EXAMINING THE RELATIONSHIP BETWEEN SPECIES RICHNESS OF FISH COMMUNITIES AND THEIR BIOMASS IN FRESHWATER ECOSYSTEMS

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Abstract

Models used to predict fish biomass in freshwater ecosystems are integral to fisheries management, however, are to date limited to predictions from either chemical (total phosphorus, nitrogen) or physical (morphometric) variables, and do not consider the implications of species and their influence on trophic energy transfer. Here, using empirical data, we first demonstrate that a significant relationship exists between species richness and fish biomass, which behaves similar to models proposed in terrestrial ecosystems. Second, we demonstrate the utility of modern food web analyses to quantify functional richness in freshwater fisheries, and relate functional richness to the species richness-biomass relationship. Finally, we apply this relationship to current models predicting biomass from chemical and physical drivers, and using data compiled from over 500 sites across North America, acquired from both the literature and this project, successfully demonstrate its ability to describe much of the regional variance in existing fish biomass models.

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Introduction

Freshwater fisheries are often ascribed value according to their ability to produce fish biomass. While the capacity of such ecosystems to produce biomass is generally thought to be governed by abiotic factors, it can be argued that the efficiency at which ecosystems perform this function can be largely attributed to their biotic components. It is the collection of species, interactions and trophic structure which ultimately determine the ability of freshwater ecosystems to convert available resources into fish biomass (trophic efficiency) (Rowan and Rasmussen 1992), and it is therefore crucial that we understand the underlying mechanism within these food webs in order to adequately manage these crucial resources.

Not surprisingly, the complex nature of mutlitrophic food webs common to freshwater fisheries has left researchers with multiple investigative avenues to follow, spawning a collection of distinct yet inter-playing theories. Original research such as that on trophic cascades (Carpenter et al. 1985, McQueen et al. 1986, Carpenter and Kitchell 1993) and niche theory (Hutchinson 1957, Roughgarden 1972, 1979) have provided foundation for more recent theories such as individual specialization (Bolnick et al. 2003, Araujo et al. 2007), distinct trophic energy pathways (Vander Zanden et al. 2006, Solomon et al. 2011, Fetzer et al. 2015), the role of functional groups (Karjalainen et al. 1999, de Carvalho and Tejerina-Garro 2015, Leduc et al. 2015), and multiple novel interpretations of our definition of the niche (Leibold 1995, Newsome et al. 2007, Winemiller et al. 2015). Despite these efforts, the effect of species richness on trophic efficiency, and many of these theories, remains poorly understood in freshwater fisheries (Reiss et al. 2009).

While it may seem intuitive that the number of species populating an ecosystem would inherently have considerable effect on trophic efficiency and biomass production, a lack of empirical evidence (at least in the realm of aquatic ecosystems and fish communities) has left researches undecided as to whether this relationship is positive, negative, or even exists at all (Reiss et al. 2009). In other types of ecosystems, however, this subject has been approached, and with greater success. Studies in both terrestrial (Tilman et al. 1997a, Hector 1998, Loreau 1998a) and aquatic (Naeem and Li 1997, Gessner et al. 2004) ecosystems, although mostly limited to single trophic level systems (O'Connor et al. 2013), provide support for Tilman's (1997) theory of a positive, asymptotic relationship that exists between species richness and biomass. Such a relationship has yet to be demonstrated, empirically, in multi-trophic freshwater fishery ecosystems, though the utility of such a model for fisheries management would likely be extensive.

Moreover, the question of the species richness-biomass relationship should be of particular interest to fisheries managers and researchers across Canada, which features not only great regional diversity in fish assemblages (McPhail and Lindsey 1970, Scott and Crossman 1973) and species richness (Chu et al. 2003), but is also faced with significant challenges such as climate change (Chu et al. 2005) and anthropogenic stressors (Chu et al. 2015), including (but not limited to) habitat alteration via hydro-power development (Macnaughton et al. 2015), which earnestly threaten that great diversity.

The reality that researchers have yet to reach a consensus with regards to the existence of a relationship between fish species richness and biomass, what the shape of the relationship might, or how it may influence/be influenced by other chemical/physical drivers of fisheries biomass, is an indication of the need for more research on the subject.

Globally, fish species richness is declining at rates which draw comparison to Earth's five major extinction events (Barnosky et al. 2011). In North America, it is predicted that between 53 and 86 species will be lost by 2050, based on current imperilled species data (Burkhead 2012), and in Canada there are currently as many as 23 imperilled taxa per ecoregion (Jelks et al. 2008), representing a significant proportion of total species richness in some species-depauperate regions (Chu et al. 2003). By demonstrating that fish species richness does impose a positive effect on biomass, and additionally providing insight into the shape of the relationship, managers and researchers alike can apply this information to help predict what effect species loss might have on fish biomass, and more importantly develop strategies to mitigate these effects.

In response to the aforementioned, this thesis comprises three chapters to address the following research questions: Chapter 1 addresses whether there is there a relationship between fish species richness and biomass in freshwater ecosystems; Chapter 2 evaluates whether modern tools describing food web structure and species interactions from isotopic ratios can be used to describe community functional richness and its influence on a species richness-biomass relationship, and Chapter 3 investigates whether species and functional richness can be used in concert with other biomass models, i.e. those derived from chemical/physical drivers, to provide regionally robust predictions of fish biomass to inform Canadian fisheries management objectives.

Chapter 1

DESCRIBING THE SPECIES RICHNESS-BIOMASS RELATIONSHIP, AND THE INFLUENCE OF FUNCTIONAL RICHNESS, IN FRESHWATER FISHERIES

Introduction

A key question in ecosystems is, “what drives productivity?”. From the perspective of ecosystem management, this is important because we often ascribe value to ecosystems based on some measure of productivity, or their capacity for production (i.e. biomass), and therefore understanding what, and how, factors contribute to this value is crucial. In freshwater fisheries research, productivity can be quite variable from ecosystem to ecosystem, and it has therefore been a long-standing objective of fisheries researchers to assign this variance environmental factors, including nutrient concentrations (Dillon and Rigler 1974, Stockner and Shortreed 1978, Peterson et al. 1993), habitat availability (Williams et al. 2005, Cramer and Ackerman 2009, Cote et al. 2011), climate (Currie et al. 2004, Evans et al. 2005, Lewis 2011) and ecosystem size (Post et al. 2000, Storch et al. 2005). This research has led to the creation of a variety of predictive models, all valuable in that they allow researchers and managers to make confident predictions of community estimates, such as productivity and biomass, which would otherwise be quite costly (Portt et al. 2006), from much more cost effective measurements such as water samples or habitat surveys (Harris et al. 2003). However, one factor which has received considerably less attention among fisheries researchers, though, likely explains a considerable amount of among-system productivity and biomass, lies in the community itself: species richness.

The idea that species imposes a significant effect on the biomass, or production, of the system they comprise is not novel. The foundation of the species richness-biomass relationship originates from Tilman’s observations of grassland communities (Tilman et al. 1997a), which outlined a positive, asymptotic relationship which is widely accepted amongst ecologists. In the years following the publication of their model, it was determined that the relationship could be attributed to two factors: the selection effect, which states that greater species richness increases community biomass by virtue of a greater likelihood that the community contains a highly productive species (Loreau 1998b, 2000), and the complementarity effect which describes the cumulative effects of functional relationships, or complementarity, among species that contribute to biomass production (Hector 1998). This work is significant, as it was the first to demonstrate that species richness does explain a significant amount of the variation in among-system variation in biomass and could therefore be used as a predictive tool. Furthermore, while demonstrating the selection effect proved quite challenging, Tilman did successfully demonstrate that functional richness could be used to explain variance in among-system biomass, in addition to that of species richness, supporting the complementarity effect hypothesis (Tilman 1997, Tilman et al. 1997a). For a more detailed account of the development of this model and its theoretical considerations, consult Appendix A.

Given its underlying theory, that species and their interactions are responsible for the formation of the complex networks which transfer energy upwards through food webs, ultimately leading to biomass (Tilman et al. 1997b, Loreau 1998a), it seems reasonable that the SpR-Biomass model could be applied to aquatic ecosystems and fish communities. However, a lack of empirical evidence in fisheries literature has left researches undecided as to whether this relationship is positive, negative, or even exists at all (Petchey et al. 2002, Reiss et al. 2009). Certainly, both measures of species richness and biomass have been studied extensively in the fisheries ecology literature, with respect to their role as either a response, or an effect, to productivity (Srivastava and Lawton 1998, Storch et al. 2005), community stability (Naeem and Li 1997, Aoki and Mizushima

2001), as well as a suite of ecosystem functions (Gessner et al. 2004, Giller et al. 2004, Humbert and Dorigo 2005, Gamfeldt and Hillebrand 2008, Hargrave 2009, Eloranta et al. 2015), in their own right. Yet rarely has their influence on one-another been reported, even when both are considered in the same study (for example Cote et al. (2011), and far rarer are studies whose primary objective is to examine the species richness-biomass relationship (Petchey et al. 2002, Reiss et al. 2009).

This lack of empirical evidence in fisheries ecology could be due to several factors. First, and perhaps most likely, is that due to the tremendous variability in among-system productivity/biomass, in combination with the wide assortment of possible confounding factors typical of freshwater ecosystems, the effect of species richness is either masked by the data or overlooked/not considered by the researcher. In one of the few examples where the SpR-Biomass has been tested in an aquatic ecosystem, Naeem et. al. were able to provide evidence in support of the theory, in part due to their experimental apparatus of aquatic mesocausms for which they could control any confounding variables (Naeem and Li 1997). Although a significant step for aquatic research, the study focused only on single-trophic bacterial communities and is therefore somewhat lacking applicability regarding larger scale management.

A second explanation, not independent of the first, is that it is reasonable to expect that because fish species are more variable in their feeding strategies than grass species (Nikolski 1974, Pavlov and Kasumyan 2002), there may inherently be more variation and statistical noise surrounding a fisheries SpR-Biomass relationship, making it harder to elucidate. In Tilman’s examination of grassland communities (1997a), he considered a maximum of five functional roles for grasses. By comparison, a recent synthesis of life histories among Canadian fish species revealed at least 14 distinct functional roles (Rasmussen et al., unpublished). Considering these two factors, both outlining the incredible variability that exists among aquatic ecosystems, attempts to provide empirical evidence for the SpR-Biomass relationship in such systems will require considerable efforts to minimize the effects of confounding factors, as well as control for substantial differences in functional feeding ecology of fishes.

A third factor, though more of a critique on sample design than the first two, is that most prior studies investigating the effects of species richness on ecosystem function have selected productivity as a response variable, rather than biomass (Waide et al. 1999, Mittelbach et al. 2001). Although seemingly an inconsequential design choice, as the two measures have been linked as strong correlates in recent studies (Randall and Minns 2000), these two measures of "ecosystem function" may in fact respond quite differently to the effects of species richness. To demonstrate this, consider the "selection effect" aspect of Tilman's theory; A substantial portion of Canada's freshwater fish diversity is attributed to the Cyprinid family (Scott and Crossman 1973), generally characterized by small bodied fishes which, because of their rapid growth rates and quick turnover (Ruiz-Navarro et al. 2016), may contribute substantially to productivity, but less to biomass. In contrast, much rarer than cyprinids are large bodied species, such as Catostomids which, once mature, contribute significantly to biomass but much less to overall ecosystem productivity due to a decline in growth rate (Grabowski et al. 2012). Because of this ratio, the selection effect, with regards to its influence on the species richness effect, suggests that communities with greater species richness will have a greater likelihood of containing a larger bodied species. If this is true, then increases in species richness, resulting from the addition of a more rare, large bodied species, would have a positive effect on biomass, though perhaps negligible effects on productivity.

While perhaps an arduous task, the determination of the SpR-Biomass relationship should be of particular interest to fisheries managers and researchers across Canada, which features tremendous regional diversity in fish assemblages (McPhail and Lindsey 1970, Scott and Crossman 1973) and species richness (Chu et al. 2015) resulting from historical access to post-glacial refugia. Central regions such as Ontario and Quebec are species rich, as these regions were populated by the Mississippian refugium (Legendre and Legendre 1984). Marginal regions such as the Western Cordillera, which lacks many pelagic specialists (Nelson and Paetz 1992, McPhail 2007), and insular Newfoundland, which lacks many true detritivores (Scott and Crossman 1973), are relatively species depauperate. Certainly, these differences in species pools, and associated lack of functional roles therein, may pose a considerable effect on regional fisheries biomass (FB). This theory, however, remains to be investigated. Furthermore, for Canadian fisheries faced with significant challenges such as climate change (Tonn 1990, Chu et al. 2005, Breeggemann et al. 2015, Carlson et al. 2015) and anthropogenic stressors (Chu et al. 2015), including (but not limited to) habitat alteration via hydro-power development (Macnaughton et al. 2015, Vezza et al. 2015), the need for such research has never been more critical.

The objectives of this study are to test, using empirical data from multi-trophic freshwater ecosystems, whether the observed relationship among species richness and biomass in terrestrial ecology also applies to fisheries, to assess whether functional groups from life history accounts can be used to help further describe this relationship, and to discuss the implications of such a relationship to current and future management of Canadian freshwater fisheries.

Methods

Site Selection

The main objective when selecting sampling locations was to optimize the range of fish species richness, per lake, while restricting differences among physical and chemical lake properties. Access to post-glacial refugia has led to great variance in regional fish species biodiversity in Canada (Legendre and Legendre, 1984; Mandrak and Crossman, 1992; Chu, 2003). Exploiting this to achieve an adequate range of fish species richness, per lake/stream in the data set, three main regions were selected from which sampling would occur: North-Central British Columbia (species poor), Southwestern Alberta – Southern British Columbia (poor to moderate species richness), and Northwestern Ontario (species rich).

Within each of these regions, lakes and streams were selected based on a suite of metrics thought to have measurable influence on FB; size (Carey and Wahl 2011, Eloranta et al. 2015), littoral/pelagic ratio (Vander Zanden et al. 2006), primary production (total phosphorus and Secchi depth) (Rasmussen and Kalff 1987), latitude (Christie and Regier 1988), angler access/pressure (Hunt et al. 2011), and fish community composition for lakes, and size (Vannote et al. 1980), latitude (Petersen and Kitchell 2001, Melcher et al. 2013), substrate (Pilgrim et al. 2013), dissolved oxygen (Sternecker et al. 2013) quality of pool habitat (Cramer and Ackerman 2009) and community composition for streams. In total, 13 lakes, ranging from 2-species to 10-species communities, and 13 streams, ranging from 2-species to 6-species communities, were selected for this study (Figure 1, Table 1).

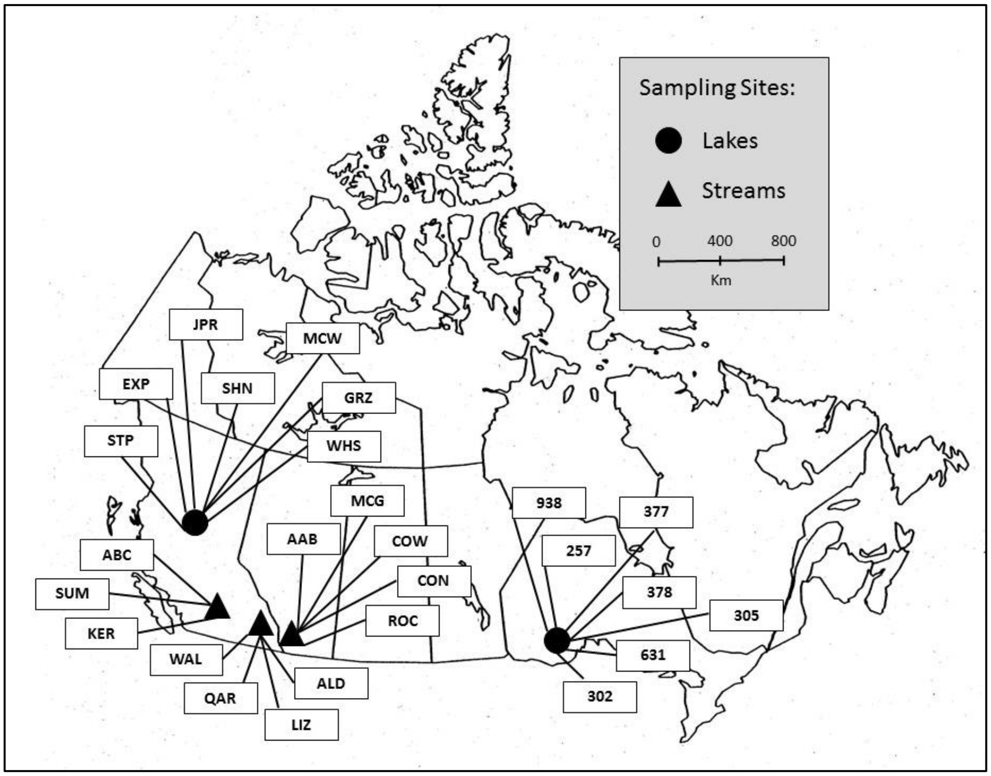

Figure 1.1. Map of site locations.

Fish Community

Lake fish community sampling occurred over a 3-year period (2013-2015), each year beginning in the late spring and finishing in early summer (June/July). A decision to limit lake surface area to 50ha and depth to 15m was made with intentions of ensuring a high level of confidence in FB measures, as estimates of FB generally become less confident with increasing lake size and depth (Morgan and Snucins 2005). Sample design was adapted from the Nordic sampling method and the protocol outlined by Morgan and Snucins (2005), with modifications to reduce fish mortality. The Nordic method targets all species and size classes present in a system using a 12-panel gill net array (each panel a different mesh size, ranging from 5mm to 55mm knot-to-knot).

Table 1.1. Name, abreviation, size and UTM of sample sites.

Waterbody	Abr.	Size*	UTM
Lakes			
McEwan Lake	MCW	47	10.530581.6030792
Grizzly Lake	GRZ	55	10.533668.6031013
Shanley Lake	SHN	32	10.445422.5998682
Whitestone Lake	WHS	30	10.565174.5811940
Stump Lake	STP	27	10.461089.5865477
Expected Lake	EXP	29	10.431437.6001771
Jumping Rabbit Lake	JPR	29	10.471567.6037683
Lake 257	257	25	15.440945.5504358
Lake 631	631	36	15.440100.5506021
Lake 378	378	24	15.444082.5506738
Lake 938	938	20	15.430666.5502680
Lake 377	377	27	15.444176.5507818
Lake 305	305	54	15.449899.5504379
Streams			
Allison Creek(AB)	AAB	4.0	11.674277.5500724
McGillivry Creek	MCG	3.9	11.679009.5501466
Rock Creek	ROC	3.8	11.700142.5495969
Connelly Creek	CON	4.2	11.702209.5499463
Cow Creek	COW	4.2	11.702324.5508926
Allison Creek (BC)	ABC	4.5	10.680088.5497380
Summers Creek	SUM	4.5	10.692467.5504304
Keremeos Creek	KER	4.3	11.294397.5463856
Aldridge Creek	ALD	4.5	11.649009.5578000
Lizard Creek	LIZ	5.6	11.638664.5481359
Quarrie Creek	QAR	6.1	11.644433.5569646
West Alexander Creek	WAL	5.7	11.663796.5504228

*Size represents surface area (ha) for lakes, wetted width (m) for streams

Sampling is depth stratified, with equal effort being afforded to littoral and pelagic habitat (predetermined from bathymetric maps and Secchi depth). Net gangs were 30 m long, consisting of 12 - 2.5m panels which were 1.5m deep. Nets were set prior to sunrise, usually between 03:30 and 05:00, and allowed to soak for approximately 3hrs prior to retrieval (± 20 minutes for travel time), modified from the original protocol which outlines 24hrs soak time. This reduction of soak time was applied in effort to reduce mortality. A total of 12-16 gillnets were deployed on each lake, depending on surface area and max depth, deployed evenly among the pelagic and littoral sampling strata. Fish were removed from gillnets and transferred to on-boat recovery tanks prior to being identified, weighed and measured (fork length). All captured fish were released, however, 10 individuals of each species (or feeding guild for species known to undergo ontogenetic niche shifts) were sacrificed for stable isotope and stomach content analysis.

Stream fish communities were assessed during low flow periods (late August and September) in 2014 and 2015. Stream sizes were limited to widths which could be accurately sampled via multi-pass depletion electrofishing, with a Smith Root LR-24 backpack electrofisher and a 2-person crew. Three reaches, per stream, of 300m length were selected for sampling, having met the following criteria; 1-reaches featured 300m of continuous habitat which could be sufficiently sampled via backpack electrofishing (i.e. no pools deeper than the equipment would permit, or overgrown bank vegetation hindering upstream movement of technicians),2-reaches had sufficient riffle-pool sequences to be representative of the stream, 3-reaches were a minimum of 1km away from other selected reaches (to ensure reach independence), 4-reaches featured reasonable access for transportation of equipment. Once a reach was selected, block nets were set at opposite ends of the reach and the first electrofishing pass would begin at approximately 10 am. Fish captured during this pass were identified and measured (weight and fork length) and placed in live wells upstream of the enclosed reach. A second pass would begin at approximately noon, and captures were once more identified, measured, and the placed in live wells with those from the first pass. To standardize efforts among sequential passes, total electrofishing seconds were constantly monitored and kept consistent for all reaches (of all streams). If the total catch of the second pass was greater than 25% of the that of the first pass, a third pass was performed (Peterson et al. 2004). Not once did this occur, therefore all reach population estimates were derived from only 2 passes. Once sampling was complete, fish were released back into the reach. As with lakes, 10 individuals of each species (or feeding guild for species known to undergo ontogenetic niche shifts) were sacrificed for stable isotope and stomach content analysis.

Species Richness and Functional Group Determination

For lakes, species richness was determined from presence in gillnets, and corroborated by a variety of other sampling gears such as minnow traps, beach seins and electrofishing, deployed randomly where habitat permitted. For streams, species richness was determined from electrofishing captures, and corroborated by minnow traps and angler surveys deployed at various other locations along streams (outside of the electrofished reaches).

Functional richness estimates were inferred from life history data and confirmed from stable isotopes and stomach content prior to further analysis. All lakes and streams were sorted into 3 functional categories: high, low and base. During the site selection process, community compositions from historical studies were considered with the objective of selecting groups of lakes and streams, within the data set, with similar species richness but variable functional richness. The intention was to enable the analysis to parse the effects of species richness and functional richness. The criteria for designation of functional group was as follows: lakes and streams were first placed into groups of similar species richness (3 groups for lakes [2-3spp, 5-6spp, 9-10spp], 3 groups for streams [2-3spp, 4-5spp, 6spp]). Second, a key functional role within each group was identified (initially identified from life history, later confirmed with isotope bi-plots and stomach content), which was either present or absent in the lakes/streams within that group, and individual systems within the group were then assigned to the high/low functional group based on the occurrence of the identified functional role. For instance, lakes in the data set with 5-6 species all comprised a combination of cyprinid foragers and catostomid benthivores, however, 3 lakes also contained a large bodied, pelagic zooplanktivore, while the other 3 were limited to the former 2 functional groups. As such, the 3 lakes containing the zooplanktivore were assigned to the "high" functional group, while the remaining three lakes within the group were relegated to the "low" functional group. To reiterate a previous point, the differences being discussed here were anticipated from the sample design, however, could not be confirmed until present day sampling had occurred and dietary functional assumptions were supported with stable isotope and stomach content analysis. Finally, lakes and streams consisting of 3 or fewer species were simply designated as "base" functional richness because they simply did not consist of enough species to distinguish them by functionality.

Physical/Water Quality

For lakes, thermal and dissolved oxygen profiles, Secchi depth, and water samples for total phosphorus analysis and were obtained from each lake. D.O. and temperature profiles were acquired with a YSI. Water samples for phosphorus analysis were taken at depth using a Van Dorn water sampler, stored at 3˚C, and sent to the University of Alberta to be analyzed. Morphometric indices, such as surface area, max depth and mean depth were retrieved from bathymetric maps. For streams, habitat variables such as thalweg depth, wetted width, number of pools and average pool depth, as well as temperature and dissolved oxygen were measured (via YSI).

Statistical Analysis

For lakes, average FB per net was calculated for each habitat strata per lake (pelagic and littoral), which were then standardized to whole lake FB estimates by correcting for the strata area ratio (i.e. multiplying FB per littoral/pelagic net by the proportion of littoral/pelagic strata area, and summing the totals). For streams, FB estimates were calculated per reach by $B_{Total} = (B_{P1})^2 / (B_{P1} – B_{P2})$ (where B_{P1} = FB from electrofishing pass #1, and B_{P2} = FB from pass #2), and an average FB per stream was calculated from their respective reaches.

Although efforts were made to standardize habitat indices across systems, it was nevertheless imperative to determine if these metrics, known from the literature to have influence on ecosystem productivity, had any influence on FB estimates. As such, a series of linear regressions were performed between each of the habitat variables outlined above and their respective (lake or stream) FB estimates. The distribution of values describing each habitat metric, as well as those for lake and stream FB, were tested for normality (Shapiro-Wilk Test) and homoscedasticity (Levene's Test). Any data which deviated from these assumptions were $\log_{10}$ transformed prior to analysis. Any variables imposing a significant effect on FB estimates would be added to the final species richness-biomass model.

Linear regression was performed to determine the effect of species richness on FB. The distributions of species richness and FB, for both lakes and streams, were tested for normality and homoscedasticity and did not require transformation to meet these assumptions. To determine if functional richness designations could help explain variance in the data, residuals produced from the linear regression, attributed to either "high" or "low" functional group members, among both lakes and streams, were compared with a t-test. To further examine the potential influence of functional richness on the species richness-FB relationship, linear regressions were performed between species richness and FB for each functional group (high and low), and data set (lakes and stream) separately, and slopes were compared with a z-test. All statistical analysis were performed in R (R-Development-Core-Team 2008).

