Food webs in the lower Waikato River and the role of hydrogeomorphic complexity

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Abstract

Large rivers are fundamental to human societies and consequently their ecosystems have come under increasing pressure from a range of developments and uses. Despite this, there is still a major knowledge gap understanding food webs supporting fisheries of large river ecosystems. Quantifying the contributions of carbon sources that support food webs is an important and growing field of ecological research, with implications for future management and rehabilitation of large rivers. I reviewed theoretical concepts addressing carbon flow in large river food webs where organic matter from floodplains (Flood Pulse Concept), local aquatic sources (Riverine Productivity Model), or leakage from upstream processing of terrestrial organic matter (River Continuum Concept) can fuel secondary production. Recent empirical evidence highlights the importance of autochthonous carbon, especially in the form of benthic algae and phytoplankton, to food webs in a variety of large rivers along with a range of secondary carbon sources that can assume importance depending on temporal and spatial variation in hydrogeomorphic conditions. The geographic spread of studies addressing carbon flow in large river food webs is steadily increasing, although information remains sparse on temperate Southern Hemisphere rivers and long-term data sets on carbon flow are generally lacking. I measured natural abundances of stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes to quantify spatial and temporal patterns of carbon flow through aquatic food webs in the lowland section of New Zealand's longest river, the Waikato River. Zones of potential ecological importance influencing carbon transfer along the lower Waikato River were identified using a combination of (i) high-frequency, along-river water quality measurements collected during four seasons and (ii) river channel morphology data derived from aerial photos. A multivariate statistical approach was developed to identify three hydrogeomorphic zones shaped by the physical complexity and channel character of constituent river reaches, and characterised by shifts, sometimes transitional, of physico-chemical variables. Changes in water clarity, chlorophyll fluorescence and specific conductance were driven by tributary inflows and tidal influence.

Carbon flow estimated using the mixing model IsoSource supported predictions of the Riverine Productivity Model, with autochthonous algae and biofilms (phytomicrobenthos) the most important basal carbon sources contributing to consumer biomass in all three zones. These sources were often supported by C_3 aquatic macrophytes and allochthonous C_3 riparian plants. However, the relative importance of organic carbon sources appeared to change depending on season and zone, likely in response to variations in water temperature and flow, particularly in the unconstrained zone of the lower river. It was also demonstrated that to draw robust conclusions, consideration must be given to quantifying the isotopic signatures of organisms lower in the food web, as these can change significantly between sampling times and hydrogeomorphic zones.

Tributary confluences can be hotspots for biological production and provide novel carbon sources from donor sub-catchments in large river systems. Littoral food webs and water quality were compared between two main stem habitats (constrained and unconstrained hydrogeomorphic zones) and tributary junctions representing those fed by streams, lakes and wetlands during seasonal low flows when these habitats were likely to be most different. $\delta^{13}C$ and $\delta^{15}N$ isotopes were then employed using the Bayesian statistics R package Stable Isotope Analysis in R (SIAR) to estimate carbon flow through food webs and also to estimate measures of trophic structure. Pathways were also tested using analysis of fish stomach contents. SIAR mixing models confirmed that autochthonous benthic carbon was the most important carbon source to littoral food webs in all habitats. Riparian carbon appeared to be the most important secondary carbon source to fish consumers, and estimates of its contribution were often greater in tributary junctions compared to fish of the same species in the main stem. Trophic patterns of fish species collected in both the main stem and tributary junctions were similar amongst habitats, as were community metrics estimated using stable isotope signatures and SIAR. This study demonstrates that, while they may add to the lateral complexity of the riverscape, permanently connected habitats such as tributary junctions do not necessarily contribute to overall food web complexity. In this study tributary junctions tended to be steep-sided, and complex littoral habitats containing woody debris and macrophytes were typically rare, potentially limiting the development of more complex food webs.

These results contribute to the ever-improving data regarding food web ecology in large rivers, particularly with regard to carbon flow, and the role played by lateral habitats and hydrogeomorphic zones in shaping these processes.

This study also provides information and recommendations that provide direction for future research and management actions aimed at aiding the rehabilitation of the lower Waikato River, its riverscape and biological communities.

