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Declines in predatory fish promote bloom-forming macroalgae

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Abstract. In the Baltic Sea, increased dominance of ephemeral and bloom-forming algae is presently attributed to increased nutrient loads. Simultaneously, coastal predatory fish are in strong decline. Using field data from nine areas covering a 700-km coastline, we examined whether formation of macroalgal blooms could be linked to the composition of the fish community. We then tested whether predator or nutrient availability could explain the field patterns in two small-scale field experiments, by comparing joint effects on algal net production from nutrient enrichment with agricultural fertilizer and exclusion of larger predatory fish with cages. We also manipulated the presence of invertebrate grazers.

The abundance of piscivorous fish had a strong negative correlation with the large-scale distribution of bloom-forming macroalgae. Areas with depleted top-predator communities displayed massive increases in their prey, small-bodied fish, and high covers of ephemeral algae. Combining the results from the two experiments showed that excluding larger piscivorous fish: (1) increased the abundance of small-bodied predatory fish; (2) changed the size distribution of the dominating grazers, decreasing the smaller gastropod scrapers; and (3) increased the net production of ephemeral macroalgae. Effects of removing top predators and nutrient enrichment were similar and additive, together increasing the abundance of ephemeral algae many times. Predator effects depended on invertebrate grazers; in the absence of invertebrates there were no significant effects of predator exclusion on algal production. Our results provide strong support for regional declines of larger predatory fish in the Baltic Sea promoting algal production by decreasing invertebrate grazer control. This highlights the importance of trophic interactions for ecosystem responses to eutrophication. The view emerges that to achieve management goals for water quality we need to consider the interplay between top-down and bottom-up processes in future ecosystem management of marine resources.

Key words: Baltic Sea; bloom-forming algae; coastal management; eutrophication; mesopredator release; nutrient enrichment experiment; piscivorous fish; trophic cascades.

INTRODUCTION

The structure of marine food webs has been altered on a global scale through commercial fishing and degradation of fish habitats (Pauly et al. 1998, Turner et al. 1999, Myers and Worm 2003). Consequently, we now detect cascading food web effects from declines of larger predatory fish in both pelagic and coastal systems (Jackson et al. 2001, Frank et al. 2005, Daskalov et al. 2007, Casini et al. 2008). Another global threat is coastal eutrophication, which is associated with mass development of algae that increase turbidity, suffocate other vegetation, and deplete oxygen (Valiela et al. 1997,

Cloern 2001, McGlathery 2001). Reducing nutrient loads to combat the development of algal blooms is therefore a central aim for the majority of water management programs and strategies for restoration of marine environments (e.g., European Union Water Framework Directive, United States Clean Water Act). However, increasing experimental evidence shows that system productivity and higher trophic level consumers jointly control algal production, suggesting that nutrient effects on the development of algal blooms depend also on top-down forcing (Carpenter et al. 2001, Worm et al. 2002, Deegan et al. 2007).

Declines in larger piscivorous fish may generate strong increases in smaller predatory fish, mesopredator release (Jackson et al. 2001, Frank et al. 2005, Myers et al. 2007). Increased predation subsequently generates different scenarios for lower trophic levels, depending

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on the functional diversity of the prey and system productivity (Pace et al. 1999, Duffy 2002, Elmhagen and Rushton 2007). In the simplest scenario, the abundance of the prey community decreases, generating a reciprocal predator-prey chain of effects (Pace et al. 1999, Scheffer et al. 2005). Such trophic cascades are only expected in systems in which interaction strengths are determined by few functionally dominant species (Duffy 2002, Moksnes et al. 2008). In systems with higher diversity of prey defenses, the prey community may change in species composition rather than abundance if there are inedible species that can proliferate from released competition (Duffy 2002, Vasas et al. 2007). In some ecological communities mesopredator release effects are strongly limited by system productivity (Elmhagen and Rushton 2007). This suggests that declines of top predators may also promote a switch from a predominantly top-down to a predominantly bottom-up controlled ecosystem, with increasing abundances of all lower trophic levels when productivity is high. Thus, we have only recently started to realize the complexity of effects from large-scale declines in predatory fish for the status of marine communities, in which the release of consumer control may interact with local conditions such as nutrient loads (Jackson et al. 2001, Scheffer et al. 2005).

In the Baltic Sea, long-term trends are dominated both by large-scale eutrophication and notorious depletion of top predators (Österblom et al. 2007). Primary production is estimated to have more than doubled since the 1920–1940s (Elmgren 1989), and an associated increased production of phytoplankton and ephemeral macroalgae is currently considered as one of the most serious environmental problems in the entire Baltic Sea region (Bonsdorff et al. 1997, Jansson and Dahlberg 1999, Swedish Environmental Protection Agency 2006). Berglund et al. (2003) showed that from 1997 to 2000, 40% of the inlets in an archipelago area in the northern Baltic Sea were covered by drifting algal mats (Åland archipelago). Parallel to increased primary production, the majority of larger predatory fish species have declined during the last decades (ICES 2006). In the open sea, overfishing and unfavorable hydrological conditions for reproduction of cod (*Gadus morhua*) have resulted in an increase of zooplanktivorous sprat (*Sprattus sprattus*), which contributes strongly to a documented large-scale decrease in zooplankton biomass and a simultaneous increase in phytoplankton production (Casini et al. 2008). In the coastal zone, the dominant piscivore predators, perch (*Perca fluviatilis* L.) and pike (*Esox lucius* L.), have shown strong regional declines since the early 1990s (Nilsson et al. 2004, Adjers et al. 2006). Declines of perch and pike are likely caused by recruitment failures due to resource limitation, where the spatial distribution and timing of failures indicate that there may be a connection to the system shift in the open sea (L. Ljunggren, *personal observation*). Coincident with recruitment failure areas for pike and perch,

high abundances of small-bodied fish (size 5–10 cm) have been observed, particularly the three-spined stickleback (*Gasterosteus aculeatus* L.) (Nilsson et al. 2004).

In this study we explore whether declines in coastal predatory fish have cascading effects on the development of bloom-forming filamentous algae. Larger perch and pike are strong consumers of smaller predatory fish (Fago 1977, Willemsen 1977), who in turn are important predators of invertebrate grazers (Wiederholm and Thorman 1986). Invertebrate grazing and nutrient availability jointly control macroalgal production on rocky shores (Worm and Lotze 2006). Thus, piscivorous fish may indirectly control the accumulation of filamentous algae in the coastal zone by regulating predation pressure on invertebrate grazers. We therefore hypothesize that declining predator abundances generate effects similar to nutrient enrichment by promoting algal blooms. To test this hypothesis, we first analyzed a data set covering a 700-km coastline of the Baltic Sea for large-scale relationships between piscivorous fish and ephemeral filamentous algae. Second, we tested for causality in two small-scale field experiments by comparing effects of excluding larger fish and adding nutrients on the development of algal biomass.