Results

In total, 13 lakes and 13 streams were included in the analyses. Among lakes, 31 species were encountered. Species richness per lake ranged from 2 to 10 (median = 5), with cyprinids receiving the greatest representation. Among streams, the species pool comprised only 11 species. Species richness ranged from 1-6 (median = 4), and was generally dominated by salmonids.

Seven lentic habitat variables were measured among the 13 lakes in the data set. A summary of mean values, as well as range, for each habitat metric is available in Table 2. Five habitat variables, size, max depth, mean depth, % littoral and TP were $\log_{10}$ transformed to meet assumptions of normality. A suite of single regressions among habitat variables and lake FB determined that FB estimates were not significantly influenced by any of the habitat variables considered (Table 2).

Table 1.2. Mean and range of habitat values and results from single regression analyses of lake and stream habitat varables against FB.

				Regression				
Habitat variable	Min	Mean	Max	Intercept	Slope	R^2	F-value (d.f.)	P
Lakes								
Size (ha)*	20	32.6	55	6538	-3053	0.0263	1.34(1,12)	0.2683
Max Depth (m)*	7	13.4	30**	1751	210.1	0.0824	0.009(1,12)	0.9245
Mean Depth (m)*	2.9	5.4	14.3**	561	2029	0.0096	0.875(1,12)	0.3678
D.O. (mg/l)	7.8	8.6	9.8	5686	-430.4	0.0425	0.469(1,12)	0.5063
% Littoral*	32	54	68	2148	-3.08	0.0824	0.009(1,12)	0.923
Secchi (m)	3.5	4.1	5.5	3194	-300.4	0.0371	0.535(1,12)	0.4785
Total P (µg/l)*	4.4	17.5	32.2	2225	124	0.0818	0.016(1,12)	0.9013
Streams								
Wetted Width (m)*	3.8	4.6	6.1	4.978	-3.392	0.0721	0.019(1,11)	0.669
Depth (cm)	25.5	29.4	35.1	7.594	-16.43	0.0226	0.734(1,11)	0.4098
Pools per Reach	9.3	12.5	15	1.163	0.127	0.0752	0.160(1,11)	0.6962
Mean Pool Depth (cm)	39.6	44.1	51	-2.596	13.18	0.073	0.456(1,7)	0.5212
Temperature	9.9	11.3	12.9	-1.941	0.417	0.0439	0.495(1,11)	0.4964
D.O. (mg/l)	9.2	10.1	11.1	8.311	-0.548	0.0523	0.404(1,11)	0.538

*Variable was $\log_{10}$ transformed prior to regression
**Lake 305 was 15m deeper than the next deepest lake

Similarly, 6 lotic habitat variables were considered among the 13 streams in the data set, and a summary of their values is found in Table 2. One variable, wetted width, was $\log_{10}$ transformed to meet assumptions of normality. A suite of single regressions among habitat variables and FB determined that stream FB estimates were not significantly influenced by any of the habitat variables considered. (Table 2).

Lake FB estimates varied by an order of magnitude, ranging from 34g/net to 3828g/net (mean ± s.e. = 1981g/net ± 353g/net). Distribution analysis was performed on the data set, which satisfied the requirements of normality and heteroscedasticity and was therefore not transformed prior to regression analysis. Species richness explained a significant amount of the variation observed in FB among lakes, as determined from linear regression ($R^2 = 0.525$, $p = 0.0056$, Figure 2). Residuals from the regression performed on the entire lake data set, along with a priori designation of functional group, is available in Table 3. The mean of the residuals (± s.e.) for lakes in the “high” functional group was 881 ± 189, which was significantly greater than that of the residuals for lakes in the “low” group, which was -679 ± 204 (t-test, $p = 0.0010$). Regression analysis performed on subgroups of the data, distinguished by functional richness, revealed that species richness explained a greater amount of the variance in both groups (high functional richness: $R^2 = 0.736$, $p = 0.0031$; low functional richness: $R^2 = 0.760$, $p = 0.0048$), and that both groups produced significantly different slopes (z-test, $p = 0.0391$, Figure 3).

Stream FB estimates also varied by an order of magnitude, ranging from 0.47g/m^2 to 5.59g/m^2 (mean ± s.e. = 2.76g/m^2 ± 0.48g/m^2). Distribution analysis was performed on the data set, which satisfied the requirements of normality and heteroscedasticity and was therefore not transformed prior to regression analysis. Species richness explained a slightly greater amount of the variation observed in FB among streams than in lakes, determined from linear regression ($R^2 = 0.652$, $p = 0.0008$, Figure 4). The mean of the residuals (± s.e.) for streams in the “high” functional group was 1.14 ± 0.25, which was significantly greater than that of the residuals for streams in the “low” group, which was -1.21 ± 0.29 (t-test, $p = 0.0007$).

Regression analysis performed on subgroups of the data (as with lakes) revealed that species richness again explained a greater amount of the variance in both groups (high functional richness: $R^2 = 0.904$, $p = 0.0003$; low functional richness: $R^2 = 0.862$, $p =$

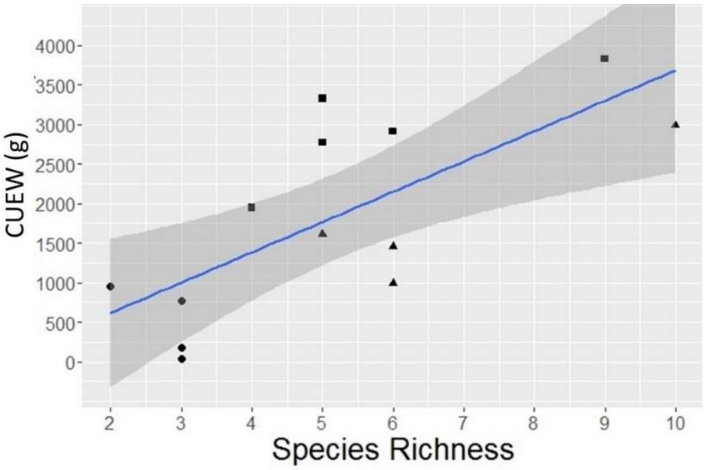

Figure 1.2. Linear regression of species richness and FB (catch per unit weight) among all lakes in the data set. Circles, triangles and squares represent base(n/a), low and high functional richness designations, respectively, determined a priori.

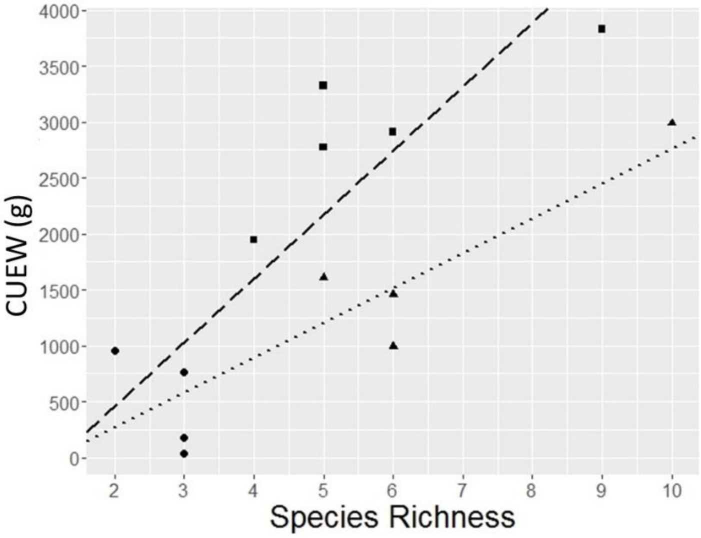

Figure 1.3. Overlaying individual linear regressions of species richness and FB (catch per unit weight) for lakes designated as high functional richness (dashed) and low functional richness (dotted).

0.0009), and just as with the lake data set, that both groups produced significantly different slopes (z-test, p = 0.0001, Figure 5). Residuals from the regression performed on the entire lake data set, along with a priori designation of functional group, is available in Table 3.

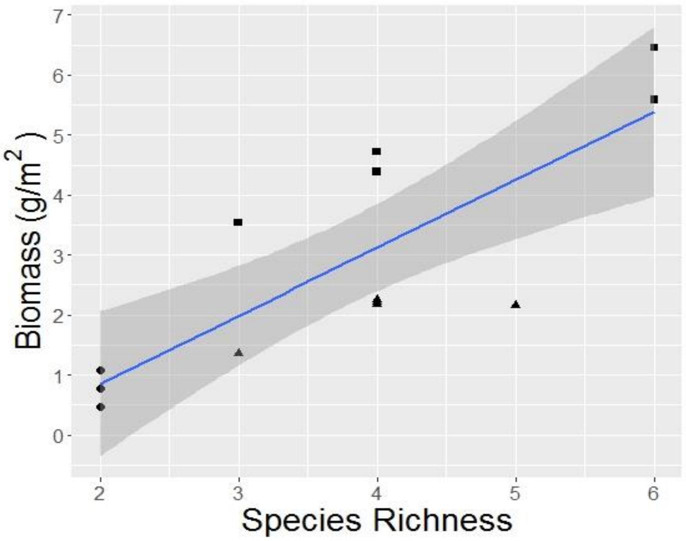

Figure 1.4. Linear regression for species richness and FB among all streams in the data set. Circles, triangles and squares represent base(n/a), low and high functional richness designations, respectively, determined a priori.

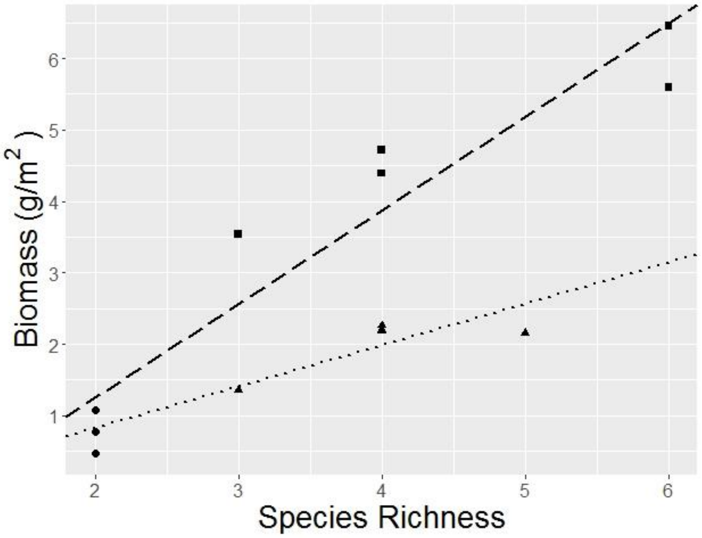

Figure 1.5. Overlaying individual linear regressions of species richness and FB for streams designated as high functional richness (dashed) and low functional richness (dotted).

Table 1.3. Residuals from species richness against FB linear regressions, for complete data sets of lakes and streams.

Waterbody	Species Richness	Functional Richness	Regression Residual
Lakes			
McEwan Lake	2	n/a	338.07
Grizzly Lake	3	n/a	-821.21
Shanley Lake	3	n/a	-967.51
Whitestone Lake	3	n/a	-239.51
Lake 257	6	low	-1162.6
Lake 631	5	low	-159.79
Lake 377	6	low	-697.08
Lake 938	10	low	-697.24
Stump Lake	4	high	559.5
Expected Lake	5	high	1005.2
Jumping Rabbit Lake	5	high	1557.2
Lake 378	6	high	758.91
Lake 305	9	high	526.04
Streams			
West Alexander Creek	2	n/a	0.2266
McGillivry Creek Above	2	n/a	-0.3822
Rock Creek	2	n/a	-0.0845
Lizard Creek	3	low	-0.6265
McGillivry Creek Below	4	low	-0.8899
Aldridge Creek	4	low	-0.9395
Quarrie Creek	4	low	-0.9095
Allison Creek (AB)	5	low	-2.0942
Keremeos Creek	3	high	1.5549
Allison Creek (BC)	4	high	1.6001
Summers Creek	4	high	1.2735
Connelly Creek	7	high	0.2039
Cow Creek	6	high	1.067

Discussion

To the knowledge of the authors, this research is the first to empirically investigate, and successfully demonstrate, the positive relationship between species richness and FB, as proposed by Tilman et al. (1997), in multi-trophic freshwater fisheries. Until now, support for this relationship has remained limited to terrestrial (Tilman et al. 1997a, Hector 1998, Loreau 1998a) and/or single trophic aquatic communities (Naeem and Li 1997, Gessner et al. 2004, O'Connor et al. 2013), or been purely theoretical (Fox 2003, Fox 2004b, Fox 2005a). As such this work represents a significant step forward for fisheries researchers and managers alike.

The previous lack of evidential support for this theory, among the fish ecology community, could be attributed to several factors which are described above and which have been addressed with this work. First, was the decision to consider FB as an "ecosystem function" response variable to species richness, rather than productivity, which has been examined in previous research producing variable results (Reiss et al. 2009). The measure of FB appears to have captured an important attribute of species richness, which is that as it increases so too does the probability that a community contains one or more large bodies species, which in Canada are rarer than their small bodied counterparts (Scott and Crossman 1973). This attribute of species richness is referred to as the selection effect (Loreau 1998b, Wardle 1999), and is relevant to this work in that the contribution of large bodied, long lived and mature species is more distinctly characterized with the measure of FB, compared to productivity (Banse and Mosher 1980, Peters 1983), enabling the analysis thereof to better describe the effect of species richness. Secondly, and of significant consequence for the statistical determination of the SpR-Biomass relationship, was the fastidious criteria of habitat indices required of ecosystems to be included in the study. By controlling for factors which would otherwise impart significant influence on the response variable, and then demonstrating the statistical independence of those factors from the response variable as a result, we were able to sufficiently isolate the influence of species richness from said factors and determine its true, and significant influence on FB.

Once it was determined that a positive relationship existed between species richness and FB, the next step was to investigate its underlying mechanisms; the selection and complementarity effects. While describing the former was simply outside of the scope of this project, the complementarity effect describes, essentially, the difference between adding a functionally unique species to a community vs adding a functionally redundant species. This difference is demonstrated in figures 3 (lakes) and 5 (streams). Among the lakes considered in this analysis, the addition of functionally redundant species resulted in below average FB gains, but above average FB gains were observed with the addition of a functionally complementary pelagic zooplanktivore. This biomass-underperformance of lakes is a not a reflection of nutrient paucity, nor lack of suitable habitat, but rather an indication of the ineffectiveness of the fish consumer population to exploit the entire range of the available carbon food base in the ecosystem. While other functional roles are similarly important to the overall transfer of energy upwards through aquatic food webs, such as detritivores, microbenthivores, deposit feeders, algavores or herbivores (McPhail and Lindsey 1970, Scott and Crossman 1973, Gelwick and Matthews 1992, Nelson and Paetz 1992, Vander Zanden and Vadeboncoeur 2002a, Solomon et al. 2011), the presence/absence of a pelagic specialist is particularly of relevance with respect to regional differences post-glacial colonization phenomena. Western cordillera fisheries are, in general, dominated by species which do not complete the entirety of their life cycles in lentic environments, but rather spend a significant portion of their adult lives in rivers and streams, such as salmonids (Clarke and Scruton 1999, Cote 2007, Cote et al.

2011). As such, these systems lack many of the pelagic specialists which are abundant in central Canadian regions such as Ontario (Mandrak and Crossman 1992), rendering them incapable of achieving their maximum FB potential.

Considering the lotic ecosystems examined here, the same biomass-underperformance is apparent in streams lacking a true detritivore. Although the absence of functional detritivores, for instance catostomids, in select streams considered in this study cannot be attributed to post-glacial colonization events, impedances in access to lentic habitat (fish passage barriers) did appear to be a factor contributing to the absence of detritivores in the salmonid dominated streams here, and corresponding below average FB production in these systems. In contrast, all streams which did have access to lake habitat, either upstream or downstream, also featured at least one functional detritivore and likewise produced above average FB. In a regional context, barriers to fish passage along stream networks, such as impassable waterfalls or hydropower operations (Hatry et al. 2013), are much more prevalent among typically high gradient cordilleran systems; therefore, it may be reasonable to expect that functional under-saturation of streams may also be more frequent among these ecosystems.

Also lending credence to the hypothesis that higher FB can be attributed to greater functional diversity is the analysis of residuals produced by the linear regression models for both lakes and streams (Figure 2 & 4, Table 3). While the sample size is perhaps low (lakes, n=9, streams n=10), it is nevertheless impressive that the basic assessments of functional richness from life history strategies, a priori to analysis, made of the systems examined in this study were 100% accurate in determining the sign of residuals produced by their respective species richness-biomass models. For both lakes and streams, systems allocated to the “high functional richness” group all produced positive residuals, and all systems allocated to the “low functional richness” group produced negative residuals, thus providing managers with a potentially valuable tool when making pairwise, comparative evaluations of FB potential from simple species distributions. However, what these basic functional assessments from species life histories do not show, but is likely a valid assumption, is how/if functional richness may also be able to determine the size of the residuals. To test such a hypothesis, empirically, would require a continuous measurement of functional richness, rather than the categorical measure given here (presence/absence of one specific functional role). However, theoretical support for this assumption can be found in current literature. First, we must accept the theory of Loreau’s (1998) selection effect, which suggests that as species richness increases, the likelihood that an additional species will offer a complementary functional role to the current community will decrease. It follows, that if size of the residuals produced by the species richness-biomass model are determined by functional richness, that the potential range of residuals will be largest (and more variable) at low species richness values due to increased sensitivity to functional increases/decreases from addition/subtraction of species. This idea is conceptualized in figure 6.

Positive residual ranges are distributed as described above, with potential variance decreasing with increasing species richness. The range of negative residuals at low species richness values would be limited by the fact that FB cannot be negative, but otherwise follow a similar progression to the ranges of positive residuals. If we then trace a curved line intersecting each of the most extreme potential positive residual values for

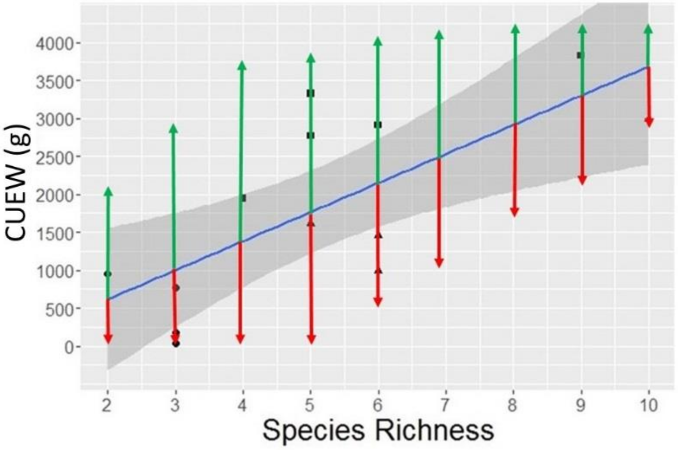

Figure 1.6. Linear regression of species richness and FB (catch per unit weight) among all lakes in the data set, overlain with proposed maximum and minimum, negative and positive functional richness residuals.

each level of species richness, that curve would describe the species richness-biomass response assuming maximum functional potential of fisheries, or rather, fishery functional saturation (FFS). Likewise, doing so for the negative residuals would produce a curve describing the lowest potential for functional richness, or fishery functional under-saturation (FFU). Examining these two functional curves further, the FFS curve can be best described as an asymptotic response, mirroring that of grassland biomass to functional richness described by Tilman et. al. (1997) in their controlled experiments of grassland plots which is widely accepted in the ecological community (Figure 7).

Support for the theory of a FFU curve is not as conspicuous in the literature, but evidence for it can be found in a recent study by Cote et. al. (2011) of biomass along salmonid dominated streams in insular Newfoundland, Canada. Similar to cordilleran systems, insular Newfoundland fish species richness is also limited by post-glacial recolonization phenomena, resulting in communities heavily dominated by salmonid species and lacking a variety of functional role-players, such as detritivores (Scott and Crossman 1973).

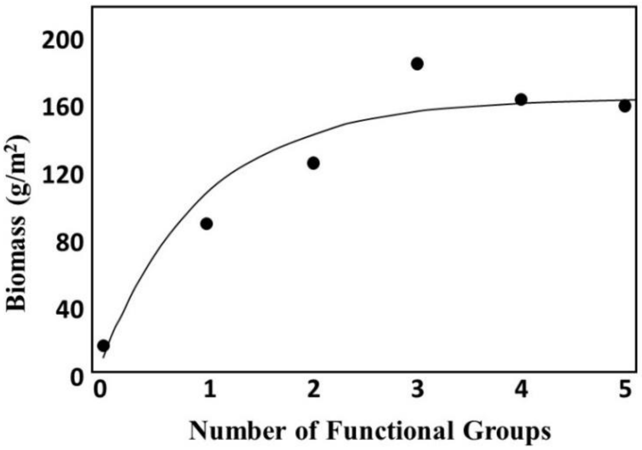

Figure 1.7. Asymptotic regression of functional richness against biomass, adapted from Tilman et. al., 1997.

Although species richness ranges from 1-6, most species are functionally redundant, resulting in functionally under-saturated systems. Although the authors do not explicitly examine the relationship between species richness and FB in their study, the species richness-abundance curve in figure 8 is produced from their published data.

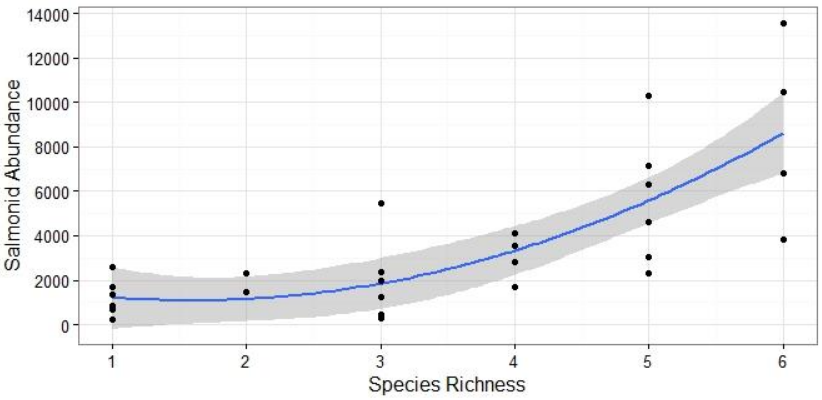

Figure 1.8. Polynomial regression of species richness and Salmonid Abundance from Cote et. al. 2011; $R^2 = 0.619$, $p < 0.0001$.

The upward swinging polynomial-2 regression response curve produced by this data, if we are correct in assuming that salmonid dominated streams of Newfoundland are functionally under-saturated, then supports our proposed FFU response curve.

Strengthening our understanding of the specific mechanisms, related to species and functional richness, that govern FB should be the next step in the progression of this research. Previous research, in both lentic and lotic realms, have provided substantial gains towards the understanding of trophic interactions (Carpenter et al. 1985, Browne and Rasmussen 2009, Jones and Post 2013, Zou et al. 2015), community structure (Vander Zanden et al. 1999, Vander Zanden et al. 2000) and energy transfer (Vander Zanden and Vadeboncoeur 2002b, Vander Zanden et al. 2006, Solomon et al. 2011), all of which are undoubtedly dependent on species. Moreover, the study of these subjects has also led to the development of several innovative methods to describe community structure (Layman et al. 2007, Layman et al. 2012), niche characteristics (Bearhop et al. 2004, Jackson et al. 2011) and trophic interactions(Swanson et al. 2015), however, such estimates of community metrics have yet to be linked to any empirically driven estimate of community FB, such as that presented here. Interestingly, it could be argued that these methods, while describing various community attributes, also provide unique estimates of community function. Furthermore, unlike the categorical estimates of functional richness used in this study, these tests produce continuous estimates of community function and therefore may be useful in quantifying functional richness in a way which accurately predicts the sizes of regression residuals here, as previously discussed. If so, not only would it lend support to our hypothesis, but would also increase the “real world” applicability of these models with respect to community ecology.

Quantifying the influence that species richness imposes on FB should be of tremendous interest to fisheries researchers and managers alike. However, in applying this knowledge to future studies and/or management decisions, it would be naïve not to consider its effects in conjunction with other phenomena known to affect fisheries productivity. For instance, phosphorus concentration in aquatic ecosystems has long been considered an effective predictor of fisheries productivity (Dillon and Rigler 1974, Stockner and Shortreed 1978, Peterson et al. 1993), and this widely accepted theory has provided the foundation for a variety of bottom up models linking TP to FB. However, it has become apparent from these empirical models that the TP-FB relationship varies substantially from region to region (Hanson and Peters 1984, Yurk and Ney 1989, Hoyer and Canfield 1991, Bachmann et al. 1996), for reasons that remain poorly understood and rather under-investigated. It is certainly possible, given the great regional implications discussed here, that the effect of species richness on FB may help to explain the regional variance observed in the TP-FB relationship, and further investigation into this among the Canadian fisheries research community is warranted.

