

Bottom–up and cascading top–down control of macroalgae along a depth gradient

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Abstract

On marine rocky shores, macroalgal herbivory is often intense, such that the cascading effects of fish predation may contribute to the control of algal communities. To estimate the magnitudes of top–down and bottom–up control on a macroalgal community, we manipulated the access of carnivorous fish to macroalgal colonization substrates, as well as nutrient availability, at two sublittoral depths. There were three levels of fish manipulation: natural fish community, no fish and the enclosure of one common species, the perch, *Perca fluviatilis*. We found a clear cascade effect of fish predation on both the total density and several individual species of macroalgae, which was more pronounced in deep than shallow water. The density of the dominant grazers, i.e. snails, increased in nutrient-enriched conditions; perch were inefficient in controlling herbivores, and had therefore no cascading effect on algal densities under such conditions. Although nutrients enhanced the growth of opportunistic algae, herbivores, in the absence of fish, inhibited this response. While algal diversity was higher in shallow than in deep water, the enrichment effect was opposite at the two depths with lowered diversity in the shallows and increased at depth. Our results indicate that fish predation is an efficient regulator of meso-herbivores and that its effect thereby cascades onto the producer trophic level such that both perennial and opportunistic algae benefit from the presence of fish. This cascade effect is probably stronger at depth where predation efficiency is less disturbed by wave motion.

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1. Introduction

The debate over plant–consumer interactions, since the “green world” hypothesis, has refined the general understanding of community regulation (Hairston et al., 1960; Menge and Sutherland, 1976, 1987; Fretwell, 1977; Oksanen et al., 1981; Carpenter et al., 1985; Polis and Strong, 1996; Menge et al., 1997; Forrester et al., 1999). The model of Hairston, Smith, and Slobodkin

(1960, hereafter HSS) stated that plants were regulated by abiotic resources, herbivores by carnivores, and carnivores by their food resource, the herbivores. Conversely, the productivity models (Fretwell, 1977; Oksanen et al., 1981) emphasized bottom–up forces in determining the number of trophic levels. This fervent discussion over the HSS model stimulated further research, and led to a form of compromise, i.e. that the main ecosystem types, such as terrestrial, freshwater and marine ecosystems, may have different prevalent mechanisms (Menge and Sutherland, 1976; Carpenter et al., 1985; Hairston and Hairston, 1993; Shurin et al.,

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2002). For example, trophic cascades are more pronounced in aquatic than terrestrial environments, and experiments conducted in marine benthos in particular, have often found strong predator effects on communities (Shurin et al., 2002).

In the case of intertidal rocky shores, Menge and Sutherland proposed an “environmental stress model” (ESM; Menge and Sutherland, 1976, 1987; Menge and Olson, 1990), which takes into account changes in the number of trophic levels along a stress gradient, such as wave exposure, such that in protected sites the trophic structure has more levels than under strong wave motion. The ESM predicts that in physically more benign environments the relative roles of grazing and predation of grazers will increase. This model also suggests that the role of consumption increases lower in the trophic structure; thus, it is more significant in grazer–plant interaction than in carnivore–grazer interaction, where the role of physical factors is greater.

Recent research in aquatic littoral community regulation has integrated top–down and bottom–up views and has tested their combined impact on plant abundance (e.g. Bosman and Hockey, 1986; Hunter and Price, 1992; Menge et al., 1997; Valiela et al., 1997; Forrester et al., 1999; Lapointe, 1999; Heck et al., 2000; Menge, 2000; Nielsen, 2001, 2003). These studies indicate that top–down forces, i.e. predation and grazing, primarily affect the abundance of macroalgae on rocky shores, in stream ecosystems, or the epiphytes on seagrass. However, bottom–up forces increase the growth of opportunistic algae (Valiela et al., 1997; Heck et al., 2000; Nielsen, 2001) and have a strong influence on a regional scale in eutrophicated areas (Lotze et al., 2001), up-welling regions (Menge et al., 1997), or in the vicinity of sea-bird colonies (Bosman and Hockey, 1986). Under the strong joint impact of nutrients and avian predators, Bosman and Hockey (1986) observed lush macroalgal cover with only few limpets, in contrast with the barren areas outside the limited area of those forces. Similarly, Forrester et al. (1999) found a clear cascade in a stream, from fish via mesograzers to algae, and a simultaneous bottom–up effect from nutrients via algae to grazers. Such trophic cascades obviously only occur in relatively simple food chains (Polis and Strong, 1996; Heck et al., 2000). Experiments investigating the relative roles of bottom–up and cascading top–down control in a marine sub-littoral are scarce. The studies on the cascading effects of predators on macroalgae are biased to systems with urchin herbivores (reviews by Sala et al., 1998; Shurin et al., 2002; Borer et al., 2005). Very few studies on systems with snail and crustacean grazers and fish predators exist, although grazer effects

on algae, and consequently potential for cascades, may be very strong in these groups due to their high densities (Sala and Graham, 2002; Korpinen et al., in press).

The control of plant communities has been studied among sites of differing wave exposure (e.g. Lubchenco, 1986; Nielsen, 2001), but variation in top–down and bottom–up control along the depth gradient typical of sub-littoral environments has not previously been studied. Environmental stress, however, decreases with the increasing depth, and the original ESM predicts changes in regulation along the stress gradient: the role of consumption decreases in high-stress habitats (Menge and Sutherland, 1976, 1987; Menge and Olson, 1990). Wave-generated disturbance influences the trophic structure of the shore by affecting herbivore (Nielsen, 2001) and fish (Robles and Robb, 1993) abundance, and by modifying algal species composition by inhibiting the dominance of superior competitors (Lubchenco and Gaines, 1981). Sublittoral depth also influences macroalgal regulation by bottom–up control in terms of both light availability and water motion, which enhance nutrient uptake and algal growth (reviewed by Hurd, 2000; Nielsen, 2003).

