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PRIMARY RESEARCH PAPER

Higher abundance of adult pike in Baltic Sea coastal areas adjacent to restored wetlands compared to reference bays

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Abstract The abundance of pike, a keystone top-predator, have declined dramatically in the Baltic Sea since the 1990s likely owing to recruitment failure. It has been proposed that wetland restoration can aid the recovery of the pike stock by increasing the number of recruits produced by anadromous populations. Yet, no previous studies have addressed whether wetland restorations are associated with higher abundances of adult pike in the coastal habitat. To address this, we performed standardised rod-and-reel survey fishing in paired bays with and without wetlands across three coastal areas and 3 years. To estimate dispersal and the contribution of wetland pike to the coastal stock, we tagged captured pike with passive integrated responders (PIT) and employed PIT reader stations in wetland inlets. The results showed that pike abundances were on average 90% higher in bays with an adjacent wetland although the effect varied among areas. Moreover, PIT-data uncovered that wetland pike constituted a high proportion of the pike found in adjacent coastal habitats and that some wetland fish dispersed up to 10 km. These results support that wetland restoration is a valuable tool to aid the coastal pike stock and ultimately restore the function and services of the coastal ecosystem.

Keywords Conservation · Fish · Habitat restoration · Management · Spawning · Standardized rod-and-reel fishing

Introduction

The coastal ecosystems of the Baltic Sea have during the last decades changed at an alarming rate owing to anthropogenic impacts such as eutrophication, climate change, habitat exploitation, and overfishing (Elmgren, 2001; Reusch et al., 2018). The negative consequences for biodiversity and the function and services of the ecosystem have been vast and include collapse of coastal fisheries (Lajus et al., 2013; Björkvik et al., 2020), enhanced eutrophication effects (Eriksson et al., 2009; Savage et al., 2010; Sieben et al., 2011), as well as altered fish community (Bergström et al., 2016b) and food-web dynamics (Eklöf et al., 2020). Several of these consequences are inherently connected to the severe declines of the coastal predatory fish species pike (*Esox lucius* L.) and perch (*Perca fluviatilis* L.) (Ådjers et al., 2006; Lehtonen et al., 2009; Ljunggren et al., 2010; Nilsson

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et al., 2019; Olsson, 2019), which may exert top-down control on the ecosystem (Donadi et al., 2017; Eklöf et al., 2020). To restore the function and services of the Baltic coastal ecosystem it is thus important with management and conservation efforts to aid the recovery of pike and perch populations. However, this has proven challenging since the actual cause(s) of the decline are still up for debate and seem to vary across time and space (Larsson et al., 2015; Bergström et al., 2016a; Olsson 2019).

At large, there is consensus that the decline of coastal predators, which was first identified in the Central Baltic Sea during the 1990s, relates to impaired recruitment (Nilsson et al., 2004, 2019; Lehtonen et al., 2009; Ljunggren et al., 2010) although increased (sub-)adult mortality caused by fisheries as well as growing populations of cormorants (*Phalacrocorax carbo sinensis* L.) and grey seals (*Halichoerus grypus* Fabricius) may also contribute (Lehtonen et al., 2009; Hansson et al., 2018; Bergström et al., 2022). Managing the factors that cause increased adult mortality is, at least hypothetically, rather straight forward by implementing fisheries restrictions and/or reducing the numbers of cormorants and seals whereas measures to mitigate poor recruitment are generally more complex owing to that it is influenced by numerous, and interacting, biotic, abiotic and anthropogenic factors (Larsson et al., 2015; Brosset et al., 2020; Hall et al., 2021). For instance, impaired recruitment of Baltic pike and/or perch have been attributed to increased resource competition with planktivorous species (Ljunggren et al., 2010), predation on early life-stages by the three-spined stickleback (*Gasterosteus aculeatus* L) (Nilsson, 2006; Bergström et al., 2015; Byström et al., 2015; Nilsson et al., 2019), toxic algae blooms (Persson et al., 2011) and degradation of coastal recruitment habitats due to exploitation (Sundblad et al., 2013; Sundblad and Bergström, 2014). Moreover, it has been proposed that Baltic Sea coastal predators are also challenged by climate change which may alter hydrological regimes in spawning habitats of anadromous ecotypes (Larsson et al., 2015; Tamario et al., 2019), and modify species interactions in the coastal habitat (Tamario et al., 2019; Donadi et al., 2020).

