

Temporal mismatches in predator–herbivore abundance control algal blooms in nutrient-enriched seagrass ecosystems

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ABSTRACT: Blooming filamentous algae recurrently overgrow macroalgae and seagrass in many coastal ecosystems, leading to potential losses in the functions and services these habitats provide. The seasonal reoccurrence of algal blooms is partly caused by excessive input of nutrients into coastal ecosystems. At the same time, overfishing of top predators has led to increased densities of smaller predators that reduce herbivore abundance. Managers of coastal ecosystems are in urgent need of information on how overfishing may act synergistically with eutrophication to promote algal blooms. In the present study, we model the interaction between the opportunistic filamentous algae *Ulva* spp. and the effective mesograzer (small invertebrate herbivore) *Gammarus locusta* L. under different nutrient regimes and predation rates by intermediate-size fish (4 to 12 cm). The aim is to assess how productivity, herbivory and predation interact to regulate seasonal algal growth under a range of scenarios, including temporal matching or mismatching between trophic groups. The model is parameterised with nutrient and demographic data from a seagrass ecosystem on the west coast of Sweden. Model simulations show that both nutrient level and herbivore abundance regulate seasonal algal biomass in the seagrass meadow. Their relative importance is dynamic and sensitive to the arrival times of herbivores in relation to the start of algal development in spring. Thus, herbivore presence and timing are crucial factors for the control of algal biomass, particularly during times when resource levels are ambient to slightly elevated. Simulations also show that it is mainly the predation rate and timing of predators, rather than food limitation, that limit herbivore abundance. As predation rates by invertebrates and smaller fish can be linked to the presence of larger and commercially targeted fish, overfishing may have similar effects to eutrophication in the seagrass ecosystems.

KEY WORDS: Seagrass · Trophodynamics · Nutrient enrichment · Filamentous algae · Herbivore efficiency · Predation · Match-mismatch · Bottom-up effects · Top-down control · Overfishing

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INTRODUCTION

Seagrass meadows are among the most productive ecosystems in the world and provide food and shelter to a diverse range of species, including many commercially targeted crustaceans and fish (e.g. Jackson

et al. 2001, Duarte et al. 2008). Over the last 2 decades, average seagrass cover has declined globally by 30% (Green & Short 2003, Waycott et al. 2009), and in some areas, losses of up to 60% have been recorded (e.g. Baden et al. 2003, Nyqvist et al. 2009).

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Traditionally, seagrass meadows have been considered bottom-up driven, and declines in seagrass cover have been attributed to elevated nutrient levels leading to increased growth of phytoplankton and epiphytic and filamentous algae (via eutrophication), which compete with seagrass for light and nutrients (e.g. Twilley et al. 1985, Hauxwell et al. 2003). Additional negative impacts on seagrasses have been detected as decomposing algae cause hypoxia and increased levels of hydrogen sulphide in the sediment that intrude into the plant (Holmer & Bondgaard 2001, 2009). But apart from resource regulation, it is known that grazing by small invertebrate herbivores (mesograzers) can have a large impact on the abundance of filamentous algae in seagrass meadows, while seagrass itself is a less preferred food (e.g. Howard 1982, Heck et al. 2000, Baden et al. 2010). The abundance of mesograzers is in turn indirectly regulated by the permanent or fluctuating presence of large predatory fish, which control the abundance of smaller predators that feed on the herbivore assemblage (Daskalov et al. 2007, Eriksson et al. 2009, Baden et al. 2012). Such cascading effects on food web structure have been found in marine, terrestrial and freshwater ecosystems (see Estes et al. 2011 for a review), and the subject bears much complicated theory (e.g. Paine 1980, Oksanen & Oksanen 2000, Shurin et al. 2002).

Another important source of variation in seasonally fluctuating environments is the temporal matching and mismatching of species (e.g. Vadas 1989, Fabina et al. 2010, Yang & Rudolf 2010). This theory builds on the match-mismatch hypothesis, which was developed to explain how recruitment success in pelagic fish depends on the matching of fish larvae with blooms of phytoplankton (Cushing 1981, 1990). How these processes manifest in heavily exploited and disturbed ecosystems is not known, but excessive fishing during certain times of the year may mimic a mismatch scenario, allowing the predicted prey to overexploit their food sources. Other species in the food web that are directly or indirectly linked to these processes will then also be affected (Paine 1980, Power 1992).

Like seagrass meadows worldwide, the eelgrass *Zostera marina* (L.) on the northwest coast of Sweden suffers from shading by overgrowing and drifting filamentous algae (*Ulva* spp.), which are known to bloom with experimental nutrient additions (Moksnes et al. 2008, Baden et al. 2010). However, despite greater availability of algal food, the natural herbivore community in this region, previously dominated by *Gammarus locusta* L. and *Idotea* spp. (Baden &

