CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

Ecological Monographs, 86(1), 2016, pp. 4–19

The adaptive capacity of lake food webs: from individuals to ecosystems

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Abstract. Aquatic ecosystems support size structured food webs, wherein predator-prey body sizes span orders of magnitude. As such, these food webs are replete with extremely generalized feeding strategies, especially among the larger bodied, higher trophic position taxa. The movement scale of aquatic organisms also generally increases with body size and trophic position. Together, these body size, mobility, and foraging relationships suggest that organisms lower in the food web generate relatively distinct energetic pathways by feeding over smaller spatial areas. Concurrently, the potential capacity for generalist foraging and spatial coupling of these pathways often increases, on average, moving up the food web toward higher trophic levels. We argue that these attributes make for a food web architecture that is inherently 'adaptive' in its response to environmental conditions. This is because variation in lower trophic level dynamics is dampened by the capacity of predators to flexibly alter their foraging behavior. We argue that empirical, theoretical, and applied research needs to embrace this inherently adaptive architecture if we are to understand the relationship between structure and function in the face of ongoing environmental change. Toward this goal, we discuss empirical patterns in the structure of lake food webs to suggest that ecosystems change consistently, from individual traits to the structure of whole food webs, under changing environmental conditions. We then explore an empirical example to reveal that explicitly unfolding the mechanisms that drive these adaptive responses offers insight into how human-driven impacts, such as climate change, invasive species, and fisheries harvest, ought to influence ecosystem structure and function (e.g., stability, secondary productivity, maintenance of major energy pathways). We end by arguing that such a directed food web research program promises a powerful across-scale framework for more effective ecosystem monitoring and management.

Key words: behavior; biomonitoring; climate change; ecosystems; environmental gradients; populations.

Introduction

With increasing awareness of human impacts on ecosystem biodiversity and function (Chapin et al. 2000, DeFries et al. 2004), scientists and governments have begun the intrepid task of developing policy that helps sustain ecosystem functions in the face of ongoing environmental change (IPCC 2001, Carpenter and Brock 2004, Friberg et al. 2011). While much of this research has focused on the role of biodiversity in its narrow sense of species richness (Hooper et al. 2005, Dudgeon et al. 2006), emerging work is arguing for management that goes beyond conserving species numbers and towards protecting the biological structure and functional species interactions that are responsible for sustaining energy and nutrient flow at an ecosystem level (Soulé et al. 2003, Gray et al. 2014, Mace et al. 2014, Travis et al. 2014). It is this biological structure, not species number per se, that is most linked to ecosystem function (Hilborn et al. 2003, McCann 2007) and likely enables ecosystems to respond to variation by acting as complex adaptive systems (*sensu* Levin 1998). Here, we use 'adaptive' (and 'adaptive capacity') to mean the ability (or potential) of a system to make adjustments

Manuscript received 13 February 2015; revised 29 July 2015; accepted 17 August 2015. Corresponding Editor: S. P. Lawler.

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in behavior or structure in response to external stress (Smit and Pilifosova 2001, Adger et al. 2004). Knowledge of what characteristics make a system adaptive are crucial for ecosystem management (Travis et al. 2014), but we still know very little about how ecosystems respond to environmental change, and even less about how human impacts might alter these adaptive responses.

Ecologists have long sought to describe the structural attributes of food webs (e.g., food chain length; Pimm 1982). Most often, this work has focused on identifying similarities across different ecosystems (e.g., connectivity; Cohen et al. 1990), instead of investigating how food web structure in the same ecosystem type (e.g., lakes) changes across natural environmental gradients (Fee and Hecky 1992, Layer et al. 2013, Tanentzap et al. 2014). While both research objectives are clearly valuable, the latter approach provides an opportunity to study how the machinery of a given system responds to variation, including major environmental perturbations such as climate change. Gradients act like 'natural experiments' and can provide insight into the effects of abiotic variation across the ecological hierarchy, from individual physiology and behavior to ecosystem-level nutrient and energy flows (O'Gorman et al. 2012). Finding evidence for consistent structural responses across levels may: (1) offer insight into adaptive capacity of whole systems, and (2) help develop general theory that incorporates these adaptive structures with their functional importance (e.g., for stability, secondary productivity). These insights may prove highly valuable as increasing human demands threaten the capacity of ecosystems to withstand and respond to environmental change.

Understanding how ecosystems respond adaptively to environmental variation may require that we consider how macroscopic food web pathways are related to and arise from organism-level traits (e.g., behavior). The ability for motile organisms to use different habitats and consume different prey in response to changing conditions is a historically underused aspect of food web ecology that ought to play a major role in driving ecosystem adaptive capacity (Schmitz and Barton 2013). Here, we argue that simple attributes linking body size and food web structure with behavior suggest that a fundamental module (hereafter, the generalist module), which repeats itself across spatial scales from micro- to macrohabitats, acts as a major component of aquatic ecosystem adaptive capacity.

Within the context of this common, spatial scale-invariant food web module, we review a well studied aquatic ecosystem—inland lakes in North America with Lake Trout, *Salvelinus namaycushas* (Walbaum, 1972), as an apex predator—as a case study to show that the generalist module changes predictably across natural environmental gradients. We highlight that changes in empirical patterns in ecosystem and food web structure are concurrent with changes at the individual level (e.g., in life history characteristics) and demonstrate how such investigations provide insight into the possible consequences of human impacts. We discuss the broad application of our approach, because the generalist module appears to be a widespread attribute of food webs, and end by arguing for the development of research programs that combine knowledge of this adaptive food web architecture with ecological tracers and tools to (1) monitor the individual to ecosystem level effects of human impacts, and (2) signal for possible losses in ecosystem adaptive capacity.

The Generalist Module as a Fundamental Food Web Attribute

Body size, mobility, and aquatic food web structure

While well-resolved description of food webs has proven elusive, ecological tracers (mainly stable isotopes) complemented by stomach content analysis have rapidly increased the ability to grossly identify major energy flows in aquatic food webs (Vander Zanden et al. 1999, Vander Zanden and Vadeboncoeur 2002, Layer et al. 2013). Below, we argue that empirical animal body size relationships align with and have a strong effect on the gross structure of aquatic food webs (Peters 1986, McCann and Rooney 2009, Gilljam et al. 2011).

Body size is a major structuring force in food webs (Petchey et al. 2008) that increases with trophic level in most aquatic ecosystems (Vander Zanden et al. 2000, Jennings et al. 2001, Gilljam et al. 2011). This simple relationship suggests that mobility ought to increase with trophic position, as well, since the cost of movement per unit of weight decreases with increasing body size (McCann et al. 2005, Rooney et al. 2008). This suggestion is supported by the observation that body size predicts the home range size of freshwater fish (Minns 1995). As size increases with trophic position, so too does the tendency for generalist feeding behavior (Petchey et al. 2008). All else equal, more mobile organisms are exposed to and capable of consuming a greater variety of prey types in a wider range of habitats (i.e., encounter probability is positively related to mobility; Pyke et al. 1977). This patterning in organismal traits, whereby larger animals are more mobile and more generalized in their feeding than smaller animals, has implications for food web structure. Simply by moving up the food web, we expect each successive trophic level to couple (move throughout and forage among) larger and larger habitat divisions (Pimm and Lawton 1980). Moving higher up in the food web also increases the number of available prey types vertically at each trophic level below a predator (Holt 1996). As a result, the likelihood for omnivory (feeding on multiple trophic levels) also increases with trophic level (Gilljam et al. 2011). Together, these relationships argue for a common structuring within food webs that we have termed the generalist module (depicted in Fig. 1A at the whole lake ecosystem level). The architecture of the generalist module is also important for food web stability based on theory (discussed below; McCann et al. 2005, Gross et al. 2009).

