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# Integrated network models for predicting ecological thresholds:

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1 **Integrated network models for predicting ecological thresholds: microbial – carbon**
2 **interactions in coastal marine systems**

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12    **Abstract**

13    This proof of concept study presents a Bayesian Network (BN) approach that integrates

14    relevant biological and physical-chemical variables across spatial (two water layers) and

15    temporal scales to identify the main contributing microbial mechanisms regulating POC

16    accumulation in the northern Adriatic Sea. Three scenario tests (diatom, nanoflagellate and

17    dinoflagellate blooms) using the BN predicted diatom blooms to produce high chlorophyll *a*

18    at the water surface while nanoflagellate blooms were predicted to occur also at lower depths

19    (> 5m) in the water column and to produce lower chlorophyll *a* concentrations. A sensitivity

20    analysis using all available data identified the variables with the greatest influence on POC

21    accumulation being the enzymes, which highlights the importance of microbial community

22    interactions. However, the incorporation of experimental and field data changed the

23    sensitivity of the model nodes ≥25% in the BN and therefore, is an important consideration

24    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 the model 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 with 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 et al., 2005 and references

62  therein). The pathways and rates of dissolved and particulate carbon cycles may be affected

63  by sources, composition and transformations of aggregates in the environment (Turner, 2014

64  and references therein). The microbial communities and biogeochemical processes of the OM

65  continuum furthermore control the habitat templates and resources for higher trophic

66  organisms (Green and Dagg, 1997). Currently, marine POC formation, accumulation and

67  sedimentation processes are being explored as potential pathways to remove $CO_2$ from the

68  atmosphere through sequestration *via* photosynthetic fixation of $CO_2$ into biomass by

69  phytoplankton.

70

71  Current models for predicting microbial community changes, such as function based models

72  and bioclimatic models as opposed to a BN approach, have limited ability to link processes to

73  environmental changes in the marine ecosystem and conduct scenario tests on scales relevant

74  for monitoring and management (Larsen et al., 2012). Complex NPHZ-V multi-trophic

75  models (Weitz et al., 2015) have been developed to integrate the complex inter-relationships

76  between viruses, plankton and bacteria but do not reflect the impacts of physio-chemical

77  conditions. Several numerical models have been implemented previously to investigate

78  oceanographic properties linked to atmospheric forces that coincided with large organic

79  aggregates (mucilage) events (Oddo et al., 2005), or to analyse the physical-chemical

80  mechanisms that may regulate aggregation events (Signell et al., 2005) in the Adriatic Sea.

81  Numerical models such as Phytoplankton Aggregation Model (PAM), Snow Aggregate

82  Model (SAM) integrate processes of the microbial cycle but are limited in their application

83  due to their parameterisation requirements and demands on the specialist numerical modeller

84  (Kriest, 2002). The PAM and SAM models aim to characterise the marine snow aggregates

85  by size, density and composition rather than aiming to predict what physical-chemical and

86  biological conditions lead to aggregate events. Cossarini and Solidoro (2008) performed a

87  trophodynamic model to highlight the most important factors for POM accumulation, such as

88  phytoplankton, total phosphorous concentrations, decay rate of particulate organic

89  phosphorous, and mortality rate of bacteria for the Gulf of Trieste. The Mucilage Aggregate

90  Index (MAI) approach was proposed to characterise the aggregate characteristics (size and

91  distribution in the water column) to environmental parameters with correlations (Bragato et

92  al., 2006). These approaches fail to identify and quantify the mechanisms influencing OM

93  aggregates along gradients of physical and chemical attributes that vary spatially and

94  temporally in marine environments. Therefore, there has been a demand for network based

4

95 models, such as BNs, that can be applied by scientists and managers to investigate the
96 mechanisms of OM aggregates in data limited conditions (Hurwitz et al., 2014).

97

98 The sporadic occurrence and lack of knowledge on the mechanisms of POC accumulation
99 events has resulted in incomplete and limited datasets on the changes within and between
100 ecosystem variables that precede aggregate formation. Integrating multiple data sources, such
101 as expert elicitation with field observations in fuzzy logic approaches, has been commonly
102 used to supplement quantitative information in the development of BNs under data limited
103 conditions (Ban et al., 2014; Isci et al., 2014; Scholton et al., 2012). Combining different
104 sources of *a priori* data, such as combining simulation and field data, can introduce bias and
105 increase uncertainty in the posterior (output) probabilities of BNs that require assessment and
106 in some cases the ranking of data sources (Hamilton et al., 2015). However, the inclusion of
107 manipulative experimental datasets in *a priori* data to fill information gaps in data limited
108 conditions and the consequences on the uncertainty and bias of the resulting posterior
109 probabilities is undetermined.

110

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

123

124 Within the model, experimental and field data on microbial activity, including phytoplankton
125 and bacteria communities, was combined with the physical-chemical parameters. Scenario

126    tests using the set of data available for this case study were conducted to investigate the
127    important processes involved in the POC formation and accumulation. The scenario test
128    assessed the most probable environmental conditions occurring during: (i) a diatom bloom,
129    (ii) a nanoflagellate bloom and (iii) a dinoflagellate bloom. A sensitivity analysis was
130    conducted to assess the causal structure of the BN and the variables that most influence the
131    output probabilities in the three scenario tests. Our hypotheses were that: 1) Phytoplankton
132    community structure and primary production are important factors in POC formation and
133    accumulation; and 2) Bacterial enzymatic activities controlling the transitions between POC
134    and DOC are important factors in POC accumulation. Additionally, we assess the influence
135    of incorporating experimental and field *a priori* data on the posterior probabilities of the BN.

136

137    **2. Methods**

138    *2.1 Study area*

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

158 *Delta-* and *Epsilonproteobacteria*, *Sphingobacteria*, *Cytophaga*, *Planctomycetes*,
159 *Actinobacteria*, *Verrucomicrobia* and *Deferribacteres*. Seasonal and spatial distribution of
160 bacterial community dynamics is influenced by temperature, freshwater-born nutrients and
161 phytoplankton blooms (Tinta et al., 2015).

162

163 *2.2 Experimental and field data*

164 Two sources of a *priori* data were used to inform the models posterior probabilities
165 (described in detail in the *Model development* section of this paper): a mesocosm experiment
166 and a field study (monitoring), both conducted in the GT.

167

168 An extensive (in terms of biogeochemical parameters analysed) 64-day mesocosm was
169 carried out in October 2007 in order to study carbon and phosphorus fluxes mediated via
170 microbial mechanisms and how interaction between carbon (C) and phosphorus (P) may lead
171 to DOC accumulation and persistence (Malfatti et al., 2014). Natural plankton assemblages
172 (bacteria and phytoplankton while larger herbivores were removed using 50 μm mesh)
173 collected in the south-eastern part of the GT were firstly spiked with nutrients except P at
174 F/10 concentration (Guillard and Ryther, 1962). After, three replicate carboys (P+) received
175 0.5 μM $PO_4^{3-}$ (approx. 10-times higher concentration compared to average phosphate
176 concentration in the sea water) while no $PO_4^{3-}$ was added to the other three (P-) control
177 carboys. The six carboys were incubated *in situ* at 2 m depth. The mesocosm experimental
178 design, parameters sampled and methods used are explained in details in Malfatti et al.
179 (2014). In particular, POC and DOC were measured in samples that were retained on or
180 passed through combusted GF/F filters, respectively, following standard procedures.

181

182 The other set of data originated from a two-year field survey (2009-2010) carried out in
183 fortnightly intervals at the marine field station 00BF (45° 32.93' N, 13° 33.03' E, 1.3 NM off
184 the coast, depth of 22 m), where oceanographic buoy Vida is located, in the south-eastern part
185 of the GT. Samples were collected at the surface (5 m) and near the bottom (20 m) of the
186 water column. The main objective of this study was to examine the seasonal dynamic of the
187 bacterial community of a coastal ecosystem and to investigate potential links between
188 bacterial and phytoplankton community and environmental parameters (for details see Tinta

189  et al., 2015). Field station 00BF is the same site where the sea water was collected for the

190  mesocosm experiment in 2007 and defines relatively undisturbed open waters of the Gulf.

191  The location also represents one of the longest time-series of the whole GT (Mozetič et al.,

192  2010); some parameters (*e.g*., dissolved oxygen and chlorophyll *a*) have been continuously

193  measured on a monthly basis from mid 80s onwards. Besides, the location makes part of the

194  grid of sampling stations, which is included in the national monitoring programme and

195  combines, when possible, with stations on the Italian side of GT into a complete coverage of

196  the Gulf's surface.

197

198  *2.3 Model development*

199  The iterative development of the BN model commenced with a conceptual model to identify

200  the variables (nodes) incorporated into sub-models and conditional relationships between

201  nodes from the available data (Fig. 1). The causal relationships connecting respective nodes

202  were determined by an extensive literature review and expert knowledge of the authors of this

203  paper on the considered processes in the northern Adriatic Sea. A BN was developed from

204  the conceptual model in Fig. 1 using the modelling software Netica 4.16 (Norsys Software

205  Corporation, 2010).

206

207  The conceptual model was initially developed into a network model in which the conditional

208  probabilities were derived from cause and effect relationships (Fig. 1). This model was

209  assessed with sensitivity analysis to investigate the propagation of probabilities through the

210  network structure. The bacterial and phytoplankton sub-models were then further developed

211  to include the taxonomy of phytoplankton and bacteria community structure using naïve

212  Bayesian network (NBN) relationships. The NBN structure assumes independence between

213  each taxonomical variable in the network (Flores et al., 2014). This NBN approach is

214  considered a more simplistic, hence naïve, representation of environmental relationships than

215  the cause and effect approach in defining the conditional structure of the model (Costa et al.,

216  2013). Despite this simplified assumption NBN approaches have strong mathematical

217  foundations and are effective in large, complex models with data limited conditions or for

218  unstructured data (Li and Li, 2013; Xu and Ma, 2014). The BN with both causal and naïve

219  structure was then assessed again with a sensitivity analysis and the results are outlined in

this paper. The development of the bacteria and phytoplankton community composition sub-models into the NBN structure provides important information on the abundance of each taxonomical class rather than only the dominant taxa in the initial cause and effect model structure that was developed (Fig. 1). A sensitivity analysis was used to assess model propagation through the final network structure and identify any insensitive or poorly informed nodes which could indicate to problems in the network structure.
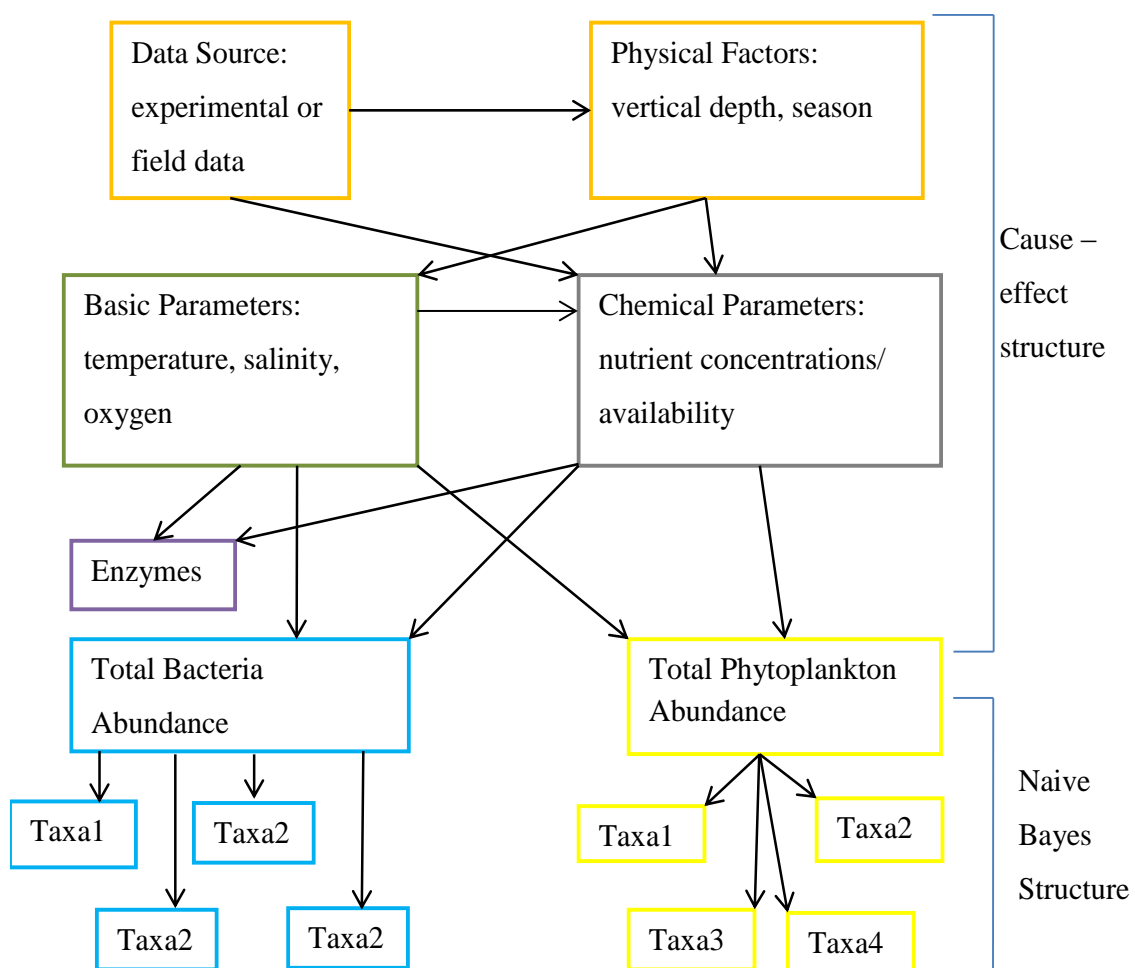


**Fig. 1** Conceptual model of the main causal relationships between sub-models of nodes in the network describing processes and process interactions leading to the higher POC concentrations. The arrows indicate conditional dependencies between sub-models.

