# Recruitment failure and decreasing catches of perch (*Perca fluviatilis* L.) and pike (*Esox lucius* L.) in the coastal waters of southeast Sweden

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In the early 1990s, commercial and recreational fishermen in the Kalmar Sound of the Baltic Sea reported decreasing stocks of Eurasian perch (*Perca fluviatilis*) and northern pike (*Esox lucius*). Test fishing surveys confirmed regionally declining abundances of both species. Both pike and perch spawning were observed annually, but virtually no young-of-the-year were captured in surveys from 1997–1999. The rapid decrease of the stocks was probably a result of the widespread recruitment failure. Studies of potential causes of the recruitment failure were conducted in 1998–2000. Field experiments excluded suboptimal water quality in brackish water recruitment areas as regulatory factor. Laboratory tests did not indicate reproductive disturbances in parental fish that could be related to chronic toxicity or endocrine disruptions, as hatching success and yolk-sac larvae survival were not negatively affected. Exposure to filamentous algae (*Pilayella* sp.) and diatoms, common in the spawning areas, had only a slight negative effect on pike egg hatchability. Two hypotheses that could not be rejected are food deficiency during the post hatching period and egg predation.

# Introduction

The Baltic fish community is characterized by a mix of marine and limnic, mainly coastal, species. During recent decades several populations have declined or have been afflicted by reproductive disturbances. Changes were attributed to chemical pollution, eutrophication, habitat destruction and overfishing (Hansson and Rudstam 1990, Bonsdorff *et al.* 1997, Lappalainen *et al.* 2000, Sandström and Karås 2002), although the suggested mechanisms are seldom unambigu-

ous (Bengtsson *et al.* 1999, Vallin *et al.* 1999). In addition to these anthropogenic impacts, Baltic fish populations are heavily influenced by large inter- and intrayear variations in temperature, ice-cover and salinity.

In the early 1990s, commercial and recreational fishermen reported low densities of freshwater fish stocks in the Kalmar Sound area at the Swedish coast of the Baltic proper. Formerly common species like Eurasian perch (*Perca fluviatilis* L.) and northern pike (*Esox lucius* L.) had within a few years become rare in catches, and it was considered necessary to document the damage and investigate its causes. Preliminary studies in 1996 (P. Karås unpubl. data) indicated a widespread recruitment deficit, but other factors like the fast-growing cormorant (*Phalacrocorax carbo* L.) population and pulp mill effluent were suggested as likely explanations. A rapid decline of this nature may be the result of either poor recruitment or high adult mortality during subsequent years.

There are several abiotic and biotic factors with the potential to affect critical life history stages in fish. Fertilization and embryo development are influenced by temperature, oxygen and salinity conditions, which may become critical for freshwater species in the Baltic (e.g. Raat 1988, Klinkhardt and Winkler 1989). Reproductive disturbance has been documented in Baltic fish (Bengtsson et al. 1999) in some cases related to toxic or endocrine active substances (Karås et al. 1991). Predation has also been shown to influence the recruitment process of marine fish (e.g. Köster and Möllmann 2000). By mathematic modelling Saulamo et al. (2001) demonstrated that predation from cormorants may contribute significantly to adult perch mortality. Whether this could deplete spawning stocks to critical levels was unclear, but predation at least may delay recoveries once recruitment is restored. The Baltic Sea suffers from large-scale eutrophication, which can influence quality of the spawning and nursery areas by changing physical as well as biotic habitats (Sandström and Karås 2002). An over-growth of filamentous algae, which has increased in some eutrophicated areas of the Baltic, could also be detrimental to fish eggs by producing toxic exudates (Aneer 1987).

The aims of the current study were: (1) to monitor the stocks of perch and pike as a response to observations of declining fisheries and (2) to investigate potential causes to reduced recruitment. The following hypotheses were tested: (1) embryo and larval survival was negatively affected by chronic reproductive disorders in the parents, (2) embryo and larval survival was negatively affected by toxic exposure or suboptimal water quality in the recruitment areas, (3) hatchability of eggs was negatively

affected by exposure to filamentous algae and/or diatoms, and (4) recruitment was affected by food deficiency during the post hatching period.