A recently proposed, and nowadays increasingly employed, management measure to aid the recruitment, and ultimately abundances, of coastal predators is to restore habitats in adjacent freshwater (streams and wetlands) to which both Baltic pike and perch may migrate for reproduction (Nilsson et al., 2014; Larsson et al., 2015; Hansen et al., 2020; Hall et al., 2022). Previous research suggests that this anadromous behaviour is common and that fish of freshwater origin may constitute a substantial proportion of the coastal stock of predators (Müller, 1986; Westin and Limburg, 2002; Engstedt et al., 2010; Rohtla et al., 2012; Hall et al., 2021; Flink et al., 2023). With a major part of rivers and wetlands along the Baltic coast severely manipulated by ditching, impoundment and migratory barriers, there are thus ample opportunities for improving spawning habitats of anadromous predators with comparatively small means with the ultimate aim of improving coastal stocks of predatory fish (Nilsson et al., 2014; Larsson et al., 2015).

Restoration and/or construction of wetlands to serve as spawning and nursery habitat have been proposed as a cost-efficient effort to aid Baltic anadromous predators, especially pike, and many (~ 100) such efforts have been conducted along the Swedish coast since the mid 2000s (Larsson et al. 2015; Engstedt et al., 2017; Hansen et al., 2020). These wetlands, known as “pike factories”, aim to offer optimal conditions for successful recruitment in terms of substrate, temperature, resources, and interspecific competition (Nilsson et al. 2014; Larsson et al., 2015; Engstedt et al., 2017). Recent studies confirm that wetland restoration have high potential to improve pike recruitment with the number of recruits increasing several orders of magnitude within a few years (Nilsson et al., 2014; Engstedt et al., 2017; Hansen et al., 2020). Moreover, increases in recruitment also seem to translate into larger census population size as suggested by increasing number of spawning adults across time (Nilsson et al., 2014; Engstedt et al., 2017; Hansen et al., 2020), a comparison facilitated by the natal homing behaviour of anadromous pike and iteroparous life-cycle where adults return annually to spawn (Engstedt et al., 2014; Forsman et al., 2015; Larsson et al., 2015; Tibblin et al., 2016b). Still, increased numbers of recruits and returning adults following wetland restoration may not, by necessity, translate into higher abundances in the coastal habitat since it may be constrained by external mortality on both juveniles and adults (Hansson et al., 2018; Nilsson et al., 2019; Bergström et al., 2022). However, the key point of whether improved pike recruitment facilitated by wetland restoration also results in higher abundance of pike in the coastal habitat have to date not been addressed.

Here, we assessed whether and how wetland restoration was associated with the abundance and size distribution of adult pike in replicated coastal areas in the south-east Baltic Sea that each comprised paired pike factory (coastal habitat with adjacent restored wetland) and reference zones (without wetland). To quantify abundances and the size distribution of adult pike, we conducted standardized rod-and-reel fishing across 3 years with replicated paired efforts (treatment and reference zones investigated simultaneously) both during spring and autumn to comprise putative spatiotemporal variation of pike abundances in the comparison. The method of standardized rod-and-reel fishing (standardized version of Niemi et al., 2023) was employed due to the unsuitability of gill-net survey fishing in estimating the abundances of pike (Holmgren, 1999; Appelberg, 2000; Bergström et al., 2022; Olsson et al., 2023). Utilising standardised rod-and-reel fishing instead of gill-net surveys also allowed us to measure, tag (with passive integrated transponders PIT) and release captured individuals to conduct mark-recapture studies. By placing PIT reader stations in the inlets to the wetlands during spawning season, we assessed to what degree individuals captured in the coastal habitat originated from the focal wetlands and estimated the spatial scale of putative impacts of wetlands on pike abundances.

Methods

The study system—Baltic anadromous pike

Pike is a large, long-lived, predatory species with circumpolar distribution where it inhabits both fresh- and brackish water environments (Craig, 1996). In the Baltic Sea, one of the largest brackish water habitats on Earth, there are two pike ecotypes (resident and anadromous) that coexist in the coastal habitat but separate during spawning which typically occur during March–May (Westin and Limburg, 2002; Engstedt et al., 2010). Resident populations spawn in shallow brackish bays whereas anadromous populations migrate to freshwater spawning habitats which are often constituted by small streams (< 5 m wide) and adjacent wetlands (Nilsson et al., 2014; Larsson et al., 2015). Previous studies have also shown that anadromous pike display natal homing and that streams/wetlands harbour genetically and phenotypically differentiated subpopulations that are locally adapted to their specific spawning habitat but are sympatric in the Baltic Sea for the large majority of the life-cycle (e.g. Tibblin et al., 2015, 2016a; Berggren et al., 2016; Nordahl et al., 2019; Sunde et al., 2022).

