



## Integrated network models for predicting ecological thresholds: Microbial – carbon interactions in coastal marine systems



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### ABSTRACT

This proof of concept study presents a Bayesian Network (BN) approach that integrates relevant biological and physical-chemical variables across spatial (two water layers) and temporal scales to identify the main contributing microbial mechanisms regulating POC accumulation in the northern Adriatic Sea. Three scenario tests (diatom, nanoflagellate and dinoflagellate blooms) using the BN predicted diatom blooms to produce high chlorophyll *a* at the water surface while nanoflagellate blooms were predicted to occur also at lower depths (>5 m) in the water column and to produce lower chlorophyll *a* concentrations. A sensitivity analysis using all available data identified the variables with the greatest influence on POC accumulation being the enzymes, which highlights the importance of microbial community interactions. However, the incorporation of experimental and field data changed the sensitivity of the model nodes  $\geq 25\%$  in the BN and therefore, is an important consideration when combining manipulated data sets in data limited conditions.

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### 1. Introduction

Bayesian Networks (BNs) are being increasingly applied to model complex ecosystem processes through the graphical and probabilistic integration of numerous interacting variables to provide a scientifically informed framework for decision making (Fletcher et al., 2014). The graphical representation of complex interactions between multiple variables can assist in the communication of BNs to end-users thereby facilitating the application of BNs into water resource management practices (McDonald et al., 2015). Although BNs are limited by the inability to model feedbacks that are important in aquatic ecosystem processes unless a computationally demanding dynamic network is developed, they have some benefits that in particular circumstances, such as data limited conditions, can outweigh this limitation (McDonald et al., 2015). A benefit of the BN approach is the ability to iteratively evolve based on the successive incorporation of available and new emerging knowledge of the investigated system into a scientifically informed framework that can be used to investigate probabilistic relationships between variables, make predictions and test

scenarios (Lowe et al., 2014; Nojavan et al., 2014). Additionally, the fact that probabilistic dependencies between variables in BNs are explicitly shown supports the communication of the model across disciplines such as management and science, and microbiology and computer science (Fletcher et al., 2014; Levontin et al., 2011). This facilitation of inter-disciplinary collaboration increases the potential for BN models to be applied not only within the scientific community but also by a wide ranging end-user community, including environmental managers, regulators and water industries without requiring in-depth understanding of the detailed modelling approach.

Aquatic ecosystems are characterised by complex interactions between variable physical, chemical and biological factors that affect primary production and carbon cycling at different spatial and temporal scales. At the microscale, the structure and strength of bacteria-phytoplankton coupling vary spatially and temporally, and are regulated by nutrient supply (Azam and Malfatti, 2007). The organic matter (OM) pool available in aquatic ecosystems can be conceptualized as a physical continuum of molecules (Verdugo et al., 2004) that spans from colloids and gel particles known as dissolved organic matter (DOC) to particulate organic carbon (POC) aggregates such as marine snow (Alldredge and Cohen, 1987) or even large aggregates of different forms and sizes (mucilage) (Giani

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et al., 2005 and references therein). The pathways and rates of dissolved and particulate carbon cycles may be affected by sources, composition and transformations of aggregates in the environment (Turner, 2014 and references therein). The microbial communities and biogeochemical processes of the OM continuum furthermore control the habitat templates and resources for higher trophic organisms (Green and Dagg, 1997). Currently, marine POC formation, accumulation and sedimentation processes are being explored as potential pathways to remove CO<sub>2</sub> from the atmosphere through sequestration via photosynthetic fixation of CO<sub>2</sub> into biomass by phytoplankton.

Current models for predicting microbial community changes, such as function based models and bioclimatic models as opposed to a BN approach, have limited ability to link processes to environmental changes in the marine ecosystem and conduct scenario tests on scales relevant for monitoring and management (Larsen et al., 2012). Complex NPHZ-V multi-trophic models (Weitz et al., 2015) have been developed to integrate the complex inter-relationships between viruses, plankton and bacteria but do not reflect the impacts of physio-chemical conditions. Several numerical models have been implemented previously to investigate oceanographic properties linked to atmospheric forces that coincided with large organic aggregates (mucilage) events (Oddo et al., 2005), or to analyse the physical-chemical mechanisms that may regulate aggregation events (Signell et al., 2005) in the Adriatic Sea. Numerical models such as Phytoplankton Aggregation Model (PAM), Snow Aggregate Model (SAM) integrate processes of the microbial cycle but are limited in their application due to their parameterization requirements and demands on the specialist numerical modeller (Kriest, 2002). The PAM and SAM models aim to characterise the marine snow aggregates by size, density and composition rather than aiming to predict what physical-chemical and biological conditions lead to aggregate events. Cossarini and Solidoro (2008) performed a trophodynamic model to highlight the most important factors for POM accumulation, such as phytoplankton, total phosphorous concentrations, decay rate of particulate organic phosphorous, and mortality rate of bacteria for the Gulf of Trieste. The Mucilage Aggregate Index (MAI) approach was proposed to characterise the aggregate characteristics (size and distribution in the water column) to environmental parameters with correlations (Bragato et al., 2006). These approaches fail to identify and quantify the mechanisms influencing OM aggregates along gradients of physical and chemical attributes that vary spatially and temporally in marine environments. Therefore, there has been a demand for network based models, such as BNs, that can be applied by scientists and managers to investigate the mechanisms of OM aggregates in data limited conditions (Hurwitz et al., 2014).

