataset used to explore catch rates of different lure types and colors. Lure types were not fully standardized and there were unequal numbers of observations between different lure types with some lures fished more frequently than others. Moreover, the categorization of both lure color and lure type remained subjective. A lure with a natural color might be highly conspicuous due to other characteristics such as movement or noise which were not accounted for. Consequently,

it is possible that results may be affected by biases or confounding factors. Future studies focusing on the effects of lure characteristics are encouraged to use more rigorous designs including standardization, randomization and systematic fishing.

Due to low frequency of pike interactions during lure trawling as a result of insufficient effort, no inferences could be drawn from the standardized lure comparison inside and outside MPAs. However, there were some indications that reactions towards the two lure types were different between pike inside and outside the MPA. Similar approaches could widen the understanding about the stimuli and mechanisms involved in lure avoidance. Given that the number of followers was found to be associated with lure timidity, the use of lure cameras is encouraged for future studies. However, as other methods in this study, the effort necessary for sufficiently high sample sizes need to be considered as the number of fish interactions should be expected to be system- and context dependent.

As a final limitations, the data on following vs. attacking depends on the visual observer, and pike might have been missed in turbid water and due to other reasons. Only if the effect was systematic in both sites the conclusions of this work are unaffected.

5 Conclusions and implications for management

The current study provided insights into fisheries-induced effects on behavior and life-history traits in a coastal northern pike populations subject to recreational and commercial exploitation by using MPAs as reference sites. While pike abundances were significantly lower in sites with fishing pressure, indicative of an impact of fishing mortality, a reduced vulnerability towards lures and growth-phenotype selective vulnerability was evident in pike from OA sites, likely in response to past angling. This phenomenon can occur as a result of learning and/or selection and evolution shaping the exploited stocks. It was not possible to quantify the absolute contribution of timidity to lower angling catch rates in OA sites, but the effect is assumed to be smaller compared to the abundance-declining effect. It can thus be concluded that while angling-induced timidity is present, its effect is overshadowed by differences in abundance between the sites, which constitute the main driver of higher catch rates inside MPAs.

Ongoing angling-induced timidity and selection of faster-growing pike can lead to genetic changes in the target populations which might be interfering with natural selection processes and therefore could lead to non-optimal outcomes by contributing to downsizing (Monk et al. 2021) and reduced vulnerability to angling. Therefore, one implication of this work is that continued angling will reduce catch rates through reduction of abundance and reduced reactivity to lures. While the former can be managed with harvest constraints to both angling and commercial fishing (Ahrens et al. 2020), the latter can only be addressed by full or temporary cessation of fishing, e.g., through rotating closures (Feary et al. 2011; Januchowski-Hartley et al. 2014; Camp et al 2015; Wegener et al. 2015; Koeck et al. 2020). The use of full or partial protected MPAs is therefore recommended to allow vulnerable pike to remain in the stock and reproduce and to provide a buffer from which reactive fish can colonize open sites. Given that exchange of pike occurs between MPA and OA sites and reproduction often takes place inside MPAs, the risk of genetic changes might not be a large concern in the present system if sufficient pike survive to reproduce. The reduction in catch rates after exposure to angling may however be to some degree be unavoidable and periods of exceedingly high rates only be transitorily happening. Regularly pausing fishing pressure and reopening it will, however, help to recover catch rates, which cannot be achieved through catch-and-release alone as the abundance-declining impact of fishing might overshadow any learning or other timidity effects. Management of catch rates for anglers must take the removal of commercial fisheries into account because the same behavioral phenotypes might be under selection (e.g., active fish) and because also commercial fisheries will reduce abundance of pike through removals. As the pike stock is strongly

declining in recent years, reductions of total fishing mortality are necessary to recover the stock. No-take MPAs may be one of many tools that can accomplish this. Others include quotas, protected seasons or new harvest limits such as harvest slots (Ahrens et al. 2020). Although a set of rules already exists in the system, it seems not sufficient to guarantee high catch rates in OA sites. The current mean catch rates in the lagoon fishery are below those expected from the average freshwater site in Mecklenburg-Vorpommern (Birdsong et al. 2022; Arlinghaus et al. 2023b).

Fisheries-induced effects on catchability bear important considerations from a management perspective as declining catch rates decrease the value of a fishery, especially to anglers (Beardmore et al. 2015; Birdsong et al. 2021). As the stock of investigation is a valuable source of tourism and therefore provides economic welfare for the region (Arlinghaus et al. 2023a, b), meeting anglers preferences is important consideration. Catch rates and the number of trophy fish have been identified as an important driver of angler satisfaction and are associated with a high willingness to pay (Koemle et al. 2022). The current catch rates in OA sites, however, provide little incentive for trips to the region, particularly for tourists and touristic effort has thus been declining recently. Currently, it is mainly anglers who are not allowed to fish in MPAs, while commercial fisheries hold exemptions. This is a problem socially as well as ecologically in terms of pike protection. The implementation of dynamic spatial regulations like rotating closures that are opened in a rotating fashion to exploitation by fishers and anglers could provide an alternative management approach. Rotating closures were found to reduce fisheries-induced effects on catch rates by avoiding ongoing selection on one hand and counteract learning effects on the other hand (Feary et al. 2011; Januchowski-Hartley et al. 2013; Camp et al. 2015; Wegener et al. 2018; Koeck et al. 2020). Such regulations would also help maintain the genetic integrity of the stock, help fast-growing phenotypes to reproduce, while providing high catch rates, therefore meeting both conservational- and management goals.

References

- Agardy MT (1994). Advances in marine conservation: the role of marine protected areas. *Trends in Ecology & Evolution* 9: 267-270.
- Ahrens RNM, Walters CJ & Christensen V (2012). Foraging arena theory. *Fish and Fisheries* 13: 41-59.
- Ahrens RNM, Allen MS, Walters C & Arlinghaus R (2020). Saving large fish through harvest slots outperforms the classical minimum-length limit when the aim is to achieve multiple harvest and catch-related fisheries objectives. *Fish and Fisheries* 21: 483-510.
- Alós J Palmer M & Arlinghaus R (2012). Consistent selection towards low activity phenotypes when catchability depends on encounters among human predators and fish. *PloS one* 7: e48030.
- Alós J & Arlinghaus R (2013). Impacts of partial marine protected areas on coastal fish communities exploited by recreational angling. *Fisheries Research* 137: 88-96.
- Alós J, Palmer M, Catalan IA, Alonso-Fernández A, Basterretxea G, Jordi A, Buttay LM, Morales-Nin B & Arlinghaus R (2014). Selective exploitation of spatially structured coastal fish populations by recreational anglers may lead to evolutionary downsizing of adults. *Marine Ecology Progress Series* 503: 219-233.
- Alós J, Palmer M, Trías P, Díaz-Gil C & Arlinghaus R (2015a). Recreational angling intensity correlates with alteration of vulnerability to fishing in a carnivorous coastal fish species. *Canadian Journal of Fisheries and Aquatic Sciences* 72: 217-225.
- Alós J, Puiggrós A, Díaz-Gil C, Palmer M, Rosselló, R & Arlinghaus R (2015b). Empirical evidence for species-specific export of fish naïveté from a no-take marine protected area in a coastal recreational hook and line fishery. *PLoSOne* 10: e0135348.
- Alós J, Palmer M, Rosselló R & Arlinghaus R (2016). Fast and behavior-selective exploitation of a marine fish targeted by anglers. *Scientific Reports* 6: 38093.
- Alós J, Campos-Candela A & Arlinghaus R (2019). A modelling approach to evaluate the impact of fish spatial behavioural types on fisheries stock assessment. *ICES Journal of Marine Science* 76: 489-500.
- Andersen KH, Marty L & Arlinghaus R (2017). Evolution of boldness and life history in response to selective harvesting. *Canadian Journal of Fisheries and Aquatic Sciences* 75: 271-281.
- Anderson RO & LeRoy Heman M (1969). Angling as a factor influencing catchability of largemouth bass. *Transactions of the American Fisheries Society* 98: 317-320.
- Arlinghaus R & Mehner T (2005). Determinants of management preferences of recreational anglers in Germany: habitat management versus fish stocking. *Limnologica* 35: 2-17.
- Arlinghaus R (2006). On the Apparently Striking Disconnect between Motivation and Satisfaction in Recreational Fishing: the Case of Catch Orientation of German Anglers. *North American Journal of Fisheries Management* 26: 592-602.

