

RESEARCH ARTICLE

Predator–prey role reversal may impair the recovery of declining pike populations

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Abstract

1. Many fish populations have experienced declines in recent decades due to anthropogenic disturbances, such as overfishing and habitat exploitation. Despite management actions, many populations show a limited capacity to recover. This may be attributed to reversal of predator–prey roles, yet empirical evidence to that effect remains scarce.
2. Here, we combine field and laboratory studies to investigate the interaction between pike (*Esox lucius*), a large keystone top predatory fish, and the small-bodied mesopredatory threespine stickleback (*Gasterosteus aculeatus*) in the Baltic Sea where pike populations have declined.
3. Our data suggest that stickleback predation on pike larvae depletes a large proportion of the recruitment and influences the size distribution through size-selective predation, which is corroborated by a gape-limitation experiment and diet analysis of wild-captured sticklebacks.
4. The effects of stickleback predation are present across several populations and years, and our data suggest that early arrival of sticklebacks has stronger effects on juvenile pike survival. Finally, we use data on pike gape-limitation and the size distribution of sticklebacks to illustrate the process of role reversal.
5. These findings suggest that mesopredator behaviour can reduce recruitment of a top predator species and impair the capacity of populations to recover. This emphasizes predator–prey role reversal as an important ecological and evolutionary driver that influences the outcome of restoration and management actions.

KEYWORDS

conservation, depensation effects, ecosystem dynamics, gape-limitation, hysteresis, interspecific interactions, intraguild predation, population recovery

1 | INTRODUCTION

Top predators have suffered catastrophic declines world-wide due to anthropogenic disturbances, such as overexploitation and habitat loss, with dramatic consequences for trophic dynamics, community organization, biodiversity and ecosystem functioning (Myers & Worm, 2003; Prugh et al., 2009; Ritchie & Johnson, 2009; Scheffer & Carpenter, 2003; Stier et al., 2016). For instance, reduced

abundances of top predators commonly result in trophic cascades with increased abundances of smaller-sized predatory species, that is a mesopredator release (Baum & Worm, 2009; Casini et al., 2009; Ritchie & Johnson, 2009). This may lead to increased interspecific resource competition or the reversal of predator–prey roles, such that the early life stages of top predators are intensively predated upon by mesopredators, which may impair recruitment and ultimately hamper the recovery of the top predator (Barkai & McQuaid, 1988; Fauchald,

2010; Hutchings, 2015; Myers & Worm, 2005). Communities may subsequently shift to irreversible alternative stable states such that large mesopredator populations suppress recruitment of top predators and thus preserve the ecosystem in a meso-predator-dominated state (Beisner, Haydon, & Cuddington, 2003; Fauchald, 2010; Gårdmark et al., 2015; Persson et al., 2007; Walters & Kitchell, 2001). Predator–prey role reversal has, especially in aquatic ecosystems, recently received a growing recognition in contributing to alternative stable states and hampering the recovery of top predators (Myers & Worm, 2005). Yet, most previous studies rely on correlative study approaches and lack experimental support that may provide important insights on the mechanistic underpinning of whether and how mesopredator behaviour impairs the recovery of top predators (Sánchez-Garduño, Miramontes, & Marquez-Lago, 2014; Stier et al., 2016).

Here, we explore predator–prey interactions between pike (*Esox lucius*), a large keystone top predatory fish, and the small-bodied mesopredatory threespine stickleback (*Gasterosteus aculeatus*, hereafter referred to as stickleback). These are two model species for ecology and evolution that coexist in freshwater and brackish water habitats throughout the northern hemisphere (Bell & Foster, 1994; Craig, 2008; Forsman et al., 2015; Gibson, 2005). Previous studies have shown that pike is a major predator on adult sticklebacks with the potential to suppress stickleback densities (Donadi et al., 2017; Eriksson et al., 2009; Frost, 1954; Leinonen, Herczeg, Cano, & Merilä, 2011). The pike–stickleback interaction in the Baltic Sea is a suitable study system in regard to evaluating predictions of the consequences of predator–prey role reversal due to a recent regime shift from top-down towards a bottom-up controlled ecosystem (Bergström et al., 2015; Donadi et al., 2017; Eriksson et al., 2009; Gårdmark et al., 2015). Notably, this regime shift involves a substantial decline of pike in the mid-1990s and an exponential increase in sticklebacks starting about a decade later (Bergström et al., 2015; Eriksson et al., 2011; Ljunggren et al., 2010; Nilsson, Andersson, Karås, & Sandström, 2004) (see Figure 1b for population trends for pike and sticklebacks in our study system). The decline of pike has been attributed to increased interspecific resource competition during early life stages, habitat exploitation and high fishing pressure (Larsson et al., 2015; Ljunggren et al., 2010). Sticklebacks have consequently been favoured by predator release partly constituted by declining pike populations (Bergström et al., 2015, 2016; Donadi et al., 2017; Sieben, Ljunggren, Bergström, & Eriksson, 2011). Many efforts, including fisheries regulation and habitat restoration, have been directed towards remediating the underlying causes for the decline, aid the recovery of pike and ultimately improve the coastal ecosystem (Engstedt, Nilsson, & Larsson, 2017; Nilsson, Engstedt, & Larsson, 2014). Still, the pike populations recover only very slowly, if at all (Bergström et al., 2016; Eriksson et al., 2009) (Figure 1b).

It has been speculated that the recovery of pike populations may be impaired by high abundances of sticklebacks (Bergström et al., 2015; Byström et al., 2015; Ljunggren et al., 2010), but the underlying mechanism has not been firmly established. In the Baltic Sea, anadromous pike forage in the coastal habitat and migrate to breed in streams and wetlands (Engstedt, Stenroth, Larsson, Ljunggren, & Elfman, 2010; Nilsson

et al., 2014; Tibblin, Forsman, Borger, & Larsson, 2016). Breeding, depending on population, occurs during March to May (Larsson et al., 2015; Tibblin, Forsman et al., 2016), and the eggs hatch after a few weeks (Berggren, Nordahl, Tibblin, Larsson, & Forsman, 2016; Craig, 2008). This recruitment period coincides with the timing of sticklebacks aggregating in coastal areas, following their migration from the offshore pelagic habitat, after which it is the most abundant fish species in many coastal areas until migrating back to the offshore pelagic in the autumn (Bergström et al., 2015; Borg, 1985; Eriksson et al., 2009; Ljunggren et al., 2010; Nilsson, 2006). Previous research has shown a negative relationship between the abundance of sticklebacks and pike juveniles (Bergström et al., 2015; Nilsson, 2006), and observational studies suggest that sticklebacks predate on pike eggs deposited in shallow coastal bays (Nilsson, 2006). However, firm evidence regarding negative effects of stickleback predation on pike recruitment is still lacking.

