Recruitment failure of coastal predatory fish in the Baltic Sea coincident with an offshore ecosystem regime shift

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The dominant coastal predatory fish in the southwestern Baltic Sea, perch and pike, have decreased markedly in abundance during the past decade. An investigation into their recruitment at 135 coastal sites showed that both species suffered from recruitment failures, mainly in open coastal areas. A detailed study of 15 sites showed that areas with recruitment problems were also notable for mortality of early-stage larvae at the onset of exogenous food-intake. At those sites, zooplankton abundance predicted 83 and 34% of the variation in young of the year perch and pike, respectively, suggesting that the declines were caused by recruitment failure attributable to zooplankton food limitation. Incidences of recruitment failure match in time an offshore trophic cascade that generated massive increases in planktivorous sprat and decreases in zooplankton biomass in the early 1990s. Therefore, sprat biomass explained 53% of the variation in perch recruitment from 1994 to 2007 at an open coastal site, where three-spined stickleback also increased exponentially after 2002. The results indicate that the dramatic change in the offshore ecosystem may have propagated to the coast causing declines of the dominating coastal predators perch and pike followed by an increase in the abundance of small-bodied fish.

Keywords: coastal fish recruitment, offshore–coastal coupling, perch, pike, stock declines, zooplankton diet.

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Introduction

Large predatory fish have declined on a global scale, generating cascading ecosystem effects in coastal and pelagic marine communities (Estes *et al*., 1998; Frank *et al*., 2005; Halpern *et al*., 2006; Daskalov *et al*., 2007). In the Baltic Sea, the catches of two dominating coastal predators, northern pike (*Esox lucius*) and Eurasian perch (*Perca fluviatilis*), decreased by 80% along the west coast of the main basin (the Baltic proper) in the 1990s (Figures 1 and 2; Supplementary material). Similar stock declines have been reported from the eastern and northern parts of the Baltic proper, although no declines have been reported from the Bothnian Sea (Ådjers *et al*., 2006). At present, coastal communities in the Baltic proper that show depleted populations of perch and pike instead contain abnormally high abundance of small-bodied facultative planktivores, notably the three-spined stickleback (*Gasterosteus aculeatus*; Eriksson *et al*., 2009). A regional study in the southwestern Baltic Sea suggests that the decline in pike and perch may have been caused by recruitment failure (Nilsson *et al*., 2004).

Fish recruitment processes are sensitive to external forces, and even small variations in the environment may produce large variations in year-class strength (Hjort, 1914). Early-stage larvae are known to be sensitive to variations, and favourable conditions at the onset of feeding have been advanced as a main driver of fish recruitment dynamics (Cushing, 1975). The larvae of top predatory fish must pass a number of ontogenetic diet shifts and have therefore been suggested to be particularly sensitive during their early life to competition for common zooplankton resources with specialized planktivorous species, as well as to predation (Persson and Greenberg, 1990). In Eurasian perch, cannibalism by older fish and strong food competition among juveniles limit year-class strength (Persson *et al*., 2000). Many fish exploit temporal pulses in food availability or avoid predation by spawning in habitats that provide shelter or during specific parts of the season (Urho, 2002). Therefore, biological processes and habitat quality have a great influence on the recruitment of fish, but are often strongly integrated with environmental factors (Alheit and Niquen, 2004; Leggett and Frank, 2008).

In response to reports on declining stocks of perch and pike along the coast of the Baltic proper, we conducted an extensive field study covering large parts of the north coast (ca. 1200 km) of the Baltic Sea. The objectives were (i) to describe the geographic patterns of recruitment of coastal predatory fish, (ii) to identify the

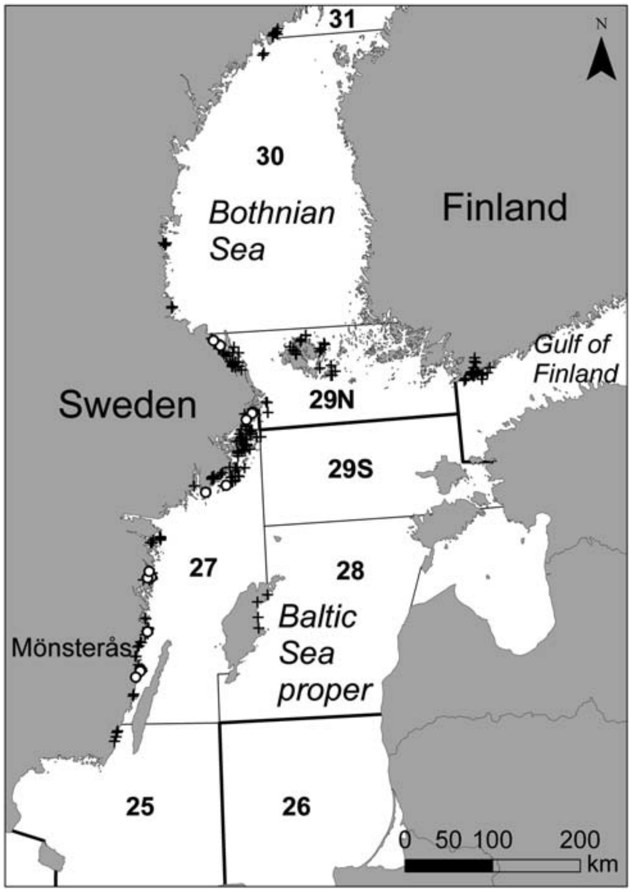

Figure 1. Map of the Baltic Sea showing sites sampled for juvenile fish in Sweden and Finland between 1996 and 2003 (plus signs). Open circles show 15 sites studied in detail in 2003 on the Swedish coast. The Bothnian Sea covers ICES Areas 29 N and 30, the Baltic Sea proper includes ICES Areas 25–29S.