The simple body-size-based predictions for lower level compartmentalization followed by higher order coupling that constitute the generalist module are met repeatedly

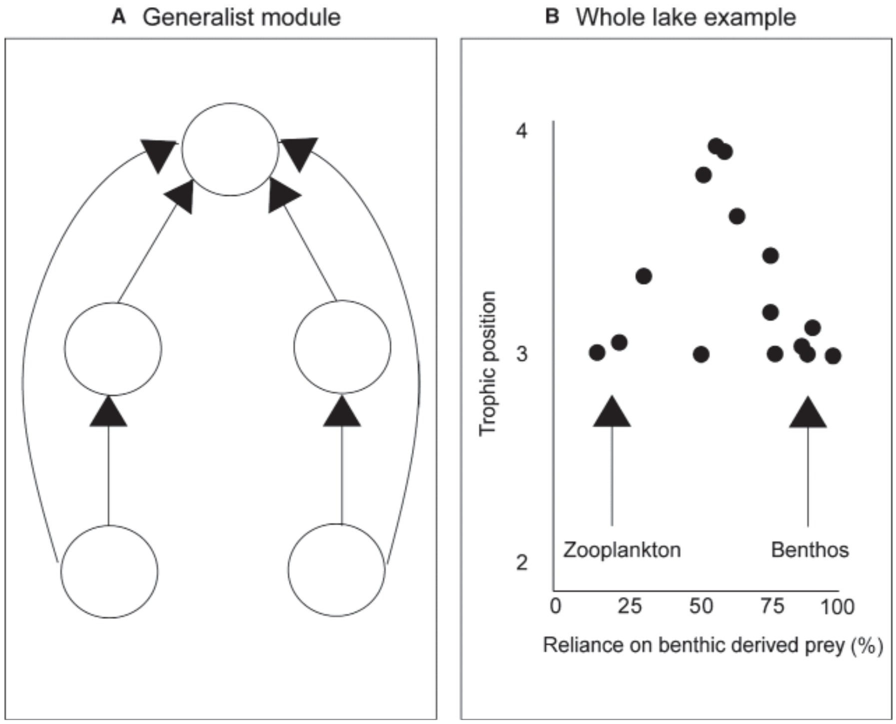

Fig. 1. (A) The generalist module, a conceptual and simplified depiction of the major energy flows through aquatic food webs, which shows a predator feeding on two consumers and omnivorously on two resources. (B) Manifestation of the generalist module in whole lakes, showing increasing benthic coupling by different fish species (filled circles) with increasing trophic position (redrawn from Vadeboncoeur et al. 2002). Trophic position 3 fish feed tend to feed on either zooplankton or benthos, whereas trophic position 4 fish consume prey from both pelagic and benthic compartments. Omnivory is also apparent because several fish have trophic positions falling between 3 and 4.

in empirically documented food webs. Based on a global survey of lentic systems, primary consumers (e.g., zooplankton or zoobenthos) tend to feed within either the pelagic or benthic habitat, respectively, and rarely on both (France 1995), setting up macrohabitat compartments. Higher up in the food web, invertivorous fish in North American temperate lakes (Fig 1B; trophic position ca. 3) also tend to consume either benthic or pelagic prey, whereas piscivores at trophic position ca. 4 feed as couplers in both habitats (Fig. 1B; Vadeboncoeur et al. 2002). A similar example, also based on combined stable isotope and stomach content data, exists from Northern European lakes where the capacity for piscivory and generalist foraging on both benthic and pelagic prey of Arctic Charr (*Salvelinus alpinus,* Linnaeus, 1758) promotes coexistence with planktivorous Whitefish (*Coregonus lavaretus,* Linnaeus, 1758) and benthivorous Grayling (*Thymallus thymallus,* Linnaeus, 1758; Eloranta et al. 2011). The extent that spatially distinct habitats are coupled therefore appears to go from low to high as trophic level increases in lake food webs (Fig. 1B). Omnivory also appears to increase with trophic level because common piscivores, such as Lake Trout and Smallmouth Bass *Micropterus dolomieu* (Lacépède, 1802), feed on a wide range of prey sizes and trophic levels and can switch to invertebrate feeding after they have suppressed their preferred fish prey (Schindler et al. 1997, Vander Zanden et al. 2000). Based on literature reviews, both aquatic and terrestrial food webs repeatedly show increased habitat coupling (Rooney et al. 2006) and increased omnivory (Thompson et al. 2007) with increasing trophic level.

Coupling can also occur at scales other than these benthic and pelagic macrohabitat examples, which suggests that the generalist module occurs at multiple scales (Rooney et al. 2008). Specifically, body size arguments suggest that smaller species lower in the food web should couple over smaller, microhabitat divisions because they are less mobile than larger, higher trophic level species capable of moving across larger ecosystem boundaries (e.g., aquatic and terrestrial, Fig. 2A). Empirical examples of this repeated structure at different spatial scales are few. Recently, McMeans et al. (2013) found evidence of multiscale coupling in an arctic marine ecosystem across benthic and pelagic compartments at the food web level by mobile predators, and across benthic and phytodetrital compartments by benthic invertebrates (Fig. 2B). Omnivory can also occur within single compartments. Predatory invertebrates within the pelagic sub-web of lakes, for example, can switch to phytoplankton consumption where zooplankton prey are rare (France 2012).

In summary, data within lakes and other aquatic ecosystems display an intriguing pattern whereby different

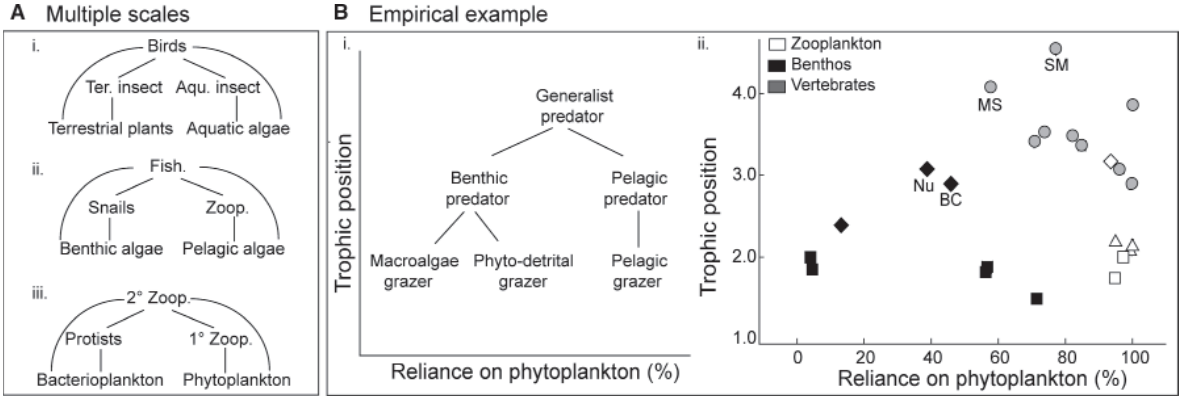

FIG. 2. (A) The generalist module in which predator coupling of food web compartments repeats itself at multiple scales: (i) across ecosystems (aquatic-terrestrial), (ii) within an ecosystem (pelagic-benthic), and (iii) within a sub-web (bacteria-phytoplankton). (B) A (i) conceptual representation and (ii) empirical example of coupling repeated at multiple scales in a coastal marine ecosystem showing that generalist predators such as *Myoxocephalus scorpius* (MS) and *Somniosus microcephalus* (SM) couple benthic and pelagic energy pathways at the food web scale, whereas and predatory benthos, such as nudibranch (Nu) and *Buccinum cyaneum* (BC), couple phytodetrital and macroalgal energy pathways at the benthic sub-web scale (redrawn from McMeans et al. 2013; squares represent herbivores; triangles, omnivores; diamonds, carnivores; and circle, vertebrates).

energy compartments are coupled by mobile generalists (Fig. 1), with the spatial scale over which this coupling occurs, increasing towards higher trophic levels (Fig. 2). The question remains as to what this pattern means for the stability of aquatic ecosystems.

