

Influence of reed beds (*Phragmites australis*) and submerged vegetation on pike (*Esox lucius*)

Niklas Niemi^a, Joakim P. Hansen^b, Johan S. Eklöf^c, Britas Klemens Eriksson^d, Henrik C. Andersson^e, Ulf Bergström^a, Örjan Östman^{a,*}

^a Swedish University of Agricultural Sciences, Department of Aquatic Resources, Box 7080, 750 07 Uppsala, Sweden

^b Stockholm University Baltic Sea Center, 106 91 Stockholm, Sweden

^c Department of Ecology, Environment and Plant Sciences (DEEP), Stockholm University, 10691 Stockholm, Sweden

^d Faculty of Science and Engineering, GELIFES — Groningen Institute for Evolutionary Life Sciences, Nijenborgh 7, 9747 AG Groningen, the Netherlands

^e Stockholm County Board, Länsstyrelsen Stockholm, Box 22067, 104 22 Stockholm, Sweden

ARTICLE INFO

Keywords:

Reed expansion
Pike
Baltic Sea
Spatial distribution
Habitat utilization
Angling
Esox lucius
Phragmites australis

ABSTRACT

Eutrophication and reduced grazing have led to an expansion of the common reed (*Phragmites australis*) in archipelago areas in the Baltic Sea, while at the same time the composition of submerged vegetation has changed. Although reed is important as nursery habitat for many fish species, extensive emergent vegetation may reduce biodiversity and abundance of predatory fish. Pike (*Esox lucius*) is a predatory fish whose larvae and young-of-the-year find both food and shelter in reed but use different micro-habitats during different life-stages. Here we investigate the influence of reed and submerged vegetation on abundance and body size of adult pike during the spawning season. We predicted that coastal bays with extensive but heterogeneous reed beds with higher cover of submerged vegetation would have more and larger pike than bays with smaller, homogenous reed belts or with less submerged vegetation. To test these predictions, we estimated abundance and size-structure of adult pike from catches in angling fishing among 22 bays in the Stockholm archipelago at the Swedish Baltic Sea coast. Our analyses show that catches of adult pike were positively associated with both extensive reed beds and cover of rooted submerged vegetation. However, pike size was not correlated with any vegetation variable, but instead increased with wave exposure and bay area. Our study suggests that reed beds and submerged vegetation are important for adult pike during the spawning season, and even the most extensive reed beds had no evident negative effect on pike populations. We could not see any clear relationship between emergent reed habitat and cover of submerged vegetation among the studied bays, and conclude that to maintain pike population during the spawning season it is important that coastal bays have sufficient amounts of both reed beds and rooted submerged vegetation.

1. Introduction

Emergent shoreline vegetation like reed (*Phragmites australis*) and cattail (*Typha* sp.) in soft sediment coastal areas is expanding due to eutrophication from allochthonous nutrient inputs (King et al., 2007; Von Numers, 2011; Pitkänen et al., 2013; Schrank and Lishawa, 2019), shoreline alterations (Burdick and Konisky, 2003; Silliman and Bertness, 2004; Bart et al., 2006; King et al., 2007; Chambers et al., 2008; Schrank and Lishawa, 2019), or reduced grazing pressure (Von Numers, 2011; Pitkänen et al., 2013). In parts of the Baltic Sea, beds of the emergent plant species common reed (*Phragmites australis*; hereafter only reed) has

become both denser and wider (Pitkänen et al., 2013) and have expanded into new areas (Von Numers, 2011). Emergent vegetation are strong competitor for light in shallow, wave-protected areas with high organic and nutrient concentrations (Li et al., 2021), which may reduce biodiversity of submerged vegetation and more homogeneous vegetation (Munsterhjelm, 1997; Pitkänen et al., 2013; Altartouri et al., 2014; Han and Cui, 2016; Schrank and Lishawa, 2019). On the other hand, reed has important functions in shallow and sheltered habitats (Altartouri et al., 2014) as it protects shorelines from wave erosion, buffers internal nutrient loading and absorbs external nutrient loadings (Kaitaranta et al., 2013), and acts as a carbon sink (Buczko et al., 2022).

* Corresponding author.

E-mail address: orjan.ostman@slu.se (Ö. Östman).

<https://doi.org/10.1016/j.fishres.2023.106621>

Received 30 May 2022; Received in revised form 13 January 2023; Accepted 15 January 2023

Available online 27 January 2023

0165-7836/© 2023 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

Reed also has a function as nesting area for birds, and spawning and nursery habitat for fish (Altartouri et al. 2014; Härmä et al. 2008; Snickars et al., 2010; Kallasvuo et al., 2011).

The northern pike (*Esox lucius*) is a piscivorous fish associated with reed and macrophyte vegetation (Bry, 1996; Casselman and Lewis, 1996; Lappalainen et al., 2008; Kallasvuo et al., 2011). Pike has shown a decline in both abundance and body size in parts of the Baltic Sea during the last decades (Berggren et al., 2022; Bergström et al., 2022; Olsson et al., 2023). There are likely several co-acting factors contributing to these declines in abundances and size, including reduced recruitment of early life-stages (Nilsson, 2006; Nilsson et al., 2019; Eklöv et al., 2020), increased adult mortality (Berggren et al., 2022; Bergström et al., 2022), and habitat degradation and isolation (Sandström et al., 2005; Nilsson et al., 2014; Sundblad and Bergström, 2014; Hansen et al., 2019).

Expanding emergent vegetation like reed and cattail (*Typha* sp.) have been shown to negatively affect fish populations, including the northern pike, in other parts of the world (Olson et al., 1998; Schrank and

Lishawa, 2019; Massa and Farrell, 2020). Although vegetation is essential for pike, in a review Casselman and Lewis (1996) concluded that abundance of juvenile and adult pike peak at a cover of submerged vegetation around 30–70 %. In shallow coastal bays of the Baltic Sea, abundance of young-of-the year (YOY) pike shows a strong positive relationship with cover of submerged vegetation up across a spatial gradient (>80 % cover) (Sandström et al., 2005; Hansen et al., 2019). Pike, however, uses different micro-habitats during different life-stages (Casselman and Lewis 1996; Eklöv 1997; Skov and Berg 1999; Hawkins et al. 2003; Hansen et al., 2019), and body size is inversely related to vegetation density of loosely structured reed and cattail (Eklöv, 1997). Hence, for pike to successfully complete its lifecycle may require vegetation and habitat of different complexity and structure (Hawkins et al., 2003; Skov and Berg, 1999; Eklöv, 1997). Decreasing habitat heterogeneity due to expansion of emergent vegetation (Schrank and Lishawa, 2019) may lower diversity and abundance of prey important for the pike life cycle (Eklöv, 1997; Hawkins et al., 2003; Massa and Farrell, 2020).

