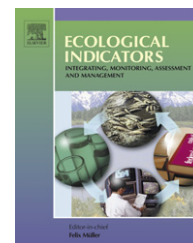


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# Empirical relationships linking distribution and abundance of marine vegetation to eutrophication

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## ABSTRACT

In order to decide on measures to preserve and restore seagrasses and macroalgae, there is a need for identifying quantitative links between eutrophication pressure and vegetation response. This study compiles existing empirical relationships between eutrophication-related variables and responses measured in terms of distribution and abundance of seagrasses and macroalgae and analyses similarities and differences between responses in different ecosystems. The compilation includes 73 relationships originating from 38 publications from the period 1982 to 2007 and covering a wide range of ecosystems. Of the 73 relationships, 38 link vegetation responses significantly to eutrophication pressure as expressed by nutrient richness or water transparency, 18 link the responses to combinations of eutrophication pressure and ecosystem characteristics and 9 link the responses to ecosystem characteristics alone. The remaining relationships are either non-significant (3) or include no information on significance levels (5). The compilation demonstrates that seagrasses and macroalgae generally respond quantitatively to changes in eutrophication pressure by growing deeper, being more abundant and more widely distributed in clear waters with low nutrient concentration as compared to more turbid and nutrient-rich ecosystems. Vegetation in deeper waters shows the strongest response because it is most markedly affected by shading effects of eutrophication. This similarity in the patterns of response indicates a wide robustness and generality of the findings. However, the sensitivity of the vegetation to shading effects of eutrophication varies widely across ecosystems. We attribute this variability to additional eutrophication effects such as anoxic events, and ecosystem characteristics such as water residence time, sediment characteristics, or presence of grazers that may modify the response of the vegetation to a given eutrophication pressure. We encourage taking into account and quantifying such effects in order to improve the predictive power of future empirical relationships.

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## 1. Introduction

Eutrophication causes marked deterioration of seagrass and macroalgal communities. Depth colonisation and abundance of the vegetation is reduced (Duarte, 1991; Nielsen et al., 2002a)

and species composition may change towards increased abundance of opportunistic macroalgae, which are fast growing and ephemeral, at the expense of seagrasses and perennial macroalgae (Duarte, 1995; Schramm, 1996). Because benthic vegetation is highly productive, constitutes habitat and refuge for invertebrates and fish and substrate for

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epiphytes, and thus enhances biodiversity and habitat diversity, such changes have serious ecosystem consequences (Schramm, 1996). Benthic vegetation also plays an important role in global carbon and nutrient cycling, stabilises flow conditions and promotes sedimentation, thereby reducing particle loads in the water as well as coastal erosion (Hemminga and Duarte, 2000).

Nutrient load, i.e., the input of nutrients to an ecosystem, affects seagrasses and macroalgae through a cascade of interactions leading to shading. Increased nutrient load causes increased nutrient concentration that stimulates phytoplankton production and thereby increases chlorophyll concentration and light attenuation. Other eutrophication effects such as increased sedimentation or anoxic events also hamper the vegetation. Though these general eutrophication effects are well-known (Duarte, 1995; Nixon, 1995; Cloern, 2001), quantitative links between eutrophication pressure and vegetation response are limited and scattered in the literature. Such quantitative information is needed in order to decide on measures to reduce nutrient load and thereby preserve and restore the vegetation. An optimal management tool would be a classical dose–response relationship with the dose being nutrient load, the variable to be managed, and the response variable being, e.g., area distribution or depth limit of seagrasses. Relationships between nutrient concentration or light attenuation and vegetation response are also useful management tools since these variables are coupled to nutrient load (Valiela et al., 2000; Tomasko et al., 2005).