Pihl 1984, Baden & Boström 2001), has declined over the last decades (Baden et al. 2012). Currently, *Idotea* spp. has almost disappeared, and only small juvenile *Gammarus* are found on the northwest coast of Sweden (e.g. Jephson et al. 2008, Baden et al. 2012). *Gammarus* and *Idotea*, together with a few other herbivores, contribute substantially to reduce algal blooms in the nearby Baltic Sea (Jephson et al. 2008, Baden et al. 2010). Cage experiments (Moksnes et al. 2008, Persson et al. 2008, Baden et al. 2010) and analyses of data collected over 3 decades (Baden et al. 2012) have demonstrated that the lower abundances of these species on the Swedish northwest coast are a result of predation from an 8- to 11-fold increased density of small fish (e.g. gobids and sticklebacks). This shift in food web structure is strongly linked to a >90% decline in the cod stock in Skagerrak during the same time period (Svedäng & Bardon 2003, Baden et al. 2012). A similar negative correlation between the abundance of cod and of small fish and crabs was found on a shallow exposed and unvegetated bottom on the southwest coast of Sweden over the last 40 yr (Eriksson et al. 2011).

Ecosystem management typically draws on mass-balanced ecosystem models to predict system development under various harvest or nutrient regimes (e.g. Christensen & Walters 2004). However, in many seagrass meadows, the human influence is so pronounced and in such constant change that the added variation in prey diversity and/or production stemming from human activities, mixed with the natural sources of variation, have created systems void of their natural 'stable' states (e.g. Duarte et al. 2008, Baden et al. 2012). During such complete shifts in or changes to producer–consumer relationships, short-term analyses that take into account transient variation are preferred over simulations based on stable systems (Diehl et al. 2000, Robinson & Frid 2003, Fox 2007).

In the present study, we use established predator–prey theory and differential equation techniques to model (i.e. iterate) the dynamic interaction between the filamentous algae *Ulva* spp. and the effective herbivore *Gammarus locusta*, which are the dominant species within their functional groups in the seagrass ecosystems on the Swedish west coast (Moksnes et al. 2008, Baden et al. 2010). The model simulates equilibrium and summer seasonal (April to September) dynamics, including scenarios with varying predation intensity by gobids and sticklebacks on their herbivore prey. Our overall objective is to assess how nutrient level, herbivory and predation interact to regulate seasonal algal biomass

under different realistic scenarios. The scenarios include varying levels of predation on herbivores and different match-mismatch situations with regard to the arrival times of herbivores and predators in relation to one another and the start of the algal growth season. Thus, we intend to show how bottom-up and top-down processes may interact with species timing, although we do not aim to accurately predict relative abundance during a particular season in the model system.

MATERIALS AND METHODS

Model system

Eelgrass *Zostera marina* is the dominant seagrass species in Swedish coastal waters, occurring in semi-exposed and protected areas at depths of 0.5 to 6 m (Baden & Boström 2001). As described for seagrass beds in general, Swedish *Z. marina* beds have been shown to support a high production of benthic fauna as well as epibenthic invertebrates and fish (Baden & Pihl 1984, Möller et al. 1985) and to serve as a nursery and feeding ground for ~40 fish species (Pihl & Wennhage 2002). *Z. marina*, in particular, has proven important for the survival of Atlantic cod of age groups 0 and 1 (Gotceitas et al. 1997, Fromentin et al. 2000, Pihl et al. 2006), and in Skagerrak, the abundances of the these groups correlate with the biomass of *Z. marina* (Fromentin et al. 2000, 2001).

The model

The model developed here simulates the temporal dynamic interaction of 2 functionally dominant species in a temperate seagrass community: the green algae *Ulva* spp. and the herbivorous crustacean *Gammarus locusta* (Moksnes et al. 2008). These 2 species operate on similar temporal and spatial scales, and the interaction can be modelled as a spatially closed system to investigate the equilibrium (long-term) and seasonal (short-term) dynamics. The spatial scale represented here is equivalent to 1 m² sea bottom with ~3 m of headspace (from the bottom to the surface) that can be extrapolated to any relevant seagrass community size. Coupled ordinary differential equations (ODEs) are used to describe the interplay between algae and herbivores over an essentially unlimited time period divided into discrete intervals represented by days,

allowing for equilibrium to be reached. Different levels of algal growth were used to represent an environment with ambient or elevated nutrient levels. In some scenarios, we include predation on herbivores, which is incorporated as a fixed (for each simulation) consumption rate. Seasonal (i.e. transient) and match-mismatch patterns are explored by limiting time to the number of days representing the time from April to September (183 d) and introducing herbivores and, in some simulations, predation at arbitrary times for the different patterns of algal growth (i.e. type of season). The ODEs are solved through the implementation of the ODE 45 solver (based on an explicit Runge-Kutta formula, the Dormand-Prince pair) using the software Matlab (Mathworks).

Filamentous algae grow logistically while being consumed by herbivores, and the ODE thus reads:

$$\frac{da}{dt} = r_a \left(1 - \frac{a}{K_a}\right) a - c_h h \left(\frac{a}{w_a h + a}\right) \quad (1)$$

where a is the biomass of algae (g), r_a is the intrinsic growth rate of algae, K_a determines the carrying capacity of algae in the absence of grazers, h is the number of herbivores, and c_h is the maximum algal biomass consumed per herbivore and day (t).