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To my wife Emily, thank you so much for all your support and for reminding me that there was more to life than just this thesis.

Table of contents

List of figures

List of tables

Preface

The main body of this thesis comprises six chapters; Chapters 2–5 were prepared as individual papers for submission to peer–reviewed scientific journals. For this reason there is some repetition of methodological details and referencing styles may vary between chapters.

Together, these chapters form a coherent portfolio of work that makes an original contribution to my chosen thesis topic. Except where stated otherwise, the work in this thesis, including study design, field and laboratory work, data analyses and writing, was undertaken by me while under the supervision of Professor David Hamilton (University of Waikato), Associate Professor Kevin Collier (University of Waikato and Waikato Regional Council), Associate Professor Brendan Hicks (University of Waikato) and Dr Bruno David (Waikato Regional Council).

Co–authors for each chapter are listed below. All co–authors reviewed relevant chapters and provided advice where necessary.

Chapter 2 has been published as "Carbon sources supporting large river food webs: A review of ecological theories and evidence from stable isotopes" in the journal Freshwater Reviews. Authors: M Pingram, K Collier, D Hamilton, B David and B Hicks (2012).

Chapter 3 is a modified version of a paper submitted to the journal River Systems as: "High intensity data survey and multivariate statistics reveal ecological zones along the longitudinal profile of a large, temperate, lowland river", and is currently under revision following peer review. Authors: M Pingram, K Collier, D Hamilton, B David and B Hicks.

Chapter 4 has been published as "Spatial and temporal patterns of carbon flow in a temperate large river food web" in the journal Hydrobiologia. Authors: M Pingram, K Collier, D Hamilton, B Hicks and B David (2012).

Chapter 5 has been prepared for submission to a relevant scientific journal as "Trophic patterns and carbon flow in main stem and tributary junction habitats in a large temperate riverscape" Authors: M Pingram, K Collier, D Hamilton, B Hicks and B David.

1 General introduction

1.1 Large rivers

Large rivers provide important goods and services to human societies and consequently their ecosystems come under pressure from a range of developments and uses (Allan & Flecker, 1993; Nilsson et al., 2005; Vörösmarty et al., 2010). Large rivers have longitudinal, lateral, vertical and temporal dimensions and can occur as single or multi-branched channels (Ward, 1989; Power et al., 1995; Thorp et al., 2008). Longitudinally rivers can undergo changes in water quality, habitat complexity and species composition, as catchment size and flow increase with distance downstream (Vannote et al., 1980). From a lateral perspective, fast-flowing main and secondary channel habitats can be supplemented by a mosaic of low-flow habitats including backwaters, side channels, bays, tributary confluences, lagoons, littoral zones and floodplain lakes and wetlands (Schiemer & Hein, 2007; Thorp et al., 2008). Contributing watercourses provide additional complexity to the riverscape, offering habitat out of the main flow, structuring physical characteristics downstream, donating carbon subsidies, and providing linkages with other habitats such as lakes, wetlands and headwater streams (Kiffney et al., 2006; Rice et al., 2006; Rosales et al., 2007; Rice et al., 2008).

Large floodplain river ecosystems can change temporally in response to seasonal flow pulses that affect connectivity with lateral habitats and changes that alter physical habitat, water temperatures and quality, composition of biotic communities and food web structure (Tockner et al., 2000; Fisher et al., 2001). The diversity, distribution, connectivity and scale of these lateral habitats are therefore important to ecological function, particularly in structurally complex river systems (Thorp et al., 2006). Interdisciplinary approaches, such as eco-geomorphology, have revealed hierarchical patterns of physical and biological associations across a range of spatial scales in riverine ecosystems (Thoms & Parsons, 2002; Parsons & Thoms, 2007). The recent integration of hierarchical patch dynamics, geomorphology and landscape ecology has expanded scientific perspectives to recognise the importance of environmental heterogeneity and discontinuities in lotic ecosystems generally (Poole, 2002; Winemiller et al., 2010).

