

Temporal scales of drivers of community dynamics: from microbes to macrofauna across the salinity gradient.

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Abstract

The abundance and distribution of organisms in aquatic systems are affected by drivers operating at diverse temporal and spatial scales. Understanding interactions among organisms and with their environments is dependent on matching population and community dynamics with drivers at relevant scales, which can range from hours to decades. Here, we review how physical, chemical, and biological processes operating at these varying scales affect the abundance and the distribution of organisms in aquatic ecosystems spanning the “salinity gradient”: lake, stream, and coastal ocean. We highlight ecosystems that are representative of the different aquatic regimes and perform a conceptual synthesis of the similarities and differences among those systems. Our review underscores the important role drivers related to annual cycles of heat, light, and wind and water movement, for instance, play in structuring the physical, chemical, and biological constituents across fluid aquatic environments. Interannual to decadal variability in population dynamics across the salinity gradient is often related to long-term shifts in climate cycles or climate change; however, climate has differential effects in the coastal ocean (e.g. shifts in current strength), lakes (e.g. climatological variability in ice cover) and streams (e.g. decadal oscillations impacting salmon runs). We identify several potential avenues for future research, including long-term forcing in lakes and streams; the drivers and effects of high-frequency, episodic disturbance events; the influence of variability on eco-evolutionary feedbacks; and nonlinear effects of climate forces on ecosystems. We recommend maximizing the effectiveness of investigations across multiple temporal scales through programs using a variety of approaches including long-term monitoring and short-term, event-driven responses, and a new generation of tools and analytical approaches capable of resolving nonlinear dynamics over time in complex aquatic ecosystems.

Section 1. Introduction

The abundance and distribution of organisms in aquatic systems are impacted by drivers operating at diverse temporal and spatial scales. Differences in processes acting on short- or long-term or near and distant scales can represent the time or space required for change to occur in community

descriptors (e.g., abundance or biomass; Powell 1995). These scales can also indicate the time or space required for recovery of ecosystems following disturbance (i.e., resilience). While the multiple scales of variability acting simultaneously on an ecosystem may represent an obstacle to study, the scales over which different drivers act may also inform us about the importance of different driving processes within an ecosystem (Kratz et al. 1987). Our ability to understand interactions among organisms and with their environments is therefore dependent on matching population and community dynamics with the scales of the relevant drivers. These scales can range from hours and days, to seasons, years, and decades.

A comprehensive understanding of the temporal scales at which important physical, chemical, and biological processes operate in aquatic environments is further necessary to understand their response to anthropogenic disturbances,

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which involve simultaneous changes in multiple parameters (Paine et al. 1998) and may induce regime shifts (Beisner et al. 2003; Carpenter 2003; Scheffer et al. 2001). Organisms can differ in their responses to the same disturbance depending on its frequency of occurrence, intensity, and temporal extent (i.e., pulsed versus chronic). Such response diversity may be related to the frequency of dominant drivers in their respective ecosystems (Elmqvist et al. 2003). For example, intermediate levels of disturbance in time (and space) in a habitat can contribute to the maintenance of biodiversity whereas high levels of disturbance can degrade it (Connell 1978). Maintaining biodiversity has the potential to drive further evolutionary development via both sympatric and allopatric speciation (Feder et al. 2003; Filchak et al. 2000). Variability in organisms' responses to short- and long-term drivers may also be related to rates of metabolism, reproduction, adaptation, and evolution, all of which scale with organism size and trophic level (Anderson-Teixeira et al. 2001; Peters 1983). For these reasons, consideration of the scales at which physical, chemical, and biological drivers operate and their effects on organisms, populations, and communities is fundamental to any ecological study (Levin 1992).

