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Inferring time-variable effects of nutrient enrichment on marine ecosystems using inverse modelling and ecological network analysis

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HIGHLIGHTS

- We use LIM and ENA to assess the effects of nutrient addition on marine ecosystems.
- Increasing nutrient supply enhanced net primary production and system activity.
- Food web efficiency and FCI decreased with increasing nutrient addition rates.
- Detritus was dominant food source, regardless of the nutrient addition rates.

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ABSTRACT

We combined data from an outdoor mesocosm experiment with carbon budget modelling and an ecological network analysis to assess the effects of continuous nutrient additions on the structural and functional dynamics of a marine planktonic ecosystem. The food web receiving no nutrient additions was fuelled by detritus, as zooplankton consumed 7.2 times more detritus than they consumed algae. Nutrient supply instantly promoted herbivory so that it was comparable to detritivory at the highest nutrient addition rate. Nutrient-induced food web restructuring reduced carbon cycling and decreased the average number of compartments a unit flow of carbon crosses before dissipation. Also, the efficiency of copepod production, the link to higher trophic levels harvestable by man, was lowered up to 35 times by nutrient addition, but showed signs of recovery after 9 to 11 days. The dependency of the food web on exogenous input was not changed by the nutrient additions.

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1. Introduction

Marine ecosystems are under increasing anthropogenic pressure (Lotze, 2006). Increasing nutrient inputs causing elevated nitrogen (N) and phosphorus (P) concentrations are a main concern for ecosystem conservation (Andersen et al., 2004; Andersen et al., 2006).

Elevated nutrient supply may cause intensive algal blooms, which indeed may have ecosystem-level consequences such as decreased transparency, oxygen depletion in deeper water layers due to increased sedimentation, and changes in fish community composition (Bonsdorff et al., 1997; Cloern, 2001; Ryther, 1954; Shadiul Islam and Tanaka, 2004). As a result, effects of anthropogenic nutrient enrichment on the structure and functioning of marine ecosystems have been increasingly studied (Cloern, 2001). Concurrently, environmental impact assessments have shifted attention from biomasses of functional groups to interactions between these groups (Kones et al., 2009). In recent decades it has also been increasingly noted that a purely topological perspective (i.e. who eats whom) on food webs is insufficient to understand the functioning of natural food webs, and that the magnitudes of the energy and material flows within food webs need to be taken into account (Berlow et al., 2004; Van Oevelen et al., 2010).

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Linear inverse modelling is a tool to quantify energy or material flows in predefined food webs. It was first applied in ecology by Vezina and Platt (1988) and subsequently used widely in ecological modelling (e.g. De Laender et al., 2010b; Kones et al., 2006; Van Oevelen et al., 2010). The goal of a linear inverse model (LIM) is to estimate elemental flows (e.g. nutrients) or energy flows in food webs, i.e. networks of species and resources interacting through feeding relationships and dissipation processes (Klepper and Vandekamer, 1987; Van Oevelen et al., 2010; Vezina and Platt, 1988). The ability to estimate the magnitudes of unknown flows from incomplete data sets (Marquis et al., 2007; Niquil et al., 1999; Olsen et al., 2006; Olsen et al., 2007; Van Oevelen et al., 2010) allows ecologists to (1) perform a system-level analysis yielding insight to processes that are hardly measurable in the field and (2) compare food webs from different regions (Daniels et al., 2006). LIM has been successfully applied to unravel elemental budgets in a variety of natural food webs (De Laender et al., 2010b; van Oevelen et al., 2006) and food webs experimentally exposed to stressors (De Laender et al., 2010a; De Laender et al., 2009). However, these studies usually investigate the time-averaged material/energy budget or one particular moment in time providing a snapshot of ecosystem status. Temporal dynamics are typically not considered by these studies.

Food web flows estimated by a LIM can be synthesized into structural and functional ecosystem properties using Ecological Network Analysis (ENA). ENA comprises various kinds of network indices as reviewed by Latham (2006). ENA has been used in several ecosystem types and is an essential tool in aquatic ecology (Baird et al., 2011; Chen et al., 2010; Christian et al., 2009; Link et al., 2009; Meihls et al., 2009). For example, ENA was used for quantifying the status of specific marine ecosystems (Heymans et al., 2007; Niquil et al., 1999), for characterizing seasonal changes within one ecosystem (Borrett et al., 2006), or for comparing different ecosystems (Baird et al., 1991; Baird and Ulanowicz, 1993; Heymans et al., 2002; Monaco and Ulanowicz, 1997). However, using ENA for among-ecosystem comparisons can be done only when certain criteria are fulfilled (Baird et al., 1991; Monaco and Ulanowicz, 1997). Firstly, the topology and the degree of trophic aggregation must be the same among the ecosystems to be compared. Secondly, the same currency must be used across all ecosystems (e.g. carbon flows cannot yet be compared with nitrogen transfers).