1.2 Carbon flow in large river food webs

Studies addressing energy flow through large river food webs are important as they can identify specific habitats and carbon sources that are important for sustaining riverine productivity, thereby providing information to support improved management and restoration of lowland floodplain rivers (Johnson et al., 1995; Thorp et al., 2006, 2008). Several different theories have been developed to account for carbon flow through large river food webs and to stimulate discussion around this and other key aspects of large river ecological function. Significant and widely-tested models describing energy flow driving biotic communities in large rivers include the River Continuum Concept (Vannote et al., 1980; Minshall et al., 1985), the Flood Pulse Concept (Junk et al., 1989), and the Riverine Productivity Model (Thorp & Delong, 1994, 2002). Each of the above models focuses on carbon originating from different parts of the riverscape (see Chapter 2 for a detailed discussion). More recently, the Riverine Ecosystem Synthesis has sought to build on and integrate previous theories by bringing together elements of ecology, fluvial geomorphology, a terrestrial landscape patch dynamic model, and aspects of other aquatic models to provide a framework for understanding the broad and often complex patterns of temporal, longitudinal and lateral dimensions of river networks that affect trophic complexity and carbon flow (Thorp et al., 2006, 2008). Fundamental to this synthesis is the concept of the functional process zone, which can be loosely defined as a fluvial geomorphic unit of scale between a valley and a reach (Thorp et al., 2008). The Riverine Ecosystem Synthesis regards rivers as arrangements of these large hydrogeomorphic patches formed by catchment geomorphology and climate that may recur longitudinally along the river network. With regard to carbon flow, the predictions Riverine Ecosystem Synthesis are in keeping with those of the Riverine Productivity Model.

Testing of these theories has been advanced through the use of stable isotope analysis, which has proven to be an invaluable technique for elucidating trophic interactions in aquatic ecosystems generally, allowing quantification of carbon flow through food webs and providing insights to other aspects of food web structure. Food webs describe the trophic interactions between consumers and resources, such as the transfer and utilisation of energy and nutrients, and they have become a central theme in ecology (Polis et al., 1997; Woodward & Hildrew, 2002; de Ruiter et al., 2005). Freshwater ecology made early use of stable isotope analysis to advance food web theory (Thompson et al., 2012), by providing a time-integrated measure of energy flow and trophic interactions (Post, 2002). Stable isotope analyses have also been applied to investigate trophic position (Vander Zanden & Rasmussen, 1999; Post, 2002), food web linkages (Fisher et al., 2001), fish movements (Rasmussen et al., 2009) and habitat use (Fry, 2002), seasonal food web patterns (Herwig et al., 2007), the effects of introduced species (Martinez et al., 2001), catchment geochemistry and land use (Chang et al., 2002; Jepsen & Winemiller, 2007; Winemiller et al., 2011), and other human impacts on aquatic ecosystems (Kohzu et al., 2009). Much of our knowledge of carbon flow in large river food webs derived from stable isotope analysis comes from North (e.g. Thorp et al., 1998; Herwig et al., 2007; Delong, 2010) and South (e.g. Hoeinghaus et al., 2007; Jepsen & Winemiller, 2007) American rivers. In addition, there is growing body of research from Australian river systems, across a range of arid (e.g. Bunn et al., 2003; Burford et al., 2008; Leigh et al., 2010) and tropical (e.g. Douglas et al., 2005; Hunt et al., 2011) climates. However, comparatively little is known about carbon flow is southern temperate rivers and whether they conform to theories developed elsewhere.

1.3 The Waikato River

The Waikato River, New Zealand's longest river, is highly significant in terms of its cultural, ecological and economic status. It is a 7th order river, with a mean annual discharge of c. 450 $m^3 s^{-1}$ at the mouth (Brown, 2010), conforming to the various definitions of a large river used elsewhere (Vannote et al., 1980; Dynesius & Nilsson, 1994; Johnson et al., 1995; Nilsson et al., 2005). The river drains a catchment of around 14,500 km^2 (or 13 % of the North Island), and flows in a roughly northerly direction for over 400 km from Lake Taupo to the sea at Port Waikato (Brown, 2010). Eight hydroelectric dams have been constructed on the upper river, providing around 13 % of the nation’s electricity supply and up to 25 % at peak demand (up to 1,100 MW) (Brown, 2010; NIWA, 2010). As well as supplying water for electricity the river provides drinking water to four major settlements, including the cities of Auckland and Hamilton, and also for industrial and agricultural uses (Brown, 2010; NIWA, 2010). The Waikato River and the major lower river tributary, Waipa River, are culturally, spiritually and historically important to tangata whenua, who have a significant interest in the well-being of these rivers. Their respect for and relationship with the river lies at the heart of tribal culture and identity (Crown, 2010; O'Sullivan & Te Hiko, 2010; Watene-Rawiri & Flavell, 2010).

