Lake Food Web Responses Across Environmental Gradients

by

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ABSTRACT

LAKE FOOD WEB RESPONSES ACROSS ENVIRONMENTAL GRADIENTS

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This PhD thesis incorporates environmental conditions into notions about what mediates the structure of major trophic pathways and the biomass structure of food webs. The result is a set of new ideas that extend understanding of how changes in environmental conditions impact the structure of food webs. Unlike many traditional studies that present binary, static food webs in a homogenous environment, here I consider changes in relative trophic interaction strengths and make simple spatial arguments about habitat differences to link food web structural shifts to environmental conditions (for example, ecosystem size, climate, and visibility). I argue that the adjustments organisms make to avoid, or to exploit, the mosaic environment regulates the major trophic pathways that fuel whole food webs. I develop a set of theoretical predictions and use literature data and a substantial new dataset that I have assembled from Canadian lakes to show that trophic pathways can vary in predictable ways across environmental gradients. These findings provide new insight into an emerging research area that asks how the environment determines the macroscopic properties of food webs. Furthermore, this research provides new knowledge on Canadian freshwater lakes which house a significant portion of the world’s freshwater life, as well as, socially and economically important fisheries. I discuss the potential implications of the food web structural changes documented for the persistence of species in natural systems. Since many organisms experience the world as an environmental mosaic, and humans act to modify this natural variety, changes in key food web structures across important environmental gradients provide an initial understanding of some of the changes ongoing as contemporary ecosystems face unprecedented change.
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Table of Contents

Chapter 1  Prologue .................................................................................................................................... 1

1.1 General Problem and Motivation ...................................................................................................... 1

1.2 Conceptualizing a Spatially Coupled Food Web ................................................................. 5

1.3 Stable Isotope Food Webs Across Gradients ............................................................................. 8

1.4 Lakes are Ideal Natural Systems to Study Food Web Change ........................................... 10

1.5 Contributions ............................................................................................................................. 10

1.5.1 Food webs expand and contract ......................................................................................... 11

1.5.2 Differential warming affects complex communities ........................................................ 12

1.5.3 Water transparency predicts a habitat coupling shift for a light sensitive predator ......... 13

1.6 Ideas for Moving Forward ........................................................................................................... 14

1.7 References .................................................................................................................................. 15

Chapter 2  Food web expansion and contraction in response to changing environmental conditions... 20

2.1 Abstract ....................................................................................................................................... 20

2.2 Introduction ................................................................................................................................ 20

2.3 Model Motivation ....................................................................................................................... 23

2.3.1 Biological assumptions and the food web model .................................................................. 23

2.4 Results ......................................................................................................................................... 27

2.4.1 Theoretical results ............................................................................................................... 27

2.4.2 Food web changes across a gradient of ecosystem size ..................................................... 30

2.4.3 Food web changes across a gradient of relative littoral habitat ........................................ 32

2.5 Discussion .................................................................................................................................... 32

2.6 Methods ...................................................................................................................................... 37

2.6.1 Relationship between model and real food webs .............................................................. 37

2.6.2 Numerical simulations ........................................................................................................ 39

2.6.3 Empirical analysis ............................................................................................................... 40

2.6.4 Statistical analysis ............................................................................................................... 42

2.7 References .................................................................................................................................. 43

2.8 Acknowledgements..................................................................................................................... 46

2.9 Supplementary Information........................................................................................................ 47

2.10 Supplementary Discussion ........................................................................................................ 49
2.10.1 A spatially implicit representation of a prey gradient ........................................................ 50
2.10.2 Use of (α) as a resource scaling parameter ................................................................. 53
2.11 Supplementary Methods ................................................................................................. 55
  2.11.1 Determining biomass proportions from gut contents .............................................. 55
  2.11.2 Empirical resource gradient data ............................................................................. 56

Chapter 3 Effects of differential habitat warming on complex communities ....................... 57
  3.1 Abstract .......................................................................................................................... 57
  3.2 Introduction .................................................................................................................... 58
  3.3 Results and Discussion .................................................................................................. 61
    3.3.1 Focal predator alters habitat use in response to climate ....................................... 63
    3.3.2 Non-focal predators and the food web shift ......................................................... 64
    3.3.3 Prey abundance in relation to climate gradient ................................................... 64
  3.4 Conclusions .................................................................................................................. 66
  3.5 Materials and Methods ................................................................................................. 70
    3.5.1 General lake sampling ......................................................................................... 70
    3.5.2 Stable isotope data collection ............................................................................. 71
    3.5.3 Stable isotopes based food web measures ......................................................... 73
    3.5.4 Catch data analysis ............................................................................................. 74
    3.5.5 Statistical approach ............................................................................................ 75
  3.6 References .................................................................................................................... 75
  3.7 Acknowledgements ....................................................................................................... 79
  3.8 Supplementary Information ......................................................................................... 80
  3.9 Supplementary Discussion .......................................................................................... 83

Chapter 4 Blinded by the light? Habitat coupling shift in a dim light preferring predator with reduced water transparency ................................................................. 85
  4.1 Abstract ......................................................................................................................... 85
  4.2 Introduction .................................................................................................................. 86
    4.2.1 Study system and predictions ............................................................................... 89
  4.3 Materials and Methods ................................................................................................. 90
    4.3.1 Relative production model estimates ................................................................. 93
    4.3.2 Isotope data collection ....................................................................................... 94
    4.3.3 Stable isotopes based food web measures ......................................................... 95

v
4.3.4 Statistical analysis ................................................................. 96
4.4 Results ........................................................................................................ 96
  4.4.1 General lake characteristics ......................................................... 96
  4.4.2 Isotopic description of trophic groups ......................................... 97
  4.4.3 Pelagic carbon contribution increases with water transparency ........ 100
  4.4.4 Predator coupling strength and other lake characteristics ............. 101
4.5 Discussion ............................................................................................. 105
4.6 References .............................................................................................. 111
4.7 Supplementary Information ............................................................... 115
Chapter 5 Epilogue ...................................................................................... 117

List of Tables
Table 4.1 Summary of study lake characteristics ........................................ 98
Table 4.2 Summary of model selection for predictors of predator reliance on pelagic resources .... 103

List of Supplementary Tables
Supplementary Table S 2.1 Units for food web model .................................. 48
Supplementary Table S 3.1 ................................................................. 81
Supplementary Table S 3.2 Relationship between lake trout food web structure and five temperature metrics. ......................................................... 82
Supplementary Table S 4.1 Definitions of production model parameters with units. Input values are given when not available directly from lake surveys (with modification from Vadeboncoeur et al. 2008). ........................................ 115
Supplementary Table S 4.2 Equations for the production model ( Vadeboncoeur et al. 2008 with modification see Methods) .................................. 116

Table of Figures
Figure 1.1 Conceptualized food webs for (a) a generic food chain, (b) a spatially coupled food web and (c) a lake food web ......................................................... 7
Figure 2.1 | Predicting food web structure: from theory to nature .................. 24
Figure 2.2 | Theoretical food web responses to changing accessibility ............. 29
Figure 2.3 | Relationships between lake size and food web structure ................. 31
Figure 2.4 | Relationships between relative littoral habitat and food web structure ........ 33
Figure 3.1 Relationship between temperature, trophic structure and, predator habitat use across individual lake ecosystems ........................................ 62
Figure 3.2 Relationship between habitat coupling and temperature is independent of measured indicators of indirect effects in study lakes ......................... 65
Figure 3.3 Simple schematic showing effects of differential warming on habitat coupling (horizontal-axis) and habitat use (vertical-axis) by lake trout in cold (top) and warm (bottom) conditions. 67

Figure 4.1 Conceptualized lake food web where walleye couple offshore and near-shore habitat compartments and expected influence of water transparency on consumption. 91

Figure 4.2 Potential determinants of the reliance of a light sensitive predator on pelagic and littoral benthic resources. 92

Figure 4.3 Stable isotope ratios of carbon ($\delta^{13}$C) and nitrogen ($\delta^{15}$N) distinguish baseline indicators and focal predator in study lakes. 99

Figure 4.4 Relationship between predator reliance on pelagic derived carbon and water transparency and three measures of the proportion of pelagic resources in each lake. 102

Figure 4.5 Relationship between predator reliance on pelagic derived carbon and water transparency after removing the variance explained by the proportion of pelagic prey fish in a lake. 104

Table of Supplementary Figures

Supplementary Figure S 2.1 Relating foraging scale to habitat accessibility for (a) a small and (b) a large alternate habitat. 47

Supplementary Figure S 2.2 Empirical littoral forage fish distribution data from 90 Canadian post glacial lakes. 47

Supplementary Figure S 2.3 Scaling peak resource density to mean resource density for different values of $\alpha$. 48

Supplementary Figure S 3.1 Relationship between climatic gradient and lake size. 80
Chapter 1  Prologue

1.1 General Problem and Motivation

Stephen Forbes (1887) made a foundational contribution to ecology as he peered into a lake and with a sense of fascination described an ‘organic complex’ that at the gross scale appeared unchanged since ancient glacial times (Forbes 1925). On closer inspection, Forbes noted flexibility in the system of interactions that seemed to sustain this apparent consistency despite wildly fluctuating conditions. Forbes’ description suggests that it is the response of the ecosystems architecture to the variable world that is responsible for the consistency in the local species assemblage. Since Forbes’ early observations, the importance of species interactions for the persistence of ecosystems has been stressed repeatedly (MacArthur 1955; May 1973; Pimm 2002; Ives & Carpenter 2007; McCann 2012), where patterns in the presence and strength of species interactions are now considered paramount to the stability or collapse of natural systems. Given the general importance of food web structure, the way species interactions respond to environmental conditions should have significant implications for ecosystem function, but generally the ways that food web structures change in response to either expected natural variability or rapid global change remain poorly understood (Schmitz 2010; McCann 2012).

The conditions of the natural world are perhaps not as constant as once thought. Rather it seems that Earth is undergoing a period of rapid change (Post 2013). Recent local species losses and changes in species distributions have been documented; however, a great deal of uncertainty remains regarding how continued global change will shape future ecosystems. A number of researchers have argued that to address these unknowns requires a better understand how
environmental changes will modify species interactions (Tylianakis et al. 2008; Gilman et al. 2010; Schmitz 2010; McCann 2012; Post 2013). In agreement with these sentiments, I argue that understanding how the consumptive pathways in food webs respond to environmental conditions may help with conserving the ecosystem functions we humans rely on. This notion is the primary motivation of my thesis research where I confront the challenges of documenting, and evaluating some underlying explanations for fundamental food web structure responses to changing environmental conditions.

Understanding the impact of environmental conditions on food webs requires a different approach from much of the traditional food web research. In general, most classic research on food web structure does not consider environmental conditions, although there were exceptions, for example, food web compartments were thought to correspond to habitat boundaries (Pimm 2002). Instead, perhaps due to a massive effort to determine the relationship between species diversity and ecosystem stability (McCann 2000; Ives & Carpenter 2007), differences in the structure of food webs is traditionally limited to changes in the species assemblage. In other words, in many studies food web structure is considered static unless there is a species change. This approach was used to elucidate interaction structures that were common to many different ecosystems as it was expected that these structures had stabilizing properties.

To contrast this classic approach, recent theory argues cogently that even for a constant species assemblage food web structure is flexible and that the organizing structure beneath natural systems is the result of local selective processes (Levin 1998). Further, a number of empirical researchers have found that the food webs they studied could be quite variable in time and space (Winemiller 1990; Polis 1991). To address this apparent variability, ecologists have begun to consider organism traits, such as behaviour, for a more mechanistic understanding of
variability in the structure and function of food webs (Schmitz 2010). I adopt this kind of thinking and address hypotheses that incorporate expected predator species behaviour responses to the environment. Rather than look for patterns in food web structure across different ecosystem types (e.g., aquatic versus terrestrial), I ask how structures in a given food web changes across natural environmental gradients. As part of this approach, I extend logic built on organism behaviour in attempt to understand how food web structure responses to environmental variation. That is, the expected organism response to the environment (e.g., temperature) is used to develop predictions for changes in food web structure.

My approach considers another feature of natural systems that is often overlooked in food web research, but is widely recognized as a key aspect of nature - that the environment is not uniform within a food web, but rather the environment is better described as a natural mosaic (Hutchinson 1959). In my research, it is the differences among habitats that will provide the backdrop for incorporating ideas about consumer behaviour into food web structure. I expect that in one location the abiotic environment might restrict a consumer from a given habitat (e.g., too hot) while in another location the same habitat might be more accessible (e.g., preferred temperature). Ideas about how consumer responses and nature’s environmental mosaic relate to the consumptive pathways that link food webs across habitats are a major emphasis of this thesis.

Recent food web studies suggest that the susceptibility of higher-order consumers to rapid environmental change may seriously erode the fundamental structures that maintain balance in food webs (Rooney et al. 2006; Ripple et al. 2014). By way of their mobility consumers are also important in food web spatial structure as they link food chains across habitats in space (France 1995; Holt 1996; Vander Zanden & Vadeboncoeur 2002; McCauley et al. 2012). Such linkages allow consumers to escape several ecological restrictions imposed by a
single habitat. For example, access to prey in alternate habitats can allow consumer populations to overcome limits on production. Further, multiple habitat use may allow consumers to respond to disturbances that affect resources in any one habitat by moving among habitats (Fryxell et al. 2005; McCann et al. 2005; Abrams 2010; Barton and Schmitz 2009). For the whole food web, predator habitat coupling under the right conditions may stabilize localised food chains, if for example, weak coupling acts to dampen prey dynamics (Rooney et al. 2006). It is because of the expected losses of top predators and mobile consumers from ecosystems, combined with the ubiquity and potential importance of consumer coupling across habitats, that I focus my research on this spatial aspect of food web structure.

Environmental changes that regulate the ability of organisms to capture prey may restructure the food web and change the patterns of biomass accumulation. Imagine a sudden environmental change that improves the consumptive abilities of a predator in a particular habitat (e.g. increased snowfall favours wolf predation of moose (Post et al. 1999)). The existing interactions among lower trophic level species may drastically change given the onset of predation. Now higher order consumers can suppress herbivore prey (or alter the behaviour of prey (Schmitz 2010) in the new conditions and this suppression may liberate primary productivity (Carpenter et al. 1985, 1987; Shurin et al. 2002).

My thesis is guided by recent ideas that recognise food web interactions change with environmental conditions, and uses key environmental gradients, to determine the influence of environmental conditions on major trophic pathways in food webs. I repeatedly argue throughout my main three chapters that the interplay between consumer traits and habitat features may be an important determinant of the structure of spatially coupled food webs. It is widely recognized among behavioural ecologist that predators often do not find the full density of a prey species to
be available for consumption (Sutherland 1996). Rather, environmental conditions can mediate prey availability to predators and this can influence trophic structure (Barton and Schmitz 2009; Schmitz 2010). My general conjecture is that habitat features may often mediate prey susceptibility to predators and as a consequence, the degree that predators couple to consumptive pathways may depend on environmental differences among habitats. To test this assertion, I ask how changes in a given food web structure varies across environmental conditions in freshwater lakes. I address direct consumer and environment based explanations for food web patterns in comparison to alternative species driven and relative bottom-up explanations for food web structural changes. I expect that limitations on mobile predators afforded by conditions present in different habitats may be a key determinant of how pockets of localized interactions (within an ecosystem) are coupled by higher order consumers on the landscape. Regulation of this important pathway may have consequences for other structures that are used to characterize food webs (e.g., food chain lengths). Such food web restructuring across environmental conditions is expected to impact species dynamics and therefore alter several of the products of ecosystems, such as, biomass of harvested species that are important to mankind.

In what follows in this prologue, I provide a brief introduction to my study systems and some of the methodology that appears in later chapters. I then briefly outline each of my three main contributing chapters. I end with a summary of points which highlight some key ideas to consider when reading through the main contributions of this work which are found in chapters two through four.

1.2 Conceptualizing a Spatially Coupled Food Web

Natural systems are very complex and attempts to understand their structure require a degree of abstraction. One way to tractably simplify the complexity of food web structure is to identify
patterns of gross trophic pathways among the tangled interactions. Roughly this can be done if your eyes squint while looking at a food web until the details of individual species interactions blur but the general shape of the gross interaction pathways are retained. An example familiar to ecologists is a food chain (Elton 2001), which represents the systematic feeding transfers from prey to predators up a food web (Fig. 1.1a). A basic food chain is usually presented to have three levels but, because I want to make a connection between the conceptual ball and arrow model and a lake food web, I describe a four level chain. This food chain begins with primary resource, often a plant, which is grazed by an herbivore, the herbivore is prey for an intermediate predator, which is eaten by an apex predator (Fig. 1.1a). Despite a blurring of species detail within trophic levels, food chains are exceptional for developing understanding of several key ecosystem functions including regulation of production at different trophic levels (i.e. trophic control) (Carpenter et al. 1985; Schmitz et al. 2004; Schmitz 2010), nutrient cycling, and accumulation of contaminants in food webs (Cabana & Rasmussen 1994).

In this thesis, I focus on a simple extension of the food chain where a mobile predator couples across habitat boundaries to link food chains in space (known as habitat coupling (Schindler & Scheuerell 2002)) (Fig. 1.1b). This coupled food web allows me to consider how environmental conditions might regulate the biomass and energy flow among habitats within a food web. For my research, I largely follow two trophic pathways from basal resources to a key predator in two lake habitats by tracing the carbon isotope ratios in predator muscle tissue to baseline organisms in near-shore and offshore habitats in lakes. This consumer coupled structure of food chains is expected to be common in nature (Schindler and Scheuerall 2002; Vander Zanden and VandeBoncoer 2002; Rooney et al. 2006). Arguments have been made that higher trophic level consumers should on average be relatively more likely to couple prey resources
Figure 1.1 Conceptualized food webs for (a) a generic food chain, (b) a spatially coupled food web and (c) a lake food web. (a,b) Black circles reflect populations of predators (P), intermediate consumers (Cp,A) and secondary resources (Rp,A) and basal resource (BRp,A). (a-c) Arrows represent the direction of trophic interactions. Subscripts refer to primary habitat (p) and an alternative habitat (A). Basal resources in (c) represent phytoplankton (BRp) and periphyton (BR\textsubscript{A}) these were not fully labeled in the diagram for clarity of presentation.
from different habitats based on them typically being larger, and moving relatively faster than smaller species (McCann 2005; Rooney et al. 2008). Empirical research has documented this arc-shaped food web structure across traditional habitat boundaries (e.g. offshore and near-shore zones in lakes) (France 1995; Vander Zanden et al. 1999; Schindler & Scheuerell 2002; Dolson et al. 2009).

Importantly the coupling of food chains also has implications for other food web structures, the biomass accumulation, and stability of the food web (Post et al. 2000a; McCann et al. 2005). The degree of spatial coupling can alter food chain lengths through predator addition, as a predator coupling to a shorter food chain by definition will increase the shorter chain’s length. Spatial coupling may also influence food chain length through trophic control. When spatial coupling increases top down suppression of a consumer’s primary prey, but releases lower trophic level prey simultaneously then overall food chain length may decrease if the predator becomes more omnivorous. These kinds of changes are thought to be important because such modification of fundamental food web structures are expected to impact food web dynamics. For example, if spatial coupling increases so that a predator population now grows where it once barely persisted (low population size) the population will now be more stable in terms of its ability to persistence in that location. But if the predator population becomes too large and the predator strongly suppresses prey species then increased coupling has the potential to drive species loss (McCann et al. 2005).