- Arlinghaus R, Klefoth T, Kobler A & Cooke SJ (2008). Size selectivity injury handling time and determinants of initial hooking mortality in recreational angling for northern pike: the influence of type and size of bait. *North American Journal of Fisheries Management* 28: 123-134.
- Arlinghaus R, Matsumura S & Dieckmann U (2009). Quantifying selection differentials caused by recreational fishing: development of modeling framework and application to reproductive investment in pike (*Esox lucius*). *Evolutionary Applications* 2: 335-355.
- Arlinghaus R, Matsumura S & Dieckmann U (2010). The conservation and fishery benefits of protecting large pike (*Esox lucius* L) by harvest regulations in recreational fishing. *Biological Conservation* 143: 1444-1459.
- Arlinghaus R, Tillner R & Bork M (2015). Explaining participation rates in recreational fishing across industrialised countries. *Fisheries Management and Ecology* 22: 45-55.
- Arlinghaus R, Alós J, Klefoth T, Laskowski K, Monk CT, Nakayama S & Schröder A (2016a). Consumptive Tourism Causes Timidity, Rather Than Boldness, Syndromes: A Response to Geffroy et al. *Trends in Ecology & Evolution* 31: 92-94.
- Arlinghaus R, Pagel T, Hühn T & Rapp T (2016b). Einheitsfanganalysen als praxisnahes Hilfsmittel zur Abschätzung der Fischbestandsentwicklung in Binnengewässern. *Fischerei & Fischmarkt in Mecklenburg-Vorpommern* 2: 30-41.
- Arlinghaus R, Alós J, Pieterek T & Klefoth T (2017a). Determinants of angling catch of northern pike (*Esox lucius*) as revealed by a controlled whole-lake catch-and-release angling experiment - The role of abiotic and biotic factors spatial encounters and lure type. *Fisheries Research* 186: 648-657.
- Arlinghaus R, Laskowski KL, Alós J, Klefoth T, Monk CT, Nakayama S & Schröder A (2017b). Passive gear-induced timidity syndrome in wild fish populations and its potential ecological and managerial implications. *Fish and Fisheries* 18: 360-373.
- Arlinghaus R, Abbott JK, Fenichel EP, Carpenter SR, Hunt LM, Alós J, Klefoth T, Cooke SJ, Hilborn R, Jensen OP, Wilberg MJ, Post JR & Manfredo MJ (2019). Governing the recreational dimension of global fisheries. *Proceedings of the National Academy of Sciences* 116: 5209-5213.
- Arlinghaus R, Lucas J, Weltersbach MS, Komle D, Winkler HM, Riepe C, Kühn C, Strehlow HV (2021). Niche overlap among anglers, fishers and cormorants and their removals of fish biomass: a case from brackish lagoon ecosystems in the southern Baltic Sea. *Fisheries Research* 238: 105894.
- Arlinghaus R, Rittweg T, Dhellemmes F, Koemle D, van Gemert R, Schubert H, Niessner D, Möller S, Droll J, Friedland R, Lewin WC, Dorow M, Westphal L, Ehrlich E, Strehlow HV, Weltersbach MS, Roser P, Braun M, Feldhege F & Winkler H (2023a). A synthesis of a coastal northern pike (*Esox lucius*) fishery and its social-ecological environment in the southern Baltic Sea: Implications for the management of mixed commercial-recreational fisheries. *Fisheries Research* 263: 106663.
- Arlinghaus R, Koemle D, Riepe C, Strehlow H, Weltersbach & Lewin WC (2023b). Angelfischerei. *Berichte des IGB* 33: 121-136.
- Arlinghaus R, Ehrlich E, Aspagilla E, Dhellemmes F, Lukyanova O & Radinger J (2023d). Regulierungen des Fangaufwands: Schonzeiten und Schutzgebiete. *Berichte des IGB* 33: 622-646.

- Árnason E, Hernandez UB & Kristinsson K (2009). Intense habitat-specific fisheries-induced selection at the molecular Pan I locus predicts imminent collapse of a major cod fishery. *PLoS One* 4: e5529.
- Askey PJ, Richards SA, Post JR & Parkinson EA (2006). Linking angling catch rates and fish learning under catch-and-release regulations. *North American Journal of Fisheries Management* 26: 1020-1029.
- Baccante D (1995). Assessing catch inequality in walleye angling fisheries. *North American Journal of Fisheries Management* 15: 661-665.
- Baktoft H, Aarestrup K, Berg S, Boel M, Jacobsen L, Koed A, Pedersen MW, Svendsen JC & Skov C (2013). Effects of angling and manual handling on pike behaviour investigated by high-resolution positional telemetry. *Fisheries Management and Ecology* 20: 518-525.
- Bartholomew A & Bohnsack JA (2005). A review of catch-and-release angling mortality with implications for no-take reserves. *Reviews in Fish Biology and Fisheries* 15: 129-154.
- Bates D, Maechler M, Bolker B & Walker S (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* 67: 1-48.
- Beardmore B, Hunt LM, Haider W, Dorow M & Arlinghaus R (2015). Effectively managing angler satisfaction in recreational fisheries requires understanding the fish species and the anglers. *Canadian Journal of Fisheries and Aquatic Sciences* 72: 500-513.
- Berggren T, Bergström U, Sundblad G & Östman Ö (2022). Warmer water increases early body growth of northern pike (*Esox lucius*), but mortality has larger impact on decreasing body sizes. *Canadian Journal of Fisheries and Aquatic Sciences* 79: 771-781.
- Bergström U, Ask L, Degerman E, Svedäng H, Svenson A, och Ulmestrand M (2007). Effekter av fredningsområden på fisk och kräddjur i svenska vatten. *Finno* 2007:2.
- Bergström U, Eggertsen M, Fredriksson R, Florin AB, Lundström K, Ovegård M, Nilsson J, Fredriksson S (2022a). No-take zone for pikeperch, pike and perch in the Stockholm Archipelago (Gålö), Baltic Sea. In: Bergström U, Berkström C, Sköld M, Börjesson P, Eggertsen M, Fetterplace L, Florin AB, Fredriksson R, Fredriksson S, Kraufvelin P, Lundström K, Nilsson J, Ovegård M, Hammar Perry D, Sacre E, Sundelöf A, Wikström A & Wennhage H (2022). Long-term effects of no-take zones in Swedish waters. *Aqua reports* 2022: 20, Swedish University of Agricultural Sciences: 72-110.
- Bergström U, Eggertsen M, Ovegård M, Fredriksson R (2022b). No-take zone for pike and perch in Licknevarpefjärden, Baltic Sea. In: Bergström U, Berkström C, Sköld M, Börjesson P, Eggertsen M, Fetterplace L, Florin AB, Fredriksson R, Fredriksson S, Kraufvelin P, Lundström K, Nilsson J, Ovegård M, Hammar Perry D, Sacre E, Sundelöf A, Wikström A & Wennhage H (2022). Long-term effects of no-take zones in Swedish waters. *Aqua reports* 2022: 20, Swedish University of Agricultural Sciences: 138-161.
- Berkström C, Wennerström L & Bergström U (2022). Ecological connectivity of the marine protected area network in the Baltic Sea, Kattegat and Skagerrak: Current knowledge and management needs. *Ambio*: 51, 1485-1503.
- Beukema JJ (1969). Angling experiments with carp (*Cyprinus carpio* L.). *Netherlands Journal of Zoology* 20: 81-92.
- Beukema JJ (1970). Acquired hook-avoidance in the pike *Esox Lucius* L. fished with artificial and natural baits. *Journal of Fish Biology* 2: 155-160.