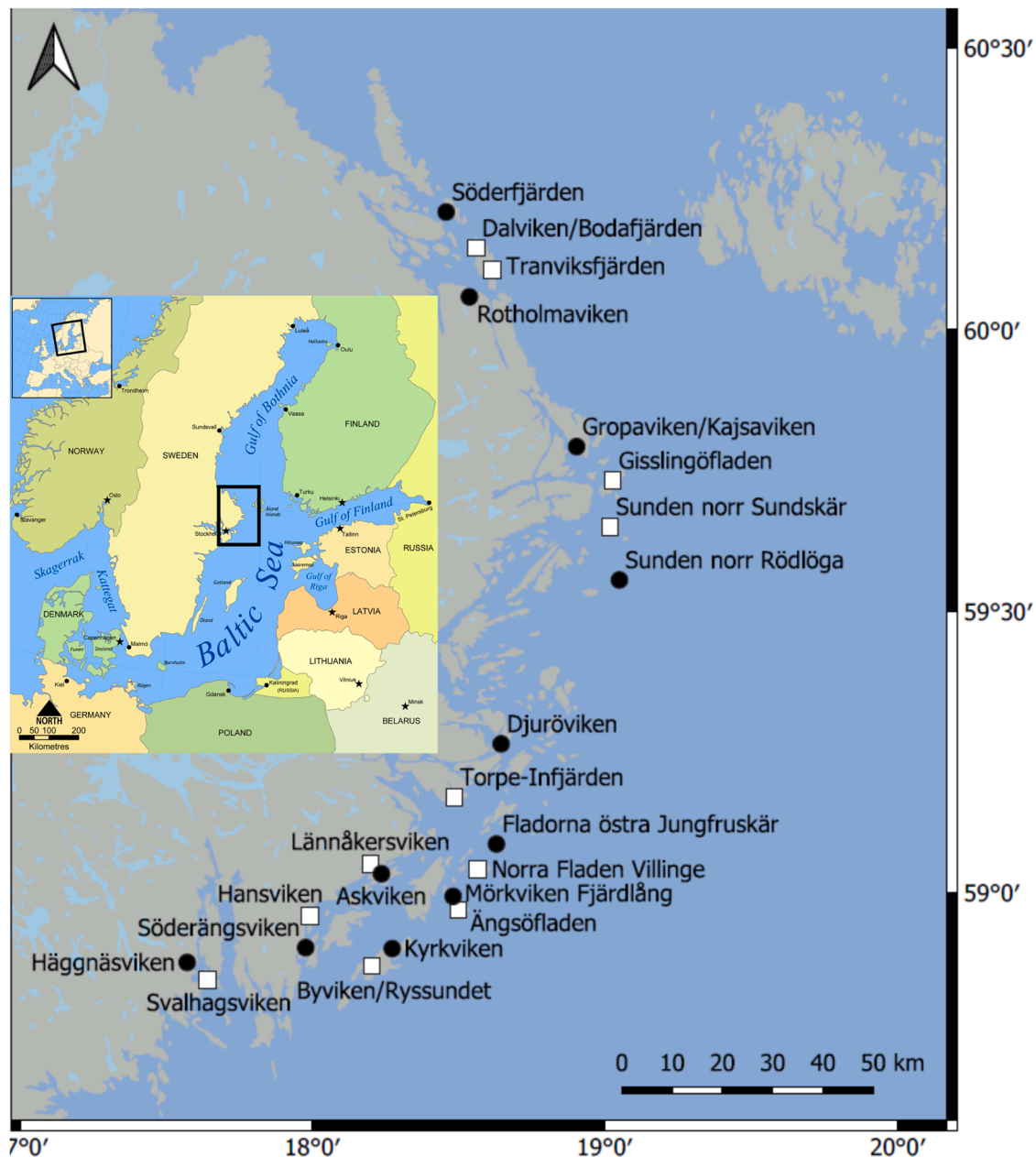


Fig. 1. Map of the study areas in the northwestern Baltic Sea with locations and names of the 22 studied bays: □ = closures, ● = reference areas. Insert maps show northern Europe and the Baltic Sea (NormanEinstein, CC BY-SA 3.0, <https://commons.wikimedia.org>).

Although there are no studies on adult pike size in relation to reed bed expansion or cutting, Olson et al. (1998) showed in a lake manipulation that increased heterogeneity of vegetation from cut lanes through emergent vegetation resulted in increased body growth of piscivore fish, bluegill (*Lepomis macrochirus*) and largemouth bass (*Micropterus salmoides*). While expanding reed habitat can be positive for juvenile pike, too dense and homogenous reed beds may delimit recruitment and body growth of adult pike.

Here we studied catch per unit effort and size of adult pike during the spawning season in relation to extension and configuration of reed beds, and cover of submerged vegetation among 22 coastal bays in the Stockholm archipelago at the Swedish coast of the Baltic Sea (Fig. 1). In addition, we also included the influence of shoreline constructions and wave exposure; factors previously shown to influence abundances of younger pike (Sandström et al. 2005; Sundblad and Bergström 2014; Kallasvuori et al. 2011; Hansen et al., 2019). We predicted that pike abundance and body size will increase with increasing heterogeneity of reed beds and submerged vegetation.

2. Materials and methods

2.1. Pike and fish data

We here use data on pike catches in 22 coastal bays in the archipelago around Stockholm at the western Baltic Sea coast (Fig. 1). Pike data was obtained from the “ReFisk” project that aims to study the effects of fishing closure during spawning time on fish communities, coordinated by the County Administrative Board of Stockholm. Half (eleven) of the bays were closed for fishing during spawning (1 Apr – 31 May) and the other half were open for fishing. Spawning protection was implemented in the bays in the mid 2000-ies (except two bays where protection was implemented 2010 and 2014), and the eleven reference bays were chosen to pair with a protected bay in the same archipelago area with similar size, depth and wave exposure.