Our goal here is to provide a qualitative review of drivers affecting different trophic levels at various temporal scales in aquatic ecosystems spanning the "salinity gradient:" lake, stream, and coastal ocean. Humans' perception of organisms in space and time is heavily influenced by scales of variability (e.g., Condon et al. 2012), and hence consideration of scale is particularly critical when designing field investigations and when multiple trophic levels or whole watersheds are involved. This chapter differs from other reviews of the importance of scales (e.g., Colijn 1998; Powell 1995) through consideration of aquatic ecosystems ranging from freshwater to the coastal ocean and integration of bottom-up (environmental) and top-down (trophic) drivers. Our ultimate goal is to provide the reader with an appreciation for the different temporal scales at which environmental drivers operate in different aquatic ecosystems, and the relative importance of time scale to different trophic levels. We do this by presenting case studies that are representative of different aquatic ecosystems, and performing a qualitative synthesis of the similarities and differences among those systems.

Section 2. Case study sites

To simplify the discussion of dominant temporal scales across trophic levels and aquatic ecosystems, three case study sites were identified that each exemplifies a different aquatic ecosystem. Sites were chosen that had a rich scientific history, revealing long-term trends while also employing high frequency sampling to investigate variability at shorter time-scales. The North Temperate Lakes (NTL) and California Current Ecosystem (CCE) sites are part of the Long-term Ecological Research (LTER) program, funded by the National Science Foundation. Datasets from Hubbard Brook in New

Hampshire, USA, were combined with those from Chester County in Pennsylvania, USA, and Broadstone Creek in the southeastern region of the U.K. to provide a range of parameters measured in streams at a range of temporal resolutions.

Drivers considered include physical, chemical, and biological processes which affect biomass and the distribution of species at several trophic levels. Multiple time scales allowed us to evaluate not only seasonal and annual changes, but also short-term events that are physical (e.g., flood events), chemical (e.g., pollution), or biological (e.g., invasive species) in nature. The chosen study sites measured overlapping parameters of all three broad types. Temporal variability is discussed in the following sections in the context of these identified parameters at the chosen case study sites.

Streams

Stream environments change rapidly along the continuum from small headwater streams to large rivers and the important temporal drivers of communities shift along that gradient as well. Small streams tend to be much more temporally variable environments than larger streams and rivers (Poff and Ward 1989). In smaller systems the metabolism varies from year to year, across seasons, from day to day, on a diel basis, and in response to major disturbances (Holtgrieve and Schindler 2011; Roberts et al. 2007).

The natural flow regime is an important part of the stability of a stream community (Poff et al. 1997). At short ecological time scales (monthly to annual), changes in flow regime (e.g., spring floods and summer droughts) can be major disturbances wiping out whole populations of invertebrates present in smaller systems whereas these same events may have minimal impacts in larger downstream rivers and can actually lead to greater system stability in the long-term (i.e., decadal time-scales). Droughts can lead to drying and the elimination of above ground wetted habitat (Beche et al. 2009; Lake 2003). Whereas some species are able to persist in hyporheic pockets of subsurface flow (Collins et al. 2007), these events are a strong environmental filter extirpating many species including fish and macroinvertebrates (Chase 2007; Clarke et al. 2010). Storms can have similarly devastating effects to the biota of small streams. Significant flows can create scour that destroys the benthos (Walsh et al. 2005). Washouts and inputs of terrestrial material in earth slides can similarly extirpate entire reaches of biota (Gomi et al. 2002).

Resources change predictably throughout the year in temperate forested streams. Notable seasonal pulses include spring algal growth when water temperatures are warming and light is still penetrating the open canopy, and the contribution of carbon and nutrients to the system from autumn leaf fall (Roberts et al. 2007; Webster and Benfield 1986). These changes in resources may lead to predictable shifts from heterotrophy in the fall to periods of autotrophy in the spring. Small streams have species that are adapted to variable environments and many have morphological adaptations to drought

(Brown et al. 2011). Fish are less common in small streams and the resident invertebrates tend to be colonizers able to rapidly (within a year) return after an extirpation event (Patrick and Swan 2011).

Downstream systems display less variability in terms of resources, disturbances, and intra-annual variation in temperature (Vannote and Sweeney 1980; Vannote et al. 1980). Whereas the same factors (drought and floods) will have an effect on larger creeks and rivers, the magnitude of the effect on the biota is less. Downstream invertebrate species tend to be more generalist, taking advantage of the range of resources being exported from upstream systems. These larger streams and rivers have more trophic levels, in the form of insectivorous and piscivorous fish, as well as phytoplankton eating fish in large rivers (Thorpe et al. 2006; Vannote et al. 1980).

