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Published in:
 Fisheries Research

DOI:
[10.1016/j.fishres.2023.106674](https://doi.org/10.1016/j.fishres.2023.106674)

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Document Version
 Publisher's PDF, also known as Version of record

Publication date:
 2023

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Eklöf, J. S., Hansen, J. P., Eriksson, B. K., Östman, Ö., Austin, Å. N., Yanos, C., Fredriksson, R., Bergström, U., & Andersson, H. C. (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, Article 106674. <https://doi.org/10.1016/j.fishres.2023.106674>

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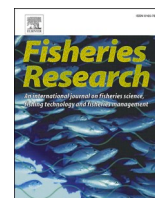
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Effects of seasonal spawning closures on pike (*Esox lucius* L.) and perch (*Perca fluviatilis* L.) catches and coastal food webs in the western Baltic Sea

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ARTICLE INFO

Handled by Robert Arlinghaus

Keywords:

Knock-on effect
Spawning closures
Marine reserves
Ecosystem-based management
Ecology of fear

ABSTRACT

Marine protected areas have become one of the main tools in the battle to curb marine biodiversity loss and habitat degradation. Yet, implementation of permanent fishery closures has often generated resource user conflicts that ultimately undermine conservation goals. Here we assessed the influence of an alternative and often more accepted measure – seasonal fish spawning closures – on large predatory fish and coastal food webs in the western Baltic Sea (Sweden). In spring 2017, we conducted a multivariable field survey in 11 seasonal closures and 11 paired reference areas open to fishing. In each area, pike was sampled through angling, and perch and mesopredators through gillnet surveys. To assess trophic cascades, we measured zooplankton abundance and loss of tethered gammarids from predation. Catches per unit effort of northern pike (*Esox lucius*) – the main target species in recreational fisheries – were ca. 2.5 times higher per unit effort in closures than reference areas; an effect that may be caused by higher abundance and/or higher catchability of pike in the absence of fishing. Catch and weight per unit effort of the more common predator European perch (*Perca fluviatilis*), and the mesopredators roach (*Rutilus rutilus*) and three-spined stickleback (*Gasterosteus aculeatus*) in survey nets were, however, unaffected by closures. Moreover, a previously hypothesized trophic cascade from perch to zooplankton via three-spined stickleback was supported by the analyses, but appeared independent of closures. Yet, predation risk for tethered gammarid amphipods (a prey of stickleback and an important grazer on macroalgae) was three times higher in fished areas than in closures; a cascading closure effect that may potentially be caused by small predatory fish being less active in protected areas to avoid pike predation. Overall, our results suggest that spawning closures impact pike abundance and/or behavior and could help limit the effects of fishing, but that more research is needed to disentangle i) what mechanism(s) that underlie the protection effect on pike catches, ii) the apparently weaker closure impacts on other fish species, as well as iii) the potential for cascading effects on lower trophic levels. Therefore, new seasonal spawning closures should be implemented in addition to (and not instead of) much-needed permanent closures, which have well-known effects on the wider ecosystem.

1. Introduction

Marine protected areas (hereafter MPAs), which often include some form of fishery closures, have become a cornerstone in marine conservation (Gronrud-Colvert et al., 2021). No-take areas are highly effective at increasing the size, biomass, and abundance of exploited fish (Edgar et al., 2014; Lester et al., 2009); effects that typically increase in strength

with the size and age of the no-take area, and the degree of isolation from other human impacts (Edgar et al., 2014). Old (>10 years) no-take areas typically also strengthen predator top-down control of lower trophic levels (Eger and Baum, 2020), which can benefit foundation species like reef-forming corals and macroalgae through trophic cascades (Clemente et al., 2009; McClanahan and Muthiga, 2016; Shears and Babcock, 2003). There is even some evidence that MPAs may help

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<https://doi.org/10.1016/j.fishres.2023.106674>

Received 7 July 2022; Received in revised form 17 February 2023; Accepted 18 February 2023

Available online 15 March 2023

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mitigate climate change impacts (Jacquemont et al., 2022), but see (Bates et al., 2019). As a consequence of such closure effects, the global conservation community is pushing hard to drastically increase the number and the size of MPAs to 30 % of ocean areas (of which one third as strictly protected areas) by 2030 (O'Leary et al., 2016; Waldron et al., 2020).

While no-take closures typically are considered an ecological 'success story', their socio-economic impacts are more mixed (Mizrahi et al., 2019; Schratzberger et al., 2019). For example, the extent of 'spillover' of fish from MPAs to fished areas (typically one of the main arguments for implementing MPAs from a fishery perspective) is a highly debated issue, where some studies show strong fishery benefits from large MPAs (Medoff et al., 2022), while others suggest 'spillover' is limited to areas with the most poorly managed fisheries (Buxton et al., 2014) and areas just outside MPAs (Di Lorenzo et al., 2020). Moreover, poorly anchored implementation of many no-take areas with stakeholders has often generated infected resource use conflicts (Cánovas-Molina and García-Frapolli, 2020), contributing to poaching (Iacarella et al., 2021). The ecological MPA research community has gradually realized the need to engage stakeholders early on in the protection process to increase compliance with restrictions (Giakoumi et al., 2018). However, there are contexts where permanent fishery closures are deemed either impossible or unnecessary to implement. In such cases, 'partial' fishery closures (a. k.a. 'partially-protected areas'), which include areas with gear restrictions as well as periodic protection, may be a more sustainable option (Bartlett et al., 2009; Cohen and Foale, 2013). Partial closures date centuries back and constitute nearly 70 % of all MPAs (Turnbull et al., 2021). One of the most common forms are seasonal spawning closures, typically aimed to protect fish when they aggregate for spawning and are easily caught and stressed (van Overzee and Rijnsdorp, 2015). Meta-analyses suggest that partial closures do increase the biomass and abundance of fishery target species, but not to the same extent as full no-take areas (Lester and Halpern, 2008; Sala and Giakoumi, 2018; Sciberras et al., 2015; Zupan et al., 2018). There are, however, notable exceptions; for example, a recent study along the Australian East coast found that partial closures were ineffective and acted as 'red herrings' for conservation, stealing resources and attention from more effective measures such as permanent closures (Turnbull et al., 2021). In addition, a simple literature search conducted by us suggests there is very limited knowledge about the extent to which partial closures can generate cascading or 'knock-on' ecosystem effects through marine food webs, in the way that particularly no-take closures are known to do (Supplemental material).

Here we assessed the effect of seasonal fishery closures on large predatory fish, as well as the potential for indirect (cascading) closure effects on lower trophic levels, along the central Swedish coast in the western Baltic Sea; a large brackish marginal sea in north-western Europe. In the study area, coastal fisheries are today dominated by recreational angling for large predatory fish such as northern pike (*Esox lucius*, hereafter 'pike') and European perch (*Perca fluviatilis*, hereafter 'perch'), while the landings of these species in the commercial coastal fishery are much smaller (Swedish Agency for Marine and Water Management, 2021). Pike is a large-bodied top predator whose populations have declined dramatically along most of the Swedish coastline, particularly in wave-exposed areas closest to the open sea (Bergström et al., 2022; Eriksson et al., 2011; Ljunggren et al., 2010; Olsson, 2019). The drivers behind the decline are most likely a combination of i) historical overfishing, ii) increasing predation from grey seals and cormorants (Bergström et al., 2022; Hansson et al., 2018), iii) predation on pike eggs and juveniles from other fish such as the three-spined stickleback (Byström et al., 2015; Nilsson et al., 2019), and iv) the historical loss of recruitment areas such as coastal wetlands (Nilsson et al., 2004). Commercial catches of pike have declined by 80 % over the last half century, and are today very low, partly due to socio-economic and cultural changes in archipelago societies (Bergström et al., 2022). Harvest from recreational angling increased until the 1990s, to then steadily

decline due to increased propensity of catch-release (C&R) fishery, especially following the introduction of bag limits (max three individuals day⁻¹) and slot length limits (40–75 cm) in 2010 (Bergström et al., 2022). Nevertheless, recreational fisheries today harvest > 10 times as much pike as the commercial fisheries. Consequently, angling harvest is likely to have contributed to the pike decline (Bergström et al., 2022), but i) the very few fishery closures that can be used to assess angling effects, and ii) the use of passive gear ill-suited to sample pike in the national fish monitoring program (Olsson, 2019), have made it difficult to assess the actual causes. Catch-and-release (C&R) is sometimes assumed to be harmless to the fish, but can be a short-term stressor for pike that restricts movement (Arlinghaus et al., 2009) and feeding (Stålhammar et al., 2012), which pike may learn to avoid (Kuparinen et al., 2010). Coastal populations of perch, another large-bodied piscivore which is naturally much more abundant than pike, are declining in some areas and stable or increasing in others (Olsson, 2019). A study comparing perch CPUE in a permanent no-take area vs. several fished areas suggested strong negative effects of fishing (Bergström et al., 2019). Meanwhile, fishing-induced mortality is probably lower than mortality from seals and cormorants (Bergström et al., 2022; Hansson et al., 2018). Consequently, there is a clear need for more and better replicated studies of closure effects, and indirectly the impact of fishing, on both pike and perch.

