### In This Issue:

# ET&C FOCUS

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# How Do Aquatic Communities Respond to Contaminants? It Depends on the Ecological Context

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Upstream to downstream: A shaded headwater stream, open canopy mid-order stream, and a larger river. Photos by William Clements.

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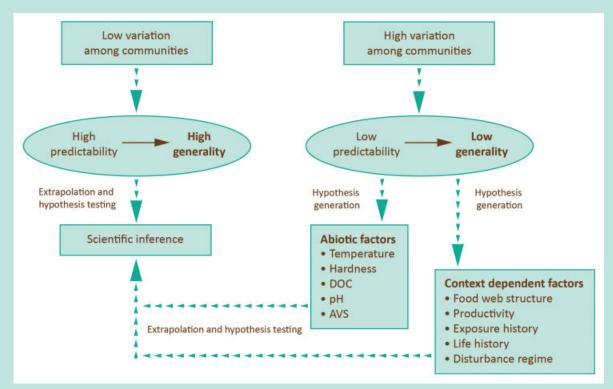
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Abstract—Context dependency refers to variation in ecological patterns and processes across environmental or spatiotemporal gradients. Research on context dependency in basic ecology has focused primarily on variation in the relative importance of species interactions (e.g., competition and predation) among communities. In this Focus article, the authors extend this concept to include variation in responses of communities to contaminants and other anthropogenic stressors. Because the structure of communities varies naturally along environmental gradients, their responses to contaminants may also vary. Similar to the way in which aquatic toxicologists assess abiotic factors associated with contaminant bioavailability, observations about context dependency could be used to test hypotheses about ecological mechanisms responsible for differences in sensitivity among communities. Environ. Toxicol. Chem. 2012;31:1932–1940. © 2012 SETAC

Keywords—Aquatic communities; Ecological context; Natural variability

Recognizing patterns in nature and using these observations to generate and test hypotheses are fundamental components of scientific inquiry [1]. The science of ecotoxicology aims to identify patterns that describe population and community responses to contaminants. Our ability to predict these responses is generally greatest for communities that change consistently in response to a specific contaminant or class of contaminants, thereby providing a direct path to extrapolation, hypothesis testing, and scientific inference (see Predicting the Effects of Contaminants). Although evidence suggests that some communities respond similarly to both natural and anthropogenic stressors [2], we know that regional variation in how communities are composed as a result of environmental, historical, biogeographical, or climatic factors complicates our ability to identify general patterns. Several studies have reported that the effects of contaminants on populations and communities vary along environmental

## **Predicting the Effects of Contaminants**



One of the major goals of the science of ecotoxicology is to describe population and community responses to contaminants. Our ability to predict effects of contaminants and make scientific inferences is greatest for communities that respond consistently to a specific chemical or class of chemicals. In situations where responses are highly variable, understanding the mechanisms responsible for differences among locations is essential. The figure above illustrates how we extrapoloate and generate hypotheses based on abiotic or context-dependent factors. For example, aquatic toxicologists have known for many years that certain physicochemical characteristics of aquatic ecosystems (e.g., temperature, pH, water hardness, and dissolved organic carbon) greatly influence the toxicity and bioavailability of some contaminants. These abiotic factors basically represent testable alternative hypotheses that may help explain site-specific variation in contaminant effects. In contrast to our well-developed understanding of how abiotic factors influence toxicity, we know relatively little about variation in sensitivity among communities. In fact, much of this variation is treated as noise and considered an impediment to our ability to predict responses and make scientific inferences. We believe that natural variation among communities also represents an opportunity to generate hypotheses and to identify ecological factors that influence contaminant fate and effects. We introduce the concept of context dependency, which refers to variation in ecological patterns and processes across environmental or spatiotemporal gradients. Specifically, we hypothesize that many of the natural environmental factors that structure communities in aquatic ecosystems (e.g., food web structure, disturbance, primary productivity, exposure history) also determine their responses to contaminants. Similar to the way in which we assess abiotic factors associated with contaminant bioavailability, observations about context dependency could be used to test hypotheses about underlying ecological mechanisms responsible for differences among communities. Rather than treating variation as a nuisance that impedes our ability to detect statistical significance, we believe that natural variation can be exploited to better understand ecological processes that influence community responses to contaminants.

gradients [3]—varying altitudes, temperatures, depths, ocean proximity, or soil humidity—or across broad geographic regions [4–6]. Few attempts have been made, however, to identify the mechanisms that cause this variation. We believe that significant advances in bioassessment and predictive ecotoxicology could result from developing approaches that consider spatial and temporal variation in the sensitivity of aquatic communities to anthropogenic stressors.

