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REVIEW

Top-down control as important as nutrient enrichment for eutrophication effects in North Atlantic coastal ecosystems

Örjan Östman[1]*, Johan Eklöf[2], Britas Klemens Eriksson[3], Jens Olsson[1], Per-Olav Moksnes[4] and Ulf Bergström[1]

[1]Department of Aquatic Resources, Institute of Coastal Research, Swedish University of Agricultural Sciences, Skolgatan 6, 742 42 Öregrund, Sweden; [2]Department of Ecology, Environment and Plant Sciences (DEEP), Stockholm University, Svante Arrhenius väg 20A, S-106 91 Stockholm, Sweden; [3]Groningen Institute for Evolutionary Life Sciences, GELIFES, University of Groningen, Nijenborgh 7, 9747 AG Groningen, The Netherlands; and [4]Department of Marine Sciences, University of Gothenburg, Box 461, SE-405 30 Göteborg, Sweden

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Summary

1. Seagrass and seaweed habitats constitute hotspots for diversity and ecosystem services in coastal ecosystems. These habitats are subject to anthropogenic pressures, of which eutrophication is one major stressor. Eutrophication favours fast-growing ephemeral algae over perennial macroalgae and seagrasses, causing habitat degradation. However, changes in top-down control, caused by, for example, overfishing, may also have negative impacts on such habitats by decreasing grazer control of ephemeral algae. Meanwhile, systematic analyses estimating top-down effects of predator manipulations across a wide range of studies are missing, limiting the potential use of top-down control measures in coastal management.

2. Here, we review the literature on experiments that test top-down and bottom-up controls in seagrass *Zostera marina* and seaweed *Fucus* spp. food webs in the North Atlantic. Using meta-analysis and meta-regression, we compare effect sizes of consumer and nutrient manipulations on primary producers, grazers and mesopredators.

3. Presence of mesopredators on average doubled the biomass of ephemeral algae through trophic cascades, mainly mediated via negative effects on amphipods and isopods. Of the grazers, gastropods had twice as strong a negative effect on ephemeral algae as amphipods/isopods, but responded weakly to both predators and fertilization. In accordance with theory, top-down effects became stronger with eutrophication.

4. Across studies, top-down effects on ephemeral algae at all trophic levels are on par with eutrophication effects. However, the few studies manipulating piscivorous fish make estimates of their top-down effects uncertain.

5. *Synthesis and applications*. Consistently strong top-down effects in coastal ecosystems call for an integrated ecosystem perspective. Management should consider measures to improve stocks of predatory fish and reduce mesopredators for restoration and conservation of essential seagrass and seaweed habitats, thereby increasing the long-term viability of ecosystem services from coastal habitats.

Key-words: bottom-up, coastal food webs, conservation, eutrophication, indirect interactions, marine fisheries management, meta-analysis, overfishing, restoration, review

Introduction

In shallow coastal waters, perennial seagrass and seaweed beds provide food and shelter for numerous invertebrates and fishes, and the habitats they form are global hotspots for marine diversity and production (Walker & Kendrick 1998; Williams & Heck 2001; Waycott *et al.* 2009; Barbier, Leslie & Micheli 2013). These habitats are exposed to several anthropogenic pressures, such as increasing nutrient levels and physical habitat modification, while

*Correspondence author. E-mail: orjan.ostman@slu.se populations within these habitats may be overexploited (Waycott *et al.* 2009; Worm & Lenihan 2013; Seitz *et al.* 2014). As a result, seagrass beds have declined globally by up to 7% per year since 1990 (Waycott *et al.* 2009) and perennial macroalga (e.g. *Fucus* spp.) habitats have decreased in many coastal areas (Kautsky *et al.* 1986; Vogt & Schramm 1991; Munda 1993). One well-recognized major human-induced threat is enhanced nutrient levels resulting in increased biomass of ephemeral micro- and macroalgae, causing shading and oxygen deficiency of perennial plants and algae (Walker & Kendrick 1998; Williams & Heck 2001; Berger *et al.* 2004; Wahl *et al.* 2011; Duffy, Hughes & Moksnes 2013). More recently, overfishing of large predatory fish has also been suggested to contribute to the decline and degradation of seagrass and seaweed habitats (Eriksson *et al.* 2011a; Baden *et al.* 2012). Loss of top predators results in a mesopredator release, which reduces grazer density and increases fouling by ephemeral algae (Heck *et al.* 2000; Williams & Heck 2001; Korpinen *et al.* 2007; Moksnes *et al.* 2008; Eriksson *et al.* 2009; Duffy, Hughes & Moksnes 2013).

Studies conceptualizing and quantifying bottom-up and top-down processes are readily available for both seagrass and seaweed food webs (e.g. Williams & Heck 2001; Hillebrand 2002; Hughes *et al.* 2004; Korpinen *et al.* 2007; Eriksson *et al.* 2011a; Poore *et al.* 2012; Wahl *et al.* 2011; Duffy, Hughes & Moksnes 2013). The evidence of positive bottom-up effects of nutrients on biomass of ephemeral algae and top-down control by invertebrate mesograzers (amphipods, isopods and gastropods) on the total biomass of all primary producers is mounting (Hillebrand 2002, 2009; Hughes *et al.* 2004; Wahl *et al.* 2011; Poore *et al.* 2012; Duffy, Hughes & Moksnes 2013; Reynolds, Richardson & Duffy 2014). In addition, there is both correlative and experimental field evidence of cascading effects from mesopredators and piscivores on seagrass and seaweed biomass (Heck *et al.* 2000; Moksnes *et al.* 2008; Eriksson *et al.* 2009, 2011a; Baden *et al.* 2010, 2012; Sieben, Rippen & Eriksson 2011). However, the cascading effects of loss of piscivorous fish can have a wide range of consequences for perennial vegetation depending on the feeding biology of dominant mesopredators and mesograzers (reviewed by Duffy, Hughes & Moksnes 2013). Mesopredators may have a negative effect on perennial macrophytes by reducing mesograzers that control fast-growing ephemeral algae, as described by the ‘mutualistic mesograzer’ model (*sensu* Duffy, Hughes & Moksnes 2013). Alternatively, mesopredators may have positive effects on perennial macrophytes if they: (i) reduce the density of mesograzers that feed (e.g. limpets) or foul (e.g. tube-building amphipods) the perennial macrophytes (Lewis & Anderson 2012), or (ii) feed directly on ephemeral algae (Heck *et al.* 2000). Further, the functional diversity and complex trophic interactions in the food web (e.g. omnivory, intraguild predation) may affect the strength and penetrance of trophic cascades (Strong 1992; Abrams 1993; Duffy 2002; Duffy, Richardson & France 2005; Duffy *et al.* 2015). Thus, simple models of food web interactions cannot necessarily be generalized from one area to another. Consequently, there is a need to improve our understanding of factors that regulate bottom-up and top-down processes in coastal ecosystems, and assess whether general predictions can be made for different systems. Although there are many food web models and studies available, few syntheses are available, and top-down effects of mesopredators and piscivorous fish have not been estimated across studies before. This information is crucial for providing advice to management on how to deal with top-down processes in the context of eutrophication mitigation.

