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LETTER

Intermittent instability is widespread in plankton communities

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Abstract

Chaotic dynamics appear to be prevalent in short-lived organisms including plankton and may limit long-term predictability. However, few studies have explored how dynamical stability varies through time, across space and at different taxonomic resolutions. Using plankton time series data from 17 lakes and 4 marine sites, we found seasonal patterns of local instability in many species, that short-term predictability was related to local instability, and that local instability occurred most often in the spring, associated with periods of high growth. Taxonomic aggregates were more stable and more predictable than finer groupings. Across sites, higher latitude locations had higher Lyapunov exponents and greater seasonality in local instability, but only at coarser taxonomic resolution. Overall, these results suggest that prediction accuracy, sensitivity to change and management efficacy may be greater at certain times of year and that prediction will be more feasible for taxonomic aggregates.

KEYWORDS
chaos, empirical dynamic modelling, local stability, Lyapunov exponent, phytoplankton, seasonality, S-map, zooplankton

INTRODUCTION

The discovery of chaos in ecological models in the 1970s heralded an extensive search for chaos in ecological time series that peaked in the 1990s. The theoretical conditions for chaos (i.e. bounded, deterministic and aperiodic dynamics that depend sensitively on initial conditions) have been extensively studied in ecological models (e.g. Hastings & Powell, 1991; Huisman & Weissing, 1999; Pearce et al., 2020), and chaos has been experimentally demonstrated in protists (Becks et al., 2005), plankton (Benincà et al., 2008) and insects (Desharnais et al., 2001). While there had been limited evidence for chaos in naturally occurring populations (Sibly et al., 2007), a recent meta-analysis found evidence for chaos in upwards of 30% of ecological time series examined, with higher prevalence among short-lived species including plankton (Rogers et al., 2022).

While these studies considered the prevalence of global instability (i.e. long-run growth of small perturbations to

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species abundances, an indication chaos), time-varying local instability (i.e. short-run growth of small perturbations at a particular point in time) has received less attention. This includes the possibility that globally stable (i.e. non-chaotic) time series can exhibit periods of local instability. Populations situated at the 'edge of chaos' are prone to alternating between periods of locally stable and unstable dynamics. This alternation means that in the near-term, there will be periods when perturbations will be dampened, and other periods when they will be amplified. Such intermittent instability could arise either because of changes in stability as the system moves through phase space (i.e. as a result of internal dynamics), or as the system is influenced by some external driver. If common, intermittent instability would affect ecological forecast horizons (Petchey et al., 2015) and present barriers beyond which precise forecasts could not be generated (Abarbanel, 2013; Cenci & Saavedra, 2019).

Two recent studies have demonstrated intermittent instabilities. In a rocky intertidal community in New Zealand, near-cyclic changes in substratum occupation by barnacles, mussels and algae exhibited periods of intermittent instability (Benincà et al., 2015). Similarly, the fish community of Maizuru Bay, Japan exhibited approximately annual periods of intermittent instability (Ushio et al., 2018). To date, however, there has not been a systematic evaluation of the conditions under which intermittent instability occurs in natural systems. Moreover, both of these seminal demonstrations centre on communities whose dynamics are dominated by fluxes of individuals from outside the system. In the rocky intertidal case, succession is forced by tidally driven losses of mussel beds followed by recolonisation by planktonic barnacle larvae. In Maizuru Bay, temporal patterns in fish abundance are dominated by seasonal migration as individuals move into and out of the estuary. As a consequence, it is unclear whether we should expect intermittent instability to appear under more general ecological conditions. Specifically, is intermittent instability simply the result of migration or dispersal in open systems, or is it intrinsic to ecological dynamics more generally? As yet, there are no comparative studies on the magnitude and frequency of intermittent instabilities.

Aggregated community and ecosystem metrics are often less temporally variable than their constituent population time series, but this does not guarantee increased dynamical stability. Populations often fluctuate asynchronously: declines in some species are offset by increases in others, a phenomenon referred to as portfolio effects (Doak et al., 2008; Tilman et al., 1998) or the insurance hypothesis (Yachi & Loreau, 1999). Asynchronous fluctuations could arise due to stochasticity, differential responses to the environment, successional processes or chaos (Dakos et al., 2009; Huisman & Weissing, 1999). However, the fact that the aggregate is less *variable* than the constituents does not imply that it is more predictable or that dynamical stability has increased. Thus far, one study using data from a single marine location found that aggregation made phytoplankton time series more predictable, at least for some taxonomic groups (Agarwal et al., 2021). However, it is unclear how widespread this pattern is or whether increased predictability at coarser taxonomic resolution corresponds with increased stability. Theory shows that high-dimensional models with many species tend to be unstable (Gross et al., 2005; Ispolatov et al., 2015; Pearce et al., 2020), but ecologists often formulate models in terms of species aggregates (e.g. total phytoplankton biomass). Whether this is an empirically reasonable approach depends on how taxonomic aggregation affects stability and predictability in real ecosystems. Exploring the effects of aggregation on both stability and predictability could help better understand community dynamics and have implications for resource management.

To address these questions, we sought to (1) examine systems that are relatively closed, such that abundance changes are less dominated by external fluxes relative to marine systems, (2) focus on species with short generation times such that abundance changes reflect population dynamics rather than movement and (3) combine observations from multiple systems that span a wide range of environmental conditions and seasonal forcing. Phytoplankton and zooplankton time series from lakes (which are relatively closed systems) and marine ecosystems (which are more open systems) are ideal for analysis, as plankton also have short generation times (on the order of days to weeks), and many locations around the world have been sampled at relatively high frequency for extended intervals. Models of plankton dynamics often exhibit chaos, particularly when combined with seasonal forcing (Doveri et al., 1993; Huisman & Weissing, 1999; Moroz et al., 2016; Popova et al., 1997; Scheffer, 1991), and although a handful of empirical investigations have looked for chaos in plankton time series (Ascioti et al., 1993; Benincà et al., 2008; Medvinsky et al., 2015; Rogers et al., 2022; Sugihara & May, 1990), none have assessed the frequency of intermittent instability or the effects of taxonomic resolution.