1.3 Stable Isotope Food Webs Across Gradients

A historical boundary to conducting food web research across environmental conditions has been the difficulty in collecting data on the feeding interactions for multiple systems. In the past, researchers sought to piece together detailed food webs from gut contents or observations from
as many individual species of the community as possible. Use of stable isotope ratios as dietary tracers allows researchers to obtain time integrated data of trophic flows in food webs quite rapidly. A single piece of tissue used for stable isotope analysis represents a time integrated diet that reflects many individual gut snapshots. Isotope tracers are well suited to studies where major material pathways are of interest, such as, in determining food chain length or identifying material flows from different primary resources. As understanding of stable isotopes increases researchers are more often using this approach to investigate food webs. Increasingly studies use stable isotope ratios to address the impacts environmental conditions food webs including; changes in food chain length across ecosystem size and production (Vander Zanden et al. 1999b; Post et al. 2000b), niche width and habitat fragmentation (Layman et al. 2007), and the effects of species invasions (Vander Zanden et al. 1999a).

To compare isotope based trophic structure among systems requires a tissue sample from a focal organism and also samples from organisms at the base on the food web. Baselines are required for each system sampled because baselines that represent a particular habitat can also vary among systems. I use nitrogen ($\delta^{15}\text{N}$) to measure the vertical position of a consumer in the food web (also called trophic position). Trophic position is calculated as the difference in $\delta^{15}\text{N}$ between the focal organism and the baseline organisms and divided by a fractionation factor (3-4‰) between predators and prey (DeNiro & Epstein 1981; Fry 2007). Carbon isotope ratios exhibit very little to no carbon fractionation with vertical transfer in the food web and therefore carbon can be use to trace the origin of a consumers diet (DeNiro & Epstein 1978; Fry 2007). To use carbon isotope ratios to identify consumer diet origins requires that basal resources can be differentiated by carbon isotope ratios $\delta^{13}\text{C}$. 
1.4 Lakes are Ideal Natural Systems to Study Food Web Change

Freshwater ecosystems are highly impacted by a range of interacting physical, chemical, and biotic drivers (Carpenter et al. 1992, 2011) and consequently, freshwater biodiversity may be more imperiled than any other habitat. Freshwater lakes possess several characteristics that also make them a well suited natural system to test ideas about the relationship between environmental conditions and food web structure. Habitat features, such as, temperature and light, differ within lakes and these vary among shallow near-shore habitat (littoral zone) and deep water offshore habitat (pelagic zone) (Kalff 2002). Further, while there can be some connectivity among lakes aquatic organisms have limited dispersal ability (Woodward et al. 2010). As such, the biota in lakes and their interactions may be largely influenced by differential environmental conditions that operate between near-shore habitats and offshore habitats.

Consumer integration of offshore (pelagic) and near-shore (benthic) habitats is a fundamental food web structure in lakes (Fig. 1.1c) (Vander Zanden & Vadeboncoeur 2002). Conveniently, differences in the carbon isotope ratios of basal resources in offshore and near-shore lake habitats can be used to trace the trophic interactions and accompanying material flows through the food web to the higher order consumers that couple these habitats (that can also be mapped to other diet metrics) (France 1995; Vander Zanden et al. 1999a). I use extensive stable isotope diet tracer knowledge from previous lake food web research as a guide in order to acquire isotopic representations of predator consumptive pathways in the boreal lakes of Ontario, Canada.

1.5 Contributions

I present my research in three papers under the common theme of understanding how food webs respond to changes in environmental conditions. I test the idea that within ecosystem habitat
differentials may govern the relative strength of trophic flows across habitats. I begin to consider how restrictions on predators might lead to a suite of changes in the macroscopic properties of food webs. Specifically, I find evidence for space, temperature, and water transparency as key environmental determinants of food web structure in freshwater lakes.

1.5.1 Food webs expand and contract

A major challenge for ecologists is to predict how ecosystems change with environmental conditions. Ecologists have noticed that food chains can be variable in their length (Elton 2001) and several studies have tested and discussed determinants of this vertical food web structure (Schoener 1989; Vander Zanden et al. 1999b; Post et al. 2000b; Takimoto et al. 2008; Sabo et al. 2010; Townsend 2010). It is somewhat surprising then that there has been little attempt to connect conditional changes, like ecosystem size, to other macroscopic food web properties.

In chapter two I argue, using theoretical and empirical approaches, that a suite of fundamental macroscopic food web structures respond to changes in habitat accessibility using post glacial lakes as model ecosystems. I build upon current theory and use existing data to develop a resource accessibility argument for the structure coupled food webs. Rather than the presence and absence of binary links, my approach relies on the relative strengths of trophic interactions and combines notions of predator access to multiple habitats to production, omnivory, and trophic control. I argue that food webs may expand (i.e. increased coupling of near-shore habitat by predator) and contract (reduced trophic position of predator) as a predator’s alternative habitat becomes more accessible. I present a theoretical approach for determining food web structure changes in model food webs. I also synthesize existing data across gradients of lake size and shape that have been used to relate conditions in lakes to changes in the food web. Predictions from relatively simple food web models that alter prey accessibility are
remarkably consistent with a number of empirical relationships between lake morphometry and several structural properties of the food web. Therefore, this research encourages further work aimed at testing this potentially powerful theory.

1.5.2 Differential warming affects complex communities

Climate change is now well accepted. What remains is to understand how this looming change impacts whole ecosystems. This problem is especially vexing as most research on the responses of nature’s complex systems assumes a uniform local environment. This simplification overlooks (i) nature’s thermal mosaic which reflects temperature differentials that exist among different habitats within ecosystems (e.g., above and below ground or shallow and deep water) and (ii) that organisms are not always hostage to a single thermal environment. Instead, given a variable world, mobile consumers may adjust their behaviour to stay cool given differential temperature in the local environment. Some recent research has begun to consider the role of behavior in food webs responses to climate conditions (Post et al. 1999; Barton and Schmitz 2009) and that prey organisms can use thermal heterogeneity to avoid predation (Barton and Schmitz 2009).

My third chapter considers how behavioural responses to thermal habitat may restructure the consumptive pathways of a spatially coupled food web. First I use a simple model as a building block to focus a general argument for the temperature dependence of consumption. I then extend this argument by considering impacts of differences in warming on the consumptive pathways that couple across habitats and may determine food chain length. I use boreal lakes containing lake trout, a predator likely to face thermal restrictions within lake ecosystems to different extents across my study range. I use stable isotope techniques to amass signatures of dominant trophic pathways in 54 food webs from Canada’s iconic boreal lakes across a 5°C
climate gradient. I show that temperature differentials govern important trophic pathways that structure these ecosystems.

1.5.3 Water transparency predicts a habitat coupling shift for a light sensitive predator

Water transparency is an important lake characteristic, as water transparency regulates the visual condition of the habitat that may impact predator-prey interactions (Bartels et al. 2012) and also the light available for primary production at depth (Vadeboncoeur et al. 2008a; Karlsson et al. 2009). In my final data chapter I document food web structure changes across a gradient of water transparency. I consider two general hypotheses for the way that a predator’s reliance on benthic and pelagic resource channels changes across a water transparency gradient in lakes. One hypothesis I refer to as ‘proportional assimilation’, is based on the idea that a predator integrates resources from different habitats in proportion to the relative resource levels in those habitats (e.g., proportional estimates of prey abundance and production). A second explanation for variation in reliance benthic and pelagic resources argues that predator traits interact with the environment such that prey availability is regulated by conditions that limit predator access and prey catchability.

Corresponding to chapter two and three, prey availability represents the way that the environment can alter the relationship between consumption and prey density. What is novel to chapter four is that I consider a different environmental condition (water transparency) and a predator expected to increase foraging success in dim-light conditions (walleye (Sander vitreus)).

I use previous knowledge about a predator in boreal lakes, walleye, to argue an expectation for the way water transparency should influence the ability of walleye to couple habitats. For the gradient I sampled, I expect walleye to have increased consumptive abilities in
the near-shore habitat under the least clear conditions relative to clearer water conditions. I find
that the proportion of pelagic and benthic carbon resource contributions to walleye diets is
related to lake water transparency.

1.6 Ideas for Moving Forward

I conclude this introductory section with three points that motivate the research that follows,

1) Biodiversity is more than a species inventory. All species are interconnected in webs (we
humans are part of this system) to other species. These interactions are an important part
of biodiversity as they mediate the flow of materials and energy in ecosystems linking
species to food web dynamics and ecosystem functions.

2) Food webs are structured by more than community demographics (presence and numbers
of species) as species interactions are also governed by the physical environment. In a
sense a community possesses a set of traits that in a vacuum are like the potential web
(like fundamental niche). Now this potential web has to operate within a physical habitat
that places an additional set of restrictions from which the actual food web topology and
interaction strengths are bound.

3) Skyscrapers are built considering variation in the environment (e.g., wind and
earthquakes). The integrity of the building depends on those structures that buffer in the
face of environmental conditions. When conditions change a skyscraper built for a
uniform environment may be prone to collapse. We need to better understand how
environmental conditions might erode nature’s architecture in order to conserve the
biological structural elements that prevent ecological collapse.
1.7 References


46. 


Chapter 2  Food web expansion and contraction in response to changing environmental conditions

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2.1 Abstract

Macroscopic ecosystem properties, such as major material pathways and community biomass structure, underlie the ecosystem services on which humans rely. While ecologists have long sought to identify the determinants of the trophic height of food webs (food chain length), it is somewhat surprising how little research effort is invested in understanding changes among other food web properties across environmental conditions. Here, we theoretically and empirically show how a suite of fundamental macroscopic food web structures respond, in concert, to changes in habitat accessibility using post glacial lakes as model ecosystems. We argue that as resource accessibility increases in coupled food webs, food chain length contracts (i.e., reduced predator trophic position), habitat coupling expands (i.e., increasingly coupled macrohabitats), and biomass pyramid structure becomes more top heavy. Our results further support an emerging theoretical view of flexible food webs that provides a foundation for generally understanding ecosystem responses to changing environmental conditions.

2.2 Introduction

Food webs provide the architecture that underlies species diversity patterns, and thus mediate system dynamics1,2 and determine key ecosystem functions (e.g. nutrient cycling3, contaminant
bioaccumulation\textsuperscript{4}). Often, in order to simplify these diverse systems, studies focus on dominant food chains\textsuperscript{5–7} and therefore food chain length is a common, and successful metric for capturing ecosystem structure\textsuperscript{8,9}. Nonetheless, recent work considers that food webs are not so isolated\textsuperscript{10–13}, and often higher order mobile consumers couple food webs (i.e. link food chains) in space\textsuperscript{14–18}. The extent that mobile predators couple spatially distinct macrohabitats is a measure of spatial coupling width on the landscape. As such, habitat coupling can be thought of as a spatial analog to food chain length. Here we consider habitat coupling to be maximal when distinct resource chains, in different habitats, are equally coupled. This approach combines both topology, increases in the number of links to new resource pathways, and interaction strength. According to this usage, in the absence of habitat coupling, a food web is a chain. Habitat coupling increases topologically by the linking of additional habitat resource chains and reaches a maximum width for a given topology when all distinct habitats are equally coupled. The extent that conditions mediate predator coupling across subsystems has potential implications for the general structure, function and persistence of ecosystems\textsuperscript{14,19}.

A recent response to the challenge of predicting ecosystem change considers how fundamental food web structures vary across conditions. Ecologists have long noticed that food chain lengths vary among ecosystems\textsuperscript{6} and have sought to understand the primary determinants of these changes\textsuperscript{7,20–25}. Empirical studies consistently find that at a regional level food chain length shortens with reduced ecosystem size\textsuperscript{7,19,20,22,25,26}, yet the mechanisms for this relationship remain largely uncertain\textsuperscript{9}. Diversity may play a role in this empirical outcome, as larger systems can be more diverse, and thus more likely to contain higher order consumer species and longer food chains\textsuperscript{7}. However, research also suggests that organism behaviour may functionally modify food chain length through changes in the amount of omnivory\textsuperscript{9,19,22}. Omnivory may increase, for
example, if a predator suppresses intermediate consumer densities through strong consumption, releasing shared prey to thrive. Now more numerous, these low trophic position prey organisms are consumed in greater proportion thereby reducing predator trophic positions\textsuperscript{19}. In addition to omnivory, habitat coupling strength can functionally alter food webs as coupling regulates the energy available to upper trophic levels (i.e. predators) through access to novel production across habitats\textsuperscript{14,19,15}. Given that space plays a role in accessibility, changing spatial conditions may alter coupling and thus space can be an important regulator of production to upper trophic levels with implications for fundamental food web properties such as dominant food chain length, omnivory, and biomass structure.

In what follows we provide a process driven theory for changes to a suite of key food web properties across different environmental conditions. Using a coupled food web approach we develop a simple spatially implicit resource accessibility argument that extends core ecological concepts from food chains, trophic cascades and spatial food webs\textsuperscript{5,9,12}. Notably, rather than a strict topological approach where feeding links are either present or absent, our theory generates empirically tractable top predator interaction strengths and trophic control. We then empirically test our theory with real food web data across two natural gradients that alter the spatial characteristics and thus the accessibility of lake systems: overall lake size, and the relative size of the littoral habitat. Our approach is synthetic in that we draw from a number of published studies adding new data and analyses to develop our theory. To conclude, we discuss the general implications of changing food webs for ecosystem structure and sustainability in a rapidly changing world.
2.3 Model Motivation

2.3.1 Biological assumptions and the food web model

Our general conjecture is that constraints (e.g., physiological, morphological) often mediate prey susceptibility to predators, and that this susceptibility then varies across environmental conditions fundamentally altering an ecosystem’s response to change. Recent research argues that food chain length and the coupling of habitats by mobile predators are influenced by ecosystem size\textsuperscript{19,20,22}. Here we present prey accessibility as a trait-mediated mechanism link to these phenomena to each other and to ecosystem biomass structure.

From behavioural ecology, it is generally accepted that consumers cannot access the full population density of their prey under all conditions\textsuperscript{27}. This is premised by the idea that predators are constrained to consume prey within their sensory capabilities (e.g. their foraging scale) and the distribution of their prey. As such, prey may take refuge, elevating their densities, in areas that are difficult for predators to access. When facing restrictive conditions predators may search less of the existing habitat and therefore, prey find themselves in a refuge from predation in unsearchable habitat (Fig. 2.1c; Supplementary Fig. S2.1). This idea extends to a system-level context under the premise that larger ecosystems tend to have greater habitat heterogeneity\textsuperscript{28} and thus more potential prey refugia compared to smaller ecosystems. Therefore, limited access across sub-habitats may reduce prey availability in larger systems compared to those systems that are smaller. Based on these ideas we further develop a general theory using an empirical case to help communicate model mechanics and our assumptions.

The predatory fish, lake trout (\textit{Salvelinus namaycush}), is an excellent example of an organism that exhibits this type of trait-mediated response to changing environmental conditions.
Figure 2.1 | Predicting food web structure: from theory to nature. (a) Food chain length and spatial coupling depend on the direction (arrow) and relative proportion (thickness) of material flow, pF’s, through feeding links calculated from Eqns. 1. P, C and R densities are represented by black circle size. Hatched lines delineate habitat boundaries. Hatched arrows on the axes show the direction of increasing food chain length and coupling strength. Symbols (γ) and (ω2) refer to food chain length and coupling strength estimates calculated using Eqns. 9 and Eqns. 6 respectively. (b) Lake food web structure. Pelagic and littoral resources chains, each containing fish and invertebrate prey, are coupled by lake trout. Chain dependence is delimited by stable isotope δ¹³C and vertical position in the web by δ¹⁵N (also calculated with stomach content data). Littoral coupling strength estimates are based on the CA and RA contribution to P’s total consumption. Food chain length is reported as predator trophic position (tppredator) (i.e. trophic transfer between baseline production and predator of the sink web). (c-e) A conceptual model of accessibility. (c) Foraging scale (arrow) is equal to habitat scale (hatched lines) and all prey (black dots) are potentially accessible (shaded area). (d) At intermediate scales, a fraction of prey (x) is not accessible. Here the highest prey density is located beyond the foraging scale of the predator. For completeness we show the end point where prey in Ha are not accessible to the predator (e). Dotted line visually separates habitats (Hp and Ha). Dashed box visually contains Ha prey and if not shaded is not accessible.
Lake trout tend to reside in the cold pelagic zone of northern post glacial lakes (Fig. 1), avoiding the warm near shore littoral habitat during the summer months. While lake trout forage on the cold water pelagic food chain they are still capable of making short foraging bouts into the warmer near shore food chain\textsuperscript{29}. Littoral coupling strength however, depends on environmental conditions (e.g., littoral habitat size) \textsuperscript{30}. Small littoral habitats are readily accessible by lake trout even over a short foraging bout, while larger littoral habitats have areas that are thermally inaccessible.

We derived a simple spatially-implicit food web model based on three empirically motivated assumptions. Lake trout prefer cold water habitats (8-12°C)\textsuperscript{31,32}, and so are thermally constrained to limited foraging bouts in the warm near shore habitat during summer months (~20°C average summer water temperature at the southern end of their zoogeographic range) (A.1, Supplementary Discussion). In the southern end of their distribution where most data are collected, for example, lake trout are capable of short foraging bouts into the warm littoral zone\textsuperscript{29}. Since prey distributions in the near shore zone also tend to show the highest densities at the lake edge (A.2, Supplementary Fig. S2.2) the furthest distance from the deep pelagic habitat preferred by lake trout, littoral prey can be difficult to access by lake trout. Additionally, the peak near shore littoral prey density does not change in a predictable way across lakes (A.3, Supplementary Fig. S2.2). Given these physiological constraints and the prey spatial distribution, we argue that as the littoral warm water habitat gets smaller lake trout should be able to more easily access littoral prey. Similarly, as littoral habitat increases in size prey should find themselves in thermal refugia from predatory lake trout.

The general application of the above assumptions allows us to derive a spatially-implicit scaling parameter, $\alpha$, that links foraging scale to mean resource density and habitat size
(Supplementary Fig. S2.1-S2.3). A unitless parameter, $\alpha$, reflects the ratio that scales mean prey density available to total mean prey density$^{-1}$ for a habitat and is derived from a constant area foraged, $f$, divided by total habita area, $H_A$ ($H_A = \text{area foraged} (f') + \text{area inaccessible} (I); H_A \geq f$) such that when $I = 0$, all resources are accessible, $\alpha=1$, and when $\alpha=0$ resources are inaccessible (Fig. 1c; see Supplementary Fig. S1 and S2 for full derivation). With this scaling parameter, we employ the following Lotka-Volterra model, with logistic resource growth, and linear functional responses to represent a three trophic level spatially coupled food web (Fig. 2.1a):

\[ \frac{dR_p}{dt} = R_p \left( r_p \left(1 - \frac{R_p}{K_p}\right) - a_{CpRp} C_p - a_{PRp} P \right) \]
\[ \frac{dR_A}{dt} = R_A \left( r_A \left(1 - \frac{R_A}{K_A}\right) - a_{C_AR_A} C_A - \alpha(a_{PR_A} P) \right) \]
\[ \frac{dC_p}{dt} = C_p \left(-M_C - (a_{PCp} P) + e_C a_{CpRp} R_p \right) \]  
\[ (1) \]
\[ \frac{dC_A}{dt} = C_A \left(-M_C - \alpha (a_{PC_A} P) + e_C a_{C_AR_A} R_A \right) \]
\[ \frac{dP}{dt} = P \left(-M_p + e_p a_{PRp} R_p + e_p a_{PCp} C_p + \alpha(e_p a_{PR_A} R_A + e_p a_{PC_A} C_A) \right) , \]

where, $r_i$ is the maximum intrinsic rate of increase for each resource for the preferred, $p$, and the alternate, $A$, habitats respectively and, $K_i$ is the carrying capacity of each resource (density). The attack rate of the consumer on the resources is defined as, $a_{C_i R_i}$. Similarly, $a_{PR_i}$, is the attack rate of the predator on each resource and, $a_{PC_i}$, the predators attack rate on each consumer. Finally,
$M_{c,P}$ and, $M_P$, are the mortality rates for $C_i$ and $P$, $e_{C,P}$ is the rate that prey are converted to $C$’s or $P$ (for units see Supplementary Table S2.1).

