The application of network analysis to assess the structure and function of aquatic food webs

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Abstract

The health of aquatic communities is under threat globally by anthropogenic impacts. A healthy ecological community is one that maintains its structure and function over time in the face of disturbance (i.e., they are stable). If we are to effectively monitor change in ecological health and instigate appropriate environmental management responses, then we first need to measure ecological health appropriately. Most methods of indicating ecological health in rivers measure structural aspects of a community, with little attention given to functional aspects. Ecological network analysis (ENA) provides a range of food web metrics that can measure both structural and functional aspects of ecological communities. The aim of this thesis was to apply ENA metrics to assess the structure and function of aquatic ecosystems and explore how they may change with habitat. In a general comparison of aquatic ecosystems, I found that rivers, lakes and estuaries have structurally similar food webs, except have lower neighbourhood connectivity which is reminiscent of unstable habitats. Through species extinction simulations of aquatic energy flow networks, I showed that aquatic food webs were most stable when trophic cascades were weak and average trophic levels were small. In examining the effects of riparian deforestation in Taranaki rivers, dietary changes altered the structure of riverine macroinvertebrate communities considerably and drove greater community respiration. In the Hutt River, I modelled changes in the biomass of trout (exotic predator) and periphyton, and showed that more periphyton, but not more trout, can result in greater community temporal variability. Furthermore, increased trout and periphyton can drive more interspecific competition. I also demonstrated the need for managers to consider the impacts of decisions on adjacent ecosystems as well as target ecosystem by showing that the Hutt River and Wellington Harbour respond substantially different to increases in algal biomass. Finally in rivers differing in nutrient enrichment the Manawatu, I showed that food webs in enriched rivers may be more stable to random species loss but more susceptible to species loss from floods. Similarly to riparian deforestation, highly enriched rivers had greater community respiration (excluding microbial activity), which may exacerbate hypoxic conditions and drive the loss of sensitive species.

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Dr Mike Joy, I am also appreciative of your co-supervision and support throughout my PhD journey.

Finally, I thank my family, friends and University support staff who have supported me throughout the PhD, especially when I’ve been stressed, unmotivated or too busy to socialize.

Further chapter-specific acknowledgements are included in the manuscript.

Preface

Each chapter of this thesis has been written as a standalone manuscript. As a consequence, there is some repetition of material between chapters. Chapters 1-8 are primarily my own work with, with input from my supervisors.

My chief supervisor, Professor Russell Death, provided guidance on methodology, manuscript development and editing, as such he is a co-author on all manuscripts prepared.

Erna Zimmermann is also a co-author on chapter four as she collected and provided the raw macroinvertebrate and physicochemical data for analysis.

Statements of Author contributions are in Appendix A.

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Chapter one:

General Introduction

Waterways are akin to the lymphatic system and kidneys of the land in that they drain and process pollutants produced on the land. However, like lymphatic systems and kidneys, if stressed excessively the health of the entire system deteriorates. Anthropogenic stressors of limnotic systems include nutrient enrichment, urbanisation, deforestation, water abstraction, engineering works, sedimentation, climate change and introduced predatory fish (Dudgeon *et al.*, 2006a, Dewson *et al.*, 2007b, Woodward *et al.*, 2010, Cucherousset and Olden, 2011, Dudgeon, 2014, Foote *et al.*, 2015a). A healthy ecosystem is one that maintains both its structure (organization) and function (vigour) in the face of stress or disturbance (i.e., stability) (Costanza and Mageau, 1999). Structure or organization includes species diversity, community composition and food web topology. Whereas function or vigour includes productivity, throughput, cycling, and flow based mutualism and synergism. Despite considerable recognition of the need to manage ecosystems for ecological health (Steedman, 1994), most research on aquatic ecological health has been focussed on understanding the drivers of structural aspects of healthy ecosystems with functional aspects seldom investigated (Friberg *et al.*, 2011). If we are to protect or enhance aquatic ecological health, then we must first identify the mechanisms to measure inclusive ecological health and then understand the key drivers of that ecological health.

Assessment of both structural and functional aspects of ecosystem health has been notoriously difficult because of the challenges in measuring higher order emergent properties (Steedman, 1994, Rapport *et al.*, 2009, Friberg *et al.*, 2011). Food webs are networks that not only represent ecological community structure but also depict energy flows between species and provide the opportunity for more holistic assessment of energy flows and potential trophic cascades. Binary food webs are those that show qualitative flows between species and allow computation of metrics characterising link distribution, connectivity and food chain length. Binary food webs are assembled by sampling the presence/absence of species across all trophic levels within a community; with dietary relationships also derived as presence/absence usually from gut samples or information from the literature (Paine, 1980, Pimm, 1982). Weighted food webs have quantified stocks and flows, and their derivation and analysis primarily stems from classic Leontief (1936) input-output economic tables. Weighted food webs are often referred to in the literature as Ecological Networks, although technically weighted food webs are a subset of Ecological Networks. Throughout the thesis there will be times where I refer to weighted food webs as Ecological Networks to maintain parallels with the existing literature. Weighted food webs are complex and time consuming to assemble. More detail can be found on their construction in Fath *et al.* (2007), but here I will provide a brief overview.

To assemble a weighted food web, one needs to thoroughly sample the density of all species across all trophic levels within a community. Often the currency of weighted food webs is in terms of carbon biomass or energy, in which it is necessary to convert count density estimates into biomass density estimates. The conversion is usually done through a combination of direct biomass measurements, or size estimates followed by conversion through published empirical size-mass relationships. Currency conversion ratios are often drawn from typical literature values. As flows between species are not readily quantifiable, flow quantums are estimated by mass-balancing the losses in energy/biomass through production, respiration and excretion. Production can be estimated directly through estimates of growth, such as the size-frequency method (Hamilton, 1969), mass turnover rates (Elwood and Nelson, 1972), observed growth rates (McIntire and Phinney, 1965), or indirectly through models of direct measures of production from the same or similar species (e.g., Robertson, 1979, Brey, 2012). Respiration rates are almost always estimated from chamber experiments that measure oxygen depletion under different scenarios (e.g., McIntire and Phinney, 1965, Elliott, 1976, Forster, 1981). Although, many species have never been assessed in a respirometer and their respiration is estimated from empirical models of similar species (Robinson *et al.*, 1983, Clarke and Johnston, 1999, Gillooly *et al.*, 2001). Direct measures of excretion rates include measuring faecal biomass or mass turnover rates under experimental conditions (Pandian and Marian, 1986); as with many species, excretion rates have never been estimated and are usually inferred from similar species. In accordance with thermodynamic principals, all inputs to a species should balance the outputs, i.e., consumption = production + respiration + excretion. If there is data on consumption, though data on another component is missing (e.g., respiration), then the equation above can be used to estimate the missing component (Fath *et al.*, 2007).

To ascertain where the energy/biomass for each consumer enters from the food web, the feeding links and dietary proportions need to be estimated. Dietary composition can either be measured directly from gut content analysis (at the site or from previous analysis in a similar system) or indirectly from biochemical analysis or functional feeding groups (Fath *et al.*, 2007, Hladyz *et al.*, 2011a). Once the flows between all species have been quantified, typically there are discrepancies in the data or from natural patterns that mean the food web is not at steady state, that is the network inputs do not balance outputs. Network analysis often relies on the webs being a steady-state snapshot; therefore, webs are often balanced by adjusting the flows between species and/or system imports and exports – this is usually done manually or by applying a balancing algorithm (e.g., Allesina and Bondavalli, 2003, Baird *et al.*, 2009). Once balanced, the network structure and functioning can then be assessed and validated (Fath *et al.*, 2007). If one wishes to simulate temporal dynamics within a food web then the webs are not balanced to steady-state, rather a differential equation (with pre-defined directions of control, i.e., bottom up, top down or mixed) is written for each link within a food web (such as a Lotka-Volterra equation or similar) and these are each integrated (solved) across time-steps.

Ecological Network Analysis (ENA) provides an assortment of metrics for food web properties that can potentially serve as indicators of both structural and functional aspects of ecological health (Jørgensen *et al.*, 2010), such as measures of energy flow distribution and efficiency, the dominance and nature of indirect flows, cycling, stability and mutualistic predator-prey interactions (Fath and Patten, 1999b, Fath and Borrett, 2006, Latham Ii, 2006). These are all measures of emergent properties that cannot be readily calculated without a complete food web. Table 1.1 summarizes the biological relevance/interpretation of key ENA variables, whilst the mathematics of the various ENA metrics are well described in literature (Ulanowicz, 1997b, Fath and Patten, 1999b, Ulanowicz, 2004, Fath and Borrett, 2006, Latham Ii, 2006).

Table 1.1. Summary of key ENA metrics and their interpretation.

Metric	Interpretation	Reference
Node count	The number of taxa included in the food web	
Mean linkage density	The average number of links per taxa	
Connectance	The per-capital average number of links or the proportion of potential links that are realized.	
Trophic proportions	The proportions of all taxa within a given trophic level.	
Mean short-weighted trophic level	The average of the average trophic level and the shortest path to basal species. It is an indicator of food chain length.	(Williams and Martinez, 2004)
Mean shortest chain to a basal species	The average length of the shortest food chain to a basal species.	(Williams and Martinez, 2004)
Characteristic path length	The average food chain length.	(Williams and Martinez, 2004)
Mean clustering coefficient	Measures the connectivity of neighbouring species.	(Lewis, 2011)
Diet discontinuity	Measures food web intervality or the number of dimensions characterising niches within a food web.	(Stouffer *et al.*, 2006)
Nestedness based on overlap and decreasing fill	Measures the extent to which specialist's diets are a subset of generalist's diets.	(Almeida- Neto *et al.*, 2008)
The entropy and standard deviations of link distributions	Indicates on the spread of the links. It may be focussed on the generality distribution (a species consumption links) or vulnerability distribution (a species predator links). A high entropy indicates links are more evenly (randomly) spread.	(Williams, 2010b)
Relative Ascendency	Measures the constraint of energy flows. A high relative ascendency indicates a web with many specialists and energy throughput. A low relative ascendency indicates a web with many generalists and low throughput.	(Ulanowicz, 1997b)
Indirect/Direct flows	The proportion of indirect flow arising from an initial movement of from one species to the next. Indirect flows are those between two species via at least one other species. It is a measure of trophic cascade strength.	(Fath and Patten, 1999b)
Indirect/Boundary flows	The proportion of indirect flows relative to the amount of energy entering/exiting the system.	(Fath and Patten, 1999b)
Indirect Flow Intensity	Proportion of total flows from indirect flows.	(Borrett *et al.*, 2006)
Average Omnivory Index	Indicates on the level of consumption across multiple trophic levels.	(Christensen and Pauly, 1993)
Average Trophic Level	Provides the energy/biomass weighted mean trophic level of all species.	(Christensen and Pauly, 1993)
Finn's Cycling Index	Measures the proportion of total energy/biomass flow that is recycled.	(Finn, 1976)
Total system throughflow	Sum of energy flows entering or exiting all taxa.	(Finn, 1976)
Respiration flows	Sum of all energy lost from respiration	
Export flows	Sum of all energy leaving the system	
Network aggradation	Average path length based on weighted energy flows. How far will a quantum of energy travel before it is dissipated?	(Finn, 1976)
Homogenization	Measures the uniformity of flow distribution	(Fath and Patten, 1999a)
Total system storage	Sum of energy stored in all taxa	(Finn, 1976)
Mutualism (flow)	Measure of the obligatory positive feedback flows	(Fath, 2007)
Synergism (flow)	Measure of the non-obligatory positive feedback flows	(Fath and Patten, 1998)

To date, weighted food webs and their analysis (using ENA) has been primarily focused on marine ecosystems, particularly with a focus on investigating the impacts of fisheries and, to a lesser extent, eutrophication. Ecopath with Ecosim (EwE) (Pauly *et al.*, 2000, Christensen and Walters, 2004, Christensen *et al.*, 2005) has become a very popular platform for modelling weighted food webs with well over 400 EwE models now assembled (Colléter *et al.*, 2013). Ecopath with Ecosim allows for the assembly of food webs including fishery harvests, time dynamic simulations (with routines to understand historical dynamics), spatial biomass modelling, Monte Carlo sensitivity analysis, the calculation of ENA metrics and estimates of fishery landing profits – providing an end-to-end solution within a graphical user interface. The EcoNetwrk software (Ulanowicz and Kay, 1991), Windows Application for Network analysis Digraphs (WAND) (Allesina and Bondavalli, 2004), the Matlab functions for Network Environ Analysis (Fath and Borrett, 2006), and the R packages NetIndices (Soetaert and Kones, 2008) and enaR (Borrett and Lau, 2014) all provide alternative methods of analysing weighted food webs using a more extensive range of ENA metrics than EwE.

Although the uptake of ENA in marine fisheries ecology is growing rapidly, there has been minimal application in riverine ecosystems (Colléter *et al.*, 2013). ENA may provide environmental managers with a more complete insight into ecological health (i.e., by assessing components of structure, function and stability) and drive more informed management decisions.

This PhD seeks to use ENA to advance the understanding of how habitat (primarily the anthropogenic changes on lotic habitats) influences aquatic food webs. The objectives of the remaining chapters are as follows:

- **Chapter two** examines the differences in food web structure between rivers, lakes and estuaries, and then investigates whether structural differences translate into differing robustness to cascading species extinction. Identifying whether and/or how food web structure differs between limnotic habitats is important for identifying structurally sensitive habitats and whether alternate management approaches are needed for different ecosystems.

- **Chapter three** defines a new method of measuring the stability of energy flows and investigates how limnotic food web structure and function affects their ability to conserve energy flow following species extinction. This chapter seeks to identify what indicators are most crucial to food web stability and bridge understanding of theoretical and empirical studies on what drives food web stability.
- **Chapter four** investigates whether forested or grassland riparian zones affect the macroinvertebrate trophic network structure and stability in streams on Mt Taranaki. Riparian zones influence stream communities in a range of ways including maintaining in-stream habitat, supporting the adult life stages of invertebrates, and providing allochthonous dietary resources. Deforestation of riparian zones is a wide spread impact on streams and has been shown to affect topological food web structure but the influence on quantified energy flows has not been investigated.
- **Chapter five** is a case study that models the potential influence of introduced predator density and periphyton abundance on the Hutt River (New Zealand) food web and potential changes in energy flow stability. Trout are a widespread sport fish throughout New Zealand; however, some studies suggest that they drive strong trophic cascades that result in periphyton blooms and altered macroinvertebrate communities. Prolific periphyton growth is currently being exacerbated by deforestation, nutrient inputs and changes in hydrological regimes. High periphyton biomass has been shown to drive changes in macroinvertebrate communities towards those dominated by grazers rather than piercers and filter feeders.

- **Chapter six** is another case study that models the potential effects of phytoplankton density on the food web of the Wellington Harbour (New Zealand) at the sub-tidal zone near the Hutt River outflow. Phytoplankton density may also be altered by nutrient inputs and influence food webs by pushing energy supply more through phytoplankton supported chains. The differences in influence of algal density between the sub-tidal estuarine food web and the Hutt River food web abundance in river (chapter five) are also compared.
- **Chapter seven** examines riverine food webs in streams and rivers throughout the Manawatu differing in nutrient enrichment. Nutrient enrichment can reduce abundance of species sensitive to enrichment, such as mayflies and stoneflies, and increase enrichment-tolerant species, such as chironomids and snails, potentially altering the food web. The relative importance of disturbance sensitive taxa on the overall food web structure is also investigated.
- **Chapter eight** I briefly synthesise the findings of the six manuscript chapters.

Chapter two:

Food web structure but not robustness differ between rivers, lakes and estuaries

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Abstract

The pervading physical habitat differences between lakes, rivers and estuaries should result in structural and thus stability differences in food webs in these three differing aquatic habitats. We compared 24 metrics of food web structure and the robustness to loss of both well-connected and random species of 18 well-resolved food webs from 6 lakes, 6 rivers and 6 estuaries. Robustness measures the proportion of species that need to be removed for 50% of all species to be lost/disconnected. Riverine food webs had low neighborhood clustering and greater variability in prey vulnerability than estuaries and lakes. Typically, rivers are disturbed relatively more frequently and with greater severity than estuaries and lakes. This may drive rivers to have lower clustering and compose greater portions of early successional taxa that are mobile and have little armor, and hence greater variability in their vulnerability to predation. Despite differences in food web structure, food web robustness did not differ between the three habitats. Similarities in robustness may be a result of freshwater organisms having similar body-size ratios between predator and prey/resource taxa thereby driving similar link distributions.

Introduction

Globally freshwater biodiversity is under considerable threat, in North America alone freshwater ecosystems are experiencing extinction rates five times higher than terrestrial ecosystems (Ricciardi and Rasmussen, 1999, Dudgeon *et al.*, 2006b, Dudgeon, 2010, Vorosmarty *et al.*, 2010). These declines in biodiversity have has resulted from multiple interacting stressors (Matthaei *et al.*, 2010, Wagenhoff *et al.*, 2011, Piggott *et al.*, 2012, Leps *et al.*, 2015) including water abstraction for consumptive and agricultural needs (Dewson *et al.*, 2007a, Poff and Zimmerman, 2010, McDowell *et al.*, 2011), invasive species (Olden *et al.*, 2010, Collier and Grainger, 2015), channelization, sedimentation, eutrophication (Carpenter *et al.*, 1998, Allan, 2004) and changing climate regimes (Palmer *et al.*, 2008, Death *et al.*, 2015).

Whilst lakes, rivers and estuaries are all impacted by these stressors, the habitat differences may yield differences in community structure that affect the ability of the community to respond to or resist such disturbances. Lakes are relatively large, deep, standing bodies of water with soft sediment bottoms; communities are typically pelagic and heavily influenced by internal thermal stratification and seasonal mixing. Rivers are flowing bodies of water, with constant mixing, variable flows and typically gravel bottoms; communities are heavily influenced by allochthonous inputs, gravel movement and flow. Estuaries represent the inland mixing zone between a river outflow and coastal waters, are usually soft bottomed and not only experience variable river flows but also semi-diurnal water fluctuations from tidal movement. Estuarine communities are typically a hybrid of the riverine and coastal communities and impacted by continual sediment deposition and disruption.

If the differences between freshwater habitats cause any of the food webs to have skewed degree distributions and/or long food chains, then they will likely have reduced topological robustness. Robustness is one measure of food web stability that assesses the capacity of a web to maintain topological structure following species extinction (Dunne *et al.*, 2002b, Dunne *et al.*, 2005, Donohue *et al.*, 2016). Food webs with more dietary links per capita (greater connectance) and a greater abundance of generalists (networks with uniform degree distributions) are hypothesized to have greater topological robustness to cascading extinctions (Sole and Montoya, 2001, Dunne *et al.*, 2002b, Ulanowicz *et al.*, 2009). Broad diets allow alternative energy pathways to continue supporting predators should other pathways be perturbed; whereas the rigid and narrow diet of specialists may prevent the compensatory effects of alternative links. (Sole and Montoya, 2001, Dunne *et al.*, 2002b, Ulanowicz *et al.*, 2009). Long food chains may also reduce robustness because the loss of basal species will cascade further up the food chain, thereby impacting more species (Freedman and So, 1985, Rooney *et al.*, 2006, Rooney and McCann, 2012, Saint-Béat *et al.*, 2015).

Both the distribution of links across species (degree distribution) and food chain length may be influenced by disturbance. Highly disturbed communities are often observed to be composed largely of generalists with broad diets, while communities in more stable environments tend to have a greater proportion of specialist species (Kitahara *et al.*, 2000, Marvier *et al.*, 2004, Devictor *et al.*, 2008). It is, therefore, plausible that disturbance can affect the composition of generalist/specialist taxa, which can in turn affect the overall food web link (degree) distribution and consequential robustness to species loss (Vázquez and Simberloff, 2002, May, 2006, Ulanowicz *et al.*, 2009). Highly disturbed ecosystems also tend to have shorter food chains and may, therefore, have greater robustness to cascading species extinction (Jenkins *et al.*, 1992, Post, 2002, McHugh *et al.*, 2010, Sabo *et al.*, 2010b).

Lakes tend to have more constant environmental conditions than estuaries and rivers as they do not experience large changes in flow regime and sediment/gravel movement from floods or tides (Wetzel, 2001). Lake communities tend to be regulated by internal feedbacks and biotic interactions (Scheffer and van Nes, 2007), whereas the diversity of river communities is often driven, at least in part, by flood regimes (Resh *et al.*, 1988, Death and Winterbourn, 1995, Lake, 2000, Death, 2008a). The environmental constancy of lakes may result in low robustness to cascading species extinction by allowing skewed degree distributions and long food chains to occur creating vulnerable hubs. Therefore, lakes may maybe more susceptible to collapse than riverine and estuarine communities (Briand, 1985, Jake Vander Zanden and Fetzer, 2007).

Lake food webs also have greater nutrient uptake and retention than estuaries and rivers, and thus provide greater opportunity for communities to take up and utilize nutrients (Saunders and Kalff, 2001). Greater assimilation of a limiting nutrient can permit higher primary productivity, which in turn allows for more energy to flow through to higher trophic levels, leading to longer food chains (Vander Zanden *et al.*, 1999, Marks *et al.*, 2000). Furthermore, if the assimilation of nutrients does not occur evenly across taxa, then some species may have considerably higher productivity than the majority. This may result in more species consuming the highly productive taxa, skewing the link distribution and making the web vulnerable to the loss of the well-connected taxa (Ulanowicz, 1997b, Dunne *et al.*, 2002b). The larger uptake and retention of nutrients in lakes may result in webs with longer chains, more skewed link distributions and consequently lower robustness than rivers and estuaries (Briand, 1985, Jake Vander Zanden and Fetzer, 2007).

If we are able to identify and protect the most sensitive freshwater habitats then we may be able reduce or halt the continued decline of freshwater species (Ricciardi and Rasmussen, 1999, Dudgeon *et al.*, 2006b, Dudgeon, 2010, Vorosmarty *et al.*, 2010). The recent availability of more complete and relatively well-resolved food webs across a range of freshwater ecosystems (Thompson and Townsend, 2004, e.g., Hechinger *et al.*, 2011, Sánchez-Hernández *et al.*, 2015) allows for comparisons in food web structure and robustness between freshwater habitats to be made. In this study, we test the hypothesis that lake, estuarine and riverine ecosystems differ in food web topology and as a result differ in robustness. We predict that river food webs, being most disturbed, will have the shortest food chains, most uniform degree distributions and greatest robustness, and lakes will have the longest food chains, most skewed degree distributions and be the least robust.

Methods

We compiled 18 well resolved (71 – 96% resolved to genus or species) aquatic food webs (Table 2.1). To assess resolution, we measured the proportion of taxa identified to species or genus level. Six webs were from estuaries, six from lakes and six from rivers; whilst there were many river food webs most were from similar and nearby rivers to those included in the study, and there were very few lake and estuarine food webs of similar resolution publicly available.

For each food web, Network 3D (Yoon *et al.*, 2004, Williams, 2010a) was used to calculate 24 metrics of food web topology including connectance, mean linkage density, trophic level proportions (by species), mean cluster coefficient, as well as measures of food chain length, degree distributions (including generality and vulnerability), nestedness, energy pathway channelization and redundancy (Table 2.2).

Table 2.1. The habitat, location, taxonomic richness, connectance and reference source for 18 freshwater food webs.

Food web	Habitat	Location	Number of taxa	Connectance	Resolution[1]	Citation
Lake Nyasa	Lake	Tanzania	37	0.055	83.8%	(Fryer, 1959)
Bridge Brook	Lake	New York, USA	75	0.098	95.0%	(Havens, 1992)
Little Rock	Lake	Wisconsin, USA	181	0.072	93.0%	(Brezonik *et al.*, 1986)
Skipworth	Lake	England	35	0.310	91.0%	(Warren, 1989)
Cimera	Lake	Spain	79	0.103	85.7%	(Sánchez-Hernández *et al.*, 2015)
Grande de Gredos	Lake	Spain	85	0.074	91.8%	(Sánchez-Hernández *et al.*, 2015)
Deep Creek	River	Idaho, USA	32	0.137	90.6%	(Koslucher and Minshall, 1973)
Bere Stream	River	England	142	0.069	91.5%	(Woodward *et al.*, 2008)
River Aire	River	England	60	0.051	83.3%	(Percival and Whitehead, 1929)
River Dee	River	Wales	34	0.092	76.5%	(Badcock, 1949)
Akatore	River	New Zealand	84	0.032	96.4%	(Thompson and Townsend, 2004)
Martins	River	Maine, USA	105	0.031	96.2%	(Thompson and Townsend, 2003)
Upper Tagus Estuary	Estuary	Portugal	29	0.086	79.3%	(Moreira *et al.*, 1992)
Carpinteria Salt Marsh	Estuary	California, USA	272	0.054	71.3%	(Hechinger *et al.*, 2011)
Estero de Punta Banda	Estuary	Mexico	355	0.048	63.1%	(Hechinger *et al.*, 2011)
Bahía Falsa	Estuary	Mexico	289	0.048	63.3%	(Hechinger *et al.*, 2011)
Ythan Estuary	Estuary	Scotland	93	0.049	86.0%	(Milne and Dunnet, 1972)
St Marks	Estuary	Florida, USA	51	0.104	71.0%	(Baird *et al.*, 1998)

[1] Resolution is the percentage of taxa nodes identified to species or genus level.

Table 2.2. Mean food web metrics for six lakes, six estuaries and six rivers. F-statistics and P-values are from ANOVASs testing differences between habitats. Degrees of freedom are 1 and 16.

Metrics	L	Est	R	F	P
Node count	8	181	5	0	0
Mean linkage density	7	9.6	3.	1	0
Connectance	0	0.0	0.	2	0
Fraction of top taxa	0	0.1	0.	6	0
Fraction of intermediate taxa	0	0.7	0.	3	0
Fraction of basal taxa	0	0.1	0.	0	0
Fraction of herbivores	0	0.2	0.	0	0
Fraction of cannibals	0	0.0	0.	6	0
Fraction of taxa within loop	0	0.1	0.	0	0
Mean short-weight trophic level (Williams and	1	2.9	1.	0	0
Mean shortest chain to a basal species (Williams and	1	2.3	1.	0	0
Fraction of omnivores (taxa feeding on multiple	0	0.5	0.	0	0
Characteristic path length (Williams and Martinez,	2	2.2	2.	0	0
Mean clustering coefficient	0	0.1	0.	1	0
Diet discontinuity (Stouffer *et al.*, 2006)	0	0.0	0.	4	0
Nestedness based on overlap and decreasing fill	0	0.2	0.	0	0
Standard deviation of consumer restricted generality	1	1.2	0.	1	0
Standard deviation of resource restricted vulnerability	0	0.7	1.	1	0
The standard deviation of the link distribution	0	0.8	0.	1	0
The entropy of the consumer restricted generality	2	2.5	2.	0	0
The entropy of the resource restricted vulnerability	2	2.7	2.	0	0
The entropy of the link distribution (Williams, 2010b)	2	3.2	2.	0	0
The percentage of resource taxa	8	86.	6	6	0
The percentage of consumers	7	86.	6	0	0

Food web robustness is defined as the percentage of taxa that need to be removed for 50% of all nodes to become extinct (Dunne *et al.*, 2002b). Food web robustness was calculated for each web by sequentially removing taxa using either of two removal sequences: 1) removal of the most connected taxa, or 2) random removal of taxa (averaged from 1000 iterations with replacement each time). Species deletion analysis was also carried out in Network 3D (Yoon *et al.*, 2004, Williams, 2010a). Secondary extinctions occurred when a species had no available dietary links remaining or completely disconnected if it is a basal species.

Using Primer 6 (Clarke and Gorley, 2006) with PERMANOVA+ (Anderson *et al.*, 2008), Non-parametric Multidimensional Scaling (NMDS) was used to examine the multivariate similarities in food web topology between the three habitat types (Clarke, 1993). For this Euclidian dissimilarity distances were used, calculated from all 24 metrics of topology (normalized). One-way Permutational Multivariate Analysis of Variance (PERMANOVA) with 9999 permutations was used to test the difference in overall web topology between the three habitats (Anderson *et al.*, 2008).

The differences in each of the food web metrics and robustness score between the three ecosystems was examined using One-way Analysis of Variance (ANOVA) in R 3.0.3 (R Development Core Team, 2012). Tukey's Honest Significant Difference post-hoc test was used to examine metrics where ANOVA differences were significant. The Holm's sequential Bonferonni procedure was applied during all multiple comparison significance testing.

Results

Species richness ranged from 29 to 355, connectance from 0.03 to 0.31, and mean shortest chain length from 1.47 to 2.58 across the 18 webs, though there was no significant difference in species richness, connectance and food chain length between the three habitats.

In an NMDS, river food webs were plotted to the left of axis one and estuaries to the right, with most lakes in the centre (Fig. 2.1). The food webs from the three habitat types differed in their structure although there was some overlap (F=2.92, p=0.009).