We assembled monthly plankton time series data from 21 globally distributed sites, which included 17 lakes and 4 marine sites. For a given site, we analysed time series at three different levels of taxonomic resolution (species, functional group and trophic level) to the extent that the data resolution allowed. For each time series, we used time delay embedding (Takens, 1981) to reconstruct Jacobian matrices (Nychka et al., 1992; Rogers et al., 2022) at each time point using local linear regression (S-map, Sugihara, 1994). From these local Jacobians, we estimated the effective Lyapunov exponent (LE, an indicator of dynamical stability over the whole time series) and local (monthly) eigenvalues as measures of local stability. Extensive simulations demonstrate that this approach to LE estimation classifies series (as chaotic or not chaotic) with high accuracy (Rogers et al., 2022).

We then assessed (1) the prevalence of chaotic dynamics and seasonal fluctuations in local stability; (2) the relationship between local stability, population growth rate, population abundance and step-ahead forecast error; (3) across-site variation in chaotic dynamics and the seasonality of local stability, including relationships with environmental covariates; and (4) how these results are affected by the level of taxonomic resolution.

METHODS

Data

We compiled data on zooplankton abundance, phytoplankton abundance and water temperature from 17 lakes and 4 marine locations sampled at monthly intervals (Table S1). If multiple observations were taken during a month, these were averaged. Depending on the taxonomic resolution of the data available at each site, we assembled time series at three different levels of aggregation: species, functional group and trophic level. 'Species'-level series were the lowest resolution available for each taxon, typically species, genus or family. Functional group series were generated by adding together species-level series as appropriate. For lakes, the functional groups were typically copepods, large cladocerans, small cladocerans, predators and rotifers. For marine sites, which had more taxonomically diverse zooplankton assemblages, functional groups were typically herbivores and carnivores. Trophic-level series reflected total zooplankton and total phytoplankton abundance at each site. Total zooplankton was obtained by adding together functional group-level series as appropriate, excluding rotifers, as they were not enumerated in most data sets. As a proxy for total phytoplankton, we used chlorophyll-a (chl-a) concentration ($\mu g\,L^{-1}$) or phytoplankton cell density if chl-a data were unavailable. Specific functional group and trophic-level aggregates used for each site are given in Table S1. For all zooplankton series, we used density data unless only biomass data were available. If measurements of chl-a and temperature were taken at multiple depths, we averaged measurements taken at depths ≤2 m.

After assembling all time series, we retained for analysis only those for which <60% of non-missing observations were zeros, the longest string of consecutive non-missing values was at least 24 and the effective sample size was at least 40 for an embedding dimension of 2 and time delay of 1. Effective sample size was defined as the number of valid coordinate delay vectors obtained after accounting for missing data (see next section for definitions of embedding dimension, time delay, and delay coordinate vector). We also included only series which had at least 4 local stability estimates in each of at least 10 months of the year, so as to ensure that seasonal dynamics were adequately represented. This resulted in 154 species level, 48 functional group level and 41 trophic level time series from 21 sites.

Prior to analysis, all time series were rescaled to unit variance by dividing by the standard deviation. To allow for log transformations, all time series containing zeros were rescaled after adding a constant (1 if all values were integers, the minimum non-zero value if the series contained non-integers or the minimum non-zero value was >100). Leaving the zeros intact and using only model forms that did not require log transformations produced similar results.

Analysis

We computed metrics of global and local stability from reconstructed state-dependent Jacobian matrices. Jacobian matrices were reconstructed by fitting a model with the form:

$$x_t = f\left(x_{t-\tau}, x_{t-2\tau}, \dots, x_{t-E\tau}\right)$$

where $\{x_{t-\tau}, x_{t-2\tau}, \dots, x_{t-E\tau}\}$ is the 'delay coordinate vector' for time t. For each time series, we fit f using local linear regression (S-map, Sugihara, 1994), which has been used in prior studies to estimate time-varying stability (Ushio et al., 2018). We specifically used the procedure detailed in Rogers et al. (2022), which has been optimised for chaos detection. This method uses leave-one-out cross-validation to select the optimal embedding dimension (E), time delay (τ) and local weighting parameter (θ) for each time series. The parameter θ determines the local weighting of points: a model with $\theta = 0$ is linear, and models with higher values are more non-linear. For this analysis, we fit models with E values from 1 to 6, τ values from 1 to 12, and 12 values of θ (0, 0.1, 0.3, 0.5, 0.75, 1, 1.5, 2, 3, 4, 6 and 8) in all combinations. From the set of best performing models (those with leave-one-out R^2 values for abundance within 0.01 of the highest obtained), we selected the model with the lowest τ, θ and E (in that order). This procedure was repeated for three different model forms (first difference $x_t - x_{t-\tau}$ as a function of abundance, population growth rate $\ln(x_t / x_{t-\tau})$ as a function of abundance, and population growth rate as a function of log abundance), and the form with the highest R^2 was selected as the final model. Jacobian matrices, $J(x_t)$, were then constructed from the local regression coefficients and were formulated (for comparison across series) in units of scaled abundance. Here, $J(x_t)$ is an E x E matrix whose top row is $J_{1,j} = \partial f / \partial x_{t-j}$ for $j = 1, \dots, E$, whose first subdiagonal is $J_{j,\,j-1} = 1$ for $j = 2, \dots, E$, and all other elements are 0.