Although responses to contaminants vary considerably, understanding the mechanisms responsible for differences among locations has important practical applications. For example, aquatic toxicologists have known for many years that the physicochemical features of aquatic ecosystems such as pH, temperature, water hardness, and dissolved organic carbon influence the toxicity and bioavailability of contaminants. Because the mechanisms for interactions between water quality and toxicity are well understood, these physicochemical characteristics are routinely included in establishing water quality criteria. In contrast to our welldeveloped understanding of how abiotic factors influence toxicity, we know relatively little about how community composition influences responses to contaminants. In fact, much of this variation is treated as noise and often considered

an impediment in our ability to predict ecological responses [7,8]. Although one of the major goals of ecotoxicological research is to isolate specific factors associated with the effects of contaminants, in reality the importance of many environmental variables is often context dependent. In this Focus article, we suggest that variation among communities and along environmental gradients represents an opportunity to identify specific ecological factors that influence contaminant fate and effects. Rather than considering this variation as an obstacle, we believe variability among communities can be exploited to understand the basic mechanisms at work. With this insight, our ability to predict the effects of contaminants in aquatic ecosystems can be significantly improved if we recognize that responses to stressors often depend on the context and consequently developing a mechanistic understanding of this "context dependency."

### **Context-Dependent Responses**

Context dependency refers to variation in ecological patterns and processes across environmental or spatiotemporal gradients. Ecologists have long recognized that community patterns and processes often depend on environmental context [9,10]. For example, the relative importance of a species in stream ecosystems can vary longitudinally [8] or across its range of distribution [11]. Much of the research on context dependency in basic ecology has focused on quantifying the strength of biotic interactions, especially those involving keystone or other dominant species, along an environmental gradient. In fact, Menge and Sutherland [12] proposed the most widely cited example of context dependency in ecology. They hypothesized that the relative importance of competition and predation varied along disturbance gradients. In other words, at low disturbance, more competitive organisms dominate the ecosystem, pushing out less competitive species. At high disturbance, such as a forest fire or human interventions, all species are at risk. After this seminal paper was published, other investigators reported context-dependent responses in a wide variety of marine [13] and freshwater [14,15] ecosystems. Because context dependency complicates our ability to generalize about important ecological processes, it has undoubtedly contributed to many contentious debates in ecology. Indeed, several major controversies in ecology, such as the importance of how species interact, the role of disturbance, and the relationship between species diversity and ecosystem function, can be resolved after recognizing the context dependency of these processes.

# Context-Dependent Responses in Ecotoxicology

In this Focus article, we propose that responses of aquatic communities to contaminants are often context dependent and vary along environmental gradients. Specifically, we hypothesize that many of the environmental factors that structure communities in aquatic ecosystems (e.g., food web structure, disturbance regime, life history characteristics, primary productivity, exposure history) also determine community responses to contaminants. These relationships may be relatively simple, in which responses to contaminants change monotonically. For example, the effects of some contaminants decrease with increasing ecosystem productivity or a history of previous exposure. More complex responses in which effects are greatest (or lowest) at some intermediate level are also possible. We know that communities subjected to moderate levels of natural disturbance may tolerate contaminants and other forms of anthropogenic disturbance much better [2]. Therefore, we predict that the effects of contaminants will be greatest in highly stable communities, decrease at some intermediate level of disturbance, and then increase as a result of potential interactions between the natural and chemical stressors.

Context-dependent responses to contaminants have been identified using both experimental and comparative approaches. Results of mesocosm experiments have routinely shown that contaminants can alter community structure, but Relyea et al. [16] also demonstrated that the magnitude of these effects depended on the types of predators present (e.g., invertebrate vs vertebrates). Similarly, Rohr and Crumrine [17] reported that initial community composition determined the direct and indirect effects of pesticides on pond communities. Stream ecologists used a comparative approach as part of the lotic intersite nitrogen experiment (LINX), a largescale research program designed to quantify factors that control nitrogen export [18]. A similar approach could be developed in ecotoxicology to examine ecological factors that determine contaminant fate and effects. The basic experimental design would be to locate communities along an important environmental gradient (e.g., watershed area) or in different geographical regions (e.g., tropical vs temperate streams) that receive the same or similar stressors. Observing similar responses along this gradient would suggest no context dependency, allowing investigators to make broader inferences about contaminant effects. In contrast, significant variation in responses among communities would support the hypothesis of context dependency. Here, our interests would be primarily in identifying the ecological factors responsible for these differences.

The most convincing examples of context dependency based on field studies are drawn from remote ecosystems that receive similar concentrations of a specific contaminant but differ markedly in some important ecological characteristic. For example, concentrations of organochlorines and methyl mercury (methyl Hg) in top predators from remote lakes are known to vary with factors such as watershed area, surface area, trophic status, and the length of the food chain [19–22]. Site-specific variation in the effects of contaminants attributable to physicochemical characteristics that determine bioavailability are well known to aquatic toxicologists. These differences in physicochemical characteristics in general are not considered examples of context dependency and are not discussed here. Instead, we focus on variation in community composition and how this variation may influence responses to contaminants. For example, we know that the structure and composition of macroinvertebrate communities varies naturally from headwater streams to larger rivers. We also know that the effects of contaminants on these communities also vary, most likely as a result of previous exposure or disturbance history [3,23]. In the following sections, we discuss examples of context-dependent responses associated with trophic transfer and ecological effects of contaminants. In addition to the practical goal of improving our ability to predict contaminant fate and effects in different ecosystems, a major objective of these studies is to identify mechanisms that are responsible for differences among communities.