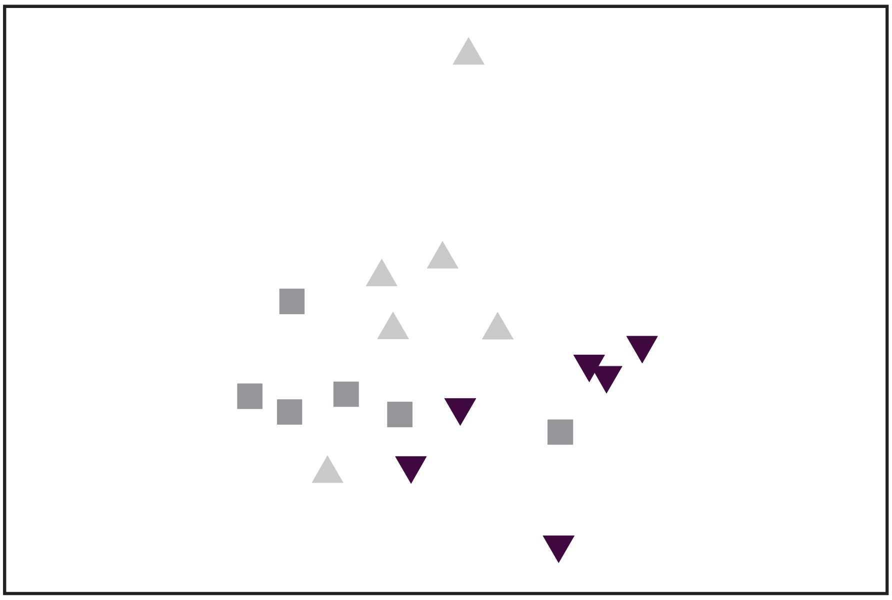

Fig 2.1. NMDS plot of food web metrics for 18 aquatic communities (stress = 0.11). Lakes are represented by light grey triangles, rivers by mid-grey squares, and estuaries by black inverted triangles. See Table 2.1 for more detail on locations and primary references.

The three habitats differed in their mean cluster coefficients ($F_{1,16}$=10.07, p=0.006, Fig. 2.2 (top)), and their standard deviation in vulnerability (number of predator) distribution ($F_{1,16}$=10.02, p=0.006, Fig. 2.2 (bottom)). Rivers had low mean cluster coefficients than lakes (p=0.008), there was no difference between lakes and estuaries (p=0.09). Rivers had a much larger variation (standard deviation) in vulnerability (number of predator) distribution than lakes (p=0.006), there was no difference between lakes and estuaries (p=0.56). The fraction of top taxa was also marginally significantly greater for rivers than estuaries and lakes ($F_{1,16}$=6.71, p=0.02).

Food web robustness did not differ significantly between the three habitats when the most connected taxa were preferentially removed ($F_{1,16}$=0.15, p=0.86, Fig. 2.3 (top), or when taxa were removed randomly ($F_{1,16}$=0.72, p=0.50, Fig. 3 (bottom)).

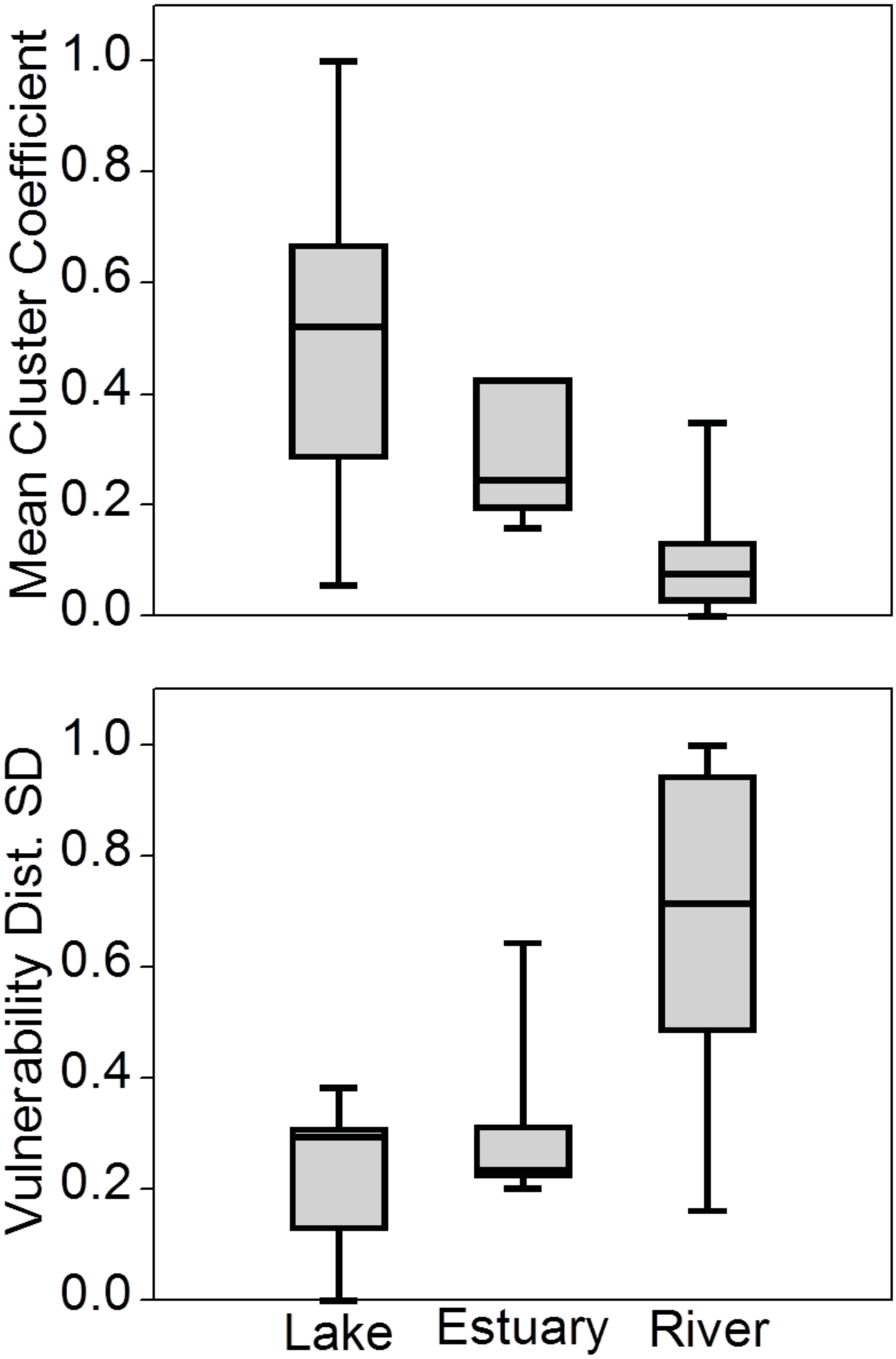

Fig 2.2. The mean cluster coefficient (top) and the standard deviation of the normalized vulnerability distribution (bottom) for 18 aquatic food webs depending on their habitat.

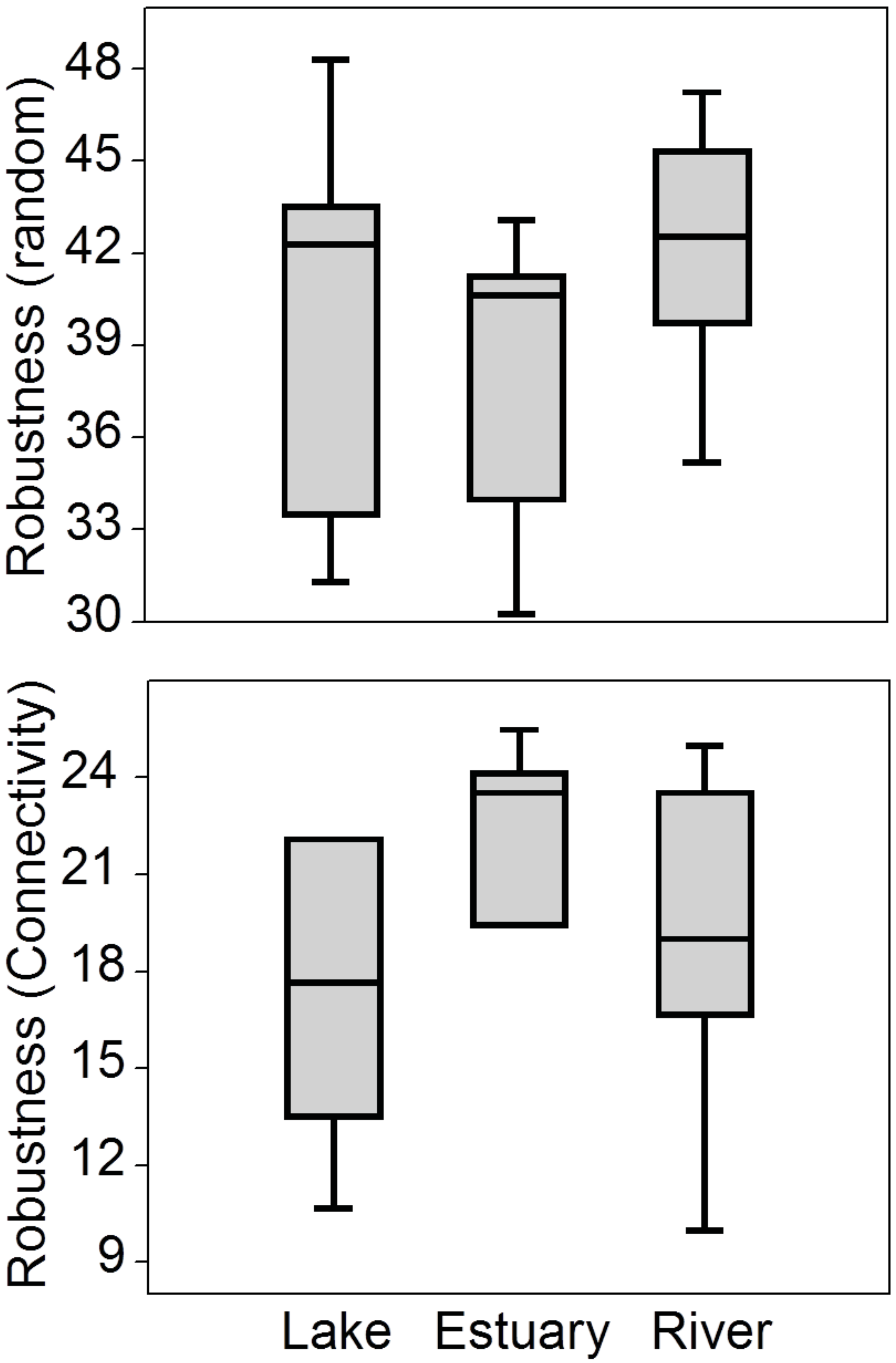

Fig 2.3. The network robustness of 18 aquatic food webs to the loss of random taxa (top) and the most connected taxa (bottom) depending on their habitat. Robustness is the proportion of direct removals required for >50% of species to be lost.

Discussion

Food web structure differed between the three habitat types. River food webs showed significantly lower node clustering (neighborhood connectivity) than estuaries and lakes. Previous studies have suggested that mean cluster coefficient can be driven by species diversity and connectance (Camacho *et al.*, 2002, Dunne *et al.*, 2002a, Belgrano *et al.*, 2004); however, neither the number of nodes nor connectance differed significantly between the three habitats. Species deletion experiments of empirical food webs have consistently shown that clustering decreases with increasing perturbation (Estrada, 2007, Navia *et al.*, 2012). Furthermore, empirical observations suggest that perturbations impact further than three links away from the initial perturbation (Schoener, 1989, Montoya and Sole, 2002, Williams *et al.*, 2002); therefore, low clustering may be advantageous in webs where species with high neighborhood connectivity are perturbed. Rivers typically face regular and harsh flood disturbances that scour away almost completely all basal taxa and remove substantial portions of invertebrates and fish (Biggs and Close, 1989, Death, 2008a). The flood disturbances that rivers face may be relatively more deleterious than the cyclic mixing and sedimentation experienced by estuaries and the internal seiches and stratification-mixing regimes in lakes (Wetzel, 2001). It is, therefore, plausible that the relatively more severe perturbations of floods in rivers reduces the amount of clustering compared to estuaries and lakes. In general, food webs tend not to have clustering coefficients typical of small-world networks (Watts and Strogatz, 1998, Camacho *et al.*, 2002, Dunne *et al.*, 2002a); our analysis suggests that food webs from some habitats may be more similar to small world networks than others.

Rivers also tend to have greater variability in the vulnerability (number of species consuming prey, or the output links of a node) distribution than estuaries and lakes. Power *et al.* (1996) found that after scouring floods the early successional community consists largely of taxa highly vulnerable to predation, which tended to be mobile and unarmored, or lightly armored, invertebrates, such as mayfly nymphs. Throughout the duration of the flood free period, predator-vulnerable taxa were replaced with less vulnerable taxa that were armored, had silk retreats, and/or were sessile, thus driving greater variation in prey vulnerability. In lakes and estuaries, however, many of the taxa are sessile and retreat into the benthic sediment (Fuller and Rand, 1990, Saha *et al.*, 2009). In consequence, high prey vulnerability may drive strong top down control, whereas low prey vulnerability may drive strong bottom up control (Power *et al.*, 1992, Atlas and Palen, 2014).

Early studies suggested that food webs had an invariant structure regardless of web size or habitat type (Briand and Cohen, 1984, Sugihara *et al.*, 1989). These findings have been severely criticised for the use of poorly resolved webs, with the current thinking that there is large variation between webs across habitat types (Havens, 1992, Bengtsson, 1994, Martinez, 1994, Petchey *et al.*, 2004). Our assessment of these well-resolved webs supports the view that neighbourhood connectivity and vulnerability differs significantly between habitat types (Petchey *et al.*, 2004, Jake Vander Zanden and Fetzer, 2007).

However, despite the differences in food web structure, robustness did not differ between habitats, irrespective of the sequence of species removal used. This is surprising given that lakes, rivers and estuaries differ considerably in their disturbance regimes, physical habitat structure, and nutrient dynamics (Wetzel, 2001); all of which can potentially alter food chain length and link distributions (both of which can drive food web robustness) (Saint-Béat *et al.*, 2015, Mougi and Kondoh, 2016). In the webs we examined, neither food chain length, nor degree nor generality distributions differed significantly between habitats. Despite the obvious differences in physical structure and disturbance between the three habitats, it may simply be that disturbance has little influence on link distribution and robustness or that the webs face similar levels of disturbance except in different forms. For example, rivers are often disturbed by floods, estuaries by sedimentation and lakes by internal seiches and stratification-mixing regimes (Wetzel, 2001).

Alternatively, recent analysis suggests that allometric scaling may enhance stability (including topological robustness) by altering dietary breadth which can alter connectance and population dynamics (Woodward *et al.*, 2005, Brose *et al.*, 2006b, Brose, 2010, Kartascheff *et al.*, 2010, Digel *et al.*, 2011, Thierry *et al.*, 2011, Heckmann *et al.*, 2012). The analysis of a large, global database of the body masses of consumers and prey found animals from lakes and streams to have very similar body size ratios compared to marine and terrestrial ecosystems (Brose *et al.*, 2006a). Therefore, the similarities in body size may translate to the similarities in link distribution and robustness observed. Instead, the differences between lakes, rivers and estuaries were around the neighbourhood connectivity and vulnerability distributions affect topological robustness (Rooney and McCann, 2012, Saint-Béat *et al.*, 2015, Mougi and Kondoh, 2016).

Whilst we did not detect any differences in robustness, this does not mean that there are no differences in community stability between the three ecosystems. Robustness, resilience, resistance, invasibility and persistence all contribute to community stability (Saint-Béat *et al.*, 2015). Therefore, even if robustness does not differ, other aspects of stability may still differ. We also only measured web robustness to the loss of both randomly selected and well connected species loss, hence robustness may still differ under different deletion sequences. Furthermore, our assessment of topological robustness assumes webs are bottom up controlled and ignores energetic dynamics, which may mask the effects on trophic cascades of neighbourhood connectivity and vulnerability variation. As explained above, the differences in vulnerability may affect the direction of trophic control which can, in turn, drive differences in stability and other emergent properties such as mutualism and synergism (Ives and Cardinale, 2004, O'Gorman *et al.*, 2010).

In summary, rivers have lower neighbourhood connectivity and greater variability in the vulnerability of predators than lakes and estuaries. These differences, however, did not translate into differences in topological robustness to cascading species extinction when species were removed randomly or by their connectivity. The similarities in link distribution and robustness between lakes, rivers and estuaries may instead be driven by freshwater ecosystems having similar body-size ratios (Brose *et al.*, 2006a).

Chapter three:

Trophic cascade direction and flow determine network flow stability

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Abstract

The mechanisms for maintenance of food web structure and function in the face of frequent disturbance has been a question in ecology for many years. Local point-wise stability of theoretical food webs or robustness assessment of empirical binary food webs are the two principal techniques that have been used to address this question. However, many theoretical webs are often small, constructed randomly or from theoretical algorithms (such as Cascade or Niche models), and assume Lotka-Volterra dynamics. Whilst the binary webs used also assume all interactions are equal and that webs are donor controlled. Recent dynamic stability analysis of empirical quantitative webs has sought to improve this assessment. Here we investigate how aquatic food web structure and the direction of trophic cascades interact to affect the robustness of total carbon flow between species after a disturbance. The robustness of the 18 food webs is higher if predator control dominates. Webs with predator control were however stabilised by weak indirect interactions and short food chains.

Introduction

The complex nature of food webs (biological, directed networks of who eats whom within an ecosystem) makes it difficult to predict the cascading impacts of species loss following disturbance. However, with a growing global population, human impacts on ecological communities are increasing and the cascading impacts of these activities are difficult to predict and/or manage. Just one example of the many trophic cascades driven by anthropogenic disturbance is recorded by Ripple & Beschta (2006) who found increased visitors to Zion National Park, decreased cougar density that in turn increased Mule Deer density. The increased grazing of deer on cottonwoods increased soil erosion and reduced abundance and diversity of both terrestrial and aquatic taxa (Ripple and Beschta, 2006). This illustrates how disturbance can ripple through a web producing unforeseen outcomes. If it was possible to identify potential cascade pathways, then similar adverse chain reactions may be mitigated or avoided.

Although the influence of food web structure on stability has been extensively studied, it is still unclear exactly what the key parameters are for determining stability (Rooney and McCann, 2012, Saint-Béat *et al.*, 2015). Here we consider stability to be a general term for the maintenance of food web structure and function over time, it includes various aspects such as equilibrium, persistence, resilience, robustness and resistance (Dunne *et al.*, 2005). Complexity (i.e., aspects including diversity, connectance, pathway proliferation and link distribution) promotes stability (by supporting predators with multiple energy pathways and dampening disruptive oscillations) or destabilizes it by spreading disruptive oscillations (McCann, 2000, Rooney and McCann, 2012, Saint-Béat *et al.*, 2015, Zhao *et al.*, 2016). It is unclear whether long food chains (network paths) are always unstable or whether the stability is dependent on the underlying trophic dynamics in those food chains (Rooney and McCann, 2012, Saint-Béat *et al.*, 2015). It is also unclear whether omnivory (feeding on multiple trophic levels) increases or reduces stability by suppressing or increasing oscillations (Gellner and McCann, 2012, Saint-Béat *et al.*, 2015).

Much of the uncertainty around what drives stability arises because of differing methods for assessing stability, and/or differences in the implied trophic dynamics of the webs (McCann, 2000). Early exploration by Gardner and Ashby (1970) and May (1972) showed that random large, well-connected food webs with Lotka-Volterra dynamics are unlikely to be stable. Whilst this was opposite to what Ecologists had hypothesized (MacArthur, 1955, Odum, 1969), it challenged Ecologists to understand what drives natural ecosystems to be stable. It was quickly identified that randomly generated webs with Lotka-Volterra dynamics are unrealistic assumptions for most food webs (Dunne *et al.*, 2005); also, point-wise linear stability (i.e., eigenvalue analysis) may not reflect the stability of the entire food web (Ulanowicz, 1972). De Angelis (1975) used a similar modelling approach to May (1972); however, he showed that highly connected food webs could be stable if they had low assimilation efficiencies and a bias towards donor-control. More recently, McCann *et al.* (1998) showed, using theoretically generated food webs with empirically mimicked interaction strengths, Holling type III responses and non-equilibrium dynamics, that generalist-dominance and weak interactions stabilize webs by dampening oscillations. In addition, also primarily via theoretical studies, adaptive foraging with a mixture of strong and weak interactions (asymmetrical flows) are predicted to confer stability (Kondoh, 2003, Kondoh, 2006, Rooney *et al.*, 2006, Uchida and Drossel, 2007). Adaptive foraging prevents cascading perturbations by allowing alternative energy supplies to establish should a link become perturbed. Consumers with both strong and weak interactions are able to feed on abundant species and exert recipient control; the less abundant species are consumed less allowing their populations to grow whilst the dominant competitor is kept in check (Rooney and McCann, 2012, Saint-Béat *et al.*, 2015).

Despite these advancements in model food webs, whether these factors drive stability in empirically derived food webs has received much less attention. Most analysis of empirically derived webs has involved the assessment of topological robustness which involves simulating cascading extinction following initial species extinction (Sole and Montoya, 2001, Dunne *et al.*, 2002b). The advantage of this approach is that empirically derived food webs can be used, it indicates on whole-system responses, and a variety of perturbation events effects on whole web stability examined. However, to date this approach has mostly been applied to topological webs (interaction strengths are not quantified) (Dunne *et al.*, 2005). They also assume webs are driven entirely by donor control dynamics (Sole and Montoya, 2001, Dunne *et al.*, 2002b). This methodology suggests that high connectance yields high robustness, and that highly skewed food webs are robust to poorly connected species but sensitive to the loss of well-connected species (Sole and Montoya, 2001, Dunne *et al.*, 2002b, Ives and Cardinale, 2004, Gilbert, 2009). Both eigenvalue analysis of theoretical webs and robustness of binary webs, therefore, have several limitations to their use and applicability in understanding and managing real ecosystems. Furthermore, Curtsdotter *et al.* (2011) showed that, in niche model generated webs, purely topological robustness tends to overstate robustness compared with dynamical robustness.

Dynamical robustness allows for the incorporation of indirect effects (via flow weighted food webs) and both predator control and donor control cascades, thus making them more realistic simulations. Recently, Zhao *et al.* (2016) applied dynamical robustness and found that food webs are most sensitive to secondary extinction when species are removed by their link weights rather than connectivity. Both diversity and connectance reduced robustness, in contrast to topological studies that found connectance increased robustness (Dunne *et al.*, 2002b, Zhao *et al.*, 2016). They also found donor control cascades caused only half of the secondary extinctions, highlighting the importance for also assessing predator control along with donor control. Thereby highlighting the need for food web stability studies to move beyond theoretical models and empirically-derived topological webs to the assessment of flow-weighted food webs. With the increasing availability of well-defined flow-weighted food webs and ecological network analysis metrics (Latham Ii, 2006, Borrett and Lau, 2014), it is now possible to explore the drivers of dynamic robustness of empirically derived food webs. Greater analysis of empirical food web stability may also close the gap between theoretical constructs and conservation/management actions.

Ecosystem management is increasingly recognizing the importance of managing for ecosystem health in addition to traditional single species conservation approaches (Steedman, 1994). Healthy ecosystems are ones that maintain structure (organization) and function (vigor) over time in the face of disturbance (stability) (Costanza and Mageau, 1999). Structure or organization includes concepts such as species diversity, average mutual information and topological predictability. Whereas function or vigor includes concepts such as productivity, throughput, cycling, and flow based mutualism and synergism. Identifying stressors and understanding how they may distress the natural lifespan of an ecosystem's structure and function is, therefore, vital to the conservation of ecosystem health. To our knowledge, all studies of the stability of empirical webs have focused on the maintenance of organization (e.g., species richness) with few studies investigating the global stability of vigor – an equally vital component of ecosystem health (Saint-Béat *et al.*, 2015, Mougi and Kondoh, 2016). Our study seeks to partially fill that gap by using 18 Carbon flow weighted food webs to explore the structural and dynamic drivers of total Carbon through-flow stability (a measure of vigor) following random mass extinctions.

Methods

Eighteen aquatic food webs, spanning a range of diversity and complexity, with quantified carbon stores and flows were analyzed for their structure and dynamic robustness of carbon throughput (Table 3.1). The webs spanned a range of diversity and complexity, this is likely partly influenced by differing levels of resolution. However, the range of weighted webs publicly available is small and we only chose webs that had more than 12 compartments to reduce the scaling constraints of small webs (Bersier and Sugihara, 1997).

The following network metrics of structure and carbon flow were calculated in R 3.0.3 (R Development Core Team, 2012) with packages NetIndices (Soetaert and Kones, 2008) and enaR (Borrett and Lau, 2014): the number of nodes, connectance (the per capita linkage density), Finn's Cycling Index (Finn, 1976), relative ascendency (Ulanowicz, 1997b), the ratio of Indirect/Direct flows (inputs idealized) (Fath and Patten, 1999b, Borrett *et al.*, 2006, Latham Ii, 2006), the ratio of Indirect/Boundary flows, the Indirect Flow Intensity (Borrett *et al.*, 2006), the average flow-based trophic level (Christensen and Pauly, 1993), and the average omnivory index (Christensen and Pauly, 1993).

Table 3.1. The name, first year published, location, number of compartments (N), connectance (C), and total system throughflow (TST) of eighteen aquatic ecological networks.

Web Name and Citation	Year Published	Location	N	C	TST
Cypress Marshes – Dry Season (Ulanowicz *et al.*, 1997)	1997	Florida, USA	68	0.12	1918.35
Florida Bay – Dry Season (Ulanowicz *et al.*, 1998)	1998	Florida, USA	125	0.13	1778.933
Graminoids Marshes (Ulanowicz *et al.*, 2000)	2000	Florida, USA	66	0.18	7519.759
Mangroves (Ulanowicz *et al.*, 1999)	1999	Florida, USA	94	0.15	3272.262
Chesapeake Bay (Baird *et al.*, 1991)	1989	Eastern USA	36	0.09	3227453
Northern Benguela Upwelling (Heymans and Baird, 2000)	2000	Namibia	24	0.21	6607.753
Neuse River Estuary Late Summer (Baird *et al.*, 2004b)	2004	North Carolina, USA	30	0.10	15031.33
St Marks Seagrass Site 4 (Feb) – Apalachee bay (Baird *et al.*, 1998)	1998	Florida, USA	51	0.08	2865.47
Sylt-Romo Bight (Baird *et al.*, 2004a)	2004	Netherlands to Denmark	59	0.08	1780964
Charca de Maspalomas Lagoon (Almunia, 1999)	1999	Canary Islands	21	0.12	6010331
Gulf of Maine (Link *et al.*, 2008)	2008	North-east USA	31	0.34	18381.9
Baltic Sea (Baird *et al.*, 1991)	1991	Northern Europe	15	0.17	1973.593
Crystal River – control (Ulanowicz, 1986)	1986	Florida, USA	21	0.19	15062.54
Lake Oneida – pre ZM (Miehls *et al.*, 2009a)	2009	New York State, USA	76	0.22	1365.096
Bay of Quinte – pre ZM (Miehls *et al.*, 2009b)	2009	Ontario, Canada	80	0.21	1925.026
Peruvian Upwelling (Baird *et al.*, 1991)	1991	Southwest Pacific, Peru	16	0.22	33496.09
Swartkops Estuary (Baird *et al.*, 1991)	1991	Southern Africa	15	0.17	13996.24
Ythan Estuary (Baird and Milne, 1981)	1991	Scotland	13	0.23	4181.8

Dynamic robustness, our indicator of stability, was defined as the percent of the original, pre-perturbed, web total system throughflow (the sum of all flows within a network) that occurred at a new steady state following the random loss of 25% of the nodes. The post-perturbation re-balancing followed the methods described by Allesina and Bondavalli (2003) and were carried out using the enaR (Borrett and Lau, 2014) package in R 3.0.3 (R Development Core Team, 2012). We chose a 25% extinction rate because in 2008 approximately one quarter of marine species assessed were listed in threatened categories (Critically Endangered, Endangered or Vulnerable) (Polidoro *et al.*, 2009). Secondary species extinctions were not enumerated because it is unlikely that a compartment will be driven to zero completely in the model and there is insufficient data published on Allee Effects to estimate density dependent thresholds for each compartment; furthermore, the focus of our study was on the stability of ecosystem vigor rather than organization. The dynamic robustness was calculated for each web for three dynamic scenarios (each iterated with replacement 20,000 times):

1. Donor-control (bottom up) dynamics - the webs were re-balanced by keeping inputs constant, using Allesina and Bondavalli (2003) input balancing method, which yields steady-state webs identical to those derived by donor controlled simulations (C Kazanci & S Whipple, pers. comm.).
2. Predator-control (top down) dynamics - the webs were re-balanced by keeping outputs constant, using Allesina and Bondavalli (2003) output balancing method, which yields steady-state webs identical to those derived by recipient (predator) controlled simulations (C Kazanci & S Whipple, pers. comm.).
3. Averaged dynamics - the coefficients were the average of those derived from either controlling inputs or outputs, following the average (AVG) rebalancing method of Allesina and Bondavalli (2003). Whilst this approach successfully rebalances webs, it

does not yield balanced webs equivalent to those derived with equal donor-recipient control, which tend to oscillate and rarely achieve steady-state (C Kazanci & S Whipple, pers. comm.).