The implications for freshwater fisheries management in Canada, as a result of this research, are various. In North America, it is predicted that between 53 and 86 fish species will be lost by 2050, based on current imperilled species data (Burkhead 2012), and in Canada there are currently as many as 23 imperilled taxa per ecoregion (Jelks et al. 2008), representing a significant proportion of total species richness in some species-depauperate regions (Chu et al. 2003). Ricciardi and Rasmussen (1999) further exemplify this perilous outlook for North American aquatic species with their work, projecting rates of species loss in North America of 4% per decade, the same rate at which species loss is occurring in the planet’s tropical rainforests. Our results demonstrate clearly that Canadian freshwater ecosystems will respond differently to species loss, depending on both the species richness of the community and the functional role of the species being lost, and will provide managers with a tool to estimate, from FB loss, which systems may be more sensitive to change and reallocate conservation resources accordingly.

In contrast to their application with respect to species loss, the results here may also provide opportunity to enhance fisheries via species addition, i.e. stocking. Take for example effects of habitat alteration (and subsequent community alteration) arising from hydro-power development. The new pelagic, littoral and benthic habitats associated with reservoir formation may initially displace native species, but will also create new opportunity (ecological niches) for adaptation and recolonization (Vezza et al. 2015). In Alberta, the course of action has generally been to stock these new pelagic habitats with sportfish, often walleye (*Sander vitreus*) (Park 2007), rather than a pelagic specialist zooplanktivore, such as lake whitefish (*Coregonus clupeaformis*). Stocking efforts costs approximately $7.3M/annum in the province (Park 2007) and are carried out despite the fact that very little is understood as to the potential ramifications to the system's total FB production. Moreover, a recent report suggests that the current stocking practices in Alberta are not generating adequate return to justify this spending, even in terms of angler satisfaction (Patterson 2011). Finally, a recent study by Campen (2016) of Southern Alberta reservoirs demonstrated that those with stocked walleye, which also featured an established lake whitefish population, were far more productive than reservoirs without lake whitefish. Considering Campen's results and ours, it seems likely that stocking practices focused on increasing functional richness, rather than simply stocking target species, would provide substantial gains in terms of both FB as well as angler satisfaction.

Chapter 2

USING COMMUNITY AND SPECIES INTERACTION METRICS TO QUANTIFY FUNCTIONAL RICHNESS IN FRESHWATER ECOSYSTEMS

Introduction

Freshwater ecosystems, from a mechanistic point of view, perform a variety of ecological functions (EF), likely so many that it would be unreasonable to assume we will ever even identify the full suite, much less be able to measure them. As such, when assessing functions to draw conclusions with respect to ecosystem health, researchers generally elect to focus on functions which lend themselves to logistically reasonable evaluation, for instance stability (May 1973, Aoki and Mizushima 2001, Worm and Duffy 2003), persistence (Naeem and Li 1997, Thébault and Fontaine 2010, Stouffer and Bascompte 2011), or productivity (Carpenter et al. 2001, Mittelbach et al. 2001). Such research has led to a diverse collection of theories, detailing the partial dependence of EFs on a variety of factors, including nutrient concentrations (Dillon and Rigler 1974, Jones and Bachmann 1975, Stockner and Shortreed 1978, Peterson et al. 1993), flow regime (Poff and Zimmerman 2010), light availability (Dickman et al. 2008) and landscape/morphometry (Huryn and Wallace 1987, Sandin 2009).

In addition to the aforementioned abiotic factors, it is also theorized that all EFs are to some extent dependant on the species which inhabit the ecosystem. For instance, it is widely accepted that species richness imposes at least some influence on the transfer and accumulation of fish biomass (FB) in food webs, which researchers have attributed to variation among feeding strategies of freshwater fish (Karjalainen et al. 1999, Pavlov and Kasumyan 2002, Fox 2005a, Humbert and Dorigo 2005, Vander Zanden et al. 2006, Syvaranta et al. 2011, de Carvalho and Tejerina-Garro 2015, Zou et al. 2015). Examples of this diversity of feeding strategies include littoral and pelagic specialists, benthivores and detritivores, and planktivores and piscivores, to name a few, each of which are responsible for energy transfer through unique bottom up mechanisms (Vander Zanden and Vadeboncoeur 2002a, Solomon et al. 2011, Vander Zanden et al. 2011, Zou et al. 2015) (for a more detailed list of Freshwater fish feeding strategies, see Appendix A.)

Apart from life history accounts, which among other shortcomings do not consider intra-species variation (which can have considerable effects on functional assumptions (Bolnick et al. 2003, Matthews and Mazumder 2004, Svanbäck et al. 2015)), researchers have been left with little else to quantify functional richness. This has been problematic, as current species richness/biomass models (as they relate to freshwater fisheries) remain afflicted with high amounts of variation, an artifact of which is an unresolved debate as to what the true influence of species richness is on biomass (Mittelbach et al. 2001, Petchey et al. 2002, Reiss et al. 2009). We posit that this influence could reasonably be explained by functional indices (chapter 1) if more detailed estimations of said indices were available.

Recently, however, following significant advances in our understanding of stable isotopes in aquatic food webs (Vander Zanden et al. 1997, Vander Zanden and Rasmussen 1999, Vander Zanden and Vadeboncoeur 2002a, Solomon et al. 2011) and further statistical applications (Layman et al. 2012) , the development of a suite of new models have provided researchers with statistical means to quantify a variety of community attributes (Layman et al. 2007), species dietary niches (Bearhop et al. 2004, Jackson et al. 2011) and species interactions (Swanson et al. 2015). Moreover, it has more recently been suggested that these analyses can provide informed estimates of functional richness (Rigolet et al. 2015). If it is valid to assume what is suggested by Rigolet et al, then it is reasonable to assume either one, or some combination, of these metrics could help to explain some portion of the remaining variance in the SpR-Bm model proposed by Lennox and Rasmussen, as the authors suggest.

In chapter one of this thesis, the influence of species, and to a certain extent functional, richness on biomass in freshwater fisheries is quantified in the form of a linear regression model, and we posit that more descriptive measures of functional richness should help to explain a portion of the remaining variance in the model.

Methods

Site Selection

Study locations were selected from two distinct regions in Canada: North-Central British Columbia (species poor) and Northwestern Ontario (species rich). Access to post-glacial refugia has led to great variance in regional fish species biodiversity in Canada (Legendre and Legendre 1984, Mandrak and Crossman 1992, Chu et al. 2003) facilitating the inclusion of a wide range of species richness in the data set under a multi-regional sampling framework. Although significant differences exist among these regions at broad landscape scales (Chu et al. 2003), the lakes selected for this study were quite similar, among regions, in local scale habitat indices.

Lakes were selected based on a suite of metrics thought to have measurable influence on FB; size (Carey and Wahl 2011, Eloranta et al. 2015), littoral/pelagic ratio (Vander Zanden et al. 2006), primary production (total phosphorus and Secchi depth) (Rasmussen and Kalff 1987), temperature (Christie and Regier 1988), angler access/pressure (Hunt et al. 2011), and fish community composition. Best efforts were made to limit between-lake variance among these indices to reduce the influence of confounding variables on the species richness/ FB relationship. In total, 13 lakes, ranging from 2-species to 10-species communities were included in the analyses (Figure 1, Table 1).

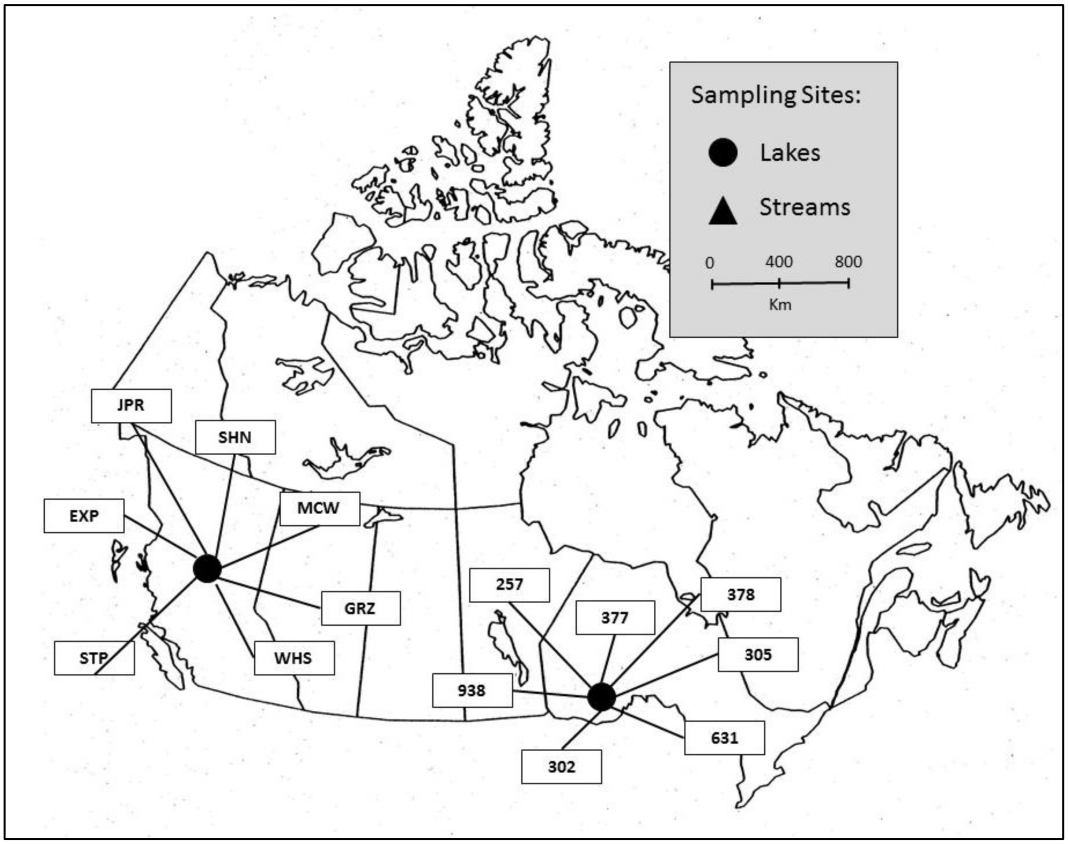

Figure 2.1. Map of site locations.

Fish Community Sampling

Fish community sampling occurred over a 3-year period (2013-2015), each year beginning in the late spring and finishing in early summer (June/July). Sample design was adapted from the Nordic sampling method and the protocol outlined by Morgan and Snucins (2005), with modifications to reduce fish mortality. Net gangs were 30 m long, consisting of 12 - 2.5m panels, of varying knot-to-knot sizes, which were 1.5m deep.

Table 2.1. Name, abreviation, size and UTM of sample sites.

Waterbody	Abr.	Area	UTM
Lakes			
McEwan Lake	MCW	47	10.530581.6030792
Grizzly Lake	GRZ	55	10.533668.6031013
Shanley Lake	SHN	32	10.445422.5998682
Whitestone Lake	WHS	30	10.565174.5811940
Stump Lake	STP	27	10.461089.5865477
Expected Lake	EXP	29	10.431437.6001771
Jumping Rabbit Lake	JPR	29	10.471567.6037683
Lake 257	257	25	15.440945.5504358
Lake 631	631	36	15.440100.5506021
Lake 378	378	24	15.444082.5506738
Lake 938	938	20	15.430666.5502680
Lake 377	377	27	15.444176.5507818
Lake 305	305	54	15.449899.5504379

Nets were set prior to sunrise, usually between 03:30 and 05:00, and allowed to soak for approximately 3hrs prior to retrieval (± 20 minutes for travel time), modified from the original protocol which outlines 24hrs soak time. A total of 12-16 gillnets were deployed on each lake, depending on surface area and max depth, deployed evenly among the pelagic and littoral sampling strata. Fish were removed from gillnets and transferred to on-boat recovery tanks prior to being identified, weighed and measured (fork length). All captured fish were released, however, 10 individuals of each species (or feeding guild for species known to undergo ontogenetic niche shifts) were sacrificed for stable isotope and stomach content analysis. Estimates of species richness were made from presence in gillnets, and corroborated by a variety of other sampling gears such as minnow traps, beach seins and electrofishing, deployed randomly where habitat permitted.

Invertebrate Community Sampling

The invertebrate communities of the lakes in this study were assessed to help quantify any potential bottom-up influence exuded on the fish community. Invertebrate sampling occurred congruently with fish community sampling via a combination of gears suitable for a variety of habitat types. Once an inventory of habitat was acquired for a given lake, each distinct habitat type would receive 5 sampling events, at locations distributed across the lake. Invertebrates were preserved in 10% ethanol and returned to lab for identification to the family level. Specimens within a family were then pooled together, dried and prepared for stable isotope analysis.

Isotopic Analysis

Because different tissues and structures assimilate diet sources over different timescales, dorsal muscle tissue was obtained from all fish and used for analysis. This was logistically unreasonable for aquatic invertebrates, therefore whole body samples were used, and where one individual could not provide a large enough sample for isotopic analysis, samples of a sufficient number of individuals were pooled. Tissues were ground into fine powder, and 0.5mg samples were packed into tin capsules to facilitate combustion. Analyses were performed using a Costech elemental analyzer in combination with a Thermo Delta V Advantage isotopic ratio mass spectrometer and IsoDat 3.0 computer software. Due to reported inter-species variance in lipid content of dorsal muscle tissue, and the potential for this variance to influence stable Carbon and Nitrogen isotope ratios (Logan et al. 2008, Braun et al. 2014), a-posteriori lipid corrections were performed on data adhering to mass balance methodologies proposed by Fry et al. (2003).

Statistical Analysis

FB per net was calculated for each habitat strata per lake (pelagic and littoral), and then standardized to whole lake FB estimates by correcting for the strata area ratio (i.e. multiplying FB per littoral/pelagic net by the proportion of littoral/pelagic strata area, and summing the totals). Prior to analysis of the species richness-biomass relationship, a series of linear regressions were performed among a variety of habitat indices (a list of these indices is available Chapter 1, Table 2) and FB estimates to determine if any confounding variables imposed a significant effect on FB. These analyses are available in Chapter 1, and will not be repeated here (though the results of said analyses will contribute to the discussion of Chapter 2).

In Chapter one of this thesis, a linear regression is preformed between FB and species richness (Chapter 1, Figure 3) among the same lakes considered in this chapter. Though it would be redundant to repeat the analysis here, the residuals produced from this linear model (henceforth referred to as SpRBm-r) will be used in various analyses throughout Chapter 2 as a measure of functional richness independent of the influence of species richness (support for its use in such a capacity is given in Chapter 1). All statistical analysis were performed in R (R-Development-Core-Team 2008).

Community/ Niche Metrics

Layman community metrics (Layman et al. 2007) were calculated to estimate various community food web characteristics, including Total Area (TA), Range of δ^{13}C (dCR), Range of δ^{15}N (dNR), Distance to Centroid (CD), Mean Nearest Neighbour Distance (MNND), and Standard Deviation of Nearest Neighbour Distance (SDNND) (see Layman et al. 2007 for a detailed description of these metrics). Layman's original design calculated these metrics using convex hulls traced around the outer members of the community. However, more recent methodologies proposed by Jackson et al. (2011) allow for these same metrics to be calculated with ellipses, which are less sensitive to strong outliers in the community, and therefore a more robust estimate of community niche size (Layman et al. 2012). For this reason, the ellipse methodology was selected to calculate Layman community metrics, using the SIBER statistical package in R (R-Development-Core-Team 2008, Jackson et al. 2011).

Standard Ellipse Area (SEA) metrics were calculated to estimate niche size of individual species, within each lake, using the SIBER - R statistical package developed by Jackson et al (2011). Due to rare instances where sample sizes of a particular species, within a lake, was less than 10, the SEA calculation 'corrected for sample size' (SEAc), as well as the bayesian methodology (SEAb) were also included in the analyses (See Jackson et al. 2011 for a full description of these methodologies). Because the SIBER model generates ellipses for individual species (rather than whole communities as the Layman metrics), values per lake were reported as mean, variance and sum of Standard Ellipse Area (mSEA, vSEA and sSEA, respectively).

Finally, to assess the level of overlap among species' niche sizes, within lakes, Swanson et al.'s (2015) nicheROVER statistical package was employed. Essentially, this methodology uses standard ellipse areas (such as those discussed above) and estimates how much the ellipses overlap, among all pairs of species in a community, as a percentage relative to the size of the individual species' SEA (see Swanson et al. 2015 for a full description of methodology). From these estimates, four metrics were derived:

mean community overlap, sum of total number of interactions (sINT), interactions greater than 20% as a proportion of maximum possible community interactions (INT>20), and interactions greater than 50% as a proportion of maximum possible community interactions (INT>50).

Community/Niche Metrics and Fish Biomass

The distributions of each of the above community and niche metrics were tested for normality (Shapiro-Wilk Test) and homoscedasticity (Levene's Test), and any data which deviated from these assumptions were $\log_{10}$ transformed. A suite of these metrics were then regressed against FB, individually, with statistical significance being evaluated following bonferroni correction for repeated tests. Metrics which produced statistically significant relationships were then included in a forward and backward stepping regression analysis, and models were evaluated using Akaike's Information Criterion (AIC).

Community/Niche Metrics and Functional Richness (SpRBm-r)

A smaller subset of community/niche metrics (than that used in the aforementioned FB regressions), determined a-priori to be most likely to correlated with functional richness, were selected to be regressed against SpRBm-r to evaluate their influence on food web functional richness, independent of the influence of species richness. These same metrics were also combined in forward and backward stepping regression analysis, and candidate models were evaluated via AIC. Finally, one suite of niche metrics (the three estimates of mean niche size) were also selected, a-posteriori, to be non-linearly regressed against SpRBm-r.

For each fish community, estimates of niche size of the food base (invertebrate community) were made to determine whether they could be used to “standardize” isotopic estimates across ecosystems, such as $\delta^{13}C$ range (dCR), $\delta^{15}N$ range (dNR), and Standard Ellipse Area (SEA). This was done by expressing fish community metrics relative to their invertebrate counterparts, and creating a set of “food base corrected” community/niche metrics. These metrics were tested for normality and homoscedasticity, and regressed against FB and SpRBm-r estimates.

Results

In total, 13 lakes were included in the analyses, represented by a combined pool consisting of 31 species. Species richness per lake ranged from 2 to 10 (median = 5), and was generally dominated by cyprinid richness. Habitat structure for these lakes, and potential influences of such on FB, are described and reviewed in chapter one of this thesis.

Lake FB estimates ranged from 34g/net to 3828g/net (mean ± s.e. = 1981g/net ± 353g/net). A significant positive relationship among species richness and FB ($R^2 = 0.525$, $p = 0.0056$) is described in Chapter 1, the residuals from which are available in Table 2.

Community/Niche Metrics and Fish Biomass

Layman community metrics were calculated and are summarized in Table 3. Among these six metrics, four were positively correlated with the number of species in the system, and also returned statistically significant positive relationships when regressed against FB: logTA ($r^2=0.5889$, $p<0.01$), logdCR ($r^2=0.3593$, $p=0.021$), dNR ($r^2=0.5352$, $p<0.01$), and CD ($r^2=0.3609$, $p<0.023$).

Table 2.2. Residuals from species richness against FB linear regressions (see Ch.1) for each lake in the data set.

Lakes	Species Richness	Functional Richness	Regression Residual
McEwan Lake	2	n/a	338.07
Grizzly Lake	3	n/a	-821.21
Shanley Lake	3	n/a	-967.51
Whitestone Lake	3	n/a	-239.51
Lake 257	6	low	-1162.6
Lake 631	5	low	-159.79
Lake 377	6	low	-697.08
Lake 938	10	low	-697.24
Stump Lake	4	high	559.5
Expected Lake	5	high	1005.2
Jumping Rabbit Lake	5	high	1557.2
Lake 378	6	high	758.91
Lake 305	9	high	526.04

Lakes classified as “low” are all, at minimum, lacking a pelagic specialist.

Table 2.3. Layman community metrics calculated for each lake in the data set.

		Layman Community Metrics					
Lakes	SpR	TA	dCR	dNR	CD	MNND	SDNND
McEwan Lake	2	0.169	0.480	1.290	0.692	1.385	0.125
Grizzly Lake	3	1.382	3.530	1.112	1.552	1.667	1.382
Shanley Lake	3	0.169	0.683	0.615	0.382	0.558	0.125
Whitestone Lake	3	3.202	4.302	1.505	1.617	1.616	0.700
Stump Lake	4	4.952	3.014	3.266	1.421	1.158	0.708
Expected Lake	5	3.997	4.004	1.553	1.457	1.073	0.557
Jumping Rabbit Lake	5	5.495	4.716	2.726	1.441	1.297	0.907
Lake 257	6	2.542	3.793	1.497	1.169	0.965	0.857
Lake 631	5	8.469	6.014	3.154	2.285	1.593	0.624
Lake 378	6	12.890	6.907	3.878	2.167	1.766	1.378
Lake 938	10	7.477	4.814	3.048	1.386	0.918	0.511
Lake 377	6	2.784	6.410	1.670	2.016	0.981	0.847
Lake 305	9	24.610	14.710	2.800	3.807	1.608	0.719

Layman metrics: Total Area (TA), Range of $\delta^{13}C$ (dCR), Range of $\delta^{15}N$ (dNR), Distance to Centroid (CD), Mean Nearest Neighbour Distance (MNND), and Standard Deviation of Nearest Neighbour Distance (SDNND).

These four metrics were further assessed against FB using forwards and backwards stepping regression analysis, which, following evaluation of all model combinations by

Akaike's Information Criterion, revealed that the combination of logTA and dCR was most effective in explaining the variance in FB, followed by logTA alone.

Table 2.4. SIBER (niche area) and NicheROVER (niche overlap) metrics calculated for each lake in the data set.

		SIBER Niche Metrics			NicheROVER Overlap Metrics		
Lakes	SpR	mSEA	mSEAc	mSEAb	mOVER	INT>20	INT>50
McEwan Lake	2	2.895	3.224	2.968	24.360	0.500	0.000
Grizzly Lake	3	3.121	3.507	2.906	42.840	0.667	0.500
Shanley Lake	3	1.154	1.297	1.128	66.310	1.000	1.000
Whitestone Lake	3	1.059	1.201	1.004	19.100	0.333	0.333
Stump Lake	4	1.020	1.192	0.918	18.260	0.417	0.000
Expected Lake	5	1.711	1.937	1.635	27.970	0.650	0.350
Jumping Rabbit Lake	5	1.791	2.017	1.747	28.990	0.800	0.350
Lake 257	6	1.282	1.451	1.125	34.510	0.500	0.233
Lake 631	5	3.049	3.446	2.289	32.200	0.250	0.150
Lake 378	6	1.583	1.773	1.449	30.040	0.333	0.233
Lake 938	10	1.206	1.356	1.225	30.020	0.256	0.100
Lake 377	6	0.962	1.099	0.845	34.060	0.533	0.267
Lake 305	9	1.368	1.615	1.202	20.200	0.250	0.056

SIBER metrics: Mean Standard Ellipse Area (mSEA), Mean Standard Ellipse Area – sampled corrected method mSEAc), and Mean Standard Ellipse Area – bayesian method (mSEAb). NicheROVER metrics: Mean Overlap (mOVER), proportion of maximum possible interactions which feature greater than 20% overlapjust a (INT>20), and proportion of maximum possible interactions which feature greater than 50% overlap (INT>50)

Standard Ellipse Area (SEA) metrics were calculated using the SIBER - R statistical package developed by Jackson et al. (2011). Mean, variance and sum of Standard Ellipse Area (mSEA, vSEA and sSEA, respectively) were calculated, and a summary of mSEA, mSEAc, and mSEAb values are provided in Table 4. Among the nine variables calculated, only three produced significantly positive relationships when regressed against biomass, and all were also positively correlated with the number of species in the system. These were the three 'sum of' SEA estimates; sSEA (r^2=0.4514, p=0.011), sSEAc (r^2=0.4596, p=0.010), and sSEAb (r^2=0.5740, p<0.01).

Niche overlap was calculated using Swanson et al.'s (2013) NicheROVER package in R. Values for mean community overlap (mOVER), interactions greater than 20% as a proportion of maximum possible community interactions (INT>20), and interactions greater than 50% as a proportion of maximum possible community interactions (INT>50) are available in Table 4. When regressed against FB, sINT produced a significant positive linear relationship and was positively correlated with the number of species in the system ($r^2=0.5932$, $p<.01$), however, mOVER produced a slightly negative relationship (only significant with 90% confidence, $p=.090$) when regressed against FB, and was not correlated with species richness.

A second forward and backward stepping suite of regressions was performed including the following metrics pooled from all three methodologies: logTA, logdCR, dNR, CD, sSEAb, logmOVER and sINT. Following evaluation of all model combinations by AIC, the model most effective in explaining the variance in FB included dNR, sSEAb and sINT.

Invertebrate community/niche metrics were in no instance significantly correlated with fish species richness, FB estimates, or any of the fish community/niche indices considered here. As such, they were omitted from any further analysis.

Community/Niche Metrics and Functional Richness

Layman's, Jackson's, and Swanson's metrics were linearly regressed against the residuals produced from the Species Richness-Biomass regression (see Chapter 1 for analysis, Table 2 for values), with only two producing relationships significant at the 90% level of confidence: logdNR (pos., r^2=0.2392, p=0.0899, figure 2) and logmOVER (neg., r^2=0.2831, p=0.0613, figure 3).