- Bieber JF, Louison MJ & Suski CD (2023a). Capture Is Predicted by Behavior and Size Not Metabolism in Muskellunge. *North American Journal of Fisheries Management* 43: 231-243.
- Bieber JF, MacDougall-Shackleton SA & Suski CD (2023b). Food availability influences angling vulnerability in muskellunge. *Fisheries Management and Ecology*.
- Birdsong M, Hunt LM & Arlinghaus R (2021). Recreational angler satisfaction: What drives it?. *Fish and Fisheries* 22: 682-706.
- Birdsong M, Hunt LM, Beardmore B, Dorow M, Pagel T & Arlinghaus R (2022). Does the relevance of catch for angler satisfaction vary with social-ecological context? A study involving angler cultures from West and East Germany. *Fisheries Research* 254, 106414.
- Biro PA, Abrahams MV, Post JR & Parkinson EA (2004). Predators select against high growth rates and risk-taking behaviour in domestic trout populations. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 271: 2233-2237.
- Biro PA & Post JR (2008). Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. *PNAS* 105: 2919-2922.
- Blackwell BG, Ward MJ & Kaufmann TM (2023). Angling of hybrid sunfish from a hatchery pond with potential implications for community fisheries. *Aquaculture and Fisheries* 8: 91-95.
- Bols RJ (1977). Display reinforcement in the Siamese fighting fish *Betta splendens*: Aggressive motivation or curiosity? *Journal of Comparative and Physiological Psychology* 91: 233.
- Braun M (2022). The influence of fluorescing lure color on catch outcomes in European perch (*Perca fluviatilis*) angling. Study Project, Humboldt-Universität zu Berlin, Germany.
- Bryan JE (1974). Hunger and the capture of grayling and char. *Journal of the Fisheries Board of Canada* 31: 1945-1948.
- Camp EV, Poorten BTV & Walters CJ (2015). Evaluating short openings as a management tool to maximize catch-related utility in catch-and-release fisheries. *North American Journal of Fisheries Management* 35: 1106-1120.
- Carlson SM, Edeline E, Asbjørn Vøllestad L, Haugen TO, Winfield IJ, Fletcher JM & Stenseth NC (2007). Four decades of opposing natural and human-induced artificial selection acting on Windermere pike (*Esox lucius*). *Ecology letters* 10: 512-521.
- Casselman JM (1974). External sex determination of northern pike *Esox lucius* Linnaeus. *Transactions of the American Fisheries Society* 103: 343-347.
- Casselman J (1978): Effects of environmental factors on growth survival activity and exploitation of northern pike. *American Fisheries Society Special Publication* 11: 114 - 128.
- Casselman JM & Lewis CA (1996). Habitat requirements of northern pike (*Esox lucius*). *Canadian Journal of Fisheries and Aquatic Sciences* 53: 161-174.
- Chen LX & Zeng LQ (2022). Previous experience alters individual vulnerability to angling of crucian carp (*Carassius auratus*). *Behavioural Processes* 195: 104565.

- Claireaux M, Jørgensen C & Enberg K (2018). Evolutionary effects of fishing gear on foraging behavior and life-history traits. *Ecology and evolution* 8: 10711-10721.
- Coble DW, Farabee GB & Anderson RO (1985). Comparative learning ability of selected fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 42: 791-796.
- Colefax AP, Haywood MD & Tibbetts IR (2016). Effect of angling intensity on feeding behaviour and community structure of subtropical reef-associated fishes. *Marine biology* 163: 85.
- Coleman FC, Figueira WF, Ueland JS & Crowder LB (2004). The impact of United States recreational fisheries on marine fish populations. *Science* 305: 1958-1960.
- Conrad JL, Weinersmith KL, Brodin T, Saltz JB & Sih A (2011). Behavioural syndromes in fishes: a review with implications for ecology and fisheries management. *Journal of fish biology* 78: 395-435.
- Cooke SJ, Suski CD, Ostrand KG, Wahl DH & Philipp DP (2007). Physiological and behavioral consequences of long-term artificial selection for vulnerability to recreational angling in a teleost fish. *Physiological and Biochemical Zoology* 80: 480-490.
- Côté, IM, Mosqueira I & Reynolds JD (2001). Effects of marine reserve characteristics on the protection of fish populations: a meta-analysis. *Journal of Fish biology* 59: 178-189.
- Craig JF & Babaluk JA (1989). Relationship of condition of walleye (*Stizostedion vitreum*) and northern pike (*Esox lucius*) to water clarity with special reference to Dauphin Lake Manitoba. *Canadian Journal of Fisheries and Aquatic Sciences* 46: 1581-1586.
- Crossman EJ (1996). Taxonomy and Distribution. In: Craig JF (editor). *Pike biology and exploitation*. 1996 Chapman & Hall, London: 1-11.
- Csányi V & Dóka A (1993). Learning interactions between prey and predator fish. *Marine & Freshwater Behaviour & Physiology* 23: 63-78.
- Czapla P, Wallerius ML, Monk CT, Cooke SJ & Arlinghaus R (2023). Reexamining one-trial learning in common carp (*Cyprinus carpio*) through private and social cues: No evidence for hook avoidance lasting more than seven months. *Fisheries Research* 259: 106573.
- de Moraes KR, Souza AT, Bartoň, D, Blabolil P, Muška M, Prchalová, M & Kubečka J (2023). Can a Protected Area Help Improve Fish Populations under Heavy Recreation Fishing? *Water* 15: 632.
- Dhellemmes F, Aspillaga E, Rittweg T, Alós J, Möller P & Arlinghaus R (2023a). Body size scaling of space use in coastal pike (*Esox lucius*) in brackish lagoons of the southern Baltic Sea. *Fisheries Research* 260, 106560.
- Dhellemmes F, Lukyanova O, Radinger J, Aspagilla E, Möller P, Friedland R, Arlinghaus R (2023b). Bewegungsökologie des Boddenhechts: Standhecht oder Wanderhecht und die Rolle der Umwelt. *Berichte des IGB* 33: 237-365.
- Dhellemmes F, Lukyanova O, Roser P, Arlinghaus R (2023c). Anadromie und Homing von Boddenhechten. *Berichte des IGB* 33: 2023. 227-296.
- Diana JS (1980). Diel activity pattern and swimming speeds of northern pike (*Esox lucius*) in Lac Ste. Anne Alberta. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 1454-1458.

- Diaz Pauli B & Sih A (2017). Behavioural responses to human-induced change: Why fishing should not be ignored. *Evolutionary Applications* 10: 231-240.
- Dochtermann NA, Schwab T & Sih A (2015). The contribution of additive genetic variation to personality variation: heritability of personality. *Proceedings of the Royal Society B: Biological Sciences* 282: 20142201.
- Donadi S, Austin Å. N, Bergström U, Eriksson BK, Hansen JP, Jacobson P & Eklöf JS (2017). Across-scale trophic cascade from large predatory fish to algae in coastal ecosystems. *Proceedings of the Royal Society B: Biological Sciences* 284: 20170045.
- Douglas Bates, Martin Maechler, Ben Bolker, Steve Walker (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67: 1-48. doi:10.18637/jss.v067.i01.
- Dudgeon CL, Pollock KH, Braccini JM, Semmens JM & Barnett A (2015). Integrating acoustic telemetry into mark–recapture models to improve the precision of apparent survival and abundance estimates. *Oecologia* 178: 761-772.
- Edeline E, Carlson SM, Stige LC, Winfield IJ, Fletcher JM, James JB & Stenseth NC (2007). Trait changes in a harvested population are driven by a dynamic tug-of-war between natural and harvest selection. *Proceedings of the National Academy of Sciences* 104: 15799-15804.
- Edgren J (2005). Effects of a no-take reserve in the Baltic Sea on the top predator, northern pike (*Esox lucius*). Stockholms Universitet. Examensarbete 28.
- Eikeset AM, Dunlop ES, Heino M, Størvik G, Stenseth NC & Dieckmann U (2016). Roles of density-dependent growth and life history evolution in accounting for fisheries-induced trait changes. *Proceedings of the National Academy of Sciences* 113(52), 15030-15035.
- Eklöf JS, Hansen JP, Eriksson BK, Östman Ö., Austin Å. N, Yanos C, Fredriksson R, Bergström U & Andersson HC (2023). Effects of seasonal spawning closures on pike (*Esox lucius* L) and perch (*Perca fluviatilis* L) catches and coastal food webs in the western Baltic Sea. *Fisheries Research* 263: 106674.
- Eklöv P (1997). Effects of habitat complexity and prey abundance on the spatial and temporal distributions of perch (*Perca fluviatilis*) and pike (*Esox lucius*). *Can. JFish. Aquat. Sci.* 54:1520-1531.
- Eriksson BK, Ljunggren L, Sandström A, Johansson G, Mattila J, Rubach A, Råberg S & Snickars M (2009). Declines in predatory fish promote bloom-forming macroalgae. *Ecological Applications* 19: 1975-1988.
- Erismann BE, Allen LG, Claisse JT, Pondella DJ, Miller EF & Murray JH (2011). The illusion of plenty: hyperstability masks collapses in two recreational fisheries that target fish spawning aggregations. *Canadian Journal of Fisheries and Aquatic Sciences* 68: 1705-1716.
- Feary DA, Cinner JE, Graham NA & Januchowski-Hartley FA (2011). Effects of customary marine closures on fish behavior spear-fishing success and underwater visual surveys. *Conservation Biology* 25: 341-349.
- Feldhege F, Roser P, Braun M, Monaghan M & Arlinghaus R (2023). Eignung von Methoden zur Einschätzung des Hechtbestandes an den Bodden. *Berichte des IGB* 33: 707-721.

