

Diagnosis of planktonic trophic network dynamics with sharp qualitative changes

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ABSTRACT

Trophic interaction networks are notoriously difficult to understand and to diagnose (i.e., to identify contrasted network functioning regimes). Such ecological networks have many direct and indirect connections between species and these connections are not static, but often vary in time. Such ecological networks welcome numerous feedbacks between species and populations and are not frozen at all, as soon as we observe them over a long enough term. These topological changes, as opposed to a dynamics on a static (frozen) network, may be triggered by natural forcings (e.g., seasons) and/or by human influences (e.g., nutrient or pollution inputs). Aquatic trophic networks are especially dynamics and versatile, thus supporting suggesting new approaches for diagnosing-identifying network structures and functioning dynamics in a comprehensive way.

In this study, we build a possibilistic qualitative model was build for this purpose. Borrowing discrete-event models to-from theoretical computer sciences, we developed a mechanistic and qualitative model were developed allowing computing exhaustive dynamics of a given trophic network and its environment. Once the model definition is assumed, it provides all possible pathways-trajectories of the trophic-network from a chosen initial state. In a rigorous and analytical approach, for the first time, we validated the model on one theoretical and two observed trajectories recorded at freshwater stations in La Rochelle region (Western France). The model appears easy to build and intuitive, and it-provides other additional relevant trajectories pathways to the expert community. We hope such mathematical-formal approach to open a new avenue in diagnosing-identifying and predicting trophic (and non-trophic) ecological networks.

Keywords: Interaction network; Freshwater ecosystem; Qualitative model; Discrete-Discrete-event model, Plankton

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IntroductionINTRODUCTION

45 Trophic networks (TNs) form the backbone of ecosystem functioning, as they simultaneously condition
 46 food acquisition, prey and predator demography, individual and population behaviours, and phenotype
 47 selection, among other consequences (Lindeman 1942, Johnson 2000, Majdi et al. 2018). Trophic processes
 48 are responsible for most matter and energy fluxes within ecosystems, but the fates and properties of
 49 ecosystems are hardly predictable mainly due to the lack of knowledges (Mouquet et al. 2015). Trophic
 50 processes have been well studied in ecology, although ~~mainly~~ mostly considered as frozen in time, ~~i.e.~~ with
 51 a fixed (or static) topology and fixed signed ~~relationships~~ interactions. This simplification may be due to ~~data~~
 52 lacking ~~data~~ over the long term ~~and as well as~~ to equation-based models dedicated to flux and abundance
 53 variations on a frozen network (e.g. e.g., Thébault and Fontaine 2010, Kéfi et al. 2015). In this study, we
 54 provided an original framework to handle ~~trophic network~~ TNs with sharply changing structures ~~and to model~~
 55 ~~their possible dynamics~~.

57 So far, ~~trophic network~~ TNs are difficult to understand and to handle, ~~in other words, hard to~~ diagnose
 58 ~~between constricted functioning under changing environmental conditions. Any new functioning involves~~
 59 ~~specific ecosystemic components and interactions, justifying why we will focus on qualitative functioning~~
 60 ~~regimes rather than quantitative component abundances and interaction intensities. First of all~~ In addition,
 61 ~~they~~ TNs usually gather a large number of populations or species in an even larger number of trophic
 62 interactions. Hence, to understand trophic dynamics would require not only to model a large and realistic
 63 number of components, but also to be able to calibrate the weights (coefficients) of each component and each
 64 interaction involved (Ings et al. 2009, Wallach et al. 2017, Majdi et al. 2018). For this reason, most trophic
 65 models focus on wide categories of populations, with a functional ~~approach~~ categories, such as carnivores,
 66 herbivores and/or detritivores (e.g. e.g., Thébault and Fontaine 2010), and approximate their trophic
 67 parameters. Even powerful models intending to bypass such limitations, such as qualitative models based on
 68 differential equation systems are limited in size (May 1973, Dambacher et al. 2003).

70 There is ~~a~~ an even stronger limitation of trophic studies in ecology: they mostly assume a frozen network
 71 of interaction (Thébault and Fontaine 2010, Kéfi et al. 2016). Not only is it harder to handle a ~~changing~~
 72 ~~changing in topology (structure)~~, but we have no idea on how such a network may change (~~typologically~~) in
 73 time, and, ~~thus~~, how to model it. Indeed, as soon as the study covers several generations of some of the species
 74 involved in the network, some other species may invade and/or go extinct (Mooney and Hobbs 2001, Warren
 75 et al. 2005). Hence, these events strongly modify the network structure and, in turn, the system dynamics.
 76 Equation-based models are not well adapted to handle dynamical systems ~~on~~ dynamical structures (sometimes
 77 called DS², Giavitto and Michel 2003), whereas some tools developed in theoretical computer sciences are
 78 perfectly adapted to this task. In particular, discrete-event systems such as graph transformations or Petri nets
 79 are able to handle sharply changing networks ~~by formalizing the way components and interactions may appear~~
 80 ~~and disappear~~ (König et al. 2018, Gaucherel and Pommereau 2019). ~~While graph transformations are directly~~
 81 ~~adding/removing some nodes and edges, Petri nets are only mimicking such addition/removal by marking with~~
 82 ~~some tokens the presence/absence of the handled nodes and edges~~ REFS. In this study, we ~~developed will~~
 83 ~~provide~~ a Petri net to model any ~~trophic interaction~~ network ~~topological~~ change, and will illustrate it on a
 84 realistic planktonic ~~trophic network~~ TN.