$\frac{a}{w_a h + a}$ is a ratio-dependent functional response determining actual herbivore consumption depending on algal biomass, where w_a is the half saturation rate (the concentration of prey at which the predation rate is half saturated). The ratio-dependent functional response used here is expressed in terms of the ratio of prey to predator abundance according to Ruan et al. (2010) (see also Arditi & Ginzburg 1989 for the benefits of this approach in predator–prey dynamics). *Gammarus locusta* is a very efficient herbivore, and w_a is estimated to take on values representing 0.8- to 1.2-fold the theoretical maximum consumption rate c_h (Andersson et al. 2009).

In the model, algal growth (r_a) ranges between 0.32 and 0.85 g d⁻¹ representing growth in ambient to severe nutrient-enriched environments (Table 1) (calculated from Pihl et al. 1996 and Moksnes et al. 2008). Moreover, we assume that all herbivores are of equal size and have the same c_h . Since herbivores never completely eliminate their algal resources because algal remnants or spores 'hide' and persist in minute crevices, we also include an absolute lower boundary condition for algal biomass. This is set to 0.16 g m⁻² based on field data (Moksnes et al. 2008). Hence, there are always algae available for production and recovery.

Table 1. Model parameters derived from data (see Pihl et al. 1996, Christie & Kraufvelin 2004, Moksnes et al. 2008, Andersson et al. 2009)

Parameter	Description	Rate
r_a	Maximum daily growth in <i>Ulva</i> spp. ($\text{g g}^{-1} \text{d}^{-1}$)	0.32 (ambient) 0.85 (enriched)
K_a	Maximum biomass of <i>Ulva</i> spp. (g m^{-2})	300
r_h	Maximum daily population growth for <i>Gammarus</i> (ind. ind. $^{-1} \text{d}^{-1}$)	0.44
K_h	Maximum density of <i>Gammarus</i> (ind. m^{-2})	12 000
c_h	Maximum weight <i>Ulva</i> spp. consumed per <i>Gammarus</i> (10 mm) and day ($\text{g ind.}^{-1} \text{d}^{-1}$)	0.0049
w_a	Half saturation rate in Eq. (1)	0.0039 to 0.0059
m_h	Intrinsic mortality (ind. ind. $^{-1} \text{d}^{-1}$) of <i>Gammarus</i>	0.02
P	Number of predators (gobid fish) (P m^{-2})	0, 2 or 8
c_p	Maximum number of <i>Gammarus</i> consumed per gobid fish and day (ind. $\text{P}^{-1} \text{d}^{-1}$)	10
w_h	Half saturation rate in Eq. (2)	10 to 20

The herbivore population grows logistically and is at the same time affected by intrinsic mortality and by relative algal biomass. In addition, larger crustaceans and fish, in our case represented by an arbitrary predator P , consume herbivores. The ODE for the herbivore population thus reads:

$$\frac{dh}{dt} = r_h \left(1 - \frac{h}{K_h}\right) \left(\frac{a}{w_h h + a} - m_h\right) h - \frac{h}{w_h P + h} c_p P \quad (2)$$

where h is the number of herbivores, r_h is the intrinsic growth rate (equivalent to the conversion factor in Ruan et al. 2010), K_h is the carrying capacity limiting growth through space limitation, m_h is the intrinsic herbivore mortality, P is the abundance of predators, and c_p is the maximum number of herbivores consumed per predator and day (t). $\frac{h}{w_h P + h}$ is the ratio-dependent functional response (see above) determining the actual predation level consumption depending on herbivore density, where w_h is the half saturation rate (the concentration of prey at which the predation rate is half saturated). w_h ranges from 1.2- to 1.8-fold greater than the maximum consumption rate (c_p). Thus, although the number of predators in the system remains constant in each simulation, their predation efficiency decreases as the ratio of predator to prey increases. The rationale behind this design is that predators such as gobid and stickleback fish species are highly mobile and also feed on other prey outside the system (e.g. Pihl & Wennhage 2002).

Equilibrium dynamics and the seasonal dynamics between interacting herbivores and algae were simulated. To test for sensitivity of the model output to changes in the half saturation values (w_h for herbivores and w_p for predators), simulations were performed with a range of possible w -values (see

above). Further, we wanted to mimic realistic scenarios of seasonal variability in resources. The simulated algal growth rate during different months of a season was therefore related to monthly measurements of dissolved inorganic nitrogen (DIN) from the modelled area on the Swedish west coast. Although nitrogen is the main limiting resource for filamentous algae in this region, using nitrogen as a sole resource may not adequately reflect the whole resource spectra as both temperature and light regimes can be important determinants of productivity. However, N levels demonstrate how the growth of algal resources changes over time in this region, and while light and temperature vary little among years, the external input of nitrogen varies greatly and has increased on average 4 to 6 times since the 1930s (Granéli et al. 1990, Rosenberg et al. 1990).