In our study, the physical-chemical and biological parameters that might be relevant for formation and accumulation of POC were integrated into a network model. The *a priori* data

235 used to calculate posterior probabilities for each node in the network combined data from
236 two-year field survey (2009-2010) with a mesocosm experiment (described in detail in the
237 *Experimental and field data* section of this paper) into one case file (Supporting Information
238 1). The BN is developed with a data node that can be used to distinguish between the data
239 sources (Fig. 1). The inclusion of experimental data to supplement the field data was
240 important to fill information gaps that exist in the 2-year monitoring campaign, such as data
241 on enzyme availability and nutrient thresholds. Therefore, the experimental data are
242 important to inform the relationships among variables in the model and quantify trends that
243 the biweekly to monthly monitoring scheme may not detect. The posterior probabilities
244 derived from only field data and only experimental data are assessed using the data node
245 embedded in the network and a sensitivity analysis conducted to investigate changes in
246 influences between variables between the two data sources.

247

248 The BN in our study was developed to the best-practice principles outlined in McDonald et
249 al. (2015) as a proof of concept for modelling microbial community interactions in aquatic
250 environments using BNs. Therefore, it is intended that the model is in the initial phase of
251 construction to assess the approach and will be developed in the future prior to being applied
252 to ecosystem management. The states for each node (Mild, Mean, Moderate, Maximum) were
253 defined by percentiles of all available data which is a common method in data limited
254 conditions (Pollino et al., 2007). The ecological importance of each node included in the
255 network is outlined in Supporting Information 1. Conditional probability tables (CPTs) were
256 calculated from the data using the Expectation Maximization (EM) algorithm due to the
257 limited number of cases (data points) for each node (cases are provided in Supporting
258 Information 1; CPTs and further model configuration is available from the lead author on
259 request). The CPTs produced in this unconditioned model represent the base case (the
260 parameterized model prior to a user defined scenario being entered) or the probabilities based
261 on all possible outcomes of the *a priori* data (McDonald et al., 2016).

262

263 *2.4 Scenario testing*

264 The complex interactions between mechanisms regulating POC accumulation and microbial
265 community structure in the unconditioned BN model developed have been furthermore tested

266   in three user-defined scenarios. Assuming that a chosen model structure is accurate, scenario
267   tests (where the model is conditioned to have a specific CPT outcome for at least one node)
268   can provide information on ecosystem responses under specific conditions (Mantyka-Pringle
269   et al., 2014; Van Grieken et al., 2013). The first scenario test investigated the ecosystem
270   responses under a high abundance of diatoms, the second scenario test a high abundance of
271   nanoflagellates, and the third scenario test included a high abundance of dinoflagellates.
272   Scenario tests were conducted by setting the abundance node for the phytoplankton group in
273   question (nanoflagellates, dinoflagellates or diatoms) to 100% probability of the state
274   representing the highest possible concentrations occurring and the dominant phytoplankton
275   node finding to 100% probability of occurrence for the same group being investigated in the
276   scenario test (*i.e.* diatom, dinoflagellate or nanoflagellate, respectively) (Supporting
277   Information 2). Thereby, predicting the probable influence a bloom event of a particular
278   phytoplankton group being investigated on the microbial community and POC. The
279   predictions for investigating the ecosystem responses in this study were conducted using both
280   the forward and backward propagation techniques (McDonald et al., 2015). These scenario
281   tests were used by the authors to investigate both the interactions between phytoplankton
282   community composition and the physical-chemical factors regulating carbon accumulation
283   and degradation processes in the GT.

284

285   *2.5 Microbial mechanisms*

286   Microbial interactions with POC aggregate formation were investigated using the scenario
287   testing technique outlined above and compared to the posterior probabilities in the
288   unconditioned model. The microbial mechanisms were investigated by conducting a scenario
289   test in which the POC node was set maximum state threshold and all parent nodes remained
290   unconditioned during the scenario test (Supporting Information 2). Thereby, the scenario test
291   investigated the most probable environmental and microbial conditions present under the
292   highest POC conditions in the *a priori* data were assessed using the BN model.

293

294   *2.6 Sensitivity analysis*

295   The sensitivity analysis, combined with the scenario testing, identified the nodes that are
296   most sensitive to changes in the posterior probabilities (calculated in the conditional

297  probability tables (CTPs)) with different outcomes in network. A sensitivity analysis was
298  conducted on the nodes of interest such as POC, phytoplankton and bacteria abundance. All
299  parent nodes remained unconditioned during the sensitivity analysis. The variance reduction
300  (VR) method in the Netica software was used to calculate the sensitivity between nodes in the
301  network.

302

303  Sensitivity analysis was furthermore used to investigate the mechanisms regulating POC
304  increase based on the model being informed by: (i) all the *a priori* data available, (ii) only the
305  experimental data and (iii) only the field data available. The changes in mechanisms of POC
306  accumulation identified by the sensitivity analysis were investigated by conducting scenario
307  tests on the unconditioned model for the all available data case study. The different data
308  sources were then investigated by setting data node to 100% probability of field data or 100%
309  probability of experimental data being used to derive the model outputs. Inferring differences
310  between the sources of the *a priori* data (field and experimental) aimed to identify the
311  variability that may be introduced into the model through the incorporation of manipulated
312  experimental data to fill information gaps in field (monitoring) data.

313

314  **3.  Results**

315  The output probabilities in the unconditioned BN predict a mean POC concentration to be the
316  most likely (48.0%) under all possible outcomes (base case) from the *a priori* data (Fig. 2;
317  Table 1). The most probable outcome for chlorophyll *a* concentrations was predicted to fall
318  within maximum threshold (26%) or within mean threshold (21.4%). The abundance of total
319  phytoplankton (25.7%) and rates of primary production (41.7%) were predicted to be in the
320  mean state range. The concentrations of DOC are predicted to fall within the minimum
321  threshold range (51.8%). The dominant bacteria order is predicted to be SAR 11 (38.9%)
322  based on all possible outcomes from the *a priori* data (Fig. 2). Nanoflagellates have the
323  highest probability of being the dominant phytoplankton group (40.5%).

324
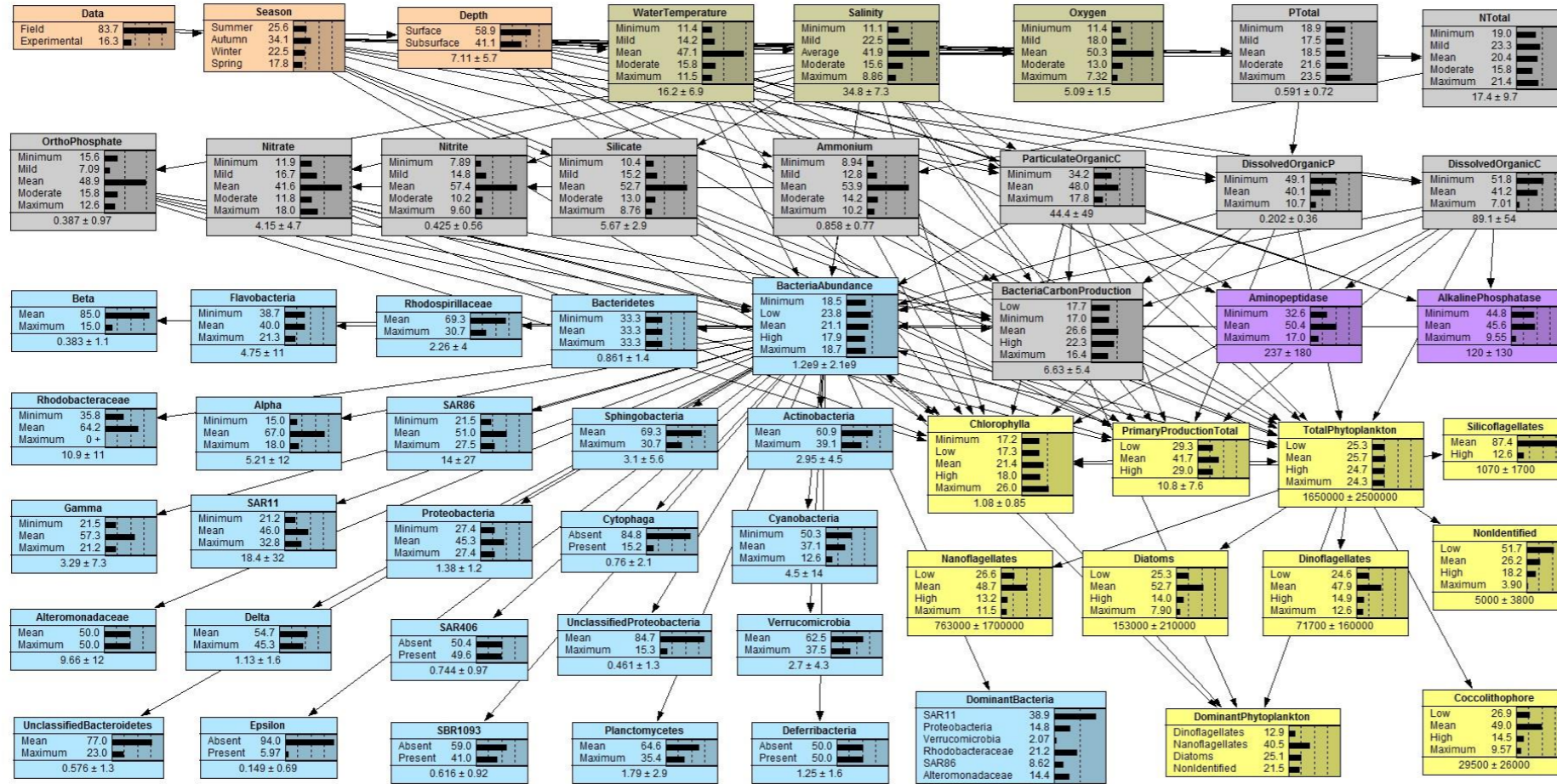
**Fig. 2** The unconditioned BN developed for investigating microbial mechanisms that lead to POC accumulation in marine environments. The network comprises of the spatial and temporal variables (orange), the basic physical-chemical parameters (green), the inorganic and organic nutrients (grey), enzyme activities (purple), bacteria community composition (blue) and phytoplankton community composition (yellow). Bottom layer (20 m) is regarded here as the subsurface layer.