METHODS

Field study

The Baltic Sea is a nontidal brackish water system with rocky archipelagos consisting of thousands of differently sized shallow inlets. These shallow coastal areas are normally characterized by soft sediment bottoms with a macrophyte community mainly consisting of submerged species such as pondweeds (*Potamogeton* spp.), stoneworts (*Chara* spp.), milfoils (*Myriophyllum* spp.), and reed (*Phragmites australis* L.), as well as bladderwrack (*Fucus vesiculosus* L.) on harder substrates. We explored field patterns for a relationship between predatory fish and bloom-forming ephemeral algae using records of juvenile pike and perch abundance and algal cover on submerged vegetation from 57 shallow inlets scattered over nine larger coastal areas and covering most of the west and north shores of the Baltic proper (Fig. 1). Each area covered a coastline of at least 10 km. All data were collected in 2003 by the Swedish Board of Fisheries and Åbo Akademi University, to document and test the distribution and possible causes of the reported recruitment failure of coastal fish (Nilsson et al. 2004; L. Ljunggren, *personal observation*). The sites were therefore distributed both throughout the areas where recruitment problems have been reported and in reference areas where recruitment failures have not occurred. Sites were chosen by stratified randomization in order to achieve considerable variation in site characteristics, including salinity and wind and wave exposure both on the large archipelago and the small-site scale. The randomization process was also stratified according to a categorical inner/mid/outer zone archipelago subdivision (Schernewski and Wielgat

2004). The sampled sites spanned a gradient in salinity from ~ 7 practical salinity units (psu) in the south to 4 psu in the north and covered a wide variety of bottom and morphometry types.

Vegetation was surveyed on two occasions in 2003: in May–early June and simultaneously with sampling of young-of-the-year (YOY) fish in late July–August. At each site, the percent cover of the vegetation was estimated every 10 m along parallel transect lines (~ 50 m apart, length 20–480 m, four to eight lines per site) drawn perpendicular to the length axis from one shore to the opposite shore until the entire site was covered. Percentage cover was measured in 0.50×0.50 m quadrates; the number of quadrates per site varied from 24 to 230, depending on the inlet size. Plots with $>25\%$ of vegetation and other substrate covered by ephemeral algae were designated as having “high” cover of bloom-forming algae.

Sampling of YOY fish was conducted in late July–August 2003. The majority of the important piscivorous fish species spawn in spring and at the time of sampling in late summer have undergone metamorphosis and aggregate in shallow, vegetated, and near-shore areas. The YOY fish were monitored by point abundance sampling with low-impact pressure waves (LIMP), derived by igniting small underwater detonations (1-g explosives) which stun small fish within an area of ~ 15 m² (Snickars et al. 2007). This method allows sampling of fish (in the size range of 15–150 mm) with well-developed swim bladders in all habitats, including dense vegetation. The number of samples in each inlet was proportional to the area of the site and varied from 9 to 47. The total number of analyzed samples was 1250. Adult fish were not included in the 2003 field samplings. However, in the Baltic Sea the variation in year class strength of perch is positively correlated to autumn abundances of YOY fish (Karås 1996). We therefore assumed that juvenile densities reflected differences in adult stocks when testing the relationship between piscivorous fish and ephemeral algae (this relation was also tested). For analysis of a relation between YOY fish and ephemeral algae we scaled the data by averaging across all sites within each of the nine large archipelago areas (Fig. 1), since predatory fish easily invade locally depleted inlets (see, e.g., Nilsson et al. 2004).

We examined the relationship between YOY and adult fish densities by comparing our field data with results from permanent monitoring programs targeting larger fish (Swedish National Board of Fisheries). Such programs are carried out in the same locations of six of our nine study areas in the Baltic proper (Fig. 1). Adult fish communities are monitored by standardized gill net surveys in August, the same time period as we collected YOY fish. The spatial distribution of the gill net programs overlaps our study areas significantly in all of the six areas, but are sampled on a different scale. Our samples of YOY fish represent single inlets, and 35 inlets were sampled within the six larger areas covered by the

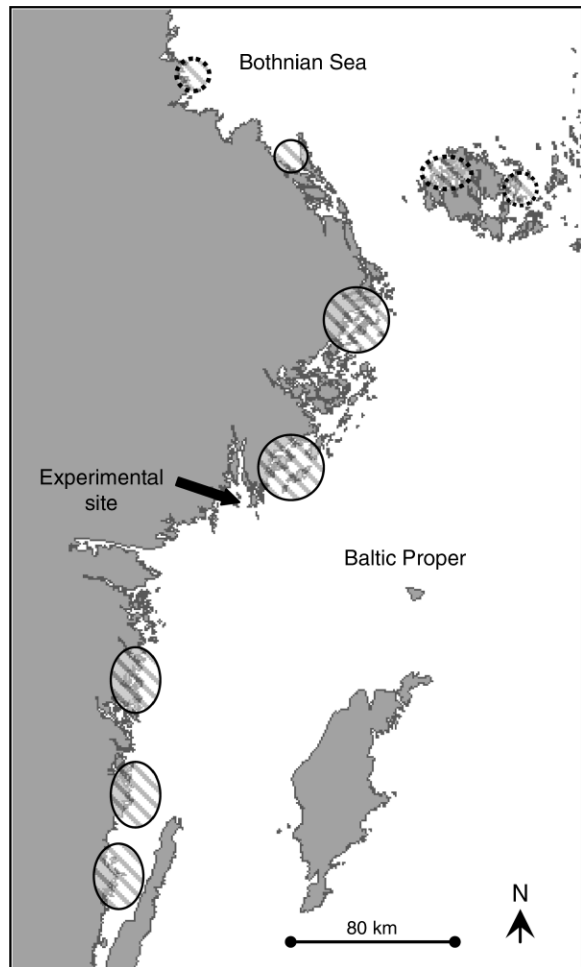


FIG. 1. Map of monitored study areas and the experimental site along the coastline of the western Baltic Sea. Shaded areas marked by solid outlines indicate the location of study areas where additional data from a beach seine survey and permanent fish monitoring programs were also obtained. Shaded areas marked by broken outlines represent study areas where only data on algae and young fishes were available.

monitoring programs (4–10 inlets in each larger area). The gill net sampling stations are instead distributed over a range of depths (1–20 m) and wave exposure gradients at a total of 45 sites in each area, to be representative of a larger region (see Ådjers et al. 2006 for more details). Unfortunately, two different gear types were used, coupled single-mesh gill nets in three of the areas and Nordic multi-mesh gill nets in the other remaining three. Since these cannot be compared quantitatively we scaled piscivore mass in each larger area by calculating the percentage deviance from the mean catch per surface area net, in comparable mesh-sizes for each specific gear separately (mass per square meter gill net). We used gill net data from the same year as the other field surveys were conducted (2003). Since gill nets do not catch small-bodied fish species such as sticklebacks, we conducted complementary sampling

with a beach seine in late May and early June in the six study areas where data on adult fish were available. We sampled a subset of the inlets where YOY fish and ephemeral algae were sampled (16 sites total, two to three per study area). These subsets of sites were randomly chosen among the available inlets. The survey method allowed us to get a measure of small-bodied fish during late spring and early summer when particularly the three-spined stickleback aggregate in shallow areas during their spawning period. At each site, the seine was pulled toward the shoreline at four randomly allocated locations. The seine was 2 m deep with 10 m long arms, 5-mm mesh size in arms and 2-mm mesh size in the cod end. Beach seine data were analyzed by comparing inlets from areas where adult piscivorous fish abundance showed a positive deviation from the mean (high piscivorous abundance) with inlets where adult piscivorous fish abundance showed a negative deviation from the mean (low piscivorous abundance). Adult fish data for the division were obtained from the permanent monitoring program.

Field experiments

We tested effects of larger piscivorous fish and nutrient enrichment on lower trophic levels including smaller fish, invertebrate grazers, and macroalgae, in two consecutive field experiments in 2005 and 2006. We used cages to exclude larger fish and agricultural fertilizer to mimic eutrophication. The experiments were performed at Askö laboratory, Stockholm University, on the island of Askö, 80 km south of Stockholm, northern Baltic Sea proper, Sweden (58°48' N, 17°40' E; Fig. 1). Askö is part of a rocky archipelago where salinity is ~6.5 psu. For the experiments we used connected shallow and sheltered bays that support a well-developed subtidal macroalgal community (Appendix A).