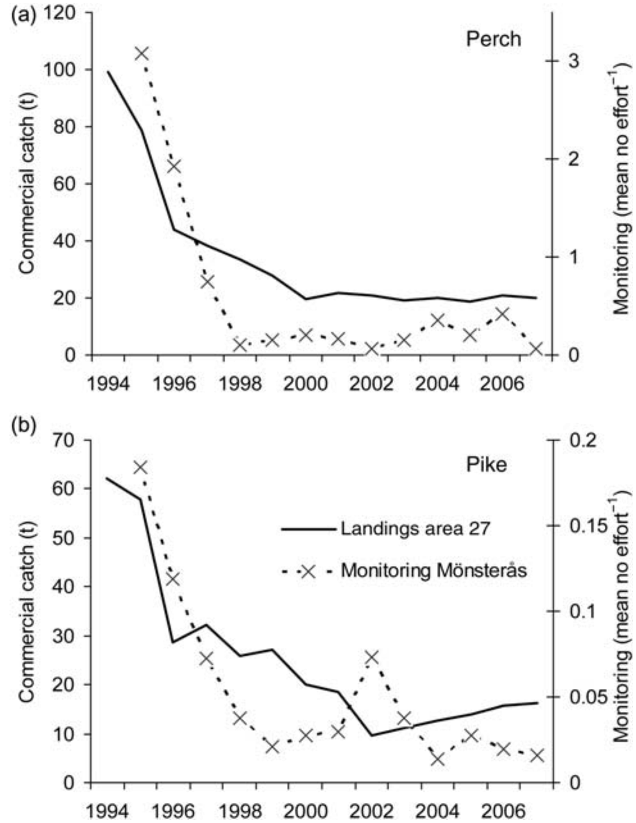

Figure 2. Trends in (a) perch and (b) pike catches and abundance trends in the Baltic proper. Commercial catches are those from ICES Subdivision 27, which cover most of the west coast of the Baltic proper (solid line), and the monitoring data (cpue, shown as mean numbers per unit of effort) are from Mönsterås on the southeast coast of Sweden (crosses and dotted lines, respectively). The monitoring data only include fish >3 years old as determined from otoliths to match the composition of the commercial catch. Catch data are based on information from the Swedish Board of Fisheries (Anon., 2008). For locations, see Figure 1.

most critical life stages for recruitment, and (iii) to correlate recruitment with potential regulatory factors to find a plausible mechanism for the decline. We identified two large-scale processes that may have had negative effects on the recruitment of perch and pike; changes in recruitment habitats caused by a combination of intensified coastal exploitation and eutrophication, which both impact the vegetation used as nursery grounds (Sandström *et al.*, 2005), and changes in foodweb composition in the offshore ecosystem (Casini *et al.*, 2008; Möllmann *et al.*, 2008). In the late 1980s, before the decline in perch and pike, there was a fishery- and climate-induced trophic cascade in the offshore ecosystem of the Baltic proper. Instead of a foodweb dominated by cod (*Gadus morhua*) as top predator, the planktivorous mesopredator sprat (*Sprattus sprattus*) became dominant, resulting in decreased levels of zooplankton (Casini *et al.*, 2008). Our hypothesis is that perch and pike suffer from recruitment failures in areas with documented stock declines and that (i) deteriorating habitat quality (vegetation) in nursery areas, (ii) decreased abundance of zooplankton for juvenile fish to eat, and/or (iii) increased predation on fish eggs and larvae from the increased abundances of mesopredatory fish may have contributed to the decline in pike and perch recruitment.

Methods

Spatial patterns in recruitment

The present status of perch and pike was investigated by analysing the spatial distribution of young of the year (YOY) in coastal areas in the western and northern Baltic Sea (Figure 1). These parts of the brackish Baltic Sea have a nearshore salinity range of 3–7 psu and include parts of two main basins, the Bothnian Sea and the Baltic proper. The coastal regions studied are not tidal and have a complex morphometry, with many islands and inlets of varying size. The shallow coastal areas where perch and pike normally spawn are generally <3 m deep, sheltered, and characterized by a mix of soft-sediment substrata dominated by submerged phanerogams and harder substrata dominated by subtidal bladderwrack (*Fucus vesiculosus*; Sandström *et al.*, 2005). YOY fish were monitored from July to early September by point abundance sampling, using small detonations that stun small fish within an area of ca. 15 m^2 (the method is evaluated and described in more detail in the Supplementary material and by Snickars *et al.*, 2007). Data were collected mainly in 2003 ($n = 72$ sites), but to enhance the spatial analyses and to avoid biases attributable to temporal variation in recruitment, data collected with similar methods from 1996 to 2002 by the Swedish Board of Fisheries were also analysed ($n = 63$ sites). We consider the abundance of YOY in late summer to be a relevant measure of recruitment. Variations in year-class strength are considered to be set at that point (Kjellman *et al.*, 2003), when recruits have passed through the most critical bottlenecks. Sites were chosen by stratified randomization along wave-exposure gradients (Bekkby and Isaeus, 2008) to represent larger regions of the coast with varying catch development of perch and pike. As we suspected reproductive disturbance related to processes in the open sea, the study sites were divided into sheltered or open sites according to their water exchange with the open sea (Schernewski and Wielgat, 2004); sheltered sites had estimated water residence times of >7 d, and open sites residence times of <7 d.