In order to examine the influence of the bottom–up effect of nutrients and the cascading top–down effect of carnivore fish predation on the macroalgal community, we manipulated both the access of fish to the macroalgal community and the availability of nutrients at the colonization phase. We were particularly interested in the variation of bottom–up and top–down regulation along the depth gradient. We therefore conducted manipulations at two depths, i.e. at the shallow and the deep end of the bladderwrack (*Fucus vesiculosus*, L.) zone. The fish in our study area are non-herbivorous species, and possible fish effects on macroalgae thus cascade via their regulation of the grazer trophic level. We hypothesized that herbivores limit algae more efficiently in the absence than in the presence of fish. More specifically, we expected algal colonization success and growth to decrease in fish exclosures, compared to that in the presence of fish (hypothesis 1, Fig. 1). We also hypothesized that nutrient enhancement would increase colonization success and growth of opportunistic algae, and that this increase would be particularly high under fish predation, where both the bottom–up and top–down forces favor the algae (hypothesis 2; Fig 1; Bosman and Hockey, 1986; Forrester et al., 1999; Heck et al., 2000). Consequently, we expected non-opportunistic species to suffer due to poorer competitive ability. Our primary interest, however, was the comparison of the two depths, and thus in testing the applicability of the ESM (Menge and Sutherland, 1976, 1987) and the

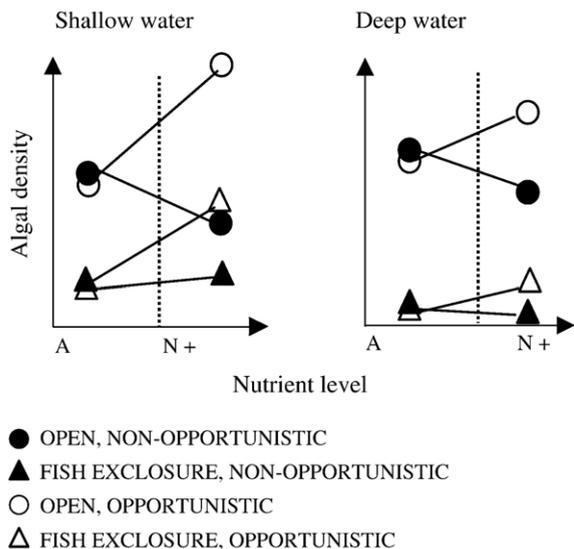


Fig. 1. Hypothetical responses of opportunistic and non-opportunistic macroalgae to fish predation (OPEN versus FISH EXCLOSURE cages) and to nutrient enrichment (A=ambient and N+=nutrient-enriched).

hypothesis of integrated bottom–up and top–down control to explain depth-related variation in the regulation of algal communities (Menge et al., 1997; Forrester et al., 1999; Lapointe, 1999; Heck et al., 2000; Menge, 2000; Nielsen, 2001, 2003). Thus, we further hypothesized that in deep water, top–down control will be more effective in affecting algae than in shallow water due to the less severe wave motion and lower light availability than close to the surface (hypothesis 3; Fig. 1). We expected both fish and mesoherbivores to be efficient regulators in deep water, thereby enhancing the cascade effect. We also expected changes in macroalgal diversity, but these are complex to predict due to the interactive effects of productivity and disturbance in determining species richness (reviewed by Proulx and Mazumder, 1998) and insufficient local information as to the relative strengths of abiotic *versus* biotic impacts in determining species richness. We discuss the results of this experiment by comparing them with a simultaneous experiment conducted at the same site, where we manipulated the herbivore trophic level (Korpinen et al., *in press*), which enabled us to evaluate direct *versus* cascading top–down effects on the algal community.

2. Methods

2.1. Study site

The experiment was carried out in a moderately wave-exposed bay of Jurmo island at the margin of the open sea

in the Archipelago Sea in SW Finland (northern Baltic Sea; 59°49,51' N, 21° 35,26' E) between late-May and mid-August 2003. The Baltic Sea is a tideless brackish-water sea, which is affected by anthropogenic eutrophication. The surface water salinity in the area varies between 5.5 and 6 psu. The surface water concentrations of inorganic nitrogen and phosphate between the summer and autumn vary between 2–200 $\mu\text{g N l}^{-1}$ and 1–40 $\mu\text{g P l}^{-1}$ (database of Finnish Environment Institute); lower concentrations prevail between June and August, increasing during the autumn.

In the study site, the abiotic conditions change quickly with depth. The significant wave height in the nearby pelagic region between May and August was on average <1 m (database of Finnish Institute of Marine Research), and the bay was partly protected from pelagic waves by some islands and skerries. Based on weekly SCUBA diving at the site, wave motion was usually clearly perceptible at a depth of one, but not at 3 m. Similarly, the amount of light decreases rapidly with depth. On a sunny day in July 2003, the proportion of photosynthetically active light off bottom in relation to that at the surface was $86.0 \pm 4.1\%$ (mean \pm SE, $n=3$) and $25.1 \pm 3.6\%$ ($n=4$), at one and 3 m depth respectively (measured with a Li188B integrating photometer, Li-Cor Inc). The actual light intensities were 677 ± 14 and $143 \pm 12 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR, respectively (one-way ANOVA: $F_{1,3}=592.1$, $p<0.001$).

A belt of *F. vesiculosus* with associated filamentous macroalgal species covered the shallow rocky bottom of the bay. The *F. vesiculosus* zone extended from 0.6 m to about 3 m. At 3 m depth, the bottom became more sandy and shelved less steeply than closer to the surface. Mats of loose-lying, partly decaying filamentous algae were common during the summer months.

We did not survey the local fish fauna in detail, but based on SCUBA observations and a local fisherman, we assumed it resembled that published for adjacent islands and the surrounding region. Among the most common species are perch (*P. fluviatilis* L.) and roach (*Rutilus rutilus* L.; Sundell, 1994; Rajasilta et al., 1999; Lappalainen et al., 2000a,b). Perch feed on crustaceans, while roach feed mainly on gastropods and mollusks (Lappalainen et al., 2000b). Gobies (e.g. *Gobius niger* L. and *Pomatoschistus minutus* Pallas) were very abundant at the site (authors' personal observations), and the site is known as a good fishing ground for flounder (*Platichthys flesus* L.). Other potential predators of herbivore fauna include white bream (*Blicca bjoerkna* L.), bream (*Abramis brama* L.), eelpout (*Zoarces viviparus* L.), and bullhead (*Cottus gobio* L.) (Sundell, 1994; Rajasilta et al., 1999;

Lappalainen et al., 2000a,b; J. Hänninen and M. Kurkilahti, (pers. comm.).