My research was conducted on the lower Waikato River downstream of Karapiro Dam which acts as a barrier to the natural upstream movement of aquatic fauna. The lower Waikato River flows through a predominantly pastoral landscape along a low-gradient channel, falling 22 m over the c. 150 km passage to the sea (Brown, 2010; Collier et al., 2010). Along its course it is fed by several major tributaries, the largest and most significant being the Waipa River which augments mean flow by c. 25 % and contributes significant amounts of agriculturally-derived nutrients and sediment to the main stem, particularly during winter and spring high flows (Chapman, 1996; Brown, 2010). Below Huntly the river once interacted with an extensive floodplain characterised by wetlands and riverine lakes, some of which feed other major tributaries. Flooding is now managed and restricted by a flood protection scheme that includes 242 km of stopbanks, 269 floodgates and 69 pump stations, disconnecting 47 % (172 km^2) of the original floodplain (Chapman, 1996; Mulholland, 2010; Speirs et al., 2010). In the lower reaches the river’s flow becomes tidally influenced, although saline intrusion does not occur above an expansive delta near Port Waikato (Brown, 2003).

The riparian zone of the lower Waikato River is dominated by introduced deciduous trees and pasture for stock grazing (Champion & Clayton, 2010b). Similarly, the aquatic flora is almost exclusively dominated by exotic macrophytes (Collier & Lill, 2008; Champion & Clayton, 2010a). The planktonic algal assemblage is mostly made up of species of green algae, diatoms and blue-green algae, while the zooplankton assemblage is dominated by small-sized rotifers (Hamilton & Duggan, 2010). Littoral macroinvertebrate faunas are characterised by taxa with a preference for soft, silty bottom sediments, including several species of annelids, nematodes, roundworms, ribbonworms, molluscs and midge larvae (Collier & Lill 2008). High abundances of the amphipod *Paracalliope fluviatilis* and the diadromous shrimp *Paratya curvirostris* occur along river margins (Collier & Hogg, 2010).

According to the New Zealand Freshwater Fish Database there are 19 species of native fish found in the Waikato River and its tributaries. This is significant, as New Zealand’s native freshwater fish diversity, although unique, is low by international standards, having only around 40 species, some of which are genetic complexes or have evolved from landlocked diadromous species (McDowall, 2000; David & Speirs, 2010). While some of the native fish species are resident in and close to the main stem of the lower river, for others the main stem acts as an important conduit to and from headwater streams (David & Speirs, 2010). At least ten introduced fish species are known to be present in the Waikato River and its tributaries (Hicks et al., 2010). Most of these have been recorded in the lower river where they are generally widespread and can occur in high densities. Several of these species have been introduced to establish recreational sports fisheries while others have been introduced illegally or by accident (McDowall, 1990; Hicks et al., 2010). Some of these introduced species have become pests and have detrimental impacts on water quality, native species and ecosystems in the lower Waikato River (Hicks et al., 2010). The lower Waikato River has been relatively little studied in the last few decades, and a recent co-management agreement has highlighted the need for information to support future restoration initiatives aimed at enhancing the mauri (life force) of the river, in accordance with Objective M of the Vision and Strategy for the Waikato River (Waikato River Authority, 2008).

1.4 Aim and objectives

The overall aim of this thesis was to contribute to global understanding of large river food webs and provide information on food webs in the lower Waikato River that could be used to assist river rehabilitation. The first objective was to identify a likely carbon flow scenario for food webs in the lower Waikato River through (i) review of empirical evidence from recently published international studies derived from stable isotope analysis, and (ii) critical evaluation of support for existing ecological concepts largely developed in large temperate and tropical rivers, notably the River Continuum Concept, Flood Pulse Concept and Riverine Productivity Model.