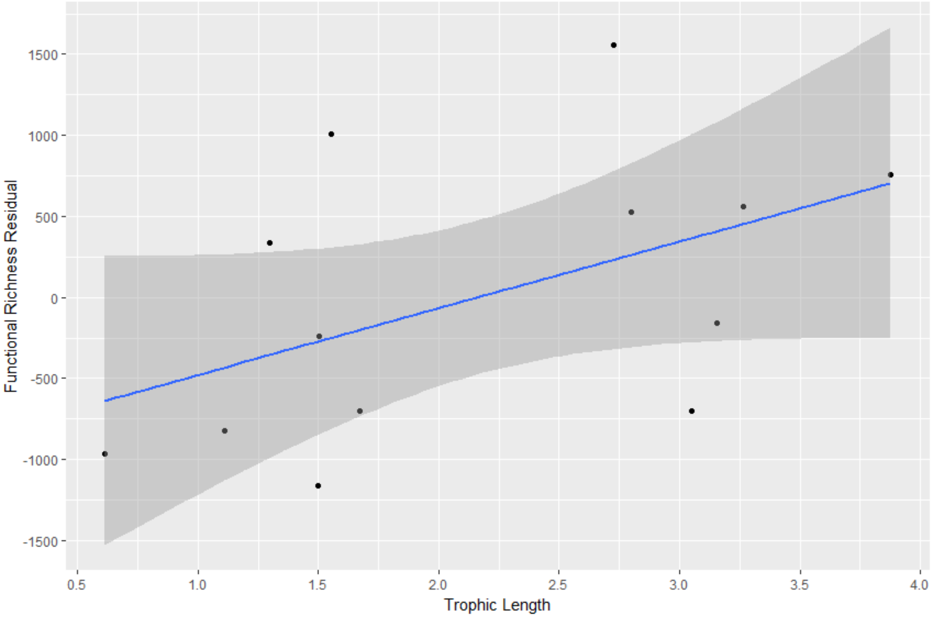

Figure 2.2. Linear regression of trophic length and Functional Residual among all lakes in the data set.

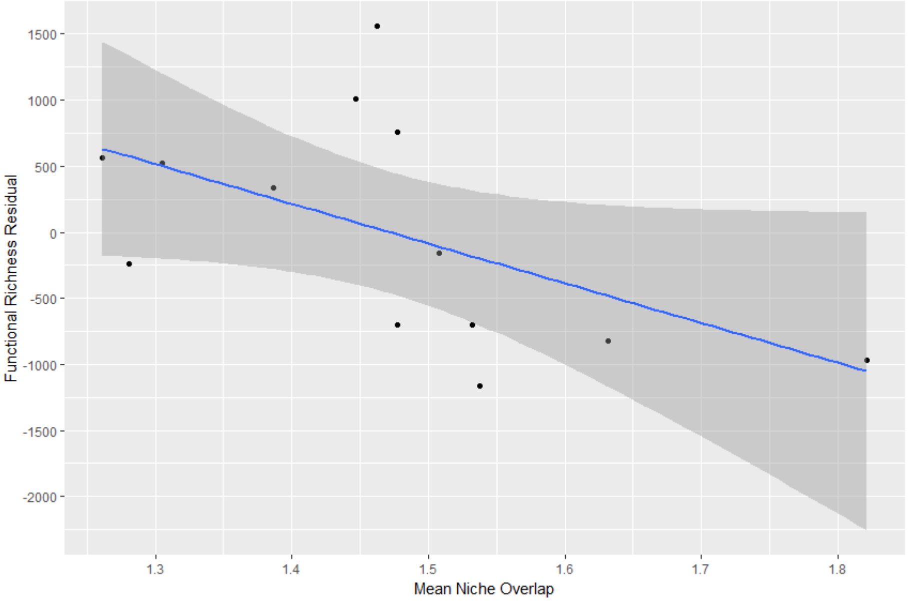

Figure 2.3. Linear regression of mean niche overlap and Functional Residual among all lakes in the data set.

Results from forward and backward stepping regressions, performed on the eight variables presumed to have the greatest influence on functional richness, revealed upon evaluation by AIC that the model featuring only logmOVER was most efficient in explaining variance in functional richness estimates, followed secondly by the model combining logmOVER and dNR. Polynomial regression performed on the three estimates of mean niche size, mSEA, mSEAc, and mSEAb, produced non-significant relationships, although, that of logmSEAc (sample size corrected methodology) was significant at the 90% level of confidence ((r^2=3820, p=0.0902, figure 4).

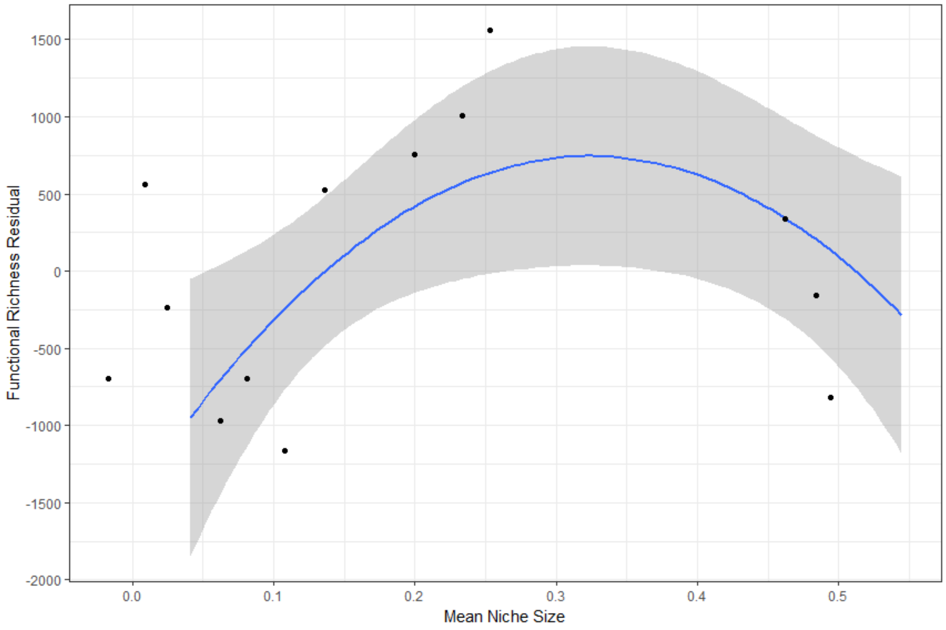

Figure 2.4. Second-order polynomial regression of mean niche size and Functional Residual among all lakes in the data set.

Discussion

In chapter 1 of this thesis, we elucidate a positive relationship among species richness and FB in multi-trophic level freshwater fisheries, and provide support for the hypothesis that the residuals produced in that model may provide a quantifiable estimate of functional richness. Furthermore, we suggest that more descriptive, and continuous, measures of ecosystem function and trophic structure could potentially be used to predict those residuals, thereby providing researchers with a means to measure functional richness, in food webs, as it applies to energy transfer and total FB. Here, through a series of regressions and model evaluations, we have successfully demonstrated that measures of community function (Layman et al. 2007, Jackson et al. 2011) and species interaction (Swanson et al. 2015) can be useful predictors of both FB and functional richness.

Layman's community metrics provide characterizations of communities which describe the width, length, and size of food webs , and as we've shown, these measures seem to provide a useful conduit for predicting FB in freshwater ecosystems. When regressed against FB estimates from the lentic systems considered here, four of the six metrics returned significant, positive relationships: Total Area (TA), Range of $\delta^{13}C$ (dCR), Range of $\delta^{15}N$ (dNR), Distance to Centroid (CD). Not surprisingly, given the positive relationship between specie richness and FB demonstrated in Chapter 1, all four of these measures correlated positively with the number of species in the system, although each describes a unique aspect of species richness.

Total Area increases alongside species richness at a greater rate when additional species are complementary, rather than redundant, and so it makes intuitive sense that FB would increase with TA, as was similarly shown in Tilman's original grassland study demonstrating the strong effect of additional unique functional groups on biomass production (Tilman et al. 1997a, Tilman et al. 1997b). Range of $\delta^{13}C$ and Range of $\delta^{15}N$ are similarly influenced by the addition of unique species, however, describe separate mechanisms for how species influence trophic structure and energy transfer. The respective strength of the relationships between these two variables and FB, presented here, may provide insight to the relative importance of specific functional groups being added to a system, either widening the food web, or elongating it. For instance, increases in dCR, or trophic width, arise when species are added to a trophic level already occupied, but utilize a resource that is either more benthically, or pelagically derived in relation to the already present community (Vander Zanden and Vadeboncoeur 2002a, Solomon et al. 2011). This widening of the food web increases a system's capacity for FB through the addition of energy pathways, such as the addition of a pelagic energy pathway to complement a littoral pathway (Vander Zanden and Vadeboncoeur 2002a, Vander Zanden et al. 2006). This appears to be one mechanism through which the addition of species led to corresponding increases in functional richness and FB in our lakes, as is evident from the comparison between systems with and without a pelagic specialist, presented in Chapter 1 and as indicated in Table 2 (high vs low richness) here. A second mechanism, which appears to have had a stronger influence on FB than trophic widening, was lengthening of the food web, or otherwise stated, an increase in dNR through the addition of a piscivore, or at least some functional group which added a new trophic level to the system. Rather than adding additional energy pathways, the introduction of a piscivore may increase the system's capacity for FB by acting as a trophic coupler (Vander Zanden and Vadeboncoeur 2002a, Quevedo et al. 2009, Bartels et al. 2016), amalgamating resources from multiple energy pathways, and storing it as large bodied individuals with longer lifespans and slower turnover (Scott and Crossman 1973, Grabowski et al. 2012). Though the presence of a predator can also impose deleterious effects on prey population (Chalcraft and Resetarits 2003, O'Connor et al. 2013, Ryabov et al. 2015) and hence prey biomass (Fox 2004b, Fox 2005a, 2007, Raborn et al. 2007), in stable food webs such as those considered here (presumed to have only minimal fluctuations in predator-prey cycles), our results suggest that this negative effect is superseded by the benefits of having a trophic coupler present.

As previously mentioned, among the lakes considered in this study, the most conceptual example of the positive effect of TA, dCR and dNR on FB is offered in the paired comparison of lakes with similar species richness which either feature, or lack, a pelagic specialist (Table 2). In these comparisons, the presence of either Rainbow Trout, Lake Trout, or in the case of Stump lake, an adult White Sucker population, led to an increase in trophic width and/or length, as well as a corresponding increase in FB (for an example, see Figure 5, Lake 257 vs Lake 378). However, there was one exception which is perhaps indicative of the limitations of using Layman's metrics as a predictor of functional richness and FB. Lake 631, though lacking any of the aforementioned pelagic specialists, features much greater TA, dCR and dNR than would be expected given the FB regressions produced by the larger data set. The lake is characterized by a simple cyprinid/catostomid community in which most species (Long Nose Sucker, in particular) are extremely generalist, each occupying a relatively large area of "stable isotope space" compared to lakes with similar species richness. As such, though the community appears to be utilizing a substantial portion of the available resource, they are perhaps not using it efficiently, and the examination of standard community metrics alone leave us with little to determine a cause for this inefficient energy transfer.

Broad community metrics, such as those discussed above, do effectively capture the effect of species richness on FB, and, as demonstrated, may even provide us with a more descriptive account of the relationships underlying mechanisms governing energy transfer. However, they do not provide us with any insight with regard to trophic interactions which, as we suggest, may explain additional variance in the FB model not captured simply by the number of species in the system. We regressed such metrics, of niche size and overlap, against the residuals produced in the species richness-biomass model and found variance in the residuals could be partially explained by estimates of both measures.

Mean Niche Overlap, an estimate of the degree to which species are competing for similar resources, had a negative influence on FB among systems with similar numbers of species (Figure 3), suggesting that energy transfer efficiency is increased with lower degrees of interspecies competition. This observation aligns itself with popular co-existence theory, which suggests that species co-existence is facilitated, and sustained, by niche partitioning among species which once competed for similar resources (Amarasekare et al. 2004, Fargione and Tilman 2005, Quevedo et al. 2009, Di Bitetti et al. 2010, Turnbull et al. 2013, Hart et al. 2016). If the phenomenon of niche partitioning is prevalent in ecological communities, and if coexistence is a selective strategy, our results suggest that it is a successful strategy. This, however, may not be the case. In a recent review, Poisot et al.(2015) performed a meta-analysis of 175 ecological networks ranging from low connectedness (high compartmentalization) to high connectedness, and found that species richness (co-existence) was most often greatest among communities of intermediate connectedness. The authors did report, however, that strategy diversity (functional groups) was maximized in communities with lower connectedness. It remains unclear whether the strategy of niche partitioning serves mainly to maximize species coexistence or maximum energy transfer efficiency, a topic which should be further investigated.

To take a different approach, consider the outcome of niche partitioning for an individual species, rather than the community: niche specialization. From both a functional and species perspective, ecologists continue to debate whether specialism or generalism is the superior strategy. Current theory suggests that while communities comprised of specialists are more efficient in energy transfer (Bernays 1998, Bernays et al. 2004), communities comprised of generalists are better suited to cope with disturbance, characterizing them with greater resilience at the expense of reduced foraging and energy transfer efficiency (Svanbäck and Peter 2003, Vanderpham et al. 2013, Polito et al. 2015). Interestingly, among the communities considered in this analysis, we observed a hump-shaped response between mean niche size and functional richness of communities, indicating that energy transfer efficiency is optimized when a community is neither dominated by specialists or generalists, but rather features a mix of both strategies. From this, it is perhaps reasonable to consider that niche partitioning may tend to both maximize energy transfer and promote co-existence simultaneously, as it appears that optimal energy transfer efficiency can be attained through selective niche partitioning only until some low-end threshold of connectedness (and competition) as achieved. A visual aid to demonstrate niche overlap as it relates to competition and functional richness is offered in Figure 5. It depicts three pairwise comparisons of lakes featuring similar species richness, but very different functional richness resulting from lower degrees of niche overlap and community connectedness. Note that the functionally rich systems are also comprised of a mix of specialist (small ellipses) and generalists (large ellipses).

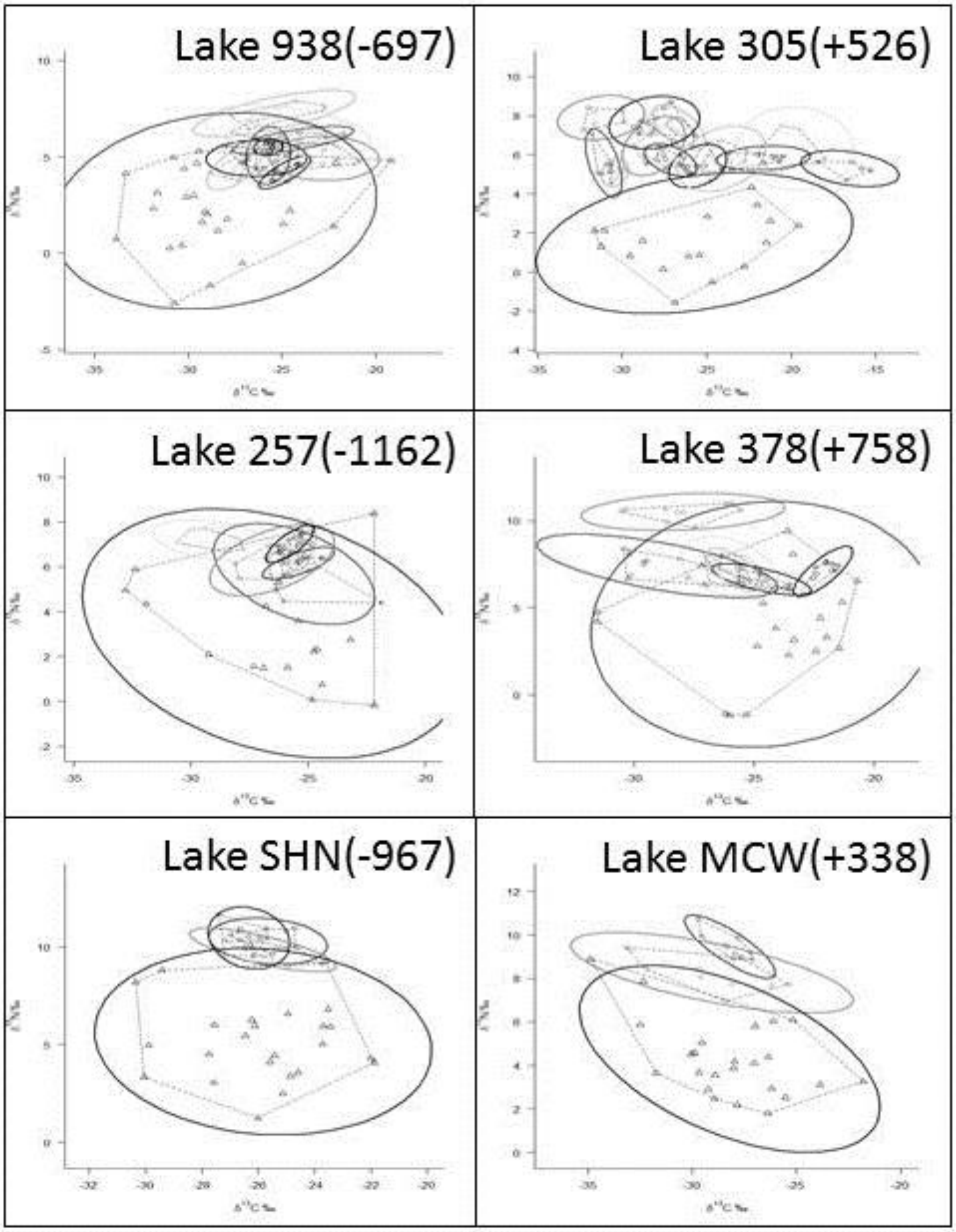

Figure 2.5. Standard Ellipse plots demonstrating differential niche overlap and functional residual in community pairs with similar species richness. From top to bottom: comparison of niche overlap among fish species in communities with high species richness (Lake938-10spp/Lake305-9spp), moderate richness (Lake257-6spp/Lake378-6spp), and low richness (LakeSHN-3spp/LakeMCW-2spp). From left to right: comparison of functional residual (given in brackets) among communities with HIGH mean niche overlap to communities with LOW mean niche overlap. Largest, "base trophic level" ellipse represents the invertebrate community niche of each lake, and is not factored into fish overlap calculations.

A somewhat surprising result here is the apparent lack of a relationship between community niche width (dCR) and functional richness. One would expect that a community which exploits a greater proportion of the available basal resources would also feature greater trophic energy transfer efficiency. This result is further confounded by our results demonstrating that increases in both total niche area (TA) and trophic length (dNR) did in fact lead to corresponding increases in functional richness; however, we posit that this discrepancy may have been an artifact of our sample design. Earlier, we discussed that the greatest influence on trophic length was the addition of a piscivore predator, and the greatest influence on trophic width was the addition of a pelagic specialist. Across our study, increases in trophic length were almost exclusively a result of the addition of a piscivore, implying that any observed increase in trophic length was the direct result of a substantial functional role being added to the system. Observed increases in trophic width across our study, however, were not exclusively the result of the addition of a pelagic specialist. Therefore, the response of functional richness to increases in trophic width may have been more variable across ecosystems, masking its effect on functional richness relative to trophic length and total niche area.

Also surprising was the inability to explain additional variance in the model by standardizing community metrics by a community's available resource, though this was almost certainly an artifact of incomplete representation of that food source in our sample. When comparing community metrics such as trophic width, or length, across multiple unique ecosystems, inferences of trophic efficiency should ideally consider the influence of the food source on its consumers. For instance, consider two distinct ecosystems (A and B), each with only two available resources, though community A's resources have more distinct stable isotope signatures than community B. If consumer communities in both A and B are both perfectly efficient at exploiting the available resources, community A will have greater trophic width relative to community B, leading to under-estimation of its influence on functional richness and energy transfer efficiency. Instances such as this may have led to the aforementioned lack of relationship among functional richness and trophic width observed here. Conversely, consider that community A's food resource offers twice the isotopic breath relative to community B, but at the cost of individual food sources being less abundant. If both consumer communities have similar trophic widths (incomplete exploitation by community A), the influence of trophic width on functional richness may be over-estimated.

Considerations such as these are painfully complex, and acquiring samples that comprehensively describe the food base can be logistically challenging to say the least. As such, most aquatic researchers have simply ignored the influence of primary consumer prey on higher trophic levels, or tried to oversimplify the resource in the application of mixing models (Phillips 2001, Phillips et al. 2005, Moore and Semmens 2008, Jackson et al. 2009). Nevertheless, it is important to recognize the potential value of comprehensive food base data to fish consumer food web analyses, and suggest that future research should strive to attain such lofty sampling goals. As a caveat, even in the failed pursuit of such a comprehensive sample (as demonstrated here), partially complete representation of the food base can still offer value in visual interpretation of food web comparisons (see Figure 5).

With this work we have successfully demonstrated that tools which employ stable isotope ratios to describe food web size and shape, as well as individual niche size and community connectedness, can be used to describe functional richness (with respect to trophic energy transfer) to a degree which goes beyond life history accounts. Going forward, these models should be tested on larger data sets, comprising a greater diversity of ecosystem types that were outside the scope the survey design here. Moreover, they should be applied in concert with other environmental factors towards predictions of FB that can be used to inform fisheries management objectives across Canada. Alas, this will require that two substantial hurdles be navigated: first, that stable isotope analyses become more common and be applied more frequently in fisheries studies across the country, and second, that a model predicting FB, from large regional data sets describing chemical, physical and biological drivers, be developed for which to assess the ability of functional richness estimates to describe residual variance. The former will require both time and resources (or for the current cost of stable isotope analysis to be reduced) to establish the necessary database, while the latter will be addressed in Chapter 3 of this thesis.

Chapter 3

EMPIRICAL MODELS RELATING FISH COMMUNITY BIOMASS TO NUTRIENTS, BIODIVERSITY AND MORPHOMETRY IN LAKES AND RIVERS

Introduction

The use of empirical models to predict the biomass of primary producers from concentrations of chemical nutrients (P, N, and Si) has been an important goal for limnology for decades (Bachmann and Jones 1974, Dillon and Rigler 1974, Stockner and Shortreed 1978). Similarly, fisheries scientists, recognizing the key role that bottom up processes play in ecological energetics, have also developed models linking fish biomass, and production to nutrient concentrations, mainly the total phosphorus (TP) concentration of the water. The link between fish and nutrients has been fundamental to the management of wild fisheries (Bennett 1970).

The relationship between nutrients and fish, in addition to its fundamental importance to aquatic ecosystems can also be controversial; in fact, fishery managers, outfitters and others whose livelihood depends on fisheries, often perceive nutrient abatement programs aimed at water quality enhancement to be at least partly detrimental to the success and sustainability of fisheries (Yurk and Ney 1989, Ney 1996). Regulatory agencies, whose task is to balance conflicts among stakeholders, and conserve and manage fisheries and other aquatic resources in the face of strong pressures for development, require simple and general models relating fish abundance to nutrient status as a benchmark from which to evaluate potentially detrimental environmental impacts.

HydroNet, an NSERC funded research network partnered with Fisheries and Oceans Canada, Manitoba Hydro and BC Hydro sought to develop simple and effective tools to better assess, minimize and mitigate effects of hydropower development on fish and their habitats, and thus strengthen the regulation process and the conservation of fisheries in Canada (Smokorowski et al. 2011). One of the goals of HydroNet was to develop better empirical model to predict fish biomass in both lotic and lentic ecosystems with strong applicability across systems and across regions. While several simple empirical models linking fish biomass to TP have been developed, the models have low precision, but more importantly the relationship between fish biomass and TP differs greatly among regions (Hanson and Leggett 1982, Yurk and Ney 1989, Hoyer and Canfield 1991, Randall et al. 1995, Bachmann et al. 1996) for reason that are not well understood.

While the relationship between nutrients and fish is often viewed as a simple ‘bottom up” causal chain, it is clear that many fundamental ecosystem processes can significantly affect it, and all of these modifying processes are highly variable among systems and regions. Many physical processes affect the cycling of nutrients within ecosystems, and influence the efficiency with which nutrients are taken up by primary producers, and passed up the food chain to fish. Thus hydrological processes, i.e. the flow regime, and associated processes such as thermal stratification and wave action, combined with the process of sedimentation can strongly influence the efficiency with which nutrients are passed from primary producers to fish. Interactions between the light regime, and morphometry will determine the relative importance of planktonic vs benthic primary producers. Benthic primary producers can directly access nutrients from the substrate and the trophic chain can also experience subsidies of allochthonous organic matter (i.e. terrestrial insects and leaf litter) which can fuel secondary production. While such processes are likely somewhat predictable from morphometry, since they are not directly linked to water column nutrient concentrations, they are likely to weaken the relationship between fish biomass and water column nutrient concentrations. All of these processes can of course be influenced by climatic and geographic factors that can vary greatly across regions.

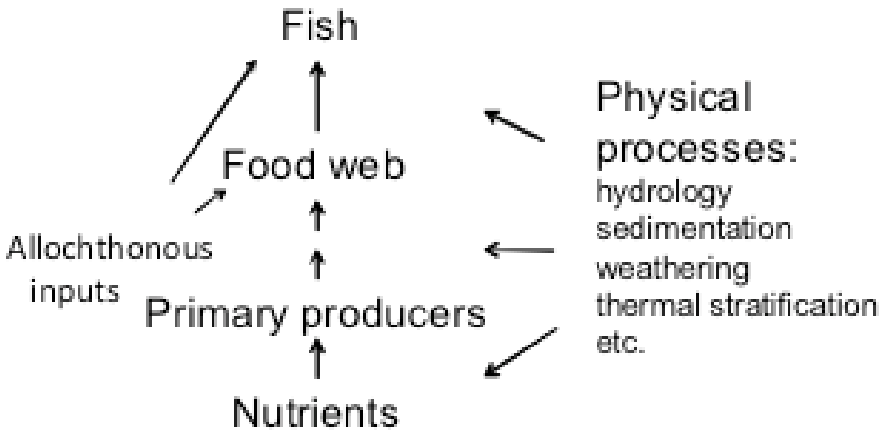

Figure 3.1. The dependence of fish abundance and productivity on the underlying trophic regime, and ultimately the nutrient regime, and the impact of physical factors that shape fish habitat.