2.2. Experimental design

We designed a completely randomized three-way factorial experiment, in which we manipulated both the presence of fish (OPEN, FISH ENCLOSURE and FISH EXCLOSURE) and the nutrient concentration (ambient and enriched) at two sub-littoral depths. Within each factor combination, we used three replicate cages, totaling 36 cages. We placed the cages at depths of 0.5–1 and 2.5–3.5 m (hereafter shallow and deep water); the most diverse algal community is found there and both wave action and light intensity diminish steeply within this range (See Section 2.1. Study site).

The FISH ENCLOSURE and FISH EXCLOSURE cages were steel-framed (40×50×60 cm, length×width×height) with a plastic-covered metal mesh net (mesh size one cm), which allowed free entrance of grazers but prevented fish of a size able to prey on them. The steel-framed OPEN cages (50×70×30 cm, length×width×height) allowed the presence of both herbivores and natural fish predation. In order to ensure that any differences between the fish enclosure and open cages were attributable to the presence/absence of fish rather than some arbitrary cage effects, we also included a treatment with enclosed fish (FISH ENCLOSURE). This was conducted by placing two perch (*P. fluviatilis*, size 18±2 cm [mean±SD]) inside each fish enclosure. This density is high for perch or any single fish species, but may well reflect the overall density of the local fish community (Pihl and Wennhage, 2002; Ziliukas, 2005). Conversely, the feeding activity of captive fish is likely lower than that of the free-ranging ones. After the experiment, we surveyed the stomach contents of the enclosed perch. While the open cages represented the natural system with all predator species present and the fish enclosures had all predators excluded, the fish enclosures had only a single predator species present.

We checked the cages weekly to clean the periphyton from mesh-nets and to inspect and when necessary, replace the perch. We conducted the experiment concurrently with another factorial experiment, where we directly manipulated the entrance of grazers using 1-mm mesh-nets (Korpinen et al., in press). In the context of that experiment, we analyzed the difference between the open cages and cages roofed with a one-mm mesh net. The analyses showed that roofing had no effect on the densities of macroalgal species. In the current experiment, we expected the possible mesh-net effects to be even smaller due to much larger mesh size

and we therefore did not include in the design a treatment level with roofed cages.

The manipulation of nutrient availability had two treatment levels, i.e. ambient and enriched. For the nutrient-enriched treatment, we used 1 kg of a controlled release fertilizer (Osmocote Exact Standard 3–4, 16N:5P:9K, Scotts Company), packed into two elongated diffusion pouches, inside each nutrient enrichment cage (see Worm et al., 2000 for methodology). We replaced the fertilizer pouches after 5 weeks and dry-weighed the old pouches to ensure sufficient release of the fertilizer; over 30% of the original weight of the fertilizer remained at the time of replacement. The ambient and enriched nutrient concentrations (mean±SE) obtained from water samples (pooled over three successive dates between July and September) taken from the cages were 8.14±0.14 ($n=7$) and 108.3±35.7 ($n=21$) $\mu\text{g DIN l}^{-1}$, and 10.6±3.4 ($n=7$) and 25.6±5.67 ($n=22$) $\mu\text{g DIP l}^{-1}$, respectively. The enriched nutrient level of inorganic nitrogen and that of phosphorus thus corresponds to a 12- and 2.5-fold increase respectively of the ambient nutrient concentration. These values lie within the summer and autumn maxima in the study area (See Section 2.1. Study site).

Since we did not want the nutrient enrichment to affect the cages at the ambient nutrient level, we maintained at least a 10-meter distance between cages belonging to different nutrient treatments. This distance was sufficient, as the nutrients clearly differed between the ambient and enriched levels. However, because placing all 36 cages 10 m apart would have required a large area, we aggregated the cages within the same nutrient level into groups of one to three random cages. We had 13 such aggregations; within an ‘aggregate’, we placed the cages 1 to 5 m apart. This aggregation was merely a safety measure against contamination from the nutrient enrichment cages; it does not represent blocks in a statistical sense, and is therefore not included in the analyses.

2.3. Estimation of grazer density

The sub-littoral grazer fauna in the northern Baltic Sea consists of small invertebrates. To estimate the density of grazers in July and September, tiles ($n=16$, size 10×20 cm) were deployed adjacent to each of the cages in both nutrient and depth treatments in June for a period of 4 and 14 weeks. SCUBA divers collected the tiles by enclosing them in mesh-bags. Grazers were brought to laboratory, identified and counted within a day of collection. As the detailed data is presented elsewhere (Korpinen et al., in press), here we present a summary of the most common taxa (Fig. 2).

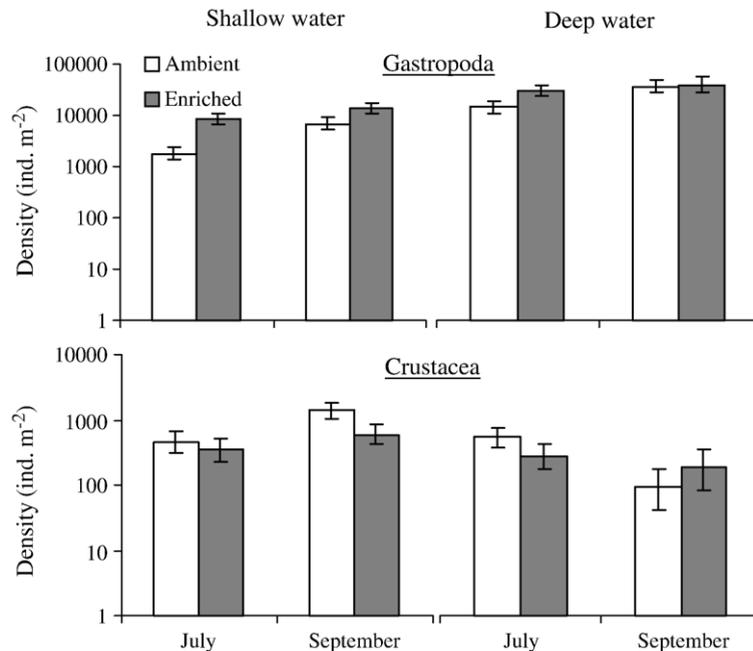


Fig. 2. Density (ind. m⁻²; least squares mean ± SE) of gastropod and crustacean species at the study site under ambient and enriched nutrient conditions in shallow (1 m) and deep (3 m) strata.