Analysis of Variance (ANOVA) and post-hoc paired t-tests were used to compare the average robustness scores between the three dynamic scenarios. Relationships were then explored with linear regressions between robustness derived from each of the three dynamic scenarios and each of the structural metrics. The Holm's Sequential Bonferonni correction was applied during all significance testing. All statistical analysis was carried out using R 3.0.3 (R Development Core Team, 2012).

Results

The eighteen webs analyzed had an average of 45.9 nodes, connectance ranged from 0.08 to 0.35, the Indirect/Direct (idealized) ranged from 0.86 to 5.73, and the average trophic level ranged from 3.10 to 8.00 (Table 3.2).

Table 3.2. The mean, standard deviation, maximum and minimum values for eight structural metrics of eighteen aquatic ecological networks.

Metric	Mean	Standard Deviation	Minimum	Maximum
Number of taxa (N)	46.7	31.5	13	125
Connectance (C)	0.17	0.07	0.08	0.35
Relative Ascendency	0.39	0.07	0.26	0.53
Indirect/Direct Flows (Idealized)	1.84	0.62	0.86	3.15
Average Omnivory Index	0.60	0.28	0.10	1.13
Average Trophic Level	4.20	0.59	3.10	5.43
Finn's Cycling Index	0.11	0.11	0.0002	0.47

Overall, robustness differed with the direction of dynamic control ($F_{1,2}$=7.97, p=0.001; Fig. 1.). The webs that were re-balanced with donor-control dynamics had lower robustness than those rebalanced with predator-control dynamics ($t_{1,17}$=2.88, p=0.01) or the average of donor and predator control ($t_{1,17}$=3.26, p=0.004). There was no difference in robustness between those rebalanced with predator-control dynamics and the averaged dynamics ($t_{1,34}$=1.06, p=0.30).

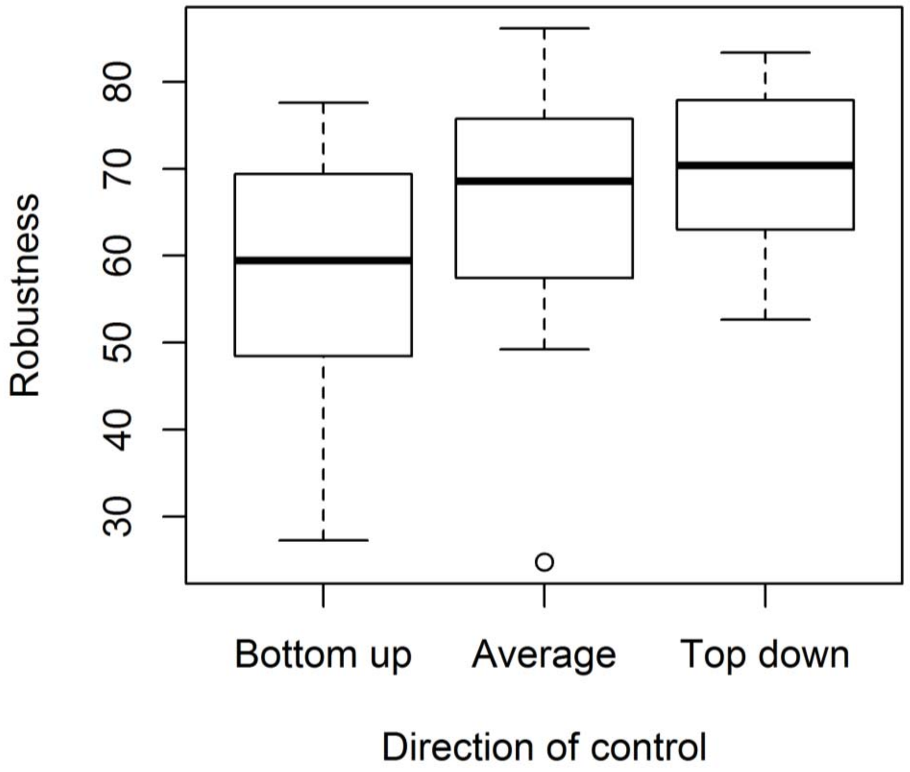

Fig. 3.1. The median and range of robustness scores for 18 aquatic food webs dependent on the imposed trophic cascade direction.

When cascades were donor controlled there was only a marginally significant decrease in robustness with increasing average trophic level; however, when cascades were predator controlled robustness decreased significantly with the Indirect/Direct (Idealized) (Table 3.3, Fig. 3.3). Interestingly, when the webs were rebalanced with averaged dynamics then robustness decreased with increasing the Indirect/Direct (Idealized), average trophic level, and average omnivory index. Neither taxonomic richness, connectance, relative ascendency, or carbon recycling were linked with robustness regardless of cascade direction (Table 3.3).

Table 3.3. Linear regressions between network metrics and the dynamic robustness of eighteen aquatic ecological networks as with either donor controlled cascades, predator controlled cascades, or an average of cascades in both directions. F-statistics (degrees of freedom 1 and 16) and p-values are calculated from ANOVAs testing slope = 0 using R 3.0.3 (R Development Core Team, 2012). Holm's Sequential Bonferroni correction applied during multiple comparisons. Bold values indicate significant relationships, whereas * indicates marginal significance. $^{+}$Indicates where an outlier was removed prior to testing.

Metric	Donor controlled			Predator controlled			Average of both directions		
	R^2	F-statistic	p-value	R^2	F-statistic	p-value	R^2	F-statistic	p-value
Number of taxa (N)	-	1.62	0.22	-	2.84	0.11	-	0.08	0.79
Connectance (C)	-	0.28	0.60	-	0.002	0.97^{+}	-	0.31	0.58^{+}
Relative Ascendency	-	0.01	0.92	-	0.64	0.43	-	0.42	0.53
Indirect/Direct flows (Idealized)	0.22	4.55	0.05*	**0.52**	**19.46**	**<0.01**	**0.53**	**20.12**	**<0.01**
Indirect/Boundary flows	-	3.07	0.10	0.25	5.4	0.04*	0.22	4.56	0.05*
Indirect Flow Intensity	-	4.17	0.06	0.23	4.82	0.04*	0.22	4.46	0.05*
Average Omnivory Index	0.26	5.67	0.03*	-	3.43	0.08	**0.39**	**11.72**	**<0.01**
Average Trophic Level	0.19	5.00	0.04*	0.19	5.00	0.04*	**0.32**	**9.07**	**<0.01**
Finn's Cycling Index	-	0.005	0.95	-	1.42	0.25	-	0.25	0.63

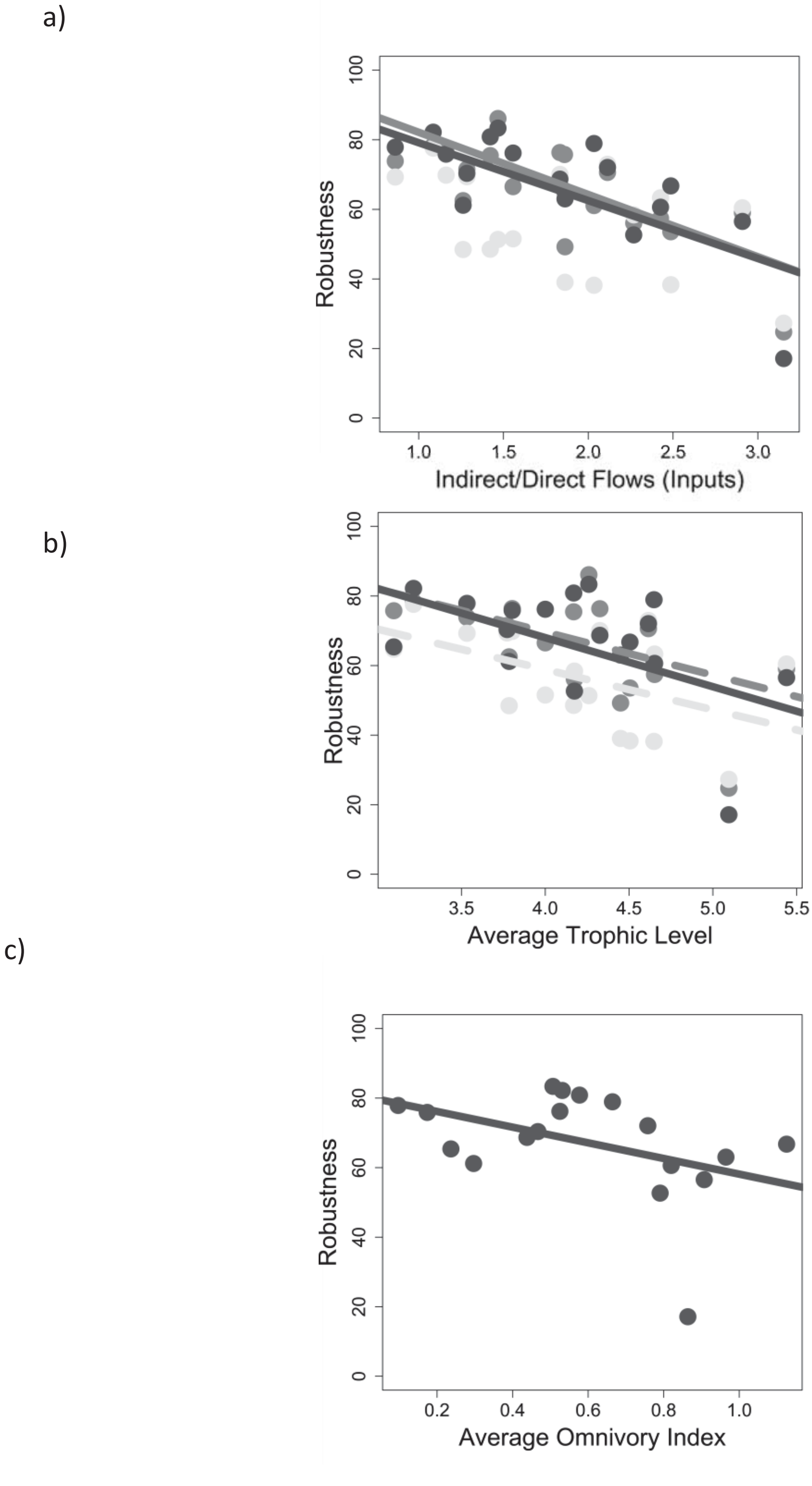

Fig. 3.2. The robustness of 18 aquatic ecological networks versus the Indirect/Direct (Idealized) (**A**), the mean trophic level (**B**), and the mean omnivory index (**C**). Light grey indicates when donor control dominates, dark grey when predator control dominates and mid grey when cascades are averaged in both directions. Dashed lines indicate marginal significance.

Discussion

Webs with low Indirect/Direct flows (Idealized) were highly robust to the loss of energy flow when webs were rebalanced via predator-control cascades or with averaged dynamics (Table 3.3, Fig. 3.2 (a)). Indirect effects occur when a change in one species affects another species via an intermediate species or pathway (Wootton, 1994). Wootton (1994) identified five ways that indirect effects may present themselves in food webs including interspecific competition, trophic cascades, apparent competition, mutual interference, and mutual exploitation. All of these indirect pathways are likely to naturally occur in the webs we examined and all depend to some degree on strong predator competition for food (Wootton, 1994). In the flow models examined, strong indirect effects present as trophic cascades that permeate the effects of species extinction along food chains and severely impacting other species, thereby reducing robustness (May, 1971, Saint-Béat *et al.*, 2015, Zhao *et al.*, 2016). A system's total through-flow is composed of boundary, direct and indirect flows with indirect flows being dependent on the direct and boundary flows (Borrett *et al.*, 2006). Therefore, the greater the proportion of total flow generated from indirect flows, the more total through-flow will be impacted when boundary and direct flows are perturbed. These patterns did not occur when cascades were donor controlled, perhaps because if prey go extinct then dependent predators also suffer regardless of the strength of indirect flows (Pimm, 1991). Furthermore, with donor control dynamics the densities of basal taxa are unaffected by changes in predator densities, therefore the impacts of species extinction are confined to higher trophic levels.

Regardless of cascade direction, webs with on average shorter food chains (as proxied by the average trophic level) were more robust than those with longer chains. This effect was most pronounced when webs were rebalanced with averaged dynamics, and weakly significant when rebalanced with donor or predator controlled cascades (Fig. 3.2 (b)). Long food chains may allow the changing densities caused by predator controlled dynamics to cascade further and impact more species; whilst donor control dynamics mean that when a resource species suffers from a drastic reduction or extinction (from top down consumption) then all the species dependent on that resource species will be affected (Pimm and Lawton, 1977, Post, 2002, Saint-Béat *et al.*, 2015). The strong effect of reduced robustness from cascades through the long chains may account for a substantial portion of the indirect effects which also affects robustness (Wootton, 1994).

As with food chain length, when cascades from both directions were averaged, the average level of omnivory decreased robustness (Fig. 3.2 (c)). Gellner and McCann (2012) have identified numerous configurations of omnivorous interactions that can either be stabilizing or destabilizing. The polyphagy present in omnivorous interactions can mean diets are more adaptable, composed with a mixture of weak links, and the dominant competitor of key prey may be kept in check, thereby preventing loss by energy transfer inefficiencies (longer chains require more energy) (Fagan, 1997, Montoya *et al.*, 2006, Saint-Béat *et al.*, 2015). Regardless of food web configuration, strong omnivorous interactions were more destabilizing than weak ones (Gellner and McCann, 2012). Vandermeer (2006) has shown that simple three species omnivorous configurations can often resemble (or occur on a gradient toward) either a linear food chain (if the link between the apex predator and the basal species is weak), or interspecific competition (if the link between the apex predator and the intermediate species is weak), or apparent competition (if the link between the basal resource and the intermediate species is weak). If the omnivory present resembled linear food chains, then the omnivory-robustness relationship observed may be reflecting the destabilizing effect of long food chains (Allesina *et al.*, 2009).

Across the metrics tested, those with the most pronounced and significant relationships with robustness occurred when webs were rebalanced with averaged cascades. This effect may have arisen because the average balancing approach tends to result in less variation than unidirectional balancing (Allesina and Bondavalli, 2003), thereby sharpening the observed relationships.

Despite considerable debate about whether food web complexity, including diversity and connectance, increases or decreases stability (McCann, 2000, Rooney and McCann, 2012, Saint-Béat *et al.*, 2015). Our study suggests there is no linear relationship between measured aspects of complexity (i.e., diversity, connectance and relative ascendency) and stability. Recent analysis of donor-controlled binary webs indicates that web robustness depends on the distribution of the links (Sole and Montoya, 2001, Dunne *et al.*, 2002b). However, connectance does not account for links highly dependent on a few keystone species (making vulnerable hubs), whereas relative ascendency does account for potential perturbation of these vulnerable hubs on flow distribution (Ulanowicz, 1997b). Although it has been hypothesized that robustness decreases with increased relative ascendency (Ulanowicz, 1997b, Ulanowicz *et al.*, 2009), we found no such relationship (Table 3.3). In addition, the information theory based robustness, as used in Mukherjee *et al.* (2015), is also unlikely to correlate with dynamic robustness estimated here because of the strong correlation it had with relative ascendency in Mukherjee *et al.* (2015). This may be because relative ascendency indicates overall structure and total system flows and not the influence of indirect effects (Ulanowicz, 1997b, Allesina *et al.*, 2009). It is plausible that flow dynamics override the effects of topological structure in determining robustness. Nevertheless, given that most of the webs had similar levels of relative ascendency (Table 3.2; Ulanowicz, 2009), more research with webs incorporating a wider range of relative ascendency or broader topological differences is required. Furthermore, the food webs used had some level of species aggregation, this tends to increase flow redundancy and reduce species redundancy (Pinnegar *et al.*, 2005, Baird *et al.*, 2009), which may distort how the modelled web responds to perturbations. For example, two species may have the same trophic links yet be aggregated and both removed simultaneously during perturbation simulations. In reality, the two species may have completely different abilities to respond to a given disturbance and one may be able to persist and provide alternative energy channels when the other is perturbed. Therefore, the effect of taxonomic resolution on robustness requires examination.

Overall, predator controlled webs were more robust than donor controlled webs. This is contrary to theoretical explorations of stability that suggest donor controlled webs should be more stable (DeAngelis *et al.*, 1989, Saint-Béat *et al.*, 2015). The contrast between our results and those from more theoretical studies may be because stability in those studies was assessed using local resilience (which measures the time for a network to recover from a small disturbance) (DeAngelis *et al.*, 1989, Saint-Béat *et al.*, 2015). Instead, our research compares the total carbon flow of the new equilibrated state with that of the pre-disturbance state. When species go extinct with donor control dynamics then all species supported by that species suffer correspondingly, whilst those further down in the trophic cascade remain unchanged. Conversely, with predator control a predator affected by a partial loss of its prey will maintain its densities and dietary carbon flow by increasing consumption of other prey. When the indirect effects are weak then predator control cascades are likely to be easily dampened allowing carbon flows to be recovered with minimal cascading damage (McCann *et al.*, 1998).

In summary, we found that weak indirect effects and short food chains stabilize communities from the loss of carbon flows following species extinction. However, weak indirect interactions are more effective at stabilizing flows when communities have predator control dynamics than donor control dynamics. Identifying and conserving species that are important to the maintenance of overall indirect to direct flow ratio are likely to be crucial in conserving nutrient/energy flows within many ecological communities. Furthermore, pollution, invasive species, harvesting, land use change, and climate change all have the potential to switch a food web from one with predator control to one with donor control (or vice-versa). Therefore, not only do conservation plans need to be tailored depending on the direction of energetic control, they also need to be sufficiently adaptive to ensure the strategic re-prioritization of conservation objectives should disturbance cause a switch in the dominant direction of cascades.

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Chapter four:

Forest canopy affects stream macroinvertebrate community structure but not stability

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Abstract

Understanding the determinates of community structure and function has been a central theme in community ecology for many years. The form of energy supply to food webs is often one of the strongest influences on community structure and function. It is postulated that trophic stability is strongly influenced by the nature of these energy pathways and whether they are external (allochthonous) or internal (autochthonous) to the ecosystem. In this study, we investigated whether stream invertebrate communities under forest canopy or in open grassland differ in community composition, energetic network structure and stability. Stability was tested as the conservation of energy flow following species extinctions. The forest stream communities were dominated by filter feeders and shredders, whilst the grassland communities were dominated by grazers. However, there was no significant differences in trophic network structure or stability. As stream systems, particularly in mountainous areas like New Zealand, are exposed to regular and large physical disturbance from flooding it may simply be that the floods result in generalist species dominating communities irrespective of the energy source.

Introduction

The influence of energy supply on community structure and stability is a central theme in community ecology (McCann, 2005, Ives, 2007, McCann, 2011). This has become even more important as humans continue to alter habitats and change the nature of energy supplies by deforestation. Despite extensive research documenting changes in species composition (and to a lesser extent trophic structure) as a result of habitat change (Ceballos *et al.*, 2015, Peters *et al.*, 2015), there is limited research on the corresponding changes to community stability and energetic flow pathways (Saint-Béat *et al.*, 2015, Mougi and Kondoh, 2016). This research has been impeded by the lack of suitably quantified data on community trophic structure and the limited methods for assessing stability (Rooney and McCann, 2012, Saint-Béat *et al.*, 2015).

Stability is a broad term used to describe a state whereby community structure and function is maintained over time despite disturbance. Stability is often composed of resistance, persistence, resilience, robustness and dynamic equilibrium (Dunne *et al.*, 2005). To date the majority of food web stability studies have used theoretical rather than empirical webs (Saint-Béat *et al.*, 2015). These webs have been criticized for being unrealistic, randomly assembled or bound by configuration rules that lack justification (De Angelis, 1975, McCann, 2000, Rooney and McCann, 2012). Furthermore, most empirical analyses of trophic stability have used binary webs and only assessed topological robustness (Sole and Montoya, 2001, Dunne *et al.*, 2002b). Using simple binary webs ignores the influence of interaction strength and assumes trophic cascades occur solely from the bottom up. It is, therefore, unclear whether these approaches yield realistic predictions suitable for understanding natural systems. However, advances in ecological network analysis (ENA) allow for the rebalanced state of a disturbed, empirically derived, weighted trophic network to be simulated which may provide a more realistic assessment of trophic network stability. Zhao *et al.* (2016) found that weighted food webs were most sensitive to the loss of species with high direct and indirect effects. Furthermore, Canning and Death (2017b) used ENA to show that indirect flow intensity is a key driver of the stability of energy flows, consistent with theoretical analysis that weak flows stabilize webs by dampening destructive flows yet maintaining alternative energy pathways (Rooney and McCann, 2012, Saint-Béat *et al.*, 2015, Mougi and Kondoh, 2016). Hence, if a food web is altered in way that affects the dominance or distribution of indirect flows then that may also alter food web stability.

One of the dominant habitat changes brought about by humans is the removal of forest (Carpenter *et al.*, 1992, Scanlon *et al.*, 2007). In New Zealand streams, native forested reaches were dominated by mayflies, stoneflies and caddisflies, whereas reaches in pasture streams were dominated by chironomids and snails, and pine forest reaches had communities intermediate between these (Quinn *et al.*, 1997a). Removal of forested riparian areas changes the energy supply for aquatic food webs by reducing allochthonous litter input and increasing periphyton growth (Naiman and Décamps, 1997). Theoretical explorations of low-speciose food webs suggest that low to moderate (relative) inputs of allochthonous material can stabilize an autochthonous based community. The low to moderate allochthonous inputs provide an alternative energy supply, which allows for the maintenance of greater population carrying capacities and the dampening of disruptive cascades, thereby increasing community resilience. However, if allochthonous inputs are too high then the community may become overly reliant on, and consequently sensitive to the loss of, the allochthonous inputs, in turn reducing the positive effect on resilience. (Huxel and McCann, 1998, Jefferies, 2000, Huxel *et al.*, 2002). Furthermore, changes in stream invertebrate species composition as a result can change the dietary makeup of communities and thus trophic stability. The removal of riparian forest may not only dramatically change the composition the aquatic communities but their stability to disturbance as well.

Mount Taranaki in New Zealand has streams arising in a forested national park, where allochthonous litter sources dominate, before transitioning into agricultural grassland, where autochthonous algal production rapidly dominates the energy source (Death and Zimmermann, 2005). Whilst Death and Zimmermann (2005) found no difference in species richness between forested and grassland sites in ten Taranaki streams, they did find the grassland sites on the same streams had greater evenness and higher densities of invertebrates. We postulate that the changes in allochthonous contributions (relative to autochthonous contributions) from forest removal has altered the stream macroinvertebrate community composition which has, in turn, driven differences in the structure and stability of the macroinvertebrate trophic networks.

Methods

Study sites

Ten streams in close proximity and similar geological origin were sampled on slopes of Mount Taranaki, New Zealand, a dormant andesitic cone volcano. The streams emerged from the Rimu-Rata-Kamahi forested Egmont National Park and transition sharply to low intensity agricultural grassland (completely absent of forest) at the Park boundary. Each stream was sampled in two locations, one approximately 50 m upstream of the Park boundary in forest, and several hundred metres downstream in low intensity agriculture grassland. The sites all had similar physicochemical characteristics and substrate size composition (predominately large cobbles), and were 400-500 m above sea level (Death and Zimmermann, 2005).

Periphyton sampling

Periphyton biomass was assessed indirectly by measuring Chlorophyll *a*, which has been found to be well correlated with biomass (r^2=0.63) in an extensive review (Morin *et al.*, 1999). Four stones (maximum planar dimension <60 mm) were collected monthly (between April 1999 and January 2000) from random locations in riffles at each site and frozen. In the lab, pigments were extracted by soaking each stone in a known volume of 90% acetone at 5°C in the dark for 24 hours. Using a Varian Cary 50 UV-visible Spectrophotometer, the absorbance of each solution was read and converted to pigment concentration (Steinman *et al.*, 1996b). Pigment concentration was then corrected for stone surface are (calculated by wrapping the stones in aluminium foil of known weight per unit area). Stone surface area was divided by two as periphyton is typically only on the upper, exposed surface.

Macroinvertebrate sampling

Macroinvertebrate communities were sampled in riffles at the end of April, July and October 1999 and January 2000 using five Surber samples (0.1 m^2 area with 250 µm mesh). Samples were sorted to the lowest taxonomic level possible using available keys (Cowley, 1978, Winterbourn *et al.*, 1989, Towns and Peters, 1996). See Death and Zimmermann (2005) for greater detail on the macroinvertebrate communities. The remaining particulate organic matter (POM) after invertebrates had been removed was dried at 80°C for five days, weighed, and ashed at 600°C for two hours then re-weighed, the difference in weight yielding ash free mass of particulate matter.

Data analysis of community composition

Using Primer 6 (Anderson *et al.*, 2008), Non-metric Multi-dimensional Scaling

(NMDS) was used to compare annual average macroinvertebrate community composition (using Bray-Curtis similarity) between sites. Analysis of Similarities (ANOSIM) with 999 permutations was used to evaluate the significance of observed differences between forested and grassland sites. SIMPER analysis, in Primer 6 (Anderson *et al.*, 2008), was used to examine the contribution of each species to differences in the two reach types.

Trophic network construction

At each of the 20 sites on the ten streams (Table 4.1), trophic networks of macroinvertebrate energy flow were assembled for the averaged communities sampled throughout 1999/2000. Mean individual lengths for each species were derived from the literature and mean individual biomasses for each species were determined from length-biomass regressions (Winterbourn *et al.*, 1989, Towers *et al.*, 1994, Moore, 1998, Stoffels *et al.*, 2003). Stocks were quantified as Joules/m^2, whilst flows were quantified as Joules/m^2 (year^{-1}). Energy (measured in Joules) stored by each species was determined from a mass to energy conversion database for aquatic organisms (Brey *et al.*, 2010b). Production/Biomass (P/B (year^{-1})) rates were estimated from Brey's (2012) artificial neural network model for aquatic benthic invertebrates. Respiration/Biomass (R/B (year^{-1})) rates were estimated using Brey's (2010) model for aquatic benthic invertebrates.

Dietary links between species were estimated from their functional feeding group (see Appendix B) and predator diets were established from the literature (Devonport and Winterbourn, 1976, McFarlane, 1976, Cowley, 1978, Winterbourn, 1978, Winterbourn, 1982, Winterbourn *et al.*, 1984, Rounick and Hicks, 1985, Winterbourn *et al.*, 1989, Towns and Peters, 1996, Winterbourn, 1996, Jaarsma *et al.*, 1998, Winterbourn, 2000, Hollows *et al.*, 2002, Polegatto and Froehlich, 2003, Collier *et al.*, 2004, Thompson and Townsend, 2004). Dietary intake of each resource was assumed proportional to the productivity of prey/basal taxa unless literature indicated there was strong dietary preference. The assimilation efficiency (assimilation/ingestion) of dietary components were the same as those used in Benke *et al.* (2001). Consumption was assumed equal to productivity + respiration + unassimilated food.

Basal nodes comprised of particulate organic matter (POM) and periphyton. POM and periphyton compartments were balanced to steady-state by assuming imports (i.e., upstream vegetation and detritus flowing into the reach or autotrophic growth) equalled the outputs from invertebrate consumption. Exports (energy leaving the system) for each species were equal to the estimated net growth as the networks were analysed as steady-state snapshots. In reality, exports represent the energetic output, such as consumption by higher trophic predators, downstream flow, death, and microbial decomposition for detritus.

Trophic network metric analysis

Measured trophic network metrics were calculated using enaR package (Borrett and Lau, 2014) in R 3.0.3 (R Development Core Team, 2012) . The number of nodes, relative ascendency (Ulanowicz, 1997b), average path length (Finn, 1976), indirect/direct flows (inputs) (Fath and Patten, 1999b, Borrett *et al.*, 2006, Latham Ii, 2006), yearly consumptions of POM and periphyton, and the total energetic exports were determined from macroinvertebrates at each site.

Differences in each network metric between forested and grassland sites were analysed using One-Way Analysis of Variance (ANOVA), calculated in R 3.0.3 (2012).

Table 4.1. The location, altitude, stream order, distance between paired sites, POM/Chlorophyll *a* ratio, and trophic network fragility for paired sites (one in upstream forest, the other in downstream grassland) at ten Taranaki (NZ) ring plain streams in the Austral Summer 2000.