#### Fate of contaminants

Contaminant concentrations in aquatic organisms vary over time and space because of the influences of natural processes and human activities. Within one species such as lake trout, contaminants that bioaccumulate and biomagnify (e.g., methyl Hg and persistent organic pollutants [POPs]) can be 5- to 10-fold higher in one lake than in another neighboring system because of inherent differences in the species' ecology, the systems' characteristics, or the activities occurring in the watershed. Understanding variability in fish contaminants and how it is affected by context has been a major focus of ecotoxicology for decades and is critical for contaminants that affect aquatic biota or their consumers. Although we have identified several key influences on the bioavailability of contaminants to the base of the food web (e.g., Hg in biota is affected by pH, dissolved organic carbon, lake temperature), the transfer of contaminants across trophic levels (e.g., rate of biomagnification) also differs among systems. Whether context dependency is a critical driver of this process is not clear; however, a clear path forward is presented to compare biomagnification of contaminants across ecosystems given the increasing use of stable isotope analyses to quantify trophic transfer.

Incorporating stable isotope analyses into biomagnification studies has allowed broader comparisons to assess the effects of ecological context on contaminant fate in food webs. Stable isotopes of nitrogen, carbon, and, more recently, sulfur have added considerably to our understanding, because they trace sources of nutrients to consumers ( $\delta^{13}C$  and  $\delta^{34}S$ ) and measure relative trophic position of the biota ( $\delta^{15}$ N) [24]. A popular application of stable isotopes in ecotoxicology is using  $\delta^{15}N$  to quantify the rates at which contaminants biomagnify, because concentrations of POPs or methyl Hg are significantly and positively related to trophic position [24-26]. Both POPs (polychlorinated biphenyls [PCBs], DDT, toxaphene, polybrominated diphenyl ethers, and so forth) or methyl Hg and the heavier isotope of N  $(^{15}N)$ increase as energy is transferred from prey to predator. Significant relationships between contaminants and  $\delta^{15}N$ have been found in marine and freshwater systems in arctic, temperate, and tropical regions and in a range of ecosystems (streams, lakes, reservoirs, estuaries, coastal zones). The slope of the relationship is considered to be the average rate of contaminant transfer through the food web, whereas the

intercept represents the inputs of contaminants to the base of the food web [27]. Within the limited comparisons that have been completed, model slopes vary from one system to another. For example, Houde et al. [28] found higher biomagnification rates for some POPs in larger, deeper lakes or lakes that were at a higher latitude or longitude. Across broader scales, models can and should be contrasted to assess how context affects biomagnification.

A compilation of existing contaminant- $\delta^{15}$ N datasets could allow one to determine whether higher contaminant concentrations in top predators are attributable to greater rates of food web processing (model slopes) or inputs to the base of the food web (model intercepts), and whether the magnitude of these coefficients are context dependent. Higher contaminant concentrations in top predators in one lake compared to another could be explained three different ways: first, if the rates of trophic transfer are the same, but inputs to the base of one food web are higher (Fig. 1A); second, if the basal inputs are the same, but the rate of biomagnification differs (Fig. 1B); and third, if the rates and inputs are the same, but the food webs have different lengths (Fig. 1C). Several interesting questions related to context dependency can be examined by comparing the current literature or by de novo designing studies of food webs across gradients (e.g., latitude). For example: Do systems with higher productivity have lower rates of contaminant biomagnification, perhaps because of higher biomass or growth dilution within the food web? Are contaminants transferred at a greater rate in lotic than lentic systems? Does community complexity affect the trophic transfer of contaminants?

The length of an aquatic food chain is another key ecological factor that determines the concentrations of methyl Hg and POPs in top predator fishes, because these chemicals biomagnify from prey to predator. Rasmussen and colleagues [20,29] unequivocally demonstrated this when they grouped temperate lakes into three classes based on the length of the pelagic food chain leading to the top predator, lake trout. Concentrations of PCBs and Hg in lake trout increased 3.5and 2.0-fold, respectively, with each additional increase in the length of the underlying food chain. As a result, contaminant exposure (and related effects) for upper-trophic-level fishes (and fish-eating wildlife and humans) was highest for systems supporting the longest food webs.