Study areas

The study was conducted in three coastal areas (Mönsterås North, MN; Mönsterås South, MS; Öland, OL) in the western Baltic Sea and comprised both inner (MN and MS) and outer (OL) archipelagic habitats (Fig. 1). In each area, reference (REF) and pike factory (PF) zones were selected to represent equal

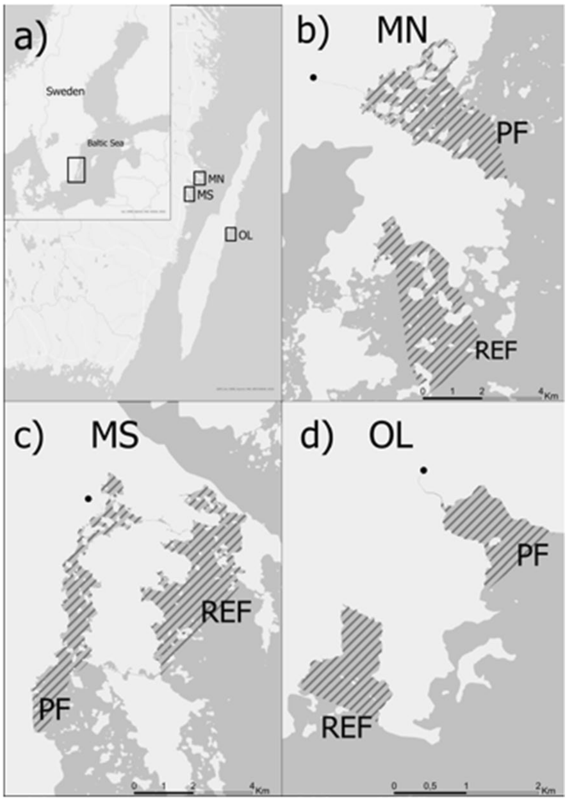

Fig. 1 Map of study area. **a** shows the study location in south-east Sweden, **b–d** shows REF and PF zones (striped dark grey) for each specific study area, respectively. Filled black bullets denote location of restored wetlands to aid pike recruitment. *MN* Mönsterås North; *MS* Mönsterås South; *OL* Öland; *PF* zone with restored wetland; *REF* zone without wetland

sized habitats (0.3–3 km^2 depending on coastal area) with similar depth profiles, available spawning habitat (shallow and sheltered bays with soft bottom and vegetation cover) and separated from each other by peninsulas (Fig. 1). No wetlands or streams were available in REF zones whereas in the PF zones there were adjacent restored wetlands in their innermost parts to facilitate pike recruitment (Fig. 1). These wetlands (Lervik in MN, Okne-Kronobäck in MS and Harfjärden in OL) were all designed to favour pike recruitment and were chosen for this study to comprise variation in characteristics, size (0.015–0.065 km^2) and type of coastal habitat (for details, please see Nilsson et al., 2014 for Lervik and Okne-Kronobäck, and Sunde et al., 2018 and Flink et al., 2021 for Harfjärden).

Standardized rod-and-reel fishing to quantify abundances of adult pike

To estimate the abundances of adult pike in the coastal habitat, we employed standardised rod-and-reel fishing from boat. For each survey (day of fishing), two teams (á 2 fishermen each) simultaneously fished for pike during 5.5 h (with a few exceptions due to strong winds when the fishing time in both paired zones were reduced) in the specific coastal area (MN, MS or OL) with one team in each of the paired zones (REF or PF). All fishing were conducted using standardised spinning gear such that each fisherman used the same rod-and-reel (ABU Velocity spinning rod 9′ 40–80 g, ABU Revo spinning reel) and had a fixed variety of five lure types (spinner, soft plastic, crankbait, plastic spoon and metal spoon) available in two specific colours (natural and bright) to choose from. All efforts were conducted during daytime (approx. 9:30–15:00) to avoid potential bias by altered activity of pike during twilight (Kobler et al., 2008; Baktoft et al., 2012; Nordahl et al., 2020).