We tested differences between sea basin (Bothnian Sea or Baltic proper) and openess (sheltered or open coastal site) with a two-way ANOVA together with Tukey's *post hoc* test (Statistica 8.0, General Linear Model Module). Assumptions of heterogeneous variance were tested using Cochran's test. We also tested whether there was an association between the presence of YOY (recruitment registered or not) and the interaction between sea basin and openness using a simple Chi-squared goodness-of-fit test.

Critical life stages

In 2003, 15 sites were selected for a detailed study of critical life stages and the potential mechanisms regulating recruitment (Figure 1). Identification of critical life stages was conducted by sampling the eggs, various stages of larvae, and metamorphosed YOY perch (sampled by detonation—see Supplementary material). Mapping of perch egg strands was conducted three times from late April to mid-June, at intervals of 14–20 d. The surveys were conducted by snorkelling along transect lines covering the sites (length 20–480 m, 4–8 lines per site depending on area; for detail of the transect grid and the variables sampled, see the Supplementary material and Eriksson *et al.*, 2009). Pelagic fish larvae were sampled with a gulf Olympia sampler (mouth diameter 0.38 m), trawled from a boat along the transect lines twice from mid-May to mid-June at intervals of 14–20 d. As the variances were strongly heterogeneous, we tested differences between areas using the non-parametric Kruskal–Wallis rank-sum test.

Variables potentially determining recruitment

In the 15 intensively studied sites in 2003, we also sampled the submerged vegetation (total cover, composition, and abundance of filamentous algae), small-bodied fish, zooplankton, temperature, salinity, and turbidity to detect potential regulating factors of perch and pike recruitment. To test correlations between habitat quality and recruitment, the vegetation was surveyed along the transect grid in spring (April to early June). The vegetation composition was included in the analysis as the first and second axis scores from a PCA (principal component analysis) ordination based on mean coverage of all macrophytic species at each site (see the Supplementary material for detailed results of the ordination). To evaluate the food availability for fish larvae, the zooplankton was also sampled along the whole transect grid using a 60-μm plankton net. To estimate potential predation on fish recruits, the fish community was sampled by beach-seine in late May and June. The survey method provided an estimate of the abundance of fish in a size range making them potential predators of zooplankton, fish eggs, and small larvae during late spring and early summer (Persson *et al.*, 2000; Nilsson, 2006). The beach-seine was pulled towards the shore at four randomly allocated locations per site. The beach-seine itself was 2 m deep with arms 10 m long, and mesh sizes of 5 mm in the arms and 2 mm in the codend. Water temperature was measured at 2-h intervals 1 m deep in the central part of each of the selected 15 sites, using automatic recorders (INTAB© TinyTag Temp). Temperature was included in the analyses as the number of day-degrees >10°C between mid-May and the end of July (days × the number of degrees >10°), because this temperature has been shown previously to explain variations in the year-class strength of perch (Kjellman *et al.*, 2003), and because temperatures <10°C cause increased mortality of fish larvae (Hokansson, 1977). At the same position, we measured salinity in spring and summer and extracted triplicate water samples for analysis of turbidity with a formacin-calibrated turbidimeter (HACH 2100P©). Depth was measured in each vegetation square along the transect grid.

We tested the factors that best explained the spatial distribution of YOY perch and pike using general linear regression. As the number of determining factors with possible interactions was much larger than the number of replicate sites, variables were included into the regression model using a forward stepwise selection procedure (Statistica 8.0, General Regression Module). We allowed variables to be in the model if they had a *p*-value of <0.1. Variables that did not meet the assumption of normally distributed and homogeneous residuals were $\log_{10}$-transformed. Spatial autocorrelation was tested on the Pearson residuals from the best linear models for perch and pike, using spline correlograms with 95% pointwise bootstrap confidence intervals (Zuur *et al.*, 2010). Mean autocorrelation remained close to zero at all lag distances, demonstrating that there was no spatial structure left in the residuals.

Temporal trends

We analysed the potential causes of temporal trends in recruitment using time-series of perch taken from a permanent gillnet monitoring programme in Mönsterås, the site of the Swedish coastal monitoring programme that best represents open coastal sites in the Baltic proper. Strong declines in both perch and pike populations have been documented there by local fishers and authorities (Figures 1 and 2; Supplementary material; Nilsson *et al.*, 2004). At Mönsterås, we also had access to *in situ* monitoring data on YOY abundance of perch in 1989 and 1990, and most years from 1997 to 2007 (Swedish Board of Fisheries).

The gillnet monitoring method is designed to sample perch and has varied between 420 and 576 gillnet operations (nets × nights) per year between 1995 and 2008 (Ådjers *et al.*, 2006). A subsample of the perch catches has been sampled for age using operculae or otoliths, allowing us to calculate variations in recruitment success from year-class strength. Three-year-old perch were best represented in the gear, so we used variations in catch per unit effort (cpue) of 3-year-old fish as a relative measure of recruitment.