86 Planktonic ~~trophic network~~ TN models are usually composed of fixed number of functional nodes that
 87 gather groups of individuals sharing the same ecological function. Mass fluxes (usually in carbon or nitrogen)
 88 between nodes are predefined according to trophic ~~links~~ interactions. In a context of ~~an~~ emerging biological
 89 oceanography discipline and regarding the limited computing resources, first planktonic TN (or ~~food-web~~ food
 90 ~~web~~) models simply consisted in mass fluxes between nutrients, phytoplankton and zooplankton nodes (Steele
 91 1958, 1974). These so-called NPZ models (NPZD, NPZDB or even NPZF when detritus, bacteria or fishes are
 92 comprised, respectively) coupled to observed or simulated physical conditions demonstrate their predictive
 93 ability to capture bulk system properties (biomass and primary production) at both regional and global scale
 94 (Mitra et al. 2007, Kriest et al. 2010, Oke et al. 2013, Hernández-Carrasco et al. 2014, Turner et al. 2014, Kumar
 95 and Kumari 2015).

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96 ~~However, in order to~~To better understand biogeochemical cycling (e.g., export fluxes, carbon
97 sequestration, organic matter recycling, microbial loop), planktonic ~~food-web-TN~~ should be delineated and
98 planktonic compartments in models could thus be refined into Planktonic Functional Types (PFTs). Plankton
99 groups are thus defined according to common ecological functions (e.g., nitrogen fixers, calcifiers and
100 silicifiers), sizes (e.g., picophytoplankton, nanophytoplankton, microphytoplankton) and/or key taxonomic
101 groups (e.g., diatoms, flagellates) (Le Fouest et al. 2013, Villaescusa et al. 2016, Kerimoglu et al. 2017,
102 Petersen et al. 2017, Maar et al. 2018, Meddeb et al. 2019). However, refinements of planktonic ~~food-web-TN~~
103 models ~~meets-greatly-complicate-with~~ model ~~formulations-formalization~~, parametrization and ~~requires~~
104 ~~more-lack-of~~ data, which increases uncertainties with model outcomes and ~~in~~ fluxes between defined groups
105 (Anderson 2005).

106
107 ~~To face~~Facing gaps in ecological knowledge and ~~lacks~~ of data, inverse modelling ~~intend to~~ derives flows of
108 energy within ~~trophic-network-TNs~~ from simple biomass estimates and rates measurements. Vézina and Platt
109 (1988) were the first to use it for inferring mass fluxes through a planktonic ~~trophic-network-TN~~ in the English
110 Channel. Inverse modelling is therefore advantageous when dealing with underdetermined systems and
111 results into a space of possible solutions that fulfil a set of linear equalities and inequalities. A ~~unique-preferred~~
112 solution is then selected from optimization or statistical methods. While vital rates and biomass can be easily
113 measured for high trophic levels (e.g., fishes), their quantification for low trophic levels (e.g., bacteria,
114 autotroph plankton) remains uncertain and questions the robustness of inverse modelling for planktonic
115 compartments study (Vernet et al. 2017, Saint-Béat et al. 2018). Overall, biological constants (production,
116 consumption, assimilation), biomass and ecological interactions are therefore not easy to measure in
117 planktonic ~~food-webs-TNs~~, resulting into an over-simplification of planktonic ~~food-web-TN~~ models (Anderson
118 2005, Flynn 2006). ~~For all these reasons, our main objective in this study consists in developing a model able~~
119 ~~to identify (to diagnose) any qualitative functioning regimes of the same TN under changing environmental~~
120 ~~conditions.~~

121
122
123 We addressed here the leading question: what are all the possible trajectories (pathways) of such an
124 aquatic TN? A trajectory is defined here as a sequence of TN states (regimes) and transitions in time, possibly
125 exhibiting bifurcations and not necessarily being quantitative. ~~More precisely, we question the various~~
126 ~~qualitative regimes this network can reach from winter to summer environmental conditions.~~ As a second sub-
127 question, we wonder whether a detailed model could exhibit new or counter-intuitive TN trajectories. ~~To~~
128 ~~address these issues, we propose here to develop a qualitative and discrete model providing all possible~~
129 ~~trajectories (or pathways) of the trophic network under study, in order to keep a rigorous (mathematical)~~
130 ~~control on the model. This assumption allows~~We assume here that the system ~~to-become-finite~~may be
131 ~~qualified~~ and ~~to~~thus exhibit a finite number of states, ~~automatically-computed~~ and ~~gathered~~ into a so-
132 ~~called~~Petri net state space (Pommereau 2010, Reising 2013). Then, a detailed and automatic analysis of this
133 state space exhaustively provides the possible fates (e.g., ~~trajectories~~, stabilities, collapses, if any) of the
134 studied system. We chose to illustrate this original method on a well-studied plankton ~~trophic-network-TN~~ in
135 wetlands, freshwater marshes of Charente Maritime region (Western France, Tortajada et al. 2011). Such a
136 system is well instrumented (~~measured~~) and will provide an expected theoretical trajectory of changing ~~trophic~~
137 ~~network-TN~~, as well as two observed trajectories at different stations (Masclaux et al. 2014). The succession of
138 planktonic ~~trophic-network-TN~~ and the different regimes of the planktonic ~~trophic-network-TN~~ are well known
139 according to the season (Masclaux et al. 2014). We will develop the corresponding Petri net of this system and
140 then validate it, ~~for the first time~~, on theoretical and observed trajectories. We will finally discuss the power
141 and drawbacks of such discrete and qualitative models for trophic ecology.