This study is the first to combine LIMs and ENA to quantify the temporal dynamics of the structure and functioning of a marine intertidal ecosystem exposed to seven nutrient enrichment conditions, using a data set from a previously conducted mesocosm experiment. In contrast to earlier modelling efforts by Olsen et al. (2007), where time-averaged carbon flows were calculated, this study quantifies the temporal dynamics of the carbon budget. To this end, we constructed and solved 70 LIMs (seven nutrient treatments times ten points in time). The 70 carbon budgets were used to infer time-variable effects of nutrient enrichment on net primary production and on its importance as a food source for zooplankton, relative to detritus and bacteria. Additionally, the 70 carbon budgets were used as an input to ENA to assess effects on (1) the trophic level of copepods and food web efficiency for copepod production; (2) carbon cycling, using the average path length (APL), Finn's cycling index (FCI) and the dominance of indirect effects (ID); and (3) the system activity and organization (i.e. total system throughput and relative ascendancy).

Table 1
Daily nutrient addition rates applied in the 7 mesocosms (L_N, L_P and L_S for nitrogen, phosphorous and silica, respectively, in µg/l/d). N was added as NH_4NO_3, P as Na_2HPO_4, and Si as SiO_2.

Nutrient addition	Bag 1	Bag 2	Bag 3	Bag 4	Bag 5	Bag 6	Bag 7
L_N	0.00	2.13	3.61	6.14	10.40	17.80	30.20
L_P	0.00	0.29	0.50	0.85	1.45	2.46	4.18
L_S	0.00	4.27	7.25	12.30	21.00	35.60	60.60

2. Material and methods

2.1. The mesocosm data

A mesocosm experiment was previously conducted in a tidally driven lagoon system on the west coast of central Norway (Olsen et al., 2007). This experiment consisted of 7 mesocosms (bags 1 to 7) with a volume of about 38 m^3 each and moored on floating stands. This was a single factor experiment (variable nutrient addition rates with an element ratio of 16:16:1 for Si:N:P) lasting 18 days (from 19 August to 5 September 1997). Nutrients were added on a daily basis (Table 1).

During the experiment, integrated samples over the whole water column (0–10 m) were collected every 2 days, i.e. on a total of 10 sampling occasions. Olsen et al. (2007) classified the planktonic organisms in the samples based on their size and carbon source (i.e. autotrophic and heterotrophic organism). They determined the standing stocks (in µgC/l/d) of the different phytoplankton and small zooplankton groups, either by conversion factors or by using group-specific regressions between carbon content and cell volume. The biomass of copepods was based on length-carbon biomass relations estimated during the experiment, whereas length–weight relationships for other mesozooplankton taxa were taken from the literature. Also measured by Olsen et al. (2007) were the standing stocks (in µgC/l/d) of dead matter including dissolved organic carbon (DOC) and detritus (DET) by using catalytic high-temperature combustion in combination with infrared detection and a CHN analyser, respectively. A selection of carbon flows (in µgC/l/d) was measured, including gross primary production (GPP) for each phytoplankton group (A1, A2, A3, see Table 2), and heterotrophic bacterial production. All details can be consulted in Olsen et al. (2007).

2.2. Estimation of nutrient addition effects on carbon flows by linear inverse modelling

2.2.1. Conceptual framework

We used linear inverse modelling as recently proposed (De Laender et al., 2010a) to estimate the carbon flows in the food web at different nutrient treatments and at different points in time. For every combination of the 10 sampling days and 7 nutrient addition rates (6 treatments and 1 control), a linear inverse model (LIM) was built to estimate the carbon flows between the food web compartments using (1) the standing stocks, primary and bacterial production measured on the specific sampling day, (2) the physiological constraints of the involved taxa, and (3) the mass balances of the food web compartments. Thus, a total of 70 LIMs were constructed.

A LIM is defined by three linear matrix equations: approximate equalities that have to be met as closely as possible (Eq. (1)), equalities that have to be met exactly (Eq. (2)) and inequalities (Eq. (3)):

$$\mathbf{A} \cdot \mathbf{x} \approx \mathbf{b} \tag{1}$$

$$\mathbf{E} \cdot \mathbf{x} = \mathbf{f} \tag{2}$$

$$\mathbf{G} \cdot \mathbf{x} \geq \mathbf{h}. \tag{3}$$

In these equations, $\mathbf{x}$ is the vector of unknown carbon flows that needs to be estimated; $\mathbf{A}$, $\mathbf{E}$, and $\mathbf{G}$ are the matrices containing coefficients of linear expressions of the carbon flows and vectors $\mathbf{b}$, $\mathbf{f}$, and $\mathbf{h}$ hold numerical data (Van Oevelen et al., 2009; Van Oevelen et al., 2010; Vezina and Platt, 1988). Often, a linear inverse model only contains equalities and inequalities, while approximate equalities are added to single out one solution for $\mathbf{x}$. Solving the three matrix expressions results in an estimate for all carbon flows in the food web. Details can be found in Van Oevelen et al. (2009); Van Oevelen et al. (2010).