Adult pike and perch both predate on smaller fish such as three-spined stickleback (*Gasterosteus aculeatus*, hereafter 'stickleback') and roach (*Rutilus rutilus*) (Jacobson et al., 2019). The former is a small mesopredator that has undergone an 'explosive' population increase along the Baltic Sea western coast (Olin et al., 2022). Correlative field survey data (Donadi et al., 2017) and predator enclosure experiments in the field (Eriksson et al., 2009) show that locally abundant perch and pike suppress abundances of adult stickleback in spring, indirectly suppressing stickleback recruitment (Eklöf et al., 2020). Sticklebacks are in turn efficient predators that can suppress abundances of small invertebrates including algal-feeding zooplankton (Ljunggren et al., 2010) and gammarid amphipods, indirectly releasing algae from top-down control (Sieben et al., 2011). Consequently, abundant perch and pike populations can, by controlling stickleback abundance, generate trophic cascades that help control the biomass of 'nuisance' algae (Donadi et al., 2017). Such algae may otherwise overgrow and smother habitat-forming macrophytes such as bladderwrack (Donadi et al., 2017; Eriksson et al., 2009) — organisms that are important habitats for juvenile pike and perch (Hansen et al., 2019). These findings lead us to hypothesize that seasonal no-take areas may be effective at not only benefitting declining pike and perch populations, but also generating ecosystem-level effects. So far, however, this hypothesis has not been tested, particularly with regard to spawning closures.

In this study we assessed the ecological effects of seasonal spawning closures in the Stockholm archipelago (Sweden). To the best of our knowledge, this study is the first to assess the effects of seasonal fishery (including spawning) closures on northern pike. We hypothesized that catches of pike and perch would be higher in the closures than in the reference areas due to the lack of fishing, and that this closure effect would indirectly affect prey species (primarily three-spined stickleback and roach), and cascade to their prey including zooplankton and benthic amphipods.

2. Material & methods

This study was conducted in the vast Stockholm archipelago in the western part of the Baltic Sea; the world's largest brackish water body (Snoeijs-Leijonmalm et al., 2017). This large and broad archipelago area (extending >20 km from the coastline) has a salinity of 4.5–6 ppt, and consists of thousands of islands with numerous shallow inlets and bays, which constitute important spawning and nursery areas for many Baltic fish species (Hansen et al., 2012, 2019).

2.1. Survey design

In 2004 and 2006 (and in 2014 for one area), the county administrative board of Stockholm established 25 seasonal fishery closures in small shallow bays ($0.035\text{--}1.46\text{ km}^2$) spread across the Stockholm archipelago, which have a ban on all fishing from April 1 to June 15. The foremost goal was to protect pike, but also perch and pikeperch (*Sander lucioperca*), during the spring spawning season, which for pike starts when the water temperature reaches ca. $4\text{--}10\text{ }^\circ\text{C}$ (Sunde et al., 2019). The specific bays were chosen as spawning closures for two main reasons: i) they (like many other bays) had suitable habitat characteristics for pike and perch spawning, and ii) a high willingness among the local fishing right owners to set their fishing areas aside for springtime closures.

The ‘gold’ standard in the design of closure effect studies is the ‘MBACI’ principle (Multiple Before-After, Control-Impact), i.e. sampling both prior to and after closures are implemented, in both fished reference areas and closure sites (Downes, 2002). As in most cases when closures are implemented, however, no before-sampling was conducted in our study area. Therefore, we used a ‘site-for-time’ replacement design, comparing data from 2017 collected in 11 closures and 11 paired reference bays. The reference bays were chosen to be situated close to (within 15 km of) their paired closure, in the same archipelago area (distance from mainland and open sea, as well as latitude) and have a similar depth, wave-exposure, and topographic openness to nearby waters (Fig. 1).

2.2. Pike survey using angling

In April 2017, we estimated pike abundance and biomass per unit effort (CPUE vs. WPUE) using catch-and-release (C&R) by actively casting with spinning rod and reel. This survey method was chosen for two reasons; i) it is the most common fishing method in the actual pike fisheries, and ii) it is the most cost-effective way of catching pike, and therefore assessing CPUE and WPUE, in these habitats. The sampling was approved by the Ethical Board on Animal Experiments of the County Court of southern Stockholm (permit S-33-15).

Fishing was done by two-person teams consisting of highly experienced pike anglers, fishing from boats in shallow ($\leq 2.5\text{ m}$) water using artificial lure(s) of personal choice. To reduce the influence of factors such as time of the day, weather conditions, and time of the spawning season, all bays were fished on four days split up into two occasions. One randomly chosen bay in each pair was first fished for half a day before noon (ca. $4\text{ h} \times 2$ fishers), and then the paired bay was fished in the afternoon for half a day (ca. $4\text{ h} \times 2$ fishers). This procedure was repeated the following day, but reversing the order of the two bays. Consequently, each closure and its paired reference were fished in both the morning and the afternoon. This two-day procedure was repeated during a second occasion ≥ 7 days later, resulting in each bay being fished for a total of ca. 16 h by each team, i.e. 32 person-hours. The total number of replicate samplings (two-person fishing sessions) was 88 ($N = 22\text{ bays} \times 4$ occasions). The fishers were instructed to catch pike to the best of their ability, freely choosing lures and exactly where in the bays to fish. The pike caught were brought up into the boat using rubber

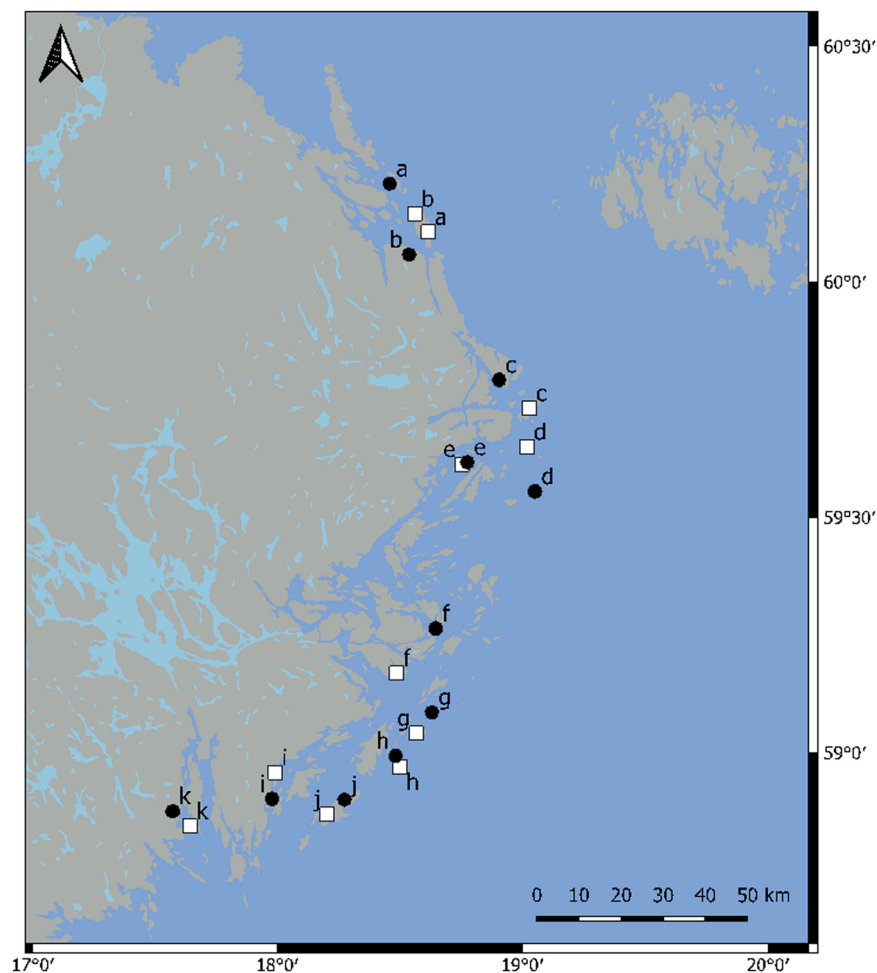


Fig. 1. Study area. Map of the study area along the central Swedish east coast in the Baltic Sea, highlighting the position of the 22 bays. \square = closures, \bullet = reference areas, letters (a-k) = bay pairs. For more information about the individual bays, see Table 1.

nets, then sexed, measured (closest cm), weighted (closest g), tagged with yellow TBA standard anchor t-bar tags of Hallprint type, and released, all within 1.5 min.