2.4. Measuring the algal assemblage

Rough-surfaced concrete tiles (10 × 20 cm) were used as the substrates for monitoring algal colonization and growth. Macroalgal filaments were counted on four random 2 × 2 cm squares from each tile. Each cage contained four tiles, two of which were collected at the two sampling times in early July 2003, 5 weeks after the start, and in mid-August, 5 weeks after the first sampling. A cage was used as a replicate in the statistical analyses, and the number of filaments was therefore summed, or the filament length was averaged, over the two tiles in the cage.

Algae were identified and counted under a dissecting microscope. When the algal density on a square was very high, a sub-sample the size of the microscope view (~0.25 cm²) was randomly taken from the square and its result was extrapolated for the whole square. We counted the algae within 1 to 6 days after transfer from the growing site. Before counting, tiles were stored underwater in a dark room at 4 °C. When the filaments were too small for identification, they were pooled to the nearest possible taxon. For example, small individuals of *Pilayella littoralis* (L.) Kjellman and *Ectocarpus siliculosus* (Dillwyn) (Lyngbye) were pooled as filamentous brown algae. We used these larger taxa in the statistical analysis. Some species were handled at the genus, some at taxon level, e.g. filamentous brown

algae, were combined such that the estimates of diversity and species richness represent minimum values. In August 2003, we also measured the maximum filament length (to 1 mm accuracy) of the dominant species, i.e. the green alga *Cladophora glomerata* (L.) Kützling.

Due to the low species richness of macroalgae in the northern Baltic Sea, species-level effects easily explain characteristics of the community; we therefore present the densities of the five most common taxa in addition to the community variables. We analyzed the treatment effects at the species and/or taxa level choosing the date (of the two sampling dates) when density was highest. Community variables, diversity, species richness and pooled algal density, are presented and analyzed for the more advanced community in August.

2.5. Data analyses

Algal and grazer densities, as well as the count data of stomach contents of the enclosed perch, were aggregated as indicated by the negative binomial distribution of these variables. We therefore used generalized linear models in the analyses, which are based on the maximum likelihood estimation and the hypothesis testing on the χ^2 -distribution. The model fit was evaluated separately for each data set based on the ratio of deviance and degrees of freedom (df); a value

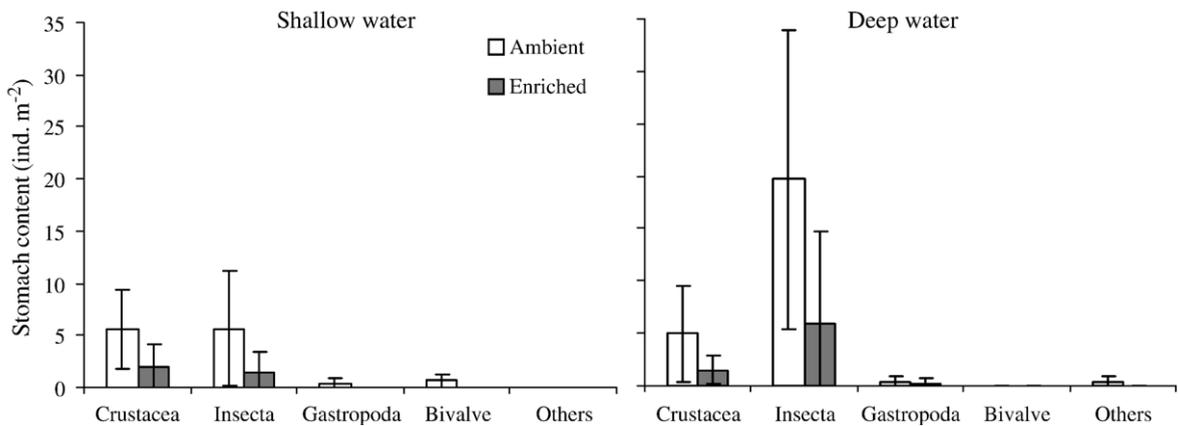


Fig. 3. Stomach contents (ind. per stomach; mean±SE) of the perch *Perca fluviatilis* in the fish enclosure treatment under ambient and enriched nutrient conditions in shallow (1 m) and deep (3 m) strata.

close to one indicates a good fit (SAS Institute, 1999). In addition, we checked the normality of the residual variation. Generalized linear models are more flexible than general linear models; they allow various sample distributions and do not assume homoscedasticity of variances (Dobson, 2003). We ran all the analyses using the SAS GENMOD procedure (SAS Institute, 1999).

In the analysis of algal density, we treated the main and interactive effects of nutrients, depth, and fish treatment as independent factors and conducted the analyses separately for each taxon and for the pooled density of all taxa. In the analysis of grazer densities, we conducted separate analyses for pooled gastropods and pooled crustaceans, with the depth, nutrient treatment, sampling time and their interaction as independent factors. In the analysis of stomach contents of the enclosed perch, we analyzed each food taxon separately although the separate taxa in a stomach are dependent on each other. However, as we were more interested in the differences in diet between the depths and nutrient treatment levels than in differences of abundance between taxa, this posed no concern to the results.

The diversity of the macroalgal community was estimated using both the Shannon–Wiener diversity index (H' , for calculation see Krebs, 1989) and species richness (S). H' and S were calculated from a combined area from two tiles (32 cm²) in each cage. We analyzed the diversity indices, as well as the filament length of *Cladophora glomerata*, using a three-way ANOVA (nutrient × fish × depth) run by the SAS GLM procedure (SAS Institute, 1999). To achieve normally-distributed response variables we log-transformed H' , S and filament lengths, and judged the fulfillment of the homoscedasticity assumption of ANOVA by Levene's tests.

3. Results

3.1. Grazer densities and the diet of the enclosed perch

Gastropods were the most abundant grazer taxon. The pooled density of all gastropod species was higher in September than July ($\chi^2=10.89$, $p=0.001$; Fig. 2). Density was higher in deep than in shallow water ('depth': $\chi^2=23.77$, $p<0.0001$; Fig. 2). Pooled crustaceans were more abundant in shallow than in deep water in September, while in July the densities did not differ between the depths ('depth × time' for pooled crustaceans: $\chi^2=7.09$, $p<0.01$; Fig. 2). Nutrient enrichment increased the abundance of gastropods ('nutrient' $\chi^2=10.82$, $p=0.001$; Fig. 2), whereas the crustacean densities did not differ between nutrient levels ('nutrient' $\chi^2=1.49$, $p>0.1$; Fig. 2).