Invasive species and context-dependent responses. Clearly, invasive species have affected the structure of aquatic food webs by outcompeting some species, causing shifts in habitat use by others, and providing an alternate food source for predators. These changes in food web structure could influence contaminant concentrations in top predators if the invasions (1) increased the length of the food chain supporting a species or (2) resulted in diet shifts from a higher to lower or lower to higher source of contaminants. In lakes invaded by the zooplankton predator *Bythotrephes*, fish occupied a higher trophic position because of invasioninduced changes in zooplankton communities. Although this

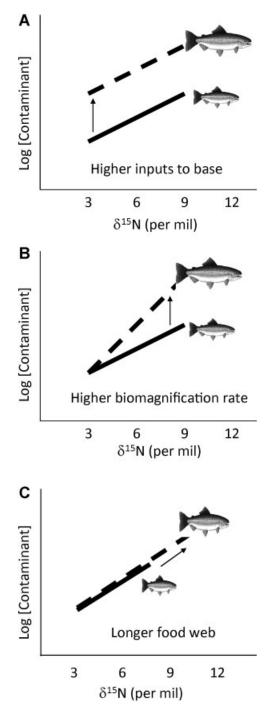


FIGURE 1: Conceptual models of how contaminant concentrations in top predators (relative concentrations indicated by size) could vary because of (A) similar rates of trophic transfer (slopes of log[contaminant] vs  $\delta^{15}$ N but a higher input to the base of the food web; (B) similar inputs to the base of the food web but a higher rate of biomagnifications; and (C) similar rates of biomagnification but a longer food web (modified from Kidd et al. [47]).

longer food web was predicted to increase Hg concentrations in fish [25] (Fig. 2), a regional survey of lakes showed no effects of *Bythotrephes* invasions [26]. Similarly, Hg concentrations in several species of piscivorous fishes did not change after planktivorous smelt invaded the ecosystem [30]. In contrast to these findings, the invasive round goby likely influenced Hg levels in piscivorous fish. Despite decreases in Hg inputs to Lake Erie, Hg in piscivorous fishes either remained constant or increased after goby invasions, perhaps because of increased recycling of sediment-associated contaminants through the goby's benthic diet [31] (Fig. 2). Similarly, invasion of zebra mussels in the Great Lakes likely maintained elevated concentrations of PCBs in spottail shiner, even though PCB inputs were declining [32]. Finally, in a lake invaded by a planktivorous fish, native forage fish shifted their diet to benthic carbon, resulting in a 50% increase in their Hg concentrations [33]. In summary, although the effects of invasive species on contaminant concentrations in other consumers are variable, these situations provide excellent opportunities to test context-dependent responses.

#### **Effects of contaminants**

Because community structure and ecosystem processes vary naturally along environmental gradients, likely responses to contaminants will also differ among locations. Identifying these context-dependent responses in ecotoxicology goes beyond quantifying simple stressor-response relationships and examines how communities inhabiting different locations respond to the same or similar stressors. In other words, we are especially interested in knowing how the slopes of concentration-response relationships vary among ecosystems. Identifying mechanisms responsible for context-dependent responses may help explain why stressors have significant effects in some environments but not in others. The basic approach would be similar to that used in laboratory studies designed to investigate abiotic factors that modify toxicity and bioavailability (e.g., water hardness, pH, dissolved organic carbon, temperature). Rather than focusing on physicochemical characteristics, however, we would identify communities along some important environmental gradient and assess variation in responses to a specific contaminant along this gradient.

Longitudinal variation in species richness, community composition, and functional processes is perhaps the most important unifying paradigm in stream ecology [34]. Because stream communities often change predictably from headwater streams to large rivers (Fig. 3), responses to contaminants likely will also vary along this gradient. Compared with headwaters, mid-order (4th-6th) streams are characterized by greater primary production, lower amounts of coarse particulate organic material, higher species richness, abundant grazers, and a more variable flow regime. Although these specific longitudinal patterns will differ depending on location, each of these factors could influence community responses to contaminants. Microcosm experiments conducted with macroinvertebrate communities collected along a longitudinal gradient showed that headwater communities were more sensitive to heavy metals than those from midorder reaches [3]. Differences in the natural disturbance regime were likely responsible for this variation, suggesting that communities from variable environments were "preadapted" to moderate levels of anthropogenic stress [2]. In this example, we have a reasonable understanding of the mechanism responsible for this variation. Because commun-

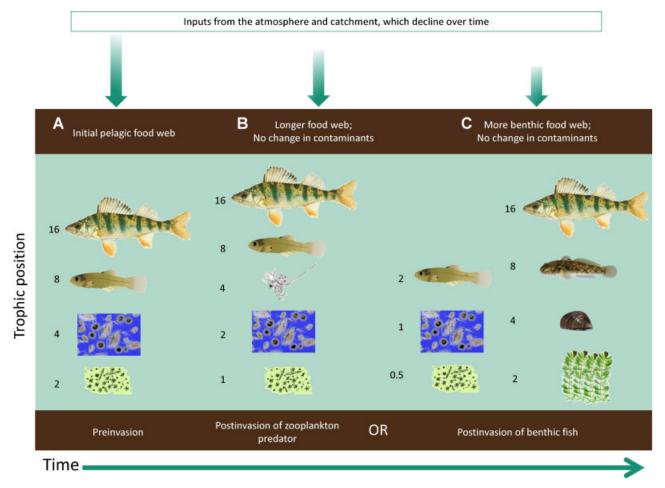


FIGURE 2: Shifts in food web structure that can result after species invasions and their effects on hypothetical contaminant concentrations (represented by the numbers adjacent to each trophic level) in biota during a period of declining atmospheric and catchment inputs. (A) Initial pelagic food web with hypothetical contaminant concentrations. (B) Despite reductions in inputs of contaminants to the base of the food web, invasion of a zooplankton predator (e.g., *Bythotrephes*) leads to a longer food web and no change in fish contaminant concentrations. (C) Continuing declines in contaminant inputs to lakes are not reflected in top predator fish because they shift to a benthic and more contaminated diet after invasion by a benthic fish (e.g., round goby).