Water temperature is a strong predictor of fish catches in these habitats (Donadi et al., 2017), partly because of its correlation with seasonality, but primarily because the physical activity of poikilotherms such as pike is highly dependent on the temperature of the surrounding medium. We therefore measured water temperature at the time of fishing using digital thermometers in the boat echo sounders, and used this as a covariate in the statistical analyses.

2.3. Fish community survey using multimesh gillnets

In May 2017, after the pike angling was completed, we assessed the effects of spawning closures on the rest of the fish community using standardized fish sampling with Nordic multimesh survey gillnets (European Union standardized method EN 14757: 2005). The sampling procedure was approved by the Ethical Board on Animal Experiments of the County Court of Uppsala, Sweden (permit C 139/13). Each bay was fished during one night with 3–5 nets (number of nets being proportional to bay size), placed at 1–3 m depth at 4–7 pm, and lifted ca. 12 h later. All individual fish caught were identified to species and measured for total length (closest cm). Length-weight correlations from the Swedish national database for coastal fish (www.slu.se/kul) were used to calculate the wet body mass (closest 1 g) of individual fish. These weights were summed up per species and net, enabling us to express catches as both CPUE (number of individuals caught per net night) and WPUE (fish weight per net night).

Temperature of the surface water was measured using handheld thermometers at the start and end of each net fishing occasion. Technical problems with some of the start measurements resulted in that we only used the temperature at the lifting of the nets as a predictor in the statistical analyses (see below).

We also measured turbidity of surface water next to three of the nets per bay (those where zooplankton were sampled, see below), using a hand held turbidimeter (Aquafluor, Turner Designs, USA). We did not include this as a predictor in all analyses, because missing data from 1 to 2 nets in many bays would reduce the overall sample size. Instead, we tested the possibility of an influence of turbidity for a subset of variables (see Statistical analyses).

2.4. Benthic vegetation around nets

The percentage cover of macroscopic benthic vegetation was estimated within two 5-m radius circles (Bergström et al., 2021), placed near the ends of each net. A snorkeler visually identified, and estimated the percentage cover of all macroscopic macrophyte species, except filamentous algae that was estimated as one functional group. We then calculated four different measures of vegetation cover, known to often influence fish abundance in similar habitats; i) *total cover* (0–100 %, estimated as 100 % - % bare seabed), ii) *cumulative cover of vegetation, except filamentous algae* (the sum of the % cover of each individual vegetation species; 0- >100 %), iii) *cumulative cover of rooted vegetation* (0- >100 %), and iv) *% cover of filamentous algae* (0–100 %).

2.5. Zooplankton sampling

Zooplankton is an important food source for many small fish including young-of-the-year perch and pike, but also adult three-spined stickleback, potentially resulting in competition for food (Ljunggren et al., 2010). To assess to what extent the fishery closures may indirectly influence zooplankton abundance, we sampled zooplankton next to three of the gillnets in each bay. In the morning (7–9 am), zooplankton was sampled using a 25 cm diameter Epstein net (80 µm), slowly pulled vertically from ca. 0.7 m above the seabed to the water surface. The length of the haul was noted to the closest 10 cm and the content

emptied into a bottle with formalin, yielding a 5 % formalin:seawater solution. This procedure was repeated two times, pooling the three samples to form one sample per net. In the lab, all zooplankton (including cladocerans, copepods and rotifers) were counted under a stereo lens and identified to species. Here, however, we only used the total abundance as a response, given that previous studies have shown this variable responds to the fish community (Ljunggren et al., 2010).

2.6. Predation rates on tethered amphipods and fish trap catches

Predation rate of fish on lower trophic levels can be strongly affected by fishery closures, because the absence of fishing affects predator abundance and/or hunting activity (Rhoades et al., 2019). Here, we assessed closure effects on predation rates on tethered gammarid amphipods; a key group of aquatic consumers that may exert strong top-down control on filamentous green algae, reducing eutrophication symptoms (Östman et al., 2016). We used a method previously tested in the same general study area (Donadi et al., 2017), with details outlined below, where tethered gammarids were placed in the innermost parts of bays overnight. Simultaneously, we sampled the local fish assemblage using stationary traps (Donadi et al., 2020) and estimated the percentage cover of the main groups of benthic vegetation. First, live gammarids were collected by hand from loose-lying *Fucus* macroalgae in the shallow wash zone, and transferred to the lab in sea water. The gammarids were then measured (to the closest 1 mm, from tip of head to end of telson) and glued with their dorsal side to the end of a 0.04 mm transparent, 10 cm long monofilament line (Fireline™) using waterproof superglue (Loctite™). The other end of the line was glued to the end of a 30 cm transparent acrylic rod (ø = 5 mm), together forming a ‘tether’. Ten tethers were transported in seawater to each bay. In the innermost part of each bay, five sampling stations spaced ca. 5 m apart along the shoreline at 0.5–1 m depth were then marked using plastic floats tied to led weights. Between 4 and 6 pm, two tethers with live amphipods were placed ca. 0.5 m apart at each station, by pushing the acrylic rod ca. 5 cm down into the sediment. Then we placed a crayfish trap (KAYOBA, Skara, Sweden, dimensions 45 × 24 × 24 cm; 1 × w × h, mesh size 3 mm) at each station, with a round opening of 5.5 cm diameter (located on one of the short sides) facing the shoreline. We visually estimated the percentage cover (0–100 %) of four main types of benthic vegetation (filamentous algae, *Fucus vesiculosus*, rooted aquatic plants, and reed) within 0.5 m of each tether.

The next morning (6–9 am) each amphipod was visually scored as being either *alive, eaten* (with a small part of the body remaining), *missing* (whole amphipod gone, including glue remains, or even the whole tether gone) or *molted* (just the gammarid exoskeleton remaining, still glued to the line). Prior to data analyses, all missing or molted amphipods were excluded from the data. However, in most bays all ten amphipods (a minimum of eight) were scored as either alive or eaten. The trap openings were then sealed and the traps were lifted onto a boat, opened, and the catch (consisting of small fish and crustaceans) was gently poured into a large crate filled with seawater. All fish caught were identified to species. The catches were dominated by three-spined stickleback, the main predator on gammarid amphipods in these habitats based on earlier studies (Donadi et al., 2017).

2.7. Estimation of wave exposure, bay openness and distance to baseline

Shallow bay fish communities in the study area are known to be strongly influenced by wave exposure, bay openness to outside water bodies, and bay position in the archipelago in relation to the open sea (Hansen et al., 2019; Snickars et al., 2009). To account for the influence of such gradients on sampled variables, we estimated wave exposure, bay topographic openness, and distance to the baseline for each of the 22 bays using GIS-based methods described in detail in a recent study (Eklöf et al., 2020). Wave exposure and bay openness are often correlated and may individually influence shallow bay organisms, but due to our

limited sample size we could not assess their joint influence. Therefore, we used a principal components analysis based on bay-level estimations of wave exposure and bay openness (Hansen et al., 2012). The first principal component (explaining 62 % of the between-bay variability) was used to describe the joint influence of the two variables, and referred to as ‘bay isolation’ with decreasing wave exposure and topographic openness with increased ‘bay isolation’-value.

2.8. Statistical analyses

All statistical analyses and model plotting were conducted in the R environment v. 4.0.0 (R Core Team, 2017).

To statistically assess if fish habitat conditions differed between the seasonal closures and the reference areas, and thus may confound our assessment of closure effects, we first combined bay-level average levels of eight environmental variables into a new dataset; distance to baseline, wave exposure, water retention time, water depth and temperature (both from the net fishing), total vegetation cover, turbidity, and salinity. Because of missing estimations of salinity, temperature and depth in some bays, the final dataset included 18 (of the 22) bays. After scaling each variable by dividing each value by its maximum, we tested if multivariate dispersion (variability within groups) differed between closures and reference areas, using the *betadisper()* function in the *vegan* package (Oksanen et al., 2022). The results showed no difference in multivariate dispersion ($F = 0.2$, $P = 0.6$). Second, we used a permuted analysis of variance with 9999 permutations to test whether there was an influence of closures on the mean multivariate habitat condition, using the *adonis()* function in *vegan*. Also here there was no difference between closures and reference areas ($F = 0.5$, $P = 0.8$, $R^2 = 0.03$, Supplementary Fig. 1).

