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Plankton interaction networks under human pressure

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ABSTRACT

Planktonic systems form complex interaction networks that are pivotal to marine ecosystem health and stability. However, the long-term responses of these interactions to multiple stressors, especially in dynamic coastal and estuarine ecosystems, remain poorly understood. We applied an information-theoretic modeling approach to monthly abundance data of 74 plankton taxa (2000–2020) from Helgoland Roads (German Bight, North Sea) to reconstruct dynamic interaction networks. Our aim was to explore community- and system-level network properties and their relationships with potential environmental drivers. On the community-level, we found that interaction types encompassing predator–prey relationships among species strengthened under high light availability and nitrogen-to-phosphorus ratios of 20–25, whereas interaction types involving both predator–prey and competitive relationships among species (e.g., mixotrophs that can both prey on and compete with autotrophs) intensified under low light and nutrient availability. The latter interactions intensified particularly after 2006. Since then, links from grazers to primary producers have also strengthened, closely associated with a decline in ambient nitrogen-to-phosphorus ratios slightly below the Redfield ratio of 16:1. The system-level properties of connectedness and resilience provided an abstract view of network behavior, revealing that the system's maturation process was non-linearly driven by salinity and nutrient availability. Consistent with complex-systems theory, the interplay between connectedness and resilience indicated that under low environmental variability, the system became highly sensitive to small nutrient changes, potentially triggering a reorganization of the interaction structure. These results highlight the system's dynamic response to environmental changes and advance understanding of plankton network functionality in coastal ecosystems.

1. Introduction

Plankton communities are an essential part of marine ecosystems, playing a key role in nutrient cycling and energy transfer to higher trophic levels (D'Alelio, 2019). Plankton exhibit remarkable taxonomic diversity, encompassing both unicellular and multicellular organisms, as well as autotrophic, heterotrophic, and mixotrophic species (D'Alelio et al., 2016). They constitute trophic and non-trophic (e.g., facilitation and competition) interaction networks, which depend on abiotic factors such as light, nutrient availability, and temperature (Lima-Mendez et al., 2015). Recent studies provide evidence that current human pressures, such as climate change and nutrient pollution, affect links and strength of interactions among plankton, potentially altering the ecosystem services that rely on them (Scharfe and Wiltshire, 2019; Trombetta et al., 2021; Anderson et al., 2022; Merz et al., 2023; Loschi et al., 2023; Zhang et al., 2024).

In coastal and estuarine ecosystems, plankton interactions are influenced by the complex interplay of natural variability and anthropogenic forcing (Trombetta et al., 2021; Loschi et al., 2023; Romillac et al., 2023). Positioned at the interface between land and sea, coastal plankton populations are frequently subject to substantial variations from fresh- and seawater inputs (Wiltshire et al., 2015). Anthropogenic influences such as nutrient enrichment, fishing pressure, and the increasing frequency of extreme weather events further modify plankton community composition (Paerl, 2006; Reid et al., 2000; Ding et al.,

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2023; Fu et al., 2024). These changes facilitate the persistence of some species, the exclusion of others, and the arrival of newcomers, thereby reshaping community structure and assembly processes (Loschi et al., 2023; Montoya and Raffaelli, 2010). Given ongoing climate warming, intensifying extreme events (Gruber et al., 2021), and the continued growth of coastal human populations (Cosby et al., 2024), it is increasingly urgent to understand how plankton interaction networks respond to the interplay of multiple environmental factors over the long term in such highly dynamic environments.

The German Bight, a shallow coastal region of the North Sea, provides an ideal setting for studying changes in plankton interactions due to its extensive data resources, dynamic environmental conditions, and significant human pressures. The region is shaped by both natural and anthropogenic drivers. Freshwater inputs from major European rivers (e.g., the Elbe, Weser, Rhine, and Meuse) (Van Beusekom et al., 2019) deliver nutrients that directly affect plankton growth, while tidal and wind forcing (Speidel et al., 2024; Rubinetti et al., 2023) indirectly influence plankton dynamics through sediment and nutrient resuspension and changes in turbidity (Wiltshire et al., 2015; Van Beusekom et al., 2019).

Over the past six decades, the German Bight has undergone pronounced environmental changes, including human-induced shifts in riverine nutrient loads (Van Beusekom et al., 2019; Wiltshire et al., 2010; Balkoni et al., 2023), rising sea surface temperatures (Wiltshire et al., 2010; Amorim et al., 2023), and an increase in extreme events, such as floods and droughts (Kaiser et al., 2023; Rewrie et al., 2023; Nguyen et al., 2024). During this period, seawater nitrogen-to-phosphorus ratios have frequently exceeded the Redfield ratio of 16:1, potentially reducing the nutritional quality of phytoplankton for higher trophic levels (Boersma et al., 2015). These changes have been shown to impact plankton communities (Scharfe and Wiltshire, 2019; Wiltshire et al., 2010; Sarker et al., 2020), driving a rapid reorganization of both phytoplankton (Di Pane et al., 2022) and zooplankton functional structures (Deschamps et al., 2023; Di Pane et al., 2023). Although the relationships between various environmental factors and the individual dynamics of phyto- and zooplankton abundances in this region are well-understood (Scharfe and Wiltshire, 2019; Wiltshire et al., 2015; Sarker et al., 2020; Di Pane et al., 2022, 2023; Boersma et al., 2015; Marques et al., 2023), it remains unclear how interactions within the plankton community respond to these environmental stressors.

Understanding such interactions requires an appropriate quantitative measure of interaction strength, yet this concept is defined in various ways depending on data availability, ecological context, and analytical objectives (Wootton and Emmerson, 2005). Here, we consider interaction strength as the size of the effect that one species has on another, encompassing trophic interactions, direct mutualism, and competition. Ideally, such information on a system would be gained by direct measurement of physical flows (Habedank et al., 2024) and interventional experiments. However, in reality, such measurements and experiments are only scarcely practicable, and therefore, corresponding data, and especially over the long term, is rarely available (Habedank et al., 2024). Typically, the most accessible type of information is observational time series of species abundances.

Throughout the last decades, a multitude of indicators have been developed to derive interaction strength from abundance data. Those indicators can be roughly divided into two classes: (i) indicators exploiting the deterministic nature of ecosystems, like Sugihara's convergent cross mapping (Sugihara et al., 2012) or S-map framework (Miki et al., 2025), and (ii) indicators leveraging the stochasticity of natural systems, like Granger causality (Granger, 1969) or information flow (Ay and Polani, 2008). Among the latter, one of the by now most established measures is Schreiber's transfer entropy (Schreiber, 2000). This information-theoretical approach quantifies the amount of information that one can gain about the next state of species B by considering not only the present state of B itself, but also the present state of species A. It thereby provides an indicator of directed transfer of information.

Based on the assumption that every effective interaction between two taxa leads to a transfer of information, previous publications have demonstrated the suitability of transfer entropy for capturing interactions in ecosystems (Wang et al., 2012; Zoller et al., 2024; Jeung et al., 2025). Acknowledging the inherently dynamic nature of ecological interaction networks (Holling, 1973), we applied Schreiber's transfer entropy to monthly abundance data of 74 plankton taxa, using 36-month moving windows between 2000 and 2020, at the Helgoland Roads monitoring site in the German Bight (Fig. 1). Considering species as nodes in a network and interaction strength as the corresponding edges, this approach yields a series of directed, weighted networks of information transfer, representing the system's evolving interaction structure. Earlier studies have demonstrated that dynamic interaction networks are valuable tools for examining how environmental change affects ecological communities and for providing early indicators of large-scale ecosystem shifts (Merz et al., 2023; Zhang et al., 2024).

We analyzed the properties of the plankton information networks at both community and system levels. At the community level, we grouped network nodes into five trophic categories – autotrophs, mixotrophs, herbivores, omnivores, and carnivores – and examined how interaction types and directionality varied among them. We distinguished two interaction types: trophic strengths, representing predator–prey relationships, and hybrid strengths, involving both predation and competition (e.g., mixotrophs can both prey on and compete with autotrophs). To assess directionality, we quantified top-down strengths, representing edges from grazers to primary producers, and bottom-up strengths, representing edges from primary producers to grazers.

At the system level, we aimed to capture the overall organization and dynamics of the network beyond trophic categories. To gain a more holistic perspective on the system dynamics, we adopted the perspective of the adaptive cycle metaphor (Gunderson and Holling, 2002). According to this conceptual model of change, system development is shaped by three systemic variables: its potential available for change (here approximated by the total system throughput); its connectedness, i.e., the internal controllability among its components and processes; and its resilience in light of unpredicted shocks.

In this framework, the interplay of these variables defines four sequential phases of system development: exploitation, conservation, release, and reorganization. While a particularly high connectedness and low resilience indicate a late conservation phase – during which the system is highly efficient but also highly vulnerable – low connectedness and high resilience characterize the reorganization phase, when internal organization and the cost of failure are low. By repeatedly running through these phases, systems alternate between growth and stability in the first two phases and change and unpredictability in the latter two. This alternation is key to the adaptive capacity of complex systems in changing environments.

Earlier studies have demonstrated the value of this framework in assessing ecosystem dynamics (Schrenk et al., 2022b), including those of plankton communities in the Baltic Sea (Angeler et al., 2016). In this study, we followed the conceptualization of the adaptive cycle suggested by zu Castell and Schrenk (2020) and Schrenk et al. (2022a), who used Schreiber's transfer entropy to estimate networks of information transfer. These networks then served as the basis for calculating potential, connectedness, and resilience via information-theoretical and spectral graph-theoretical measures, respectively.