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142 MATERIALS AND METHODSMethods

143 Aquatic trophic networks

144 The Charente-Maritime marshes of the French Atlantic coast (Fig. 1) are the second largest French wetland
145 zone (over 100,000 hectareskm²). The type of freshwater marshes is the unreplenished drained marshes which
146 constitute a significant artificial hydrographic network of channels and ditches. To mitigate and prevent drying
147 of marshes, locks control the channels and ditches (for more details, see Masclaux et al. 2014). Samples of the

198 **Petri Nets and a simplistic Prey-Predator model**

199 We first summarize the successive steps required to build any ecosystem Petri net and will then illustrate
200 these steps with a toy-model. Our generic approach to model ecosystems has been called the EDEN (Ecological
201 Discrete-Event Network) modeling framework and is here specifically applied to an aquatic trophic TN. Any
202 ecosystem Petri net is developed in three successive steps (Fig. 3): i) an intuitive graph (i.e., i.e., a set of
203 components-nodes and edges-their related-processes) is built to represent the studied ecosystem with its
204 components and their related processes, focusing based on the leading question addressed by the model (Fig.
205 3a); ii) we transform this ecosystemic graph, now called the interaction network, is then transformed into a
206 formal model based on a discrete-event Petri net and its associated rules (as explained in the next paragraph,
207 Fig. 3b); iii) each rule is finally normalized to make it simpler and unambiguous for allowing a rigorous handling
208 of the network changes. Then, the Petri net is run (computed, Fig. 3c) and analyzed (Fig. 3d) to determine the
209 whole range of the ecosystem dynamics. However, the Petri net (steps i and ii) is hidden to the (ecologist) user
210 and is automatically built (in Python language, see Suppl. Mat.) once the ecosystem graph components and
211 processes have been chosen-has been defined by the ecologists. We first illustrate here the functioning of the
212 model using a simplistic prey-predator system (Fig. 3a). Additional technical details on the principle and uses
213 of Petri nets, in particular the way they are computed, can be found in the literature (Pommereau 2010, Reisig
214 2013, Gaucherel and Pommereau 2019).

215
216 We illustrated here the basic functioning of the model using a simplistic prey-predator system (Fig. 3). Any
217 ecosystem network can be represented as a multi-digraph (i.e., a directed graph (with parallel edges). In this
218 graph, every material component of the ecosystem (e.g., e.g., abiotic: temperature; biotic: a population;
219 anthropogenic: nitrate inputs) is represented by a node (or variable), with two Boolean states: "present" (the
220 component is functionally present in the system, or above a chosen threshold, also denoted "+") and "absent"
221 (functionally absent of the system, or below the same threshold, or noted "-"). In the prey-predator
222 example toy-model, only two nodes are defined: the prey and the predator populations. Any state of the
223 ecosystem is defined by the set of "+" and "-" nodes (Fig. 3b3b), and "+" in tables of this paper, when they may
224 oscillate between successive states. The maximal number of possible system states is 2#nodes and grows
225 exponentially with the node number. The state of a node depends on the nodes to which it is connected, while
226 a connection between nodes is assumed as soon as one process explicitly connects the different components
227 (Fig. 3b3a-b). The rules correspond to any physicochemical, and/or bio-ecological and/or possibly socio-
228 economic processes (e.g., e.g., if the prey population is neglectable below a chosen threshold (-), the predator
229 population becomes below its associated threshold neglectable too), and thus represent all possible
230 interactions between nodes-components composing the studied ecosystem-studied. In the prey-predator
231 system, two rules only are defined: R1, the predation itself: the predator eats the prey, and R2, the mortality:
232 without prey, the predator dies (Fig. 3a and 3c). In the Petri net language, nodes are called places and rules
233 are called transitions, both being connected through (oriented) arcs (Fig. 3b3b).

234
235 **Figure 3** - Illustration of a simplistic prey-predator system (a), with its associated Petri net (b), its
236 qualitative dynamics (c), and the computed marking graph also called state space (d). The system is made
237 up of two components, the prey (N) and predator (P) populations, and two interactions connecting them
238 (rules R1 and R2), (as seen on the automaton (a)). The corresponding Petri net is made up of four places
239 (P+, P-, N+, N-) and two transitions R1 and R2, where linked by unlabeled and unweighted arcs (b). Starting
240 with the presence of both populations, it is possible to list all system states encountered (d₁, d₂, d₃) (c),
241 and to connect them with the rules (absent nodes and inactivated rules are displayed in grey). The net is
242 depicted in the initial state (c), and the successive states may be deduced from the token (black dot in
243 (a)) circulation seen in the dynamics movements between places (b). The marking graph of the Petri net
244 (d) is depicted with each state number (S₀, S₁, S₂) (d₀, d₁, d₂) referring to the dynamics described above
245 (b). Notice that a specific state of the system (d₃) (S₃) may not be reached from this initial condition and
246 with these rules (d).

247 **Discrete and qualitative dynamics**

248 A separate rule describes Any rule of such discrete-event models combines the left-hand condition and a
249 right-hand realization parts as: "transition's name: condition >> realization". For a rule to be applied, the state
250 of the node (variable) must satisfy its application condition; the rule is then said "enabled". If so, the application

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251 of the rule modifies the state of the nodes as stipulated in its realization part; the rule is then fired (i.e.,
252 executed or applied). In the prey-predator system (Fig. 3), the rules are written as R1: P+, N+ >> N- and R2: N-
253 , P+ >> P-. Since the rules modify node states, they change the overall system state (i.e.-i.e., the state of the
254 system aggregates all node states). Therefore, the entire system shifts from one state to another one through
255 the successive applications of enabled rules (Fig. 3c). The computation of the defined Petri net produces the
256 state space, which provides the set of all system states reachable by the rules defined (Fig. 3d). As a corollary,
257 the system states are connected to each other by some of these rules in the state space too. The size of this
258 state space is usually much smaller than the number of possible system states (2ⁿ, with n the number of
259 components or nodes/variables), because the computation starts from a specific initial condition and because
260 rules have specific application conditions. We Following the computer science community, we developed some
261 tools to automatically divide large state spaces into merged (simplified) state spaces, as explained in the next
262 sub-section.