Monthly measurements of DIN are known for the Gullmar fjord from 1986 to 2004 (SMHI 2004), producing an annual curve with mean \pm SD for each month. By relating each month's highest (+1 SD), mean and lowest (-1 SD) nitrogen value to the highest DIN value in the whole time-series, we produce 3 estimates of proportional enrichment for each month and year. By multiplying these proportions with maximum algal growth ($r_a = 0.85$) we get 3 levels of algal growth rates (low, medium and high) during the different months and season types (Fig. 1). In ambient surroundings, independent data suggest that the algal growth rate averages 0.3 g d^{-1} (see Pihl et al. 1996), which here corresponds to the estimated lower monthly growth rates (the -SD curve in Fig. 1). We therefore let -SD, mean and +SD values represent ambient, enriched and severely enriched environments, respectively. Because of data limitation, it is assumed that each day in a month has the same growth rate.

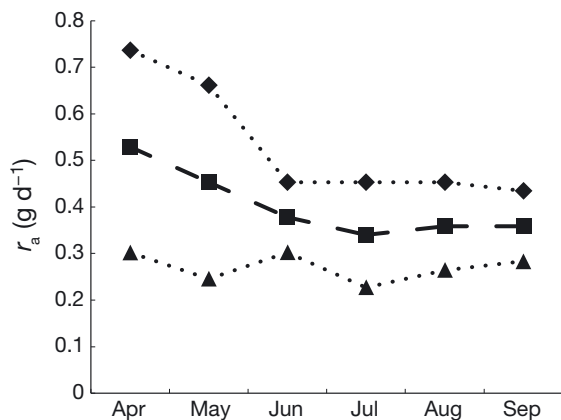


Fig. 1. Estimated algal growth rates (r_a) from the beginning of April until the end of September under seasons with ambient (\blacktriangle), enriched (\blacksquare) and severely enriched (\blacklozenge) nitrogen levels. The 3 types of seasons equal the mean \pm 1 SD and was estimated by relating algal growth to 19 yr (1986 to 2004) of monthly measurements of DIN in Gullmarsfjorden on the Swedish west coast (SMHI 2004)

Model simulations

No predation on herbivores

Equilibrium. Even if the system is unlikely to reach equilibrium within 6 mo, such simulations can provide valuable information on algal and herbivore development. Equilibrium was explored using a range of different starting values for herbivore numbers, ranging from 1 to 300 ind. m^{-2} . Initial algal biomass was held at the absolute lower boundary condition for algal biomass of 0.16 $g\ m^{-2}$ since algae is usually absent after the winter season. Simulations continued until algal biomass and herbivore abundances were constant or showed repetitive fluctuations that remained over >1000 d. By calculating the equilibrium herbivore numbers when the predators are absent under algal growth in ambient ($r_a = 0.32$) vs. severely enriched ($r_a = 0.85$) environments, we could assess how increased productivity transferred into algal and herbivore abundance.

Seasonal dynamics. The simulation time it took to reach system equilibrium exceeded that of a season, and algal biomass during spring, summer and autumn depended on herbivore abundance. Scenarios of match-mismatch were tested by simulating an algal season of 183 d (April–September), beginning the season with an algal biomass at its lower boundary level (0.16 $g\ m^{-2}$). Assuming that intermediate-sized individuals form the bulk of the *Gammarus locusta* population (see Andersson et al. 2009 for the different size classes), 10 intermediate-sized herbivores

m^{-2} were introduced at an arbitrary time (day) during algal production, and the subsequent dynamics were recorded. Herbivore arrival times, ranging from Days 1 to 30, were tested separately for each of the 3 types of seasons, i.e. ambient, enriched and severely enriched environments.

Predation on herbivores

Equilibrium. In this analysis, we focused on the equilibrium dynamics during which algal abundance fluctuated around its lower boundary level (0.16 $g\ m^{-2}$) controlled by a population of herbivores. Using this as a starting point in simulations and by setting $P = 1$ in Eq. (2), we could determine the threshold consumption rate (prey consumed $m^{-2}\ d^{-1}$) required to reduce herbivore abundance and produce an alternative equilibrium state of algal bloom ($>200\ g\ m^{-2}$). These simulations were performed for both low and high levels of algal growth (Table 1, Fig. 1).

Seasonal dynamics. As for herbivores, predators may either be absent or present at different times during the season, and there are an infinite number of match-mismatch scenarios between the different functional groups. To illustrate the potential impact of predation timing at the beginning of the season, we focused on a few scenarios during a season in which 10 reproducing herbivores m^{-2} are present from Day 1 of the simulations. Starting times for predation range from Days 1 to 30, and the subsequent dynamics were recorded. We used 2 predation rates: one moderate rate based on 2 predators m^{-2} (a maximum of 20 prey consumed $m^{-2}\ d^{-1}$; Table 1) and one high rate based on 8 predators m^{-2} (a maximum of 80 prey consumed $m^{-2}\ d^{-1}$; Table 1). The former is equivalent to the historical predation rates found in eelgrass beds along the Swedish west coast in the 1980s (Baden et al. 2012), while the latter equals the high predation pressure on herbivores found in the same areas today (Moksnes et al. 2008, Baden et al. 2012). The procedure was repeated for all 3 types of seasons, i.e. ambient, enriched and severely enriched environments.