As a measure of global stability, we computed the Lyapunov exponent (LE). Positive LEs indicate long-term sensitivity to initial conditions and global instability (i.e. chaos). The LE is computed by multiplying sequential Jacobian matrices and taking the log absolute value of the dominant eigenvalue, Λ_1, of this product. The LE is formally defined as time series length $T \to \infty$, but for finite time series, the effective LE is calculated over all available data.

$$\mathrm{LE} = \frac{1}{T}\ln\left|\Lambda_1\left(\prod_{t=1}^{T} J(x_t)\right)\right|$$

In the case of missing data, we computed the LE over the longest consecutive sequence of non-missing values. We obtained LEs and constructed confidence intervals as described in Rogers et al. (2022). Series with LE significantly >0.01 were classified as chaotic.

Local stability can be computed in several different ways from the individual Jacobian matrices, $J(x_t)$. The largest singular value of the Jacobian (eigenvalue of $J(x_t)J(x_t)^{\mathrm{T}}$) quantifies the maximum growth rate of a local perturbation over the next timestep (Neubert & Caswell, 1997). However, singular values are not scale invariant and are sensitive to the use of delay coordinates. Thus, we opted to use the log absolute value of the dominant eigenvalue of $J(x_t)$ (hereafter, the 'local eigenvalue') as our measure of local instability (values >0 indicating instability). We evaluated the local eigenvalue at each point to test for intermittent instability. We note that evaluated over a longer time interval, the eigenvalue would estimate the local LE, used to indicate 'intermittent chaos' in physical systems (Abarbanel et al., 1992). Although the dominant eigenvalue reflects asymptotic stability as opposed to perturbation growth after a single timestep (which may include transient expansion), eigenvalues are invariant to similarity transformations (i.e. J and SJS^{-1} have the same eigenvalues, where S is an arbitrary non-singular matrix, such as the transformation between native and delay coordinates), so are consequently relatively insensitive to the use of delay coordinates and present a conservative lower bound on the true step-ahead perturbation growth rate for the system. As a less conservative measure of local short-term perturbation growth, we also computed the log variance expansion ratio (VER) given by the trace of $J(x_t)J(x_t)^{\mathrm{T}}$. In an idealised setting, the VER measures the ratio of total variance at the next timestep to the total variance at the current timestep. This quantity is analogous to the 'volume contraction rate', which Cenci and Saavedra (2019) used to quantify local structural stability.

To examine seasonality in local eigenvalues, standardised power spectra were computed for the local eigenvalue time series using penalised (ridge) regression onto sine and cosine basis functions with frequencies $2\pi k/T$, where $k = 1, 2, \dots T/2$ and T is the time series length. This was done in lieu of a discrete Fourier transform because all time series contained missing values. Local eigenvalue time series were rescaled to mean 0 and unit variance prior to decomposition, and the penalty was set to 0.01. Power at each frequency was calculated from the sine and cosine coefficients. We separately evaluated the power for period 12 by regression onto basis functions, since this exact frequency was not always included in the basis set. Series were classified as 'seasonal' if the period with maximum power was between 11.5 and 12.5 months. The magnitude of seasonality for local eigenvalues was computed as the difference between the minimum and maximum monthly median eigenvalues. Relative eigenvalue seasonality was calculated similarly, but after scaling the local eigenvalue time series to unit variance.

We next examined the relationship between local stability and time of year, abundance, growth rate and predictability for all series with at least one positive local eigenvalue and some seasonality in local eigenvalues (difference between minimum and maximum monthly medians >0.25). We identified the month with greatest median local instability across all years. We also computed the Pearson cross-correlation between local eigenvalues, growth rate ($\ln(x_{t+1}/x_t)$) and log scaled abundance, and we identified the lag with the maximum correlation. We examined the relationship between step-ahead leave-one-out forecast error (log absolute value of the prediction residual) and either the local eigenvalue or VER across all time series for each level of aggregation. At the site level, we examined how median variability (coefficient of variation, CV) and predictability (R^2) varied with level of aggregation.

Lastly, we evaluated the relationship between site-level stability metrics (LE, proportion-positive local eigenvalues, local eigenvalue seasonality and relative local eigenvalue seasonality) and two environmental covariates: mean temperature (which was highly correlated with latitude, photoperiod range and productivity as measured by mean log chl-a; Pearson $r = -0.95, -0.90, 0.66$ respectively) and temperature range (difference between minimum and maximum monthly means, which was not strongly correlated with mean temperature, Pearson $r = -0.06$, as it is additionally affected by system size, depth and stratification). We also examined whether these relationships depended on the level of aggregation. We used average values for each site, at each level of aggregation, and used additive linear models. We also fit a model using individual data points with site as a random effect.

Analyses were performed in R version 3.6.3 (R Core Team, 2019). The S-map models were fit using the package 'rEDM' version 0.7.4 (Ye et al., 2018).

RESULTS

Chaotic dynamics (LE significantly >0) were found in many time series, particularly at finer taxonomic resolution (Figure 1). The proportion of time series classified as chaotic was 52% for species (80 of 154 total time series), 42% for functional groups (20 of 48) and 7% for

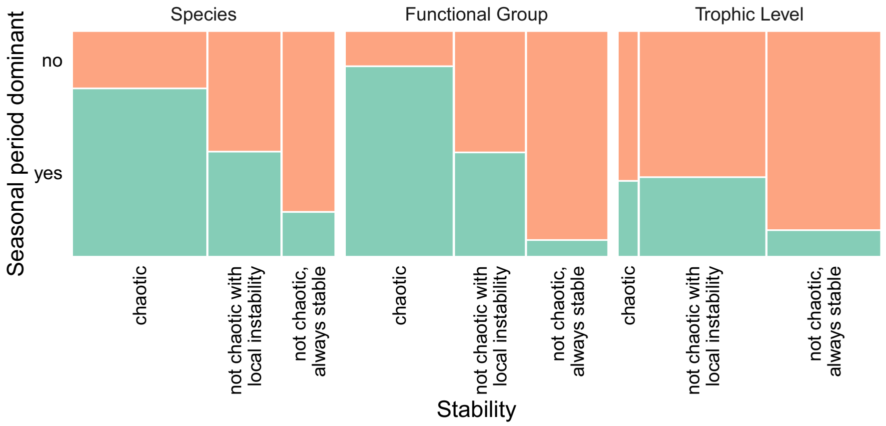

FIGURE 1 Mosaic plot indicating stability and seasonality of time series at three levels of taxonomic resolution. Axes show the relative frequency of each category. Series were classified as chaotic if LE >0. Series that were not chaotic but had at least one local eigenvalue >0 are classified as 'not chaotic with local instability'. Within each stability category, a series was considered to have a dominant seasonal period if the period of the local eigenvalue Fourier spectrum with maximum power was between 11.5 and 12.5 months.