# Materials and methods

#### Study area

The field studies were carried out from 1995 to 2001 in Kalmar Sound and reference areas (Fig. 1). Data for retrospective comparisons were also available from investigations in 1989-1990 (P. Karås, unpubl. data). The coastal waters in the narrow archipelago of Kalmar Sound are shallow with water depths rarely exceeding 9 m. The salinity in the outer archipelago seldom exceeds 7% and decreases successively toward the mainland and nearby freshwater streams and to a minor extent to the north. The fish community is dominated by stationary limnic species such as perch, pike, roach (Rutilus rutilus L.) and silver bream (Abramis bjoerkna L.). These coastal fish species spawn both in the archipelago and in adjacent freshwaters. Among typically marine species, herring (Clupea harengus L.) and flounder (Platichthys flesus L.) dominate.

#### **Field studies**

#### Test fishing

Monitoring of fish abundance was carried out between the end of July and mid-August in 1995-2001 at four sites in Kalmar Sound and at four reference sites (Fig. 1). The sites in Kalmar Sound were partly influenced by pulp mill effluent. Reference site 4 was monitored only in 1995, 1997 and 2001. Net sets, composed of four 1.8-m-deep and 27-m-long gill nets, with mesh sizes 17, 22, 25 and 30 mm (knot to knot), were used in the test fishing. The fishing was carried out on six nights at fixed stations with one net set per station (Thoresson 1996). The results are expressed as number of individuals per net and night. In 1998, monitoring was expanded to cover additional sites to document the geographical pattern of fish abundance.

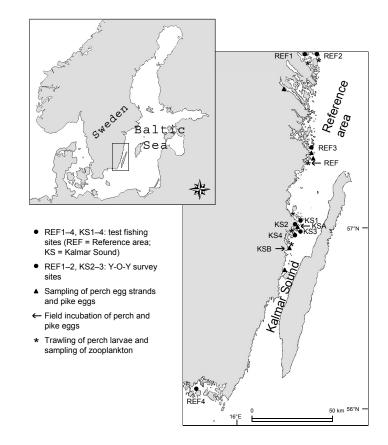


Fig. 1. The study area.

## Y-O-Y (young-of-the-year) fish

The abundance of Y-O-Y was monitored at the end of the first growth season in September 1989-1990 and 1997-1999 at KS2 and KS3 in Kalmar Sound, and in 1990 and 1997-1999 at REF1 and REF2 in the reference area (Fig. 1). The Y-O-Y survey was expanded with additional sites in 1998. Small explosive charges were detonated underwater at approximately half the water depth in shallow (1-3 m) and sheltered areas potentially suitable as nurseries for the targeted fish. Detonations stunned or killed fish within an area of about 50 m<sup>2</sup>. All fish floating to the surface were collected and counted. The aim was to collect fish from fifteen stations at each site. Perch, pike and roach were identified to species, whereas nine-spined stickleback (Pungitius pungitus L.) and three-spined stickleback (Gasterosteus aculeatus L.) were pooled and referred to as sticklebacks. Other species were only occasionally occurring in the catches and were excluded from the study.

#### Perch larvae and zooplankton

Trawling for perch larvae was carried out at three sites in both Kalmar Sound and the reference area where perch spawning was observed (Fig. 1). Sampling was conducted over five consecutive weeks in May and June in 1999 with a Gulf-Olympia sampler to compare the relative abundance and development of perch larvae between the areas (Hudd *et al.* 1983). The sampler was towed through the water column for approximately 5 minutes at a speed of 3 knots. At each site and occasion, ten hauls at 0.5 and 1.0 m depth were made. After preservation in ethanol (70%), the perch larvae were counted and measured in the laboratory. The larval food supply was studied by collecting zooplankton samples in duplicate at each trawling site. Twenty litres of water were pumped up and filtered through a 25  $\mu$ m net. The samples were preserved in ethanol (70%). Zooplankton was counted under a microscope at ×63 magnification and separated into the categories: rotifers, nauplii, copepodites, adult copepods and cladocerans.