Surveys in each of the three areas (MN, MS, OL) were replicated among and within years to comprise spatiotemporal variation in activity and/or abundances of pike. Each area (and PF and REF zones there within) were surveyed in spring (February–March with the exception of 2018 when it was done in early June due to ice cover and fishery closure during April–May) and autumn (October–November) across three years (autumn 2017–spring 2020) with surveys replicated three times in each period ($N_{\text{total}} = 53$ paired surveys, one survey in the OL area was cancelled). Both spring and autumn were surveyed since the former (spring) represents the spawning period during which pike aggregate close to spawning habitats whereas, in autumn, pike have dispersed throughout the forage habitat (Jacobsen et al., 2017; Nordahl et al., 2020; Flink et al., 2023). Including both seasons thus generate unbiased estimates of pike abundances in the coastal habitat. All nine surveys (three per area) for each period were conducted within 4 weeks with a minimum of 3 days between repeated surveys of the same area (MN, MS or OL). All surveys (fishing) were performed by a confined group of 14 experienced fishermen constituted by the authors and field personnel (please see 'Author contributions' and 'Acknowledgements' for details) which were randomly assigned to the teams, zones, and areas throughout the project to avoid bias by potential skill differences among fishermen.

Surveys were conducted with the objective to maximize the number of captured pike in the focal zone. All captured individuals were landed with a rubber net, measured for total length (to the closest cm), sampled for DNA (fin clip), sex determined and tagged with a PIT-tag (HDX23, Biomark, Boise, Idaho, USA) that were inserted into the pelvic girdle. Before release, the location (GPS-coordinates) and time of the capture was recorded.

Estimating the contribution of wetland spawning pike to the coastal stock

To assess the proportion of individuals captured in the coastal habitat that originated from wetlands and inform about the spatial scale of putative influences of wetland on the coastal pike stock, we employed PIT reader stations close to inlets in each of the three focal wetlands. Each PIT reader station used two antennas that were made out of looped copper wiring, customized to each site and tested to ensure that the detection range encompass the full cross-section of the inlet. The antennas create magnetic fields and thereby enable the station to detect PIT-tagged individuals that pass through (see Skov et al. 2013 for more details). Using two antennas per station add reliability through redundancy, increase the detection probability and allow for identifying the direction of movements. These stations monitored the arrival of PIT-tagged fish with known capture location across the spawning season (early March–Late May) except for the 2018 spawning season in Okne-Kronobäck due to a technical failure.

Data analysis and statistics

Comparing the abundances of pike in coastal habitats with and without adjacent restored wetlands

To investigate whether the abundances of pike differed between coastal habitats with and without restored wetlands, we performed 53 paired (i.e. REF versus PF zones) surveys using standardized rod-and-reel fishing. To analyse data, we first calculated catch per unit effort (CPUE) for each survey (fishing day/zone) by dividing the total catch (of a 2-man team) by the fishing time (normally 5.5 h) multiplied by number of fishermen (2) to generate number of pike per rod hour as CPUE estimate. Movement data showed that wetland pike also dispersed to the REF zones (especially in the OL area where 47% of the captured fish was of wetland origin, see Sect. Results below). With the paired study design relying on that pike abundances in REF zones were not impacted by the wetlands (i.e. representing control bays, hence the separation of peninsulas), dispersing pike (as identified by PIT-tag detections) were subsequently excluded in the CPUE estimates for REF zones (see S1 for analysis of data and results without excluding wetland pike in REF zones). To support the decision to exclude wetland fish in REF zones to avoid confounding the treatment (PF)—control (REF) comparison, we conducted an additional analysis (linear mixed model, same settings as below) with wetland fish excluded from both zones (PF and REF) (see S2 for analysis of data and results). This revealed that there was no significant difference ($P = 0.69$) between zones in CPUE corrected for wetland fish which illustrated that the presence of wetlands modulated the abundances (S2, Fig. S3).

To evaluate whether overall CPUEs differed between coastal habitats with (PF) and without (REF) restored wetland, we first performed a paired t-test with stats package (v4.2.1). Next, to evaluate whether the effect of zone varied according to coastal area, we fitted a linear mixed model with log transformed CPUE values as response variable, zone, and coastal area, as well as the interaction between them, as fixed explanatory variables. Pairwise fishing efforts in each coastal area was set as random factor to account for the possibility that pike densities might vary among coastal areas, years, seasons, and fishing occasions. However, we also evaluated whether the potential differences of CPUE between zones varied among seasons by adding an interaction between zone and season, but this interaction was not significant. The interaction between coastal area and zone was significant, hence we evaluated the potential difference in CPUE between zones in separate models for each coastal area.