Based on this review, a second objective was to test the hypothesis that the majority of carbon fuelling littoral, main-channel food webs in the lower Waikato River would be derived from suspended and benthic algae, conforming to predictions of the Riverine Productivity Model which has been supported by evidence from a variety of river systems (Thorp & Delong, 1994, 2002)

(Hypothesis 1; Chapter 4). Littoral food webs are likely to play a major role in carbon transfer through large river food webs because habitat complexity is greater along edges and hydrological conditions are favoured by a range of fish and invertebrate species (Thorp & Delong, 1994; Schiemer et al., 2001). In addition, in line with the concept of functional process zones articulated in the River Ecosystem Synthesis, it was hypothesised that carbon contributions and food web structure would differ between hydrogeomorphically distinct sections of river (Hypothesis 2; Chapters 3 and 4) and that lateral habitats would add to overall food web complexity (Hypothesis 3; Chapter 5) (Thorp et al., 2006, 2008). The focal lateral habitat for testing Hypothesis 3 was tributary junctions, which can contribute novel carbon sources to main stem habitats, provide refugia for aquatic flora and fauna from higher flow velocities in the main stem and contribute to the overall biodiversity in large river systems (Fernandes et al., 2004; Collier & Lill, 2008).

1.5 Thesis overview

This thesis comprises four main chapters (Chapters 2–5) which have been prepared for, or published in, peer–reviewed scientific journals to address the objectives above.

Chapter 2 describes theoretical concepts accounting for carbon flow through aquatic food webs in large rivers globally and then reviews recent empirical evidence from studies using stable isotope analysis. Large rivers were defined as those which conformed to either of two definitions: (i) 7th order or greater based on the Strahler concept (Vannote et al., 1980; Johnson et al., 1995), or (ii) virgin mean annual discharge of ≥ 350 m^3 s^{-1} (Dynesius & Nilsson, 1994; Nilsson et al., 2005). The review focuses on studies undertaken since the publication of the Riverine Ecosystem Synthesis (Thorp et al., 2006), specifically between 2006 and 2012.

To define zones for the testing of food web concepts in Chapter 4, Chapter 3 employs multivariate statistics to identify and characterise river zones of potential ecological importance at a scale relevant to management actions along the lower Waikato River. Data were collected using a combination of (i) high-frequency, along-river water quality measurements collected in four seasons and (ii) river channel morphology data derived from aerial photos.

In Chapter 4 natural abundances of stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes were used to quantify spatial and temporal patterns of carbon flow through littoral food webs in three different zones identified in Chapter 3. Samples were collected from littoral habitats of the main channel of the lower Waikato River across a range of seasonal conditions, and carbon contributions were estimated using a linear mixing model (IsoSource).

In Chapter 5 aspects of food web structure were compared between main channel and tributary sites along the lower Waikato River. Natural abundances of stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes were again used to estimate carbon flow through food webs, augmented with fish gut content analyses. Results were also used to estimate food web parameters such as trophic position and diversity. For this chapter the R package Stable Isotope Analysis in R (SIAR Parnell et al., 2010; Jackson et al., 2011) was used to estimate carbon flow and community food web metrics. SIAR employs Bayesian statistics to provide probability estimates, and also allows variability in carbon source and consumer isotopic signatures and that surrounding trophic fractionation estimates to be incorporated into mixing model estimates.

Chapter 6 synthesises the main conclusions of the preceding chapters, and also suggests avenues for management and research that would further advance rehabilitation and understanding of energy flow in large river ecosystems, in particular the Waikato River.

1.6 References

Allan, J. D. & A. S. Flecker, 1993. Biodiversity conservation in running waters. Bioscience 43: 32-43.

Waikato River Authority, 2008. Restoring and protecting the health and wellbeing of the Waikato River: Vision and strategy for the Waikato River. Guardians Establishment Committee.

Brown, E. J., 2003. Hydraulic travel time of major Waikato rivers. Environment Waikato Technical Report 2003/02. Environment Waikato, Hamilton.

Brown, E. J., 2010. Flow regime and water use. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, Hamilton, p 29-46.

Bunn, S. E., P. M. Davies & M. Winning, 2003. Sources of organic carbon supporting the food web of an arid zone floodplain river. Freshwater Biology 48: 619-635.