Pike abundance and size structure was estimated from pike angling in 1–29 April 2017, during the pike spawning period. Angling was chosen as it was considered to be the most time effective way of catching pike and assessing CPUE in these habitats. Two anglers per boat fished for four hours per bay and after four hours they switched to another bay and fished for another four hours. The next day they switch order of bays and fished for four hours in each bay. After a minimum of seven days these bays were fished again with the same method by two other anglers. The instruction to anglers was to maximize the pike catch (numbers) within the bay for each 4 h period. Hence, anglers changed lure depending on habitat and conditions, and could fish longer in parts where catches seemed higher or more likely. All angling was done during the spawning period but catch rate may depend on weather and water temperature. Therefore each bay was fished four times by two different teams to reduce influence of variation between anglers and weather conditions. All participants were highly experience pike anglers. For all catches the position, sex, total body length and water temperature were recorded, and all pike were marked with an individual tag (anchor T-bar tags). We here disregarded all recaptured pike from the data. Sampling and tagging were done under ethical permits from Stockholm, south Ethical Board permit Dnr S-33–15 and Uppsala Ethical Board permit Dnr C 139/13.

From the sampled size distributions of pike in each bay we calculated the mean body length (in cm), *mL*. To avoid stochastic variation in *mL* due to low sample size we omitted nine bays with less than 20 pike measured (i.e. 13 bays had a catch of more than 20 pikes).

2.2. Reed distribution

We measured spatial extent (area) and perimeter of the reed beds in the 22 bays (Fig. 1) using geographically referenced RGB aerial photos from the Swedish mapping, cadastral and land registration authority

(Lantmäteriet) with a precision of 0.5 m placed as template to digitally mark reed beds (Suppl. Fig. S1). Aerial photos were from May 2019, i.e. two years after the pike sampling, when the reed has not started to grow for the season. Reed beds may have changed somewhat over years due to ice conditions (removing reed) and water levels (low water levels due to variation in air pressures across the Baltic Sea in summer facilitate reed expansion). However, the difference is not more than a couple of meters between years so between year variation is marginal relative to the between bay variation and will thus be considered as random measurement errors. Reed beds from aerial photos in spring were sometimes difficult to distinguish from banks and shallow waters because reed was not green. We therefore used satellite images from a commercial national map service (eniro.se/kartor, Eniro Sverige AB) taken later during 2019 to verify the classification of reed beds in uncertain cases. Satellite images were added as an overlay image on the aerial photo by georeferencing photos in the software Qgis (version 3.4.15, Qgis.org 2020). Polygons were digitized by manually tracing reed from the photo layers (Suppl. Fig. S1), thereby obtaining vector graphic of reed bed shape in each of the 22 bays, from which reed area and perimeter were estimated using Qgis tools.

Reed grows past the waterline on to land and therefore crosses the shoreline border, which is not possible to identify from aerial photos. To objectively define the coastline we used the official Swedish shoreline, produced in a collaboration project between the Swedish Maritime Administration and the Swedish Mapping, Cadastral and Land registration authority, called “National shoreline” (NSL). NSL is the projected line at a certain height relative long-term average water level between reference points from aerial photos (Sjöhed et al., 2020). This shoreline was used as the inner boundary of the reed beds in bays. The NSL is not perfect and in many shallow areas the shoreline is diffuse (Sjöhed et al., 2020) but gives a good, and most importantly objective, estimate of the shoreline. To create polygons of the reed beds, the areas were delineated along the perimeter of the beds and patches in the aerial photos (Suppl. Fig. S1) from each bay. We visually checked that NSL did not seem to differ markedly from the observable parts of the coastline from the aerial photos (no obvious major deviation detected).

2.3. Calculations of reed area and heterogeneity

We checked for errors, using Qgis “Check for validity” function to control that there was no crossings of polygon lines or other malfunctions with polygons. Once a reed bed was judged as valid we used the polygon area and line length tools in Qgis to calculate:

- a) Total reed area (*RA*)
- b) Total reed perimeter (*RP*, excluding the coastline)
- c) Reed cover (in % of bay; *RC*) = $RA/Total\ bay\ area$
- d) Average Reed belt width (in meters; *RD*) = $RA/Coastline\ length$
- e) Reed ratio (%; *RR*) = $(Reed\ perimeter - Coastline\ length)/(Coastline\ length)$,

The Reed ratio is an estimate of how much longer or shorter the reed perimeter is relative to the coastline of the reed habitat. A higher ratio indicates a more complex interface between reed and water whereas a lower (can be negative) ratio indicates a straight boundary between reed and open water.

2.4. Submerged vegetation

In each bay, the abundance of submerged vegetation was surveyed by free-diving in May 2017 at 3–5 sites per bay, with a higher number of sites per bay with increasing bay area. To gain a representative sampling of the whole bay area, sampling sites were haphazardly distributed across wave exposure and depth gradients in the bays (maximum sampling depth set at 3.5 m). At each sampling site, we estimated the percent seabed cover of aquatic vegetation in two stations placed ca

30 m apart. Each station consisted of a seabed area with a 5-m radius (78.5 m²) following the protocol of Bergström et al. (2021) and similar to the method used in other recent studies in the area (e.g. Hansen et al., 2019). The percentage cover of each taxon, except filamentous algae that was treated as a specific group (Fil. alg.), was estimated separately and identified to species level in the field. The cumulative sum of all taxa, rooted angiosperms except reed, and habitat-forming coarsely structured macroalgae was calculated for each station (hereafter denoted 'Total cover', 'Rooted submerged vegetation' and 'Macroalgae', respectively). The cumulative sum could exceed 100 % when species grew on top and/or overlay each other. For each bay we calculated the grand mean of each vegetation variable.

2.5. Jetties and wave exposure

We used available data on jetties/piers and wave exposure in the bays. For jetties and piers, we used a shapefile of Sweden's jetties, piers and small buildings (e.g. boathouses) mapped 2015–2016 by Törnqvist et al. (2020). The layer show length of each jetty, pier and small building but not width. There were no harbors or other major linear elements along the coast in the bays. Since piers and jetties can cross the coastline and sometimes reach far up on land, all objects were cut at the NSL so that only the lengths on water were used. The total length of jetties, piers and small buildings per bay was transformed into an index of 'jetty density', estimated as jetty/pier/boathouse-meters per hectare. The jetties, piers and small buildings were mapped 2–3 years before pike surveys and we may therefore have underestimated the true density of jetties in bays at the time of sampling. However, number of jetties changes little over such short time periods (see Fig S1 in Hansen et al., 2019). Wave exposure data (m²/s) was obtained from modelled data for the complete Swedish coast (Isæus, 2004; Sundblad et al., 2014) as the average value of pixels within each bay.

