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Stochastic effects on plankton dynamics: Insights from a realistic 0-dimensional marine biogeochemical model

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ABSTRACT

Marine ecosystems exist in a noisy and uncertain environment, not governed by deterministic laws. The development of ecological communities is significantly influenced by variability, and the interaction between nonlinearity and stochastic processes can lead to phenomena that deterministic models cannot explain. Plankton, forming the base of the marine food web, are highly affected by stochastic fluctuations due to their short reproductive timescales. Investigating the effects of noise on plankton growth is essential for accurately describing and predicting marine health. We present a realistic biogeochemical model where multiplicative white noise represents environmental stochasticity affecting plankton. The model suggests ergodic properties in the presence of stochastic fluctuations, with temporal and ensemble distributions being coherent. Analytical and numerical analyses reveal that, given sufficiently low noise intensity, dynamics near equilibrium resemble an Ornstein-Uhlenbeck additive process. With higher noise intensities, resonance occurs, particularly when endogenous dynamics are periodic. The results indicate that low noise intensity can positively influence plankton persistence with an higher number of species coexisting, while higher noise intensity can establish a new equilibrium in the system.

1. Introduction

Plankton are crucial to ocean biogeochemical cycles and ecosystems, significantly influencing the carbon cycle (Buesseler et al., 2007; Falkowski et al., 1998), nutrient dynamics (Falkowski et al., 2000), climate regulation (Falkowski, 2012), and food production (Cermeño et al., 2016; Ryther, 1969). Accurate prediction of plankton dynamics is essential for assessing the health of aquatic ecosystems. Anthropogenic climate changes, such as rising global temperatures and ocean acidification, are shifting phytoplankton communities, altering food webs, and impacting marine ecosystem productivity (Behrenfeld et al., 2006; Doney et al., 2009). Therefore, the need to anticipate the future state of the ocean. Advanced tools for predicting plankton dynamics are biogeochemical models, which numerically integrate differential equations to simulate interactions between plankton species, microbial loops, and nutrient cycles (Fennel et al., 2022). These models provide comprehensive insights into the state, variability, and changes in the global ocean, informing scientists, policymakers, and the public, as demonstrated by initiatives like the European Copernicus Marine Service (CMS) and the Coupled Model Intercomparison Project Phase 6 (CMIP6) (Eyring et al., 2016).

Recent advancements in ocean biogeochemical models include increased biodiversity representation of plankton species (Henson et al., 2021; Shimoda et al., 2016; Shimoda and Arhonditsis, 2016), simulation of plankton trait evolution through adaptive dynamics (Le Gland et al., 2021), the integration of water quality modules to model the pollution loading inputs of rivers (Zhao et al., 2020), studies of zooplankton mortality as first step to coupling fish and biogeochemical models (Hill Cruz et al., 2021). While modern ocean biogeochemical models describe a complex range of processes, they often lack sufficient empirical knowledge of the systems they study. Additionally, these models sometimes simulate more processes than can be observed in field studies, leading to uncertainties in model parameterization and, consequently, in the interpretation of model results (Cai et al., 2023). To address these challenges, several advanced techniques have been employed. Sensitivity analysis of model parameters has been applied using advanced statistical and machine learning techniques (Cai et al., 2023). Data assimilation tools have been integrated to optimally

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combine observations with model predictions (Bruggeman et al., 2023; Spada et al., 2023). Automated calibration methods that combine parameter inference with sensitivity analysis through machine learning approaches have also been developed (Álvarez et al., 2023; Piccioni et al., 2022). Furthermore, deep learning models that integrate both observational and model data have been created to more accurately reproduce biogeochemical variables (Pietropolli et al., 2022).

While significant efforts have been made to address uncertainties in model parameters (Álvarez et al., 2023; Bruggeman et al., 2023; Cai et al., 2023; Piccioni et al., 2022; Spada et al., 2023), another critical source of uncertainty requires further investigation: environmental stochasticity. Ocean biogeochemical models operate within inherently random and uncertain marine environments, as most natural phenomena do not follow strictly deterministic laws, but rather oscillate randomly around an average behaviour (Beddington and May, 1977). Even the most precise meteorological data and fine-gridded circulation models cannot fully capture marine environmental variability, leading to inherent uncertainties. This phenomenon, known as environmental stochasticity, is defined as random changes in environmental variables among times or locations that affect the survival and reproduction of populations (Steiner et al., 2021; Valenti et al., 2016). Other stochastic phenomena in ecology include immigration stochasticity and demographic stochasticity (Arnoldi et al., 2019; Steiner et al., 2021). The latter describes the random fluctuations in population size that occur because the birth and death of each individual is a discrete and probabilistic event (Lindo et al., 2023; Melbourne, 2012) (this is particularly relevant for populations with a small number of individua (Gurney and Nisbet, 1998)). Demographic stochasticity proved to increase the realism of a population ecological model (Kaitala et al., 2006). Immigration stochasticity causes a change in the growth rate due to random immigration (or emigration) of individua of a population (Arnoldi et al., 2019). It is crucial to distinguish between selective and non-selective causes of variation (Steiner et al., 2021); a study of selective stochastic processes can be found, for example, in (Dieckmann and Law, 1996), where a derivation of evolutionary dynamics is presented. We will restrict ourselves to the non-selective ones and in particular to environmental stochasticity. Plankton growth is determined by environmental conditions and in particular by solar irradiance (Álvarez et al., 2022), temperature (Rhee and Gotham, 1981) and nutrients (Rhee and Gotham, 1981). Therefore, incorporating environmental variability into biogeochemical models can increase the accuracy of ocean state predictions. When a species or a population is subjected to environmental stochasticity its individuals respond synchronously to the stochastic perturbation, which effect will be thus proportional to the abundance of the perturbed population. This phenomenon can be modeled with multiplicative white noise (Arnoldi et al., 2019; Liao, 2023; Liu and Wang, 2011).

Stochasticity in ecological models often arises from simplifying or summarizing numerous processes across different scales (Boettiger, 2018). Models based on stochastic differential equations address uncertainties from unmodeled processes, while sensitivity analysis and model calibration tackle uncertainties from parameterization of modeled processes. These approaches can intersect, as parameterization depends on which processes are included or excluded in the model. While stochasticity has yet to be widely implemented in operational biogeochemical models, it has received considerable attention in ecology. This stems for the fact that stochasticity or noise, beside representing the uncertainty of under-described processes, is often responsible for the emergence of ordered phenomena from disordered dynamics (Boettiger, 2018). Such subtle mechanisms are proving fundamental in determining the dynamical properties of systems at all length scales, from microscopic physical systems such as glasses (Biscari and Parisi, 1995; Charbonneau et al., 2014) to macroscopic ecological systems (Benzi et al., 1982). Noise can produce intriguing and counterintuitive dynamical effects in living systems, such as stochastic resonance (Benzi et al., 1982; Gammaitoni et al., 1998; Mantegna et al., 2000; Mantegna and Spagnolo, 1994) and noise-enhanced stability (Mantegna and Spagnolo, 1996; Spagnolo et al., 2004a; Yu and Ma, 2023; Zeng et al., 2015), which do not otherwise occur in deterministic dynamics. The key element of these unpredictable effects is the simultaneous presence of nonlinear interactions and random fluctuations characteristic of natural complex systems. Indeed, marine ecosystems are characterized by nonlinear interactions (Valenti et al., 2012) and non-stationary dynamics (Occhipinti et al., 2023; Perhar and Arhonditsis, 2012) as well as deterministic forcings (daily and seasonal cycles) (Di Biagio et al., 2019; Lazzari et al., 2012; Terzić et al., 2019) and random fluctuations of physical variables (Chichigina et al., 2005; Spagnolo et al., 2004b; Valenti et al., 2004). Considering the above points of view, the effects of stochastic environmental fluctuations have a great impact on the parameters included in an ecosystem model, such as growth rate, mortality rate and more (May, 2001).

Randomness in the marine environment was initially introduced in plankton ecological models as noise over the temperature (Benincà et al., 2011; Freund et al., 2006). Then, recently, the effect of noise over temperature was studied in a ocean biogeochemical model of realistic complexity (Lazzari et al., 2021), the Biogechemical Flux Model (BFM) (Vichi et al., 2020), used in the Copernicus Marine Service. In the zero-dimensional box model configuration of the BFM the temperature is described as a stochastic process driven by an additive self-correlated Gaussian noise, (Lazzari et al., 2021) found a correlation between noise intensity and the coexistence of the modeled plankton species. A similar study was performed introducing stochasticity in solar irradiance as multiplicative Ornstein-Uhlenbeck process (Grimaudo et al., 2022). Plankton experienced a non-monotonic response to the intensity and the correlation time of the noise, further a transition to an out-of-equilibrium state occurred (Grimaudo et al., 2022).

In this context, we used the same deterministic configuration of the biogeochemical model of (Grimaudo et al., 2022; Lazzari et al., 2021) and studied the response of plankton to environmental stochasticity. Up to our knowledge, it is the first time that environmental stochasticity is introduced as multiplicative white noise in a biogeochemical model of realistic complexity, in particular we provide an analysis of small perturbation regime and consider the model behaviour when perturbation increases leading to non-linear fluctuations. Further, it is the first time that stochastic resonance is observed in a high complexity biogeochemical model, highlighting the key role of noise in shaping plankton dynamics. Similar studies were conducted in simpler trophic networks, such as in the phytoplankton-zooplankton model (Liao, 2023) and in the nutrient-phytoplankton model (Valenti et al., 2016), or with noise affecting a single environmental variable (Grimaudo et al., 2022; Lazzari et al., 2021) instead of generally affecting the population growth (Arnoldi et al., 2019). In this work, we investigate the effects of environmental stochasticity in a planktonic community with three main objectives. First, given that endogenous oscillations are found in plankton populations (Occhipinti et al., 2023; Perhar and Arhonditsis, 2012), we want to evaluate the possibility of amplification of non-stationary dynamics by means of stochastic resonance. Second, we evaluate whether stochasticity is able to lead the system to new equilibria or whether it only generates fluctuations around the deterministic solution. Third, we aim to investigate the influence of environmental stochasticity, on plankton persistence and coexistence, as suggested by (Mubayi et al., 2019; Sarker et al., 2020; Yu et al., 2019a; Yu et al., 2019b). A further examination of the mathematical properties of the stochastic differential equations that define the model can be found in Sect.3.

2. Methods

2.1. The deterministic model

The deterministic model used is the Biogeochemical Flux Model (BFM), formulated in terms of deterministic partial differential

equations that account for the main biogeochemical processes in pelagic marine ecosystems (Sarmiento, 2006) (depicted in Fig. 1a). The BFM (Biogeochemical Flux Model) is a model of reasonable complexity, consisting of 54 state variables. It is employed for various purposes including operational studies (Salon et al., 2019), process research (Lazzari et al., 2012; Lazzari et al., 2016), and climate studies (Reale et al., 2022; Solidoro et al., 2022). The model is versatile, being used at both the basin scale (Lazzari et al., 2012) and the local scale (Lamon et al., 2014). Specifically, the BFM is utilized to simulate the biogeochemical aspects, referred to as "Med-BIO," within the framework of "The Mediterranean Sea Monitoring and Forecasting Centre (Med-MFC)". The BFM has undergone rigorous validation against various observational datasets, including satellite data, literature, climatology records, and BGC-Argo floats. This validation process has confirmed the model's consistency in simulating key features of Mediterranean biogeochemistry and its accuracy in routinely reproducing observations at specific times and locations (Salon et al., 2019). Therefore, the BFM is considered a state-of-the-art model for marine biogeochemistry.