The perch enclosed into the FISH ENCLOSURE cages evidently ate during the experiment. Perch had eaten mainly insects, i.e. larvae of Hydroptilidae and *Phryganea* spp. [Trichoptera] and adult *Notonecta glauca* L. [Heteroptera], including crustaceans (e.g. *Gammarus*—amphipods and *Idotea*—isopods) (Fig. 3). Insects were consumed more in the deep than in shallow water and at the ambient than at the enriched nutrient level ('depth' $\chi^2=6.88$, $p<0.01$; 'nutrient' $\chi^2=7.00$, $p<0.01$; 'depth × nutrient' $\chi^2=0.01$, $p>0.1$; Fig. 3). Crustaceans were eaten more in the ambient than in the enriched nutrient concentration ('nutrient' $\chi^2=7.77$, $p<0.01$), whereas the amount of eaten crustaceans did not differ between shallow and deep water ('depth' $\chi^2=0.28$, $p>0.1$; Fig. 3). Only a few gastropods (*Hydrobia* sp. and *Lymnea* sp.) and bivalves (*Mytilus trossulus* Gould and *Cerastoderma glaucum* Poiret) were found from the stomach contents (Fig. 3).

Table 1

Statistical analyses on the effects of depth, nutrient enrichment and manipulation of fish presence on algal diversity (H'), species richness (S), and total density in August 2003

Source	Diversity (H')				Species richness (S)			Total density	
	df	MS	F	p	MS	F	p	χ^2	p
Depth	1	0.57	22.9	<0.0001	1.13	8.3	<0.01	5.2	<0.05
Nutrient	1	0.05	1.9	N.S.	0.38	2.8	N.S.	16.6	<0.0001
Fish	2	0.06	2.3	N.S.	0.10	0.8	N.S.	19.7	<0.0001
$D \times N$	1	0.32	12.8	<0.01	0.02	0.1	N.S.	0.6	N.S.
$D \times F$	2	0.001	0.04	N.S.	0.06	0.4	N.S.	9.6	<0.01
$N \times F$	2	0.10	3.9	<0.05	0.06	0.5	N.S.	3.4	N.S.
$D \times N \times F$	2	0.03	1.2	N.S.	0.06	0.4	N.S.	1.1	N.S.
Error	24	0.03			0.14				

H' and S were analyzed using a 3-way ANOVA and total density using a generalized linear model (See Section 2.5. Data analyses). The ratio of deviance to degrees of freedom (df) is a measure of the model fit.

3.2. Macroalgal community-level responses

There was a marked difference in diversity (H') between shallow and deep water particularly in the ambient nutrient treatment: in the deep, H' decreased to about 10–20% of that in shallow water. In the nutrient enrichment, on the other hand, diversity values were quite similar at both depths, about half of those in the ambient nutrient concentration in shallow water ('depth \times nutrient' in Table 1; Fig. 4a,b). The fish manipulation had no main effect on H' (Table 1; Fig. 4a,b), but, in the FISH ENCLOSURE, H' decreased significantly with the nutrient enrichment ('nutrient \times fish' in Table 1; Fig. 4a,b).

Species richness (S) varied from one to five taxa depending on the treatment combination. The shallow assemblages had more species (least squares mean 2.99 [$-0.33, +0.36$ SE], $n=3$) than those of the deep-water (least squares mean 1.03 [$-0.23, +0.25$ SE], $n=3$; 'depth' in Table 1). Nutrient enrichment and fish manipulation had no main or interactive effect on species richness (Table 1).

Total algal density was lowest in the fish exclusion cages (FISH EXCLUSION), thus supporting our first hypothesis ('fish' in Table 1; Fig. 4c,d). Moreover, the cascading effects of fish were even more pronounced in deep than in shallow water, supporting hypothesis 3 ('depth \times fish' in Table 1; Fig. 4c,d). The nutrient enrichment reduced total algal density at both depths ('nutrient' in Table 1; Fig. 4c,d). Although the shallow-water macroalgal assemblage included most of the algal species, it was dominated by *C. glomerata* and filamentous brown algae (Fig. 5). In deep water, the assemblage consisted mainly of *C. glomerata* and the filamentous browns only (Fig. 5).

3.3. Macroalgal species-level responses

The five commonest macroalgal taxa responded differently to the manipulations of nutrient availability and presence of fish, the response often depending on

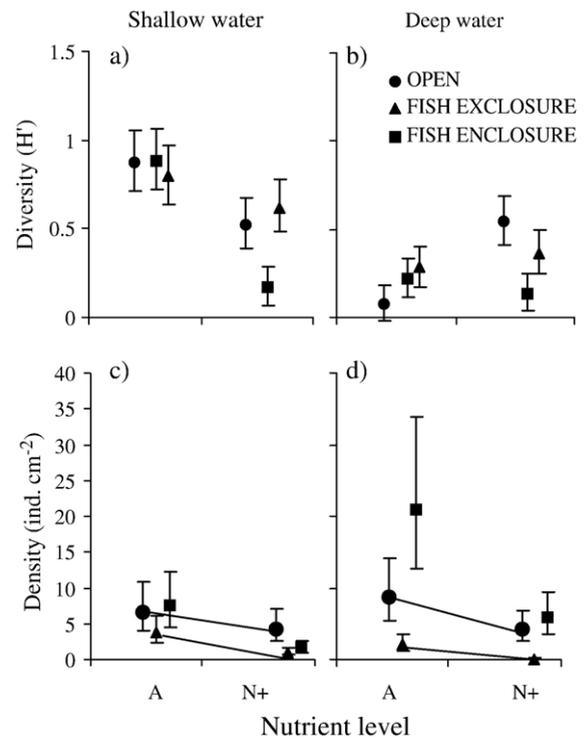


Fig. 4. Algal diversity (H' ; a, b) and total density (ind. cm⁻²; c, d) (least squares mean \pm SE) under natural predation (OPEN), controlled fish predation (FISH ENCLOSURE), and no fish predation (FISH EXCLUSION) in shallow (1 m) and deep (3 m) water and ambient (A) and enriched (N+) nutrient conditions in August 2003. Lines are drawn only for comparison with Fig. 1.