2.6. Statistical analysis

All statistical analyses were done in R version 4.0.4 (R Core Team, 2021). To get an overview of strengths of single correlations between predictor variables and pike CPUE (average number of pike per fishing hour in a bay) we did a correlation matrix. We did a separate correlation matrix for *mL* as it could only be calculated for 13 bays. Pike CPUE and predictor variables were log-transformed to better fit normal distributions.

As several reed characters and estimates of submerged vegetation were inter-correlated (Suppl. Fig. S2) we transformed the vegetation variables into principal components. We used the three first principal components that had eigenvalues >1 (explaining 87 % of cumulative variation of vegetation parameters) to study if and which PC-variables that explained significant variation in pike catches in generalized mixed models with a negative binomial distribution of catches as dependent variable and fishing hours as an offset to adjust for different effort with the `glmer.nb`-function in the `lme4` package for R (Bates et al., 2015). Beside principal components, bay area, wave exposure, jetty density and mean water temperature (surface temperature at the four fishing occasions) were added as explanatory variables. As half the bays were chosen to study the effect of spawning protection and the other half were reference areas open to fishing, bay was nested under spawning protection/reference as random factor to account for any variation in relation to spawning protection. For body size we used linear mixed models with body length as dependent variable in the `lmer`-function, also in the `lme4` package for R, with bay nested under spawning protection/reference as random factor and the same fixed factors as for pike catches. As there is a size dimorphism, sex was used as a fixed factor in this analysis. Fixed factors were added or removed in a stepwise selection based on p-values, adding variables with the lowest p-value < 0.05 and removing the variable with highest p-value >0.1. Parameter estimates and standard errors for the full models including all variables are

provided in Table S1. Partial *r*²-values for each variable was calculated as differences in marginal pseudo R² values for generalized mixed models (Nakagawa and Schielzeth, 2013) when that variable was removed relative the full model using the '`r.squaredGLMM`' function in the `MuMIn` package for R (Barton, 2022).

3. Results

Variables of reed characteristics were generally positively correlated (*r*_p > 0.6; Suppl. Fig. S2) and grouped along the first PC axis (Fig. 2) that explained 47 % of total variation in vegetation. Hence, the more reed in a bay in general also meant higher perimeter, proportion and heterogeneity between water and reed belts. Total cover of submerged vegetation and cover of rooted submerged vegetation grouped along the second PC-axis (21 %), whereas the third PC axis (11 %) separated out cover of macro- and filamentous algae (Fig. 2).

In the stepwise model selection (generalized mixed models), pike catches controlled for effort increased with PC1 (*F*_{1,18} = 18, *p* < 0.001; Fig. 3A) and PC2 (*F*_{1,18} = 11, *p* < 0.001, Fig. 3A), and decreased with wave exposure (*F*_{1,18} = 5.8, *p* = 0.02). Together, these three variable explained 77 % of marginal variation in pike catches. No other variable was included in the stepwise regression, and the full model did not show any qualitative differences of significant variables (Table S1).

As single Pearson's correlations, pike CPUE showed strongest correlations to reed perimeter (*r*_p = 0.76), reed area (*r*_p = 0.74), reed cover (*r*_p = 0.67), and with cover of rooted submerged vegetation (*r*_p = 0.63; Suppl. Fig. S2), and to lesser degree to reed ratio (*r*_p = 0.59) and reed depth (*r*_p = 0.55). Mean length of pike in each bay, *mL*, showed no correlation with CPUE of pike (*r*_p = -0.14; Suppl. Fig. S3) but positively correlated with the proportion of females (*r*_p = 0.69; Fig. S3). The environmental variables showing strongest single correlation with *mL* were positive relationships with wave exposure (*r*_p = 0.84; Fig. S3) and bay area (*r*_p = 0.68; Fig. S3).

In the stepwise model selection of pike body length (mixed linear models) when controlling for sex (*F*_{1,1101.5} = 378, *p* < 0.001, Fig. 3B), only wave exposure was significantly negatively associated with body length (*F*_{1,11.4} = 19, *p* = 0.001, Fig. 3B), explaining 10 % of marginal variation of the final model. However, in the full model with all environmental variables included, wave exposure was not significant and explained only 2 % of marginal variation (Table S1), indicating that wave exposure and bay area were confounding each other's effect (*r*_p = 0.78) in the full model. No PC axis of vegetation explained any significant variation in body length (*F*_{1,9} < 0.5, *p* > 0.5, Table S1).

4. Discussion

As predicted, catches (CPUE) of adult pike were associated with both reed and submerged vegetation, and hence vegetation heterogeneity, among the 22 studied bays. Different characteristics of reed beds had a high positive covariance, as larger reed beds also had a more complex interface between reed and water, making it impossible to single out which reed properties that are most important for pike. In general, large reed beds with high perimeter seemed favorable for pike with no indications of a decline in catch in bays with the largest reed beds. Reed beds and submerged vegetation showed no evident association between each other and pike catches also increased with increasing coverage of submerged vegetation. Pike body length, in contrast, was not significantly related to any vegetation variable, nor pike catches, but increased with increasing wave exposure. Females was also larger than males and the sex ratio was skewed towards more females in bays with higher wave exposure.