13

**Table 1.** The predicted probabilities of states for key physical and chemical drivers of POC accumulation in each of the scenarios (to 1 decimal

331 place).

| Node | State | All probable outcomes | High Diatom abundance | High Dinoflagellate abundance | High Nanoflagellate abundance | Maximum POC |
|---|---|---|---|---|---|---|
| Season | Summer | 25.6 | 27.5 | 24.5 | 26.1 | 9.7 |
| | Autumn | 34.1 | 36.4 | 33.9 | 36.9 | 35.0 |
| | Winter | 22.5 | 17.8 | 23.9 | 16.1 | 17.1 |
| | Spring | 17.8 | 18.2 | 17.7 | 20.9 | 38.1 |
| Temperature | Minimum | 11.4 | 10.6 | 11.1 | 11.4 | 7.8 |
| | Mild | 14.2 | 12.6 | 14.4 | 11.1 | 27.4 |
| | Mean | 47.1 | 46.5 | 46.9 | 50.5 | 46.2 |
| | Moderate | 15.8 | 17.1 | 15.7 | 15.8 | 13.0 |
| | Maximum | 11.5 | 13.2 | 11.9 | 11.2 | 5.5 |
| Depth | Surface | 58.9 | 59.1 | 61.8 | 55.8 | 71.3 |
| | Bottom | 41.1 | 40.9 | 38.2 | 44.2 | 28.1 |
| Dissolved oxygen | Minimum | 11.4 | 12.4 | 11.3 | 12.1 | 5.69 |
| (DO) | Mild | 18.0 | 19.0 | 17.7 | 19.5 | 22.1 |
| | Mean | 50.3 | 48.2 | 51.2 | 47.1 | 53.6 |
| | Moderate | 13.0 | 13.0 | 13.0 | 13.1 | 15.3 |
| | Maximum | 7.3 | 7.4 | 6.8 | 8.1 | 3.4 |
| Ammonium | Minimum | 8.9 | 8.62 | 10.5 | 7.3 | 8.96 |
| | Mild | 12.8 | 12.9 | 13.8 | 11.2 | 13.5 |

| | | | | | | |
|---|---|---|---|---|---|---|
| | Mean | 53.9 | 53.9 | 53.0 | 53.7 | 62.8 |
| | Moderate | 14.2 | 14.3 | 13.6 | 16.4 | 5.24 |
| | Maximum | 10.2 | 10.3 | 9.08 | 11.4 | 9.53 |
| Ortho-phosphate | Minimum | 15.6 | 16.6 | 16.0 | 15.1 | 10.9 |
| | Mild | 7.09 | 7.4 | 7.6 | 6.4 | 11.2 |
| | Mean | 48.9 | 46.4 | 47.0 | 51.8 | 47.5 |
| | Moderate | 15.8 | 15.4 | 15.9 | 15.3 | 17.1 |
| | Maximum | 12.6 | 14.2 | 13.5 | 11.3 | 13.4 |
| Total Phosphorus | Minimum | 18.9 | 19.1 | 18.8 | 19.3 | 15.3 |
| | Mild | 17.5 | 17.4 | 17.4 | 17.6 | 15.0 |
| | Mean | 18.5 | 18.2 | 18.4 | 18.6 | 15.9 |
| | Moderate | 21.6 | 21.5 | 21.6 | 21.3 | 14.9 |
| | Maximum | 23.5 | 23.8 | 23.8 | 23.2 | 38.8 |

332

333

*3.1 Scenario testing*

335     The BN model predicts increased probability of POC accumulation in autumn in the

336     unconditioned network from the *a priori* data (34.1%), that increased in the nanoflagellate

337     bloom scenario test (36.9%) and in the diatom bloom scenario test (36.4%) but decreased in

338     the dinoflagellate bloom scenario test (33.9%),  (Table 1; Supporting Information 2). Diatom

339     abundance is predicted to increase with water temperatures in the high 17.1% or maximum

340     13.2% node states. The model output predicts the vertical distribution of diatom (59.1%) and

341     dinoflagellate (61.8%) with higher abundance in the upper water column, while

342     nanoflagellates are more evenly distributed between the surface (55.8%) and bottom layer

343     (44.2%).

344

345     *3.2 Microbial mechanisms*

346     The maximum POC scenario is predicted to occur in spring (38.1%) at the surface (71.3%)

347     (Table 1; Supporting Information 2). The maximum concentrations of total phosphorous

348     (38.8%) in the *a priori* data are predicted to occur during POC accumulation events. During

349     the maximum state POC concentrations the probability of low DO concentrations (in the mild

350     (22.1%), mean (53.6%) and moderate (15.3%) node state ranges) increases from the

351     probabilities at base case in the unconditioned model.

352

353     Elevated dinoflagellate abundance is reflected in increase of the chlorophyll *a* concentration

354     within the maximum threshold state of 35.5%, an increase from 26% based on all probable

355     outcomes (base case) in the unconditioned network, 11.2% in high nanoflagellate conditions

356     and 30% in high diatom conditions (Table 2). Predictions for phytoplankton abundance

357     falling within the maximum threshold state was greatest in the diatom scenario (50.8%),

358     which increased from 26% in the unconditioned network. The probability of a maximum

359     phytoplankton abundance decreased with a nanoflagellate (13.7%) bloom and a dinoflagellate

360     (5.7%) bloom. The probability of primary production in the high range increased from 29%

361     in the unconditioned network to 30.1% with high diatom abundance and 30.7% with high

362     nanoflagellate abundance. The probability of bacteria abundance occurring within the

363     maximum node state range also increased from 18.7% in the unconditioned network to 23.1%

364     in the diatom scenario test and 19.8% in the nanoflagellate scenario test. The maximum

365 concentrations of POC were expected to increase from 17.8% to 18.7% in the diatom

366 scenario and 18.4% in the dinoflagellate scenario for POC (Table 2; Supporting Information

367 2). The probability of higher DOC concentration increased from 7.07% to 7.8%, based on all

368 probable outcomes in the unconditioned network, with high diatom abundance and even more

369 (7.2%) with high dinoflagellate abundance.

370

**Table 2.** The BN output probabilities (%) for key variables that indicate changes in biotic community structure and carbon accumulation (to 1 decimal place). The states with the highest probable outcome are in bold (Full model outputs are provided in Supporting Information 2).

| Node | State | All probable outcomes | High diatom abundance | High dinoflagellate abundance | High nanoflagellate abundance | Maximum POC |
|---|---|---|---|---|---|---|
| Chlorophyll *a* | Minimum | 17.2 | 15.1 | 19.8 | 16.8 | 17.9 |
| | Low | 17.3 | 11.2 | 24.5 | 14.8 | 18.9 |
| | Mean | 21.4 | 6.4 | 0 | **42.9** | 20.3 |
| | High | 18.0 | **37.3** | 20.3 | 14.3 | 17.7 |
| | Maximum | **26.0** | 30.0 | **35.3** | 11.2 | **25.2** |
| Phytoplankton abundance | Low | 25.3 | 0 | 0 | 0 | **25.5** |
| | Mean | **25.7** | 18.4 | 4.0 | 8.1 | 24.8 |
| | High | 24.7 | 30.8 | **90.3** | **77.4** | 24.5 |
| | Maximum | 24.3 | **50.8** | 5.7 | 13.7 | 25.2 |
| Net Primary production | Low | 29.3 | 30.5 | 28.5 | 30.4 | 30.8 |
| | Mean | **41.7** | **39.5** | **43.3** | **38.9** | **38.6** |
| | High | 29.0 | 30.1 | 28.1 | 30.7 | 30.6 |
| Bacterial abundance | Minimum | 18.5 | 15.1 | 21.8 | 15.7 | 19.7 |
| | Low | **23.8** | 17.1 | **27.5** | 21.1 | **21.9** |
| | Mean | 21.1 | **27.6** | 18.2 | 20.3 | 20.3 |
| | High | 17.9 | 17.0 | 15.5 | **23.1** | 18.4 |
| | Maximum | 18.7 | 23.1 | 17.1 | 19.8 | 19.7 |
| POC | Minimum | 34.2 | 34.8 | 33.2 | 36.0 | 0 |

|  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|
|  | Mean | **48.0** | **46.6** | **48.4** | **46.6** | 0 |
|  | Maximum | 17.8 | 18.7 | 18.4 | 17.4 | 100 |
| DOC | Minimum | **51.8** | **55.2** | **50.4** | **55.7** | **44.9** |
|  | Mean | 41.2 | 37.0 | 38.9 | 37.4 | 27.3 |
|  | Maximum | 7.0 | 7.8 | 7.2 | 6.9 | 27.7 |

373

374  The BN predicted chlorophyll *a* concentrations in the maximum state range and low total
375  phytoplankton abundance (25.5%) to be the most probable for POC concentrations in the
376  maximum node state (Table 2; Supporting Information 3). The most likely bacteria
377  abundance during maximum POC concentrations is predicted to be within the low state
378  concentrations (21.9%). The minimum node state concentrations of DOC were the most
379  probable (44.9%) to occur during events where the POC is within the maximum
380  concentrations.

381

382  *3.3 Sensitivity analysis*

383  The variables with the greatest influence on the probability of POC accumulation in the
384  model were aminopeptidase (10.5%) and alkaline phosphatases (8.3%) (Fig. 3; Supporting
385  Information 3). The POC output probabilities were sensitive to salinity (4.7%). The seawater
386  temperature (3.3%) and silicate (3.3%) were also key factors influencing the probability of
387  POC accumulation in the system that may account for some of probabilistic changes in the
388  community composition scenarios investigated in this paper. The dominant phytoplankton
389  class probabilities were most sensitive to changes in the chlorophyll *a* (8.7%) and
390  phytoplankton abundance (3.3%) nodes. The probabilities of phytoplankton community
391  composition nodes, such as coccolithophorids (1.5%) and dinoflagellates (1.4%), were
392  identified as key variables influencing the model output probabilities for dominant
393  phytoplankton class. Probabilities for the bacteria abundance node were most sensitive to
394  changes in the probabilities of the dominant bacteria (53.2%) node (Supporting Information
395  3). Bacteria community composition nodes, such as *Flavobacteria* (38.6%) and SAR11
396  (37.8%), were also key nodes influencing the probabilities of the bacteria abundance.

397
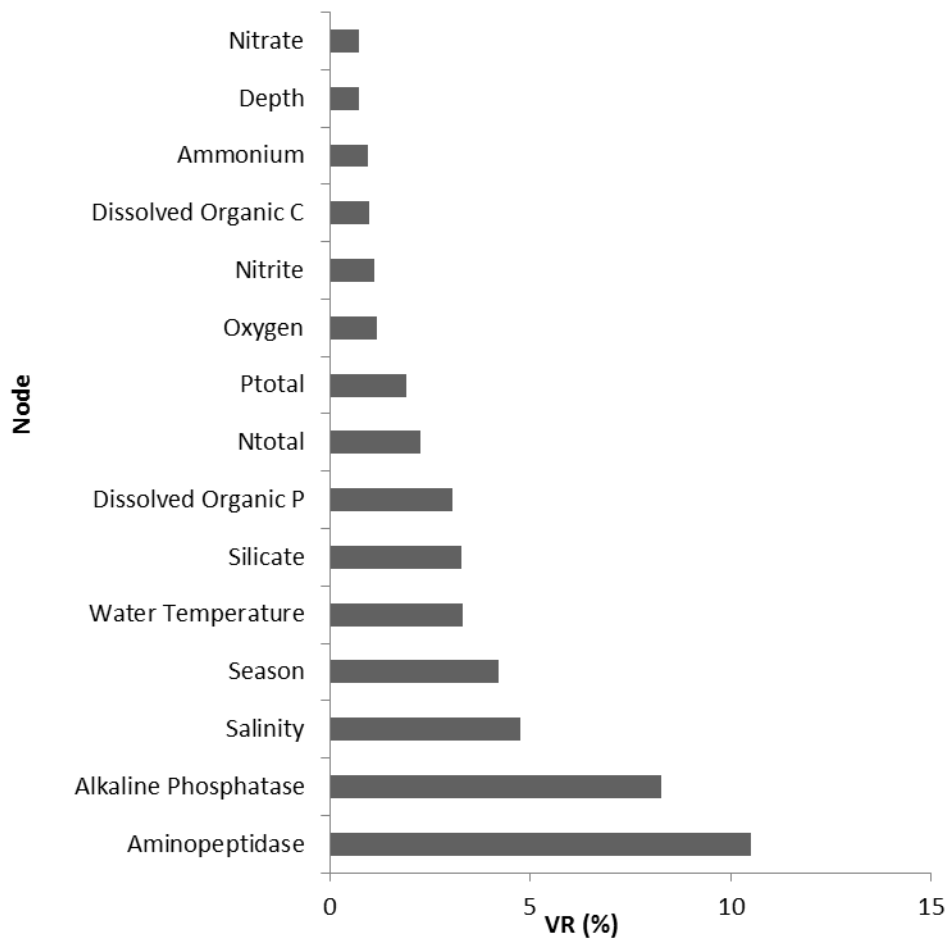
**Fig. 3** Sensitivity analysis indicating the variables that have the greatest influence on the POC node based on all available data being used to inform the model. Nodes are provided for values up to ≥1% VR change.

*3.4 Microbial mechanisms by data source*

The embedded data node in the BN structure distinguished between posterior probabilities derived from manipulated experimental and field data. The posterior probabilities of nodes populated with experimental data predict higher temperatures (Maximum 18%), lower salinities (Mild 54%), lower oxygen (Mild 29%), and increased DOC (Maximum 24%) and DOP (Maximum 28%), than if the model was populated by only field data (Supporting Information 4). Additionally, the posterior probability of the season node predicts the seasons that the experiments were conducted in (autumn 81% and winter 19%) when informed by only the experimental data. The BN populated with experimental data predicts higher bacteria abundance (21%), increased total phytoplankton (25%) and a shift in the dominant bacteria

413 (*Rhodobacteraceae* 20%). The posterior probabilities of nodes informed with field data

414 predict a broader range of probabilities among all node states than the probabilities from only

415 experimental data. For example, lower bacteria abundance (Maximum 19%), and increased

416 ammonium (11%), silicate (10%), nitrite (10%), nitrate (15%) and orthophosphate (13%) was

417 predicted in the BN informed by only the field data.