RESULTS

No predation on herbivores

Equilibrium

The equilibrium dynamics under algal growth in an ambient environment ($r_a = 0.32$) were independent of

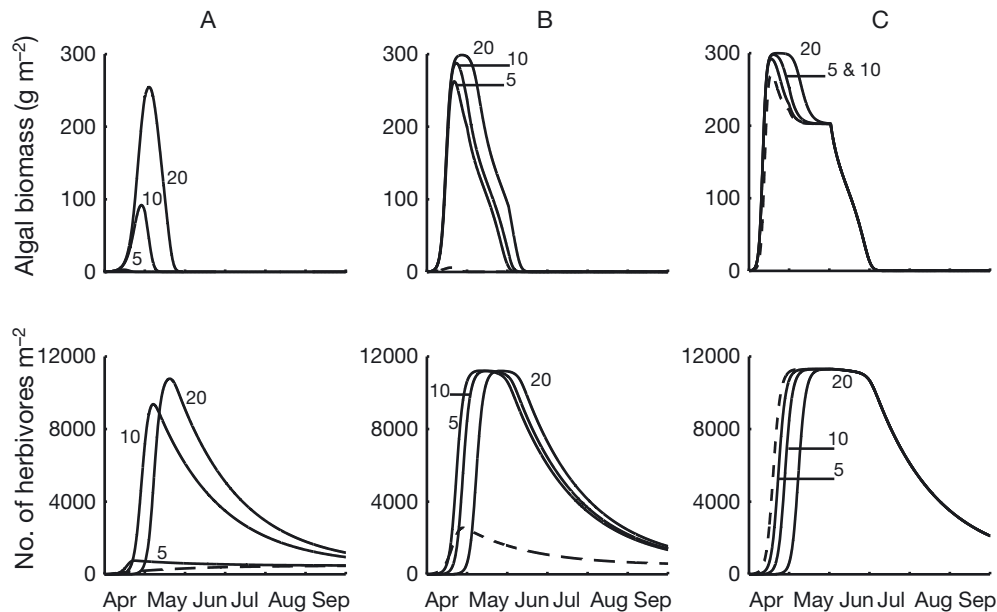


Fig. 2. Seasonal (183 d) algal biomass and number of herbivores per m^2 in (A) ambient, (B) enriched and (C) strongly enriched environments for 4 different scenarios regarding the delay between the start of algal growth and herbivore appearance where predation on herbivores is excluded. $w_h = c_h$. Dashed lines are when algae and herbivores are both present from Day 1. Herbivore delays of 5, 10 and 20 d are illustrated

the initial number of herbivores. Algae biomass fluctuated around the lower boundary value 0.16 g m^{-2} , sustaining a herbivore population of 487 individuals. In a severely enriched environment, the algal growth rate ($r_a = 0.85$) exceeded the maximum herbivore population growth rate ($r_h = 0.44$), enabling 2 potential equilibrium states depending on the initial number of herbivores. When the initial herbivore number was $>110 \text{ ind. m}^{-2}$, algal biomass was suppressed and fluctuated around the lower boundary value 0.16 g m^{-2} . Despite the low density of algae, it sustained a herbivore population of 617 individuals. Hence, the 2.65-fold ($0.85/0.32$) increase in algal growth rate transferred to a 0.26-fold increase in herbivore numbers. When initial herbivore numbers were $<110 \text{ ind. m}^{-2}$, algal biomass stabilised at 232 g m^{-2} (i.e. an algal bloom) and sustained 11 324 herbivores.

Seasonal dynamics

Varying w_h had little impact on overall simulation results, and here, we present results from simulations of the average $w_h = c_h$. In the absence of predators, the 10 initial herbivores and their offspring could control algal biomass within the seasonal window in both the ambient and enriched environments but not in the severely enriched environment. However, herbivores could only prevent algal blooms in ambient en-

vironments if they were present early (from Days 1 to 12) in the season (Fig. 2A,B). Arrival delays of herbivores that were $>4 \text{ d}$ led to algal blooms in the enriched environment (algal density $> 200 \text{ g m}^{-2}$), and longer delays extended the duration of the bloom by up to 2 mo in the severely enriched environment. As nitrogen levels and thus algal growth rates decreased later in the year in all environments (Fig. 1), the herbivores were always able to reduce algal biomass during the end of the summer (Fig. 2A,B). During an algal bloom, the unlimited food supply led to herbivores quickly approaching their carrying capacity of 12 000 individuals. These densities have never been observed in the field but are often observed in the laboratory in the absence of predators (data not shown, P.-O. Mosknes). In a severely enriched environment, algae always outgrew the herbivore population and bloomed (Fig. 2C). Only after the drop in productivity (i.e. algal growth rate) in June (Fig. 1) could herbivores begin to reduce algal biomass.