Burford, M. A., A. J. Cook, C. S. Fellows, S. R. Balcombe & S. E. Bunn, 2008. Sources of carbon fuelling production in an arid floodplain river. Marine and Freshwater Research 59: 224-234.

Champion, P. D. & J. S. Clayton, 2010a. Native macrophytes and aquatic weeds. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, p 153-172.

Champion, P. D. & J. S. Clayton, 2010b. Box 14.1: Riparian vegetation. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, p 268.

Chang, C. C. Y., C. Kendall, S. R. Silva, W. A. Battaglin & D. H. Campbell, 2002. Nitrate stable isotopes: tools for determining nitrate sources among different land uses in the Mississippi River Basin. Canadian Journal of Fisheries and Aquatic Sciences 59: 1874-1885.

Chapman, M. A., 1996. Human impacts on the Waikato river system, New Zealand. GeoJournal 40: 85-99.

Collier, K. J. & A. Lill, 2008. Spatial patterns in the composition of shallow-water macroinvertebrate communities of a large New Zealand river. New Zealand Journal of Marine and Freshwater Research 42: 129-141.

Collier, K. J. & I. D. Hogg, 2010. Macroinvertebrates. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest River. Waikato Regional Council, Hamilton, p 175-192.

Collier, K. J., E. M. Watene-Rawiri & J. D. McCraw, 2010. Geography and history. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, p 1-12.

Crown, P., 2010. Box 1.4: Significance of the Waipa to Maniapoto. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, p 10.

David, B. O. & D. A. Speirs, 2010. Native fish. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, p 193-208.

de Ruiter, P. C., V. Wolters & J. C. Moore, 2005. Dynamic food webs. In de Ruiter, P. C., V. Wolters & J. C. Moore (eds), Dynamic Food Webs: Multispecies assemblages, ecosystem development and environmental change. Academic Press, p 3-9.

Delong, M. D., 2010. Food webs and the Upper Mississippi River: contributions to our understanding of ecosystem function in large rivers. Hydrobiologia 640: 89-101.

Douglas, M. M., S. E. Bunn & P. M. Davies, 2005. River and wetland food webs in Australia's wet-dry tropics: general principles and implications for management. Marine and Freshwater Research 56: 329-342.

Dynesius, M. & C. Nilsson, 1994. Fragmentation and flow regulation of river systems in the northern third of the world. Science 266: 753-762.

Fernandes, C. C., J. L. Podos & J. G. Lundberg, 2004. Amazonian ecology: Tributaries enhance the diversity of electric fishes. Science 305: 1960-1962.

Fisher, S. J., M. L. Brown & D. W. Willis, 2001. Temporal food web variability in an upper Missouri River backwater: energy origination points and transfer mechanisms. Ecology of Freshwater Fish 10: 154-167.

Fry, B., 2002. Stable isotopic indicators of habitat use by Mississippi River fish. Journal of the North American Benthological Society 21: 676-685.

Hamilton, D. P. & I. C. Duggan, 2010. Plankton. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, p 117-131.

Herwig, B. R., D. H. Wahl, J. M. Dettmers & D. A. Soluk, 2007. Spatial and temporal patterns in the food web structure of a large floodplain river assessed using stable isotopes. Canadian Journal of Fisheries and Aquatic Sciences 64: 495-508.

Hicks, B. J., N. Ling & B. J. Wilson, 2010. Introduced fish. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the

Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, p 209-228.

Hoeinghaus, D. J., K. O. Winemiller & A. A. Agostinho, 2007. Landscape-scale hydrologic characteristics differentiate patterns of carbon flow in large-river food webs. Ecosystems 10: 1019-1033.

Hunt, R. J., T. D. Jardine, S. K. Hamilton & S. E. Bunn, 2011. Temporal and spatial variation in ecosystem metabolism and food web carbon transfer in a wet-dry tropical river. Freshwater Biology: doi: 10.1111/j.1365-2427.2011.02708.x.

Jackson, A. L., R. Inger, A. C. Parnell & S. Bearhop, 2011. Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R. The Journal of animal ecology 80: 595-602.