418

419 The nodes that had the greatest influence over the outcomes of POC in the model varied

420 between whether all data, only experimental data or only field data were used to inform the

421 posterior probabilities. The variables with the greatest influence on POC using all available

422 data to inform the probabilities were: aminopeptidase (10.5%) and alkaline phosphatases

423 activities (8.3%), salinity (4.7%), and season (4.2%). The variables with the greatest

424 influence on POC using only field data were: salinity (28.9%), total phosphorus (14.8%),

425 DOP (11.5%), and total nitrogen (11.4%). The variables with the greatest influence on POC

426 using only experimental data were: aminopeptidase (11.3%) and alkaline phosphatases

427 activities (9.2%), season (5.1%), and water temperature (3.8%). Changes in the sensitivity of

428 the POC node from the base case probabilities (all available data in the unconditioned model)

429 were greatest for the season node which increased by 0.9% and the salinity node which

430 decreased by 2% in the field data (Fig. 4). In the experimental data the sensitivity of the POC

431 node increased 24.16% to salinity and season decreased by 2.9% from the base case with all

432 available data.
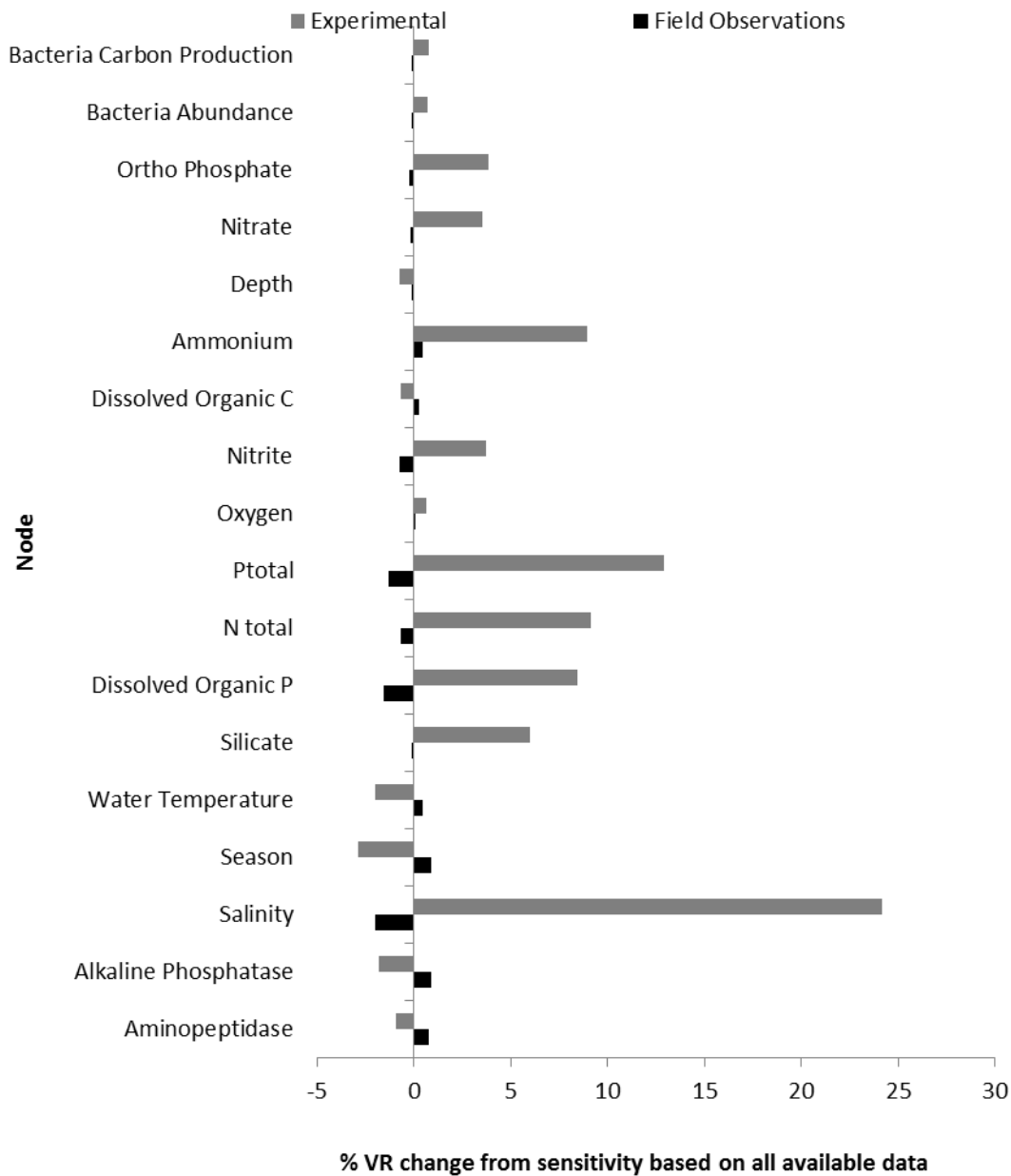
**Fig. 4** The % deviation from the VR (%) of the model at base case (all probable outcomes) when the model is informed by either only field data, or only experimental data. Nodes are provided for values up to ≥1% VR change.

437

## 4. Discussion

The integration of numerous sources of data is a key strength of the BN approach for data limited conditions (Ban et al., 2015; Li et al., 2010) when the node states, network structure and learning algorithms are carefully selected and applied (Lucena-Moya et al., 2015; Lui et al., 2007). Data from experimental ecosystems provide valuable information for predictive models on ecological thresholds that have not been exceeded and thus, are not detected in field datasets (Perlinski et al., 2014; Van Dam et al., 2014). However, including manipulated experimental data into predictive models can skew the output probabilities away from trends observed in the nature. By embedding a data source node into the network the posterior probabilities and interactions between variables can be investigated by end-users without manipulative data if bias is suspected. End-users can then determine the confidence in the model outputs and make informed decisions accordingly. Therefore, by incorporating manipulated date in the BN the interactions between variables in the predictive model can be informed from all available knowledge of the system in data limited conditions.

452

Understanding the possible uncertainty and bias in the *a priori* data, such as manipulated experimental data, is essential for managers and scientists to make informed interpretations of the model predictions. Salinity had the greatest variability in the sensitivity of the POC node and was more important in the experimental data (25% VR difference from the unconditioned model probabilities) and less important in the field data (-3% VR difference from the unconditioned model probabilities). This variability in the sensitivity of the POC node, and therefore POC aggregates, to salinity could be influenced by the lack of seasonal freshwater fluxes and depth profile in the simplified representations of the environment in the mesocosm experiments (Puddu et al., 1997; Monticelli et al., 2014). The sensitivity of the POC node to nutrient availability and turnover was also higher in the experimental data to the field data and highlights the influence of the nutrient enrichment on POC and system function. The enzymatic activity (alkaline phosphatase and aminopeptidase) remained among the most influential nodes on POC in both the manipulated and experimental data. However, alkaline phosphatase and aminopeptidase dropped from being the most influential nodes on POC when the model is informed by the manipulated experimental data which could be a result of the lack of data informing the nodes under the scenario. Similarly to the inclusion of

469    simulation or qualitative data into BNs, the inclusion of experimental data in the *a priori* data

470    is an acceptable method to fill information gaps or provide information on event that are yet

471    to occur (McDonald et al., 2015). In our BN, the manipulated experimental data provided

472    essential information on P thresholds for POC aggregates and filled information gaps on

473    interactions between nutrient availability, microbial community structure and enzymatic

474    activity. However, assessing the differences in the sensitivity of a target variable to the

475    different data sources is important to effectively interpret the model predictions, particularly

476    in relation to regulatory mechanisms.

477

478    Overall, the posterior probabilities of our BN under the scenarios presented in this paper

479    support the current understanding of coastal ecosystem functioning (e.g., Malej et al., 1995;

480    Mozetič et al., 2012; Malfatti et al., 2014; Tinta et al., 2015) such as node states in the high

481    and mean chlorophyll *a* concentrations will most probably develop during a diatom (37%)

482    and nanoflagellate (43%) bloom, respectively. In the GT, diatoms have been observed to be

483    responsible for the highest seasonal blooms, which usually occur in autumn (October-

484    November) and recently also in mid-summer (June-July) (Mozetič et al., 2012; Tinta et al.,

485    2015). These observations clearly support the BN prediction of a high probability of high

486    diatom abundance in autumn in the surface layer and indicate that the model is propagating

487    probabilities from the *a priori* data well in the current absence of validation. In general,

488    diatoms are known to thrive under conditions of elevated nutrients (Fawcett and Ward, 2011)

489    and grow at sufficiently high rates to maintain a major contribution to the biomass (Goericke,

490    2002). In a recent study Talaber et al. (2014) found abundance of diatoms in the surface layer

491    most closely related to high concentrations of total inorganic nitrogen and slightly less to

492    silicate, which corresponded to periods of diatom abundance peaks in late autumn and spring

493    – summer. Tamše et al. (2014) suggested that, besides mixing of waters of different origin,

494    phytoplankton uptake controlled the distribution and isotopic composition of nitrate in the

495    marine system and was more extensive in spring, while in autumn ammonium, not nitrate,

496    was the dominant source for phytoplankton. Indeed, the posteriror probabilities of the POC

497    node in our BN was also more sensitive to changes in ammonium than nitrate.

498

499    Nanoflagellates, which are on the annual basis prevailing and most abundant group in the GT,

500    have not been identified to contribute as much as diatoms or dinoflagellates to chlorophyll *a*

biomass. The model prediction that mean chlorophyll *a* concentrations will most probably occur during periods of high nanoflagellate abundance, therefore reflects the real situation of the GT (Mozetič et al., 2012) and of other temperate coastal areas, e.g. Gulf of Naples (Ribera d'Alcalá et al., 2004) and western Black Sea (Yunev et al., 2007). Lastly, the prediction of the model that the maximum state of chlorophyll *a* is most probably achieved during the third scenario of high dinoflagellate abundance is overestimated due to an unusually high abundance of dinoflagellates in the year, which was used to populate the BN.

Our model also predicted the highest probability (44.2%) that a nanoflagellate bloom will develop in the deeper water column layer (>5m) than a diatom bloom (<5m). An explanation could be the fact that flagellates can perform active swimming, which permits these organisms to access the water layer with an adequate quantity of inorganic nutrients, thereby improving their retrieval (Smayda, 1997). It, however, failed to detect dinoflagellates using the same advantageous characteristic, vertical mobility, according to the probability (38.2%) that a dinoflagellate bloom will develop in the bottom layer (>5m).

In the BN model of this study, probabilities for the bacteria abundance node were most sensitive to changes in the probabilities of the dominant bacteria (53%) node, with *Flavobacteria* (37%) and SAR11 (38%) as key nodes with high VR value. These observations clearly support our previous results and significant relationships between diatom blooms and shift in bacterial community composition within *Alphaproteobacteria* (from SAR11 to *Rhodobacteraceae*) and increase of *Gammaproteobacteria* (within which mostly *Alteromonadaceae*, SAR86 and *Vibrionaceae*) (Tinta et al., 2015) in accordance with others (Gilbert et al., 2012; Teeling et al., 2012). *Gammaproteobacteria* appear to be dominant colonizers of diatom detritus (Bidle and Azam, 2001) and marine snow aggregates (DeLong et al., 1993). High variability in bacterial and phytoplankton community composition has been observed in the aggregates during periods of mucilage formation in the northern Adriatic (Najdek et al., 2002).

Together with complex network structure, an importance of enzyme activity during large aggregates events in the GT has been observed (Del Negro et al., 2005; Ivančić et al., 2009;

532   Turk et al., 2010), changing quality of the DOC (Faganeli et al., 1995; Giani et al., 2005;

533   Malfatti et al., 2014). These observations support our BN model output, since the POC node

534   is most sensitive to changes in the bacterial aminopeptidase and alkaline phosphatase

535   activities nodes in model at base case (all probable outcomes) and the probabilities predicted

536   from only field and only the experimental data. Bacterial extracellular enzymes such as

537   aminopeptidase, lipase, glucosidase, N-acetylglucosaminidase in addition to alkaline

538   phosphatase are important catalysts in the degradation of POC to DOC (Smith et al., 1995).

539   The BN outputs highlight that further investigation of interactions between enzyme

540   availability and bacteria community composition and abundance should be conducted to

541   quantify the relationship as a mechanism in the degradation of aggregates.