We tested which of the factors best explained the temporal changes in the recruitment index (cpue index) of perch at Mönsterås from 1992 to 2005, including time-series of temperature, potential competitors for zooplankton (sprat, herring, and stickleback biomass), a proxy for zooplankton quantity (sprat and herring condition; Casini *et al.*, 2006), potential predators on eggs (stickleback biomass), and potential cannibalism on YOY (perch 1–2 years old; Persson *et al.*, 2000). Temperature sums (the number of day-degrees >10°C × the number of degrees >10°C between mid-May and the end of July) were calculated from daily temperature data collected in a coastal area north of Kalmar sound, ca. 100 km north of Mönsterås. The biomasses of sprat, herring (*Clupea harengus*), and stickleback were extracted from the Baltic International Acoustic Surveys (BIAS) database for subdivision 27, which covers the area outside Mönsterås (for more information on BIAS, see the Supplementary material and ICES, 2008). At present, there are no available zooplankton time-series from the area studied. However, growth and condition of sprat in the Baltic Sea is density-dependent and mediated by competition for the zooplankton on which they feed (Casini *et al*., 2006). As an indication of feeding conditions determined by zooplankton quantity, we therefore calculated the body condition of herring and sprat according to the method described in Casini *et al*. (2006). The relative abundance of perch 1–2 years old was also calculated from the year-class strength of 3-year-old perch, because 1–2-year olds were poorly sampled by the gillnets.

We selected the best subset of explanatory variables for the time-series of perch recruitment (1992–2005) using Mallow's C_p, including all factorial interactions of all variables (Quinn and Keough, 2002; Statistica 8.0, General Regression Module). Model selection was also tested using Akaike's information criterion (AIC), including all interactions to the second degree (Statistica 8.0, Generalised Linear Models Module). For all variables, we tested the assumptions of normal and homogeneous residuals. In all analyses, the cpue index for perch recruitment was square-root transformed before model-fitting to normalize the distribution. The autocorrelation function (Statistica 8.0) evidenced a slight autocorrelation at the second lag for the time-series of stickleback, but no significant autocorrelation (lags 1–5) for any other time-series variables used in the analyses. We therefore ran the analyses assuming independence.

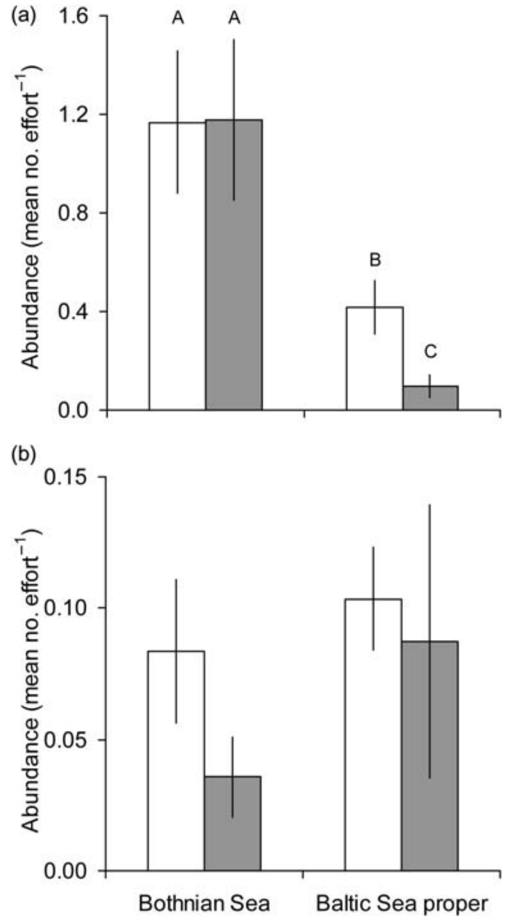

Figure 3. Cpue (expressed as the mean numbers per unit of effort) of (a) YOY perch, and (b) YOY pike, in sheltered (white bars) and open areas (grey bars) in the Bothnian Sea and Baltic Sea proper. Data are based on surveys from 1996 to 2003. Error bars show +1 s.d. Different letters above the bars denote significant differences ($p < 0.05$) based on Tukey's *post hoc* test; A (sheltered and open areas in the Bothnian Sea) shows a significantly higher mean catch than B (sheltered areas in the Baltic Sea, $p = 0.003$) and C (open areas in the Baltic Sea, $p < 0.001$), and B shows a significantly higher mean catch than C ($p = 0.0015$). No significant pairwise differences were found for pike.

Results

Spatial patterns in recruitment

The large-scale field survey from 1996 to 2003 showed that the coastal predators perch and pike suffered from recruitment failure in parts of the Baltic Sea. For perch, the abundance of YOY was three times higher in the Bothnian Sea than in the Baltic proper. Moreover, in the Baltic proper, open sites had significantly fewer YOY perch than sheltered sites [significant interaction effect between sea basin (Bothnian Sea or Baltic proper) and openness (sheltered or open coastal site): $F_{1,131} = 4.43$, $p = 0.037$; Figure 3a]. For pike, the abundance of YOY was generally lower in open than in sheltered sites, but there were no significant differences between the Bothnian Sea and the Baltic proper (significant main effect of site openness only: $F_{1,131} = 5.34$, $p = 0.022$; Figure 3b).