To investigate how these community- and system-level properties respond to environmental variability, we related them to several environmental factors–sea surface temperature, salinity, Secchi depth, and nutrient concentrations and ratios–using change point analysis, correlations, and multivariate S-maps. S-maps is a time series prediction algorithm that applies locally weighted linear regression to reconstructed state spaces, enabling to capture nonlinear dynamics and forecast how environmental changes influence network behavior over time (Sugihara et al., 1994; Dixon et al., 1999; Deyle et al., 2016; Sugihara et al., 2012; Chang et al., 2017).

While we included a broad set of environmental variables to comprehensively capture the main physical, chemical, and optical drivers of the system, our specific hypotheses focus on the key mechanisms identified in earlier studies of similar plankton systems. Based on this evidence, we hypothesize that (i) hybrid interaction strengths will dominate over trophic strengths over the long term under increasing sea surface temperatures and decreasing resources, such as light and nutrients. This expectation arises from the anticipated increase in the intensification of multiple types of biotic interactions, such as competition, under these conditions (Kordas et al., 2011; Rothhaupt, 1996). We further hypothesize that (ii) bottom-up strength will prevail over top-down strength under conditions of increasing light availability and elevated nitrogen-to-phosphorus ratios. These conditions are expected to increase carbon-to-phosphorus ratios in primary producers, leading to lower food quality for zooplankton (Wiltshire et al., 2015; Di Pane et al., 2022; Boersma et al., 2015, 2008). This shift in nutrient composition can constrain zooplankton growth and reproduction, thereby amplifying the influence of bottom-up processes. Finally, based on general complex systems theory, we hypothesize that (iii) the total system throughput, its connectedness, and its resilience will indicate a decrease in the system's stability in consequence of the changing environment (Gunderson and Holling, 2002).

2. Material and methods

2.1. Study site and data

Our analyses were based on the long-term dataset from the Helgoland Roads monitoring site (54°11.30'N, 7°54.00'E) (Dummermuth et al., 2023) (https://www.pangaea.de/). This site is located approximately 60 km from the German mainland, in a channel between the main island of Helgoland and the Düne (Fig. 1). Helgoland lies in the transition zone between the coastal and offshore waters of the German Bight, a highly dynamic coastal region of the North Sea, bounded by the Netherlands and Germany to the south, and Denmark and Germany to the east. The region's hydrodynamics are complex due to the interactions of discharges from major European rivers, North Sea water, Atlantic water entering through the English Channel, and tidal and atmospheric forces (Van Beusekom et al., 2019; Rubinetti et al., 2023; Becker et al., 1992; Chegini et al., 2020). The water depth does not exceed 20 m at Helgoland Roads and the water column is continuously mixed, with salinity ranging from approximately 30 to 34, depending on the season (Wiltshire et al., 2015).

Since 1962, phytoplankton have been sampled on a work-daily basis, along with measurements of temperature, salinity, nutrient concentrations, and Secchi depth (Wiltshire et al., 2008). Phytoplankton samples were preserved in brown glass bottles using Lugol's solution (final concentration: 0.1% Lugol) (Wiltshire et al., 2015). Phytoplankton were identified to the lowest feasible taxonomic level, often to species, and counted using the Utermöhl method (Lund et al., 1958; Wiltshire and Dürselen, 2004). Nutrients were measured in a filtered subsample immediately after sampling in the laboratory using standard colourimetric methods (Grasshoff et al., 2009; Raabe and Wiltshire, 2009). The same subsample was also used to measure salinity (Raabe and Wiltshire, 2009). The Secchi depth, representing the transparency of water bodies at Helgoland Roads, was measured directly on station using a Secchi disc (Wiltshire et al., 2010). In 1974, meso- and macrozooplankton sampling was set up on three days per week (Greve et al., 2004). The sampling was done through oblique hauls with a quantitative collection device net (150 μm mesh size, aperture 17 cm, net length 100 cm) (see details on zooplankton in Boersma et al. (2015) and references therein).

This study used data collected from 2000 to 2020 to maximize taxonomic consistency and inclusiveness across taxa (Wiltshire and Dürselen, 2004). Using computational or conceptual frameworks (network models) that incorporate as many taxa as possible is crucial for accurately representing the complexity of aquatic ecosystems (D'Alelio et al., 2016; Loschi et al., 2023). Plankton communities are highly diverse, with a wide range of trophic strategies and interactions that drive essential processes like energy transfer and nutrient cycling. Simplified models might overlook these intricate relationships, leading to an incomplete understanding of ecosystem dynamics (Abarca-Arenas and Ulanowicz, 2002). By including detailed, hierarchical interactions across multiple taxonomic levels, conceptual and numerical network models can better capture the roles of specific organisms and their contributions to ecosystem functions, improving predictions of how these systems respond to environmental changes (D'Alelio et al., 2016; Loschi et al., 2023). Our analyses incorporated 74 phytoplankton and zooplankton taxa, detailed in Table A.3, exceeding the minimum threshold of 40 functional nodes necessary for ecological network studies (Abarca-Arenas and Ulanowicz, 2002).

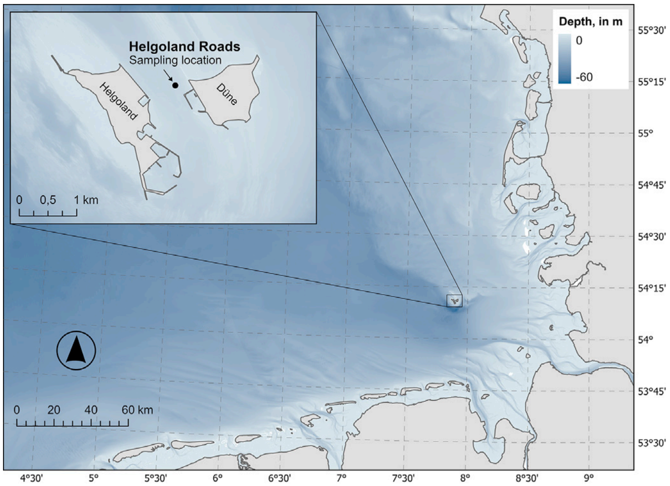


Fig. 1. Bathymetric map of the German Bight and location of the Helgoland Roads sampling location.

2.2. Data preparation

We first calculated the monthly average values for the abundance of each taxon and for each environmental parameter. This step was undertaken to smooth the data and establish a consistent time interval, which is essential for the following time series analyses (Di Pane et al., 2022). The environmental dataset included sea surface temperature (SST, °C), Secchi depth (m), salinity, and nutrient concentrations ($\mu molL^{-1}$) for silicate (SiO_4^{4-}), phosphate (PO_4^{3-}), and dissolved inorganic nitrogen (DIN), which was defined as the sum of ammonium (NH_4^+), nitrate (NO_3^-), and nitrite (NO_2^-). Dissolved inorganic nitrogen-to-phosphorus ratios (DIN:DIP) were also included and computed as monthly medians (Balkoni et al., 2023).

Each time series (taxon abundances and environmental variables) was decomposed into three components: seasonality, trend, and residual, in order to focus on general trends and avoid seasonal variations. We used the trend component of each taxon for constructing the plankton networks and the trend component of environmental parameters to investigate their relationships with the network properties (Di Pane et al., 2022). The time series decomposition was implemented using classical additive decomposition via the decompose() function in the R stats package.

2.3. Estimating interaction networks

We modeled interaction networks as networks of information transfer, which can be derived from time series of abundance data (see,

Table 1
Description of network properties and their ecological interpretation.

Level	Network property	Description	Interpretation
Community-level	Trophic strength (TR)	Sum over the average edge weight between two trophic groups in a predator–prey relationship	Information transfer between predator–prey interactions
	Hybrid strength (HY)	Sum over the average edge weight between two trophic groups in a predator–prey and competition relationship	Information transfer between predator–prey and competition interactions
	Top-down strength (TD)	Sum over the average edge weight from grazers to primary producers	Information transfer from grazers to primary producers
	Bottom-up strength (BU)	Sum over the average edge weight from primary producers to grazers	Information transfer from primary producers to grazers
System-level	Total System Throughput (TST)	Sum over all edge weights	Total interactive activity within the system
	Connectedness (Con.)	Average mutual information between in- and outflow of nodes	Degree of maturation or specialization of the network's internal structure
	Resilience (Res.)	The lowest 10% of the nonzero real parts of the eigenvalues of the network's Laplacian matrices	The amount of disturbance the system can absorb before changing its identity

e.g., zu Castell and Schrenk, 2020; Schrenk et al., 2022b). Here, network construction was based on the trend components of taxon abundances. As a measure of information transfer, we used Schreiber's *transfer entropy* (Schreiber, 2000). Denote by A and B the time series of abundances of two taxa. Transfer entropy $B \to A$ measures the amount of uncertainty about the next outcome of A that is reduced by knowledge of the past outcomes of B. Note that transfer entropy $B \to A$ does not require or imply causality between B and A (Lizier and Prokopenko, 2008). It should rather be understood as the "explanatory power" that B possesses over A. The reasons for such explanatory power can be manifold. In the context of a trophic network, for example, bad food quality can lead to an increase of explanatory power from primary producers to grazers; or high grazing pressure can be a reason for an increase in explanatory power from grazers to primary producers.

In this study, the length of the past time points of B to take into account in an estimation $B \to A$, the history length, has been set to one month. This choice is based on an analysis of the time series' "memory", which can be approached via the measure of active information storage (see, e.g., Lizier et al. (2012) and compare Fig. A.9).

We created a time series of interaction networks by estimating transfer entropy in a 36-month moving window. Each taxon defines a node in this network. Edge weights are given by the respective transfer entropy. The choice of the window size is always a trade-off: while a certain amount of data points is needed to receive statistically significant results, a very large window size may "blur" short-time effects. The main trends in the results have been shown to be stable across different window sizes (Fig. A.10).