In 2005, the experiment was designed in a factorial combination of larger predatory fish presence (predator exclusion/predator access/no cages) and nutrients (ambient nutrients/nutrient enriched) with three replicates ($n = 18$ plots). Plots were set up at ~1-m depth in a randomized block design with three blocks placed next to one another parallel to the shore in one of the bays. Each plot was separated by at least 3 m from the neighboring ones.

Larger predatory fish were excluded using steel cages (0.5 × 0.5 m wide and 1.0 m high) covered with a thin plastic net with 14-mm diagonal mesh size that limits light penetration insignificantly. To separate effects of caging from true predator effects on macroalgal development, we compared closed cages (predator exclusion) with cages with two 15 × 15 cm holes cut in the net on non-opposite sides (predator access). We also determined cage effects on macroalgal development by comparing experimental effects in plots with no cages with effects in predator access cages.

Nutrients were enriched by supplying 120 g of slow-release nitrogen-phosphorus-potassium (NPK) fertilizer pellets (Plantacote Depot 6 M, Urania Agrochem, Hamburg, Germany). Pellets were applied in plastic net bags, which were changed every five to six weeks (Worm et al. 2000). Nutrient enrichment increased dissolved inorganic nitrogen (DIN) and phosphorus (PO_4) by 35.7% and 54.8%, respectively, compared to plots with ambient water concentrations of 1.90 ± 0.21 μmol DIN/L and 0.10 ± 0.005 μmol PO_4 /L, during the experiment in August 2005 (mean \pm SE; ANOVA, $N = 18$, $F_{1,16} = 4.38$, $P < 0.05$ and $F_{1,16} = 7.13$, $P < 0.05$, respectively).

The experiment ran from 7 July to 13 September in 2005 (experimental time = 10 weeks). In the beginning of the experiment, artificial substrates were introduced to all plots in order to allow colonization of algae and invertebrates. We used bricks (25 × 12 cm) and ceramic tiles (5 × 5 cm) as artificial colonization units. Two tiles and one brick were placed in each experimental unit. At the end of the experiment, we sampled the substrates in plastic bags under water and analyzed the abundance of macroalgae (dry mass) and invertebrate fauna (number of individuals) in the laboratory.

In 2006, we used larger predator exclusion cages where we could include canopy cover to look at interactive effects between predators, nutrients, and habitat complexity. In addition, larger cages allowed us to include smaller grazer exclusion cages to specifically look at grazing effects in the different predator treatments. The larger predation exclusion cages (0.55 × 1.2 m wide and 1.2 m high) were covered with the same thin plastic net as for treatments excluding large predatory fish (14 mm diagonal mesh size). Also here we compared closed cages (predator exclusion) with open cages, constructed by cutting a 25 × 15 cm hole on one of the short sides and a 50 × 50 cm hole on one of the long sides (predator access). Nutrients were enriched following the scheme from 2005. Instead of two, we placed four bags with 120 g of slow release NPK fertilizer pellets in each nutrient enrichment cage, to compensate for the larger size of the cage. Canopy cover was manipulated by adding six larger *Fucus vesiculosus* thalli to half of the cages, creating a sparse (~50%) cover. The *Fucus* thalli were fastened by cable ties to the steel frame on the bottom sides of the cage.

The experiment in 2006 was designed in a factorial combination of larger predatory fish presence (predator exclusion/predator access) and nutrients (ambient nutrients/nutrient enriched), and canopy cover (canopy cover/no canopy cover) with three replicates ($n = 24$ plots). Plots were set up at ~1 m depth in a randomized block design with three blocks placed in adjacent bays. Each plot was separated by at least 3 m. Unfortunately, plots in one bay had to be discarded due to over-sedimentation, limiting replicates of the full factorial design to two ($n = 16$).

The experiment ran from 27 April to 13 September in 2006 (experimental time = 20 weeks). In the beginning of the experiment, we added artificial substrates to all plots: one brick with four ceramic tiles ($5 \times 5 \text{ cm} \times 4$) for colonization of algae and one brick ($12 \times 12 \text{ cm}$) for quantification of invertebrates. At the end of the experiment, we sampled the substrates in plastic bags under water and analyzed the abundance of all species of macroalgae (dry mass) and invertebrate fauna (number of individuals) in the laboratory. In 2006 we assigned the invertebrates both to species and size classes: small (0–2 mm) and large (>2 mm). At the end of August we measured the effect of the predator cage treatment on the fish community: fish associated with the cages were sampled using underwater detonations (LIMP; Snickars et al. 2007). We collected all fish on the bottom inside and 0.4 m outside of predator exclusion and predator access cages and recorded all swimming fish inside cages during sampling.

In 2006 we also tested grazing effects on algal recruitment in the different treatments. Grazer presence was manipulated by including two smaller steel cages ($25 \times 25 \times 25 \text{ cm}$) covered with 1.0-mm transparent net inside the larger predator manipulation cages: one closed (grazer exclusion) and one open (grazer access, with two $15 \times 10 \text{ cm}$ holes cut in the net on non-opposite sides) in each larger cage (see Eriksson et al. [2007] for specifics on cage design). The net excluded all gastropod and crustacean grazers. Grazer cages were included later in the experiment (on 13 July 2006; experimental time = 92 d) to avoid degenerating conditions from developing inside the closed cages, either from increased sedimentation or mass recruitment from larval stages penetrating the net. Each cage contained a ceramic tile ($5 \times 5 \text{ cm}$) on which all algal recruits were counted at the end of the experiment. We analyzed the grazing effect by testing open and closed cages separately using the full design of predator exclusion and nutrient enrichment and comparing the results. Canopy cover was not included in the design for grazer effects, since the canopies were too low to cover the cages.

Data analysis

For the field study, we correlated high covers of ephemeral algae with piscivorous YOY fish abundance (perch and pike) and abiotic variables including latitude, longitude, inlet size, and mean depth of sites, using all nine areas. The YOY fish counts were Poisson distributed in all samplings, and we therefore used Spearman's rank correlation when including YOY fish. All counts of small-bodied fish, invertebrates, and algal recruit data from both the beach seine and experimental studies were Poisson distributed, and differences in means for all counts were therefore analyzed using generalized linear models (GLM) with Poisson error distributions and log-link functions (McCullagh and Nelder 1989). We used the log-likelihood ratio as test statistic, since it is robust to small sample sizes. All

GLM models were corrected for overdispersion. Differences in algal cover data from the field study were analyzed with ANOVA using arcsine transformation, while differences among experiment treatments on algal biomass data were analyzed with factorial MANOVA using \log_{10} transformation when necessary to obtain homogeneous variances according to Cochran's test. Difference in algal biomass between no cage and predator access cages (cage effects) in 2005 were only tested as a main effect (no factorial design).

RESULTS

Field study

Summer development of ephemeral algae clearly increased with declining abundance of piscivorous juveniles (perch and pike), across the nine larger archipelago areas. Perch dominated the YOY piscivorous fish community (for YOY species composition see Appendix B), while the ephemeral algae consisted both of fast-growing filamentous (mainly *Cladophora* spp., *Ectocarpus siliculosus*, *Pylaiella littoralis*, and *Spirogyra* spp.) and sheet-forming (*Ulva* spp. and *Monostroma* spp.) algae. There was a significant negative correlation between high cover of ephemeral algae and YOY piscivores that increased from moderate in May (Spearman's rank correlation, $R = -0.76$, $P = 0.028$) to very strong in August (Spearman's $R = -0.95$, $P < 0.001$). The increase in fit from May to August was largely explained by a marked increase in ephemeral algal load, restricted to areas with low density of YOY piscivores (Fig. 2). No measured geographic or environmental pattern correlated significantly with ephemeral algal abundance (Appendix C).