Second, to assess the relative influence of spawning closures and environmental covariates on each specific response variable, while accounting for the hierarchical sampling design, we used generalized linear mixed models as implemented in the *glmmadmb* package (Fourrier et al., 2012). In the analyses of pike angling catches we initially included ‘protection’ (two levels: closure vs. reference), ‘temperature’ (continuous) and ‘bay isolation’ (continuous) as fixed factors, based on i) the focus of the study, ii) prior knowledge about the influence of water temperature and bay openness on pike catches, and iii) initial plotting of raw data, indicating that they all had an influence. We also tried models where we replaced ‘bay isolation’ with ‘distance to baseline’, but these fitted the data much worse. As random factors we included i) ‘Bay ID’ (22 unique levels) nested under ‘protection’ (to account for the hierarchical sampling design and true replication of closures, $n = 11$), ii) ‘Bay pair’ (11 levels, one for each closure-reference pair), and iii) ‘sampling day’ (unique day) nested under ‘sampling occasion’ (two levels). We did not include vegetation cover or turbidity as predictors in these models, as these variables were only measured during the gillnet fishing 1 month later. We used the number of caught pike as the response variable, and the log of the number of fishing hours (6–8) as an offset, resulting in that the model tests predictors of CPUE. The first set of models of CPUE of all pike and large pike (>60 cm) used a Poisson error distribution and a log link function. As these were overdispersed, we switched to a negative binomial error distribution, which was also used for pike biomass. In the models of pike length (mean length across all pike caught during a session) we first excluded the 21 of the 88 sampling sessions where no pike were caught (resulting in $N = 67$). The length model used a gamma error distribution and a log link function. In all analyses we identified the most parsimonious model(s) using a backwards selection based on Akaike’s Information Criterion (AIC), where models with a delta AIC ≤ 2 were deemed to have a similar fit. In this process we also included an intercepts-only model. Finally, we plotted the influence of the fixed factors in the best-fitting model(s) as partial regression plots using the *visreg* package (Breheny and Burchett, 2017).

For the analyses of CPUE of all perch, CUPE of large perch (> 25 cm), perch weight per effort (WPUE), roach CPUE, roach WPUE, stickleback

CPUE, and stickleback WPUE (all caught in the Nordic survey nets) we used a similar approach but with some alterations. First, besides ‘protection’ we included ‘water temperature’ as fixed factors in all initial models, as temperature is known to have a major influence of fish catches (Donadi et al., 2017). The limited sample size prevented us from including all possible predictors in the same model. Therefore, we also compared the relative fit with models that included either ‘bay isolation’, ‘vegetation cover’ and ‘distance to baseline’. In the models of stickleback CPUE and WPUE we also included catches of perch (CPUE or WPUE) as a predictor, given the known role of perch as an efficient predator of stickleback (Jacobson et al., 2019), able to regulate stickleback abundance in spring (Donadi et al., 2017; Eklöf et al., 2020). As net sampling was only done once per bay, we only included the random factors ‘Bay ID’ (22 levels) nested under ‘protection’, and ‘Bay pair’ (11 levels, random intercept), in all models. The models based on abundances used a Poisson error distribution or, if overdispersed, a negative binomial distribution, whereas models based on fish biomass used a negative binomial distribution. Catches of pike in the nets were low (22 in total; 14 in closures and 8 in reference areas), as expected given that these gillnets are known to poorly sample pike (Donadi et al., 2017; Olsson, 2019). Therefore, we did not assess the closure effects on pike in gillnet catches. For the analyses of zooplankton abundance, we also used negative binomial mixed models with protection, vegetation cover, temperature and stickleback CPUE as fixed factors, and zooplankton abundance per sample as the response, and the log of the filtered water volume (L) as an offset.

Pike regularly feed on stickleback in these coastal habitats, and stickleback can form > 50 % of the stomach content of large (> 60 cm) individuals (Jacobson et al., 2019). To be able to assess the possible influence of pike on stickleback abundance (CPUE) despite the poor catches of pike in the gillnets, we included pike catches from the preceding rod fishing (CPUE of all pike or large pike > 60 cm) as predictors in a mixed model based on bay-level averages ($N = 22$). We used bay-level averages here to avoid pseudo-replicating pike catches, which could vary considerably between the different parts of the bays where the gillnets were placed. We also included the best combination of predictors from the original stickleback CPUE model (see above and Results); temperature and perch CPUE. Finally, to account for the paired design, we included ‘Bay pair’ (11 levels) as a random intercept.

For the analyses of gammarid survival (0/1) we used a mixed binomial regression model with ‘protection’, ‘gammarid size’ (continuous) and ‘stickleback CPUE’ (number of stickleback caught in the traps) as fixed factors, and ‘Bay ID’ nested under ‘protection’ and ‘trap ID’ (5 unique levels) nested under ‘Bay ID’, as random factors. As evident by the results, there was a strong positive effect of closures on gammarid survival (see Results). To try to shed more light on the possible mechanism(s), we also assessed whether bay-level averages of three other potential predictors – water turbidity, pike CPUE from the rod fishing, and CPUE of large pike (>60 cm) – may explain bay-level mean survival of tethered gammarids (and in turn contribute to the observed protection effect). This was done using a bay-mean glmm ($N = 22$) with a binomial error distribution and ‘Bay pair’ (11 levels) as a random factor (random intercept). The reasoning for assessing these particular predictors was that i) high (vs. low) turbidity may reduce hunting success of visual hunters (thus increasing gammarid survival), and that ii) even though adult pike are not predators on gammarids, their presence and activity may scare smaller predatory fish such as stickleback, to the extent that they reduce their foraging (Heins et al., 1999), thus increasing gammarid survival.

Finally, for the analyses of stickleback catches in the crayfish traps, we used a similar model structure with ‘protection’ and ‘temperature’ as main predictors and the same random structure, but also tested the influence of either the percentage cover of i) bladder wrack *Fucus vesiculosus*, ii) reed *Phragmites australis* or iii) filamentous algae, as a fixed factor with a negative binomial error distribution.

3. Results

3.1. Pike catches from experimental angling

In total, 425 northern pike (*Esox lucius*) were caught in 692 h of catch-and-release angling in the 22 bays in April 2017. Across all bays, 74 % of the catches were done in closures and 26 % in reference areas. Eight catches (1.9 %) were recaptures; seven in closures and one in a reference area.

The best-fitting model of catch per unit effort (CPUE) of all pike included positive effects of protection and water temperature (Table 2, Fig. 2a-b). After controlling for random spatial and temporal variability and the temperature effect, pike angling CPUE was 2.35 (95 % CI: 1.18–4.65) times higher in closures than in the reference areas. The model of pike biomass showed a similar effect, with 2.66 (1.32–5.28) times higher biomass per unit effort (WPUE) in closures than reference areas, along with a positive effect of temperature (Table 2, Fig. 2c-d). CPUE of large pike (> 60 cm), which made up 62 % of all catches, was 2.47 (1.10–5.56) times higher in closures than references and positively affected by temperature (Table 2, Fig. 2e-f). Finally, the mean size of the pike did not differ between closures and fished areas, and was also unaffected by temperature and bay isolation (Table 2, figure not shown).

3.2. Gillnet fish catches

The best-fitting model of perch CPUE (number of individuals per net night) showed positive effects of water temperature and bay isolation, but no effect of closures or vegetation cover (Table 3, Fig. 3a-b). Catches of large perch (>25 cm) were positively influenced by temperature and negatively influenced by % cover of all vegetation, but there was no effect of closure or bay isolation (Table 3, figure not shown). Finally, perch biomass was positively influenced by bay isolation, but there was no effect of closure, vegetation cover or temperature (Table 3, figure not shown).

The best-fitting model of catches per unit effort of three-spined stickleback (number of individuals per net night) showed negative effects of temperature and perch CPUE, but no effect of closure or vegetation cover (Table 3, Fig. 3e-f). Stickleback biomass per unit effort (WPUE) was also unaffected by protection, and negatively influenced by bay isolation (Table 3, figure not shown). Follow-up models based on bay-level averages of stickleback CPUE, which also included pike CPUE from the angling (of all pike or only large >60 cm) as a predictor to be

Table 1

Information about the 22 bays (11 seasonal closures + 11 paired reference bays).

