

Multiscalarity of the Nutrient–Chlorophyll Relationship in Coastal Phytoplankton

William K. W. Li · Marlon R. Lewis · W. Glen Harrison

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Abstract The relationship between nitrogen (N) and phytoplankton chlorophyll *a* (Chl) establishes a basis for understanding eutrophication in coastal marine ecosystems. A substantial literature exists on cross-ecosystem analysis of this relationship, but there is little information on cross-scale patterns. A collection of observational records in Bedford Basin (Canada) was used to construct the N–Chl relationship at four time scales: intra-day, intra-annual, interannual, and interdecadal. Additionally, a dataset of contingent observations from 16 biogeochemical ocean provinces was used to construct the N–Chl relationship at large spatial scale. In Bedford Basin, N statistically predicts Chl at time scales that are short (intra-day, intra-annual) and long (interdecadal) but not intermediate (interannual). There is an apparent stoichiometric regularity in the dependence of Chl on N that crosses time scales. Further, an apparent similitude exists between the local pattern at long time scale and the global pattern at large space scale.

Keywords Chlorophyll · Eutrophication · Macroecology · Multiscale patterns · Nitrogen

Introduction

In recent decades, accelerated production of reactive nitrogen from global human activity has intensified delivery of nutrients from land to sea through riverine and

atmospheric transport (Galloway et al. 2004). As a result, many coastal marine ecosystems in which nitrogen is the limiting nutrient now show systemic cascading change in biogeochemistry and ecology (Howarth and Marino 2006; Galloway et al. 2008). In Canada as a whole, nitrogen releases to air and water are relatively low, with little evidence of coastal eutrophication (Schindler et al. 2006). However in Atlantic Canada, Halifax Harbour receives urban effluents that are largely from domestic sources and high in nitrogen, phosphorus, and organic content (Petrie and Yeats 1990; Chambers et al. 2001). Historical reconstructions using benthic foraminiferal assemblages retrieved from sediment cores document recent rapid urban growth by the appearance of species tolerant of high organic carbon (Scott et al. 2005).

Nutrient control of eutrophication starts at the level of primary producers, and a strong statistical response of phytoplankton biomass to nutrient enrichment is evident in comparative analysis of worldwide coastal ecosystems (Smith 2006). However at local scales, a signal of changing nutrient concentration does not always elicit a response of changing phytoplankton biomass or production. A limited explanation may lie first in the modulation of response by system-specific attributes, such as water residence time, and second in the complexity of biotic responses. These biotic responses can be direct, such as shifts in phytoplankton community composition, or indirect, such as concomitant shifts in grazer community composition. More generally, a comprehensive explanation must include the effects of other simultaneous stressors, such as climate change (Cloern 2001). Evidently, patterns of mean state across space established by comparative ecosystem measurements need to be reconciled with patterns of dynamic state through time constructed from monitoring observations.

Whereas the canonical relationship between nitrogen (N) and chlorophyll *a* (Chl) is well established across diverse

W. K. W. Li (✉) · W. G. Harrison
Ecosystem Research Division, Bedford Institute of Oceanography,
Dartmouth, NS, Canada, B2Y 4A2
e-mail: LiB@mar.dfo-mpo.gc.ca

M. R. Lewis
Department of Oceanography, Dalhousie University,
Halifax, NS, Canada, B3H 4J1

marine ecosystems (Guildford and Hecky 2000; Smith 2006), little appears to have been published concerning this relationship at different scales of time. The fundamental requirement for detecting phytoplankton change is a time series of observations that adequately accounts for periodic forcing due to the annual and diel cycles of earth orbit and forcing at the important meteorological scales (Lewis and Platt 1982). Both eutrophication and climate change are components of lower frequency variability which are not purely periodic; hence, the effects of such environmental forcing on phytoplankton can only be discerned over long time periods. Here, we show that in Halifax Harbour, N statistically predicts Chl at time scales that are short (diel, intra-annual) and long (decades) but not intermediate (interannual). Furthermore, there is apparent similitude between the local pattern at long time scale and the global pattern at large space scale.