Comparing the size distribution of pike in coastal habitats with and without adjacent restored wetlands

To test whether the size distribution of pike (total length cm) differed between the zones, data were fitted using a linear mixed model with length as a response variable, and sex and zone as fixed main explanatory variables. Since the study was replicated in three different coastal areas (MN, MS and OL) that might house pike of different size distributions, we allowed the intercepts to vary according to area by including it as a random factor and also included an interaction between coastal area and zone as a random effect. Due to the presence of an interaction effect between area and zone, we also added separate analyzes for each location evaluating whether size distributions differed according to zone or sex. In these cases, we used function *lm* in the stats package and all results are reported in Table 1.

Linear mixed models were fitted with function *lme* in the package nlme (v3.1-159) (R Core Team, 2013; Pinheiro et al., 2019; RStudio Team, 2019). Categorical variables with no expected baseline were assigned orthogonal contrasts. To evaluate best model fit, we

Table 1 Results from separate linear regressions evaluating the effects of zone and sex on pike length distributions within each location respectively

Location	Predictors	df	*F* value	*P* value
MN	Zone	1, 374	23.8	< 0.001
	Sex		95.8	< 0.001
MS	Zone	1, 349	2.70	0.10
	Sex		113	< 0.001
OL	Zone	1, 170	30.4	< 0.001
	Sex		19.2	< 0.001

performed log-likelihood tests of mixed models fitted with maximum likelihood using function *anova* in the stats package. Significance of terms was evaluated with the function *Anova* (using type 3 sums of squares in the presence of an interaction) in the car package (v3.1-0). To evaluate model fit and test assumptions we used visual inspection of residuals and standardized residuals against fitted values generated with functions *qqnorm* and *plot,* respectively (R Core Team, 2013; RStudio Team, 2019). All other plots were generated with ggplot2 (v3.3.6) and ggpubr (v0.4.0) (Wickham, 2016; Kassambara, 2019).

Results

Restored wetlands associated with higher abundances of pike in the coastal habitat

During 53 paired surveys that constituted 1119 rod hours, we captured, and released 914 pike (Total mean length ± SD = 64 ± 11 cm; range: 33–112 cm). In total, 560 and 354 pike were captured in PF and REF zones respectively out of which 52 individuals in the REF zones originated from the wetlands and were subsequently excluded (for results without exclusion of wetland fish, please see S1). The average CPUE (number of pike / rod hour) was 0.97 for PF and 0.51 for REF zones respectively which equal an 89.9% higher average CPUE in PF zones (Fig. 2A). During the 53 paired surveys, rank data showed that PF zones generated the highest number of captured pike in 74% of the occasions (i.e. 39 out of 53 surveys) whereas REF zones had highest capture in 17% of the surveys while in 9% of the surveys the catch was equal between zones (Fig. 2B). Pairwise analysis of CPUE showed that abundances of pike as estimated by standardized rod-and-reel fishing were overall significantly higher in coastal habitats with adjacent restored wetlands to aid pike recruitment (Paired *t* test: $t = 4.34$, $df = 52$, $p < 0.0001$; Fig. 2B). The difference in CPUE between PF and REF zones did not vary over seasons (effect of interaction between zone