Living species are divided into functional types, i.e. groups that have a common ecological function. The deterministic configuration of the BFM was developed to accurately reproduce the dynamics of the following plankton functional types (PFTs): primary producers (phytoplankton), predators (zooplankton), and decomposers (bacteria). Within these PFTs, more specific subgroups are identified to better describe the planktonic food web, in total $N_{bio} = 9$ plankton subgroups are described. Each functional type is characterized by the cell size (ESD) as morphological trait, and by several parameters describing photosynthesis and nutrient uptake as physiological traits. Heterotrophic anaerobic and aerobic bacteria are grouped into a single type called bacteria (B1), characterized by the function of converting organic material into inorganic macro-components such as nitrate (PO_4) and phosphate (NO_3). Phytoplankton, which includes cyanobacteria and photosynthetic protists, is divided into 4 plankton functional types (PFTs): (i) diatoms (P1), unicellular eukaryotes enclosed by a silica frustule, $ESD = 20 - 200\mu m$; (ii) autotrophic nanoflagellates (P2), motile unicellular eukaryotes comprising smaller dinoflagellates and other autotrophic microplanktonic flagellates, $ESD = 2 - 20\mu m$; iii) picophytoplankton (P3), prokaryotic organisms generally referred to as non-diazotrophic autotrophic bacteria such as Prochlorococcus and Synechococcus, but also as mixed eukaryotic species, $ESD = 0.2 - 2\mu m$; iv) dinoflagellates (P4), large, slow-growing phytoplankton representing a broad group of phytoplankton species that includes larger species belonging to the previous groups (e.g. dinoflagellates), but also those that develop a form of (chemical) defence against predator attacks during a certain period of the year. This group generally has low growth rates and small food matrix values with respect to the micro- and mesozooplankton groups, $ESD > 100\mu m$. Zooplankton are subdived in 4 PFTs: i) carnivorous mesozooplankton (Z3), any carnivorous zooplankton between $200\mu m$ and $4cm$ long as an adult, also embracing many species that are traditionally considered part of the microzooplankton when in juveniles stages; ii) omnivorous mesozooplankton (Z4), as the previous PFT but comprising omnivourous species, mainly calanoid copepods; iii) microzooplankton (Z5), representing the microzooplankton with *ESD* in the range $20 - 200\mu m$, excluding flagellates and naupliar/larval stages of multicellular zooplankton or meroplanktonic larvae of benthicorganisms; iv) heterotrophic nanoflagellates (Z6) protozoa with dimensions between 2 and 20 μm, mainly grazing upon picophytoplankton and bacteria. The trophic web of grazing and predation relationships is shown in Fig. 1b. In the following text, we refer to the subgroups as biological species. Each functional group of plankton is defined by a vector of components, each of which refers to an element or constituent relevant to physiological functions. For phytoplankton, these elements include carbon, nitrogen, phosphorus, silicon, and chlorophyll molecules containing photosynthetic pigments. In this work, we consider a spatially homogeneous system, described by a zero-dimensional (0-D) configuration of the BFM. This model is formulated as a system of $N_{tot} = 54$ ordinary nonlinear differential equations and represented by a 54-dimensional state vector $\boldsymbol{x}$. The time derivatives of a generic phytoplankton carbon component (e.g., carbon in diatom, $x^i = P1_c$) and the corresponding nutrient intracellular concentration (e.g., nitrogen in diatom, $x^j = P1_n$) are given by:

$$\frac{\partial x^i}{\partial t} = f_c^{gpp}(\boldsymbol{x}) - f_c^{rsp}(\boldsymbol{x}) - f_c^{exc}(\boldsymbol{x}) - f_c^{prd}(\boldsymbol{x}), \tag{1}$$

$$\frac{\partial x^j}{\partial t} = f_n^{upt}(\boldsymbol{x}) - f_n^{rel}(\boldsymbol{x}) - f_n^{prd}(\boldsymbol{x}). \tag{2}$$

The f terms are functions representing the biogeochemical fluxes associated with the main physiological processes. Gross primary production (*gpp*) is expressed in $mgCm^{-3}day^{-1}$ and represents photosynthesis or the flux of inorganic CO_2 to organic compounds. Respiration (*rsp*) is the release of carbon as CO_2. Excretion (*exc*) is related to the metabolic activities of the cells and the need to balance the internal carbon against other elements. *prd* is predation or grazing by zooplankton. The f terms can be factorized in several regulating functions:

$$f_{gpp}(\boldsymbol{x}) = r_{max} f_T(T) f_I(I) f_{nut}(\boldsymbol{x}) x^i, \tag{3}$$

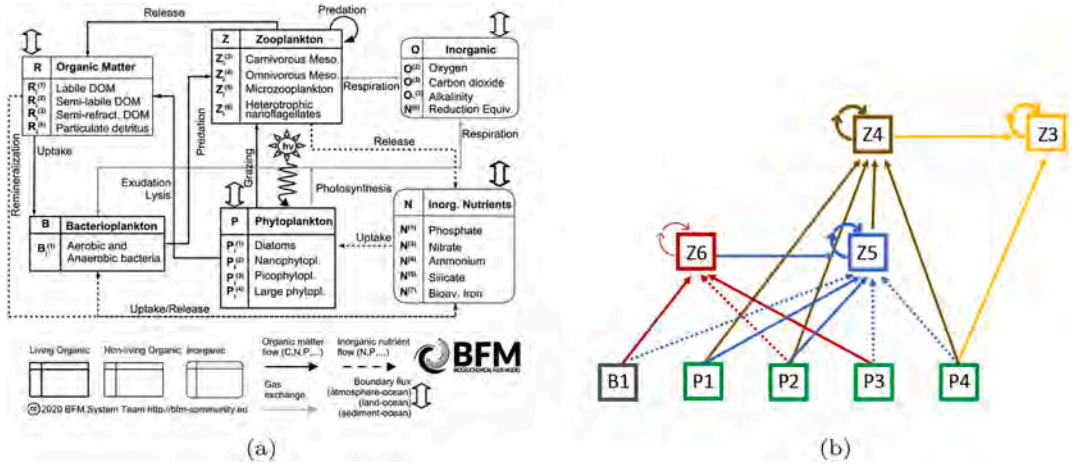


Fig. 1. (a) Scheme of the biogeochemical interactions between organisms within the BFM model; (b) Scheme of trophic web of BFM model. An arrow directed from one box to another indicates a predation flux. Solid arrows denote a higher preference for a specific prey, while dashed ones indicate a lower preference. A looping arrow on the box denotes cannibalism.

where r_{max} is the species-specific maximum growth rate, $f_I(I)$ is a solar irradiance I harvest factor, $f_T(T)$ represents the dependence of metabolic rates on temperature T, and $f_{nut}(\boldsymbol{x})$ defines the limitations to growth caused by nutrient-depleted conditions. The equations for zooplankton are analogous to those for phytoplankton, with the photosynthetic growth term replaced by the grazing term (f_{gra}). For instance, in the case of carnivorous mesozooplankton carbon component $x^i = Z3_c$, we have:

$$\frac{\partial x^i}{\partial t} = f_{gra}(\boldsymbol{x}) - f_{rsp}(\boldsymbol{x}) - f_{rel}(\boldsymbol{x}) - f_{prd}(\boldsymbol{x}). \tag{4}$$

The total amount of food available to zooplankton is determined by summing the possible prey items (see Fig. 1b) weighted by the predator's food preferences. The grazing term follows a type 2 functional response (Gentleman et al., 2003):

$$f_{gra}(\boldsymbol{x}) = f_T(T) r_{max} \frac{F_c}{F_c + h_z} x^i, \tag{5}$$

$$F_c = \sum_{j \in preyC} \delta^j e^j x^j, \tag{6}$$

$$e^j = \frac{x^j}{x^j + \mu_Z}, \tag{7}$$

where h_z is a parameter inversely related to the mobility and searching volume of the organism, x^j is the carbon content in the prey, and δ^j is the preference for a specific prey.

In addition to describing the food web, the BFM also considers the major biogeochemical processes that characterize the dynamics of a pelagic marine ecosystem (e.g., cycles of nitrogen, phosphorus, silica, carbon, and oxygen in water due to plankton activity). In this work, solar irradiance I and temperature T are considered constant, in order to neglect externally induced fluctuations. Thus, if the solution of the model is non-stationary, it is due to inherent properties of the system under study. The endogenous dynamics in the deterministic BFM has been studied in a previous work, (Occhipinti et al., 2023), performing a sensitivity analysis in the domain of realistic parameter values. The analysis of the model behaviour indicated that the model is stationary in the majority of the parameter space configurations. Chaotic solutions correspond approximately to 1% of the considered parameter space hyper volume. Periodic solutions are characterized by small amplitude fluctuations ($CV \approx 10^{-3}$) and correspond approximately to 30% of the parameter space. The effects of variability of I and T on the same system has been investigated in dedicated studies (Grimaudo et al., 2022; Lazzari et al., 2021). For more details and the complete list of equations and processes included in the BFM, (Lazzari et al., 2012) and the BFM code manual (Vichi et al., 2020) are recommended.

2.2. The stochastic model

In the stochastic BFM we added multiplicative white noise to the biomass (carbon concentration) growth rate of each planktonic species, a general differential equation for a model state variable can be written as follows

$$\begin{cases} dx^i = BFM_{x^i}(xt)dt + Dx^i dW & \text{if } i = 1, ..., N_{bio} \\ dx^i = BFM_{x^i}(xt)dt & \text{if } i = N_{bio}+1, ..., N_{tot} \end{cases}, \tag{8}$$

where BFM_{x^i} denotes the deterministic dynamics (or deterministic skeleton) of the variable x^i, which for example corresponds to Eq.(1) for the carbon component of diatoms. $\boldsymbol{x}$ is the vector of the N_{tot} model state variables, of which the first N_{bio} elements are the biomass of the plankton species, and W is a Wiener process. The factor Dx^i is typically referred to as noise intensity (e.g. in (Sieber et al., 2007)). However, for the sake of simplicity in notation, we will henceforth use D to represent the noise intensity. We decided to use the same D for all plankton biomasses to maintain a consistent level of noise. While assigning different noise intensities to each plankton functional type would be more realistic, it would overly complicate the study. The noise is linearly proportional to the biomass x^i of the affected species, since the environmental stochasticity affects all individuals of a species in the same way (Arnoldi et al., 2019). The stochastic model is numerically solved using the Ito scheme, so Eq.(8) is solved as

$$\begin{cases} x^i_{t+1} = x^i_t + BFM_{x^i}(x_t t)\delta t + Dx^i_t \sqrt{\delta t}\,\xi & \text{if } i = 1, ..., N_{bio} \\ x^i_{t+1} = x^i_t + BFM_{x^i}(x_t t)\delta t & \text{if } i = N_{bio}+1, ..., N_{tot} \end{cases}, \tag{9}$$

where δt is the timestep and ξ is a random variable with mean 0 and variance 1. The solution of a simulation is obtained by averaging 1000 simulation realizations. Due to the nonlinear character of the BFM, averaging over different realizations does not rule out the effects stemming from random environmental fluctuations (Grimaudo et al., 2022). In a linear model, indeed, the mean value of a generic variable is not affected by stochastic perturbations.