trophic levels (3 of 41). Similar results were seen within individual sites that had all three resolutions represented (Figure S1). It was also common for series to show intermittently unstable dynamics (positive local eigenvalues) when the dynamics were globally stable (58% of non-chaotic series for species, 46% for functional groups and 53% for trophic levels; Figure 1). Variability in local eigenvalues was seasonal (displayed a dominant annual periodicity) for many time series, particularly at finer taxonomic resolutions (56% for species, 50% for functional groups and 24% for trophic levels; Figure 1). Seasonality was more common in stable series with intermittent local instability than in series that were always stable, and at the species and functional group resolutions, seasonality was present in the majority of chaotic series (Figure 1).

The proportion of local eigenvalues that were positive also decreased at coarser levels of taxonomic resolution. Across time series, the average proportion of eigenvalues that were positive was 50%, 39% and 21% for species, functional groups and trophic levels respectively. Of series that were not chaotic (LE ≤0), 54% had at least one local eigenvalue that was positive, and 38% had at least a quarter of local eigenvalues that were positive (Figure 2b). For chaotic series, 49–96% of local eigenvalues were positive.

The magnitude of seasonality for local eigenvalues was typically low for non-chaotic series, although seasonality could be high when a large percentage of the eigenvalues were positive (Figure 2). For chaotic series, the magnitude of seasonality ranged from very low to very high (Figure 2). Time series displayed greater seasonality at finer taxonomic resolution, and these patterns were similar for both lake and marine sites. Representative time series of abundance and local eigenvalues, along with power spectra for local eigenvalues are shown in Figure 3, showing a range of different behaviour and seasonality. For example, series 1 is chaotic (LE>0) with local eigenvalues that are highly seasonal and alternate between positive and negative values. In contrast, series 6 is non-chaotic with local eigenvalues that are always negative and show very little seasonality.

Across all species-level series with at least one positive local eigenvalue and some seasonality in local eigenvalues (>0.25), the month with greatest median local instability occurred most often in spring (Figure S2), although there was variation among series. For functional group and trophic-level series, the month with greatest instability also occurred most often in spring for marine sites, but was more variable for lakes. Based on the Pearson cross-correlation function, the month with greatest local instability tended to coincide with, or just follow, the month with maximum growth rate, and to precede the month with maximum abundance (Figure S3). Local eigenvalues did not show a strong relationship with step-ahead predictability, however, a larger VER was associated with lower step-ahead predictability (greater step-ahead forecast error; Figure 4). This association was stronger, and the spread of VER values larger, at the species level than at coarser taxonomic resolutions. At the site level, time series variability decreased (Figure 5a) and predictability increased (Figure 5b) as the level of taxonomic aggregation increased.

Across sites, the proportion-positive local eigenvalues and local eigenvalue seasonality did not show significant relationships with any of the covariates (Figure 6a,b; Table S2). Relative local eigenvalue seasonality was higher at lower mean temperature at the functional group level ($p = 0.054$) and trophic level ($p = 0.007$, Figure 6c,d; Table S2). The LE was higher at lower mean temperatures at the functional group level ($p = 0.004$) and trophic level ($p = 0.087$), and lower temperature range at the trophic level ($p = 0.018$, Figure 6e,f; Table S2). Similar results were obtained using individual data points with site as a random effect, except the relationship between mean temperature and the LE at the trophic level and relative seasonality at the function group level were statistically significant ($p = 0.047$, 0.011 respectively).