Comparisons with the relative abundances of piscivorous fish from the monitoring programs indicated that the YOY stock was a relevant proxy for adult densities. Percentage of deviation from the two means revealed a strong positive correlation between large-scale YOY abundance and relative adult catch of piscivorous fish (mainly perch and pike; common sizes 15–40 and 30–80 cm, respectively; Fig. 3; general regression model [GRM], $N = 6$, $R^2 = 0.82$, $P < 0.05$). Based on a positive or negative deviation from the mean, there was a clear division between regions with high and low abundances of piscivorous fish, both for the monitoring programs of adult fish and the YOY samplings (see dotted line in Fig. 3). Regions with high abundances included three larger monitoring areas with 19 inlets sampled for YOY. Regions with low abundances included three larger monitoring areas with 16 inlets sampled for YOY. Beach seine data on smaller bodied fish (size = 5–10 cm) also showed a clear division between inlets within sampling areas with high or low abundance of piscivorous fish. Of the 16 inlets selected for the beach seine sampling, eight belonged to regions with high abundances of piscivorous fish and eight to regions with low. Inlets within regional areas with low abundances of piscivorous fish had both significantly

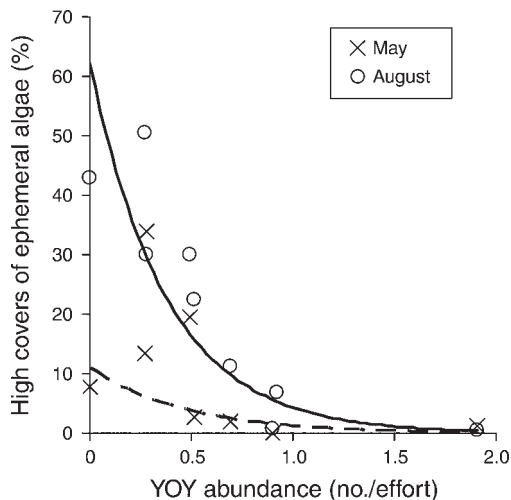


FIG. 2. The relation between young-of-the-year (YOY) piscivorous fish and high loads of ephemeral algae in May and August, including 43 inlets from six areas in the western Baltic Sea, eight inlets from one area in the western Bothnian Sea (Gävle), and six inlets from two areas in the Åland archipelago. The lines show exponential trends between YOY and a high percentage cover of ephemeral algae in June (lower broken line) and in August (upper solid line). A high percentage cover of ephemeral algae was assigned to plots where cover of filamentous algae on vegetation and other substrates exceeded 25%. The YOY fish were sampled with low-impact pressure waves, and effort denotes catch per detonation.

higher abundances of smaller bodied fish and significantly higher covers of ephemeral macroalgae, compared to inlets within regional areas with high abundances of piscivorous fish ($N = 16$, $\chi^2 = 12.0$, $P < 0.001$ and $N = 16$, $F_{1,14} = 9.26$, $P < 0.01$, respectively; Fig. 4). The three-spined stickleback dominated the smaller bodied fish fauna (Fig. 4; for details of species composition and sizes, see Appendix B).

Field experiment 1 (2005)

The 2005 experiment showed that small-bodied predatory fish had significant effects on invertebrate community composition and on the production of ephemeral algae. The results support the positive relationship between the abundance of small-bodied predatory fish and ephemeral algae observed in the field study. The invertebrate fauna was dominated by filter-feeding mussels, herbivorous scrapers (gastropods), and herbivorous shredders (amphipods: *Gammarus* spp.). Excluding larger predatory fish favored mussels and disfavored smaller species of grazing gastropods. The mussels *Cardium* spp. and *Mytilus* sp. both increased by a factor of two in the closed predator exclusion cages compared to the open predator access cages, and this increase was strengthened by nutrient enrichment (Table 1, Fig. 5). There were no significant differences in the abundance of shredders, *Gammarus* spp., or the larger sized gastropods scrapers, *Theodoxus fluviatilis* L. (adult size, 10 mm) and *Radix balthica* L. (adult size, 15–20

mm), between the predator treatments (Table 1, Fig. 5). *Radix balthica* decreased significantly with nutrient enrichment, from 5.5 ± 1.3 individuals/dm² in ambient conditions to 2.5 ± 1.0 individuals/dm² when adding nutrients (mean \pm SE; Table 1). The small gastropod scrapers, *Hydrobia* spp. (adult size, 4–5 mm) and *Limapontia capitata* Müller (adult size, 2–4 mm) decreased significantly in number when larger predatory fish were excluded (significant main effects, Table 1, Fig. 5). *Limapontia capitata* increased strongly from nutrient enrichment (2.3 ± 0.9 and 6.6 ± 2.6 individuals/dm² in ambient and enriched conditions, respectively; Table 1).

Excluding larger predatory fish generated a clear increase in the net production of bloom-forming ephemeral algae (Fig. 6). Three species of filamentous and opportunistic macroalgae (*Cladophora glomerata*, *Pylaiella littoralis*, and *Ulva* spp.), which commonly contribute to ephemeral blooms in the Baltic Sea, colonized the substrates. An overall analysis of all species demonstrated that there was a significant main effect from excluding larger predatory fish (MANOVA results, $F_{3,6} = 5.16$, $P = 0.042$), but no significant effect from nutrient enrichment. *Ulva* spp. dominated biomass and contributed together with *P. littoralis* to the strong increase in net production from predator exclusion (comparison between predator exclusion and predator access cages; Table 2, Fig. 6). The absence of significant

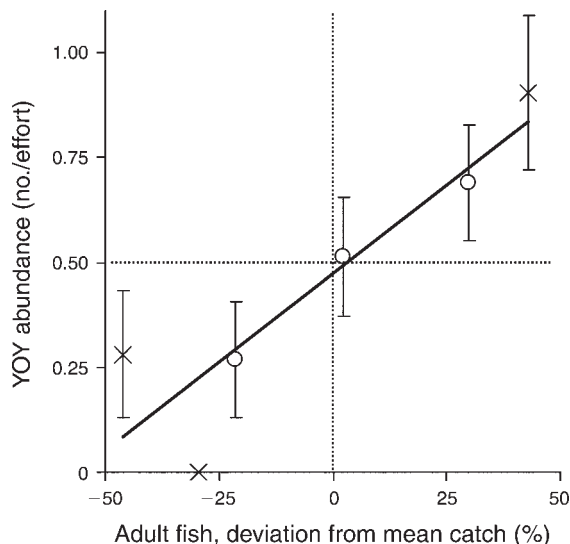


FIG. 3. The relation between adult and young-of-the-year (YOY) piscivorous fish in six areas in the western Baltic Sea. The symbols denote different gear types: Nordic multi-mesh gill nets (open circles) and coupled single-mesh gill nets with varying mesh sizes (crosses). Adult catch was normalized between different gear types by calculating the percentage of deviance from the mean catch. The dotted lines show a division between samplings characterized by low or high abundances of piscivorous fish, both considering the relative abundance of adult larger fish and YOY densities. The YOY fish were sampled with low-impact pressure waves, and effort denotes catch per detonation. Error bars show \pm SE.