542

543   The explicit quantification of uncertainty in the model output probabilities and

544   parameterization of the node states from the *a priori* data will be quantitatively assessed as

545   the model is updated and further developed. Qualitative indications of the uncertainty in our

546   model were investigated through the iterative model development (set of alternate models)

547   and the validation posterior probabilities and node sensitivity against known behaviour of the

548   system (Melbourne-Thomas et al., 2012). Uncertainty is expected to arise from the inclusion

549   of field and manipulated experimental data and the lack of feedback loops, such as the

550   microbial loop, in the model structure. Additionally, the short time series and data limited

551   conditions could inhibit the model from detecting long term trends or highly sporadic events

552   outside the available data. Therefore, until our model is updated and uncertainty within our

553   model is numerically quantified, the posterior probabilities have limited ability to inform

554   decision making processes. However, our model outputs can indicate the key nodes, variable

555   interactions and information gaps that are important to direct the future development of the

556   model and scientific investigations of POC aggregate events.

557

558   The BN framework developed in this study demonstrated exceptional potential to be

559   developed into a model that can be applied to investigate POC accumulation and microbial

560   dynamics in marine environments. The posterior probabilities captured the statistical trends in

561   the *a priori* data, reported in Tinta et al. (2015) and Malfatti et al. (2014), through the

562   propagation of probabilities in the network indicating the network structure adequately

563   represents current knowledge on ecosystem interactions. Furthermore, the model structure

564 was sensitive to changes in the CPTs and contained a very small number insensitive or poorly
565 informed nodes particularly for the model size and data availability. Therefore, further
566 development of the model may provide valuable information for managers and scientists on
567 the microbial interactions that regulate POC accumulation and are lacking in current models
568 used for characterising aggregate formation. However, the model was developed as a proof of
569 concept that inherently included two notable limitations. Data availability limitations
570 currently existing in the model can in future be overcome by updating with additional data
571 and conducting an uncertainty analysis as it becomes available. The inclusion of incomplete
572 datasets collected over sporadic timeframes is another key benefit of BNs in predicting data
573 limited environmental events (Ban et al., 2014; Metcalf et al., 2014). A further limitation is
574 that all field data used to inform the BN model was obtained from one location in the GT.
575 Data from additional locations, particularly from the Italian coast near the largest river
576 inflows, may be added in the future for the model to derive probabilities across the spatial
577 extent of the GT. Despite these limitations the BN created in this study advances previously
578 developed complex numerical models such as trophodynamic models (Cossarini and
579 Solidaro, 2008) by integrating physical, chemical and biological variables to investigate the
580 mechanisms for marine POC accumulation in a framework that has the potential to be used
581 by managers, scientists and stakeholders.

582

583 A benefit of the BN approach is the adaptability of the approach to be integrated into adaptive
584 management strategies and frameworks (McDonald et al., 2015). The BN presented in this
585 study could allow scientists and managers to identify and prioritise research on information
586 gaps on the poorly understood and complex relationships between the chemical parameters
587 and microbial activity. Our BN model identifies that carbon and nitrogen availability (and
588 turnover) is an important indicator of POC aggregate events, and interactions between
589 enzyme activity and bacterial community composition is important in regulating POC
590 conditions in marine ecosystems. However, little data is available on enzyme activity and
591 including enzymes in microbial monitoring schemes is currently not a common practice.
592 Consequently, quantifying the dynamic relationships between bacteria community structure
593 and enzyme activity remains poorly understood in the lead up to, during and decomposition
594 of POC aggregates. Our BN structure is a transparent and scientifically informed framework
595 to identify and targeted variables for managing POC aggregates that has the potential to be
596 implemented across international borders such as the Adriatic Sea. Further updating with

597　information from additional sites the model framework developed in this study could be
598　coupled with a GIS interface that scientists and managers could integrate into informed
599　decision making frameworks (Kocabas et al., 2012; Stelzenmuller et al., 2013). Therefore, a
600　BN approach that integrates physical, chemical and biological factors into a decision making
601　framework is an important step forward in predicting and managing POC aggregate events in
602　the future.

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**Supporting Information 1:** Node configuration

**Table S1.1** The definition and scientific rationale for each node in the network.

| Node | Definition | States | Ecological Importance | Cases |
|---|---|---|---|---|
| Data | The source of the data used. | Field Observations<br>Experimental | Experimental ecosystems can produce unreliable results (Elskens et al. 2005; Brock et al., 2015) | 129 |
| Season | Calendar seasons | Summer<br>Autumn<br>Winter<br>Spring | The seasonal variability of physical and chemical mechanisms in the system can influence the microbial processes occurring in the ecosystem (Tinta et al., 2015). | 129 |
| Depth (m) | Probabilities extrapolated from Tinta et al. (2015). | Surface (5)<br>Bottom (20) | Vertical distribution of physical-chemical parameters that influence the growth and abundance of plankton organisms (e.g., Fehling et al., 2012). | 129 |
| Water Temperature (ºC) | States derived from <10, 10-25, 25- 75, 75-90, >90 percentiles of data from Tinta et al. (2015). | Minimum 0 - 9.78<br>Mild 9.78- 11.73<br>Mean 11.73 – 19.69<br>Moderate 19.69 -23.03<br>Maximum >23.03 | Temperature influences the rate of biological processes (Pomeroy and Wiebe, 2001). | 100 |
| Salinity | States derived from <10, 10-25, 25- 75, 75-90, >90 percentiles of data from Tinta et al. (2015). | Minimum 0 – 34.52<br>Mild 34.52 – 36.13<br>Mean 36.13 – 37.57<br>Moderate 37.57 – 37.69 | The salinity governs physical, chemical and biological processes (Levinton, 2013). | 100 |

| | | Maximum >37.69 | | |
|---|---|---|---|---|
| Dissolved oxygen (mg/L) | States derived from <10, 10-25, 25- 75, 75-90, >90 percentiles of data from Tinta et al. (2015). | Minimum 0 - 4.03 <br> Mild 4.03 - 4.80 <br> Mean 4.80 - 5.80 <br> Moderate 5.80 - 6.45 <br> Maximum >6.45 | The dissolved oxygen concentration is the one of the major factor that determines the type and abundance of organisms as well as biochemical processes (O'Connor and Di Toro, 1970; Lee and Lee, 1995). | 90 |
| Total Nitrogen (TN) (µmol/L) | States derived from <10, 10-25, 25- 75, 75-90, >90 percentiles of data from Tinta et al. (2015) and Malfatti et al. (2014). | Minimum 0-9.07 <br> Mild 9.07-11.63 <br> Mean 11.63-23.50 <br> Moderate 23.50- 26.31 <br> Maximum >26.31 | Giani et al. (2012) reported POC aggregate accumulation has a hyperbolic relationship to TN concentrations. | 127 |
| Total Phosphorus (TP) (µmol/L) | States derived from <10, 10-25, 25- 75, 75-90, >90 percentiles of data from Tinta et al. (2015) and Malfatti et al. (2014). | Minimum 0-0.19 <br> Mild 0.24-0.19 <br> Mean 0.24-0.35 <br> Moderate 0.35-0.4 <br> Maximum >0.4 | Giani et al. (2012) reported POC aggregate accumulation has a linear relationship to TP concentrations. | 127 |
| Ammonium ($NH_4^+$) (µmol/L) | States derived from <10, 10-25, 25- 75, 75-90, >90 percentiles of data outlined in Tinta et al. (2015) and Malfatti et al. (2014). | Minimum 0-0.20 <br> Mild 0.20-0.32 <br> Mean 0.32-0.98 <br> Moderate 0.98-1.57 <br> Maximum >1.57 | A by-product of OM degradation that increases in concentrations in the water column through release from sediment, excretion of zooplankton (Wright, 1995) and inputs from land (e.g., sewage) (Brigolin et al., 2011). It is a bioavailable form of N for the biota and can serve as an energy source for bacteria (Miller, | 127 |

| | | | | |
|---|---|---|---|---|
| | | | 2004). | |
| Nitrite ($NO_2^-$) (µmol/L) | States derived from <10, 10-25, 25-75, 75-90, >90 percentiles of data outlined in Tinta et al. (2015) and Malfatti et al. (2014). | Minimum 0-0.04 Mild 0.04-0.09 Mean 0.09-0.46 Moderate 0.46-0.88 Maximum >0.88 | A bioavailable form of N that is required for photosynthetic processes and microbial processes (Miller, 2004). | 127 |
| Nitrate ($NO_3^-$) (µmol/L) | States derived from <10, 10-25, 25-75, 75-90, >90 percentiles of data outlined in Tinta et al. (2015) and Malfatti et al. (2014). | Minimum 0-0.45 Mild 0.45-0.83 Mean 0.83-4.39 Moderate 4.39-5.86 Maximum >5.86 | A bioavailable form of N that is required for photosynthetic processes and microbial processes (Miller, 2004). | 125 |
| Silicate $SiO_4^{4-}$ (µmol/L) | States derived from <10, 10-25, 25-75, 75-90, >90 percentiles of data outlined in Tinta et al. (2015) and Malfatti et al. (2014) | Minimum 0-2.69 Mild 2.69-5.44 Mean 5.44-7.31 Moderate 7.31-9.35 Maximum >9.35 | Silicon (in the form of orthosilicate ion) is a major nutrient for diatoms and silicoflagellates (Miller, 2004). | 127 |
| Orthophosphate ($PO_4^{3-}$) (µmol/L) | States derived from <10, 10-25, 25-75, 75-90, >90 percentiles of data outlined in Tinta et al. (2015) and Malfatti et al. (2014). | Minimum 0-0.04 Mild 0.04-0.05 Mean 0.05-0.1 Moderate 0.1 – 0.15 Maximum 0.15- 5 | A bioavailable form of P that is required for photosynthetic processes and microbial processes (Krom et al., 1991). | 127 |
| Dissolved Organic Phosphorus (DOP) | States derived from <25, 25-75, >75 percentiles of data outlined | Minimum 0-0.11 Mean 0.11-0.18 | Organic phosphorus pool that is cleaved by the alkaline phosphatase enzyme present in bacteria | 19 |

| | | Maximum >0.18 | and phytoplankton (Ivančić et al. 2009) | |
| --- | --- | --- | --- | --- |
| (μmol/L) | in Malfatti et al. (2014). | Maximum >0.18 | and phytoplankton (Ivančić et al. 2009) | |
| Particulate Organic Carbon (POC) (μmol/L) | Percentiles of data outlined in Malfatti et al. (2014). | Minimum 0 - 9.82<br>Mean 9.82 - 68.33<br>Maximum >68.33 | The origin and variation in chemical composition vary annually and can be affected by type of microbial community provoking blooms (Faganeli et al., 1995) | 16 |
| Dissolved Organic Carbon (DOC) (μmol/L) | States derived from <25, 25-75, >75 percentiles of data outlined in Malfatti et al. (2014). | Minimum 0-91.29<br>Mean 91.29-160.23<br>Maximum >160.23 | During algal growth substantial amount of DOC could be released and subsequently utilised by heterotrophic bacteria and influence the accumulation (Azam et al., 1983). | 20 |
| Chlorophyll *a* (μg/L) (Chl *a*) | States derived from <10, 10-25, 25- 75, 75-90, >90 percentiles of data from Tinta et al. (2015) and Malfatti et al. (2014). | Minimum 0 - 0.31<br>Low 0.31 - 0.42<br>Mean 0.42 - 0.99<br>High 0.99 - 1.62<br>Maximum >1.62 | The concentration of chlorophyll *a* indicates the biomass of phytoplankton, i.e. phytoplankton stock in the water column and is the key light-absorbing pigment involved in photosynthesis (Miller, 2004). | 124 |
| Total Phytoplankton abundance (cells/L) | States derived from <25, 25- 75, 75-90, >90 percentiles of data outlined in Tinta et al. (2015) and Malfatti et al. (2014). | Low 0 - 300000<br>Mean 300000 - 600000<br>High 600000 - 900000<br>Maximum >900000 | The amount of photosynthesised carbon can strongly vary with changes in the phytoplankton abundance and composition (Fonda Umani et al., 2005). | 95 |
| Net Primary Production (PP) (μg C/L h) | States derived from <25, 25-75, >75 percentiles of data outlined in and Malfatti et al. (2014). | Minimum 0 - 4.07<br>Mean 4.07 - 16.33<br>Maximum >16.33 | Net PP indicates the amount of inorganic C fixed into autotrophic biomass via photosynthetic processes within a specified time period and is subsequently available to higher trophic levels (Lindeman, 1942). | 17 |