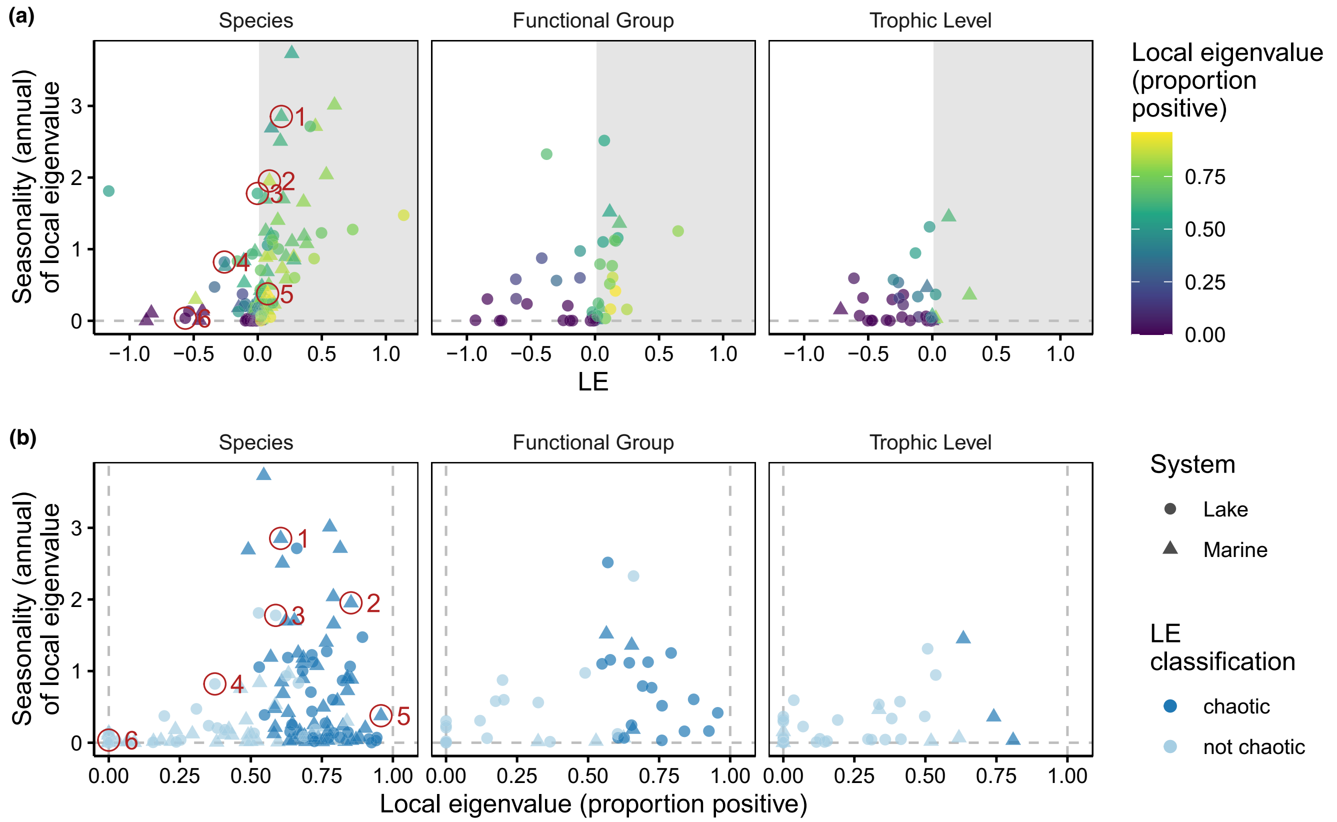

FIGURE 2 Seasonality of local eigenvalues (difference between minimum and maximum monthly medians) for each level of taxonomic resolution, plotted against (a) Lyapunov exponent (LE), colour indicating proportion-positive local eigenvalues, and (b) proportion-positive local eigenvalues, colour indicating chaos classification. Circled points are representative time series displayed in Figure 3.

DISCUSSION

Our results demonstrate that intermittent instabilities are common in natural plankton systems, both in relatively closed (lake) and relatively open (marine) ecosystems. Time series displayed a wide range of dynamical behaviour (e.g. chaotic and intermittently unstable, not chaotic and intermittently unstable, not chaotic and always stable). Chaos was also prevalent, supporting other results that chaos is widespread in plankton (Medvinsky et al., 2015; Rogers et al., 2022). However, the most novel finding was that, even among series not classified as chaotic, local eigenvalues fluctuated above and below 0 with an annual/semi-annual periodicity, indicating that intermittent instabilities are both common and strongly seasonal.

Chaos was most prevalent at the species level, and less common as the level of interspecies aggregation increased. Asynchronous, chaotic fluctuations in species abundances due to non-equilibrial (Huisman & Weissing, 1999) or near-neutral (Pearce et al., 2020; Rodríguez-Sánchez et al., 2020) dynamics can allow for the coexistence of more species than the number of resources, maintaining a higher level of diversity than would otherwise be possible. In this context, our results are consistent with the hypothesis that chaos may resolve the paradox of the plankton (Hutchinson, 1961; Scheffer et al., 2003), though there are other, non-exclusive hypotheses. In nutrient–phytoplankton–zooplankton (NPZ) models, chaos is sometimes seen as problematic, and models are often altered (by addition of closure terms) so that the dynamics are stable (Caswell & Neubert, 1998). Our results suggest that while this may be a reasonable thing to do for plankton aggregates (e.g. total chlorophyll), such ad hoc stabilisation of models may be misguided for models of particular species or functional groups.

Variability and stability are often used interchangeably when examining population dynamics. However, if species fluctuate independently, data aggregation would decrease variability as a result of statistical averaging, but this would not necessarily increase stability or predictability. Here, data aggregation decreased variability and increased predictability, which is more consistent with species fluctuating out of phase due to complementarity (compensatory dynamics, response diversity, e.g. Jochimsen et al., 2013). Observed changes in predictability were related to changes in global stability (aggregates were less chaotic) and local stability (aggregates had less variable VER). Along these lines, non-seasonal plankton competition models can exhibit chaotic succession of many different species, but near constant aggregate biomass (Huisman & Weissing, 1999). In models with a