Here, we use a meta-analytical approach to estimate effect sizes of top-down effects of consumers (grazers, mesopredators and piscivores) on different trophic levels and guilds in temperate seagrass and seaweed food webs, and compare these with effect sizes of experimental fertilization. We restrict our analysis to *Zostera marina* (L.) and *Fucus* spp. habitats in the North Atlantic, as these represent structurally similar food webs with gastropods, amphipods and isopods as the main grazers of ephemeral algae, and crabs, shrimp and smaller fish as mesopredators. In large parts of this area, large piscivorous fish like gadoids, tunas and sharks have declined during the last decades, which is believed to have resulted in a mesopredator release (Korpinen *et al.* 2007; Myers *et al.* 2007; Eriksson *et al.* 2011a; Duffy, Hughes & Moksnes 2013; McCain *et al.* 2016). To also infer what factors regulate the strength of trophic cascades, we conduct meta-regressions with nutrient levels, abiotic factors and number of trophic levels as covariates of effect sizes. By tracking the main paths of trophic cascades and quantifying their strength in relation to bottom-up effects, we finally discuss how management of top-down processes may be used to relieve the negative consequences of eutrophication.

Materials and methods

We identified the available scientific literature on top-down and/or bottom-up experiments in coastal seagrass *Zostera marina* and seaweed *Fucus* spp. habitats using the ISI Web of Science Core Collection data base (1945–2014). The following search string in the topic was used: (graz* or herbiv*) and exp* and coast* and (macrophyte* or alg*or seagrass* or seaweed* or *Zostera* or *Fucus*), resulting in 296 hits. Only studies conducted in the northern part of the Atlantic Ocean, including the Baltic Sea and that contained either *Fucus* spp. or *Zostera marina* and ephemeral macro- and microepiphytic algae were used. Consequently, we excluded studies that did not involve ephemeral algae (e.g. mesocosm experiment with *Zostera* or *Fucus* spp. as sole primary producer). In addition, we searched through previously published reviews and meta-analyses on top-down and bottom-up effects in coastal ecosystems for additional studies (Hillebrand 2002, 2009; Hughes *et al.* 2004; Korpinen *et al.* 2007; Gruner *et al.* 2008; Wahl *et al.* 2011; Poore *et al.* 2012; Duffy, Hughes & Moksnes 2013). In total, we included data from 48 independent studies (but each study included several different experiments (Table S1 in Supporting Information), for which we recorded the following eight variables: (i) type of experiment (mesocosm, enclosure, exclosure, ambient), (ii) substrate type (soft, hard, mixed), (iii) volume and (iv) area of experimental unit (ranging~1 L to >600 m^3), (v) average water temperature (7–27 °C), (vi) salinity (5–32 psu), (vii) duration of experiment (4–250 days) and (viii) season (spring, summer, autumn or whole season). For each treatment (fertilization or density manipulations of different consumers), we recorded average treatment levels, standard errors and sample size for the focal groups. If values were not available in tables, we used the ruler in Adobe Acrobat to estimate means and standard errors (SE) from figures. In a few cases where SE was not presented, we obtained data directly from authors. In addition, we collected information on ambient and treatment N and P concentrations as μM dissolved N or P, and grazer abundances. Only 10 studies reported abundances of mesopredators, which gives too little statistical power to be meaningful in metaregressions with several explanatory variables.

To better reveal how bottom-up and top-down effects penetrate the foods, we divided trophic levels into different groups. Ephemeral algae were divided into macroalgae (epiphytic or mat-forming filamentous or sheath-like algae) and microephiphytes (unicellular algae, for example diatoms), because they are to a large extent eaten by different grazers and represent different energy paths in the food web (Råberg & Kautsky 2007; Eriksson *et al.* 2011b). Ephemeral macroalgae were further divided into green and red/brown algae because of their different light requirement, growth and palatability (Eklöf *et al.* 2012). Grazers were divided into crustaceans (amphipods and isopods) and gastropods, as the two groups have different capacities to graze different algal species and respond to blooms of ephemeral algae, and may also show differences in vulnerability to predation (Eklöf *et al.* 2012). Amphipods and isopods often have a short generation time with direct development allowing them to respond quickly to local blooms of ephemeral algae. They are also mobile swimmers that feed by chewing and can graze mats of ephemeral macroalgae, which may not be accessible to gastropods. In contrast, gastropod grazers are slow-moving crawlers that typically feed by grazing and have longer generation times that often involve pelagic larval stages. Mesopredators were divided into fish and crustaceans (crabs and shrimps), and the most common mesopredators in the studies were stickleback, gobies and blue crab. The most common piscivorous fish species were cod, pike and large perch.