The effects of noise are evaluated in the presence of different endogenous dynamics: stationary, periodic, chaotic. Here we study the stochastic BFM in four configurations (parameter sets) taken from (Occhipinti et al., 2023), which yield deterministic solutions with the following characteristics.

The first configuration exhibits stationary endogenous dynamics and consists of the standard configuration of BFM parameters, representing a generic, well-mixed temperate coastal sea with mean depth $5m$ (Vichi et al., 2020).

The second configuration shows periodic dynamics with increasing amplitude (but always with a coefficient of variation on the order of 10^{-3}) for diatoms (P1), while the other plankton species show stationary dynamics.

The third configuration shows chaotic dynamics for all plankton species, except for nanoflagellates (P2), which are extincted after a few years of simulation. The second and third configurations are generated by perturbing the default parameters in a realistic range of values (Occhipinti et al., 2023), so that the model solutions still represent a well-mixed temperate coastal sea.

A fourth configuration of the model is used, the parameters of the model are the same as for the stationary configuration, but in this case the noise is applied to a single plankton species, in particular we choose the microzooplankton Z5. The solutions of the deterministic and the stochastic BFM are shown in Fig. 2 for the four model configurations.

2.3. Sensitivity analysis

In this study, we conducted a sensitivity analysis to investigate the impact of initial conditions and parameter variations on the persistence of plankton species. We simultaneously perturbed all 200 model parameters and 54 initial conditions, excluding the noise intensity D, which will be generically referred to as model parameters. The perturbation magnitude for these parameters was set within ±30% of their reference values [48], except for the initial conditions of nutrients. Nutrient values were randomly sampled within the intervals $[0.01, 2.0]$ for PO_4, $[0.01, 32.0]$ for NO_3, NH_4, and SiO_3, and $[5.0, 390.0]$ for dissolved oxygen (Occhipinti et al., 2023). Using the Parsac tool (Bruggeman and Bolding, 2020), we randomly sampled the parameters to generate 35,000 parameter sets. We then performed 35,000 Monte Carlo simulations, each with a unique parameter set, and recorded whether at least one plankton species went extinct or all species survived. A species was considered extinct if its biomass dropped below $10^{-4}\,\mathrm{mgC\,m^{-3}}$. The primary objective of this sensitivity analysis was to compute the ratio of the parameter space that supports the coexistence of all plankton species.

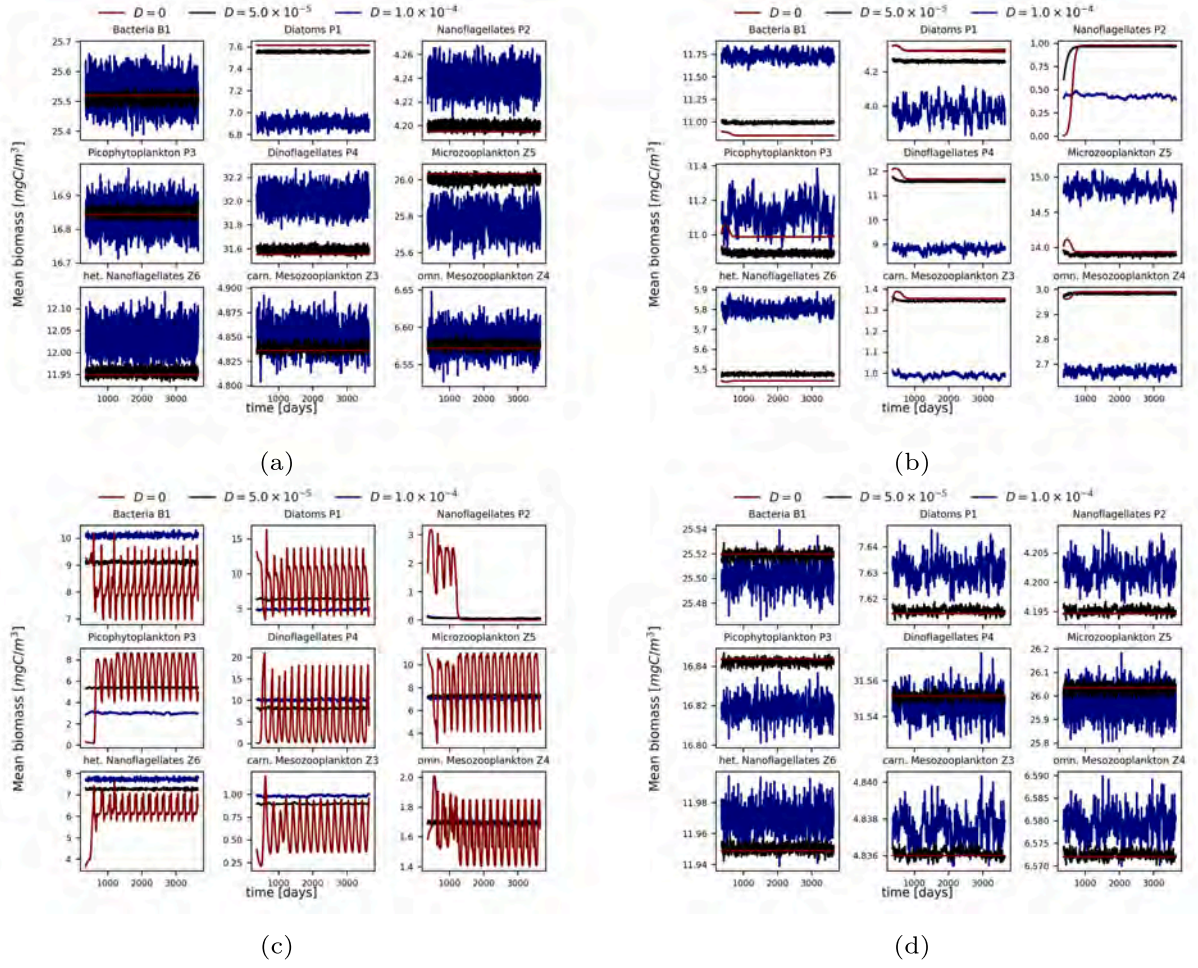


Fig. 2. Biomass time series for the BFM biological species obtained by the average of the stochastic ensemble. In red the deterministic solution ($D = 0s^{-1/2}$), in black ($D = 5.0 \times 10^{-5}s^{-1/2}$) and blue ($D = 1.0 \times 10^{-4}s^{-1/2}$) the solutions with the addition of stochastic noise for 4 model setups: (a) stationary configuration, (b) periodic configuration, (c) chaotic configuration. (d) here, the noise is applied only to the microzooplankton biomass and the stationary configuration is used. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

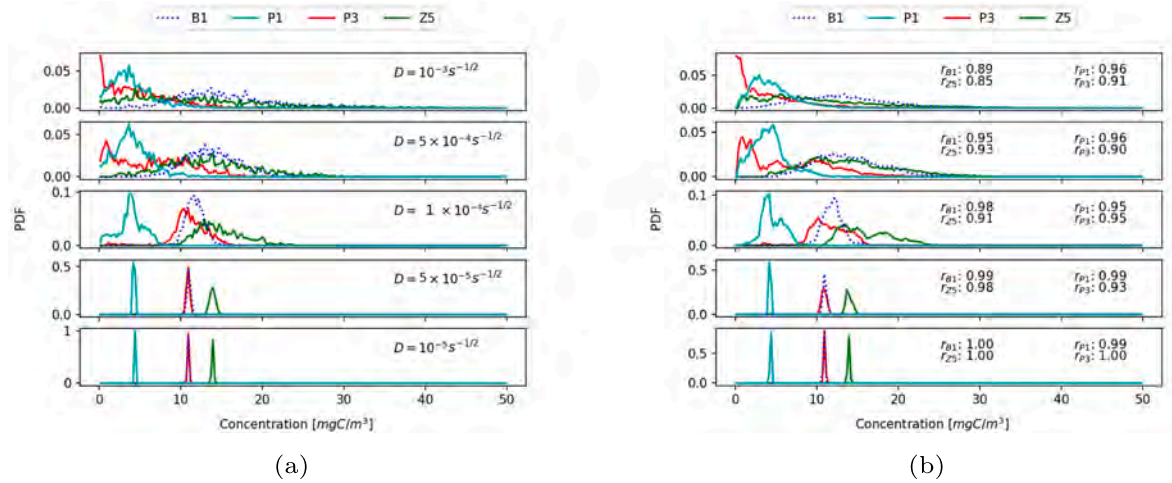


Fig. 3. Probability density function (PDF) for the bacteria (B1), diatoms (P1), picophytoplankton (P3), microzooplankton (Z5) for different levels of noise intensity D: (a) computed over an ensemble of 1000 solutions, on the right of each box is annotated D; (b) computed over an ensemble of 9000 time steps of a single solution, on the right of each box is annotated the Pearson correlation coefficient r between the PDFs in (a) and in (b).

3. Theory

3.1. Ergodicity

One property of an ergodic system is that it satisfies the equality of the infinite time averages and the phase averages, i.e. expectation values with respect to the microcanonical measure on the phase space (Van Lith, 2001). In the context of stochastic processes, the phase average stands for the average over the ensemble of stochastic simulations. Therefore, when studying an ergodic stochastic process, it is not necessary to run an ensemble of simulations, but the statistics can be derived from the temporal evolution of the process, which reduces the computational effort. We compared the probability density function (PDF) of the plankton biomasses constructed over an ensemble of 1000 stochastic simulations with the PDF constructed from 9000 time steps of a single simulation (see Fig. 3) using the periodic configuration (see Fig. 2b). The two PDFs are compared using the Pearson correlation coefficient r (see Fig. 2b) for each selected plankton species. The PDFs are found to be correlated and the p-values (not shown) confirm statistical significance, suggesting that the stochastic 0-D BFM has ergodic properties. For a generic stochastic system, it is possible to prove ergodicity mathematically (e.g. (Rihan et al., 2022; Rihan and Rajivganthi, 2021)). However, the model used in this study is too complex for an analytical assessment of ergodicity, so we relied on the numerical analysis described above.