Differential response and behavior as components of ecosystem adaptive capacity

Recent food web theory argues that different resource compartments do not always respond synchronously with changing environmental conditions (McCann and Rooney 2009). This is important because synchronized resources tend to amplify interaction strengths and increase system variability, whereas asychronized resources dampen variation and promote stability (McCann et al. 2005, Rooney et al. 2006, Sinclair et al. 2013). In aquatic ecosystems, resource asynchrony can manifest at the interspecific level (e.g., phytoplankton community succession *sensu* Sommer et al. 1986), but can also occur among entire functional guilds. For example, across a gradient of increasing lake depth, the relative contribution of zooplankton to total lake secondary production increases while that of zoobenthos decreases (Fig. 3A; Vadeboncoeur et al. 2002). Similarly, aquatic and terrestrial prey availability in streams peak at different times of the year (Fig 3B; Nakano and Murakami 2001). Terrestrial examples include herbivores in the Serengeti responding differently to decadal climate oscillations (Sinclair et al. 2013) and consumers of fungi and bacteria fluctuating out of phase with one another in soil food webs (Moore and de Ruiter 1991). Differential species and habitat responses can be more bottom-up (e.g., McMeans et al. 2013, Tanentzap et al. 2014) or top-down driven (e.g., Rooney et al. 2006, Tunney et al. 2012), but both serve to create a spatial mosaic of resource productivity that varies through time.

Mobile and generalist organisms are, in turn, capable of rapid behavioral responses to asynchronously varying resources. Specifically, if one habitat is thriving while another is not, then a mobile predator can respond by increasing foraging activity in the more productive habitat (called the birdfeeder effect; Eveleigh et al. 2007). Generalist Lake Trout, for example, forage more strongly on zoobenthos in smaller lakes as compared to larger lakes (Fig. 3C; Vadeboncoeur et al. 2002). Stream fish also increase terrestrial prey use when terrestrial prey influx is highest (Fig. 3D; Nakano and Murakami 2001). On land, shrubland birds readily switch between foraging on insect and fruit resources that fluctuate asynchronously with season (Carnicer et al. 2008). Such adaptive generalist foraging acts to minimize the potential for any single species, or sets of species, to monopolize available nutrients and energy, therefore promoting food web stability (Gross et al. 2009) and the maintenance of a diverse and variable assemblage of organisms (McCann et al. 2005, Carnicer et al. 2008, Rooney et al. 2008).

An important component of this theory, however, is that conditions which yield very strong coupling into multiple habitats, such as large subsidies (Huxel and McCann 1998) or small ecosystems (McCann et al. 2005), can be destabilizing if they allow generalist predators to reach such high densities that they dangerously suppress preferred prey (akin to apparent competition; Holt 1977). Behavioral responses must also be rapid for predation to be stabilizing, because slow responses generate destabilizing lags (Abrams 2006).

Together, these results suggest that the generalist module (Fig. 1A) is both a theoretically motivated and empirically appropriate characterization of the major carbon flow pathways through food webs. According to this theory, ecosystem adaptive capacity is generated by differential responses of resources at a variety of spatial

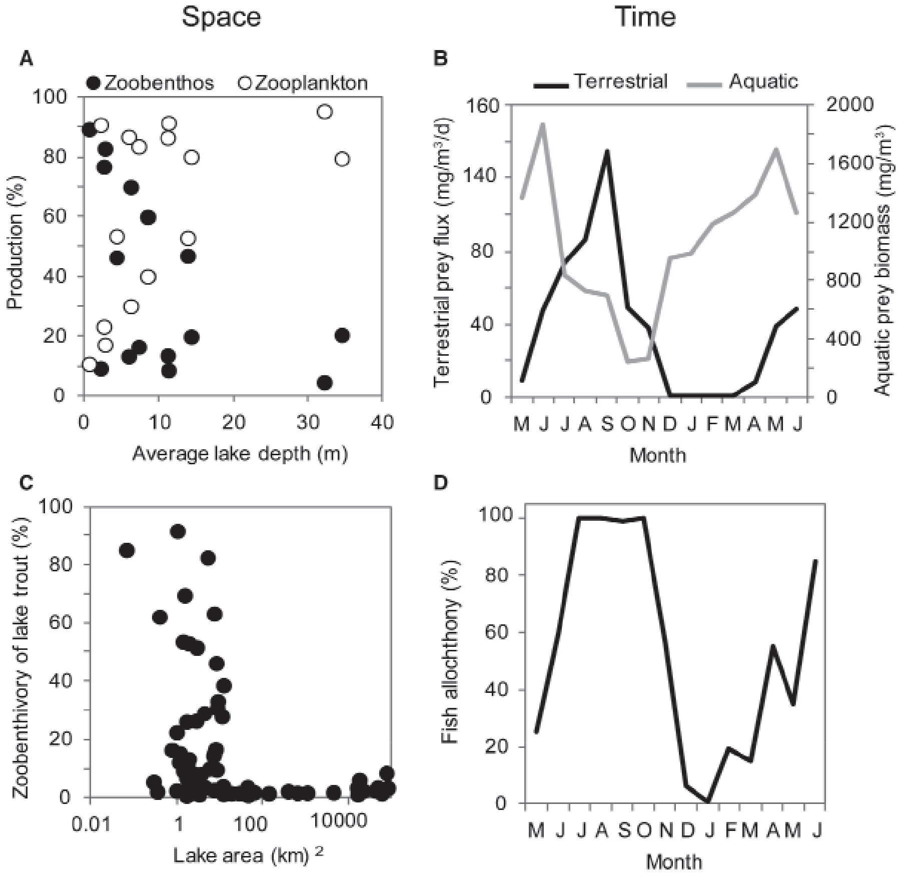

Fig. 3. Differential responses of resources (A, B) and rapid response of fish predators (C, D) in space and time. (A) Percent contribution of zoobenthos and zooplankton to total secondary production (i.e., zooplankton + zoobenthos) across a gradient of average lake depth (meters). (B) Seasonal change in terrestrial prey flux to and aquatic prey biomass within a Japanese stream. (C) Decreasing consumption of zoobenthos by Lake Trout in response to reduced access to littoral prey with increasing lake size (area, kilo meters squared). (D) Seasonal changes in reliance on terrestrial (vs. aquatic) prey by *Oncorhynchus masou* due to underlying changes in terrestrial prey flux to a Japanese stream. Data redrawn from Vadeboncoeur et al. 2002 (A, C) and Nakano and Murakami 2001 (B, D).

and temporal scales and integration of this variation by shifts in predator foraging behavior, with the range of scales being integrated increasing with predator size and trophic position. We now examine a well-studied case of northern lake ecosystems with Lake Trout as the top predator to identify how this adaptive architecture (Fig. 1A) responds to changing conditions.