263
264 Firing a rule independently to some others often leads to unrealistic trajectories (e.g.-e.g., removing
265 flushing water without removing fishes-plankton in it). Therefore, we defined new-objects-called constraints,
266 preventing the model from simulating such unrealistic (socio-ecological) trajectories. Constraints have a
267 condition and a realisation part, just as rules stricto sensu do, and model inevitable (mandatory) events
268 transitions given the system state. The sole difference between rules and constraints is that constraints have
269 priority on rules stricto sensu. In the prey-predator system, the system state S1-d₁ = {(N-, P+)+} is unrealistic;
270 so, the rule R2 has to be transformed into a constraint (C1: N-, P+ >> P-). From a given state, the model first
271 simulates all trajectories opened up by the defined constraints and then only, when all the system states
272 obtained are realistic (i.e.-i.e., there is no longer any enabled constraint), the enabled rules are fired (Fig. 3d).
273 Notice that the modelled system may stay an indefinite time in any of the computed states, as no rule forces
274 it to leave the qualitative state (i.e., the system may experience quantitative dynamics yet without sharp
275 qualitative changes). In brief, the discrete model proposed here is qualitative, mechanistic (processes are
276 explicit), non-deterministic (no stochasticity yet several possible outcomes from each state) and asynchronous
277 (i.e., all rules are applied as soon as possible, no rule conflict) (Reisig 2013, Gaucherel and Pommereau 2019).
278 The EDEN models are also causal and chronological yet non-temporized, i.e., transitions and time steps are not
279 quantified (and not probabilized).

281 Methodology and TN trajectories and validation methodology

282 The theoretical plankton trophic network TN modeled here combines nine different nodes/components,
283 associated to the dominant functional groups possibly present in the channel freshwater marshes, and two
284 additional components/nodes featuring environmental conditions (Table 1, Fig. 2). To link-connect them, we
285 defined 34 processes and seven constraints encompassing at least four trophic levels (Table 2, Fig. 2). To
286 validate the TN model, one theoretical trajectory (T1) has been defined and two observed trajectories
287 (T2-3) were recorded the studied system at two distant stations (Table 3 Supplementary Materials, Table SM1-
288 2). For the model to be validated, we expect As a validation stage, we intend not only to detect these successive
289 states (e.g., {S0, S1, S2, S3}) in the modeled state space, but also to detect them in the correct succession
290 orders. The model always starts in winter conditions or with a flush in summer conditions, with the node
291 Renew present only, which brings back some source of inorganic nitrogen in the system (Table 1). To see
292 whether the model was able to recover the expected trophic regimes, we We tested two variants of the model:
293 i) the full model intending to grasp the TN functioning and, ii) the same similar model (called seasonal) yet
294 without return in winter conditions (R3, called the "seasonal model"0, Table 2), thus getting the model stuck
295 in summer conditions. The model starts in winter conditions or with a flush in summer conditions, with the
296 node Renew present only, which brings back some source of inorganic nitrogen in the system (Table 1).

297
298 For the full and seasonal each models, we will compute the state space and the merged state space, and
299 will check whether observed trajectories T1 to T3 are correctly recovered. A merged state space is a simplified
300 state space gathering under the same nodes the sets of mutually reachable states of the modelled system, a
301 topological structure called a structural stability. Such structure is interpreted as a stable regime as, by
302 definition, any state in this stability may be reached by any other state belonging to it. Other stabilities may be
303 automatically identified, such as terminal stabilities, from which the system can no more exit, basins gathering

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304 states having the same following states, and *deadlocks*, which are single states from which the system can no
 305 more exit. Merged states spaces are much more compact than full state spaces, and summarized trajectories
 306 are easily revealed.

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307 **Table 1** - The plankton model-TN components and their associated modelled nodes-variables in the TN
 308 interaction network, with their abbreviations, and descriptions. Whether these ecological components
 309 are present (+) or absent (-) in the initial state is also displayed (second column).

Acronym	In initial state	Description
Bact	-	Bacteria
PicoP	-	Picophytoplankton
NanoP	-	Nanophytoplankton
MicrP	-	Microphytoplankton
Proto	-	Protozoa
MicrZ	-	Microzooplankton (metazoa)
MesoZ	-	Mesozooplankton
DOC	-	Dissolved organic matter
Nit	-	Nitrates, linked to seasons or flush
Envir	-	Environmental and climate conditions
Renew	+	Water and Nitrate inputs (rain or humans)

310

311 **Table 2** - Trajectories of the theoretical expert elicitation and observed at stations A and B. For each
 312 trajectory, theoretical and observed regimes are listed in columns and present (+)/absent (-) components
 313 of the trophic network-TN are listed in lines. The corresponding regimes displayed in Fig. 5a-c are listed in
 314 the last line of each trajectory, with a single index A1 to A3 and B1 to B4 for successive regimes.

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Commenté [g7]: EN FAIT, j'enlèverais cette table, qui me semble redondante avec la première des Supp. Mat. (elle est plus détaillée, mais n'apporte que de la confusion selon moi). D'ailleurs, elle était mal numérotée. A discuter...