ities from highly variable environments are often dominated by opportunistic or r-selected species capable of reproducing and recolonizing rapidly, we would expect them to show greater resistance or resilience to contaminants. Similarly, we expect that communities with a long-term history of exposure to a specific stressor would show greater tolerance to that stressor. Microcosm experiments have shown that communities collected from metal-contaminated streams were more resistant to metals compared with reference communities [35]. These patterns are consistent with the pollution-induced community tolerance hypothesis, which states that increased tolerance occurs when sensitive species are eliminated from a community [36]. Interestingly, the increased tolerance for one set of stressors often results in greater susceptibility to other, novel stressors. Stream microcosm experiments have shown that metal-tolerant communities were more susceptible to acidification [37], UV-B radiation [38], and predation [35] compared with reference communities. These findings suggest that communities retain a long-term record of exposure that may persist long after a contaminant has dissipated or degraded [39].

Variation in landscape features such as vegetation, topology, elevation, and geology directly influences community composition and provide an opportunity to investigate context-dependent responses at larger spatial scales. Spatially extensive surveys of streams in North America, Europe, New Zealand, and other regions have been used to identify regional reference conditions [40] and to classify watersheds based on landscape features [41]. We know from these studies that underlying geomorphological characteristics of a watershed determine local water quality [42] and contaminant bioavailability; however, we know relatively little about how these features will affect ecological responses to contaminants. In a regional assessment of geology, water quality, and macroinvertebrate communities in the Colorado Rocky Mountains, Schmidt et al. [43] showed that variation in the effects of metals among watersheds was likely a result of underlying geology. These studies highlight the importance of considering regional variation in community composition when assessing potential effects of contaminants on aquatic communities.

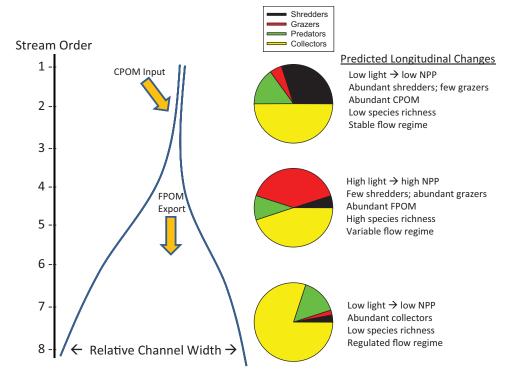


FIGURE 3: Longitudinal variation in community composition and function of stream ecosystems as predicted by the river continuum concept [34]. We hypothesize that natural variation in aquatic communities from upstream to downstream could result in context-dependent responses to contaminants and other stressors. CPOM = coarse particulate organic material; FPOM = fine particulate organic material; NPP = net primary productivity.

# Comparative studies across broad geographic regions

Natural populations and communities are characterized by spatial heterogeneity, with unique species assemblages inhabiting polar, temperate, and tropical environments. Because the communities associated with these broad geographic regions differ both in species composition and in food-web structure, their sensitivity to contaminants may also differ. Community susceptibility to contaminants is a function of both biological diversity and inherent species sensitivity. The diversity of species is generally considered to increase toward the tropics, indicating that the number of species that potentially could be affected by pollutants is greater [4]. Our ability to determine community sensitivity to contaminants is largely limited to single-species laboratory and multi-species mesocosm studies. These studies are constrained by the scale of the exposure systems, thus excluding larger predators, and limited to species performing well in such systems. Datasets are also biased toward temperate regions, where most studies have been undertaken (i.e., North America, Europe) and are very limited for more extreme environments (e.g., Antarctica) and for some key species groups (e.g., marine corals).

Studies aimed at validating the protective value of toxicity thresholds have compared sensitivities of species using a species sensitivity distributions approach. Dyer et al. [6] compared the species sensitivity distributions of acute toxicity data for 95 species of temperate, coldwater, and tropical fish for six organic compounds. Fish from the regional groups showed comparable threshold sensitivity to DDT, with tropical fish generally being less sensitive, whereas no significant difference in sensitivity was found for other compounds. Brock et al. [5] reviewed the published data assessing spatial extrapolation in ecological effects and concluded that although the composition of freshwater communities varies across biogeographical regions, climatic zones, and habitat types, the distribution of species threshold sensitivities does not vary markedly. Tropical freshwater fish species are not generally more sensitive to environmental contaminants than temperate fish species. When compared with temperate species, a trend is seen of a slight increase in the sensitivity of tropical invertebrates to a few selected chemicals, whereas for a few other chemicals the reverse was observed.