We estimated average effect size of treatments as log response ratios, $LRR = \ln(X_t/X_c)$, where X_t is mean treatment level and X_c is mean level in controls (Hedges, Gurevitch & Curtis 1999; Gruner *et al.* 2008). A within-study, variance-weighted mixed-model meta-analysis was applied to estimate the average effect size of treatments with the respective 95% confidence intervals, CI (Hedges, Gurevitch & Curtis 1999; Hillebrand 2009). For groups and treatments with low sample sizes (<30), we used standard errors corrected for low sample size (Hedges, Gurevitch & Curtis 1999). If 95% CI did not include zero, the average effect size was considered to be significant (at $\alpha = 0{\cdot}05$). To avoid pseudo-replicating studies that (in addition to controls) included more than one treatment level (e.g. low, medium and high nutrient or grazer levels), we only included the ‘high’ level if two levels were present, or the ‘medium’ level if three levels were assessed (high-level nutrient additions were extremely high in some studies of three levels of nutrient additions so we always chose medium levels to be consistent; no study had more than three treatment levels). However, several treatments from the same study were included if they were qualitatively different (e.g. presence/absence of grazers or mesopredators). We also included several observations from the same study if they were done at different points in time (>30 days from the end of one experiment to the start of the next) or at different sites (>50 km apart), but each time point/site was then treated as a separate experiment (i.e. it did not affect within-experiment variation but only between-experiment variation). From the studies that had done full factorial manipulations of nutrients and consumers, we estimated the interaction term of nutrient and grazing/predation effects (for details, see Appendix S1).

As manipulated levels of nutrients and biomasses of grazers and mesopredators differed between studies, we wanted to study how different experimental levels influenced effect sizes. We therefore did meta-regressions, a technique that also assesses the influence of continuous predictor variables on effect size in meta-analyses, which accounts for the non-independence of multiple experimental levels in a study (Gurevitch & Hedges 1999; Poore *et al.* 2012). This also allows accounting for other variables potentially confounding the results between studies. Specifically, we tested the influence, measured as *t*-values, of (i) continuous treatment variables (dissolved inorganic nitrogen [*DIN_T*], phosphorus [*DIP_T*], and grazer biomass in treatments [*G_T*]), (ii) ambient grazer biomass [*G_C*], (iii) ambient dissolved nitrogen [*DIN*], phosphorous [*DIP*], salinity [*Salinity*] and temperature [*Temp*], and (iv) the duration of experiment [*Days*], on effect sizes (see also Poore *et al.* 2012). In the meta-regressions, we use biomass, mg ash free dry weight (AFDW) per square metre using the conversion rates in Table S2, as a common unit rather than abundance as the size differs between different grazer species. For gastropods, we excluded the estimated weight of the calcareous shell in the calculations of AFDW. Experimental type ([*ExpType*]; exclosure, enclosure/mesocosm, open cage) and different functional groups [*Grazer* or *Algae groups*] were used as categorical variables in the meta-regressions. Initially, we wanted to include the number of trophic levels as an explanatory factor, but the importance of bottom-up and top-down effects are likely not linear responses to the number of trophic levels (Oksanen *et al.* 1981). Therefore, we instead used odd- vs. even-numbered food chain lengths as a categorical variable. The rationale here was that for odd-numbered food chains, primary producers and every second trophic level above (including mesopredators) are primarily bottom-up controlled and herbivores are top-down controlled, whereas for even-numbered food chains, the opposite pattern may exist. Variation in *LRR* was analysed in relation to categorical factors and continuous predictor variables using the ‘lmer’-function in the *lme4* package of R. 3.1.1 (Bates *et al.* 2014). Predictors were set as fixed factors and experiment as a random factor. All treatments of a study were included in the model even if they had more than one treatment level + control, as different levels could be set as a covariate and experiment as a random factor (to account for within-experiment dependency of treatments). To select the fixed factors most relevant for explaining variation in effect size of a treatment, we, using a backward selection process, removed the factor with the highest *P*-value in an ANOVA, using the ‘car’-function for R (Fox & Weisberg 2011), until only significant factors ($P < 0{\cdot}05$) remained. To visualize the results from the meta-regression, we show partial regressions using the ‘visreg’-package for R (Breheny & Burchett 2012) and calculate partial r^2-values for the fixed factors using the ‘MuMIn’-package for R (Barton 2016).

Results

EPHEMERAL MACROALGAE

Across all studies, the magnitudes of top-down and bottom-up controls on ephemeral macroalgae were similar. On average, nutrient additions ($LRR = 0{\cdot}92 \pm 0{\cdot}39$; mean ± 95% CI; $P < 0{\cdot}001$; $N = 56$; Fig. 1a) and mesopredators ($0{\cdot}76 \pm 0{\cdot}43$; $P < 0{\cdot}001$; $N = 24$; Fig. 1a) approximately doubled, whereas grazers halved the biomass of ephemeral macroalgae ($-0{\cdot}72 \pm 0{\cdot}10$; $P < 0{\cdot}001$; $N = 77$; Fig. 1a). Piscivorous fish had only been manipulated in six experiments, and although the mean effect size of top-down control of piscivorous fish on the biomass of ephemeral macroalgae was negative, it was only marginally significant ($-0{\cdot}51 \pm 0{\cdot}055$, $P = 0{\cdot}06$; Fig. 1a).

Meta-regressions showed that the positive bottom-up effect of nutrient additions on ephemeral macroalgae increased with treatment nitrogen levels ($t_{99} = 6{\cdot}1$, $P < 0{\cdot}001$; Fig 2a) and was larger in odd-level than in even-level food chains ($t_{99} = 3{\cdot}7$, $P < 0{\cdot}001$; Fig. 2a, Table S3). After controlling for nitrogen, there was no significant treatment effect of phosphorus on ephemeral macroalgae ($t_{98} = -0{\cdot}4$, $P = 0{\cdot}7$). The top-down effects of grazers and mesopredators on ephemeral macroalgae were amplified with increasing dissolved nitrogen levels in treatments ($t_{95} = -2{\cdot}4$, $P = 0{\cdot}02$ and $t_{17} = 3{\cdot}8$, $P = 0{\cdot}001$, respectively; Fig 2b,c, Table S3). The results from the experiments crossing nutrient additions with consumer manipulations indicated a larger top-down effect of grazers, but not of mesopredators or piscivorous fish, on ephemeral macroalgae in the presence of nutrient additions than in controls (Appendix S1).