Unfolding the Adaptive Capacity of Lake Ecosystems

Lake Trout are top predators that naturally inhabit deep and cold North American lakes. In the southern part of this distribution, these lakes contain pelagic year-round thermal refuges separated by a thermocline from a warmer surface layer that is uninhabitable to Lake Trout for long periods each year. The trophic relationships of this system have been studied extensively using stomach contents combined with stable isotopes of carbon ($\delta^{13}C$) to track littoral vs. pelagic carbon source use and nitrogen ($\delta^{15}N$) to estimate trophic position (Post et al. 2000, Vander Zanden and Vadeboncoeur 2002, Tunney et al. 2012, 2014). To build on previous explorations of how lake food webs respond to gradients in lake size (Vander Zanden et al. 1999, Post et al. 2000, Vadeboncoeur et al. 2002, McCann et al. 2005), Tunney et al. (2012) used theoretical models and empirical data to argue that lake food webs may restructure in predictable ways as environmental conditions change. Specifically, historical and recent data from lakes with similar prey communities showed that Lake Trout decreased littoral habitat coupling and omnivorous foraging on littoral invertebrates across a gradient of increasing lake size (moving from left to right on Fig. 4A,B).

Increased nearshore coupling in smaller lakes facilitates increased energy flow to and density of Lake Trout, which may drive a trophic cascade (suppression of preferred pelagic and littoral fish prey and release of littoral invertebrates and zooplankton) that renders omnivorous feeding on littoral invertebrates more beneficial in smaller systems

(Fig. 4B). While biomass pyramid information was not available for Lake Trout, Cyr and Peters (1996) showed that smaller lakes did support more top-heavy food webs (increased fish: zooplankton ratios) than larger lakes. Based on this work, lake food web structure and ecosystem-level biomass and energy flows restructured across a gradient of ecosystem size. Although not measured by Tunney et al. (2012), it is likely that changes in food web structure and fish foraging behavior were also accompanied by shifts in nutrient cycling through these ecosystems, because fish predators are known to affect littoral to pelagic nutrient transport in lakes (Schindler et al. 1993, Vanni 2002).

The responses of lake systems to environmental variation also appear to manifest at the individual level via altered life history attributes. Shuter et al. (1998) have found that across a similar lake size gradient explored in Tunney et al. (2012), although for different lakes, individual-level attributes of Lake Trout also change in a consistent way. Lake Trout maximum length (Fig. 4C) and length at maturation (Fig. 4D) both decline while density (data not shown) increases with decreasing lake size (Shuter et al. 1998). Reduced body size in smaller lakes is consistent with maximum size predictions from bioenergetic models (Kerr and Ryder 1977, Sherwood et al. 2002), which have empirically argued that reduced prey size or richness drives reduced maximum predator sizes.

Temperature-driven changes to prey availability (i.e., access + density) could explain these observed shifts in Lake Trout foraging behavior and resultant food web structure. Specifically, the larger area of the warm littoral zone in larger lakes would reduce the availability of littoral prey to cold water Lake Trout. High temperatures above physiological capabilities are broadly known to restrict foraging in warm habitats by cold water ectotherms (Brett

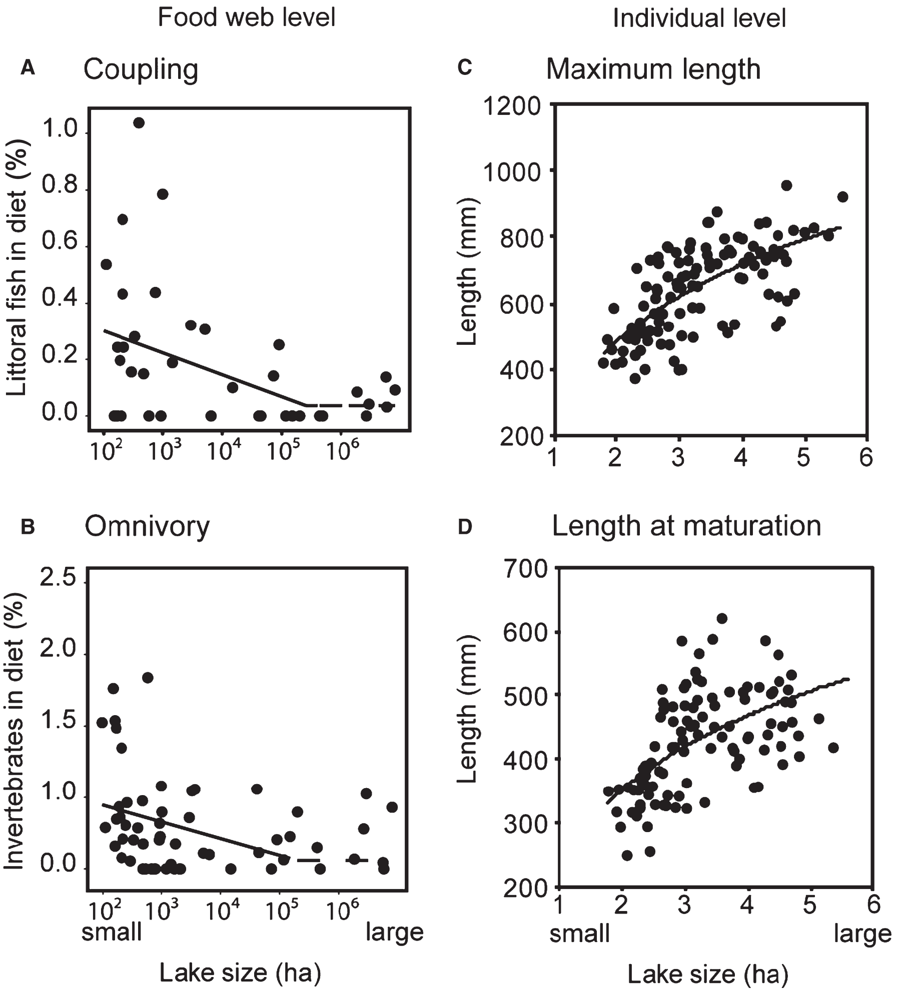

FIG. 4. Food web (A, B) and individual/population level (C, D) responses to a lake size gradient (all x axes show log transformed lake area in hectares). The top predator, Lake Trout, exhibits increased coupling (A: increased consumption of littoral prey) and omnivory (B: reduced trophic position) in smaller lakes, as well as smaller maximum length (C) and length at maturation (D). A and B are redrawn from Tunney et al. (2012) and C and D are from Shuter et al. (1998).

1971, Stefan et al. 2001, Plumb and Blanchfield 2009). Even at temperatures below such thermal thresholds, foraging behavior is likely mediated by a tradeoff between an organism's potential for successful foraging bouts and increased metabolic demands in a thermally inhospitable environment (Petchey et al. 2010, Nowicki et al. 2012, Rall et al. 2012). For example, in lakes where temperature does not exceed physiological thresholds, or where predators can move rapidly in and out of intolerably warm environments and still acquire prey, littoral–pelagic coupling should be maintained. In larger lakes with larger littoral zones that provide greater spatial refuge for prey and thermally limit search times, coupling should decline, which is consistent with the data provided by Tunney et al. (2012).