#### Hatching success

#### Laboratory and field incubation of eggs

To indicate possible chronic reproductive disorders in the adult perch and pike populations, hatching success and yolk-sac larvae survival were investigated on egg samples from a total of 60 females of each species. Naturally deposited perch egg strands were collected at three sites in Kalmar Sound and at three reference sites between 26 April and 6 May 1999 (Fig. 1). From ten strands at each site, pieces of  $285 \pm 26$  (mean  $\pm$  SD) eggs were cut out and put in plastic jars, and brought to the laboratory within two hours.

Pike were caught at the end of April and beginning of May in 1999 with fyke nets at three sites in Kalmar Sound and at three reference sites (Fig. 1). To prevent spawning in captivity males and females were held in separate tanks. Eggs for artificial fertilization were obtained by stripping the females. The eggs from individual females were placed in dry beakers and droplets of milt from at least two males were added. Eggs and milt were mixed gently for about 20 seconds, and then water with a temperature of 10 °C and salinity of 4‰ was added. During fertilization the eggs were kept completely still for two minutes. To prevent later moulding, the eggs were gently rinsed with brackish water. The eggs from each female were divided into subsamples (509  $\pm$  82 eggs; mean  $\pm$ SD) and kept in plastic jars in a cool box at 10 °C for two hours before transportation.

In an indoor hatchery provided with a flowthrough system of filtered and aerated brackish water, the egg samples were incubated on nets (0.8 mm mesh size for pike and 0.5 mm mesh size for perch) in polyethylene beakers, each with a separate water supply. The salinity and water temperature were maintained at 3.9% $\pm 0.5\%$  and  $10.7 \pm 0.4$  °C, respectively. Light was provided by fluorescent tubes and the light: dark period was 12:12 h. At about three weeks after incubation, thirty larvae from each brood with the yolk resorbed or almost resorbed were preserved in ethanol and their total length subsequently measured. To investigate whether the water quality in the brackish recruitment areas were negatively affecting hatching success or larval survival, artificially fertilized pike eggs and collected perch egg strands from three sites in the reference area, were incubated in one recruitment site in the reference area and two recruitment sites in Kalmar Sound (Fig. 1). At each of the three collecting sites, eggs originated from ten females of both species. These eggs were incubated at each of the three study sites, giving a total of 30 replicates of both species in each study site. The eggs were placed on a net, 0.8 mm for pike and 0.5 mm for perch, in the bottom of PVC pipes randomly mounted in floating net cages. Water temperature varied between a minimum of 7.3-8.9 °C and a maximum of 15.8-17.3 °C, with the lowest values at station KSA and the highest at the reference site. Salinity varied between a minimum of 5.3%-5.5% and a maximum of 5.6%-6.6%, with the lowest values at station REF and the highest at KSB (Fig. 1).

Hatching success was calculated by dividing the number of eggs hatched by the number of eggs incubated. Yolk-sac larvae survival was calculated by dividing the number of surviving larvae by the number of hatched embryos.

#### Exposure to filamentous algae and diatoms

To test if benthic algae common in pike spawning grounds affected the hatchability of pike eggs, a laboratory experiment was conducted in May 2000. At the time of pike embryo development, filamentous brown algae (*Pilayella* sp.) and benthic diatoms (dominated by *Fragilaria*, *Melosira*, *Nitzschia* and *Tabellaria*) were collected. The gathered *Pilayella* sp. was carefully rinsed in filtered seawater to remove attached diatoms. Polyethylene jars (1.5 l) were prepared for four different treatments: (1) *Pilayella* sp., (2) diatoms, (3) *Pilayella* and diatoms, and (4) controls without algae. Each treatment was replicated 12 times. The algae were placed at the bottom of the jar and covered by a net (0.25 mm). Roe from three pike was mixed to minimize inter-female variation, and artificially fertilized as described above. Equal amounts of eggs  $(n = 94 \pm 2, \text{ mean } \pm \text{SE})$  were placed on a net (0.80 mm) 5 cm above the algae. Each jar had an individual water supply from a small Teflon pipe ending at the bottom of the jar, with the water running off through a small hole in the upper part of the jar. To mimic field conditions, the temperature was set at 11 °C at the beginning of the experiment and was progressively raised to 14 °C. The salinity was 6.9‰. The water flow gave a retention time of 2 h. The light:dark period was 16:8 h, which was similar to natural conditions. The quantity of light during the experiment was 900  $\mu$ E s<sup>-1</sup> m<sup>-2</sup>. The jars were continuously aerated, resulting in oxygen values > 80% saturation during the experiment.