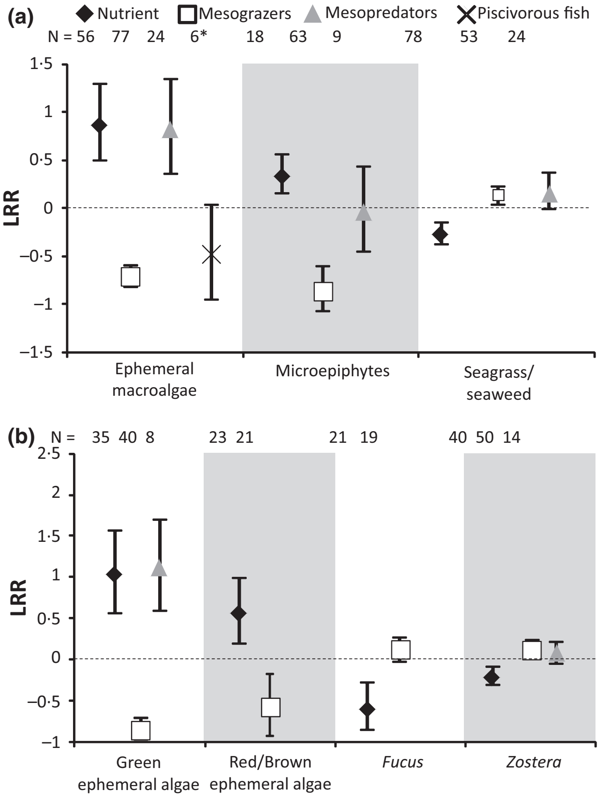

Fig. 1. Mean effect sizes (log response ratios, *LRR*) of treatments. (a) *LRR* of bottom-up effects (nutrients, filled diamonds), and top-down effects (grazers = open squares; mesopredators = grey triangles; piscivorous fish = crosses) on the different main groups of primary producers in coastal food webs from experimental studies. (b) *LRR* of bottom-up and top-down effects divided for specific groups of ephemeral macroalgae (see Materials and methods) and *Fucus*/*Zostera*. Error bars indicate 95% confidence intervals. N indicates the number of experimental studies used in the calculation of *LRR*.

Both nutrient addition and grazers had larger average effect sizes on green macroalgae than on red or brown ephemeral macroalgae (nutrients: $1{\cdot}08 \pm 0{\cdot}52$, $N = 35$ vs. $0{\cdot}59 \pm 0{\cdot}40$, $N = 23$; Grazers: $-0{\cdot}83 \pm 0{\cdot}1$, $N = 40$ vs. $-0{\cdot}55 \pm 0{\cdot}37$, $N = 21$; Fig. 1b). The meta-regressions revealed that the positive bottom-up nutrient effect on green macroalgae increased with increasing nitrogen levels ($t_{35} = 6{\cdot}0$; $P < 0{\cdot}001$), and tended to be larger in food chains with one or three trophic levels than those with two or four trophic levels ($t_{35} = 1{\cdot}8$, $P = 0{\cdot}07$). The positive bottom-up effect of nutrients on red and brown ephemeral macroalgae was stronger in the absence of grazers ($t_{19} = 3{\cdot}6$, $P < 0{\cdot}001$), but was not related to nitrogen or phosphorus treatment levels (Table S2).

Of the two grazer groups, gastropods ($-1{\cdot}01 \pm 0{\cdot}53$, $N = 18$) had a twice as large negative top-down effect on ephemeral macroalgae as amphipods/isopods ($-0{\cdot}47 \pm 0{\cdot}35$, $N = 28$; Fig. 3). The negative top-down effect of amphipods/isopods on ephemeral macroalgae was stronger with increasing phosphorus (ambient or added) levels ($t_{35} = -5{\cdot}2$, $P < 0{\cdot}001$, Fig. 2d). Too few observations ($n = 12$) were available for meta-regressions to be meaningful for estimating the effect of gastropods on ephemeral macroalgae.

MICROEPIPHYTES

Across studies, microepiphytes were more strongly affected by top-down effects from grazers ($-0{\cdot}96 \pm 0{\cdot}15$, $P < 0{\cdot}001$, $N = 63$; Fig. 1a) than bottom-up effects from nutrients ($0{\cdot}35 \pm 0{\cdot}23$, $P = 0{\cdot}005$, $N = 18$; Fig. 1a). There were similar negative top-down effects of gastropods ($-0{\cdot}95 \pm 0{\cdot}25$, $N = 11$) and amphipods/isopods ($-0{\cdot}98 \pm 0{\cdot}25$, $N = 24$; Fig. 3) on microepiphytes. The average effect size of mesopredators on microepiphytes was close to zero, but sample size was low ($0{\cdot}01 \pm 0{\cdot}44$, $N = 9$; Fig. 1a). No study quantified the effect of predatory fish on microepiphytes. Meta-regressions showed that the positive bottom-up effect of nutrients on microepiphytes increased with increasing treatment nitrogen levels ($t_{21} = 7{\cdot}3$; $P < 0{\cdot}001$) and that the negative effect of grazers became stronger