As discussed above, this food web model consists of a mobile predator, $P$, that forages on two distinct food chains each containing a consumer, $C$, and a resource, $R$ (Fig. 1a). Biologically, the model includes the ability for food web structure to change in two important ways. First, the predators’ ability to forage in the alternative habitat depends on that habitat’s size. Thus, changing alternative habitat size affects coupling strength into both habitats (i.e. degree of habitat coupling) (Fig. 2.1c). Second, dynamic changes in predator densities $P$ ultimately influence the densities of $R$ to $C$ in both habitats, and so drives a change in the amount of omnivory (Fig. 2.1a). As an example, if $C$ is suppressed by elevated $P$ densities with increased resource accessibility, then $R$ is released to flourish, and $P$ naturally begins to consume more prey lower in the food web. Such a scenario decreases food chain length and increases omnivory. The general, three level, two channel, trophic structure of the theoretical structure above maps to natural lake trout food web topologically (equation (1); Fig. 2.1a,b; Methods).

2.4 Results

2.4.1 Theoretical results

With the model system described above (equation (1)) we conduct a theoretical experiment that changes the mean prey density available in a two habitat system by effectively reducing one habitat’s size. As size is reduced by increasing $\alpha$, the model system becomes effectively smaller (i.e., move from right to left on the x-axis Fig. 2.2) and the predator perceives prey in the alternative habitat compartment as more accessible. In a sense, changing the food web accessibility here has a direct influence on the amount of secondary habitat prey that can be
consumed by the predator. Thus, our theory predicts (1) that as a secondary habitat is more accessible predators consume more prey from that habitat and thus coupling increases (Fig. 2.2a). This secondary habitat coupling increase allows the predator population to increase its intake compared to the single habitat and now suppresses primary consumer prey. Notice that with strong top-down suppression in small systems, secondary consumers are low in density relative to their prey (i.e. due to the top heavy pyramid; Fig. 2.2b). So increased coupling drives a second prediction (2) that the trophic pyramid of the system shifts from the more classic Eltonian pyramid\(^6\) to a more top heavy pyramid (Fig. 2.2b) with increased predator to consumer densities (Fig. 2.2b inset). The changing biomass pyramid releases \(R\) relative to \(C\). Thus, for small systems the top predator has a greater propensity to feed on lower trophic levels (i.e. feeds more on \(R\) which is high relative to \(C\)). The consumption of \(R\) maintains the predator with the suppression of \(C\) and the accompanying reduction in \(C_A\) production. This effect is our third prediction (3) that omnivory increases in small or high accessibility ecosystems (Fig. 2.2c). As omnivory increases the predator is supported proportionally by more prey from lower trophic levels. From this result, we arrive at a fourth and final related prediction (4) that food web length contracts with decreases in ecosystem size (i.e., increased omnivory; Fig. 2.2d).

Our results are robust, as 100 replicates of the experiment, each with randomly chosen parameters, yielded the identical qualitative response 100% of the time, e.g. an overall increasing or saturating predator density with resource accessibility, although 44% showed a hump shape response at higher resource accessibility. This humped shape outcome is not too surprising. Like other consumer resource models, reversals appear to occur at conditions near bifurcation points\(^{33}\) and when exploitation rates are high (e.g., high attack rates)\(^{34}\). More specifically in our model food web, near the loss of \(C_A\) from the system, \(P\) begins to fall with higher \(\alpha\) and \(C_\rho\) is
Figure 2.2 | Theoretical food web responses to changing accessibility. As the system becomes effectively smaller, secondary habitat prey become more accessible. Macroscopic system properties change such that (a) habitat coupling increases, (b) generally the predator:consumer biomass ratio increases, and predator biomass density increases (inset), (c) percent omnivory increases, and (d) food chain length decreases (for metric calculations see Materials and Methods). Predictions are simulated using a simple spatially implicit food web model (Eqns 1.). Predator accessibility (a) is increased (0-1). All other parameter values are held constant. Parameter values for displayed data are as follows: $r = 1.5$, $K_P = 5.0$, $K_A = 5.0$, $eC_P = 0.80$, $aPR_p = 0.02$, $aPC_p = 0.35$, $aPR_A = 0.02$, $aPC_P = 0.35$, $MC_P = 0.45$, $MC_A = 0.45$, $MP = 0.20$, $aCR_p = 1.90$, $aCR_A = 1.90$. 
simultaneously released. In this case $C_A$ production approaches zero and increasing predator consumption even further will quickly lead to the loss of $C_A$ from the system. Interestingly, the above conditions provide an indication of instability and extinction in our model web.

Our theory generates four main predictions regarding the dependence of food web structure on the spatial properties of ecosystems (note: the results are robust to the inclusion of a switching response (Unpublished data; see Supplementary Discussion)). We test spatial resource accessibility predictions against empirical web structure across two natural gradients: overall size, and the relative size of littoral habitat.

2.4.2 Food web changes across a gradient of ecosystem size

Empirical data collected across a wide range in lake size (Surface Area min = $1.10 \times 10^2$ha, max = $8.33 \times 10^6$ha) exhibit patterns that are remarkably consistent with predictions generated from hypothesized accessibility. In agreement with the first prediction lake trout are more strongly coupled to littoral habitats in smaller lakes (Fig. 2.3a). While biomass pyramid data are not currently available for lake trout food webs, published data from a broad sample of freshwater lakes demonstrate that biomass size spectra become more top heavy with decreasing lake size and suggest that biomass pyramids can even be inverted in small systems. Biomass ratios calculated from these data show that top consumers (fish) are elevated compared to secondary pelagic consumers (zooplankton) (Fig. 2.3b) and marginally elevated for combined whole system secondary consumer biomass (zooplankton + zoobenthos, $R^2 = 0.17$, $n = 21$, $p = 0.06$) as lakes become smaller. Lake trout density data are available for a set of low productivity, unexploited, systems. In concurrence with prediction two lake trout biomass densities in these lakes decrease as lakes increase in size (Fig. 2.3b inset). The third prediction that omnivory is higher in smaller
Figure 2.3 | Relationships between lake size and food web structure. (a) Habitat coupling (hockey stick regression, break-point = 5.4, $R^2 = 0.16$, n = 40, p = 0.036), (b) biomass ratio (linear regression, $y = -0.297(\log_{10}x) + 0.204$, $R^2 = 0.39$, n = 21, p = 0.002) and predator biomass density (inset) (linear regression, $y = -0.11(\log_{10}x) + 1.32$, $R^2 = 0.42$, n = 10, p = 0.04), (c) omnivory (hockey stick regression, break-point = 5.3, $R^2 = 0.12$, n = 56, p = 0.04), and (d) food chain length (hockey stick regression, break-point = 4.0, $R^2 = 0.48$, n = 40, p = 0.04). Dashed lines represent right hand segments with slopes set to zero.
lakes is also supported by these empirical data (Fig. 2.3c). Finally, consistent with the fourth prediction the food web truncates as lake size decreases (Fig. 2.3d).

2.4.3 Food web changes across a gradient of relative littoral habitat

We further test our theory with a set of seven similar sized lakes from the same geographic location. These lakes varied in shape such that percent littoral habitat differs widely across lakes (% Littoral Area min = 32, max = 79). This natural experiment changes the size of the non-preferred habitat and so alters the accessibility of the nearshore zone. Furthermore, we expect that the greater the littoral area, the greater the opportunity for prey to take up refuge far from the pelagic littoral boundary and, consequently, the lower the predators’ ability to consume those prey resources. Similar predictions therefore apply since lakes with small relative littoral areas should drive stronger coupling, top heavy biomass pyramids, and increased omnivory. Consistent with these predictions, food webs in lakes with relatively small littoral areas are more strongly coupled (Fig. 2.4a) and exhibit more omnivory (Fig. 2.4b) than lakes with relatively large littoral areas. Food chain length and the relative littoral habitat do not vary significantly, for a linear model, but notably, in agreement with prediction four, the linear trend line slope is positive (Fig. 2.4c). For food chain length an analysis of variance showed that a quadratic model improved fit over the linear model despite a degrees of freedom penalty (Fig. 2.4c). In support of predictions, an increasing curve significantly explained the relationship (Fig. 2.4c), but with seven systems we are cautious to presume the exact shape of this relationship.

2.5 Discussion

Little research combines theory and environmental gradients (e.g., ecosystem size, temperature) to address mechanisms that influence macroscopic patterns of food web interactions and biomass structure across environmental conditions. Our theoretical food web shortened, and broadened in
Figure 2.4 | Relationships between relative littoral habitat and food web structure. (a) Habitat coupling (%) decreases ($\logit(y) = -1.64\logit(x) - 0.90, R^2 = 0.71, n = 7, p = 0.03$), (b) omnivory (%) decreases ($\logit(y) = -0.74\logit(x) - 1.91, R^2 = 0.75, n = 7, p = 0.03$), (c) food chain length increases (linear: $y = 0.14\logit(x) + 4.519, R^2 = 0.28, n = 7, p = 0.2$) as relative littoral habitat increases. Proportional data were logit transformed. Linear regression is used for all three statistical tests. For food chain length an increasing quadratic model was significant (quadratic: $y = 0.28\logit(x)-0.30(\logit(x))^2+4.66, R^2 = 0.78, n = 7, p = 0.046$) and was a better predictor than a straight line (ANOVA; $F = 9.21, df = 1, p = 0.038$). Structure is based on $\delta^{13}C$ and $\delta^{15}N$ stable isotope signatures (see Methods).
habitat coupling, as resource accessibility (mediated by alternate habitat size) decreased. This food web response is generally accompanied by a biomass shift from a classic Eltonian pyramid to one more top heavy in shape. This general trait mediated response is supported by empirical evidence from lake ecosystems. Further, and interestingly, omnivory and compartmentation are known stabilizing structures under the same environmental conditions in which we find them here. In large ecosystems, for example, theory shows that weak coupling to alternate compartments can allow diverse multi-habitat ecosystems to persist, while in small ecosystems, where interactions couple habitats so that the web behaves like a strong linear chain, omnivory is a potent stabilizing force. Similarly, prey dispersal among patches in expansive systems may facilitate omnivory when top down forces are strong enough to exclude intermediate consumers. Such expansion and contraction of food web structure ought to have implications for the stability and persistence of food webs in general. These results add to an emerging literature that is piecing together the role of space in food web structure and dynamics.

Empirical patterns show differences in food web structure across two meaningful spatial gradients that are remarkably similar to those predicted by theory. Combined, empirical data suggest that food webs are longer and coupled more narrowly, with lower predator biomass, in lakes where littoral resources are effectively far from the predator, and are shorter and more broadly coupled, where littoral resources are more accessible (Fig. 2.4). Our approach differs from traditional studies in several novel ways. First, we argue that a traditional non-spatial theory would obviously not predict the same changes in omnivory, biomass structure and food chain length across systems, all else equal. Second we limit our study to lakes with essentially the same prey trophic groups. We did this to minimize possible influences of system
size on prey diversity (e.g., littoral coupling and omnivory in small lakes can be driven by the sheer absence of pelagic fish). Finally, coupling strength decreases with the relative littoral habitat size. As such, data support a resource accessibility theory to a greater extent than increased relative productive space, which predicts the opposite trend, or strict prey diversity arguments alone.

Our findings also emphasize the notion that certain important food web structures may not be ubiquitous. Ecologists, for example, have sought compartments in food webs since Gardner and Ashby noted that real complex systems may persist due to incomplete connectedness and Robert May extended this result to food web compartments. Our results clearly indicate that, in nature, compartments may only exist under certain conditions. In expansive systems, we find that food chains are weakly connected across macrohabitats, and therefore are compartmentalized, whereas in small, highly connected ecosystems mobile predators strongly couple multiple energy channels and thus remove compartmentalization. Similarly, empirical studies of omnivory are somewhat conflicting and are likely to be more productive if focused on assessing how omnivory, or omnivory strength varies by following food webs in space or time.

The general theory employed here argues that our results are not exclusive to lake ecosystems. On land, research from Bahamian islands suggests that smaller islands tend to have shorter food chains and stronger trophic cascades. From their island studies, Schoener and Spiller hypothesized that refugia reduce trophic cascades on large islands. They also noticed that long points or peninsulas tend to maintain higher spider densities compared to adjacent more central habitats and suggest that these areas may be less accessed by lizard predators. It is worth mentioning that this island shape feature is analogous to long shallow bays common to lakes.
with large relative littoral habitat that are inaccessible to cold water predatory fish. On the mainland, few studies link food web structure to resource conditions. A recent study shows that a balsam fir food web appears to topologically expand (i.e., increase trophic position) in response to budworm outbreaks, and contract (i.e., decrease trophic position) during the decline phase of the budworm cycle \(^{44}\).

These collective results argue that food webs may generally expand and contract in response to changing conditions in space and time. This idea raises the question of whether modification of material pathways is likely fundamental for maintenance of topology, stability, and thus ecosystem function in water, on land, and among other ecosystem types. Furthermore, given the changing capacity of food webs, it becomes critical that we understand how human impact alters not only common food web structures, but also their variability in space and time. Climate change, for example, may increase littoral temperature in northern lakes to the point that the littoral zone becomes inaccessible to cold water fish and hence eliminates the capacity for these lake food webs to alter habitat coupling. Tools such as stable isotope analysis then, take on an additional importance as a means to rapidly procure and diagnose this potential deterioration in food web structure. Isotope approaches have effectively addressed human impacts such as the effects of flow regulation on food chain length in rivers\(^{21}\), habitat fragmentation on community niche space\(^{45}\), and species invasion on food web structure\(^{46}\) to name a few. Finally, we argue if food webs often change in consistent ways (e.g., food chains lengthen with ecosystem size), then by identifying these consistencies, we will be in a better position to monitor food web structure and look for ecosystem-level warning signals of deleterious human change.
2.6 Methods

2.6.1 Relationship between model and real food webs

From the system outlined above (Eqns. 1) we use functional responses to simulate (see below) measures of food web structure in the same way that empirists use stable isotope and stomach content data to construct real webs. The theoretical model reflects a sink food web module that is commonly found in nature \(^{16}\) where percent carbon is used to delinate dependence on macrohabitats (habitat coupling), and nitrogen to determine vertical position in the web with respect to the number of trophic transfers (food chain length). In lake systems, lake trout couple a pelagic habitat channel driven by phytoplankton and a littoral habitat channel supported by attached algae and detritus\(^{30,35}\). Basal resources in the pelagic and littoral habitats have distinct carbon signatures making them suitable to delineate trophic groups with stable isotope approaches that also correspond to prey species habitat preferences (pelagic forage fish (e.g., Corigonids), pelagic invertebrates (e.g., Copepods), littoral forage fish (e.g., Cyprinids) and littoral invertebrates (e.g., Ephemeroptera) and therefore make sense for use with traditional diet data as well (Fig. 1b; Supplementary Methods). Thus, both our model and empirical data are posed to measure food chain length and habitat coupling width.

Using the model system, we generate predator-prey interactions based on biomass flow calculated from predator functional responses. We calculate proportion of \(C_i\) or \(R_i\) (e.g. \(C_p \rightarrow P\) in Fig. 1c) in predator diets simply as:

\[
p_{FPx} = \frac{e_{FPx}}{\sum_i e_{FPx}} ,
\]  

(2)
where \( pF_{P_x} \) is the proportion of any single interaction (e.g. \( F_{PC_p} \)) to all interactions (\( \Sigma_i F_{P_x} \)) for the given web.

Simulated data are comparable to empirical stable isotope or stomach contents data. As an example a two source isotope mixing model provides the proportion of a sample that is the sum of diet isotope signatures \(^{47}\).

**Stable isotope interactions**

\[
psource_1 + psource_2 = 1 \tag{3}
\]

\[
psource_1 = \frac{(\delta_{sample} - \delta_{source_2})}{(\delta_{source_1} - \delta_{source_2})}, \tag{4}
\]

where \( source_i \) is the stable isotope (e.g. \(^{13}\)C) signature for a dietary item, and \( sample \) is predator diet \(^{47}\). We used this two source approach to calculate habitat coupling \(^{35}\) and a modified equation for food chain length \(^{22}\). For omnivory we used a Bayesian multi-source isotope mixing model (SIAR\(^{48}\)) that includes \(^{13}\)C and \(^{15}\)N for four dietary sources.

Theoretical interactions can also be tested with traditional gut content data, although diet is not assimilated as in stable isotope analyses.

**Stomach content interactions**

\[
%\text{prey}_1 = \frac{\text{prey}_1}{\text{prey}_1 + \text{prey}_2} \times 100 \tag{5}
\]
2.6.2 Numerical simulations

We performed an experiment where we simulated system dynamics over a range of spatial conditions \((\alpha = 0 - 1)\). For each condition we sampled a time series and took the mean densities of each trophic group \((P, C’s\) and \(R’s\)) on the attractor between 4000-5000 time steps. We next determined the proportion of each prey type consumed by the top predator as a direct measure of proportional interaction strength. Four food web metrics were calculated using these simulated data: (i) habitat coupling, (ii) biomass pyramid shape, (iii) omnivory, and (iv) food chain length.

(i) Habitat coupling \((\omega_2)\) measured here as the proportion of prey (material) consumed by the predator from the alternative habitat chain \((C_A-R_A)\).

\[
\omega_2 = \frac{F_{PC_A} + F_{PR_A}}{F_{PC_I} + F_{PR_I}}
\]  

\((6)\)

\(F_{PC_I}\) and \(F_{PR_I}\) are the function responses for \(P\) feeding on \(C\) and \(R\) respectively.

(ii) Biomass pyramid shape \((\chi)\) captures changes in the biomass structure among trophic levels.

\[
\chi = \frac{P}{C_p + C_A},
\]

\((7)\)

Here we simply used the ratio of predators to consumer biomass density.

(iii) Omnivory \((\psi)\) is determined as the resource biomass \((R’s)\) consumed by the predator divided by the total biomass.

\[
\psi = \frac{F_{PR_I}}{F_{PR_I} + F_{PC_I}}
\]

\((8)\)

(iv) Food chain length \((\gamma)\) is predicted as the trophic position of the apex predator.

\[
\gamma = 1 + \frac{F_{PC_I}}{F_{PR_I} + F_{PC_I}} 2 + \frac{F_{PR_I}}{F_{PR_I} + F_{PC_I}} 1
\]

\((9)\)
This method weighs the contribution of each trophic level by the relative consumption of the predator and adds 1 to account for transfer to the predator\(^8\).

Results are shown for one parameter set (aside from manipulating \(\alpha\)), but are consistent over a range of parameter values. We chose the particular parameter set shown as it produced an interior equilibrium when matching parameters were set equal for both habitats. To test the generality of our findings, we ran the experiment with randomly chosen parameters until we obtained 100 parameter sets that produced an interior equilibrium (~2000 random sets; \(r_i = 0.01-3.0\), \(a_cR_i = 0.8-2.0\), \(a_{PC_j} = 0.8-2.0\), \(a_{PR_i} = 0.0005-0.20\), \(\varepsilon = 0.5-0.9\), \(M = 0.05-0.5\), \(MC_i = 0.05-0.5\), \(K_i = 4.0-10.0\)). Essentially this process provided 100 replicates of our experiment without species extinctions where each parameter value was selected at random. We then determined the proportion of replicates that match our predictions.

### 2.6.3 Empirical analysis

Our empirical analyses combined new data from recent lake surveys with data published in several studies. The ecosystem size analyses used published data\(^49\) and added new data from a subset of lakes to calculate habitat coupling and omnivory. We only used lakes that contained a secondary consumer fish species in both habitats (pelagic fish are absent in some small lakes), so that the empirical food webs topologically match the food web model. For our new data, fish remains found in stomach contents were often not identified to species, which was used to determine habitat origin. We only added new food webs to the habitat coupling dataset when three or more species were identified for a population. Identification was not an issue for omnivory calculations, as the more coarse categories of fish or invertebrate were resolved for nearly all stomach contents. Both habitat coupling and omnivory metrics were reported as the biomass proportions of each trophic group in lake trout diets\(^49\) (Supplementary Methods). We
then calculated habitat coupling as the proportion of littoral fish biomass to total fish biomass (littoral + pelagic) and omnivory was calculated as the invertebrate biomass to total organisms (invertebrates + fish) in gut contents. Measures of food chain length reflect the pathways leading to a single predator (i.e., a sink food web), calculated as mean lake trout trophic position, and were obtained from the literature\textsuperscript{19}. To be consistent with recent literature that defines food chain length as maximum trophic position, recognize that lake trout often, but not always, hold the maximum trophic position in lakes. Lake trout mean trophic position is then a reasonable estimate of system food chain length for our study. This is also more likely as we excluded smaller lakes without pelagic forage where smallmouth bass (\textit{Micropterus dolomieu}) tend to hold higher trophic positions than lake trout.