Bay-pair	Bay name	Protection	Bay no.	Year established	Distance to baseline (m)	Wave exposure (m ² /s)	Area (km ²)
a	Tranviksfjärden	Closure	15	2004	6477	1432.1	0.156
a	Söderfjärden, Sladdarön	Reference	16		17,139	1369.5	0.246
b	Dalviken/Bodafjärden	Closure	19	2004	13,992	2371.9	0.254
b	Rotholmaviken	Reference	20		11,840	3461.2	0.437
c	Gisslingöfladen	Closure	13	2006	9877	1481.7	0.092
c	Gropaviken/Kajsaviken	Reference	14		12,909	1277.0	0.060
d	Sunden norr Sundskär	Closure	17	2006	16,819	1079.8	0.234
d	Sunden norr Rödlöga	Reference	18		22,247	1567.9	0.068
e	Söderfladen	Closure	11	2004	32,473	1429.0	0.072
e	Eknövik	Reference	12		29,600	1259.4	0.079
f	Torpe-Infjärden, Björnöfjärden	Closure	21	2014	27,154	2544.8	1.445
f	Djurövik	Reference	22		31,450	1841.0	0.182
g	Norra Fladen, Villinge	Closure	9	2004	10,511	3448.9	0.433
g	Fladorna östra Jungfruskär	Reference	10		12,338	1819.7	0.259
h	Ångsöfladen	Closure	5	2006	7497	7953.0	0.115
h	Mörkviken, Fjärdlång	Reference	6		12,409	2211.4	0.087
i	Hansviken	Closure	7	2004	27,752	2444.9	0.035
i	Söderängsviken, Herrön	Reference	8		25,670	3052.8	0.073
J	Byviken	Closure	3	2004	11,188	1732.8	0.130
j	Kyrkviken, Utö	Reference	4		14,399	2600.2	0.360
k	Svalhagsviken	Closure	1	2006	30,576	3645.0	1.462
k	Hägnäsviken	Reference	2		35,789	6839.0	0.748

Table 2

Summary of the best-fitting GLMMs from backward selection on AIC on catches of pike. All models include an effect of seasonal closures for A) CPUE (catch per unit effort) of all pike, B) WPUE (weight per unit effort) of all pike, C) CPUE of large pike (>60 cm), and D) mean length (cm) of caught pike. Random effects are not shown.

	Beta	SD	Z	P
A. CPUE all pike				
Intercept	-3.68	0.648	-5.68	< 0.001
Protection:Closure	0.861	0.351	2.45	0.014
Temperature	0.359	0.091	3.94	< 0.001
B. WPUE all pike				
Intercept	-5.021	0.703	-7.15	< 0.001
Protection:Closure	0.97	0.354	2.74	0.006
Temperature	0.366	0.102	3.6	< 0.001
C. CPUE large pike				
Intercept	-4.273	0.5597	-7.63	< 0.001
Protection:Closure	0.9626	0.4263	2.26	0.024
Temperature	0.368	0.0744	4.94	< 0.001
D. Mean length of caught pike				
Intercept	4.1478	0.0241	172.3	< 0.001
Protection:Closure	0.0446	0.0308	1.45	0.150

able to compare the pike vs. perch influence, again showed that only perch catches influenced stickleback catches (Table 5, figure not shown).

Finally, the best-fitting models for roach CPUE and biomass per unit effort both showed a positive influence of bay isolation and temperature, but no effect of closures or vegetation cover (Table 4, Fig. 3g-i).

3.3. Zooplankton abundance

The best-fitting model of total zooplankton abundance showed a positive effect of water temperature and a negative effect of stickleback CPUE (Table 3, Fig. 3g-h). There were, however, no effects of closures, bay isolation or distance to the open sea.

3.4. Predation pressure on tethered gammarids

Three models fit the data equally well (AIC <2) and all showed a very similar result; the risk for individual gammarids to be eaten was ca. three times higher in reference areas than in closures (ca. 10 vs. 30 %), and there were no effects of gammarid size, trap catches of stickleback, or temperature (Table 4, Fig. 4). A follow-up model based on bay-level

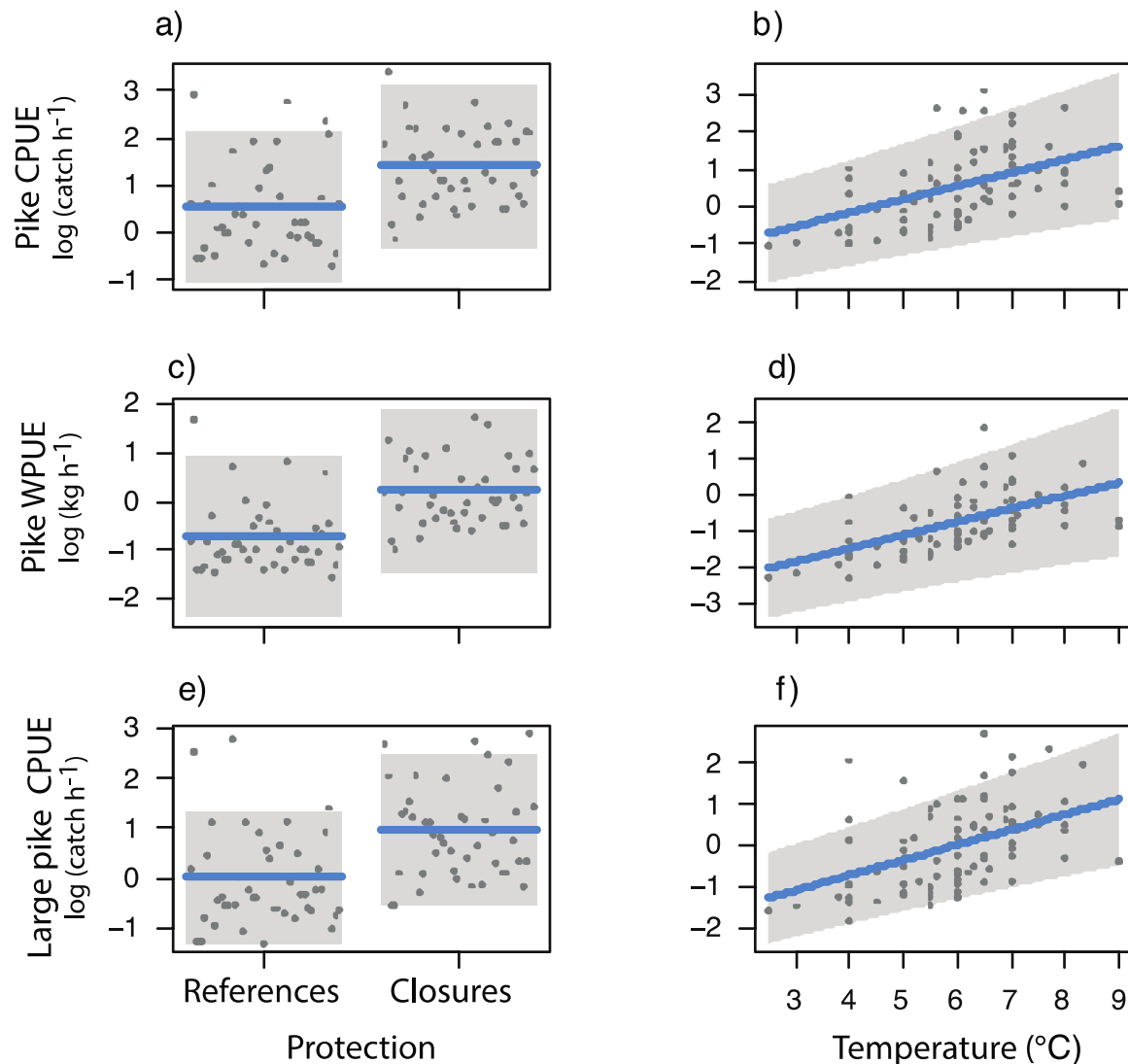


Fig. 2. Pike angling catches. Partial regression plots displaying the influence of spawning closures and water temperature on a-b) pike CPUE (log of catch h⁻¹), c-d) pike WPUE (log kg h⁻¹), and e-f) CPUE of large pike (log catch of pike ≥ 60 cm h⁻¹) CPUE.

averages suggested that gammarid survival was not explained by water turbidity, or by CPUE of pike or large pike (> 60 cm) from the preceding angling (Table 5, figure not shown). Finally, the best-fitting model of stickleback catches in the traps included a non-significant negative influence of temperature, and there were no effects of closures or vegetation cover (Table 4, figure not shown).