Commenté [CD8R7]: C'est la théorie et cela décrit un peu plus les réseaux trouvés à la figure 5, non ? Je le garderais.

THEORY	Stage-1	Stage-2	Stage-3	Stage-4	Stage-5	Stage-6
Bact	-	-	-	+	+	+
PicoP	-	-	-	+	+	+
NanoP	-	+	+	+	-	-
MicrP	-	+	+	-	-	-
Proto	-	-	-	+	+	-
MicrZ	-	-	+	+	+	-
MesoZ	-	-	+	+	-	-
Nit	+	+	+	-	-	-
DOC	-	-	+	+	+	+
Envir	-	+	+	+	+	+
Renew	+	+	-	-	-	-
Regimes (Fig. 5)	Biological winter	Low herbivorous TN	Herbivorous TN	Multivorous/ Strong multivorous TN	Microbial TN	Microbial loop

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317 ResultsRESULTS

318 State spaces and computed dynamics

319 The full model provides a state space made up of 765 states gathered into a unique dynamical structure (a
 320 so-called structural stability, Fig. SM1aa-Suppl.). This structure was interpreted as a stable and highly resilient
 321 dynamics as, by definition, any state in this stability may be reach by any other state belonging to it. Yet, when

322 ~~rule zero (R0, seasonal oscillation) is deactivated,~~ The seasonal model gets stuck into a high number (12, plus
 323 two basins) of successive structural stabilities of various sizes (Fig. 4 and SM1b-Suppl.). When oriented
 324 downward in time (i.e., following causality and chronology), the whole system inexorably-inevitably converges
 325 toward a small terminal stability (made up of four states) in which the system appears in a biological winter
 326 (i.e.-i.e., few living species, in green, Fig. SM1b-Suppl.). Some of the reached stabilities exhibit a large number
 327 of states and may keep the system into such specific stabilities during indefinite time (in purple, Fig. 4 and
 328 SM1b-Suppl.). In brief, the seasonal model displays the same state space than the full model, but with a
 329 possible return to the initial biological winter regime thus connecting the bottom states (in red, Fig. 4a) to the
 330 top states (in pink, Fig. 4a). This is why we observe a single cycling stability in the full model state space (Fig.
 331 SM1a). We call such structural stabilities TN "regimes", i.e. a set of interconnected states displaying a coherent
 332 TN behaviour.

333 **Table 3** - Rules and constraints used in both full and seasonal models, with their formal expression (first
 334 column) and descriptions (second column). Only the rule N°0 (in italic and bold) is discarded in the
 335 seasonal version of the model.

CONSTRAINTS

CONSTRAINTS	Descriptions
DOC- >> Bact-	C1 Without organic matter (DOC), Bacteria disappear
Nit- >> NanoP-, MicrP-, DOC+	C2 Without Nitrates, all kinds of phytoplankton except Pico disappear (and produce organic matter)
Bact+, PicoP-, NanoP- >> Proto-, DOC+	C3 Without all its preys (but Bacteria), Protozoa disappear (and produce organic matter)
Bact-, Proto-, PicoP-, NanoP- >> MicrZ-, DOC+	C4 Without all its preys (but Bacteria), Microzooplankton disappear (and produces organic matter)
Proto-, MicrZ-, NanoP-, MicrP- >> MesoZ-, DOC+	C5 Without all its preys, Mesozooplankton disappear (and produces organic matter)
Envir- >> PicoP-, NanoP-, MicrP-	C6 In winter, all Phytoplankton disappear (and do not produce organic matter)
PicoP+, NanoP+, MicrP+ >> Nit-	C7 With all Phytoplankton (present), Nitrates disappear

RULES

<i>Envir+ >> Envir-, Renew+</i>	<i>R0 After summer (and spring) comes winter</i>
Envir- >> Envir+	R1 After winter comes summer (and spring), with a bloom
Envir+, Renew+ >> Nit+, Renew-	R2 Nitrate input is due to water flush from human management or rainfall
Envir-, Renew+ >> Nit+, DOC-, Bact-, Proto-, PicoP-, NanoP-, MicrP-, MicrZ-, MesoZ-	R3 In winter, the Reset of the system is due to water flush from rainfall (but there is a Nitrate inputs)
Envir-, Renew+ >> Renew-	R4 In winter, we stop the flush after its action (reset)
DOC+ >> Bact+	R5 Bacteria use organic matter, without removing it
Bact+, DOC+ >> DOC-	R6 Bacteria use organic matter and remove it
Envir+, Nit+ >> MicrP+, NanoP+	R7 Microphytoplankton and Nanophytoplankton use Nitrates in summer, without removing them
Envir+, Nit+ >> PicoP+	R8 Picophytoplankton use Nitrates, without removing them
Bact+ >> Proto+	R9 Protozoa graze on Bacteria, without removing them
Bact+, Proto+ >> Bact-, DOC+	R10 Protozoa graze on Bacteria, which disappear and produce organic matter
PicoP+ >> Proto+	R11 Protozoa graze on Picophytoplankton, without removing it
PicoP+, Proto+ >> PicoP-, DOC+	R12 Protozoa graze on Picophytoplankton, which disappears and produce organic matter