We examined trophic control with biomass pyramid shape calculated using predator: consumer ratios with data from a published study\textsuperscript{36}. To calculate this ratio the biomass of the published trophic groups, fish, zooplankton, phytoplankton were used. Lake trout biomass density data were collected by the Ontario Ministry of Natural Resources (OMNR) and Ministere des Resources Natural et de la Faune Quebec (MRNFQ) from calibrated netting surveys and mark recapture studies. Biomass density was calculated based on the biomass (kg) of lake trout per area (ha) of habitat.

Our littoral size data are from a published study\textsuperscript{30} and we recalculated coupling, omnivory and food chain length, again calculated as mean lake trout trophic position, according to published methods\textsuperscript{47}. Lake characteristic details, including description of fish communities and isotope collection methods are available from a published study\textsuperscript{30}. For each lake, littoral habitat area proportion was calculated as the area of substrate above the 10\textdegree C isotherm in the lake divided by the total area. Measures of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were obtained from muscle tissue
samples from fish and invertebrates. Habitat coupling was calculated using a simple two source mixing model to determine the contribution of littoral carbon to predator populations according to a previously published equation:\textsuperscript{35}

\[
\% \text{ littoral carbon} = \frac{\left( \delta^{13}C_P - \delta^{13}C_{PB} \right)}{\left( \delta^{13}C_LB - \delta^{13}C_{PB} \right)} \times 100 \text{ , (10)}
\]

where mean $\delta^{13}C$ for predators, pelagic and littoral baseline are indicated by subscripts $P$, $PB$ and $LB$. We used $\delta^{13}C$ from Unionid mussels for the pelagic baseline and the mean $\delta^{13}C$ snails and inverts as a baseline for benthic production in the littoral zone. Food chain length was calculated using mean lake trout $\delta^{15}N$ and mean pelagic $\delta^{15}N$ and littoral baselines $\delta^{15}N$ as in coupling calculation given above\textsuperscript{22}. To calculate omnivory we used a Bayesian multi-source mixing model, SIAR\textsuperscript{48}, for $R^{50}$, to determine the proportion of four dietary source groups in predator diets: zooplankton, pelagic forage fish, littoral macro invertebrates, and littoral forage fish. Mean lake trout isotope values were used and the mean isotope values and standard deviation of four dietary sources. Isotope values were corrected for lipid content\textsuperscript{51} and $\delta^{13}C$ (0.4±0.1) and $\delta^{15}N$ (3.4±0.1) fractionation from prey to predator\textsuperscript{47}. From these mixtures, omnivory was determined according to the theoretical metrics above (Eqn. 8). Trends were robust over several fractionation values published for temperate lakes and lake trout systems\textsuperscript{52}.

2.6.4 Statistical analysis

We used linear, hockey-stick, and quadratic regression statistical models. For the relationship between food chain length and littoral habitat proportion (Fig. 4c) we report quadratic regression results in addition to linear regression results and use analysis of variance to compare the two statistical models. We transformed data according to statistical requirements. Logit transforms were used for isotope proportions and littoral habitat proportions. Due to several zero
observations in the dataset, stomach content data were transformed by taking the arcsine of the square root of prey biomass proportions.

2.7 References


### 2.8 Acknowledgements

We thank S. Sandstrom (OMNR) for providing lake trout biomass data. G. Gellner provided programming advice. Fish images are modified from originals that are used with permission of the New York State Department of Environmental Conservation. This work was supported by NSERC grants to K.M. and B.S.
2.9 Supplementary Information

Supplementary Figure 2.1 Relating foraging scale to habitat accessibility for (a) a small and (b) a large alternate habitat.

Supplementary Figure 2.2 Empirical littoral forage fish distribution data from 90 Canadian post glacial lakes
Supplementary Figure S 2.3 Scaling peak resource density to mean resource density for different values of $\alpha$.

Supplementary Table S 2.1 Units for food web model

<table>
<thead>
<tr>
<th>Description</th>
<th>Symbol</th>
<th>Units</th>
</tr>
</thead>
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<tr>
<td>Variables</td>
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<td></td>
</tr>
<tr>
<td>Predator population</td>
<td>$P$</td>
<td>density (biomass.area$^{-1}$)</td>
</tr>
<tr>
<td>Consumer population</td>
<td>$C$</td>
<td>density (biomass.area$^{-1}$)</td>
</tr>
<tr>
<td>Resource population</td>
<td>$R$</td>
<td>density (biomass.area$^{-1}$)</td>
</tr>
<tr>
<td>Parameters</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intrinsic rate of growth</td>
<td>$r$</td>
<td>proportion.time$^{-1}$</td>
</tr>
<tr>
<td>Carrying capacity</td>
<td>$K$</td>
<td>density (biomass.area$^{-1}$)</td>
</tr>
<tr>
<td>Accessibility</td>
<td>$\alpha$</td>
<td>proportion (area.area$^{-1}$).time$^{-1}$</td>
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<tr>
<td>Conversion efficiency</td>
<td>$e$</td>
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<tr>
<td>Attack rate</td>
<td>$a$</td>
<td>area .biomass$^{-1}$.time$^{-1}$</td>
</tr>
<tr>
<td>Mortality rate</td>
<td>$m$</td>
<td>proportion.time$^{-1}$</td>
</tr>
</tbody>
</table>

* Here we provide units for the food web model (equation (1)). We report units based on biomass.area$^{-1}$ of the populations. Of course, for this general model the units are simply defined by the chosen currency. For example, the number of individuals can also be used.
2.10 Supplementary Discussion

As discussed in the main text, we put forward a food web model where a consumer forages over two habitats. In one, the preferred habitat \((p)\), resources are entirely accessible to the foraging consumer, while habitat size constrains resource accessibility of the alternate habitat \((A)\). In what follows we elaborate on our argument that prey distribution in the alternate habitat contributes to greater prey availability in small versus large lakes (Supplementary Fig. S1, small = ABC, large = AED). Below, we define the parameter, \(\alpha\), as the ratio of the foraging scale, \(f\), to the alternative habitat area, \(H_A\). We prove that this ratio allows us to determine the accessible resource density, which in turn determines the alternate habitat resource consumption, \(a(\alpha C)P\), where, \(\alpha\), is the spatial scaling parameter, and, \(a\), is the attack rate for the functional response of the predator, \(P\), on intermediate consumers, \(C\).

We parenthesize \((\alpha C)\) here because our theory scales prey densities. At present there is no empirical reason expect that other parameter, such as, \(a\) or \(e\) (conversion efficiency), necessarily decrease as a function of alternate habitat size. In general, a similar food web expansion and contraction should occur if an environmental condition is asymmetrically changed to alter consumption rates for other coupled food web models. We chose a parsimonious model, motivated by empirical data, however, a more complex model with density dependent spatial preference, and a spatial condition amplifies but does not change the response (unpublished data). Further research will need to piece apart the degree to which space, and switching, alone may contribute to the expansion and contraction of food webs.
2.10.1 A spatially implicit representation of a prey gradient

Here we elaborate on how three assumptions contribute to resource accessibility in an alternate habitat.

(A.1) Predators foraging scale is constant.

(A.2) Available alternate habitat resource density increase linearly with the area searched.

(A.3) Peak resource density does not vary with system size.

First, we assume that the predators foraging scale is constant (assumption A.1, also depicted in Fig. 2.1 and Supplementary Fig. S2.1). Consequently, foraging predators can access a restricted search area into the alternate habitat \( f \), while the remaining alternate habitat is inaccessible and is denoted as \( I \). Therefore the total area of the alternate habitat is \( H_A = f + I \).

Note here that because \( H_A = f + I \), the ratio \( f/H_A = f/(f + I) \) and when \( I = 0, f/H_A = f/f = 1 \), and the system is bound by the constraint \( f \leq H_A \). This is important to understand because this means that the habitat size does not get smaller than the predators foraging area. Thus what the predator eats is limited by the predators' constant attack rate \( a \) and the available prey density \( \alpha R_2 \). The foraging scale constraint is empirically motivated by the idea that animals face trade-offs and are therefore constrained by time and by their traits (physiology) from the use of all habitats equally. For example, in temperate lakes coldwater species (e.g. lake trout) are limited to short foraging bouts into warm littoral habitats during summer months when water temperatures often greatly exceed preferred temperatures.

Our second assumption follows that alternate habitat is structured by a simple linear increase in resource density (assumption A.2 depicted in Fig.2.1 and Supplementary Fig. S2.1).
recognize in real systems resource distributions may be nonlinear, however, the argument below holds for more complex shaped resource distributions, as long as resource density in the alternate habitat increases with distance from the habitat boundary (i.e. pelagic zone). This is a reasonable assumption, for our lake example, as both the peak and mean catch per unit effort of 26 species of littoral fish generally increase as depth decreases (i.e. away from the preferred habitat) in 90 Canadian lake trout lakes (Supplementary Fig. S2.2).

Third, we also assume that the peak density is the same, on average, in any alternative habitat regardless of size (assumption A.3; BC = ED =D’). Empirical data from lakes containing lake trout motivate our assumption, as peak catch.net⁻¹ of littoral prey fish show no compelling trend with lake size (R² = 0.02, p = 0.16, n = 90; Supplementary Fig. S2.2).

Based on these assumptions, the consumer necessarily sees lower resource density in a large habitat and greater resource density in a small habitat (i.e., the resource slope of the small habitat is greater than the slope of the large habitat; Supplementary Fig. S2.1). We can state this more formally by pointing out that as we increase (AB) (i.e., alternate habitat size increases such that AB approaches AE), then the side opposite the angle, θ , (i.e., BF, the peak accessible resource density) necessarily decreases (Supplementary Fig. S2.1). Therefore, as the alternative habitat size increases relative to the foraging scale, then the peak accessible resource density necessarily decreases. Now consider an ecosystem size experiment, if we start from an alternate habitat of size, f = Hₐ (Hₐ = Hₐ), then the consumer sees a mean resource density that is consistent with seeing the entire habitat (Supplementary Fig. S2.1). At the other extreme, if we make the habitat infinitely large, the angle θ approaches zero, and the predator approaches a resource accessibility of zero (Supplementary Fig. S2.1). Thus, if we allow a scaling parameter (α) that modulates how much of the resource is actually accessible to the predator, we know:
(i) at the smallest alternative habitat size \( (f = H_s) \), all resources are available for potential consumption (e.g. accessible resources \( = \alpha D' = D' \); \( \alpha = 1 \)), and;

(ii) at the largest size (infinity) the slope of the resources approaches zero and so the accessible resource density approaches zero \( (\alpha D' \to 0; \alpha \to 0) \).

Thus, the simple linear parameter, \( \alpha \), allows us to move from the smallest lake (e.g. \( H_{S}; H_A = H_S \)) to large lakes (e.g. \( H_L; H_A = H_L \)) by decreasing alpha from 1 to 0 (Supplementary Fig. S2.1). In fact, this implies that resource availability \( (\alpha = f / H_A) \) scales linearly with the foraging scale to habitat size ratio (see below for scaling proof).

Based on these arguments, we expect that a larger lake can have greater total resource carrying capacity (abundance, or standing crop) because of its size, but there is no obvious reason it is elevated in resource density relative to a smaller lake. For clarification, we point out that from the geometry of triangles ABC and AED that the total biomass capacity, \( B_{tot} \), of the alternate habitat equals the area under the hypotenuse of a right triangle (\( AC \) in ABC and AD in AED; Supplementary Fig. S2.1). Therefore, for different sized lakes the total biomass of resources in the alternative habitat is determined by:

Small habitat: \( B_{tot} = f*D'/2; \) \hspace{1cm} (S1)

Large habitat: \( B_{tot} = (f+I)*D'/2; \) \hspace{1cm} (S2)

where \( B_{tot} \) is the total biomass, \( f \) is the predator foraging scale, \( I \) is the inaccessible portion of the habitat, \( D' \) is the peak resource density (Supplementary Fig. S2.1). Given the assumption of a constant mean peak density of prey \( (D') \), a large littoral habitat lake necessarily has more total biomass than a small littoral habitat lake (i.e., Supplementary equation (S2) > Supplementary
equation (S1). In contrast, though, the total biomass accessible, $B_{\text{acc}}$, is lower in a larger lake compared to a smaller lake. To see this, one simply compares the accessible area of ABC (small lake) to ABF (large lake) identified in Supplementary Fig. S2.1.

### 2.10.2 Use of ($\alpha$) as a resource scaling parameter

Here we show in two steps that the ratio of foraging scale, $f$, to the secondary habitat size, $H_s$, scales linearly with prey accessibility. In order to simplify the spatially explicit resource assumption above, we chose to approximate the linear increasing resource density in the alternate habitat by following the mean resource density (e.g. $D_S$, $D_L$). Supplementary Fig. S2.3 graphically depicts this simplification.

**Step 1.** *Proof that the ratio of foraging scale (AB) to secondary habitat size (AE) scales peak resource density (BC or AE) with peak available resource density (BC or BF).*

To start, for all right triangles, the tangent of an angle, $\theta$, equals the ratio of the opposite side over the adjacent side (Supplementary Fig. S2.3). According to this definition we can state that any right triangle (e.g., ABF) contained within another right triangle (e.g., AED), and having common angle (e.g., $\theta$), necessarily has the same ratio between the opposite to adjacent sides. We can state this simply with the following equality;

$$\tan \theta = \frac{BF}{AB} = \frac{ED}{AE}.$$ 

Given $BC = ED$ (Supplementary Fig. S2.1, A.2), then we substitute BC for ED yielding:

$$\tan \theta = \frac{BC}{AE}.$$ 

Therefore, it is also true that;
\[ \frac{BF}{AB} = \frac{BC}{AE}, \]

rearranging,

\[ BF = BC \left( \frac{AB}{AE} \right). \]

Finally, given that \( \frac{AB}{AE} = \alpha \), then \( BF = BC(\alpha) \), and so;

\[ \alpha = \frac{BF}{BC}. \]

Thus, the scaling parameter, \( \alpha = \frac{AB}{AE} \), scales the accessible resource density, \( BF \), relative to the resource peak density \( (BC = ED) \). Thus, for example, the functional response for a predator \( P \) in an alternate habitat with intermediate consumer, \( C \), has a consumption rate: \( a(\alpha C)P \), where \( \alpha C \) is the mean density of resources within the consumers foraging scale.

Step 2. *Proof that \( \alpha \) scales mean resource density in a small habitat to a large habitat*

Here we show that we can scale mean resource density with \( \alpha \). In Supplementary Fig. S2.3 we represent mean resource densities by converting triangles to rectangles of equal area. Notice that a constant predator foraging scale is also maintained.

To begin the proof we simply state the area of ABC, the triangle that represents an alternative habitat with a base (AB) equal to \( f \), and a peak resource density BC so that;

\[ \text{Area } ABC = \frac{1}{2} (BC * AB). \quad (S3) \]
The height of the rectangle with the same area approximates the mean resource density, and this height is determined by (Supplementary Fig. S2.3);

\[ \text{Area } ABC = \text{Area } ABHG; \text{ where } AG = BH = \frac{1}{2} (BC). \]

Next moving to Supplementary Fig. S2.3 we state the equivalent equation for the accessible portion of a larger habitat (AED) which is bound by ABF;

\[ \text{Area } ABF = \text{Area } ABJI; \text{ where } AI = BJ = \frac{1}{2} (BF). \]

By cancelling terms we now show that \( \alpha \) scales Area ABHG to Area ABJI, and thus scales the mean resource density accessible in the two habitats, such that:

\[
\frac{\text{Area \ ABJI}}{\text{Area \ ABHG}} = \frac{\frac{1}{2}BF \cdot AB}{\frac{1}{2}BC \cdot AB} = \frac{BF}{BC} = \alpha \quad (S4)
\]

Here, we have effectively transformed the simple increasing linear spatial resource representation into a uniform spatial resource representation, making sure the uniform representation has the same mean density. Our simple spatially-implicit equations, therefore, following mean accessible resource densities.

### 2.11 Supplementary Methods

#### 2.11.1 Determining biomass proportions from gut contents

Detailed methods used to determine percent biomass from stomach contents are published elsewhere\(^49\). In a nutshell, biomass volumes were determined from stomach contents using one of three methods. Either (i) each dietary items biomass was directly measured from stomach contents and expressed as a percentage of the total biomass, (ii) percent biomass was calculated
as the frequency occurrence of each dietary item multiplied by the average biomass of an item of that type (e.g. benthic invertebrates = 0.23g) and divided by the total mass of all prey items, or (iii) an equation was used to estimate percent biomass volume from frequency of occurrence: 

\[
\text{%volume} = -0.62 -1.13(\text{%frequency}) -0.27(\text{%frequency})\log(\text{predator:prey biomass ratio}); R^2 = 0.83, n= 578. 
\]

For the new data, (not in Vander Zanden and Rasmussen\textsuperscript{49}) gut contents were converted to biomass proportions using this frequency occurrence equation.

### 2.11.2 Empirical resource gradient data

In the Supplementary Discussion we motivate two assumptions, A.2 and A.3, with empirical data from Ontario Ministry of Natural Resources surveys of 90 Canadian lake trout lakes (Supplementary Fig. S2.2). We use 26 littoral fish species to calculate three littoral fish depth distribution metrics; (i) catch.net\textsuperscript{-1} by depth strata (number of fish captured per net for each depth stratum (m) 1-3, 3-6, 6-12, 12-19.9), (ii) peak depth (for each lake the depth that had the highest catch.net\textsuperscript{-1}), (iii) catch.net\textsuperscript{-1} at the peak depth (the number of fish captured per net at the depth with the highest catch.net\textsuperscript{-1} per lake). We use these data as a basis for arguing for a littoral resource gradient.
Chapter 3  Effects of differential habitat warming on complex communities

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3.1 Abstract

Food webs unfold across a mosaic of micro and macro habitats, with each habitat coupled by mobile consumers that behave in response to local environmental conditions. Despite this fundamental characteristic of nature, research on how climate change will affect whole ecosystems has overlooked: (i) that climate warming will generally affect habitats differently, and; (ii) that mobile consumers may respond to this differential change in a manner that may fundamentally alter the energy pathways that sustain ecosystems. This reasoning suggests a powerful, but largely unexplored, avenue for studying the impacts of climate change on ecosystem functioning. Here we use lake ecosystems to show that predictable behavioral adjustments to local temperature differentials govern a fundamental structural shift across 54 food webs. Data show that the trophic pathways from basal resources to a cold adapted predator shift toward greater reliance on a cold-water refuge habitat, and food chain length increases, as air temperatures rise. Notably, cold-adapted predator behavior may substantially drive this decoupling effect across the climatic range in our study independent of warmer adapted species responses (for example, changes in near-shore species biomass and predator absence). Such
modifications reflect a flexible food web architecture that requires more attention from climate change research. The trophic pathway restructuring documented here is expected to alter biomass accumulation, through the regulation of energy fluxes to predators, and thus potentially threatens ecosystem sustainability in times of rapid environmental change.

3.2 Introduction

Natural systems are inherently complex entities, wherein organisms act as agents of material and biomass transport (1) weaving food webs through a mosaic thermal environment. Direct temperature effects on trophic interactions arise through thermal regulation of an organism’s physiology and behavior (2–5). For ectotherms, (that is, organisms whose body temperature is aligned with ambient temperature) several biological rates show unimodal responses to temperature (2, 3, 6), and correspondingly, studies have shown that consumption rates initially rise with warming to a peak rate and then fall rapidly approaching a critical temperature (6). Understanding the ways that these organism responses alter food webs, and how these food web responses affect ecosystem function, are key requirements to predicting climate change impacts on ecosystems (7–11).