Within streams and rivers, the macroinvertebrate community undergoes predictable intra-annual shifts in community composition following the seasons. Many of the organisms are univoltine, and their temporal niches are off-set to take advantage of the changing resources throughout the year and reduce interspecific competition. Stream benthic communities can be significantly different in the fall, winter, spring, and summer, and higher trophic levels that live for multiple years show less intra-annual variation in community composition.

There are a number of other factors potentially affecting the temporal dynamics and stability of stream systems. Acidification, or drop in pH, is one example of a well-studied phenomenon in stream ecosystems (Likens et al. 1996). pH declines occurred as a multi-decadal trend in temperate North America and Europe during the twentieth century because of deposition of aerosolized nitrogen and sulfur species, NO_x and SO_x (Layer et al. 2011). This acidification led to gradual shifts in species composition and loss of game fish in areas with low buffering capacity, whereas streams with a strong buffering capacity (i.e., limestone or dolomite) were able to resist large changes (Schlesinger 1997). In this context, spatial variation in underlying geology led to spatial variation in temporal patterns of the response to a press disturbance (i.e., acid rain).

While acidification is on the decline, new stressors are emerging. For example, the effect of chemical road salts on streams is becoming a larger issue in urbanized regions (Kaushal et al. 2005). Road salts (NaCl) used to winterize roads accumulate in soils and make their way into freshwater systems. Preliminary work on this contaminant shows that increases in the salinity of inland waters can have a variety of impacts on aquatic biota, particularly amphibians (Karraker et al. 2008). Furthermore, the effect of road salts appears to be compounding over time as the buffer capacity of soils is reduced (Kaushal et al. 2005).

Understanding the different scales of temporal variability that affect stream communities, and the spatial variation in that temporal variability, is a crucial part of predicting how streams will respond to human impacts and climate change.

The collection of high resolution long-term data sets and experiments at varying time scales are necessary first steps to forecasting into the future. Our search for a single stream data set that included high resolution sampling (intra-annual) for fish, invertebrates, and the physical environment over decadal time scales was unsuccessful, though discrete datasets at either high resolution (e.g., US Geological Survey Water Quality Watch, <http://waterwatch.usgs.gov/wqwatch/>) or sustained over several years (e.g., US Environmental Protection Agency Rapid Bioassessment program, <http://water.epa.gov/scitech/monitoring/rsl/bioassessment/>) do exist. This gap suggests a need for this type of temporally integrated monitoring that is not currently being met.

Northern temperate lakes

In areas subjected to glaciation, lakes occur in high densities, such as in the Northern Highland Lake District in northern Wisconsin where the North Temperate Lakes Long Term Ecological Research site (NTL-LTER) is located. Since the early 1980s, this research program has sought to understand the long-term ecology of lakes and their interactions with terrestrial, atmospheric, and human processes. Lakes within this area share the same geology (silicate sand) which allows significant groundwater fluxes and determines key water-chemical parameters. The close spatial proximity also results in similar weather and climate conditions for these lakes, which drive temperature and light regimes. Yet, despite the shared basic characteristics, lakes within the district differ in nutrient load, ionic composition, acidity, and species richness (Kratz et al. 2003).

The position of a lake in the landscape provides a further basis for understanding variability in physicochemical characteristics and biotic dynamics. Lakes receive water from surface runoff, groundwater inflow and precipitation, and in general, lakes higher in a landscape receive relatively more water from precipitation than lakes lower in the landscape (Lottig et al. 2011). This shifting balance of water sources to lakes along an elevation gradient results in predictable changes in physical, chemical, and biological factors. For instance, using semi-conservative cations as tracer, Webster et al. (1996) could show that a lake's landscape position influenced the limnochemical response to drought. However, as lake size increases their biogeochemical attributes converge due to a diversification of flow paths to larger systems, greater biogeochemical processing, and changes in landscape composition (Lottig et al. 2011).