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NanoP+ >> Proto+	R13 Protozoa graze on Nanophytoplankton, without removing it
NanoP+, Proto+ >> NanoP-, DOC+	R14 Protozoa graze on Nanophytoplankton, which disappears and produce organic matter
MicrP+ >> MesoZ+	R15 Mesozooplankton graze on Microphytoplankton (its PREFERRED prey), without removing it
MicrP+, MesoZ+ >> MicrP-, DOC+	R16 Mesozooplankton graze on Microphytoplankton, which disappears and produces organic matter
MicrP-, NanoP+ >> MesoZ+	R17 Mesozooplankton graze on Nanophytoplankton, without removing it
MicrP-, NanoP+, MesoZ+ >> NanoP-, DOC+	R18 Mesozooplankton graze on Nanophytoplankton (secondary preferential prey), which disappears and produces organic matter
MicrP-, Proto+ >> MesoZ+	R19 Mesozooplankton graze on Protozoa, without removing them
MicrP-, Proto+, MesoZ+ >> Proto-, DOC+	R20 Mesozooplankton graze on Protozoa, which disappears and produces organic matter
NanoP+ >> MicrZ+	R21 Microzooplankton graze on Nanophytoplankton (its PREFERRED prey), without removing it
NanoP+, MicrZ+ >> NanoP-, DOC+	R22 Microzooplankton graze on Nanophytoplankton, which disappear and produce organic matter
NanoP-, PicoP+ >> MicrZ+	R23 Microzooplankton graze on Picophytoplankton (secondary preferential prey), without removing it
NanoP-, PicoP+, MicrZ+ >> PicoP-, DOC+	R24 Microzooplankton graze on Picophytoplankton, which disappear and produce organic matter
NanoP-, Proto+ >> MicrZ+	R25 Microzooplankton graze on Protozoa, without removing them
NanoP-, Proto+, MicrZ+ >> Proto-, DOC+	R26 Microzooplankton graze on Protozoa, which disappear and produce organic matter
NanoP-, Bact+ >> MicrZ+	R27 Microzooplankton graze on Bacteria, without removing them
NanoP-, Bact+, MicrZ+ >> Bact-, DOC+	R28 Microzooplankton graze on Bacteria, which disappear and produce organic matter
MicrZ+ >> MesoZ+	R29 Mesozooplankton graze on Microzooplankton, without removing it
MicrZ+, MesoZ+ >> MicrZ-, DOC+	R30 Mesozooplankton graze on Microzooplankton, which disappears and produces organic matter

336

337 Four **TN** regimes were revealed by the **full and seasonal** models (Fig. 4a and Table **SM1-Suppl.**): **the S0}**
338 biological winter regimes, without planktonic bloom, with oscillations of both zooplankton feeding on bacteria
339 and organic matter; **the S1}-a** regime in which all components are present because the environment is
340 favourable to the development of organisms with many fluctuations of them; **the S2}** a-multivorous **TN**-regime
341 with a mix of preys and various predators such as protozoa and both zooplankton (MicrZ and MesoZ), and
342 finally, **the S3}-a** regime centred on protozoa and mesozooplankton with a few preys but the oscillation of
343 Bacteria (Fig. 4a, Table **SM1-Suppl.**). The trajectories passing through different regimes were diverse and
344 depend on the rules fired from the initial state (Fig. 4b): either the TN system shifts between various types of
345 S0 regimes, or it crosses successively regimes S0 to S1, S2, S3 (with possible ways back) and then back to S0.
346

347

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348 **Figure 4** - The merged state spaces of the seasonal model (a, as in Fig. SM1a-Suppl.), on which each node
349 corresponds to a structural stability (i.e., i.e., a set of TN mutually reachable states), and each edge
350 corresponds to specific irreversible transitions between two successive stabilities. Here, structural
351 stabilities are labeled with system components that are systematically present (+) in their associated
352 states (see Fig. SM2). To see components that are systematically absent in stabilities. This figure helps
353 identifying the various regimes (b, and Table SM1-Suppl.) reached by the trophic network TN system along
354 to the (downward) trajectories computed.

355 Model validation

356 All states of the theoretical trajectory are correctly recovered predicted by the model and, as the model
357 exhibited a single stability, the system is certain to successively reach all these states (although we do not know
358 by which complex-complicated trajectories, Fig. 4a, Table SM1-Suppl.). This observation definitely validates the
359 model. The theoretical planktonic TN trajectory (Table 2 and Fig. 5a) started by an immature regime, here
360 found during named a the biological winter. They It then evolved toward low herbivorous TN, herbivorous TN
361 and variable multivorous TN (from weak to strong multivorous regimes, with protozoa, microzooplankton or
362 mesozooplankton, respectively), and microbial TN regime, and to finally reach a microbial loop regime. When
363 water in the marshes is renewed (Renew+), the TN returned to an immature biological winter regime, as may
364 the herbivorous and biological winter regimes too. All these TN regimes are recovered by the model (Fig. 5a),
365 yet with slightly different stabilities. The figure 5 is not intending to demonstrate this validation stage (already
366 done by identifying the successive trajectory states), rather than showing that all predicted states (coloured
367 nodes) are correctly recovered into the computed state space, and indeed connected through successive
368 transitions (bold edges). Note that this modeled trajectory is crossing many other intermediate states (Fig. 5a)
369 not found in the observations of (Masclaux et al. 2014). When in the seasonal oscillation model (rule R0) is
370 deactivated, the theoretical trajectory is predicted too (colored states, Fig. 5a), yet in a reverse order for with
371 the last two states (blue states at the bottom): in the reverse order, as the fourth multivorous regime may
372 directly reach the last depleted one.