This study investigates whether and how mesopredatory sticklebacks through predation on juvenile life stages influence the recruitment in top predatory pike populations. If recruitment of pike is affected by stickleback predation, we would predict that (a) mortality of pike juveniles coincides with sticklebacks arriving to the recruitment areas, (b) stickleback induced mortality is high and affects the majority of a size cohort, (c) pike mortality is size-dependent and corresponds to the stickleback gape-limitation, and that (d) in recruitment areas where sticklebacks arrive before pike have reached the critical size determined by gape-limitation there will be hardly any recruitment, whereas in recruitment areas where pike breed early (such that juveniles can grow beyond the critical size) before sticklebacks arrive the survival will be high.

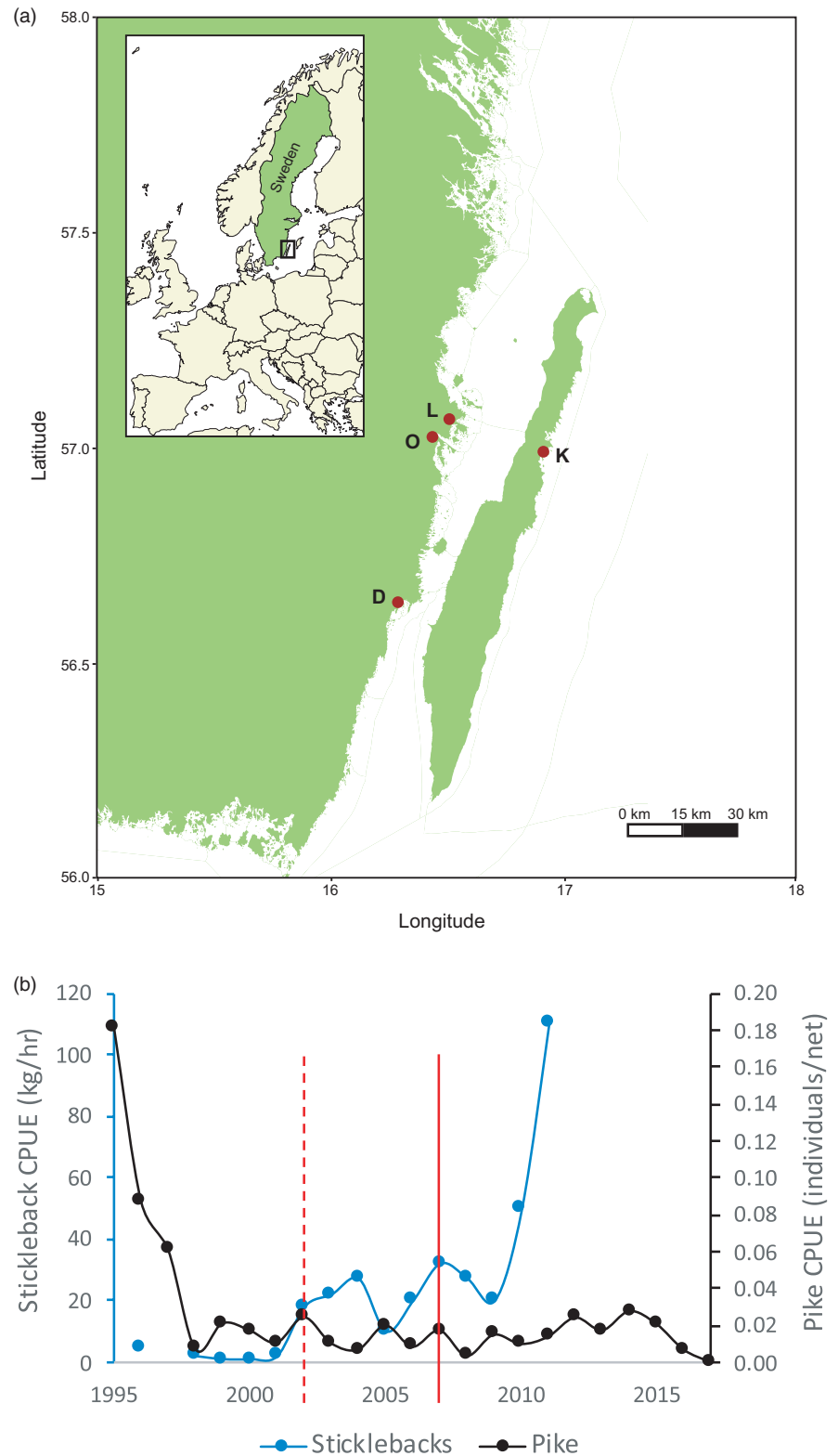
We tested these predictions by investigating spatial and temporal variation in effects of stickleback predation on the recruitment success of anadromous pike that breed in wetlands connected to the Baltic Sea. Using data from four populations collected over five years, we quantified the size distributions and abundances of emigrating pike juvenile cohorts in the presence and absence of sticklebacks within streams due to barriers restricting sticklebacks reaching upstream areas adjacent to the breeding habitats in wetlands. We also performed a gape-limitation experiment and analysed the diet of sticklebacks captured in the stream mouths to test whether gape-limitation of sticklebacks corresponds to size-selective disappearance of pike juveniles. Finally, to visualize the process of predator–prey reversal, we used data on gape-limitations of pike and the size distribution of sticklebacks in our study area to assess at what size range pike switch from being prey to become predator.

2 | MATERIALS AND METHODS

2.1 | Anadromous pike – a suitable system to study the pike–stickleback interaction

In this study, we take advantage of that anadromous pike populations breed in shallow vegetated wetlands that are out of reach for sticklebacks, provide suitable breeding substrate, high zooplankton production and low interspecific competition/predation (Engstedt et al., 2017; Nilsson

FIGURE 1 (a) Map of breeding sites (coordinates below) of pike populations investigated for effects of stickleback predation. L (N57°04.400'; E16°31.100'), O (N57°01.200'; E16°26.700'), D (N56°38.200'; E16°14.800') and K (N56°57.500'; E16°53.000'). Population abbreviations please see Table 1; (b) Trends in abundances of pike (black) and stickleback (blue) in or adjacent to the study area with the timing of major management efforts marked out. Data for pike abundances derived from survey fishing efforts using gillnets in the coastal area outside the sampling streams for populations O and L. Data for stickleback abundances are derived from figure 2 in Bergström et al. (2015) and represent catches of sticklebacks during pelagic trawl hauls in zones SD27-29 in the offshore central Baltic Sea most adjacent to our study area. Vertical red lines represent the timing of the partial closure of the pike fishery (dashed line) and the initiation of spawning habitat restorations (solid line)



et al., 2014). These wetlands are typically located 200–700 m upstream from the Baltic coast and associated with small streams (generally 2–3 m wide and with an annual mean water flow of less than 0.5 m³/s) through which they are connected by outlets, rifles and/or fishways making them inaccessible to species with smaller body size and/or lesser swimming ability (e.g. the stickleback) (Engstedt et al., 2017; Nilsson, 2006).