| | | | | |
|---|---|---|---|---|
| Bacterial Carbon Production (µgC/L day) | States derived from <10, 10-25, 25- 75, 75-90, >90 percentiles of data outlined in Tinta et al. (2015) and Malfatti et al. (2014). | Minimum 0 - 1.07 Low 1.07 - 2.1 Mean 2.1 - 8.75 High 8.75 - 11.44 Maximum >11.44 | Bacterial growth rate is dependent on nutrient availability and on temperature (Hagström and Larsson, 1984). | 99 |
| Bacteria Abundance (cells x $10^8$/L) | States derived from <10, 10-25, 25- 75, 75-90, >90 percentiles of data outlined in Tinta et al. (2015) and Malfatti et al. (2014). | Minimum < 1.45 Low 1.45 -2.06 Mean 2.06 -5.71 High 5.71- 9.57 Maximum >  9.57 | Bacteria abundance varies seasonally and depends to a large extend on vertical physical processes and nutrient concentrations (Wikner and Hagström, 1991). | 109 |
| Alkaline phosphatase (nM/h) | States derived from percentiles of data outlined in Malfatti et al. (2014). | Minimum 0 - 24.28 Mean 24.28 - 325.52 Maximum > 325.52 | Enzyme that hydrolyses phosphate from phosphorus rich compounds (Celussi and Del Negro, 2011). | 14 |
| Aminopeptidase (nM/h) | States derived from percentiles of data outlined in Malfatti et al. (2014). | Minimum 0 - 80.48 Mean 80.48 - 466.90 Maximum > 466.90 | Enzyme that hydrolyses aminoacids from proteins (Celussi and Del Negro, 2011). | 14 |
| Dominant phytoplankton | States derived from percentiles of data outlined in Tinta et al. (2015) and Malfatti et al. (2014). | Nanoflagellates Diatoms Dinoflagellates Unidentified | Seasonal shifts in phytoplankton community composition that influences autotrophic C availability e.g., a diatom or nanoflagellate dominated community structure (Mozetič et al., 2012; Moran et al., 2012; Taylor et al., 2014). | 95 |
| Nanoflagellates (cells/L) | States derived from <25, 25-75, 75-90, >90 percentiles of data | Low 0 - 100000 Mean 100000 - 500000 | The abundance of each phytoplankton class/group reflects growth rates of that group, | 95 |

| | | | | |
|---|---|---|---|---|
| | outlined in Tinta et al. (2015) and Malfatti et al. (2014). | High 500000 - 900000<br>Maximum >900000 | but also physical processes (advection, horizontal mixing) that can promote different types of phytoplankton (Miller, 2004). | |
| Diatoms (cells/L) | States derived from <25, 25-75, 75-90, >90 percentiles of data outlined in Tinta et al. (2015) and Malfatti et al. (2014). | Low 0 - 4500<br>Mean 4500 - 174875<br>High 174875 - 487556<br>Maximum >487556 | | 95 |
| Dinoflagellates (cells/L) | States derived from <25, 25-75, 75-90, >90 percentiles of data outlined in Tinta et al. (2015) and Malfatti et al. (2014). | Low 0 - 6000<br>Mean 6000 - 37628.50<br>High 37628.50 - 52900<br>Maximum >52900 | | 95 |
| Coccolithophorids (cells/L) | States derived from <25, 25-75, 75-90, >90 percentiles of data outlined in Tinta et al. (2015) and Malfatti et al. (2014). | Low 0 - 6650<br>Mean 6650 - 42750<br>High 42750 - 69900<br>Maximum >69900 | | 95 |
| Silicoflagellates (cells/L) | States derived from <75, >75 percentiles of data outlined in Tinta et al. (2015) and Malfatti et al. (2014). | Mean 0 - 1000<br>High >1000 | | 95 |
| Non identified algae (cells/L) | States derived from <25, 25-75, 75-90, >90 percentiles of data from Tinta et al. (2015) and Malfatti et al. (2014). | Low 0 - 4000<br>Mean 4000 - 8000<br>High 8000 - 11900<br>Maximum >11900 | | 95 |
| Alphaproteobacteria | States derived from percentiles | Minimum 0 - 0.27 | Variable environmental parameters (biotic and | 16 |

| | | | | |
|---|---|---|---|---|
| (Relative abundance) | of data outlined in Tinta et al. (2015) and Malfatti et al. (2014). | Mean 0.27 - 0.37<br>Maximum >0.37 | abiotic) affect bacterial community composition (Fuhrman et al., 2006; Gilbert et al., 2012). Different phylotypes of bacteria have diverse metabolism that influence the carbon degradation and accumulation processes (Fuhrman et al., 2006; Teeling et al., 2012). Sequence taxonomic identities (at > 97% similarity) were assigned using the genome Basic Local Alignment Search Tool (BLAST) at the National Center for Biotechnology Information (NCBI). Classification was done down to the bacterial family level. In order to take into account the libraries with different sequencing depths we expressed the contributions of distinct bacterial families as a percentage of the total number of sequences in each library (relative abundance) (Tinta et al., 2015). | |
| Rhodospirillaceae and Rhodobacteraceae (Relative abundance) | States derived from <75, >75 percentiles of data outlined in Tinta et al. (2015) and Malfatti et al. (2014). | Mean 0 - 0.143<br>High >0.143 | | 16 |
| Gamma-Proteobacteria (Relative abundance) | States derived from <25, 25-75, >75 percentiles of data outlined in Tinta et al. (2015) and Malfatti et al. (2014). | Low 0 – 0.149<br>Mean 0.149 - 0.181<br>High >0.181 | | 16 |
| Alteromonadaceae (Relative abundance) | States derived from percentiles of data outlined in Tinta et al. (2015) and Malfatti et al. (2014). | Mean 0 - 0.39<br>Maximum >0.39 | | 16 |
| SAR11 (Relative abundance) | States derived from percentiles of data outlined in Tinta et al. (2015) and Malfatti et al. (2014). | Minimum 0 – 0.28<br>Mean 0.28 - 0.68<br>Maximum > 0.68 | | 16 |
| SAR86 (Relative abundance) | States derived from percentiles of data outlined in Tinta et al. (2015) and Malfatti et al. (2014). | Minimum 0 – 0. 0.16<br>Mean 0.16 – 0.53<br>Maximum >0.53 | | 16 |
| Betaproteobacteria (Relative abundance) | States derived from <90, >90%percentiles of data outlined in Tinta et al. (2015) and | Mean 0 – 0.02<br>Maximum >0.02 | | 16 |

| | | | | |
|---|---|---|---|---|
| | Malfatti et al. (2014). | | | |
| Deltaproteobacteria (Relative abundance) | States derived from <90, >90%percentiles of data outlined in Tinta et al. (2015) and Malfatti et al. (2014). | Mean 0 - 0.003 Maximum > 0.003 | | 16 |
| Epsilonproteobacteria (Relative abundance) | States derived from percentiles of data outlined in Tinta et al. (2015) and Malfatti et al. (2014). | Present Absent | | 16 |
| Unclassified Proteobacteria (Relative abundance) | States derived from <90, >90%percentiles of data outlined in Tinta et al. (2015) and Malfatti et al. (2014). | Mean 0 - 0.003 Maximum > 0.003 | | 16 |
| Flavobacteria (Relative abundance) | States derived from percentiles of data outlined in Tinta et al. (2015) and Malfatti et al. (2014). | Minimum 0 – 0.07 Mean 0.07 - 0.23 Maximum >0.23 | | 16 |
| Sphingobacteria (Relative abundance) | States derived from percentiles of data outlined in Tinta et al. (2015). | Mean 0 - 0.05 Maximum >0.05 | | 16 |
| Cytophaga (Relative abundance) | States derived from percentiles of data outlined in Tinta et al. (2015) and Malfatti et al. (2014). | Mean 0 – 0.0001 Maximum >0.0001 | | 16 |
| Unclassified Bacteroidetes | States derived from <90, >90%percentiles of data outlined | Mean 0 - 0.003 Maximum >0.003 | | 23 |

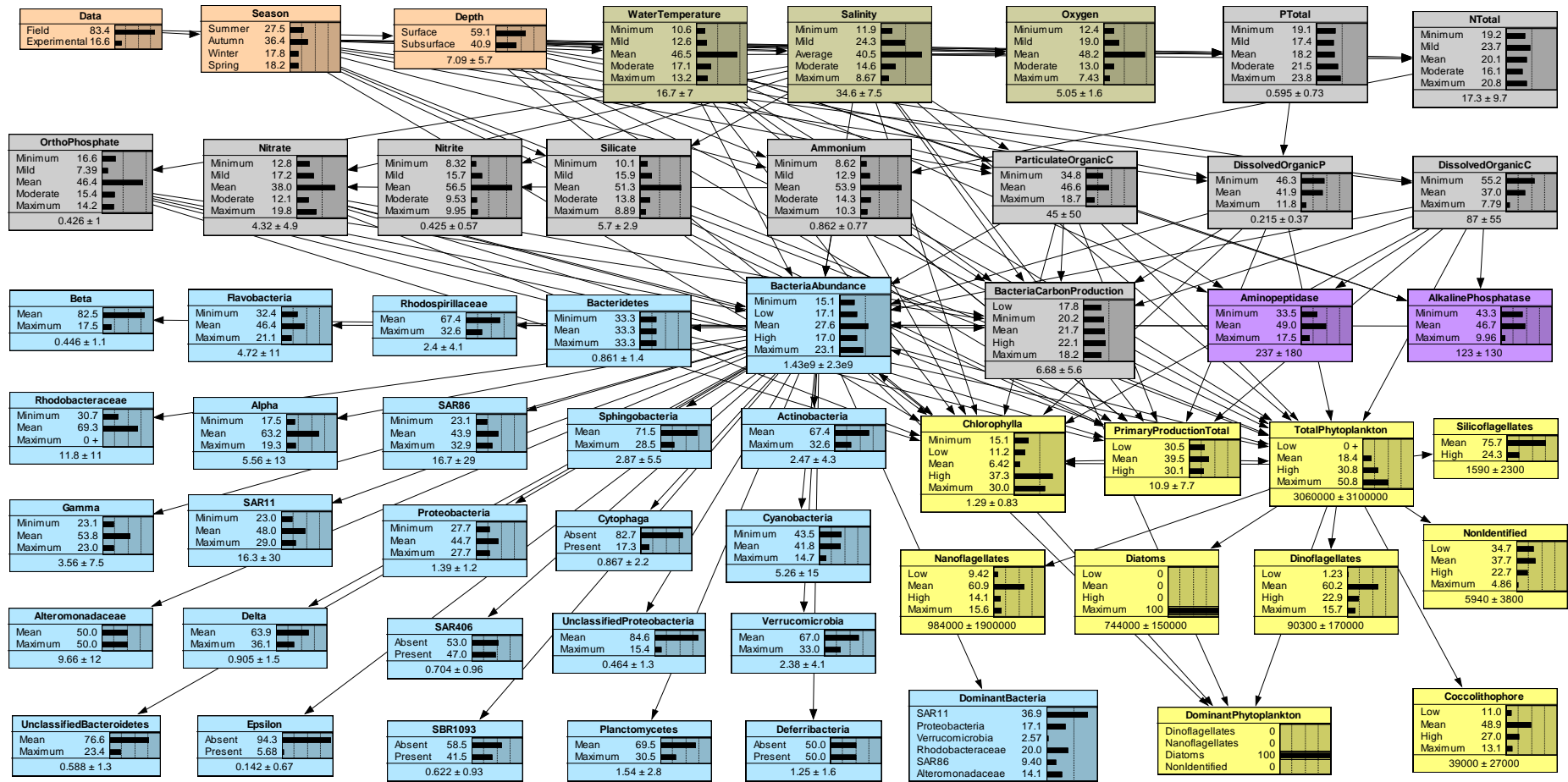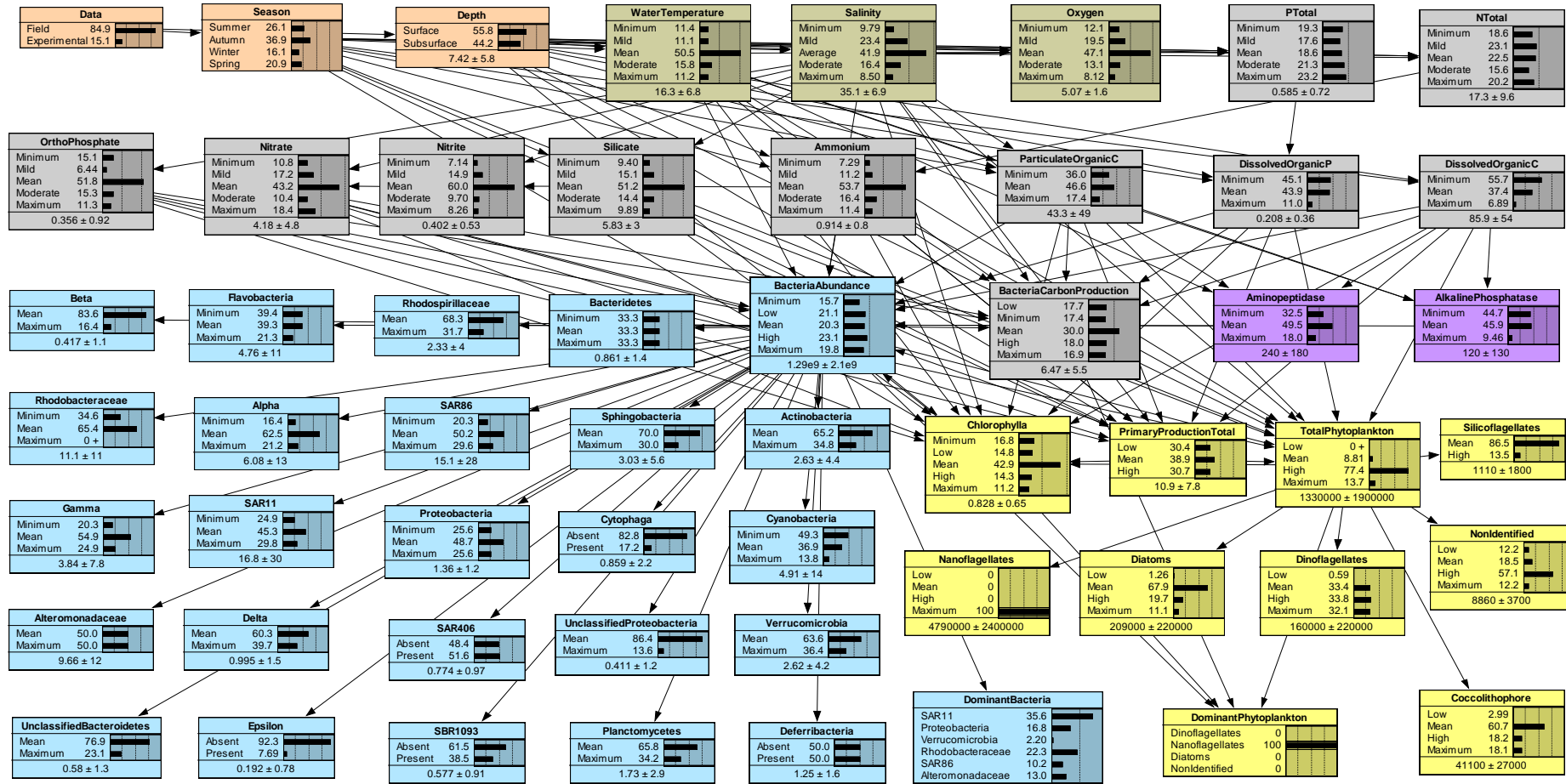| | | | | |
|---|---|---|---|---|
| (Relative abundance) | in Tinta et al. (2015) and Malfatti et al. (2014). | | | |
| Actinobacteria (Relative abundance) | States derived from <90, >90%percentiles of data outlined in Tinta et al. (2015) and Malfatti et al. (2014). | Mean 0 – 0.05 Maximum >0.05 | | 16 |
| Cyanobacteria (Relative abundance) | States derived from percentiles of data outlined in Tinta et al. (2015) and Malfatti et al. (2014). | Minimum 0-0.07 Mean 0.07 - 0.26 Maximum >0.26 | | 23 |
| Planctomycetes (Relative abundance) | States derived from <90, >90%percentiles of data outlined in Tinta et al. (2015) and Malfatti et al. (2014). | Mean 0 - 0.04 Maximum >0.04 | | 23 |
| Verrumcomicrobia (Relative abundance) | States derived from percentiles of data outlined in Tinta et al. (2015) and Malfatti et al. (2014). | Mean 0 - 0.04 Maximum >0.04 | | 23 |
| Deferribacteria (Relative abundance) | States derived from <90, >90%percentiles of data outlined in Tinta et al. (2015) and Malfatti et al. (2014). | Absent Present | | 16 |
| Dominant Bacteria (Relative abundance) | States derived from percentiles of data outlined in Tinta et al. (2015) and Malfatti et al. (2014). | SAR11 Proteobacteria | The bacteria present in the highest abundance at each observation point. | 23 |