- Fernö A & Huse I (1983). The effect of experience on the behaviour of cod (*Gadus morhua* L.) towards a baited hook. *Fisheries Research* 2: 19-28.
- Ferter K, Hartmann K, Kleiven AR, Moland E & Olsen EM (2015). Catch-and-release of Atlantic cod (*Gadus morhua*): port-release behavior of acoustically pretagged fish in a natural marine environment. *Canadian Journal of Fisheries and Aquatic Sciences* 72: 252-261.
- Fischer JR & Quist MC (2014). Gear and seasonal bias associated with abundance and size structure estimates for lentic freshwater fishes. *Journal of Fish and Wildlife Management* 5: 394-412.
- Fitzgerald CJ, Droll JS, Shephard S, Monk CT, Rittweg T & Arlinghaus R (2023). Length-based assessment of an exploited coastal pike (*Esox lucius*) stock (Rügen southern Baltic Sea) underscores the crucial relevance of growth and natural mortality for assessment outcomes. *Fisheries Research* 263: 106667.
- Flink H, Tibblin P, Hall M, Hellström G & Nordahl O (2023). Variation among bays in spatiotemporal aggregation of Baltic Sea pike highlights management complexity. *Fisheries Research* 259: 106579.
- Fox J & Weisberg S (2019). *An R Companion to Applied Regression*, Third edition. Sage, Thousand Oaks CA. <<https://socialsciences.mcmaster.ca/jfox/Books/Companion/>>.
- Franks B, Gaffney LP, Graham C & Weary DM (2023). Curiosity in zebrafish (*Danio rerio*)? Behavioral responses to 30 novel objects. *Frontiers in Veterinary Science* 9: 1062420.
- Gabelhouse DW (1984). A length-categorization system to assess fish stocks. *North American Journal of Fisheries Management* 4: 273-285.
- García-Rubies A, Hereu B & Zabala M (2013). Long-term recovery patterns and limited spillover of large predatory fish in a Mediterranean MPA. *PLoS One* 8: e73922.
- Goedde LE & Coble DW (1981). Effects of angling on a previously fished and an unfished warmwater fish community in two Wisconsin lakes. *Transactions of the American Fisheries Society* 110: 594-603.
- Goetze JS, Januchowski-Hartley FA, Claudet J, Langlois TJ, Wilson SK & Jupiter SD (2017). Fish wariness is a more sensitive indicator to changes in fishing pressure than abundance length or biomass. *Ecological Applications* 27: 1178-1189.
- Grant GC, Schwartz Y, Weisberg S & Schupp DH (2004). Trends in abundance and mean size of fish captured in gill nets from Minnesota lakes 1983–1997. *North American Journal of Fisheries Management* 24: 417-428.
- Grimm MP & Klinge M (1996). Pike and some aspects of its dependence on vegetation. In *Pike: biology and exploitation* (pp. 125-156). Dordrecht: Springer Netherlands.
- Gwinn DC, Allen MS, Johnston FD, Brown P, Todd CR & Arlinghaus R (2015). Rethinking length-based fisheries regulations: the value of protecting old and large fish with harvest slots. *Fish and Fisheries* 16: 259-281.
- Hangsleben MA, Allen MS & Gwinn DC (2013). Evaluation of electrofishing catch per unit effort for indexing fish abundance in Florida lakes. *Transactions of the American Fisheries Society* 142: 247-256.
- Härkönen L, Hyvärinen P, Paappanen J & Vainikka A (2014). Explorative behavior increases vulnerability to angling in hatchery-reared brown trout (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic Sciences* 71: 1900-1909.

- Härkönen L, Hyvärinen P, Niemelä, PT & Vainikka A (2016). Behavioural variation in Eurasian perch populations with respect to relative catchability. *Acta Ethologica* 19: 21-31.
- Heino M & Godø OR (2002). Fisheries-induced selection pressures in the context of sustainable fisheries. *Bulletin of marine science* 70: 639-656.
- Heino M, Díaz Pauli B & Dieckmann U (2015). Fisheries-induced evolution. *Annual Review of Ecology Evolution and Systematics* 46: 461-480.
- Hilborn R & Walters CJ (1992). *Quantitative Fisheries Stock Assessment - Choice, Dynamics & Uncertainty*. 1992 Springer Science+Business Media, Dordrecht: 58.
- Hilborn R, Amoroso RO, Anderson CM, Baum JK, Branch TA, Costello C, de Moor C, Faraj A, Hively D, Jensen OP, Kurota H, Little RL, Mace P, McClanahan T, Melnychuk MC, Minto C, Osio GC, Parma AM, Pons M, Segurado S, Szuwalski CS, Wilson JR &
- Holmgren K (1999). Between-year variation in community structure and biomass-size distributions of benthic lake fish communities. *Journal of Fish Biology* 55: 535-552.
- Ye Y (2020). Effective fisheries management instrumental in improving fish stock status. *Proceedings of the National Academy of Sciences* 117: 2218-2224.
- Hoolihan JP, Luo J, Abascal FJ, Campana SE, De Metrio G, Dewar H, Domeier ML, Howey LA, Lutcavage ME, Musyl MK, Neilson JD, Orbesen ES, Prince ED & Rooker JR (2011). Evaluating post-release behaviour modification in large pelagic fish deployed with pop-up satellite archival tags. *ICES Journal of Marine Science* 68: 880-889.
- Hsieh KY, Huang BQ, Wu RL & Chen CT (2001). Color effects of lures on the hooking rates of mackerel longline fishing. *Fisheries science* 67: 408-414.
- Hunt LM, Camp E, van Poorten B & Arlinghaus R (2019). Catch and non-catch-related determinants of where anglers fish: a review of three decades of site choice research in recreational fisheries. *Reviews in Fisheries Science & Aquaculture* 27: 261-286.
- Huntingford FA & Wright PJ (1992). Inherited population differences in avoidance conditioning in three-spined sticklebacks *Gasterosteus aculeatus*. *Behaviour* 264-273.
- Isaeus, M. (2004). *Factors Structuring Fucus Communities at Open and Complex Coastlines in the Baltic Sea*. Department of Botany, Stockholm University, Stockholm, Sweden. Ph. D. thesis.
- Jackson JB, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ & Warner RR (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293: 629-637.
- Jansen T, Arlinghaus R, Als TD & Skov C (2013). Voluntary angler logbooks reveal long-term changes in a lentic pike *Esox lucius* population. *Fisheries Management and Ecology* 20: 125-136.
- Januchowski-Hartley FA, Graham NA, Feary DA, Morove T & Cinner JE (2011). Fear of fishers: human predation explains behavioral changes in coral reef fishes. *PLoS One* 6: e22761.