Adult pike migrate from the Baltic Sea and arrive to the wetlands during March–May (depending on the population), after which the reproduction commences (Larsson et al., 2015). Eggs hatch after about 10 days, and hatched larvae remain in the wetlands a few weeks before emigrating towards the Baltic Sea. Within hours after leaving the wetland, juveniles passively drift (with the current) and/

TABLE 1 Data of sampled pike populations, sampling years, starting dates of pike emigration and stickleback arrival, population census sizes and sample sizes

Population	Okneback (O)					Lervik (L)	Dunö (D)	Kårehamn (K)
Year	2007	2008	2009	2013	2014	2014	2014	2014
Start of juvenile pike emigration	27 April	23 April	25 April	10 May	26 April	13 May	06 May	29 April
Stickleback arrival	18 May	13 May	13 May	28 May	15 May	<13 May	<06 May	<29 Apr
No. of days from emigration start to stickleback arrival	21	20	18	18	19	0	0	0
Population census size of pike	n/a	n/a	n/a	n/a	3,086	625 ^a	450	323
No. of captured pike (no-pred/pred traps)	612/126	4,401/1,853	15,018/3,444	6,774/1,858	3,400/2,530	1,063/49	2,638/106	411/3

^aIndicates that the census population size in population L is based on investigations ending in 2011 (Tibblin, Forsman et al., 2016). No-predation and predation traps were located upstream and downstream respectively within each stream/population.

or actively swim through the streams. The emigration of juveniles is relatively synchronous, and within one month after emigration begins, about 80–95% of the cohorts have left the wetlands (Larsson et al., 2015; Nilsson et al., 2014). Recent research suggests that these wetlands have a vast potential for producing recruits that may contribute to the coastal pike stock with an annual production of several hundred thousand juveniles in some wetlands/populations (Engstedt et al., 2017; Nilsson et al., 2014). Given the substantial decline of pike, together with historical intense exploitation of wetlands areas, much effort has been directed towards restoration and construction of wetlands optimized for pike recruitment (Engstedt et al., 2017). These systems also offer valuable opportunities for scientific studies. The defined routes through narrow streams and fishways/outlets through which fish (adults and juveniles) pass allow for controlled quantification of migration and emigration, phenology as well as population dynamics (Larsson et al., 2015; Nilsson et al., 2014; Tibblin et al., 2015; Tibblin, Forsman et al., 2016).

In the present study, we assess influences of stickleback predation on pike recruitment by investigating cohorts of emigrating pike juveniles from four populations (D, K, L, O, see Table 1 for abbreviations) that reproduce in wetlands connected to the southwest Baltic Sea (Figure 1a; Table 1). Furthermore, in population O (Table 1) we sampled across five years to examine temporal variation in stickleback predation effects across breeding seasons. Previous research has shown that these populations display homing behaviour (Tibblin, Forsman et al., 2016), fine-spatial-scale genetic population differentiation (Larsson et al., 2015) and local adaptations to specific streams/wetlands (Berggren et al., 2016; Sunde, Tamario, Tibblin, Larsson, & Forsman, 2018; Tibblin, Berggren, Nordahl, Larsson, & Forsman, 2016; Tibblin et al., 2015). Moreover, our study area experienced the most extreme decline of pike in the Baltic Sea during the 1990s and abundances are still very low despite that the pike fishery is partially closed and strictly regulated through bag and size limits (Figure 1b) (Bergström et al., 2016; Ljunggren et al., 2010; Nilsson et al., 2004). Recent studies suggest that adult census population

sizes of pike in our study populations vary between approximately 300 and 3,000 adults (Table 1; Nilsson et al., 2014; Larsson et al., 2015; Tibblin, Forsman et al., 2016; P. Tibblin, unpubl data).

2.2 | Stickleback predation influences pike recruitment

To evaluate effects of stickleback predation, we investigated the abundances and size distributions of emigrating juvenile pike cohorts through simultaneous sampling of juveniles at predation (sticklebacks present) and at no-predation sites (sticklebacks excluded) within each population/stream, respectively. We sampled using traps specifically developed for passive capture of juvenile pike during emigration (Nilsson et al., 2014). No-predation traps were placed in the streams precisely downstream the outlets of the wetlands where sticklebacks have never been observed, whereas the predation traps were placed a few hundred metres further downstream where sticklebacks have been observed each year. Traps had squared entrance openings (30–50 cm depending on the size of the stream) followed by a conical net (1 mm mesh size) leading into a collecting container (Nilsson et al., 2014). In each stream respectively, the no-predation and predation traps were set in locations with similar water flow, depth and stream width such that the amount of water directed through the traps was equal (25–100% of the water flow depending on stream and water flow). All sampled streams are ditched and straightened and provide little or none suitable habitat for pike reproduction or sustaining larval and juvenile life stages; instead, these streams merely offer a route towards the Baltic Sea through which larvae pass within hours after leaving the wetland (Nilsson et al., 2014). As such, it is unlikely that environmental variation influenced catchability of juvenile pike to any important degree. Moreover, to prevent sticklebacks entering and predate within the traps we fitted the entrances with a stickleback-safe net (6 mm mesh size). In population O, the stickleback-safe net was removed during efforts in 2013–2014 to avoid interfering with the capture of pike juveniles in the upper size range. The capture of sticklebacks in the trap

during this period was low and the relative capture of pike between predation and no-predation traps was similar to previous years, thus suggesting stickleback predation within traps to be negligible (Table 1).

The sampling was initiated prior to the start of pike emigration based on visual observations, timing of breeding activity and the white plate method where a 30-cm white disc was slowly moved over the bottom to quantify free-swimming larvae (Lappalainen, Harma, Kuningas, & Urho, 2008; Nilsson et al., 2014). To comprise the majority of the emigrating cohort, once the emigration had started we sampled each stream during six weeks with traps being emptied daily, or, during periods of more extensive emigration twice a day. The size distributions of pike juveniles were determined based on random subsamples of individuals collected every 5–7 days. The difference in predator regimes (i.e. predation vs. no-predation) between traps/sites was confirmed by daily stickleback census. In all five years of studies in population O, sticklebacks arrived to the predation site at a time when the emigration of juvenile pike had already lasted for 18–21 days, whereas in the other three populations (D, K, L) sticklebacks were present at the onset of pike emigration (Table 1).

Additionally, we validated stickleback densities and the potential presence of other putative predators by electrofishing and seine fishing in the predation sites. Electrofishing, which was only possible in population K due to high conductivity in the other streams, resulted in about 10 individuals/m², yielding an estimated total abundance of more than 20,000 sticklebacks in the stream during juvenile pike emigration. Apart from sticklebacks, electrofishing identified only one more potential predator, the ninespine stickleback (*Pungitius pungitius*). However, this species was caught only sporadically and in much lower numbers. In the other streams, seine fishing revealed a similar pattern with sticklebacks being the dominant predator. During the daily visits to our study sites, we also took special notice in observing other putative predators, for instance reptile (grass snake *Natrix natrix* and adder *Vipera berus*) and avian predators (Common merganser *Mergus merganser*, Grey heron *Ardea cinerea* among others), but such species were only present sporadically and in very low numbers. That our study design actually reflected variation in stickleback predation on pike juveniles rather than effects of other putative predators or environmental variation was further supported by a lack of difference between traps in size distributions and abundances of captured emigrating pike juveniles prior to stickleback arrival (LMM on log length: effect of predation: $\chi = 2.50$, $p = 0.131$; LMM on log abundances: effect of predation: $\chi = 0.02$, $p = 0.96$).