Stream	**Site**	**Co-ordinates (WPS 84)**	**Altitude (m)**	**Stream Order**	**Distance between paired sites**	**POM/ Chlorophyll *a***	**Dynamic stability**
Waipuku Stream	F1	174 10 09 E 39 17 15 S	560	1	1650	1.08	79.71
	G1	174 11 15 E 39 17 00 S	480	1		0.00	72.77
Waipuku Tributary Stream	F2	174 10 30 E 39 17 28 S	529	1	400	1.36	78.97
	G2	174 14 46 E 39 17 25 S	520	1		0.51	81.82
Mangatoki Stream	F3	174 09 10 E 39 20 46 S	540	2	3800	5.03	81.09
	G3	174 10 56 E 39 22 29 S	400	5		0.95	74.03
Kaupokonui East Tributary Stream	F4	174 08 12 E 39 21 37 S	515	2	600	19.05	80.27
	G4	174 08 27 E 39 21 53 S	485	2		0.00	75.63
Kaupokoni East Stream	F5	174 07 53 E 39 21 49 S	505	2	300	4.17	81.40
	G5	174 08 02 E 39 21 55 S	490	2		2.94	79.05
Dunns Creek	F6	174 06 57 E 39 22 15 S	500	1	1000	2.67	82.32
	G6	174 07 19 E 39 22 44 S	455	1		0.56	79.98
Little Dunns Creek	F7	174 06 47 E 39 22 22 S	500	1	750	6.03	81.71
	G7	174 06 45 E 39 22 44 S	460	1		3.13	80.69
Ouri Stream	F8	174 03 00 E 39 22 50 S	450	3	225	2.33	82.45
	G8	174 02 58 E 39 23 00 S	435	3		0.82	81.19
Cold Stream	F9	174 01 07 E 39 22 28 S	400	1	900	9.81	80.27
	G9	174 00 44 E 39 22 48 S	370	1		0.00	76.56
Kapoaiaia Stream	F10	173 57 17 E 39 17 30 S	410	3	750	7.73	77.38
	G10	173 56 47 E 39 17 31 S	380	3		1.26	82.77

Trophic stability analysis

Dynamic trophic stability, an indicator the conservation of total energy flows following species perturbation, was derived for each network. Following the methods described by Canning and Death (2017b), dynamic stability is defined as the percent of the original, pre-perturbed, network energy throughflow (the sum of all flows within a network) that occurred at a new steady state following the random loss of 25% of the nodes. Webs were re-balanced to steady-state using the average (AVG) approach described by Allesina & Bondavalli (2003) and performed in the enaR package (Borrett and Lau, 2014). This balancing method averages the flows from a bottom up balanced web equally with the flows from a top down balanced web and has been shown by Allesina & Bondavalli (2003) to have the least variability in structure post-balancing. Perturbations were iterated with replacement 20,000 times.

Using R 3.0.3 (2012), ANCOVA was used to assess differences in dynamic stability between forested and grassland sites (categorical variable) across a range of POM/Chlorophyll a ratios (i.e. an independent variable representing the energetic contributions from allochthonous inputs relative to the autochthonous inputs).

Results

Community composition

Community composition differed between forested and grassland sites (Global R=0.2, p=0.008; Fig. 4.1). Both forested and grassland sites had similar proportions of *Deleatidium spp.* (mayfly), with the forested site having greater proportions of *Coloburiscus humeralis* (mayfly) and *Orthopsyche thomasi* (net-building caddisfly), and proportionally fewer *Orthocladiinae grp.* (chironomid midge), *Aphrophila neozelandica* (cranefly), and *Maoridiamesa spp.* (chironomid midge) than grassland sites.

Average monthly chlorophyll *a* density, was approximately three times greater in grassland (21.0 mg/m^2) than in forested (7.2 mg/m^2) sites ($F_{1,18}$=21.2, p<0.01). Whereas average POM did not differ significantly (marginal) between forested (3.4g/0.1m^2) and grassland (1.7g/0.1m^2) sites ($F_{1,18}$=4.05, p=0.06).

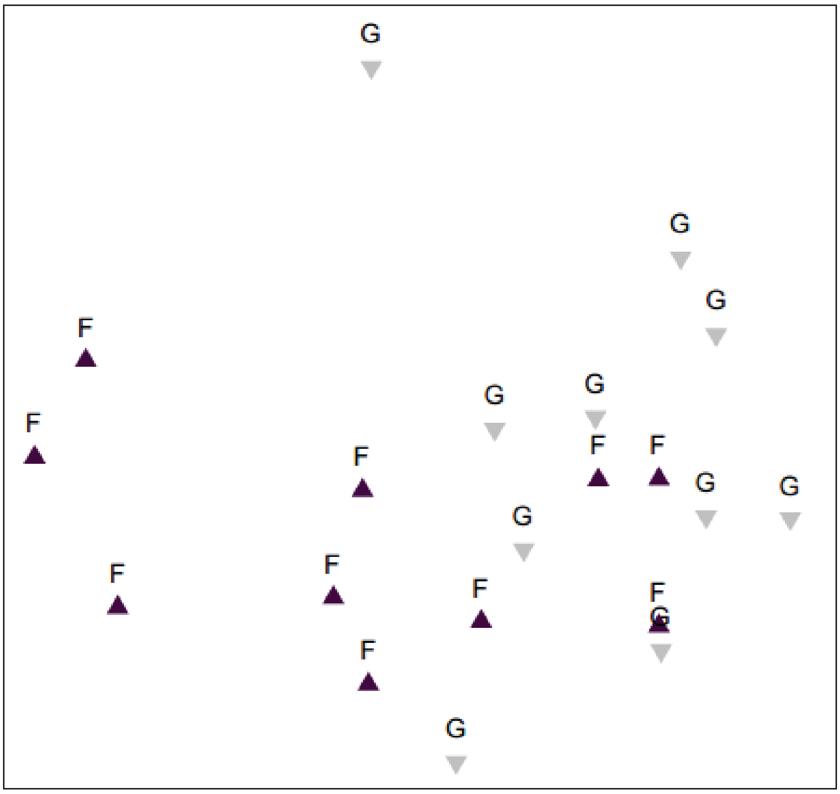

Fig. 4.1. NMDS (stress=0.11) based on Bray-Curtis dissimilarity of macroinvertebrates at paired sites (upstream forested and downstream grassland) on ten Taranaki (NZ) ring plain streams sampled during the Austral Summer January 2000. F (black triangle) indicates forested riparian sites, and G (grey inverted triangle) indicates grassland riparian sites.

Trophic network metrics and stability

Following the data quality scoring framework proposed by Costanza *et al.* (1992), the macroinvertebrate and chlorophyll a densities have high confidence, whereas the macroinvertebrate and periphyton biomass conversions, productivity and respiration estimates, and macroinvertebrate diets all have medium confidence.

The macroinvertebrate community at the grassland sites consumed significantly more periphyton and had greater energetic exports per square metre than the forested sites (Table 4.2). There were no differences in relative ascendency, indirect flow intensity, average path length and POM consumption between forested and grassland sites (Table 4.2). Figure 4.2 is an example trophic network derived from the forested reach of Waipuku Stream Tributary.

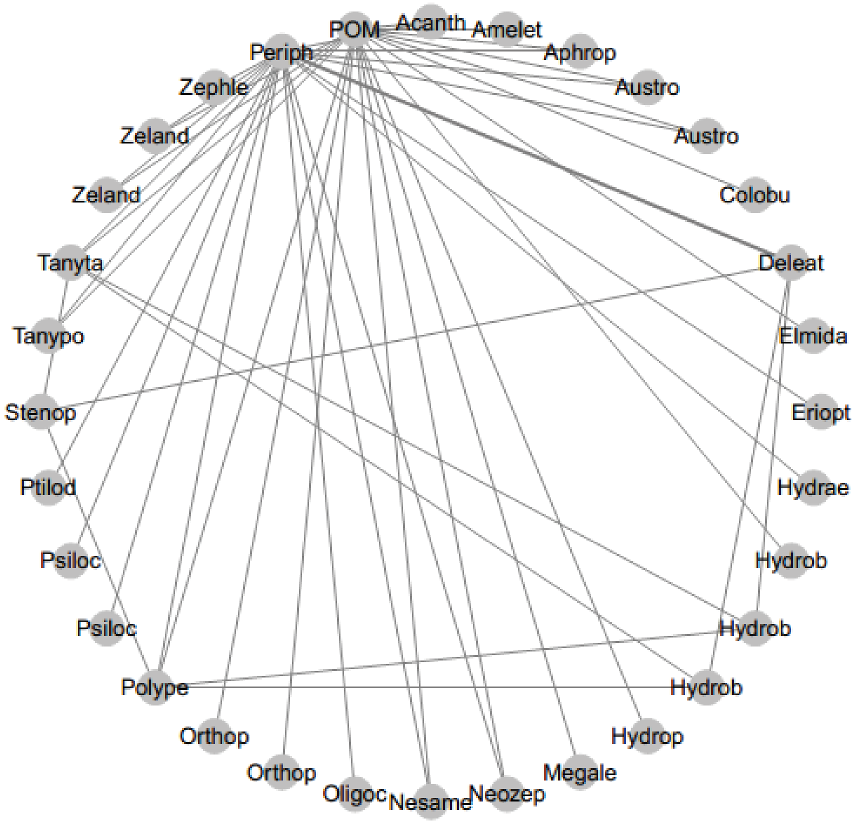

Fig. 4.2. The macroinvertebrate trophic network from the forested reach of Waipuku Stream Tributary. Line width is proportional to the size of flow.

Dynamic stability did not differ significantly between the forested and grassland sites (t=-1.09, p=0.29) or with the ratio of POM/Chlorophyll a (t=0.38, p=0.71), nor were both factors significant together (r^2=0.05, $F_{2,17}$=1.52, p=0.25).

Table 4.2. The mean metrics for stream macroinvertebrate trophic structure at paired sites on ten Taranaki (NZ) ring-plain streams (one in upstream forest and one in downstream grassland) sampled during the Austral Summer 2000. P and F-test values for ANOVAs comparing forested and grassland sites, df=1,18.

Statistic	Forested Canopy	Grassland Canopy	F-test for differences between Forested and Grassland sites	P-value for differences between Forested and Grassland sites
Number of nodes	30.6	34.6	5.81	0.04
Relative ascendency	0.36	0.36	0.98	0.35
Indirect/direct flows (inputs	0.11	0.12	1.98	0.19
Average path length	2.01	2.02	2.56	0.14
Total consumption of Periphyton (Joules/m^2 (year^{-1}))	533868	910930	11.03	>0.01
Total consumption of POM (Joules/m^2 (year^{-1}))	371830	467411	1.52	0.25
Total macroinvertebrate exports (Joules/m^2 (year^{-1}))	124644	177963	6.58	0.03
Macroinvertebrate community respiration (Joules/m^2(year^{-1}))	781054	1200377	8.69	>0.01
Dynamic stability	80.56	78.44	2.87	0.12

Discussion

All sites were dominated by the diatom scraper *Deleatidium spp.* The forested sites were dominated by filter-feeders (*Coloburiscus humeralis* and *Orthopsyche*) which feed on particulate organic matter in the water column. In contrast, the grassland sites were dominated by chironomid midges (*Orthocladinae grp., and Maoridiamesa spp.*) and cranefly (*Aphrophila neozelandica*); both chironomid midges and cranefly larvae feed primarily on diatoms and filamentous algae. This is consistent with Quinn *et al.* (1997a) who found forested streams were dominated by mayflies, stoneflies and caddisflies, whilst pasture streams were dominated by chironomids and snails. Artificial shading experiments of pasture streams have shown that shade increases filter feeding on fine particulate organic matter and reduces grazers, but has no influence on species that feed on course detritus (Towns, 1981, Quinn *et al.*, 1997b). Therefore, differences in community composition are most likely related to both differences in food resources between particulate organic matter dominated forest streams and algae dominated grassland streams.

As there was a greater basal energy supply at grassland sites, it is not surprising that there was considerably greater energetic (biomass) export and respiration from the macroinvertebrate community. A larger energy supply also means a greater predator (i.e., fish) biomass can be supported thus resulting in greater growth of community biomass. Interestingly, despite greater macroinvertebrate biomass and total growth at the grassland sites, there was no difference in the average path length of the macroinvertebrate trophic networks despite predatory invertebrates being present. That is, a larger energy supply did not result in a greater biomass of macroinvertebrate secondary consumers, instead the macroinvertebrate trophic network grew laterally (macroinvertebrate primary consumer biomass increased). The increased macroinvertebrate exports in grassland sites may also influence the energetic flows of higher trophic levels beyond the macroinvertebrate community, such as fish. Whilst higher trophic levels may benefit from greater macroinvertebrate production, it comes at the cost of greater community respiration which may exacerbate or cause hypoxic events. The macroinvertebrate communities at grassland sites had approximately 50% greater than those at forested sites. Given that water has limited oxygen retention, increased respiration may drive oxygen levels to drop to stressful or lethal levels more frequently (Dodds, 2007, Smith and Schindler, 2009, Franklin, 2013).

Despite there being some differences in energetic uptake and exports between the forested and grassland macroinvertebrate communities, there was no difference in stability. Theoretical studies suggest that low to moderate inputs of allochthonous material can help stabilise autochthonous food webs by providing multiple food chain options should one disappear, supporting greater carrying capacities and dampening disruptive oscillations (Huxel and McCann, 1998, Huxel *et al.*, 2002). At high levels of allochthonous input, polarising aggregation may also destabilise the community if allochthonous inputs are perturbed (Jefferies, 2000, Huxel *et al.*, 2002). However, we found that regardless of the relative levels of POM to periphyton in either forest or grassland streams, stability did not differ. Previous studies of empirical trophic networks suggest that relative ascendency, indirect/direct flows and average path length can all also influence stability (Ulanowicz, 2009, Ulanowicz *et al.*, 2009, Rooney and McCann, 2012, Saint-Béat *et al.*, 2015, Canning and Death, 2017b). However, none of these metrics differed between forested and grassland streams, even though energy supply and community composition differed (Death and Zimmermann, 2005).

It may simply be that food web stability is similar between forested and grassland sites because of regular flood disturbances (Winterbourn, 1997, Death, 2008b, Death, 2010). Highly disturbed ecosystems have been found to have highly indeterminate energy pathways, short food chains and weak interactions – all factors suggested to drive stability (Townsend *et al.*, 1998, Post, 2002, Ulanowicz, 2009, McHugh *et al.*, 2010, Sabo *et al.*, 2010a, Saint-Béat *et al.*, 2015). Frequent flooding has already been postulated to explain the highly flexible nature of feeding and life history characteristics of New Zealand aquatic macroinvertebrates, like many other mountainous areas around the world, and may, therefore, also explain the constant stability of New Zealand riverine macroinvertebrate trophic networks (Townsend *et al.*, 1997, Winterbourn, 1997, Death, 2008b, Death, 2010).

In summary, we found that the absence of riparian forest results in macroinvertebrate communities dominated by algae grazers rather than filter feeders. The grassland stream macroinvertebrate communities also had greater energy exports and respiration which may mean greater energetic support for higher trophic levels, however may also exacerbate hypoxic events. But differences in the energy base of the food web did not affect the stability of the macroinvertebrate communities.

Chapter five:

The potential influence of increasing trout and algal biomass on a New Zealand riverine food web

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Abstract

Environmental management is increasingly recognising the need to manage both the structure and function of ecological communities. A healthy ecosystem is one that has a stable structure and where ecosystem processes occur with natural bounds. Food web modelling and analysis provides a methodology by which potential future environmental effects on ecosystems can be assessed in terms of the overall (or emergent) properties, such as total energy throughflow, energy-flow mutualism and synergism, the dominance of indirect effects, and the robustness of energy flows to species extinction. We applied food web modelling and analysis to assess the effects of different trout and algae biomasses on emergent properties of a food web for the Hutt River New Zealand. We find that an increase in algal biomass increased food web robustness to random species extinctions, but it also increased population variability and interspecific competition. An increase in trout had no influence on the robustness, population variability or total energy flow, but did increase competition between trout and native fish.

Introduction

The maintenance and/or enhancement of ecosystem health has been widely adopted as an objective in many legislative resource management frameworks (Steedman, 1994, Rapport *et al.*, 1999). A healthy ecosystem is one that can maintain its structure and function over time in the face of disturbance (Costanza and Mageau, 1999). Structure typically includes species richness, species abundance distributions and community composition. Whereas function includes productivity, energy flow dynamics, system throughput, cycling, and flow based mutualism and synergism. Popular measures of riverine ecosystem health include: taxonomic sensitivity scores, such as Hilsenhoff's (1988) Family-level Biotic Index in the USA and Stark's (1993) Macroinvertebrate Community Index in New Zealand; metrics that compare species present with those expected to occur under reference conditions , such as RIVPACS (Wright *et al.*, 1993) and RICT (Davy-Bowker *et al.*, 2008) in the UK and the AUSRIVAS (Simpson and Norris, 2000) in Australia; and multi-metric techniques, such as the Index of Biotic Integrity applied to periphyton, invertebrate and fish communities throughout many regions around the globe (Karr *et al.*, 1986). However, none of these structural indicators assess ecosystem processes or function, although it is often assumed that structure and function are correlated (Friberg *et al.*, 2011), despite the importance of functional measures becoming increasingly considered in resource management (Townsend and Riley, 1999, Hladyz *et al.*, 2011a, Hladyz *et al.*, 2011b). The few common biomonitoring measures that do include some measure of function are based on oxygen demand or leaf-litter breakdown (Friberg *et al.*, 2011). However, they do not provide any assessment of stability, energy flow distribution, energy utility, the dominance of indirect effects, and mutualistic/synergistic relationships - all important components of ecological health (Gamfeldt *et al.*, 2008, Reiss *et al.*, 2009, Jørgensen *et* *al.*, 2010, Ptacnik *et al.*, 2010). Unless ecosystem health is measured appropriately it will be extremely difficult to monitor and/or manage.

Accurate assessment of ecosystem health has been notoriously difficult because of the higher order emergent properties encapsulated in the term (Steedman, 1994, Arkema and Samhouri, 2009, Rapport *et al.*, 2009). Developments in network analysis and simulation may provide suitable techniques to assess current and potentially future health scenarios (Ulanowicz, 1992, Xu *et al.*, 1999, Jørgensen *et al.*, 2010). The Ecopath with Ecosim (EwE) software constitutes a popular part of this development and allows for the assembly, simulation and analysis of quantitative food webs (Christensen and Walters, 2004). EwE provides a platform to explore the effects of policy decisions on food web structure. Although it has been primarily designed and used to explore the ecological impacts of fisheries, and, to a lesser extent, nutrient regimes it can be used to model and simulate any impact on food webs (Pauly *et al.*, 2000). Given the complexity of interactions in most food webs, ecological network analysis (ENA) comprises a wide range of mathematical measures that can be calculated from a food web to quantify ecological characteristics such as energy (or other quantified unit) flow amplification, cycling, flow homogenization, flow distribution and mutualism (Fath and Patten, 1999b, Latham Ii, 2006). The coupling of dynamic network simulation and ecological network analysis is becoming an effective alternative to traditional community indices in providing insight into managing anthropogenic stressors to minimise ecosystem health degradation (Pauly *et al.*, 2000, Arkema and Samhouri, 2009).

Despite many rivers worldwide being impacted by anthropogenic stressors (Dudgeon, 2014, Garcia-Moreno *et al.*, 2014), the application of ENA to measure ecosystem health in rivers has seldom been conducted (e.g., Mathews, 1993, Angelini and Agostinho, 2005, Sawusdee *et al.*, 2009, Angelini *et al.*, 2010). There is no study, to our knowledge, applying ENA to understand the impacts of multiple stressors in lotic systems. Like many rivers around the world, the Hutt River in New Zealand's capital city Wellington is impacted by multiple stressors including nutrient enrichment, urbanisation, water abstraction, river engineering, sedimentation and exotic fish (Perrie *et al.*, 2012, Joy, 2014, Miller, 2015). To date, the primary measure of ecosystem health in the Hutt River has been the Macroinvertebrate Community Index (MCI) which, like all species organic enrichment sensitivity indices, is a measure of structural not functional aspects of ecosystem health (Stark, 1993, Young and Collier, 2009, Jørgensen *et al.*, 2010, Friberg *et al.*, 2011, Clapcott *et al.*, 2012). Furthermore, the metric is relatively insensitive to impacts other than organic enrichment, such as sedimentation and heavy metals (Quinn and Hickey, 1990, Stark, 1993, Collier *et al.*, 1998, Hickey and Clements, 1998, Clapcott *et al.*, 2012, Ramezani *et al.*, 2014). Given that the Hutt River has been extensively surveyed over the past few decades, it provides an ideal case study to investigate how functional aspects of ecosystem health might be affected by multiple stressors, namely excessive periphyton growth and exotic species, using EwE and ENA.

Excessive Periphyton growth, whether caused by nutrient enrichment, reduced shade or altered flow regimes, can alter riverine food webs from one dominated by shredding and filter feeding invertebrates to one dominated by algae grazers (Death and Zimmermann, 2005, Wagenhoff *et al.*, 2012, Tonkin *et al.*, 2013). High periphyton biomass may skew the distribution of energy pathways within a food web, resulting in a reduction in robustness to potential losses of well-connected species (Townsend *et al.*, 1998, Dunne *et al.*, 2002b, Power and Dietrich, 2002). Increased periphyton productivity can also increase the biomass of higher trophic consumers which in turn may lead to a greater top-down primacy in food chains (Power and Dietrich, 2002).

Introduced predatory brown trout *Salmo trutta* may also alter the food web by modifying the indirect food web effects and driving top down trophic cascades (Wootton, 1994, McIntosh *et al.*, 2010). Trout have been shown to drive these cascades by predating invertebrates, reducing control of algae and reducing the food supply for native fish (Flecker and Townsend, 1996, Huryn, 1996a, Townsend, 1996, Huryn, 1998, Townsend, 2003). Coupled with the trout's relatively high productivity (Hopkins, 1971), this may skew energy flows in food webs to the point where native fish are outcompeted and web stability is compromised (Rooney and McCann, 2012, Saint-Béat *et al.*, 2015, Mougi and Kondoh, 2016, Zhao *et al.*, 2016). If trout density affects community functioning then active management of trout density may assist in the conservation of the natural community (Flecker and Townsend, 1996).

Here we explore, using dynamic food web simulations, the potential impacts of varying densities of algae and trout on the overall food web structure, function and stability (ecological health) in the Hutt River (NZ).

Methods

Study site

The Hutt River is a popular river for recreation passing through the Upper Hutt and Lower Hutt suburbs of New Zealand's capital city Wellington. It flows from the Tararua Ranges for 56 km along the Wellington fault line into Wellington Harbour. Our study site was a 300 m reach in the lower reaches at Boulcott (above WGS-84 174°55'19.89" E 41°11'52.66" S).

Monthly monitoring of the Hutt River by the local Regional Council at Boulcott between July 2008 and June 2011 recorded water temperature ranges between 8.2°C and 21.5°C (median = 13.6°C); conductivity ranges between 67 µS/cm and 114 µS/cm (median = 86 μS/cm); total organic carbon (pelagic) ranges between 1.1 mg/L and 9.8 mg/L (median = 2.3mg/L); dissolved inorganic nitrogen ranges between 0.044 mg/L and 1.500 mg/L (median = 0.176 mg/L); and dissolved reactive phosphorus ranges between 0.004 mg/L and 0.011 mg/L (median = 0.004mg/L) (Perrie *et al.*, 2012).

Food web construction

The food web was assembled in Ecopath with Ecosim (EwE) v6.5 (Christensen and Walters, 2004, Christensen *et al.*, 2005). Ecopath uses two master equations:

(1) Production = predation + fishery + other mortality + biomass accumulation + net migration.
(2) Consumption = Production + Respiration + Unassimilated food.

Basal components

Periphyton biomass was approximated from ten cobbles (transferred to the lab on ice) randomly collected annually between 2009 and 2016 (inclusive) during regional council monitoring (Keenan and Morar, 2015). Periphyton was scrubbed and scrapped (with a razor blade) off each cobble, blended with a known volume of 95% ethanol, boiled at 78°C for five minutes, and stored in a dark refrigerator for 24h. Spectrophotometry readings of the samples were taken at 665 and 750 nm both with and without 0.1 mL of 0.3-M HCl. Chlorophyll a biomass (mg) and density (from stone surface area) was determined following Biggs and Kilroy (2000). Periphyton species composition was estimated by randomly collecting ten cobbles during February 2016, periphyton was scrapped off all cobbles using a razor blade and mixed briskly with water. Using an Olympus BX51 polarizing light microscope with 60x magnification, 300 cells were identified using the identification keys in Biggs and Kilroy (2000). Representative biovolumes were estimated for each taxa by measuring the dimensions of up to ten cells using cellSens Dimension 1.6 software. Biovolumes were derived using the geometric formula that best represented the taxa's shape (Biggs and Kilroy, 2000). The biomass of each species of algae was determined by apportioning the total periphyton biomass to taxa based on the relative density (biovolume x cells) of that taxa and then converted to Joules (Banse, 1977, Brey *et al.*, 2010a). Periphyton annual production/biomass (P/B) was estimated to be approximately 35, derived by assuming P/B was similar to that calculated by in a temperate (10 to 22°C) Southeastern USA stream where $^{32}PO_4$ uptake was measured, and similar to the studies summarised, by Elwood and Nelson (1972). Annual respiration/biomass (R/B (year^{-1})) rate was approximated to be 10.95, this follows an approximate daily R/B of 0.03 (0.03 over 365 days is 10.95) calculated by McIntire and Phinney (1965) in similarly temperate laboratory mesocosm respiration chambers.

Invertebrate components

The National Institute of Water and Atmospheric Research (NIWA) have sampled invertebrates once a year (between January and March) from 1990 to 2016 (inclusive) using seven randomly placed Surber samplers (0.1 m^2 and 250µm mesh). Invertebrates within the 0.1 m^2 quadrat were scrubbed off all cobbles and fine sediment stirred to a depth of 10 cm for one minute. Samples were preserved in 50% Isopropyl alcohol, sorted and enumerated to the lowest practicable taxonomic level (Quinn and Hickey, 1990, Smith and McBride, 1990, Scarsbrook *et al.*, 2000).

Mean individual lengths and biomasses for each species were determined from the literature and length-biomass regressions (Winterbourn *et al.*, 1989, Towers *et al.*, 1994, Moore, 1998, Stoffels *et al.*, 2003). Invertebrate biomass (dry weight) was converted to

Joules following Brey *et al.* (2010a). The annual production and respiration was estimated using empirical models for aquatic invertebrates with a median annual temperature of 13.6°C (Brey, 2010, Brey, 2012). The estimated production rates were similar to those derived for the same and similar taxa throughout other parts of New Zealand (Hopkins, 1976, Huryn, 1996b, Winterbourn, 1996, Huryn, 1998, Collier *et al.*, 2004). Consumption was assumed equal to productivity + respiration + unassimilated food.

Dietary links between species were estimated from their functional feeding group (see Appendix B) and predator diets were established from the literature (Devonport and Winterbourn, 1976, McFarlane, 1976, Cowley, 1978, Winterbourn, 1978, Winterbourn, 1982, Winterbourn *et al.*, 1984, Rounick and Hicks, 1985, Winterbourn *et al.*, 1989, Towns and Peters, 1996, Winterbourn, 1996, Jaarsma *et al.*, 1998, Winterbourn, 2000, Hollows *et al.*, 2002, Polegatto and Froehlich, 2003, Collier *et al.*, 2004, Thompson and Townsend, 2004). Dietary intake of each resource was assumed proportional to the productivity of prey/basal taxa unless literature indicated there was strong dietary preference. The assimilation efficiency (assimilation/ingestion) of dietary components were the same as those used in Benke *et al.* (2001).

Fish components

Native fish density and approximate lengths were determined by spotlighting the entire 300 m reach on three occasions between January and March 2016 (Allibone, 2013, Joy *et al.*, 2013). Average densities and lengths were used for web construction. They were similar to those fish assemblages found with electric fishing surveys in 2007/8 (Atkinson, 2008).

Brown trout (*Salmo trutta*) density was estimated annually from 1990 to 2016 (between December and March) by the Wellington Fish and Game Council. Each year, trout were surveyed by drift diving seven 1 km lengths of the Hutt River between the Kaitoke weir and the river mouth. Drift divers spanned the wetted channel width and were spaced 2-3 m apart, counting trout and conversing regularly to reduce multiple counts of the same fish. Given that trout are highly mobile (Young *et al.*, 2010), we used the average density across all reaches dived as this showed considerably less variation than density estimates from a single reach.

Fish biomass was estimated from approximate lengths following Jellyman *et al.* (2013). Fish productivity rates were assumed to be the same as those determined in neighbouring streams by Hopkins (1971). The empirical relationships between individual biomass, temperature and respiration determined by Clarke and Johnston (1999) were used to estimate respiration rates assuming temperature is 13.6°C.

Fish diet was determined from published dietary studies and flows determined as proportional to the abundance of prey biomass unless the literature indicated a higher dietary preference (Cadwallader, 1975, Main and Winterbourn, 1987, Glova and Sagar, 1989, Glova and Sagar, 1991, Kusabs and Swales, 1991, Sagar and Glova, 1995, Jellyman, 1996, Montori *et al.*, 2006).

Annual trout catch by anglers was estimated from angler usage surveys conducted in 1994/5, 2001/2, 2007/8 and 2014/15 (Unwin, 1996, Unwin, 2003, Unwin, 2009, Unwin, 2016). Catch estimates for the years in between surveys were linearly interpolated.

Detrital compartments

Two detrital compartments were used in the model to represent pelagic and benthic/other detritus. Average annual (2008-2012) pelagic detritus was estimated from monthly total organic carbon sampling carried out by the Regional Council (Perrie *et al.*, 2012). To offset pelagic detritus outputs, benthic/other detritus was assumed to break down and enter the pelagic detritus pool. All organisms that died from causes other than consumption entered the benthic/other detritus pool. Consumption of benthic/other detritus was determined by summing estimated consumption by both microbes and invertebrate consumers. Consumption of benthic/other detritus exceeded detritus input from death, this was corrected by setting imports (i.e., upstream vegetation and detritus flowing into the reach) equal to the difference to ensure detritus inputs equalled the outputs.