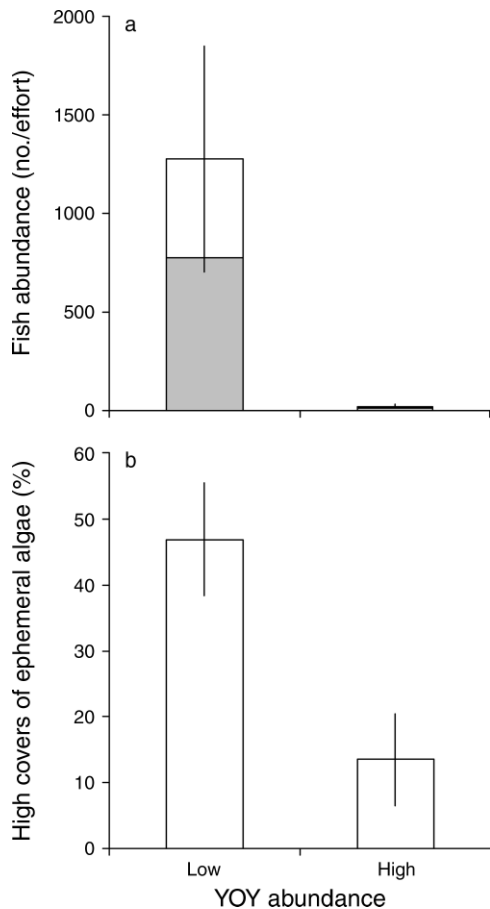


FIG. 4. Differences in the abundance of (a) small-bodied fish (5–10 cm) and (b) high loads of ephemeral algae in August (the percentage of vegetation plots where ephemeral cover exceeded 25%) in areas characterized by low vs. high abundances of both young-of-the-year (YOY) and adult piscivorous fish (lesser or higher than relative or absolute mean catch; based on Fig. 3). Data are from 16 inlets in the Baltic proper that were sampled with a beach seine. Effort denotes catch for each pull with the beach seine. The gray area shows abundance of three-spined sticklebacks (*Gasterosteus aculeatus*) that dominated the smaller-bodied fish fauna. Error bars show \pm SE.

nutrient effects in the overall analysis depended on strong cage effects (one-way MANOVA results from comparing open cages with predator access and with no-cage plots, $F_{3,8} = 9.88$, $P < 0.01$). The biomass development of *Ulva* spp. was not influenced by caging (univariate ANOVA results, $F_{1,10} = 1.77$, $P = 0.21$), but both *C. glomerata* and *P. littoralis* decreased significantly in cages with predator access compared to no-cage plots (negative cage effects; univariate ANOVA results, $F_{1,10} = 23.12$, $P < 0.001$ and $F_{1,10} = 12.96$, $P < 0.01$ for *C. glomerata* and *P. littoralis*, respectively). Cage effects on *P. littoralis* were limited; nutrients more than doubled biomass inside the cages (significant univariate nutrient effect; Table 2, Fig. 6). For *C. glomerata* caging limited net production by almost 90%, and outside the

cages in the no-cage treatment nutrient enrichment more than doubled *C. glomerata* biomass (2.1 times the ambient conditions; t test, $df = 4$, $t = 2.7$, $P = 0.056$). This indicated that *C. glomerata* should be omitted from the analysis of predator \times nutrient effects. For *P. littoralis* and *Ulva* spp., nutrient enrichment and predator removal had similar and independent additive effects that together increased the net algal production more than fourfold; nutrient enrichment increased the biomass of *P. littoralis* and *Ulva* spp. 2.3 times, which is similar to a 2.4-fold increase by predator exclusion cages (significant univariate nutrient effects; Table 2, Fig. 6).

Field experiment 2 (2006)

The 2006 experiment demonstrated that declines in larger predatory fish induce a chain of events cascading down the food web, including (1) an increase of smaller bodied fish, (2) changes in the size distribution of invertebrate grazers, (3) increased biomass development

TABLE 1. Generalized linear model results for the abundance of dominating invertebrate species from the 2005 experiment along the coastline of the western Baltic Sea.

Source	df	χ^2	P
Mussels			
<i>Cardium</i> spp.			
Nutrient enrichment (N)	1	0.15	0.695
Predation (P)	1	4.38	0.036
N \times P	1	3.73	0.053
Error	8		
<i>Mytilus</i> spp.			
Nutrient enrichment (N)	1	2.53	0.112
Predation (P)	1	11.84	<0.001
N \times P	1	9.19	0.002
Error	8		
Amphipod shredders			
<i>Gammarus</i> spp.			
Nutrient enrichment (N)	1	1.48	0.224
Predation (P)	1	0.02	0.88
N \times P	1	1.55	0.213
Error	8		
Gastropod scrapers			
<i>Limapontia capitata</i>			
Nutrient enrichment (N)	1	13.05	<0.001
Predation (P)	1	7.59	0.006
N \times P	1	1.10	0.295
Error	8		
<i>Hydrobia</i> spp.			
Nutrient enrichment (N)	1	0.34	0.562
Predation (P)	1	4.36	0.037
N \times P	1	0.00	0.944
Error	8		
<i>Radix balthica</i>			
Nutrient enrichment (N)	1	6.92	0.009
Predation (P)	1	0.33	0.563
N \times P	1	0.49	0.482
Error	8		
<i>Theodoxus fluviatilis</i>			
Nutrient enrichment (N)	1	1.26	0.262
Predation (P)	1	0.00	0.961
N \times P	1	0.07	0.794
Error	8		

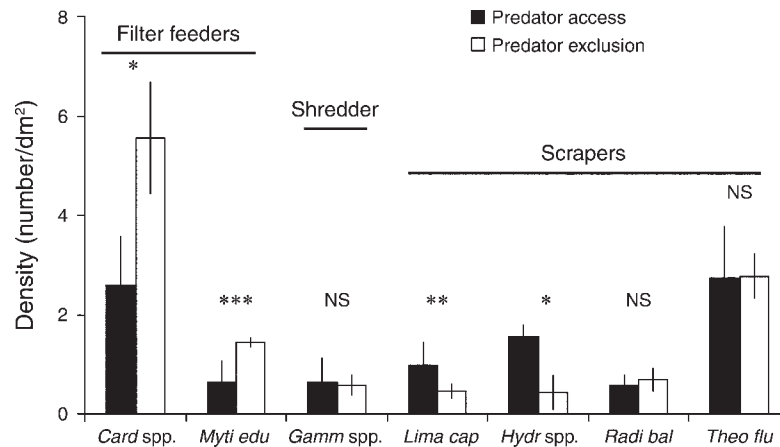


FIG. 5. Effects of exclusion of larger piscivorous fish on the density (mean \pm SE) of the dominating filter-feeding and herbivorous invertebrates in the 2005 experiment: black bars show open predator access cages and white bars show closed predator exclusion cages. Abbreviations are: *Card spp.*, *Cardium* spp.; *Myti edu*, *Mytilus edulis*; *Gamm spp.*, *Gammarus* spp.; *Lima cap*, *Limapontia capitata*; *Hydr spp.*, *Hydrobia* spp.; *Radi bal*, *Radix balthica*; *Theo flu*, *Theodoxus fluviatilis*.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS, nonsignificant.