One of the main research focuses on the NTL-LTER has been on synchrony and coherence of variables between lakes over large regional scales and within seasons (Baines et al. 2000; Kratz et al. 2003). Observing regional synchrony in distinct ecosystems was used to deduce the influence of climate variability on lake water temperature, pH, and water color (Baines et al. 2000; Pace and Cole 2002) using data collected during more than a decade. Surface temperature which is mainly determined by insolation, air temperature, and wind, actually showed a high degree of synchrony among the lakes

(Magnuson et al. 1990). While environmental and chemical variables and their temporal variability have been recognized as drivers of biological processes, population dynamics of zooplankton (Rusak et al. 1999, 2002, 2008), primary producers (Baines et al. 2000; Marshall and Peters 1989), and fish (Olden et al. 2006) have been explicitly addressed in more focused publications.

Eutrophication of lakes worldwide is linked to overfertilization by phosphorus which stimulates algal blooms, resulting in the accumulation of toxins, modified foodwebs, and diversity loss. Assessment of phosphorus (P) loads spanning several decades has shown that during extended periods of drought, P loads, and summer total P concentrations decline. Studying the Yahara River chain of lakes (Mendota, Monona, Waubesa, and Kegonsa near Madison, Wisconsin, USA), Lathrop and Carpenter (2014) showed that in years when P loads are high due to major runoff events, summer total P in these lakes was high, ultimately releasing algae growth from P limitation. Moreover, landscape position determines P input, because P is passed from one lake to another and increases with flushing rates, allowing for probabilistic modeling of management actions in lakes across different regions (Carpenter and Lathrop 2014).

A prominent sign of climate forcing on lake ecosystems is the time of formation and disappearance of lake ice, with profound effects on lake ecosystems, such as water level fluctuations or the formation of anoxia. Using datasets starting in the 1850s, variability in lake ice cover has been used to identify extreme events, i.e., extremely early or late freeze or breakup, respectively (Benson et al. 2012). Mean ice duration has been shown to decline, driven mainly by earlier break-up dates, and this decline has accelerated during the last decades.

As a result of this rich history of research, limnologists have quantified seasonal and regional drivers of temporal variability and synchrony relatively well. Regional comparisons on multiple timescales are perhaps unique in this context (Kratz et al. 1991); however, there is a dearth of published information regarding the effects of disturbance or extreme events on temporal dynamics across multiple trophic levels.

Coastal ocean

At the intersection of the land, open sea, and atmosphere, coastal oceans are arguably among the most dynamic of all the marine ecosystems. Among them, the California Current ecosystem (CCE) is one of the most extensively studied given its ecological and socio-economic import. The CC is the eastern extent of the anticyclonic North Pacific Gyre, transporting cool, low salinity subarctic water south (Venrick 2009). As a result of the equator-ward flow of the CC, the CCE is as a coastal upwelling biome, supporting high levels of primary production and a large number of active fisheries. The California Cooperative Oceanic Fisheries Investigations (CalCOFI) program has been conducting quarterly research cruises off the coast of California for almost 70 years in

response to the collapse of the sardine fisheries in the late 1940s. More recently, the CCE-LTER site has built upon the ongoing CalCOFI dataset, specifically focusing on mechanisms leading to transitions over time between different states of the pelagic ecosystem.

Physical, chemical, and to some extent, biological parameters in the CCE are dominated by seasonal, interannual, and decadal scales of variability. Water temperature in the CCE varies seasonally, with the most pronounced fluctuations at the surface, and on interannual and decadal scales in conjunction with the El Niño Southern Oscillation (ENSO), Pacific Decadal Oscillation (PDO), and North Pacific Gyre Oscillation (NPGO; Kim et al. 2009; Venrick 2009). Decadal signals are also apparent in salinity in the CCE, correlated mainly with climate indices including the PDO and NPGO (Kim et al. 2009).