Methods

Land/Ocean Biogeochemical Observatory Hourly resolved concentrations of nitrate and Chl were measured in the surface water of the Northwest Arm (44°37'45" N, 63°35'29" W) of Halifax Harbour by Land/Ocean Biogeochemical Observatory, which is an autonomous floating platform of in situ sensors that monitor physical, chemical, and biological properties (Comeau et al. 2007). Nitrate is sensed by in situ ultraviolet spectrophotometry (Johnson and Coletti 2002), and Chl is sensed by in vivo red fluorescence.

Bedford Basin Plankton Monitoring Program Weekly resolved concentrations of nutrients (nitrate, phosphate, and silicate) and Chl have been measured at 1, 5, and 10 m in the Bedford Basin (44°41'37" N, 63°38'25" W) of Halifax Harbour since 1992 (Li and Dickie 2001; Li and Harrison 2008). Earlier measurements made intermittently since 1967 were extracted from 11 historical reports listed in Li et al. (1998). Chl is measured by in vitro fluorescence of acetone extracts from seston retained on glass fiber filters. Nutrient analyses are performed using colorimetric techniques on an autoanalyzer. The analysis of nitrate is based on the measurement of a diazo dye formed by the reaction between sulfanilamide and nitrite, which in turn has been produced by the reduction of nitrate to nitrite on a copperized cadmium column. Because the analysis is based on the reduction of nitrate to nitrite, the method actually determines the sum of the nitrate and nitrite concentrations (Mitchell et al. 2002).

Macroecological Analysis Data of the North Atlantic Ocean including its subpolar gyre in the Labrador Sea

were compiled from 34 cruises of *CCGS* Hudson extending 18 years (1990–2007). Hydrographic stations were located across seven biogeochemical provinces (Longhurst 2007): mainly in the Atlantic Arctic (ARCT), Boreal Polar (BPLR), Northwest Atlantic Shelves (NWCS), and Gulf Stream (GFST); to a much lesser extent in the North Atlantic Subtropical Gyre East (NASE), North Atlantic Subtropical Gyre West (NASW), and the North Atlantic Drift (NADR). The seasonal and geographic distributions of these stations are uneven, following the contingent requirements of hydrographic surveys (Li et al. 2004, 2006). Other data were compiled from the Blue Earth Global Expedition (BEAGLE), which was a 7-month circumnavigation along 20–34°S, sampling the Pacific Ocean in winter, the Atlantic Ocean in spring, and the Indian Ocean in summer (Bouman et al. 2006), covering nine provinces: East Australian Coastal (AUSE), Archipelagic Deep Basins (ARCH), Benguela Current Coastal (BENG), Brazil Current Coastal (BRAZ), Eastern Africa Coastal (EAFR), Humboldt Current Coastal (HUMB), Indian South Subtropical Gyre (ISSG), South Atlantic Gyral (SATL), and South Pacific Subtropical Gyre (SPSG). Only data from the upper 20 m were included in this analysis.

Results

Intra-day Pattern The record of in vivo Chl fluorescence for each hour of almost every day in 2007 (Fig. 1) shows a strong midday depression, which is due to diel photo-inhibition of cellular fluorescence (Kiefer 1973). On average over each diel cycle, the initial (0 h) and final (23 h) Chl values are almost identical. However, a slight within-day maximum occurs at night, on average at 20 h. The concurrent record of NO₃ (Fig. 2) also indicates little change between initial and final diel values, but a slight minimum in this nutrient occurs at night, on average coincident in time with the Chl maximum. Seemingly imperceptible change from 1 day to the next grows with time, so it becomes possible to discern intra-month variability and inter-month progression (Figs. 1 and 2), which can be displayed in familiar time series form (Comeau et al. 2007).