A simple way to think about temperatures effects on any single trophic interaction is through the general linear consumption function:

\[
\text{Consumption (per capita)} = e \cdot a \cdot t_s \cdot R, \quad \text{(Eqn 1)}
\]

where \( e \) is the efficiency of converting prey to biomass, \( a \) is the attack rate, \( t_s \) is the time searching, and \( R \) is the resource density. Assuming \( e \) is temperature independent (9), the direct effects of temperature on an organism’s consumption may largely depend on \( a \) and \( t_s \). The
argument for the temperature dependence of attack rate is straightforward. Temperature mediates foraging velocity (3), and considering all else equal, velocity determines encounter rates and prey capture success. The influence of temperature on time searching is a little more complex, but the general expectation is that its influence will be shaped by the requirement that the organism allocate its feeding time in different patches or habitats to increase its fitness (5). Such thermal limitation of search time would lead to reductions of interaction strength in warming habitats – in effect, temperature would mediate prey availability. What remains to complete the consumption equation above is the effect of temperature on \( R \), both direct effects (for example, the impact of warming on \( R \)’s productivity) and indirect effects (for example, impact of warming on the number and efficiency of consumers competing for \( R \) ) (12, 13).

Here we extend the logic that underlies this simple representation of temperature dependent consumption to develop hypotheses that link temperature differentials, through direct and indirect means, to spatial food web structure. Spatially simple laboratory studies of food webs suggest that larger bodied, higher trophic level organisms are likely to have high extinction risk with ambient warming (14). In natural systems, these higher order predators provide a spatially unifying component to food webs: their high mobility enables them to forage among different habitats, coupling food chains with unique basal resource groups (15–17). This coupling structure can be an important part of sustaining higher order consumers with consequences for food chain length, trophic control, and ecosystem stability (15, 18–20). For example, theory argues that reduced access to a novel resource compartment may decrease a consumer’s biomass (18, 19) thereby increasing the chance of local extinction from a random event. When accessibility is limited reduced coupling may alter food chain length if habitats contain prey that differ in trophic position (21) or if higher level prey increase, with reduced
trophic control, and consequently predators become less omnivorous (18, 20). Given that temperature change can drive asymmetric responses in species that differ in thermal tolerance, the influence of spatially structuring elements on the response of a food web to warming will depend, not only on the direct responses of consumers to temperature (2, 3, 5), but also those responses of other interacting community members (12, 13, 22). We test notions of the structuring effects of differential temperature on spatially coupled food webs (thermal-accessibility hypothesis), using boreal lakes as a model ecosystem. To make this test, we assembled one of the largest comparative food web data sets on record: 54 ecosystems, characterized using >3000 isotope (N and C) samples.

Freshwater lakes are particularly sensitive to climate change as lake habitats are structured by climate driven water temperature and biota are vulnerable to ambient temperature change (23). A key habitat feature of boreal lakes is thermal stratification, an effect of antagonistic physical forces of mixing by wind energy and resistance to mixing by solar heating that separates cold more dense water (hypolimnion) from warmer less dense surface water (epilimnion) (24). The stratification process creates a potential for temperature differentials between deeper offshore and shallower near-shore sub-habitats within a lake, as temperatures remain relatively constant in deep habitats whereas shallower near-shore temperatures are strongly influenced by air temperatures (25). Monitoring in the boreal region (26, 27) has shown that rising air temperature warms surface waters, accelerates the stratification process, and extends the duration of stratification; thus air temperature is a primary determinant of lake thermal heterogeneity.

Most aquatic organisms (e.g. invertebrates, amphibians, fish) are ectotherms, therefore the demands of the thermal environment arguably form the most influential set of abiotic factor
aquatic organisms must satisfy (28, 29) (including increased oxygen requirements in warmer water). Thermal differentiation in lakes typically corresponds with the species differences that characterize offshore and near-shore habitats. Conveniently, biomass flow from these habitats through a food web can be traced using stable carbon and nitrogen isotope ratios due to isotope differences at the base of the food web between phytoplankton (offshore) and benthic algae (near-shore) (17, 21, 30, 31).

We focus our study on the trophic pathways that flow from basal resources to lake trout (*Salvelinus namaycush*) a vulnerable, cold adapted (10-12°C preference) apex predator (32) estimated to reside in 66, 500 Canadian lakes (33). Previous studies show that lake trout play a keystone structural role in integrating resource pools in offshore and near-shore habitats (17, 20, 21, 30). In what follows, we test the direct and indirect effects of differential warming on this model system (lake trout food web) across a summer mean temperature gradient ranging 15-20°C. At the warmer end of this range surface temperatures will often exceed the physiological tolerance of lake trout and should restrict accessibility into the near-shore habitat. This thermal-accessibility mediated restructuring of the food web is considered along with complementary notions of warm tolerant competitor effects and relative prey abundance changes with climate.

### 3.3 Results and Discussion

**Food web structure shifts in response to climate**

Resource contributions from near-shore exposed habitats to lake trout were clearly reduced relative to open coldwater habitats in warmer temperatures (Fig. 3.1A, B). Under these warmer conditions lake trout carbon signatures shifted toward cold water baseline sources (Fig. 3.1A), indicating a proportionally stronger dependence on offshore phytoplankton production. In
Figure 3.1 Relationship between temperature, trophic structure and predator habitat use across individual lake ecosystems. (A) As temperature increases the contribution of material derived from basal resources in near-shore habitat to lake trout diet (near-shore coupling) is reduced (linear regression, $R^2 = 0.18$, df = 53, $p = 0.001$). (B) Similarly higher temperatures are related a reduced contribution of near-shore relative to offshore (linear regression, $R^2 = 0.18$, df = 36, $p = 0.008$) indicating the decreased reliance on prey fish from habitat in warmer temperatures. (C) Trophic position of lake trout estimated as the population mean (linear regression, $R^2 = 0.07$, df = 53, $p = 0.045$) and the highest individual value recorded for each lake (linear regression, $R^2 = 0.13$, df = 53, $p = 0.007$). (D) The proportion of the lake trout population captured near-shore ($< 6$m) in each lake decreased with summer air temperature indicating a shift to offshore habitat use (logistic regression (binomial), $D$ explained = 0.45, df = 39, $p < 2.0 \times 10^{-16}$). Summer air temperature is the mean monthly temperature averaged for June, July, and August for the year each lake was sampled. Near-shore coupling is the proportional contribution of $\delta^{13}C$ from near-shore basal resources relative to offshore basal resources ultimately assimilated in lake trout tissue (see Materials and Methods).
addition, this shift toward offshore carbon sources was accompanied by a parallel diet shift toward more coldwater prey fish (Fig. 3.1B). Concurrently, the trophic position of lake trout increased with warmer temperatures (Fig. 3.1C). Hence, a shift in consumption to deepwater resources seems to correspond with a lengthening of the trophic pathways to lake trout (Pearson’s $r = -0.28$, df = 53, $p = 0.032$). Lake trout typically hold the highest trophic position in temperate lakes (31) and so for many lakes this increased trophic position likely amounts to an increase in overall food chain length. Further this food web response agrees with a previous study that theoretically and empirically argues that altering accessibility in these lakes results in an expansion and contraction of the food web (34). Our new findings show that temperature can be an important mediator of this effect.

### 3.3.1 Focal predator alters habitat use in response to climate

The general food web structure shift corresponds with data on lake trout habitat use. Abundance data from lakes used in the trophic analysis show that the relative proportion of lake trout caught in near-shore habitat decreased as temperatures increase (Fig. 3.1D). Field studies find that lake trout behaviorally thermoregulate seeking cold-water refuges in the summer months (32, 35, 36). Despite use of cold water below the thermocline, summer tracking data have shown that lake trout occasionally take short forays into the littoral zone, in the summer, which is expected to be driven by the search for prey (35). Finally, anecdotal reports suggest fishermen notice that in northern areas lake trout can easily be caught from shore all year long while at the southern end of the species’ range this is not the case. Considering our findings with previous observations we argue that predator behavior is an important component of the food web responses documented here.
3.3.2 Non-focal predators and the food web shift

Smallmouth bass (*Microterus dolomieu*) and walleye (*Sanders vitreus*) are apex predators that inhabit the near-shore zone in many lake trout lakes. Because these species are expected to benefit from warmer summer temperatures over the climate range of our study (25), they may be an indirect cause of the overall decoupling effect observed across the climate gradient. In contrast to the prediction that warm-water predators are the primary driver of decoupling across a warming climatic gradient, our analysis of lakes without bass and walleye shows a similar if not stronger relationship between warming and the decoupling of lake habitats (Fig. 3.2A). Furthermore, bass abundance estimates in lakes where these species are present are independent of the temperature gradient measured in our study and walleye abundance is somewhat higher but not significantly so in the colder lakes (Fig. 3.2B). Note that our findings do not discount the previous findings that competitors may act to decouple lake trout from near-shore fish production (21), nor that their distribution is restricted by climate (25). In fact bass are more likely to be present on average in our warmer study lakes (F = 4.393, n = 54, p = 0.041). Our findings instead suggest that the existence of these predators is not the force driving the relationship between air temperature and trophic structure across the climatic gradient. Said differently, temperature may alter the accessibility of resources to predators in a similar way but independently of its affects on other components of the food web.

3.3.3 Prey abundance in relation to climate gradient

Examination of prey abundance in the exposed littoral habitat further contradicts the idea that indirect effects account for the observed food web restructuring. Prey abundance estimates did not vary predictably with warmer temperature conditions (Fig. 3.2C). This result suggests that abiotic limitation like temperature may explain exceptions to the general prediction that habitat
Figure 3.2 Relationship between habitat coupling and temperature is independent of measured indicators of indirect effects in study lakes. (A) The negative relationship between temperature and near-shore coupling (logit($\delta^{13}$Clake trout – $\delta^{13}$Cmussel)/( $\delta^{13}$Csnail – $\delta^{13}$Cmussel)) occurs with smallmouth bass absent (black line (black circle); $R^2 = 0.33$, df = 17, $p = 0.009$), walleye absent (dark grey line (grey triangle); $R^2 = 0.22$, df = 24, $p = 0.01$) and both near-shore predators absent (light grey line (grey square); $R^2 = 0.35$, df = 11, $p = 0.03$). (B) Smallmouth bass ((black circle); $R^2=0.007$, df = 30, $p = 0.65$ and walleye ((grey circle); $R^2 = 0.12$, df = 26, $p = 0.07$) biomass per net are not significantly related of the temperature gradient in lakes where these predators are present. (C) Near-shore prey biomass per net is independent of the climatic gradient ($R^2 = 0.0064$, df = 43, $p = 0.599$). Summer air temperature is the mean monthly temperature averaged for June, July, and August for the year each lake was sampled. Near-shore coupling is the proportional contribution of $\delta^{13}$C from near-shore basal resources relative to offshore basal resources ultimately assimilated in lake trout tissue. Data reported in all panels are from the same lake dataset.
coupling may depend on relative prey abundance in an alternate habitat (16). Taken together with the predator effects mentioned above (Fig. 3.2A,B), we argue that temperature differentials can decouple food web interactions across habitats independent of the complex indirect interactions between cold-water predators and warm-water fish species (Fig. 3.3).

### 3.4 Conclusions

Historically climate change research on communities has largely focused on the magnitude of regional temperature change and focal species thermal sensitivity (9). Increasingly researchers recognize that predicting organism responses to climate change is more ecologically complex than simple thermal limitations of species (5). Some recent research suggests that inconsistencies in mapping climate change to organism responses may be reduced by considering biotic interactions (8, 12). Until recently however, few studies considered the impacts of any directional environmental change on the fundamental consumptive pathways that structure food webs (but see (31, 37–39)) and thus climate change impacts on food web structure remain elusive. Our finding, that air temperature mediates a predictable shift in food web structure that integrates different habitats, contributes to an emerging research area that considers biotic interactions in climate change effects. Moreover these findings support the general idea that consumptive effects and spatial conditions in food webs cannot be overlooked if we aim to understand climate impacts on communities (12, 22).

With ongoing climate change ecotherms in aquatic and terrestrial systems may increasingly face the challenge of staying cool. By shifting from warm habitats (for example, aquatic = near-shore, terrestrial = direct sun) to cold refuge habitats (for example, aquatic = offshore, terrestrial = shade) organisms avoid detrimental and potentially lethal thermal exposure in their environment. Indeed, we found that the apex predator in these boreal lakes did, in fact,
Figure 3.3 Simple schematic showing effects of differential warming on habitat coupling (horizontal-axis) and habitat use (vertical-axis) by lake trout in cold (top) and warm (bottom) conditions. Lake trout couple into the thermally exposed resource channel less (Fig 1A, B) and are rarely captured (proportionally) in that habitat (Fig 1D) under warmer conditions (indicated by lake trout position). Arrows direction and thickness accentuate coupling direction and strength. Letters in the top diagram identify trophic groups used in both upper (cold) and warm lake depictions; lake trout (a), pelagic forage fish (b), pelagic invertebrates (c), pelagic phytoplankton (d), littoral fish (e), littoral invertebrates (f), benthic algae (g). To the right in the diagram we show thermal profile data contrasting temperature at depth from Victora lake (cold; summer air temperature = 15.5°C, lat = 49.62306, long = -91.54889) and Charleston lake (warm; summer air temperature = 19.7°C, lat = 44.53611, long = -76.01194) taken at the time of sampling. Temperature is visually highlighted with darker blue (cold) and darker red (warm) hues. These lakes experience temperatures near the cold and warm endpoints for our data set, are of the same order of magnitude in size, and both had thermal profiles to 30m.
alter its habitat use in a manner expected by its thermal tolerance (36, 40), as we detected a
decreased proportion of lake trout in near-shore habitat with relatively warmer air temperatures
Fig 3). Such behavioral thermal buffering by organisms is well known for individual species (5),
but the implications of this climate mediated behavior on the integration of food web pathways
has until now not been studied.

Data show that over a climatic gradient the trophic pathway that couples two lake habitats
contracts, and the height of the food chain pathway between basal resources to the focal predator
lengthens, as warming air temperature drives a thermal differential within lakes (Fig. 3.3). This
decoupling of resource pathways and increased predator trophic position occurs independently of
the abundance of near-shore prey species and the presence of two warm tolerant predators that
can be found in some of systems we studied. We recognize that this may not always be the case
and expect that warm water predators and negative temperature effects on prey species along
with indirect behavioral effects (12) can magnify the consumptive shift we indentify. We do
argue that our study provides evidence that thermal accessibility can be an important mediator of
the biomass uptake by predators from different habitats and thus influences the structure of food
webs across climatic conditions. This result aligns with previous food chain research that has
argued that behavioral responses and altered habitat use to climatic conditions can mediate prey
encounter and biomass structure at different trophic levels (12). Our findings extend previous
knowledge by showing that thermal effects act to shift consumptive pathways according to
spatial temperature features across systems. In a general sense, this result supports recent
research that argues for spatial conditions as an important regulator of the fundamental pathways
of energy flow from basal resources to predators in food webs (18, 20, 31, 39).

Importantly the habitat avoidance and the shift in trophic interactions we document may
have important implications for the sustainability of these lakes and more generally in complex
food webs. A reduced energy flux to predators can lower predator population size (18, 19) and
leave predators more susceptible to extinction by other stressors in their environment (for
example, harvest). In addition to the potential for consumer extinction from lowered access to
production, intolerable conditions also limit a predator’s ability to switch habitats in response to
prey variability. Such behavior can reduce the potential for ‘adaptive’ stabilization of the web.
For example, if prey species have the potential to oscillate predators may suppress this potential
by switching from prey at low abundance to feed on abundant prey. In the absence of this
flexibility, predators may continue to reduce prey in disturbed habitats or food chains may be
more prone to rapid dynamic fluctuations with improved conditions (15, 18, 19). These kinds of
responses are recognized as potential implications of this food web structural shift on community
dynamics, and sustainability. Understanding nature of interaction changes on food web dynamics
remains a challenge for climate research and clarifying the relationship between structure and
function of food webs is a central problem in ecology.

Our study uses a novel approach to relate climate to the biodiversity inherent in the
world’s ecosystems. In particular we expect our findings to have major implications for climate
impacts on an integral part of global freshwater biodiversity on which mankind relies. Boreal
lakes in particular house a large part of Canada’s 37% share of global freshwater (33).
Furthermore, the freshwater communities in these lakes support recreational and subsistence
fisheries of substantial social and economic value (e.g., Canadian recreational fishery value > 4.9
billion dollars annually) (41). Aside from the dynamic implications of food web shifts, increased
trophic positions of the predators in these systems has been linked to greater accumulation
contaminants and thus adds another element of concern for the services that humans rely on in
these ecosystems. More generally given the widespread recognition of consumer thermoregulation such a fundamental shift in dominant trophic pathways may extend to a number of aquatic and terrestrial ecosystems. Finally, we suggest that flexible food web structure may serve as an important diagnostic tool for the impacts of changing climate and so we urge for more research on the responses of food web structure for ecosystem conservation efforts.

3.5 Materials and Methods

3.5.1 General lake sampling

In 2009, we began collecting data to estimate food web relationships using stable isotope techniques from lakes across the Canadian province of Ontario in conjunction with ongoing Ontario Ministry of Natural Resources (OMNR) lake biodiversity surveys. Full details for the fish community netting protocol and isotope collection can be found elsewhere (44). Our general methodology for isotope processing and analysis follows previously published studies (17, 21, 31). We also supplemented the whole lake sampling with isotope data collected from Ontario lakes in 2007 and less intensive sampling effort that was performed on a few lakes in attempt to extend our sampling range. Since we did not have standardized whole lake catch estimates from these lakes that were not sampled with the full survey, these lakes could not be used in our analysis of the relationships between fish abundance and the climate gradient. In what follows we provide details necessary to understand our general methodology and data analysis.

Lakes were sampled across a summer air temperature gradient (average June-August monthly mean) of roughly 5°C (range = 15°C-20°C). Sampled lakes were chosen at random within management zones, from these we focused on those known to contain lake trout and we obtained isotope samples from these lakes covering as wide a climatic zone as possible.
Sampling began in the middle of June and continued through to September. Summer air temperature data were obtained for each lake for the year the lake was sampled from a climate database (HCAT) maintained by the OMNR (42). Five additional temperature measures along with some general study lake characteristics were used in analyses appearing in the Supplementary Information (OMNR database and Environment Canada database (43)). Lake characteristic measurements were obtained from historical government (OMNR) databases or were measured during the biological survey.

### 3.5.2 Stable isotope data collection

To rapidly procure estimates of gross food web structure we collected tissue for stable isotope analysis from a representative set of organisms in the lake trout food web of boreal lakes (see Figure 3). The collection included seven types of samples that included lake trout, near-shore and offshore prey fish, near-shore insects, offshore zooplankton, and mussels and snails. Mussels and snails consume phytoplankton and benthic algae respectively and were used as indicators of habitat baselines. These lakes are well suited for the use of stable isotope techniques as the general isotope signatures for many organisms in these lakes have been identified (21, 30, 31, 45) and stable isotope based food web estimates ($\delta^{13}$C and $\delta^{15}$N) agree with stomach content diet data for many species (45). We used carbon as a tracer of spatial structure in these lake food webs as isotope ratios ($\delta^{13}$C) exhibit little to no ($<1\%$) $^{13}$C enrichment with transfer among trophic levels. In these boreal lake systems, mussels and snails can be used to capture $\delta^{13}$C differentiation between primary producers in offshore and near-shore habitats respectively (21, 30, 31). Nitrogen ($\delta^{15}$N) is used to estimate an organism’s vertical position in a food web. This estimate reflects the number of trophic transfers in the pathway from basal resource to an apex predator. This is possible as nitrogen isotope ratios exhibit a 3-4‰ fractionation between
predators and prey (31, 39). Using this approach we are positioned to obtain estimates of the 
reliance of lake trout on near-shore and offshore resources (habitat coupling) and the food chain 
length of the sink food web that leads to lake trout.