2.3 | Characterizing sticklebacks as a predator on pike juveniles

2.3.1 | Gape-limitation experiment

To estimate gape-limitations of stickleback predation on pike juveniles, we performed a feeding experiment where we exposed differently sized pike juveniles to adult sticklebacks. The experiment was conducted during the spring of 2010 at Linnaeus University, Kalmar, Sweden. Sticklebacks (65 ± 2 mm; mean \pm SD total length, $n = 168$)

were caught with traps in shallow bays close to the breeding wetland of population O, transported to the laboratory and held in groups of ten individuals in 35-L holding aquariums with aerated stream-specific water. Holding aquaria were provided with gravel and plastic vegetation as shelter. Sticklebacks were fed live cladocerans and frozen chironomid larvae daily, and starved for at least four hours prior to each experiment. Pike juveniles of different sizes (range: 12–58 mm, $n = 84$) were caught with traps in population O. To obtain pike juveniles of different sizes, the sampling was conducted at seven occasions along the experimental period. Juveniles were transported to the laboratory and thereafter put separately in twelve 20-L experimental aquaria. All experimental aquaria that were used were provided with a layer of gravel, a piece of plastic 'vegetation' ranging from the bottom to the surface as shelter, and aerated water originating from population O. Three of four sides of each aquarium were covered with black plastic during the experiments and water temperature followed outside conditions (12–18°C) throughout the experimental period. At the onset of each trial, a juvenile pike acclimatized in the experimental aquarium for one hour prior to the introduction of two sticklebacks with all subjects used only for one trial. The experiment was terminated either when the pike was consumed, fatally injured or after four hours if predation did not occur.

2.3.2 | Gape-limitation of sticklebacks estimated by morphometrics

In order to estimate the body depth and the corresponding maximum length of pike juveniles that can be eaten by sticklebacks, we measured morphometrics of juvenile pike (29 ± 8 mm; mean \pm SD total length, range 15–47 mm, $n = 228$) and sticklebacks (62 ± 7 mm, range 47–76 mm, $n = 100$) randomly sampled in our study populations. We measured total length to the nearest mm, while body depth of pike juveniles and gape-limitation of sticklebacks were measured to the nearest 0.1 mm. Gape-limitation was measured as the distance between the upper and lower jaw at a gape angle of 90°, using a stereomicroscope (method adopted by Byström et al., 2015). The gape-limitation among the sampled sticklebacks ranged from 2.8 to 4.9 mm, whereas the body depth among pike juveniles ranged from 2.1 to 6.6 mm. Stickleback gape size increased with total length (TL) according to $\text{gape size} = 0.0527 \times \text{TL} + 0.7145$ (linear regression, $R^2 = 0.68$, $F_{1,98} = 212$, $p < 0.001$), whereas pike juvenile body depth increased with total length according to $\text{body depth} = 0.1513 \times \text{TL} - 0.2043$ (linear regression, $R^2 = 0.92$, $F_{1,226} = 2,486$, $p < 0.001$).

2.3.3 | Diet analysis of sticklebacks present at the predator sites

To investigate whether the critical size of pike for stickleback predation, estimated by gape-limitations of sticklebacks, corresponds to natural predation, we randomly sampled sticklebacks (60 ± 7 mm, range 43–80 mm, $n = 739$) at the predation site of population O for diet analysis. Following capture, each individual was immediately killed and preserved in a 4% formalin solution buffered with borax. Out of 739 examined individuals, 241 guts contained prey that we

classified according to taxonomic group by microscope. To assess the contribution of pike as part of the stickleback diet, we measured all consumed pike juveniles to the closest mm and calculated the frequency (%) of sticklebacks that had consumed pike.

2.4 | Characterizing pike as predator on adult sticklebacks

We examined the role of pike as predator on sticklebacks by measuring gape-limitations on later stages of juvenile pike residing in the coastal habitat (105 ± 47 mm, range 39–208 mm: $n = 53$) in relation to the size distribution of adult sticklebacks (61 ± 6 mm, range 40–80 mm: $n = 1684$) randomly sampled in our study area. The gape-limitation of pike was determined to the nearest mm by inserting a plastic cone with increasing cross-sectional diameter into the mouth of the pike according to the method presented by Nilsson and Brönmark (2000). Body depth and total length of sticklebacks were determined to the nearest mm using digital calipers in a subsample of sticklebacks (55 ± 8 mm range 40–73 mm: $n = 92$). Pike gape size increased with total length (TL) according to gape size = $0.0944 \times \text{TL} + 0.1588$ (linear regression, $R^2 = 0.99$, $F_{1,52} = 4517$, $p < 0.001$). The body depth of sticklebacks increased with total length according to body depth = $y = 0.233 \times \text{TL} - 1.8612$ (linear regression, $R^2 = 0.88$, $F_{1,90} = 686$, $p < 0.001$).

2.5 | Statistical analysis

To test whether the size distributions and abundances of emigrating pike juveniles were affected by stickleback predation, we analysed data using linear mixed models (LMM), with the maximum likelihood (ML) as estimation method (Bates, Mächler, Bolker, & Walker, 2015; Luke, 2017). We evaluated temporal effects in stickleback predation using data representing five years in population O, and we ran separate LMM for the two dependent variables (size and abundances). Predation regime (no-predation/predation) was treated as fixed factor and year as random factor, and we included the predator regime \times year interaction as random factor to evaluate whether the magnitude of predation effects varied across years. We also included sampling occasion (date) as a random factor to the models and to take into account the covariance of repeated measures within predator regime. However, we were not interested in evaluating or quantifying the random effects of sampling occasion and year (and population below) per se, and thus, parameter estimates and associated statistical significance levels for these factors are not reported. To examine spatial variation in stickleback predation effects, we analysed data representing four populations using the same statistical approach as for temporal variation. Predation regime was treated as fixed factor, whereas population and sampling date were set as random factors. To answer whether the magnitude of predation effects varied across populations, we also included the predator regime \times population interaction as random factor. Assumptions of all LMMs were checked by visual inspections of diagnostic plots using the *mcheck* function in R STUDIO (Crawley, 2013). To normalize distributions and homogenize

variances, data were log-transformed. Significance levels of fixed factors were evaluated using log-likelihood ratio tests with 1 *df* (Bolker et al., 2009; Luke, 2017). To analyse the effects of stickleback predation on abundances, we also applied a generalized linear mixed models (GLMM) with a Poisson distribution generally suitable to analyse counts. This generated similar results as our LMMs; however, based on diagnostic plots the GLMMs did not fit data equally well, and thus, we adhere to the LMMs in the results below. All presented models were estimated using the package LME4 (Bates, Maechler, & Bollinger, 2011) in R STUDIO v.1.0.136, with R v.3.3.2 (R Core Team, 2016).