3.2. Near-equilibrium dynamics

The study of near-equilibrium dynamics often allows to understand the properties of complex systems, thanks to the assumptions that can be made in such a regime. In the BFM, we can assume that the deterministic growth rate of plankton near equilibrium is directly proportional to the respective biomass. We extend such approximation to the other chemical variables of the model. Therefore the following approximation holds for any of the model state variables $x^i \in \boldsymbol{x}$,

$$BFM_{x^i}(\boldsymbol{x},t) : -\gamma^i\left(x^i - x_0^i\right), \tag{10}$$

where the minus sign is due to the fact that the dynamical response is expected to balance fluctuations and bring the system to equilibrium, and γ^i is an effective growth rate with units $\left[s^{-1}\right]$, characteristic of each variable x^i. If the deterministic equilibrium state is characterized by a stationary dynamic, the variable x^i can be assumed to have negligible relative fluctuations near a mean value x_0^i, $|x^i - x_0^i| = x_0^i$. In fact, when the noise intensity D is small, we can consider the fluctuations around the mean to be negligible in the coefficient of the Wiener process of (8),:

$$\begin{cases} dx^i = -\gamma\left(x^i - x_0^i\right)dt + Dx_0^i dW & \text{if } i = 1,\ldots,N_{bio} \\ dx^i = -\gamma\left(x^i - x_0^i\right)dt & \text{if } i = N_{bio}+1,\ldots,N_{tot} \end{cases}. \tag{11}$$

Therefore, the near-equilibrium dynamics of plankton resembles an additive Ornstein-Uhlenbeck process, described by the following stochastic differential equation (Gardiner, 1985).

$$dx^i = -\gamma^i\left(x^i - x_0^i\right)dt + \sqrt{D^i}dW_t \quad \mathrm{i} = 1,\ldots,N_{bio}, \tag{12}$$

which is equal to Eq.(11) with the substitution $D^i = D^2 {x_0^i}^2$. The Ornstein-Uhlenbeck process stabilizes (for $t > 1/\gamma^i$) to a distribution with standard deviation σ_{OU}^i satisfying the following relation

$$\sigma_{OU}^i = \sqrt{\frac{D^i}{2\gamma^i}} = \frac{Dx_0^i}{\sqrt{2\gamma^i}}. \tag{13}$$

where the plankton dynamics stabilise to a Gaussian distribution with mean x_0^i and standard deviation σ_{OU}^i for any biomass variable ($i = 1,..,N_{bio}$) in the presence of weak noise, while the other model variables ($i = N_{bio}+1,\ldots,N_{tot}$) stabilise to a distribution with mean x_0^i and standard deviation 0. We would like to evidence again that these results hold in the near equilibrium and small noise limit ($|x^i - x_0^i| = x_0^i$ and $D = 1$). Since we assume that the 0-D BFM has ergodic properties, the deviation in the distribution is reflected in the time series such that σ_{OU}^i is related to the magnitude of the fluctuation of the plankton biomass around the mean. We test these findings numerically in the Results section.

3.3. Fokker-Planck equations

The stochastic differential eq. (8) can be written in the general form

$$dx = A(x,t)dt + B(x,t)dW(t), \tag{14}$$

where $\boldsymbol{x}$ is the vector of the N_{tot} state variables of the BFM, $A^i = BFM_{x^i}$ is the time derivative of x^i in the deterministic BFM, $i = 1,\ldots,N_{tot}$, $B(\boldsymbol{x},t)$ is a matrix which describes the interaction between the noise and the model, $\boldsymbol{W}$ is a N_{tot} dimensional Wiener process.

In particular in our study we set the matrix B to:

$$\begin{cases} B^{ij} = Dx^i\delta^{ij} & \text{if i,j} = 1,\ldots,N_{bio} \\ B^{ij} = 0 & \text{if i,j} = N_{bio}+1,\ldots,N_{tot} \end{cases} \tag{15}$$

in this notation, the first N_{bio} variables are the biomass of the plankton functional types.

The eq. (14) is associated to the Fokker-Planck equation (Gardiner, 1985):

$$\partial_t p(\boldsymbol{x},t) = -\sum_i \partial^i\left[A^i(\boldsymbol{x},t)p\right] + \frac{1}{2}\sum_{i,j}\partial^i\partial^j\left\{\left[B(\boldsymbol{x},t)B^T(\boldsymbol{x},t)\right]^{ij}p\right\} \tag{16}$$

which describes the probability $p(\boldsymbol{x},t)$ that the state variables of the BFM have value $\boldsymbol{x}$ at time t.

Since B is a diagonal matrix the following equality holds:

$$\begin{cases} \left[B(xt)B^T(xt)\right]^{ij} = D^2x^{i2}\delta^{ij} & \text{if i,j} = 1,\ldots,N_{bio} \\ \left[B(xt)B^T(xt)\right]^{ij} = 0 & \text{if i,j} = N_{bio}+1,\ldots,N_{tot} \end{cases} \tag{17}$$

and so the eq. (16) simplifies to

$$\partial_t p = -\sum_i^{N_{tot}} \partial^i\left[A^i(\boldsymbol{x},t)p\right] + \frac{1}{2}D^2\sum_i^{N_{bio}}\partial^{i2}\left(x^{i2}p\right) \tag{18}$$

This equation alone defines the evolution of the state of the system in the stochastic BFM. In Eq.18 the model shows its complexity, the numerical solution of the problem should be formulated in a N_{tot}-dimensional space, which is currently impossible to handle even with modern state-of-the-art computing facilities.

When the system reaches a steady-state the following equality holds:

$$D^{-2}\sum_i^{N_{tot}}\partial^i\left[A^i(\boldsymbol{x})p(\boldsymbol{x})\right] = \frac{1}{2}\sum_i^{N_{bio}}\partial^{i2}\left(x^{i2}p(\boldsymbol{x})\right). \tag{19}$$

In Eq.19, we can apply the same assumption of near-equilibrium dynamics, assume linearity and hypothesize that the interactions within the trophic web are of second order in terms of noise propagation, for the biomass of the N_{bio} plankton species holds the following equation:

$$\dot{q}\left(x^i\right) = 2C^i - 2\gamma^i\frac{x^i - x_0^i}{\left(Dx^i\right)^2}q\left(x^i\right) \quad \mathrm{i} = 1,\ldots,N_{bio}, \tag{20}$$

where $q\left(x^i\right) = x^{i2}p\left(x^i\right)$ and $A^i(\boldsymbol{x}) \approx -\gamma^i\left(x^i - x_0^i\right)$, thanks to linearity, and C^i is a normalization constant. While for the other state variables Eq. (19) simplifies to

$$-\gamma^i\left(x^i - x_0^i\right)p\left(x^i\right) = 0 \quad \mathrm{i} = N_{bio}+1,\ldots,N_{tot}. \tag{21}$$

Eq.21 has a Dirac delta as solution $p(x^i) = \delta\left(x^i - x_0^i\right)$, the noise in this approximation affects only the variables on which it is applied. Eq.20

can be solved analytically

$$q(x^i) = Cx^{i-2\gamma^i D^{-2}} e^{-2\gamma^i D^{-2} x_0^i x^{i-1}} \quad i = 1, \ldots, N_{bio}, \tag{22}$$

where C is a constant factor. $q(x^i)$ has a maximum in x_0^i, it is zero in $x^i = 0$ and goes to 0 for $x^i \to \infty$. For very small values of D, the analytical solution is difficult to manipulate. We can perform additional transformations of Eq.20, setting $r(x'^i) = q(x^i - x_0^i)$ assuming $x'^i = (x^i - x_0^i) = x_0^i$, we get a simple ODE valid around x_0^i,

$$\dot{r}(x'^i) = -2\gamma^i \frac{x'^i}{(Dx_0^i)^2} r(x'^i) \tag{23}$$

The solution of this equation is a Gaussian with standard deviation $Dx_0^i/\sqrt{2\gamma^i}$, consistently with what found in the previous section. The solution for $p(x^i)$ will be the Gaussian with mean x_0^i divided by a factor x^{i2}.

The solution $p(x^i)$ shows a deviation for the mode of the distribution increasing with higher noise intensity (see Fig. 4), but in the linear regimes for any noise amplitude the average value of the $p(x^i)$ distribution is not affected. Fig. 5 shows the the probability density function (PDF) of the BFM state variables, the probability is computed as a time distribution thanks to the ergodic property suggested in Sect.3.1, separately for each state variable x^i. Comparing state variables PDFs with different noise it is clear how lower noise produce in general Gaussian distributions, Fig. 5a, that becomes more irregular with higher noise regimes, Fig. 5b. In the latter regime noise diffuse from the plankton biomass through the whole state variables.

3.4. Resonance

The analysis of Fokker-Planck equations indicates that noise can propagate within the trophic web, therefore it is interesting to investigate possible resonance effects. In particular we explore the occurrence and the implications of resonance between white noise and endogenous non-stationary dynamics. In literature there are several definitions and examples of resonance, from the classical resonance to the stochastic resonance. We describe, briefly, here a few of them.

Classical Resonance. Systems described by second-order ordinary differential equations may exhibit periodic solutions characterized by fluctuations with frequency ω_0. When such a system is subjected to an external periodic forcing, with frequency ω, the observed fluctuations may increase (or decrease) in amplitude or lose their periodicity. Classical resonance is defined as the phenomenon in which the amplitude of the fluctuations increases infinitely with time when the two frequencies (ω_0 and ω) are integer multiples of each other.

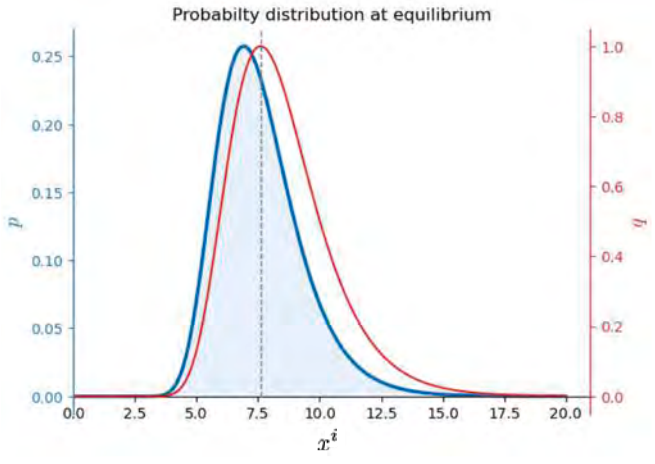


Fig. 4. Analytic solutions $q(x^i)$ and $p(x^i)$ for the parameters $\frac{2\gamma^i}{D^2} = 2$ and $x_0^i = 7.6$ indicated with a dashed vertical line. The plot and calculation has been performed using the SageMath python package (see Sect.7), with the floating point numeric precision increased to 512 bits. The average of the numerically calculated distribution $p(x^i)$ corresponds to x_0^i for any value of D.