Microbial compartments

Two microbial compartments were used in the model, one for the decomposition of pelagic detritus, the second for decomposition of benthic/other detritus.

The pelagic microbial respiration was calculated from 5-day Biochemical Oxygen Demand tested monthly by NIWA’s national monitoring program from 1998-2002 (Smith and McBride, 1990, Warr, 2002). As there has been little physicochemical change since then we assumed present microbial activity to be similar (Keenan and Morar, 2015). Using the respiration versus biomass relationship presented in Stelzer *et al.* (2003), we estimated the annual respiration to biomass ratio (R/B (year^{-1})) for river microbes to be approximately 28. We assumed that the Hutt River microbes would have a similar ratio and back-calculated an estimate of pelagic microbial biomass. Using the empirical model derived by White *et al.* (1991), for a median temperature of 13.6°C we estimate the annual microbial production/biomass ratio (P/B (year^{-1})) to be approximately 80. Microbial assimilation efficiency of detritus was assumed to be 0.7

(Ho and Payne, 1979). Consumption was estimated to be equal to production + respiration + unassimilated food.

The benthic/other microbes were assumed to account for the remainder of per capita community respiration once all other respiration by both producers and consumers had been accounted for. Community respiration was determined from continuous dissolved oxygen saturation monitoring carried out by Miller (2015) between January 2012 and April 2015. The median dissolved oxygen saturation was 96.3% (10.24 g/m^3), average maximum was 108.3% (11.51 g/m^3) and average minimum was 85.5% (9.08 g/m^3). Assuming a typical depth of 0.4 m (Hudson, 2010), average community respiration was estimated to be ~710 gO_2/m^2 (year^{-1}) (~10004796 J/m^2 (year^{-1}) (Brey *et al.*, 2010a)). The P/B, R/B and assimilation efficiencies determined above were also applied to the benthic/other microbe group. The benthic/other microbe biomass was calculated by dividing their yearly respiration by R/B.

Ecosim vulnerability fitting

To simulate changes in biomass over time, it is critical to understand whether trophic interactions are donor controlled, recipient controlled or donor-recipient controlled. Ecosim deals with the direction of control by incorporating 'vulnerability' parameters into the underlying Lotka-Volterra equations. Vulnerability scores exist for each predator-prey interaction and dictate the extent to which an increase in predator will increase prey mortality. For example, a species that has the ability to hide and avoid predation will have a lower vulnerability than those that are more easily predated. Using the Fit to Time Series function within Ecosim, the vulnerability parameters were estimated from time-series data to attain more realistic system dynamics. The time-series data used included density estimates (J/m^2) for the 15 most prevalent (by biomass) invertebrates for each year from 1990-2016 (inclusive) and *Salmo trutta* density for each year from 1995-2016. The best fitting vulnerability values were modelled using three routines, with the best routine being selected using AIC:

1. The first routine searched each predator-prey interaction for the sensitivity of that interaction to a very small change in the vulnerability parameter on the overall fit to the time series data (lowest Sum of Squares). Once the potentially sensitive interactions were identified, vulnerability parameters were searched iteratively until there was no improvement in fit between the model and time series data. Ecosim uses a Marquardt nonlinear search algorithm with trust region modification of the Marquardt steps to search for vulnerabilities (Christensen and Walters, 2004, Christensen *et al.*, 2005).
2. The second routine was similar to the first routine except it searched the vulnerabilities for all of a predator's foraging arena.
3. Routine three is also similar to routine one except it only searched the groups with the time series data. This routine had the lowest AIC and Sum of Squares, therefore the vulnerability values identified by this routine were adopted in the model.

Stable Isotope Analysis

To validate the food web model's ability to predict a species trophic level, we regressed the $\delta^{15}N$ isotope ratio of nineteen taxa with their predicted trophic level (Table. 5.1, Fig. 5.1). Species at higher trophic levels have greater levels of $\delta^{15}N$ fractionation and should have greater $\delta^{15}N$ concentrations than lower trophic levels. Analysis of Variance (ANOVA) tested whether the slope was equal to zero.

Species used for stable isotope analysis (SIA) were obtained separately (during April 2016) from the sampling occasions used to assemble food webs. Macroinvertebrates and detritus were collected from riffles using five kick net samples (250µm mesh). Fish tissue was provided by the Fish and Game Council collected in their surveys in January 2016. Filamentous algae were collected by cutting mats ~3 mm thick from the base of ten cobbles and pooling the samples. Diatoms were collected by scraping from ten cobbles with a razor blade. All samples were transferred on ice to the lab where they were processed immediately.

Samples were dried at 65°C for 96 hours and ground using a mortar and pestle. Macroinvertebrates were identified to the same level as used in the model, guts removed and dried whole (Winterbourn *et al.*, 1989, Moore, 1998). Approximately 2g of fish muscle was removed from each fish for drying. Filamentous and diatom algae were not separated to species level but processed whole. Dried and ground samples were sent to the Waikato Stable Isotope Unit where they were ball milled and tested for their δ^{15}N isotope ratio.

Table 5.1. The δ^{15}N stable isotope ratio and modelled trophic level for taxa in Hutt River (NZ).

Taxa	Number of individuals	Trophic level	Stable isotope δ^{15}N
Archichauliodes diversus	7	3.07	5.7
Coloburiscus humeralis	26	2.53	5
Deleatidium spp.	52	2.74	4.4
Hexatomini	8	3.71	6.9
Hydrobiosella spp.	9	2.67	5.8
Elmidae	26	2.67	4.3
Neurochorema spp.	11	2.47	5
Psilochorema spp.	7	2.59	4.5
Pycnocentria sp.	5	2.47	3.9
Maoridiamesa	76	2.24	3.5
Stenoperla spp.	2	3.67	6.7
Zephlebia spp.	21	2.47	4.9
Un ID Juveniles	17	3.63	8.6
Galaxias brevipinnis	4	3.60	8.7
Salmo trutta	10	3.65	9.2
Anguilla australis	5	3.65	9.4
Diatom	N/A	1	1.4
POM	N/A	1.3	2.4
Filamentous	N/A	1	1.9

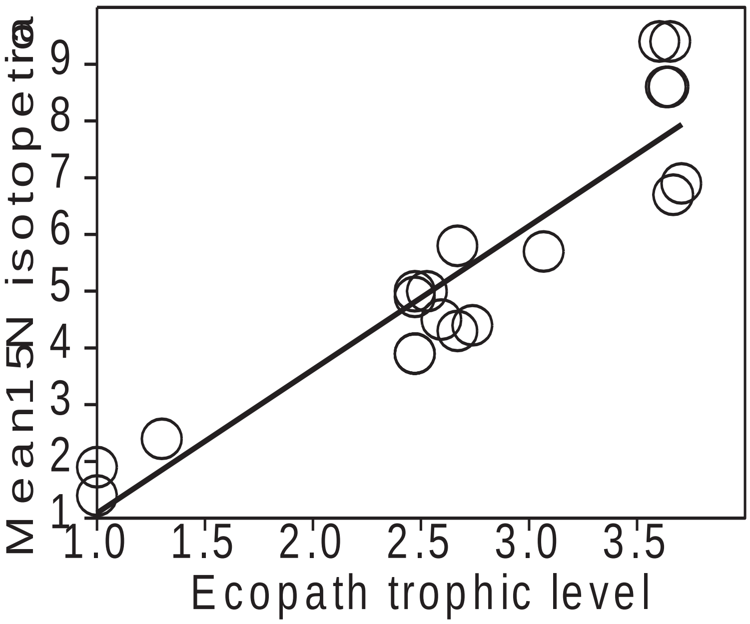

Fig 5.1. Relationship between the δ^{15}N stable isotope ratio and the modelled trophic level for 19 taxa in Hutt River (NZ). $F_{1,17}=96.71$, $p<0.01$, $r^2=0.85$.

Scenario simulations

We simulated how the food web might change over a 15-year period (using monthly iterations) between 2016 and 2030 to five different starting densities of algae (status quo (2016 levels), 33% of status quo, 66% of status quo, 133% of status quo and 166% of status quo) and five different densities of trout (status quo (2016 levels), 33% of status quo, 66% of status quo, 133% of status quo and 166% of status quo). We explored all 25 possible combinations of algae and trout density for the final year of simulation (2030) produced.

Ecological network and stability analysis

Following the data quality rating framework proposed by Costanza *et al.* (1992), confidence levels were assigned to model parameters for each group (Table 5.2).

Table 5.2. The confidence ratings of model parameters in the Hutt River model following Costanza *et al.* (1992)

Group	Individual densities	Biomass conversion	Productivity	Respiration	Assimilation efficiency	Diet	Boundary flows
Basal	High	Medium	Medium	Medium	N/A	N/A	Low
Invertebrates	High	Medium	Medium	Medium	Medium	Medium	Low
Fish	High	Medium	Medium	Medium	Medium	Medium	Low
Detritus	N/A	Low	N/A	N/A	N/A	N/A	Low
Microbes	N/A	Medium	Low	High	N/A	High	Low

All final year webs were manually converted into WAND format (Allesina and Bondavalli, 2004) prior to ecological network analysis in R 3.3.1 (R Development Core Team, 2012) using the enaR package (Borrett and Lau, 2014). Each of the food webs were initially balanced using the AVG method described by Allesina and Bondavalli (2003) prior to calculating the following metrics: total system through-flow (Finn, 1976), network aggradation (Finn, 1976), Finn's cycling index (Finn, 1976), indirect/direct flows (inputs idealized) (Borrett *et al.*, 2006), input network homogenization (Fath and Patten, 1999a), strong measure of input network amplification (Patten *et al.*, 1990), internal first passage flow (mode 1) (Higashi *et al.*, 1993, Fath *et al.*, 2001), cycled flow (mode 2) (Higashi *et al.*, 1993, Fath *et al.*, 2001), relative ascendency (Ulanowicz, 1997b), consumer-restricted relative ascendency, flow-based network synergism (Fath and Patten, 1998), and the flow-based network mutualism (Fath, 2007).

The dynamic robustness, an aspect of stability, of each predicted food web was calculated as the average proportion of total system throughput conserved following the random loss of 25% of the species and rebalanced to steady-state (iterated with replacement 10,000 times). Webs were rebalanced using the average (AVG) approach described by Allesina & Bondavalli (2003) and performed in the enaR package (Borrett and Lau, 2014). This balancing method averages the flows from a donor controlled balanced web equally with the flows from a predator controlled balanced web and has been shown by Allesina & Bondavalli (2003) to have the least variability in structure post-balancing.

Food web variability, another aspect of stability, is the variance in population densities over time. For each simulated web, variability was estimated by averaging the coefficient of variation in biomass density over the final five years of simulation for the twenty densest species.

ANOVAs tested the significances of multiple regressions that predicted each of the metrics (including robustness and variability) from the densities of Trout and Algae (Metric ~ Trout + Algae). Mixed trophic impacts (MTI) analysis was used to explore interactions between species and explain the observed patterns (Ulanowicz and Puccia, 1990).

Results

The Hutt River at Boulcott food web (Fig. 5.2) had 73 taxonomic groups, comprising of four fish groups (*Anguilla australis, Galaxias brevipinnis, Salmo trutta* and unidentified juveniles), 40 macroinvertebrate taxa (*Deleatidium spp.* (grazer)*, Orthocladiinae* (collector-gatherer) and *Coloburiscus humeralis* (filter feeder) were the three largest groups), and 22 algae taxa (*Stigeoclonium spp.,* and *Gomphonema sp.* were the two largest groups). The original web had a connectance of 0.13, a total system throughflow of 156 MJ/m^2(year^{-1}), and a dynamic robustness score of 30.67 (Table 5.3). Predicted trophic level of taxa was also well correlated with the δ^{15}N isotope ratio ($F_{1,17}$=96.71, p<0.01, r^2=0.85, Table 5.1, Fig. 5.1).

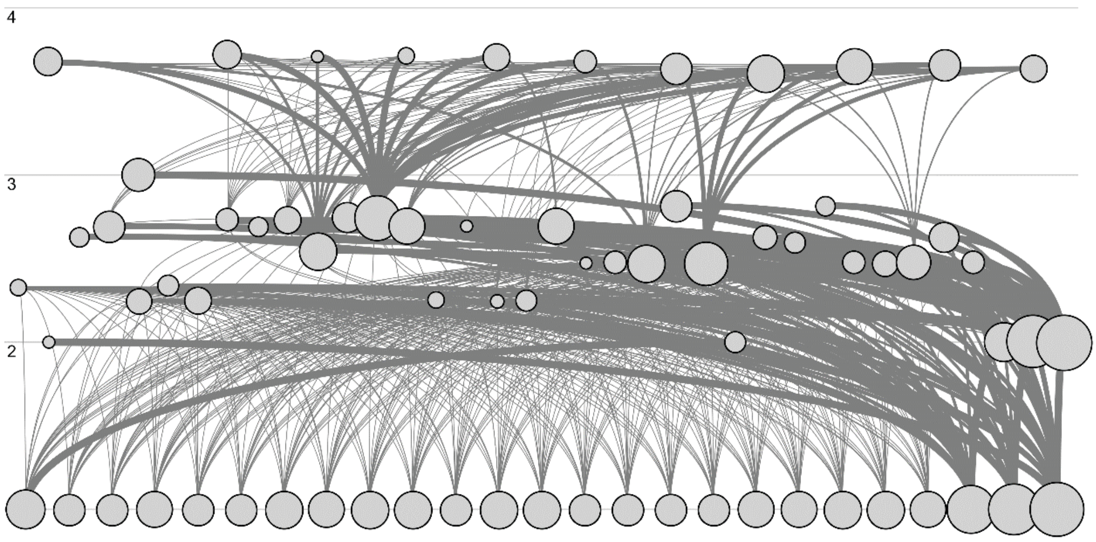

Fig. 5.2. Food web model with energy flow weighted nodes and links of the Hutt River at Boulcott.

Increasing trout biomass (controlling for periphyton) had no significant effect on the estimated food web robustness, variability, or any of the other measured metrics, except for marginally significant reductions in both the flow-based network synergism and mutualism (Table 5.3, Fig. 5.3.). Increasing periphyton (controlling for trout) lead to increases in robustness and variability, network homogenization and cycled flow, along with a decrease in network synergism (Table 5.3, Fig. 5.3.).

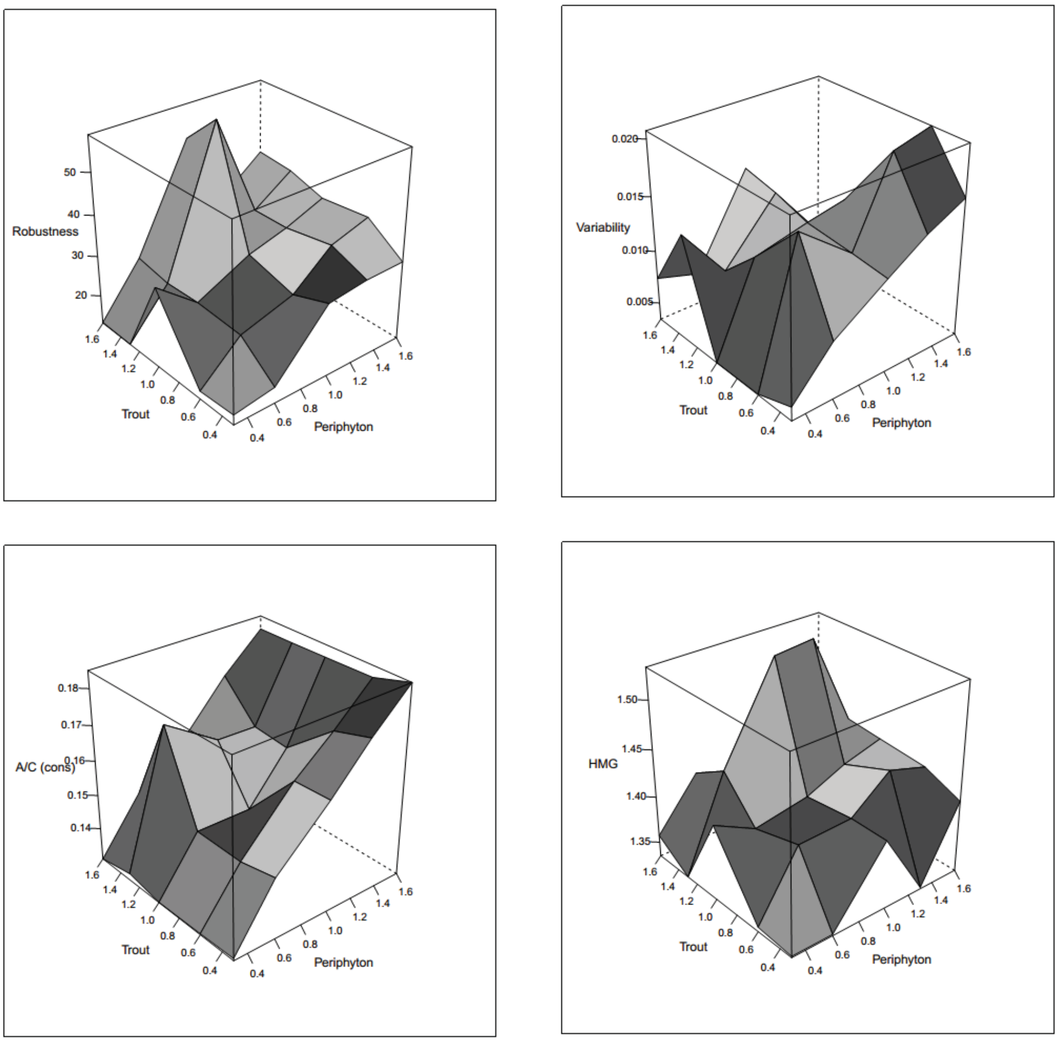

Fig. 5.3. The robustness (top left), variability (top right), consumer-restricted relative ascendency (bottom left) and Homogenization (bottom right) versus the proportion of original trout and periphyton biomass, as simulated by an EwE food web of the Hutt River at Boulcott (NZ).

Table 5.3. The ecological network metrics for the status quo (2016 assemblage) of the Hutt River (NZ) food web and the range of metric variation caused by simulated changes in trout or algae biomass density. Direction (coefficient sign) and p-values are for multiple regressions controlling for other factor.

Metric	Status quo network	Range	Factor	Direction	P-value
Robustness	30.67	12.84-58.45	Trout	+	0.08
			Algae	+	0.0002
Variability	1.27	0.34-2.07	Trout	-	0.10
			Algae	+	0.008
Total system through-flow	156m	131m-440m	Trout	+	0.04
			Algae	+	0.04
Network aggradation	9.85	2.14-10.60	Trout	-	0.13
			Algae	-	0.83
Finn’s Cycling Index	0.75	0.20-0.75	Trout	-	0.10
			Algae	-	0.59
Indirect/Direct flows (input idealized)	6.44	1.85-7.08	Trout	-	0.35
			Algae	+	0.77
Input network homogenization	1.40	1.33-1.53	Trout	+	0.04
			Algae	+	0.005
Strong measure of input network amplification	129	42-143	Trout	-	0.75
			Algae	+	0.18
Internal first passage flow (mode 1)	23.7m	18.9m-148m	Trout	+	0.06
			Algae	+	0.26
Cycled flow (mode 2)	116m	87.1m-170m	Trout	+	0.44
			Algae	+	0.003
Relative ascendency	0.54	0.41-0.58	Trout	+	0.95
			Algae	+	0.18
Relative ascendency (consumer-restricted)	0.16	0.13-0.18	Trout	-	0.77
			Algae	+	<0.0001
Flow-based network synergism	10.88	3.83-12.94	Trout	-	0.02
			Algae	-	0.009
Flow-based network mutualism	0.84	0.74-0.85	Trout	-	0.02
			Algae	-	0.23

Discussion

Our model suggests that the robustness of the Hutt River food web to random species loss will increase with increasing algal biomass but not with increases in trout biomass. Canning and Death (2017b) suggested that dynamic robustness is determined primarily by the amplification of indirect flows from direct flows, and to a lesser extent the average trophic level. Yet the indirect/direct flow ratio did not change significantly with either a change in algae and/or trout densities and is, therefore, unlikely to explain robustness in this case. An alternative explanation could be the larger energy flows through more pronounced energy pathways among consumers with increasing algae (indicated by the increasing consumer-restricted relative ascendency with algae). It may be that as algae biomass increases the majority of energy flows through only a few pathways, with other pathways relatively weaker. An increase in relatively weaker links could also explain the increase in network homogenization with increasing algae biomass, as the majority of flows become more similar (Fath and Patten, 1999a). Therefore, when species are removed at random the probability of removing a high-energy pathway declines, thereby minimising the relative effects on total energy throughflow. The increase in relatively weaker links may also prevent the disturbing effects of perturbation from cascading further (McCann *et al.*, 1998, Neutel *et al.*, 2002, Pinnegar *et al.*, 2005, Rooney and McCann, 2012, Saint-Béat *et al.*, 2015, Mougi and Kondoh, 2016). This contrasts with Ulanowicz's (1997b) hypothesis that increased relative ascendency reduces stability by reducing energy pathway redundancy. However, the range of consumer-restricted relative ascendency values derived in our study was small, and may not represent the breadth of stability responses that could potentially occur.

Increasing algal biomass, but not trout, also increased overall temporal variability of energy stored by each species. More variable communities may be at greater risk of species extinction and reduced resilience (Pimm, 1991). An examination of simulations with high algae density reveals that the ten most variable taxa are (in order from most variable): *Psilochorema* spp., *Hydrobiosis* spp., Hexatomini, *Neurochorema* spp., *Salmo trutta*, *Stenoperla* spp., *Gobiomorphus hubbsi*, *Archichauliodes diversus*, *Galaxias brevipinnis* and *Deleatidium* spp. All of these taxa, with the exception of *Deleatidium* spp., are predators and share *Deleatidium* spp. (single gill mayfly) and *Coloburiscus humeralis* (spiny gilled mayfly) as prey with high input flows. The diets of the first four taxa appeared more constrained and more reliant on the shared mayflies than the less variable predators, which either have broader diets or higher energetic inputs from species other than the two mayflies. *Deleatidium* spp. is a grazer that scrapes diatomic algae from rock surfaces and is a primary beneficiary of an increase in algae. *Coloburiscus humeralis* is a filter feeder that feeds on drifting food particles and is, therefore, influenced less directly by increases in algae. An increase in algae may have increased abundance of *Deleatidium* spp. which, in turn, increased energy throughflow to predators. The increase in predators would have increased the top down control on *Deleatidium* spp., resulting in predator-prey oscillations that caused some of the variation in *Deleatidium*. Interestingly, *Deleatidium* spp. was much less variable than its predators. Perhaps the bottom up control by *Deleatidium* spp. was slightly stronger than the top down predator control. Interspecific competition between predators for *Deleatidium* spp. may also have driven oscillations amongst the predators, with those most reliant on *Deleatidium* spp. being more variable, while the slightly less variable taxa are buffered by alternative energy inputs (prey). The unbiased interspecific competition may also explain the greater homogenization of flows (a tendency for a more even flow distribution) with increasing algae as a dominant competitor did not establish.

High cycling can both increase and reduce robustness, cycling can buffer against large changes following perturbation; however, if the cycle is disrupted by perturbation then this may reduce total throughflow (Saint-Béat *et al.*, 2015). The total flow being cycled increased with increasing algal density but not increasing trout density. It is likely that increased algae caused increased growth, but that this subsequently died rather than being consumed fuelling the detritus compartments and driving cycling. The absolute increase in cycling did not, however, cause the webs to have greater portions of total throughflow driven from cycles (there was no change in Finn's Cycling Index). Studies to date have only compared relative levels of cycling with stability (Saint-Béat *et al.*, 2015); therefore, it is unclear whether absolute differences in cycling can influence stability.

Network synergism (flow-based) reduced with both increasing algae and trout biomass. Synergism is the non-obligatory interaction between two or more species that produces a total effect greater than the sum of the parts (Fath and Patten, 1998, Fath and Patten, 1999b). This is similar to mutualism which involves obligatory interactions. A reduction in synergism or mutualism suggests either a weakening of synergistic relationships or an increase in competition. From the mixed trophic impact analysis, an example of an antagonistic or competitive relationship is between *Deleatidium* spp. and *Orthocladinae* spp. They both have a very similar diet and potentially compete for algae, though via different feeding mechanisms. An increase in algae causes growth in both species which could fuel their competition as they begin to exert top down control. Strong competition may also occur between *Salmo trutta* and *Galaxias brevipinnis* (a native fish) as they too have a similar diet. Therefore, both an increase in algae and increase in trout caused stronger interspecific competition and potentially reduced the strength of existing synergistic relationships.

One caveat of our study is that it does not account for the hypoxic and hyperoxic perturbations that may result from high levels of algal growth. Rivers naturally experience a certain level of diurnal dissolved oxygen fluctuation as algae become a net producer of oxygen during the day and net user of oxygen at night. However, when epilithic algae growth becomes prolific the lower layers begin to rot and the decomposition process uses high volumes of oxygen; at night time this oxygen can cause dissolved oxygen to plummet to fatal levels. During the day time, excessive oxygen fixation may supersaturate water resulting in fish and invertebrates developing air embolisms which may also be stressful and perturbing (Hilton *et al.*, 2006, Smith *et al.*, 2006). The relationship between algae biomass and dissolved oxygen has not been well quantified and is consequently not included in the model. Our model only assesses the food web effects of increased algae and/or trout and assumes perturbation from hypoxia or hyperoxia does not occur.

In conclusion, an increase in algal growth may increase food web robustness by increasing the proportion of weak links; however, increased algal growth may increase the variability in species densities and drive increased interspecific competition. An increase in trout had no influence on the robustness or species density variability but did increase competition with other fish.

Chapter six:

The influence of primary production on estuarine food web structure

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Abstract

Coastal and estuarine ecosystems are increasingly being stressed by algal blooms driven by increasing nutrient loads from agriculture and sewerage. Increased algal biomass can change the base of food web and may result in hypoxic conditions arising that reduce the occurrence of species sensitive to organic enrichment. If increased algal biomass changes the ecological communities, then that may also drive changes in the structure and function of the food web. This study used dynamic food web modelling and ecological network analysis to examine the impact of phytoplankton biomass on a sub-tidal food web within New Zealand’s Wellington Harbour. Increased phytoplankton biomass resulted in more energy flowing through the food web and more energy being stored by species within the food web. However, these increases came at the cost of small reductions in mutualistic energy flows. Despite having larger energy flows, the distribution of energy flows remained relatively similar. We also showed clear differences in the food web responses of increased algal biomass between the Wellington Harbour food web and those previously modelled in the up-stream and adjacent Hutt River food web. This reinforces the need for managers to consider the impacts of decisions on adjacent ecosystems as well as the target ecosystem.

Introduction

Estuarine and coastal marine environments are increasingly impacted by anthropogenic nutrient inputs (particularly nitrogen) with many becoming eutrophic (Smith *et al.*, 2006, Howarth, 2008, Paerl, 2009). In the US, approximately 65% of estuaries showed moderate to high levels of eutrophication, with two-thirds expected to continue to decline (Bricker *et al.*, 2008). High nutrient loads can result in excessive phytoplankton growth with a consequential increase in oxygen demand and potentially hypoxia sensitive species extinction (Hilton *et al.*, 2006, Smith *et al.*, 2006). Although nutrient loads are the main driver of phytoplankton blooms, they are often exacerbated by sediment-nutrient release, low turbidity, high temperature and stratification (Davis and Koop, 2006). In many phytoplankton based communities, increased primary productivity drives greater grazer density yielding greater fish densities and fishery landings (Nixon, 1988, Worm *et al.*, 2000, Nixon and Buckley, 2002). Whilst eutrophic systems (with hypoxic events) have high algal biomass but fewer crustaceans, polychaetes and fish, that is the paradox of enrichment occurs and results in a dominant competitor reducing diversity (Rosenzweig, 1971, Anderson *et al.*, 2002, Sutherland *et al.*, 2007, Bricker *et al.*, 2008, Smith and Schindler, 2009). Whether an enriched coastal environment becomes hypoxic is dependent on a variety of factors including light, temperature, hydrological mixing and the site of decomposition. If light is sufficient then excessive algal growth may occur and its decomposition may reduce dissolved oxygen. Warmer waters are more easily oxygen saturated so have less capacity to buffer oxygen used in decomposition. If hydrological mixing is poor, then thick algal layers may occur and shade lower layers (leading to their decomposition) and limit oxygen dispersion. Also, highly localised decomposition is more likely to result in hypoxia than well-dispersed decomposition (Diaz, 2001, Smith *et al.*, 2006, Painting *et al.*, 2007, Smith and Schindler, 2009, Howarth *et al.*, 2011).