#### Statistical analyses

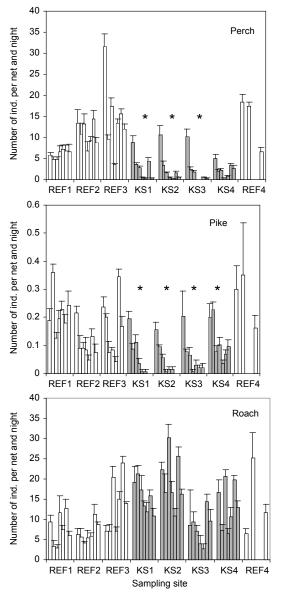
The statistics were calculated using the software Statistica TM 99. When ANOVA or linear regression was used, the homogeneity of variances was tested with Cochran's test. Prior to analyses the data were log transformed except for the data on hatching success and larval survival where percentages were arc sin square root transformed when necessary. In cases where the assumptions of an ANOVA could not be met a non-parametric Mann Whitney U-test or a Kruskal Wallis test was used. In the field incubation experiment repeated measures analyses of variance (RM ANOVA) were used to test differences in hatching success and larval survival between the study sites. RM ANOVA was used; as eggs from the same set of females were used at all three study sites.

## Results

#### **Field studies**

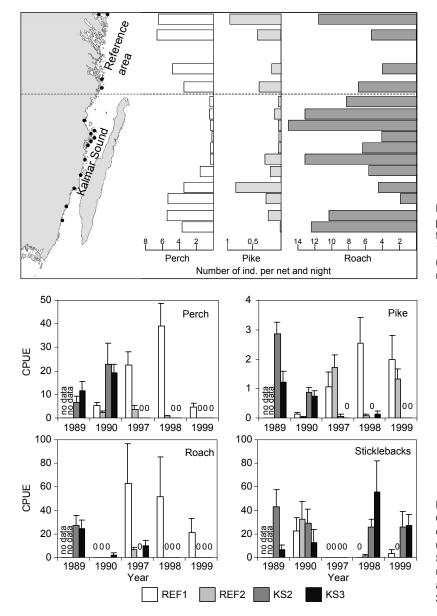
#### Test fishing

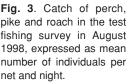
Regression analyses on number of individuals per net and night and year revealed decreasing catches of perch ( $R^2 = 0.35-0.40$ , p < 0.001),



**Fig. 2.** Catch of perch, pike and roach in July–August 1995–2001 (mean + SE, n = 6) at reference sites (REF1–4) and Kalmar Sound sites (KS1–4). \*p < 0.005.

and pike ( $R^2 = 0.18-0.56$ , p < 0.005), at all sites in Kalmar Sound from 1995–2001 (Fig. 2), except for perch at KS4 (p = 0.329), but no significant change in roach catches. No decline was observed in any of the three analysed species at the reference sites (Fig. 2; p > 0.05). A contrast analysis where 1995 was compared with 2001 revealed decreasing catches of perch ranging from 48% to 97% and decreasing catches of pike





**Fig. 4.** Abundance of Y-O-Y fish in September, expressed as catch-perunit-effort (CPUE) (mean + SE, n = 15) at sites in the reference area (REF1–2) and Kalmar Sound (KS2–3).

ranging from 50% to 100% at the four sites in Kalmar Sound (ANOVA planned comparisons: p < 0.05). The expanded test fishing survey in 1998 documented low abundances of perch and pike in the central and northern areas of Kalmar Sound, but no similar pattern was found in the catches of roach (Fig. 3).