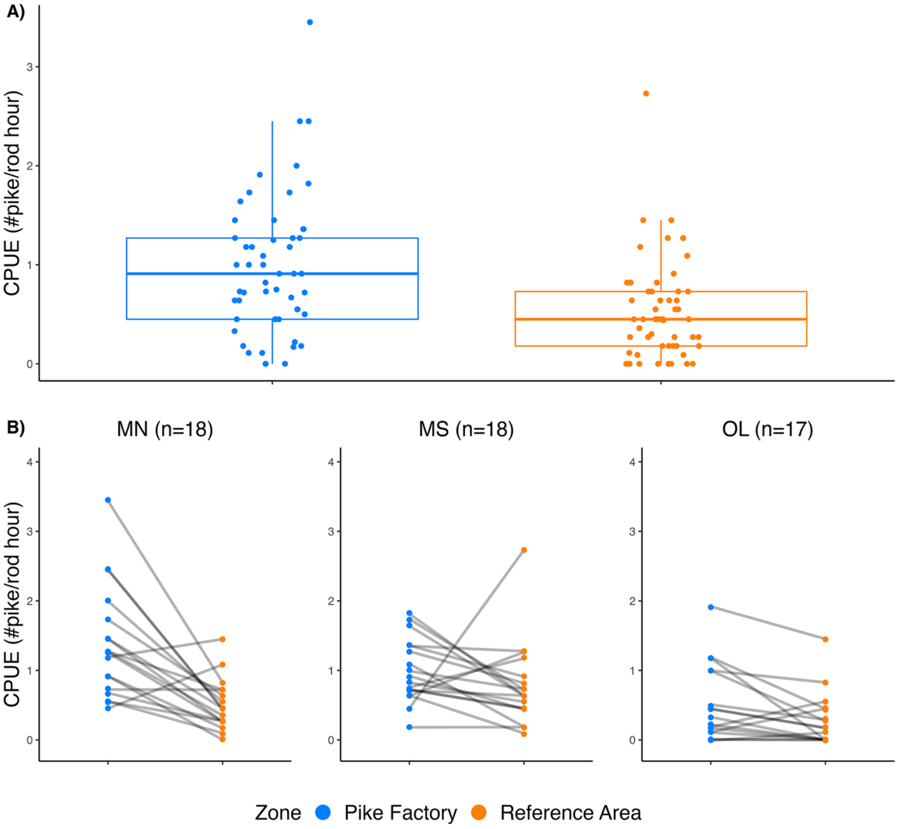

Fig. 2 Differences in abundances of pike estimated by standardized rod-and-reel fishing. **A** Overall catch per unit effort (CPUE: number of pike per rod hour) for PF and REF zones respectively based on 53 fishing surveys totaling 1119 rod hours. **B** Pairwise comparisons of CPUE for each survey (paired efforts in REF and PF) among coastal areas (MN, MS, OL). Fish originated from the wetlands were excluded when calculating CPUEs for REF zones. *MN* Mönsterås North; *MS* Mönsterås South; *OL* Öland; *PF* zone with restored wetland; *REF* zone without wetland

and season: $\chi^2 = 5.64$, $df = 12$, $P = 0.23$), but among coastal areas (effect of interaction between zone and coastal area: $\chi^2 = 9.70$, $df = 8$, $P = 0.01$). In separate analyzes for each coastal area, the positive effect of a restored wetland was significant in MN and OL (mean CPUE: $MN_{PF} = 1.37$, $MN_{REF} = 0.50$; $OL_{PF} = 0.52$, $OL_{REF} = 0.28$) but not MS (mean CPUE: $MS_{PF} = 0.99$, $MS_{REF} = 0.77$) (effect of zone in MN: $\chi^2 = 924.7$, $df = 1$, $P < 0.0001$; OL: $\chi^2 = 6.20$, $df = 1$, $P = 0.013$; MS: $\chi^2 = 1.98$, $df = 1$, $P = 0.16$).

Wetland fish constitutes a major proportion of the coastal stock

PIT-tag data showed that a high proportion of individuals captured in the coastal habitat utilized the wetlands for spawning. The average proportion of captured pike pooled across the three coastal areas (MN, MS, OL) that were detected in the wetlands, without controlling for mortality, were 46% and 20% for PF and REF zones respectively, although the proportion varied considerably among coastal areas ($MN_{PF} = 60\%$, $MN_{REF} = 8\%$; $MS_{PF} = 14\%$, $MS_{REF} = 5\%$; $OL_{PF} = 63\%$, $OL_{REF} = 47\%$). In all three coastal areas, there were individuals captured in REF zones that migrated to the wetlands for spawning which reflected dispersal events of up to 10 km swimming distance (measured from location of capture).

Associations between restored wetlands and the size structure of the coastal pike stock

Analysis of the size structure of pike uncovered a significant interaction effect between zone and coastal area ($\chi^2 = 25.5$, $df = 9$, $P < 0.0001$). There was a significant difference in length distributions according to zone and sex (main effect of zone: $\chi^2 = 25.9$, $df = 1$, $P < 0.0001$; main effect of sex: $\chi^2 = 226$, $P < 0.001$; Fig. 3), such that pike caught in PF zones were generally smaller (average total length ± SD: $PF_{females} = 65.9 \pm 10.3$ cm, $PF_{males} = 55.8 \pm 7.0$ cm, $REF_{females} = 69.8 \pm 11.0$ cm, $REF_{males} = 58.6 \pm 7.0$ cm) and females generally larger than males (average total length ± SD: Females = 67.4 ± 10.7 cm, Males = 56.9 ± 7.1 cm). Analyzing the three locations separately revealed that this pattern was similar for all coastal areas (Table 1), although the trend of larger pikes in the REF zone was not significant in the MS area ($P = 0.10$; Table 1; Fig. 3).