- Januchowski-Hartley FA, Graham NA, Cinner JE & Russ GR (2013). Spillover of fish naïveté from marine reserves. *Ecology letters* 16: 191-197.
- Januchowski-Hartley FA, Cinner JE & Graham NA (2014). Fishery benefits from behavioural modification of fishes in periodically harvested fisheries closures. *Aquatic Conservation: Marine and Freshwater Ecosystems* 24: 777-790.
- Jansen T, Arlinghaus R, Als TD & Skov C (2013). Voluntary angler logbooks reveal long-term changes in a lentic pike *Esox lucius* population. *Fisheries Management and Ecology* 20: 125-136.
- Jolley JC, Willis DW, DeBates TJ & Graham DD (2008). The effects of mechanically reducing northern pike density on the sport fish community of West Long Lake Nebraska USA. *Fisheries Management and Ecology* 15: 251-258.
- Juan-Jordá, MJ, Mosqueira I, Cooper AB, Freire J & Dulvy NK (2011). Global population trajectories of tunas and their relatives. *Proceedings of the National Academy of Sciences* 108: 20650-20655.
- Keiling TD, Louison MJ & Suski CD (2020). Big hungry fish get the lure: Size and food availability determine capture over boldness and exploratory behaviors. *Fisheries Research* 227: 105554.
- Karås P & Lehtonen H (1993). Patterns of movement and migration of pike (*Esox lucius* L) in the Baltic Sea. *Nordic Journal of Freshwater Research* 68: 72-79.
- Karlsson E, Ogonowski M, Sundblad G, Sundin J, Svensson O, Nousiainen I & Vasemägi A (2022). Strong positive relationships between eDNA concentrations and biomass in juvenile and adult pike (*Esox lucius*) under controlled conditions: Implications for monitoring. *Environmental DNA* 4: 881-893.
- Keiling TD, Louison MJ & Suski CD (2020). Big hungry fish get the lure: Size and food availability determine capture over boldness and exploratory behaviors. *Fisheries Research* 227, 105554.
- Kekäläinen J, Podgorniak T, Puolakka T, Hyvärinen P & Vainikka A (2014). Individually assessed boldness predicts *Perca fluviatilis* behaviour in shoals but is not associated with the capture order or angling method. *Journal of Fish Biology* 85: 1603-1616.
- Klefoth T, Kobler A & Arlinghaus R (2008). The impact of catch-and-release angling on short-term behavior and habitat choice of northern pike (*Esox lucius* L.). *Hydrobiologia* 601: 99-110.
- Klefoth T, Kobler A & Arlinghaus R (2011). Behavioural and fitness consequences of direct and indirect non-lethal disturbances in a catch-and-release northern pike (*Esox lucius* L.) fishery. *Knowledge and Management of Aquatic Ecosystems* 403: 11.
- Klefoth T, Skov C, Krause J & Arlinghaus R (2012). The role of ecological context and predation risk-stimuli in revealing the true picture about the genetic basis of boldness evolution in fish. *Behavioral Ecology and Sociobiology* 66: 547-559.
- Klefoth T, Pieterek T & Arlinghaus T (2013). Impacts of domestication on angling vulnerability of common carp, *Cyprinus carpio*: the role of learning, foraging behavior and food preferences. *Fisheries Management and Ecology* 20: 174-186.

- Klefoth T, Skov C, Kuparinen A & Arlinghaus R (2017). Toward a mechanistic understanding of vulnerability to hook-and-line fishing: Boldness as the basic target of angling-induced selection. *Evolutionary Applications* 10: 994-1006.
- Kobler A, Klefoth T, Mehner T & Arlinghaus R (2009). Coexistence of behavioural types in an aquatic top predator: a response to resource limitation?. *Oecologia* 161: 837-847.
- Kuparinen A, Klefoth T & Arlinghaus R (2010). Abiotic and fishing-related correlates of angling catch rates in pike (*Esox lucius*). *Fisheries Research* 105: 111-117.
- Kuparinen A, Alho JS, Olin M & Lehtonen H (2012). Estimation of northern pike population sizes via mark–recapture monitoring. *Fisheries Management and Ecology* 19: 323-332.
- Koeck B, Wallerius ML, Arlinghaus R & Johnsson JI (2020). Behavioural adjustment of fish to temporal variation in fishing pressure affects catchability: an experiment with angled trout. *Canadian Journal of Fisheries and Aquatic Sciences* 77: 188-193.
- Koemle D, Beardmore B, Dorow M & Arlinghaus R (2021). The human dimensions of recreational anglers targeting freshwater species in coastal ecosystems, with implications for management. *North American Journal of Fisheries Management* 41: 1572–1590.
- Koemle D, Meyerhoff J & Arlinghaus R (2022). How catch uncertainty and harvest regulations drive anglers' choice for pike (*Esox lucius*) fishing in the Baltic Sea. *Fisheries Research* 256, 106480.
- Lacoursière-Roussel A, Rosabal M & Bernatchez L (2016). Estimating fish abundance and biomass from eDNA concentrations: variability among capture methods and environmental conditions. *Molecular ecology resources* 16: 1401-1414.
- Laskowski KL, Monk CT, Poverino G, Alós J, Nakayama S, Staaks G & Arlinghaus R (2016). Behaviour in a standardized assay but not metabolic or growth rate predicts behavioural variation in an adult aquatic top predator *Esox lucius* in the wild. *Journal of Fish Biology* 88: 1544-1563.
- Law R (2000). Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science* 57: 659-668.
- Lenth R (2023). emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.8.5, <https://CRAN.R-project.org/package=emmeans>
- Lennox RJ, Diserud OH, Cooke SJ, Thorstad EB, Whoriskey FG, Solem Ø, Havn TB, & Uglem I (2016). Influence of gear switching on recapture of Atlantic salmon (*Salmo salar*) in catch-and-release fisheries. *Ecology of Freshwater Fish* 25: 422-428.
- Lennox RJ, Alós J, Arlinghaus R, Horodysky A, Klefoth T, Monk CT & Cooke SJ (2017). What makes fish vulnerable to capture by hooks? A conceptual framework and a review of key determinants. *Fish and Fisheries* 18: 986-1010.
- Lester SE, Halpern BS, Grorud-Colvert K, Lubchenco J, Ruttenberg BI, Gaines SD, Airamé S & Warner RR (2009). Biological effects within no-take marine reserves: a global synthesis. *Marine Ecology Progress Series* 384: 33-46.

- Lewin WC, Arlinghaus R & Mehner T (2006). Documented and Potential Biological Impacts of Recreational Fishing: Insights for Management and Conservation. *Fisheries Sciences* 14: 305-367.
- Lucas J, Ros A, Geist J & Brinker A (2023). Effects of behavioral strategies on catchability, bait selectivity, and hunting behavior in northern pike (*Esox lucius*). *Canadian Journal of Fisheries and Aquatic Sciences*: <https://doi.org/10.1139/cjfas-2023-0004>
- Louison MJ, Suski CD & Stein JA (2019). Largemouth bass use prior experience but not information from experienced conspecifics to avoid capture by anglers. *Fisheries Management and Ecology* 26: 600-610.
- Lovén Wallerius M, Gräns A, Koeck B, Berger D, Sandblom E, Ekström A, Arlinghaus R & Johnsson JI (2019). Socially induced stress and behavioural inhibition in response to angling exposure in rainbow trout. *Fisheries Management and Ecology* 26: 611-620.
- Lovén Wallerius M, Johnsson JI, Cooke SJ & Arlinghaus R (2020). Hook avoidance induced by private and social learning in common carp. *Transactions of the American Fisheries Society* 149: 498-511.
- Mann RHK (1996). Fisheries and Economics. In: Craig JF (editor). Pike biology and exploitation. 1996 Chapman & Hall, London: 219-241.
- Margenau TL, Gilbert SJ & Hatzenbeler GR (2003). Angler catch and harvest of northern pike in northern Wisconsin lakes. *North American Journal of Fisheries Management* 23: 307-312.
- Mas-Muñoz J, Komen H, Schneider O, Visch SW & Schrama JW (2011). Feeding behaviour, swimming activity and boldness explain variation in feed intake and growth of sole (*Solea solea*) reared in captivity. *PLoS One* 6: e21393.
- Mason F (2002). The Newfoundland cod stock collapse: a review and analysis of social factors. *Electronic Green Journal* 1: 17.
- Matsumura S, Arlinghaus R & Dieckmann U (2011). Assessing evolutionary consequences of size-selective recreational fishing on multiple life-history traits with an application to northern pike (*Esox lucius*). *Evolutionary Ecology* 25, 711-735.
- McCormick MI & Choat JH (1987). Estimating total abundance of a large temperate-reef fish using visual strip-transects. *Marine biology* 96: 469-478.
- Mollie E. Brooks, Kasper Kristensen, Koen J. van Benthem, Arni Magnusson, Casper W. Berg, Anders Nielsen, Hans J. Skaug, Martin Maechler and Benjamin M. Bolker (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal*, 9: 378-400. doi: 10.32614/RJ-2017-066.
- Monk CT (2014). Mining the behavioural reality of fish-fisher interactions to understand vulnerability to hook-and-line fishing. Doctoral Dissertatin, Humboldt-Universität zu Berlin.
- Monk CT, Bekkevold D, Klefoth T, Pagel T, Palmer M & Arlinghaus R (2021). The battle between harvest and natural selection creates small and shy fish. *Proceedings of the National Academy of Sciences* 118: e2009451118.
- Moraga AD, Wilson AD & Cooke SJ (2015). Does lure colour influence catch per unit effort fish capture size and hooking injury in angled largemouth bass? *Fisheries Research* 172: 1-6.