Quantifying effects on the vegetation of specific factors such as nutrient load, nutrient concentration or water transparency is not straight-forward since a complex of factors varying on both temporal and spatial scales interacts to regulate the vegetation. The regulating factors include not only the eutrophication related variables listed above, but also climatic variables like insolation, temperature and wind events, other physico-chemical variables such as substratum conditions and salinity, and biological variables like grazing and disease. Effects of specific factors may be identified through laboratory experiments, where relevant parameters are manipulated and plant responses monitored. Mechanistic models that predict responses at the population or community level are often based on multiple studies of plant response at the individual plant or physiological level (Farmer and Adams, 1989; Carr et al., 1997) but such small-scale studies are insufficient for describing plant responses at the scale of populations and communities in the field.

A useful method for analysing large-scale patterns of plant response is through the establishment of empirical relationships between, e.g., nutrient load and vegetation response based on large data sets representing a wide range of habitat conditions and responses occurring in the field. Such data sets allow discriminating between effects of the above-mentioned abiotic triggers of vegetation response and thereby identifying relationships between eutrophication pressure and vegetation response. Though a correlation between two variables does not document a causal relationship it does provide an indication of such, especially when reflecting well-documented regulation mechanisms such as light control of depth limits. This approach has been applied in lakes since the 1960s and was initiated by predictive relationships between nutrient load/

concentration and phytoplankton chlorophyll/production. The most classic example is the ‘Vollenweider plot’ relating phytoplankton chlorophyll to nutrient load (Vollenweider, 1976). Later analyses included relationships between transparency and depth limits of lake macrophytes (Chambers and Kalff, 1985; Duarte and Kalff, 1987). The Vollenweider approach inspired similar large-scale comparisons of eutrophication effects in marine mesocosms and coastal areas (Boynton et al., 1982; Oviatt et al., 1986). Soon after, the establishment of predictive relationships between physico-chemical variables and benthic vegetation variables in coastal areas followed (Dennison, 1987; Sand-Jensen and Borum, 1991; Terrados et al., 1998; Nielsen et al., 2002a; Fourqurean et al., 2003).

This study aims to (1) identify quantitative links between eutrophication pressure and responses of seagrasses and macroalgae in coastal waters based on large-scale empirical relationships compiled from the literature and (2) analyse similarities and differences between responses in different ecosystems. The benthic vegetation responds in various ways to eutrophication pressure, so a wide array of possible response variables exists. They encompass genetic indicators, chemical and isotopic composition, processes such as growth rates as well as indicators of distribution and abundance (Borum et al., 2004). We have here considered responses in terms of distribution and abundance of seagrasses and macroalgae which both form critical habitats in many coastal ecosystems.

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## 2. Materials and methods

We searched the international literature for empirical relationships based on field data linking water quality variables to the distribution and abundance of seagrasses and macroalgae preferably through correlation or linear regression analyses. We compiled the relationships but did not compile the data sets behind the relationships. We searched through the Web of Science and supplemented the search by cross-referencing. We searched for the following response variables: (1) ‘depth limit of seagrasses and macroalgae’, known to depend on transparency (Dennison, 1987; Duarte, 1991), (2) ‘abundance of seagrasses and macroalgae at specific water depths’ also depending on transparency (Duarte, 1991; Dahl and Carstensen, 2005), (3) ‘area distribution of seagrasses’ which depends on both depth limits and abundance at specific depths and therefore also should respond to changes in transparency, and (4) ‘abundance of opportunistic algae’ which is expected to increase relative to the abundance of perennial algae with increased nutrient richness (Pedersen, 1995). We included studies describing seagrasses either as one group or as individual species and macroalgae either as the entire community, larger taxonomic algal groups or individual species. We also included depth limits representing the depth of the deepest-growing specimen, of continuous vegetation or of algal belts and abundance expressed as presence, cover, biomass, or shoot density.

Studies were included which related or attempted to relate vegetation response to one or more of the following predictor variables reflecting eutrophication pressure: (1) ‘nitrogen and phosphorus load’, (2) ‘concentrations of total and inorganic nitrogen and phosphorus’, (3) factors directly affecting water

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