Intra-annual Pattern The record of Chl concentration measured by in vitro fluorescence for almost every week of each year from 1992 to 2007 (Fig. 3) shows phytoplankton blooms in spring and autumn, on average peaking at weeks 13 and 39, respectively. The concurrent record of NO₃ (Fig. 3) shows spring depletion and autumn recharge as expected in the stereotype of temperate coastal waters.

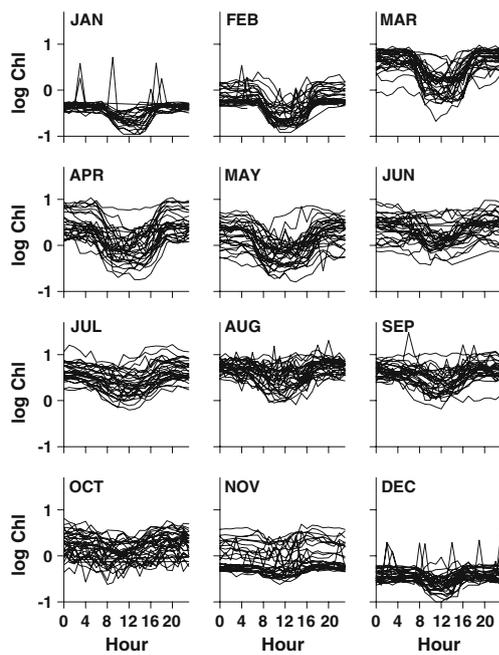


Fig. 1 Hourly records of in vivo fluorescence indicating chlorophyll ($\log \text{mg m}^{-3}$) over the 24-h daily cycle from January 10 to December 31, 2007 in the Northwest Arm, displayed by month

Inter-annual Pattern Annual average concentrations of Chl and NO_3 have not remained constant in the past 40 years, but there is no visually discernible evidence of supra-annual cycles (Fig. 4). The inter-annual increase of NO_3 is highly

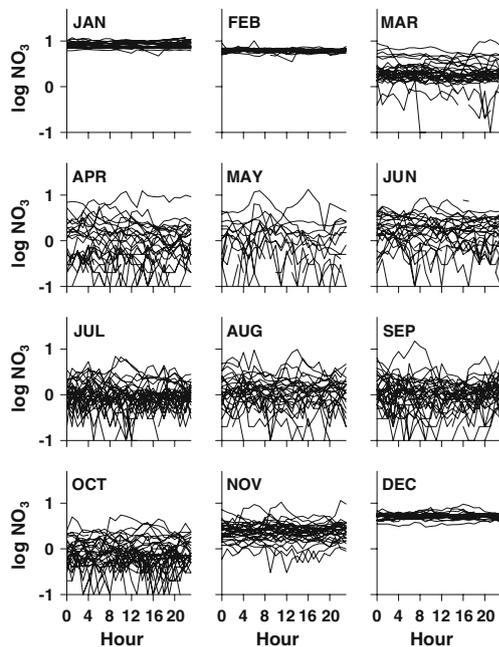


Fig. 2 Hourly records of nitrate ($\log \text{mmol m}^{-3}$) over the 24-h daily cycle from January 10 to December 31, 2007 in the Northwest Arm, displayed by month

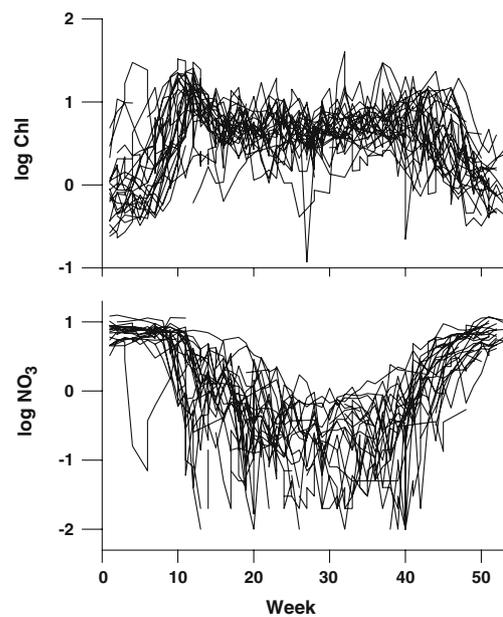


Fig. 3 Weekly records of chlorophyll ($\log \text{mg m}^{-3}$) and nitrate ($\log \text{mmol m}^{-3}$) over the 52-week annual cycle from 1967 to 2007 in the Bedford Basin