Subdivision of the data into sites with total absence of YOY perch and pike and sites with YOY revealed a distinct geographic pattern with non-functional recruitment mainly in open areas in the Baltic proper. For perch, 80% of the sites in open areas of the Baltic proper lacked YOY fish, whereas the corresponding number was 20–30% for the Bothnian Sea and the sheltered sites in the Baltic proper (significant association χ^2 test: d.f. = 1, $\chi^2 = 68.2$, $p < 0.01$; Figure 4a). For pike, the pattern was less clear, but the open sites in the Baltic proper still showed the highest degree of the absence of YOY (significant association χ^2 test: d.f. = 3, $\chi^2 = 14.3$, $p < 0.01$; Figure 4b). Therefore, recruitment of perch was clearly best in the Bothnian Sea and in sheltered areas in the Baltic proper. For pike, YOY were generally more abundant in sheltered archipelagos, regardless of the sea basin. In summary, therefore, the absence of YOY of coastal predatory fish was mainly associated with areas with rapid water exchange with the open Baltic proper.

Critical life stages

An analysis of perch survival during their first summer in 2003 indicated that lower recruitment in the open coastal areas of the Baltic proper was attributable to increased mortality of the larvae. The subset of 15 sites selected for more-detailed studies included only three sites from the Bothnian Sea. Those sites were pooled and compared with the sheltered and open sites of the Baltic proper. The abundance of perch eggs did not differ between the regions (the Kruskal–Wallis rank-sum test: $H_{1,16} = 0.24$, $p = 0.88$), but the abundance of larvae and juveniles at the open coastal sites in the Baltic proper was lower than

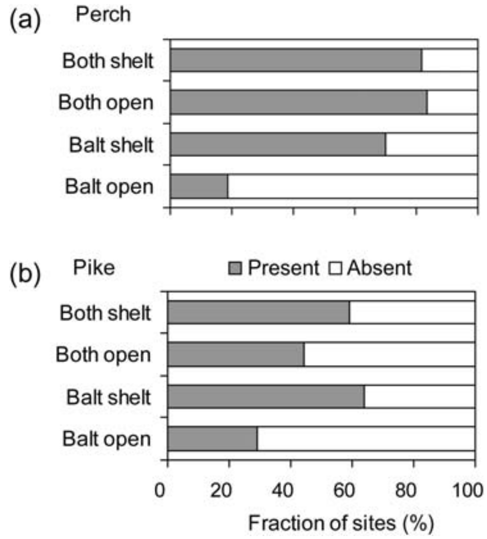

Figure 4. Presence/absence patterns of (a) perch and (b) pike in sheltered (shelt) and open coastal areas of the Bothnian Sea (Both) and Baltic Sea proper (Balt). Grey bars show the percentage of sites with YOY perch or pike present in the samples, and white bars show the percentage of sites with YOY perch or pike absent from the samples, i.e. sites with no recruitment registered. Data are based on surveys from 1996 to 2003.

at the sheltered sites in the Baltic proper and Bothnian Sea (Kruskal–Wallis rank-sum test: weak trend for larvae, $H_{1,16} = 4.67$, $p = 0.097$; significant difference for YOY, $H_{1,16} = 7.38$, $p = 0.025$; Figure 5a). At the open coastal sites in the Baltic proper, no larvae >7 mm were found (Figure 5b) and that is the size at which perch larvae start exogenous feeding (Treasurer, 1992). Clearly, the perch eggs hatched normally, but the early larvae suffered increased mortality at the onset of feeding.

Variables potentially determining recruitment

Recruitment of perch and pike was best explained by zooplankton abundance in the regression analyses of potential causal factors from the 15 intensively studied sites in 2003. For perch, the forward selection procedure selected zooplankton abundance as the only significant predictor of YOY abundance (log-transformed zooplankton abundance: multiple $r^2 = 0.83$, $F = 64.0$, $p < 0.001$). For pike, zooplankton abundance was the strongest predictor of YOY abundance (partial $r = 0.58$, $p = 0.013$), but vegetation cover was included as a moderate trend (partial $r = 0.39$, $p = 0.073$). The best full model was log-transformed zooplankton abundance + vegetation cover: multiple $r^2 = 0.53$, $F = 6.67$, $p = 0.011$). YOY of both perch and pike showed an initial strong increase with increasing zooplankton density that levelled off at higher zooplankton abundance (Figure 6). Therefore, we conclude that food availability determined by zooplankton abundance was limiting the recruitment of coastal perch and pike in areas with low-to-moderate levels of recruitment in the Baltic Sea.

In 2003, the zooplankton community in the study area was numerically dominated by rotifers, particularly by *Keratella* spp., *Asplanchna* spp., and *Synchaeta* spp., followed by, in order of abundance, copepods of the families Cyclopidae (*Cyclops* spp.), Temoridae (*Eurytemora* spp.), Centropagidae (*Centropages* spp.), and Acartiidae (*Acartia* spp.), and cladocerans. All these zooplankton groups were strongly correlated with the total abundance