We used the function `QtAC` from the corresponding R-package for the estimations of transfer entropy (Schrenk et al., 2022a) and tested the significance of each estimation via the built-in bootstrapping test. Every transfer entropy whose p-value exceeded a threshold of $p = 0.05$ was set to zero. Active information storage is estimated via `QtAC_AIS`. We used the built-in bootstrapping test to determine the significance of each estimation and, again, set every active information storage whose p-value exceeded a threshold of $p = 0.05$ to zero.

Since the information-theoretic estimators require the addition of a certain amount of Gaussian noise to the input data, results can vary slightly across repetitions. The results presented in this manuscript are averages of 25 repetitions of the estimation procedure.

2.4. Computing network properties

To understand community-level responses, we categorized each plankton taxon, represented as nodes in the networks, into trophic groups (autotrophs, mixotrophs, herbivores, omnivores, and carnivores, Table A.3) and modeled interaction strength between these trophic groups as the average transfer entropy between them. Average transfer entropy from one trophic group G_1 to another trophic group G_2 was computed as the sum of all transfers from taxa belonging to G_1 to taxa belonging to G_2, divided by the number of taxa in G_1 times the number of taxa in G_2. This scaling factor diminishes the influence of size effects on the interaction network. Hence, the strength of a transfer from group G_1 to group G_2 represents the average amount of information that current abundances of G_1 provide on future abundances of G_2. Fig. A.11 exemplarily illustrates this procedure for the first time step. Temporal variability of the aggregated networks is exemplarily displayed for January of each year in Fig. A.12.

Then, we computed the total (i) trophic strength (TR) as the sum of edges primarily representing predator–prey relationships (autotrophs-herbivores, autotrophs-omnivores, herbivores-carnivores, and omnivores-carnivores); (ii) hybrid strength (HY) as the sum of edges combining predation and competition (autotrophs-mixotrophs, mixotrophs-herbivores, mixotrophs-omnivores, and herbivores-omnivores); top-down strength (TD) as the sum of edges directed from grazers to primary producers (from herbivores to autotrophs and from omnivores to autotrophs); and bottom-up strength (BU) as the sum of edges directed from primary producers to grazers (from autotrophs to herbivores and from autotrophs to omnivores) (Table 1). We then derived relative strengths, expressed as the ratios of total trophic to hybrid strength (TR/HY) and top-down to bottom-up strength (TD/BU), to compare the proportional contributions of different interaction types. Relative interaction strengths are ecologically more meaningful than absolute values (Gasparini and Castelt, 1997; D'Alelio et al., 2019; Mitra, 2024), therefore, the subsequent analyses primarily focus on these relative measures.

Additionally, for a more holistic assessment of the system dynamics, we considered three systemic properties which have been identified as drivers of system maturation in the adaptive cycle framework (Gunderson and Holling, 2002): a system's potential (here approximated via the total system throughput), its connectedness, and its resilience. We estimated these properties on base of the interaction network of taxons (Table 1).

Connectedness has been defined as the degree of "maturation" or "specialization" of a system's internal structure (Gunderson and Holling, 2002). Translated to a system's interaction network, connectedness can be understood as the level of "concentration" of edge weight and the efficiency of pathways. This property is typically quantified via the expected mutual information between the outflow of one node and the inflow of another node in the network, scaled by the sum over all edge weights –known as total system throughput (TST) (Ulanowicz et al., 2009). Here, we considered these two factors separately. This allowed us to isolate the topological component of connectedness from the strong influence of TST. As isolated measure, the latter can be understood as total "interactive activity".

A system's resilience has been heuristically defined as the amount of disturbance that a system can absorb before changing its "identity" (Gunderson and Holling, 2002). This concept has been transferred to interaction networks by measuring the vulnerability of existing

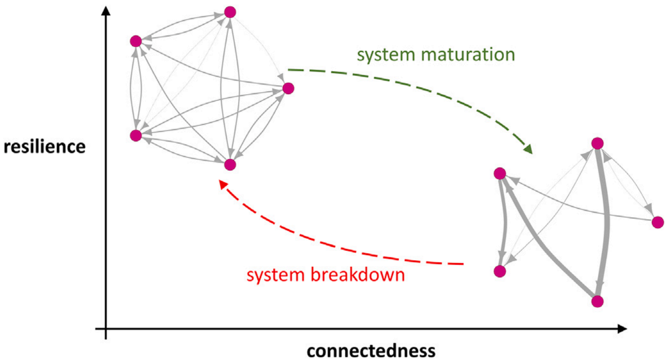


Fig. 2. The interaction structure of a complex system typically alternates between phases of high connectedness and low resilience ("mature" phases) and phases of low connectedness and high resilience (ready for reorganization after system "breakdown"). After a system breakdown, edge weights in the interaction network become more evenly distributed, with most pathways maintained through alternative routes. In the mature stage, the total edge weight is more "concentrated", differences between edge weights are larger, and there is not much redundancy (no "safety net").

pathways towards the loss of single edges (zu Castell and Schrenk, 2020). As a quantification of this property, the smallest non-zero real part of the eigenvalues of the network's Laplacian matrices were suggested (Schrenk et al., 2022a). Here, we slightly modified this definition to take into account not only the smallest eigenvalue but the lowest ten percent of the non-zero real parts. This modification turns resilience –originally prone to estimating artifacts due to its locally defined nature– into a more stable measure (see Fig. A.13 for a direct comparison of the classical and our modified version of the resilience indicator). Fig. A.14 demonstrates the stability of resilience with respect to the chosen percentage of the spectrum.

During the classical maturation process of a complex system, as conceptualized in the adaptive cycle metaphor, connectedness and resilience act largely as counterparts (see, e.g., Holling, 2001; Gunderson and Holling, 2002). The increase in efficiency and specialization in a system's interaction structure typically goes along with a decrease in redundancy and flexibility and therefore comes at the cost of resilience. A system "breakdown" is characterized by a sudden decrease in connectedness and a simultaneous increase in resilience. The prevailing randomness and redundancies provide the basis for the subsequent reorganization of the interaction structure. See Fig. 2 for an illustrating example of the topology of a high-connectedness-low-resilience network and vice versa. Note that in the context of the adaptive cycle metaphor, the term "breakdown" does not describe a total collapse of a system. It instead refers to a (partial) decomposition of the current interaction structure and does not necessarily become apparent in metrics like carrying capacity or diversity.

2.5. Relationships between network properties and environmental parameters

Understanding the response of plankton communities to environmental perturbations is particularly challenging in coastal zones, where environmental variables act and interact across a variety of spatial and temporal scales (Hewitt et al., 2016). In these dynamic systems, interactions between environmental variables and nonlinear ecological responses are likely ubiquitous (Hewitt et al., 2016; Allen and Polimene, 2011). Traditional linear statistical approaches can obscure correlations between variables in such studies, making non-parametric methods more suitable (Dixon et al., 1999; Sugihara et al., 2012; Chang et al., 2017).

This study explored the relationships between network properties and environmental parameters in three steps. First, we detected potential change-points (years) in both the environmental parameters (trends) and the network properties to identify common years of change. We applied Pettitt's test, which identifies a change-point in a time series when two periods have different averages (PETTrrr, 1979). The results were evaluated for significance at the 5% level ($\alpha = 0.05$). Both Pettitt's and the significance tests were implemented using the pyHomogeneity package in Python.

Next, we examined the relationships between plankton network properties and each environmental parameter using Spearman's rank correlation coefficient to assess linear relationships. The trend component of the environmental parameters were averaged using 36-month moving windows, to match the temporal scale of the modeled network properties. Due to the presence of temporal autocorrelation in several time-series variables, the significance testing procedure for correlations was conservatively adjusted (Pyper and Peterman, 1998). This adjustment involved reducing the effective degrees of freedom, which consequently increased the p-values in accordance with the degree of autocorrelation. Autocorrelation was tested using the ACF function from the statsmodels.tsa module, and Spearman's correlation was computed using the spearmanr function from scipy.stats in Python.

Lastly, to understand the interactive effects between pairs of environmental variables on plankton network properties and the degree of non-linear responses, we employed multivariate S-maps (Merz et al., 2023; Sugihara et al., 1994; Dixon et al., 1999; Deyle et al., 2016). S-map is a time series prediction algorithm within the framework of Empirical Dynamic Modeling (EDM). The underlying idea is to reconstruct the state space of a system based on local, linear estimates by computing local, weighted linear regressions (Deyle et al., 2016). Doing so, the method overcomes the limitations of traditional (linear) statistical methods, in particular in cases where the attractor has a highly non-linear geometry (Sugihara et al., 1994, 2012; Dixon et al., 1999; Chang et al., 2017). Localization in S-maps is using the weight function

$$w = \exp\left(-\theta \frac{d}{D}\right),$$

where d is the distance from the query point to the given data, D is the average distance given by the data, and θ is a localization parameter (https://sugiharalab.github.io/EDM_Documentation/SMap_Demo/). The θ parameter controls the weighting strength balancing between global tendencies ($\theta = 0$ enforcing linearity) and local control ($\theta > 0$) (https://ha0ye.github.io/rEDM/articles/rEDM.html).

We implemented the S-map models between pairs of exogenous (sea surface temperature, salinity, Secchi depth) and endogenous (nutrient concentrations and ratios) parameters using rEDM (v.0.7.5) (Merz et al., 2023). While Secchi depth can be influenced by increasing phytoplankton biomass in the water column, studies at Helgoland Roads have shown that this impact is negligible, and Secchi depth primarily serves as a surrogate for light availability (e.g., Wiltshire et al., 2015). Therefore, we treated Secchi depth as an exogenous environmental factor. We calculated the variance for each S-map by determining the standard deviation across 100 predictions. We selected 100 values for each environmental parameter, ranging from the minimum to the maximum values of the averaged time series within 36-month moving windows. Similar to Merz et al. (2023), the exclusion radius was set to 12 to minimize high temporal autocorrelation, and θ was selected to maximize the predictive skill (ρ) varied over a list of values ranging from 0 to 8.