Jepsen, D. B. & K. O. Winemiller, 2007. Basin geochemistry and isotopic ratios of fishes and basal production sources in four neotropical rivers. Ecology of Freshwater Fish 16: 267-281.

Johnson, B. L., W. B. Richardson & T. J. Naimo, 1995. Past, present, and future concepts in large river ecology. Bioscience 45: 134-141.

Junk, W. J., P. B. Bayley & R. E. Sparks, 1989. The flood pulse concept in river-floodplain systems. In Dodge, DP (ed) Proceedings of the International Large River Symposium, Canadian Special Publication of Fisheries and Aquatic Sciences 106: 110-127.

Kiffney, P. M., C. M. Greene, J. E. Hall & J. R. Davies, 2006. Tributary streams create serial discontinuities in habitat, biological productivity, and diversity in mainstem rivers. Canadian Journal of Fisheries and Aquatic Sciences 63: 2518-2530.

Kohzu, A., I. Tayasu, C. Yoshimizu, A. Maruyama, Y. Kohmatsu, F. Hyodo, Y. Onoda, A. Igeta, K. Matsui, T. Nakano, E. Wada, T. Nagata & Y. Takemon, 2009. Nitrogen-stable isotopic signatures of basal food items, primary consumers and omnivores in rivers with different levels of human impact. Ecological Research 24: 127-136.

Leigh, C., M. A. Burford, F. Sheldon & S. E. Bunn, 2010. Dynamic stability in dry season food webs within tropical floodplain rivers. Marine and Freshwater Research 61: 357-368.

Martinez, P. J., B. M. Johnson & J. D. Hobgood, 2001. Stable isotope signatures of native and nonnative fishes in Upper Colorado River backwaters and ponds. Southwestern Naturalist 46: 311-322.

McDowall, R. M., 1990. New Zealand Freshwater Fishes: A natural history and guide. Heinemann Reed, Auckland.

McDowall, R. M., 2000. The Reed Field Guide to Fishes of New Zealand. Reed Books, Auckland.

Minshall, G. W., K. W. Cummins, R. C. Petersen, C. E. Cushing, D. A. Bruns, J. Sedell, R. & R. L. Vannote, 1985. Developments in stream ecosystem theory. Canadian Journal of Fisheries and Aquatic Sciences 42: 1045-1055.

Mulholland, W. M., 2010. Box 2.2: History of the lower Waikato Flood Protection Scheme. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, Hamilton, p 16.

Nilsson, C., C. A. Reidy, M. Dynesius & C. Revenga, 2005. Fragmentation and flow regulation of the world's large river systems. Science 308: 405-408.

NIWA, 2010. Waikato River independent scoping study. NIWA Client Report HAM2010-032, Hamilton.

O'Sullivan, S. J. O. & N. H. Te Hiko, 2010. Box 1.3: Raukawa and the River. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, p 9.

Parnell, A. C., R. Inger, S. Bearhop & A. L. Jackson, 2010. Source partitioning using stable isotopes: coping with too much variation. PloS one 5: e9672.

Parsons, M. & M. C. Thoms, 2007. Hierarchical patterns of physical - biological associations in river ecosystems. Geomorphology 89: 127-146.

Polis, G. A., W. B. Anderson & R. D. Holt, 1997. Toward and integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. Annual Review of Ecological Systematics 28: 289-316.

Poole, G. C., 2002. Fluvial landscape ecology: addressing uniqueness within the river discontinuum. Freshwater Biology 47: 641-660.

Post, D. M., 2002. Using stable isotopes to estimate trophic position: Models, methods, and assumptions. Ecology 83: 703-718.

Power, M. E., A. Sun, G. Parker, W. E. Dietrich & J. T. Wootton, 1995. Hydraulic food-chain models. Bioscience 45: 159-167.

Rasmussen, J. B., V. Trudeau & G. Morinville, 2009. Estimating the scale of fish feeding movements in rivers using delta C-13 signature gradients. Journal of Animal Ecology 78: 674-685.

Rice, S. P., R. I. Fergusson & T. B. Hoey, 2006. Tributary control of physical heterogeneity and biological diversity at river confluences. Canadian Journal of Fisheries and Aquatic Sciences 63: 2553-2566.