of filamentous macroalgae, and (4) reduced grazing control on the phytobenthos. The small-bodied fish fauna at the study site was dominated by the predatory three-spined stickleback and the omnivorous Eurasian minnow (*Phoxinus phoxinus* L.), while perch dominated the piscivorous fish community (reference sampling outside the experiment area). Excluding the larger predatory fish and adding nutrients both increased the number of smaller bodied fish dramatically. Small-bodied fish were almost 10 times more abundant in the predator exclusion cages than in the predator access cages and five times more abundant in the nutrient enrichment cages than in the ambient nutrient cages (Fig. 7a; GLM, significant main effects only, $N = 16$, $df = 1$, $\chi^2 = 17.1$, $P < 0.001$ and $\chi^2 = 10.9$, $P < 0.001$ for predator and nutrient treatments, respectively). The data

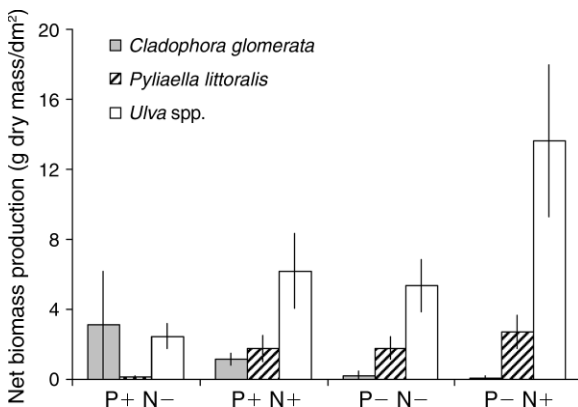


FIG. 6. Effects of exclusion of larger piscivorous fish and nutrient enrichment on ephemeral bloom-forming macroalgae in the 2005 experiment. Abbreviations are: P+, larger predatory fish present; P-, larger predatory fish excluded; N-, ambient nutrient concentrations; N+, nutrient enrichment. Error bars show \pm SE.

were highly aggregated and did not permit a full factorial analysis including the canopy treatment (the limited replication resulted in treatment combinations with zero variance). The exclusion cages effectively excluded the larger predators (Appendix D); piscivorous perch exclusively entered the predator access cages (four individuals were found in open cages during fish sampling, none in the closed cages).

In 2006, excluding larger predatory fish changed the response of the herbivore community to nutrient enrichment, while mussels increased independently of the nutrient treatment. The herbivore fauna was dominated by gastropod grazers; we only found a few individuals of amphipod and isopod grazers and therefore excluded them from the analyses in 2006. For scraping gastropods, there was a trend toward a significant interaction effect between the predator and nutrient treatments that depended on smaller individuals

TABLE 2. Univariate MANOVA results for the production of dominating ephemeral algae from the 2005 experiment.

Source	df	F	P
<i>Cladophora glomerata</i>			
Nutrient enrichment (N)	1	0.03	0.869
Predation (P)	1	4.17	0.076
N \times P	1	0.23	0.643
Error	8		
<i>Pylaiella littoralis</i>			
Nutrient enrichment (N)	1	8.59	0.019
Predation (P)	1	8.52	0.019
N \times P	1	3.76	0.089
Error	8		
<i>Ulva</i> spp.			
Nutrient enrichment (N)	1	5.75	0.043
Predation (P)	1	4.97	0.056
N \times P	1	0.00	0.953
Error	8		

increasing from nutrient enrichment, but only when excluding predators (small = 0–2 mm; included all *Limapontia capitata*, small *Hydrobia* spp., juvenile *Theodoxus fluviatilis*, and juvenile *Radix balthica*; Table 3, Fig. 7b). In ambient nutrient conditions, the smaller scrapers decreased significantly when excluding larger predators. For larger scrapers there were no significant effects by the predator or nutrient treatments (Table 3). All mussels increased strongly in the absence of larger predators, regardless of size and nutrients treatments: there were three times as many mussels in the closed predator exclusion cages as in the open predator access cages (Table 3, Fig. 7c). All invertebrates reacted negatively to canopy cover (Table 3). The variation created by the canopy treatment was important in the statistical models, but did not change the predator and nutrient effects on the invertebrates (statistical trends and significant interaction effects with the canopy treatment were in some cases created by very strong declines in all canopy treatment combinations; Table 3).

Larger predatory fish, nutrients, and canopy cover together controlled the development of macroalgal biomass (Fig. 8); predator and nutrient effects were similar to the results in 2005. Also in 2006 the algae were dominated by *Cladophora glomerata*, *Pylaiella littoralis*, and *Ulva* spp. Analyzing all species together (MANOVA) demonstrated interaction effects between the predator and nutrient treatments (a trend, $F_{3,6} = 4.16$, $P = 0.065$) and between the nutrient and canopy treatments ($F_{3,6} = 1.34$, $P < 0.01$). These interaction effects depended on a strong increase in the biomass of *Ulva* spp. when excluding larger predators in combination with nutrient enrichment and no canopy cover, increasing the total biomass production of macroalgae at least twofold compared with all other treatment combinations (Table 4, Fig. 8). There were no significant univariate treatment effects on *Pylaiella littoralis* or *Cladophora glomerata* (Table 4).

Grazer control mediated significant cascading effects of larger predatory fish on algal recruitment. Recruitment of algal propagules to the tiles consisted of filamentous macroalgae, but also colonies of cyanobacteria and single-stranded green algae. The individual propagules that recruited were small, from microscopic to 2–3 mm long, and could not be determined to species with accuracy. We therefore only analyzed total number of recruits. When grazers had access to the recruitment tiles in open grazer cages, algal recruitment increased significantly both by adding nutrients and excluding larger predatory fish (in predator exclusion cages) (GLM results; predation [P]: $df = 1$, $\chi^2 = 4.06$, $P = 0.044$; nutrients [N]: $df = 1$, $\chi^2 = 11.03$, $P < 0.001$; P × N: $df = 1$, $\chi^2 = 0.01$, $P = 0.903$). Nutrient and predator effects reinforced one another, creating a many times higher production of recruits when combining nutrient enrichment with predator exclusion cages (Fig. 9, black bars). When grazer effects were deleted by putting the tiles in closed grazer cages (grazer exclusion cages), there

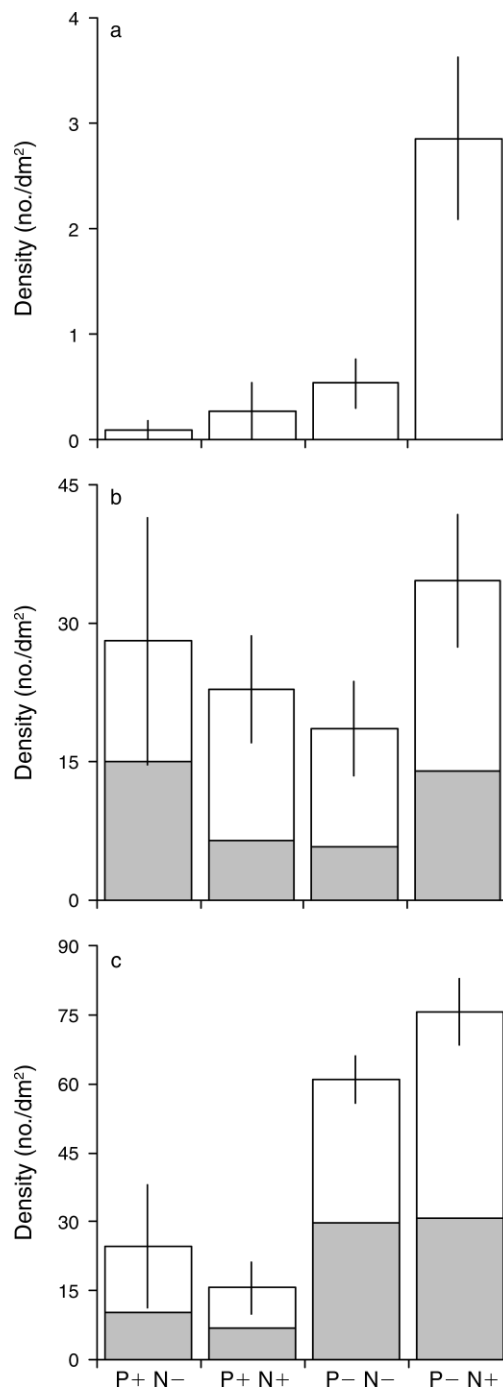


FIG. 7. Effects of exclusion of larger piscivorous fish and nutrient enrichment on density (mean \pm SE) of (a) smaller bodied predatory fish, (b) gastropod scrapers, and (c) filter-feeding mussels in the 2006 experiment. In panels (b) and (c) the gray parts of the bars show the abundance of small individuals (0–2 mm), and the white parts of the bars show the abundance of larger individuals (>2 mm). Abbreviations are as in Fig. 6.