- Mosindy TE, Momot WT & Colby PJ (1987). Impact of angling on the production and yield of mature walleyes and northern pike in a small boreal lake in Ontario. *North American Journal of Fisheries Management* 7: 493-501.
- Myers RA & Worm B (2005). Extinction survival or recovery of large predatory fishes. *Philosophical Transactions of the Royal Society B: Biological Sciences* 360: 13-20.
- Neumann RM & Willis DW (1995). Seasonal variation in gill-net sample indexes for northern pike collected from a glacial prairie lake. *North American Journal of Fisheries Management* 15: 838-844.
- Nieman CL, Bruskotter JT, Braig IV, EC & Gray SM (2020). You can't just use gold: Elevated turbidity alters successful lure color for recreational Walleye fishing. *Journal of Great Lakes Research* 46: 589-596.
- Niemi N, Hansen JP, Eklöf JS, Eriksson BK, Andersson HC, Bergström U & Östman Ö (2023). Influence of reed beds (*Phragmites australis*) and submerged vegetation on pike (*Esox lucius*). *Fisheries Research* 261: 106621.
- Niessner D, Rittweg TD, Schubert H, Roser P & Arlinghaus R (2023a). Naturräumliche Einordnung. *Berichte des IGB* 33: 26-38.
- Niessner D, Rittweg TD, Roser P & Arlinghaus R (2023b). Schon- und Schutzbestimmungen mit Bezug zur Fischerei. *Berichte des IGB* 33: 136-152.
- Nuhfer AJ & Alexander GR (1994). Growth survival and vulnerability to angling of three wild brook trout strains exposed to different levels of angler exploitation. *North American Journal of Fisheries Management* 14: 423-434.
- Nyqvist MJ, Gozlan RE, Cucherousset J & Britton JR (2012). Behavioural syndrome in a solitary predator is independent of body size and growth rate. *PLoS One* 7: e31619.
- Nyqvist MJ, Cucherousset J, Gozlan RE & Britton JR (2018). Relationships between individual movement trophic position and growth of juvenile pike (*Esox lucius*). *Ecology of Freshwater Fish* 27: 398-407.
- Ogonowski M, Karlsson E, Vasemägi A, Sundin J, Bohman P & Sundblad G (2022). Temperature moderates eDNA–biomass relationships in northern pike. *Environmental DNA*.
- Ojeda-Martínez C, Bayle-Sempere JT, Sanchez-Jerez P, Forcada A & Valle C (2007). Detecting conservation benefits in spatially protected fish populations with meta-analysis of long-term monitoring data. *Marine Biology* 151: 1153-1161.
- Oele DL, Rypel AL, Lyons J, Cunningham P & Simonson T (2016). Do higher size and reduced bag limits improve Northern Pike size structure in Wisconsin lakes?. *North American Journal of Fisheries Management* 36: 982-994.
- Olson DE & Cunningham PK (1989). Sport-fisheries trends shown by an annual Minnesota fishing contest over a 58-year period. *North American Journal of Fisheries Management* 9: 287-297.
- Olsson J (2019). Past and current trends of coastal predatory fish in the Baltic Sea with a focus on perch pike and pikeperch. *Fishes* 4: 7.
- Olsson J, Andersson ML, Bergström U, Arlinghaus R, Audzijonyte A, Berg S, Briekemane L, Dainys J, Dalby Rayn, Droll J, Dziemian L, Fey DP, Van Gemert R, Greszkiewicz M, Grochiwski A, Jakubavičiūtė E, Luzys L, Leijk AM, Mustamäki N, Naddafi R, Olin M, Saks L, Skov C, Smolinski S, Svrigsden R, Tiainen J & Östman Ö (2023). A pan-Baltic

- assessment of temporal trends in coastal pike populations. *Fisheries Research* 260: 106594.
- Pauly D, Christensen V, Dalsgaard J, Froese R & Torres Jr F (1998). Fishing down marine food webs. *Science* 279: 860-863.
- Pauly D, Christensen V, Gu  nette S, Pitcher TJ, Sumaila UR, Walters CJ, Watson R & Zeller D (2002). Towards sustainability in world fisheries. *Nature* 418: 689-695.
- Philipp DP, Cooke SJ, Claussen JE, Koppelman JB, Suski CD & Burkett (2009). Selection for Vulnerability to Angling in Largemouth Bass. *Transactions of the American Fisheries Society* 138: 189-199.
- Pierce RB (1997). Variable catchability and bias in population estimates for northern pike. *Transactions of the American Fisheries Society* 126: 658-664.
- Pierce RB (2012). Northern pike: ecology, conservation, and management history. University of Minnesota Press, Minneapolis, London.
- Pierce RB, Tomcko CM & Schupp DH (1995). Exploitation of northern pike in seven small north-central Minnesota lakes. *North American Journal of Fisheries Management* 15: 601-609.
- Pieterek TP (2014). Determinanten der anglerischen Fangbarkeit von Hechten (*Esox lucius*). Master thesis, Humboldt-Universit  t zu Berlin.
- Pierce RB & Tomcko CM (2003). Variation in gill-net and angling catchability with changing density of northern pike in a small Minnesota lake. *Transactions of the American Fisheries Society* 132: 771-779.
- Pierce RB, Tomcko CM, Pereira DL & Staples DF (2010). Differing catchability among lakes: influences of lake basin morphology and other factors on gill-net catchability of northern pike. *Transactions of the American Fisheries Society* 139: 1109-1120.
- Pieterek T (2014). Determinanten der anglerischen Fangbarkeit von Hechten (*Esox lucius*). Master Thesis, Humboldt-Universit  t zu Berlin, Germany.
- Pitcher TJ, Green DA & Magurran AE (1986). Dicing with death: predator inspection behaviour in minnow shoals. *Journal of Fish Biology* 28: 439-448.
- Pitcher T (1991). Who dares wins: the function and evolution of predator inspection behaviour in shoaling fish. *Netherlands Journal of Zoology* 42: 371-391.
- Pope KL, Wilde GR & Bauer DL (2005). Maximum size of fish caught with standard gears and recreational angling. *Fisheries research* 76: 117-122.
- Post JR, Sullivan M, Cox S, Lester NP, Walters CJ, Parkinson EA, Andrew JP, Leyland J & Shuter BJ (2002). Canada's recreational fisheries: the invisible collapse? *Fisheries* 27: 6-17.
- Pursiainen A, Veneranta L, Kuningas S, Saarinen A & Kallasvuori M (2021). The more sheltered the better–Coastal bays and lagoons are important reproduction habitats for pike in the northern Baltic Sea. *Estuarine Coastal and Shelf Science* 259: 107477.