significant ($0.033 \text{ mmol m}^{-3} \text{ year}^{-1}$, $r^2=0.51$, $p=0.0001$), but that of Chl is only weakly significant ($0.034 \text{ mg m}^{-3} \text{ year}^{-1}$, $r^2=0.13$, $p=0.10$). Increases are also strongly evident in annual averages of NH_4 ($0.043 \text{ mmol m}^{-3} \text{ year}^{-1}$, $r^2=0.70$, $p=0.0007$) and PO_4 ($0.0075 \text{ mmol m}^{-3} \text{ year}^{-1}$, $r^2=0.63$, $p=0.000006$) but not in SiO_3 ($-0.024 \text{ mmol m}^{-3} \text{ year}^{-1}$, $r^2=0.09$, $p=0.16$; Fig. 5).

Inter-decadal Pattern Decadal concentration, calculated as the intra-decade average of annual average values, has

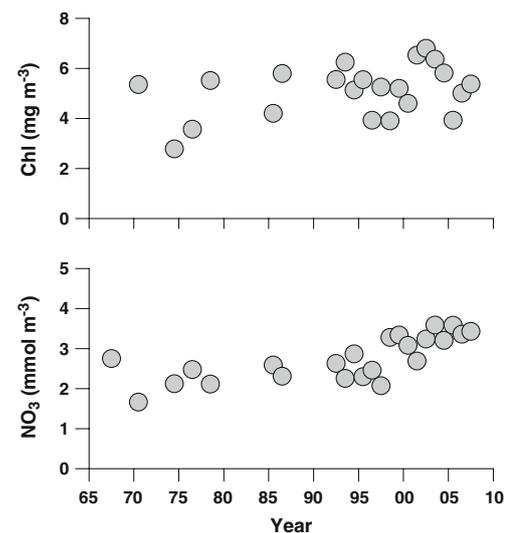


Fig. 4 Time series of chlorophyll (mg m^{-3}) and nitrate (mmol m^{-3}) averaged on an annual basis

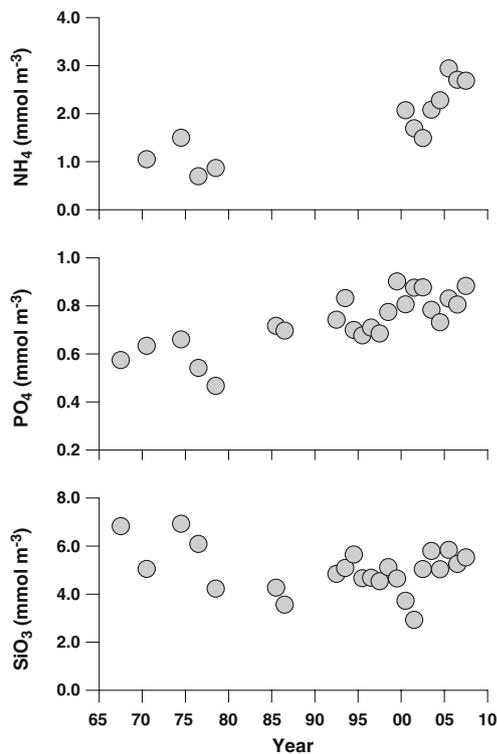


Fig. 5 Time series of ammonium (mmol m^{-3}), phosphate (mmol m^{-3}), and silicate (mmol m^{-3}) averaged on an annual basis

increased for both Chl ($0.38 \text{ mg m}^{-3} \text{ decade}^{-1}$, $r^2=0.93$, $p=0.04$) and NO_3 ($0.37 \text{ mmol m}^{-3} \text{ decade}^{-1}$, $r^2=0.95$, $p=0.02$; Fig. 6).