Although nutrient enrichment clearly drives changes in food web composition, the effects on the emergent properties of those webs has seldom been explored (Smith and Schindler, 2009, Baeta *et al.*, 2011, Mukherjee *et al.*, 2015). Examining an overall food web using ecological network analysis (ENA) may provide insight into the emergent properties of the energy flow network, such as flow amplification, cycling, flow homogenization, flow distribution and mutualism (Fath and Patten, 1999b, Fath and Borrett, 2006, Latham Ii, 2006). ENA provides mechanisms for measuring the structural and functional aspects of ecological health such as energy use efficiency and distribution, stability, beneficial interactions and changes in competition (Costanza and Mageau, 1999, Fath and Patten, 1999b). Whereas most methods of indicating ecological health (e.g., species sensitivity indicators and observed/expected rations) only measure structural components (Friberg *et al.*, 2011). It has been hypothesised that energy flow confinement (measured by the average mutual information) and the total sum of energy flows (total system throughput) should both increase with nutrient enrichment (Ulanowicz, 1997b, Mageau *et al.*, 1998). Yet there have been few empirical tests of this hypothesis with findings unclear. For example, across an enrichment gradient within the Mondego Estuary (Portugal), the oligotrophic and eutrophic sites had more confined energy flows, and lower connectivity and cycling, with total energy flows larger than at the mesotrophic site (Patrício *et al.*, 2004, Patrício and Marques, 2006, Baeta *et al.*, 2011). Whereas in Mdloti estuary (South Africa), increasing algae biomass was modelled to increase total sum of energy flows, and decrease energy flow confinement and cycling (Mukherjee *et al.*, 2015). Therefore, it is likely that nutrient enrichment affects the emergent properties and ecological health of estuarine food webs, though no general patterns have been established.

Dynamic food web simulations that model standing stocks and energy flows, such as that offered in Ecopath with Ecosim (EwE) (Pauly *et al.*, 2000, Christensen and Walters, 2004, Christensen *et al.*, 2005), provide an avenue in which plausible food web states can be generated for a given empirical food web. Network analysis can then be applied to those hypothetical webs and the potential impacts on emergent properties examined. Canning and Death (2017a) used dynamic food web simulations to illustrate that in the Hutt River in New Zealand increased periphyton growth can increase the proportion of weak links, thereby increasing food web robustness by dampening disruptive cascades. Yet the increased robustness came at the cost of increased variability of the periphyton population and reduced energy flow based synergism. If riverine periphyton biomass is managed at any given level through reduced nutrient loadings, then the outflow nutrient loads may also impact algal growth, and ecological communities in downstream estuarine ecosystems (Alber, 2002).

Given the growing awareness of the need to manage for ecological health in adjacent ecosystems as well as the directly impacted ecosystem (Alber, 2002, Kundzewicz *et al.*, 2007), we assembled an energy-weighted food web model of the sub-tidal zone in Wellington Harbour near the Hutt River outflow. Using simulations generated in EwE (Christensen *et al.*, 2005) and ENA, we investigated whether phytoplankton biomass (assuming hypoxic conditions do not occur) is likely to affect the structure of the food web and compared the changes to those modelled to occur with algal blooms in Htt River (Canning and Death, 2017a).

Methods

Study site

The food web was compiled for the sub-tidal zone of the Wellington Harbour, New Zealand, approximately 1-2 km from the Hutt River mouth, the only major river draining into the harbour (Fig. 6.1). Given the salinity gradient and sheer size of Wellington Harbour (Booth, 1975), our study is only representative of the immediate area and does not depict dynamics in the entire harbour. The Hutt River catchment is composed of approximately 35% native forest, 25% urban and 40% agriculture. Wellington Harbour is largely surrounded by urban Wellington (New Zealand's capital city).

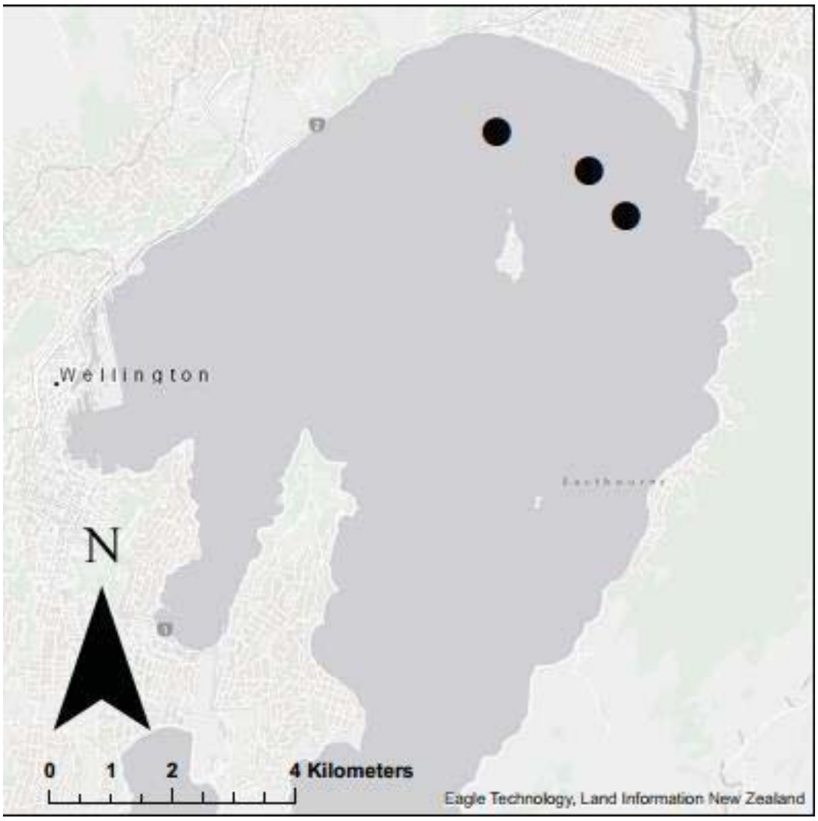

Fig 6.1. The centre locations of the benthic invertebrate surveys in Wellington Harbour (NZ). The Hutt River is visible draining into the northern section of the Harbour.

Food web assembly

Basal compartments

Phytoplankton density was estimated from surface Chlorophyll-a estimates derived from MODIS (Moderate Resolution Imaging Spectroradiometer) Aqua images ocean colour (resolution 500m x 500m) (NASA Goddard Space Flight Center *et al.*, 2016) and processed using SeaDAS v7.3.1 (Fu *et al.*, 1998). An average Chlorophyll-a density (mg/m^3) was taken from monthly images captured from January 2011 through to December 2015 (NASA Goddard Space Flight Center *et al.*, 2016). It was assumed that the Chlorophyll-a density only extended as deep as the median Secchi depth of 4.5 m measured by Booth (1975). The phytoplankton energy density was determined using (Riemann *et al.*, 1989) estimates of carbon content and converted to joules using Brey *et al.* (2010a). Phytoplankton species composition and relative densities were assumed to be the same as nearby Kenepuru Sound (Mackenzie *et al.*, 1986), which contained a similar array of species to earlier qualitative observations of phytoplankton within Wellington Harbour by Norris (1964). The annual ratio of production/biomass (P/B(year^{-1})) for phytoplankton was estimated to be 320 – the same as that derived by Lundquist and Pinkerton (2008) for the nearby Te Tapuwae o Rongokako Marine Reserve ecosystem model.

Macroalgae was surveyed in January 2015 using a 0.25 m^2 photoquadrat (12-megapixel camera with 400 lumens of light) at 10 m intervals along four 50 m transects extending north, south, east and west from three locations. The three locations were: 1) approximately 1.25 km south of Petone Wharf at 174°51′43.6″E 41°14′23.8″S; 2) approximately 1.1 km south-west of Hutt River mouth at 174°53′15.7″E and 41°15′06.9″S; and 3) 1.75 km west-south-west of Hutt River mouth at 174°52'49.20"E and 41°14'43.35"S. No macroalgae was observed, probably because of the low light and high sediment, therefore biomass and net productivity were not determined.

Invertebrate compartments

Stephenson *et al.* (2011) surveyed the benthic invertebrates in 2011 by SCUBA diving the same three locations surveyed for the basal compartments. Eight 200 mm diameter by 250 mm sediment cores were taken at random points within a 20 m radius of each of three locations where macroalgae was surveyed. Benthic invertebrate biomass density estimates were converted to J/m^2 using Brey *et al.* (2010a). Zooplankton density was determined from monthly surveys between 1961 and 1963 by Wear (1965b). We assumed a typical depth of 17 m (Stephenson *et al.*, 2011) and that the community would still be similar as catchment land use has changed little since the surveys. Zooplankton biomass density estimates were converted to J/m^2 following Wiebe *et al.* (1975).

The P/B(year^{-1}) for each invertebrate species was estimated using an empirically derived artificial neural network model by Brey (2012). The annual respiration/biomass (R/B(year^{-1})) for each invertebrate species was estimated using the empirical model by Brey (2010). We assumed 20% of the total consumption by invertebrates was unassimilated. Total consumption was equal to production + respiration + unassimilated ingestion.

Invertebrate dietary links were obtained from feeding groups identified in the literature and energy flows were assumed proportional to the production of each prey item, unless it was indicated that species had a strong dietary preference (Cannon, 1934, Dennell, 1934, Lebour, 1940, Morton, 1957, Hyman, 1959, Greenwood, 1965, Wear, 1965a, Dingle and Caldwell, 1978, Fielder and Jones, 1978, Fauchald and Jumars, 1979, Brusca and Iverson, 1985, McDermott and Roe, 1985, Lopez and Levinton, 1987, Silberstein, 1987, Cadien and Ranasinghe, 2001, Blazewicz-Paszkowycz and Ligowski, 2002, Yokoyama and Ishihi, 2003, Walsby, 2004, Lundquist and Pinkerton, 2008, Saiz and Calbet, 2010, Vannier *et al.*, 2010).

Fish compartments

Fish densities and individual lengths were estimated from the raw data surveys used by Francis *et al.* (2011), and Livingston (1987). Biomass was determined from length-mass equations following Froese *et al.* (2014) and converted to Joules following Hartman and Brandt (1995). The P/B(year^{-1}) for each species was estimated using the empirical model presented in Haedrich and Merrett (1992). The annual food consumption/biomass (Q/B(year^{-1})) was estimated using the empirical multivariate model presented in Palomares and Pauly (1998). Fish dietary links were also obtained from feeding groups identified in the literature and energy flows were assumed proportional to the production of each prey item, unless it was indicated that a species had a strong dietary preference (Baker, 1971, Russell, 1983, Livingston, 1987, Taylor and Paul, 1998, Stevens *et al.*, 2011).

Food web assembly

The initial web was assembled in Ecopath with Ecosim, which uses two master equations:

(1) Production = predation + fishery + other mortality + biomass accumulation + net migration.

(2) Consumption = Production + Respiration + Unassimilated food.

Microbes were excluded because there was a lack of suitable data and the large energy flow through a single microbial compartment may result in highly uneven resolution. Food webs were balanced to steady-state by first assuming imports (i.e., from incoming drift) to each node corrected any net losses in biomass, then outputs corrected any net gains in a species biomass (i.e., outgoing drift, death and microbial processing). The ecotrophic efficiency was left as the default of 0.95.

The quality of model parameters for each coarse group has also been assessed against the framework proposed by Costanza *et al.* (1992) and is presented in Table 6.1.

Table 6.1. The confidence ratings of model parameters in Wellington Harbour model following Costanza *et al.* (1992)

Group	Individual densities	Biomass conversion	Productivity	Respiration	Assimilation efficiency	Diet	Boundary flows
Phytoplankton	Medium	Medium	Medium	Medium	N/A	N/A	Low
Benthos	High	Medium	Medium	Medium	Medium	Medium	Low
Zooplankton	Medium	Medium	Medium	Medium	Medium	Medium	Low
Fish	High	Medium	Medium	Medium	Medium	Medium	Low
Detritus	N/A	Low	N/A	N/A	N/A	N/A	Low

Scenario simulations

Using forcing functions with EwE, we simulated the effect of increasing phytoplankton productivity by 25%, 50%, 75% and 100%, and decreasing phytoplankton productivity by 25%, 50% and 75%. Each simulation ran for 20 computational years (monthly step size).

EwE uses an adapted version of the Lotka-Volterra equations that incorporates foraging by regulating simulated predation by vulnerability values. Vulnerability values exist for each predator-prey interaction and represent the ability of prey to avoid being consumed – a low value represents donor-control, whereas a high value represents recipient-control. As we did not have any historical data, we were unable to estimate vulnerability parameters. Instead, as a sensitivity analysis, we simulated each scenario three times, whereby all vulnerability values were set at 20 (donor-control), 50 (donor-recipient control) or 80 (recipient-control) respectively.

Ecological network analysis

The final food webs assembled for each scenario were converted manually into WAND (Windows Application for Network Analysis Digraphs) (Allesina and Bondavalli, 2004) format and then analysed using enaR (Borrett and Lau, 2014) in R 3.3.1 (R Development Core Team, 2012). Ecological network metrics determined were total system through-flow, relative ascendency, Finn's cycling index, total system storage, indirect flow intensity, network aggradation, flow-based mutualism, flow-based synergism, output network homogenization, and the output network amplification.

In R 3.3.1 (R Core Team, 2016), we used multiple regression analysis to test relationships between each metric and algae biomass while controlling for vulnerability (formula: metric ~ algae biomass + vulnerability). The critical p-value of 0.05 was adjusted during interpretation following the Sequential-Holms Bonferonni method.

Results

The assembled food web was composed of 135 taxa and 3408 feeding links, with a connectance of 0.187, total system throughflow of 8.08 x 10^8 J/m^2($year^{-1}$), average path length (network aggradation) of 1.67 and relative ascendency of 0.365 (Table 6.1, Figure 6.2).

As algal biomass increased so did total amount of energy stored in the system (Fig. 6.3) and total system throughput (Fig. 6.4), whilst flow-based mutualism reduced slightly (Table 6.1.). Temporal variability, Indirect/Direct flows, network amplification and flow-based synergism were unaffected by simulated changes in algal biomass. Resource vulnerability did not have a significant influence on any of the metric-algae biomass relationships (Table 6.1).

Table 6.1. Regressions between ecological network metrics and simulated differences in algal biomass in the Wellington Harbour (Hutt outflow) food web. Statistics are for ANCOVAs testing the regression: network metric ~ algae biomass + vulnerability. Sensitivity analyses varied vulnerability (vuln) – a modelling parameter that alters the extent to which donor or recipient control occurs in simulations. Factor p-values provide the significance of a single factor while accounting for the other factor. The status-quo network represents the present-day network at steady-state without any simulated changes in algal biomass.

Network metric	Status quo network	Range	Factor	Coefficient	Factor p-value	Adjusted r^2	F-stat	p-value
Temporal variability	N/A	6.70-75.9	Algae	-6.83	0.40	-0.05	0.49	0.62
			Vuln.	9.33 x 10^{-2}	0.64			
Total system throughput	8.08 x 10^{8}	8.07-8.09 x 10^{8}	Algae	1.15 x 10^{6}	<0.01	0.90	95.56	<0.01
			Vuln.	3.78 x 10^{3}	0.09			
Network aggradation	1.644	1.643-1.644	Algae	3.97 x 10^{-4}	<0.01	0.80	40.15	<0.01
			Vuln.	3.81 x 10^{-7}	0.73			
Finn's Cycling Index	6.51 x 10^{-6}	5.69-11.5 x 10^{-6}	Algae	-2.63 x 10^{-6}	<0.01	0.71	25.79	<0.01
			Vuln.	-5.24 x 10^{-10}	0.96			
Indirect/Direct flows (output network, idealized)	0.68	0.293-1.07	Algae	7.04 x 10-^{2}	0.48	-0.07	0.26	0.77
			Vuln.	-1.10 x 10^{-5}	0.96			
Output network homogenization	1.31	1.20-1.53	Algae	-8.72 x 10^{-2}	<0.01	0.28	4.93	0.02
			Vuln.	-1.61 x 10^{-4}	0.82			
Strong measure of output network amplification	125	110-171	Algae	2.56	0.71	-0.07	0.32	0.73
			Vuln.	0.119	0.49			
Relative ascendency	0.365	0.365-0.366	Algae	3.65 x 10^{-4}	<0.01	0.31	5.41	0.01
			Vuln.	2.08 x 10^{-4}	0.44			
Total system storage	3.063 x 10^{7}	3.061-3.064 x 10^{7}	Algae	3.65 x 10^{4}	<0.01	0.91	104.9	<0.01
			Vuln.	38.9	0.20			
Flow-based network synergism	0.840	0.833-0.849	Algae	1.70 x 10^{-3}	0.36	0.04	1.37	0.28
			Vuln.	-6.09 x 10^{-5}	0.19			
Flow-based network mutualism	2.58	2.48-2.68	Algae	-9.35 x 10^{-2}	<0.01	0.91	107.2	<0.01
			Vuln.	-3.26 x 10^{-4}	0.06			

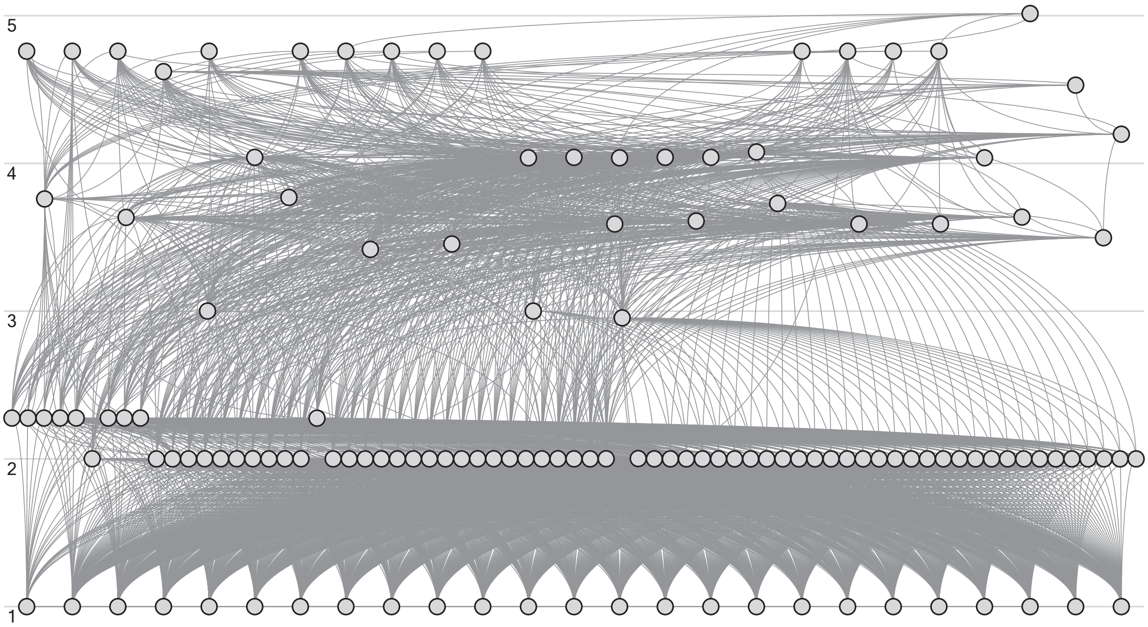

Fig 6.2. Energy flow pathways between taxa in a sub-tidal zone of Wellington Harbour.

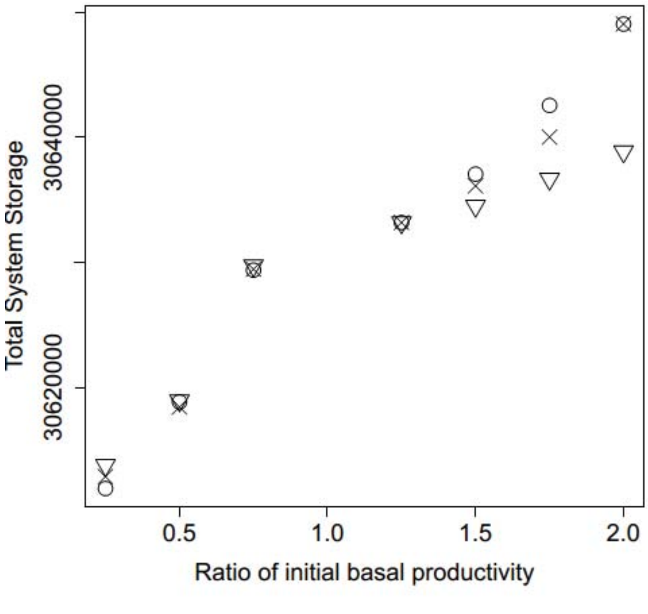

Fig. 6.3. The predicted total system storage of the Wellington Harbour food web with differing ratios of the initial basal productivity. Circles indicate an Ecosim vulnerability of 80, crosses a vulnerability of 50 and inverted triangles a vulnerability of 20.

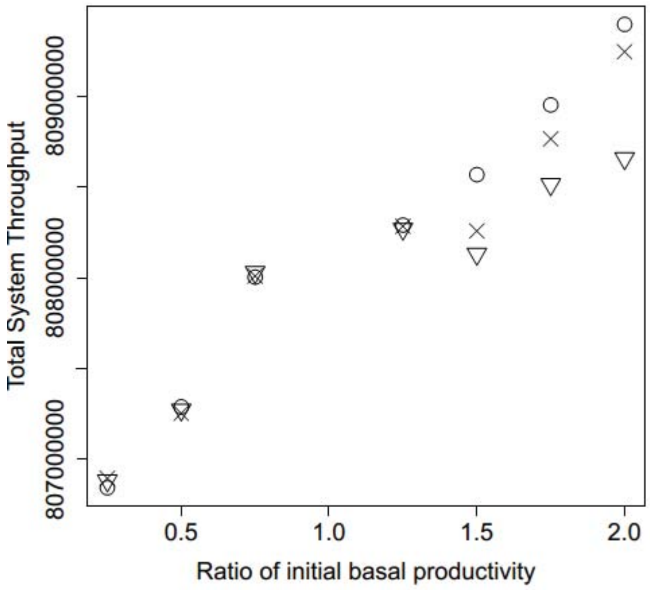

Fig. 6.4. The predicted total system throughput of the Wellington Harbour food web with differing ratios of the initial basal productivity. Circles indicate an Ecosim vulnerability of 80, crosses a vulnerability of 50 and inverted triangles a vulnerability of 20.

Discussion

The vulnerability of resource species to predation had no significant influence on the Harbour food web properties. When resource vulnerability is high, they are easily consumed by predators and are consequently recipient controlled. Conversely when resource vulnerability is low, they are more able to avoid being eaten and exert donor control. Compared to many other published food webs, flows in the Wellington Harbour food web were more redundant and evenly distributed (relative ascendency was lower) (Zorach and Ulanowicz, 2003, Ulanowicz, 2009). This may indicate predators having relatively unconstrained/broad diets whose downward control is spread evenly across prey; thereby, reducing the influence of control direction on the relative distribution of energy flows.

Increased algal biomass (controlling for species vulnerability) increased both total energetic throughput and total system storage in both the Harbour and Hutt River food web (Canning and Death, 2017a). Mukherjee *et al.* (2015) also found in Mdloti Estuary (South Africa) that increasing algal biomass increased total system throughput. Higher algal productivity means greater energetic output flowing through the web. This, in turn, leads to greater energy storage among species. Despite the increase in throughput, this did not drive substantial changes to the relative distribution of flows throughout the Harbour web – as indicated by very small differences in relative ascendency, homogenization and aggradation. Phytoplankton dominates the base of the food web; therefore, equal increases in phytoplankton productivity largely drive equal increases in productivity of all consumers, rather than one particularly dominant competitor (the decreases in homogenization with increasing phytoplankton productivity were small). By comparison, increasing algae productivity in the Hutt River food web drives large increases of flow through a few pathways with the majority of trophic links having relatively small increases in throughput (Canning and Death, 2017a). Thus, this drove increases in the dominance of relatively weaker links and give the appearance of increasing network homogenization.

A mixture of several strong and many weak interactions has been hypothesised to increase food web stability in both theoretical web explorations and perturbation simulations of empirically derived webs (Rooney and McCann, 2012, Saint-Béat *et al.*, 2015, Mougi and Kondoh, 2016, Zhao *et al.*, 2016, Canning and Death, 2017b). Many weak links reduce the probability of strong interactions being exterminated during random perturbations, localising the impacts by dampening cascading disruptions. The amplification of indirect flows from direct flows, and the relative channelization of energy flows, were not influenced by algal productivity in the Harbour food web. That is, phytoplankton productivity did not affect the strength of trophic cascades or skew energy flows and is, therefore, unlikely to affect food web stability. Whereas in the Hutt River food web, whilst increases in algal productivity did not drive differences in the amplification of indirect flows from direct flows, the relative increase in proportion of weak links is predicted to increase web robustness to random species loss.

Increasing algal productivity had no significant influence on the temporal variability of the Harbour web. This is perhaps not surprising given there was no change in homogenization, amplification and relative energy flow distribution. However, the temporal variability in the Hutt River food web increased significantly with increasing algae productivity (Canning and Death, 2017a). More variable communities are predicted to have reduced resilience and greater risk of species extinction (Pimm, 1991). Food web stability is a multifaceted concept, with robustness composing only one aspect along with resilience, persistence, resistance and variability (Rooney and McCann, 2012, Saint-Béat *et al.*, 2015, Mougi and Kondoh, 2016). Although the robustness of the Hutt River food web is predicted to increase with algae productivity, the increased variability may reduce the overall stability.

Mutualism is predicted to reduce with increasing algae productivity in both the Wellington Harbour and Hutt River food webs. In the Harbour food web there was a small reduction in obligatory beneficial interactions (mutualism) with increasing algal productivity. Whilst in the Hutt River food web there was a corresponding reduction in non-obligatory beneficial interactions (synergism). Reductions in beneficial interactions suggests either an increase in competition or decrease in positive feedback. In both webs, increased algae may fuel the growth of two or more competitors. Alternatively, if a species is partially positively affected by algae and positively via a synergistic relationship with another species, then an increase in algae may dominate the support and negate the reliance on the synergistic relationship – thereby reduce overall synergism.

This study highlights the potential effects of differing algae productivity on food web structure as driven by changes in predator-prey interactions. There are a multitude of factors that could also affect food web structure, such as changes in hydrology that alter imports and exports, dietary switching, and the effects of hypoxia. High algae productivity frequently causes hypoxic conditions across the breadth of aquatic ecosystems and has occurred previously in the Wellington Harbour (Jones and Rhodes, 1994, Wear and Gardner, 2001, Kröger *et al.*, 2006). Hypoxic conditions can arise when algal blooms, die and sink to benthos and decompose. Bacterial decomposition depletes large volumes of oxygen from the local environment. Further exacerbated by warmer temperatures as warm water holds less oxygen; deep stratified layers that receive little oxygen from algae oxygen fixation within the photic zone; and diurnal oscillations in oxygen fixation as algae becomes a net user of oxygen at night when photosynthesis does not occur. Examining the effects of hypoxic conditions on food web structure would be an interesting advance for future studies as hypoxia-sensitive species would be perturbed and web considerably reconfigured.

Often environmental management plans focus on one ecosystem at a time without considering the effects of neighbouring or indirectly connected ecosystems. In New Zealand, most catchment plans aim to manage nutrient levels for the riverine ecosystem without considering the outflow of nutrients to estuarine and coastal habitats. Here we show that managing for a particular state (i.e., a desired change in algal productivity) in the Hutt River does not necessarily result in the downstream Wellington Harbour food web benefiting from that management. Consider a hypothetical scenario, whereby environmental managers were to solely manage nutrient leaching limits within the Hutt River catchment to allow a doubling of algae in the Wellington Harbour, while ignoring the Hutt River food web state. In that scenario, assuming abundant dissolved oxygen, the Harbour may show little impact from the increase in nutrients other than an increase in fish. However, that scenario would overlook the negative impacts of increased species variability and the alteration of the strong and weak flow composition occurring within the Hutt River. This case study reaffirms the need for environmental managers to consider the emergent properties of connecting ecosystems as well as target ecosystems when setting management plans.

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Chapter seven:

The influence of nutrient enrichment on riverine food webs: Are the energy flow defences compromised?

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Abstract

Nutrient enrichment of rivers and lakes has been increasing rapidly over the past few decades, primarily because of agricultural intensification. Although the fact that nutrient enrichment can result in excessive periphyton growth and changes in biological community composition, how the resulting emergent properties of the food web change is poorly understood. We used ecological network analysis (ENA) to examine the emergent properties of 12 riverine food webs across a nutrient enrichment gradient in the Manawatu, New Zealand. Nutrient enrichment resulted in communities composed of energy inefficient species with high community (excluding microbes) respiration. Community respiration was several times greater in enriched communities and this may drive hypoxic conditions even without concomitant changes in microbial respiration. Enriched communities also had weaker trophic cascades, which may yield greater robustness to energy flow loss. Interestingly, enriched communities were also more structurally and functionally affected by species sensitive to flow disturbance making these communities more vulnerable to species extinction during floods.