## Y-O-Y fish

Perch, sticklebacks and roach dominated the

littoral young fish community at sites KS2 and KS3 in Kalmar Sound in 1989 and 1990 (Fig. 4). Pike were also found at these sites but in lower numbers. In 1990, Y-O-Y perch and pike were more abundant in Kalmar Sound than at the reference sites (Kruskal-Wallis test: p < 0.05), whereas sticklebacks were found in equal amounts (p = 0.43). Very few Y-O-Y perch, pike or roach were observed in Kalmar Sound in 1997–1999. In the reference area, these species always occurred at higher densities in the inner archipelago (REF1 compared with REF2; Mann-

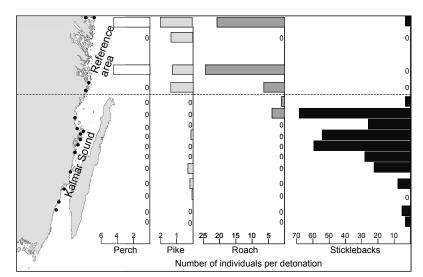
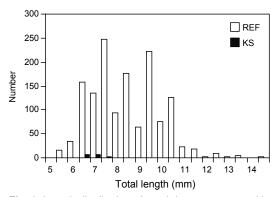


Fig. 5. Abundance of Y-O-Y fish in September 1998, expressed as mean number of individuals per detonation.

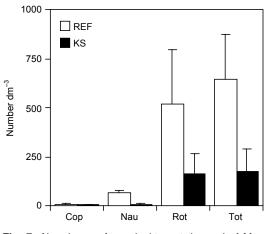


**Fig. 6**. Length distribution of perch larvae, separated in 0.5 mm length groups, caught in May–June 1999 in the reference area (REF) and Kalmar Sound (KS).

Whitney *U*-test: p < 0.05), except for perch and roach in 1997 and pike in 1997 and 1999 (Fig. 4). The expanded survey in 1998 revealed that Y-O-Y perch, roach and pike were common at most reference sites (Fig. 5), but that they were almost totally absent along the mainland coast in Kalmar Sound. Sticklebacks, mainly the threespined stickleback, were abundant, especially in the central and northern parts of the Sound.

#### Perch larvae and zooplankton

The highest catch per unit effort of perch larvae was found in the reference area (Mann-Whitney *U*-test: p < 0.05). The mean number of larvae per haul varied between 0.3 and 12.6 in the reference



**Fig. 7.** Abundance of zooplankton at the end of May 1999 (mean + SD, n = 6) in the reference area (REF) and Kalmar Sound (KS) (Cop = copepodites, Nau = nauplii, Rot = rotifers and Tot = total).

area and between 0 and 0.2 in Kalmar Sound. Length distribution data showed that almost all larvae from the Kalmar Sound were in the yolk sac stage (< 7 mm), while larger and consequently more developed larvae were common in the reference area (Fig. 6).

The zooplankton analyses in 1999 showed that there were differences in abundance and community structure between Kalmar Sound and the reference area (Fig. 7). Thus, the total abundance as well as the abundance of rotifers and nauplii was higher in the reference area (Mann-Whitney *U*-test: p < 0.05). Among rotifers, *Keratella* spp. was most abundant in the

Perch Pike 100 100 80 80 60 60 40 40 20 20 0 0 HS IS HS LS REF KS Perch Pike 100 100 80 80 60 60 40 40 20 20 . 0 0 HS LS HS LS REF KSA KSB

Fig. 8. Hatching success (HS) and larvae survival (LS) of artificially fertilized pike eggs and pieces of naturally deposited perch egg strands collected in the reference area (REF) and Kalmar Sound (KS) and then incubated in the laboratory, May 1999 (mean + SE, n = 30).