4. Discussion

Partially protected areas such as fish spawning closures are the most common form of marine protected areas globally (Turnbull et al., 2021), mainly because they are more readily accepted among resource users than complete (permanent) closures. Yet, knowledge about their ecological effectiveness is limited, particularly when it comes to indirect ('knock-on') effects on non-target species. In this study we used a comparative field survey to assess the effects of springtime spawning closures on large predatory fish – northern pike (*Esox lucius*) and European perch (*Perca fluviatilis*) – in coastal areas of the western Baltic Sea, and start exploring to what extent the closures may generate cascading effects through the food web. We found that the closures greatly increased catch and weight per unit effort of pike, but not of perch, roach or three-spined stickleback (the three most abundant fish species in our gillnet survey, together making up >80 % of all fish caught). However,

predation pressure on tethered gammarids – which are key grazers on filamentous algae – was three times higher in reference areas than in closures, suggesting that there may be a cascading closure effect on the benthic food web. We also found support for a trophic cascade where perch indirectly benefitted zooplankton by decreasing stickleback abundances, but this effect occurred independent of closures. Below we discuss these results in greater detail and outline their potential implications from both fundamental and applied perspectives.

In line with the main hypothesis, our results support what appears to be a strong, positive spawning closure effect on angling catches of northern pike (*Esox lucius*); the main target species in recreational angling fishing and one of the focal species when the closures were created. There are several possible and complementary explanations to this positive effect, which should be explored in future studies. First, the higher pike CPUE may reflect that pike is more abundant in closures due to an absence of fishing-induced mortality, as has been shown for partial closures in general (Lester and Halpern, 2008; Sala and Giakoumi, 2018; Sciberras et al., 2015; Zupan et al., 2018). We do, however, question that this large difference would be from reduced pike mortality alone, because fishing mortality in our area may be considerably lower than natural mortality, thereby limiting the potential effect of fishing closures on pike populations. Most importantly, a recent study from the same archipelago area shows that annual pike harvest from fisheries

Table 3

Summary of the best-fitting GLMMs, but also including effects of seasonal closures, for A) CPUE (individuals per net night) of all perch (*Perca fluviatilis*), B) biomass (wet weight) of all perch, C) CPUE of large perch (>25 cm), D) CPUE of three-spined stickleback (*Gasterosteus aculeatus*), E) biomass of three-spined stickleback, F) CPUE of roach (*Rutilus rutilus*), G) biomass of caught roach, and H) zooplankton density (individuals per liter). Note that random effects are not shown.

	Beta	SD	Z	P
A) CPUE all perch				
Intercept	0.867	0.483	1.8	0.072
Protection:Closure	-0.064	0.281	-0.23	0.819
Temperature	0.121	0.039	3.11	0.002
Bay isolation	1.38	0.284	4.86	< 0.001
B) Biomass all perch				
Intercept	0.249	0.279	0.89	0.371
Protection:Closure	-0.094	0.251	-0.38	0.707
Bay isolation	2.181	0.546	3.99	< 0.001
% cover all vegetation	-0.008	0.004	-2.03	0.042
C) CPUE large perch				
Intercept	0.778	0.337	2.31	0.021
Protection:Closure	-0.283	0.261	-1.08	0.280
Bay isolation	2.741	0.526	5.21	< 0.001
% cover all vegetation	-0.013	0.004	-2.76	0.006
D) CPUE three-spined stickleback				
Intercept	8.681	2.018	4.3	< 0.001
Protection:Closure	0.658	0.544	1.21	0.226
Temperature	-0.520	0.171	-3.03	0.002
Catch all perch	-0.094	0.025	-3.74	< 0.001
E) Biomass three-spined stickleback				
Intercept	-2.604	0.707	-3.68	< 0.001
Protection	0.310	0.529	0.57	0.568
Bay isolation	-1.462	0.608	-2.41	0.016
% cumulative vegetation cover	0.012	0.008	1.58	0.114
F) CPUE roach				
Intercept	1.141	0.863	1.32	0.186
Protection:Closure	-0.190	0.162	-1.17	0.24
Temperature	0.173	0.066	2.6	0.009
Bay isolation	0.875	0.377	2.32	0.020
G) Biomass roach				
Intercept	-2.23	1.03	-2.16	0.031
Protection:Closure	-0.002	0.172	-0.01	0.99
Temperature	0.127	0.064	1.98	0.048
Bay isolation	0.958	0.419	2.29	0.022
Distance to baseline	0.001	0.001	1.95	<i>0.051</i>
H) Zooplankton density				
Intercept	-0.012	0.776	-0.02	0.988
Protection:Closure	-0.298	0.484	-0.61	0.539
Temperature	0.450	0.061	7.36	< 0.001
CPUE three-spined stickleback	-0.002	0.001	-2.02	0.044

(commercial and recreational combined) over the last decades was in the order of 5–20 % of the harvest by grey seal (*Halichoerus grypus*) and great cormorant (*Phalacrocorax carbo*); two top predators whose abundances have increased greatly over the last decades (Bergström et al., 2022). Moreover, spawning closures are open to fishing during 80 % of the year, further limiting the possible effects of closures on fishing-induced mortality. Consequently, we find it unlikely that the ca. 2.5 times higher pike catches in closures could be caused solely by differences in fishing-induced mortality.

A second possible explanation to the higher pike CPUE in closures is a lower degree of stress from catch-and-release, resulting in higher pike catchability. C&R constitutes a direct stress on caught pike, which increases stress hormone levels and can reduce movement and activity the following hours (Arlinghaus et al., 2017b, 2009). However, pike appear to quickly learn to avoid artificial lures, resulting in that pike in heavily fished areas/time periods become significantly harder to catch, which lowers CPUE even when abundances remain constant (Arlinghaus et al., 2017a; Kuparinen et al., 2010). The ‘flipside’ to these types of behavioral fishing effects is that the absence of fishing in no-take areas can strongly increase fish willingness to hunt (Rhoades et al., 2019). This in turn makes protected fish more naïve to fishing gear, and therefore more

easily caught just outside closures – thus contributing to the MPA ‘spillover’ effect (Januchowski-Hartley et al., 2013). Against this background, we hypothesize that a considerable part of the much higher pike CPUE in the seasonal closures is explained by higher catchability of less weary, more active pike. However, to separate the effects on pike mortality and activity, better estimates of actual pike abundance, possibly combined with behavioral studies, are needed.

Third, there is a possibility that the spawning closures increase pike abundance by increasing pike spawning success, as shown for other types of spawning closures (van Overzee and Rijnsdorp, 2015). A previous experimental study along the SW Swedish coast suggested that C&R on female pike did not reduce spawning success (Flink et al., 2021). However, the study did not test for effects on recruitment, and most of the fish were experimentally caught only once, most likely underestimating the amount of fishing-induced stress that pike individuals in popular angling areas (who are likely to be caught many times) experience during a spawning season. Consequently, there is need to assess how spawning closures like these may affect pike spawning and recruitment.

Finally, even though we statistically controlled for relevant environmental predictor, and also showed that general habitat conditions did not differ between closures and reference areas, the lack of data collected before the closures were implemented makes it impossible to completely exclude the possibility that currently unknown site differences contribute to the closure effect. This is a common problem in many MPA effect studies, which is typically addressed by (as in this study) including relevant environmental drivers as covariates (Edgar et al., 2014). To complement our study, we in 2018 started a before-vs-after MPA study in the same geographical area with sampling both before and after a new set of spawning closures were implemented in another set of shallow bays, each paired with a reference area. This study will assess how long time it takes for the closure effects to develop and help shed more light on the mechanism(s) involved. So far, we argue that the results we present here, combined with the general literature on effects of partial closures, clearly suggest that seasonal spawning closures do benefit pike catchability and/or abundance.