- R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Raat AJP (1985). Analysis of angling vulnerability of common carp in catch-and-release angling in ponds. *Aquaculture Research* 16: 171-187.
- Raat AJ (1988). Synopsis of biological data on the northern pike: *Esox lucius* Linnaeus 1758 (No. 30). Food & Agriculture Org.
- Raat AJP (1991). Production growth condition and angling vulnerability of zander *Stizostedion lucioperca* (L), in relation to the availability of prey fish in ponds. *Aquaculture Research* 22: 93-104.
- Radinger J, Koemle D, Ehrlich E, Dhellemmes F, Palder J, Matern S, Arlinghaus R (2023). Wirkung der beruflichen Vorlaichfischerei auf den Hechtbestand an den Bodden. *Berichte des IGB* 33: 528-542.
- Radinger J & Arlinghaus R (2023). Fischereiliche Sterblichkeit abgeschätzt aus Fang-Markierung-Wiederfang-Daten. *Berichte des IGB* 33: 2023: 508-528.
- Réale D, Reader SM, Sol D, McDougall PT & Dingemanse NJ (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews* 82: 291-318.
- Redpath TD, Cooke SJ, Arlinghaus R, Wahl DH & Philipp DP (2009). Life-history traits and energetic status in relation to vulnerability to angling in an experimentally selected teleost fish. *Evolutionary Applications* 2: 312-323.
- Redpath TD, Cooke SJ, Suski CD, Arlinghaus R, Couture P, Wahl DH & Philipp DP (2010). The metabolic and biochemical basis of vulnerability to recreational angling after three generations of angling-induced selection in a teleost fish. *Canadian Journal of Fisheries and Aquatic Sciences* 67: 1983-1992.
- Ricker WE (1958) Handbook of computations for biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada: 1-300.
- Riepe C, Koemle D & Arlinghaus R (2023). Angelfischerei an den Bodden heute. *Berichte des IGB* 33: 356-379.
- Rittweg TD, Palder J, Braun M, Arlinghaus R, Möller S & Winkler H (2023). Wachstum, Kondition und Ernährung von Boddenhechten früher und heute. *Berichte des IGB* 33: 193-232.
- Roser P, Lukyanova O, Dhellemmes F, Schütt J, Möller S, Kühn C & Arlinghaus R (2023). Historische und aktuelle Laichgebiete in den Bodden und Zuflüssen. *Berichte des IGB* 33: 265-277.
- Røste AS (2020). How Northern pike's (*Esox lucius*) traits environmental factors and angler characteristics influence angling vulnerability explored through an angling experiment in Aremarksjøen. Master thesis, Norwegian University of Life Sciences Ås.
- Rourke ML, Fowler AM, Hughes JM, Broadhurst MK, DiBattista JD, Fielder S & Furlan EM (2022). Environmental DNA (eDNA) as a tool for assessing fish biomass: A review of approaches and future considerations for resource surveys. *Environmental DNA* 4: 9-33.
- Saura M, Moran P, Brotherstone S, Caballero A, Alvarez J & Villanueva B (2010). Predictions of response to selection caused by angling in a wild population of Atlantic salmon (*Salmo salar*). *Freshwater Biology* 55: 923-930.

- Sbragaglia V, Morroni L, Bramanti L, Weitzmann B, Arlinghaus R & Azzurro E (2018). Spearfishing modulates flight initiation distance of fishes: the effects of protection individual size and bearing a speargun. *ICES Journal of Marine Science* 75: 1779-1789.
- Seekell DA, Brosseau CJ, Cline TJ, Winchcombe RJ & Zinn LJ (2011). Long-term changes in recreational catch inequality in a trout stream. *North American Journal of Fisheries Management* 31: 1100-1105.
- Sharma CM & Borgström R (2008). Increased population density of pike *Esox Lucius* – a result of selective harvest of large individuals. *Ecology of freshwater fish* 17: 590-596.
- Skov C, Berg S, Jacobsen L & Jepsen N (2002). Habitat use and foraging success of 0+ pike (*Esox lucius* L) in experimental ponds related to prey fish water transparency and light intensity. *Ecology of Freshwater Fish* 11: 65-73.
- Skov C, Nilsson PA, Jacobsen L & Brönmark C (2007). Habitat-choice interactions between pike predators and perch prey depend on water transparency. *Journal of Fish Biology* 70: 298-302.
- Stålhammar M, Fränstam T, Lindström J, Höjesjö, J, Arlinghaus R & Nilsson PA (2014). Effects of lure type fish size and water temperature on hooking location and bleeding in northern pike (*Esox lucius*) angled in the Baltic Sea. *Fisheries Research* 157: 164-169.
- Stamps JA (2007). Growth-mortality tradeoffs and 'personality traits' in animals. *Ecology letters* 10: 355-363.
- Suski CD & Philipp DP (2004). Factors affecting the vulnerability to angling of nesting male largemouth and smallmouth bass. *Transactions of the American Fisheries Society* 133: 1100-1106.
- Sutter DA, Suski CD, Philipp DP, Klefoth T, Wahl DH, Kersten P, Cooke SJ & Arlinghaus R (2012). Recreational fishing selectively captures individuals with the highest fitness potential. *Proceedings of the National Academy of Sciences* 109: 20960-20965.
- Tibblin P, Forsman A, Borger T & Larsson P (2016). Causes and consequences of repeatability flexibility and individual fine-tuning of migratory timing in pike. *Journal of Animal Ecology* 85: 136-145.
- Tibblin P, Bergström K, Flink H, Hall M, Berggren H, Nordahl O & Larsson P (2023). Higher abundance of adult pike in Baltic Sea coastal areas adjacent to restored wetlands compared to reference bays. *Hydrobiologia* 1-12.
- Tiainen JM, Olin MJ, Lehtonen HVT, Nyberg KB & Ruuhijärvi J (2017). The capability of harvestable slot-length limit regulation in conserving large and old northern pike (*Esox lucius*). *Boreal Environment Research*.
- Tsuboi J, Morita K, Klefoth T, Endou S & Arlinghaus R (2016). Behaviour-mediated alteration of positively size-dependent vulnerability to angling in response to historical fishing pressure in a freshwater salmonid. *Canadian Journal of Fisheries and Aquatic Sciences* 73: 461-468.
- Uusi-Heikkilä, S, Wolter C, Klefoth T & Arlinghaus R (2008). A behavioral perspective on fishing-induced evolution. *Trends in Ecology & Evolution* 23: 419-421.
- Uusi-Heikkilä S, Whiteley AR, Kuparinen A, Marsumura S, Venturelli PA, Wolte C, Slate J, Primmer CR, Meinelt T, Killen S, Bierbach D, Polverino G, Ludwig A & Arlinghaus R (2015). The evolutionary legacy of size-selective harvesting extends from genes to populations. *Evolutionary Applications* 8: 597-620.

- van Densen WLT & Vijverberg J (1982). The relations between 0+ fish density zooplankton size and the vulnerability of pikeperch *Stizostedion lucioperca* to angling in the Frisian lakes. *Hydrobiologia* 95: 321-336.
- van Gemert R, Koemle D, Winkler H & Arlinghaus R (2022). Data-poor stock assessment of fish stocks co-exploited by commercial and recreational fisheries: applications to pike *Esox lucius* in the western Baltic Sea. *Fisheries Management and Ecology* 29: 16–28.
- Vainikka A, Tammela I & Hyvärinen P (2015). Does boldness explain vulnerability to angling in Eurasian perch *Perca fluviatilis*?. *Current Zoology* 62: 109-115.
- Van Poorten B & Post JR (2005). Seasonal Fishery Dynamics of a Previously Unexploited Rainbow Trout Population with Contrasts to Established Fisheries. *North American Journal of Fisheries Management* 25: 329-345.
- Vogt A (2020). Understanding stakeholder conflicts in coastal fisheries: evidence from the brackish lagoons around Rügen. Master Thesis, Humboldt-Universität zu Berlin, Germany.
- Walters CJ & Bonfil R (1999). Multispecies spatial assessment models for the British Columbia groundfish trawl fishery. *Canadian Journal of Fisheries and Aquatic Sciences* 56: 601-628.
- Waters TF (1960). The development of population estimate procedures in small trout lakes. *Transactions of the American Fisheries Society* 89: 287-294.
- Wegener MG, Schramm HL, Neal JW & Gerard PD (2018). Effects of fishing effort on catch rate and catchability of largemouth bass in small impoundments. *Fisheries Management and Ecology* 25: 66-76.
- Wickham H, François R, Henry L, Müller K, Vaughan D (2023). *_dplyr: A Grammar of Data Manipulation_*. R package version 1.1.0
- Wilde GR, Pope KL & Durham BW (2003). Lure-size restrictions in recreational fisheries. *Fisheries* 28: 18-26.
- Wilson AD, Binder TR, McGrath KP, Cooke SJ & Godin JGJ (2011). Capture technique and fish personality: angling targets timid bluegill sunfish *Lepomis macrochirus*. *Canadian Journal of Fisheries and Aquatic Sciences* 68: 749-757.
- Wilson AD, Brownscombe JW, Sullivan B, Jain-Schlaepfer S & Cooke SJ (2015). Does angling technique selectively target fishes based on their behavioural type?. *PloSone* 10: e0135848.
- Winkler HM (1989). Fische und Fangertrage im Greifswalder Bodden. *Meer und Museum* 5 - Greifswalder Bodden: 52-58.
- Winkler HM (1991). Changes of structure and stock in exploited fish communities in estuaries of the southern Baltic coast (Mecklenburg-Vorpommern Germany). *Internationale Revue der gesamten Hydrobiologie und Hydrographie* 76: 413-422.
- Wickham H (2016) *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York, 2016.
- Young RG & Hayes JW (2004). Angling pressure and trout catchability: behavioral observations of brown trout in two New Zealand backcountry rivers. *North American Journal of Fisheries Management* 24: 1203-1213.