373
374 The data of recorder at stations A and B, and associated to observed trajectories were correctly recovered
375 too. At station A, three regimes succeed along time, from A1 to A3 (Table SM2-Suppl., Fig. 5b). The TN started
376 by biological winter during four weeks with presence of nitrates and organic matter, but did not reach
377 favourable conditions for biological development. Then, the favourable conditions at week 5-five allowed the
378 development of phytoplankton (micro- and pico-plankton), and thus their zooplankton predators with
379 bacteria. This situation was typical of situations between herbivorous and multivorous TNs. Then, a
380 multivorous regime of TN settled until the week 8-eight. At station B, the observed succession displayed four
381 regimes, from B1 to B4 (Table SM2-Suppl., Fig. 5c). The TN started by biological winter during three weeks and
382 favourable conditions arrived occurring at week 4-four which allowed a presence of multivorous TN ("weak
383 multivorous TN" according to (Masclaux et al. 2014)) and at week 5-five an herbivorous TN. Then, a multivorous
384 regime of TN settled from week 6-six to week 8-eight.

385

386 **Figure 5** - The full (not merged) seasonal state space highlighting the three trajectories used in this study
387 (Table 2), namely the theoretical (a), station A (b) and station B (c) ones (Table 2 Suppl.). Here, each node
388 corresponds to a trophic network TN state, connected to each other by downward transitions. The specific
389 states building the three trajectories are highlighted by node colors other than red and identifiers
390 corresponding to their numbers (last lines of trajectories in Table 2) and by bold edges.

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391

DiscussionDISCUSSION

392 The ~~discrete-discrete~~-event and qualitative model of trophic network (TN) presented here is computed
393 ~~almost~~-instantaneously (< 0.01s) and provided, once the model is defined and assumed, all possible
394 trajectories of this system (Fig. 4). ~~Such approaches are called possibilistic (i.e. non-deterministic and non-~~
395 ~~probabilistic) and appear relevant for most ecological studies.~~ To our knowledge, it is the first attempt to
396 model exhaustively a detailed TN (11 components, Table 1) and to accurately validate its qualitative
397 dynamics) trophic network (but see Baldan et al. 2015, Gaucherel and Pommereau 2019), and to accurately
398 validate its qualitative dynamics.

399 Complex dynamics of aquatic trophic networks

400 In the Charente-Maritime trophic system, we discovered that this ~~trophic system~~TN may have followed
401 other trajectories than the one identified by experts in the theoretical model and in the ones observed (Fig.
402 5 and Supplementary Materials tables). First, the station B proves that DOC may be present in winter, thus
403 with the ~~trophic network~~TN fluctuating in intermediary states before reaching the usual trajectory
404 observed in Masclaux et al. (2014). Indeed, DOC in winter could be an allochthonous input from terrestrial
405 environment (Del Gorgio and Davis 2003). After winter (~~i.e. i.e.~~, when Renew+ and Envir+ were present,
406 Table 1), all the modeled trajectories and all the TN regimes appeared at reach. The TN may come back to
407 ~~immature-biological winter~~ system states due to the nitrate inputs (Nit+, with R2) and to anthropogenic
408 activities (Tortajada et al. 2011). This situation happens when the water renewal is important and no
409 planktonic biomass accumulation is possible (David et al. 2020). Also, rainfall could happen and favour
410 nitrate leaching (R3), then pushing back the planktonic ~~trophic network~~TN to ~~immature-biological winter~~
411 system states. The model confirmed the key role of organic matter (DOC), as the system trajectories
412 differed when organic matter was present or absent at the beginning of winter.

413
414 From the initial state of the TN, the trajectories could be passing through slightly different biological
415 winter regimes (Fig. 4a-b) with oscillations of organic matter, bacteria, micro- and meso-zooplankton.
416 Similarly, Masclaux et al. (2014) found two types of Biological winter regimes, mainly depending on the
417 presence or absence of bacteria, and on some preys and predators combinations. The model correctly
418 recovered different states of biological winters. The regime of multivorous TN was well recovered by the
419 model too (Masclaux et al. 2014). The multivorous TN is known to be highly stable (Legendre and
420 Rassoulzadegan 1995). However, the microbial loop, which has a transient nature (Legendre and
421 Rassoulzadegan 1995) did not appeared as a structural stability in the model either.

422
423 The regime gathering protozoa and mesozooplankton (Proto/MesoZ cycles) characterized by the
424 presence of predators with a few preys but the oscillation of bacteria was not found in the observations
425 (Masclaux et al. 2014). The modeled trajectory is crossing many intermediate states (Fig. 5a-c) not sampled
426 in the field. The field sampling frequency or the structural characteristics of the sampled wetlands likely
427 did not allow capturing all the possible states of TN: this reveals the ability of the model for exploring many
428 other possible states of the planktonic TNs and other trajectories of TN. In particular, the predicted
429 Proto/MesoZ regime has not yet been identified at the Charente Maritime sites, but work in progress at
430 other Atlantic arc territories has identified related TNs (F.-X. Robin ROBIN, pers. Comm.). Finally, bacteria
431 were frequently present in the ecosystem, and occupied a large place in the model (Table SM1-2-Suppl.,
432 Table 2, Table 2-Suppl.). Bacteria seemed to frequently oscillate (Fig. 4a), although not visible in the merged
433 state space (~~i.e.~~, bacteria frequently appear and disappear within structural stabilities). The model
434 confirmed that bacteria are frequently grazed by their grazers, as small protists are (Pernthaler 2005, Šimek
435 et al. 2013). Indeed, we know the strong control of bacteria by the protozoa in freshwater ecosystems.

436 Power and drawbacks of ~~discrete-discrete~~-event models

437 An increasing number of ~~trophic network~~TN models are being developed today (Mitra et al. 2007, Kriest
438 et al. 2010, Thébault and Fontaine 2010, Turnet et al. 2014, Kéfi et al. 2016, Hansen and Visser 2016,
439 Kloosterman et al. 2016). But they still have three main limitations: a limited size and complexity, and a
440 frozen (static) network with frozen (~~i.e.~~, topology) interactions. In this study, we proposed an original

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Commenté [g9]: Ici et plus haut, on aurait dû ajouter plus de refs des modèles NPZ, mentionnées par le reviewer 1 et ici dans l'intro...