Multiscale Correlations On an hourly average basis (Fig. 7a), during the dark period of the diel cycle when

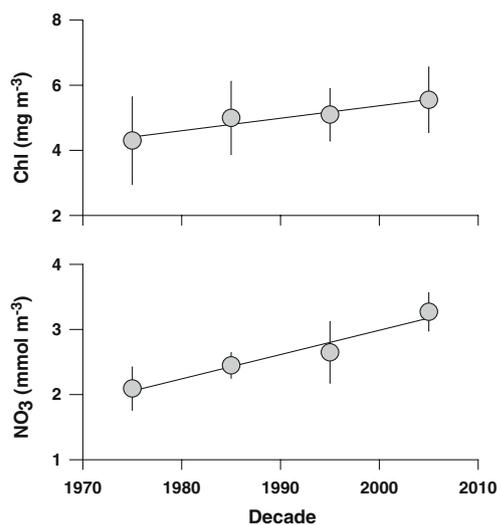


Fig. 6 Time series of chlorophyll (mg m^{-3}) and nitrate (mmol m^{-3}) averaged on a decadal basis. Error bars indicate intra-decade standard deviation

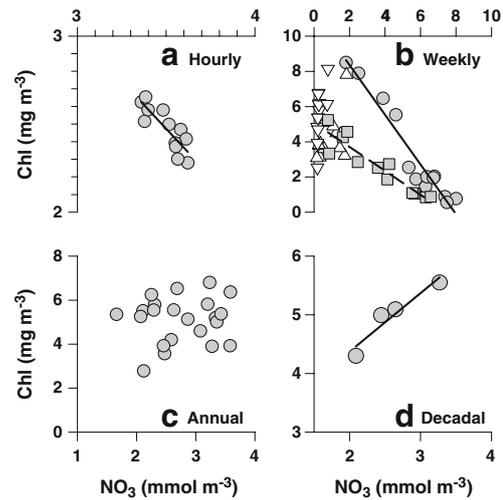


Fig. 7 The nitrate–chlorophyll relationship at various time scales. **a** Hourly averages during the dark period (1800–0600 hours). **b** Weekly averages partitioned by quarters: weeks 1–13 (filled circles), weeks 14–26 (open triangles), weeks 27–39 (open inverted triangles), and weeks 40–52 (filled squares). **c** Annual averages. **d** Decadal averages. Linear regression statistics are given in the text

phytoplankton are not photoinhibited, there is a strong negative relationship between NO_3 and Chl ($-1.08 \text{ mg Chl m}^{-3} (\text{mmol N m}^{-3})^{-1}$, $r^2=0.71$, $p=5 \times 10^{-4}$). On a weekly average basis (Fig. 7b), during the first quarter of the year (weeks 1–13), a similar negative relationship exists ($-1.41 \text{ mg Chl m}^{-3} (\text{mmol N m}^{-3})^{-1}$, $r^2=0.94$, $p=6 \times 10^{-8}$). The relationship dissolves in the second and third quarters but is re-established in the fourth quarter (weeks 40–52) at a lower level of response ($-0.68 \text{ mg Chl m}^{-3} (\text{mmol N m}^{-3})^{-1}$, $r^2=0.88$, $p=3 \times 10^{-6}$).

On an annual average basis (Fig. 7c), NO_3 and Chl are uncorrelated ($r^2=0.009$, $p=0.68$). Including NH_4 as a component of dissolved inorganic nitrogen still fails to yield a predictive relationship ($r^2=0.04$, $p=0.55$). However, on a decade average basis (Fig. 7d), a strong positive relationship emerges ($1.00 \text{ mg Chl m}^{-3} (\text{mmol N m}^{-3})^{-1}$, $r^2=0.91$, $p=0.04$).