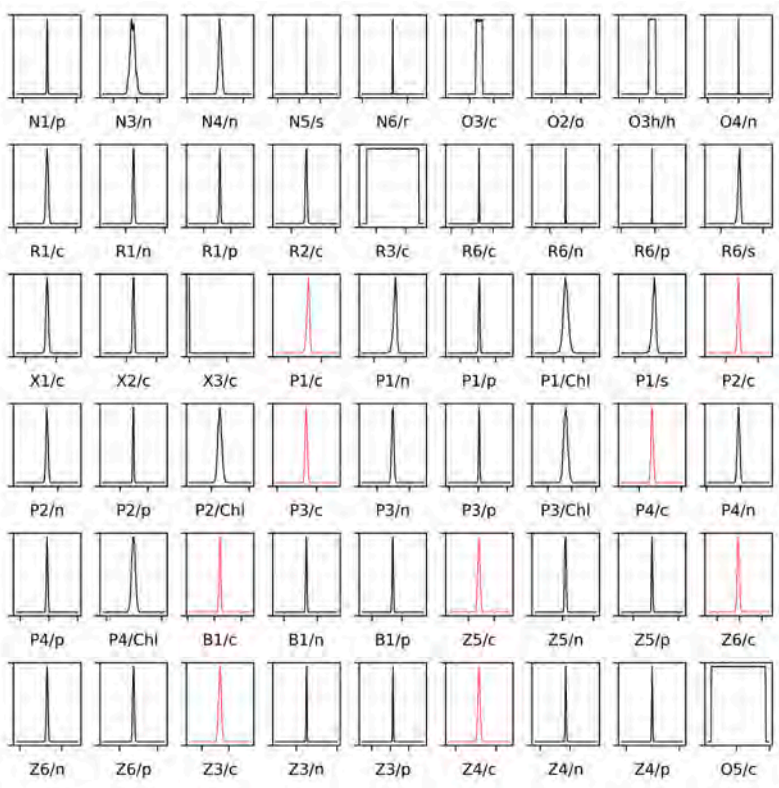
Resonance with white noise. Resonance can also be observed when a system that exhibits periodic dynamics is subjected to white noise. This phenomenon is able to explain the glaciation cycle caused by the interaction between random fluctuations and the long-term periodicity of an astronomical forcing (Benzi et al., 1982; Benzi et al., 1983). Here, the resonance is no longer defined as an increase in the fluctuations amplitude, but as the presence of a correlation between the jumping time (between one equilibrium and another) and the periodic astronomical forcing. This means that the jumping time is of the same order of magnitude as the period of the forcing, although it has not to be exactly the same since the white noise covers a wide frequency spectrum (Benzi et al., 1982). Another possible definition of resonance in this case comes from observing the peak of the power spectrum (P) of the temperature time series. A peak in the plot of P above the intensity of the noise indicates the presence of a resonance (Benzi et al., 1983). This particular resonance between a periodic signal and white noise is often referred to as a stochastic resonance.

Resonance with red noise. The interaction of periodic fluctuation of a dynamical system and red noise can cause resonance phenomena. Red noise has a characteristic time scale τ and is used to model fluctuations that exhibit memory or persistence in time, e.g., temperature fluctuations in aquatic ecosystems (Benincà et al., 2011). In this case, resonance amplifies the periodic fluctuations and can be detected by examining the power spectral density: resonance occurs at the τ corresponding to the maximum of the power spectral density. In particular, resonance is observed when the characteristic time scale τ of the red noise is a fraction of the period of the deterministic fluctuations that characterize the system (Benincà et al., 2011).

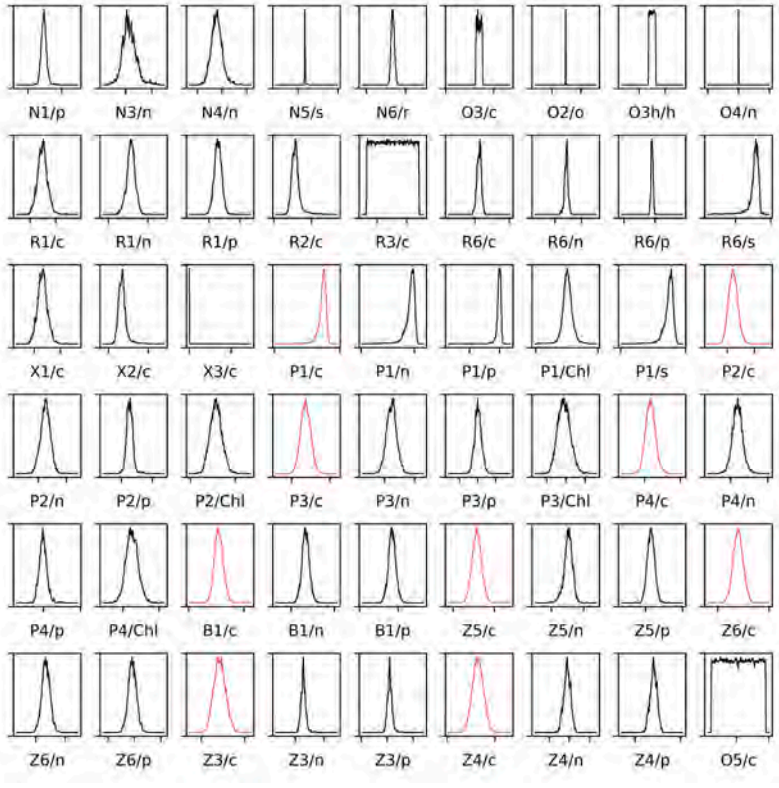
In this work we study the resonance between white noise and non-stationary dynamics, extending the definition of stochastic resonance of (Benzi et al., 1982; Benzi et al., 1983) considering also the interplay between noise and chaotic dynamics. Moreover, the situation we study is different from the examples given above. White noise is applied directly to plankton biomass, which may therefore no longer exhibit the periodic or chaotic dynamics related to the deterministic skeleton of the model. Instead, in the example of (Benzi et al., 1982; Benzi et al., 1983), the periodic astronomical forcing cannot be eliminated by the noise. Therefore, to study such a complex scenario, we can use a more general definition: stochastic resonance (SR) is observed when an increase in the level of unpredictable fluctuations - e.g., random noise - leads to an increase in a metric of signal transmission quality or detection performance rather than a decrease (McDonnell and Abbott, 2009). Using the peak of the power spectrum, similar to (Benzi et al., 1983), as a metric proved too computationally expensive, so to assess the presence of SR we tested two different metrics. The peak in the power spectrum can correspond to a peak in the noise amplification (NA) (Benincà et al., 2011), defined as

$$NA = \frac{CV_{noise} - CV_{det}}{D}, \tag{24}$$

where CV_{noise}, CV_{det} are the coefficients of variation (variance over mean) of the noisy signal and of the deterministic signal before the noise addition and which is less computationally expensive than the evaluation of the power spectrum and therefore we use it as first metric. Stochastic resonance between aperiodic signals and noise can be individuated by using the power norm (PN) (Collins et al., 1995). Since in our model the noise is internal in the dynamics of the plankton, it can be expected that resonance exists between the dynamics of the different plankton species. Diatoms are used as a reference for two reasons: they



(a)



(b)

Fig. 5. Probability density function $p(x_i)$ of the BFM state variables x_i, the x-axis is limited to ±30% of the mean value of the respective state variable. (a) Noise intensity is set to $D = 10^{-5}s^{-1/2}$; (b) Noise intensity is set to $D = 10^{-4}s^{-1/2}$, the state variables where noise is applied are in red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

are at the base of the food web and are the only species that shows periodic behaviour in the periodic configuration. Thus, we define the power norm as

$$PN^i = \frac{\langle (x^i(t) - \langle x^i(t) \rangle)(x^{P1}(t) - \langle x^{P1}(t) \rangle) \rangle}{\sqrt{\left\langle (x^i(t) - \langle x^i(t) \rangle)^2 \right\rangle \left\langle (x^{P1}(t) - \langle x^{P1}(t) \rangle)^2 \right\rangle}}, \quad (25)$$

where x^i is the biomass of plankton species i in the stochastic solution of the model, x^{P1} is the biomass of diatoms in the stochastic solution of the model. The biomass is determined from the ensemble average, and the brackets denote the mean value over time. PN is the cross-correlation between the deviations from the mean of the biomass of a plankton species and the diatoms, normalized by their standard deviation. Maximizing this metric corresponds to maximizing the shape matching of the fluctuations around the mean of a general species and the diatoms (Collins et al., 1995). PN is appropriate when the noise effect (Collins et al., 1995) has no time lag, and we use it as our second metric.

4. Results

Near-equilibrium dynamics. In the Theory section we found that in the stationary configuration, the standard deviation of plankton biomass should theoretically be equal to the standard deviation of an Ornstein-Uhlenbeck process (Eq.(13)) if the noise is weak enough to produce only small fluctuations around a mean value. We tested this theoretical result numerically confronting the standard deviation of the time series of each plankton species and the theoretical Ornstein-Uhlenbeck standard deviation for different values of noise intensity D. The noise intensity range explored is selected from very low values ($D = 10^{-5} s^{-1/2}$) and increased till the model is no more numerically integrable ($D = 10^{-3} s^{-1/2}$). The theoretical and the time series standard deviations are coherent for low noise values but begin to diverge with higher noise intensity ($D = 10^{-4} s^{-1/2}$). As an example, the standard deviation values calculated from the biomass time series and the Ornstein-Uhlenbeck one are reported in Table 1 for $D = 5.0 \times 10^{-5} s^{-1/2}$ and $D = 1.0 \times 10^{-4} s^{-1/2}$. The fact that the Ornstein-Uhlenbeck approximation breaks down near $D = 10^{-4} s^{-1/2}$ may be related to a break in the linearity of the system response to noise. This break in linearity can be seen in Fig. 6, where the distributions of biomass mean and CV in the stationary configuration are shown as a function of noise intensity. The deterministic equilibrium is (approximately) represented by the leftmost point in the distribution, which corresponds to the solution with the lowest noise intensity. The biomass is bounded near the deterministic equilibrium until the CV does not become too large, which happens near $D = 10^{-4} s^{-1/2}$. The effect of the noise is to perturb the equilibrium of the deterministic model by 10% to 30% for phytoplankton, while mesozooplanton is less affected with noise dependent fluctuations below 10%. All phytoplankton species and only the top predator Z3 show a non-monotonic behaviour in terms of biomass concentration, while the CV variation is always monotonic and bounded below 5%. The analysis of the Fokker-Planck equation in the linear regimes shows that the steady state solution preserves the average values obtained with the deterministic configuration, so that the observed deviations are due to nonlinear interactions between noise and the deterministic skeleton.

Table 1
Standard deviation of the biomass of the plankton species (std) and its theoretical value as standard deviation of an Ornstein-Uhlenbeck process (σ_{OU}), two simulations are performed with the stationary configuration using different noise intensities D. In the bottom row are reported the Pearson correlation coefficient and the p-value between std. and σ_{OU} for each simulation.

	$D = 5.0 \times 10^{-5} s^{-1/2}$		$D = 1.0 \times 10^{-4} s^{-1/2}$	
var	std $[mgCm^{-3}]$	σ_{OU} $[mgCm^{-3}]$	std $[mgCm^{-3}]$	σ_{OU} $[mgCm^{-3}]$
P1_c	0.18	0.13	1.21	0.05
P2_c	0.07	0.07	0.26	0.10
P3_c	0.27	0.24	1.03	0.51
P4_c	0.56	0.52	2.23	1.40
B1_c	0.32	0.35	1.22	1.94
Z5_c	0.46	0.62	1.80	4.41
Z6_c	0.20	0.18	0.74	0.23
Z3_c	0.10	0.10	0.38	0.70
Z4_c	0.11	0.12	0.42	0.38
	r	p	r	p
	0.93	10^{-4}	0.61	0.08

Stochastic Resonance. We studied the occurrence of SR for three parameter configurations of the BFM characterized by different endogenous deterministic dynamics (Occhipinti et al., 2023): stationary, periodic, chaotic (Fig. 2a,b,c). In order to assess the possibility of SR we perturbed randomly the noise intensity D in the interval $[10^{-5}, 10^{-3}] s^{-1/2}$, taking 100 samples for each configuration. The analysis of the mean biomass and the corresponding standard deviations indicates a clear non-monotonic behaviour also in the cyclic configuration for diatoms and mesozooplankton, while CV is monotonically increasing, Fig. 7b. The chaotic configuration, Fig. 7c, shows a non-monotonic behaviour for the nanoflagellates P2, the microzooplankton Z5 and carn. mesozooplankton Z5. In this configuration, CV shows a complex dependence on the noise intensity. Applying the noise to only one class of organisms, in this case Z5, leads to the simplest results with small deviations with respect to the deterministic case and monotonic behaviour for biomasses and coefficients of variation (see Fig. 7d).