Commenté [CD10R9]: J'ai rajouté

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441 model family (called the EDEN framework (Gaucherel and Pommereau 2019, Cosme et al. 2022)) to bypass
442 these limitations. It is based on a discrete-event system, well-known by computer scientists and more
443 recently by some molecular biologists (Thomas and Kaufman 2001, Reisig 2013). The price to pay by using
444 our qualitative model is that no ~~more~~-quantitative and detailed dynamics is available; but in turn, no
445 difficult parameterization and construction isare required. Consequently, such approach is fully
446 complementary to already existing models in (trophic) ecology. Here, we provide for the first time to our
447 knowledge a discrete and qualitative model of TN to bypass such limitations. By the way, in the continuity
448 to previous theoretical attempts (May 1973, Dambacher et al. 2003), we open here new avenue for using
449 such original qualitative models in (ecosystem and trophic) ecology. The foundations of this proposition,
450 yet out of the scope here, are based on a theoretical ground assuming that ecosystems are informational
451 systems made up of material components and immaterial processes (Gaucherel 2019) ~~represented in~~
452 summarized into theirthe interaction networks.

453
454 Such a model is intuitive, easy to build, tractable and rigorous (~~i.e.~~-i.e., no trajectories have been
455 forgotten or added according to the mathematical Petri net engine). In addition, we said that it does not
456 require any detailed and quantitative calibration, as no parameter is required. The central assumption of
457 this approach is that it is possible to summarize ecological processes into qualitative rules, possibly
458 interpreted as long term and discrete-discrete events. Other studies show that this approach is not limited
459 to trophic processes and may be applied to a high diversity of social-ecosystems (Gaucherel and
460 Pommereau 2019, Mao et al. 2021). In this study, we were lucky enough to collate several theoretical and
461 observed trajectories ~~on-with~~ which to validate the model, thus confirming that it is conform and accurate
462 (Fig. 5). Another quality of this type of models is to be heuristic, to force scientists questioning the
463 knowledge they have on the studied system and to collate it into a single coherent framework.

464
465 As perspectives, it appears at hand to model many TN stressors such as pollution, cleaning, drought,
466 invasive species and/or climate changes (Mooney and Hobbs 2001, Mouquet et al. 2015). Any
467 complexification of the studied social-ecosystem is also possible, in theory, as the model is still far from
468 reaching its limits in terms of components, processes and of their nature diversity. It may then be used in
469 a more applied way, exploring other scenarios by changing initial conditions. Coupling this model with
470 other components describing the mechanisms behind these stressors would provide a relevant
471 territorialized model to anticipate trends in a context of global warming and coastline change. In a near
472 future, it would be relevant not only to improve the model realism, but also to develop analysing tools
473 already used in similar studies focusing on social-ecological systems (Mao et al. 2021, Cosme et al. 2022).
474 ~~Indeed, with more components and processes, the computed state space may become increasingly huge~~
475 ~~and difficult to interpret (Reisig 2013). A way to proceed~~Additionally, it would be relevant to develop
476 methods based on model checking already in use in computer sciences (Burch et al. 1992). Another relevant
477 line to explore is to complexify our discrete and qualitative approach by using quantitative and multivalued
478 scheme, so that we will bridge the gap with more traditional (~~e.g.~~-e.g., equation-based or individual-based)
479 models (Vézina and Platt 1988, Kéfi et al. 2016).

480
481 In brief, by modeling trophic networks ~~with~~ an original (EDEN) framework, we recovered ~~observed and~~
482 theoretical as well as observed trajectories. With such possibilistic-qualitative models, we understood its
483 dynamics and predicted new states and new trophic network TN-functioning regimes that may be observed
484 in the field. We illustrated them on a specific and well instrumented-measured freshwater ~~TN trophic~~
485 network. Such models provide an intuitive and robust approach to diagnose any trophic (and non-trophic)
486 network by computing all possible trajectories it may reach from a chosen initial state. The known
487 processes at play in the system help identifying all possible dynamics and thus studying the
488 contingencycounter-intuitive trajectories of such complex (social-eco-)systems. To connect such biotic
489 dynamics to human related componentsactivities would reveal even more insightful understanding of
490 complex trophic ecosystems.

491 AppendicesAPPENDICES

492 Additional Tables and Figures (Appendix 1)

493

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494

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495

DATA SCRIPTS CODE AND SUPPLEMENTARY MATERIAL AVAILABILITYData, scripts, code, and supplementary information availability

496

497

Data are available in this article (Tables and Figures) (*citation of the data* Gaucherel et al, 2023);

498

Scripts and code are available online: DOI:10.1111/2041-210X.13242 of the webpage hosting the data

499

<https://github.com/fpom/ecco> (*citation of the scripts and code* Pommereau et al., 2022);

500

Supplementary information is available online: XXXXDOI of the webpage hosting the data

501

<https://doi.org/10.5802/fake3.doi> (*citation of the scripts and code* Gaucherel et al, 2023);

502

[The references of the datasets, scripts and codes should also be present in the reference list and cited in the text.]

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CONFLICT OF INTEREST DISCLOSUREConflict of interest disclosure

505

The authors declare that they comply with the PCI rule of having no financial conflicts of interest in relation to the content of the article. [C. Gaucherel is a recommender PCI ecology]

506

507

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509

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