Fig. 9. Hatching success (HS) and larvae survival (LS) of artificially fertilized pike eggs and pieces of naturally deposited perch egg strands collected in the reference area and then incubated at one reference site (REF) and at two study sites in Kalmar Sound (KSA and KSB) in May 1999 (mean + SE, n = 30).

reference area, while Synchaeta spp. dominated in Kalmar Sound (Mann-Whitney U-test: p < 0.05). Copepodites were sparse and adult copepods and cladocerans practically were absent in both areas.

## Hatching analyses

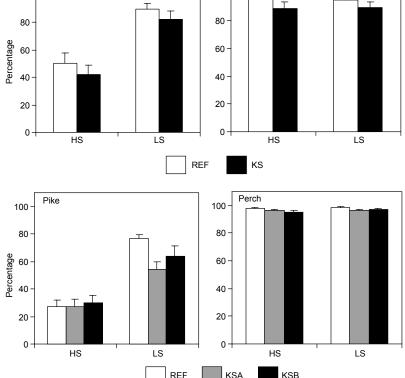
#### Laboratory and field incubation of eggs

There were no differences in hatching success (ANOVA: p = 0.59) or yolk-sac larvae survival (ANOVA: p = 0.59) among samples from Kalmar Sound and the reference area when pike eggs were incubated in the laboratory in 1999 (Fig. 8). About 45% of the eggs hatched and about 85% of the yolk-sac larvae survived. Four of the 60 incubated broods, two from each area, did not hatch at all. In six cases all eggs hatched and larval survival was 100%. About three weeks after incubation when the yolk was

consumed, there were no differences in total length (ANOVA: p = 0.082) between pike larvae from Kalmar Sound  $(13.1 \pm 0.1 \text{ mm})$  and the reference area  $(12.6 \pm 0.2 \text{ mm})$ .

No differences were found in hatching success (ANOVA: p = 0.66) or yolk-sac larvae survival (ANOVA: p = 0.98) among samples from Kalmar Sound and the reference area when perch eggs were incubated in the laboratory in 1999 (Fig. 8). The hatching success and yolk sac larvae survival was about 90%. Of the incubated 60 egg strands, 37 showed 100% hatching while only two had a hatching rate below 50%. No differences existed in the total length of larvae (ANOVA: p = 0.057) comparing Kalmar Sound ( $6.9 \pm 0.1$  mm) and the reference area  $(6.5 \pm 0.1 \text{ mm})$ .

There were no differences between Kalmar Sound and the reference area in either hatching success or yolk-sac larvae survival of perch or pike when eggs from the reference area were incubated in the field in 1999 (Fig. 9; RM ANOVA: p > 0.05).



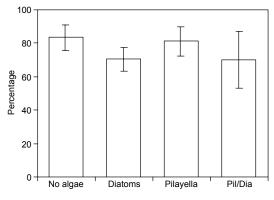
Exposure to filamentous algae and diatoms

The hatching success of pike eggs in 2000 varied between 70%–83% when incubated together with algae in the laboratory. The different algae had only a slight negative effect on hatchability (Fig. 10). Hatching success was lowest in the treatments with algae, but only the diatom treatment differed from the control (Kruskal-Wallis test: p < 0.01).

## Discussion

The abundance of perch and pike in Kalmar Sound decreased substantially since monitoring started in 1995 and in 2001 reached low levels as compared with the references. The depleted stocks were most likely a result of a recruitment failure during subsequent years, indicated by the almost total absence of Y-O-Y fish. At the reference sites, there was no indication of a similar recruitment problem. Consequently, the low production of Y-O-Y in Kalmar Sound seems to be connected to a rapid change in regional environmental conditions as Y-O-Y abundance was considered to be normal in 1989-1990 (Fig. 4). The expanded survey in 1998 showed that the recruitment failure covered the whole mainland coast of the Sound, but the decrease in abundance of older fish was most pronounced in its central and northern parts. The recruitment of roach also was affected. However, no negative development could be seen in the test fishing, which may be explained by a comparatively slow growth and high mean age in this species, delaying the impact of periodic recruitment deficits on the adult population.