TABLE 3. Generalized linear model results for the abundance of dominating invertebrate species from the 2006 experiment, by size classes.

Source	df	Total abundance		Small (0–2 mm)		Large (>2 mm)	
		χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>
Gastropods							
Predation (P)	1	0.04	0.849	0.15	0.694	0.28	0.597
Nutrient enrichment (N)	1	0.75	0.388	0.01	0.937	1.90	0.168
Canopy cover (C)	1	9.01	0.003	13.50	<0.001	5.89	0.015
P × N	1	2.94	0.087	12.32	<0.001	0.24	0.623
P × C	1	0.67	0.414	0.00	0.992	1.45	0.228
N × C	1	2.00	0.157	1.22	0.269	2.77	0.096
P × N × C	1	0.83	0.362	4.04	0.044	0.14	0.710
Mussels							
Predation (P)	1	17.54	<0.001	14.51	<0.001	18.77	<0.001
Nutrient enrichment (N)	1	0.06	0.813	0.04	0.846	0.39	0.531
Canopy cover (C)	1	15.69	<0.001	14.11	<0.001	15.67	<0.001
P × N	1	1.12	0.290	0.36	0.549	2.08	0.150
P × C	1	1.93	0.165	0.47	0.495	3.78	0.052
N × C	1	1.99	0.158	1.78	0.182	2.11	0.147
P × N × C	1	0.02	0.882	0.01	0.941	0.16	0.688

was a significant increase by adding nutrients but no effect of excluding predators (GLM results; P, $df=1$, $\chi^2=0.58$, $P=0.447$; N, $df=1$, $\chi^2=29.97$, $P<0.001$; P × N: $df=1$, $\chi^2=0.19$, $P=0.666$); creating a 12-fold higher production from nutrient enrichment regardless of the predator treatment (Fig. 9, white bars). Thus, the significant increases in algal recruitment by excluding larger predatory fish depended on the presence of grazers: when excluding grazers the predatory fish had no significant effect on algal recruitment.

DISCUSSION

Our results provide strong support for the importance of top-down forcing in the coastal zone and suggest that declines in larger predatory fish and nutrient enrichment together promote the development of macroalgal blooms in the Baltic Sea. In the large-scale field study,

we found that high covers of ephemeral algae coincide both with low abundances of piscivorous fish and high abundances of small-bodied fish that feed on invertebrate grazers. In the field experiments we demonstrate that the abundance of larger piscivorous fish controls the abundance of smaller bodied prey fish, the composition and size distribution of invertebrate grazers, and the production of ephemeral macroalgae. Excluding larger predatory fish, adding nutrients, and removing canopy cover together generated strong increases in algal production. This is the first example of joint control of primary production by higher trophic level predators, nutrient availability, and habitat complexity. Furthermore, we show that declines in larger predatory fish promote algal recruitment, but only in the presence of grazers; excluding invertebrate grazers deleted all significant predator effects. Thus, our results indicate

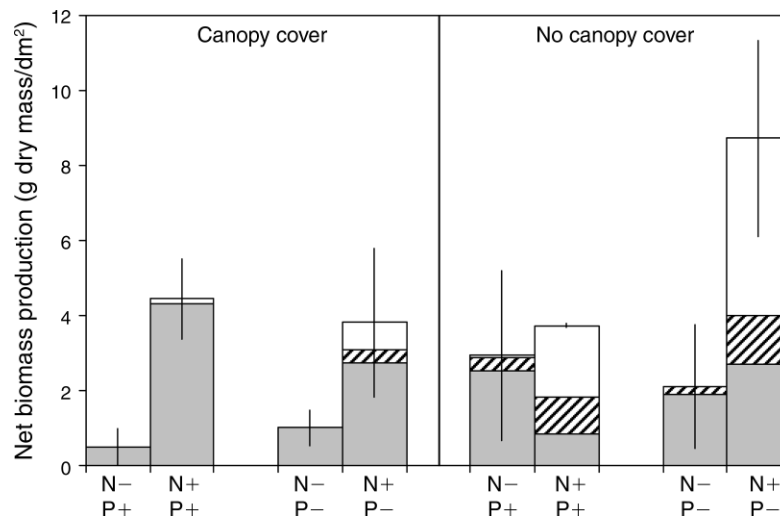


FIG. 8. Effects of exclusion of larger piscivorous fish, nutrient enrichment, and canopy cover on production (mean \pm SE) of ephemeral bloom-forming macroalgae in the 2006 experiment. Abbreviations and bar fills are as in Fig. 6.

TABLE 4. Univariate MANOVA results for the biomass production of macroalgal species from the 2006 experiment.

Source	df	<i>Cladophora glomerata</i>		<i>Pylaiella littoralis</i>		<i>Ulva</i> spp.	
		F	P	F	P	F	P
Predation (P)	1	0.00	0.976	0.20	0.666	7.82	0.023
Nutrient enrichment (N)	1	1.18	0.308	2.97	0.123	38.22	<0.001
Canopy cover (C)	1	0.02	0.897	4.29	0.072	23.57	0.001
P × N	1	0.01	0.929	0.46	0.518	8.29	0.021
P × C	1	0.29	0.606	0.03	0.876	3.18	0.112
N × C	1	2.20	0.176	1.24	0.297	22.77	0.001
P × N × C	1	1.15	0.315	0.01	0.935	3.49	0.099
Error	8						

cascading effects across four trophic levels. Declines in larger predatory fish generate a mesopredator release, increasing the abundance of smaller bodied predatory fish. This mesopredator release subsequently decreases grazer control on algal recruitment through effects on the invertebrate grazer community composition and thereby promotes algal production. In particular, our results provide strong evidence that decreased top-down forcing from regionally depleted predator communities contributes to regionally high abundances of bloom-forming ephemeral algae in the Baltic Sea.

Predatory fish changed invertebrate size and species distributions in both experiments, with negative effects on smaller gastropods in almost all treatment combinations. This indicates that increased predation mainly affected smaller herbivores and not the weight of the whole trophic level. Resulting changes in herbivore composition may have significant effects on grazing rates by loss of complementarity effects if herbivore species diversity decreases (Duffy et al. 2003) or by loss of functionally important herbivore species if selection conditions change from efficient food uptake to predator defenses (see Moksnes et al. 2008). The strong increase of mussels in the predator exclusion cages most probably resulted from the fact that the cages also excluded the main predator on mussels, roach (*Rutilus rutilus*; Lappalainen et al. 2005). In the 2006 experiment, predator and nutrient effects interacted: gastropods increased with nutrient enrichment but only when predatory fish were excluded from the community. This suggests that when we removed the top predators, nutrient enrichment may have shifted the community from a top-down controlled system to a bottom-up controlled system, increasing both primary and secondary producers. This is supported by both smaller bodied fish and herbivores being most abundant in the predator exclusion × nutrient enrichment treatment. In a similar system in the eastern Baltic Sea, Korpinen et al. (2007) provided indications that nutrients may overrule predator control under disturbed conditions, generating switches between top-down and bottom-up control. Thus, the specific changes driving the demonstrated trophic cascade probably depend both on changes in grazer efficiency and an increased influence of bottom-

up control. Here we show that excluding larger predatory fish decreases grazer control of algae. Further studies are needed to explore how the connection between predators and properties of the herbivore community contribute to grazing efficiency.