For most lakes, lake trout and forage fish tissue samples were collected according to the 
standard methodology utilised for OMNR biodiversity surveys (44). These surveys used a depth 
stratified sample design that targeted whole fish communities with multi-mesh gill nets. The 
sampling effort was standardized across lakes based on lake size and nets were assigned to 
random locations based on a depth stratified design (44). Predator fish were captured using a 
large mesh net that targets fish over 200mm with mesh sizes (38-127mm). Prey species were also 
caught in large mesh nets, but were targeted with a small mesh (13-38mm) net (44). Lake trout 
tissue samples for stable isotopes were taken from the first 20 fish captured, or for the complete 
sample of fish obtained in lake surveys. Prey fish were sampled from both the littoral (target = 40 
fish) and pelagic (target = 20 fish) habitats to represent the forage species found in each lake.

Invertebrate collections were made to obtain organism used to establish the baseline 
isotope signatures for near-shore and offshore habitat in each lake. Excluding zooplankton 
samples, collections of invertebrates reflect multiple sites within each lake with more sites used 
in the larger lakes. Mussels (Unionidae, zebra mussels used for two lakes) were collected by 
snorkeling or with use of dip nets and were used as an integrated indicator of pelagic isotope 
baselines. Gastropods were used as indicators of the near-shore resource baseline and were 
collected by essentially the same methods as mussels. Near-shore benthic insects were also 
obtained for the near-shore zone using a kick net and by hand picking from the rocks and wood 
debris in each lake. Zooplankton were sampled with 150-200µm mesh nets retrieved five times 
from below 20m of the water’s surface from the deepest part of the lake.
Once collected, tissue was sampled from larger fish in the field while smaller fish and invertebrates were stored whole and dissected in the laboratory. These samples were packed in ice filled coolers and samples were immediately frozen following return from the field. For each of the larger fish a muscle sample (~2g) was removed from behind the dorsal fin and above the lateral line to keep the tissue sample consistent (44). Forage fish were thawed and dorsal muscle tissue was removed in the laboratory (the aim was to obtain a 500µg dried sample). Mussels and snails were removed from their shell so that only soft tissue was used. Zooplankton and near-shore invertebrates were kept whole. Samples were dried at 65-70°C for 48-72 hours. Dried samples were ground into powder and were sent to the University of New Hampshire stable isotope lab for analysis.

3.5.3 Stable isotopes based food web measures

We used established methodology and two source mixing models to determine the contribution of near-shore carbon in lake trout diets and their trophic position. We used lakes that ranged in the number of lake trout isotope samples obtained (2-24) with an average of 13 individual trout sampled per lake. Lake trout 250mm and larger were used as fish this size were expected to be capable of predating on fish as well as invertebrates. We only used lakes where both littoral and pelagic forage fish were present in attempt to preserve the general trophic structure across lakes. Forage fish were processed individually by species and then the mean for each habitat based trophic group was used in the mixing models.

If one of the key baseline organisms (that is, mussels or snails) was not collected, which occurred in a few lakes, we used linear regression models to estimate missing baseline values from other organism’s from the same lake. Carbon isotope ratios were estimated with the equations: $\delta^{13}C_{mussel} = 0.7071(\delta^{13}C_{pelagic forage fish}) - 7.9513 \ (R^2 = 0.35)$ and $\delta^{13}C_{snail} =$
1.0377(δ^{13}C_{mussel}) + 9.5952 (R^2 = 0.17). Nitrogen baseline values were estimated in the same way e.g., δ^{15}N_{snail} = 0.895(δ^{15}N_{mussel}) - 0.3275 (R^2 = 0.71).

Carbon pathways from offshore and near-shore habitats were determined as the proportion of carbon assimilated in predator fish tissue relative to baseline δ^{13}C. These habitat delineations were combined with nitrogen measurements in a model to estimate trophic position. Estimates of near-shore coupling are based on the mean δ^{13}C for lake trout, mussel and snails in each lake using the following the equation (21): proportion near-shore carbon in lake trout diet = (δ^{13}C_{lake trout} − δ^{13}C_{mussel})/(δ^{13}C_{snail} − δ^{13}C_{mussel}). The same equation was used for the forage fish based calculation with δ^{13}C_{pelagic forage fish} and δ^{13}C_{littoral forage fish} replacing δ^{13}C_{mussel} and δ^{13}C_{snail} respectively. Proportion near-shore fish carbon in lake trout diet = (δ^{13}C_{lake trout} − δ^{13}C_{pelagic forage fish})/(δ^{13}C_{littoral forage fish} − δ^{13}C_{pelagic forage fish}). Trophic position of lake trout was calculated using the equation (31): trophic position = 2 + (δ^{15}N_{lake trout} − (δ^{15}N_{mussel} × (1−α) + δ^{15}N_{snail} × α))/3.4, where 3.4 is the assumed per trophic level increase due to fractionation in ^{15}N, 2 is the trophic position of the organism used to estimate baseline values, α is the proportion of littoral carbon and weights the trophic position estimate according to baseline contributions. We present two measures of trophic position one is the average of all fish collected and TP_{max} is the trophic position of the highest individual lake trout recorded in the lake.

3.5.4 Catch data analysis

Catch estimates were obtained from lakes used in the isotope analysis that were sampled using standardized netting protocols (44). Near-shore habitat use by lake trout was determined as the number of lake trout caught from nets in less than 6m of water relative to the total catch for the whole lake. Presence and absence of smallmouth bass and walleye was determined by a combination of the biodiversity surveys and historical records for each lake. Catch per unit effort
estimates for smallmouth bass, walleye and littoral species were estimated for the whole lake and predator catch estimates were area weighted by depth stratum using lake bathymetry. The basic unit of the catch estimate used in our analysis of predator fish is kilograms of fish per gang, where a gang is the equivalent to 25m of net. The number of individuals per gang is used for the forage species and reflects the combine catch for 34 species according to their presence in each lake.

3.5.5 Statistical approach

We used linear, logistic (binomial), and multivariate regression models in our analyses. We transformed data according to statistical requirements (46). Logit transforms were used for isotope proportion data (47). Catch per unit effort estimates used as fish abundance measures were log transformed. To avoid extreme zero inflated catch distributions, we analyzed smallmouth bass and walleye biomass per net for lakes where the species are present and where we had catch data. We felt this was an appropriate way to meet statistical assumptions and considering we examined the effects of the absence of these predator species in another analysis. We excluded an outlier from the analysis for Fig 1 (b) and in the near-shore fish coupling summary in the Supplementary Information. This single measure had a large effect on the linear regression model as identified by Cook’s distance (47) and was the highest value in the dataset. All analyses were performed using the R language statistical environment.

3.6 References


3.7 Acknowledgements

We thank biologists and technical staff at the OMNR Broad-scale Monitoring Program for assistance with sample collection. S. Sandstrom, K. Armstrong and J. Wright were particularly helpful with logistics and offered sampling advice. A number of people assisted in additional fieldwork and sample processing in the lab these include J. Simpson, A. Fraser, R. Lee, R. Saint, T. Bartley, L. Jarvis, E. Perrier and R. Cornell. We also acknowledge the efforts of A. Oulimette and R. Mixon at U.N.H. Stable Isotope Lab. Helpful discussion related to this work included McCann lab members, NSERC strategic group “Impacts of climate change on limnetic biodiversity and fisheries in Ontario and Quebec”, Canadian Institute of Ecology and Evolution (CIEE) working group “Thermal Scaling and Body Size: the next frontier in climate change” and, NCEAS working group “Synthesizing theory and databases to advance a general framework for how warming affects trophic interactions”. This work was supported by grants from the Natural Sciences and Engineering Research Council of Canada and the Climate Change Program of the Ontario Ministry of Natural Resources. Additional support came through a CRC tier 2 research chair held by K.S.M.
Supplementary Figure S 3.1 Relationship between climatic gradient and lake size. Lake size measured as area (A) ($R^2 = 0.0004$, df = 53, p=0.64) and volume (B) ($R^2 = 0.0479$, df = 30, p = 0.23) does not vary with the temperature gradient used in our study. Summer air temperature is the average of monthly mean temperatures for June, July and August for each location for the year the lake was sampled.
Supplementary Table S 3.1  Summary of temperature metrics and other physical characteristics for study lakes. Variables are summarized as the number of observations (n), minimum value (min), maximum value (max), mean value (mean), and standard deviation (SD).

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† Summer air temperature is the average monthly mean for June, July and August for each lake during the sampling year. †† Summer air temperature max is the average of the mean of daily maximum temperatures for the same months. ‡ Month air temperature is the mean temperature for the month the lake was sampled in the sampling year (note: when the sampling date is prior to the fifth of the month then the previous month is used). ‡‡ Month air temperature max is the mean of daily maximum temperatures the month the lake was sampled. * Depth of 10°C isotherm is the depth from the lakes surface that water temperature first measured 10°C and is determined from a temperature profile measured during the sampling period.
### Supplementary Table S 3.2 Relationship between lake trout food web structure and five temperature metrics.

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† Summer air temperature is the average monthly mean for June, July and August for each lake measured in the sampling year. †† Summer air temperature max is the average of the mean of daily maximum temperatures for the same months. ‡ Month air temperature is the mean temperature for the month the lake was sampled in the sampling year (note: when the sampling date is prior to the fifth of the month then the previous month is used). ‡‡ Month air temperature max is the mean of daily maximum temperatures the month the lake was sampled. *Depth of 10°C isotherm is the depth from the lakes surface that water temperature first measured 10°C and is determined from a temperature profile measured during the sampling period.
3.9 Supplementary Discussion

This supplementary information provides a summary description our study systems (Table S3.1) and provides additional analyses that relate food web structure to additional temperature metrics (Table S3.2). We reported summer air temperature in the main text as it is a good predictor relative to other temperature measures (Table S3.2). We added a global temperature model to each of the three food web metrics used in our analyses and found little improvement in the variance explained by the model compared to using summer air temperature alone. None of the global models were significant according to a p < 0.05 threshold. Furthermore, summer temperature is known to be a good predictor of other important seasonal climate indicators such as stratification timing and duration\textsuperscript{23}, and the summer ice free season is a period of increased production in boreal lakes where air temperature strongly maps to surface water temperatures (compared to winter when ice forms on these lakes).

Generally the slope of the relationship between food web structure and temperature is the same across temperature metrics although in several cases these are not significant. Essentially all of the temperature effects on near-shore coupling (both for baseline organisms and fish) have a negative slope (Table S3.2). Meanwhile trophic position tends to increase with these warming measures. Note that the mean daily maximum air temperatures can be more than 10°C higher than what is reported as the preferred temperature for the apex predator lake trout (\textasciitilde10°C) and exceed upper thresholds reported from lab studies.

As mentioned in the main text, few studies have used environmental gradients to capture change in food webs. There is however consistency in the relationship between ecosystem size and food chain length. Similarly lake size has been related to lake trout coupling to near-shore fish\textsuperscript{4}. For our study the climate gradient was independent of lake size measured as area
(Fig.S3.1A) and volume (Fig.S3.1B). In our lakes trophic position of lake trout and isotope mixing models with forage fish show the same directional trend - an increase in trophic position and a decrease in near-shore fish in lake trout diet but the results are not significant. This is not too surprising for our study lakes as the size range in our study systems is less than previous studies than show this pattern and there tends to be variation among systems within the size range we observed.

We also included pH and water clarity measures in the summary table. Lake trout systems are known to contain several pH sensitive species. Low pH through industrial acidification can substantially alter lake community composition and has lead to the extirpation of lake trout from some lakes. Our study lakes have pH levels above critical levels. Similarly lake trout tend to be found in clear lakes and so secchi and dissolved organic carbon (two measures that reflect water clarity) are provided as background data for research specialists of these lake systems.
Chapter 4  Blinded by the light? Habitat coupling shift in a dim light preferring predator with reduced water transparency

4.1 Abstract

Increasingly ecologists recognise that food web interactions can cross traditional habitat boundaries when key top predator species couple otherwise relatively distinct material or energy flow pathways. This habitat coupling has been argued to play a major role in governing other macroscopic properties (e.g., biomass structure and stability) of whole ecosystems. Despite this, traditional food web approaches have rarely explored how this food web link may change across large-scale environmental gradients. We consider two plausible mechanisms governing the degree of habitat coupling. First, predator coupling is strictly mediated by the proportion of prey that exists among different habitats (*proportional assimilation hypothesis*). Second, changes in environmental conditions impose constraints on consumers and these constraints govern access and ease of prey capture (*realized prey availability hypothesis*). Here we evaluate how these hypotheses predict whether walleye, a top predator that prefers dim light, couples into pelagic and littoral pathways across a gradient in water transparency. In lakes, water transparency alters light penetration which effects the visual environment a predator will experience in near-shore (littoral) and offshore (pelagic) habitats and therefore also regulates primary and in turn, secondary production. Data from 32 lakes show that habitat coupling by walleye shifts towards near-shore habitats as water transparency decreased. Increased reliance on near-shore prey by walleye appears to be a combination of improved light conditions for walleye foraging (*realized prey availability*) and to a lesser extent an increased proportion of near-shore prey (*proportional assimilation*). Our findings support a general idea that food webs respond through consumer behaviour to environmental conditions that influence prey availability. Identifying when physical habitat change regulates trophic interaction strengths across habitats is an important step toward understanding the fate of ecosystems in a changing world.
4.2 Introduction

Habitat boundaries are traditionally used to delineate food chains and food webs. Such abstraction has been a successful way to advance our understanding of complex natural systems. Several studies have argued for the existence of habitat compartments or resource channels (interactions extending from basal resources within a particular habitat, such that where many and/or stronger interactions exist within a habitat than between habitats) in food webs (Moore et al. 1989; Krause et al. 2003). That habitats are compartmented supports the idea that habitat boundaries may provide a natural partition in food web structure. Some recent research however, recognises that interactions across habitats are common in nature, and aims to uncover how these linkages influence food web dynamics (Polis & Strong 1996; Huxel & McCann 1998; Huxel et al. 2002). Indeed, trophic flows can move across several traditional habitat boundaries including; marine (Polis & Hurd 1995; Polis et al. 1997) and freshwater habitats (Nakano et al. 1999; Nakano & Murakami 2001; Gratton et al. 2008) and terrestrial habitats, open-water pelagic and near-shore benthic habitats (Vander Zanden & Vadeboncoeur 2002; Tunney et al. 2012), above ground and below ground habitats, and between canopy and understory habitats (Pringle & Fox-Dobbs 2008). The importance of spatially coupled structure for food web stability has also been stressed repeatedly (Polis & Strong 1996; Huxel & McCann 1998; Post et al. 2000; McCann et al. 2005; Rooney et al. 2006), but the mechanisms that govern the relative strength of connections among subsystems are not well understood.

Recent work on habitat coupling points to predators as a major functional component of spatial food web structure, where higher-order mobile predators are able to rapidly forage over large areas integrating over resources in distinct habitats (Schindler & Scheuerell 2002; McCann et al. 2005; McCauley et al. 2012; Tunney et al. 2014). By linking resource pools among habitats
mobile predators join energy pathways and therefore free themselves from the restrictions on primary production restrictions imposed in a single habitat (Post et al. 2000; McCann et al. 2005; Tunney et al. 2012). Previous research has argued that when predator habitat linkages increase overall predator energy consumption, such shifts can suppress lower trophic levels and predator populations may increase relative to their prey (top heavy biomass pyramids) (Schindler & Scheuerell 2002; McCann et al. 2005; Tunney et al. 2012). At the same time, when multiple resource pathways are used, a consumer may reduce the dynamic risks of reliance on one resource pathway (Post et al. 2000; Rooney et al. 2006). In a single habitat, environmental disturbances that imperil prey populations, or make foraging difficult, may reduce consumer intake, and impact the resulting population dynamics. On the other hand, an ability to access many resource pools may reduce the effects of a localized disturbance on a consumer given that the consumer can move habitats, and provided that there is some degree of spatial asynchrony among habitats (e.g. prey are differently affected among habitats) (Rooney et al. 2006).

Environmental change at the landscape scale may often manifest differentially among habitats according to specific conditions. Here we consider two general explanations to better understand how differences between habitats across environmental conditions may determine the degree that consumers couple subsystems within food webs. From a traditional perspective, where consumer vital rates (e.g., attack rate) are constant within a species, it might be argued that the relative strength of habitat linkages by higher-order consumers are determine by ‘proportional assimilation’ - the relative differences in resource abundance among habitats or relative productive potential of a habitat (e.g., proportional habitat contribution to total primary production) . An alternative idea is that the environment imposes limitations on consumers that govern the relationship between the actual prey density in a given habitat and a ‘realized prey
availability' based on access and ease of prey capture (hereafter, realized prey availability).

Previous theory has argued that differences in prey accessibility among habitats, a component of realized availability, may generally impact the relative strength of interactions that couple prey from different food chains (Dolson et al. 2009; Tunney et al. 2012). These two hypotheses are not necessarily mutually exclusive because variation on resource abundance at a large enough scale could influence realized prey availability and because the relevant scale of habitats and their homogeneity may not be completely known. Nevertheless, understanding the importance of these two hypotheses across different environmental gradients is a convenient way to gain insight for anticipating responses of fundamental food web structure to changes in the environment.

Water transparency varies among lake ecosystems and mediates differential light levels between shallow near-shore habitats and deeper offshore habitats. Transparency can rapidly change in lakes, and several factors have been linked to ongoing water transparency shifts (e.g. seasonality, climate change, invaders, and nutrient loading). During eutrophication from nutrient loading (e.g. phosphorus inputs) water can become green and turbid with greater algal growth in the water column, thereby reducing visibility for biota (Schindler 1977; Vadeboncoeur et al. 2003). Increased dissolved organic matter associated with brown colour in lakes can reduce transparency as well (Kalff 2002; Karlsson et al. 2009). Importantly, water transparency determines how light attenuates with depth which can alter the visual environment for organisms and the primary productivity in a given habitat (Vadeboncoeur et al. 2008a; Karlsson et al. 2009; Bartels et al. 2012). Water transparency can also influence consumption by altering the visual environment (Einfalt et al. 2012) and may mediate the reliance of visual consumers on different aquatic habitats (Bartels et al. 2012).
We conducted a large scale field study across a gradient of water transparency in 32 lakes. Our study uses stable isotope ratios to determine whether water transparency may explain predator reliance on distinct trophic pathways. We document patterns in food web structure, and we test whether relative habitat coupling is predicted by proportional assimilation of resources and environment mediated realized prey availability based on predator responses to water transparency. We end by speculating about the potential implications of documented changes for trophic control in these lake systems.

### 4.2.1 Study system and predictions

We address the general question of how habitat coupling is altered by environmental conditions using northern boreal lake ecosystems. Studies have repeatedly documented spatial trophic structure in lakes, where predators integrate over near-shore and offshore habitats characterized by benthic periphyton production and open water phytoplankton production respectively (Vander Zanden & Vadeboncoeur 2002) (Figure 4.1).

Walleye (*Sander vitreus*) is a predatory fish in North American freshwater lakes that consumes prey in littoral and pelagic habitats (Figure 4.1). Interestingly, walleye eyes are morphologically adapted to dim light conditions (Vandenbyllaardt *et al.* 1991). This visual characteristic has motivated behavioural investigations of captive walleye that shows preferentially use of habitat according to light intensity (Einfalt *et al.* 2012) and greater consumption under dim light conditions (Vandenbyllaardt *et al.* 1991; Einfalt *et al.* 2012). Direct observations of walleye activity in lakes have revealed greater activity in near-shore habitats which increased with high light attenuation (~ 1-3m secchi depth) compared to those with high light penetration (Ryder 1977). Under clearer conditions walleye are inactive during the day near-shore (Ryder 1977; Kelso 1978), and seek shelter to avoid bright light (Ryder 1977), but
become active at dawn and dusk. Furthermore, in clear lakes walleye seem to track light as they feed. Researchers detect walleye in deeper waters when ambient light at the surface was more intense, but are progressively caught in shallower waters as daylight recedes (Ryder 1977; Kelso 1978).