Seasonal variability in phytoplankton biomass is largely apparent as climatological spring blooms of diatoms in the CCE, while interannual and decadal variability on the scale of 20-30 years is also evident and largely correlated with ENSO, PDO, and NPGO (Kim et al. 2009; Mantyla et al. 2008). The 1997-1999 El Niño-La Niña transition, for example, is evident in time series of chlorophyll (Mantyla et al. 2008), while magnitude and timing of the spring bloom at the Scripps Pier has shown three distinct climatologies since the 1980s (Kim et al. 2009). Phytoplankton community composition in the CCE shows distinct variability on seasonal timescales, as siliceous phytoplankton flux peaks strongly in the spring, and interannually with ENSO (Venrick et al. 2008). Similarly, net primary production (NPP) varies on an annual cycle, driven largely by transitions between the relatively stable, high-light water columns of summer to the turbulent, low-light winter water columns (Mantyla et al. 2008), and on decadal cycles, as suggested by multi-year increases in satellite-derived NPP annual maxima from 1997-2007 (Kahru et al. 2009). At higher trophic levels, variation in zooplankton and ichthyoplankton biomass on seasonal scales can be attributed to several different processes depending on the time of year, including increased phytoplankton production during spring and fall turn-over, advection of nutrients, and biomass with changes in the strength of the CCE, coastal and wind-stress curl induced upwelling, and the development of coastal jets and eddies (Macías et al. 2012; Roesler and Chelton 1987).

In addition to strong seasonal and interannual variability in algal bloom magnitude and duration (Santoro et al. 2010), phytoplankton biomass also shows episodic, high frequency variability in the nearshore environment, as blooms tend to occur on the order of weeks-months (Kim et al. 2009; Ryan et al. 2009). Higher frequency temporal variability has been shown to play an important role in chemical and biological constituents of the CCE. Inorganic nutrients, such as nitrate, ammonium, and phosphate show high frequency (days-weeks) variability likely due to wind-driven convection (Mantyla et al. 2008) and upwelling (Omand et al. 2012), both of which inject

significant nutrients into the surface layer. On shorter time-scales (e.g., hours), these nutrients are also strongly influenced by the stage of diurnal tides (Santoro et al. 2010).

Variability in zooplankton and fish populations on longer time-scales (interannual-decadal) in the CCE are driven both directly and indirectly by basin-wide and regional-scale climatic forcing. Changes in biomass, assemblage diversity, and species geographic ranges have been linked to shifts in several atmospheric phenomena, including NPGO (Di Lorenzo et al. 2008), ENSO (Chavez et al. 2003, McGowan et al. 1998), the North Oscillation (Schwing et al. 2002), and the PDO (Mantua et al. 1997) through their effects on biophysical conditions in the northeast Pacific. ENSO is a dominant driver of interannual variability in CCE plankton and demersal and forage fish populations, with shifts in community structure, biomass, and productivity often responding to changes induced by El Niño or La Niña events every 5.0-6.3 years (Lavaniegos and Ohman 2007; Miller and Schiff 2012; Smith and Moser 2003). Such decadal and multi-decadal variations in zooplankton, ichthyoplankton, and fish populations have been a topic of great interest given implications for the management of the Pacific sardine (*Sardinops sagax*), anchovy (*Engraulis mordax*), and the Pacific salmon (*Onchorhynchus* spp.) fisheries. Low-frequency changes in northeast Pacific conditions are thought to be driven by shifts in PDO that occur every 15-25 years (Mantua and Hare 2002) as well as NPGO (Di Lorenzo et al. 2008). Changes in the PDO over the past fifty years (i.e., 'regime shifts') are thought to have occurred in 1947, 1978, and 1998 and have had effects on zooplankton biovolume (Roemmich and McGowan 1995) and species composition (Lavaniegos and Ohman 2003); geographic distributions of larval oceanic fishes and historically offshore taxa (Hsieh et al. 2009; Smith and Moser 2003); forage fish abundances (McClatchie et al. 2008); and chinook and coho salmon survival (Peterson and Schwing 2003).

Section 3. Synthesis and discussion

Similarities and differences across aquatic ecosystems.