Inter-province Pattern In the northern hemisphere and in both Atlantic and Pacific Oceans, a general south-to-north increase is observed in Chl and NO_3 when values are averaged within biogeochemical provinces (Fig. 8; see also Lewis et al. 1988). However, there is substantial idiosyncrasy and discontinuity in this geographic pattern because only three of the provinces (ARCT, BPLR, NWCS) are sampled extensively and regularly. The pattern is not as clear in our data in the southern hemisphere provinces since they were only sampled within a narrow latitudinal band, missing both the equator and pole. In spite of sampling non-uniformity, a strong

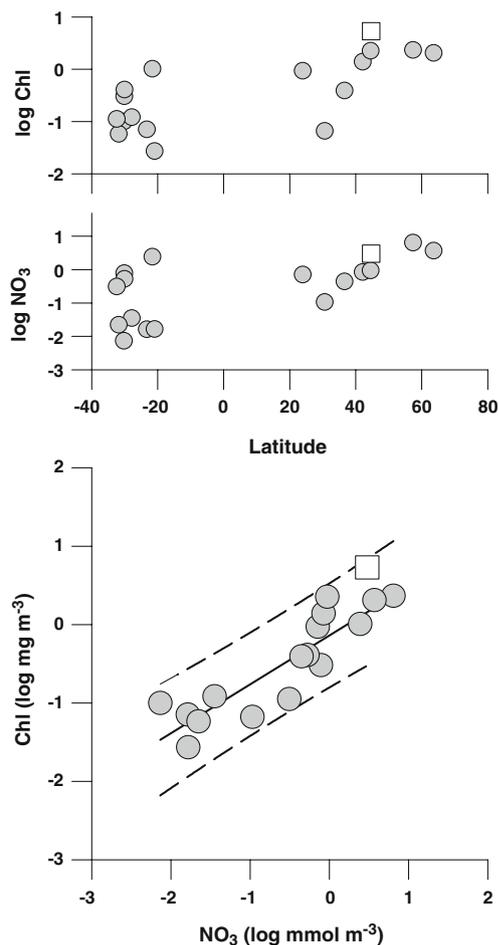


Fig. 8 Chlorophyll and nitrate concentrations in surface waters averaged into 16 biogeochemical ocean provinces indicating spatial distribution by latitude (*upper panels*) and the bivariate relationship, showing linear regression (*solid line*), 95% prediction limits (*dashed lines*), and long-term average state in Bedford Basin (*open square*)

positive relationship exists between the variables: $\log \text{Chl} = -0.14 + 0.62 \log \text{NO}_3$ ($r^2 = 0.79$, $p = 4 \times 10^{-6}$). The long-term average values in Bedford Basin are within the 95% prediction limits of this relationship (Fig. 8).

Discussion

Ecological patterns are widely observed tendencies in nature, but even for the same objects, patterns differ according to the scale of perception (Li 2007). The relationship of pattern and scale is thus of central concern in ecology but presents a difficulty to ocean management because the dynamics of environmental change and human behavioral response are mismatched (Levin 2000). This difficulty is exacerbated in coastal waters because environmental change is driven by many factors acting simulta-

neously but with different time scales (e.g., Lewis and Platt 1982). For example, nutrient enrichment and climate change are globally important, but local stressors such as toxic contaminants, hydrologic manipulations, and others cannot be discounted (Cloern 2001). The problem of understanding phytoplankton change in coastal waters can be approached by first recognizing the biotic response to natural forcing as a result of Earth's orbit around its own axis and around the sun, then by discerning coherent variation of driver and response at longer time scales, and finally by seeking a spatial similitude. This is not an ineluctable prescription, but we will show that our empirical results provide clear demonstration of a tenet concerning general laws in ecology.