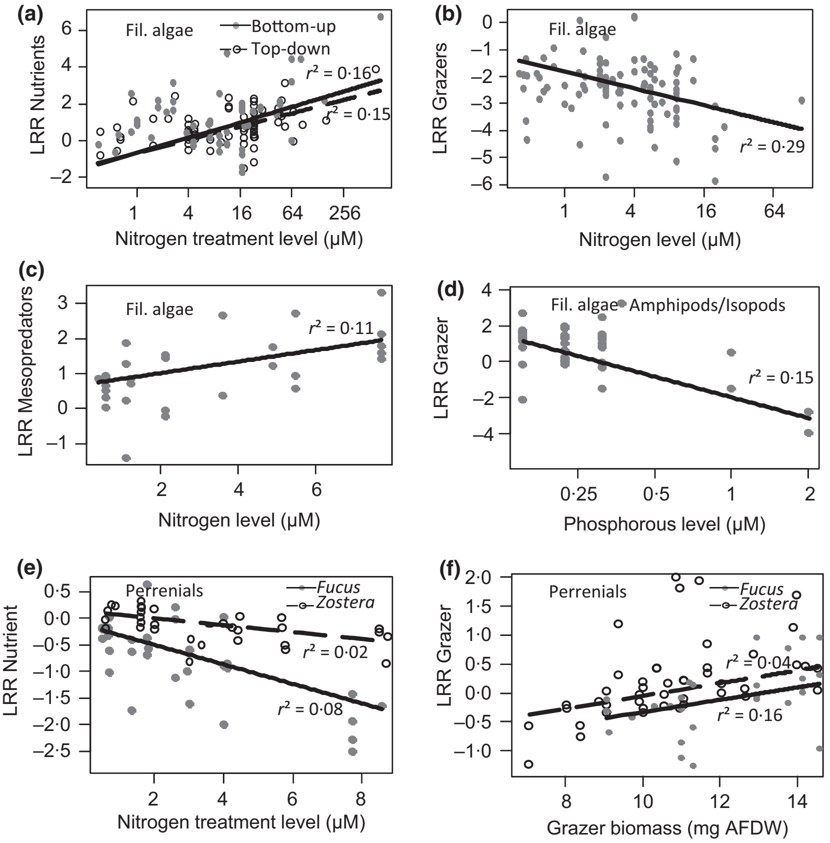

Fig. 2. Partial regressions of effect size, *LRR* (log response ratios), from the meta-regressions. In covariates are (a–e) nutrient levels and (f) grazer abundance. (a–d) show results of different covariates on effect size of different treatments on filamentous algae. In (a), *LRR* of filamentous algae is separated for when bottom-up controlled (primary producers alone or mesopredators as the top trophic level; solid circles and full line) and top-down controlled (grazers or piscivorous fish as the top trophic level; open circles and hatched line). (e–f) show results of covariates on the effect size of nutrient additions and grazers on *Fucus* (solid) and *Zostera* (open). r^2-values are partial r^2-values for the fixed variable calculated from the mixed model using the MuMln package in R 3.1.1.

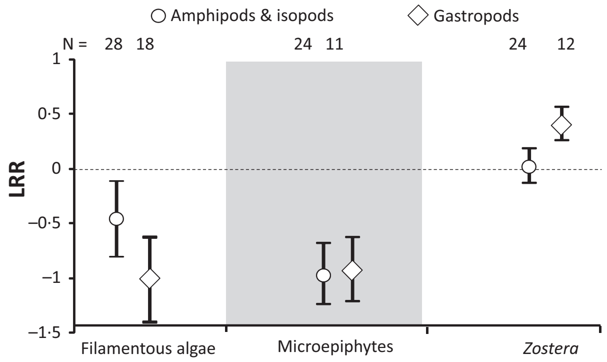

Fig. 3. Mean effect size (*LRR*) of grazer groups, on algae and *Zostera*. Too few studies to estimate effects on *Fucus* spp. Error bars indicate 95% confidence intervals. N indicates the number of experimental studies used in the calculation of *LRR*.

with increasing treatment grazer abundance ($t_{56} = -2{\cdot}0$; $P = 0{\cdot}05$; Table S3).

ZOSTERA/FUCUS

Perennial macrophytes as a group responded more strongly to bottom-up effects of nutrients than top-down effects of consumers. Nutrient additions had a negative net effect on seagrass/seaweed (−0·25 ± 0·10, $P < 0{\cdot}001$, $N = 50$, Fig. 1a), but *LRR* was on average three times stronger for *Fucus* (−0·57 ± 0·29, $P < 0{\cdot}005$, $N = 21$; Fig. 1b) than for *Zostera* (−0·18 ± 0·11, $P = 0{\cdot}002$, $N = 40$; Fig. 1b). Meta-regressions (Table S3) indicate that the negative nutrient effects on *Fucus* and *Zostera* increased with increasing treatment nitrogen levels ($t_{32} = -2{\cdot}2$, $P = 0{\cdot}03$, and $t_{39} = -2{\cdot}2$, $P = 0{\cdot}03$; Fig. 2e). Results from full factorial experiments did, however, not indicate any interactive effects of bottom-up and top-down manipulations on seagrass and seaweed (Appendix S1).

Across all studies grazers had relatively small but significant positive net top-down effects on seagrass/seaweed (0·12 ± 0·09, $P = 0{\cdot}01$, $N = 69$; Fig. 1a), which were similarly strong for *Zostera* (0·12 ± 0·11, $P = 0{\cdot}03$, $N = 50$) and *Fucus* (0·13 ± 0·14, $P = 0{\cdot}09$, $N = 19$; Fig. 1b). The meta-regression revealed the positive top-down effect of grazing on *Fucus* and *Zostera* increased with increasing grazer biomass ($t_{28} = 2{\cdot}1$, $P = 0{\cdot}05$ and $t_{57} = 3{\cdot}3$, $P = 0{\cdot}002$, respectively; Table S3), but was not related to nitrogen or phosphorus levels (Table S3). Across all studies on *Zostera*, the positive top-down effect of grazing depended on gastropod abundance (0·42 ± 0·12; $P < 0{\cdot}001$, $N = 12$), while the average effect of amphipods/isopod abundance was non-significant (0·07 ± 0·16, $P = 0{\cdot}5$, $N = 24$; Fig. 3). Only one and three studies had separated *Fucus* responses to manipulation of amphipods/isopods and gastropods, respectively, so a comparison between grazer groups was not meaningful. Mesopredators had a non-significant effect on seagrass/seaweed

(0·09 ± 0·15, P = 0·2, N = 24; Fig. 1a). No study had estimated the effect of piscivores on seagrass/seaweed.