Case studies presented here illustrate the importance of light and temperature, water level fluctuation, and nutrient availability as environmental drivers in all aquatic biomes, suggesting that findings from one aquatic biome may stimulate research in another. For instance, the effects of varied light availability in streams due to canopy cover could possibly be translated to ice cover in lakes and to turbidity and shading from microalgal blooms and macrophytes in coastal marine environments. Similarly, water level fluctuations have been intensely studied in streams in the context of flood and drought and in coastal ecosystems in relation to tidal dynamics; however, much less information is available about the effects of water level fluctuation in lakes. However, the scales of temporal variation considered as relevant in these distinct aquatic habitats differs, and the question remains to what extent this is caused by scientific tradition and limitations

in technology and funding to carry out high resolution or long-term observations, rather than actual relevance. In this section, we pinpoint some of the similarities and differences in temporal scales of environmental drivers (Table 1), and we hope that such cross-system comparison may advance different aquatic disciplines to test applicability of concepts across the salinity gradient.

Across aquatic ecosystems, drivers related to annual cycles of heat, light, and wind and water movement play a large role in structuring the physical, chemical, and biological constituents of the fluid environments. Annual timescales might reflect the life span of aquatic organisms such as invertebrates and fish, and annual variation in physical environments often impact ontogenetic processes with potential evolutionary consequences. Most of our knowledge, however, is based on research conducted in temperate regions of the northern hemisphere and the dearth of research on tropical ecosystems limits our understanding of temporal dynamics in the absence of seasonality. Similarly, temporal dynamics of populations and communities in polar regions, with their extremes of heat and light, should also be a priority for providing further insights into such eco-evolutionary coupling.

Interannual to decadal variability is often related to longer term shifts in climate cycles or climate change while short-term, episodic events can have significant impacts on the ecosystems as sources of disturbance. In general, decadal and multi-decadal scales play a primary role in structuring coastal marine ecosystems (e.g., CCE) through variability in current strength, temperature patterns, and general climatological conditions. Long-term processes are less well studied in temperate lakes or streams. Decadal processes are evident in lakes as variability of the duration of ice cover or nutrient loads, with strong effects on timing of phytoplankton blooms and mixing (Benson et al. 2012; Lathrop and Carpenter 2014). Streams affected strongly by runs of salmon, driven in part by decadal oscillations, show long-term coupling as well (Naiman et al. 2002). While these few examples of long-term forcing in lakes and streams are not exhaustive, it is also possible that they represent a gap in the freshwater literature rather than lesser influence of long-term processes in these aquatic ecosystems. These relatively few examples may also be tied to a unique feature of stream ecosystems, namely their spatial gradients of temporal variability with smaller, upstream bodies being more highly variable than their larger, downstream counterparts.

Across all ecosystems, there is a general dearth of information regarding the drivers and effects of high-frequency, often episodic disturbance events. Using an automated monitoring system deployed for several years in an Alpine stream, Peter et al. (2014) reported seasonal, diurnal, and event-driven dynamics of CO₂ partial pressure related to catchment processes (soil respiration, bedrock weathering), metabolic processes, and dilution. Temperature and light-dependent metabolic processes tended to build up diurnal amplitudes of CO₂, whereas

Table 1. Summary of dominant drivers at the scales of hours-day, days-week, seasonal, annual, decadal in streams, lakes, and the coastal ocean. This synthesis is based on literature from the case studies presented in the manuscript. NPP, net primary production; PDO, Pacific Decadal Oscillation; ENSO, El Niño Southern Oscillation; NPGO, North Pacific Gyre Oscillation; AMO, Atlantic Multidecadal Oscillation; NAO, North Atlantic Oscillation; MJO, Madden-Julian Oscillation; NPP, net primary productivity.