3 | RESULTS

3.1 | Stickleback presence affects pike survival and size distributions

Predator regime (stickleback presence or absence) was associated with significant differences in both size distributions and abundances of pike juveniles emigrating from population O during five years of recruitment, albeit the magnitude of the differences in abundances varied across years (LMM on log-transformed total length: predation regime $\chi^2 = 9.15$, $p = 0.002$, predation regime \times year $\chi^2 = 1.39$, $p = 0.239$, $n = 2,561$; LMM on log-transformed abundances: predation regime $\chi^2 = 6.58$, $p = 0.010$, predation regime \times year $\chi^2 = 4.58$, $p = 0.032$, $n = 182$; Figures 2a and 3a). Similar associations with predator regime were also evident when analysing data representing four different populations, with significant differences in abundances and size distributions although the magnitude of the differences varied across populations (LMM on log-transformed total length: predation regime $\chi^2 = 5.94$, $p = 0.015$, predation regime \times population $\chi^2 = 32.89$, $p < 0.001$, $n = 649$; LMM on log-transformed abundances: predation regime $\chi^2 = 6.68$, $p = 0.001$, predation regime \times population $\chi^2 = 26.69$, $p < 0.001$, $n = 118$; Figures 2b and 3b).

Pike juveniles were continuously captured in large numbers at the no-predation sites in all populations, whereas very few individuals (that had not yet reached a size of 33 mm or larger) were simultaneously captured at the predation sites (Figure 4a). The average loss of emigrating juveniles to stickleback predation during 2014 was estimated to $79 \pm 36\%$ (mean across populations \pm SD, range: 26–99%, Table 1) and 64% of total abundances across populations, respectively (Table 1; Figure 4). In population O, where sticklebacks arrived after the pike emigration had started, there was an instant decrease in juveniles in the predation trap by $61 \pm 14\%$ (mean across five years \pm SD) the day after stickleback arrival, whereas in the no-predation trap, the decrease was negligible ($3 \pm 8\%$) (Figure 5).

3.2 | Size-selective disappearance of pike juveniles corresponds to stickleback gape-limitation and gut content

The stickleback gape-limitation and pike body depth relationship suggest that the estimated maximum pike length (PL) that a stickleback can consume increases with stickleback length (SL) according

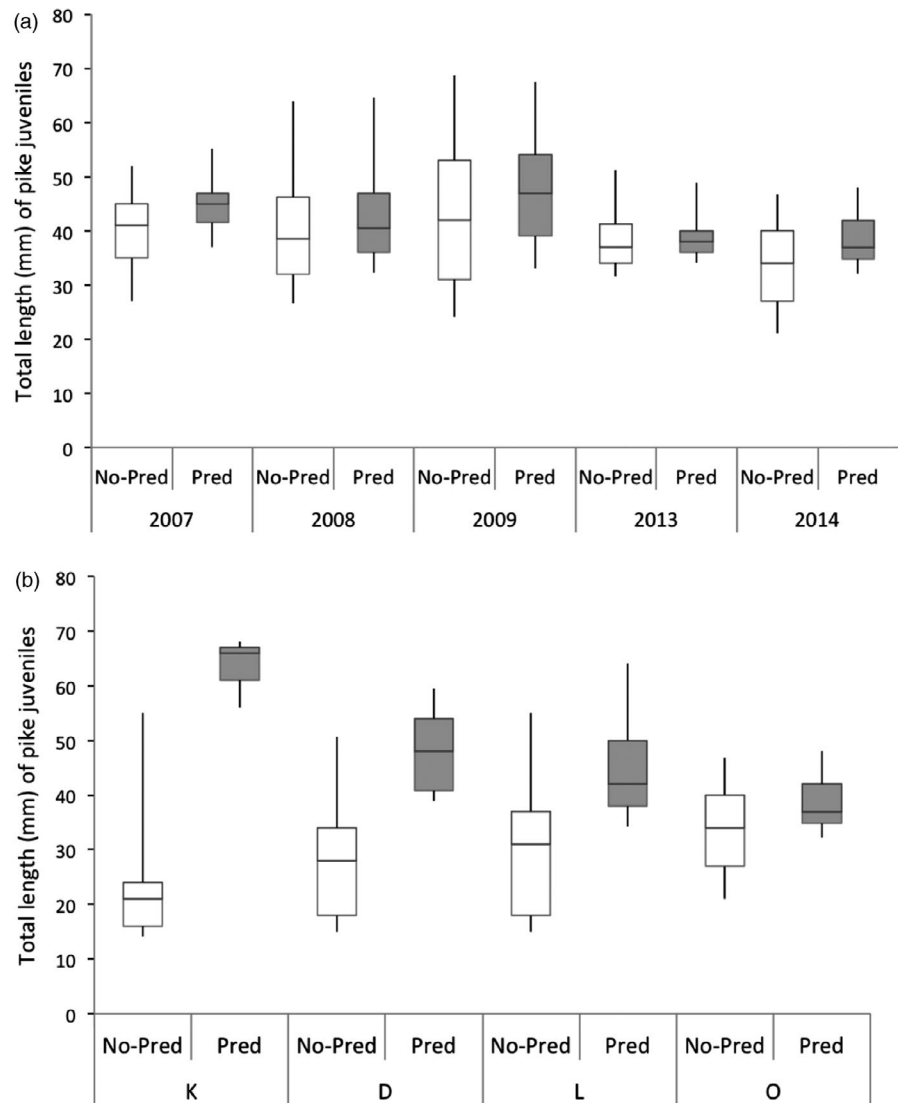


FIGURE 2 Effects of stickleback predation on size distribution of emigrating pike juveniles. (a) Year-to-year variation in the effects of stickleback predation in population O. (b) Stickleback predation effects in four populations during 2014. Population abbreviations please see Table 1. Two sites with different predator regimes: No-Pred = unreachable for sticklebacks; Pred = sticklebacks present. The solid lines within the boxes indicate medians, the boundaries of the box indicate 25th and 75th percentiles, and the whiskers below and above indicate 5th and 95th percentiles, respectively

to $PL = 0.3483 \times SL + 6.073$. Based on the total lengths of sampled sticklebacks (40–80 mm, $n = 1,684$), we estimated that 33 mm was the critical size of pike for outgrowing the stickleback predation window (Figure 6). This critical size also largely corresponds to the results of the feeding experiment and the diet analysis of wild-captured sticklebacks. The feeding experiment uncovered that sticklebacks consumed 97% of pike under 35 mm ($n = 62$) and only 5% of the ones longer than 35 mm ($n = 22$) (Figure 4b). The diet analysis showed that 14% of the examined sticklebacks had preyed upon pike and all consumed pike juveniles were shorter than 32 mm. These estimates of the critical size of pike for stickleback predation largely conform with the size-selective disappearance found in the field (Figure 4a).