Both perch and pike are considered as sedentary species. Mark-recapture experiments with perch show that 80% of the recaptures are made within 10 km from the tagging place (Böhling and Lehtonen 1984). Corresponding figures for pike are 90% within 3 km (Karås and Lehtonen 1993). The closest reference site (REF3) is situated approximately 50 km from the study area and the distance to the northernmost reference sites is more than 100 km. These data imply that we quite reasonably can assume that fish



**Fig. 10.** Hatching success of pike eggs incubated in May 2000 without (no algae) and with algae in three treatments: diatoms, *Pilayella* and *Pilayella*/diatoms (mean  $\pm$  SD, n = 12).

populations in the study area and control area are not affected by each other on any time scale relevant to this study. The distance between the test fishing sites in Kalmar Sound (KS1–4) is approximately 2.5 km. We cannot guarantee that these sites are "closed" and thereby independent replicates. However, this analysis was conducted to detect regional trends in stock development and consequently is not a comment on changes at single sites.

Apparently the structure of the fish community in Kalmar Sound changed dramatically during the 1990s, and at present sticklebacks, mainly the three-spined stickleback, dominate the littoral fish community. Similar changes in the fish community structure, i.e. a decrease in perch and pike and a synchronous dominance of sticklebacks, were described from Puck Bay in the southern Baltic Sea (Sapota and Skóra 1996, Skóra 1996). A high supply of nutrients and also harvesting of perennial macroalgae in the bay resulted in dense growth of filamentous algae and a decrease in the previously dominant submersed vegetation (Pliński and Florczyk 1984). The decrease of perch and pike is attributed to this alteration and deterioration of the spawning and nursery grounds.

When the poor recruitment became obvious in Kalmar Sound in 1997, the causes were not evident. Both perch and pike spawning were observed annually but virtually no Y-O-Y were found later in autumn. Thus, the impact likely

affected life stages during the first summer. Walters and Kitchell (2001) suggested that absent or delayed recovery of large commercial fish, sometimes despite severe restrictions on fishing pressure, could be a result of depensation effects. According to the Y-O-Y investigations in September, the three-spined sticklebacks dominated the small fish community in Kalmar Sound. At present this dominance is even more pronounced in spring and early summer (J. Nilsson unpubl. data), when migrating sticklebacks return from their winter feeding areas (see e.g. Sundell 1994, Sapota and Skóra 1996, Ziliukas et al. 1998). Data on stickleback abundance do not confirm an increase at the two sites in Kalmar Sound when the period 1989-1990 is compared with 1998-1999. However, with the current low perch and pike stocks, egg consumption by sticklebacks or other predators may negatively affect recruitment. Observations in spawning grounds in Kalmar Sound indicated that aggregating sticklebacks ate many eggs (J. Nilsson unpubl. data).

Predation by fish-eating birds is also a possible explanation for the stock decline. Large colonies of nesting cormorants are found in central and southern Kalmar Sound. An exponential increase in nesting birds took place in the late 1980s and early 1990s. Thereafter the population varied between 6000 and 8000 nesting pairs, by far the highest density in Sweden (Engström 2001). A predation model for perch indicates that cormorant predation could have a strong impact on perch population size at current bird densities in Kalmar Sound (Saulamo et al. 2000). However, cormorants prefer perch of a larger size than Y-O-Y, and an impact on recruitment is only possible if they have depleted the spawning stocks below critical levels.

There was no indication that suboptimal temperatures or salinities could explain the poor recruitment, as no negative effects on hatching success or larval survival were observed in the field tests. Both pike and perch are freshwater species, and their reproduction in the brackish water in the southern Baltic Sea is probably limited by salinity (Raat 1988, Klinkhardt and Winkler 1989). However, measurements conducted in the southern Baltic Sea actually demonstrate a decreasing salinity over the last two decades (Winsor *et al.* 2001). Both species also spawn in freshwater estuaries, and even in these habitats Y-O-Y were rare (J. Nilsson unpubl. data).