The degree of nonlinearity was measured by $\Delta\rho$, i.e., the average estimation error between the nonlinear model (when $\theta > 0$) and the linear model (when $\theta = 0$) (Dixon et al., 1999). Values of $\Delta\rho$ above zero indicated non-linear dynamics, whereas values of $\Delta\rho$ near zero suggested linear relationships. A high and positive $\Delta\rho$ indicates an expected significant improvement in predictability building on non-linear state-dependent dynamics. $\Delta\rho$ values closer to 1 represent a greater improvement. Here, we focused only on the pairs of variables which provided the most significant improvement in predicting the network properties (i.e., $\Delta\rho$ values closer to 1). To assess the response of the system's interaction structure to variations in environmental parameters, we considered only pairs that showed an increase in predictive skill for all systemic measures: total system throughput (TST), connectedness, and resilience.

3. Results

In our analyses, we focused on three aspects of the plankton networks: (i) the type of interactions, (ii) the directionality of interactions, and (iii) systemic measurements. The first two aspects were explored using a conceptual trophic network through the estimation of the ratio of trophic strength to hybrid strength (TR/HY) and the ratio of top-down to bottom-up strength (TD/BU). The third aspect was investigated from properties estimated directly from the taxon networks (i.e., each node represents a taxon) and included total system throughput (TST), connectedness, and resilience. Our results indicated that all network properties derived from both the conceptual trophic networks and the taxon networks exhibited variability over time, displaying distinct trends during different periods. These properties responded to environmental factors in both linear and non-linear ways, with Secchi depth, nutrient availability, and salinity emerging as key predictors of the system. In the following sections, we will first describe the environmental conditions at Helgoland Roads and their potential links to the temporal variation of plankton network properties. Next, we will present the results of the correlation analysis. Finally, we will present the results of the interactive effects between pairs of environmental variables on plankton network properties.

3.1. Environmental parameters and plankton network properties

Our analyses showed that both sea surface temperature (SST) and salinity have exhibited higher levels and reduced variability at Helgoland Roads post-2014 (Fig. 3). During the same period, dissolved inorganic nitrogen (DIN) and phosphate (PO_4^{3-}) concentrations and their ratios (DIN:DIP) decreased, with the ratio falling well below the Redfield ratio (16:1) in some years.

Secchi depth and silicate (SiO_4^{4-}) concentrations also showed a decrease in variability, with a significant change point identified in 2007 for both parameters. After 2007, Secchi depth exhibited fewer extremes, while silicate levels had an overall higher mean value than before. The identification of a common year of change between these two parameters is intriguing. Secchi depth is positively correlated with annual algal biomass in this system and serves as a proxy for light availability for algal growth at Helgoland Roads (Wiltshire et al., 2008, 2010, 2015). Meanwhile, silicate is crucial for diatom growth, and diatoms constitute over 80% of the phytoplankton biomass at Helgoland Roads (Wiltshire et al., 2015). Combined with the trend of autotrophs in our dataset (Fig. A.15), this suggests that the drop in silicate levels at the beginning of the time series may be caused by increased phytoplankton biomass. Overall, the variability across all environmental variables analyzed was notably higher at the beginning of the time series, followed by a general reduction in variability in recent years.

In general, change points in plankton network properties did not coincide with those in environmental parameters (Fig. 4). Only the top-down to bottom-up strength ratio (TD/BU) revealed a significant change point in 2007 –the same year that Secchi depth and silicate did. Bottom-up strength prevailed from 2003 to 2007, indicating that bottom-up control might be favored under conditions of higher light availability. Since then, top-down strength has intensified, with a drop in 2016. An opposite overall pattern was observed for the trophic to hybrid strength ratio (TR/HY), with a significant change point one year before (2006). The strength of trophic links within the plankton networks was highest in 2004 and 2014. Then, the TR/HY ratio decreased from 2005 to 2007 and again towards the end of the time series, from 2015 to 2019, indicating that hybrid strength prevailed during these periods.

Total system throughput (TST), connectedness, and resilience varied over time, each displaying unique temporal patterns during different periods (Fig. 4). TST showed cyclic behavior with two peaks: one at the beginning of the time series in 2005 and another in 2014, and two drops: one during 2009–2010 and another in 2016. A significant change point was identified in 2008. Connectedness was more variable, with an overall increase after 2010. Resilience showed a change point in the same year as SST and salinity (2014). However, it was not statistically significant.

3.2. Correlations between network properties and environmental parameters

Spearman's correlations revealed that the top-down relative to bottom-up strengths (TD/BU) was negatively related to Secchi depth ($r_s = -0.45$, $p_{adj} < 0.01$) and positively related to silicate levels ($r_s = 0.45$, $p_{adj} < 0.01$) (Table 2). This relationship was primarily driven by bottom-up strength, which showed the strongest correlation with Secchi depth ($r_s = 0.47$, $p_{adj} < 0.01$) (Table A.4 and Fig. A.16), indicating that bottom-up strength dominated under conditions of higher light availability. The negative relationship between bottom-up strength and silicate ($r_s = -0.44$, $p_{adj} < 0.01$) (Table A.4 and Fig. A.16) is likely due to the reverse relation of autotrophs with silicate levels (see Section 3.1).

The trophic relative to hybrid strengths (TR/HY) was positively related to Secchi depth ($r_s = 0.32$, $p_{adj} < 0.01$) and negatively related to silicate levels ($r_s = -0.26$, $p_{adj} < 0.01$). We found that both trophic and hybrid strengths were positively related to Secchi depth; however, trophic strength had the strongest correlation coefficient ($r_s = 0.66$, $p_{adj} < 0.01$) (Table A.4 and Fig. A.16), indicating that trophic links in the plankton networks strengthen significantly under higher light availability. Regarding silicate, both trophic and hybrid strengths decreased under higher concentrations. However, the correlation between silicate and trophic strength ($r_s = -0.53$, $p_{adj} < 0.01$) was stronger than that for hybrid strength ($r_s = -0.28$, $p_{adj} < 0.01$), indicating that trophic links prevailed under low silicate levels (Table A.4 and Fig. A.16).

We also found a moderate negative correlation between the TR/HY strength ratio and salinity ($r_s = -0.51$, $p_{adj} < 0.01$) (Table 2). Total system throughput (TST) and TD/BU strength were also related to salinity. TST showed a weak but significant negative relationship ($r_s = -0.34$, $p_{adj} < 0.01$), while TD/BU strength was positively related to salinity ($r_s = 0.32$, $p_{adj} < 0.01$), suggesting that under high salinity levels, bottom-up strength decreased (Table A.4).

Weak positive relationships were identified between both nitrogen and phosphate concentrations and TR/HY strength and TST, whereas the relationship between these nutrients and TD/BU strength was weakly negative (Table 2). Increases in sea surface temperature were associated with decreases in TR/HY strength ($r_s = -0.39$, $p_{adj} < 0.01$) and in TST ($r_s = -0.21$, $p_{adj} < 0.01$) (Table 2). We did not identify any significant relationships for connectedness and resilience.

3.3. Interactive effects and nonlinear responses

To explore the interactive effects of environmental factors on plankton networks, we examined the degree of nonlinearity between pairs of environmental parameters (exogenous vs. endogenous) and modeled their interactive effects on the network properties using S-maps. We assessed these effects using the predictive skill improvement ($\Delta\rho$) and the optimal parameter value (θ) (Table A.5). $\Delta\rho$ values closer to 1 represent greater improvement. For community-level responses, we focused on TR/HY and TD/BU ratios, examining the interplay of parameters with the highest $\Delta\rho$ value. To evaluate how the system's interaction structure

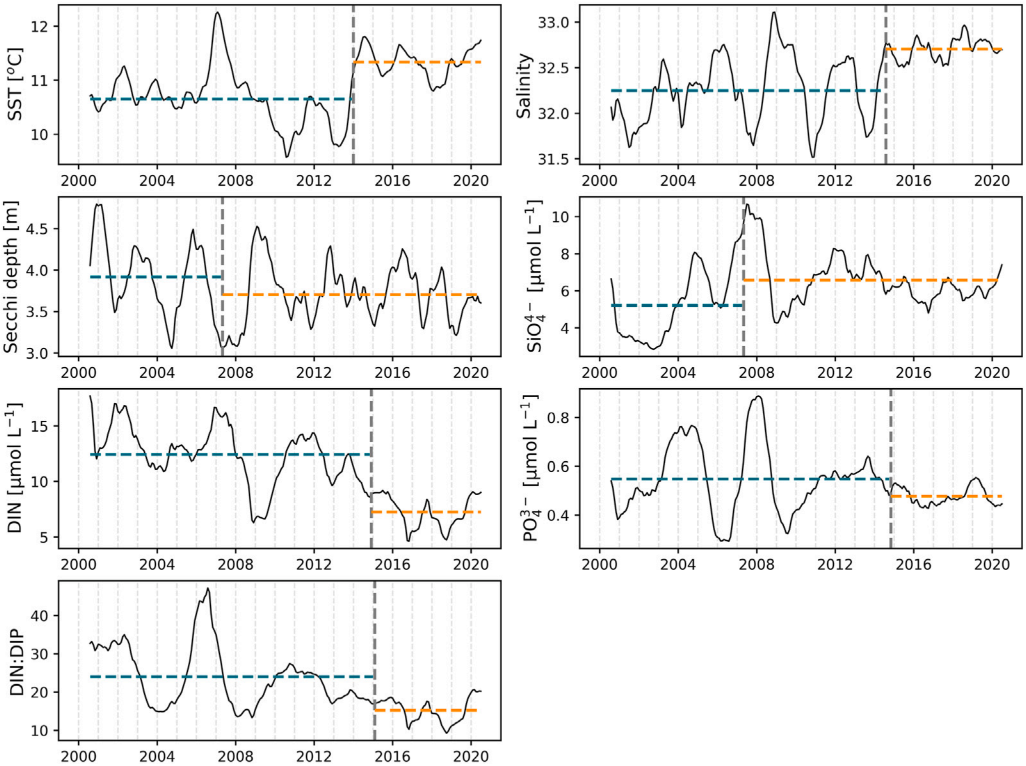


Fig. 3. Trends in environmental parameters at Helgoland Roads from 2000 to 2020. Vertical dashed lines mark statistically significant ($p<0.05$) change points identified by the Pettitt's test. Horizontal dashed lines represent the mean values of each parameter before and after the change point, depicted in green and orange, respectively.