Biological factors, notably the makeup of fish communities also vary greatly both within and among regions, which mostly reflects the zoogeographical history of the system. Lakes and rivers, even in species poor glaciated regions like Canada, often contain a broad diversity of species, and life history stages, and sometimes ecotypes, each of which can differ in their resource requirements, and thus the pathway through which they are affected by the underlying 'food regime' (Chu et al. 2003). The greater the variety a system supports, the broader should be the range of resources and habitats that contribute to fish production, and the greater the potential biomass of the community. Thus, as complex as the energy flow path shown in Figure 1 is, it remains a considerable oversimplification of reality. Since the richness of species and functional groups in different aquatic habitats differ greatly from region to region, reflecting both large-scale historical zoogeographical factors, local colonization and extirpation process, human introductions and removals, and pure chance as well (Mandrak and Crossman 1992), fish biodiversity may explain a considerable amount of the regional variability, and perhaps local variability as well, in the relationship between fish biomass and TP.

The purpose of this analysis is to establish a relationship between community biomass of fish (FB) and the total phosphorus concentration of the water column, and test for the ability secondary nutrients (TN:TP ratio), morphometric variables (mean and max depth, lake area, stream width), and community biodiversity (fish species richness, and functional group structure) to add to the predictive power of the relationship. Residuals from the models were used to compare rivers with regulated flow regimes, ie. rivers < 10 km downstream of a dam or impoundment will be compared rivers that are open or upstream of reservoirs, and to artificial lakes, i.e. reservoirs to natural lakes. These relationships would be established using data collected from the literature, plus 28 rivers and streams from across Canada studied during the 2009-14 NSERC HydroNet program (Smokorowski et al. 2011).

First, we expect TP will be the best predictor of FB, and will be the main chemical driver of freshwater ecosystem FB (Deegan and Peterson 1992, Downing and Plante 1993, Hyatt et al. 2004). We do not expect that TN will have a measurable effect, though TN:TP may influence FB where the ratio is low (Downing and McCauley 1992). Secondly, due to the greater range of resources available in littoral habitat (relative to pelagic), we expect FB will be a negative function of depth and surface area in lakes. In rivers, we expect a similar negative response of FB to river size, following theoretical implications of the river continuum concept (Vannote et al. 1980). Furthermore, because pelagic resources, i.e. plankton, are more dependent on water column nutrient richness than littorally derived primary resources (which more readily access nutrients in the benthos), we expect the FB-TP relationship to be stronger in deeper lakes and larger rivers, relative to shallow lakes and small rivers. Finally, we hypothesize that, in support of our findings in chapter one, greater fish diversity (number of species and functional groups) will beget greater FB in both rivers and lakes (where TP is constant) as a result of greater trophic energy transfer efficiency, as demonstrated in chapter two. Moreover, due to regional variability in fish diversity resulting from post glacial colonization patterns, we expect that fish diversity might explain much of the regional variance in the FB-TP relationship observed in previous studies.

Methods

The relationship between fish biomass (FB) (g/m^2) and the total phosphorus (TP) and total Nitrogen (TN) concentration of the water (mg/m^3) was determined empirically for a wide range of published and unpublished studies including 28 sites from across Canada studied during the HydroNet project (2010-14). In total, data on FB, TP, species composition and morphometry were obtained for 295 lentic sites, and 208 lotic sites. Data were obtained from a wide range of different types of fish habitats representing both flowing and standing water environments, ranging widely in size and depth, from shallow littoral systems to deep thermally stratified lakes and reservoirs. Rivers range from small headwater streams (2nd & 3rd order) to 5th - 6th order rivers, and included rivers regulated by dams and other impoundments, as well as free-flowing systems, where fish can enter or leave freely. Except for the Arctic tundra region, most of the geographic range of North America is represented including the boreal forest, the Canadian Shield, the Appalachians, the prairie and the mid-west, to the Western Cordillera, and oceanic islands on both coasts. In addition to representing a very broad range of physical conditions, the fish communities range widely in terms of taxonomic and trophic diversity from highly species rich and functionally diverse communities in the Appalachians, and central U.S.A, to the species poor lakes and rivers of the Cordillera and the islands of both coasts. While the majority of the data compiled in our database were from North America, European studies were included whenever possible.

Estimates of fish biomass were obtained from a very broad range of sources, including scientific journals, government reports, theses and dissertations, consulting reports, as well as websites and unpublished sources, and were based on a wide variety of methods. Most estimates for rivers and streams were based on electrofishing, either backpack methods for small streams, or boat-based protocols for larger rivers. Some were based on mark and recapture methods, and in many cases a combination of these methods. Estimates for small lakes and ponds were obtained from mark and recapture methods, seining, index gill netting, beach or purse seining, rotenone poisoning, direct counts following pond draining, or a combination of these methods. Estimates for large lakes and reservoirs were obtained from primarily from hydroacoustic studies, usually employing dual-beam methodologies, supplemented with information on the relative abundance of species obtained from mid or deep-water trawls, gill-netting or purse seining and/or quantitative surveys of runs of outmigrating fish such as salmon smolts. Analyses of this kind have contributed a substantial amount of data on the impact of nutrient fertilization on fish abundance, especially for west coast sockeye salmon lakes. Often in studies using hydroacoustic and/or mark-recapture methods, no actual biomass estimates were produced by the authors; however, when possible, we converted such estimates of fish density to biomass by multiplying by average size, when information on fish size structure was available, either from the same source or from concurrent studies. Data on nutrients, morphometry and the composition of the fish community were obtained either from the same published or unpublished reports as the fish data or from sources that they cited, or concurrent studies. However, often this information had to be retrieved from other publications or reports on the respective water bodies, published within a decade of the fish biomass estimates. In some cases, nutrient information was obtained from large-scale studies of nutrient export trends, either published or available on government websites, for whole river systems or regions, where location data as well as historical information allowed good estimates for the appropriate water bodies. Data on river widths, when not available in the published report, were estimated from 'Google Earth'.

During our HydroNet study nutrient sampling and auxiliary site measurements were carried out together with the fish sampling, under baseflow conditions. Three replicate water samples were collected for nutrient analysis. Samples were taken in 500mL acid washed polyethylene Nalgene bottles and nutrient concentrations were measured on unfiltered water as Total Phosphorus (TP) and Total Nitrogen (TN). TP was determined using persulfate oxidation, and TN was analyzed with the chemical digestion flow injection method. Water was cooled at 4°C and shipped to the University of Alberta Biogeochemical lab for analysis. While it was usually not possible to ensure that literature data was collected and analyzed by the same methodology, whenever possible we chose data that had been collected by similar methods.

The species list at each site included all species that made up 1% or more of the community biomass, however, it was not possible to adhere strictly to this standard, since the data sources used were not always sufficiently precise to allow this. Moreover, for about 20% of the sites, the species composition of the fish community was obtained from independent studies or from provincial or state fishery databases, and therefore can only be considered as approximate.

Species data were organized into functional groups (see Appendix B) based on feeding ecology and habitat use of commonly occurring species, as outlined by: (McPhail and Lindsey 1970, Scott and Crossman 1973, Ploskey and Jenkins 1982, Power et al. 1985, Matthews 1986, Nelson and Paetz 1992, Matthews 1998, McPhail 2007).

Statistical Analysis

Log/Log linear regressions are usually highly robust because they transform data in such a way as to deliver linear relationships, reducing the need for interaction terms, and homoscedastic, normally distributed residuals (Shapiro-Wilk test (Shapiro and Wilk 1965)), that reflect uncertainty in a proportionate, rather than absolute manner, over orders of magnitude variation ranges in both dependent and independent variables.

While not all of the log/log regressions tried met all of these criteria, none of the untransformed regressions produced strong models with homoscedastic normally distributed residuals.

While other transformations, such as power transformations (e.g. square, cube and fourth roots), sometimes produced well behaved models, log/log transformations met the above criteria the best, and their advantage was highest in multiple regressions with three to four variables.

Results

Comparison of Fish Biomass, Nutrients and Species Richness among Regions

Significant and important differences among regions and ecosystem types can be seen in Figure 2 and Table 1. Regions differed significantly for all of the variables in Table 1 with the F_R among regions being greater for SpR (189) > FB (105) > TP (58) > N:P (29). Thus SpR and FB varied the most across regions, with Western/Cordillera < Newfoundland < Central Canada < Central USA. TP also differed among regions, with Western/Cordillera < Newfoundland, Central Canada and Central USA; however, its variability among regions was considerably less than SpR and FB. Regions also differed for N:P with Western Cordillera < other regions; however all N:P ratios in this data set were higher than the 16:1 Redfield Ratio, and thus there was no reason to suspect that Nitrogen limitation was a significant contributor to FB variability. FB was also highly variable within regions as judged by (within group RMS/ pooled mean). FB (1.55) > SpR (0.47) > TP (0.37) > N:P (0.28).

While lakes and rivers differed significantly in FB in three of the four regions, there was no consistent pattern to this difference. In the Western Cordillera where lakes are very deep and tend to be large and oligotrophic, FB in rivers was significantly higher than in lakes, and this was true as well in Newfoundland; however, in Central Canada the difference was not statistically significant. Moreover, in the Central USA lakes and reservoirs both had higher FB than rivers; in fact, FB in reservoirs in this region were the highest in the entire data set.

Table 3.1. Mean values of FB, TP, SpR and N among regions and ecosystem types.

	Fish Biomass (FB) g/m^2	Total Phosphorus (TP) mg/m^3	TN:TP	Species Richness (SpR) #Sp	N
Western Cordillera Lakes	1.33±0.31; 0.36±21.5% 0.39, 0.04, 3.1	5.74±0.62; 4.13±10.0% 4.5, 1.2, 12	18.1±2.0; 14.8±7.1% 13.3, 7.6, 37.5	2.9 ± 0.19; 2.6 ± 5.2% 2, 1, 5	75
Western Cordillera Rivers	3.52±0.51; 1.87±15.7% 1.95, 0.3, 8.5	12.6±1.91; 7.21±13.8% 7.0, 2.0, 41.5	30.5 ± 6.13; 15.2 ± 14.8% 8.68, 4.3, 107	2.7 ± 0.23; 2.2 ± 8.5% 2, 1, 6	66
Central Canada Lakes	4.90 ± 0. 66 3.03 ±15.9% 3.0, 0.67, 12.4	12.5 ±1.72; 9.71 ± 9.8% 9.0, 4.9, 21.0	46.9 ± 3.18; 40.6 ± 8.7% 40.1,17.8,84.9	6.5 ± 1.85; 3.5 ±12.9% 4, 1, 10	50
Central Canada Rivers	7.12 ± 1.30 3.01± 22.1% 1.96,1.48,25.9	15.3 ± 1.49; 11.9 ± 11.1% 10, 4.50, 21.9	32.9 ± 1.6; 31.1± 10.2% 30.2, 18.2, 50	8.4 ± 0.74; 6.8 ± 10.4% 7.5, 3.0, 17.1	48
Central USA Lakes	14.1 ± 1.44; 10.2 ± 11.5% 9.6, 4.04,29.8	25.3 ± 3.54; 14.9 ± 14.6% 19.1,2.20,63.2	53.7 ± 6.53; 39.2 ± 10.2% 36.7, 16.5,133	18.8 ± 1.09; 17.1 ± 5.9% 17, 9.4, 32.8	63
Central USA Reservoirs	64.6 ± 6.28; 48.3 ± 13.1% 9.6, 4.04, 29.8	53.4 ± 5.68; 38.4 ± 13.2% 44.5,11.0, 125	30.6 ± 3.72; 23.7 ± 9.9% 21.3,12.4,60.8	25.3 ± 1.95; 22.5 ± 8.7% 29.2,11.1, 40.3	50
Central USA Rivers	9.26 ± 1.82; 2.81 ± 30.1% 1.36,0.35,33.4	32.1 ± 4.08; 16.7 ± 58.7% 12.0,4.20,92.5	40.4 ± 3.54; 33.1 ± 40.7% 31.4,13.5, 80.2	6.3 ± 2.5; 3.8 ± 20.4% 4, 1, 16.4	37
NL Lakes	0.61 ± 0.09; 0.51 ± 11.8% 0.52,0.18,1.20	26.2 ± 1.76; 25.1 ±10.7% 22, 15, 37	28.5 ± 6.50; 24.1 ± 21% ------	2.4 ± 0.3; 2.1 ± 13% 2, 1, 4	15
NL Rivers	5.5 ± 2.48; 1.68 ± 10.1% 1.8, 1.1, 7.5	21.2 ± 5.42; 19.9 ±13% 16.6, 6.0, 56	--- ---	2.4 ± 0.2; 2.0 ± 20% 2, 1, 3	30
Overall	11.7±2.8; 7.4±16% 7.2, 1.5, 22.5	60.1±11.3; 35.4±20% 22.6, 8.0, 95	25.5±4.52; 22.8 ±22% 22.5, 12.5, 65	6.3 ±1.2; 4.3±16% 4, 2, 18	434

Values represent arithmetic mean ± SE, geometric mean ± error factor (%), and median +10th & 90th %iles of FB, TP, SpR and N. Geometric mean = 10^mean $\log_{10}$, and error factor (%) is $[(10^{(1+SE_{log10})})-10]/10] * 100$.

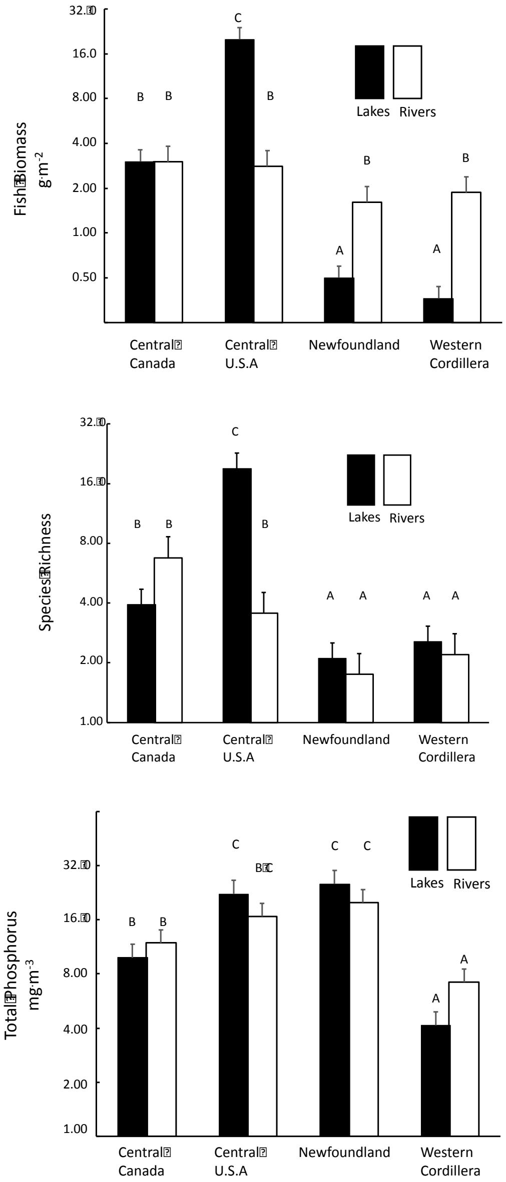

Figure 3.2. Comparison of FB, SpR and TP across regions and between lentic and lotic ecosystems. From top to bottom: fish biomass (a) fish species richness (b) total phosphorus concentration (c), across geographic regions, and between lakes (filled bars) and rivers (open bars). Central Canada = Ontario & Quebec; Central USA= Appalachian states, midwestern states and Florida; Newfoundland = Insular NL; Western Cordillera includes Vancouver Island, Interior British Columbia, Northwestern states, foothills provinces and states. Axes are log2 transformed. Two-way ANOVA, on Log transformed variables with Tukey *post hoc* comparisons; bars sharing the same letter are not significantly different ($p<0.05$).

FB, $F_{Tot,3,1,3,426}=154$; $F_{RG,3}=105$, $p<0.0001$; $F_{LR,1}=3.2$ $p<0.07$; $F_{RG*LR,3}=46$, $p<0.0001$;

SpR, $F_{Tot,3,1,3,426}=348$; $F_{RG,3}=189$, $p<0.0001$; $F_{LR,1}=140$, $p<0.0001$; $F_{RG*LR,3}=18.7$, $p<0.0001$;

TP, $F_{Tot,3,1,3,426}=63$; $F_{RG,3}=58$, $p<0.0001$; $F_{LR,1}=0.0$,$_{ns}$; $F_{RG*LR,3}=5.2$, $p<0.002$

N:P, $F_{Tot,3,1,3,426}=31$; $F_{RG,3}=29$, $p<0.0001$; $F_{LR,1}=1.3$,$_{ns}$; $F_{RG*LR,3}=0.3$,$_{ns}$;

Under-Saturation of Fish Biomass in some Species-Poor Lakes.

All sites where FB was reported to be < 0.1 g.m-2 occurred in the Western Cordillera and in Newfoundland in lakes where species richness was very low; in fact, in all cases only 1 or 2 species, both salmonids, were present; 15 such lakes were from Newfoundland and contained only brook trout and Atlantic salmon (Clarke and Scruton 1999), and 30 such lakes were from British Columbia (Shortreed et al. 2001, Hyatt et al. 2004) and usually contained only sockeye and sometimes kokanee salmon. The estimates available for FB in the NL lakes, were uncorrelated with TP concentrations, despite considerable range in TP values (Cote et al. 2011), and size of Atlantic salmon parr from these lakes was not not correlated with numerical density (Ryan 1986). Since the efforts to enhance the production of sockeye salmon smolts in B.C. lakes involve considerable effort and expense to purchase and administer P and N fertilizers, considerable effort was expended to identify lakes where sockeye production was unlikely to be nutrient limited, and thus unlikely to be enhanced by fertilization. Thus for the 30 sockeye salmon lakes referred to above FB was uncorrelated with either TP or TN levels, or N:P ratios, and moreover, mean size of fry or outmigrating smolts was uncorrelated to abundance (Hyatt and Stockner 1985). The most common reason cited for sockeye and kokanee populations in these lakes being below capacity was recruitment limitation resulting from limited access to good spawning habitat in associated rivers and streams, with migration barriers also an often-cited factor (Shortreed et al. 2001). Like sockeye and kokanee salmon, neither Atlantic salmon nor brook trout typically use lakes for spawning, and only move into lakes from nursery rivers and streams later in their juvenile life-history; thus it is likely that biomass of these salmonids in these ‘under-saturated’ is similarly recruitment limited.

Since the effort to build empirical models in this study is based on the principle of nutrient limitation, the 45 lakes cited above, whose FB was clearly not a function of nutrient status, were not included in the dataset used to generate our empirical models. With the exception of NL lakes, whose under-saturation has been outlined, Log TP was a highly significant predictor of Log FB for both lakes and rivers; however, the strength of the relationship was highly variable. R^2 ranged from 0.35 – 0.74, which was similar to the range to that reported in previous studies (0.24 – 0.83). Intercepts ranged from -1.29 to +0.21, with lakes and rivers broadly similar, a broader range than reported in previous studies (-0.29 – 0.55). Slope estimates were also highly variable ranging from +0.81 – 1.64, compared to 0.32 – 1.02 in previous studies. River slopes were all higher than that previously published for rivers (Hoyer and Canfield 1991). Overall, lakes did not differ significantly from rivers with regard to intercept, slope or R^2 (Figure 3, Table 2).

The highest intercept was found in Central U.S.A lakes (Table 2), the region with highest biodiversity. The Western Cordillera and NL the regions, with the lowest biodiversity, had low intercepts; intercept was correlated with mean Log SpR ($r = 0.57$, $p = 0.07$). For lakes, the slopes were similar (near 1) in all regions (Figure 3a, Table 2); however, an extremely low slope was reported by Bachmann et al. 1996 for a set of shallow, predominantly littoral Florida lakes. Consistent with this, when lakes were broken down into three depth groups (mean depth < 3m, 3 – 15 m, > 15 m), there was a very consistent pattern in regard to both intercept and slope, with intercept highest, and slope lowest in the shallow lakes, and the intercept lowest and slope highest in the deepest lakes (Figure 3b).

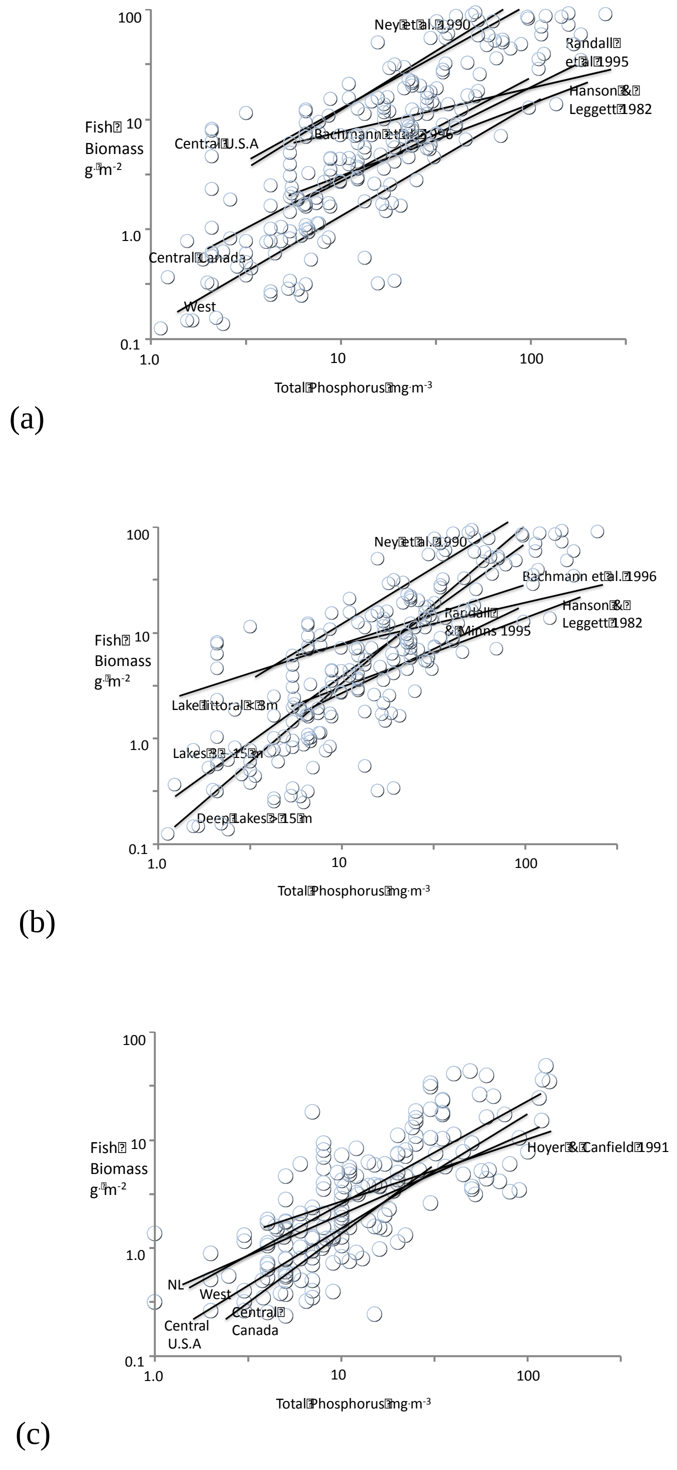

Figure 3.3: Log FB vs Log TP Relationships for lakes and streams compared to previously published relationships. From top to bottom: (a) lakes categorized by region (b) lakes categorized by depth (c) rivers categorized by region. Regression models are listed in Table 2.

Table 3.2: Comparison of intercepts and slopes from regressions in Figure 3.

Log$_{10}$ FB = Intercept + slope * Log$_{10}$ TP	Intercept ± SE	Slope ± SE	RMS, R^2	Log SpR	N
Central Canada lakes	-0.46 ±0.19	+0.94 ± 0.18	0.39, 0.35	0.58	49
Central Canada rivers	-1.29 ± 0.16	+1.64±0.14	0.31, 0.74	0.92	48
Western Cordillera lakes	-0.76 ± 0.12	+0.92 ± 0.17	0.43, 0.35	0.44	58
Western Cordillera rivers	-0.42 ± 0.18	+0.81 ± 0.10	0.37, 0.51	0.34	65
Central U.S.A lakes	0.21 ± 0.09	+0.81 ± 0.06	0.33, 0.59	1.29	113
Central U.S.A rivers	-0.92 ± 0.10	+1.12 ± 0.10	0.43, 0.66	0.50	65
Newfoundland rivers	-0.52 ± 0.25	+0.89 ± 0.18	0.36, 0.48	-0.52	30
All lake data	-0.66 ± 0.07	+1.28 ± 0.06	0.47, 0.65	0.91	220
All river data	-0.66 ±0.07	+1.00 ±0 .06	0.39, 0.59	0.51	218
Hanson & Leggett 1982	-0.23	+0.71	----, 0.75	----	18 lakes Central
Ney et al. 1990	0.24	1.02	----, 0.84	1.70	21 central U.S.A. Reservoirs
Randall et al. 1995	-0.29 ± 0.16	0.63 ± 0.11	0.28, 0.65	----	18 Global lakes & rivers
Hoyer & Canfield 1991	-0.18	+0.59	----, 0.64	----	79 rivers Canada & U.S.A
Bachmann et al. 1996	+0.55	+0.32	----, 0.24	1.5	65 Florida lakes

Multiple Regression Models relating FB to TP and Biodiversity

Both TP and SpR were highly significant predictors of FB in every region, and in both lakes and rivers. The intercepts of these models as well as the slope coefficients for TP and SpR both varied greatly among regions for both lakes and rivers. Intercepts were all negative, more strongly so in lakes than rivers, and ranged from -0.20 in Central USA lakes to -1.33 in Central Canada rivers. The slope coefficient for Log TP was similar for lakes and rivers, but varied overall from +0.59 in Central U.S.A rivers to +1.18 in Central Canada rivers, and the coefficient for Log SpR was smaller for rivers than lakes, and varied overall from +0.35 in Central U.S.A. lakes to +1.39 in NL rivers. No interaction between Log TP and Log SpR was significant in any of the regions for either lakes or rivers. Although the inclusion of Log SpR in the models helped explain considerable variation both within and among regions compared to models that contained only Log TP, considerable variability among regions remained.