Predation on herbivores

Equilibrium

The predation rate required to change the system from herbivore control toward algal dominance was $8.1 \text{ herbivores consumed m}^{-2} \text{ d}^{-1}$ and 8.9 herbivores

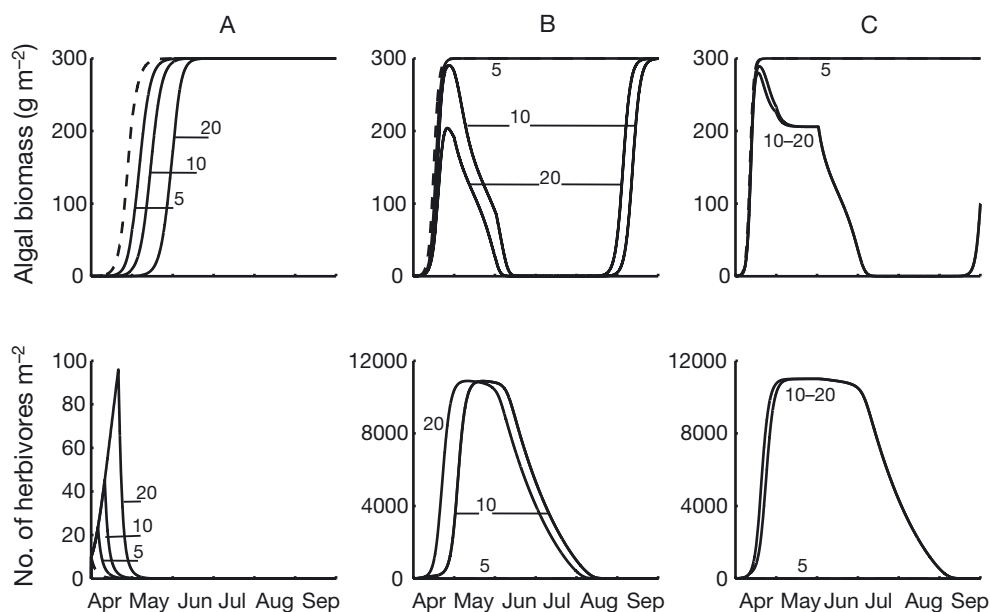


Fig. 3. Seasonal (183 d) algal biomass and number of herbivores per m^2 in (A) ambient, (B) enriched and (C) severely enriched environments for 4 different predator appearance times in relation to the start of algal and herbivore population growth. Predation is moderate (i.e. 2 predators = 20 herbivores $m^{-2} d^{-1}$), $w_h = c_h$, and $w_p = 1.5c_p$. Dashed lines are when predators are present from Day 1. Predation delays of 5, 10 and 20 d are illustrated

consumed $m^{-2} d^{-1}$ for the regular ($r_a = 0.32$) and high ($r_a = 0.85$) levels of algal growth, respectively. These numbers are equivalent to the consumption by ~1 intermediate-sized *Gobius niger* (gobid fish) (Moksnes et al. 2008) or 2 to 5 intermediate-sized *Palaeomon elegans* (grass shrimp) (Persson et al. 2008).

Seasonal dynamics

Moderate predation (2 predators m^{-2}). The overall pattern differed slightly depending on w -values, and the results presented here represent simulations where $w_h = c_h$ and $w_p = 1.5c_p$ (Fig. 3). At ambient (no enrichment) nutrient levels, moderate predation was always able to suppress the herbivore population, which led to an algal bloom during most parts of the season (Fig. 3A). In the beginning of the season, the effects of predation were emphasized by the relatively slow population development of herbivores due to the low productivity of algae. In an environment with higher algal growth, the timing of predators became more important. For delays >10 d, the herbivore population would reach its carrying capacity, allowing for control of algal biomass until late autumn (Fig. 3B). A similar pattern was found in the severely enriched environment, but here, the fast-growing algae were more resilient to herbivory, and algal biomass remained at bloom levels ($<200 g m^{-2}$)

well into June. These results show that as higher nutrient levels led to elevated algal productivity and increased herbivore resources, herbivores become more resilient to predation.

High predation (8 predators m^{-2}). For a predation pressure equal to the levels of predation found in eelgrass beds today, the herbivore population was unable to grow, and algae bloomed in all simulated scenarios (Fig. 4). Herbivores were aided by higher algal productivity, and for predation delays >25 d, herbivores were able to control algal growth during part of the season (Fig. 4B,C).

DISCUSSION

The present study illustrates how the timing of the arrival of herbivores and predators at the beginning of the growing season interacts with algal productivity to shape the trophic structure in a temperate seagrass meadow. Herbivore presence early in the year is the crucial factor for the control of algal biomass, particularly when resource levels are moderately elevated (excluding effects from self-shading, anoxia, etc.). Herbivore density is in turn determined by the timing and level of predation, and at high predation intensity, comparable with the present levels of predation on the Swedish west coast, herbivores are unable to control algal growth. These results, together with