The first principal component, which was associated with large reed area, cover, perimeter reed depth and ratio to shoreline, was the variable best explaining variation in pike catches. From the aerial photos and at the scale of whole bays we could not see that larger reed beds would be more homogenous, but the opposite. Large reed beds was associated

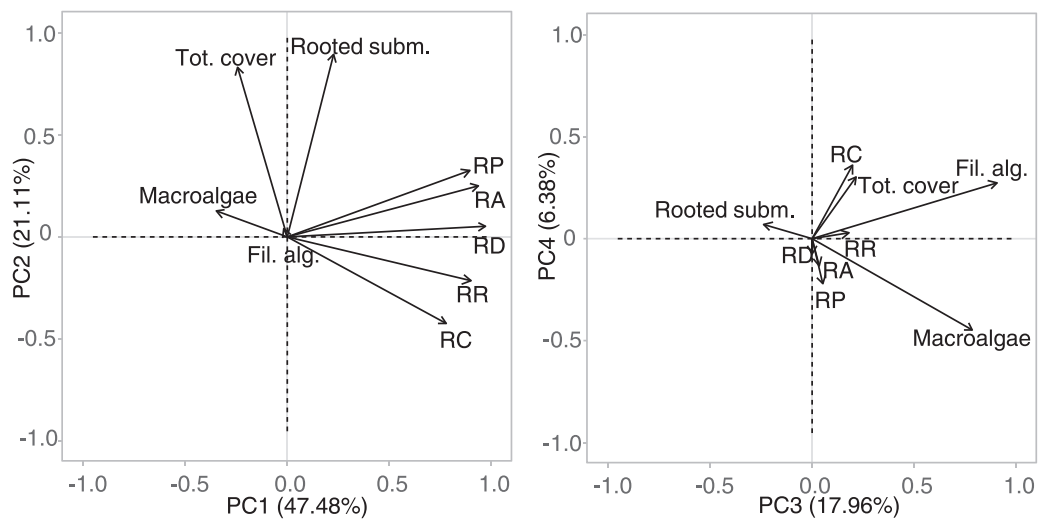


Fig. 2. Biplots of Principal Components Analysis of reed characters and submerged vegetation. ‘RP’ – reed perimeter (m), ‘RA’ – reed area (m²), ‘RD’ – reed depth (m), ‘RR’ – reed to shoreline ratio, ‘RC’ – reed cover (%), ‘Tot. cover’ – total cumulative cover (%) of submerged vegetation, ‘Rooted subm.’ – cover (%) of rooted angiosperms except reed, and ‘Fil. alg.’ – cover (%) of filamentous algae.

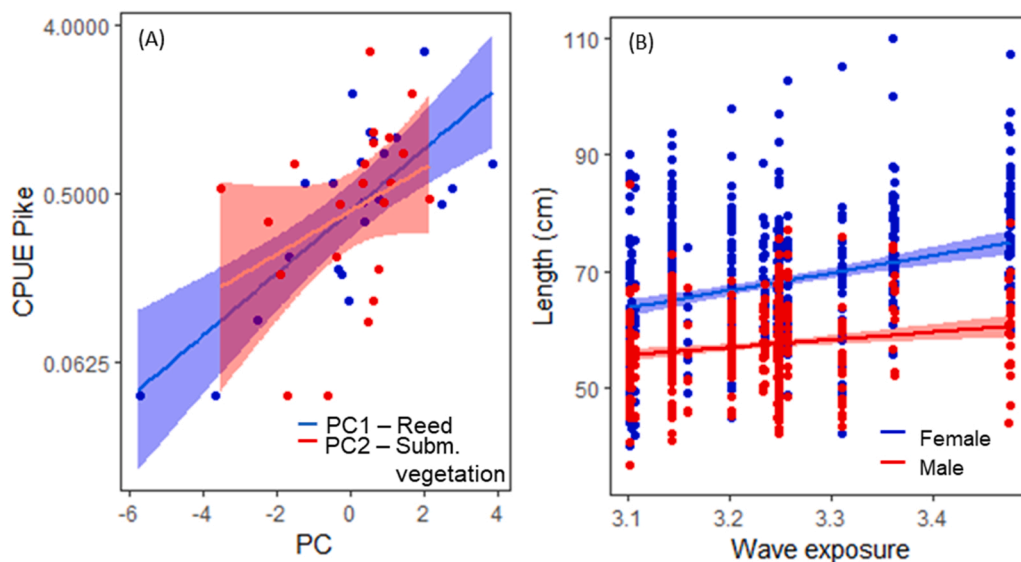


Fig. 3. (A) Relationship among the studied bays between the observed estimates of pike abundance (catch per unit effort, CPUE) from angling fishing and PC axes 1 and 2 from the vegetation PCA. PC1 (blue) was positively related to extension of reed beds and PC2 (red) to Rooted and Total cover of submerged vegetation. (B) Relationship between length of sampled pike and wave exposure divided on sex. In both figures regression lines represent best linear fit and shaded areas confidence intervals.

with a more complex interface between reed and water at a bay scale. The maximum cover of reed in the studied bays was 27 % (mean 6.7 % ± 6.4 SD), which is substantially lower than the optimum vegetation cover of 30–70 % indicated in the review by Casselman and Lewis (1996). Hence, reed beds were in these bays likely not extensive enough to have negative impact on pike at a bay scale. The extent or distribution of reed was calculated at a bay scale, whereas the cover (%) of submerged vegetation was calculated from 5 m radius plots within bays, and not the total extent. Expansion of reed, and other emergent vegetation, may reduce the abundance and diversity of submerged vegetation within bays (Munsterhjelm, 1997; Pitkänen et al., 2013; Altartouri et al., 2014; Lishawa et al., 2015; Bansal et al., 2019), but not coverage within plots, as studied here.

We found a positive association between catches (CPUE) of adult pike and cover of especially submerged rooted vegetation (associated with PC2, Figs. 2, 3). Earlier studies in the Baltic Sea show that submerged vegetation is important as nursery habitat increasing the density of young-of-the-year (YOY) pike (Sandström et al., 2005; Hansen et al., 2019). Our study suggests that the relationship also apply for adult pike

densities during spawning season, and confirms the importance of the availability of macrophytes and different micro-habitats for pike during different life-stages (Casselman and Lewis 1996; Eklöv 1997; Skov and Berg 1999; Hawkins et al. 2003; Craig, 2008). It should be noted that bay area itself showed no association with pike CPUE. Other emergent vegetation than reed was not accounted for, which may be an important factor for pike (Eklöv, 1997; Massa and Farrell, 2020). Such vegetation, were however sparse in the studied bays. We conclude that among the studied bays, reed and rooted submerged vegetation, resulting in heterogeneous vegetation, contributed independently on pike catches.