Table 3.3: Multiple regression models testing Log FB vs Log TP and Log SpR for each region, and for all lakes and rivers.

Log FB = A + B*Log TP+ C*logSpR	A ± SE	B ± SE	C ± SE	RMS,R^2	N
Central Canada Lakes	$-0.64_{\pm0.16}$	$0.76_{\pm0.16}$	$0.62_{\pm0.13}$	0.31, 0.55	49
Central Canada Rivers	$-1.33_{\pm0.15}$	$1.18_{\pm0.19}$	$0.66_{\pm0.20}$	0.28, 0.79	48
Central USA Lakes	$-0.20_{\pm0.19}$	$0.78_{\pm0.06}$	$0.35_{\pm0.14}$	0.32, 0.61	113
Central USA Rivers	$-0.72_{\pm0.14}$	$0.59_{\pm0.14}$	$0.81_{\pm0.15}$	0.32, 0.82	37
Western Lakes	$-1.00_{\pm0.14}$	$0.69_{\pm0.17}$	$0.90_{\pm0.29}$	0.39, 0.45	58
Western Rivers	$-0.51_{\pm0.09}$	$0.73_{\pm0.10}$	$0.47_{\pm0.15}$	0.34, 0.57	66
Newfoundland Rivers	$-0.55_{\pm0.21}$	$+0.66_{\pm0.17}$	$+1.39_{\pm0.46}$	0.32, 0.61	30
All Lakes	$-0.92_{\pm0.06}$	$+0.85_{\pm0.06}$	$+0.80_{\pm0.0.06}$	0.36, 0.79	30
All Rivers	$-0.69_{\pm0.06}$	$+0.79_{\pm0.06}$	$+0.51_{\pm0.0.06}$	0.35, 0.68	218

Multiple Regression Models Relating Log FB to log TP, Biodiversity and Morphometry

Our hypothesis providing rationale for why mean depth and river size should affect FB models were supported by the models developed for lakes and rivers. For lakes, the model contained a highly significant mean depth term as well as strong interaction term between depth and nutrient richness.

The model obtained was

$$ {}_{Log}FB = -\,0.27_{\pm\,0.10} + 0.48_{\pm\,0.07}\ {}_{Log}TP + 0.62_{\pm\,0.05}\ {}_{Log}S - 0.45_{\pm\,0.07}\ {}_{Log}\ Dm + 0.44_{\pm\,0.07}\ Dm{*}TP $$

$$ R^2 = 0.85;\ RMS = 0.28,\ p < 10^{-9} \text{ for all variables, } N = 227. \qquad (1) $$

Similarly for rivers, when river width (Log RW) was added, the model obtained was

$$ {}_{Log}FB = -\,0.46_{\pm\,0.07} + 0.83_{\pm\,0.05}\ {}_{Log}TP + 0.60_{\pm\,0.06}\ LogS - 0.31_{\pm\,0.05}\ LogRW \qquad (2) $$

$$ R^2 = 0.79;\ RMS = 0.28,\ p < 10^{-8} \text{ for all variables, } N = 174. $$

When the number of fish functional groups (Log FG) (see Appendix B) was added to the models in place of Log SpR, the lake model became slightly stronger

$$_{\text{Log}}\text{FB} = -\ 0.63_{\pm\ 0.10} + 0.57_{\pm\ 0.07}\ _{\text{Log}}\text{TP} + 1.83_{\pm\ 0.12}\ _{\text{Log}}\text{FG} - 0.44_{\pm\ 0.07}\ _{\text{Log}}\ \text{Dm} + 0.37_{\pm\ 0.06}\ \text{Dm*TP}$$

$$R^2 = 0.88;\ \text{RMS} = 0.26,\ p < 10^{-7} \text{ for all variables, N} = 227. \quad (3)$$

However, the river model became slightly weaker

$$_{\text{Log}}\text{FB} = -\ 0.43_{\pm\ 0.08} + 0.93_{\pm\ 0.06}\ _{\text{Log}}\text{TP} + 0.81_{\pm\ 0.15}\ \text{LogFG} - 0.26_{\pm\ 0.06}\ \text{LogRW} \quad (4)$$

$$R^2 = 0.72;\ \text{RMS} = 0.31,\ p < 10^{-5} \text{ for all variables, N} = 174.$$

No additional variance could be explained by region, latitude or longitude in either the lake or river models. Thus these models were general in that they explained the large level of regional variation in FB and in the FB vs TP relationships through a combination of biodiversity and morphometric terms. Interactions terms between TP and SpR and FG were tested, but failed to contribute significantly to either the lake or river models, and for the river model an interaction between TP and RW was also not significant. In support of hypothesis regarding species and functional richness, both Log SpR and Log FG made strong contributions to both the lake and the river model, and moreover, both the magnitude and strength of the coefficient for Log SpR was similar in both models. In addition to its strong contribution to the general models, biodiversity terms also made highly significant contribution within each region, although the magnitude and strength of the coefficients tended to be weaker when the data set was split into regions (Table 4). Even in regions such as Newfoundland and the West, where biodiversity was low and did not vary over a broad range, it still made a strong contribution to the models. The effect of species richness as reflected in Eq. 1 is displayed as a family of lines representing different SpR values, on a Log FB vs Log TP plot (Figure 4a), and directly, as a Log FB vs Log SpR plot, for different levels of TP (Figure 4b), and as with plot of untransformed FB vs SpR values, which illustrates that the underlying relationship between FB and SpR as a saturating curvilinear power function.

A considerably weaker lake model was obtained using TN in place of TP was obtained

$$_{\text{Log}}\text{FB} = -\ 2.04_{\pm\ 0.22} + 0.80_{\pm\ 0.08}\ _{\text{Log}}\text{TN} + 0.76_{\pm\ 0.07}\ _{\text{Log}}\text{SpR} - 0.13_{\pm\ 0.07}\ _{\text{Log}}\ \text{Dm} \qquad (5)$$

$R^2 = 0.74$; RMS = 0.39, $p < 0.05$ for all variables, N = 193.

For rivers the best model obtained using TN in place of TP was was also considerably weaker than the corresponding model based on TP

$$_{\text{Log}}\text{FB} = -\ 0.90_{\pm\ 0.21} + 0.46_{\pm\ 0.09}\ _{\text{Log}}\text{TN} + 0.95_{\pm\ 0.15}\ \text{LogS} - 0.38_{\pm\ 0.12}\ \text{LogRW} \qquad (6)$$

$R^2 = 0.59$; RMS = 0.37, $p < 0.01$ for all variables, N = 81.

Table 3.4: Correlation matrix for main variables used in Lake and River models

Lakes

	Log TP	Log TN	N:P	Log SpR	Log FG	Log Dm	Log FB
Log TP	----	0.79	-0.30	0.51	0.41	-0.39	0.82
Log TN	0.79	----	0.25	0.54	0.43	-0.63	0.76
N:P	-0.30	0.25	----	ns	ns	ns	ns
Log SpR	0.51	0.54	ns	----	0.85	-0.21	0.73
Log FG	0.41	0.43	ns	0.85	----	-0.07	0.70
Log Dm	-0.39	-0.63	ns	-0.21	ns	----	-0.36
Log FB	0.82	0.76	ns	0.73	0.70	-0.36	----

Rivers

	Log TP	Log TN	N:P	Log SpR	Log FG	Log RW	Log FB
Log TP	----	0.71	-0.39	0.41	0.37	ns	0.77
Log TN	0.71	----	0.27	0.54	0.57	0.37	0.65
N:P	-0.39	0.27	----	ns	ns	ns	ns
Log SpR	0.41	0.54	ns	----	0.82	0.37	0.55
Log FG	0.37	0.57	ns	0.82	----	0.39	0.41
Log RW	ns	0.37	ns	0.37	0.39	----	ns
Log FB	0.77	0.65	ns	0.55	0.41	ns	----

Analysis of Residuals

Residuals from sites containing each of the taxa listed in Table 1 were compared to sites from which each was absent; this comparison was carried out separately for lakes (Eq. 1, 29 taxa) and rivers (Eq. 2, 17 taxa) for each of the taxa found at 10 or more sites. After Bonferroni correction for the number of tests done, the only taxa for which significant presence vs absence differences were found were found were common carp, and buffalofish in lakes. Lakes with common carp (n = 50) had an average residual of 0.15 compared to -0.04 for lakes without carp ($t = 4.47$, $p = < 0.001$), and lakes with buffalofish (n = 20) had an average residual of 0.36 compared to -0.03 for lakes without them ($t = 4.83$, $p < 0.001$). Similarly, residuals from Eq. 1, were compared for lakes and reservoirs, which were not significantly different, and for Eq. 2 the 33 rivers open to migratory salmonids either from the sea or the Great Lakes had an average residual of +0.18 compared to -0.03 for streams closed to such migrations ($t = 3.54$, $p < 0.01$). This positive residual effect occurs in spite of the fact that the biomass estimates from these rivers do not include migrating anadromous adults. When the analysis was repeated with an additional species added to designate resident rainbow trout, steelhead, brook trout, and cutthroat trout in the streams that contained migratory populations of these species, the new model was

$$_{\mathrm{Log}}\mathrm{FB} = -\,0.47_{\pm\,0.07} + 0.79_{\pm\,0.05}\ {}_{\mathrm{Log}}\mathrm{TP} + 0.64_{\pm\,0.06}\ \mathrm{LogSpR} - 0.30_{\pm\,0.05}\ \mathrm{LogRW} \qquad (8)$$

$$R^2 = 0.80;\ \mathrm{RMS} = 0.26,\ p < 10^{-8} \text{ for all variables, } N = 174$$

and the difference between residuals for open and closed rivers was no longer statistically significant. In several lakes, sockeye juveniles and kokanee salmon occur together and were counted as separate species in Eq. 1.

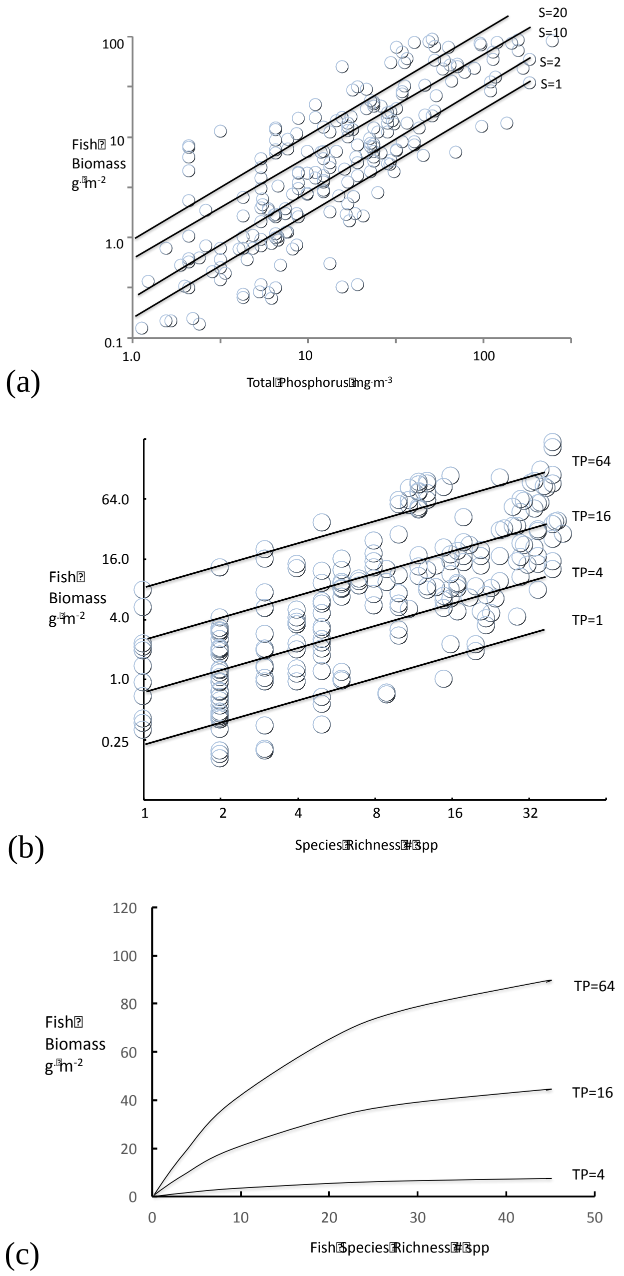

Figure 3.4: The combined influence fish of trophic richness (total phosphorus) and fish species richness on fish biomass.From top to bottom:(a) shows LogFB vs LogTP for a family of SpR values, (b) shows the Log FB vs Log SpR for different TP levels, and (c) shows the same relationship for untransformed FB and SpR. The plots are based upon Eq 1. with mean depth set to 10 m. Here Eq 1 is displayed in terms of Log_2,

$$_{Log}FB = -0.87+(0.47_{Log}TP)–(0.46_{Log}\ Dm)+(0.13* Dm*TP)$$

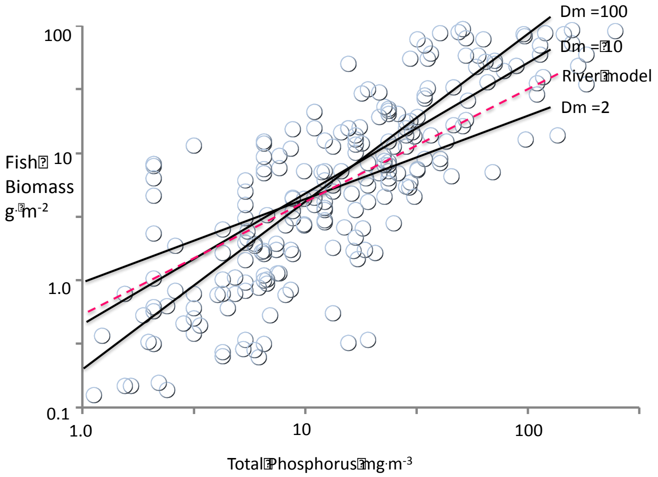

Figure 3.5: The combined influence of trophic richness (total phosphorus) and mean depth on fish biomass in lakes. The plots are based upon Eq 1. with SpR set to 5 spp. The river model is Eq 2, with S = 5 species and river width = 10 m.

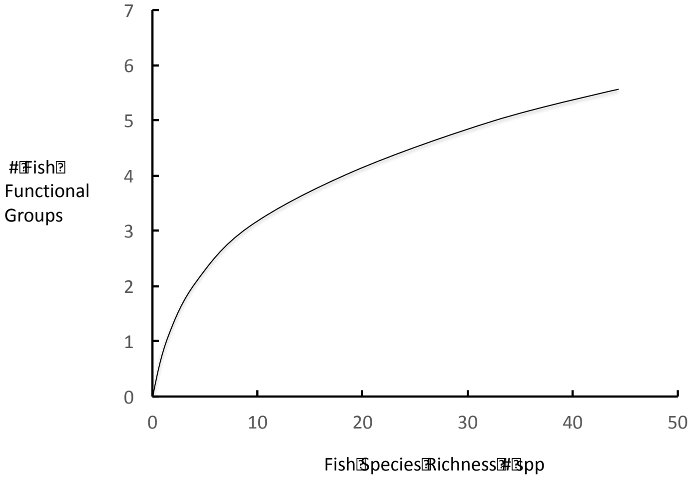

Figure 3.6: The relationship between species richness and functional groups. Functional groups determined from functional group designations available in Appendix B.

A multiple regression analysis for both species together yielded:

$$\text{Residual} = -0.04 + 0.11(0.02) * \text{Carp} + 0.21(0.08) * \text{Buffalofish} \quad (7)$$
$$R^2 = 0.11, \text{RMS} = 0.26.$$

Discussion

Fish biomass in both lakes and rivers varied over nearly three orders of magnitude, but when the variance in FB was analyzed among and within regions, about 2/3 was allocated to the regional scale, and 1/3 within region (Table 1). Variability both within and across regions could be explained by a combination of nutrient richness, fish biodiversity and morphometry, each of these factors being highly variable both within and across regions, with each of these factors contributing about equally to two empirical models that explain the variance in FB to within a factor of about two. The strength and direction of the contributions from nutrient richness, fish biodiversity and morphometry supported all outlined hypotheses.

TP was strongly linked to FB using Log-Log regressions, and this relationship was strong for both lakes and rivers (Table 2; Figure 3). Strong links between biomass and TP have been demonstrated for phytoplankton (chlorophyll a) (Bachmann and Jones 1974, Dillon and Rigler 1974), and zooplankton, and zoobenthos (Hanson and Peters 1984, Rasmussen 1988), and TP is generally regarded as the overall best statistical measure of nutrient richness. Models linking TP to fish community biomass have been published previously for lakes (Hanson and Leggett 1982, Bachmann et al. 1996) for reservoirs (Ney et al. 1990), and for rivers (Hoyer and Canfield 1991, Randall et al. 1995). While total Nitrogen (TN) is generally correlated with Total Phosphorus, and can sometimes provide reasonable predictions of trophic richness, TN was always present in excess of the Redfield ratio, and more variable than TP, and as a result is a much weaker predictor of FB in our data set.

The multiple regression models developed here, Eq. 1 & 2, express the predictive effect of log TP and Fish Biodiversity for both lakes and rivers. For lakes these effects were combined with mean depth as a morphometric variable and its interaction with TP. This shows that while FB tends to decrease with mean depth in lakes, the effect of TP (an indicator of water column richness) increases strongly with the depth of the water column. The effect of TP on FB is weaker in shallow lakes, because littoral primary and secondary production can access the sediment nutrient pool, and thus compensate for low water column richness, especially since this will be accompanied by increased light penetration (Yvonne et al. 2008). The negative effect of water column depth is most strongly felt in species poor lakes, but is compensated by increased fish biodiversity, which leads to more effective use of space within the column, and energy flow through the food web both throughout the water column, as well as in the profundal zone. Judging by the strength of the coefficients in Eq. 1 for mean depth, -0.45 for a ten-fold increase in depth, vs +0.62 for a ten-fold increase in species richness, an increase in mean depth from 2 – 20 m would be much more than compensated by an increase from 2 - 20 species. In rivers, the morphometric factor that was captured in Eq. 2 was river width, which had a coefficient of -0.33. Thus an increase in river width from 2 -20 m would be effectively compensated for by a three-fold increase in species richness. Thus the predictive power of TP, combined with biodiversity, and morphometry captures the main differences within and among regions for both lakes and rivers, and none of the residual variability could be explained by region, latitude or longitude.

Why is Biodiversity Such a Strong Predictor of Fish Community Biomass?

The power of fish species and functional group richness to influence the relationship between trophic richness and fish biomass, has been little studied, and in fact, has been rarely studied by aquatic ecologists. Since species differ in life history, habitat requirements, and sensitivity to environmental risks, species richness can potentially buffer systems against recruitment limitation, thus providing redundancy by hedging against risks, as discussed in chapter two. However, this is not likely the factor being captured in Eq. 1 - 4, since the sites that were considered to be strongly undersaturated were removed a priori from the data set. The contribution of species and functional group richness in the multiple regression models likely reflects functional diversity among species in trophic ecology. Thus the differences among taxa and functional groups in food resources they use, and the associated food web pathways that drive energy flow within the community, likely means communities with greater species richness have access to a broader base of energy and nutrient sources, and can utilize effectively a broader range of habitats, including depth zones (Carey and Wahl 2011). Although most species overlap in their food utilization to some extent, and many are ‘trophic generalists,’ our analysis indicates that the extent to which they differ appears to lead to additive effects on community biomass. To reiterate an example provided in the preceding chapters, the food chain in a lake that lacks pelagic zooplanktivores would make far less efficient use of plankton productivity than one that contained efficient zooplanktivores, and fish biomass, in the latter system should be higher. Similarly, efficient microbenthivores, herbivores, detritivores, deposit feeders, and periphyton feeders should all expand the trophic spectrum of the community significantly. This principle, the combination of redundancy and functional complementarity, has been shown to explain the observed increases in the productivity, biomass and stability of grasslands (Tilman and Downing 1994, Hooper et al. 2005) and other plant communities; however, the significance of fish biodiversity for productivity has received little consideration.

Why are Lakes in Species Poor Regions Prone to 'Under-Produce'?

In chapter 1 we draw support for the use of residuals in our species richness-biomass model to describe functional richness, from a model of functional under-saturation in species poor Newfoundland lakes (Chapter 1, Figure 8), though discuss only briefly the underlying mechanisms for this phenomenon; our results here may offer greater insight. The differences among species in life history, habitat requirements and sensitivity to environmental risks can do more than increase trophic efficiency; it can buffer systems against environmental factors that can cause recruitment limitation, thus providing redundancy by hedging against risks. The faunas of both insular Newfoundland, and the Western Cordillera, two species poor regions, are poor in lacustrine specialists, i.e. fish species that complete their entire life-cycles, from spawning to the adult stage, within the lakes (Clarke and Scruton 1999, Cote 2007, Cote et al. 2011). The fishes that comprise the limnetic faunas in these regions are primarily salmonids that spawn in rivers and streams, producing young that migrate to the lakes for a portion of their juvenile life, before leaving again and to mature elsewhere, either at sea or in larger lakes or rivers. As a result, any factor that leads to a bottleneck in recruitment, i.e. limited availability or access to good spawning or nursery habitat, or barriers that restrict movement of either outgoing juveniles or returning adults, whether they be natural or man-made, will limit populations to a fraction of the lakes productive capacity. Since the regional fish faunas are so species poor due to zoogeographical barriers that have limited post-glacial access from major refugia (McPhail and Lindsey 1970, Van Zyll de Jong et al. 2005), there are rarely other species present that are capable of compensating for such recruitment limitations, and as a result total fish biomass of such systems can be far below what the lakes could support. Recruitment limitations of this kind are not limited to lakes, but can of course occur in rivers and streams as well especially upstream of waterfalls or other barriers, but the generally greater availability of salmonid spawning and habitat, and the overall higher connectivity of rivers, makes rivers more likely to approach their productive capacity than lakes in species poor regions.

Recruitment limitation limits lake fish biomass differently in these two species poor regions. The lakes in the Cordillera are much larger and deeper, their watersheds are steeper, and their oligotrophy is much more extreme than in Newfoundland. Moreover, the salmonids that use the lakes are different, and the role of lakes in their life-history is also different. In the West, the main species utilizing the large, deep fjord lakes is the sockeye salmon (*Oncorhynchus nerka*) and their land-locked counterpart the Kokanee salmon. Both spawn primarily in streams, usually inflows, and migrate to the lakes as fry, and spend one or more years as pelagic zooplanktivores, before migrating out, either as smolts going to sea for one or more years, or as adults migrating to spawn.

Hydroacoustic fish surveys were found for 46 such ‘sockeye’ lakes, and of these, only 16 were considered to have fish communities that approached productive capacity as judged by primary productivity, zooplankton biomass and nutrient richness (Shortreed et al. 2001, Hyatt et al. 2004), and the remainder often had fish populations as much as 10-fold lower than the trophic regime was estimated to be able to support, and were considered unlikely to respond to nutrient fertilizations. For these lakes FB was uncorrelated with TP, and the mean size of fry or outmigrating smolts was uncorrelated to abundance (Hyatt and Stockner 1985). The most common reason cited for sockeye and kokanee populations being below capacity was, limited access to good spawning habitat, with migration barriers also an often-cited factor (Shortreed et al. 2001).

Restricted access to suitable spawning gravels is greatly exacerbated by the steep terrain leading to washout of fine gravels, and waterfalls and impassible ‘chutes’ near the lakes on most inflow streams. In only one case was the presence of another species, the three-spined stickleback *Gasterosteus aculeatus*, listed as a factor limiting sockeye abundance (Shortreed et al. 2001). While there are some other salmonids that do sometimes use these lakes, none are efficient pelagic zooplanktivores or lake spawners (McPhail 2007). As a result, poor species richness in the regional fauna of the Cordilleran region of Western North America makes the probability of ‘under saturation’ due to recruitment limitation greater, and this factor has its greatest impact on fish biomass in the large deep fjord lakes.

The lakes of Newfoundland are much shallower and less oligotrophic than the western fjord lakes, and while the geography of the landscape is much less steep, fine gravel can still be limiting in some areas because most glacial outwash is below sea level due to post glacial subsidence (negative uplift) and increases in marine sea level (Batterson and Liverman 2010). Many of the lakes appear as widenings along relatively low-gradient rivers to which riverine fish have ready access (Cote et al. 2011).