The NA and PN indicators expressed as function of D (see Fig. 8) are coherent both in stationary and periodic configurations. In fact, both NA and PN show SR in the stationary and periodic configuration. In these configurations (see Fig. 8a,b), we found that the peaks of the metrics occur at noise intensities between $10^{-4} s^{-1/2}$ and $10^{-3} s^{-1/2}$ (where the metrics show a peaked distribution). The magnitude of NA in the periodic configuration, Fig. 8b, is more than an order of magnitude larger (e.g. in the case of P2 and Z5) with respect to the stationary case. The high NA values for Z5 could be related to the extinction regime, in which the biomass values of Z5 become very low and cause a divergence. Based on the PN distributions in the stationary and periodic configurations (see Fig. 8 a, b), it can be seen that the correlation between diatoms and the other species can be positive or negative. A positive (negative) correlation is associated with an increase (decrease) in the biomass of the species studied, which is accompanied by an increase in the biomass of the diatoms. The case of the chaotic configuration, Fig. 8c, differs from the other two, Fig. 8a and b. NA is negative due to the strong reduction of the fluctuations caused by noise, Fig. 2c. The nanoflagellates P2 are the only species that show positive NA, which is due to the fact that they are extinct in the deterministic skeleton. We were unable to identify SR for the chaotic configuration, the NA is monotonically dependent over D, while PN shows no clear signal. The configuration with the noise source applied to Z5, Fig. 8d, shows only smaller NA for all plankton species considered, and a scattered signal for both NA and PN with no clear SR.

System equilibria. The stochastic solutions (see Fig. 2) show different biomass concentrations than the deterministic model, at least for some plankton species. To assess whether these new concentrations are equilibria of the system or are merely kept alive by the continuous stochastic forcing, another set of simulations is run in which the noise is turned off after three years over the ten simulation years. We focused on the stationary configuration because it is easier to assess whether the system relaxes to the stationary equilibrium. We then examined the time series of the plankton biomass (see Fig. 9). At high noise intensities, new equilibria occur in which the biomasses relax to a different concentration compared to the deterministic skeleton. The largest variation in biomass is observed for picophytoplankton P3, whose biomass decreases by about 10% of the deterministic value.

Persistence. The persistence response of plankton species to the variation of BFM parameters is studied. From the sensitivity analysis for

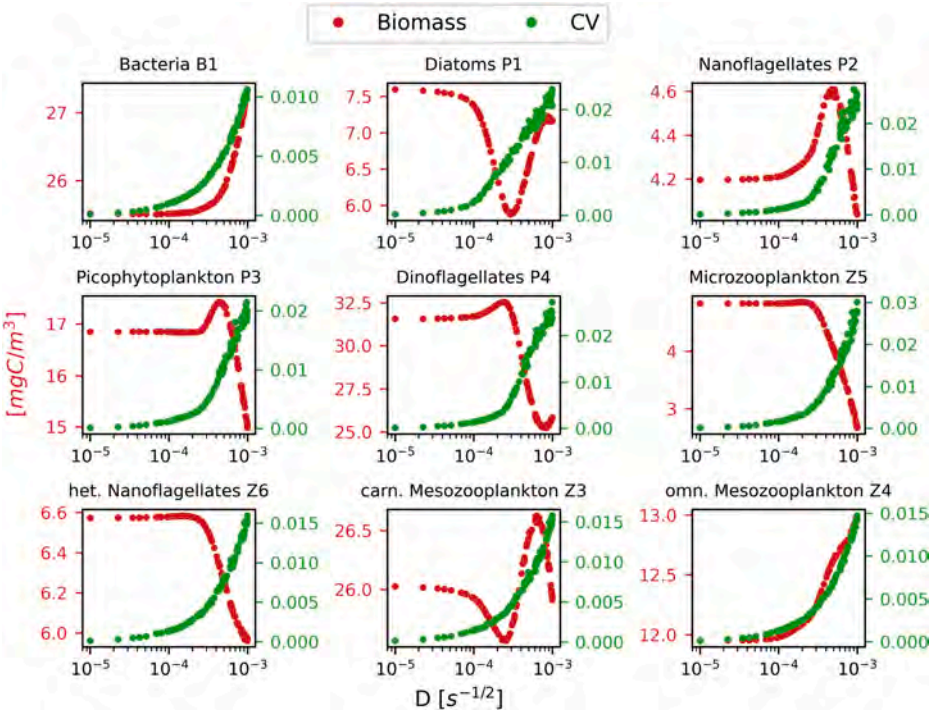


Fig. 6. Biomass (red) and coefficient of variation (CV, green) as a function of noise intensity D for the biological species of BFM with stationary deterministic skeleton configuration. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

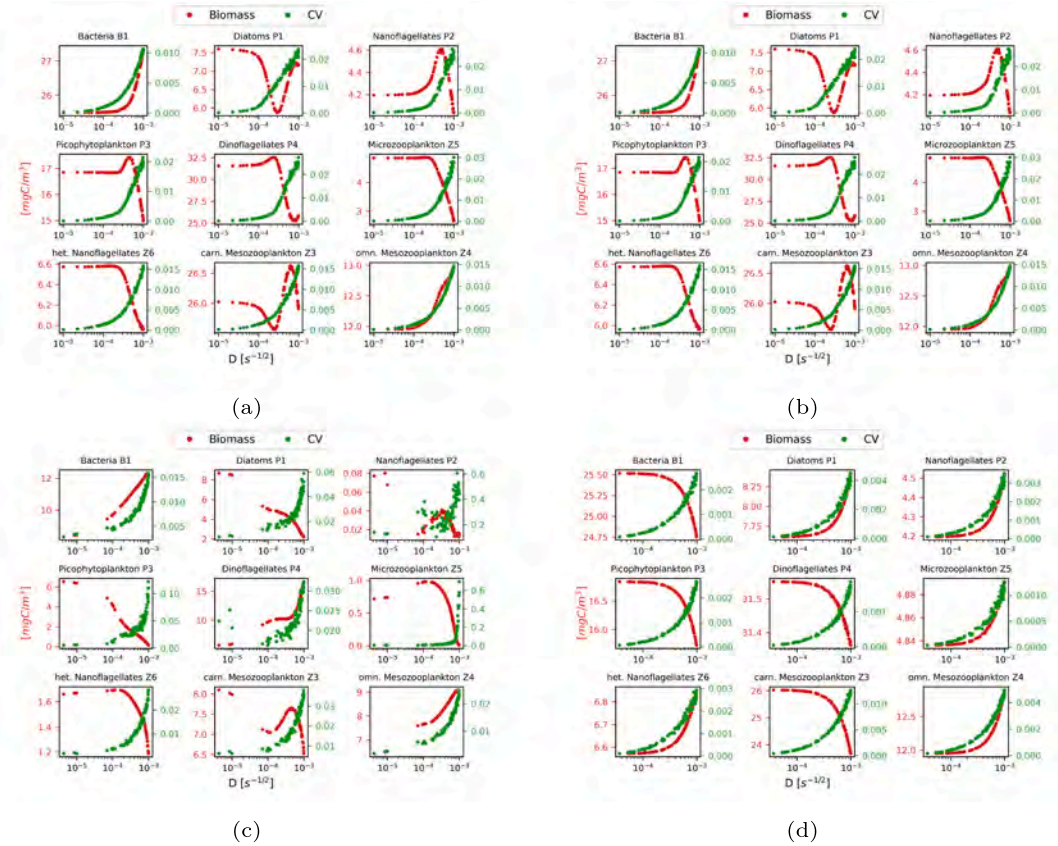


Fig. 7. Biomass (red) and coefficient of variation (CV, green) as a function of noise intensity *D* for the biological species of BFM, for 4 model setups: (a) stationary configuration, (b) periodic configuration, (c) chaotic configuration. (d) here, the noise is applied only to the microzooplankton biomass and the stationary configuration is used. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