In addition to nutrient availability and the composition of the fish community, canopy cover also regulated algal production, demonstrating the importance of habitat structure for ecological processes. Canopy-forming species control algal production by shading understory species and attracting grazers and thereby modify resource and consumer control of macroalgae (Eriksson et al. 2006, 2007). In this study, all invertebrates decreased under canopy cover because of whiplash and a “dilution” effect from preferring shelter inside the canopy. Under natural conditions *Fucus vesiculosus*, the canopy species used in this experiment, increases the abundance of the invertebrate community (Råberg and Kautsky 2007), but to detect this we also needed to sample the canopies.

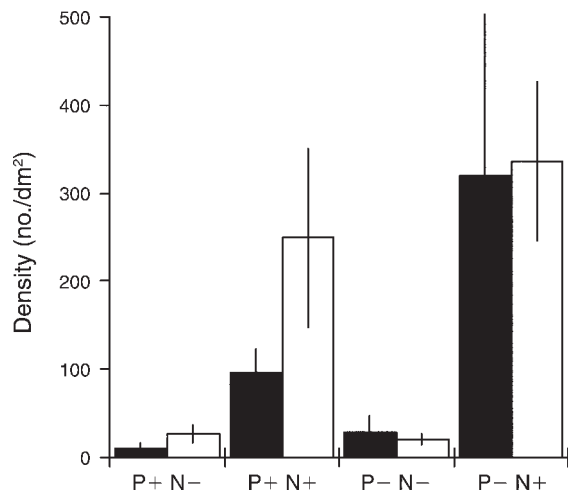


FIG. 9. Effects of exclusion of larger piscivorous fish and nutrient enrichment on algal recruitment (density, mean ± SE). Black bars show algal recruitment in the presence of invertebrate grazers (in open grazer cages), and white bars show algal recruitment in the absence of invertebrate grazers (in closed grazer cages). Abbreviations are as in Fig. 6.

The field study showed two distinct regional ecosystem configurations with either high or low abundances of piscivorous fish. There are several potential feedback mechanisms that may work in concert to maintain a community state with high abundances of smaller predatory fish and high covers of bloom-forming algae in areas with depleted piscivorous fish stocks (Österblom et al. 2007). Increased excretion of nutrients by the large biomass of small-bodied fishes at lower trophic levels may facilitate production of ephemeral algae (Hillebrand and Kahlert 2001, Liess et al. 2006). Small planktivorous fish (e.g., sticklebacks and sprat) compete for prey with younger life stages of piscivorous fish and also predate on their eggs and larvae (e.g., Köster and Möllmann 2000, Hinrichsen et al. 2003, Nilsson 2006). Lower predation rates commonly alter the size structure and condition of prey fish by increased intraspecific competition. The resulting change in food quality also has the potential to produce a negative feedback on piscivorous fish, which potentially prevents the piscivorous fish from recovering to their earlier status (DeRoos and Persson 2002). Experiences from other areas in which top predator fish stocks have been depleted demonstrate the difficulty in restoring these stocks to their earlier levels (Post et al. 2002, Frank et al. 2005).

Studies from both the Baltic Sea and a variety of other ecosystems support the importance of both top-down and bottom-up control of algal production (e.g., Burkepille and Hay 2006, Worm and Lotze 2006). Still, all focus on combating algal blooms has been put on reducing nutrient loads. Models of the Baltic Sea ecosystem indicate that it may take decades before any positive effects can be expected to come from reducing nutrient inputs due to internal loads held in sediments and fixation of nitrogen by cyanobacteria (Munkes 2005). This suggests an ecological regime shift wherein the Baltic Sea is locked in a eutrophied state (Österblom et al. 2007), which implies that present management tools alone (i.e., reduction of nutrient loads) may be insufficient to restore the ecosystem. Nonlinear community responses to nutrients are common in aquatic systems (e.g., Scheffer et al. 2001). For example, in the Great Lakes, macroalgal blooms that were successfully combated by effective reductions in nutrient loads now reemerge due to trophic effects of an invading dreissenid (Hecky et al. 2004). Our results do not in any way disregard the importance of reducing nutrient loads to the Baltic Sea, but they do suggest that effective management also needs to acknowledge top-down effects. Thus, a closer incorporation of fisheries management into the overall environmental management of the Baltic Sea is essential to accomplish reduction of problems associated with increasing primary production.

Remediation efforts to restore stronger stocks of piscivorous fishes could be divided into two main directions. First, traditional fisheries management tools such as catch limitations, gear restrictions, and protec-

tion of key areas from fishing should be enforced. Second, the most essential recruitment areas for piscivorous fishes should be restored and protected. Since the key coastal predators (perch and pike) to a large extent use recruitment areas in freshwaters, a way to enhance their recruitment and simultaneously increase the retention of nutrients would be to restore coastal wetlands. Present efforts to reduce nutrient loading in the Baltic have already partly shifted focus from managing point sources by wastewater treatment plants to managing diffuse runoff from agriculture as the next main target. Based on our findings, managing eutrophication by restoring wetlands could be much more cost efficient if the wetlands were designed to both reduce nutrients and function as recruitment areas for predatory fish. Today, many wetlands do not function as fish recruitment areas due to severe migration obstacles.

To conclude, we demonstrate a connection between the composition of the fish community, nutrient enrichment, and the production of filamentous algae in the Baltic Sea coastal ecosystem. In particular, local declines of larger predatory fish had complementary effects to nutrient enrichment, by promoting the production of benthic algae through loss of grazer control. This indicates that failures to restore eutrophication impacted coastal areas by reducing nutrient loads may depend on failures to acknowledge top-down effects from degenerated predatory fish communities. This is supported by models and large-scale analyses of both the Atlantic and the Baltic Sea offshore systems, where fisheries and eutrophication show strong and interacting effects (Hansson et al. 2007, Vasas et al. 2007, Casini et al. 2008). Our results highlight that community structure determines the responses of marine systems to eutrophication (e.g., Jackson et al. 2001, Worm and Lotze 2006, Myers et al. 2007) and indicate that managing a high trophic diversity of fish communities is important for water quality in near-shore environments. The view emerges that synergistic effects of bottom-up and top-down processes need to be incorporated into future ecosystem management of marine resources.

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APPENDIX A

Photograph of one of the bays used for experimental cages from the field experiment at Askö, western Baltic Sea, Sweden (*Ecological Archives* A019-082-A1).

APPENDIX B

Field abundances of fish determined using different sampling techniques (*Ecological Archives* A019-082-A2).

APPENDIX C

Field correlations between ephemeral macroalgae, young-of-the-year fish, and environmental variables (*Ecological Archives* A019-082-A3).

APPENDIX D

A photograph showing the cleaning of cages of filamentous drift algae during the field experiment at Askö, western Baltic Sea, Sweden (*Ecological Archives* A019-082-A4).