In contrast to the closure effect on pike, we found no closure effects on catch or biomass per unit effort of European perch (*Perca fluviatilis*); the most common piscivorous fish in the study area, which is also targeted by fisheries. There are several possible explanations to this lack of effect. First, the closures were sampled (and are only protected) during spring; a period when perch are not fished as intensely as pike. Meanwhile, the little data that exist suggest that year-round closures have a strong positive effect on perch CPUE and WPUE (Bergström et al., 2019). Second, the bays where the seasonal closures exist were primarily chosen because they are good pike habitats, which does not necessarily mean they are ideal for perch. We also did not find any indications of closure effects on roach (*Rutilus rutilus*) or three-spined stickleback (*Gasterosteus aculeatus*); both being mesopredatory fish that are eaten by pike (Jacobson et al., 2019). We did, however, find that stickleback CPUE was explained by perch CPUE; a finding supported by comparative field surveys (Donadi et al., 2017) and piscivore exclusion experiments (Sieben et al., 2011). Moreover, zooplankton abundance was negatively influenced by stickleback CPUE (but not by pike catches). A similar effect was previously suggested to show competition for food between stickleback and young-of-the-year pike and perch, potentially contributing to the pike and perch recruitment failure along parts of the coast (Ljunggren et al., 2010). When the different results from our analyses are combined, they strongly suggest that abundant perch have an indirect positive effect on zooplankton abundance by suppressing stickleback (Fig. 5); a trophic cascade that, however, does not appear to be influenced by the spawning closures. This suggests that even though the closures appear to benefit pike CPUE during the period when stickleback migrate into these bays, and individual pike can be ferocious predators on stickleback, they are perhaps not (yet) abundant and/or actively hunting enough to strongly suppress prey abundances, in the way that

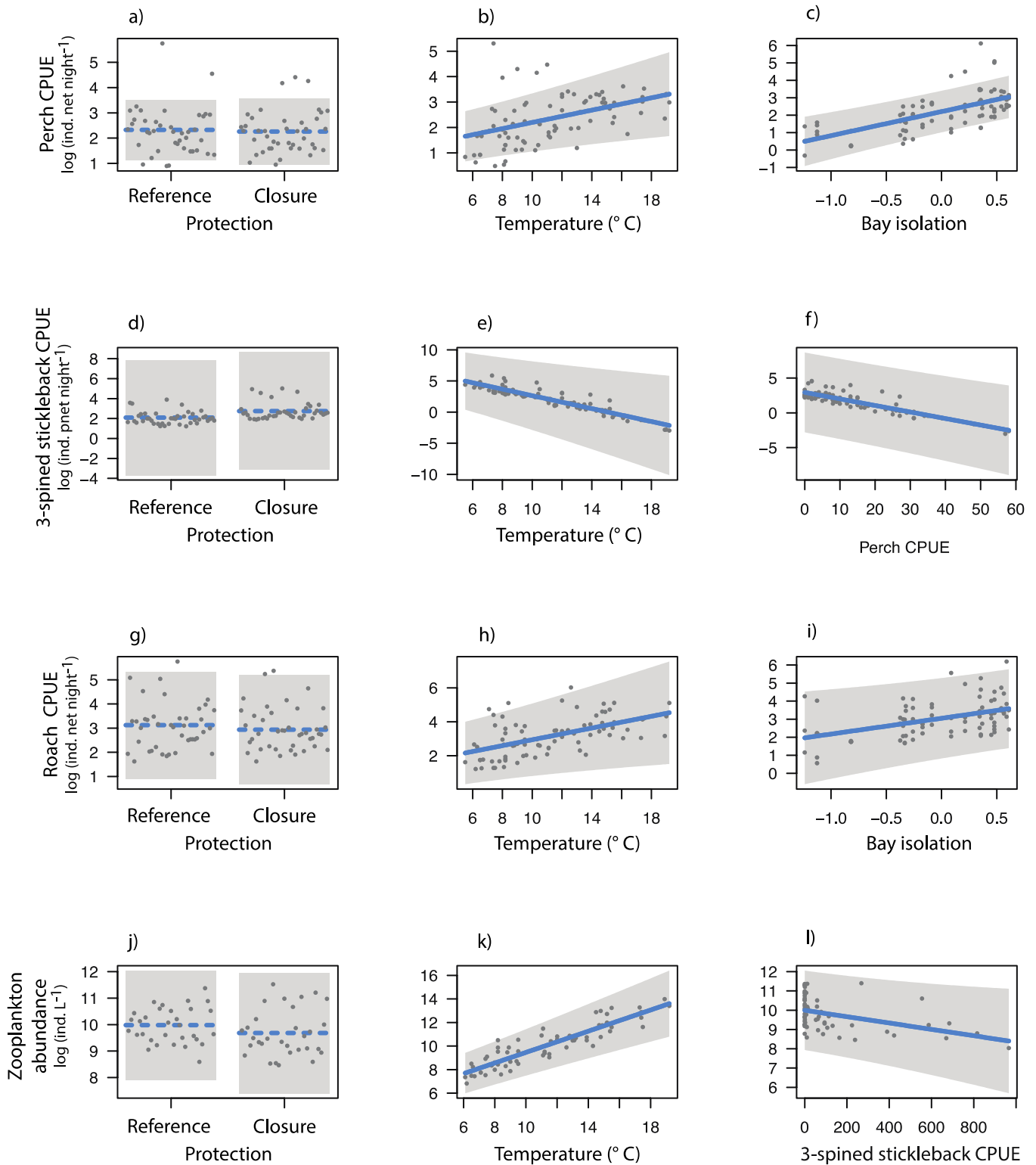


Fig. 3. Fish gillnet catches and zooplankton abundance. Partial regression plots displaying the influence of spawning closures and environmental covariates on a-c) perch CPUE, d-f) 3-spined stickleback CPUE, g-i) roach CPUE, and j-l) zooplankton abundance. Dashed lines denote non-significant effects (at $\alpha = 0.05$).

perch appear to do.

Given the absence of a closure effect on most fish species besides pike, we were surprised to find a strong, positive closure effect on survival of tethered gammarids; a key group of benthic, algal-feeding herbivores, who are eaten by small fish and shrimp, especially three-spined stickleback (Sieben et al., 2011). Tethering overestimates actual predation rates but is a common and useful method to measure the relative

strength of predation across space and time (Aronson and Heck, 1995). Here, after controlling for the possible influence of other factors, we found that predation risk was ca. three times higher in reference areas compared to closures (ca. 30 vs. 10 %, respectively); an effect of the same magnitude as the closure effect on pike CPUE (see above). Adult pike (the only fish species caught to a higher extent in the closures) do not eat gammarids, suggesting that this must be a knock-on effect

Table 4

Summary of the best-fitting GLMMs, but also including effects of seasonal closures, for A) predation pressure (binomial) on tethered gammarids, and B) catches (number of individuals per trap) of three-spined stickleback (*Gasterosteus aculeatus*). Note that random effects are not shown.

	Beta	SD	Z	P
A) Predation pressure				
Intercept	-1.673	1.172	-1.428	0.153
Protection:Closure	-1.279	0.475	-2.694	0.007
Temperature	0.082	0.100	0.819	0.412
B) Trap catch three-spined stickleback				
Intercept	4.061	2.31	1.758	0.078
Protection:Closure	-0.665	0.574	-1.158	0.247
Temperature	-0.382	0.194	-1.971	0.048
% cover filamentous algae	-0.003	0.004	-0.881	0.378

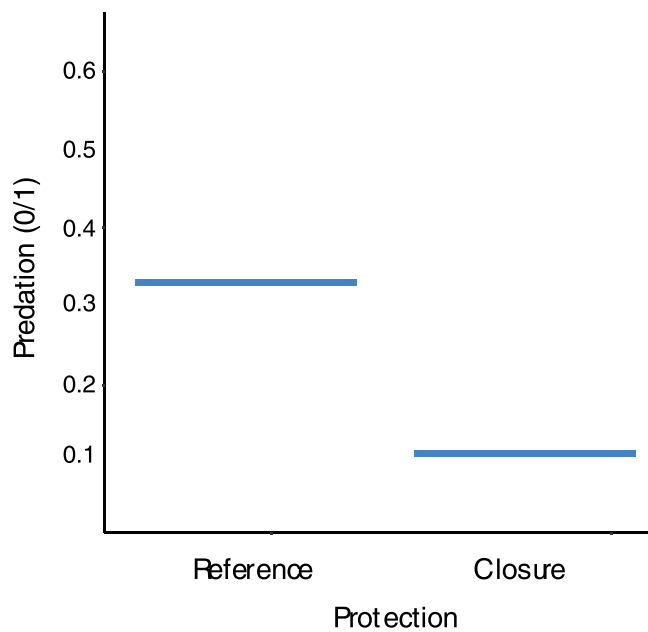


Fig. 4. Gammarid predation risk. Influence of spawning closures on predation risk (0–1) on tethered gammarids.