CONSUMERS

Across all studies and grazer groups, grazer abundance was more strongly affected by top-down than bottom-up control. Nutrient addition had no significant bottom-up effect on total grazer abundance (0·07 ± 0·17, P = 0·4, N = 47; Fig. 4a) or abundance of gastropods alone (0·07 ± 0·29, P = 0·6, N = 19), but had a positive effect on amphipod/isopod abundance (0·23 ± 0·22, P = 0·04, N = 33; Fig. 4b). Meanwhile, mesopredators had a negative top-down effect on total grazer abundance (−0·74 ± 0·38, P < 0·001, N = 42; Fig. 4a) and on amphipod/isopod abundance alone (−1·28 ± 0·49, P < 0·001, N = 25; Figs 4b and 5), but no significant effect on gastropod abundance (0·23 ± 0·49, N = 15; Figs 4b and 5). The negative top-down effect of mesopredatory fish on amphipods/isopods (−1·90 ± 1·16, P = 0·005, N = 10) was twice as strong as the effect of crabs (−0·79 ± 0·62, P = 0·02, N = 10; Figs 4b and 5). Piscivorous fish abundance (10 studies) had a marginally significant positive top-down effect on grazer abundance (0·36 ± 0·37, P = 0·057; Figs 4a and 5). Only four experiments had quantified top-down effects of piscivorous fish on mesopredators, and although mean effect size was numerically large, so were the confidence intervals (−0·71 ± 2·0; Fig. 1a). The full factorial studies of nutrients and piscivorous fish indicated a marginally significant interactive effect (0·32 ± 0·34, P = 0·059, N = 21) on intermediate trophic levels (grazers and mesopredators lumped to increase sample size; Appendix S1).

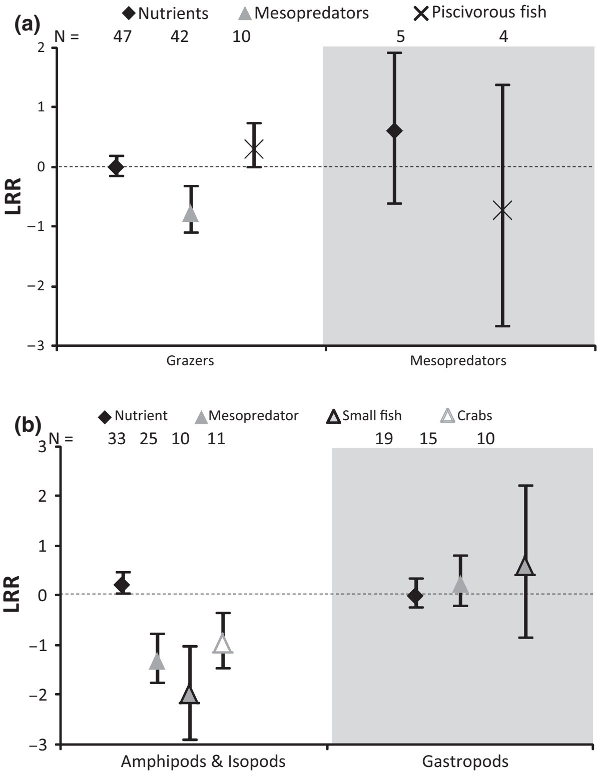

Fig. 4. Mean effect size, *LRR* (log response ratios), of treatments on higher trophic levels. (a) *LRR* of nutrients, mesopredators and piscivorous fish on mesograzers and mesopredators in coastal food webs. (b) *LRR* of nutrient and different mesopredators on two functional groups of mesograzers (amphipods/isopods vs. gastropods) in coastal food webs. Error bars indicate 95% confidence intervals. *N* indicates the number of experimental studies used in the calculation of *LRR*.

Discussion

The results of this study suggest that top-down control is evident across all trophic levels in seagrass and seaweed habitats in the North Atlantic and that these top-down effects are at least as important as nutrient effects for the structure of coastal food webs. The effect sizes of nutrient and grazer manipulations were on par with effect sizes reported in previous meta-analyses on ephemeral algae and *Zostera* (Hillebrand 2002, 2009; Hughes *et al.* 2004; Poore *et al.* 2012). Regarding *Fucus*, our analysis reports considerably stronger negative effects of nutrients and positive effects of grazers than Wahl *et al.* (2011). In contrast to that study, we only included experiments with *Fucus* if there was ephemeral algae present, not only to estimate the direct effects on *Fucus* but also to include the indirect effects from competition with ephemeral algae. Despite the fact that North Atlantic coastal food webs have functionally heterogeneous species at each trophic level, omnivorous species, and intraguild predation, which could all dilute top-down effects, we found trophic cascades in these seagrass and seaweed meadows. Mesopredator presence had a cascading top-down effect which increased biomass of ephemeral macroalgae by 113%; an effect of similar magnitude to the estimated effect of nutrient additions (150%). Consequently, mesopredator release induced by loss of piscivores, or apex predators, can be predicted to have significant cascading effects also in relatively complex coastal food webs, as previously shown for overfishing of top predators in coral reefs (Bascompte, Melián & Sala 2005) and sea otter recovery in Pacific seagrass habitats (Hughes *et al.* 2013). Our results indicate that piscivores and large predators in seagrass and seaweed beds can be important for buffering against effects of nutrient enrichment in real coastal food webs (see Hughes *et al.* 2013).

The results from this meta-analysis support that the top-down mechanisms described by the “mutualistic mesograzer model” (*sensu* Duffy, Hughes & Moksnes 2013) dominate in *Zostera* and *Fucus* communities of the North Atlantic (Fig. 5). That is, grazers – by selectively grazing on epiphytes and fast-growing ephemeral algae – reduce the competition for light or nutrients, which facilitate the growth of seagrass/seaweed. However, the strength of bottom-up and top-down effects differs between groups of plants and grazer species, affecting the penetrance of the trophic cascades.