Additional evidence for a thermally driven response of Lake Trout comes from a related study that focused on lakes of similar sizes but different shapes with respect to the littoral zone (Dolson et al. 2009). Lake Trout in these lakes decreased nearshore coupling and omnivory in response to increased spatial complexity of the lakes' littoral zones (moving from left to right on Fig. 5A,B). Lakes with more reticulate and complex littoral areas effectively act like large lakes by increasing prey refugia and thermally limiting foraging in littoral areas by Lake Trout, compared to lakes with smaller, less complex littoral zones. Individual-level data gathered during the sampling for the Dolson et al. (2009) study additionally show that Lake Trout maximum size ($P < 0.05$) and density ($P > 0.05$) increased and decreased, respectively, with increasing littoral area (Fig. 5C,D; McCann, *unpublished data*). Again, across an environmental gradient (lake shape), the system changed in a predictable way from the individual to the whole ecosystem level. We argue that such knowledge of how systems respond to variation sheds light on ecosystem adaptive capacity and could provide unprecedented insight into the possible consequences of human activities for these adaptive structures and their resultant ecosystem functions.

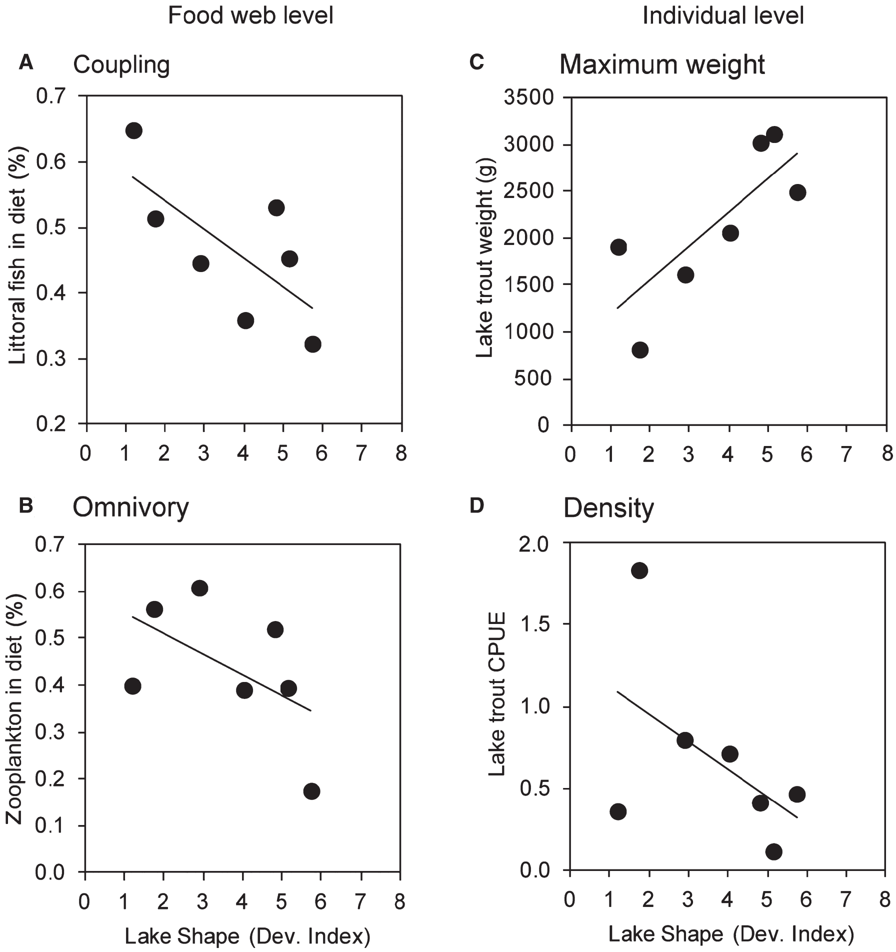

FIG. 5. Food web (A, B) and individual/population level (C, D) responses to a gradient in lake shape shown from low to high levels of shoreline development (Dev. Index, a proxy for littoral area) moving from left to right on *x* axes. Less reticulate lakes mimic small lakes in that littoral prey are more accessible. Food webs in these less reticulate lakes therefore are increasingly coupled (A) with more omnivory (B), which is accompanied by population level declines in top predator (Lake Trout) maximum weight (C) and increases in density (D). Data are from Dolson et al. 2009 (A, B) and K. McCann, *unpublished data* (C, D).

Human Impact and the Loss of Ecosystem Adaptive Capacity?

Human activities have altered lake ecosystems in a variety of ways. Eutrophication has driven shifts in lake state from clear to turbid, and the altered distribution of water and biota has impacted lake energy flow pathways (reviewed by Smith and Schindler 2009, Carpenter et al. 2011). Climate-driven temperature increases are also altering the timing of resource production in lakes, with negative consequences for consumers higher up in the food web (Winder and Schindler 2004, Woodward et al. 2010*b*). Based on the theory outlined above, these and other human impacts, which remove resource heterogeneity or the mobile predators that couple it, may also reduce the potential for the generalist module to respond to changing conditions and, therefore, threaten ecosystem adaptive capacity.

Such an example of a human impact on adaptive capacity, which has emerged from the research outlined above, is that the ability of a generalist predator to couple into multiple habitats may be lost or muted with warming temperatures (Tunney et al. 2014). In northern stratified lakes, warming tends to increase the temperature of epilimnion and nearshore zone, while reducing the size of the deep coldwater zone that remains habitable by Lake Trout (Schindler et al. 1990, Keller 2007, Cline et al. 2013). Given these characteristics, Tunney et al. (2014) used a temperature gradient approach and found that Lake Trout exhibited reduced littoral habitat coupling (Fig. 6A) and omnivorous foraging on littoral invertebrates (shown as an increase in trophic position, Fig. 6B) in lakes with higher summer temperatures. Additionally, Lake Trout appeared to respond behaviorally to warmer, increasingly less habitable littoral zones because the catch per unit effort of Lake Trout decreased in the nearshore zone in the warmer lakes (Fig. 6C).

Introductions of Smallmouth Bass in some lakes have also been suggested to reduce availability of nearshore prey and, subsequently, reduce littoral habitat coupling, growth, and reproduction in Lake Trout (Vander Zanden et al. 2004). Access to key prey is also critical for fish growth and recruitment to the piscivorous stage throughout ontogeny (Hargeby et al. 2005, Woodward et al. 2010*a*). Human-driven decoupling of fish from their key prey may therefore have detrimental consequences and serious management implications for predators if they no longer have sufficient accessible production to support viable populations. Direct removal of top predators via fisheries harvest also threatens ecosystem capacity and has been linked to decreased ecosystem stability (Britten et al. 2014). Importantly, a suite of existing tracers and tools (referred to as 'structural indicators,' Table 1) show great promise for identifying and monitoring for potential losses to ecosystem adaptive capacity across the ecological hierarchy and, correspondingly, from small to large scales (Fig. 7).