Introduction

The eutrophication of rivers, lakes and groundwater is increasing rapidly (Carpenter *et al.*, 1998, Allan, 2004, Camargo and Alonso, 2006, Hilton *et al.*, 2006, Smith and Schindler, 2009), and is among the most influential drivers of the global decline in aquatic biodiversity (Dudgeon *et al.*, 2006b, Dudgeon, 2010, Vorosmarty *et al.*, 2010). Many regions worldwide now have a 10-15 fold greater nitrogen flux through their rivers than 20 years ago, driven largely by intensive agriculture and wastewater (Howarth, 2008). Dissolved Inorganic Nitrogen (DIN) and Dissolved Reactive Phosphorus (DRP) are the dominant culprits of eutrophication and are most often limiting nutrients of algal growth in rivers and their increase usually promotes excessive periphyton growth (Camargo and Alonso, 2006, Hilton *et al.*, 2006, Smith *et al.*, 2006, Conley *et al.*, 2009, Smith and Schindler, 2009). Dissolved inorganic nitrogen (DIN) can affect freshwater organisms directly via toxic effects of ammonia and nitrite (Camargo *et al.*, 2005, Camargo and Alonso, 2006, Hickey and Martin, 2009) but can result in changes in water chemistry including hypoxia if periphyton growth increases too rapidly. With high periphyton biomass, the bottom layers of the biofilm can begin to rot with the bacterial decomposition dramatically reducing ambient dissolved oxygen levels and changing pH, which in turn have adverse effects on instream invertebrates and fish (Hilton *et al.*, 2006, Smith *et al.*, 2006). Changes in the composition of the periphyton communities from low growing diatoms to filamentous growth forms, along with hypoxic events, lead to invertebrate communities changing from mayfly, stonefly and caddisfly dominated to those dominated by worms, snails and midges (Cullen *et al.*, 2006, Tonkin *et al.*, 2013, Ballantine and Davies-Colley, 2014). Surviving fish species may have poor condition as a result of stress and the dietary changes from the altered macroinvertebrate communities (Dean and Richardson, 1999, Franklin, 2013).

Whilst it is clear that riverine community composition changes with nutrient enrichment (Camargo and Alonso, 2006, Smith and Schindler, 2009), the influence of those changes on food web emergent properties/functioning is not well understood (Dodds, 2007, Friberg *et al.*, 2011). Ecological network analysis (ENA) provides a tool box of mathematical measures of food web characteristics, such as flow amplification, cycling, flow homogenization, flow distribution and mutualism that give some indication of how food web function may have altered (Fath and Patten, 1999b, Fath and Borrett, 2006, Latham Ii, 2006). Theoretical investigations have hypothesised that nutrient enrichment should yield increases in the average mutual information (a measure of energy flow confinement), total system throughput (the sum of all energy transfers within a web) and consequently the relative ascendency as energy flows increase and become more highly confined (Ulanowicz, 1997b, Mageau *et al.*, 1998). However, the few empirical applications of ENA across enriched aquatic systems have yielded inconsistent results (Patrício *et al.*, 2004, Patrício and Marques, 2006, Baeta *et al.*, 2011, Mukherjee *et al.*, 2015).

A more difficult property of ecological communities to quantify is food web stability. Food web stability is the maintenance of food web structure and function over time, it includes resilience, persistence, equilibrium, resistance and robustness (Dunne *et al.*, 2005, Rooney and McCann, 2012, Saint-Béat *et al.*, 2015, Mougi and Kondoh, 2016). Current theory suggests that having many relatively weak indirect flows can stabilise webs by dampening the spread of destructive cascades (Rooney and McCann, 2012, Saint-Béat *et al.*, 2015, Mougi and Kondoh, 2016, Canning and Death, 2017b). When disturbances are species-specific, secondary extinctions are most likely to occur when species with the highest link weight (both direct and indirect effects) are perturbed (Zhao *et al.*, 2016). Analysis of un-weighted food webs also suggested species connectivity had high influence on secondary species extinctions (Sole and Montoya, 2001, Dunne *et al.*, 2002b, Montoya *et al.*, 2006); however, connectivity has since been shown to be unimportant in weighted food webs (Zhang *et al.*, 2016). Species with high influence on food web stability are often termed as being keystone (Mills *et al.*, 1993). Therefore, if food webs change in a way that means the most sensitive species to disturbance are also keystone species, then the food web will likely have lower stability to the said disturbance.

New Zealand, like many developed countries, has experienced considerable decline in ecological health over the last 25 years – largely from eutrophication in lowland, agriculture dominated catchments (Davies-Colley and Nagels, 2002, Ballantine and Davies-Colley, 2010, Unwin and Larned, 2013, Foote *et al.*, 2015b, Ministry for the Environment and Statistics New Zealand, 2015). In this study, we assembled weighted food webs for twelve rivers across a nutrient gradient within the Manawatu, New Zealand and examined:

1) How food web properties differ across that nutrient gradient?
2) Does nutrient enrichment affect the web-wide influence (direct and indirect) of nutrient and flood sensitive macroinvertebrates?

We show that nutrient enriched riverine communities have a reduced indirect flow intensity, which may increase stability to random species loss. However, the communities changed in a way that meant flood-sensitive species would likely have greater detrimental effect when removed. Furthermore, enrichment increased community respiration (excluding microbes) which may exacerbate hypoxic events.

Methods

Study sites

Twelve sites in the Manawatu River catchment varying in nutrient enrichment were studied (Table 1). At each site, the DIN and DRP concentrations were determined monthly between 1999 and 2006 (inclusive) as a part of state of environment monitoring (Horizons Regional Council). Samples were collected and processed in accordance with NZS/ISO/IEC 17025: 1999 protocols using methods outlined in (American Public Health Association *et al.*, 1998).

Food web construction

Basal compartments

Periphyton biomass was approximated from the average chlorophyll a (mg/m^2) measured yearly in January or February from 1999-2006 (inclusive). At each site, chlorophyll a density was estimated from five unglazed tiles (0.25m x 0.25m) and/or from five randomly collected stones. Stone surface area was estimated following Graham *et al.* (1988) with periphyton assumed to be covering half of the total surface area. Pigments were collected separately for each tile or stone in known volumes of 90% acetone at 5°C in the dark for 24 h. Pigment densities were converted from absorbances determined using a Varian Cary 50 Conc UV-visible Spectrophotometer, following Steinman *et al.* (1996b). Algal species composition was also determined from stone scrapings primarily in 2003 and also 2016 following Steinman *et al.* (1996a). The approximate biomass of each species was determined by rationing the total periphyton biomass (from chlorophyll a – biomass relationships) by relative species abundance (Banse, 1977, Brey *et al.*, 2010a, Keenan and Morar, 2015). Periphyton annual production/biomass (P/B) was estimated to be 35 by extrapolating the hourly rate determined in Elwood and Nelson (1972). The annual respiration/biomass (R/B) rate was approximated to be 10.95 following an approximate daily R/B of 0.03 (0.03 over 365 days is 10.95) calculated by McIntire and Phinney (1965).

Invertebrate compartments

At each site, macroinvertebrates were sampled using five randomly positioned Surber samplers ($0.1m^2$ and 250µm mesh) between January and March 2007. Invertebrates within the $0.1m^2$ quadrat were scrubbed off all cobbles and fine sediment stirred down to a depth of approximately 10cm for one minute. Samples were preserved in 10% formalin, sorted and enumerated to the lowest practicable taxonomic level (Winterbourn *et al.*, 1989).

Mean individual lengths and biomasses for each species were determined from the literature and length-biomass regressions (Winterbourn *et al.*, 1989, Towers *et al.*, 1994, Moore, 1998, Stoffels *et al.*, 2003). Invertebrate biomass (dry weight) was converted to Joules following Brey *et al.* (2010a). The annual production and respiration was estimated using empirical models for aquatic invertebrates with a typical annual median temperature of 14 °C (Death and Death, 2006, Brey, 2010, Brey, 2012). The estimated production rates were similar to those derived for the same or similar taxa throughout other parts of New Zealand (Hopkins, 1976, Huryn, 1996b, Winterbourn, 1996, Huryn, 1998, Collier *et al.*, 2004). Consumption was assumed equal to productivity + respiration + unassimilated food.

Dietary links between species were estimated from their functional feeding group (see Appendix B) and predator diets were established from the literature (Devonport and Winterbourn, 1976, McFarlane, 1976, Cowley, 1978, Winterbourn, 1978, Winterbourn, 1982, Winterbourn *et al.*, 1984, Rounick and Hicks, 1985, Winterbourn *et al.*, 1989, Towns and Peters, 1996, Winterbourn, 1996, Jaarsma *et al.*, 1998, Winterbourn, 2000, Hollows *et al.*, 2002, Polegatto and Froehlich, 2003, Collier *et al.*, 2004, Thompson and Townsend, 2004). Dietary intake of each resource was assumed proportional to the productivity of prey/basal taxa unless literature indicated there was strong dietary preference. The assimilation efficiency (assimilation/ingestion) of dietary components were the same as those used in Benke *et al.* (2001).

Fish compartments

Fish density and approximate lengths were determined from electric fishing surveys recorded in the New Zealand Freshwater Fish Database (Richardson, 1989) at the date closest to the 2007 macroinvertebrate surveys.

Fish biomass was estimated from approximate lengths following the length-mass equations in Jellyman *et al.* (2013). Fish productivity rates were assumed to be the same as those determined in neighbouring streams (Hopkins, 1971). Clarke and Johnston (1999) was used to estimate respiration rates assuming typical median temperature is 14°C (Death and Death, 2006).

Fish diet was determined from previous dietary studies and flows were proportional to the abundance of prey biomass unless literature indicated a high dietary preference (Cadwallader, 1975, Main and Winterbourn, 1987, Glova and Sagar, 1989, Glova and Sagar, 1991, Kusabs and Swales, 1991, Sagar and Glova, 1995, Jellyman, 1996, Montori *et al.*, 2006).

Detrital compartments

Two detrital compartments were used to represent Fine Particulate Organic Matter (FPOM) and Course Particulate Organic Matter (CPOM). All organisms that died from causes other than consumption entered the CPOM pool. Detritus compartment storages were all set to a nominal figure of 100J/m^2 and steady-state maintained by assuming imports (i.e., upstream vegetation and detritus flowing into the reach) equalled the outputs from invertebrate consumption. The nominal detritus storage value is relatively small and will have a consistent, but small, effect on the total system storage that readers should be aware of. The nominal detritus storage value will have no effect on flow based metrics.

Food web assembly and analysis

Using PAST3 (Hammer *et al.*, 2001) differences in macroinvertebrate community structure were assessed using Non-metric Multi-Dimensional Scaling (NMDS) of percent-transformed biomass density. The twelve sites were split into two groups, being the six most enriched sites (H) and the six least enriched sites (L). Permutational Multivariate Analysis of Variance (PERMANOVA) (Anderson, 2005) with 9999 permutations was used to test the differences in community composition between the two groups. Similarity Percentage Analysis (SIMPER) was used to identify the species contributing the most to the dissimilarity between the two groups.

The food webs were assembled in WAND (Allesina and Bondavalli, 2004) format (Data S1-S12). Microbes were excluded because there was a lack of suitable data available and the large energy flow through a single microbial compartment may result in uneven resolution and obscure network patterns. Food webs were balanced to steady-state by first setting imports (i.e., from upstream drift) to each node equal to any net losses in biomass, then outputs set equal to any net gains in a species biomass (i.e., drift downstream, death and microbial processing).

For each web, network metrics were calculated using R 3.3.1 (R Core Team, 2016) and the enaR package (Borrett and Lau, 2014). Initially, any remaining small imbalances were balanced using the AVG2 method described by Allesina and Bondavalli (2003) prior to calculating the following metrics: total system through-flow (Finn, 1976), sum of loss to respiration, sum of loss to exports, total system storage (Finn, 1976), network aggradation (Finn, 1976), Indirect Flow Intensity (Borrett *et al.*, 2006), homogenization (inputs) (Fath and Patten, 1999a), relative ascendency (Ulanowicz, 1997b), flow-based network synergism (Fath and Patten, 1998), and the flow-based network mutualism (Fath, 2007). Metric interpretations are included in Table 2.

Regression analysis using R 3.3.1 (R Core Team, 2016) was used to test the relationship between each network metric calculated and the respective DIN concentration for all twelve webs. Given that DIN concentration was significantly correlated with DRP (r^2=0.81, $F_{1,8}$=6.01, $p<0.01$), we only regressed metrics with DIN.

Keystone macroinvertebrate sensitivity

Two common disturbances in New Zealand rivers are increasing nutrient enrichment and floods. If keystone food web invertebrates are sensitive to high nutrients, then the web will be sensitive to increasing nutrient enrichment. Likewise, if keystone species have only one terrestrial life-stage, are crawlers, have cylindrical body forms, exposed gills and low dissemination potential then the communities may be more sensitive to flow disturbance than those with keystone taxa that have multiple terrestrial life-stages, are burrowers, have streamlined body forms, plastron respiration and high dissemination potential (Scarsbrook and Townsend, 1993, Townsend and Hildrew, 1994, Townsend *et al.*, 1997).

To investigate whether nutrient enrichment changed the web-wide influence of disturbance sensitive macroinvertebrates we calculated five keystone sensitivity indexes (KSI) for each web. Each of the five KSI's were based on five species trait categories known to be influenced by enrichment or flow disturbance, being: body form, locomotion, respiration, dispersal potential and organic enrichment sensitivity. The KSIs for each web and each trait were calculated following equation 1.

$$KSI \ = \frac{\sum_m Sensitivity\ score \times Normalised\ Average\ Environ\ Centrality}{\sum_m Normalised\ Average\ Environ\ Centrality}$$

Eqn (1)

where m is each of the macroinvertebrate species within a given food web.

The Average environ centrality is an indicator of the web-wide influence a species has and measures a species web-wide direct and indirect effect (Fann and Borrett, 2012) and were calculated for each species in each web using enaR (Borrett and Lau, 2014). The average environ centrality scores for macroinvertebrates were normalized into scores ranging from 0 to 1 to allow inter-web comparisons.

Species traits were sourced from the Freshwater Biodata Information System (National Institute for Water and Atmospheric Research, 2004) and trait-specific sensitivity scores were assigned as follows (higher values being more sensitive):

1. **Body form**: Cylindrical (3), flattened (2) and streamlined (1).
2. **Locomotion**: Crawler (3), swimmer (2) and burrower/sessile (1).
3. **Respiration of aquatic stages**: Gills/aerial (3), tegument (2) and plastron (1).
4. **Dispersal ability**: Low (3), moderate (2) and high (1)

5. **Organic enrichment sensitivity**: Individual species sensitivity scores adopted from the MCI (Stark, 1993).

Using regression analysis in R 3.3.1 (R Core Team, 2016), the relationships between each of five trait-specific KSIs and DIN concentration were examined (Table 3).

Results

The macroinvertebrate communities at the six most enriched sites had significantly different compositions from those in the six least enriched sites (F=5.24, p=0.002, Fig. 7.1). SIMPER analysis revealed the most enriched sites had markedly greater portions of biomass from Orthocladiinae, Oligochaetes and Pycnocentria, and lower portions of *Deleatidium spp*. and Elmidae than low enrichment sites (Table 7.1.).

Table 7.1. SIMPER analysis comparing the invertebrate communities of the six least enriched sites (L) with the six most enriched sites (H), showing the average % dissimilarity (Av. dissim), the % contribution to the overall dissimilarity (Contrib.), the cumulative contribution to the overall dissimilarity, and the mean portion (%) of an invertebrate community's biomass.

Taxon	Av. dissim	Contrib. %	Cumulative %	Mean L	Mean H
Deleatidium spp.	22.94	35.9	35.9	6.058	10.99
Orthocladiinae	6.748	10.56	46.46	1.81	10.46
Oligochaetes (small)	4.998	7.819	54.27	0.364	10.01
Elmidae	4.719	7.383	61.66	1.45	10.03
Pycnocentria sp.	3.933	6.153	67.81	0.209	7.97
Aoteapsyche sp.	3.254	5.092	72.9	1.62	7.17
Tanytarsini	3.158	4.941	77.84	2.77	6.45
Potamopyrgus antipodarum	2.768	4.33	82.17	1.36	6.32

Across all twelve food webs, the mean dissolved inorganic nitrogen (DIN) concentration ranged from 0.05 to 0.90 mg/L, taxonomic richness ranged from 33 to 67, and total system throughflow from 6629034 to 54782015 J/m^2(year^{-1}) (Table 7.2, Fig. 7.2).

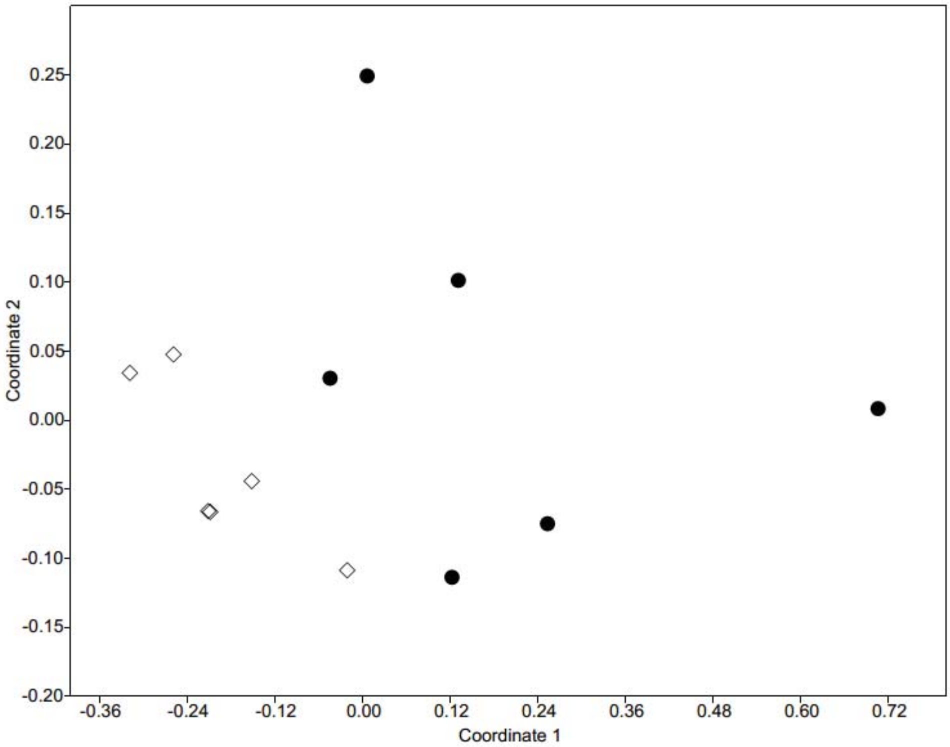

Fig 7.1. NMDS of the macroinvertebrate communities from six rivers with low nutrient enrichment (diamond) and six with high nutrient enrichment (circles) within the Manawatu region of New Zealand, collected in 2007.

As DIN concentration increased, total system throughflow, total respiration, and the indirect flow intensity all increased up to a point, after which values remained similar despite increasing DIN. Synergism declined slightly with increasing DIN also until a threshold was met, after which values remained similar with increasing DIN. There was no relationship between DIN and exports, homogenization, total system storage and mutualism. Relative ascendency increased with increasing DIN until a threshold, after which relative ascendency reduced with increasing DIN (Fig. 7.3., Table 7.3).

Of the disturbance sensitivity indices, only the body form sensitivity index increased with DIN concentration, whilst the remainder were not correlated with DIN (Fig. 7.4., Table 7.4).

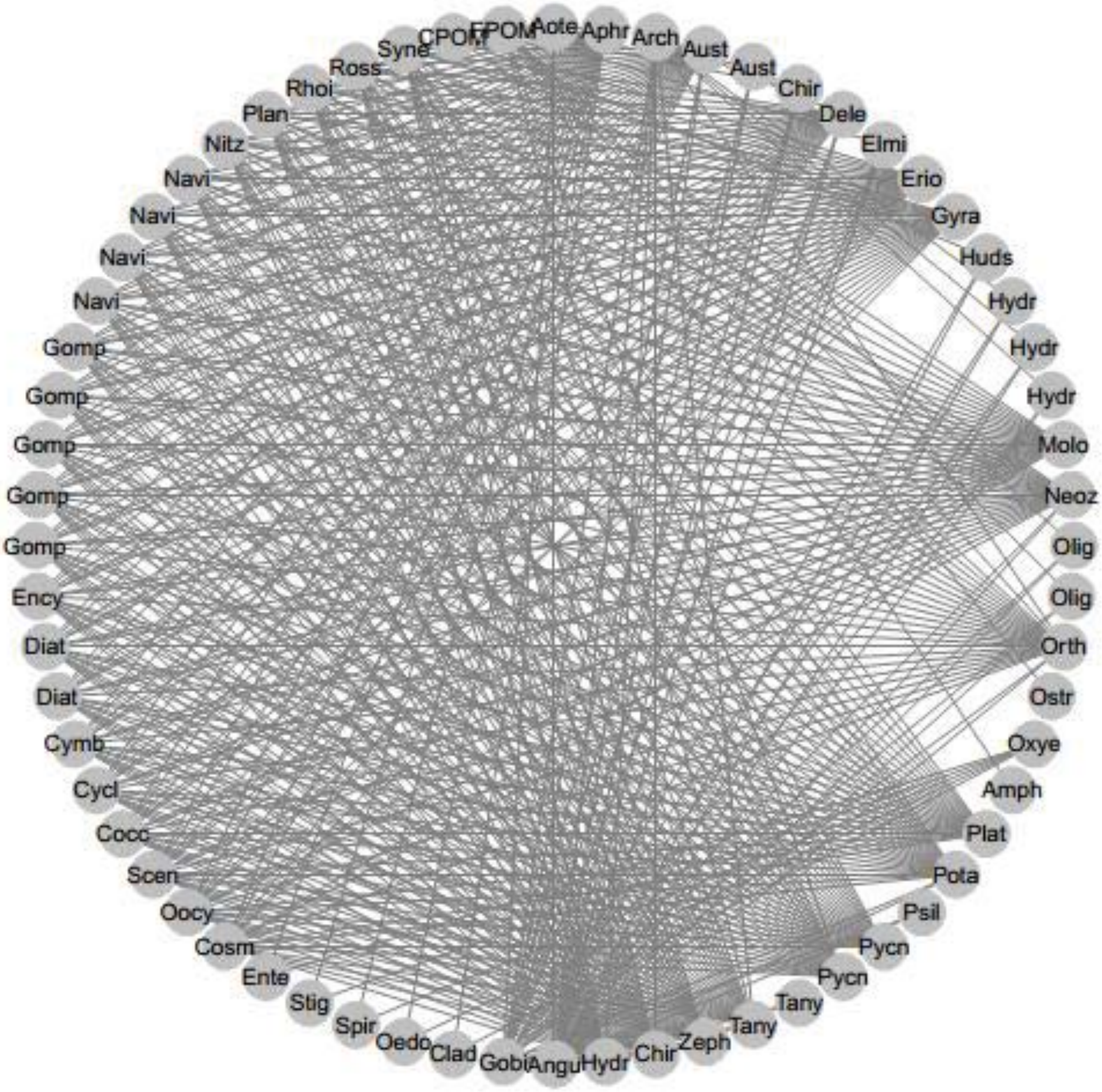

Fig. 7.2. The food web of the Manawatu River at Hopelands Road.

Table 7.2. The average dissolved inorganic nitrogen concentration (DIN, mg/L), dissolved reactive

phosphorus (DRP, mg/L), species richness (N), connectance (C), total system throughflow (TST, J/m$^{2(\text{year-1})}$) and locations (WGS 64) of twelve river food webs sampled in 2007 in the Manawatu, NZ. Nutrient concentrations were based on 84 sampling occasions, sampled monthly between 1999-2006 inclusive.

Site	Latitude	Longitude	DIN	DRP	N	C	TST
Mangatainoka River @ Putara Road	40° 40” 49.9’ S	175° 32” 50.8’ E	0.02	0.003	33	0.11	8749303
Pohangina River @ Piripiri Road	40° 03” 04.9’ S	175° 56” 11.5’ E	0.05	0.005	62	0.09	16377036
Pohangina River @ Raumai Reserve	40° 12” 26.3’ S	175° 47” 21.5’ E	0.08	0.012	53	0.12	6629034
Tokomaru River @ Horseshoe Bend Reserve	40° 29” 14.3’ S	175° 31” 33.4’ E	0.08	0.005	67	0.12	19844310
Raparapawai Stream @ Jacksons Road	40° 19” 25.2’ S	175° 59” 45.8’ E	0.15	0.030	62	0.11	20767724
Oroua River @ Nelson Street	40° 13” 50.0’ S	175° 34” 55.1’ E	0.24	0.010	38	0.12	11872967
Manawatu River @ SH2	40° 23” 60.7’ S	175° 53” 17.0’ E	0.40	0.009	64	0.12	34246823
Mangatera Stream @ SH2	40° 14” 27.1’ S	176° 05” 55.6’ E	0.44	0.141	62	0.10	54782015
Oroua River @ Awahuri Road	40° 16” 32.4’ S	175° 31” 17.6’ E	0.53	0.101	37	0.09	34819550
Mangatera Stream @ Timber Bay	40° 14” 27.1’ S	176° 05” 55.6’ E	0.81	0.141	66	0.11	40277332
Manawatu River @ Hopelands Road	40° 21” 35.3’ S	175° 57” 42.1’ E	0.90	0.024	64	0.11	22250529
Mangapapa Stream @ Troup Road	40° 20” 31.0’ S	175° 50” 52.3’ E	0.90	0.024	67	0.12	40237153

Table 7.3. The regression statistics, including permutation test results (exact method), of ten network metrics and their interpretation across twelve rivers (Manawatu, NZ) along a dissolved inorganic nitrogen (DIN) gradient. Regressions were Box-Cox transformed, where necessary, in the form metric = DIN^λ.

Network metric	Metric interpretation	Lambda (λ)	Adjusted R^2	F-statistic	p-value (>|F|)	Iterations	p-value (perm)
Total system throughflow	Sum of energy flows entering or exiting all taxa	0.7	0.58	14.86	0.004	5000	0.009
Respiration flows	Sum of all energy lost from respiration	0.42	0.40	8.42	0.02	5000	0.02
Export flows	Sum of all energy leaving the system	N/A	-0.07	0.30	0.60	74	0.58
Network aggradation	Average path length	N/A	-0.07	0.32	0.58	81	0.56
Indirect Flow Intensity	Proportion of total flows from indirect flows	0.10	0.44	8.78	0.02	5000	0.02
Homogenization (input, flow)	Measures the uniformity of flow distribution	N/A	-0.05	0.52	0.49	120	0.46
Relative ascendency	Measures the constraint of energy flows	X^2	0.54	6.97	0.02	51	0.78
		X				5000	0.005
Total system storage	Sum of energy stored in all taxa	N/A	-0.05	0.52	0.49	95	0.52
Mutualism (flow)	Measure of the obligatory positive feedback flows	N/A	0.02	1.21	0.30	263	0.28
Synergism (flow)	Measure of the non-obligatory positive feedback flows	0.83	0.53	11.95	0.007	5000	0.009

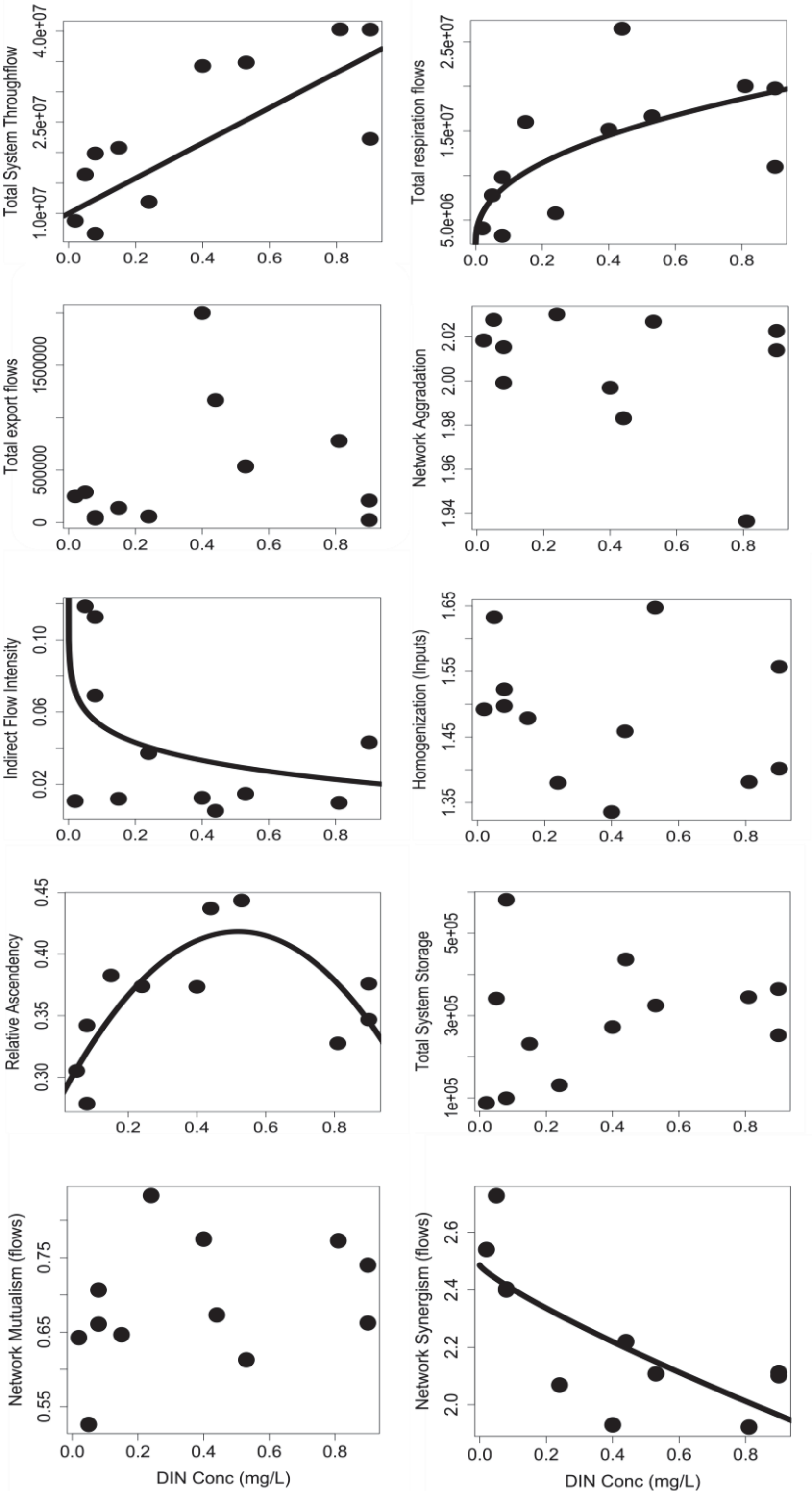

Fig 7.3. Ten network metrics from riverine food webs across a dissolved organic nitrogen (DIN, mg/L) gradient throughout the Manawatu, NZ. Lines represent statistically significant regressions ($p<0.05$, Table 7.2).