The sporadic occurrence and lack of knowledge on the mechanisms of POC accumulation events has resulted in incomplete and limited datasets on the changes within and between ecosystem variables that precede aggregate formation. Integrating multiple data sources, such as expert elicitation with field observations in fuzzy logic approaches, has been commonly used to supplement quantitative information in the development of BNs under data limited conditions (Ban et al., 2014; Isci et al., 2014; Scholton et al., 2013). Combining different sources of *a priori* data, such as combining simulation and field data, can introduce bias and increase uncertainty in the posterior (output) probabilities of BNs that require assessment and in some cases the ranking of data sources (Hamilton et al., 2015). However, the inclusion of manipulative experimental datasets in *a priori* data to fill information gaps in data limited conditions and the consequences on the uncertainty and bias of the resulting posterior probabilities is undetermined.

In this study, a BN was iteratively developed to increase our understanding of the main parameters that effect POC formation in a marine environment using a proof of concept example developed for the shallow and enclosed areas, such as the Gulf of Trieste (GT), northern Adriatic. Several recurring events, either linked to anthropogenic eutrophication or to specific natural conditions, such as hyper-production copious mucus macroaggregates (Giani et al., 2005) have characterised the whole northern Adriatic basin in the recent past. It was shown that the variations in the availability of inorganic nutrients, dissolved organic nitrogen (DON) and dissolved organic phosphorus (DOP) can strongly influence the phytoplankton primary production and the microbial degradation of OM (Cozzi et al., 2004; Danovaro et al., 2005). Under certain poorly understood conditions, the recalcitrant nature of the OM pool combined with slower microbial degradation processes can lead to an increase of the POM pool and formation of large aggregates (Fajon et al., 1999; Malfatti et al., 2014).

Within the model, experimental and field data on microbial activity, including phytoplankton and bacteria communities, was combined with the physical-chemical parameters. Scenario tests using the set of data available for this case study were conducted to investigate the important processes involved in the POC formation and accumulation. The scenario test assessed the most probable environmental conditions occurring during: (i) a diatom bloom, (ii) a nanoflagellate bloom and (iii) a dinoflagellate bloom. A sensitivity analysis was conducted to assess the causal structure of the BN and the variables that most influence the output probabilities in the three scenario tests. Our hypotheses were that: 1) Phytoplankton community structure and primary production are important factors in POC formation and accumulation; and 2) Bacterial enzymatic activities controlling the transitions between POC and DOC are important factors in POC accumulation. Additionally, we assess the influence of incorporating experimental and field *a priori* data on the posterior probabilities of the BN.

## 2. Methods

### 2.1. Study area

The semi-enclosed Gulf of Trieste (GT) is a shallow coastal area (maximal depth of about 25 m) in the northernmost end of the Adriatic Sea. Its oceanographic conditions are affected by water mass exchange with the northern Adriatic at the open boundary, by variable local meteorological conditions that induce a pronounced seasonal cycle of seawater temperature (from 6 °C in winter to summer peaks of >25 °C) (Malačić et al., 2006) and by pronounced freshwater inputs of rivers (Cozzi et al., 2012). These physical factors are ultimately reflected in strong seasonal and inter-annual variability in ecosystem structure and functioning, which primarily includes changes in plankton communities and primary production (Fonda Umani et al., 2007; Malej et al., 1995; Tinta et al., 2015). Two seasonal peaks of phytoplankton biomass and abundance regularly occur in the GT: one in spring, being mostly due to the proliferation of nanoflagellates, and the other in late autumn, which is also the highest on the annual scale and is dominated by diatoms (Mozetič et al., 2012). Dinoflagellate abundance represents, with some exceptions, only a small portion of the phytoplankton community (on average around 4%) (Francé and Mozetič, 2012). At times, phytoplankton dynamics can be altered by exceptional events such as heavy precipitation or enhanced river inputs in summer, resulting in a diatom bloom in July (Malej et al., 1997; Tinta et al., 2015). The bacterial community structure shows the importance of *Alphaproteobacteria* (mainly SAR11), *Gammaproteobacteria* (*Bacteroidetes*, mostly *Flavobacteria*) and *Cyanobacteria* (*Synechococcus*) in GT (Tinta et al., 2015). Less abundant or rare

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