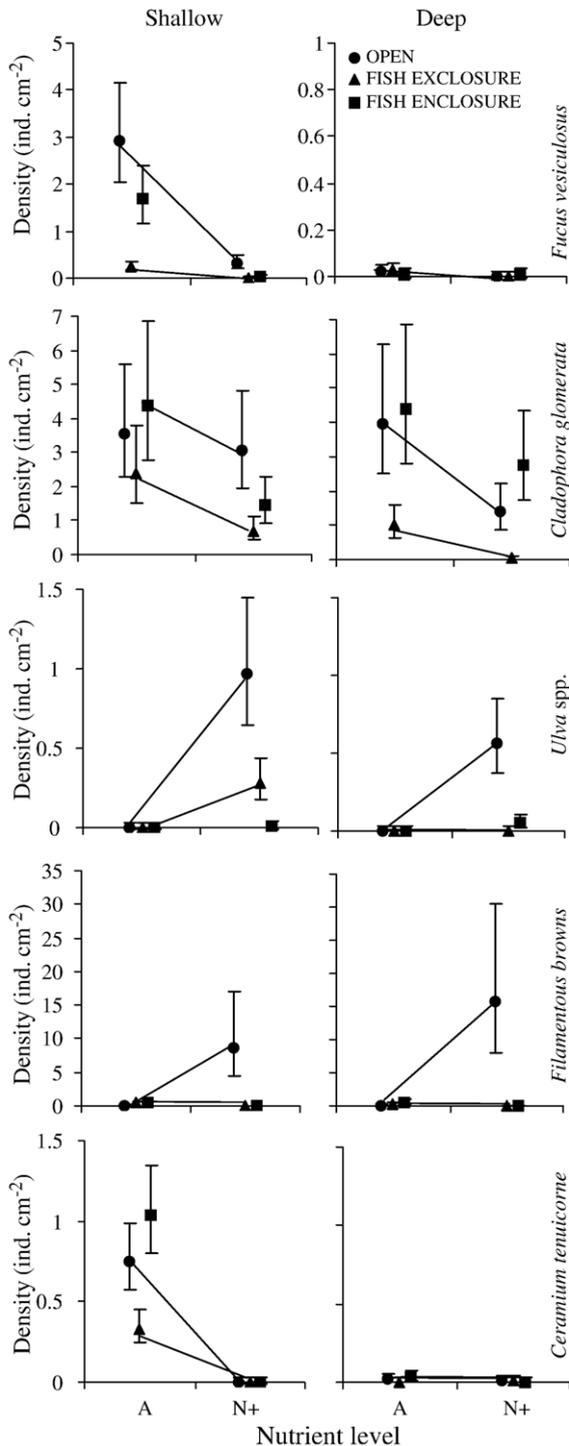


Fig. 5. Density (ind. cm⁻²; least squares mean±SE) of macroalgal species under natural predation (OPEN), controlled fish predation (FISH ENCLOSURE), and no fish predation (FISH EXCLOSURE) as well as ambient (A) and enriched (N+) nutrient conditions in both shallow (1 m) and deep (3 m) water. Filamentous brown algae indicate *Pilayella littoralis*/*Ectocarpus siliculosus*. Lines are drawn only for comparison with Fig. 1. For sampling times, see Table 2.

depth. In general, however, the presence of fish increased the density of all five species (Fig. 5), supporting our first hypothesis. *F. vesiculosus* showed the highest density and was strongly affected by fish during the colonization phase in July (Table 2); the exclusion of fish predation on grazers caused the lowest density, while in both the fish enclosures and open cages the density was higher (Fig. 5). *F. vesiculosus* colonized deep-water substrates poorly and settlement was strongly inhibited by nutrient enrichment; the effects of fish were therefore only found in the shallows at ambient nutrient levels, with significant depth×fish and depth×nutrient interactions (Table 2; Fig. 5).

In the absence of fish, herbivores decreased the density of *C. glomerata*, particularly in deep water (supporting hypotheses 1 and 3; Fig. 5; 'depth×fish' in Table 2). The nutrient enrichment treatment decreased the density of *C. glomerata* ('nutrient' in Table 2; Fig. 5). Nutrient enrichment greatly enhanced the density of the opportunistic *Ulva* sp. and of filamentous brown algae (supporting hypothesis 2; 'nutrient' and 'nutrient×fish' in Table 2; Fig. 5). Under ambient nutrient concentrations, these algae were very rare, and the effects of fish were thus found only in the enriched nutrient treatment ('nutrient×fish' interactions in Table 2). The densities of both these taxa were very much higher (almost 800- and 30-fold for the filamentous browns and *Ulva*, respectively) in the OPEN than in the FISH ENCLOSURE cages; indicating that herbivore control by the natural fish community clearly exceeds that of the two perch in the FISH ENCLOSURE cages (Fig. 5).

Manipulation of fish did not affect the density of the red alga *Ceramium tenuicorne* (Table 2; Fig. 5), probably indicating negligible grazing pressure on this species. *C. tenuicorne* mostly colonized the shallow-water substrates, and settlement was reduced in nutrient-enriched conditions ('depth' and 'depth×nutrient' in Table 2; Fig. 5).

The growth of *C. glomerata*, measured in terms of the length of the filaments, was influenced by the presence of fish, nutrient availability and depth as indicated by a 3-way interaction ('depth×nutrient×fish' $F_{1, 40}=4.25$, $p<0.05$; Fig. 6). In shallow water, nutrient enrichment resulted in better growth. However, this only occurred under natural fish predation in the OPEN cages. In the deep stratum, growth was good in the OPEN cages in ambient nutrient conditions but decreased with nutrient enrichment (Fig. 6).