|  | Rhodobacteria |
|  | SAR86 |
|  | Alteromonsdaceae |

988

**Supporting Information 2** Appendix of the scenario tests conducted in this study.
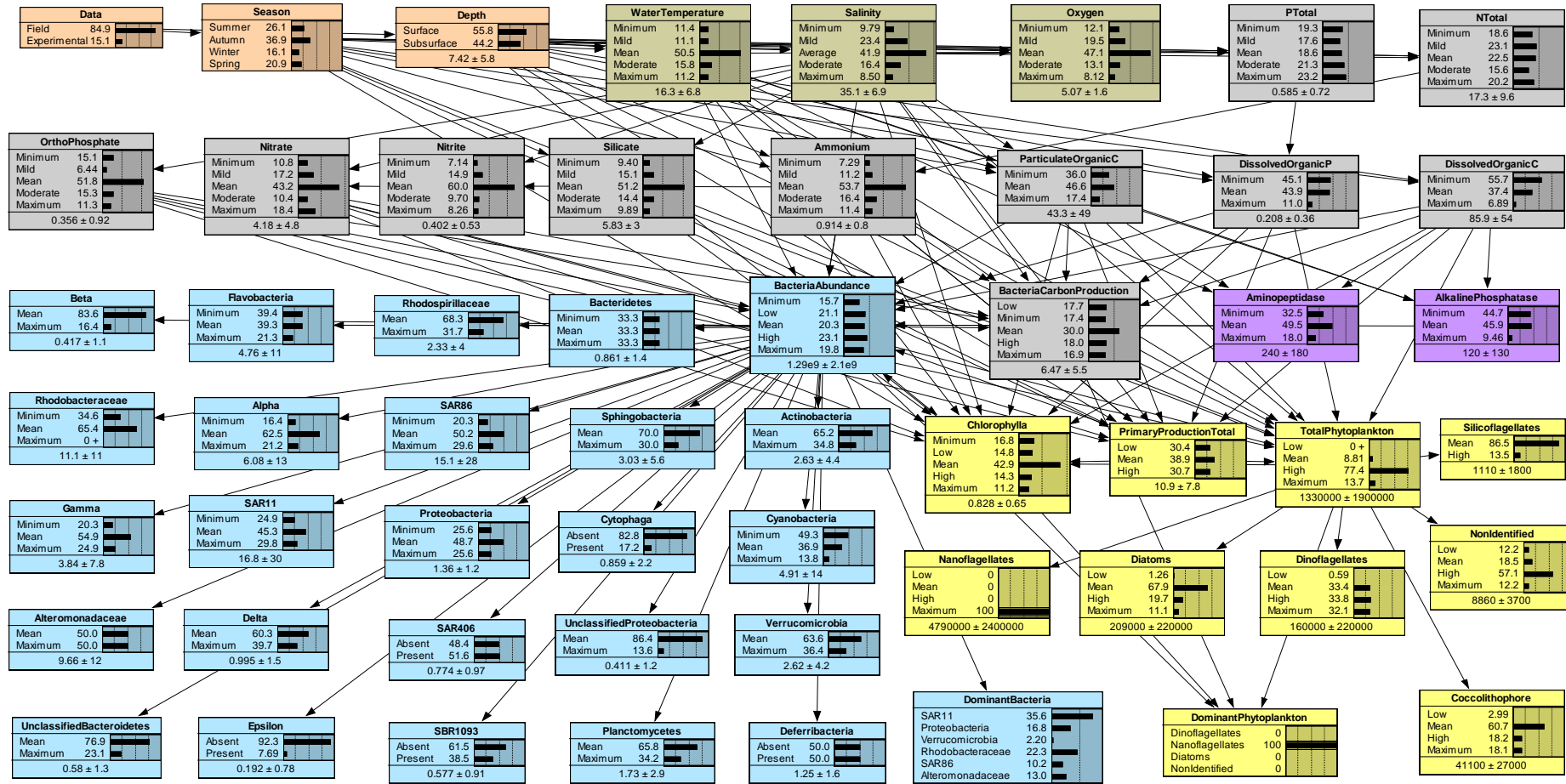
991  **Fig S2.1** Scenario test for a diatom bloom.

992

**Fig. S2.2** Scenario test for a dinoflagellate bloom.
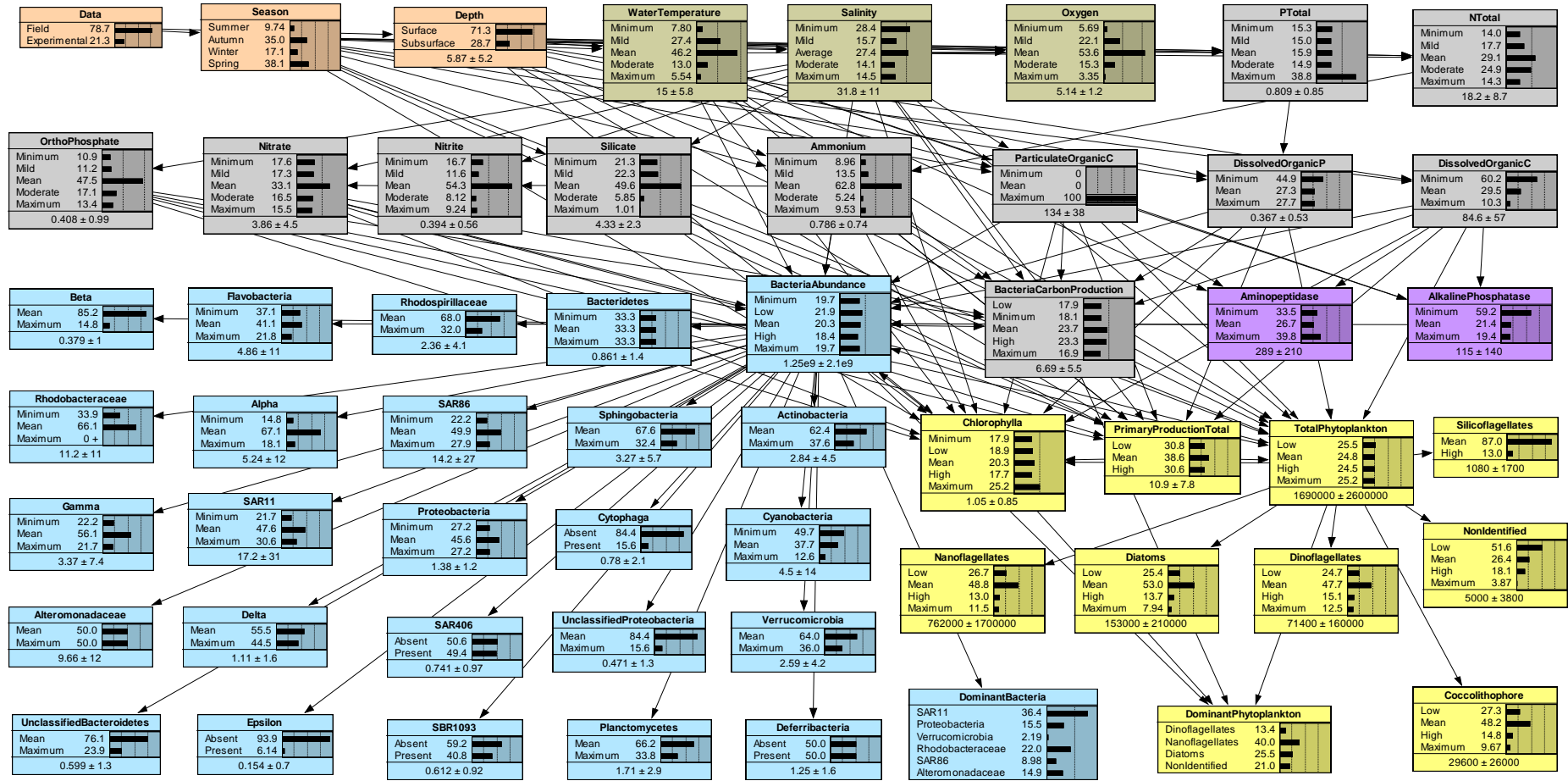
994

**Fig. S2.3** A scenario test for a nanoflagellate bloom.

998

**Fig. S2.4** Scenario test for the maximum concentrations of POC in the a priori data to occur.

1002 **Table S3.1** Sensitivity analysis for POC, dominant phytoplankton and bacterial abundance
1003 node**s** (listed to 1% VR).

| Output node | Node | VR |
|---|---|---|
| Particulate Organic Carbon (POC) | Aminopeptidase | 10.5 |
| | Alkaline Phosphatase | 8.3 |
| | Salinity | 4.7 |
| | Seawater Temperature | 3.3 |
| | Silicate | 3.3 |
| | Dissolved Organic Phosphorus (DOP) | 3.1 |
| | Total Nitrogen (TN ) | 2.3 |
| | Total Phosphorus (TP ) | 1.9 |
| | Dissolved oxygen | 1.2 |
| | Nitrite | 1.1 |
| Dominant Phytoplankton | Chlorophyll *a* | 8.7 |
| | Phytoplankton abundance | 3.3 |
| | Coccolithophorids | 1.5 |
| | Dinoflagellates | 1.4 |
| | Bacteria Abundance | 1.2 |
| Bacteria Abundance | Dominant Bacteria | 53.2 |
| | Flavobacteria | 38.6 |
| | SAR11 | 37.8 |
| | Deltaproteobacteria | 37.5 |
| | Alphaproteobacteria | 32.4 |
| | SAR86 | 27.4 |
| | Actinobacteria | 25.8 |
| | Rhodobacteraceae | 25.7 |
| | Sphingobacteria | 24 |
| | Planctomycetes | 22.7 |
| | Verrucomicrobia | 22.2 |
| | Cyanobacteria | 22 |
| | Gammaproteobacteria | 20.5 |

| | |
|---|---|
| SAR406 | 15.8 |
| Unclassified Proteobacteria | 10.8 |
| Rhodospirillaceae | 10.5 |
| Proteobacteria | 10.4 |
| Betaproteobacteria | 10.3 |
| Bacteria Carbon Production | 1.3 |
| Season | 1.2 |