3.3 | Pike juveniles switching from being prey to become predator

The gape-limitation of pike and stickleback body depth relationship suggests that the estimated maximum length of sticklebacks (SL)

that a pike juvenile can consume increases with pike length (PL) according to $SL = 0.4051 \times PL + 8.670$. This indicates that juvenile pike can start to prey upon the smaller size classes of adult sticklebacks when they reach a length of 78 mm, whereas all sticklebacks are potential prey to pike that reach 175 mm (Figure 6).

4 | DISCUSSION

Many keystone top predators have suffered dramatic declines due to anthropogenic disturbances, and this has resulted in destabilized food web dynamics, trophic cascades and regime shifts (Baum & Worm, 2009; Casini et al., 2009; DeYoung et al., 2008). This has called for intense management efforts world-wide, but only few populations have been able to recover and the global status of both aquatic and terrestrial top predators remains poor (Myers & Worm, 2003; Stier et al., 2016). A potential cause to failed recoveries of top predators is that their recruitment is impaired by predator-prey reversal (Barkai & McQuaid, 1988; Cardinale & Svedäng,

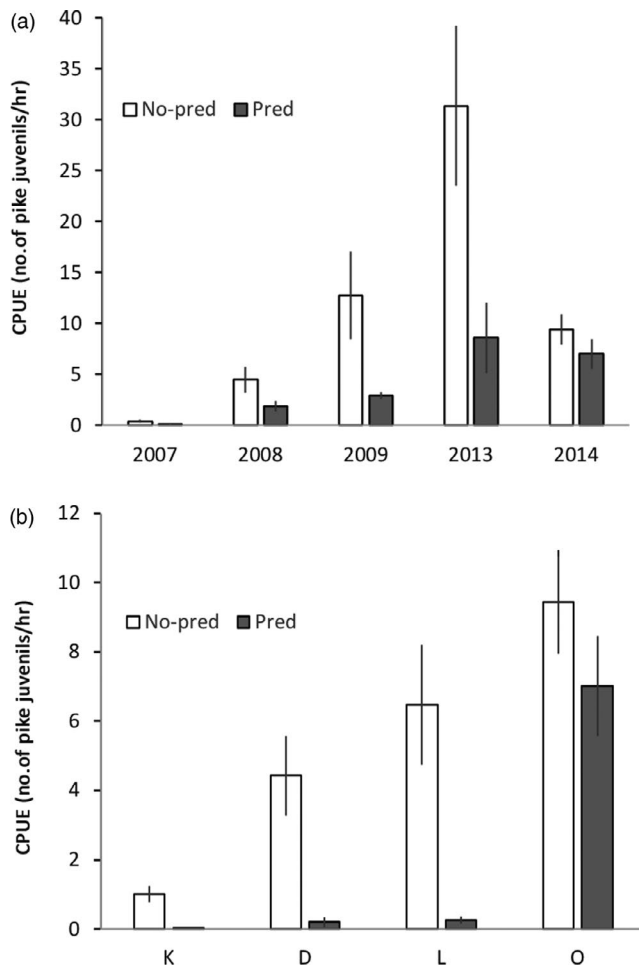


FIGURE 3 Effects of stickleback predation on abundances of juvenile pike estimated by CPUE (number of pike juveniles/hour) \pm SE. (a) Year-to-year variation in the effects of stickleback predation in population O. (b) Stickleback predation effects in four populations during 2014. Population abbreviations please see Table 1. Two sites with different predator regimes: No-Pred = unreachable for sticklebacks; Pred = sticklebacks present

2011; Fauchald, 2010; Gårdmark et al., 2015; Myers & Worm, 2005). Yet, the possible role of predator–prey reversal has commonly been overlooked and the process remains poorly understood (Barkai & McQuaid, 1988; Sánchez-Garduño et al., 2014; Stier et al., 2016; Walters & Kitchell, 2001). Here, we add to this knowledge by investigating the interaction between pike, a top predatory fish species with declining populations, and the mesopredatory stickleback in the Baltic Sea. The role of the stickleback in influencing the abundances of predatory fish is under debate, but firm evidence to such effects is still lacking and the underlying mechanism eluding (Bergström et al., 2015; Byström et al., 2015; Ljunggren et al., 2010). In this study, we combine field and laboratory studies to suggest that sticklebacks negatively impact the recruitment success of pike by intense size-selective predation, structured by gape-limitations, on early life stages of pike about to leave their recruitment habitat. This suggests that sticklebacks strongly influence population dynamics of their own top predator, impairing the capacity of weakened

populations to recover, and as a result possibly contributing to lock the ecosystem in meso-predator-dominated state.

Our data suggest that impacts of stickleback predation on size distributions and abundances of pike juveniles were present both across populations and years, albeit significant interaction effects suggest that the magnitude varied in all comparisons except in the one of temporal variation in stickleback predation effects on size distribution of pike juveniles. In those populations (D, K and L) where sticklebacks were present at the onset of emigration, it constituted a major source of mortality on the cohort of emigrating juveniles and reduced survival to less than 4% of the numbers leaving the wetlands (Table 1). In principle, the survival of pike juveniles during these circumstances was exclusively limited to individuals that emigrated at a time when they had outgrown the predation window structured by the gape-limitation of sticklebacks. However, in population O where sticklebacks consistently over five years of studies arrived at a time when a large proportion of the cohort had already emigrated, the predation effect on the recruitment was less intense in a similar way as previously shown in Baltic Sea perch (Byström et al., 2015). The late arrival of sticklebacks in relation to the emigrating timing of pike also meant that many juveniles had outgrown the predation window once sticklebacks were present, resulting in weakened predation effects on the size distribution of emigrating juveniles. Together, this indicates that temporal and spatial variation in stickleback predation effects may be important in shaping the recruitment success of different populations of pike. Potentially, these patterns may also have been caused by other predatory species than stickleback, yet our survey fishing efforts and daily observations suggested that additional putative fish-, reptile- and avian predators were in very low abundances, and therefore unlikely to have contributed to our results.

Mortality during early life stages is an important bottleneck that may structure adult abundances (Sogard, 1997). To accurately test whether the increased juvenile mortality in pike caused by sticklebacks represents a population-level bottleneck requires experimental manipulation and control of alternative sources of mortality which our study approach do not comprise. Nonetheless, the magnitude of stickleback predation effects on survival of pike juvenile cohorts across our populations corresponds to adult abundances estimated in previous studies (Larsson et al., 2015; Tibblin, Forsman et al., 2016) and indicates that stickleback predation represents a population-level bottleneck. The estimates of census population sizes (Table 1) are higher in population O where a substantial fraction of the emigrating cohort leaves the wetland before stickleback arrival than in the other populations where sticklebacks were present at the onset of pike juvenile emigration. This suggests that migratory timing is crucial for survival and recruitment success (Dingle, 1996; Quinn, Unwin, & Kinnison, 2000). Previous research has revealed that migratory timing in pike varies both among individuals and populations and that it is associated with fitness (Larsson et al., 2015; Tibblin, Forsman et al., 2016). In this context, our present results indicate that stickleback predation may be an important selective driver shaping the timing of migratory events such that it should favour early breeding and subsequent emigration prior to stickleback arrival (Bergström et al., 2015).