4. Discussion

4.1. Impact of fish on herbivore grazing

Marine littoral trophic structure is usually characterized as a simplified three or four-level system, where the

Table 2

Statistical analyses on the effects of depth, nutrient enrichment and manipulation of fish presence on densities of specific species or taxa. Analyses were conducted using a generalized linear model

Source	df	<i>Fucus vesiculosus</i> ^a		<i>Cladophora glomerata</i> ^b		<i>Ulva</i> sp. ^b		<i>Filamentous browns</i> ^a		<i>Ceramium tenuicorne</i> ^b	
		28/23		38/24		22/24		36/23		18/24	
Deviance/df		χ^2	<i>p</i>	χ^2	<i>p</i>	χ^2	<i>p</i>	χ^2	<i>p</i>	χ^2	<i>p</i>
Depth	1	34.2	<0.0001	3.4	0.06	1.0	N.S.	<0.1	N.S.	15.8	<0.001
Nutrient	1	19.6	<0.0001	13.4	<0.001	20.1	<0.0001	<0.1	N.S.	28.1	<0.0001
Fish	2	7.8	<0.05	18.9	<0.0001	9.8	<0.01	19.0	<0.0001	1.2	N.S.
<i>D</i> × <i>N</i>	1	8.7	<0.01	0.9	N.S.	1.0	N.S.	<0.1	N.S.	21.5	<0.001
<i>D</i> × <i>F</i>	2	8.7	<0.05	7.0	<0.05	2.8	N.S.	0.6	N.S.	0.2	N.S.
<i>N</i> × <i>F</i>	2	0.2	N.S.	4.0	N.S.	10.5	<0.01	29.8	<0.0001	1.9	N.S.
<i>D</i> × <i>N</i> × <i>F</i>	2	2.6	N.S.	2.3	N.S.	2.8	N.S.	0.2	N.S.	<0.1	N.S.

The ratio of deviance and degrees of freedom (*df*) is a measure of the model fit (See Section 2.5. Data analyses). Each taxon was analyzed at the date of the highest abundance, either in July (denoted a) or in August 2003 (denoted b).

top-level consists of carnivorous birds, piscivorous fish, and/or large sea mammals whose feeding effects cascade down to grazers and finally to macroalgae (e.g. Estes et al., 1998). Previous correlative studies show that carnivores significantly increase algal abundance through a reduction in herbivore density, e.g. sea urchins (Bosman and Hockey, 1986; Estes et al., 1998; Shears and Babcock, 2002). In this study, we focused on the alga–herbivore–fish food chain, where the herbivore trophic level consisted of several, highly abundant mesograzers species: amphipods, isopods and small-sized snails. We demonstrated, in a manipulative experiment, how the macroalgal density and growth depended on fish presence. In the absence of fish, macroalgal densities decreased both during the and shortly after the colonization phase, with the opposite trend under conditions of natural fish predation. Since there are no algivorous fish species in the Baltic Sea, the predation influence of fish on herbivores must have cascaded down to macroalgae. The stomach contents of the enclosed perch showed that they had mainly eaten crustacean mesograzers, which were numerous and effective in consuming macroalgal recruits (Korpinen et al., in press). According to Lappalainen et al., 2000b, the diets among the local fish species differ. Therefore, a wider array of invertebrates was consumed due to natural fish predation, which caused a more consistent increase in the algal densities than predation by perch alone.

The HSS model implied that the herbivores do not regulate plant abundance (Hairton et al., 1960). However, Menge and Sutherland (1987) proposed and provided empirical evidence (Menge et al., 1986) that the role of predation increases the closer we approach the basal level in the trophic structure under focus. In freshwater lakes, Jones and Sayer (2003) found that fish

predation inhibited herbivores and thereby increased periphyton density, but they also showed that herbivory was still more efficient than fish predation in affecting periphyton density, thus supporting the latter. In our experiment, macroalgae benefited from reduced herbivory under fish predation. By comparison, in a companion study where we directly manipulated the access of grazers to the colonization substrates (Korpinen et al., in press), maximum algal recruitment occurred in the herbivore exclosures and the maximum grazing in the fish exclosures. If the total algal density in the maximal grazing treatment (FISH EXCLOSURE) is taken as a baseline, then the achieved algal recruitment in the

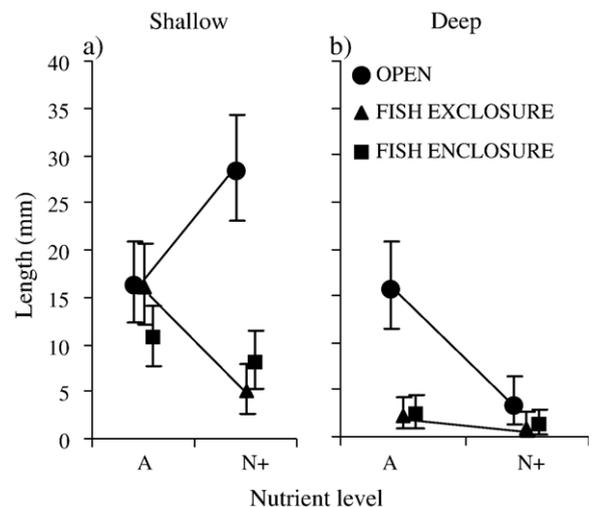


Fig. 6. Maximum filament length (mm; least squares mean±SE) of *Cladophora glomerata* at two depths in August under natural fish predation (OPEN), controlled fish predation (FISH ENCLOSURE) and no fish predation (FISH EXCLOSURE) in combination with ambient (A) and enriched (N+) nutrient conditions.

OPEN treatment, as well as the potential recruitment in the treatment where herbivores were completely excluded was 10- to 62-fold respectively (Korpinen et al., in press). The previous example concerned shallow-water nutrient-enriched conditions, where opportunistic algae were abundant. At ambient nutrient levels in shallow water, increases were 2.6 times (OPEN) and 7 times (grazer enclosure) the baseline level. In deep water, increases were 5.7 times (OPEN) and 15.6 times (grazer enclosure) and 153 times (OPEN) and 445 times (grazer enclosure) the baseline level at ambient and enriched nutrient levels, respectively. These comparisons show that the relief from herbivory provided by natural fish predation is less efficient than artificial respite. This indicates that the role of consumption on algal abundance is of greater magnitude at a lower level in the food chain, i.e. in plant–herbivore rather than in fish–herbivore interactions. Nevertheless, the existence of cascading effects from the third trophic level suggests that local variations in the abundance and structure of the fish community may potentially manifest in the macroalgal community.