Should walleye experience improved conditions throughout the day in near-shore habitats because of lower water transparency (i.e., longer periods of preferred low light) (Lester et al. 2004), then walleye should increase their near-shore consumption of prey in near-shore habitats as water transparency decreases (Figure 4.1, Top). Consequently, we predict that walleye will show increased proportions on carbon produced by near-shore sources in lower transparency lakes (Figure 4.2). Whereas, if relative habitat coupling follows proportional assimilation, then we expect that the percent pelagic carbon in walleye diets will be higher when pelagic production increases relative to benthic production (Figure 4.2).

4.3 Materials and Methods

We conducted a field study in boreal lakes in the Canadian province of Ontario to determine the effects of water transparency and relative production on the walleye food web. Data collection involved fish surveys, invertebrate sampling and obtaining lake physical characteristics. Fish sampling was conducted according to Ontario Ministry of Natural Resources (OMNR) Broad-scale monitoring program guidelines (Sandstrom et al. 2013). The program adopts a whole lake fish community sampling using standardized multi-mesh gillnets. Invertebrate collections were carried out at the same time as fish surveys and our methods for sampling invertebrates are given below with a more detailed version available elsewhere (Sandstrom et al. 2013).
Physical lake characteristics were obtained from OMNR databases (e.g., lake morphometry) or were measured during the biological survey (e.g., water transparency). Secchi depth (m) was used as an overall measure of water transparency and was obtained by lower a secchi disc attached to a rule marked line into the water column (Kalff 2002; Sandstrom

Figure 4.1 Conceptualized lake food web where walleye couple offshore and near-shore habitat compartments and expected influence of water transparency on consumption. Top figures show the expected sensitivity of walleye consumption to water transparency. For the same surface light intensity high transparency and low transparency lakes differ in light levels in near-shore and offshore habitats. Lower transparency is expected to increase walleye foraging success and activity particularly in near-shore habitats as light is reduced toward predicted peak. Arrows show direction of biomass flow. The diagram shows a single top predator walleye (a), an offshore prey fish (b), a near-shore consumer (c), zooplankton (d), near-shore benthic insects (e), phytoplankton (f), and periphyton (g), typical of study lakes.
Figure 4.2 Potential determinants of the reliance of a light sensitive predator on pelagic and littoral benthic resources. Arrow direction and thickness represent the direction and proportional interaction strength and black circles show a predator (P) and two resources (R’s). (A) A food web shift may result from changes in relative production where the relative strength of trophic structure reflects the proportion of available resources. This is shown by the relative size of the basal resources and the corresponding arrows representing trophic flows. (B) The bottom panel alternatively argues for a response related to consumption based on predator visual capabilities (where low transparency represents near optimal conditions). Here basal resources are kept constant for demonstration. It has been suggested that water transparency alters basal resources as in the top figure in the opposite direction of a consumer mediated response.
Combined these measures were used to test for relationships with predator related food web structure and also to parameterize the equations for the primary production estimate (Supplementary Table S4.1 and S4.2).

Catch per unit effort was used as a relative measure of fish abundance and was calculated for each species and summed for each habitat group. We calculated the pelagic proportion of catch in three ways and data are displayed as proportions of catch per net. First we considered 6m depth as a cut-off for the nears-shore habitat and consider all potential prey species (we excluded other large predators as by-catch) beyond 6m as being pelagic prey. Therefore the proportion of pelagic prey (>6m) is the sum of the catch per net for all potential prey fish greater than 6m depth divided by the total catch per net across all depths. The second approach used species expected habitat use. Species included in the category as potential pelagic prey were (cisco, rainbow smelt, whitefish, sculpin) and littoral included all other species that could be potential prey for walleye. We also used cisco (*Coregonus artedi*) and yellow perch (*Perca flavescens*) to verify our classification as these two species tend to have stable isotope signatures that reflect pelagic and littoral habitats respectively and dominate catches in our study lakes.

### 4.3.1 Relative production model estimates

We estimated relative benthic and littoral production using a previously developed model (Vadeboncoeur *et al.* 2008b) with minor modification (Supplementary Table S4.1 and Table S4.2). The model uses a number of established relationships between lake morphometry, light, nutrients, and properties of benthic and pelagic primary producers to estimate daily primary production for benthic and pelagic basal resources in lakes (Vadeboncoeur *et al.* 2008a; Vander Zanden *et al.* 2011). Our motivation for using this model was to produce an index of the proportion of production expected in pelagic and littoral habitats, rather than daily production
estimates, and thus we simplified the model from the original formulation by removing the time component from the calculation. To make this adjustment, we considered primary production only at the peak light intensity (termed solar noon in Vandeboncœur et al. 2008). Another difference was that we estimated light attenuation using a previously published linear empirical relationship between secchi depth and light attenuation ($R^2 = 0.89$, light attenuation $= 0.24 + 0.902$ (Secchi Depth$^{-1}$))(Koenings & Edmundson 1991). We used this model as an alternative to the traditional conversion equation because of concerns that the traditional method was specific to clear oligotrophic lakes (Kalff 2002). Like Vander Zanden (2011) we used a maximum benthic production at light saturation ($BP_{\text{max}}$) value of 30 mg C m$^{-2}$h$^{-1}$ but also calculated estimates for 300 mg C m$^{-2}$h$^{-1}$, a value at the high end of natural variation as reported that study. Finally, we used previously determined lake area (for benthic production) and volumes (for phytoplankton) at each 1 m depth specific to measured lake bathymetry for our specific lakes rather than estimates used in previous use of the model. Consequently, we calculated the amount of production for each 1m depth for surface area and volume and then summed depths over the range of the photic zone (> 1 % light at solar noon). Otherwise, our approach is similar as that presented in previous studies (Vander Zanden et al. 2011).

4.3.2 Isotope data collection

To rapidly procure food web structures from boreal lakes we collected tissue samples to acquire stable isotope data from walleye and baseline indicators. Walleye were collected with multi-mesh gill-nets as part of government surveys. Muscle tissue (~2g) was removed from behind the dorsal fin and above the lateral line for each fish and was stored on ice in the field and then frozen upon return to a lab. Unionid mussels were used as indicator of pelagic isotope baselines and were collected by snorkeling or with use of dip nets. Gastropods (i.e., snails) were
used as indicators of near-shore resource baseline and were collected by the same methods as mussels or by wading and picking near the shore. Invertebrate collections were attempted at multiple sites within each lake, with more sites used in the larger lakes. Mussels and snails were frozen whole and a piece of soft tissue was removed for analysis in the laboratory. All tissue samples were dried at 65-70°C for 48-72 hrs. These samples were individual ground into a fine powder and were sent to the University of New Hampshire stable isotope lab for analysis.

4.3.3 Stable isotopes based food web measures

Naturally occurring stable isotopes are now widely used to capture a time integrated measure of food webs structure based on material flows. Stable isotope ratios provide integrated diet characteristics over time from a single tissue sample, as opposed to the instantaneous picture obtained from a gut contents analysis. Therefore each isotope sample provides an extended (~ 4 months reported for adult fish muscle tissue) temporal average of an organism’s diet (Weidel et al. 2011).

We used established methodology and two source mixing models to determine the pathways of carbon flow from pelagic and littoral zones for walleye based on nitrogen. We calculated predator coupling to pelagic habitat using ratios $\delta^{13}C$. Carbon is consistent across trophic transfers from predator to prey with no (or very little) fractionation (<1‰) from prey to predators. For this reason, carbon isotope ratios are often used to trace the dietary sources of consumers back to primary resources. Use of this technique requires that basal resources have distinct isotope ratios. Estimates are based on the mean $\delta^{13}C$ values for each lakes for walleye, mussel and snails using the following the equation: $\%$ littoral carbon = $\left(\delta^{13}C_{\text{walleye}} - \delta^{13}C_{\text{mussel}}\right) / \left(\delta^{13}C_{\text{snail}} - \delta^{13}C_{\text{mussel}}\right)$ (Vander Zanden et al. 1999). Fish tissue samples were corrected for lipids
according to a published equation \( \delta^{13}C_{\text{corrected}} = \delta^{13}C_{\text{corrected}} - 3.32 + 0.99 \text{C:N ratio} \) (Post et al. 2007).

### 4.3.4 Statistical analysis

We tested the statistical significance of relationships between predator pelagic habitat coupling and several potential determinants using simple linear regression models. We also determined the appropriateness of multiple regression models using AIC for model selection analysis (Burnham and Anderson 2002). Models with a lower AIC value are more likely the model that best represents the data compared to models with higher AIC values. We used \( \Delta \text{AIC} \) and Akaike Weights to further determine whether any model was better than a set of competing models. \( \Delta \text{AIC} \) is the difference between the best model and other models in the set of models being examined. We used this approach to distinguish among competing hypotheses and to determine the when combined. We transformed data according to statistical requirements (Crawley 2013). We used both histograms of statistical test residuals and Shapiro-Wilks test to determine whether residuals were normally distributed. Proportions were logit transformed when residuals did not meet the assumption of normality. Catch per unit effort estimates for prey species were right skewed (dominated by many low and a few high values) and were log\(_{10}\) transformed. All statistics were performed using the R language and environment for statistical computing (R Development Core Team 2005).

### 4.4 Results

#### 4.4.1 General lake characteristics

Data from 33 boreal lakes were analysed. With the exception of one lake from southern Ontario (Bobs Lake; was not an outlier) all other lakes were located in northwestern Ontario (Table 4.1).
Importantly, water transparency as measured by secchi depth varied from 1.1m to 6.9m, 1.5m - 3m is expected to be preferred by walleye (Lester *et al.* 2004). Mean air temperature data were within the optimal growth temperature range (11-25°C) for walleye (Lester *et al.* 2004)) and pH levels were near neutral across lakes (Table 4.1). Prey catches were dominated by cisco (*Coregonus artedi*) in the offshore and yellow perch (*Perca flavescens*) in the near-shore habitat. Our estimate of the proportion of pelagic prey species catch per net to total prey species catch per net was strongly related to the proportion of cisco catch per net to cisco and yellow perch catch per net ($R^2 = 0.74$, df = 32, $p = 1.45(10^{-10})$).

### 4.4.2 Isotopic description of trophic groups

The mean isotope ratio ($\delta^{13}$C) and ($\delta^{15}$N) values for each lake ecosystem exhibited an expected triangular pattern. Predators mean $\delta^{15}$N value across all lakes was enriched by approximately two trophic levels ($\Delta^{15}$N $\sim 3.4 \pm 0.5$‰) relative to the baseline organisms (walleye – mussel = 6.88 ‰; walleye – snail = 7.49 ‰). Mussel $\delta^{15}$N (mean = 2.97 ‰) and snail $\delta^{15}$N (mean = 2.36 ‰) values differed by < 1 ‰ and suggested a generally similar trophic position for these two baseline indicators on average. As expected, mean lake $\delta^{13}$C of offshore pelagic baseline (mussel = -30.2) were more negative than near-shore benthic (snail = -20.8) baseline isotopic ratios (Figure 4.3; ANOVA, $F_{1,70} = 189.21$, $p < 0.001$). Predator ($\delta^{13}$C) mean values for all lakes were intermediate to baselines and appeared to be a mixture of the two baseline end members (Figure 4.3).

Within each trophic group there were clear differences in individual lake mean values (Figure 4.3). The variability in $\delta^{15}$N was similar among the three focal trophic groups (walleye standard deviation = 1.11; mussels standard deviation = 1.08; snails standard deviation =
\( \delta^{13}C \) variability among lakes was similar for the predator (walleye; standard deviation = 1.43), and pelagic baseline (mussels; standard deviation = 1.48), whereas, littoral baseline lake means were approximately twice as variable as the predator and pelagic baselines respectively (snails; standard deviation = 3.78). This difference seems to be due primarily to higher snail \( \delta^{13}C \) values in two lakes (i.e., less negative values, Fig 4.3).

**Table 4.1 Summary of study lake characteristics.** Summary data include the number of observations (n), the minimum observed value (min), the maximum observed value (max), the mean value (mean) and the standard deviation (SD).

<table>
<thead>
<tr>
<th>Variable</th>
<th>n</th>
<th>min</th>
<th>max</th>
<th>mean</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
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<td></td>
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<td></td>
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<tr>
<td>Longitude</td>
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<td>-94.1742</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Water Transparency</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Secchi Depth (m)</td>
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<td>6.9</td>
<td>3.68</td>
<td>1.43</td>
</tr>
<tr>
<td>True Colour (TCU)</td>
<td>31</td>
<td>4.8</td>
<td>129</td>
<td>39.73</td>
<td>32.83</td>
</tr>
<tr>
<td>Production</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total Phosphorus (mg.m(^{-3}))</td>
<td>31</td>
<td>4.2</td>
<td>16.2</td>
<td>8.68</td>
<td>3.7</td>
</tr>
<tr>
<td>% Pelagic Production Index(^\dagger)</td>
<td>31</td>
<td>0.14 (0.02)</td>
<td>0.99 (0.95)</td>
<td>0.69 (0.26)</td>
<td>0.21(0.19)</td>
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<td>Morphometry</td>
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<td>Mean Depth (m)</td>
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<td>7.54</td>
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</tr>
</tbody>
</table>

\(^\dagger\) Relative benthic production was determined using a published model. Several assumptions are made in the model and choosing parameters. Values reported reflect a low value of \( \text{BP}_{\text{max}} = 30 \) and high value \( \text{BP}_{\text{max}} = 300 \) in parentheses. See Materials and Methods and Supplementary Information for details. \(^\ddagger\) Summer air temperature is the average monthly mean for June, July and August for each lake during the sampling year. *Temperature data not available for the most southern lake.
Figure 4.3 Stable isotope ratios of carbon ($\delta^{13}$C) and nitrogen ($\delta^{15}$N) distinguish baseline indicators and focal predator in study lakes. Means for each lakes pelagic (Unionid mussels (triangle)) and benthic (Gastropods (square)) baseline indicators and predatory walleye (circles) are shown. Larger black symbols and error bars correspond to the mean and standard deviation of the each trophic group for all study systems. Data shown do not account for fractionation in the predator. Each symbol reflects an individual lake.
4.4.3 Pelagic carbon contribution increases with water transparency

We found a general trend where walleye increasingly relied on near-shore carbon sources with decreasing water transparency (Fig. 4.4A). This trend agrees with a behavioural hypothesis of realized prey availability, because walleye relied more on near-shore production as water became less transparent, which should give them a predatory advantage. This relationship appears to be driven primarily by low values of water transparency corresponding to <2.5 and > 4.5 m secchi depth. The proportion of pelagic carbon in predator diet varies by 45% between 2.5-4m secchi depth.

If the proportion of resources from different habitat carbon pathways predicts the contribution of those pathways to predator diets then consumers should proportionally assimilate habitats. We found a marginally significant relationship between the proportion of prey catch per net >6m and the reliance of walleye on pelagic resources (Figure 4.4C). Neither the proportion of pelagic prey as determined by species grouping (Figure 4.4B), or the index of the proportion of pelagic production (Figure 4.4 D) were significantly, or marginally, related to the proportion of pelagic carbon in the diets of walleye across the lakes in our study. Our qualitative results were similar for both values of maximum values of benthic primary production BP<sub>max</sub> used to estimate the proportion of primary production in each lake. Of note, in both cases (BP<sub>max</sub> = 30 and BP<sub>max</sub> = 300), we found evidence of an increasing trend in the proportion of pelagic coupling with increasing proportion of pelagic production but neither was statistically significant (BP<sub>max300</sub>, linear regression, R<sup>2</sup> = 0.07, df = 32, p = 0.14).

Because there was a marginal positive relationship between water transparency and the proportion of pelagic prey (>6m) in each lake (R<sup>2</sup> = 0.08, df = 32, p = 0.08). Therefore we considered whether water transparency explained predator reliance on offshore carbon beyond
that of the proportion of prey. As might be expected with a weak correlation, we found a significant increase in the residual proportion of pelagic carbon in a predator’s diet after linearly removing the effect of the proportion of pelagic prey (Figure 4.5). The most parsimonious model explaining the proportion of pelagic carbon in predator diets based on AIC scores was water transparency alone. Although this simple model was similar to a multivariate model that included a combination of water transparency and the proportion of pelagic prey in that the differences between AIC scores (\(\Delta AIC\)) was < 1 (Table 4.2).

### 4.4.4 Predator coupling strength and other lake characteristics

Water colour, is a main component of secchi depth estimates. Predator reliance on the near-shore production increased as water colour increased which matches our expectation and the secchi depth results presented above (\(R^2 = 0.18, df = 31, p = 0.01\)). Total phosphorus can also be correlated with water transparency, for instance, when total phosphorus promotes phytoplankton production which adds to water column turbidity. We found that total phosphorus was not a significant predictor of the relative reliance of walleye on pelagic prey (\(R^2 = 0.002, df = 31, p = 0.81\)). Lakes with lower mean depth may have relatively less pelagic habitat (shape depending), which could also influences the relative proportions of pelagic and littoral prey. The reliance of walleye on pelagic resources increased with lake depth (\(R^2 = 0.15, df = 31, p = 0.03\)). A combined model including lake mean depth and secchi depth had a lower AIC value and was weakly distinguishable from a simple model with secchi depth alone (\(\Delta AIC = 1.97\)).
Figure 4.4 Relationship between predator reliance on pelagic derived carbon and water transparency and three measures of the proportion of pelagic resources in each lake. (A) Walleye reliance on offshore carbon sources increases in clearer lakes ($R^2 = 0.23$, df = 32, $p = 0.004$). (B) The proportion pelagic carbon in walleye diet shows a marginally significant increase with the proportion of pelagic prey catch per net in > 6m of water ($R^2 = 0.11$, df = 32, $p = 0.07$). (C) There was no relationship between the proportion of pelagic derived carbon in walleye diet and the proportion of pelagic prey fish (species combined) caught per net ($R^2 = 0.01$, df = 32, $p = 0.57$). (D) The proportion of pelagic carbon in predator diet is not predicted by the proportion of pelagic primary production ($R^2 = 0.03$, df = 32, $p = 0.3$). Each data point represents an estimate from individual lakes in Ontario, Canada.
Table 4.2 Summary of model selection for predictors of predator reliance on pelagic resources

<table>
<thead>
<tr>
<th>Dependent(y)</th>
<th>Independent(x)</th>
<th>Model</th>
<th>AIC</th>
<th>△AIC</th>
<th>Likelihood</th>
<th>ω_i</th>
<th>R²</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pelagic carbon in predator diet</td>
<td>Water Transparency (WT)</td>
<td>$y = mx+b$</td>
<td>-43.1</td>
<td>0</td>
<td>1.00</td>
<td>0.35</td>
<td>0.23</td>
<td>0.004</td>
</tr>
<tr>
<td>Pelagic prey by species (Pps)</td>
<td>$y = mx+b$</td>
<td></td>
<td>-36.04</td>
<td>7.06</td>
<td>0.03</td>
<td>0.01</td>
<td>0.04</td>
<td>0.21</td>
</tr>
<tr>
<td>Pelagic prey &gt;6m (Pp6)</td>
<td>$y = mx+b$</td>
<td></td>
<td>-37.87</td>
<td>5.23</td>
<td>0.07</td>
<td>0.03</td>
<td>0.1</td>
<td>0.071</td>
</tr>
<tr>
<td>Pelagic primary production (Ppp)</td>
<td>$y = m \logit(x)+b$</td>
<td></td>
<td>-35.53</td>
<td>7.57</td>
<td>0.02</td>
<td>0.01</td>
<td>0.03</td>
<td>0.3</td>
</tr>
<tr>
<td>WT+ Pps</td>
<td>$y = m_1x_1+m_2x_2+b$</td>
<td></td>
<td>-41.33</td>
<td>1.77</td>
<td>0.41</td>
<td>0.15</td>
<td>0.23</td>
<td>0.02</td>
</tr>
<tr>
<td>WT+ Pp6</td>
<td>$y = m_1x_1+m_2x_2+b$</td>
<td></td>
<td>-42.76</td>
<td>0.34</td>
<td>0.84</td>
<td>0.30</td>
<td>0.24</td>
<td>0.009</td>
</tr>
<tr>
<td>WT+ Ppp</td>
<td>$y = m_1x_1+m_2\logit(x_2)+b$</td>
<td></td>
<td>-41.52</td>
<td>1.58</td>
<td>0.45</td>
<td>0.16</td>
<td>0.24</td>
<td>0.01</td>
</tr>
</tbody>
</table>
Figure 4.5 Relationship between the residual variation in predator reliance on pelagic derived carbon and water transparency. The proportion of pelagic source carbon in walleye diets (proportional δ^{13}C relative to mussel and snail baselines) was first linearly regressed against the proportion of prey fish capture deeper than 6m. Here, the residual variation in the proportion of pelagic source carbon is still positively related to secchi depth (m) a measure of water transparency ($R^2 = 0.18$, df = 32, p = 0.02). Residual values and secchi depth measures represent estimates for individual lakes in Ontario, Canada.
4.5 Discussion

Lake food webs can be conceptualized as energy pathways that extend from basal resources in offshore pelagic and near-shore benthic habitats up a trophic ladder to higher level consumers in either habitat or consumers that integrate trophic ladders across habitats (Hecky & Hesslein 1995; Vander Zanden & Vadeboncoeur 2002). Few studies have considered how this food web structure may be affected by differences in environmental conditions that vary among food webs. Yet, the degree that predators couple food chains in different habitats might be influenced by environmental conditions that restrict their access to prey or their performance in different habitats. Therefore, the trophic interactions that link habitats may be mediated by a predator’s realized prey availability. Alternatively, based on the idea that food webs are mediated by production at lower trophic levels, the proportion of prey abundance in each habitat might be the primary mechanism governing predator choice, as expected by optimal foraging theory. Data from 31 lakes show that predator (walleye) reliance on offshore habitat was relatively stronger compared to reliance on near-shore habitat with increased water transparency. A trophic pathway shift toward near-shore basal resources under lower water transparency is consistent with expectations that walleye can increase their consumption in near-shore environments under dim light conditions and therefore their response to variation of within lake may act to modify food web structure.