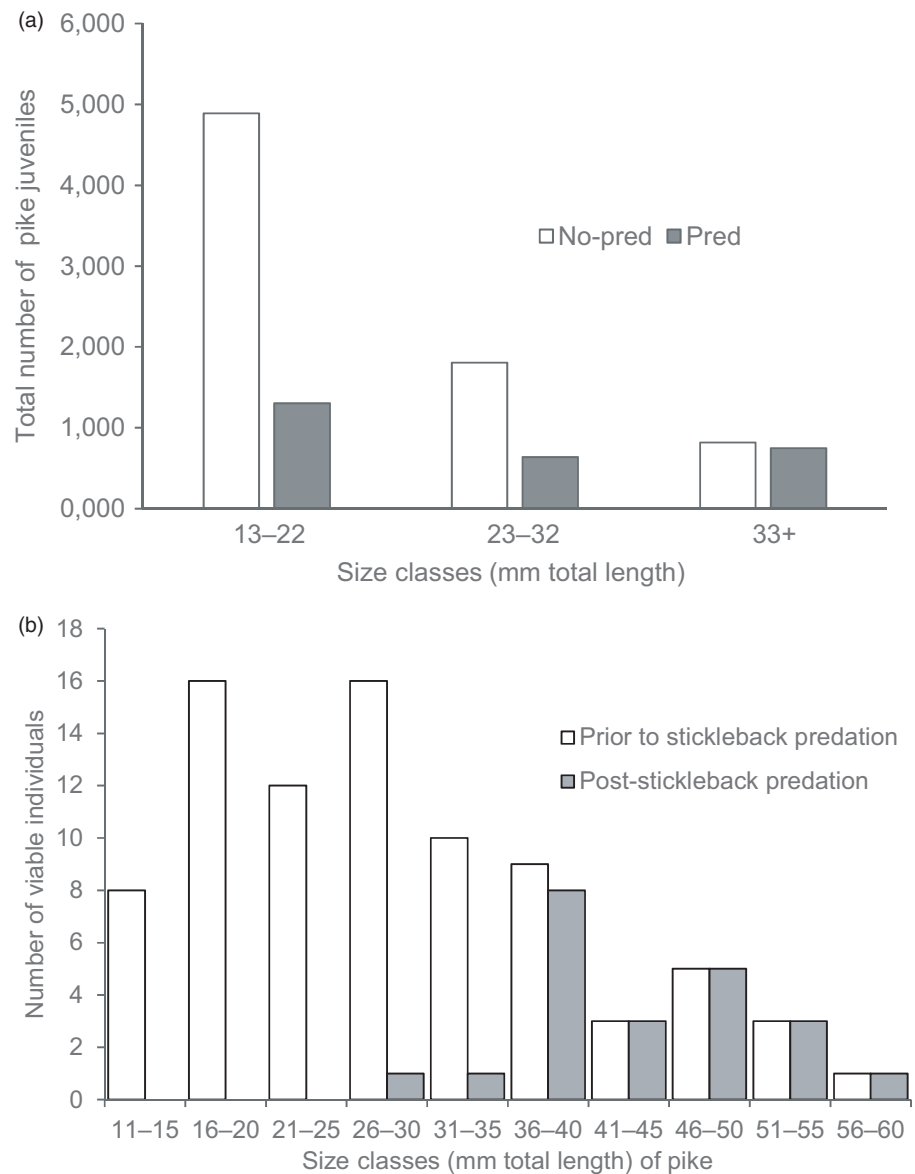


FIGURE 4 Size-selective predation by sticklebacks on pike juveniles. (a) Stickleback predation effects on pike abundances (n_{tot} : no-pred = 7,512, pred = 2,688) of three size classes of wild-captured emigrating pike juveniles representing four populations (K, D, L and O) during 2014. (b) Effects on survival and size distribution of pike juveniles exposed to stickleback predation in the laboratory experiment ($n = 84$). The shaded bars represent juveniles exposed to stickleback predation, while the non-filled bars represent data for non-exposed juveniles

It is well-established that body size and growth rates are key life-history traits influencing mortality (Persson, Andersson, Wahlström, & Eklöv, 1996; Roff, 1992). Our findings of size-selective predation on pike juveniles together with the diet analysis and established gape-limitations of sticklebacks suggest that it is crucial for pike to outgrow the stickleback predation window prior to emigration, a pattern that conforms the bigger-the-better hypothesis (Sogard, 1997). In regard to the role reversal of pike, our data also suggest that reaching the critical size of about 80 mm will allow pike juveniles to start taking advantage of the significant resource constituted by high stickleback densities, which further manifest the importance of fast juvenile growth. Earlier investigations in our study system revealed considerable differences in growth rates of early life stages attributed to adaptive genetic variation, representing local adaptations to population-specific recruitment areas (Berggren et al., 2016; Sunde et al., 2018; Tibblin et al., 2015; Tibblin, Berggren et al., 2016). The effects of size-selective stickleback predation may thus alter

life-history strategies of pike populations and potentially influence population turnover rates, age at maturity and growth trajectories (Reznick, Bryga, & Endler, 1990; Tibblin et al., 2015).

Our results indicate that stickleback predation is an important force in shaping the recruitment success of pike. This is corroborated by, and adds an explanation to, previous findings of a negative relationship between abundances of pike and sticklebacks along the Swedish Baltic coast previously attributed primarily to resource competition (Bergström et al., 2015; Ljunggren et al., 2010). Moreover, the effect sizes of stickleback predation that we show in this paper are likely conservative since predation may also be present in the coastal habitat (Nilsson, 2006). Recent investigations have also uncovered a similar negative relationship in abundances between sticklebacks and perch (*Perca fluviatilis*), another coastal top predator that have experienced a similar decline in abundances as in pike (Bergström et al., 2016). This adds to the generality of our findings and suggests that stickleback predation is an important mechanism