Table 5

Summary of the best-fitting GLMMs including effects of seasonal closures on bay-level means for A) catches per unit effort (CPUE) of three-spined stickleback (*Gasterosteus aculeatus*) in gillnets, and B) predation pressure (% predation) on tethered gammarids.

	Beta	SD	Z	P
A) CPUE 3-spined stickleback				
Intercept	5.33	2.139	2.49	0.013
Protection:Closure	0.011	0.628	0.02	0.986
Temperature	-0.109	0.222	-0.49	-0.624
Catch all perch	-0.108	0.047	-2.3	-0.022
Pike CPUE angling	0.212	0.593	-0.36	0.721
B) Predation pressure				
Intercept	-2.88	1.58	-1.823	0.068
Turbidity	0.337	0.669	0.504	0.614
Pike CPUE angling	0.131	1.014	0.129	0.897

mediated by other, smaller predators. In a previous study of 32 shallow bays along the same coastline, we found that stickleback biomass explained predation pressure on tethered gammarids, as well as the biomass of benthic mesograzers including gammarids (Donadi et al., 2017). In the present study, we found no influence of stickleback abundance or biomass on predation rates, and no closure effect on stickleback. We therefore hypothesize that the mechanism behind the

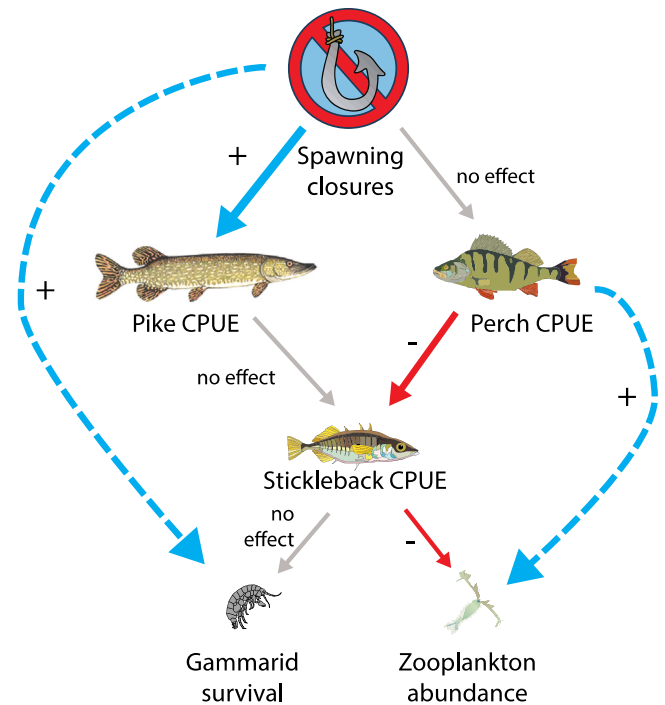


Fig. 5. Conceptual model summarizing the main findings regarding closure effects from a simplified food web perspective. Blue, red and grey arrows are positive, negative and non-significant effects, respectively. Filled and dashed arrows are direct and indirect effects, respectively. Gammarid and zooplankton symbols are courtesy of IAN Image Library, University of Maryland, USA.

closure effect on gammarid survival is not simply about numerical relationships, but instead explained by gammarid predators (such as stickleback) being more wary and spending less time foraging, potentially because of a higher risk of being eaten themselves. Stress associated with C&R has been shown to reduce the interest of pike in prey fish and increase attack time, which may affect the prey fish community (Stålhammar et al., 2012). Even though the conditions in that study differed from ours (short-term pond experiment with lower salinity, higher temperature, etc.), this gives support to the hypothesis that the higher survival of tethered amphipods in the spawning closures is a consequence of higher pike interest in, and attack rates on, stickleback as prey fish, in the absence of C&R. Also in support of this mechanisms, correlative data from North American lakes suggests that stickleback's fear of being preyed by invasive pike strongly reduces stickleback feeding rates and food intake, to the extent of starvation (Heins et al., 1999). There is, however, need for more detailed studies to establish whether C&R induces changes in pike behavior that cascades to lower trophic levels, and whether such effects are reversed in the seasonal closures.

Our study has several implications for the understanding of coastal food webs in the Baltic Sea in general, and the role of predation and large predatory fish in particular. First, our results support the hypothesis that pike and perch, as large predators high up in the food web, affect lower trophic levels and uphold cascading predation effects that benefit other organisms such as zooplankton and benthic invertebrates (Donadi et al., 2017; Östman et al., 2016); taxa that in turn contribute to important processes such as grazing, but also make up food for other organisms. Second, the higher catches of pike, and higher survival of tethered gammarids, in the closures open up for the interesting possibility that the influence of predation may involve a significant element of fear. A rich and growing literature from both terrestrial and aquatic systems shows that fear of predation alone often plays a significant role in determining where and when prey organisms are found and how they spend their time (Brown et al., 1999; Schmitz et al., 1997), and can

generate trophic cascades (Suraci et al., 2016). In the case of coastal fish in the Baltic Sea, we have previously shown that locally abundant perch and pike stocks benefit recruitment of their young-of-the-year by feeding on (and suppressing the numbers of) adult stickleback in spring, which otherwise eat perch and pike eggs and larvae (Eklöf et al., 2020). We did not assess closure effects on fish recruitment in the present study. Future studies should, however, assess the possibility that the mere presence of actively hunting adult pike in closures may instigate enough fear into stickleback to reduce predation pressure on the eggs and larvae of perch and pike.

Our study also has several implications from an applied perspective. Most importantly, the ca. 2.5 times higher catches of pike in closures suggest that closed fishing during the spawning season is a measure that results in more or abundant and/or easily caught pike. This may potentially benefit pike spawning and increase pike abundances (but see Flink et al., 2021). More studies on the topic are definitely needed, particularly those that follow areas before and after closures are implemented, and also assess closure effects on fish behavior and recruitment. In the meantime, we suggest that seasonal spawning closures should be considered to be one of several promising tools in pike conservation and fisheries management, which may help reduce the impact of fishing (Bergström et al., 2022; Olsson, 2019). That said, these spawning closures are open to fishing during 80 % of the year, and cannot be expected to protect pike in the same way as permanent closures. Similarly, the potential benefits of the spawning closures to instigate ecosystem level effects are still unclear. The lack of a protection effect on CPUE of other fish including perch – a much more abundant predator with potentially stronger effects on lower trophic levels, which instead appears to benefit from complete (year-round) closures (Bergström et al., 2019) – suggests that spawning closures cannot replace year-round closures and their multiple benefits (Jacquemont et al., 2022), and should be seen as an alternative to be used when full closures are either deemed unnecessary (for example, if fishing pressure is very low) or too difficult to implement.

Funding

This study was funded by the Swedish Agency for Marine and Water Management (Grant no. 3859-2016), the Research Council Formas (Grant no. 2013–1074 to Project PlantFish), and in-kind contribution from Stockholm University, Sweden (to JSE and JPH) and Groningen University, the Netherlands (to BKE).

CRediT authorship contribution statement

Johan S. Eklöf: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Resources, Validation, Visualization, Writing – original draft. **Joakim P. Hansen:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Validation, Visualization, Writing – review & editing. **Britas Klemens Eriksson:** Investigation, Methodology, Resources, Supervision, Validation, Writing – review & editing. **Örjan Östman:** Conceptualization, Investigation, Methodology, Validation, Writing – review & editing. **Åsa N. Austin:** Investigation, Writing – review & editing. **Casey Yanos:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Supervision, Validation, Visualization, Writing – review & editing. **Ronny Fredriksson:** Data curation, Formal analysis, Validation, Visualization, Writing – review & editing. **Ulf Bergström:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Validation, Visualization, Writing – review & editing. **Henrik C. Andersson:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Validation, Writing – review & editing.

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 thank; the water rights owners around the 11 closure bays for agreeing to create spawning closures, and those around all 22 bays for allowing us to sample for this study; A. Sandström, A. Santnér, C. Ericsson, D. Brelín, G. Almqvist, H. Schreiber, J. Andreasson, J. Lantz, J. Persson, K. Florén, L. Ljunggren, N. Sjöberg, P. Persson Holmberg, P. Lindberg and T. Fränstam for assistance with the pike angling; Naturvatten i Roslagen AB, Sveriges Vattenekologer AB, JP Aquakonsult KB and Hydrophyta Ekologikonsult for gillnet fishing and vegetation surveys; E. Heenstra for assistance with field work, and the attendees at the online Baltic Sea Pike Symposium 2021, as well as two anonymous reviewers, for constructive comments that helped improve this paper.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2023.106674.

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