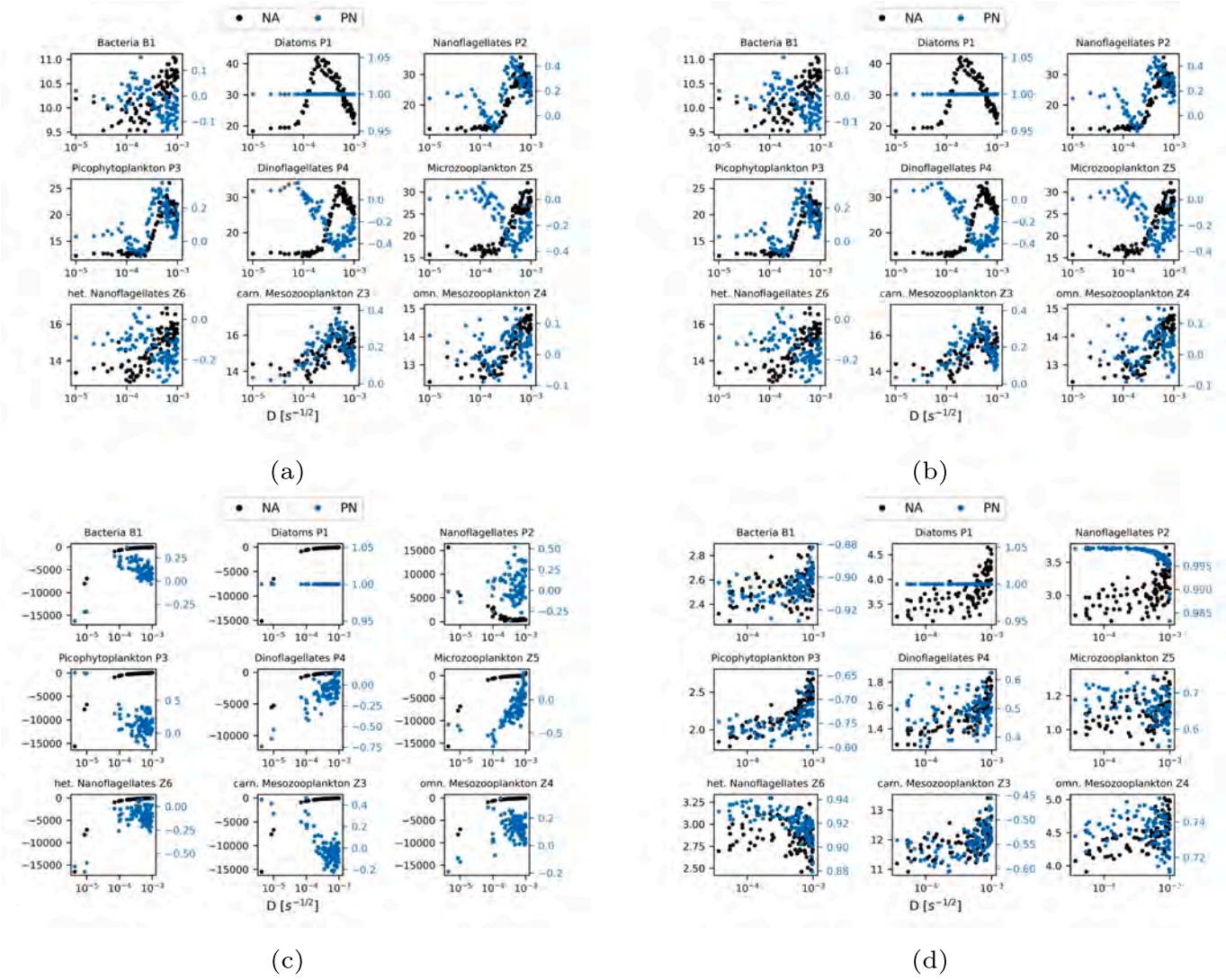


Fig. 8. Noise amplification (NA, black) and power norm (PN, blue) as a function of noise intensity D for the biological species of BFM, for 4 model setups: (a) stationary configuration, (b) periodic configuration, (c) chaotic configuration. (d) noise applied only to the microzooplankton biomass. In case (d) the stationary configuration is used. A gap in the points can be observed especially in panel (c) in the interval $D \in [10^{-5}, 10^{-4}]s^{-1/2}$, which is caused by the use of a random sampling method and the logarithmic scale of the x-axis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the deterministic BFM resulted that for about 60% of the possible parameter choices at least one species goes extinct during a 10-years simulation (Occhipinti et al., 2023). The effect of stochastic noise on plankton persistence is investigated for different values of the intensity of noise D; the fraction of samples presenting extinction is shown in Table 2. We found that in the stochastic model, plankton persistence generally increases. However, a high level of D (e.g. $D = 10^{-3}s^{-1/2}$) may have the opposite effect; the plankton are more likely to go extinct compared to the deterministic model.

5. Discussion

5.1. Methodology

In this study, we introduced environmental stochasticity into an ocean biogeochemical model of realistic complexity. We incorporated multiplicative white noise to represent the growth response of plankton biomass to environmental variability over time and space. Our findings revealed phenomena absent in the deterministic model, highlighting the importance of including stochastic processes in biogeochemical models to enhance prediction accuracy.

Stochastic models are defined in terms of probabilities, which evolve over time through stochastic differential equations (Mubayi et al., 2019), such as the Fokker-Planck equation Eq.(16). These probabilities are generated from an ensemble of solutions with the same initial conditions, as the random components of the stochastic process produce different outputs from identical inputs (Mubayi et al., 2019). Consequently, the results of stochastic models are derived from the statistical properties of these probabilities, such as the ensemble mean and variance. This probabilistic nature allows stochastic models to effectively represent the range of environmental variability and the corresponding plankton growth responses, incorporating uncertainty in environmental parameterization and thereby improving prediction accuracy. In the field of meteorology, a sophisticated stochastic technique, Stochastically Perturbed Parametrisations, is the standard for evaluating model uncertainty (Lang et al., 2021). It consists of introducing stochastic perturbations into the physical parametrisation and is currently used by the European Centre for Medium-Range Weather Forecasts (ECMWF) (Leutbecher et al., 2017). In our model, the noise describes the uncertainty of the environment, a metric indicating the uncertainty of the

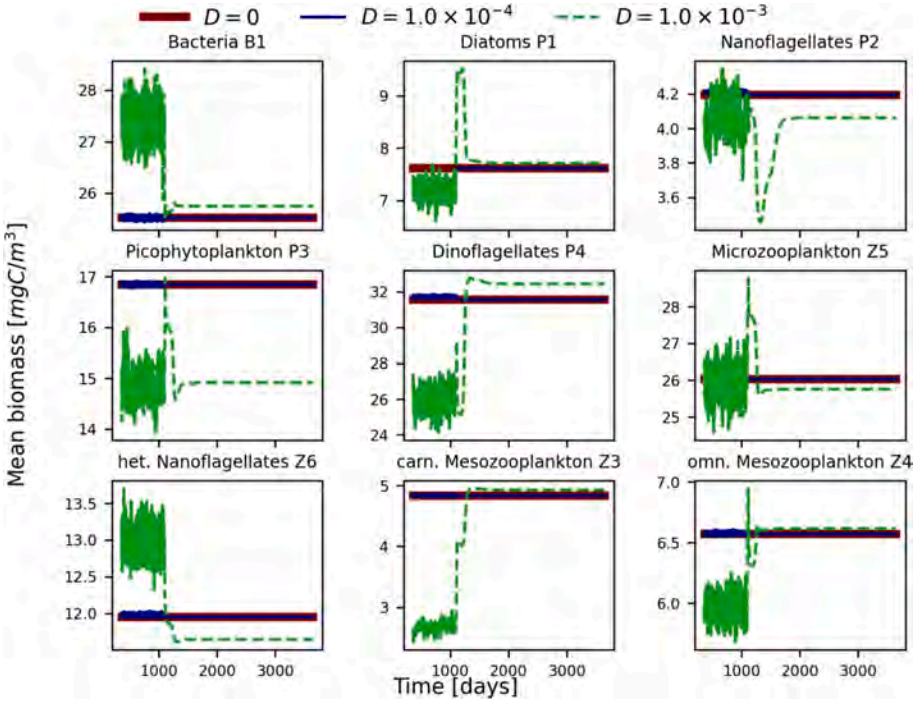


Fig. 9. Biomass time series for the BFM biological species obtained by the average of the stochastic ensemble. The stationary configuration is used and the noise is set to 0 after 3 years of simulation. In red the deterministic solution ($D = 0s^{-1/2}$), in blue ($D = 1.0 \times 10^{-4}s^{-1/2}$) and green ($D = 1.0 \times 10^{-3}s^{-1/2}$) the solutions with the addition of stochastic noise. The solution with the strongest noise intensity (green) relaxes to a different equilibrium with respect to the deterministic skeleton. The line width of deterministic time series (red) is increased to make it visible. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Probability that at least one species of plankton is extincted perturbing the parameters of the BFM in a realistic range, for different noise intensity D.

$D\ [s^{-1/2}]$	extinction [%]
0	60
1.0×10^{-6}	25
5.0×10^{-5}	30
1.0×10^{-4}	25
1.0×10^{-3}	65

model solutions is not used. The theoretical analysis performed indicates that for low noise intensity the ensemble distribution of solutions is strictly related to an Ornstein-Uhlenbeck process, while for higher noise intensity the statistic and therefore the uncertainty follow more complex distributions. Future studies in the context of ocean biogeochemical model could focus on defining an appropriate metric that quantifies the degree of uncertainty of model solutions with respect to the intensity of noise introduced into the model. This quantification can help to understand the importance of the uncertainty of unmodelled processes, in our case environmental variability, for the model solutions. We suggest that the noise amplification, Eq.(24), is a possible metric as it relates the coefficient of variation of the solutions to the noise intensity.

In contrast, deterministic models typically involve creating ensembles by perturbing initial conditions or parameters. However, this method loses the temporal aspect of environmental variability, which is inherently captured in the noise of stochastic models. Ensemble modeling is a common technique to enhance accuracy (Ganaie et al., 2022). For instance, it has improved the fit and stability of artificial neural networks in environmental modeling (Huang and Gao, 2017). Utilizing ensembles of different models is considered the best approach to address the uncertainty of a single model, offering conceptual and structural diversity that better replicates the complex dynamics of physical, chemical, and biological interactions in real-world scenarios. Ensemble modeling is widely practiced in ecology (Araujo and New, 2007; Dormann et al., 2018; Recknagel et al., 2018) and climate science (Eyring et al., 2016). It is the standard method for predicting future climate in the Intergovernmental Panel on Climate Change (IPCC). We showed that multiplicative white noise could address uncertainty from environmental variability. Other stochastic processes, such as those combining stochastic variables with Monte Carlo simulations (Schmitz et al., 2016), may be suitable for addressing different types of uncertainty. Stochastic approaches are used to provide measures of uncertainty in the planning of marine protected areas (Beech et al., 2008). We propose considering stochastic models to address and confront model uncertainty due to their intrinsic ensemble structure. The ensemble mean can describe real scenarios better than individual deterministic simulations, as the modeling of the chlorophyll concentration in (Valenti et al., 2016) shows. Incorporating stochastic processes into biogeochemical models can enhance the mechanistic understanding of ocean dynamics and provide crucial insights into the most effective strategies for managing marine ecosystems, ensuring their health and sustained services to human populations.

We found that the Biogeochemical Flux Model (BFM) in a 0-D configuration, and in the absence of exogenous forcings, exhibits ergodic properties, such as the equivalence between ensemble statistics and temporal statistics. This is a significant finding, particularly in the context of the previous discussion on ensemble modeling. Generating temporal statistics is far less computationally expensive than generating ensemble statistics, as it requires running only a single simulation. This property was demonstrated in the presence of endogenous oscillations in plankton dynamics, suggesting that the equivalence may hold even with periodic exogenous forcing. Further research should explore this hypothesis under more complex dynamics, such as the turbulence induced by ocean currents.

5.2. Ecological implications

We studied the effect of noise on plankton dynamics investigating the influence of the interaction between noise and endogenous dynamics, i.e. the dynamics resulting from the model in the deterministic configuration and in the absence of exogenous forcing, e.g. cycles in temperature and light. Therefore, plankton dynamics is determined by competition and predation relations among plankton species and by the microbial loop. Non-stationary dynamics can have severe impact on population structure, examples are the relationship between the complexity of fluctuations and the genetic structure of a population (Kaitala et al., 2006), and the influence of the strength of fluctuations on the coexistence between species (Pisa et al., 2019; Roy et al., 2020). In the deterministic BFM different configurations of parameters lead to stationary, periodic or chaotic endogenous dynamics (Occhipinti et al., 2023). The kind of endogenous dynamics resulted to lead to different responses to noise. In particular stochastic resonance is not observed when the endogenous dynamics is chaotic.

One of the major ecological questions regarding stochastic models is if environment fluctuations can sustain population fluctuations (Mubayi et al., 2019). This topic is connected to the observation of fluctuations in various animal populations with frequencies distinct from those of periodic environmental oscillations (Berryman, 1988; Hudson et al., 1992; Krebs and Myers, 1974; Moss et al., 1996; Watson et al., 1984), comprising plankton (Benincà et al., 2008; Goulden and Hornig, 1980; McCauley and Murdoch, 1987; Pratt, 1943; Rogers et al., 2022). The causes of population fluctuations have long intrigued theoretical ecologists, dating back to the work of Lotka and Volterra (Kendall et al., 1999). Several studies have shown that noise can increase the variability of plankton populations (e.g. (Benincà et al., 2011; Guo et al., 2023)). Stochastic resonance cause noise-induced fluctuations in populations (Mubayi et al., 2019) and, possibly, explain the observations. Stochastic resonance proved to be an inherent feature of the stochastic BFM, leading to an increase in biomass fluctuations. We found that such phenomenon is possible in the presence of stationary and periodic endogenous dynamics. Since resonance between noise and a stationary signal is not possible, the observed resonance must be caused by the interaction between different species, i.e., there is resonance between the noise of different species and not between the noise and the deterministic time series. This internal resonance is evidenced by the correlation (PN) between diatoms and the other plankton species (see Fig. 8a, b). In the deterministic model the configuration expressing periodic endogenous dynamics presents oscillations with an amplitude which is not experimentally observable (Occhipinti et al., 2023). Environmental stochasticity, through stochastic resonance, can amplify the amplitude of fluctuations up to an observable level. We observe a stronger amplification when noise interacts with periodic endogenous dynamics, comparing the noise amplification between panel a (stationary endogenous dynamics) and b (periodic endogenous dynamics) of Fig. 8.