Based on surveys of fish communities in nearby areas, the local fish community was diverse (Sundell, 1994; Rajasilta et al., 1999; Lappalainen et al., 2000a,b; J. Hänninen and M. Kurkilahti, pers. comm.). The diets of small littoral fish species as well as flounder include benthic animals, e.g. small snails and juvenile crustaceans (cf. fish diets at www.fishbase.org). The food preferences of some abundant fish species, however, have been studied locally; roach is an efficient consumer of gastropods while the diet of perch contains mainly crustaceans (Lappalainen et al., 2000b). Perch is among the most common species in rocky bladderwrack habitats (Lappalainen et al., 2000a,b), and the abundance of roach has increased significantly in the outer archipelago in SW Finland due to increased eutrophication of the Baltic Sea (Lappalainen et al., 2000a,b). In comparing the efficiency of local fish predation to the effects of enclosed perch individuals, some response variables, particularly at the ambient nutrient level, indicated an impact of roughly similar magnitude. This similarity may indicate that fourth trophic level predators, piscivorous fish and avian predators, have only a minor impact on the carnivore guild at the site.

The density of some algal species collapsed when only perch were present. In nutrient-enriched assemblages, the perch caused a decrease in diversity and a complete disappearance of *Ulva* sp. and filamentous brown algae. There are two possible mechanisms behind this outcome. First, a negative effect of mesh nets in the FISH ENCLOSURE cages and, secondly, differences in top–

down control by multi-versus single-predator systems. We consider the former effect relatively minor, since *C. glomerata* grew well in both the FISH ENCLOSURE and the similar FISH EXCLOSURE cages. Likewise, all the dominant species grew well in the fully-covered herbivore exclusion cages used in the companion study, indicating an absence of cage effects. On the other hand, the perch in our enclosures consumed more crustaceans and insects than gastropods, which is also consistent with the previous studies on perch diet (Lappalainen et al., 2000b). Moreover, nutrient enrichment greatly increased the density of hydrobid snails even in the presence of fish. Therefore, the interactive effect of low predation on hydrobid snails by perch and the increased abundance of the snails with nutrient enrichment may contribute to the lower colonization success of macroalgal spores. Our results suggest that the local predatory fish community was more effective at reducing the altered grazer abundance in the nutrient-enriched conditions than perch alone, thus explaining the low densities of the opportunistic algal species in both the fish enclosures and the perch enclosures.

4.2. Interactive effect of nutrients and fish

Studies evaluating the interactive effects of nutrients and cascading top–down control on three-trophic-level littoral communities are scarce (but see Bosman and Hockey, 1986; Forrester et al., 1999; Heck et al., 2000). In this study, 12-fold fertilization increase caused a decrease in diversity and species richness in shallow water, and an increase in the growth of opportunistic algae. In particular, the opportunistic species, filamentous brown and *Ulva* sp., were able to take advantage of the nutrient enrichment only when grazers were controlled by fish, i.e. when they were favored by both bottom–up and top–down forces, as we hypothesized (hypothesis 2). Not all macroalgal species benefited from nutrient enrichment. Slow-growing species, such as the red alga *C. tenuicorne* and the bladderwrack *F. vesiculosus*, were probably out competed by the opportunistic species and suffered from artificial fertilization. Similarly, the green alga *C. glomerata* decreased in abundance under nutrient-enriched conditions. There may be two reasons behind this reduction: (1) low success in competition with *Ulva* sp. and the filamentous brown algae, and/or (2) increased grazing pressure on germlings of *C. glomerata* by snails, combined with inefficient fish predation on snails. Both of these mechanisms may prevail simultaneously. Firstly, *Ulva* sp. and the filamentous browns grew very densely on nutrient-enriched substrates, whereas at the ambient nutrient level the same algae were absent. Secondly, predatory fish were evidently not able to respond fully to

the greatly increased snail density on nutrient-enriched substrates, as there was no increase in the density of *C. glomerata* (or in the total macroalgal density) in either the OPEN or the FISH ENCLOSURE treatments.

The impact of grazing and fertilization on macroalgal diversity varied with depth. Although diversity was generally higher in shallow than deep water, nutrient enrichment increased diversity in deep water, particularly in the presence of local fish fauna (the OPEN cages). Nielsen (2003) found that in wave-protected tidal pools both macroalgal diversity and cover of fleshy algal species were controlled by both nutrients and herbivores. She concluded that diversity and species richness are reduced by herbivores, but probably increase under nutrient enrichment at low grazer densities (Nielsen, 2003). However, we showed that in shallow turbulent water fertilization decreased diversity despite the fish manipulation. This may indicate that in the relatively eutrophic Baltic coastal waters, increased nutrient availability leads to dominance by the most opportunistic species independently of grazer presence.

4.3. Evaluation of ESM along depth gradient

According to the environmental stress model (ESM; Menge and Sutherland, 1976, 1987; Menge and Branch, 2001), environmental harshness increases the roles of competition and physical factors in structuring the community relative to predation. This has been documented in the rocky intertidal zone among shores differing in wave motion (e.g. Lubchenco, 1986; Nielsen, 2001). However, in their test of other features of the ESM, Menge et al. (1986) did not explore community control along the stress gradient. In the more specific consumer stress model, Menge and Olson (1990) suggested that consumers (i.e. predators or grazers) are more prone to environmental stress than prey (i.e. herbivores or algae).

In this study, we compared the role of fish in herbivore–alga interaction at two depths, which differed in wave strength but also in other depth-related factors such as light availability. Depth had no effect on top–down control by fish on the density of *Ulva* sp. or of the filamentous browns. However, there was a clear difference between the depth strata in top–down control on the density and length of *C. glomerata* as well as on total algal density. The presence of fish did not increase the density and filament length of *C. glomerata* or the total algal density in shallow water, although such top–down control was found in deep water or in nutrient-enriched conditions. The difference between depths was most obvious at the ambient nutrient level. Our results indicate that in shallow water fish did not control herbivores very efficiently, which is consistent with the

ESM predictions. Therefore, our results suggest that in a more physically benign environment such as deep water, the carnivore guild has a greater impact on the herbivore guild, and thereby on algal density and diversity, than in a more wave-exposed environment close to the surface.

5. Conclusions

Manipulation of the presence of fish affected the colonization of macroalgae; the top–down effect cascaded down to the basal level. We also found that the indirect positive effect of fish on algal densities was of lesser magnitude than the direct consumption of algae by herbivores. In addition to the clear top–down control, nutrients also affected algal density and filament length. Bottom–up and top–down influences interacted: in particular, opportunistic species were able to benefit from nutrient enrichment only in the presence of fish. Cascading top–down control also depended on depth, in a manner consistent with the prediction from the environmental stress model. Our results underline the significance of the abiotic environment, such as the depth gradient, in modifying the cascading effects on producers.

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