System	Time scale	Driver	Response variable	Stochastic low/high	Expected change to stochasticity in response to climate change
Stream	Hours-day	Diel cycle		Low	N/A
	Days-weeks	Flood	Community identity, substrate composition, geomorphology	High	Climate change may change frequency and intensity of flood events
	Seasonal	Leaf fall, temperature change	Spring algae, carbon availability, community shifts, heterotrophy versus autotrophy	Low	Climate change may change the identity of riparian species and the time at which leaf fall and leaf out occur
	Annual	Drought	Community identity	High	Climate change may change the frequency and intensity of drought events
	Decadal	Acidification	Community identity, decomposition rates	Low	N/A, although human activities which drive climate change all affect acidification
		Salinization	Community identity	Low	As precipitation regimes change during the winter so will the application of road salts or the use of water for irrigation (both of which contribute to salinization)
		PDO, ENSO	Marine-derived nutrient fluxes, heterotrophic activity, hydrologic regime	Low	Decadal climate empirical orthogonal functions may certainly change in frequency
Lake	Hours-day	Weather-related runoff events	Nutrient fluxes, NPP	High	Increase in flood frequency may increase nutrient pulses
	Days-weeks	Diel cycles	Vertical migration, damage and repair	Low	Regional climate may become drier/wetter
		Regional weather		High	
	Seasonal	Blooms	Biomass distribution, dominance	High	Higher temperature may trigger bloom formation
	Annual	Ice-cover duration, mean air temperature	Timing of food web interactions	Low	Shorter ice cover may uncouple pelagic food webs
Decadal	Eutrophication, climate change	Diversity, multiple responses	Low	Extinction risk may increase	
Coastal ocean	Hours-day	Tidal cycles, diel cycles	Nutrient fluxes, NPP, algal blooms	Low	N/A
	Days-weeks	Upwelling, wind-driven convection, freshwater inputs, cold fronts, tropical storms	Nutrient fluxes, phytoplankton and zooplankton bloom development	High	Large scale climate signals (e.g. ENSO) may alter the timing and intensity of coastal upwelling events and tropical storms
	Seasonal	Water temperature, salinity, regional weather, river discharge hypoxia, light, frontal boundaries, eddies, MJO	Phyto-, zoo-, and ichthyoplankton biomass and community structure	High	Alteration of regional weather patterns related to climate change could alter river flow regimes, nutrient inputs, and extent of hypoxia; fluctuations in the MJO affect tropical storm development
	Annual	Water column stratification, light availability;	NPP, Fish and invertebrate early life stages settling or recruiting to adult stocks; ecosystem productivity	Low	Warmer water temperatures possible coupled with increased freshwater inputs could strengthen stratification.
	Decadal	ENSO, PDO, NPGO, AMO, NAO, eutrophication, acidification	Water temperature, salinity; variability of fish populations, biomass, ecosystem productivity	Low	N/A

episodic events such as storms and snowmelt interrupted and dampened these patterns. Caron et al. (2008) showed significant impacts of high frequency but largely predictable changes in wind speed and direction on depth-resolved algal biomass distribution, and studies of lakes in North America, Asia, and Europe suggested that weather-related episodic events could have both short-term effects on thermal structure and more long-lasting effects on dissolved oxygen, water clarity, and algal biomass (Jennings et al. 2012). In the coastal temperate ocean, some studies have revealed significant short-term dynamics of microalgal blooms—biological disturbance events with the potential to throw entire food webs out of balance. In the CCE, these events occur within days and often last less than a week or two. While interannual variability is high in bloom occurrence, magnitude, and duration, such largely unpredictable events appear to be driven much more by local, high-frequency processes (Kim et al. 2009; Omand et al. 2011). In any case, organic matter export and phytoplankton bloom events represent ecologically significant phenomena driven by physical, chemical, and biological processes operating on short scales that require development of new approaches to effectively monitor.

At the other end of the spectrum, the nonlinear effects of climate forces on ecosystems are also not well understood. Climatic drivers operate over years, if not decades, and their impacts on multiple trophic levels are an open area of study. For example, the effects of match/mismatch among trophic levels due to phenological shifts in one group, but not another, represents an area in need of further study. Taxa often respond to a different set of physical or chemical cues; as a result, such investigations would require study of many parameters across multiple timescales.

Study of multiple timescales is also integral to understanding eco-evolutionary dynamics responsible for longer-term structuring of aquatic populations and communities. In the past few decades, evidence that ecological and evolutionary dynamics can occur across a range of timescales has accumulated (Hairston et al. 2005; Schoener 2011). Aquatic ecologists have begun to recognize that evolutionary processes imprint on population dynamics (Pelletier et al. 2009; Yoshida et al. 2003), alter community composition and assembly (Emerson and Gillespie 2008), and structure spatial dynamics (Urban et al. 2008). However, scale dependence of eco-evolutionary dynamics has not yet been addressed. For instance, stochastic events may interfere with eco-evolutionary dynamics whereas long-term shifts might foster rapid evolutionary adaptation. These relationships between timescale of disturbance events or trends and adaptation and evolution of individuals represent an excellent opportunity for future study.