Discussion

In the Baltic Sea, the coastal top-predator and keystone species pike has declined dramatically since the 1990s (Ljunggren et al., 2010; Nilsson et al., 2019;

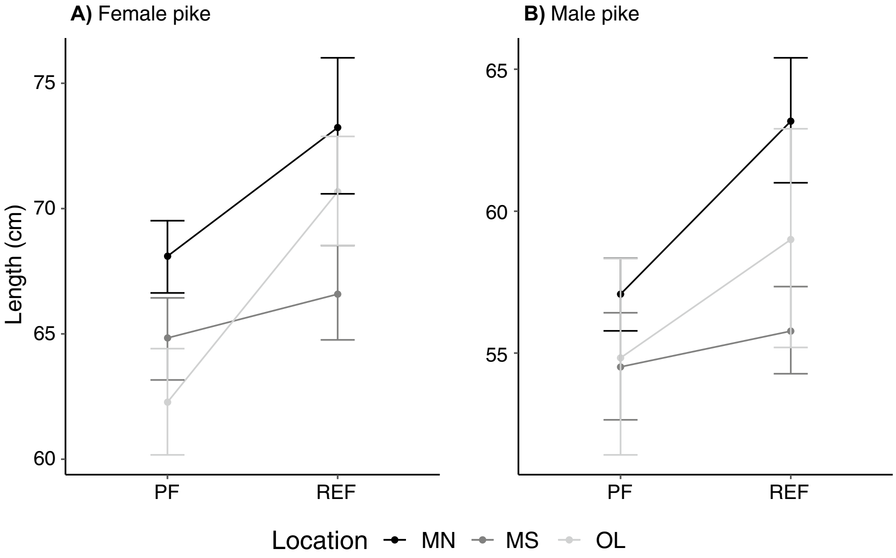

Fig. 3 Size distributions (cm total length) for each location (MN, MS, OL) and zone (PF, REF). **A** Female ($n = 639$) and **B** Male ($n = 263$), size distributions across locations and zones. *MN* Mönsterås North; *MS* Mönsterås South; *OL* Öland; *PF* zone with restored wetland; *REF* zone without wetland

Bergström et al., 2022). Recent insights about the presence of sympatric anadromous and Baltic resident ecotypes of pike (Limburg and Waldman, 2009; Engstedt et al., 2010; Rohtla et al., 2012) lead to the development of wetland restoration as a management tool to aid the recruitment of anadromous pike with the ultimate aim of strengthening the pike stock in the coastal habitat and regain a top-down controlled food-web (Larsson et al., 2015; Hansen et al., 2020; Kraufvelin et al., 2021). Although previous reports suggest that wetland restorations have the potential to substantially increase the number of recruits and spawning adults (Nilsson et al., 2014; Engstedt et al., 2017; Hansen et al., 2020), there have been no evaluation of whether wetland restorations are de facto associated with higher densities of adult pike in coastal habitats despite this being the ultimate aim from an ecosystem functioning and services perspective. The reasons to this crucial lack of knowledge are likely two-fold. First, pike typically becomes mature at an age of 3–4 years (Craig, 1996; Tibblin et al., 2015) so wetland restorations require time before any putative positive effects on abundances can be detected and the majority of pike wetlands have been restored during the last decade (Hansen et al., 2020). Second, quantifying the abundances of pike in the Baltic Sea is not suitable with traditional survey fishing methods such as gill nets or electrofishing (Holmgren, 1999; Appelberg, 2000) and pike is thus not part of regular biomonitoring such that estimates of abundances of adult pike in coastal habitats are scarce (Olsson, 2019; Bergström et al., 2022; Olsson et al., 2023).

In this study we evaluated whether and how the abundance and size structure of adult pike in coastal habitats were associated with wetlands restored to aid the recruitment of pike. In three coastal areas and across three years, we performed paired standardized rod-and-reel efforts in bays with and without adjacent restored wetlands. This uncovered that restored wetlands, despite being very small areas of less than 0.065km^2, were associated with substantially higher (89.9%) abundances (estimated by CPUE) of adult pike in the adjacent coastal habitats although the impact of wetlands varied considerably among areas. The same pattern was also evident when comparing rank data. Moreover, in bays with adjacent wetlands pike were generally smaller (and likely younger) indicative of stronger recent recruitment cohorts although putative effects of increased intraspecific competition cannot be excluded (Swales, 2006). The notion that wetland restoration is associated with higher abundances of adult pike in the coastal Baltic Sea have to date relied upon circumstantial evidence based on increasing numbers of recruits and spawning adults (Nilsson et al., 2014; Larsson et al., 2015; Engstedt et al., 2017; Hansen et al., 2020). However, this neglects the potential of other factors constraining the actual abundances on the coast. For instance, the number of recruits may not translate into higher abundances due to intense predation by sticklebacks (Nilsson et al., 2019) whereas the abundances of adults may be constrained by external mortality (Hansson et al., 2018; Bergström et al., 2022) such that increasing numbers of adult anadromous pike only result in a change of the ecotype (anadromous/resident) composition in the coastal stock (Engstedt et al., 2010). As such, this study provides novel and, from a management perspective, crucial information to the positive effect of restored wetlands for pike abundances in the coastal habitat.