Monitoring Adaptive Food Webs: an Integrated Role for Ecological Tracers and Tools

Several existing tracers and tools are capable of identifying how the theoretically derived generalist module (Fig. 1A) empirically restructures across changing conditions via altered nutrient and energy flows at the ecosystem and food web level. Stable isotope analysis is readily aligned with the generalist module because δ^{13}C can identify coupling across ecosystem and macrohabitat compartments (e.g., aquatic–terrestrial and benthic–pelagic), while δ^{15}N deciphers trophic position and omnivory (see review by Boecklen et al. (2011)). Complimentary analysis of stomach contents and fatty acid biomarkers (see review by Dalsgaard et al. (2003)) can provide better resolution and support for how predators couple across specific habitat compartments through space or time (e.g., increased importance of littoral pathways; Paterson et al. 2014). Combined analysis of stable isotopes with contaminants that biomagnify can shed further light on how human-driven changes in food web structure alter contaminant levels and transport (see review by McKinney et al. (2015)). Predaceous fish are also important for moving nutrients across habitat boundaries (Vanni 2002) and elemental stoichiometry could be applied within our framework to trace how fish foraging behavior affects nutrient transport, levels, and limitations across changing environmental conditions (see review by Elser et al. (2000)).

At a finer resolution, analysis of δ^{15}N values in individual amino acids (Chikaraishi et al. 2014) and δ^{13}C in individual fatty acids (Bec et al. 2011) are providing more robust and accurate estimates of predator diets while overcoming some of the caveats associated with 'bulk' stable isotopes analysis (reviewed by Wolf et al. (2009). Molecular techniques including DNA barcoding of gut contents provide detailed information about the makeup of predator diets and can produce more complete food webs compared to taxonomic stomach content identification (Pompanon et al. 2012, Carreon-Martinez et al. 2014). Within our framework, such highly resolved dietary information can help identify the specific trophic linkages that are driving observed shifts in ecosystem level energy, nutrient, and contaminant flows.

Also central to our approach is information about predator behavior and health. Techniques such as catch per unit effort data (Rennie et al. 2009), trace elements (Tanentzap et al. 2014), and acoustic and archival tracking technologies (Hussey et al. 2015) are providing detailed information about the habitat use and behavior of populations and individuals through space and time. Additionally, 'environmental' DNA (eDNA) obtained directly from water samples is an emerging tool for estimating aquatic species diversity, density, biomass, and occupancy in a given habitat with potentially much less effort than traditional survey methods (reviewed by Rees et al. (2014)). However, a greater understanding of how environmental factors and species traits affect eDNA production, degradation, and diffusion is currently needed before the approach can be applied to quantify variation in spatial habitat use and coupling. Finally, physiological indicators of stress (cortisol; Campbell et al. 2003), movement (lactate dehydrogenase [LDH]; Morbey et al. 2010), and nutrition (levels of the essential fatty acids 20:5n-3; Tocher 2003), when combined with information about fish growth and life history parameters (Shuter et al. 1998), could shed light on how altered resource pathways are affecting predator health and fitness.

Programs aimed at developing and integrating these tracers and tools will allow researchers to generate repeated lines of evidence for the consequences of human activity and to mechanistically link these responses across the ecological hierarchy and, consequently, from small to large scales (Fig. 7; Woodward et al. 2010*b*, Friberg et al. 2011, Hussey et al. 2015). Existing environmental gradients provide the spatial and temporal heterogeneity that allows for these adaptive structures to be identified (Fig. 7). This includes spatial gradients of lake size, shape, and temperature, as in our Lake Trout example above, and other spatial gradients that affect resource availability or consumer foraging behavior across habitats, including turbidity (Carreon-Martinez et al. 2014), vegetation cover (Tanentzap et al. 2014), and acidity (Layer et al. 2013). Studying temporal changes in resource use by aquatic predators is also informative. For example, stable isotopes, stomach contents, and fatty acids all pointed toward increased reliance on lower quality littoral prey by multiple predators in the Laurentian Great Lakes following invasion of Dreissenid mussels (*Dreissena polymorpha* and *D. bugensis*; Rennie et al. 2009, Rush et al. 2012, Paterson et al. 2014). Increased littoral catch per unit effort of Lake Whitefish *Coregonus clupeaformis* (Mitchill, 1818) provided additional evidence that the benthification of Great Lakes ecosystems by invasive mussels (shunting of energy and nutrients away from the pelagic zone) was altering food web structure, fish behavior, and fish health (Rennie et al. 2009).

Monitoring the foraging behavior of predators could also compliment time series based early warning signals and help predict the impending restructuring of entire ecosystems. This is because predators respond rapidly to changes in the composition and availability of species below them in the food web. As an example of this predictive ability, Velarde et al. (2013) recently demonstrated that shifts in the foraging behavior of birds signaled impending declines in forage fish before stocks actually collapsed. Altered predator foraging behavior, especially when simultaneously accompanied by changes in individual behavior, growth, and physiology (Fig. 7), may therefore provide a powerful framework to monitor for ecosystem level shifts before observable changes in biomass structure occur.

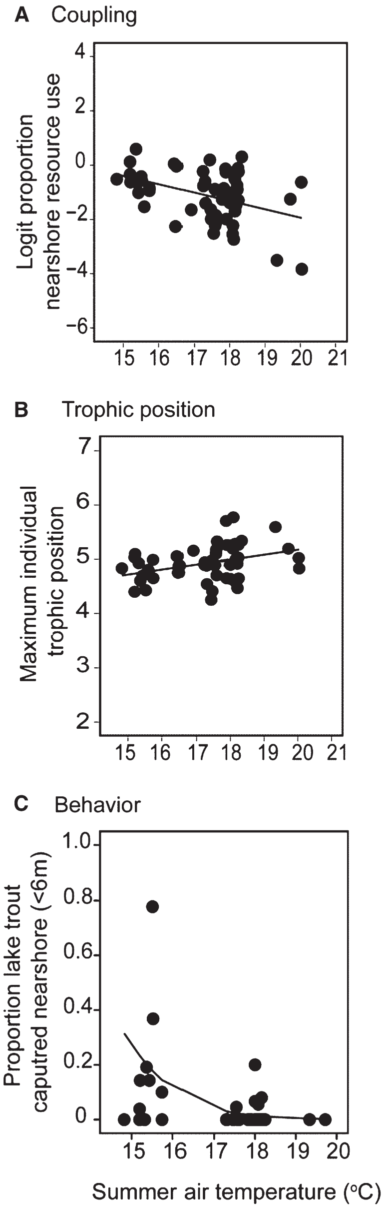

FIG. 6. Cooler lakes with more accessible littoral zones support Lake Trout populations that exhibit increased nearshore coupling (A) and reduced trophic positions (i.e., increased omnivory) of individual Lake Trout (B). These ecosystem-level shifts in energy flow are accompanied by individual-level behavioral changes whereby Lake Trout show increased use of the nearshore zone in cooler lakes (C). Data are redrawn from Tunney et al. 2014.

Developing frameworks such as those outlined in Fig. 7 may, at least initially, require increased research efforts compared to existing biomonitoring schemes. However, researchers are arguing for more theoretically based biomonitoring approaches that mechanistically assess the multilevel responses of aquatic systems to perturbations (Woodward et al. 2010*b*, Friberg et al. 2011, Gray et al. 2014). We argue that employing existing environmental gradients and a suite of ecological tracers and tools, whose costs will almost certainly continue to decline as they are further developed, provide a feasi-

Table 1. A currently available suite of ecological tracers and tools that can resolve nutrient and energy flows, movement and physiological indicators of fish nutrition and stress.