Whereas previous studies on pike in the Baltic Sea suggest mean body weight has increased as abundance decreased (Lehtonen et al., 2009; Bergström et al., 2022), we found no significant association between body length and pike catches. Only 13 bays had enough samples for assessing pike body length so the statistical power for detecting associations with body size was lower. We instead found that both females were more dominant and size of pike of both sexes were positively associated with wave exposure. The relationship with wave exposure seems to be due to both that the largest pike were found in more exposed

bays that also lacked the smallest pike (Fig. 3B). However, it should be noted that in this dataset wave exposure showed positive covariation with bay area. We cannot identify any specific mechanism for these patterns, but one factor contributing to larger pike may be that cannibalism is common in pike (Grimm, 1981; Persson et al., 2006; Craig, 2008) resulting in mainly larger pike use less sheltered or larger bays. There may be several other reasons to why larger pike are more common in wave exposed or larger bays (prey availability, optimum temperature), but for this study we conclude that vegetation structure or composition seemed to have little influence on the pike size distribution.

Pike in the Baltic Sea, and elsewhere, may migrate to the spawning sites from surrounding areas (Karås and Lehtonen, 1993; Bosworth and Farrell, 2006) so abundance and size may be related to the connectivity between the studied bays and other suitable areas (Englund et al., 2020). Surrounding habitat was not assessed here and in this study we can therefore not infer anything about the importance of surrounding habitat quality or connectivity between habitats.

As pike is an ambush predator it is poorly represented in static sampling gear (Olsson, 2019) and angling is a cost-efficient sampling method. However, angling has its demerits for some questions addressed here as the method i) cannot target pike inside dense or large reed beds, and ii) is sensitive to differences in pike catchability (how willing an individual is to hunt a lure). If we assume that pike catches reflect densities our results suggest that there are denser pike populations in bays with more reed and rooted submerged vegetation. This pattern could, at least partly, also be driven by a higher catch rate in areas with extensive reed beds if pike are more willing to attack lures in vegetated habitat. Angling was also done with the best lure for the condition according to fishers, which means different lures may be used in different types of habitat. Hence, we cannot rule out lures with a higher catchability were used in vegetated habitats. That seems unlikely to us, however, because lures used in vegetated areas can be used in more open habitat as well. On the contrary, the use of lures is more restricted in vegetation habitats as many lure types may get stuck in the vegetation, which rather may have led to use of lures with lower catchability in these habitats. We are not aware of any studies on how emergent or submerged vegetation may influence catchability, but find it unlikely that the difference in catchability would explain differences from occasional catches in some bays to hundreds of pikes angled in other bays. On the contrary, pike densities may rather be underestimated in some reed habitat as it is difficult to angle-fish pike in reed beds, but the relationship between vegetation habitat and catchability remains to be investigated.

Jetties and boating activities can affect habitats and change vegetation composition (Hansen et al., 2019) and thereby impact abundance of younger pike (Sandström et al., 2005). Here we found no evident association between jetties/ha and adult pike CPUE, but the studied bays did not have high levels of shoreline exploitation, maximum around 25 m/ha. In comparison, Sandström et al. (2005) that found negative associations between YOY pike and small boat marinas with higher jetty densities.

There are no general estimate of the increase in reed beds in coastal bays in the Baltic Sea. In one of the studied bay, Söderängsviken, the reed beds have increased with 265 % since 1960's and in another bay in the area not included here (Österbyfjärden, Gräsö) with 180 %, not accounting for land rise underestimating reed areas in the 1960 (unpublished data). Considering that pike were more abundant and the largest pikes were larger in the archipelagos before 2000 (Lehtonen et al., 2009; Berggren et al., 2022; Bergström et al., 2022), an increase in reed distribution is unlikely to be the main factor for these negative trends in pike. Several reasons for this decline have been suggested, including eutrophication (Lehtonen et al., 2009), overfishing (Bergström et al., 2022), seal predation (Bergström et al., 2022), loss of spawning habitat (Nilsson et al., 2014; Sundblad et al., 2014) and recruitment failure (Nilsson 2006; Nilsson et al. 2019; Eklöf et al. 2020). That does not imply reed or reed management would be unimportant.

On the opposite, preserving sufficient reed edges seems to be of great importance to provide both shelter and foraging habitat as it seem to be the main vegetation factor explaining abundance of pike during the spawning season.

There is a need for future studies to better separate the influence of reed distribution (area and perimeter), heterogeneity (the interface between reed and water) and reed structure (stems/m², stem thickness) on pike within bays, which was not possible in this study. A higher spatial resolution of reed characteristics within bays can better scrutinize the influence on pike behavior, body growth, distribution and abundance. Whether reed management, i.e. cutting or grazing of reed or other vegetation, or even reed planting, may have positive or negative effects on pike should be evaluated through experimental studies. Other habitat management actions, such as restoration of coastal wetlands, may be effective for restoring pike populations (Engstedt et al., 2010), but are geographically limited to suitable locations (Larsson et al., 2015) and only provide a spawning habitat and not suitable habitat for later life stages. Reed management could be a complement in many areas along the Baltic Sea coast to ensure enough reed edges, as well as in other aquatic environments where reed is dominant.

Different types of reed management, such as cutting, needs to be better studied to understand their effects (c.f. Massa and Farrell, 2020 in cattail habitat) before large-scale application. As pike populations are declining in this part of the Baltic Sea, bays with reed beds and abundant submerged vegetation may be needed for supporting pike populations. By improving habitats and developing reed management actions, the conservation of pike may be improved.

CRediT authorship contribution statement

NN & ÖÖ conceived the idea, NN compiled data on reed, whereas HCA & UB compiled pike data JH, JSE & BKE collected data on submerged vegetation, HCA was project coordinator. NN & ÖÖ analysed data, NN wrote the first draft and ÖÖ led and finished the writing. All authors contributed critically to the drafts and final version.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

We first want to thank all the water rights owners for allowing us to sample fish for this study. Second, we thank T. Fränstam and G. Almqvist and all the ReFisk pike anglers for assistance with the pike angling, and Naturvatten i Roslagen and JP Aquakonsult for the vegetation survey. We are grateful to two anonymous reviewer that provided constructive feedback on a previous version. Finally, we thank the attendees at the online Baltic Sea Pike Symposium 2021 for constructive comments that helped improve the study. This work was funded by the Swedish Agency for Water Management Dnr 3859–2016 through the “ReFisk” project, and the Swedish Research Council Formas through the PlantFish-project Dnr 2013–1074 and Baltic Waters 2030 through the “Levande vikar”-project for analyses of submerged vegetation. In kind contribution was allocated to authors from the Swedish University of Agricultural Sciences (ÖÖ, UB), Stockholm University (JSE, JPH) and Groningen University (BKE).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.fishres.2023.106621](https://doi.org/10.1016/j.fishres.2023.106621).