The interaction between noise and chaotic oscillations has a completely different effect on noise amplification compared to the periodic configuration. In this context, noise amplification (NA) is negative, meaning that the coefficient of variation (CV) of the stochastic solution is smaller than that of the deterministic solution (see Figs. 2c, 8c). This suggests the possibility of noise-enhanced stability in biogeochemical models. Noise-enhanced stability is defined as the phenomenon where noise stabilizes a fluctuating or periodically driven metastable state, causing the system to remain in this state longer than it would in the absence of noise (Spagnolo et al., 2004a). This phenomenon was initially observed in electrical circuits (Mantegna and Spagnolo, 1996) and has since been identified in ecological models as well (Yu and Ma, 2023; Zeng et al., 2015). While we cannot definitively classify the significant decrease in noise amplification as noise-enhanced stability, it provides a clue to its potential occurrence. Future research should investigate the potential occurrence of noise-enhanced stability and its implications for ecosystem stability. Another important aspect of plankton fluctuations is the interaction between noise and external periodic forcing (e.g. temperature and light), which can have a significant impact on plankton dynamics (Rinaldi et al., 1993). Understanding these interactions can provide deeper insights into the complex behaviour of plankton populations. However, investigating these effects in detail is beyond the scope of the present work.

We found that noise affects not only plankton biomasses but also permeates the entire model, as illustrated in Fig. 5. The propagation is particularly strong through species interactions and can lead to stochastic resonance in configurations with stationary endogenous dynamics. To study noise propagation from a single source, we used the same parameters as the stationary configuration but applied noise to only one species, the microzooplankton (see Fig. 2d). Microzooplankton was chosen because it is a critical species for characterizing trophic interactions in the BFM, occupying a central node in the trophic web (Occhipinti et al., 2023) (see Fig. 1b). Noise can propagate also when it has a single source, but no stochastic resonance occurs (see Fig. 8d). The phenomenon of perturbation propagation in trophic webs has been extensively studied through both experimental (Duffy et al., 2015; Pace et al., 1999) and modeling approaches (Carpenter et al., 1987; Montoya et al., 2006; Quévreux et al., 2021; Quévreux and Loreau, 2022; Simon and Vasseur, 2021). The impact of perturbations on ecosystems is closely linked to their stability and resilience (Arnoldi et al., 2016; Arnoldi et al., 2019; Darling and Côté, 2018; Donohue et al., 2013; Quévreux and Loreau, 2022).

A recent review by (Kéfi et al., 2019) highlighted the complexity-stability relationship as one of the leading open questions in ecology. This line of research began with studies on the role of diversity in stability (Elton, 2020; MacArthur, 1955; May, 2001) and continues to engage ecologists today (Allesina and Tang, 2012; Arnoldi et al., 2019; Hautier et al., 2014; Ives and Carpenter, 2007; Johnson et al., 2014; Pennekamp et al., 2018). (Kéfi et al., 2019) identified three main issues in the diversity-stability debate. The first is how to measure stability, as there is no consensus on which metrics to use or whether they convey the same information. The second issue is at what organizational level stability should be computed, whether for the whole community, groups of species, or individual species. The third issue concerns the types of perturbations used to assess stability; most studies have examined isolated perturbations over a few ecological scales, highlighting the need to study synergistic effects of multiple perturbations. In the context of plankton communities and ocean biogeochemical models, the deterministic BFM has demonstrated high stability to variations in its parameters and initial conditions (Occhipinti et al., 2023). A sensitivity analysis showed that most solutions exhibit endogenous stationary dynamics, with periodic or chaotic fluctuations being rare. It was suggested that the complex network of interactions described by the model has a damping effect on fluctuations (Occhipinti et al., 2023). The damping of perturbations originating from a single noise source (see Figs. 2d and 8d) further supports the stability role of complex networks. However, the occurrence of stochastic resonance highlights the risk of overestimating stability when the interactions between multiple perturbations are not considered.

The understanding of the coexistence of multiple species within the same ecosystem has long intrigued ecologists and population biologists (Chesson, 2000; Tilman, 1982). The impact of environmental stochasticity on coexistence has received particular attention (Chesson, 1982; Chesson and Ellner, 1989; Ellner, 1989). The interplay between endogenous and stochastic exogenous dynamics impacts coexistence in such a complex manner that its comprehension is still evolving through mathematical and ecological models (Benaïm and Schreiber, 2019; Hening et al., 2021; Majumder et al., 2021).

This research has particularly fascinated ecologists studying plankton. Marine ecosystems contain more species of plankton than the resources can support according to coexistence theory, giving rise to the yet unresolved “Paradox of the Plankton” (Hutchinson, 1961). Several stochastic processes may alter the persistence of populations. For

instance, demographic stochasticity is considered a cause of extinction (Xue and Goldenfeld, 2017), with its effect being particularly strong when population density is low (Lindo et al., 2023). In contrast, environmental noise appears to increase plankton persistence (Guo et al., 2023; Sarker et al., 2020; Yu et al., 2019a). Positive effects of noise on plankton persistence were observed in studies on the effects of global warming (Sarker et al., 2020). Although a gradual increase in temperature leads to a decrease in plankton diversity, the number of persisting species in the system with noise is higher than in the system without noise (Sarker et al., 2020). In a food chain model that accounts for seasonality, with white noise applied to the growth of plankton and nutrients, it was found that the persistence of phytoplankton depends on environmental noise (Yu et al., 2019a). In a nutrient-plankton model, environmental variability in mortality was described via stochastic regime switching, which was found to enhance the persistence of plankton populations (Guo et al., 2023). Furthermore, chaotic fluctuations in a spatially extended environment have been shown to increase the chance that populations in isolated areas will survive periods of unfavorable conditions, thereby increasing species survival chances (Petrovskii et al., 2004). This is consistent with our finding that noise in growth rates can reproduce both fluctuations, similar to the chaos studied by (Petrovskii et al., 2004), and variability in spatial conditions in a 0-dimensional model (environmental stochasticity), thus promoting species persistence.

We contribute to the understanding of plankton coexistence using a biogeochemical model of realistic complexity. Unlike simpler models, the BFM describes the major processes occurring in marine ecosystems and provides an accurate understanding of plankton dynamics. We found that plankton persistence (and the number of coexisting species) can increase or decrease as a function of noise intensity (see Table 2), suggesting that environmental stochasticity can enhance coexistence when low in intensity. When the noise approaches the scale of plankton growth (days), e.g., for $D = 10^{-3}s^{-1/2} \approx 0.3d^{-1/2}$, persistence decreases and fewer species coexist. The opposite effect is observed for smaller D, far from the growth temporal scale, where a larger number of species coexist. The use of sensitivity analysis allowed for an accurate assessment of plankton coexistence despite uncertainties in model parameters (Cai et al., 2023). The extensive number of simulations (175,000) provided a thorough investigation of the parameter space (Occhipinti et al., 2023).

Recent stochastic implementations of biogeochemical models have shown that stochastic processes do not cause a transition to a new equilibrium point but instead maintain the ecosystem in a steady state out-of-equilibrium (Grimaudo et al., 2022). However, our findings indicate that certain intensities of noise can lead the system to a different equilibrium than the deterministic one. This result may appear to contrast with (Grimaudo et al., 2022), but the noise in that study models the random fluctuations of solar irradiance. Environmental stochasticity encompasses both the random variability of the environment and the stochastic response of population growth rates to such variability. This response could explain the emergence of new equilibria at specific intensity levels (D) of the noise. Similar findings were observed in a phytoplankton-zooplankton model subjected to environmental stochasticity, where noise-induced transitions between two equilibria were noted (Zhao et al., 2022).

Our study confirms that non-selective stochastic processes can increase plankton persistence. We expect that including selective stochastic processes, for example adding a fitness function to the multiplicative noise (Dieckmann and Law, 1996), may increase further the persistence of plankton. Future research may focus on study different sources of stochasticity (e.g. demographic or immigration (Arnoldi et al., 2019)) or the evolution of one or more specific traits of plankton (e.g. the maximum growth rate (Flynn and Skibinski, 2020)), possibly in a complex model of higher spatial dimensions, in order to evaluate the effects of plankton evolution in a climate change scenario.

6. Conclusions

This study presents an investigation into a stochastic 0-dimensional marine biogeochemical model of realistic complexity. Our results show that the inclusion of stochastic processes in biogeochemical models enables the observation of new phenomena (e.g. stochastic resonance) in plankton dynamics and biogeochemical cycles. Moreover, the proposed stochastic model can effectively account for environmental uncertainties thanks to the random variability of growth rate and ensemble solutions.

The deterministic skeleton on which the stochastic model is built can exhibit different endogenous behaviours, such as stationary, periodic and chaotic dynamics. The stochastic model proves to present ergodic properties, largely decreasing the computational cost of numerical simulations. We have shown that the introduction of multiplicative white noise on the growth rate of biological species can develop a stochastic resonance, surprisingly, even when the deterministic solution of the model is stationary. The resonance can amplify the small periodic endogenous fluctuations in the plankton biomass to an experimentally observable level. This mechanism could explain the observation of non-stationary dynamics in ecosystems. In contrast, the interaction between chaos and noise appears to reduce the amplitude of fluctuations. Furthermore, a low noise intensity can have a positive effect on persistence of plankton with a larger number of species coexisting, while a higher noise intensity can induce a new equilibrium in the system.

Therefore the plankton ecosystem has a strong response to environmental noise. The occurrence of stochastic resonance and the variability in the persistence highlight the non-linearity of this response. Future studies may investigate the effect of noise in combination of deterministic external forcings (e.g. temperature and light), or even the effect of strong rare stochastic fluctuations (extreme events) on marine ecosystems.

7. Algorithms, program codes and listings

The code for the BFM and its manual can be freely downloaded at bfm-community.eu. The code of the parsac tool to perform sensitivity analysis can be freely downloaded at github.com/BoldingBruggeman/seamless-notebooks commit: 86210c6c281ce7dcb55e7c5e1ccc860da87d8424. The code developed in this work to add the stochastic noise to the BFM can be freely downloaded at (Occhipinti and Lazzari, 2023). The SageMath notebook used for the analysis of Fokker-Planck equilibrium solution can be accessed at the following url: cocalc/AnalyticSolution.ipynb and as a python notebook file in the supplementary material.

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CRediT authorship contribution statement

Guido Occhipinti: Writing – original draft, Validation, Software, Methodology, Conceptualization. **Stefano Piani:** Writing – review & editing, Software. **Paolo Lazzari:** Writing – review & editing, Validation, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The code used in this work is shared in the Algorithms, Program codes and Listings Section of the manuscript

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoinf.2024.102778.

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