1004

1005

**Table S3.2** The full sensitivity analysis for the POC node with all data (VR %), monitoring

data (VR MON %) and experimental data (VR EXP %).

| Node | VR (%) | VR MON (%) | VR EXP (%) |
|---|---|---|---|
| POC | 100 | 100 | 100 |
| Aminopeptidase | 10.5 | 11.3 | 9.56 |
| Alkaline Phosphatase | 8.28 | 9.17 | 6.49 |
| Salinity | 4.74 | 2.78 | 28.9 |
| Season | 4.21 | 5.12 | 1.33 |
| Water Temperature | 3.32 | 3.81 | 1.33 |
| Silicate | 3.29 | 3.21 | 9.27 |
| Dissolved Organic P | 3.07 | 1.5 | 11.5 |
| N total | 2.27 | 1.62 | 11.4 |
| Ptotal | 1.9 | 0.632 | 14.8 |
| Oxygen | 1.18 | 1.22 | 1.86 |
| Nitrite | 1.13 | 0.419 | 4.85 |
| Dissolved Organic C | 0.998 | 1.25 | 0.321 |
| Ammonium | 0.969 | 1.41 | 9.91 |
| Depth | 0.739 | 0.675 | 7.69E-06 |
| Nitrate | 0.732 | 0.585 | 4.27 |
| Ortho Phosphate | 0.494 | 0.29 | 4.33 |
| Bacteria Abundance | 0.363 | 0.294 | 1.07 |
| Bacteria Carbon Production | 0.285 | 0.203 | 1.08 |
| Data | 0.203 | 0 | 0 |
| SAR11 | 0.191 | 0.153 | 0.488 |
| Planctomycetes | 0.184 | 0.142 | 0.546 |
| Verrucomicrobia | 0.173 | 0.13 | 0.542 |
| Actinobacteria | 0.164 | 0.139 | 0.372 |
| Rhodobacteraceae | 0.164 | 0.13 | 0.427 |
| Delta | 0.151 | 0.139 | 0.288 |
| Flavobacteria | 0.142 | 0.113 | 0.403 |
| Dominant Bacteria | 0.137 | 0.11 | 0.381 |
| Cyanobacteria | 0.123 | 0.0985 | 0.364 |
| Alpha | 0.0969 | 0.0758 | 0.332 |
| SAR86 | 0.0905 | 0.0801 | 0.188 |
| Gamma | 0.0741 | 0.0612 | 0.18 |
| Primary Production Total | 0.0504 | 0.0273 | 0.384 |
| Chlorophyll *a* | 0.0417 | 0.041 | 0.147 |
| Beta | 0.0375 | 0.0293 | 0.135 |
| Rhodospirillaceae | 0.0342 | 0.029 | 0.0621 |
| Sphingobacteria | 0.0332 | 0.0242 | 0.108 |
| Total Phytoplankton | 0.0243 | 0.0346 | 0.0186 |
| Unclassified Bacteroidete | 0.0243 | 0.0184 | 0.0683 |
| Dominant Phytoplankton | 0.0217 | 0.0207 | 0.0714 |

| | | | |
|---|---|---|---|
| Cytophaga | 0.0195 | 0.0185 | 0.0304 |
| Unclassified Proteobacteria | 0.0173 | 0.00981 | 0.11 |
| Non-Identified | 0.013 | 0.0212 | 0.00454 |
| Epsilon | 0.0103 | 0.00783 | 0.0316 |
| Proteobacteria | 0.0093 | 0.00713 | 0.028 |
| Dinoflagellates | 0.00599 | 0.0101 | 0.00872 |
| Coccolithophore | 0.00591 | 0.00841 | 0.00779 |
| SBR1093 | 0.00535 | 0.00411 | 0.0161 |
| Nanoflagellates | 0.0044 | 0.00758 | 0.00421 |
| Diatoms | 0.00202 | 0.00351 | 0.00507 |
| Silicoflagellates | 0.00198 | 0.00232 | 0.000394 |
| SAR406 | 0.00188 | 0.000614 | 0.0256 |
| Deferribacteria | 0 | 0 | 0 |
| Alteromonadaceae | 0 | 0 | 0 |
| Bacteridetes | 0 | 0 | 0 |

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**Supporting Information 4** Posterior probabilities depending on data source
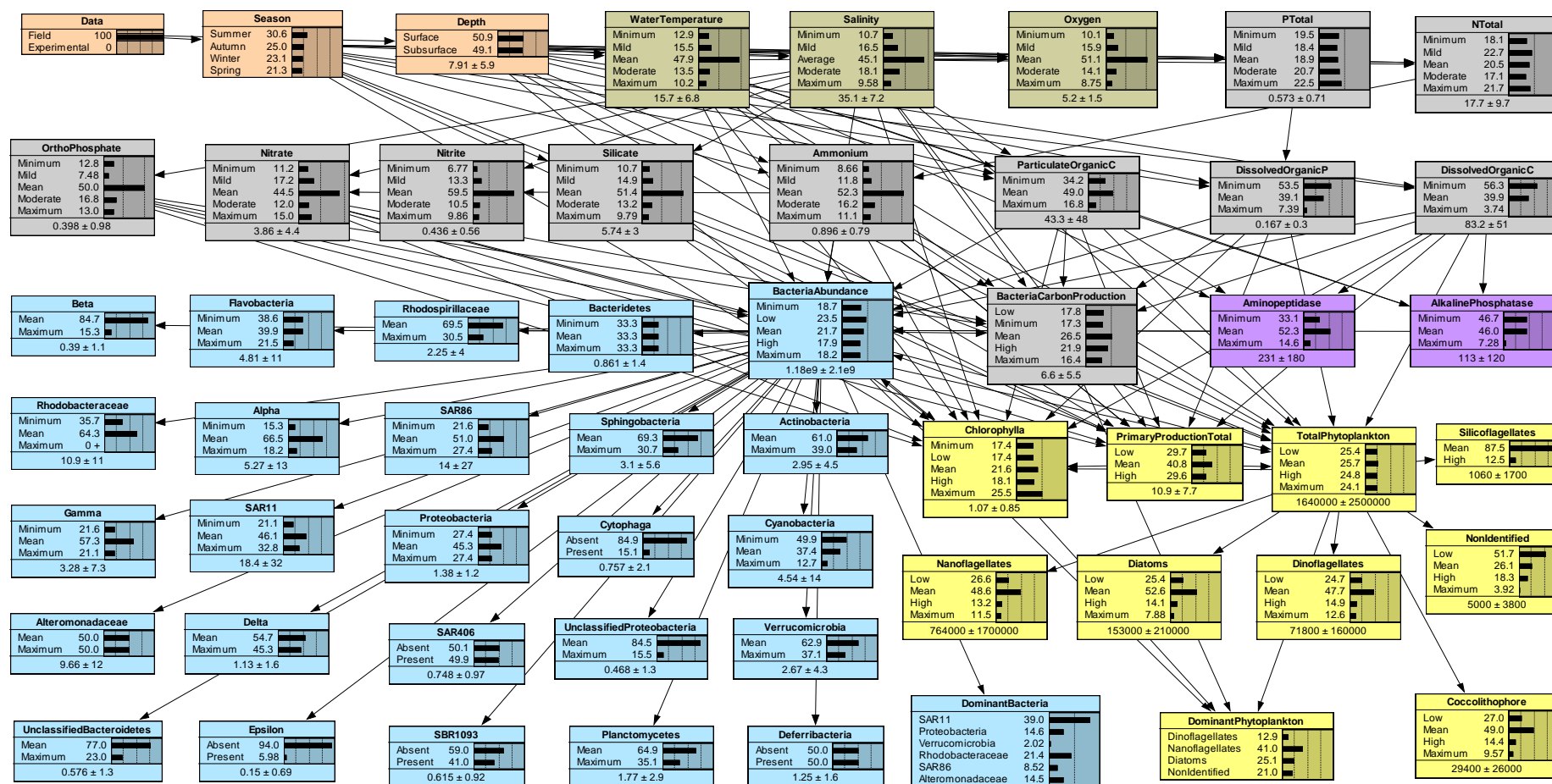
**Fig. S4.1** Posterior probabilities informed from field data only.
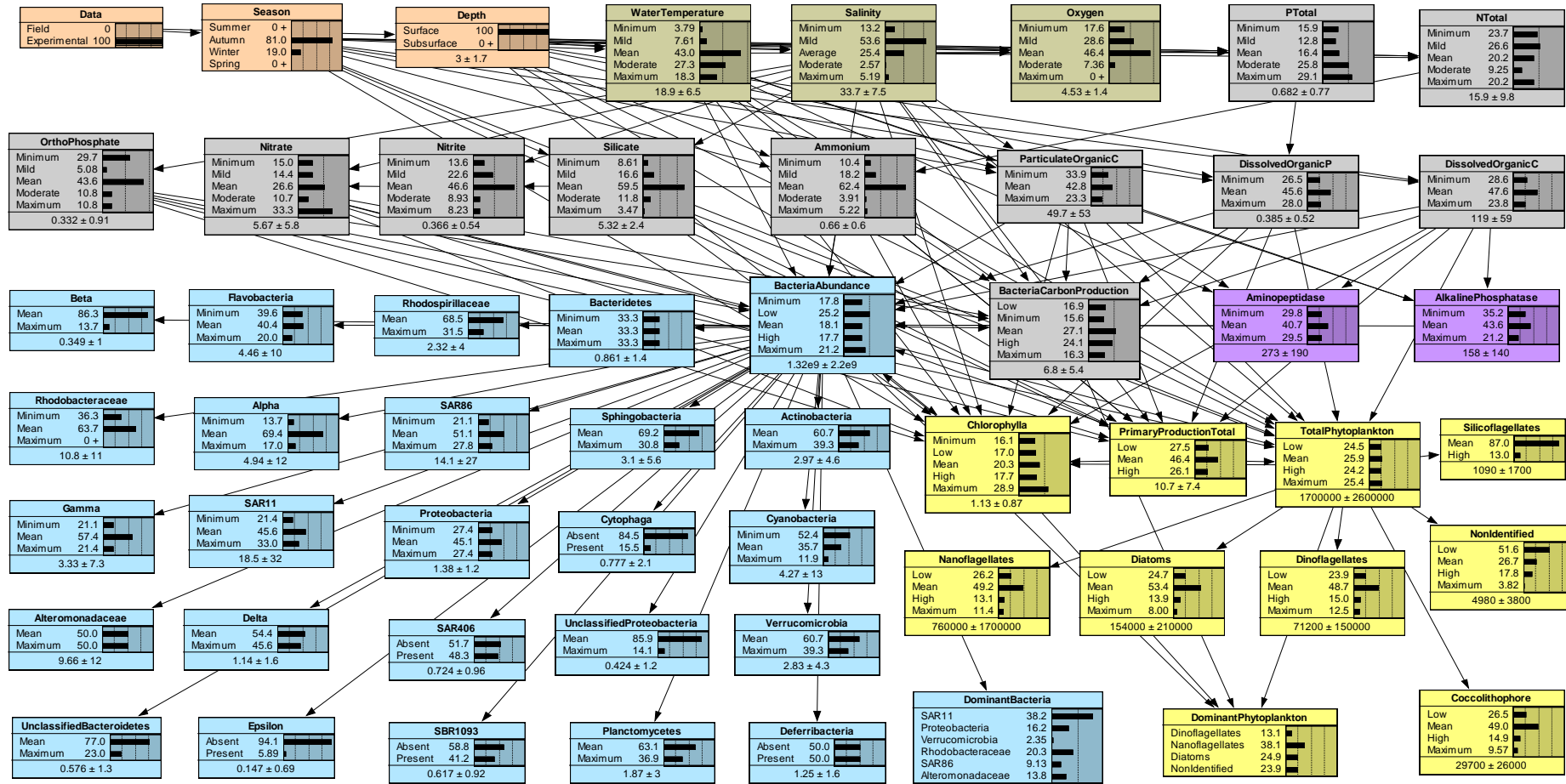
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1015 **Fig. S4.2** Posterior probabilities informed from experimental data only.