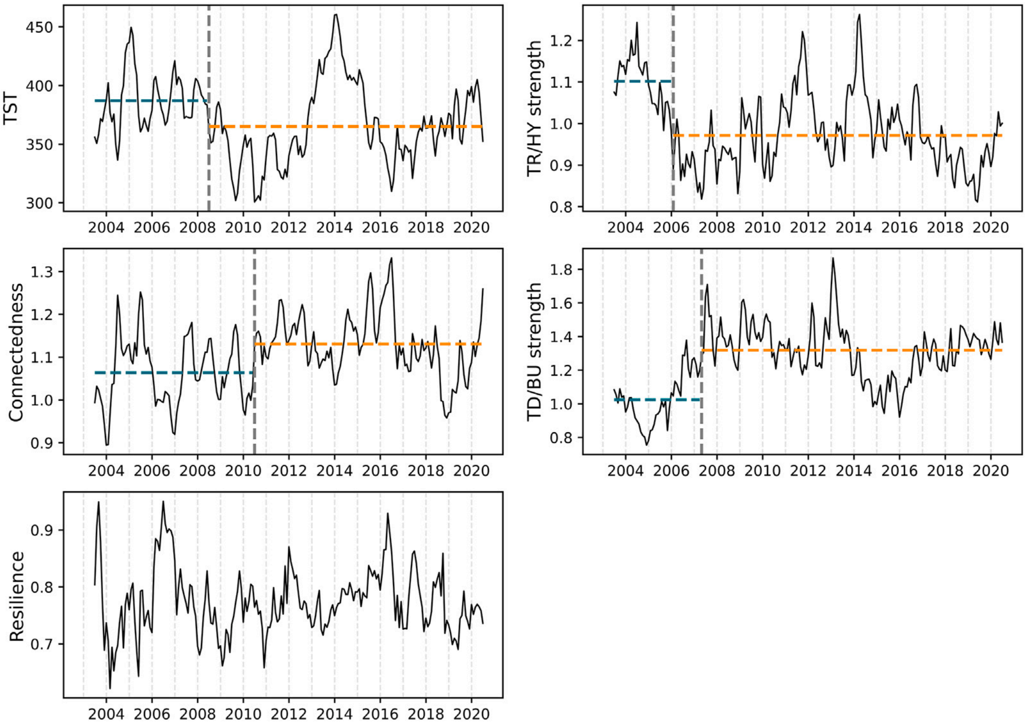
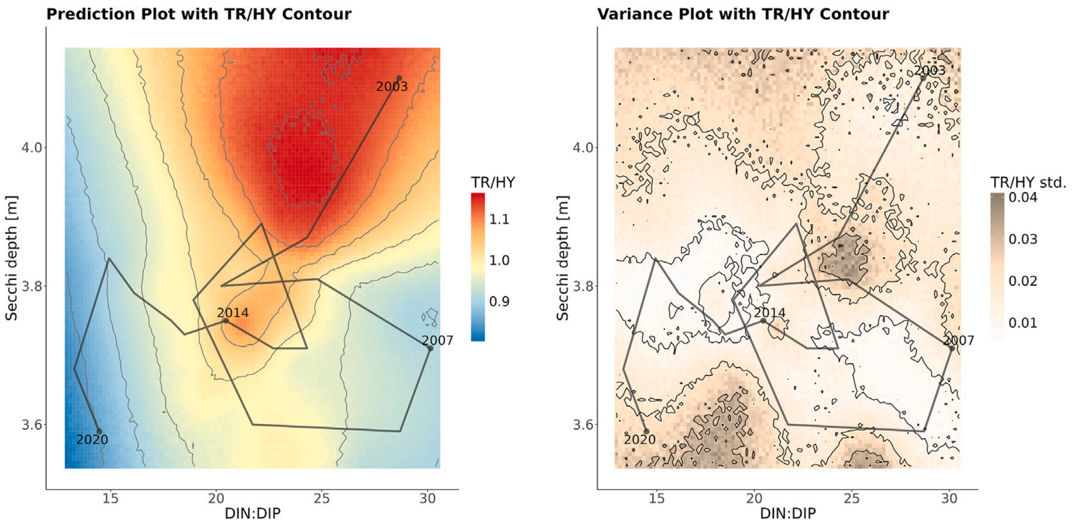


Fig. 4. Plankton network properties - total system throughput (TST), connectedness, resilience, trophic to hybrid (TR/HY) strength ratio, and top-down to bottom-up (TD/BU) strength ratio - estimated within 36-month moving windows from 2000 to 2020. Vertical dashed lines mark statistically significant ($p<0.05$) change points identified by the Pettitt's test. Horizontal dashed lines represent the mean values of each parameter before and after the change point, depicted in green and orange, respectively.

Table 2
Spearman's rank correlation coefficients (r_s) and adjusted p-values (p_{adj}) for plankton network properties and environmental parameters. Abbreviations: trophic relative to hybrid strength (TR/HY), top-down relative to bottom-up strength (TD/BU), total system throughput (TST), sea surface temperature (SST), silicate (SiO_4^{4-}), dissolved inorganic nitrogen (DIN), phosphate (PO_4^{3-}), dissolved inorganic nitrogen-to-phosphorus ratio (DIN:DIP).

	SST		Salinity		Secchi depth		SiO_4^{4-}		DIN		PO_4^{3-}		DIN:DIP	
	r_s	p_{adj}	r_s	p_{adj}	r_s	p_{adj}	r_s	p_{adj}	r_s	p_{adj}	r_s	p_{adj}	r_s	p_{adj}
TR/HY	**−0.39**	**<0.01**	**−0.51**	**<0.01**	**0.32**	**<0.01**	**−0.26**	**<0.01**	**0.26**	**<0.01**	**0.23**	**<0.01**	**0.19**	**<0.01**
TD/BU	0.14	0.15	**0.32**	**<0.01**	**−0.45**	**<0.01**	**0.45**	**<0.01**	**−0.19**	**0.02**	**−0.32**	**<0.01**	−0.04	1.00
TST	**−0.21**	**0.01**	**−0.34**	**<0.01**	−0.15	0.11	0.12	0.28	**0.34**	**<0.01**	**0.28**	**<0.01**	**0.21**	**0.01**
Connectedness	−0.15	0.09	0.01	1.00	−0.12	0.27	0.07	0.90	−0.17	0.04	−0.09	0.60	−0.14	0.11
Resilience	−0.08	0.67	0.08	0.58	0.11	0.26	0.02	1.00	−0.07	0.79	−0.06	1.00	−0.01	1.00



(a)

(b)

Fig. 5. (a) S-maps demonstrating the interactive effects of Secchi depth and dissolved inorganic nitrogen-to-phosphorus (DIN:DIP) ratios on trophic relative to hybrid strength (TR/HY). (b) Standard deviation of predicted TR/HY strength, estimated among 100 model predictions. The black solid lines on the s-maps show the annual averages of Secchi depth and DIN:DIP, indicating the directionality of time and the status of the predicted variable through the years. Years identified as significant change points in the environmental parameter trends using Pettitt's test have been displayed on the trajectories.

responds to environmental parameter variations, we focused solely on those pairs that exhibited an enhanced predictive ability across all systemic measures –total system throughput (TST), connectedness, and resilience.

3.3.1. Hybrid strength prevailed over trophic strength under low Secchi depth and DIN:DIP below the Redfield ratio

We found that the highest $\Delta\rho$ for TR/HY strength occurred with the combination of Secchi depth and the DIN:DIP ratio ($\Delta\rho = 0.54$ and $\theta = 3$, Table A.5). The S-map model predicted a maximal trophic to hybrid relation at higher Secchi depth and DIN:DIP ratios approximately between 20 and 25, while hybrid strength intensified under lower Secchi depth combined with DIN:DIP ratios well below 16:1 (Fig. 5(a)). The model demonstrated low uncertainty in predicting the trophic relative to hybrid strength for the combination of Secchi depth and DIN:DIP ratios (Fig. 5(b)).

Past trajectories from 2003 to 2010 indicate that Helgoland Roads shifted from a system where trophic strength prevailed in 2003 to one where hybrid strength has intensified in 2020. This change became particularly evident after the decrease in Secchi depth in 2007. Further reductions in Secchi depth in 2020, along with a decrease in the DIN:DIP ratio below 16, appear to be linked to the dominance of hybrid strength.