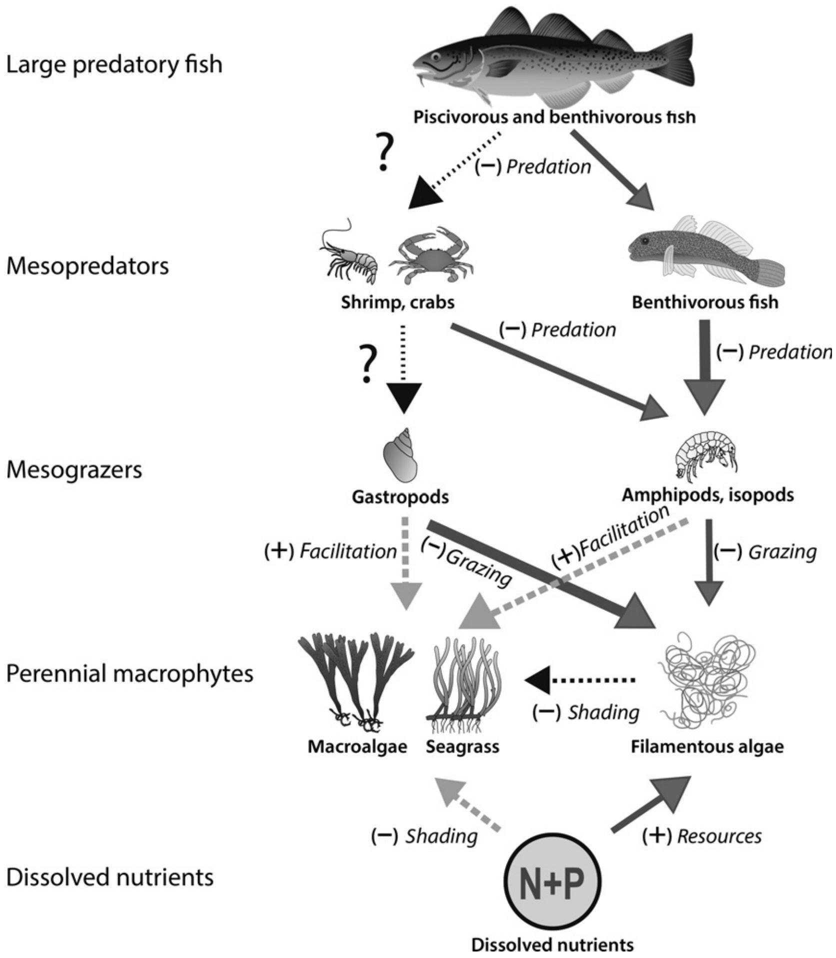

Fig. 5. Conceptualized figure of food web interactions in coastal *Fucus*/*Zostera* food webs. The thickness of the arrow is proportional to interaction strength (*LRR*). Darker solid grey arrows indicate direct effects, and hatched lighter arrows indicate indirect effects. Dotted black arrows indicate missing estimates of the interaction strength. Text in italics describes the type of interaction (e.g. predation), and (+/−) the sign of the effect on the receiving functional group. Symbols courtesy of the Integration and Application Network (IAN).

Green macroalgae and microepiphytes responded on average >30% stronger to grazer treatments than red and brown ephemeral macroalgae. In return, green macroalgae responded twice as strongly as red and brown ephemeral macroalgae and microepiphytes to nutrient enrichment (Fig. 5). This is consistent with studies showing that green macroalgae are dominant space competitors in the absence of grazers (Lotze, Worm & Sommer 2001; Moksnes *et al*. 2008; Eklöf *et al*. 2012) and dominate macroalgal blooms in the North Atlantic and elsewhere (Valiela *et al*. 1997; Pihl *et al*. 1999), but are often replaced by less palatable brown and red algal species where grazers are abundant (Lotze, Worm & Sommer 2001; Eklöf *et al*. 2012).

Even though we found strong effects of mesopredators on grazers on ephemeral algae, and a positive effect of grazers on *Zostera* and *Fucus*, there was no significant negative effect of mesopredators on the perennial macrophytes. The lower strength and penetrance of the top-down effects may in part be explained by a slow response in perennial species in combination with short-term experiments, decreasing the effect size on *Zostera* and *Fucus* (Fig. 1). It may also be partly related to different responses to trophic interactions between groups of mesograzers. Our results demonstrated that while gastropods were the most important grazers for seagrass and seaweed health, they responded weakly to both mesopredators and nutrients. Meanwhile, crustacean amphipods and isopods mediated stronger trophic cascades, responding negatively to mesopredators, as well as positively to nutrient addition. Similar results have been shown in a smaller meta-analysis (Eklöf *et al*. 2012) and suggest that cascading effects of mesopredator release to algae occur mainly through fast-growing and poorly defended crustacean grazers.

The faster response of amphipods and isopods to nutrient additions compared with gastropods has been observed elsewhere (Eriksson *et al*. 2011b; Duffy *et al*. 2015) and may partly be due to faster generation times, direct development and higher mobility, enabling relative fast responses to food additions on the small temporal and spatial scale of the investigated experiments. Gastropods have a generation time (6 months–1 year) that is typically longer than the duration of most of the experiments (ranging 4–250 days with a median around 1 month), rendering the effect of increased food availability on population biomass difficult to capture in short-term experiments. In relation to short-term nutrient pulses in natural environments, for example after upwelling episodes or heavy land run-off, the difference in response time may, however, be significant for *Fucus* and *Zostera*. In these instances, a rapid numerical response of crustacean grazers may be vital for regulating biomass of fast-growing ephemeral algae, which also respond quickly to nutrient pulses (Kiirikki & Blomster 1996).