Table 7.4. The regression statistics, including permutation test results (exact method), for Keystone Sensitive Indices (five species traits) across twelve rivers (Manawatu, NZ) along a dissolved inorganic nitrogen (DIN) gradient.

Keystone Sensitivity Index trait	Adjusted R^2	F-statistic	p-value (>|F|)	Iterations	p-value (perm)
Body form	0.33	6.02	0.04	2344	0.04
Locomotion	-0.10	0.03	0.86	51	0.92
Respiratory mechanism	-0.10	0.01	0.92	51	0.94
Dispersal potential	-0.06	0.35	0.57	92	0.52
Organic enrichment sensitivity	-0.10	0.01	0.92	51	0.94

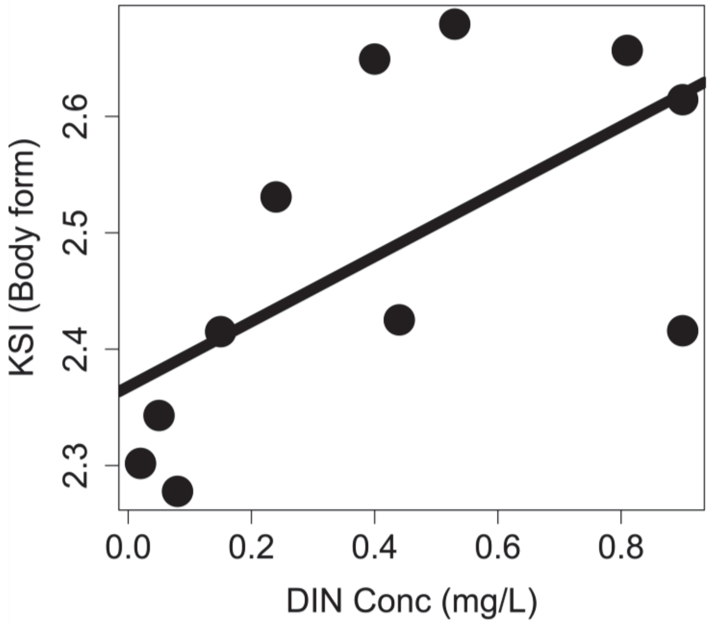

Fig 7.4. The Keystone Sensitivity Index (body form) across riverine food webs along a dissolved organic nitrogen (DIN, mg/L) gradient throughout the Manawatu, NZ. Linear regression line is statistically significant ($F_{1,10}$=6.02, p=0.04).

Discussion

Total energy flow increased (measured using TST) with increasing nutrient enrichment until a DIN concentration of approximately 0.5 mg/L after which total energy flow remained constant. The initial increase in throughflow is consistent with bottom up control theory whereby an increase in primary productivity (in this case from greater nutrient enrichment) results in increasing productivity of consumers (Rosemond *et al.*, 1993, Hillebrand, 2002). The total food web biomass was unaffected by nutrient enrichment, rather the per-capita throughflow increased instead. Thereby indicating that either: a) production increased and organisms moved across the system boundary (organisms drifted or swam out of the area or died) thereby maintaining total system biomass and increasing throughflow; or b) the webs are composed of more energetically demanding/more inefficient species that require greater energy consumption resulting in increased throughflow. Interestingly, whilst exports (non-respiratory boundary flows out of the system) remained unchanged, total community respiration increased markedly with increasing nutrient enrichment. This supports the latter hypothesis that the communities became composed of energetically inefficient species with increasing enrichment. Hypoxia is often associated with the microbial decomposition of algal blooms (de Jonge *et al.*, 2002, Hilton *et al.*, 2006, Smith *et al.*, 2006); however, our results show that at DIN concentrations greater than approximately 0.35mg/L respiratory energy demand, and consequently oxygen demand, for the entire community excluding microbes can be three to four times greater than in oligotrophic conditions. The change in invertebrate community composition could therefore also be having a considerable influence on the frequency and intensity of hypoxic conditions without the need to invoke any microbial processes.

Nutrient enrichment may have resulted in an increase in the composition of inefficient species by increasing the frequency and/or intensity of both hypoxic and substrate movement disturbances. Highly disturbed communities tend to be composed of smaller bodied species as they are typically fast growing and can recover more easily (Townsend and Hildrew, 1994, Lamouroux *et al.*, 2004, Dolédec *et al.*, 2006). Whilst a small bodied invertebrate on its own will likely have low respiration demand, when biomass differences are accounted for smaller bodied invertebrates tend to have greater respiration rates than larger invertebrates (Robinson *et al.*, 1983, Peters, 1986, Gillooly *et al.*, 2001, Brey, 2010); thus, making communities of smaller invertebrates less energy efficient than larger invertebrates assuming total biomass is the same. Eutrophic streams in general have more prolific periphyton growth. Prolific periphyton can disturb communities by increasing the frequency and intensity of hypoxic events (Hilton *et al.*, 2006, Smith *et al.*, 2006, Dodds, 2007). Also, if periphyton dominates the base of the food web then substrate movement (which scours periphyton from rocks) will also be disturbing for the invertebrates that rely on periphyton (Lake, 2000, Biggs *et al.*, 2005, Death and Zimmermann, 2005, Death, 2010). Therefore, if hypoxic events and periphyton scouring disturb the community then the increased frequency and/or intensity of stream disturbances may drive more enriched communities to be composed of small bodied, energetically inefficient species (Townsend and Hildrew, 1994, Hilton *et al.*, 2006).

Similarly to total energy flow, the confinement of energy flows (measured by relative ascendency) also increased with enrichment until an approximate DIN concentration of 0.50-0.55 mg/L, after which energy flow confinement relaxed slightly. Mageau *et al.* (1998) suggested that relative ascendency would increase with nutrient enrichment; however, they did not account for the potential effects of a dominant competitor collapsing which would revert the network to a state with relatively unconstrained energy flows (the large, specialised flows of dominant competitor are lost). In river systems, nutrient enrichment may increase algae growth and drive more energy through the algae-consumers, thereby increasing relative ascendency (Ulanowicz, 1986, Ulanowicz, 1997b, Almunia, 1999, Ulanowicz, 2003). As explained above, prolific periphyton growth may increase disturbance frequency and/or intensity (Hilton *et al.*, 2006). Disturbance often returns communities to earlier successional stages that have more uniform energy flow distributions (i.e., relative ascendency drops) (Genoni and Pahl-Wostl, 1991, Ulanowicz, 1997b, Mageau *et al.*, 1998). It is plausible that when DIN concentrations exceed 0.55 mg/L that hypoxic events occur and disturb the system sufficiently to drop relative ascendency. Ulanowicz (1997a) found that most weighted food webs have very similar relative ascendency values, which has been suggested to represent a common trade-off between adaptable yet inefficient communities and efficient yet brittle communities – termed the Window of Vitality (Ulanowicz, 2009, Ulanowicz *et al.*, 2009). Interestingly, all the webs we assessed were within the Window of Vitality, with the webs of highest relative ascendency occurring approximately at the upper boundary of the established Window.

The Indirect Flow Intensity (measures the dominance of trophic cascades) decreased sharply with increasing nutrient enrichment until an inflection at DIN concentrations of approximately 0.3-0.4mg/L, after which indirect flows remained consistently at very low levels of total system flow. Weak indirect effects have been shown to increase food web robustness as they dampen the spread of disruptive cascades induced by disturbance. On the contrary, strong indirect effects have been associated with greater biocomplexity by supporting species coexistence through increased heterogeneity in space and time. Therefore, increasing enrichment may stabilize webs yet reduce their biocomplexity by reducing the proportion of indirect flows.

Synergistic effects, being non-obligatory positive feedback relationships (Fath and Patten, 1998), also reduced slightly with increasing enrichment between DIN concentrations of approximately 0.10-0.20 mg/L, after which synergism remained unaffected by increasing DIN. Despite differences in synergism, mutualistic effects, being obligatory positive feedback relationships (Fath, 2007), were unaffected by increasing DIN. Synergistic energy flows allow for the simultaneous growth of multiple species. Since species in synergistic relationships are not reliant on each other for survival but complimented, then if one species in a synergistic loop is perturbed then the others will support the recovery of the perturbed species, thereby supporting food web resilience (the ability of a food web to recover following disturbance) (Okuyama and Holland, 2008, Saint-Béat *et al.*, 2015). The reduction in synergism with nutrient enrichment may, therefore, reduce resilience.

If nutrient enrichment causes communities to be structured in a way that means disturbance-sensitive species are in keystone (or highly influential) positions, then their loss during the next disturbance would likely be more pervasive than when they are less influential (Zhao *et al.*, 2016). We found that as nutrient enrichment increased, the community structure changed in a way that meant species whose body forms were sensitive to flood disturbances became more keystone/influential (greater environ centrality, Fig. 7.4.). Therefore, in our webs, floods are more likely to cause disruptive cascades in and destabilise webs that are highly enriched as keystone species have body forms that are more easily disturbed by flood disturbances.

In conclusion, as nutrient enrichment increased the communities became energy inefficient as community (excluding microbes) respiration increased. Increased community oxygen demand may drive or exacerbate hypoxic events. Furthermore, the strength of trophic cascades reduced with increasing enrichment, this may reduce the effects of disruptive cascades. Interestingly, enriched communities were also structured in a way that resulted in flood-sensitive species (based on body form) being more keystone than in pristine communities; therefore, the communities may more sensitive to collapse from flow disturbance.

Chapter eight:

Synthesis

The aim of this PhD was to advance the understanding of how habitat affects aquatic food webs. This was achieved by applying a relatively new analysis technique, ecological network analysis (ENA) to understand (i) the structural differences in lake, river and estuarine food webs; (ii) how aquatic food web assembly affects energy flow stability; (iii) the influence of basal composition (allochthonous-dominance vs autochthonous-dominance) on riverine macroinvertebrate trophic networks; (iv) the interaction between periphyton and trout densities on the properties of the Hutt River food web; (v) the effect of phytoplankton blooms on the Wellington Harbour food web; and (vi) the influence of nutrient enrichment on riverine food webs.

In chapter two, lake, riverine and estuarine food webs were found to be structurally similar, except that rivers had lower neighbourhood connectivity and greater variability in the number of consumers of resource taxa than in food webs from lakes and estuaries. I hypothesise that frequent disturbance from floods in rivers reduces the neighbourhood connectivity, with the frequent 'resetting' of the community favouring predator-vulnerable taxa.

In chapter three, I found that in weighted food webs energy flows are stabilised from perturbation by low indirect flow intensities (i.e., trophic cascades were weak) and lower mean trophic levels. This work supports existing theoretical hypotheses that food webs are stabilized by the dominance of weak interactions and short food chains (Rooney and McCann, 2012, Saint-Béat *et al.*, 2015, Mougi and Kondoh, 2016, Zhao *et al.*, 2016). Weak indirect interactions can dampen disruptive cascades caused by disturbance.

In chapter four, I found that across 20 paired stream sites on the Mt Taranaki ring-plain, riparian forest stream macroinvertebrate communities differed from those in grassland because of increased allochthonous inputs and reduced periphyton biomass in the former streams. Despite differences in community composition of these communities, the trophic networks and their stability did not differ. Interestingly, however, the macroinvertebrate communities in grassland had greater energy exports (i.e., drift and death) and greater community respiration.

In chapter five, I found that in the Hutt River modelled increases in periphyton increased food web robustness by increasing the proportion of relatively weak links. However, greater periphyton growth caused more population variability in taxa reliant on energy from that periphyton, potentially making the web more vulnerable to species extinction (Pimm, 1991). An increase in trout had no influence on robustness or variability but did increase competition with other fish (Flecker and Townsend, 1996, Townsend, 1996, Townsend, 2003, McIntosh *et al.*, 2010).

In chapter six, modelled phytoplankton blooms in Wellington Harbour (sub-tidal zone near Hutt River outflow) were found to increase the total quantum of energy stored and flowing within the food web but at the cost of small reductions in mutualistic energy flows. Changes in indirect effects and energy flow distribution were otherwise minimal. In comparison to the adjacent Hutt River food web (chapter five), it is clear that managing nutrients, and consequently algae growth, for the health of one ecosystem does not necessarily mean the same outcomes will be achieved in the adjacent ecosystem.

In chapter seven, I found that in 12 riverine food webs with differing nutrient enrichment that highly enriched communities had weaker indirect effects, which may increase their robustness to loss of energy when disturbed. This is consistent with findings from chapters four and five that found increased periphyton reduces indirect effects, thereby increasing the robustness of the energy flow. However, enriched webs are also likely to be more sensitive to the loss of flood-sensitive species than those with low enrichment. Furthermore, enriched communities showed community respiration (excluding microbial respiration) several times greater than communities with low enrichment. The greater respiration in enriched communities may drive more frequent and more severe hypoxic conditions and is consistent with the findings in chapter four where periphyton growth in grassland webs also resulted in macroinvertebrate communities with greater community respiration. The identification of a potential eutrophication threshold in this chapter could be significant in effectively managing New Zealand freshwater ecosystems, further analysis should re-examine the relationships found across a larger dataset.

Howard Skipper is often quoted saying “a model is a lie that helps you see the truth,” this quote also applies to the modelling presented in this thesis. Some key limitations of the modelling presented here include the lack of microbial parameters, the limited temporal resolution, the lack of environmental constraints, and the heavy reliance on other modelled data. Microbes were excluded for all but the Hutt River food web as there is no data available and to minimise the risk of a large coarsely resolved node from dominating the metrics calculated (Abarca-Arenas and Ulanowicz, 2002, Allesina *et al.*, 2005). The exclusion of microbes means that cycling (and indices that rely on cycling) will be grossly under-estimated (Hall and Meyer, 1998, Fath and Halnes, 2007, Fath *et al.*, 2007); therefore, the metrics presented only account for the flows travelling between non-microbial compartments and across boundaries. Further analysis of microbial compartments in the webs assembled in chapters six and seven would permit greater insight to the cycling occurring in those webs.

The webs assembled were also snap-shots of communities using annual average parameters and do not explore seasonal changes in the webs. Further examining seasonal differences may inform managers of the most sensitive periods for an ecosystem (Baird and Ulanowicz, 1989). In chapters five and six, I simulated the effects of changing the biomass of basal species and trout (chapter six only), what has not been accounted for in these simulations are the limits to growth or depletion of compartments depending on available habitat or allele effects. Future studies could determine likely habitat constraints and allele effects and then include them in the dynamic models. Food web models are often large aggregations of published surveys and relationships given the logistical demands of deriving all food web parameters. Whilst using existing literature from the same or similar environments and/or species is considerably less time consuming, the cumulative error of the multiple sources may have strong influence on the final analysis. In this thesis, I have not explored the influence of this error, although I have rated and presented the confidence for each parameter. Further analysis could assess the sensitivity of parameter changes to derived metrics.

Despite these limitations, this thesis highlights the potential insights that may be gained by assessing freshwater ecosystems using ecological network analysis. Key contributions include: 1) The development of a new way to measure the stability of weighted empirically-derived food webs to species extinction and that stability is greatest when indirect effects are low. 2) The construction of multiple stream food webs, which helps fill a gap in the ENA literature for riverine systems. Furthermore, these webs show how food webs can be used as a response variable to understand anthropogenic disturbances (Memmott, 2009) 3) It has been shown that changes in invertebrate community composition from deforestation and nutrient enrichment may result in communities that are more energy demanding that consume substantially greater levels of oxygen. Large changes in oxygen use within aquatic systems has traditionally been attributed to increases in microbial activity. Here it is hypothesised that disturbance leads to communities that are energetically inefficient, have greater respiration demands, and consequently may exacerbate diurnal fluctuations in dissolved oxygen and hypoxic conditions. 4) A new metric methodology is presented that may indicate a webs susceptibility to cascading collapse from a particular disturbance, such as floods. Using this metric methodology, it is suggested here that nutrient enrichment may lead to communities where flood sensitive taxa hold more influential positions within river food webs. This may mean that nutrient enriched river food webs could be more susceptible to collapse from floods.

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Appendix A

MASSEY UNIVERSITY
GRADUATE RESEARCH SCHOOL

STATEMENT OF CONTRIBUTION TO DOCTORAL THESIS CONTAINING PUBLICATIONS

(To appear at the end of each thesis chapter/section/appendix submitted as an article/paper or collected as an appendix at the end of the thesis)

We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

Name of Candidate: Adam Canning

Name/Title of Principal Supervisor: Prof Russell Death

Name of Published Research Output and full reference:

Food web structure but not robustness differ between rivers, lakes and estuaries

In which Chapter is the Published Work: Two

Please indicate either:

- The percentage of the Published Work that was contributed by the candidate:

  and / or

- Describe the contribution that the candidate has made to the Published Work:

  Adam Canning developed the hypothesis, reviewed literature, carried out the analysis, interpreted the data, wrote the manuscript. Professor Russell Death, provided guidance on conception, methodology, manuscript development and editing.

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DRC 16

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STATEMENT OF CONTRIBUTION TO DOCTORAL THESIS CONTAINING PUBLICATIONS

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Name of Candidate: Adam Canning

Name/Title of Principal Supervisor: Prof Russell Death

Name of Published Research Output and full reference:

Trophic cascade direction and flow determine network flow stability

In which Chapter is the Published Work: Three

Please indicate either:

- The percentage of the Published Work that was contributed by the candidate:

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- Describe the contribution that the candidate has made to the Published Work:

  Adam Canning developed the hypothesis, reviewed literature, carried out the analysis, interpreted the data, wrote the manuscript. Professor Russell Death, provided guidance on conception, methodology, manuscript development and editing.

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Name of Candidate: Adam Canning

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Name of Published Research Output and full reference:

Forest canopy affects stream macroinvertebrate community structure but not stability

In which Chapter is the Published Work: Four

Please indicate either:

- The percentage of the Published Work that was contributed by the candidate:

  and / or

- Describe the contribution that the candidate has made to the Published Work:

  Adam Canning developed the hypothesis, reviewed literature, carried out the analysis, interpreted the data, wrote the manuscript. Professor Russell Death, provided guidance on conception, methodology, manuscript development and editing. Erna Zimmerman collected the macroinvertebrate and physicochemical data.

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STATEMENT OF CONTRIBUTION
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We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

Name of Candidate: Adam Canning

Name/Title of Principal Supervisor: Prof Russell Death

Name of Published Research Output and full reference:

The potential influence of increasing trout and algae biomass on a New Zealand riverine food web

In which Chapter is the Published Work: Five

Please indicate either:

- The percentage of the Published Work that was contributed by the candidate:

  and / or

- Describe the contribution that the candidate has made to the Published Work:

  Adam Canning developed the hypothesis, reviewed literature, carried out the analysis, interpreted the data, wrote the manuscript. Professor Russell Death, provided guidance on conception, methodology, manuscript development and editing.

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DRC 16

MASSEY UNIVERSITY
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STATEMENT OF CONTRIBUTION TO DOCTORAL THESIS CONTAINING PUBLICATIONS

(To appear at the end of each thesis chapter/section/appendix submitted as an article/paper or collected as an appendix at the end of the thesis)

We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

Name of Candidate: Adam Canning

Name/Title of Principal Supervisor: Prof Russell Death

Name of Published Research Output and full reference:

The influence of primary production on estuarine food web structure

In which Chapter is the Published Work: Six

Please indicate either:

- The percentage of the Published Work that was contributed by the candidate:

  and / or

- Describe the contribution that the candidate has made to the Published Work:

  Adam Canning developed the hypothesis, reviewed literature, carried out the analysis, interpreted the data, wrote the manuscript. Professor Russell Death, provided guidance on conception, methodology, manuscript development and editing.

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Name of Candidate: Adam Canning

Name/Title of Principal Supervisor: Prof Russell Death

Name of Published Research Output and full reference:

The influence of nutrient enrichment on riverine food webs: Are the energy flow defences compromised?

In which Chapter is the Published Work: Seven

Please indicate either:

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- Describe the contribution that the candidate has made to the Published Work:

  Adam Canning developed the hypothesis, reviewed literature, carried out the analysis, interpreted the data, wrote the manuscript. Professor Russell Death, provided guidance on conception, methodology, manuscript development and editing.

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Appendix B

Table A1. Macroinvertebrates present at the Taranaki ring-plain (New Zealand) and their associated feeding groups.

Order	**Species**	**Functional Feeding**	**Reference**
Ephemeroptera	*Coloburiscus humeralis*	Filterer	(Winterbourn 1982; Winterbourn *et al.* 1984; Winterbourn 2000; Winterbourn *et al.* 1989)
Ephemeroptera	*Deleatidium spp.*	Grazer	(Polegatto and Froehlich 2003; Towns and Peters 1996; Winterbourn 1982; Winterbourn *et al.* 1984; Winterbourn 2000; Winterbourn *et al.* 1989)
Ephemeroptera	*Nesameletus spp.*	Browser	(Polegatto and Froehlich 2003; Towns and Peters 1996; Winterbourn 1982; Winterbourn *et al.* 1984; Winterbourn 2000; Winterbourn *et al.* 1989)
Ephemeroptera	*Zephlebia dentata*	Grazer	(Polegatto and Froehlich 2003; Towns and Peters 1996; Winterbourn 1982; Winterbourn *et al.* 1984; Winterbourn 2000; Winterbourn *et al.* 1989)
Ephemeroptera	*Acanthophlebia cruentata*	Grazer	(Polegatto and Froehlich 2003; Towns and Peters 1996; Winterbourn 1982; Winterbourn *et al.* 1984; Winterbourn 2000;

			Winterbourn *et al.* 1989)
Ephemeroptera	*Austroclima jollyae*	Grazer	(Polegatto and Froehlich 2003; Towns and Peters 1996; Winterbourn 1982; Winterbourn *et al.* 1984; Winterbourn 2000; Winterbourn *et al.* 1989)
Plecoptera	*Austroperla cyrene*	Browser	(Winterbourn 1982; Winterbourn *et al.* 1984; Winterbourn 2000; Winterbourn 2005; Winterbourn *et al.* 1989)
Plecoptera	*Megaleptoperla grandis*	Browser	(Winterbourn 1982; Winterbourn *et al.* 1984; Winterbourn 2000; Winterbourn 2005; Winterbourn *et al.* 1989)
Plecoptera	*Stenoperla prasina*	Midges and detritus	(Devonport and Winterbourn 1976; Winterbourn 1982; Winterbourn *et al.* 1984; Winterbourn 2000; Winterbourn *et al.* 1989)
Plecoptera	*Zelandobius sp.*	Collector	(Winterbourn 1982; Winterbourn *et al.* 1984; Winterbourn 2000; Winterbourn 2005; Winterbourn *et al.* 1989)
Plecoptera	*Zelandoperla decorata*	Collector	(Winterbourn 1982; Winterbourn *et al.* 1984; Winterbourn 2000; Winterbourn 2005; Winterbourn *et al.* 1989)

Trichoptera (cased)	*Baeraeoptera roria*	Collector	(Cowley 1978; Winterbourn 1982; Winterbourn *et al.* 1984; Winterbourn 2000; Winterbourn *et al.* 1989)
Trichoptera (cased)	*Confluens hamiltonii*	Collector	(Cowley 1978; Winterbourn 1982; Winterbourn *et al.* 1984; Winterbourn 2000; Winterbourn *et al.* 1989)
Trichoptera (cased)	*Helicopsychidae sp.*	Collector	(Cowley 1978; Winterbourn 1982; Winterbourn *et al.* 1984; Winterbourn 2000; Winterbourn *et al.* 1989)
Trichoptera (cased)	*Olinga feredayi*	Collector and shredder	(Cowley 1978; Winterbourn 1982; Winterbourn *et al.* 1984; Winterbourn 2000; Winterbourn *et al.* 1989)
Trichoptera (cased)	*Pycnocentrella sp.*	Collector and shredder	(Cowley 1978; Winterbourn 1982; Winterbourn *et al.* 1984; Winterbourn 2000; Winterbourn *et al.* 1989)
Trichoptera (cased)	*Pycnocentria funera*	Collector and shredder	(Cowley 1978; Winterbourn 1982; Winterbourn *et al.* 1984; Winterbourn 2000; Winterbourn *et al.* 1989)
Trichoptera (cased)	*Oxythira albiceps*	Filamentous algae	(Cowley 1978; Winterbourn 1982; Winterbourn *et al.* 1984; Winterbourn 2000; Winterbourn *et al.* 1989)

Trichoptera (uncased)	*Hydrobiosis parumbripennis*	Midges and detritus	(Cowley 1978; Crosby 1975; Winterbourn 1982; Winterbourn *et al.* 1984; Winterbourn 2000; Winterbourn *et al.* 1989)
Trichoptera (uncased)	*Aoteapsyche colonica*	Filterer	(Cowley 1978; Winterbourn 1982; Winterbourn *et al.* 1984; Winterbourn 2000; Winterbourn *et al.* 1989)
Trichoptera (uncased)	*Aoteapsyche raruraru*	Filterer	(Cowley 1978; Winterbourn 1982; Winterbourn *et al.* 1984; Winterbourn 2000; Winterbourn *et al.* 1989)
Trichoptera (uncased)	*Orthopsyche fimbriata*	Filterer	(Cowley 1978; Winterbourn 1982; Winterbourn *et al.* 1984; Winterbourn 2000; Winterbourn *et al.* 1989)
Trichoptera (uncased)	*Orthopsyche thomasi*	Filterer	(Cowley 1978; Winterbourn 1982; Winterbourn *et al.* 1984; Winterbourn 2000; Winterbourn *et al.* 1989)
Trichoptera (uncased)	*Hydrobiosella stenocerca*	Browser	(Cowley 1978; Winterbourn 1982; Winterbourn *et al.* 1984; Winterbourn 2000; Winterbourn *et al.* 1989)
Trichoptera (uncased)	Hydrobiosidae, early instar	Midges and detritus	(Cowley 1978; Winterbourn 1982; Winterbourn *et al.* 1984; Winterbourn

			2000; Winterbourn *et al.* 1989)
Coleoptera	Elmidae	Collector	(Winterbourn 1982; Winterbourn *et al.* 1984; Winterbourn 2000; Winterbourn *et al.* 1989)
Diptera	*Aphrophila neozelandica*	Browser including filamentous algae	(Winterbourn 1982; Winterbourn *et al.* 1984; Winterbourn 1996; Winterbourn 2000; Winterbourn *et al.* 1989)
Megaloptera	Archichauliodes diversus	Midges and detritus	(Devonport and Winterbourn 1976; Winterbourn 1982; Winterbourn *et al.* 1984; Winterbourn 2000; Winterbourn *et al.* 1989)
Crustacea	Paranephrops	Browser	(Hollows *et al.* 2002; Winterbourn 1982; Winterbourn *et al.* 1984; Winterbourn 2000; Winterbourn *et al.* 1989)
Oligochaeta	Oligochaeta	Deposit	(Winterbourn 1982; Winterbourn *et al.* 1984; Winterbourn 2000; Winterbourn *et al.* 1989)
Diptera	Paradixa sp.	Filterer	(Winterbourn 2000; Winterbourn *et al.* 1989)
Diptera	Orthocladinae grp.	Collector	(Winterbourn 1982; Winterbourn *et al.* 1984; Winterbourn 2000; Winterbourn *et al.* 1989)
Diptera	Polypedilum	Collector	(Winterbourn 1982; Winterbourn *et al.*

			1984; Winterbourn 2000; Winterbourn *et al.* 1989)
Diptera	Maoridiamesa	Collector	(Winterbourn 1982; Winterbourn *et al.* 1984; Winterbourn 2000; Winterbourn *et al.* 1989)
Diptera	Tanytarsus	Collector	(Winterbourn 1982; Winterbourn *et al.* 1984; Winterbourn 2000; Winterbourn *et al.* 1989)
Diptera	Podonominae	Collector	(Winterbourn 1982; Winterbourn *et al.* 1984; Winterbourn 2000; Winterbourn *et al.* 1989)

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