Category	Tracer	Example	Application	Reference
Nutrient & energy flows	Stoichiometry	N:P	Trace nutrient flows and potential limitations among ecosystem components	Elser et al. (2012)
	Stable isotopes	$\delta^{13}C$, $\delta^{15}N$	Identify major carbon flows, coupling, omnivory, niche widths, trophic position	Boecklen et al. (2011)
	Biomarker fatty acids	n-6 fatty acids	Resolve carbon source contributions to upper trophic levels (e.g., aquatic vs. terrestrial)	Dalsgaard et al. (2003)
	Compound-specific analyses	$\delta^{13}C$ of fatty acids	Better discriminate among basal carbon sources	Bec et al. (2011)
		$\delta^{15}N$ of amino acids	More accurately assign trophic positions and trace nitrogen sources	Chikaraishi et al. (2014)
	Biomagnifying contaminants	Mercury	Link food web structure with contaminant exposure and transfer	McKinney et al. (2015)
	DNA analysis of gut contents		Provide detailed profiles of predator diets	Pompanon et al. (2012)
Movement/ habitat use	Tracking technology	Acoustic or archival tags	Accurately track fish habitat use through space and time	Hussey et al. (2015)
	Trace elements	Ba, Ca, Sr	Reflects water chemistry of a particular habitat	Tanentzap et al. (2014)
	Environmental DNA		Estimate species diversity and occupancy in a given habitat	Rees et al. (2014)
	Enzymes	Lactate dehydrogenase	Indicator of swimming activity	Morbey et al. (2010)
Nutrition	Essential fatty acids	20:5n-3, 22:6n-3	Essential for fish nutrition; associated with high quality resources	Tocher 2003
Stress	Hormones	Cortisol	High levels associated with stress and potentially reduced fitness	Campbell et al. (2003)

ble pathway toward this goal in some ecosystems. Once fully developed in more ecosystem types, our framework could eventually help redirect available funds and efforts toward monitoring a reduced, select number of structural indicators that are connected to key attributes of ecosystem adaptive capacity.

Discussion

Existing theory suggests that consumer adaptive foraging behavior and food web restructuring can promote stability (Valdovinos et al. 2010, Thierry et al. 2011) and that the generalist module (Fig. 1A) contributes to food web persistence in the face of perturbations (McCann and Rooney 2009). The empirical patterns discussed above in The Generalist Module as a Fundamental Food Web Attribute whereby a top predator responds flexibly to resource variation between habitat compartments support the existence of the generalist module as an overarching food web structure. The predictable restructuring of the generalist module across environmental gradients further suggests that it plays a central role in ecosystem adaptive capacity. We suggest that advancing the use of ecological tracers and tools to study this adaptive structure will shed light on human impacts across the ecological hierarchy, from individual to ecosystem levels. This approach has the potential to further our scientific understanding of the adaptive responses to major drivers of ecosystem change and to develop more effective strategies for biodiversity and ecosystem management. Such a united research agenda is critical for a science that has long separated among different research axes (e.g., population vs. community vs. ecosystem; applied vs. fundamental).

Although not directly addressed herein, we assume that individual Lake Trout within single lakes in our case studies were at least capable of feeding as generalists (were not individual specialists *sensu* Bolnick et al. 2003). Supporting this contention: (1) recent work suggests that the extent of individual specialization declines at high trophic positions (Svanbäck et al. 2015), and (2) Lake Trout tend to be highly plastic in their feeding and to have low within- relative to among-population diet variation (Vander Zanden et al. 2000). Some evidence exists, however that Lake Trout individuals develop diet-specific morphotypes in large lake ecosystems where interspecific competition is low (Chavarie et al. 2013). Other examples of 'generalist' species exhibiting individual-level resource selection include Smallmouth Bass selecting for certain prey during years when intraspecific density was high (Schindler et al. 1997), and individual Brown Trout selecting for specific habitats or resources (Giller