References

- Altartouri, A., Nurminen, L., Jolma, A., 2014. Modeling the role of the close-range effect and environmental variables in the occurrence and spread of *Phragmites australis* in four sites on the Finnish coast of the Gulf of Finland and the Archipelago Sea. *Ecol. Evol.* 4, 987–1005.
- Bansal, S., Lishawa, S.C., Newman, S., Tangen, B.A., Wilcox, D., Albert, D., Windham-Myers, L., 2019. Typha (cattail) invasion in North American wetlands: biology, regional problems, impacts, ecosystem services, and management. *Wetlands* 39, 645–684.
- Bart, D., Burdick, D., Chambers, R., Hartman, J.M., 2006. Human facilitation of *Phragmites australis* invasions in tidal marshes: a review and synthesis. *Wetl. Ecol. Manag.* 14, 53–65.
- Barton, K. 2022. MuMIn: Multi-Model Inference. R package version 1.46.0. <https://CRAN.R-project.org/package=MuMIn>.
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Soft.* 67, 1–48.
- 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. *Can. J. Fish. Aquat. Sci.* 79, 771–781.
- Bergström, U., Sundblad, G., Fredriksson, R., Karås, P., Sandström, A., Halling, C. 2021. Fisk i kustvatten - Yngelprovfiske med tryckvåg. Övervakningsmanual, Havs- och vattenmyndigheten. Available at [visited 2022-05-06]: <https://www.havochvatten.se/download/18.50a3054d17c661dd9988430e/1634542742922/overvakningsmanual-fisk-i-kustvatten-yngelprovfiske-med-tryckvag.pdf>.
- Bergström, U., Larsson, S., Erlandsson, M., Övegård, M., Stabo, H.R., Östman, Ö., Sundblad, G., 2022. Long-term decline in northern pike (*Esox lucius* L.) populations in the Baltic Sea revealed by recreational angling data. *Fish. Res.* 251, 106307.
- Bosworth, A., Farrell, J.M., 2006. Genetic divergence among northern pike from spawning locations in the Upper St. Lawrence River. *N. Am. J. Fish. Manag.* 26, 676–684.
- Bry, C., 1996. Role of vegetation in the life cycle of pike. In: Craig, J.F. (Ed.), *Pike, Biology and Exploitation*. Chapman & Hall, London, pp. 45–67.
- Buczko, U., Jurasinski, G., Glatzel, S., Karstens, S., 2022. Blue carbon in coastal *Phragmites* wetlands along the southern Baltic Sea. *Estuaries Coasts* 45, 2274–2282.
- Burdick, D., Konisky, R., 2003. Determinants of expansion for *Phragmites australis*, reed, in natural and impacted coastal marshes. *Estuaries* 26, 407–416.
- Casselman, J.M., Lewis, C.A., 1996. Habitat requirements of northern pike (*Esox lucius*). *Can. J. Fish. Aquat. Sci.* 53, 161–174.
- Chambers, R., M. Havens, K. J., Killeen, S., Berman, M., 2008. Common reed *Phragmites australis* occurrence and adjacent land use along estuarine shoreline in Chesapeake Bay. *Wetlands* 28, 1097–1103.
- Craig, J.F., 2008. A short review of pike ecology. *Hydrobiologia* 601, 5–16.
- Eklöv, J.S., Sundblad, G., Erlandsson, M., Donadi, S., Hansen, J.P., Eriksson, B.K., Bergström, U., 2020. A spatial regime shift from predator to prey dominance in a large coastal ecosystem. *Commun. Biol.* 3, 1–9.
- 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. J. Fish. Aquat. Sci.* 54, 1520–1531.
- Englund, G., Öhlund, G., Olajos, F., Finstad, A., Bellard, C., Huguency, B., 2020. Holocene extinctions of a top predator—effects of time, habitat area and habitat subdivision. *J. Anim. Ecol.* 89, 1202–1215.
- Engstedt, O., Stenroth, P., Larsson, P., Ljunggren, L., Elfman, M., 2010. Assessment of natal origin of pike (*Esox lucius*) in the Baltic Sea using Sr:Ca in otoliths. *Environ. Biol. Fish.* 89, 547–555.
- Grimm, M.P., 1981. Intraspecific predation as a principal factor controlling the biomass of northern pike (*Esox lucius* L.). *Aquac. Res.* 12, 77–79.
- Han, Z., Cui, B., 2016. Performance of macrophyte indicators to eutrophication pressure in ponds. *Ecol. Eng.* 96, 8–19.
- Hansen, J.P., Sundblad, G., Bergström, U., Austin, Å.N., Donadi, S., Eriksson, B.K., Eklöv, J.S., 2019. Recreational boating degrades vegetation important for fish recruitment. *Ambio* 48, 539–551.
- Härmä, M., Lappalainen, A., Urho, L., 2008. Reproduction areas of roach (*Rutilus rutilus*) in the northern Baltic Sea: potential effects of climate change. *Can. J. Fish. Aquat. Sci.* 65, 2678–2688.
- Hawkins, L.A., Armstrong, J.D., Magurran, A.E., 2003. Settlement and habitat use by juvenile pike in early winter. *J. Fish. Biol.* 63, 174–186.
- Isæus, M., 2004. Factors structuring *Fucus* communities at open and complex coastlines in the Baltic Sea. Department of Botany, Stockholm University, Sweden. PhD Thesis.
- Kaitaranta, J., Niemistö, J., Buhvestova, O., Nurminen, L., 2013. Quantifying sediment resuspension and internal phosphorus loading in shallow near-shore areas in the Gulf of Finland. *Boreal Environ. Res.* 18, 473–487.
- Kallasvuo, M., Lappalainen, A., Urho, L., 2011. Coastal reed belts as fish reproduction habitats. *Boreal Environ. Res.* 16, 1–14.
- Karås, P., Lehtonen, H., 1993. Patterns of movement and migration of pike (*Esox lucius* L.) in the Baltic Sea. *Nord. J. Freshw. Res.* 68, 72–79.
- King, R., Deluca, W., Whigham, D., Marra, P., 2007. Threshold effects of coastal urbanization on *Phragmites australis* (common reed) abundance and foliar nitrogen Chesapeake Bay. *Estuaries Coasts* 30, 469–481.