Kwok et al. [4] recently undertook the most extensive comparison of temperate and tropical freshwater species for 18 chemical substances (ammonia, 9 metals, 2 narcotics, and 6 pesticides: carbaryl, chlordane, chlorpyriphos). Sensitivity comparisons were made based on the calculated threshold hazardous effect concentration for a 10% response. They found that for most metals, temperate species tended to be more sensitive than their tropical counterparts; however, for un-ionized ammonia, phenol, and some pesticides (e.g., chlorpyrifos), tropical species are probably more sensitive. The authors concluded that an extrapolation factor of 10 should be applied when water quality guidelines derived from temperate regions are used for tropical regions. Examining the species sensitivity distribution response curves, Kwok et al. [4] also showed marked differences between temperate and tropical species for several compounds, indicating differing community sensitivity once the effect threshold was exceeded. These data indicate that both a tolerance threshold and a community sensitivity measure should be used to assess the risk to ecological communities.

#### Temporal variation in contaminant effects

In addition to the natural variation among communities and along spatial gradients described, temporal variation in the abundance of sensitive species and life stages will likely influence responses to contaminants. Winner et al. [44] observed seasonal variation in the sensitivity of zooplankton communities to Cu exposure. Similarly, mesocosm experiments conducted with macroinvertebrate communities showed that summer communities, which were dominated by smaller, early instars of aquatic insects, were more sensitive to metals than communities collected in late spring [45], which were dominated by larger individuals. These investigators suggested that phenology and life history characteristics of sensitive resident species should be considered when designing biomonitoring programs and establishing water quality criteria. Results of these studies demonstrate the importance of accounting for temporal changes in community composition when assessing impacts of anthropogenic stressors.

# Should We Care About Context Dependency?

Given the rich history of ecotoxicology and bioassessment, it is surprising that context dependency of ecological responses to contaminants has received so little attention. This may be explained partially by the significant challenges associated with using descriptive approaches to identify context dependency. Because of the difficulty conducting manipulative experiments at ecologically realistic spatial or temporal scales, our ability to make causal inferences is limited. Investigating context dependency will require tradeoffs between experimental control and our ability to make broader statements about ecological factors that determine community responses. We know that unique environmental conditions and differences in community composition will likely result in significant variation in the impact of contaminants. However, we also recognize that testing the effects of all chemicals of concern on all sensitive species across all localities is not realistic [5]. Thus, a risk screening or tiered approach should be used to quantify variation in the probability of effects and to identify context-dependent responses. Developing an understanding of the importance of abiotic factors that influence contaminant bioavailability relative to contextdependent factors that determine community responses to contaminants is also important. Although we have treated abiotic and context-dependent factors independently in this Focus article, we know that physicochemical characteristics directly influence communities. Therefore, it is likely that abiotic factors will interact with context-dependent factors to determine responses to contaminants.

Understanding how different communities respond to contaminants is also difficult because multiple environmental drivers that operate across a continuum of spatial and temporal scales determine community composition. Unlike mechanistic models used to predict contaminant bioavailability (e.g., biotic ligand model; equilibrium partitioning; quantitative structural activity relationships), ecological models are considerably more complex and highly interactive. Thus, we may never have a unified theory that predicts how communities in different locations will respond to contaminants. However, comparisons of community structure among ecosystems (e.g., tropical vs temperate streams), along latitudinal gradients (e.g., headwater streams vs large rivers), or among streams in different geomorphological units, could provide insight into the underlying mechanisms responsible for context-dependent responses. Finally, an appreciation for context dependency will be necessary to understand potential interactions between contaminants and global change. By developing stressor-response relationships for communities located along well-defined gradients of temperature, hydrologic variability, UV-B radiation, or other variables associated with global change, one could possibly produce a more comprehensive understanding of how these changes may interact with contaminants [46]. Although context dependency complicates our ability to make broad generalizations in ecotoxicology, it provides an opportunity to better understand the factors responsible for variation among communities. Rather than treating natural spatiotemporal variation as a nuisance that inflates p values and impedes our ability to detect statistical significance, we encourage ecotoxicologists to consider ways to exploit this variation and test specific hypotheses about how ecological processes influence responses to contaminants.

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#### REFERENCES

- [1] Platt JR. 1964. Strong inference. Science 146:347-353.
- [2] Rapport DJ, Regier HA, Hutchinson TC. 1985. Ecosystem behavior under stress. Am Nat 125:617–640.
- [3] Kiffney PM, Clements WH. 1996. Effects of metals on stream macroinvertebrate assemblages from different altitudes. *Ecol Appl* 6:472–481.
- [4] Kwok KWH, Leung KMY, Lui GSG, Chu VKH, Lam PKS, Morritt D, Maltby L, Brock TCM, Van den Brink PJ, Warne MSJ, Crane M. 2007. Comparison of tropical and temperate freshwater animal species' acute sensitivities to chemicals: Implications for deriving safe extrapolation factors. *Integr Environ* Assess Manag 3:49–67.
- [5] Brock TCM, Maltby L, Hickey CW, Chapman J, Solomon KR. 2008. Spatial extrapolation in ecological effect assessment of chemicals. In Solomon KR, Brock TCM, de Zwart D, eds, *Extrapolation Practice for Ecological Effect Characterization of Chemicals*. SETAC/CRC, Boca Raton, FL, USA, pp 223–256.
- [6] Dyer SD, Belanger SE, Carr GJ. 1997. An initial evaluation of the use of Euro/ North American fish species for tropical effects assessments. *Chemosphere* 35:2767–2781.