The main fishes that use the lakes are Atlantic salmon parr (Salmo salar) and juvenile brook trout (*Salvelinus fontinalis*) (Clarke and Scruton 1999). Both are generalist feeders, utilizing mainly littoral benthic macroinvertbrates and neither are effective zooplanktivores. The arctic charr (*Salvelinus alpinus*) is present in Newfoundland, and its juvenile stages are efficient zooplanktivores, but the species is found in very few of the lakes (Van Zyll de Jong et al. 2005). The three-spined stickleback is also found in some of the lakes but its contribution biomass is small (Ryan 1984). Newfoundland atlantic salmon are atypical in that they often move from rivers into lakes and feed on littoral macroinvertebrates (Ryan 1986). This likely reflects the fact that Newfoundland lakes lack the diverse array littoral zone competitors found in most continental lakes (Erekinaro and Gibson 1997). Similarly, the brook trout found in Newfoundland lakes are also juveniles that have moved from stream nursery habitats to lakes as larger juveniles. Neither species spends more than a fraction of its life-cycle in the lakes; the salmon smolt and migrate to sea following their lacustrine phase, and the brook trout move to streams and spawn.

The extremely low biomass in many of the Newfoundland lakes relative to their associated rivers and to their nutrient levels, is an indication of under-saturation. Moreover, the biomass of fish in these lakes is uncorrelated to nutrient richness, despite considerable range in trophic richness (Cote et al. 2011) and size of par is not correlated with density (Ryan 1986). The abundance of both salmonid species within river systems, is likely determined by the capacity of the spawning and nursery habitat in the streams and rivers, and the abundance of fish in the larger lakes appears to bear little relation what the lake resources could support, since the lacustrine phase of the salmon and brook trout in Newfoundland is only a minor portion of their overall life-history. Thus the recruitment limitation leading to undersaturation in Newfoundland lakes likely results from lake habitat being available in higher proportion than spawning and rearing habitats for the two main salmonids that use the river systems. Just as on the west coast, the poor species richness in the Newfoundland fish fauna makes the probability of ‘under saturation’ due to recruitment limitation greater, since there is a lack of lacustrine specialists, especially zooplanktivores, whose abundance would be limited by the lake resources rather than the recruitment capacity of associated rivers and streams.

Interestingly, species-poor systems are not confined to salmonid dominated coastal regions; In Central North America and Europe, there are species poor headwater systems where the one or two species present are either yellow perch (*Perca flavescens* or *P. fluviatilis*), cyprinids (in Europe usually the roach *Rutilus rutilus*, and in North America, the northern red-belly dace and golden shiner), centrarchids (usually bluegill or pumpkinseed sunfish) or catostomids (usually white sucker) (Kelso and Johnson 1991, Horppila et al. 2010). While biomass in these lakes is invariably low compared to similar multi-species lakes, there are no cases of extreme under production, where biomass is over an order of magnitude deficient relative to trophic resources, such as the cases described in coastal salmonid lakes. The likely reason for this is that recruitment limitation is much less likely to occur in perch, minnow or sucker lakes, since these species are capable of spawning and completing their life cycles in lakes or slow-moving streams, and do not have specialized requirements such as clean fine gravels. As a result, bottlenecks related to access to spawning grounds and/or habitat fragmentation are not likely to occur in species poor perch, minnow or sucker systems.

The Relationship of Fisheries Yields to Biomass and Nutrient Status

While TP has been used to predict commercial fish yields (Hanson and Leggett 1982) as well as sportfish yields (Jones and Hoyer 1982), the precision with which this can be done is limited, since the proportion of the total fish community that actually contributes to the fishery will depend on many factors, both ecological and social. The proportion of community biomass targeted by a fishery is usually very high in boreal lakes (Rawson 1951) whose communities contain whitefish, ciscoes, perch, walleye and lake trout of targetable size to commercial and recreational fisheries. While sockeye salmon smolts are not directly targeted by fisheries, they are of course a highly valued fisheries resource, and that can constitute as much as 90% of the biomass in many west coast lakes (Hyatt et al. 2004). Alternatively, many lakes may contain significant biomass of large carp, chubs, shiners, bullheads and suckers (Carlander 1955) that are often not targeted by fisheries, and in such situations only a few percent of community biomass may be contributing to fisheries. Clearly, the proportion of the community biomass targeted by a fishery is highly variable, and will depend on the types of fish species present in a region, the structure of the food web, and to a very large extent on social factors such as which fish species are ‘desirable’ and which are not. None of these factors are direct or predictable functions of the nutrient regime, at least not on a broad scale across regions that differ broadly in their faunas and in their culture.

Conclusions

Processes that beget fish biomass in freshwater ecosystems, and which govern maximum biomass potential in our lakes and rivers, have been a focal point of fisheries research for decades. Bottom up processes, i.e. those which influence primary productivity, were the earliest to be studied and have since received the most attention, and have provided the framework for an array of models which can predict fish productivity from simple measures such as nutrient concentrations, or growing degree days, with reasonable accuracy (Dillon and Rigler 1974, Stockner and Shortreed 1978, Chezik et al. 2013). These models, however, do not offer the same accuracy when applied to predictions of fish biomass and, as such, it has been widely recognized that top down processes, i.e. predator-prey interactions, are likely also a significant contributor to this relationship (Carpenter et al. 1985, Carpenter et al. 1987, Carpenter et al. 2001). Considering this persistent knowledge gap, it seems reasonable to assume that a more wholistic approach is required to bridge these theories, which is why it is perhaps surprising that, to date, such little attention has been afforded to the role of species richness in the equation. It is the collection of species within an ecosystem which create the framework for energy transfer from basal resources to apex predators, and the mosaic of interactions among them which dictate the functionality and efficiency with which that energy is transferred. Ultimately, it is the dynamics of species richness which can bridge our theories of bottom up and top down processes in the pursuit of accurate fish biomass models, and it is precisely that which we intended to demonstrate with the research outlined in this thesis.

To assess the utility of species richness as a predictor of fish biomass, we identified three sequential questions to address: 1- Does a relationship exist among species richness and fish biomass in real world freshwater ecosystems?; 2- If a relationship does exist, what is the role of trophic function, and can this be quantified with current statistical tools?; 3-If a relationship does exist, can it be used to strengthen biomass estimates from predictors of primary productivity, such as nutrient concentrations? In our pursuit to test these hypotheses, we have drawn a series of conclusions which we hope will prompt further discussion regarding the influence of species richness in freshwater fisheries, and provide guidance for future studies wishing to further this research.

First, through the investigation of 26 freshwater ecosystems distributed across the Canadian landscape, we found a significant, positive relationship among species richness and fish biomass. Though perhaps intuitive, this was an important first step as it represents, to our knowledge, the first empirically driven, positive and significant relationship demonstrated between species richness and fish biomass in multitrophic, freshwater ecosystems. Moreover, the observed relationship here mirrors the relationship proposed by Tilman (1997a) from his study of grassland species, which is widely accepted, lending further support to our findings. Perhaps the most interesting finding in this investigation, however, came from further examination of the dataset with the consideration of trophic functional groups. Upon reviewing the residuals produced in the species richness-biomass model, it was apparent that the sign of the residual (positive or negative) could be accurately predicted from the relative number of functional groups present in an ecosystem. From this observation, we proposed the theoretical concept of a “maximum functionality” and “minimum functionality” curve to describe the upper and lower limits of the species richness-biomass relationship, and we provide empirical evidence from past examples in the literature which provide support for these theories.

Conveniently, these proposed curves lend themselves quite nicely to testing, and we would encourage future studies to provide further investigation. While testing of the “minimum functionality” curve may provide little more than proof of concept, investigations of the “maximum functionality” curve could provide valuable insight into complementarity of functional roles in freshwater ecosystems, and could possibly be used to validate assumptions of optimal species community composition with respect to biomass capacity in freshwater ecosystems.

Once the positive relationship between species richness and biomass had been established, and considerable reason existed for the assumption of an effect of trophic function, we set out to attempt to quantify the effect of function using modern analyses facilitated by stable isotope ratios. This presented not only an opportunity to quantify a portion of the residual variance in the species richness-biomass model, but also to test the utility of commonly used stable isotope analyses to describe this variance (and therefore describe trophic function), which would be a novel application of these tools. We considered metrics which described community and individual species dynamics, as well as trophic interactions, and found that components of each were successful in describing trophic function. Moreover, from the suite of metrics which successfully captured additional model variance, we were able to draw insight into a question we had not intended to address, regarding evolutionary considerations of generalist vs specialist strategies. One prominent advantage of the generalist strategy is that it enables species to be better adept at adapting to environmental perturbations, leading to greater reliance of individual species. Specialists, on the other hand, feature more efficient consumption strategies and energy transfer rates, and because species are more compartmentalized within their community, it is thought that this strategy facilitates greater species co-existence, providing the overall community with greater resilience in the face of environmental perturbations. As such, when considering the phenomenon of niche partitioning, i.e. the ability of two generalists with overlapping niches to partition the shared resource and specialize, evolutionary researchers are left with the question of whether this strategy is employed to increase productivity, or to facilitate species co-existence. Although our dataset is far too small to draw any real conclusions on the topic, is was apparent from our dataset that trophic efficiency was greatest in communities which were neither dominated by specialists, nor generalists, but rather featured a mix of both strategies. This might suggest that the strategy of niche partitioning tends to both maximize energy transfer while also promoting co-existence, and should not be viewed as a means to solely either end. Moreover, it is possible that this strategy is therefore just as likely to be driven by the breadth of the food resource available to the community as it is by species life histories, which further elucidates the importance of considering basal carbon resources in studies which make inferences about food web dynamics and evolutionary implications thereof, as we posit in our discussion in chapter two.

Our final objective was to investigate whether the relationship between species richness and biomass, as demonstrated in chapter 1, could be used to strengthen primary productivity-biomass models and resolve the unexplained regional variance associated with those models. On both accounts, we were able to confirm the affirmative, demonstrating that not only is our model compatible with the most prevalent present-day fisheries biomass models, but also that the species richness-biomass relationship proposed here is still valid when applied to larger data sets than that presented in chapter 1.

Additionally, by including nutrients as a covariate in our model, we were able to identify "under-performing" lakes based on assumptions from their trophic status, and gain further insight into the dynamics of "functional under-saturation" theorized in chapter 1. What was proposed is that the mechanisms which beget functionally under-saturated systems, such as limited species pools from post-glacial recolonization factors, and evolution of life history traits specific to regionally unique habitat, can also render populations more vulnerable to environmental perturbations which impede recruitment, which then further compounds the under-performance of these populations with regards to biomass potential. This would suggest that the "functional under-saturation" curve presented in chapter 1 is likely to some degree dependant on not only species richness, but also life history and even environmental perturbations. This exemplifies the types of inferences which can be made from analysis which consider dynamics of species richness in combination with measures of primary productivity and habitat, and the applicability of our findings here with respect to management of Canadian freshwater fisheries.

Although the species richness-biomass relationship, first demonstrated in chapter 1, was shown to hold true when applied to a much broader data set in our chapter 3 analyses, it is important to note that the inferences made here regarding trophic functionality and community efficiency were based on a relatively small dataset. Furthermore, the lakes and streams considered in the analyses from chapters 1 and 2 are limited to relatively small systems with very similar habitat characteristics and fish communities, and as such, we would encourage future studies to apply the theories examined, and proposed, here to larger data sets more representative of the true diversity of freshwater ecosystems across Canada. With that being said, we do not feel that the results presented here are any less meaningful, or applicable. For instance, large inland lake monitoring programs, such as the Broad-scale Monitoring Program in Ontario which surveys approximately 150 unique fisheries every year, rely on biological reference points such as biomass capacity to assess the health of fish populations (P. Lester et al. 2003). These reference points, however, are based mostly on indicators of primary productivity, and ignore dynamics of fish diversity which, as demonstrated here, can help to provide more robust estimates of biomass, and hence biomass potential. Given the extensive nature of their current dataset (~1500 individual monitoring events), it seems reasonable that species richness data could be applied to current models reduce error in estimates of these biological reference points.

Moreover, the findings presented here should certainly be considered by resource managers across the country when considering the implications of climate change and the expected loss of fish species. In fact, it is perhaps in this regard that the findings here will be of the greatest value. Canada’s freshwater ecosystems are entirely vulnerable to climate warming, which will inevitably alter habitat rendering it unsuitable for the collection of species which have historically adapted to it (Ricciardi and Rasmussen 1999, Chu et al. 2005, Chu et al. 2015). This is the primary mechanism through which we expect to see species being extirpated from these systems. Of course, as habitat becomes less suitable for some species, it will concurrently become more suitable for others, and it is in this regard that it may be reasonable to assume that we are entering an age where “community engineering” may become our most powerful tool in maintaining ecosystem productivity in mitigation of climate change. We discuss this in chapter 1 in the context of stocking practices of newly formed reservoirs in Alberta. In the same way that river impoundment creates habitat which is not suitable for native riverine species, but more suitable for pelagic species, climate change will alter thermal regimes of lakes across the landscape leading the populations therein to the same fate. In the case of newly formed Alberta reservoirs, it has been shown that stocking a “functionally suitable’ species, such as Lake Whitefish, produced greater results than stocking a “functionally unsuitable” species, such as Walleye (Campen 2016), and it is this functional perspective that may best serve climate change mitigation efforts in the future. The results presented, and theories proposed, here will help to not only inform best stocking practices, but also provide a framework to evaluate the effectiveness of species additions and the complementarity of their functional roles to the communities to which they’ve been introduced.

In closing, it is our assessment that the research presented here represents a significant step forward in our understanding of species richness and its influence on fish biomass in freshwater ecosystems. It is my sincere hope that this work is challenged, studied further, more broadly applied, and ultimately leads to progressive means of protecting and conserving the Canadian freshwater ecosystems that I am so passionate about.

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Appendix A

Introduction: The Succession of Biodiversity - Productivity Research

Unprecedented population growth, in combination with a global consumerist mentality, has engorged our anthropogenic footprint to a point which threatens Earth's biological communities along both local and global scales. Habitat alteration and destruction, accelerated species introductions, and a plethora of adjacent avenues have led to the overall depauperization of biological communities (Vitousek 1997, Pimm and Raven 2000, Sala et al. 2000) at rates which bear comparison to the species loss experienced during the major extinction events evident in the fossil record (Barnosky et al. 2011). As such, over the past 20 years researchers have become increasingly interested in understanding the extent to which impoverishment of species diversity might affect the basic processes performed by the ecosystems in which we all occupy. The emergent discipline of "Biodiversity-Ecosystem Function" (referred to as B.E.F. here forth) has since spanned both terrestrial (Grime 1997, Loreau et al. 2001) and aquatic (Gessner et al. 2004, Humbert and Dorigo 2005, Gamfeldt and Hillebrand 2008) systems, considering a range of biodiversity measures (Tilman et al. 1997a) as well as ecosystem functions (Aoki and Mizushima 2001, Dunne et al. 2002, Reiss et al. 2009, Franssen et al. 2011). However, the relationship which has garnered the greatest attention among B.E.F. researchers has been that of species richness and productivity (Tilman et al. 1997b, Mittelbach et al. 2001, Worm and Duffy 2003, Tilman et al. 2012).

Despite the fact that a consensus had been achieved among the scientific community, that reductions in species diversity led to corresponding impairment of ecological functions (Hooper et al. 2005), this seemed counterintuitive to the fact that in nature, the most productive plant communities often consisted of relatively few species (Huston 1994). In response to this apparent contradiction, a suite of original works were carried out which experimentally manipulated species composition, in model communities of both terrestrial (Naeem et al. 1994, Hooper and Vitousek 1997, Tilman et al. 1997a, Hector et al. 1999) and aquatic (Naeem and Li 1997) ecosystems. While these studies were perhaps limited in that they considered only primary production of single trophic level communities (with the exception of Naeem at al. 1994), their experimental design allowed for conclusions to be drawn without the "noise" of complex predator-prey interactions (O'Connor et al. 2013), and from these analysis arose the first widely accepted model predicting a positive relationship between three individual measures of species diversity (richness, functional richness and functional composition) and productivity (Tilman et al. 1997a).

However, as is generally the case in scientific research, the biggest findings are often met with a great deal of criticism along the path to validation, and Tilman's (1997a) research was no exception. One year prior to his 1997 work, Tilman produced a model which predicted that increasing species diversity significantly increased productivity in grassland communities, however, in this earlier work he included only species richness as a measure of diversity (Tilman et al. 1996). This work was immediately met with criticism, challenging that the increase in observed productivity was simply due to the fact that communities with a greater number of species also have a greater chance of having highly productive species (Aarssen 1997). Tilman arrived at this same conclusion, albeit independently from Aarssen (Tilman 1997), and it was for this reason that he demonstrated that the relationship exists even when diversity is measured as functional richness or functional composition (inferring that it was not only the number of species, but rather differences in their respective niches which led to the increase in productivity)(Tilman et al. 1997a). From this work it became clear that there were underlying mechanisms which needed to be understood in order for the advancement of the theory stemming from Tilman's model (Huston 1997). As such, two mechanisms were quickly identified, the sampling effect (see Wardle 1999) and the complementarity effect (see Hector 1998), and research was quick to follow towards the understanding of how the two mechanisms operated in tandem (Tilman et al. 1997b, Loreau 2000), as the objective had now transitioned from understanding "if" biodiversity had an effect on productivity, to "how" biodiversity affects productivity.

Efforts to arrive at a solution to this problem began with simplistic models aimed at removing the sampling effect by comparing the yields (this is a term used to describe productivity, but can also serve as a surrogate for other ecosystem functions) of mixtures, as well as individual species within those mixtures, to their respective yields in monoculture (Jolliffe 1997, Wardle et al. 1997, Hector 1998). While these early models proved successful in testing against the null hypothesis that species composition alone (the sampling effect) was accounting for differences in observed total yields, they were, however, unable to make any inference as to possible alternative hypotheses (such as differences in yield due to niche complementarity)(Loreau 1998b). At this point it was clear that a final solution would have to involve measures which considered these original approaches, however, Loreau and Hector felt that there were too many restrictions inherent with these models, and furthermore they felt that the sampling effect was actually a combination of two mechanisms: a sampling effect and a selection effect

(Loreau and Hector 2001). Through further deliberation, they determined that is was a "selection effect" which would require partitioning from the complementarity effect, rather than a sampling effect, and through a combination of Price's general theory of selection (used to determine the "selection effect" (Price 1970, Fox 2006)), and the three aforementioned models, they were able to apply an additive approach to partition these mechanism's contributions to the overall biodiversity effect (Loreau and Hector 2001).

Since its inception in 2001, the Loreau and Hector model, developed from single trophic level grassland communities, has provided the basis for models developed for aquatic (Petchey et al. 2002, Giller et al. 2004) and multi-trophic (Petchey et al. 2004, Fox 2005a) systems, and has stemmed further research into how these effects might work with other theories crucial to our understanding of ecosystem functions, such as coexistence theory (Turnbull et al. 2013). The following pages provide a detailed summation of the research fundamental to the 20 year succession of this theory, and will offer some insight as to the applicability of this work to future research.

Productivity and Ecosystem Functioning: The Role of Biodiversity

Although it has long since been assumed that the species which occupy any given ecosystem have a considerable effect on the processes performed by said ecosystem, it has really only been in the past 20 years that this concept has become a central concern of ecological research (Loreau et al. 2001). In truth, the first indirect evidence for ecosystem functions being positively influenced by functional characteristics of the species within came as early 1958 (Elton 1958), although during the 35 years which followed, a large collection of projects were carried out which produced rather equivocal results (May 1972, 1973, Anderson and King 1978), leaving many to debate whether the relationship among diversity and ecosystem function was positive or negative. Moving forward, in 1982, Leps et al. undertook a study in an attempt to replicate findings by May, and determined that functional richness (as a measure of diversity) was a better determinant of ecosystem functionality than was species richness, however they were not able to provide any additional clarity as to the nature (positive or negative) of the BEF relationship (Leps et al. 1982). It was not until 1994, by means of several concurrent studies featuring species composition manipulations in model terrestrial communities at the Ecotron in Southern England (Naeem et al. 1994) and the Ceder Creek Reserve in Minnesota (Tilman and Downing 1994), that a positive BEF relationship was elucidated which gained wide acceptance among the scientific community (Grime 1997).

The Ecotron, located at Imperial College in London, England, is a facility which houses model terrestrial ecosystems within an environment where abiotic conditions such as temperature, humidity, air flow and soil conditions, among others, can be controlled as to remove their effects from any terrestrial ecosystem experiment. As such, it was an ideal candidate for research by Naeem et al. in their attempts to discern the effects of species diversity on several ecosystem functions (Naeem et al. 1994). Their experiment included 14 terrestrial microcosms which were given one of three treatments (levels) of diversity; low diversity, containing nine species, medium diversity, containing 15 species, and high diversity, which contained 31 species. Furthermore, low species communities were subsets of higher level diversity treatments so as to emulate depauperate versions of their higher diversity counterparts. As alluded to previously, not only was this study among the first to test these hypothesis in a controlled environment, but was also among the few early examples of these theories being tested in a multi-trophic system. Species contained within each microcosm were partitioned among four trophic levels; primary producers (vascular plants), primary consumers (herbivores, such as aphids), secondary consumers (parasitoids of the various herbivores present), and decomposers (collembola, earthworms). Once these communities had been established, the authors then investigated the effects of these treatments on five ecosystem function responses; respiration (measured as CO_2 exchange), decomposition, nutrient retention (measured as total available nitrogen (N), phosphorous (P) and potassium (K) in soil), H_2O retention, and lastly plant productivity (measured as the inverse of per cent transmittance of photosynthetically transmitted active radiation). Following repeated measures ANOVA analyses, the Naeem at al. determined that species diversity had a significant effect on respiration as well as plant productivity, and therefore concluded that such species loss may indeed impair multiple ecosystem services (Naeem et al. 1994).

Concurrent to the Naeem et al. study, presented above, was a similar study undertaken by Tilman and Downing performed in a grassland community at the Cedar Creek reserve in Minnesota (Tilman and Downing 1994). Unlike the Naeem et al. study, this research was not performed within a controlled environment such as the Ecotron, however, provided perhaps a more “real world” contribution to the growing body of BEF research. The study included 207, single trophic level, four by four meter grassland plots (although 45 of the 207 were only two by four meters) partitioned among four larger fields. The project encompassed 11 years of research, beginning in 1982 with various nutrient manipulations in order to achieve a range of biodiversity values among the 207 plots. Individual plots received one of nine treatments; no nutrient addition, non-N nutrient addition, and seven other treatments of N addition at differing concentrations to promote a range of biodiversity (these latter seven plots also received the same non-N nutrient addition as the second treatment). Also differing from the Naeem et al. study, Tilman and Downing chose resistance and resilience as ecosystem function response variable, rather than any of the five considered by their colleagues in London. The ability to measure resistance/resilience was facilitated by a “1 in 50” year drought which spanned from 1987-1988, which allowed the investigators to observe both resistance to drought (measured in 1986, 87 and 88 as change in above ground plant biomass), as well as resilience in recovering from said drought (measured in 1989, 90, 91 and 92 as the remaining deviation in above ground biomass from original biomass values in 1982). Upon final measurements of above ground biomass in 1992, the authors found that only plots with less than five species remained significantly lower than their respective average biomass values from 1982-86. But perhaps of greater interest was the curvilinear relationship found following correlation analysis of species richness vs resistance (resistance considered here as $\ln[\text{biomass}_{88}/\text{biomass}_{86}]$), which suggested that communities became more resilient with the addition of more species, with a saturation effect occurring beyond ~15 species. From this, Tilman and Downing too concluded that ecosystem functioning was sensitive to species diversity (Tilman and Downing 1994).

Tilman, Wedin and Knops (1996) continued on this work with a two year study examining 147 grassland plots in which diversity was experimentally manipulated by directly planting either 1, 2, 4, 6, 8, 12, or 24 North American prairie species. As measures of diversity, the authors considered species richness, Shannon diversity index and effective species richness as a combination of the former two indices. For response variables, productivity was measured by total plant cover, biomass (estimated from light penetration) and N utilization (plots were manipulated so that N was the limiting nutrient). Following correlation analysis, the authors reported a significant correlation between species richness and all three measures of productivity, further supporting the theory that ecosystem productivity increased with species richness (Tilman et al. 1996).

The three studies just addressed provide an accurate representation of the significant contributions to the BEF relationship. It is perhaps fitting that all were performed in grassland communities, as it has been within these terrestrial ecosystems that a significant proportion of the BEF body of research has occurred, at least in its early stages of maturation (Loreau 2000, Naeem et al. 2002). However, McGrady-Steed et al.'s (1997) examination of the BEF relationship provides an example representative of the far fewer number of aquatic based works contributing to this research during its early stages of development. Here, the authors manipulated microbial species richness within aquatic microcosms to create eight initial levels of diversity (0, 3, 5, 10, 15, 20, 25 and 31 eukaryotic species). Microcosms also contained on average 24 bacterial taxa (reported as an average, as variance in the number of bacterial taxa across microcosms was inherently difficult to control due to contamination). Similar to Naeem et al. (1994), this study was among the few early examples to consider the BEF relationship in a multi-trophic community (albeit a microbial one). As such, special consideration was given to the establishment of these communities, with lower trophic levels being added to culture first, allowing them to proliferate to a degree which ensured the survival of higher trophic levels which would be added afterwards. This process of community establishment, in combination with contamination, led to some deviations in the "final" community from the initial taxa richness, "realized" community richness was considered for analyses rather than initial richness. Communities were given six weeks to proliferate, throughout which weekly measurements of two ecosystem function response variables were taken: decomposition (change in dry mass of seeds placed in microcosms) and respiration (production/ consumption of CO_2). After these first six weeks, and after measurements of decomposition and respiration were obtained, an invader taxa was added to all cultures and its change in abundance was measured following an additional 10 days as a third ecosystem response variable (invasion). Specifically, McGrady-Steed et al. were interested in the capacity of species richness to predict these three response variables, and following multiple regression analysis determined that one response, respiration, become increasingly predictable with greater species richness. Then, to complement this work, the author's investigated similar patterns of ecosystem variability offered by, including data from Naeem et al. (1994) and Tilman and Downing (1994), presented earlier, and determined that ecosystem function predictability showed a similar response to increasing biodiversity in grassland communities (McGradySteed et al. 1997).