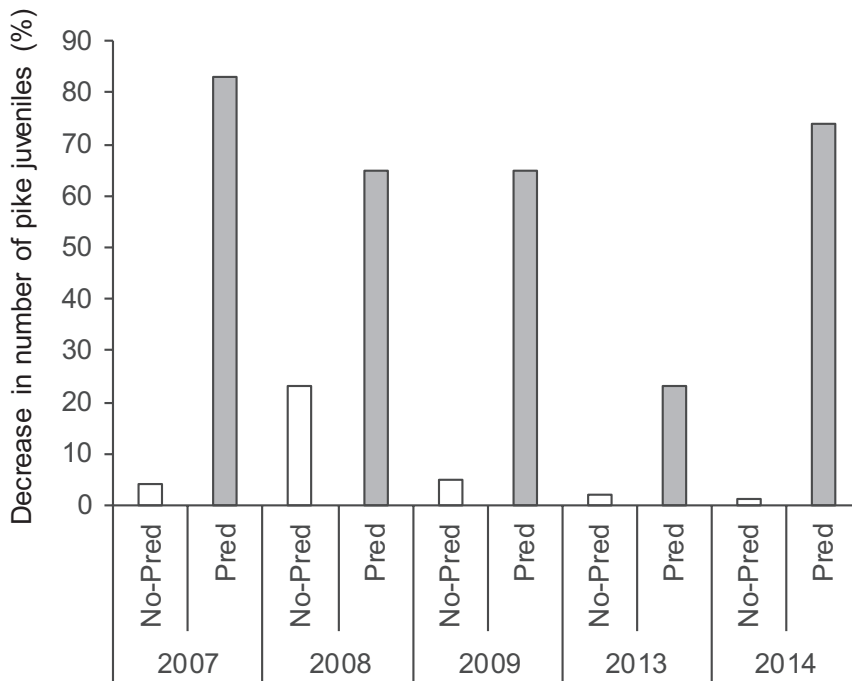


FIGURE 5 Percentage decrease in numbers of emigrating pike juveniles in population O the day after stickleback arrival in 2007–2009, 2013 and 2014. Two sites with different predator regimes: No-Pred = unreachable for sticklebacks; Pred = sticklebacks present

Ability to prey upon sticklebacks

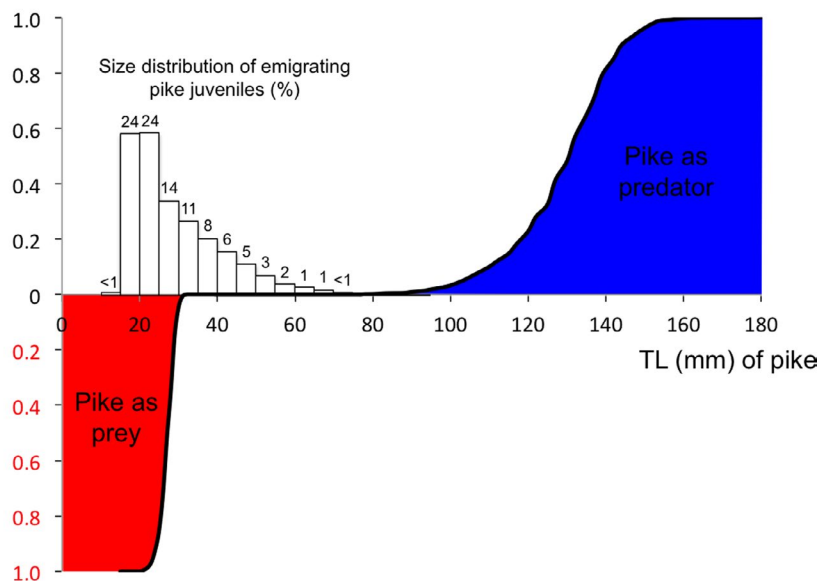


FIGURE 6 Reversal of predator–prey roles between pike and stickleback. The solid black line predicts the proportion of the size distribution of adult sticklebacks in our study area that can either prey on (red; susceptibility) or be preyed upon by (blue; ability) pike of different sizes estimated by gape-limitations of both species, respectively. The bar diagram represents the size distribution of pike juveniles emigrating from four populations ($n = 2,422$) prior to exposure to stickleback predation. The numbers above each bar denote the proportion (%) of specific size classes

Susceptibility to stickleback predation

for structuring the abundances of coastal top predators, and that it potentially impairs the recovery of weakened populations.

Our findings add important insights on the mechanistic detail of how predator–prey role reversal may hamper the recovery of top predators and ultimately prevent a return to a top-down structured ecosystem despite conservation actions aiding the top predator, which may have profound impacts on the ecosystem functioning including accelerating eutrophication effects and loss of biodiversity (Byström et al., 2015; Donadi et al., 2017; Eriksson et al., 2009; Ritchie & Johnson, 2009). Mitigating the effects of the reversal in predator–prey roles on ecosystems in general, and top predator

populations in particular, is complex due to multiple reasons facilitating the exponential increase in mesopredators (Bergström et al., 2015; Prugh et al., 2009; Ritchie & Johnson, 2009). This includes climate change, eutrophication and predator release (Candolin, Engstroem-Öst, & Salesto, 2008; Mackenzie, Gislason, Möllmann, & Köster, 2007; Prugh et al., 2009; Ritchie & Johnson, 2009; Sieben et al., 2011). Adding to the complexity, mesopredator release commonly involves declines in multiple top predatory species that may be present simultaneously or during specific stages of the mesopredator life cycle (Prugh et al., 2009; Ritchie & Johnson, 2009; Stier et al., 2016). For instance, the predator release of Baltic Sea sticklebacks

may also be associated with the collapse of the offshore top predators cod (*Gadus morhua*) and salmon (*Salmo salar*) that will drastically increase stickleback survival during its pelagic life stage (Casini et al., 2009). Collectively, this suggests that to manage the challenges of reversal in predator–prey roles and successfully aid the recovery of top predators require ecosystem-based management, for instance culling of mesopredators and reintroduction of top predators, where the complexity of different habitats, life cycles, species interactions and their connections are taken into account (Blenckner, Osterblom, Larsson, Andersson, & Elmgren, 2015; Persson et al., 2007; Ritchie & Johnson, 2009; Samhouri et al., 2017; Stier et al., 2016).

To conclude, our study suggests that the mesopredatory stickleback predation is a temporally and spatially consistent driver in shaping abundances and size distributions of the top predatory pike. These findings represent correlative evidence that mesopredator behaviour reduces recruitment of their top predator. This emphasizes predator–prey role reversal as a process with potentially major ecological and evolutionary consequences, including impaired ability to recover for weakened populations, altered life-history strategies and ecosystems locked in alternative stable states (Barkai & McQuaid, 1988; Fauchald, 2010; Sánchez-Garduño et al., 2014; Walters & Kitchell, 2001). During times when a large proportion of the fish populations are under intense anthropogenic pressure (Daskalov, Grishin, Rodionov, & Mihneva, 2007; Hutchings, 2015; Jackson et al., 2001) and in urgent need of conservation, it is imperative to regard the consequences of predator–prey role reversal in future management actions.

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AUTHORS' CONTRIBUTIONS

J.N. conceived the study and designed the research together with P.T. and H.F. J.N. and H.F. performed field and experimental studies. P.T. analysed data and wrote the first draft, and all authors contributed to revisions and approved the submitted manuscript.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.k3583p1> (Nilsson, Flink, & Tibblin, 2019).

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