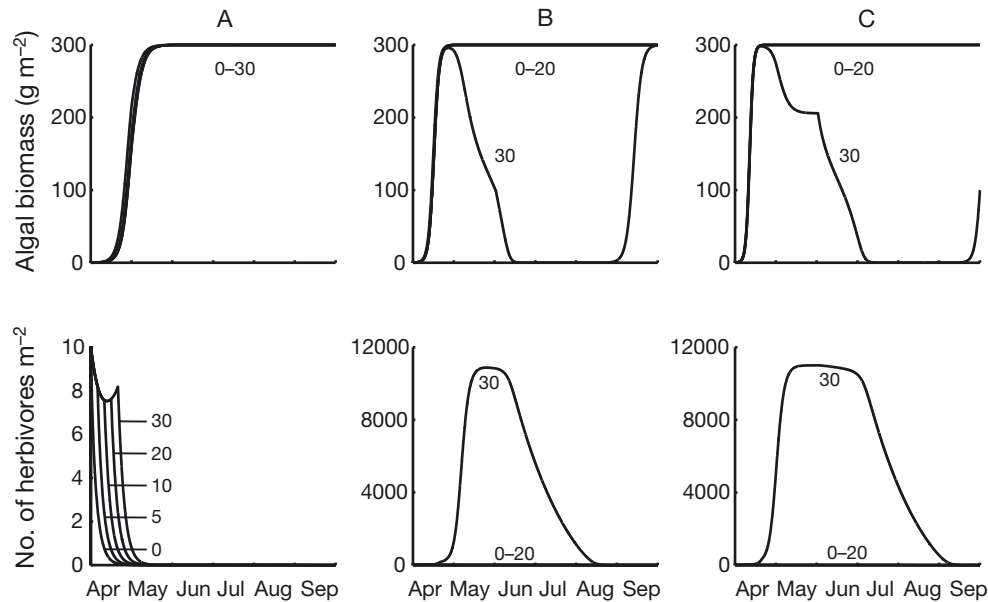


Fig. 4. Seasonal (183 d) algal biomass and number of herbivores per m^2 in (A) ambient, (B) enriched and (C) severely enriched environments for 5 different predator appearance times in relation to the start of algal and herbivore population growth. Predation is high (i.e. 8 predators = $80 \text{ herbivores m}^{-2} \text{ d}^{-1}$), $w_h = c_h$, and $w_p = 1.5c_p$. Predation from Day 0 and delays of 5, 10, 20 and 30 d are illustrated

earlier empirical studies (e.g. Kraufvelin et al. 2006, Worm & Lotze 2006, Baden et al. 2010), show that although nutrient enrichment increases the likelihood of algal blooms, it is the season-specific interaction between primary production and top-down effects that ultimately shapes algal biomass. Factors reducing herbivore establishment in the beginning of the season, such as higher densities of small predatory fish, will therefore increase the likelihood of algal blooms in seagrass beds over time.

One scenario leading to higher abundances of smaller predators and a change in trophic structure is the depletion of large predators (Heck et al. 2000, Jackson et al. 2001, Baden et al. 2012). In Skagerrak-Kattegat (west of Sweden), cod is a key large predator, and due to overfishing, its present abundance is $\sim 10\%$ of the recorded maximum (Svedäng & Bardon 2003, Ask & Westerberg 2009). Studies in Skagerrak-Kattegat (Baden et al. 2012) and other cod-dominated areas (Frank et al. 2005, Österblom et al. 2006) have shown that a depletion of cod will completely change the trophic structure of the ecosystem. Baden et al. (2012) compared drop-trap, gill and beach seine-net data from the 1980s and 2000s in *Zostera marina* on the Swedish west coast, showing that a dramatic decrease of cod during this period (Svedäng & Bardon 2003) is coupled with a significant 8-fold increase in the biomass of intermediate-sized predators (especially black goby *Gobius niger*, $\sim 70 \text{ mm}$,

but also 3-spined stickleback *Gasterosteus aculeatus*, of 46 mm size) early in the season (May to June). This is equivalent to ~ 4 intermediate-sized predatory fish m^{-2} . The pattern is emphasized later in the season (August to September) when up to 34 intermediate-sized predatory fish m^{-2} can be found in *Z. marina* beds on the Swedish northwest coast. Moreover, omnivorous *Palaemonid* shrimps, found at densities ranging from 20 to 40 m^{-2} , prey upon small herbivores. A similar negative correlation between the biomass of cod and small fish (i.e. labrid fish and black goby) and decapod predators (mainly shore crabs) has recently also been demonstrated in southwestern Sweden (Eriksson et al. 2009), adding further support to a change in the trophic structure of the Swedish west coast. As a result of the high predation pressure by small predators, adult gammarids and idoteids are virtually absent from these shores (Jephson et al. 2008, Moksnes et al. 2008, Baden et al. 2012). In contrast, in the 1980s, the abundance of adult gammarids and idoteids varied between 30 and 85 ind. m^{-2} early in the year (May), which according to the present study would be sufficient to control algal blooms. This can be compared with the present mid-season densities of adult invertebrate herbivores in *Z. marina* beds in the Baltic Sea that vary between 100 and 800 ind. m^{-2} coupled with a lack of the ephemeral mats found on the west coast of Sweden (Baden et al. 2010).

Of late, it has been suggested that climate change may induce environmental variability that could increase occurrences of mismatches between species both in the ocean and on land (e.g. Edwards & Richardson 2004, Fabina et al. 2010, Yang & Rudolf 2010). Naturally, the effects of mismatches will be unique to each system, but it is likely that simpler ecosystems with fewer key herbivores will be more susceptible to such events (Cushing 1990, present study). It can also be expected that temperate coastal regions with pronounced seasonality will be particularly sensitive to the predicted increases in temperature and extreme storm frequency since seasonal trophodynamics are determined by the interaction between the physical factors controlling productivity and the species appearances during spring and summer (Cushing 1990, Edwards & Richardson 2004, Harley et al. 2006). In the Swedish seagrass meadow, for example, an earlier onset of algal growth could offset the natural balance between algal and herbivore appearances in spring. In the same way, herbivore behaviour can be affected by changes to the physical environment, but little is known of gammarid behaviour over winter, and it is just assumed that the larger adult individuals hibernate to form the base of new populations each year. In contrast, the smaller fish that prey upon herbivores spend the winter in slightly deeper waters and then return when temperatures increase (Pihl & Wennhage 2002, Pihl et al. 2006). With warming waters and fewer larger predators feeding in the seagrass meadow, it will be difficult even for timely herbivores to control algal development.