- [7] Simberloff DS. 1980. A succession of paradigms in ecology: Essentialism to materialism and probabilism. *Synthese* 43:3–39.
- [8] Wellnitz T, Poff NL. 2001. Functional redundancy in heterogeneous environments: Implications for conservation. *Ecol Lett* 4:177–179.
- [9] Sousa WP. 1979. Disturbance in marine intertidal boulder fields: The nonequilibrium maintenance of species diversity. *Ecology* 60:1225–1239.
- [10] Cardinale BJ, Nelson K, Palmer MA. 2000. Linking species diversity to the functioning of ecosystems: On the importance of environmental context. *Oikos* 91:175–183.
- [11] Power ME, Tilman D, Estes JA, Menge BA, Bond WJ, Mills LS, Daily G, Castilla JC, Lubchenco J, Paine RT. 1996. Challenges in the quest for keystone species. *BioScience* 46:606–620.
- [12] Menge BA, Sutherland JP. 1987. Community regulation: Variation in disturbance, competition, and predation in relation to environmental stress and recruitment. Am Nat 130:730–757.
- [13] Shears NT, Babcock RC, Salomon AK. 2008. Context dependent effects of fishing: Variation in trophic cascades across environmental gradients. *Ecol Appl* 18:1860–1873.
- [14] Moore JW, Schindler DE. 2008. Biotic disturbance and benthic community dynamics in salmon-bearing streams. J Anim Ecol 77:275–284.
- [15] Nowlin WH, Drenner RW. 2000. Context-dependent effects of bluegill in experimental mesocosm communities. *Oecologia* 122:421–426.
- [16] Relyea RA, Schoeppner NM, Hoverman JT. 2005. Pesticides and amphibians: the importance of community context. *Ecol Appl* 15:1125–1134.
- [17] Rohr JR, Crumrine PW. 2005. Effects of an herbicide and an insecticide on pond community structure and processes. *Ecol Appl* 15:1135–1147.
- [18] Mulholland PJ, Tank JL, Webster JR, Bowden WB, Dodds WK, Gregory SV, Grimm NB, Hamilton SK, Johnson SL, Marti E, Mcdowell WH, Merriam JL, Meyer JL, Peterson BJ, Valett HM, Wollheim WM. 2002. Can uptake length in streams be determined by nutrient addition experiments? Results from an interbiome comparison study. J North Am Benthol Soc 21:544–560.
- [19] Bodaly RA, Rudd JWM, Fudge RJP, Kelly CA. 1993. Mercury concentrations in fish related to size of remote Canadian Shield lakes. *Can J Fish Aquat Sci* 50:980–987.
- [20] Cabana G, Tremblay A, Kalff J, Rasmussen JB. 1994. Pelagic food-chain structure in Ontario Lakes: A determinant of mercury levels in lake trout (Salvelinus namaycush). Can J Fish Aquat Sci 51:381–389.
- [21] Kidd KA, Schindler DW, Muir DCG, Lockhart WL, Hesslein RH. 1995a. High concentrations of toxaphene in fishes from a subarctic lake. *Science* 269:240–242.
- [22] Kidd KA, Paterson MJ, Hesslein RH, Muir DCG, Hecky RE. 1999. Effects of northern pike (*Esox lucius*) additions on pollutant accumulation and food web structure, as determined by delta C-13 and delta N-15, in a eutrophic and an oligotrophic lake. *Can J Fish Aquat Sci* 56:2193–2202.
- [23] Medley CN, Clements WH. 1998. Responses of diatom communities to heavy metals in streams: The influence of longitudinal variation. *Ecol Appl* 8:631–644.
- [24] Broman D, Näf C, Rolf C, Zebühr Y, Fry B, Hobbie J. 1992. Using ratios of stable nitrogen isotopes to estimate bioaccumulation and flux of polychlorinated dibenzo-p-dioxins (PCDDs) and dibenzofurans (PCDFs) in two food chains from the Northern Baltic. *Environ Toxicol Chem* 11:331–345.
- [25] Rennie MD, Strecker AL, Palmer ME. 2011. Bythotrephes invasion elevates trophic position of zooplankton and fish: Implications for contaminant biomagnification. Biol Invas 13:2621–2634.
- [26] Rennie MD, Sprules WG, Vaillancourt A. 2010. Changes in fish condition and mercury vary by region, not *Bythotrephes* invasion: A result of climate change? *Ecography* 33:471–482.
- [27] Kidd KA, Hesslein RH, Fudge RJP, Hallard KA. 1995b. The influence of trophic level as measured by delta15N on mercury concentrations in freshwater organisms. *Water Air Soil Pollut* 80:1011–1015.
- [28] Houde M, Muir DCG, Kidd KA, Guildford S, Drouillard K, Wang X, Evans MS, Whittle DM, Haffner D, Kling H. 2008. Influence of lake characteristics

on the biomagnification of persistent organic pollutants in lake trout food webs. *Environ Toxicol Chem* 27:2169–2178.