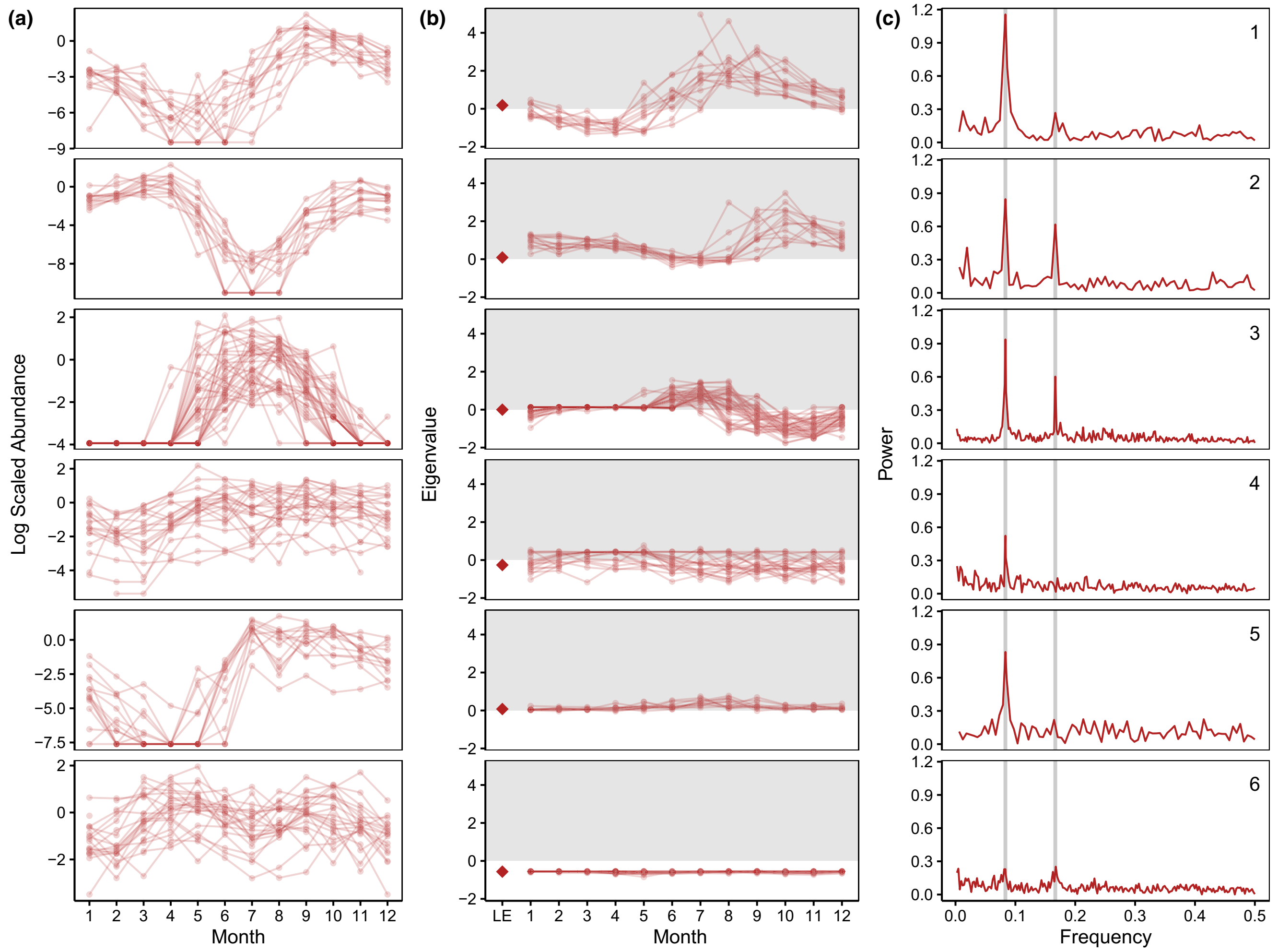

FIGURE 3 Representative time series. (a) Log-scaled abundance, lines connecting sequential values from the same year. (b) LE and local eigenvalues by month, lines connecting sequential values from the same year. LE values (top to bottom) are 0.18, 0.091, −0.0024, −0.26, 0.077 and −0.57. (c) Standardised power spectra for local eigenvalues. Vertical grey lines are frequencies 12^{-1} and 6^{-1}. Numbers in the upper right of (c) correspond to the points in Figure 2, and are (1) Port Erin Bay, *Paracalanus parvus*; (2) Port Erin Bay, *Biddulphia mobiliensis*; (3) Lake Müggelsee, *Leptodora kindtii*; (4) Loch Leven *Eudiaptomus gracilis*; (5) Narragansett Bay, *Acartia tonsa*; and (6) Lake Geneva, *Cyclops prealpinus*.

seasonal environment, aggregate dynamics can show seasonal blooms, while species-level chaos drives variability in the magnitude and composition of those blooms (Dakos et al., 2009), making species abundance less predictable than aggregate biomass (Agarwal et al., 2021; Cottingham et al., 1998; Tilman, 1995). Indeed, overall biomass behaves relatively predictably in lake ecosystems (Sommer et al., 1986).

The LE for many time series (including aggregates) was often very close to zero, and local stability often fluctuated seasonally between stable and unstable values, as seen in previous studies (Benincà et al., 2015; Ellner & Turchin, 1995; Turchin & Ellner, 2000; Ushio et al., 2018). The time of year with greatest instability tended to be during spring. Our results thus imply seasonal variation in forecastability (Abarbanel et al., 1992), with spring and summer (the time of blooms in many plankton species) being least predictable. This is consistent with findings in plankton models (Popova et al., 1997) and studies of *Daphnia* (Hovenkamp, 1990). Supporting this, the VER was related to short-term predictability, which was most pronounced in the species-level time series.

Whether seasonal instability results from 'intrinsic' variation in dynamics (e.g. species interactions) and/or variation in an external driver is unclear. For most species, instability was associated with periods of high (exponential) growth, which could result from seasonal changes in either environmental (e.g. light, nutrient) or biological (e.g. prey availability, competition, predation) conditions (Rogers et al., 2020). While useful for identifying intermittent instability, time delay embedding does not allow us to differentiate between these because it implicitly includes the driver as part of the 'system', though this can potentially be disentangled with additional data. The role of noise in inducing chaos or intermittent instability (e.g. Dwyer et al., 2004) is also difficult to evaluate using these methods. The source of intermittent instability is thus an interesting avenue for future work.

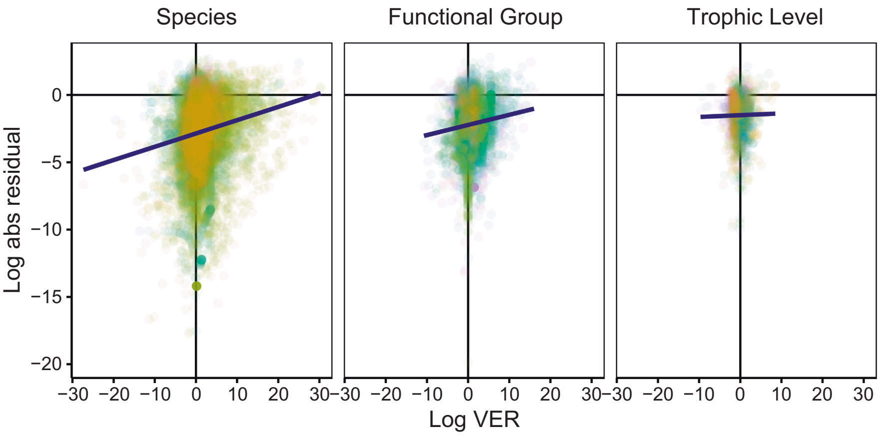

FIGURE 4 Step-ahead residual (log absolute value) versus local instability (as measured by log variance expansion ratio [VER]) for each level of taxonomic resolution, colour indicating different sites. Only results from series with proportion-positive local eigenvalues >0 and local eigenvalue seasonality (difference between minimum and maximum monthly medians) >0.25 are shown. Regression lines shown are fit to all data.