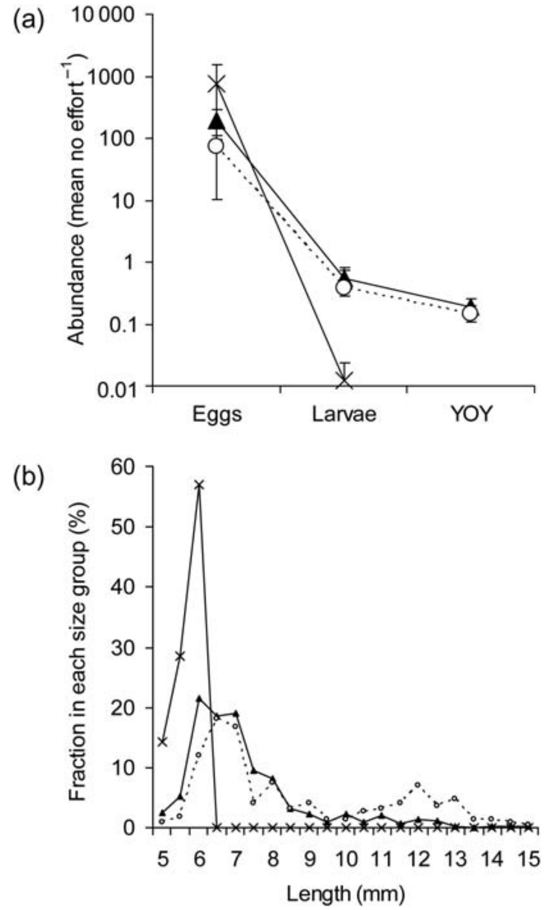

Figure 5. Abundance of different life stages of perch during summer 2003 in the Bothnian Sea (open circles and dotted line), and sheltered (triangles and solid line) and open areas (crosses and solid line) in the Baltic Sea proper. (a) Mean abundance of different life stages, and (b) percentage of the larva samples belonging to different size groups. Error bars in (a) show s.e.

of zooplankton (Pearson's correlation: $n = 16$, $r > 0.80$, $p < 0.001$), making it difficult to distinguish between the effect of the different fractions of the zooplankton community (see Supplementary material). However, the fraction of rotifers increased significantly at low total numbers of zooplankton (Pearson's correlation: $n = 16$, $r = -0.59$, $p < 0.05$).

The assemblage of small-bodied fish, i.e. potential predators on eggs and larvae, consisted almost exclusively of stickleback, whose abundance correlated negatively with the recruitment of both perch and pike (see Supplementary material for the univariate results). However, sticklebacks were poor predictors of YOY abundance. Instead, high abundance of sticklebacks was restricted to sites where the recruitment of piscivorous fish was limited or absent (four sites). YOY perch abundance also correlated positively with water temperature ($r = 0.78$, $p < 0.01$). We know that more fish larvae suffer mortality at low temperature (<10°C; Hokansson, 1977), but temperatures <10°C were not registered during the larval period at any of the sites.

Trends in time

The time-series of *in situ* quantified YOY perch and pike from Mönsterås was incomplete, but it did show the same decreasing

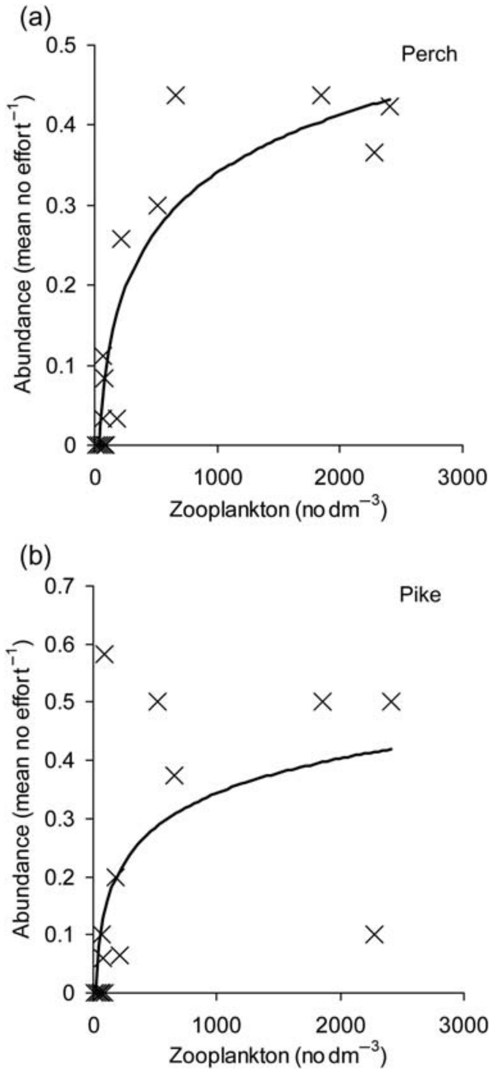

Figure 6. Logarithmic fit between zooplankton abundance (number dm^{-3}) and cpue of (a) YOY perch, and (b) YOY pike at 15 sites sampled during 2003 in the Baltic Sea.