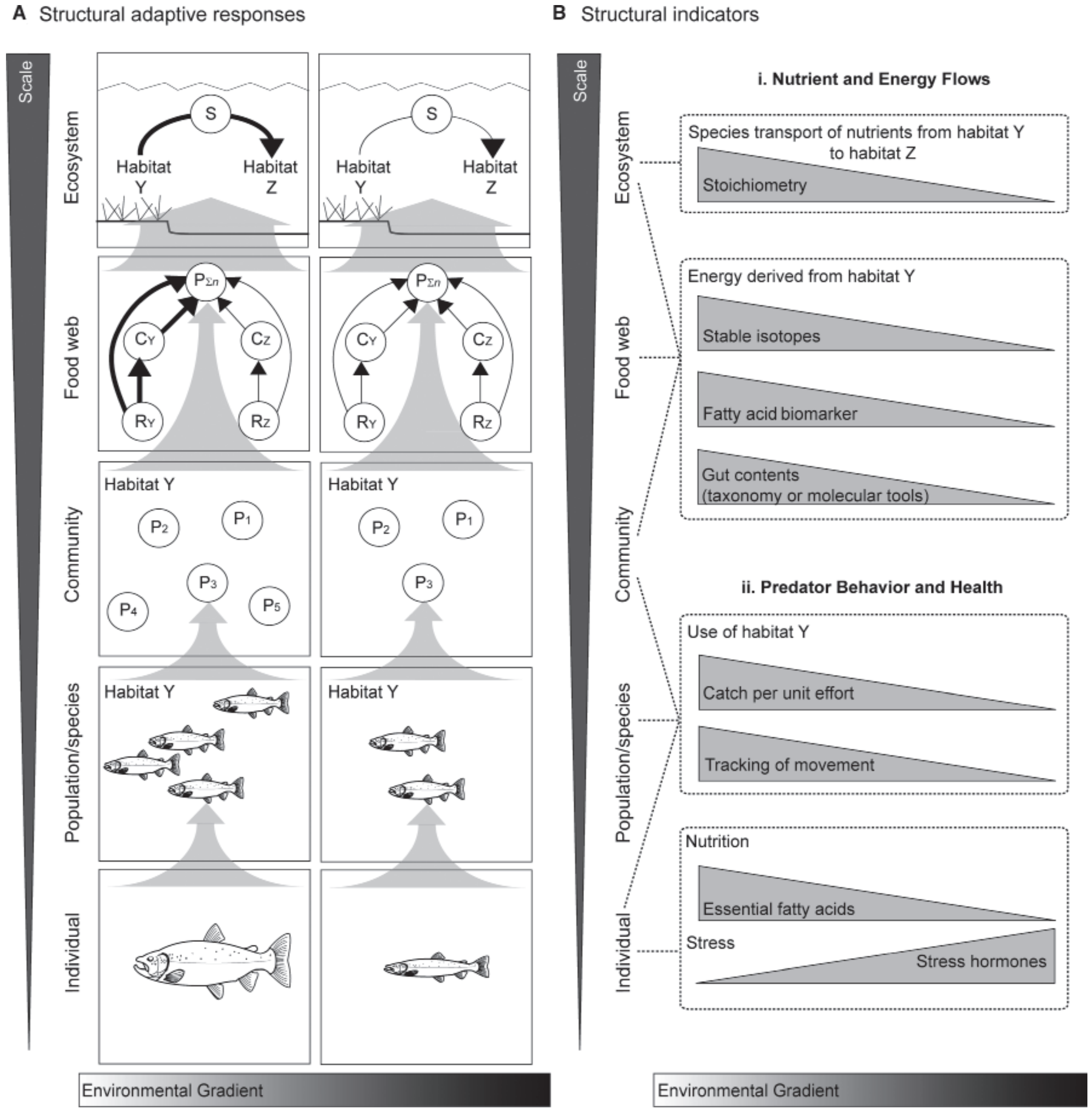

FIG. 7. (A) Conceptual framework depicting sample adaptive structural responses of a hypothetical aquatic system and (B) suites of structural indicators that can be applied to study these responses across an environmental gradient. The framework is multilevel (individuals to ecosystems) and multi-scale in both space (microhabitat to landscape) and time (days to years) because processes occurring at higher ecological levels correspond to larger scales. In this hypothetical example, moving from left to right along the gradient (*x*-axes), species (S) exhibit reduced ecosystem transport of nutrients from habitat Y to habitat Z. Focusing in on the food web reveals that predators ($P_{\Sigma n}$, refers to a single predator species or a community of *n* different predator species) acquire less energy from habitat Y prey. This is accompanied by reduced use of habitat Y in predator communities and species and reduced individual health. One suite of indicators (i) can trace these altered nutrient and energy flows at the level of ecosystems and food webs and a second (ii) can uncover accompanying species and individual level changes in behavior and health. These changes across the gradient can also be studied at the community level among different predator species. See Table 1 for a description and other examples of structural indicators.

and Greenberg 2014). The consequence of such within-population diet variation for ecosystem adaptive capacity will likely depend on the timescale over which these selective foraging behaviors are maintained and the extent to which generalist foraging capabilities are lost. Intraspecific diet variation in a broad sense, and the genetic variation underlying it, is important for allowing a population to adapt to future conditions over long timescales (Bolnick et al. 2011). From our perspective, diet variation among individuals could help promote ecosystem adaptive capacity if individuals maintain the ability to respond flexibly and opportunistically to changing conditions over short timescales (such as the Smallmouth Bass example provided above). Populations dominated by long-term individual specialists that have lost foraging flexibility, on the other hand, would respond more slowly and in our terminology, less adaptively to environmental variation (Bolnick et al. 2003). In reality, both short-term behavioral responses and long-term phenotypic variation likely contribute to observed intraspecific diet variation. Future directed efforts, including applications of the tools outlined in Table 1, will help uncover (1) the occurrence, permanency, and flexibility of observed feeding behaviors throughout the food web (Svanbäck et al. 2015), and (2) the consequences of intraspecific diet variation for ecosystem adaptive capacity.

Our framework has widespread applicability in other system types. This is because the generalist module, and the body size, mobility, and foraging relationships underlying it, appears to be a widespread attribute of food webs (McCann et al. 2005, Rooney et al. 2006, Layer et al. 2010). For example, stable isotopes uncovered that ground dwelling arthropod predators couple terrestrial and aboreal compartments in wooded grasslands (Pringle and Fox-Dobbs 2008) and that arctic foxes (*Alopex lagopus*, Linneaus, 1758) couple terrestrial and marine pathways in coastal tundras (Roth 2002). Further, American alligators (*Alligator mississippiensis*, Daudin, 1802) can couple marine and estuarine habitats based on stable isotopes and acoustic tag data (Rosenblatt and Heithaus 2011). The structural indicators outlined in Table 1 could therefore be applied to study how human impacts, beyond freshwaters, including climate-driven shifts in terrestrial plant production, sea ice-driven declines in marine resource access, and reduced marine-esturary connectivity, alter the ability of the generalist module to respond to changing conditions. Extending our approach to large systems, such as the Laurentian Great Lakes, is also feasible and presents researchers with unique opportunities to consider how multiple predators couple across an increasing number of habitat compartments both horizontally (e.g., inshore and offshore) and vertically (e.g., surface and profundal; Paterson et al. 2014, Sierszen et al. 2014, Stockwell et al. 2014). Researchers in large marine ecosystems are also combining diet analysis and archival tag data with molecular tools (expression of genes related to cold tolerance) to study the coupling of warm suface with cold deepwater habitats by tunas (Madigan et al. 2015). Important considerations and remaining questions in moving from small to very large systems include (1) what level of detail (e.g., from micro to macro habitats) is necessary for anticipating whole system- or population-specific responses to stressors like climate change and species invasions, and (2) how coexisting generalist and specialist fishes in various habitats and at different trophic positions collectively respond and sustain energy and nutrient flow in the face of changing environmental conditions.

Existing concepts in ecology lend some insight into the possible beneficial consequences of variation among species in their responses to environmental change. The portfolio effect stresses the importance of differential responses at the population and community levels for buffering environmental variability (Hilborn et al. 2003, MacDougall et al. 2013, Schindler et al. 2015). Such biocomplexity in populations and communities can be viewed as another form of adaptive capacity, which complements our focus on asynchronously fluctuating habitat compartments and the buffering capacity of predators at the food web level. Further, diet variation among predators may serve to maintain essential ecosystem functions (e.g., trophic control) by balancing trophic flows. For example, reduced coupling by one species may be balanced by increased coupling in another species. By taking advantage of existing environmental gradients, applying multiple tracers, and gathering specific information on individual taxa (e.g., behavior and physiological tolerances), researchers can begin to uncover the mechanism by which individual adaptive predators, and ultimately predator communities, respond to variation and help maintain function in a wide range of ecosystem types.

While ecosystems are considered examples of complex adaptive systems (Levin 1998) and management policy seeks to preserve this capacity to buffer ecosystems (Travis et al. 2014), little research has yet directed ecologists toward what these adaptive responses actually are. Here, we have outlined empirical work motivated by theory to propose that an individual-to-whole ecosystem's biological structure changing consistently with changing conditions offers us a glimpse of a system's adaptive capacity. Recent and ongoing development of suites of ecological tracers and tools provide an avenue to monitor for the loss of these adaptive structures, thus signaling the loss of adaptive capacity. We have provided an example whereby increasing temperature may act to decouple nearshore from offshore habitats, as mobile consumers find themselves excluded from warmed, nearshore zones. Because habitat switching may buffer variability in prey populations and prevent any species from dominating energy or spatial resources, such a condition may reduce the adaptive capacity of a food web and influence the function of whole systems. Further, these mobile, generalist food web 'stabilizers' are typically the primary targets of harvesting, and our framework could help incorporate this role in food web maintenance into harvest regulations. Collectively, our results argue for an emerging field that unites theory across the ecological hierarchy and links behavior, population dynamics, food web structure, and ecosystem functions such as secondary production and stability. Continued development of research agendas within this field would ultimately provide the basis for new biomonitoring approaches and management policies that better sustain ecosystem functions in the face of changing conditions.

Acknowledgments

The authors thank the Great Lakes Fishery Commission grants to K. S. McCann and A. T. Fisk, a National Science and

Engineering Research Council (NSERC) Discovery Grant to K. S. McCann, an NSERC Discovery Grant and Canada Research Chair funding to A. T. Fisk. Timothy Bartley and two anonymous reviewers provided helpful comments.

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Data Availability

Data associated with this paper have been deposited in Dryad: http://dx.doi.org/10.5061/dryad.f4mc7