According to the model presented here, the abundances of autotrophs and invertebrate herbivores, which have a life cycle that operates on relatively short temporal and small spatial scales, are closely and dynamically linked to seasonal circumstances in terms of herbivore arrival times and predation level. The quantitative balance between trophic levels and timing of events in these ecosystems is surprisingly sensitive, and even simple interactions can produce complex patterns in time that would be difficult to elucidate through established food web theory (Paine 1980, Power 1992, present study). As an example, we can take one of our scenarios with a predation delay of 10 d under moderate predation in an enriched environment (Fig. 3B). Sampling a random day in mid-May, we may find large amounts of algae ($<100 \text{ g m}^{-2}$) and at the same time abundant herbivores. From a static top-down perspective, such data would suggest that the herbivores are feeding on alternative food and that predation (on herbivores) is

weak. However, in our simplified ecosystem, there are no alternative foods, and each point in time is just a snapshot of a system under change. Hence, there is a risk with analysing ecosystems under change using static correlative tools or approaches assuming mass-balance (e.g. Vadas 1989, Hughes et al. 2004), and models based on these assumptions are unlikely to yield reliable predictions of trophic structures in the field (Oksanen & Oksanen 2000, Robinson & Frid 2003, Christensen & Walters 2004).

Consistent with enrichment theory (White 1978, Oksanen et al. 1981) and results from field experiments in the modelled area (Moksnes et al. 2008, Baden et al. 2010), nutrient enrichment had small effects on algal biomass and instead increased the number of herbivores. Still, the simulated boost in maximum productivity by a factor of 2.65 led to a mere 0.26-fold rise in herbivore numbers at equilibrium, indicating that increases in productivity are concealed higher up the food chain. The explanation is that it is biomass and not maximum productivity that transfers between trophic levels, and if consumers fail to optimise the use of resources, the 'bottom-up' effects will be buffered when the resource is depleted (see Diehl et al. 2000 for a similar example from a lake ecosystem). On shorter time scales (before equilibrium), the benefits for consumers from increased productivity can of course be higher, a conclusion that is supported by a 6 wk caging experiment in this system, in which herbivore biomass was 60% higher (compared with 26% at simulated equilibrium) in nutrient-enriched treatments compared to an ambient treatment (Moksnes et al. 2008). We could also see that a modelled increase in productivity resulted in faster renewal of herbivores, which in turn led to higher resistance to predation (i.e. the benefit to population growth due to higher productivity partly offset the effects from predation) (see also Diehl et al. 2000).

An important aspect of trophodynamics not included in our model is that consumers adjust their food preferences as they grow (age) (e.g. De Roos & Persson 2002) and depending on the availability of food (e.g. Holling 1965, White 1978, Oksanen & Oksanen 2000). Although *Gammarus locusta* on the Swedish west coast is an effective grazer, it exhibits omnivorous behaviour, and it is known to become more predatory and even cannibalistic as it grows larger (Moksnes et al. 2008, Andersson et al. 2009). The effects of this behaviour and possible changes in size distribution over time can be difficult to observe from field data unless abundances and sizes are measured meticulously over time (e.g. De Roos & Persson 2002). Separating

herbivores into different sizes in our model could be a way of exploring potential consequences of how size-dependent consumption interacts with top-down and bottom-up processes in these systems.

Assessing potential human causes for changes to ecosystems requires extensive knowledge of the main drivers of ecosystem function, i.e. the interaction between resource supply and consumer pressure (e.g. Power 1992, Shurin et al. 2002, Estes et al. 2011). In seagrass meadows, the effects of increased nutrient loads on the growth rate of filamentous algae are well documented (e.g. Twilley et al. 1985, Hauxwell et al. 2003), and eutrophication is known to pose a threat to these ecosystems. We show here that reductions in herbivore densities, a likely consequence of overfishing of larger predators (Carpenter & Kitchell 1993, Frank et al. 2005, Baden et al. 2012), may have similar effects as full-scale eutrophication in environments with ambient nutrient levels. However, the relative impact from the 2 threats is not static, and the sensitivity of an ecosystem to external pressures can be higher at certain times and lower at other times. Measurable effects will be further blurred by innate variability in the densities of algae, invertebrates and fish (e.g. Burkepile & Hay 2006), and the latter is linked to the state of the adjacent offshore ecosystem (e.g. Eriksson et al. 2011). Future assessments of ecosystem health thus require monitoring schemes that take into account the effects of key herbivore and predator species on trophic structure and the natural and human-induced variability in the abundances of these species.

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