Acknowledgements

I would like to express my sincere gratitude to the people who without whom this work would not have been possible. First of all, I thank my peer students and good friends Fritz Feldhege and Marlon Braun who stood by me through the highs and lows of extensive fieldwork and who had an equal contribution to the organization and execution of the majority of efforts necessary to put this work together. Similarly, I would like to thank Carlos Jimenez who was a great and reliable help for over two months of tough work and who became a valued part of our team during his time as an intern. Likewise, Brian Beyeler joined our work for several weeks and was an immense help in the realization of these efforts.

There was a bunch of highly valued people in the background who were always helpful and constituted a significant backbone in this project: Timo Rittweg who laid the foundation for this work and was a reliable and valued colleague. Felicie Dhellemmes who always had an open ear for questions and was a highly appreciated mentor for various aspects of realizing such work. Dominique Niessner, who spent many hours in explaining necessary bureaucratic processes and who was appreciated for her joyous mentality. Johannes Radinger, who patiently spent many hours with me in the office and taught me the statistical analysis necessary to make sense of our data, never getting tired of my questions. Dieter Koemle, who was a joyous and helpful colleague, likewise supporting me with advice. Sven Matern, who helped us in the field for several weeks and contributed his knowledge and great team spirit. Jan Hallermann and Alex Türck, who were valued and reliable helpers for questions regarding the technical equipment necessary. Thank you to the team of the vehicle fleet of IGB, Stefan Bednarz, Thorsten Preuer and Laura Klatt who made our frequent journeys to Rügen feasible and were forgiving of losses. I want to deeply thank Jörg Schütt, who we all learned to value not only for his perpetual dedication in helping us, but for his kindness and affection for the project and each and every one of us. Thank you to Henry Diedrich, who was always supportive and provided us with valuable advice. Moreover, I would like to thank Volker Brauer and Dieter Reiter from Ummanz e.V. who permitted us to use their facilities. Thank you to Thomas, Ben and Olaf Lindner who were highly supportive during our fieldwork. I would moreover like to thank Tommy Tiegs and Frank Schnuchel, who were always keen and reliable helpers during data collection, as well as many more voluntary anglers who offered their help. Thomas Schälke kindly allowed us the use of crucial facilities around Sellin harbor.

I would like to highlight my gratitude for the support from several official institutions and their personnel, most importantly the Nationalpark Vorpommersche Boddenlandschaft

and Biosphärenreservat Südostrügen who gave us the permission to work inside the protected areas. Additionally, I want to thank the Landesamt für Landwirtschaft, Lebensmittelsicherheit und Fischerei Mecklenburg-Vorpommern (LALLF) for the kind collaboration and additional permissions necessary to make this work possible, including the animal care protocol for tagging (Aktenzeichen 7221.3–1-052/19). Likewise, I thank the Wasserschutzpolizeistation Stralsund and Lauterbach for the friendly collaboration. The Staatliches Amt für Landwirtschaft und Umwelt Vorpommern (StALU) is thanked for granting us access to Nature Conservation Areas.

I would like to thank my first supervisor and initiator of the Project BODDENHECHT, Robert Arlinghaus, for the mental basis of this work, the number of ideas put forth, the endurance to write the applications necessary for this project, guidance along the way in many aspects and the trust to enable this project. I also thank my second supervisor, Thomas Klefoth, for his willingness to make his way through this work and the associated efforts.

Lastly, I would like to express my deepest gratitude to Arianna Cecchetto, who was my main mental support for the past years and who stood by my side despite challenging periods.

Appendix

Appendix 1 Post-hoc results (p-values) for testing the effect of site on abiotic environmental variables. No significant differences were found for any of the variables.

Area	Salinity	Temperature	Visibility
Werderbucht	0.389	0.820	1
Ummanz	0.583	0.912	0.888
Sellin	0.098	0.842	0.153

Appendix 2 Mean values and standard deviations of pike total body lengths for the three comparison areas for each site gear and site.

Area	Site	Gear	Mean total length (mm) $\pm$ SD	n
Werderbucht	MPA	A	791.9 $\pm$ 88.3	91
		S	751.9 $\pm$ 57.8	32
	OA	A	808.5 $\pm$ 107.5	24
		S	753.9 $\pm$ 54.0	12
Ummanz	MPA	A	840.8 $\pm$ 107.0	64
		S	780.5 $\pm$ 124.7	27
	OA	A	785.3 $\pm$ 81.7	9
		S	766.9 $\pm$ 107.9	17
Sellin	MPA	A	671.1 $\pm$ 151.2	52
		S	733.4 $\pm$ 85.8	19
	OA	A	715.0 $\pm$ 87.7	23
		S	739.5 $\pm$ 82.8	16

Appendix 3 Mean values and standard deviations of pike ages determined from scale reading for the three comparison areas for each site gear and site.

Area	Gear	Site	Mean age (y) $\pm$ SD	n
Werderbucht	A	MPA	4.92 $\pm$ 1.37	72
		OA	3.95 $\pm$ 1.35	21
	S	MPA	5.57 $\pm$ 1.16	30
		OA	5.55 $\pm$ 1.75	11
Ummanz	A	MPA	6.44 $\pm$ 1.56	34
		OA	3.75 $\pm$ 1.5	4
	S	MPA	4.87 $\pm$ 2.18	23
		OA	4.13 $\pm$ 1.99	16
Sellin	A	MPA	3.35 $\pm$ 2.08	34
		OA	2.73 $\pm$ 2.05	11
	S	MPA	4.74 $\pm$ 2.32	19
		OA	5.25 $\pm$ 2.26	16

Appendix 4 Mean values and standard deviations of pike size corrected growth determined from scale reading for the three comparison areas for each site gear and site. Values were first summarized by individual to account for repeated measures.

Area	Gear	Site	Mean size corrected growth (mm) $\pm$ SD	n
Werderbucht	A	MPA	437.1 $\pm$ 41.6	72
		OA	465.5 $\pm$ 56.6	21
	S	MPA	419.8 $\pm$ 36.6	30
		OA	411.5 $\pm$ 24.7	11
Ummanz	A	MPA	433.3 $\pm$ 49.5	34
		OA	435.6 $\pm$ 50.7	4
	S	MPA	443.3 $\pm$ 43.1	23
		OA	458.8 $\pm$ 66.1	16
Sellin	A	MPA	431.5 $\pm$ 92.7	33
		OA	502.5 $\pm$ 60.7	11
	S	MPA	447.8 $\pm$ 79.2	19
		OA	432.4 $\pm$ 22.1	16

Declaration of independence

Faculty of Life Sciences

Albrecht Daniel Thaer-Institute for Agricultural and Horticultural Sciences

I hereby declare that this thesis with the title

“Examining Evidence for Angling-Induced Timidity in Northern Pike (*Esox lucius* L.):
A Case Study from Lagoons in the Southern Baltic Sea”

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 study and examination regulations and/or the General Admission, Study and Examination Regulations of Humboldt-Universität zu Berlin (ZSP-HU) / Allgemeine Satzung zur Regelung von Zulassung, Studium und Prüfung der Humboldt-Universität zu Berlin (ZSP-HU).

Berlin, 20.10.2023

Place / Date / Signature