The proportion of individuals that utilized the focal wetlands for spawning (as evidenced by PIT-tag recordings) were generally high although it varied considerably among areas and zones. In the bays adjacent to the restored wetlands, on average 46% (range 14–63%) of the individuals utilized the wetlands for spawning whereas the corresponding estimate in the reference bay was 20% (range 5–47%). These estimates were not adjusted for mortality, straying or miss of detection by the PIT-antennas such that the proportion were likely underestimated which further strengthen the conclusion that a substantial proportion of pike in these areas originated from the restored wetlands. Interestingly, our result also suggests that the impact of the restored wetlands on pike abundances is not only limited to the adjacent coastal habitat with, in average, 20% of the pike captured in the reference areas also utilizing the wetlands for spawning. As such, positive effects of restored wetlands on pike abundances seem to be relevant within a radius of approximately 10 km swimming distance. That wetlands may contribute with a substantial proportion of all pike found in adjacent coastal habitats also mirrors the results of a recent study by Flink et al. (2023) who showed that 33 out of 36 (> 90%) pike captured and acoustically tagged in a coastal habitat during summer and fall utilized an adjacent restored wetland and its estuary during spawning the next year.

Together, these results support the notion that wetland restoration can be a viable and important management tool to improve the coastal Baltic Sea pike stock. The confined home-range and locally adapted population structure of anadromous pike (Tibblin et al., 2015; Sunde et al., 2022) do however suggest that large-scale positive effects on pike abundances and stabilisation of food-webs through top-down control require intense restoration efforts of wetlands along the coast. Such efforts would potentially also result in additive values on the productivity and stability of pike populations through enhanced connectivity similar to what have been shown in trout (*Salmo trutta* L.) (Tamario et al., 2021). The effects of large-scale wetland restorations for abundances of anadromous pike would potentially also indirectly aid the recovery of resident pike populations through spill-over effects (Taylor et al., 2019; Medoff et al., 2022) and top-down control of the mesopredatory three-spined stickleback that predate intensively on pike juveniles (Nilsson et al., 2019).

To conclude, this study suggests that wetland restoration to aid recruitment of Baltic Sea anadromous pike have the potential to substantially increase the abundances of adult pike in the coastal habitat. However, caution is needed regarding the generality and causation of the findings with only three areas included and since it was not possible to employ a before-after-control-impact (BACI) design. Our estimates suggest that the focal wetlands, despite being smaller than 0.065 km^2, contributed with approximately 5–63% of the pike found in adjacent coastal areas with a radius upwards of 10 km. This supports the notion that wetland restoration is a viable management strategy to aid the dwindling coastal pike stock and ultimately restore the function and services of the Baltic coastal ecosystem through top-down control of the food-web (Nilsson et al., 2014; Donadi et al., 2017; Greszkiewicz et al., 2022). Moreover, wetlands do not only constitute a key habitat for the viability of a plethora of species, including many fish, amphibian, bird and plant species, but is also central for the hydrology, water quality and nutrient cycling of aquatic systems (Kingsford et al., 2016; Tamario et al., 2019; Roegner et al., 2021). Unfortunately, the biological function of the majority of wetlands are impaired by, for instance, dredging to facilitate irrigation, agriculture and exploitation, with dramatic negative consequences both for biodiversity and the function and services of ecosystems (Davidson, 2014; Kingsford et al., 2016). Continued restoration of wetlands to aid Baltic Sea pike thus have the potential to offer synergistic effects for biodiversity conservation in general, decreased eutrophication and restored ecosystem functioning.

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Data availability The datasets generated during and/or analysed during the current study are available in the Dryad repository, https://doi.org/10.5061/dryad.3r2280gmt.

Declarations

Conflict of interest The authors do not have any conflicts of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. The study was granted ethical approvals (Dnr 39-10, Dnr 168677-2018; Dnr 19359-2019) by the Ethical Committee on Animal Experiments, Swedish Board of Agriculture, in Linköping and Stockholm.

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