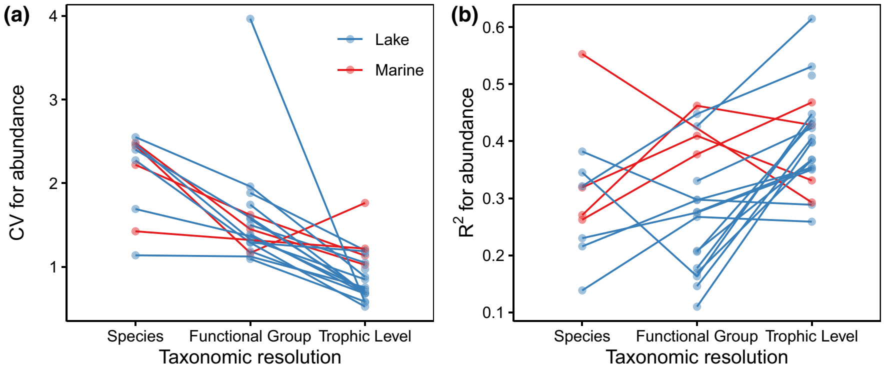

FIGURE 5 Variability and predictability of time series at different levels of taxonomic aggregation. Median coefficient of variation (CV) for abundance (a) and R^2 for abundance (b) at different levels of taxonomic resolution. Lines connect values from the same site.

Cross-site patterns in stability only emerged at coarser levels of taxonomic aggregation. Sites had higher LEs, on average, at higher latitudes, lower mean temperature and lower productivity. This is consistent with many models that found seasonality increases the probability of chaos and intermittently unstable dynamics (Dakos et al., 2009; Heilmann et al., 2016; Kot & Schaffer, 1984). However, the theoretical relationship between global stability and the amplitude of seasonality is inconsistent among studies: Steffen et al. (1997) found that the LE was sensitive to the amplitude of periodic forcing, but the relationship was complex, while Dakos et al. (2009) found no relationship. The abruptness of seasonal forcing also appears to affect dynamical stability in models (Sauve et al., 2020). We found that temperature range did not appear to be related to overall stability, although photoperiod range (correlated with latitude and mean temperature) could potentially be related. The effect of productivity is also difficult to parse since it covaries with other factors. Simulations have found chaos to be most prevalent at intermediate productivity (Dakos et al., 2009), and community stability (variability) is known to be influenced by nutrients (Lewandowska et al., 2016; Ptacnik et al., 2008) and temperature (Paerl & Huisman, 2008). However, there have been few experimental studies on how environmental conditions affect dynamical stability—an important area for future research.

Although a first hypothesis would be that seasonality in local stability is driven by environmental seasonality, we did not observe a simple relationship between these quantities. However, we did see that relative seasonality in local stability increased with latitude (lower mean temperature, lower productivity). In other words, higher latitude sites did not necessarily display greater amplitude fluctuations in local stability, but the variation in local stability that they did display was more seasonal. Again, this pattern was most apparent at coarser levels of data aggregation. Relative seasonality did not show a relationship with temperature range, which might mean that photoperiod range is a more important seasonal driver.

Chaos and intermittent instability present challenges for management in terms of establishing causal relationships, making forecasts and devising interventions or controls to achieve desired outcomes. From an empirical standpoint, establishing cause–effect relationships in chaotic systems