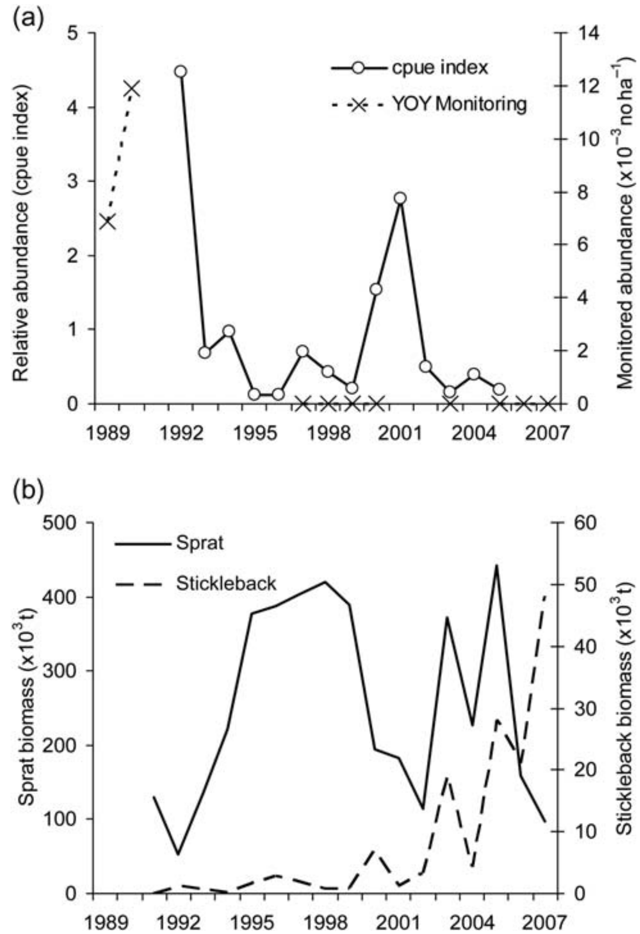

Figure 7. (a) Trends in perch recruitment at Mönsterås, an open coastal site in the Baltic Sea proper. Monitoring data on YOY were collected by detonation (crosses and dotted lines). The recruitment index (cpue index) was back-calculated from the number of 3-year-old perch caught in the permanent gillnet monitoring programme at the site (open circles and solid line). (b) Trends in biomass of sprat (solid line) and stickleback (broken line) in the Baltic Sea proper (ICES Subdivision 27). For locations, see Figure 1.

trend as the calculated recruitment index for perch (Figure 7a). In 1989 and 1990, the cpue of YOY perch and pike was 1.68 ± 0.57 and 0.23 ± 0.05, respectively ($n = 360$; mean $\pm$ s.e.), higher than the catch of YOY in any of the regions in 2003 (Figure 3). From 1997 to 2000, perch suffered a total recruitment failure and the recruitment of pike decreased dramatically ($n = 108$). From 2003 to 2007, we found no YOY of either perch or pike ($n = 75$), indicative of a change from normal to very poor recruitment during the 1990s.

Perch recruitment (cpue index) at Mönsterås for 1992–2005 was best explained by a model including just sprat biomass (Figure 7; see Supplementary material for the full model output). Sprat has dominated the biomass of planktivorous fish in ICES Subdivision 27 in the Baltic proper since the 1990s, but sticklebacks have also increased since 2002 (Figure 7b). Sprat biomass alone explained 53% of the variation in perch recruitment (dependent variable = cpue index (square-root): $r = -0.72$, $F_{12} = 13.48$, $p < 0.01$; see Supplementary material). Sprat and herring condition (ICES Subdivision 27) both correlated strongly with sprat biomass and were therefore not included in model selection (Table 1). No other factor showed a significant correlation with perch recruitment.

Discussion

Our study has demonstrated almost certainly that recruitment failure caused the documented stock declines in perch and pike in the Baltic Sea proper. The large-scale recruitment data distinguished areas with functioning recruitment in the Bothnian Sea and sheltered areas of the Baltic proper from areas with recruitment disturbance along the open coasts of the Baltic proper. Therefore, the declines in commercial catches of perch and pike during the 1990s are limited to the Baltic proper, whereas catches were stable or increasing in the Bothnian Sea (Anon., 2008). The most dramatic decreases in catches of the two species were from open areas, such as Kalmar county, where the catches of pike and perch during recent years are just 1–10% of historical landings from 1891 to 1955 (Alm, 1957; Ojaveer *et al.*, 2007). Although fishing effort has changed since historical records started, available monitoring data of pike from Kalmar show

Table 1. Univariate correlation results for all variables tested in the model of perch recruitment and the condition of clupeid fish through time (1992–2005).

		Perch recruitment		Herring condition		Sprat condition	
Variable	***n***	***r***	***p***	***r***	***p***	***r***	***p***
Herring biomass	14	0.13	0.646	0.22	0.452	0.39	0.172
Sprat biomass	14	**−0.73**	**0.003**	**−0.63**	**0.015**	**−0.81**	**<0.001**
Stickleback biomass	14	−0.31	0.277	0.25	0.383	−0.12	0.679
Temperature SUM	14	0.33	0.252	0.52	0.058	0.44	0.117
Cpue 1 year perch	11	−0.24	0.469	0.55	0.082	0.43	0.186
Cpue 1 + 2 year perch	11	−0.18	0.606	0.4	0.22	0.36	0.272

n, number of replicates; *r*, regression coefficient; *p*, probability. Emboldened values indicate significant correlations.

that average abundance was more than twice as high during the two decades before the registered decline in catch in 1995, compared with subsequently (Supplementary material). The time-series data on YOY abundance from Mönsterås show that recruitment was functioning in the open coastal areas of the Baltic proper in the early 1990s, indicating that the recruitment failure is a recent phenomenon, corresponding in time with the stock declines.

The results also show that spatial and temporal patterns in recruitment are best described by variables related to zooplankton availability. We have identified the early larval stage as the critical period of increasing mortality, approximately at the onset of feeding. YOY perch and pike abundance in late summer 2003 were closely related to zooplankton abundance in spring. In the time-series analysis, recruitment of perch was best predicted by changes in sprat biomass and correlated with changes in sprat condition. Sprat condition is strongly density-dependent and related to feeding competition in the Baltic Sea (Casini *et al*., 2006). This means that an abundance of sprat translates into low zooplankton biomass and poorer body condition of sprat (Casini *et al*., 2006). Time-series of sprat abundance from shallow coastal areas are not available, but sprat is a major zooplanktivore in coastal areas of the Baltic Sea (Rudstam *et al*., 1992; Baumann *et al*., 2006, 2007). Taken together, these results suggest that the large-scale recruitment failures of perch and pike were driven by limited food availability for their larvae, which itself may have been caused by competition with sprat for zooplankton in coastal areas.