Our study also supports a partial bottom up explanation for the variation in food web structure that we document across northern boreal lakes. It seems hard to question that the proportion of prey in each habitat is important to explain a portion of the variation in predator habitat coupling. This is not surprising, as water transparency is not totally limiting the access of walleye to either habitat under the conditions we observed. For example, in clear lakes,
favourable near-shore feeding may still occur at dawn and dusk (Lester et al. 2004). As a result, it might be expected that extreme differences in prey abundance among habitats may offset the performance losses experienced when daytime light conditions exceed preferences for walleye. As a contrast, conditions where temperature in near-shore surface waters exceeds the maximum tolerance levels of predatory fish may be more limiting as use of this habitat may be fatal. Research on a cold-water predator lake trout (Salvelinus namaycush) studied in boreal lakes provides an example of such a thermal accessibility restriction (see Chapter 3). Regardless, this research suggests that water transparency explains a significant portion of the variation in food web structure that links littoral and pelagic habitats, beyond that explained by the relative resource proportions in each habitat. In fact, across these lakes, the proportion of pelagic resources in each lake was poorer at predicting habitat use than water transparency. In addition, prey availability, as defined by the time walleye experienced preferred light conditions in near-shore habitats, explained a significant amount of variation in relative coupling by the predator after accounting for the effects of relative prey abundance (Figure 4.4). We do not conclude that prey relative abundance is unimportant in driving habitat use because models that include the proportion of pelagic prey performed similar to those without. Nonetheless, taken together we interpret these findings as strong evidence that variation in water transparency can impact predator coupling of distinct resource pools in addition to theories based on prey relative abundance.

Theoretical work on predation has long proposed that prey detection regulates consumption rates. Variation in prey detection is also often believed to influence the susceptibility of prey species to a predator (Case & Roughgarden 2000) - in a sense changing a predator’s realized prey availability. These ideas have been supported by numerous studies that
seek to understand the way that predator performance changes with the environment (e.g., water transparency and fish consumption rates) (Einfalt et al. 2012). But these ideas have not been frequently incorporated into food web research. Here, we have empirically extended the idea that a predator’s traits may mediate relative spatial coupling of habitats in a complex multi-habitat food web. Our findings agree with general predictions from a predator performance-mediated theory that recognizes that environmental factors can influence the behaviour of organisms. As evidence to this assertion, walleye show greater relative contribution of carbon from littoral resource habitat when the environment is conducive to increased consumption (i.e., reduced transparency).

Our study makes an important empirical contribution to an emerging literature that seeks to identify the contributions of near-shore and offshore habitat compartments to whole lake ecosystems. Recent research suggests that benthic contributions can be over-represented in fish relative to the benthic share of whole lake production (Vander Zanden et al. 2011). Interestingly our argument of realized prey availability provides one possible explanation for this phenomenon. That is, if consumers experience higher relative consumption in one habitat compartment relative to another, than the percent contribution from the preferred habitat compartment may exceed relative production in that habitat. How consumers may respond to changes in environmental conditions will then reflect the set of phenotypic traits that influence their performance. Research from several Swedish lakes argues that lower water transparency and resulting decreases in light penetration reduced benthic production and whole lake primary production across lakes (Karlsson et al. 2009). This production loss corresponded with a lower proportion of benthic derived carbon in Arctic char (Salvelinus alpinus) and Eurasian perch (Perca fluviatilis) and a lower estimated biomass accumulation of these species (Karlsson et al.
Foraging performance is expected to be expressed as a hump shaped curve (proposed in Fig 4.1). Walleye are expected to perform better under dim light conditions (Lester et al. 2004), like those measured at the lower seechi depth values in our study, but below these levels (i.e. <1m seechi depth) walleye performance is expected to rapidly decline again.

Ongoing water transparency changes are widely observed in freshwater ecosystems and have been attributed to environmental factors including climate, acidification (and more recently recovery), species invasions, eutrophication, and land use (Keller 2007; Karlsson et al. 2009; Carpenter et al. 2011). Climate change is expected to alter air temperature and precipitation patterns both of which alter the input of terrestrial organic matter (Keller 2007), a major contributor to water colour in boreal lake ecosystems. Many lakes in the Northern Hemisphere are becoming less transparent and recent research points to ongoing lake recovery from acidification, following global reductions in atmospheric sulphur deposition in recent decades (Monteith et al. 2007). Our study questions whether a darkening of lakes will generally reduce the reliance of fish on near-shore benthic resources. Predators that prefer low transparency may benefit from dim light to the possible detriment of clear water preferring species and susceptible prey. If true, then these effects may more strongly regulate benthic productivity in general.

We had strong a priori information on walleye that we used to make predictions about their responses to water transparency (Lester et al. 2004; Ryder 1977), but we had comparatively less information on other consumers in the food web. Based on previous studies, we adopted the notion that reduced water transparency can make walleye more successful predators, and so can increase their activity time in near-shore habitats (Ryder 1977). Future work may also explore the possibility that lower trophic levels might also be responding to changes in water transparency. A lower trophic level response would complement notions that environmental
conditions generally mediate consumer habitat coupling in food webs. Clarifying the complex influence of water transparency on the different trophic levels that exist within the spatially coupled food web we document remains a challenge for future research.

Given the importance of spatially coupled structure for food web dynamics (Post et al. 2000; McCann et al. 2005) and the potential impending environmental change, predicting the future structure and function of ecosystems requires that studies investigate the interactions that couple habitats in food webs. That consumers obtain energy and material from multiple habitat compartments in food webs is common among ecosystems and has been documented in freshwater (Vander Zanden & Vadeboncor 2002; Tunney et al. 2012), marine (McCauley et al. 2012) and terrestrial habitats (Pringle and Fox-Dobbs 2008). That food web structure shifts across habitats according to environmental conditions has implications for understanding spatial structure and other structural components of food webs. Studies have debated whether habitat compartments are common in food webs. By documenting that environmental conditions can alter a predators relative reliance on different basal energy sources, our research supports the idea that considering environmental conditions, such as light conditions, may improve our understanding of variation in natural food web structures.

The movement of energy and nutrients among habitats is expected to impact food web dynamics and nutrient cycling in ecosystems. All else equal, if the increased littoral coupling we document is due to an increase in foraging activity at low light conditions, then the observed proportional trophic shift could increase the biomass of the predator across the water transparency gradient. According to general theory, a potential for increased in consumption across habitats and an accompanied top heavy biomass distribution in the food web may lead to greater trophic control and elevated predator densities that may have cascading effects on lower
trophic levels in low transparency lakes. A previous study has argued that lower water transparency is related to higher walleye abundance (Lester et al. 2004), although the underlying food web structure has not been identified. Notably, researchers have suggested that links between pelagic and littoral habitats may potentially drive top down suppression and trophic cascades in the pelagic zones of lakes (Schindler & Scheuerell 2002). More empirical work is required to link the observed shift in food web structure to the abundance and dynamic responses of walleye in these freshwater lakes. However, knowledge about the trophic structure that we have documented should be useful in making these connections. For example, if combined with biomass estimates, these relative interaction measures can be more closely linked to theoretical notions about the regulation of biomass and persistence in food webs (McCann 2012).

To sum up, our findings demonstrate that food web structure can sometimes predictably shift in response to environmental conditions. Our result serves as a reminder that environmental conditions may not always operate independently to alter food web interactions, but rather consumers may respond to improved access to prey along with relative prey abundance, and thus alter the trophic pathways that bring food webs to life. Importantly, the biodiversity at higher trophic levels that links habitats may be particularly vulnerable to contemporary environmental changes because of the spatial requirements of these organisms (Rooney et al. 2006). That said, any ability to rapidly move across the landscape may buffer a consumer to effects in any one habitat (McCann 2005; Rooney et al. 2006). For this reason, it is important to understand how shifts in trophic structure impact the biomass structure and persistence of organisms in the food web. Given the responsive nature of the trophic structure that couples habitats, if we can link this restructuring to population or food web biomass, then monitoring habitat coupling may serve as a useful indicator of whether changes in the environment may accelerate biodiversity loss.
4.6 References


22.


### 4.7 Supplementary Information

**Supplementary Table S 4.1 Definitions of production model parameters with units. Input values are given when not available directly from lake surveys (with modification from Vadeboncoeur et al. 2008).**

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Definition</th>
<th>Assumed input value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$BP_{max}$</td>
<td>maximum benthic primary production (mg C m$^{-2}$ h$^{-1}$)</td>
<td>30, 300</td>
</tr>
<tr>
<td>$I_0$</td>
<td>surface light at solar noon (μmol m$^{-2}$ s$^{-1}$)</td>
<td>1500</td>
</tr>
<tr>
<td>$I_k$</td>
<td>light intensity at onset of saturation (μmol m$^{-2}$ s$^{-1}$)</td>
<td>180 phytoplankton; 300 periphyton</td>
</tr>
<tr>
<td>$A_z$</td>
<td>lake surface area, $A$, at depth $z$ (m$^2$)</td>
<td>Variable</td>
</tr>
<tr>
<td>$V_z$</td>
<td>lake volume, $V$, at depth $z$ (m$^3$)</td>
<td>Variable</td>
</tr>
<tr>
<td>$Z_{1%}$</td>
<td>depth at 1% incident light (m)</td>
<td>Variable</td>
</tr>
<tr>
<td>TP</td>
<td>Total Phosphorus (mg m$^{-3}$)</td>
<td>Variable</td>
</tr>
</tbody>
</table>

Parameters and definitions are modified from Vadeboncoeur et al. 2008.
### Supplementary Table S 4.2 Equations for the production model (Vadeboncoeur et al. 2008 with modification see Methods).

<table>
<thead>
<tr>
<th>Equation Number</th>
<th>Model Output</th>
<th>Equation</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>phytoplankton chlorophyll a, Chl</td>
<td>Chl = 0.41 ( TP^{0.87} )</td>
</tr>
<tr>
<td>2</td>
<td>phytoplankton productivity (mg C m(^{-3}) h(^{-1})), PP</td>
<td>( PP_{\text{max}} = 2.2 \text{Chl} )</td>
</tr>
<tr>
<td>3</td>
<td>light attenuation coefficient (m(^{-1})), ( K_d ) †</td>
<td>( K_d = 0.24 + 0.902 \times SD^{-1} )</td>
</tr>
<tr>
<td>4</td>
<td>light at depth ( z ), ( I_z )</td>
<td>( I_z = I_0 e^{-K_d z} )</td>
</tr>
<tr>
<td>5</td>
<td>phytoplankton primary production at depth ( z ) (mg C), ( PP_z )</td>
<td>( PP_z = PP_{\text{max}} \tanh(I_z/I_0)(V_z-V_z)\Delta z )</td>
</tr>
<tr>
<td>6</td>
<td>whole-lake phytoplankton phytoplankton production (mg/m(^2)), TPP</td>
<td>( TPP = \sum_{z=0}^{z=1%} PP_z \frac{A_z}{A_0} )</td>
</tr>
<tr>
<td>7</td>
<td>% TPP</td>
<td>( %TPP = TPP/(TPP+TBP) )</td>
</tr>
<tr>
<td>8</td>
<td>periphyton primary production at depth ( z ) (mg C), ( BP_z )</td>
<td>( BP_z = BP_{\text{max}} \tanh(I_z/I_0)(A_z-A_z\Delta z) )</td>
</tr>
<tr>
<td>9</td>
<td>whole lake periphyton production (mg C/m(^2)), TBP</td>
<td>( TBP = \sum_{z=0}^{z=1%} BP_z \frac{A_z}{A_0} )</td>
</tr>
<tr>
<td>10</td>
<td>% TBP</td>
<td>( %TBP = TBP/(TPP+TBP) )</td>
</tr>
</tbody>
</table>

† Equation 1 used to estimate \( K_d \) is taken from Koenings and Edmonston (1991) and not in original model. Area at depth \( A_z \) and Volume above depth \( V_z \) were calculated using the actual measurements for each lake taken from bathymetric contour maps. \( z_{1\%} \) refers to the depth at light attenuated to 1% incident light. TP is total phosphorus (mg m\(^{-3}\)).
Chapter 5 Epilogue

Nature’s complexity unfolds over a variety of biotic and abiotic dimensions. A desire to predict changes in our natural world calls for a better understanding of which dimensions alter the structure and functions of the world’s ecosystems. Food web research has argued strongly that the interactions among species influence biomass accumulation at different trophic levels (Carpenter et al. 1985; Schmitz 2010) and stability of natural systems (McCann 2012). With some notable exceptions (Schoener 1989; Vander Zanden et al. 1999; Post et al. 2000; Tylianakis et al. 2007; Takimoto et al. 2012), few empirical studies determine how consumer resource interactions and the structure of food webs might change across environmental gradients.

Unfolding the relationships between fundamental food web structure and environmental conditions has been the goal of my thesis. I have used a spatial food web comprised of two food chains coupled by an apex predator to develop intuition about how differential environmental changes between habitats may impact the trophic interactions that join them together (i.e., habitat coupling). Using gut contents (Chapter 1) and stable isotope tracers to estimate diet information, I empirically assessed patterns in the properties of this fundamental food web structure across environmental gradients in northern freshwater lakes. Data repeatedly show a directional restructuring of the food web as conditions change. This food web modification is consistent with predictions based on mobile consumer accessibility and performance differences across habitats, where habitats are more strongly linked when a consumer experiences similar conditions among habitats, but are more weakly linked where one habitat is expected to restrict a consumer’s foraging capabilities.
My research suggests that the occurrence of key food web structures may depend on environmental conditions. A longstanding notion in ecology is the existence of compartments in food webs structure (Moore et al. 1989; Krause et al. 2003), but the widespread existence of food web compartments has been debated by some researchers (see Pimm 2002). My research suggests that when conditions limit the accessibility of a habitat to consumers, interactions are more compartmentalized, whereas when a habitat is accessible to a consumer, relative habitat coupling can be strong hence, habitat compartmentalization is decreased. Interestingly what appears to be happening in lakes is that the food web may behave more like two separate food chains when lakes are larger or conditions differ among habitats such that consumers may be restricted from foraging between them. But when lakes are smaller or when conditions within habitats are not restrictive to consumers the web may function like a single food chain. This is a notable property of these food webs because apparently different outcomes, strong or weak links among habitats, can be understood via the same underlying concept. That is, consumer responses to habitat conditions mediate food web linkages across habitats. Thus, as I mention in chapter two, understanding how conditions alter food web structure may resolve some debates over the ubiquity food web properties by considering under what conditions might a particular structure exist or be important.

In my second chapter I develop new theory and synthesized existing data on spatial structure in lakes to make some predictions about how food web structure may change across environmental conditions. Both theory and empirical data suggest that food web structure may expand (increased habitat coupling) and contract (reduced predator trophic position by omnivory), and may become more top heavy with increased predator biomass as predator accessibility increases across systems.
In chapter three, I argued that climate research often overlooks two well known properties of ecosystems: 1) climate can warm local habitats differently and 2) mobile consumers can respond to this temperature differential within ecosystems. Based on these properties I expected that climate may have profound effects on the spatial coupling of habitats in lake food webs. I found that the thermal sensitivity of a predator can be a key predictor of the coupling of energy pathways, as large scale climate gradients alter thermal differentials within ecosystems. It seems that limiting abiotic factors may have a strong restrictive effect on food web structure near species thresholds, such as when temperatures approach or exceed thermal maxima.

My fourth chapter tested notions about the role of environmental conditions in the relative contribution of offshore and near-shore resources to a predator. This chapter is framed as a general test of two hypotheses. First, that the relative contribution of resources to a predator is determined by the relative proportion of resources in those habitats ‘proportional assimilation’. The second argues that the relative proportion of prey in those habitats that is available to predators is mediated by environmental conditions and so changes in conditions can mediate spatial coupling of these habitats by a predator. To be clear prey abundance must play some role in a predator’s consumption. However, it is not too hard to imagine that the prey available to a predator is restricted by other habitat features in addition to prey density. As expected based on behavioural research, data show that the proportional contribution of offshore resources to a light sensitive predator (walleye) are higher under conditions of high water transparency. Our study supports the idea that realized prey availability mediated by water transparency and to a lesser degree resource abundance influence habitat coupling by walleye across lakes. This result is of interest for conservation of freshwater lakes, as water transparency appears to be changing in many lakes in the Northern Hemisphere.
It has been a major goal of ecology to understand the role of biological structure (trophic interactions, biomass pyramids (Elton 2001)), in the functioning of ecosystems. I have presented a collection of work that aimed to consider environmental conditions in the structuring of major trophic pathways in food webs. My research repeatedly shows that the interplay between consumer traits and ‘the mosaic nature of the environment’ is a determinant of the structure of spatially coupled food webs. If predator integrated consumptive pathways are governed by a few key environmental features (e.g., temperature, nutrients, light), then it should be possible to incorporate these kinds of changes into food web models to make better predictions about the consequences of environmental change on food web sustainability.

With further research and the advance of techniques to rapidly assemble food webs, monitoring trophic structure holds promise to become a regular part of the diagnostic toolbox used by those charged with conserving natural systems. Already the cooperation of several government agencies in my research suggests that there is interest in bringing more food web knowledge to the management of fisheries in freshwater lakes. Beyond the use of food webs as an applied tool for conserving the world’s biodiversity, it is also generally interesting to study the structure of food webs as incredible examples of complex adaptive systems. For now, I am amazed that despite the overwhelming complexity of food webs it is possible to find some predictable patterns in their macroscopic structure.

References