- [29] Rasmussen JB, Rowan DJ, Lean DRS, Carey JH. 1990. Food chain structure in Ontario lakes determines PCB levels in lake trout (*Salvelinus namaycush*) and other pelagic fish. *Can J Fish Aquat Sci* 47:2030–2038.
- [30] Johnston TA, Leggett WC, Bodaly RA, Swanson HK. 2003. Temporal changes in mercury bioaccumulation by predatory fishes of boreal lakes following the invasion of an exotic forage fish. *Environ Toxicol Chem* 22:2057–2062.
- [31] Hogan LS, Marschall E, Folt C, Stein RA. 2007. How non-native species in Lake Erie influence trophic transfer of mercury and lead to top predators. *J Great Lakes Res* 33:46–61.
- [32] French TC, Petro S, Reiner EJ, Bhavsar SP, Jackson DA. 2011. Concentrations in a small invertivorous fish (*Notropis hudsonius*): An examination of post-1990 trajectory shifts in the Lower Great Lakes. *Ecosystems* 14: 415–429.
- [33] Eagles-Smith CA, Suchanek TH, Colwell AE, Anderson NL, Moyle PB. 2008. Changes in fish diets and food web mercury bioaccumulation induced by an invasive planktivorous fish. *Ecol Appl* 18:A213–A226.
- [34] Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE. 1980. The river continuum concept. Can J Fish Aquat Sci 37:130–137.
- [35] Clements WH. 1999. Metal tolerance and predator-prey interactions in benthic macroinvertebrate stream communities. *Ecol Appl* 9:1073–1084.
- [36] Blanck H, Wangberg S. 1988. Induced community tolerance in marine periphyton established under arsenate stress. *Can J Fish Aquat Sci* 45:1816– 1819.
- [37] Courtney LA, Clements WH. 2000. Sensitivity to acidic pH in benthic invertebrate assemblages with different histories of exposure to metals. *J North Am Benthol Soc* 19:112–127.
- [38] Kashian DR, Zuellig RE, Mitchell KA, Clements WH. 2007. The cost of tolerance: sensitivity of stream benthic communities to UV-B and metals. *Ecol Appl* 17:365–375.
- [39] Landis WG, Matthews RA, Matthews GB. 1996. The layered and historical nature of ecological systems and the risk assessment of pesticides. *Environ Toxicol Chem* 15:432–440.
- [40] Reynoldson TB, Norris RH, Resh VH, Day KE, Rosenberg DM. 1997. The reference condition: A comparison of multimetric and multivariate approaches to assess water-quality impairment using benthic macroinvertebrates. *J North Am Benthol Soc* 16:833–852.
- [41] Snelder TH, Biggs BJF. 2002. Multiscale river environment classification for water resources management. J Am Water Res Assoc 38:1225–1239.
- [42] Wanty RB, Verplanck PL, San Juan CA, Church SE, Schmidt TS, Fey DL, Dewitt EDH, Klein TL. 2009. Geochemistry of surface water in alpine catchments in central Colorado, USA: resolving host-rock effects at different spatial scales. *App Geochem* 24:600–610.
- [43] Schmidt TS, Clements WH, Wanty RB, Verplanck PL, Church SE, San Juan CA, Fey DL, Rockwell BW, DeWitt EH, Klein TL. 2012. Geologic processes influence the effects of mining on aquatic ecosystems. *Ecol Appl* 22:870–879.
- [44] Winner RW, Owen HA, Moore MV. 1990. Seasonal variability in the sensitivity of freshwater lentic communities to a chronic copper stress. *Aquat Toxicol* 17:75–92.
- [45] Clark JL, Clements WH. 2006. The use of in situ and stream microcosm experiments to assess population- and community-level responses to metals. *Environ Toxicol Chem* 25:2306–2312.
- [46] Clements WH, Brooks ML, Kashian DR, Zuellig RE. 2008. Changes in dissolved organic material determine exposure of stream benthic communities to UV-B radiation and heavy metals: implications for climate change. *Global Change Biol* 14:2201–2214.
- [47] Kidd K, Clayden M, Jardine T. 2012. Bioaccumulation and biomagnification of mercury through food webs. In: Liu G, Cai Y, O'Driscoll N, eds, *Environmental Chemistry and Toxicology of Mercury*. Hoboken, NJ, John Wiley & Sons.