The species composition of zooplankton was characteristic of nearshore coastal areas in the Baltic Sea (Rudstam *et al*., 1992). Rotifers dominated the zooplankton by number and are mainly freshwater plankton found in inner bays of the Baltic Sea (especially the genus *Synchaeta*; Rudstam *et al*., 1992). Moreover, the copepod community was dominated by *Cyclops* spp. and *Eurytemora* spp., both of which are common in shallow coastal waters (Rudstam *et al*., 1992), but which differ significantly from offshore communities (see Möllmann *et al*., 2000). This would support the notion that low levels of zooplankton at the coastal sites with recruitment failure of perch and pike were caused by local predation, and not by water exchange with the open Baltic proper.

The growth of larval fish does not depend solely on prey availability, but also on access to prey of high quality. A combination of an abundance of easily accessible small prey at the onset of feeding followed by a pulse of abundant and highly nutritious prey of suitable size appears to be necessary for optimal growth and survival (Ljunggren, 2002b). The preferred prey for larval perch in the size range 6–9 mm are copepod nauplii, and rotifers are selected only when the small copepods and cladocerans are scarce (Ljunggren, 2002a). In our study, the proportion of rotifers increased at low total numbers of zooplankton, which indicates that the quality of the zooplankton as prey decreased along with the decrease in total abundance.

There were still many perch eggs at the open sites in the Baltic proper, though few perch larvae or YOY perch and pike. In the open areas, the width of the egg strands were higher (see Supplementary material), suggesting that the size of spawners was significantly greater (Dubois *et al*., 1996). Perhaps egg production in those areas depends on just a few large females, which indicates that the population would be characterized by low rates of recruitment and either fast-growing or old fish.

Large-scale climate changes, as documented in changed North Atlantic Oscillation (NAO) patterns in the late 1980s, led to documented effects on the North Sea and offshore ecosystem of the Baltic Sea (Alheit *et al*., 2005). However, direct temperature effects cannot explain the declining recruitment of perch and pike, because higher temperature enhances recruitment (Karås, 1996). Lower temperature could therefore potentially decrease recruitment in open compared with sheltered areas, but temperature cannot explain the north–south differences in perch recruitment. Moreover, temperatures increased during the past decade (Alheit *et al*., 2005), and positive climate effects have been documented for local perch stocks in the inner basins of the Baltic Sea (Ådjers *et al*., 2006).

In the central Baltic Sea, the offshore ecosystem has shifted from one dominated by cod to a system dominated by sprat (ICES, 2009). This shift, induced by overfishing and climate-driven processes, has cascaded down the pelagic foodweb (Casini *et al*., 2008; Möllmann *et al*., 2008). In the early 1990s, the summer zooplankton community changed dramatically, with significant decreases in total biomass from >400 to ~ 200 mg m^{-3}. Increased predation by sprat has been identified as the main driving force behind the summer zooplankton decline (Casini *et al*., 2008), and the results here indicate that the increased biomass of sprat may also have impacted the coastal ecosystem, likely through increased predation pressure on coastal zooplankton, leading to recruitment failure of the coastal predators, perch and pike. Trophic cascades across ecosystem borders may have significant effects on the structure of adjacent ecosystems (Knight *et al*., 2005).

Our results also suggest that the cumulative decline in predators in the coastal zone released a second important mesopredator from predation, the three-spined stickleback. Since 2002, well after the declines in perch and pike, the biomass of stickleback in the Baltic proper (ICES Subdivision 27) has been increasing exponentially. Today, large parts of the Baltic coastal are dominated by the stickleback (Eriksson *et al*., 2009). Predation by sticklebacks can deplete zooplankton communities in brackish lagoons at stickleback densities of just 3–6 ind. m^{-2} (Jakobsen *et al.*, 2004); our values of stickleback density for the areas where pike and perch recruitment failed are 10–45 adults m^{-2}. Along with the potential predation on early life stages (Nilsson *et al.*, 2004; Nilsson, 2006) sticklebacks may therefore have the potential to lock the coastal system in an alternative state by depleting the food needed by perch and pike larvae (Bakun and Weeks, 2006; Baumann *et al.*, 2006; Möllmann *et al.*, 2008).

To conclude, our study has indicated a trophic cascade in the pelagic offshore ecosystem that may have propagated also to the coastal ecosystem, causing recruitment failure and declining stocks of coastal predators in the Baltic Sea. We therefore believe that further studies are needed to explore the interactions between the open sea and the coast in the Baltic Sea, preferably with greater focus on zooplankton dynamics. The recruitment failure we have demonstrated may result in consequences well beyond the obvious setbacks of the relatively small coastal fisheries sector that rely on pike and perch. The loss of top-down control in littoral coastal ecosystems is further elaborated in Eriksson *et al.* (2009), where it is shown that the effects of declines in the perch and pike populations cascade down the foodweb to increase the production of benthic algae.

Supplementary material

Supplementary material is available at *ICESJMS* online and is divided into eight sections. Section 1 provides additional support for the declines in pike, Section 2 details the LIMP method, Section 3 the sampling grid in 2003, Section 4 the PCA ordination analyses of vegetation in 2003, Section 5 provides additional information on the BIAS time-series, Section 6 presents additional results from egg-strand sampling, Section 7 gives detailed results of the spatial analysis of recruitment success through univariate correlations, and Section 8 provides detailed results of the temporal analysis of recruitment success, including model output and an extra figure.

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