In Bedford Basin, an increase in Chl accompanies a decrease in NO_3 but only at sub-annual time scales. At the hourly scale (Fig. 7a), processes of cellular physiology transform dissolved nutrient from seawater into additional particulate biomass. Cell growth occurs every day when nutrients and other resources are available. At the weekly scale, population processes (birth, death, immigration, emigration) are superposed. At the seasonal scale (Fig. 7b), community processes (competition, species interactions, succession) are further superposed. A net change of biomass at this scale is a community-wide result, and this result is different according to seasons because meteorology, hydrology, and hydrography change throughout the year (Li and Dickie 2001; Li and Harrison 2008).

It is remarkable that, when these time scales are crossed, the stoichiometric conversion of N to Chl remains essentially unchanged in spite of increased complexity. Our measurements indicate a relationship of $-1.1 \text{ mg Chl m}^{-3} (\text{mmol N m}^{-3})^{-1}$ at the intra-day scale, representing cellular conversion. Yet the relationship is not greatly different at the weekly scale during the spring bloom with a value of $-1.4 \text{ mg Chl m}^{-3} (\text{mmol N m}^{-3})^{-1}$, representing population and community processes, and close to the average of early investigations of cellular chlorophyll to nitrogen ratios of natural marine phytoplankton ($1.6 \text{ mg Chl m}^{-3} (\text{mmol N m}^{-3})^{-1}$; Yentsch and Vaccaro 1958). The incorporation of 1 mmol N into phytoplankton requires a Redfield stoichiometric balance of 6.6 mmol C, whose mass equivalent is 79 mg C. In Bedford Basin, the average C/Chl mass ratio is 70 (Harrison and Platt 1980). Therefore on average, 1 mmol N converts to 1.1 mg Chl, quod erat demonstrandum.

The apparent regularity across scales in the stoichiometric conversion of nitrogen to chlorophyll is a nontrivial result. It may depend on the fact that the Redfield ratio itself is a macroscopic property, being an empirical statistical average and not a fundamental biochemical constraint (Li 2007). Phytoplankton species differ considerably in elemental composition, and the Redfield ratio

results from an appropriate mix of stoichiometric types (Klausmeier et al. 2004). Furthermore, since elemental stoichiometry in phytoplankton depends on relative specific growth rate (Goldman 1980), the cross-scale regularity emerges from both physiology and community assembly. Notably, in winter, the relationship between NO_3 and Chl takes a different value (Fig. 7b), indicating that winter nutrient recharge by physical mixing cannot be viewed as the opposing process of spring biological nutrient draw-down. During mid-year when NO_3 is reduced to limiting concentrations, Chl is sustained by NH_4 (Fig. 5).

Bedford Basin is a location at the land–sea interface that exhibits strong and recurrent phytoplankton seasonality (Fig. 3), driven largely by temperature-dependent water stratification (Li and Harrison 2008). However, this seasonality is not universal. A recent analysis of 114 estuaries, lagoons, inland seas, bays, and shallow coastal waters around the world shows a broad continuum of seasonal patterns, as indicated by continuous distributions in the timing and amplitude of phytoplankton biomass cycles (Cloern and Jassby 2008). A strong seasonal signal of nutrient-driven phytoplankton dynamics (Fig. 7b) may not be evident in many land–sea interface systems where other drivers or multiple stressors (Cloern 2001) may dominate local and regional processes.

The regular cycles of a day and a year are both natural time scales for phytoplankton, but it is the latter that largely sets the course of community assembly, through proximal events in the annual cycles of meteorology, hydrology, and hydrography. At the end of every year, the system returns to a state not too far removed from its initial state. However stochasticity and contingency ensure that no 2 years are exactly the same, either in detail or in aggregate. To discern trends extending further in time, fine low-level details need to be suppressed so that the high level aggregate behavior can be discerned. Coarse-grain rescaling of high-resolution data into annual bins reveals the interannual relationship of Chl to N, which turns out to be statistically nonsignificant (Fig. 7c), even when NH_4 is included. This apparent failure to predict over time based on what is surmised over regional and global space is a challenge to the principle of ergodicity. Yet this space-for-time substitution is often taken for granted when macroecology is applied towards problems of global change (Kerr et al. 2007).