Finally, the responses of open biological systems to episodic stressors such as oil spills also remain relatively unknown. Such stressors tend to be unpredictable, which makes them more difficult to study with long-standing ongoing research projects. Instead, a combination of background data from

existing programs and reaction-based field campaigns is necessary for advancing understanding of such events. The investment in basic and reaction-based research in the aftermath of the Deep Water Horizon oil spill in the Gulf of Mexico will hopefully provide valuable information about the time-scales of effects and recovery across trophic levels as well as provide a model for such work.

Methodological considerations

These questions require an inherently broad view of ecosystems and the use of a wide range of tools for studying natural systems. The interconnections between synchrony, regime shifts, and the frequency and magnitude of extreme events are most relevant to the study of climate change. However, to effectively address all of these features, an investigator would need to study several similar systems (synchrony) over long periods of time and at high temporal resolution (extreme events). This trade-off between long duration and high resolution is one of the main obstacles to such investigations, but one that will hopefully become less of an impediment as *in situ*, robotic, and remote methods for persistent study become more widely adopted. The LTER program serves as an excellent example of the inclusion of teams of researchers spanning trophic levels, expertise, and scales of interest that can provide the backbone of study from which short-term and/or reaction-based field campaigns can be launched. However, opportunities to add new sites to the LTER network are severely limited. The National Ecological Observatory Network (NEON) is another program that may fulfill the need for long-term, high resolution data sets spanning ecosystems and is incorporating mobility of sites into the design to allow for flexibility in the ecosystems studied.

Finally, a new generation of analytical methods is also necessary to understand data produced from such complex investigations. Traditional methods for determining the coefficients of variation (variability, extreme events), and correlation (synchrony/coherence) must be combined with methods for detecting nonlinear, sometimes step-wise changes (e.g., Rodionov 2004, change-point analyses) and understanding time-series data in frequency-space (e.g., spectral analyses, Fourier, and wavelet transforms). Moreover, since functional traits structure communities and drive their responses to change, analysis of intra- and interspecific trait variability at different spatial scales need to be considered (Violle et al. 2012)

Lingering questions

The issue of resilience is at the forefront of ecological research as scientists, resource managers, and policy-makers struggle to predict what ecosystems are more or less vulnerable to disturbance across many scales in both space and time. Are ecosystems driven by long term variability more or less susceptible to disturbance? Do they take longer to recover? For example, if lake productivity is primarily driven by processes operating on seasonal to interannual and decadal timescales,

whereas a stream is variable at both seasonal and sub-seasonal time scales, does this mean that the stream is more resilient to disturbance? Does this relationship depend on what temporal scales are dominant? These questions can be further refined to investigate resilience across trophic levels and as whole communities, i.e., do taxa that are forced by drivers at one or a few scales represent a bottle-neck for recovery? Are there differences in resistance and resilience between different levels of biological organization, i.e., between microbes (Shade et al. 2012), primary producers, and higher trophic levels? What do the scales of dominant drivers tell us about what the potential mechanisms organisms are using to deal with variability? How do the overlapping or decoupled scales of disturbance and eco-evolutionary adaptation influence these mechanisms? These are just some of the questions that remain after our synthesis of existing literature from these case study sites.

Section 4. Conclusions

Aquatic ecosystems are driven by physical, chemical, and biological processes operating across a variety of temporal scales. There is great similarity in the dominant processes and scales along the salinity gradient, though the drivers of these processes often manifest differently in each ecosystem. Much can be gained by cross-pollinating our understanding of temporal dynamics across aquatic ecosystems, especially when generating hypotheses and designing experiments for understudied drivers or responses in a particular ecosystem. To maximize effectiveness, investigations of aquatic ecosystems across multiple temporal scales require a variety of approaches including long-term monitoring and short-term, event-driven responses, and a new generation of tools and analytical approaches.

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