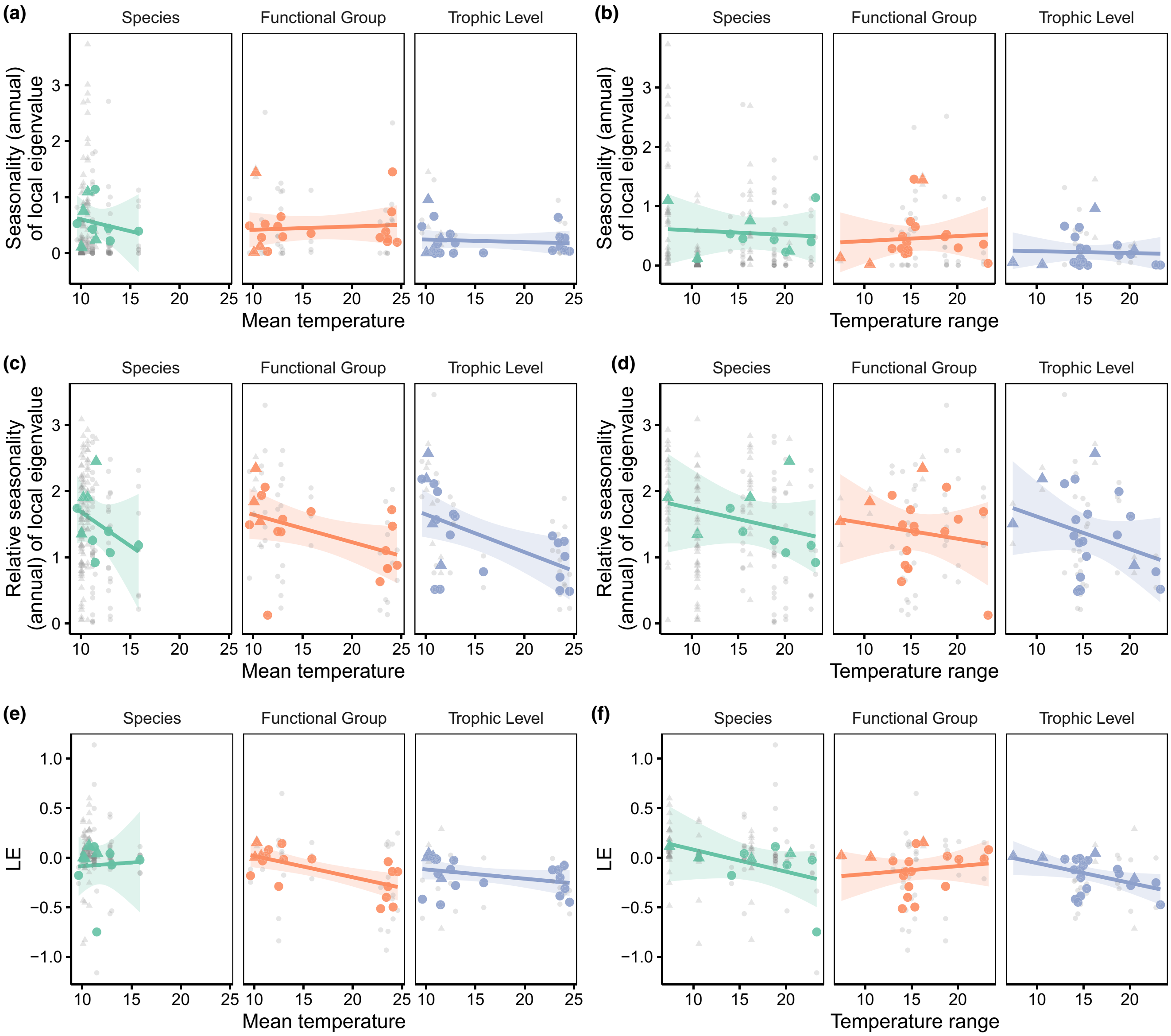

FIGURE 6 Across site patterns in seasonal instability for each level of taxonomic resolution. (a, b) Seasonality of local eigenvalues (difference between minimum and maximum monthly medians) plotted against site-level mean temperature and temperature range. (c, d) Relative seasonality of local eigenvalues (difference between minimum and maximum monthly medians, after scaling eigenvalues to unit variance) plotted against site-level mean temperature and temperature range. (e, f) Lyapunov exponent (LE) plotted against site-level mean temperature and temperature range. Lines and bands are linear regressions and 95% confidence intervals. Coloured points are site means, grey points are individual time series (not used in analysis, but plotted to show within-site variation). Circles are lakes, triangles are marine sites.

requires use of non-linear approaches (Sugihara, 1994), and because of sensitivity to small differences in initial conditions, attempts to attribute intrinsically chaotic fluctuations (e.g. spring bloom composition and magnitude) purely to environmental drivers may be futile. At the same time, attributing all unexplained variation to noise is a missed opportunity; Non-linear forecasting methods suitable for chaotic systems can generate more accurate short-term predictions than models assuming stable dynamics plus noise (e.g. Perretti & Munch, 2012).

For instance, harmful algal blooms may be highly sensitive to initial conditions. This can thwart traditional control efforts, and systems may respond to perturbations in unintended ways. However, a small perturbation during, or just prior to, an unstable period would impact the system more than the same perturbation during a stable period. Hence, there may be an optimal time to apply control measures to prevent an algal bloom (Balaji-Prasath et al., 2022). State-dependent timing of management action was effective in controlling chaotic laboratory populations (Desharnais et al., 2001), and in preventing population outbreaks and crashes in chaotic population models (Hilker & Westerhoff, 2007). Whether this can be successfully implemented in a natural system will depend on whether we can accurately reconstruct the dynamics and identify desirable perturbations. Empirical dynamic models can be combined with dynamic programming to obtain useful control policies in chaotic systems (Brias & Munch, 2021), and the extension to systems with intermittent instabilities is an important area of future research. Our results also suggest that management of species groups may be more robust than single-species approaches. This is consistent with recent suggestions that marine ecosystem management would benefit from 'balanced harvesting' (Zhou et al., 2010, 2019) albeit for fundamentally different reasons.

In terms of forecasting, accurate short-term predictions are likely more feasible for aggregated data. Predictions are also more likely to be feasible for winter and fall, when dynamics are most locally stable, though non-linear forecasting methods may improve short-term predictions during more unstable periods. Coarse-grained (climatological) predictions on an annual time scale are likely feasible as well, largely because of seasonal entrainment—for example, abundance will go up in spring and down in fall, though exactly how much is harder to say. Changes in climate, if they occur at unstable times of year, may also have outsized impacts on plankton dynamics. For example, climate change has led to warmer spring water temperatures, earlier spring ice-off and earlier onset of stratification (Woolway et al., 2020)—changes that may influence plankton dynamics more than environmental changes in other seasons (Gerten & Adrian, 2002; He et al., 2020).

There have been numerous calls to make ecology a more predictive science (Dietze, 2017; Mouquet et al., 2015), and this includes acknowledging that predictions may be more feasible during some time periods than others, and that predictability may vary with taxonomic resolution. The efficacy of management interventions may also vary temporally. Quantification of global and local instability can aid forecasting efforts in complex natural ecosystems and the approaches best used at different scales.

AUTHOR CONTRIBUTIONS

SBM conceived the study. All authors compiled data. TLR analysed data with input from SBM and made the figures. TLR, SBM and CCS drafted the article, and all authors contributed to revision.

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DATA AVAILABILITY STATEMENT

No new data were used. Data sources are given in Table S1. Code and compiled data used for the analysis can be found at https://doi.org/10.5281/zenodo.7508285. To comply with data licensing polices, the abundance and temperature time series for some data sets are omitted, but can be obtained from the sources cited.

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SUPPORTING INFORMATION

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