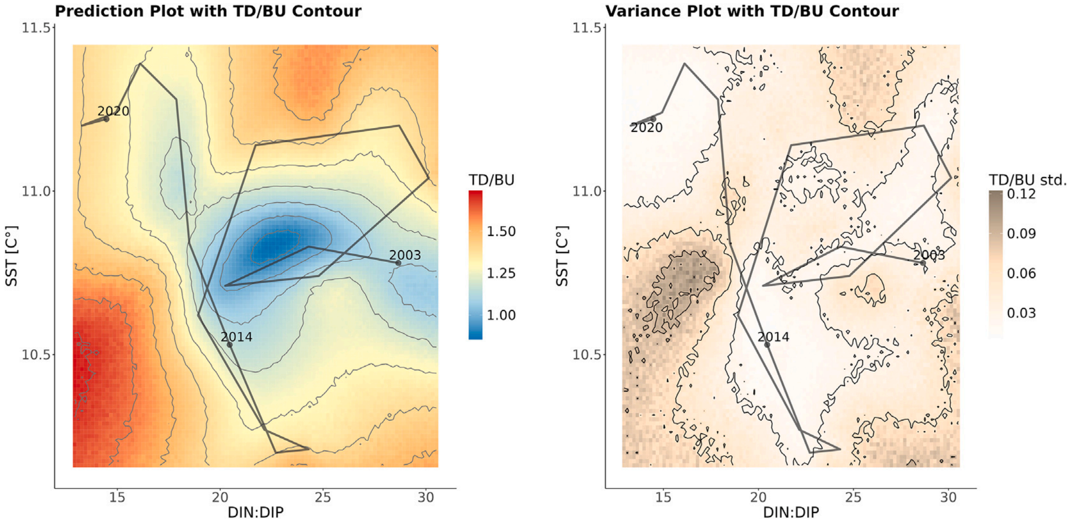
3.3.2. Bottom-up relative to top-down strength was intensified under intermediate temperature and DIN:DIP above the Redfield ratio

The interaction between SST and DIN:DIP ratios exhibited substantially non-linear effects ($\Delta\rho = 0.88$ and $\theta = 4$, Table A.5) on TD/BU, again indicating the presence of nonlinear dynamics. The S-map model showed that bottom-up strength prevailed over top-down strength under intermediate temperatures and DIN:DIP ratios between 20 and 25 (Fig. 6(a)), demonstrating low uncertainty (Fig. 6(b)). This pattern appeared to be mediated primarily by SST and nitrogen (DIN) rather than SST and phosphate (PO_4^{3-}) levels (see the high $\Delta\rho = 0.72$ for SST and DIN in Table A.5 and Fig. A.17a). However, the interplay between both nitrogen and phosphate provided the best improvement in predictive skill ($\Delta\rho$), highlighting the importance of the balance between these two nutrients.

In general, we observed that bottom-up strength intensified at intermediate temperatures, approximately between 10.5°C and 11°C, for all nutrients (nitrogen, phosphate, and silica) (Fig. A.17). Top-down strength appeared to intensify under both higher and lower sea surface temperatures within the range of 10°C to 11.5°C and primarily depended on DIN:DIP variations. Past trajectories showed that bottom-up strength prevailed over top-down strength at Helgoland Roads in 2003, but these strengths have diminished by 2020.

3.3.3. The system was more sensitive to nutrient availability under high levels of salinity

Both connectedness and TST showed strong nonlinear responses to changes in salinity and availability of silicate, phosphate, and nitrogen (Fig. 7, Fig. A.18, Table A.5). Based on the change point analysis of environmental variable trends (see Fig. 3), we distinguished two different regimes: the lower-salinity regime, characterized by salinity oscillations, and the high-salinity regime, which started in 2015, when



(a)

(b)

Fig. 6. (a) S-maps demonstrating the interactive effects of sea surface temperature (SST) and dissolved inorganic nitrogen-to-phosphorus (DIN:DIP) ratios on top-down relative to bottom-up strength (TD/BU). (b) Standard deviation of predicted TD/BU strength, estimated among 100 model predictions. The black solid lines on the s-maps show the annual averages of SST and DIN:DIP, indicating the directionality of time and the status of the predicted variable through the years. Years identified as significant change points in the environmental parameter trends using Pettitt's test have been displayed on the trajectories.

salinity stabilized at a higher plateau. Remarkably, the same patterns in connectedness and total system throughput were observable for the interplay of salinity and all three types of nutrients: The S-map models predicted overall low levels of total system throughput during the higher-salinity regime. With absolutely small changes in edge distribution having proportionally large impact on the overall structure, a system of such low levels of interactive activity is naturally prone to quick shifts between extreme system states. And indeed, connectedness was estimated to be very sensitive to nutrient availability during this regime. In other words, a slight change in the concentrations of silicate, phosphate, or nitrogen could lead to a strong reduction or increase in connectedness.

As illustrated in Fig. 2, strong increases or decreases in connectedness are usually an indicator of system maturation or breakdown, respectively. In order to better understand the predicted system changes in the high-salinity regime, we need to consider the system's resilience as well (Fig. 8, Fig. A.19). In the case of silicate, connectedness and resilience showed a typical antagonistic behavior: while in 2020, a slight increase in the availability of silicate might result in a strong increase in connectedness and decrease in resilience, a small decrease in silicate could lead to a strong decrease in connectedness and a simultaneous increase in resilience. According to the adaptive cycle framework, the latter is characteristic of a typical system breakdown in the sense of the adaptive cycle metaphor (Gunderson and Holling, 2002): the formerly efficient, specialized interaction structure dissolves in favor of a more random structure, characterized by unpredictable fluctuations and redundancies, allowing the system to reorganize and adapt to the new environmental conditions. Hence, in this sense, such a breakdown can be considered as "constructive". The same pattern, although not as clear, was visible in the case of phosphate. For higher levels of salinity and a moderate phosphate level, a small increase in phosphate might lead to a typical system breakdown, while a small decrease in phosphate could result in a system maturation.

In the case of nitrogen, the situation was clearly different: connectedness and resilience showed the same behavior with respect to changes in nitrogen availability. Here, the system breakdown resulting from a slight increase in nitrogen is characterized by a substantial decrease in both connectedness and resilience. More precisely, although the system loses its specialized structure during the breakdown, no redundancies and thereby adaptive capacities are build up, making it more difficult for the system to reorganize and restart the maturation process. Hence, once could classify this scenario as "destructive" breakdown.

Interestingly, network properties relating to bottom-up (BU) and top-down (TD) strength showed significant non-linear responses to the interplay of salinity and nutrient availability in all three cases (Fig. 8, A.5). This not only suggested a crucial role of vertical control mechanisms in system dynamics, it also allowed us to gain further insight into the possible effects of the system's sensitivity to nutrients. In the case of silicate, the system maturation resulting from a slight increase in silicate was accompanied by a strong decrease in top-down strength. Similarly, the maturation process resulting from a slight decrease in phosphate was characterized by a decrease in the TD/BU ratio. During the atypical maturation process, initialized by a slight increase in nitrogen, top-down strength was also predicted to decrease. These observations indicate that immature systems are strongly driven by top-down trophic interactions, while more mature, optimized systems are characterized by lower top-down strength. This finding was further supported by the strong negative correlation (r_s=-0.59, p_{adj} < 0.01) between top-down strength and connectedness (compare Fig. A.20).

4. Discussion

Understanding how plankton network dynamics respond to environmental drivers is essential for predicting the consequences of environmental change on ecological communities (D'Alelio et al., 2016; Merz et al., 2023; Loschi et al., 2023). While significant progress has been made in recent years (Merz et al., 2023; Zhang et al., 2024; Trombetta et al., 2021; Loschi et al., 2023), the long-term responses of plankton interaction networks to multiple environmental stressors, particularly in dynamic coastal and estuarine ecosystems, remain poorly understood. To address this knowledge gap, we analyzed plankton interaction networks in the German Bight, focusing on three aspects of the network: (i) interaction types (trophic and hybrid strengths), (ii) directionality of trophic and hybrid interactions (top-down and bottom-up strengths), and (iii) systemic properties of the network (total system throughput, connectedness, resilience). Our results revealed both linear and non-linear responses of interaction strengths and systemic network measures to environmental factors, with light, nutrient availability, and salinity emerging as key drivers of system structure and sensitivity.

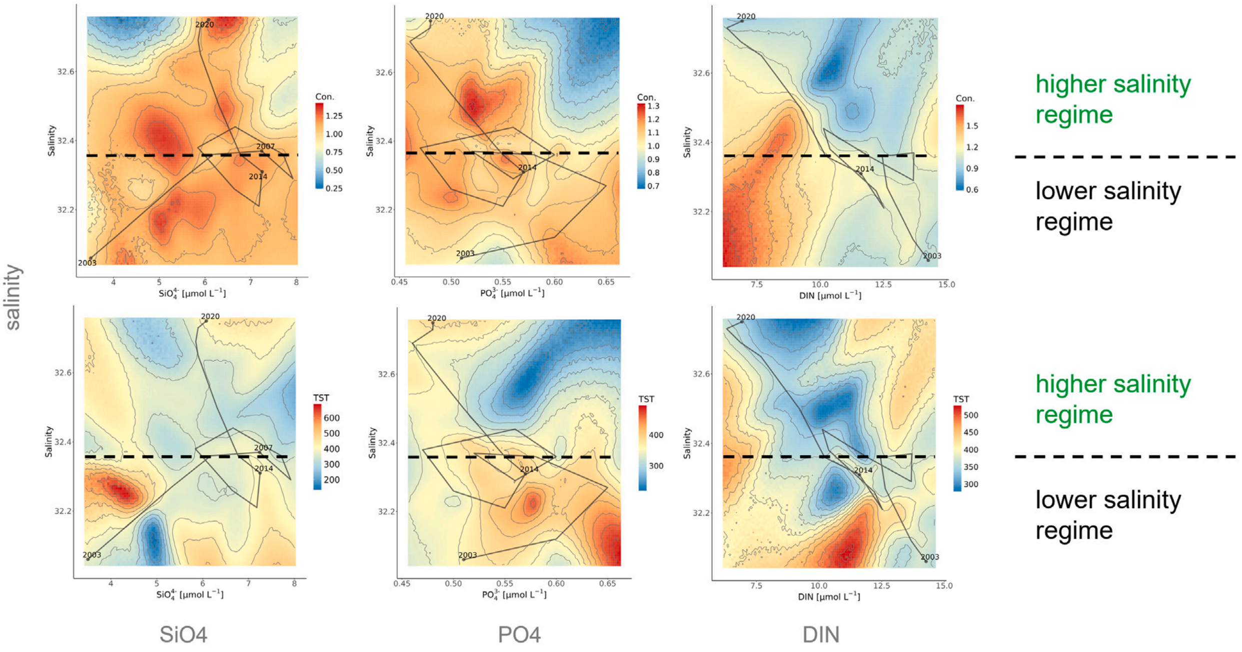


Fig. 7. Sensitivity of the system to nutrient changes during higher salinity regime. S-maps displaying the non-linear effects of salinity and availability of silicate (SiO_4^{4-}), phosphate (PO_4^{3-}), and dissolved inorganic nitrogen (DIN) on both connectedness (Con.) and total system throughput (TST). The dashed line separates the lower-salinity from the higher-salinity-regime.