In Bedford Basin, an annual increase in surface nutrients does not inevitably lead to an annual increase in Chl. The availability of nutrients to phytoplankton is proximally determined by effective mixing of the large pool of nutrient-rich water from depth, even if anthropogenic enrichment is delivered at the surface. Temperature has strong seasonal variation, but yearly averages are not very different. On the other hand, salinity has weak seasonal variation, but yearly averages are substantially different.

Thus, at the interannual scale, changes in stratification are related to changes in salinity. This is a macroscopic result derived in principle from the net summation of all temperature and salinity changes that transpire over a year. In this system, annual average Chl is related not directly to surface concentrations of NO_3 (Fig. 7c) but rather to the concentration difference between deep NO_3 and surface NO_3 , which is a reflection of stratification measured by seawater density; it relates directly to the vertical flux of nitrate from deep to surface waters (Li and Harrison 2008). Thus, the sustained increase of N in surface waters over 40 years (Fig. 4) is modulated by interannual changes in stratification to yield an indeterminate pattern in Chl (Fig. 7c). However, a reductionistic analysis of this community-wide pattern indicates differential responses by functional groups. Picoeukaryotic algae, which subsist within the microbial loop dependent largely on recycled nutrients, indeed exhibit positively correlated annual change with N (Cullen et al. 2007), whereas diatoms are strongly responsive to annual change in stratification and the resultant new production driven by vertical nutrient inputs (Li and Harrison 2008). The pattern observed at the level of bulk Chl is the net outcome of different responses at a lower level of organization.

At the longest time scale afforded by our measurements, a strong relationship exists between N and Chl (Fig. 7d). A time interval of a decade has no apparent natural basis in phytoplankton ecology, but it is a cultural norm and therefore of significant importance. At this scale, the dependence of Chl on N has essentially the same numerical value as at lower scales, but the algebraic sign is opposite. The apparent regularity of this stoichiometry at sub-annual scales is obscured at the annual scale but re-emerges at the decadal scale. At the long time scale, the interannual variations of stratification are subsumed, revealing an increase in Chl correlated with an increase in N, namely the signature of eutrophication. Our cross-scale study clearly demonstrates a general ecological tenet: at low levels of organization, organismal biology and population ecology are not complicated too much by particular circumstances of space and time; at intermediate levels, community ecology is overwhelmingly complicated by contingency; but at high levels, macroecology displays a statistical order that emerges from detail-free patterns (Lawton 1999).

We have not investigated the source of long-term nutrient enrichment in Bedford Basin and therefore cannot evaluate local (anthropogenic), regional (advective), or global (atmospheric) contributions. However, selective enhancement of N and P but not Si, as seen in Bedford Basin, is a common characteristic of human activities (Cloern 2001). Notwithstanding the source of enrichment, we find the long-term average state of Bedford Basin to be located within the

statistical boundaries of the global domain of Chl and NO₃ (Fig. 8). Parenthetically, it may be argued that the local effect of significant NH₄ contribution to phytoplankton biomass accounts for the slight positive vertical discrepancy from the line of best fit. Ultimately, at large scales of space and time, proximal events are far removed, yet the scaling of Chl on N is similar across a multitude of complex systems. Self-organization of pelagic autotrophic communities is demonstrably plausible (Follows et al. 2007). Further, “the metabolism of ecosystems is empirically more universal than their partitioning according to the roles and interactions of species” (Morowitz and Smith 2007), leading to the idea that ecosystems might be better understood as a tension between countervailing forces at different time scales (Johnson 2006). Much like weather variance propagates at different scales to climate variability (e.g., Hasselman 1976), high frequency physical and biological fluctuations propagate to long-term change in coastal ecosystems. Perception of the nutrient–phytoplankton relationship at macroscopic scale thus provides the verisimilitudinous basis for adopting ocean management strategies that are matched to the ecological dynamics of coastal eutrophication.

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