- Lappalainen, A., Härmä, M., Kuningas, S., Urho, L., 2008. Reproduction of pike (*Esox lucius*) in reed belt shores of the SW coast of Finland, Baltic Sea: a new survey approach. *Boreal Environ. Res.* 13, 370–380.
- Larsson, P., Tibblin, P., Koch-Schmidt, P., Engstedt, O., Nilsson, J., Nordahl, O., Forsman, A., 2015. Ecology, evolution, and management strategies of northern pike populations in the Baltic Sea. *Ambio* 44, 451–461.
- Lehtonen, H., Leskinen, E., Selén, R., 2009. Potential reasons for the changes in the abundance of pike, *Esox lucius*, in the western Gulf of Finland, 1939–2007. *Fish. Manag. Ecol.* 16, 484–491.
- Li, S., Sun, T., Yang, W., Yan, S., Cui, B., 2021. Interspecific relationships between submerged and emergent aquatic plants along a nitrogen gradient in a mesocosm experiment. *Ecol. Indic.* 133, 108360.
- Lishawa, S.C., Lawrence, B.A., Albert, D.A., Tuchman, N.C., 2015. Biomass harvest of invasive *Typha* promotes plant diversity in a Great Lakes coastal wetland. *Restor. Ecol.* 23, 228–237.
- Massa, E.A., Farrell, J.M., 2020. Improving habitat connectivity in a *Typha*-dominated wetland shows increased larval northern pike survival. *Wetlands* 40, 273–286.
- Munsterhjelm, R., 1997. The aquatic macrophyte vegetation of flads and gloes, south coast of Finland. *Acta Bot. Fenn.* 157, 1–68.
- Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining from generalized linear mixed-effects models. *Methods Ecol. Evol.* 4, 133–142.
- Nilsson, J., 2006. Predation of northern pike (*Esox lucius* L.) eggs: a possible cause of regionally poor recruitment in the Baltic Sea. *Hydrobiologia* 553, 161–169.
- Nilsson, J., Engstedt, O., Larsson, P., 2014. Wetlands for northern pike (*Esox lucius* L.) recruitment in the Baltic Sea. *Hydrobiologia* 721, 145–154.
- Nilsson, J., Flink, H., Tibblin, P., 2019. Predator-prey role reversal may impair the recovery of declining pike populations. *J. Anim. Ecol.* 88, 927–939.
- Olson, M.H., Carpenter, S.R., Cunningham, P., Gafny, S., Herwig, B.R., Nibbelink, N.P., Pellett, T., Storlie, C., Trebitz, A.S., Wilson, K.A., 1998. Managing macrophytes to improve fish growth: a multi-lake experiment. *Fisheries* 23, 6–12.
- 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, M.L., Bergström, U., Arlinghaus, R., Audzijonyte, A., Berg, S., Östman, Ö., 2023. A pan-Baltic assessment of temporal trends in coastal pike populations. *Fish. Res.* 260, 106594.
- Persson, L., Bertolo, A., De Roos, A.M., 2006. Temporal stability in size distributions and growth rates of three *Esox lucius* L. populations. A result of cannibalism? *J. Fish. Biol.* 69, 461–472.
- Pitkänen, H., Peuraniemi, M., Westerborn, M., Kilpi, M., von Numers, M., 2013. Long-term changes in distribution and frequency of aquatic vascular plants and charophytes in an estuary in the Baltic Sea. *Ann. Bot. Fenn.* 50, 1–54.
- R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Sandström, A., Eriksson, A., Klemens, B., Karås, P., Isæus, M., Schreiber, H., 2005. Boating and navigation activities influence the recruitment of fish in a Baltic Sea archipelago area. *Ambio* 34, 125–130.
- Schrank, A.J., Lishawa, S.C., 2019. Invasive cattail reduces fish diversity and abundance in the emergent marsh of a Great Lakes coastal wetland. *J. Great Lakes Res.* 45, 1251–1259.
- Silliman, B.R., Bertness, M.D., 2004. Shoreline development drives invasion of *Phragmites australis* and the loss of plant diversity on New England salt marshes. *Conserv. Biol.* 18, 1424–1434.
- Sjöhed, J., Nordström, K., Wallhagen M., Gustafsson, L. 2020. Specifikation -Nationell strandlinje. Rapport, NSL 01, Lantmäteriet och Sjöfartsverket. Available at: https://www.sjofartsverket.se/globalassets/sjokort-och-sjogeografi/specifikation_nsl.pdf [visited 2022-10-14].
- Skov, C., Berg, S., 1999. Utilization of natural and artificial habitats by YOY pike in a biomanipulated lake. In: Walz, N., Nixdorf, B. (Eds.), *Shallow Lakes '98*. Springer, Dordrecht, pp. 115–122.
- Snickars, M., Sundblad, G., Sandström, A., Ljunggren, L., Bergström, U., Johansson, G., Mattila, J., 2010. Habitat selectivity of substrate-spawning fish: modelling requirements for the Eurasian perch *Perca fluviatilis*. *Mar. Ecol. Prog. Ser.* 398, 235–243.
- Sundblad, G., Bergström, U., 2014. Shoreline development and degradation of coastal fish reproduction habitats. *Ambio* 43, 1020–1028.
- Sundblad, G., Bergström, U., Sandström, A., Eklöv, P., 2014. Nursery habitat availability limits adult stock sizes of predatory coastal fish. *ICES J. Mar. Sci.* 71, 672–680.
- Törnqvist, O., Klein, J., Vidissón, B., Haljestedt, S., Katif, S., Nazerian, S., Rosengren, M., Giljam, C. 2020. Fysisk störning av grunda havsområden – Kartläggning och analys av potentiell påverkanszon samt regional och nationell statistik angående störda områden. Metria AB, Stockholm. Available at: <https://www.havochvatten.se/download/18.7d45de5c174e8f2dabe8afa3/1604908758378/rapport-2020-12-fysisk-storning-i-grunda-havsomraden.pdf> [visited 2022-05-12].
- Von Numers, M., 2011. Sea shore plants of the SW Archipelago of Finland – distribution patterns and long-term changes during the 20th century. *Ann. Bot. Fenn.* 48, 1–46.