4.1. *Trophic and hybrid interaction types*

Plankton species engage in a wide range of interactions, including trophic, non-trophic, and hybrid types, which together influence community structure (D'Alelio et al., 2016; Trombetta et al., 2021; Merz et al., 2023; Zhang et al., 2024). These interaction types within a plankton network can vary in response to changes in per capita interaction strengths (Kordas et al., 2011; D'Alelio et al., 2016; Merz et al., 2023; Zhang et al., 2024). In this study, we considered trophic and hybrid interaction strengths and observed considerable temporal variability in their relative intensities (Fig. 4). The strength of trophic links within the plankton network was highest in 2004 and 2014, while hybrid links intensified during 2006–2009 and again towards the end of the time series during 2018–2020.

Our analyses revealed strong nonlinear interactions between Secchi depth and ambient DIN:DIP ratios that govern the trophic relative to hybrid strength (TR/HY) (Fig. 5(a)). Trophic strength was higher than hybrid strength at higher Secchi depth and DIN:DIP ratios above 20, whereas hybrid strength intensified under lower Secchi depth combined with DIN:DIP ratios below 15 or above 25. Correlation analyses also indicated that hybrid strengths dominated over trophic strengths under conditions of lower Secchi depth and lower nitrogen and phosphorus concentrations (Table 2). Lower Secchi depth is an indicator of reduced light availability at Helgoland Roads (Wiltshire et al., 2015). These results suggest that as resource availability decreases, interactions among (i) mixotrophs and autotrophs, (ii) mixotrophs and herbivores, and (iii) mixotrophs and omnivores, as well as between (iv) herbivores and omnivores, become more intense. The population dynamics of these groups are more tightly linked, with stronger influences of one group on another. This is expected, as reduced resource availability can intensify competition for resources such as light, nutrients, and prey (Merz et al., 2023; Rothhaupt, 1996; Litchman et al., 2015; Lombard et al., 2010), leading to heightened hybrid strengths over trophic strengths. However, it is important to note that increased hybrid interaction strength does not necessarily reflect competition alone but rather a broader intensification of multiple biotic interaction types among plankton groups under low-resource conditions. The observed intensification of hybrid interactions may arise not only from increased competition for shared resources but also from enhanced predation (Rothhaupt, 1996; Delaney, 2003; Stelzer, 1998). For instance, resource limitation has been shown to amplify competition and sequentially shift interactions among species, such as ciliates and appendicularians, from competition to predation (Lombard et al., 2010).

Temperature is a critical environmental factor influencing interaction types (Merz et al., 2023; Trombetta et al., 2021; Kordas et al., 2011; Delaney, 2003). Warming can enhance trophic cascades by accelerating metabolic rates and organism growth (Kordas et al., 2011). However, its effects are often context-dependent, as temperature influences multiple factors simultaneously, including species-specific thermal tolerances, resource availability, community composition, and the balance between primary production and consumption rates (Trombetta et al., 2021). For example, a long-term study in several Swiss lakes found that while hybrid and trophic interaction strengths generally decreased with warming, some lakes showed increases during the same period (Merz et al., 2023). In our study, light and nutrient availability emerged as more critical drivers than temperature. We found weak positive relationships between hybrid strengths and SST, partially supporting our hypothesis (i) that increasing temperatures and lower nutrient availability would intensify hybrid links. The weak relationship between interaction strengths and SST (Table A.4) in our analysis may be due to the narrow range of SST values (Fig. 3). This was because we analyzed only the trend component of the time series and further averaged it using a 36-month moving window to match the network properties. Analyzing a longer time period could help maintain a broader range of SST and reveal stronger temperature effects (Merz et al., 2023). Nevertheless, the importance of light in pelagic, highly dynamic environments is well recognized (Wiltshire et al., 2015; Loschi et al., 2023; Loebl et al., 2009; Capuzzo et al., 2015), and our results emphasize its role in shaping plankton interactions and ecosystem dynamics.

4.2. *Top-down and bottom-up trophic control*

By analyzing dynamic interaction networks from monthly abundance data of 74 plankton taxa at Helgoland Roads between 2000 and 2020, we found that the edges from primary producers to higher

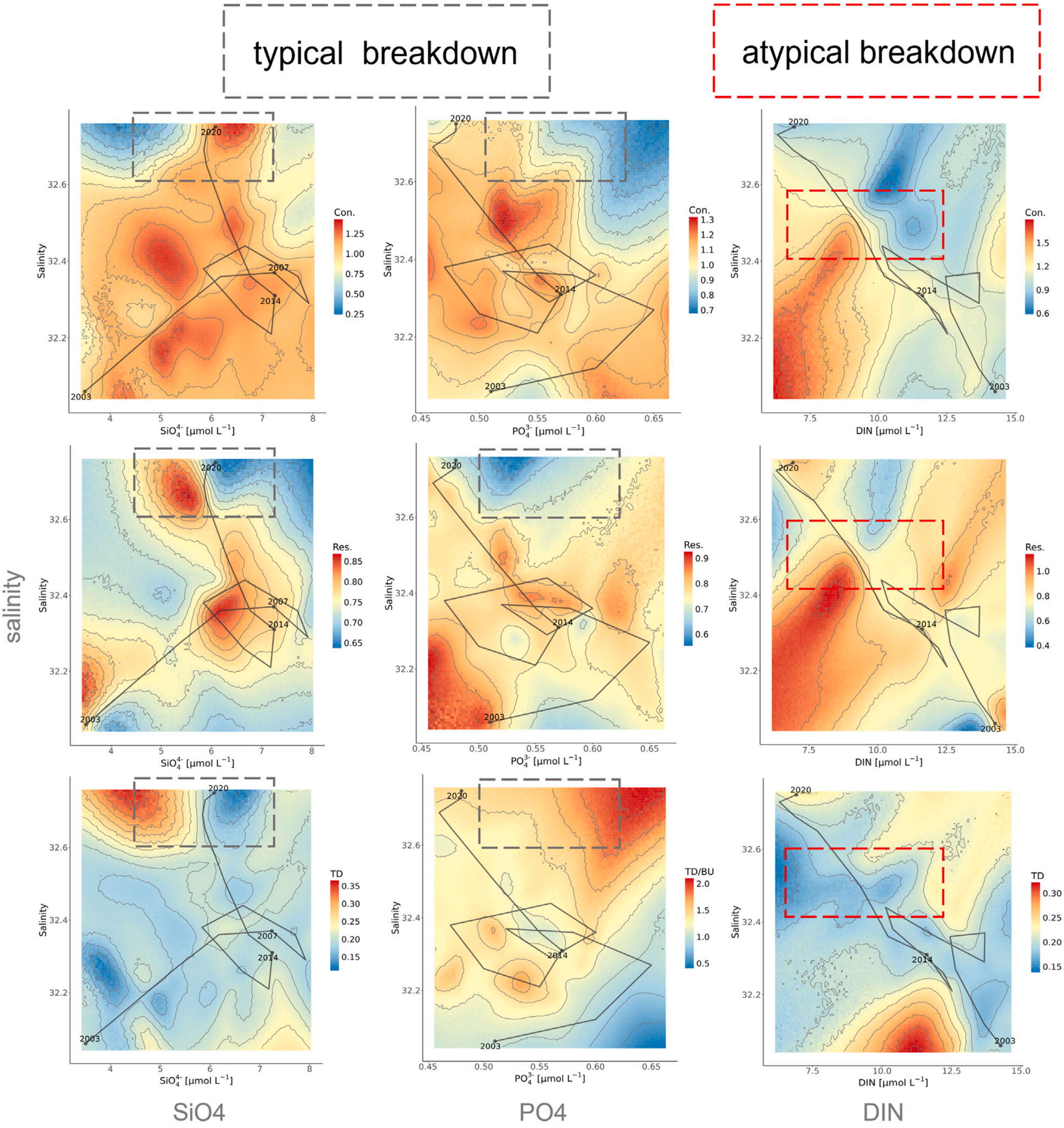


Fig. 8. Changes in nutrient concentration can lead to constructive and destructive system breakdowns during the high-salinity regime. S-maps displaying the non-linear effects of salinity and availability of silicate (SiO_4^{4-}), phosphate (PO_4^{3-}), and dissolved inorganic nitrogen (DIN) on connectedness (Con.), resilience (Res.), top-down strength (TD), and the ratio of top-down and bottom-up strength (TD/BU). Dashed boxes mark the high-sensitivity regions.

trophic levels were stronger than the reverse until 2007, suggesting bottom-up control (Fig. 4). Since then, top-down control has intensified, although it slightly weakened again after 2014.