Mesopredatory fish like wrasses, gobies and sticklebacks had a negative effect on amphipods and isopods that was twice as strong as the effects of crabs. Whereas mesopredatory fish had no significant effect on gastropod abundance, the effect of crabs on gastropods was not investigated in any of the reviewed studies, despite crabs feeding extensively on gastropods in the coastal zone (e.g. Hamilton 1976; Perez *et al.* 2009).

Nutrient effects generally increased with the level of fertilization, being positively correlated with the effect size on ephemeral algae but negatively correlated with effect size on *Fucus* and *Zostera*. Importantly, the meta-regressions also showed that the effects of mesopredators increased with increasing nutrient levels (especially nitrogen), indicating synergistic effects of nutrient enrichment and mesopredator release. The interaction term between nutrient and grazer manipulations in factorial studies was similar to estimated interaction effects in previous meta-analyses (Hillebrand 2002; Wahl *et al.* 2011), indicating that grazing partly mitigates the effect of nutrients on ephemeral algae. A similar pattern was shown by Poore *et al.* (2012), who on a global scale found a weak increasingly negative effect of grazers on total primary producer biomass with increasing nitrate levels (but see Hillebrand 2009 for an exception). These results are coherent with the 'exploitation ecosystem hypothesis' (Oksanen *et al.* 1981), stating that trophic cascades become stronger in more productive environments. Thus, synergistic effects of (i) nutrient enrichment and (ii) mesopredator release as a consequence of overfishing of piscivorous fishes highlight the risk of 'double-trouble' for *Zostera* and *Fucus* habitats.

Correlative field studies have suggested a negative association between the abundance of piscivorous fish and ephemeral algae (Eriksson *et al.* 2009, 2011a,b; Baden *et al.* 2012), but very few of the experiments in this meta-analysis manipulated piscivorous fish. Interestingly, the average effect sizes in these studies were on par with effect sizes of manipulation of lower trophic levels and of nutrients, but they were only nearly significant ($P = 0{\cdot}06$) due to the low sample size. Cascading top-down effects from large, piscivorous fish to primary producers have been observed in no-take and marine-protected areas for decades (e.g. Shears & Babcock 2003; Guidetti 2006), suggesting they are important. To improve the estimates and confirm the importance of top predators in coastal ecosystems, there is a clear need for more studies manipulating large predatory fish. Cage experiments that exclude large fish is one tested and useful approach (e.g. Eriksson *et al.* 2009), but establishing replicated no-fishing zones in shallow coastal areas in the North Atlantic would be a more realistic and relevant way to study the relative importance of top-down control from large predatory fish, and assess the generality of the trophic cascades shown in this study.

MANAGEMENT IMPLICATIONS

This meta-analysis suggests that top-down effects are typically on par with bottom-up eutrophication effects in coastal ecosystems and that nutrient enrichment and mesopredator release may synergistically increase biomass of nuisance algae and pose 'double-trouble' in *Fucus* and *Zostera* communities, just as in freshwater food webs (Carpenter *et al.* 2001). This underscores the importance of taking food webs and trophic interactions into account in management actions aiming to protect and restore essential *Zostera* and *Fucus* habitats in the North Atlantic. So far, management of eutrophication has concentrated on reducing nutrient leakage from land to coastal waters. These measures have successfully reduced nutrient loadings, but may take decades to actually lower nutrient concentrations in coastal waters (Varjopuro *et al.* 2014). Thus, eutrophication problems may remain long after reductions in nutrient loading.

As top-down processes are here shown to be almost as important as fertilization for the biomass of 'nuisance' ephemeral algae, we suggest management of fish communities towards a state with more piscivorous fish and fewer mesopredators (Eriksson *et al.* 2011a) may provide a tangible additional measure for restoring coastal food webs. Numerically, the mesopredators' assemblage of *Zostera* and *Fucus* food webs in the north Atlantic are typically dominated by small fish and crustaceans that remain mesopredators during adult life stages, for example crabs (e.g. *Carcinus maenas*), labrids (corkwing and goldsinny wrasse), croakers (spot, silver perch), gobies (e.g. black goby) and sticklebacks (Pihl & Wennhage 2002; Sobocinski *et al.* 2013). For some of these species, there are commercial fisheries, in addition to sometimes recreational fishing, such as fyke-net fisheries for wrasses used for removing sea lice from farmed salmon (Skiftesvik *et al.* 2014), and pot and trap fisheries for crabs. For migratory mesopredatory species, trawl fishing in the open sea may also be an option; for example, sticklebacks could be fished in the open sea for fish meal production. These fisheries targeting mesopredators can be used to achieve local reductions of mesopredator abundance to restore coastal food webs.

Although some of the mesopredators in *Zostera* and *Fucus* food webs are juvenile stages of piscivorous fish, primarily gadoids, the few field surveys along gradients in the density of piscivorous fish that exist suggest a negative correlation with cover of ephemeral algae (Eriksson *et al.* 2009; Baden *et al.* 2012). This indicates that the positive effect of large piscivores on seagrass/seaweed on average overwhelms the negative effect of mesopredatory life stages. Replicated no-fishing areas would be a valid way of testing whether enhancing populations of large piscivorous fish could be a complementary way of also relieving eutrophication symptoms.

This meta-analysis indicates that active management of food web structure, for example by (i) reducing the abundance of benthos-eating fish through targeted fisheries, and/or (ii) increasing the abundance of large piscivorous fish through fisheries regulations or establishment of no-take marine reserves, may improve the health and resilience of coastal ecosystems. We have here focused on food web structure to mitigate eutrophication symptoms, but seagrass and seaweed habitats may also become degraded by algal blooms stimulated by warming and acidification (Eklöf *et al.* 2012). It is therefore possible that food web structure can affect coastal resilience to a wider range of stressors than nutrient enrichment alone (see Graham *et al.* 2015).

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Data accessibility

Data of studies involved and treatments are available in Table S1.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Description and analysis of interactive effects of full factorial studies.

Table S1. Detailed information about treatments and metadata of the included studies.

Table S2. Conversion coefficients to abundances of grazers into biomass.

Table S3. Complete results from the meta-regressions.