Reproductive disorders in fish can be caused by toxic exposure (Fitzsimons 1995). A large pulp mill is situated in the northern parts of the investigated area in Kalmar Sound and mill effluents could have negative effects on reproduction (Sandström 1994). Larsson and Förlin (2002) showed that the viviparous blenny (Zoarces viviparus L.) produced male-biased broods in the vicinity of the mill. However, there were only few indications of other impact on reproduction or general health of the monitored population. Karås et al. (1991) and Sandström (1994) found that perch embryos exposed to a pulp mill effluent were significantly smaller than reference fish and had more deformations, causing increased larval mortality, but the current study demonstrated no impacts on offspring survival and development in perch and pike during experimental exposures. We could find no evidence of the M-74 syndrome, an occasionally important mortality factor in the Baltic salmon fry (Bengtsson et al. 1999). Bylund et al. (2001) as well found no evidence of M-74 in pike populations suffering from recruitment deficits in the Åland archipelago, northern Baltic Sea. Thus, chronic disorders in parent fish reproductive systems are not likely explanations for the recruitment failure. Acute effects of toxic exposure on embryo and larva could also be excluded based on the results of our field experiments.

Eutrophication has been considered one of the most important causes of the changes observed in both marine and freshwater fish communities in the Baltic Sea (Hansson and Rudstam 1990, Bonsdorff et al. 1997, Lappalainen et al. 2000, 2001, Sandström and Karås 2002). In temperate lake ecosystems, the amounts of cyprinid fish such as roach, bream (Abramis brama L.) and silver bream generally increase during an eutrophication process, and at the same time predatory fish such as perch and pike decrease (cf. Jeppesen et al. 1997). In the coastal waters of the Baltic Sea, similar responses are not generally apparent, probably due to deviating hydrological features and the presence of marine organisms. However, in some areas of the Baltic increasing abundance or a dominance of cyprinids were recorded (Neuman and Karås

1988, Ådjers et al. 2001, Lappalainen et al. 2001). In the present study, the decreasing perch and pike stocks were not accompanied by a simultaneous increase in roach abundance, suggesting that a similar eutrophication process is not an appropriate explanation for the changes. Nevertheless, eutrophication is very pronounced in Kalmar Sound, expressed as high amounts of benthic filamentous algae. Although quantitative monitoring data are lacking, observations indicate that the production of benthic algae has increased in Kalmar Sound, as reported also from other coastal areas of the Baltic Sea (Kangas et al. 1982, Pliński and Florczyk 1984, Vogt and Schramm 1991). An over-growth of filamentous algae could damage both spawning (Aneer 1987) and nursery grounds for fish (Pihl et al. 1994). Both perch and pike spawn on open substrates, preferably on vegetation. One of the most significant potential hazards for these unguarded and immobile fish eggs could be a lack of oxygen in the surrounding water (Wootton 1998). It is a well-documented phenomenon that dense stands of filamentous algae can induce hypoxia and anoxia in the water at the algal-sediment interface (Norkko and Bonsdorff 1996) and release toxic exudates (Aneer 1987). In the current study, the presence of algae had only a slight negative effect on the hatchability of pike eggs. Consequently, exudates from the algae are not a plausible explanation for the poor recruitment.

Eutrophication of shallow coastal waters may lead to a shift from pelagic to benthic primary production, with secondary effects on the zooplankton community. The study indicated differences in zooplankton community structure between Kalmar Sound and the reference area and lower abundance of suitable prey for larval fish. Suboptimal feeding conditions for the larvae could thus be a possible explanation for the poor recruitment of perch. Irreversible starvation can occur if food is unavailable or inadequate for more than a few days during the period when larvae switch from endogenous to exogenous feeding (Karås 1996).

As a conclusion, the study demonstrated a persistently low abundance of adult fish of formerly dominating species, accompanied by an almost total lack of young fish production all along the mainland coast of Kalmar Sound. Suboptimal water quality, toxic or endocrine impacts on parent fish reproduction or exposure to filamentous algae were tested but seemed to be less likely explanations. No single factor or factors could be clearly identified as responsible for the initial decline of the stocks or the subsequent recruitment failure. Further studies are needed to determine whether the absent recovery of the stocks is inhibited by predation pressure from cormorants and if the poor recruitment is caused by food deficiency during the post hatching period and/or egg predation.

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