Our analyses indicated that changes in the top-down to bottom-up ratio (TD/BU) were related to variations in light availability, nutrient ratios, and temperature, supporting our initial hypothesis (ii). Change point analysis identified significant shifts in Secchi depths and silica in 2007 (Fig. 3). Correlations showed that bottom-up strength intensified with higher Secchi depths and lower silicate levels (Fig. A.16). The first relationship is straightforward, as previous analyses have shown that Secchi depths are related to higher light availability in the water column, which is favorable for algal growth (Wiltshire et al., 2015). The negative relationship with silica can be explained by the fact that silicate dynamics were regulated by increasing algal biomass during that period (Fig. 3 and Fig. A.15). We also found that the interaction between the nitrogen-to-phosphorus ratio and SST improved the predictability of TD/BU strength. Bottom-up strength intensified under intermediate water temperatures and nitrogen-to-phosphorus ratios above the Redfield ratio of 16:1 (approximately 20 to 25), potentially indicating phosphorus-limited algae (Redfield, 1934). The increase in phytoplankton biomass due to improved light conditions, combined with reduced phosphorus concentrations relative to nitrogen, can elevate the carbon-to-phosphorus ratio (C:P) in phytoplankton biomass. This higher C:P ratio has been shown to result in food of inferior quality for zooplankton (Boersma et al., 2015; Boersma and Elser, 2006; Malzahn and Boersma, 2012). Conversely, top-down strength dominated under conditions of lower light availability, higher sea surface temperatures, and nitrogen-to-phosphorus ratios (N:P) around

15, near the Redfield ratio. This result underscores the importance of ambient N:P ratios for the nutritional quality of higher trophic levels, while phytoplankton exhibit flexibility in their nutrient uptake and do not strictly adhere to the Redfield Ratio (Hillebrand et al., 2013).

Taken together, our findings suggest that from 2000 to 2007, bottom-up control dominated the dynamics of higher trophic levels due to poor food quality. After 2007, top-down control prevailed over bottom-up control due to improved conditions favoring zooplankton growth and reduced conditions favoring algal growth, such as decreasing light availability. This is further supported by observations of the temporal dynamics of total zooplankton and fish biomass at Helgoland Roads (Di Pane et al., 2023; Marques et al., 2023). The total meso-zooplankton community experienced one of the most dramatic shifts over the past fifty years in 2007 (Di Pane et al., 2023), coinciding with the shift in our top-down relative to bottom-up time series (Fig. A.15). Specifically, it can be observed that total meso-zooplankton from 2000 to 2007 slightly decreased (see Fig. 1a in Di Pane et al., 2023). During the same period, fish biomass also showed a slight decrease (see Fig. 1 g in Marques et al., 2023). The concurrent decrease in both meso-zooplankton and fish biomass, while phytoplankton biomass increased (Wiltshire et al., 2015; Boersma et al., 2015), supports our observation of increased bottom-up strength due to bad food quality. Since 2007, total meso-zooplankton has decreased dramatically (Di Pane et al., 2023), likely due to a significant increase in fish biomass (see Fig. 1 g in Marques et al., 2023). Consequently, reduced predation on phytoplankton may lead to increased phytoplankton abundances and/or an extended growth period for phytoplankton overall (Wiltshire et al., 2015), resulting in a top-down signal in our plankton networks.

This is further supported by the study of Sguotti et al. (2022), which explored the synergistic effect of two drivers -one bottom-up (environment) and one top-down (fishing pressure)- using a stochastic cusp model in the North Sea and data from the Continuous Plankton Recorder (CPR) program. Their analyses indicated bottom-up control from 2000 to 2008, followed by top-down and then bottom-up control again (see Fig. 4 in Sguotti et al., 2022). The later shift from bottom-up to top-down control could be related to the larger spatial scale of their study, although our results are still in line.

4.3. Total system throughput, connectedness, and resilience

Between 2014 and 2015, the system's environment appears to have entered a new regime. Change point analysis reveals an increase in sea surface temperature and in salinity levels (Fig. 3). These simultaneous changes are not likely to be coincidental but rather indicative of altered hydrographic conditions in the region (Amorim et al., 2024). Over the past decade, intensified droughts in Europe (Ionita et al., 2022) have led to decreased river runoffs (Conradt et al., 2023; Kaiser et al., 2023). Consequently, less freshwater seems to be reaching the Helgoland Roads site, increasing temperature and salinity levels since then.

More striking than the concurrent change points is the fact that, subsequently, the amplitude of oscillations in all three variables significantly decreases. The new regime is characterized by stable environmental conditions - the more interesting that the system itself displays a higher "instability". This instability is particularly apparent in the strong sensitivity of profound systemic variables to nutrient availability (Fig. 7). From a system theoretical point of view, this co-occurrence of a stable environment and a highly sensitive system is conclusive. Under stable environmental conditions, a system can invest into optimization, which typically comes at the cost of its adaptive capacity (Holling, 2001; Loschi et al., 2023). These findings support initial hypothesis (iii), claiming that the systemic variables will indicate a loss of stability in consequence of the environmental changes.

Our observations further revealed that the predicted breakdowns of the system during this unstable regime are of different nature. While some slight changes in silicate and/or phosphate availability might lead to "constructive" breakdowns, likely resulting in a quick and successful adaptation to the new environmental conditions, some changes in nitrogen availability might lead to so-called "destructive" changes, during which the system loses its adaptive capacity. From a systemic view, a quick and appropriate reorganization of the system is more unlikely in this case.

The system's differing responses to the different nutrient species might be attributed to the current level of pressure as well as to the varying levels of anthropogenic share in the changes. In the German Bight, dissolved inorganic nitrogen and phosphorus levels have been significantly influenced by human activities such as population growth, industrialization, fertilizer use, and de-eutrophication strategies, whereas silicate levels have not (Van Beusekom et al., 2019). Over recent decades, both nitrogen and phosphorus levels have decreased substantially, but phosphorus reductions have been more successful, nearing thresholds for good ecological status (Heyden and Leujak, 2023). Nitrogen levels, however, remain well above these thresholds (Heyden and Leujak, 2023). Therefore, nitrogen dynamics are still strongly influenced by anthropogenic inputs, phosphorus to a lesser extent, and silicate is primarily governed by the growth of primary producers (Wiltshire et al., 2015) and re-mineralization processes. This is supported by our data, as phosphorus and silicate trends show similar patterns during 2000–2020, while nitrogen exhibits an overall decline (Fig. 3). These observations suggest that the system's coping mechanisms are more effective in light of internally regulated changes than in light of externally induces changes under high pressure.

Such examples illustrate the potential of this type of systemic analysis to find application in the evaluation and management of ecosystem change.

4.4. Limitations

In this study, we focused on a subsystem of the marine ecosystem – the planktonic community – without explicitly accounting for effects from higher or lower trophic levels. While this isolated perspective might seem restrictive, earlier studies in marine ecology and systems theory have demonstrated the validity and insightfulness of such subsystem-level analyses (e.g., Mozetič et al., 2012; Ward et al., 2013; Wiltshire et al., 2015; Angeler et al., 2016; Anneville et al., 2019; Merz et al., 2023). These approaches allow the identification of intrinsic patterns, feedbacks, and emergent properties that can serve as indicators of broader ecosystem dynamics.

From a theoretical perspective, a system can be considered as a conglomerate of nested subsystems operating at different temporal and spatial scales (compare the panarchy framework (Holling, 2001)). Each of these sub-systems is a complex system in itself and can display the typical cyclic dynamics of a maturation process. A full understanding of the overall system's dynamics requires an assessment of the processes both within and across these scales. In alignment with this theoretical perspective, including higher and lower trophic levels to our analytical framework would certainly yield valuable insights and further deepen our understanding of the dynamics observed in the planktonic community and in the larger marine ecosystem.

Leveraging information theory to derive interactions in ecosystems has become an established approach (see e.g., Wang et al., 2012; Schrenk et al., 2022b; Jeung et al., 2025). Nevertheless, it should be noted that transfer entropy, like most statistical dependency measures, just captures varying predictability across time series - some of those might be artifacts, not reflecting an actual interaction, while some actual interactions might not leave an imprint in the abundances. Moreover, transfer entropy does not reflect the reason for an increasing or decreasing cross-predictability between timeseries. Interpretation requires awareness of these facts and is necessarily context-specific.

5. Conclusions

Based on an information theoretical approach, this study provides critical insights into the dynamics of plankton interaction networks in the German Bight, emphasizing the interplay between environmental drivers and ecological complexity. Our findings suggest that hybrid interactions, which combine trophic and non-trophic elements, intensify under reduced resource conditions. Moreover, the directionality of edges between primary producers and grazers has shifted: initially driven by bottom-up strengths until 2007, followed by the emergence of top-down strengths. This shift is primarily influenced by ambient nitrogen-to-phosphorus ratios and light availability. Systemic analyses further indicate that stable environmental conditions can lead to higher system sensitivity, offering insights into potential adaptive and maladaptive responses to ecosystem changes. The methodologies applied in this study provide a robust framework that can be adapted to investigate plankton interaction networks and ecosystem dynamics in other marine or freshwater systems. Additionally, findings may be applicable to other regions with similar ecological and environmental conditions, offering valuable comparative insights into ecosystem responses to environmental change. These contributions deepen our understanding of marine ecosystem dynamics and provide a basis for informed management strategies to address the challenges posed by environmental change.

CRediT authorship contribution statement

Areti Balkoni: Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Wolfgang zu Castell:** Writing – review & editing, Validation, Methodology, Conceptualization. **Karen Helen Wiltshire:** Writing – review & editing, Resources, Funding acquisition, Conceptualization. **Maarten Boersma:** Writing – review & editing, Resources, Funding acquisition, Conceptualization. **Hannah Zoller:** Writing – original draft, Visualization, Supervision, Software, Methodology, Formal analysis, Conceptualization.

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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.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.ecocom.2026.101163.

Data availability

Phytoplankton, zooplankton, and environmental data used in this study are available in the open-access repository PANGAEA and can be accessed by following the respective links https://doi.pangaea.de/10.1594/PANGAEA.960407, https://doi.org/10.1594/PANGAEA.873032, and https://doi.org/10.1594/PANGAEA.960375.

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