Finally, no review of the BEF research, or more specifically the biodiversity-productivity relationship, would be complete without the inclusion of Tilman et al.'s work in 1997 (1997a). For this final piece of the puzzle, Tilman et al. returned to the Cedar Creek reserve where the Tilman and Downing had performed earlier research. Following the Tilman and Downing (1994) research, grassland plots were burned, the top 6cm of soil removed and the resulting landscape tilled to avoid any residual effects from the N manipulations in the 1980's. The land was then subdivided into 13m x 13m plots, and seeded in both 1994 and 1995. In an effort to continue to build off prior works, Tilman et al. wanted to consider not only species richness as a measure of diversity, and therefore included two other measures in their analyses; functional diversity (number of functional groups per plot) and functional composition (specifically which functional groups were present per plot). To facilitate these analyses, the following experimental design was employed: 167 plots contained either 1, 2, 4, 8 or 16 species (from a pool of 18 species), 76 plots were assigned 1, 2 or 3 functional groups containing 2, 4 or 8 species (an additional species pool of 16 was utilized where necessary), and 46 plots contained 32 species (of the 34 species pool). Functional groups considered were C_3 and C_4 grasses, legumes, forbs and woody species. As response variables, the authors considered peak above ground biomass as there measure of productivity, along with percent N in above ground tissue, total N in above ground tissue, soil NH_4, soil NO_3 and light penetration. Following various regression analyses among all response and explanatory variables, as well as multiple MANOVAs and ANOVAs, the authors concluded that while each explanatory factor on its own produced significant influence on many of the ecosystem functions considered, functional composition and functional diversity were able to better explain the four variables directly related to plant measurements. Furthermore, from their regression analyses between productivity and both species richness and functional richness (both statistically significant), arose the project’s most significant contribution to diversity-productivity research, presented as figures 1A and 1B, which are now widely cited in the literature (Tilman et al. 1997a).

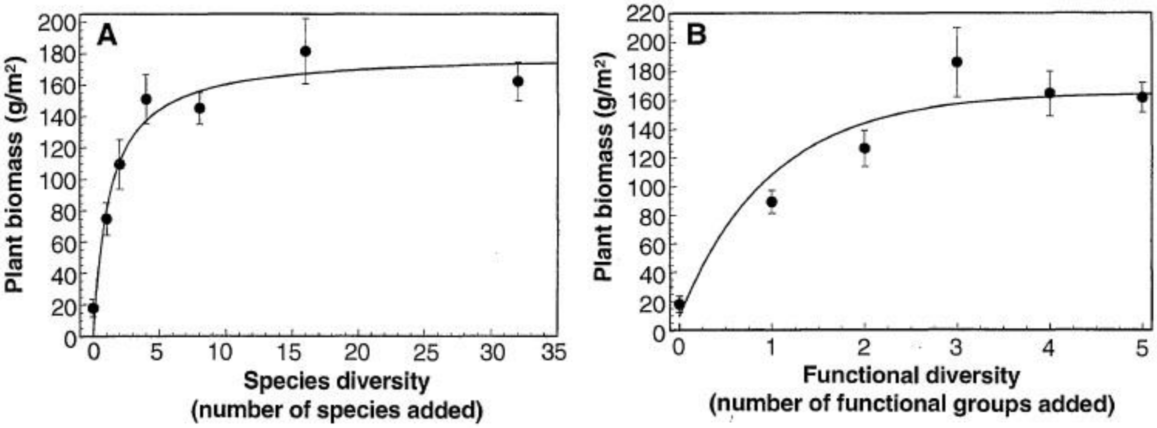

Figure 1. Relationship between species diversity and plant biomass (A) and functional diversity and plant biomass (B) (Tilman et al. 1997a).

The Debate: Complementarity or the Sampling Effect

Following Tilman at al.'s work in 1996, a controversy began to develop stemming from a report published by Aarssen (1997) which debated whether or not the biodiversity effects proposed by Tilman et al. were in fact real, or just simply just an artifact caused by a "sampling effect". In this opinion paper published in OIKOS, Aarssen argued that it may not have been a true biodiversity effect which generated a positive relationship with productivity, but rather the fact that systems with a greater number of species simply have a greater chance of including a highly productive species which would then come to dominate the system, accounting for the observed increase in productivity. Aarssen based this conviction on three points; [1] central limit theorem dictates that the productivity of individual species should be normally distributed, so that there are a much greater number of intermediary productive species than there are low or highly productive species, [2] highly productive species will outcompete less productive species and, over time, will come to dominate the systems they occupy, and [3] the probability that any given system will contain a highly productive species will increase with increasing numbers of species present in the system. Aarssen went on to refer to a study performed by Abul-Fatih and Bazzaz (1979), who found that the presence of a certain highly productive species lowered the diversity of systems by 90 per cent, but increased productivity of said systems by eight fold, and as such Aarssen concluded that it was therefore of much greater likelihood that it was simply the presence of a highly productive species which drives increases in productivity (Aarssen 1997).

As fate would have it, Tilman had actually come to this same conclusion independently, and in the same year (1997) he would publish a manuscript proposing three different models to explain the various possible mechanisms which may account for his proposed biodiversity effect (Tilman et al. 1997b). The first of his models, and the most simple, was termed the sampling effect and was directly in line with what Aarssen had proposed, featuring a situation where species competed for a single resource. The logic behind this model dictated that species could be represented by their respective resource requirements (denoted as R*), such that species with the lowest requirements for a resource would be most productive and would eventually come to dominate a system (resource competition theory, (Tilman 1982)) and therefore the R* of the system will eventually just be a reflection of the dominant species' R*. It then follows, that systems with the lowest R* values would be most productive, and if by reducing any given set of species to their range of R* values (R^*_{min}, R^*_{max}), then it would be possible to calculate the probability of a system to assume its lowest possible R* value, given its original number of species (N), with the following equation:

$$\mathbf{[Min\ R^*] = R^*_{min} + ((R^*_{max} - R^*_{min}) / (N + 1))} \qquad \mathbf{[1]}$$

This equation essentially describes the sampling effect proposed by Aarssen, and dictates that R^* approaches R^*_{min} as species diversity (N) increases, leading to corresponding increases in productivity.

The second model proposed by Tilman et al. described a system in which species compete for two resources which are spatially distributed in heterogeneous fashion. In such an instance no single species would be capable of completely dominating a system, and would rather only dominate the spatial locations where its limiting resource was found, leaving other unoccupied areas to be colonized by species in correspondence to a second limiting resource. Clearly, in this scenario the system's total productivity would not be dictated solely by the dominant species, but would rather be determined by some combination of the multiple species present, alluding to some other mechanism involved in the biodiversity effect. Their third model proposed a similar scenario, however, rather than stipulations based on multiple resources, the underlying theory behind this model was based on unique niches determined by tolerance to some combination of heterogeneously distributed environmental factors (such as soil pH and temperature). As such, whether any given species had lower resource requirements or not, they could only occupy some given niche space in accordance to their respective performance within a window of environmental variables. This model predicted that productivity would increase asymptotically with diversity (similar to the relationship demonstrated in (Tilman et al. 1997a)), and the rate at which the curve would reach the asymptote was dependant on the degree of spatial heterogeneity among the environmental variables determining niche parameters (Tilman et al. 1997b).

These latter two models, in essence, described in partial the complementarity effect, a secondary mechanism contributing the overall biodiversity effect on biomass productivity. Further theoretical considerations would follow which would determine that it was most likely some combination of complementarity and the sampling effect which was responsible for the biodiversity effect (Loreau 2000), however, the complexity in separating these effects in order to determine their exact contribution to this relationship would prove incredibly difficult. In light of this, Loreau would later come to the conclusion that the investigation of third mechanism, selection, would provide more useful in further attempts to partition the roles of these underlying mechanisms (Loreau 2000, Loreau and Hector 2001).

The Resolution: A Model to Partition the Effects

Prior to Loreau's notion of a selection effect being involved in the biodiversity-productivity relationship, work to decipher the mechanisms introduced above began with attempts to quantify the sampling effect. Of these attempts, three in particular were conceptually significant towards the work by Loreau and Hector in the years to follow. The first of which to be discussed here is that of Joliffe (1997). The relative land output model (RLO here forth) was developed as a means to compare the productivity of two-species communities to the productivity of those species in their respective monocultures in the absence of species interactions. In actuality, it compared the yield of the area of land occupied by the species present, rather than the species themselves (hence the name, relative "land" output). By comparing the productivities of species in mixture to their "expected" productivity values based on monoculture yields, this method essentially allowed for a method to test against the null hypothesis that the sampling effect had an influence on the productivity of the mixture (this same theory underpins all three models presented here). The RLO model [2] featured the following assumptions; 1, equal total densities among species in mixture; 2, equal number of individuals per species; and 3, equal land area coverage among species in mixture. The RLO model is given by:

$$\mathbf{RLO = O_T / E_T} \qquad \textbf{[2]}$$

where O_T is the sum of total observed yields of both species in mixture, and E_T is the sum of expected yields of all species in mixture, calculated from productivity values in correspondence to their respective monocultures (0.5*total yield in monoculture, assuming 50:50 ratio of species in mixture, an underlying assumption of the model as stated above). Essentially, this method eliminated any effects of individual highly productive species on the biodiversity effect, and therefore any deviations from RLO = 1 would be an indication that complementarity among species was accountable for any subsequent increase in productivity attributed to species diversity. While this method provided a convenient measure to compare the yield of a mixture to that of its monoculture counterparts, it was quite stringent in its underlying assumptions and was significantly limited by the fact that it can only be used to compare two-species mixtures (Jolliffe 1997).

A second model, quite similar to the RLO, was proposed by Wardle et al. (1997), and provided a more traditional method to estimating the same deviation described above, calculated as:

$$\mathbf{D_T = O_T - E_T / E_T} \qquad \textbf{[3]}$$

where observed and expected yields are calculated in the same manner as the RLO. This model could also be used to calculate the proportional deviation [4] and weighted average proportional deviation [5] of individuals by:

$$\mathbf{D_i = O_i - E_i / E_i} \qquad \mathbf{[4]}$$

$$\mathbf{\overline{D} = \sum_i p_i D_i} \qquad \mathbf{[5]}$$

where D_i, O_i and E_i represent the proportional deviation, observed yield and expected yield of individual species (i), and p_i is the proportion of species (i) in the mixture. This method was useful in that it could be calculated without the same stringent underlying assumptions as RLO, however was arguably less powerful for the same reasons. Upon further examination of this equation, it is clear to see how the two were related by the following:

$$\mathbf{RLO = D_T + 1} \qquad \mathbf{[6]}$$

Finally, a third method in the attempt to eliminate the sampling effect from biodiversity/ productivity calculations was developed (or rather modified) by Hector (1998), derived from the relative yield totalmethod originally proposed by Harper (1977). The relative yield total (RYT here forth) modified by Hector (1998) was similar to both methods presented above, and was calculated as follows:

$$\mathbf{RY = O_i / M_i} \qquad \mathbf{[7]}$$

$$\mathbf{RYT = \sum RY_i} \qquad \mathbf{[8]}$$

where RY is the relative yield of species I, given by the quotient of O_i (observed productivity of species “i” in mixture) divided by M_i (observed productivity of species i in monoculture), and RYT is the sum of RYs of all species present in mixture. Interestingly, it is apparent how RYT related to Wardle's proportional deviation by the following:

$$\mathbf{RYT = \bar{D} + 1} \qquad \mathbf{[9]}$$

Hector then went on to demonstrate through multiple hypothetical examples how the RYT could successfully remove the sampling effect in biodiversity-productivity experiments by testing against the null hypothesis (RYT=1) that any increase in the productivity in mixture, compared to expected values in monoculture, could be attributed to proportional contributions of any of the species present in said mixture (overyielding). The RYT method, however, fell short of being able to quantify the effects of complementarity, and therefore was burdened by the same limitations as the two prior models.

The strength of these three models presented by Jolliffe, Wardle and Hector was in their ability to detect whether or not a mechanism aside from the sampling effect (complementarity) was contributing to the observed gains in yield from increased biodiversity. However, without a means to calculate the actual contribution of this alternate effect, the debate would persist as to what the actual relationship between biodiversity and productivity was. Loreau, though, was not convinced that this was an unattainable task. In 1998, he published a review of these three models, investigating their strengths and weaknesses, and it was presumably following this review (in particular the RYT model by Hector), that he came to a significant realization which would lead to the development of a method to quantify the effects of complementarity. This realization, presented in Loreau and Hector's work in 2001, was that the sampling effect, which these three models were attempting to characterize, was actually a combination of two processes; a sampling process (as defined earlier) and a selection process which allows for more productive species to dominate any given system, thereby driving up the yield of more diverse mixtures. He then further proposed that the sampling effect actually acts upon both selection as well as complementarity (since a greater number of species present should also give rise to a greater likelihood of complementary species being present), and as such, determined that it was the selection effect, rather than the sampling effect, which would have to be partitioned from complementarity (Loreau and Hector 2001).

This decision, to develop a model to partition the effects of selection and complementarity, rather than sampling and complementarity, was significant because the two former mechanisms could be additively partitioned by employing a combination of Hector's RYT theory, Wardle's proportional deviation theory and Price's general theory of selection (Price 1970, Wardle et al. 1997, Hector 1998, Loreau and Hector 2001). The model can be broken down into three terms, and is given by the following:

$$\Delta \mathbf{Y} = \mathbf{N}\ \Delta\overline{\mathbf{RY}}\,\overline{\mathbf{M}} + \mathbf{N}\ \boldsymbol{cov}\ (\Delta \mathbf{RY}, \mathbf{M}) \qquad \mathbf{[10]}$$

where N is the number of species present, ΔY is the biodiversity effect, N $\Delta\overline{RY}\,\overline{M}$ gives the complementarity effect, N *cov* (ΔRY, M) gives the selection effect and all other terms are defined in previous equations [1-6]. Examining the terms of this equation further, it becomes apparent how they relate to prior models shown above. Firstly, ΔY relates to D_T and therefore RLO by the following:

$$\Delta \mathbf{Y} = \mathbf{D_T}\ \mathbf{Y_E} \qquad \mathbf{[11]}$$

where Y_E is the sum of the expected yields of all species in mixture, and D_T is defined in [3]. Secondly, the complementarity term relates to $\overline{D}$ [12] and RYT [13] by the following:

$$\mathbf{N\,\Delta\overline{RY}\,\overline{M} = \overline{D}\,\overline{M}} \qquad \mathbf{[12]}$$

$$\mathbf{N\,\Delta\overline{RY} = RYT - 1 = \overline{D}} \qquad \mathbf{[13]}$$

where $\overline{D}$ is defined in [5] and RYT defined in [7,8]. Finally, as previously alluded to, the selection term is derived from Price’s general theory of selection, and is given by the covariate of ΔRY [14] and M (yield in monoculture).

$$\mathbf{\Delta RY_i = RY_{Oi} - RY_{Ei}} \qquad \mathbf{[14]}$$

To summarize, the selection effect measured the covariance between the change in relative yields of species in the mixture and their yields in monoculture, and would positive or negative depending on the specific productivity (higher or lower than average, respectively) of the dominant species. The complementarity effect measured whether or not yields in mixture were higher (or lower, although this is quite rare) than what would be expected from the weighted average yields of those same species in monoculture (Loreau and Hector 2001).

Conclusions – Validity and Applicability of the Model

To test the validity of their model, Loreau and Hector applied their findings to a prior dataset from the BIODEPTH project, which investigated patterns of above ground plant biomass in experimentally manipulated European grassland communities (Hector et al. 1999). As they had anticipated, they found that the mean selection effect was not significantly different from zero, on average, across all sites (significantly positive in two localities, and significantly negative in another), and was significantly influenced by species composition but not richness. Further, they found a significantly positive effect of complementarity in four localities (and a significant overall effect across all sites), including the locality in which selection produced a significantly negative effect, demonstrating to a reliant degree that the model was successfully able to partition among these two effects (Loreau and Hector 2001).

From this work, for the first time, it was made clear that complementarity, through a likely combination of facilitation and niche differentiation, holds a significantly positive influence on ecosystem productivity. However, while these findings are crucial to our understanding of the relationship between biodiversity and primary productivity (particularly in terrestrial communities), applying this model to future research may present some difficulty for a number of reasons. The first obstacle, at least in relation to applying this model to complex animal food webs, is acquiring the necessary information in regards to the productivity of component species in “monoculture”. Of interest to many ecologists will be the ability to apply this model to multispecies ecosystems, however, finding “closed” ecosystems which feature only a single species might be an arduous endeavour for animal ecologists, and may require whole system manipulations which will inevitably present a greater task than the relatively simple manipulations of plant communities presented here. A possible solution for this may be to apply mean specific growth curves for individual species, as a surrogate of monoculture productivity, derived from multispecies systems across a wide range of environmental conditions. However, there would be obvious bias associated with these estimates and therefore this method would likely require a great deal of planning and consideration.

A second issue surrounding the application of this model, again in relation to more complex animal food webs, is the consideration of confounding effects of multiple trophic levels, and more accurately, the effects of predation. In relation to multi-trophic aquatic ecosystems, it is well understood that higher trophic levels (2°-3° consumers) are less productive than lower trophic levels (1° producers, 1° consumers)(Wetzel 2001), and therefore any conclusions which are to be drawn from entire communities will have to incorporate these discrepancies in their analyses. Further, top-down control by higher trophic levels (and similarly, bottom-up control by lower levels) will also inherently influence productivity of lower (higher) trophic levels, and understanding how these influences fit into the Loreau and Hector model will no doubt require sophisticated and innovative analyses. A more detailed synthesis of the various considerations required when attempting to apply current models to multi-trophic aquatic ecosystems is provided by Petchy et al. (2004), who outline many of the aforementioned issues relating to complex trophic interactions.

A common theme among the science and research, which has contributed to our most fundamental ecological laws and principles, is that the progression towards their complete understanding was often cyclical in nature. Through a series of theoretical inception followed by hypothesis testing, we acquire the answer to our original question whilst forming a new question simultaneously. What has been presented here, from the early BEF to Tilman's 1997 model, and then from Aarssen's (1997) criticism of a potential sampling effect through to the creation of the model to partition diversity effects (Loreau and Hector 2001), is analogous to two cycles within this framework. To complete this analogy, one could argue that we are currently in a third cycle, progressing towards a model which incorporates the complexities of "real food webs", a good example of this being the work of Jeremy Fox at the University of Calgary (Fox 2003, Fox 2004a, b, Fox 2005a, Fox 2005b, Fox 2006, 2007, Fox and Harpole 2008). Although we are currently only in the theoretical stage of this cycle, the foundation has been set for future, and even current (such as my own) research to begin incorporating these theories into design. While Loreau and Hector's (2001) model sets the current standard for partitioning among the effects of biodiversity and productivity, it is only inevitable that a more complete model, appropriate for complex multi-trophic ecosystems, is on the horizon, as such is the nature of science.

Appendix B

Functional feeding groups of common North American freshwater fish species

Standing Water fish communities			
Warmwater pelagic planktivores	Clupeidae	*Alosa pseudoharengus* (22)	alewife
		A. aestivalis (18)	blueback herring
		Dorosoma spp (57)	gizzard & threadfin shad
	Atherinopsidae	*Labidesthes sicculus* (11)	brook silversides
	Cyprinidae	*Cyprinella, Notropis spp* (29)	shiners
		Mylocheilus caurinus (2)	peamouth
		Notemigonus crysoleucas(78)	golden shiner
		Pimephales spp (9)	
		Richardsonius balteatus (6)	redside shiner
		Ptychocheilus oregonensis(7)	pikeminnow
	Fundulidae	*Fundulus notatus* (3)	topminnow
	Poeciliidae	*Gambusia affinis* (2)	mosquitofish
Coldwater pelagic zooplanktivores	Salmonidae	*Coregonus clupeaformis* (8)	lake whitefish juveniles
		C. artedi (4)	lake cisco & other ciscoes
		C. hoyi (3)	bloater chub
		Prosopium coulteri (1)	pygmy whitefish
		Oncorhynchus nerka (42)	sockeye, kokanee salmon
	Osmeridae	*Osmerus mordax* (4)	rainbow smelt
Herbivores	Cyprinidae	*Ctenopharyngodon idella*(13)	grass carp
		Carpiodes cyprinus (22)	quillback
Warmwater periphyton grazer/ detritivores, micro/ meiobenthivores	Catostomidae	*Erimyzon sucetta* (39)	lake chubsucker
		Ictiobus spp (20)	buffalofishes
		Cycleptus elongatus (2)	blue sucker
		Minytrema melanops (3)	spotted sucker
	Cichlidae	*Ochreochromus aureus* (14)	blue tilapia
	Cyprinidae	*Cyprinus carpio* (50)	common carp
		Campostoma anomalum (9)	stone rollers
		Phoxinus spp (10)	dace
Coldwater periphyton grazer/ detritivores, micro/ meiobenthivores	Catostomidae	*Catostomus catostomus* (11)	Longnose sucker
		C. commersoni (50)	white sucker
Warmwater macroinvertebrate feeders	Catostomidae	*Moxostoma spp* (17)	redhorses
	Centrarchidae	*Lepomis spp.* (105)	sunfishes
	Cyprinidae	*Couesius plumbeus* (5)	lake chub

	Moronidae	*Morone americana* (2)	juvenile white perch
	Percidae	*Perca flavescens* (52)	Juvenile yellow perch
	Sciaenidae	*Aplodinotus grunniens* (6)	freshwater drum
Coldwater macroinvertebrate feeders	Salmonidae	*Salmo,Salvelinus, Oncorhynchus*	Juvenile& small adult trout
		Coregonus clupeaformis (8)	Lake whitefish
		Prosopium spp. (2)	round & mountain whitefish
	Percopsidae	*Percopsis omiscomaycus* (3)	troutperch
	Cottidae	*Myoxocephalus thompsoni*(3)	deepwater sculpin
		Cottus spp (4)	
Warmwater piscivores	Amiidae	*Amia calva* (3)	bowfin
	Centrarchidae	*Micropterus spp* (105)	black basses
		Pomoxis spp (75)	adult crappies
	Esocidae	*Esox spp.* (28)	muskellunge & pikes
	Ictaluridae	*Ictalurus spp.* (40)	Channel & blue catfish
		Pylodictis olivaris (7)	flathead catfish
	Lepisosteidae	*Lepisosteus spp* (66)	garpikes
	Moronidae	*Morone saxatilis* (20)	striped bass
	Percidae	*Sander vitreus* (22)	yellow walleye
		S. canadensis (4)	sauger
		Perca flavescens (52)	adult yellow perch
Coldwater Piscivores	Salmonidae	*S. trutta* (5)	brown trout
		Salvelinus namaycush (5)	lake trout
		S. confluentus (7)	bull trout
		S. fontinalis (20)	brook trout
		Oncorhynchus mykiss (19)	rainbow trout
		O. kisutch (4)	coho salmon
		O. tshawytscha (4)	chinook salmon
	Gadidae	*Lota lota* (5)	burbot
Running Water Fish Communities			
River periphyton grazer; micro/ meiobenthivores		*Notropis, Luxilus spp* (44)	shiners
		Pimephales promelas (3)	Fathead minnow
		Rhinichthys spp (69)	Longnose & blacknose dace
		Semotilus atromaculatus(18)	*creek chub*
	Percidae	*Etheostoma spp* (35)	darters
Herbivores	Cyprinidae	*Ctenopharyngodon idella* (1)	grass carp
		Carpiodes cyprinus (4)	quillback

Detritivores, micro/ meiobenthivores	Catostomidae	*Carpiodes carpio* (4)	river carpsucker
		Ictiobus spp (14)	buffalofishes
		Catostomus spp (42)	white & longnose sucker
		Cycleptus elongatus (2)	blue sucker
		Minytrema melanops (2)	spotted sucker
	Cyprinidae	*Cyprinus carpio* (4)	common carp
Benthic macroinvertebrate / drift feeders	Accipenseridae	*Accipenser* (2)	sturgeons
	Catostomidae	*Moxostoma spp* (11)	Redhorses
	Cottidae	*Cottus spp* (11)	sculpins
	Centrarchidae	*Lepomis spp* (24)	sunfishes
		Ptychocheilus oregonensis(1)	pikemnnow
	Ictaluridae	*Ictalurus spp* (10)	juvenile catfish
	Salmonidae	*Prosopium spp* (18)	river whitefishes
		Oncorhynchus, Salmo spp (52)	juvenile trout & salmon
		Salvelinus spp (76)	Juvenile charrs
Piscivores	Centrarchidae	*Micropterus spp* (18)	black basses
		Pomoxis spp (2)	adult crappies
	Esocidae	*Esox spp* (6)	pikes & muskellunge
	Gadidae	*Lota lota* (4)	burbot
	Ictaluridae	*Ictalurus spp.* (10)	catfishes
	Percidae	*Sander spp* (5)	walleye, sauger
	Salmonidae	*Oncorhynchus spp* (12)	Adult rainbow/cutthroat trout
		Salmo trutta (8)	Adult brown trout
		Salvelinus spp (14)	Adult charrs