Rice, S. P., P. Kiffney, G. Correigh & G. R. Pess, 2008. The ecological importance of tributaries and confluences. In Rice, S. P., A. G. Roy & B. L. Rhoads (eds), River Confluences, Tributaries and the Fluvial Network. John Wiley & Sons, Ltd., Chichister, p 209-242.

Rosales, J., L. Blanco-Belmonte & C. Bradley, 2007. Hydrogeomorphological and ecological interactions in tropical floodplains: The significance of confluence zones in the Orinoco Basin, Venezuela. In P. J. Wood, D. M. Hannah & J. P. Sadler (eds), Hydroecology and Ecohydrology: Past, present and future John Wiley & Sons Ltd., Chichester, p 295-316.

Schiemer, F. & T. Hein, 2007. The ecological significance of hydraulic retention zones. In Wood, P. J., D. M. Hannah & J. P. Sadler (eds), Hydroecology and Ecohydrology: Past, present and future. John Wiley & Sons, Ltd, Chichester, p 405-420.

Schiemer, F., H. Keckeis, W. Reckendorfer & G. Winkler, 2001. The "inshore retention concept" and its significance for large rivers. Large Rivers 12: 509-516.

Speirs, D. A., D. G. Allen, R. M. Kelleher, M. D. Lake, A. N. Marchant, K. A. Mayes, E. M. Watene-Rawiri & B. J. Wilson, 2010. River management. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, Hamilton, p 13-26.

Thompson, R. M., J. A. Dunne & G. U. Y. Woodward, 2012. Freshwater food webs: towards a more fundamental understanding of biodiversity and community dynamics. Freshwater Biology 57: 1329-1341.

Thoms, M. C. & M. Parsons, 2002. Eco-geomorphology: an interdisciplinary approach to river science. International Association of Hydrological Sciences, Publication: 113-119.

Thorp, J. H. & M. D. Delong, 1994. The riverine productivity model: an heuristic view of carbon sources and organic processing in large river ecosystems. Oikos 70: 305-308.

Thorp, J. H. & M. D. Delong, 2002. Dominance of autochthonous autotrophic carbon in food webs of heterotrophic rivers. Oikos 96: 543-550.

Thorp, J. H., M. C. Thoms & M. D. Delong, 2006. The riverine ecosystem synthesis: Biocomplexity in river networks across space and time. River Research and Applications 22: 123-147.

Thorp, J. H., M. C. Thoms & M. D. Delong, 2008. The Riverine Ecosystem Synthesis: Towards conceptual cohesiveness in river science. Elsevier.

Thorp, J. H., M. D. Delong, K. S. Greenwood & A. F. Casper, 1998. Isotopic analysis of three food web theories in constricted and floodplain regions of a large river. Oecologia 117: 551-563.

Tockner, K., F. Malard & J. V. Ward, 2000. An extension of the flood pulse concept. Hydrological Processes 14: 2861-2883.

Vander Zanden, M. J. & J. B. Rasmussen, 1999. Primary consumer delta C-13 and delta N-15 and the trophic position of aquatic consumers. Ecology 80: 1395-1404.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell & C. E. Cushing, 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37: 130-137.

Vörösmarty, C. J., P. B. McIntyre, M. O. Gessner, D. Dudgeon, A. Prusevich, P. Green, S. Glidden, S. E. Bunn, C. A. Sullivan, C. R. Liermann & P. M. Davies, 2010. Global threats to human water security and river biodiversity. Nature 467: 555-561.

Ward, J. V., 1989. The four-dimensional nature of lotic ecosystems. Journal of the North American Benthological Society 8: 2-8.

Watene-Rawiri, E. M. & D. L. A. Flavell, 2010. Box 1.2: Significance to Waikato-Tainui. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, p 3.

Winemiller, K. O., A. S. Flecker & D. J. Hoeinghaus, 2010. Patch dynamics and environmental heterogeneity in lotic ecosystems. Society 29: 84-99.

Winemiller, K. O., D. J. Hoeinghaus, A. A. Pease, P. C. Esselman, R. L. Honeycutt, D. Gbanaador, E. Carrera & J. Payne, 2011. Stable isotope analysis reveals food web structure and watershed impacts along the fluvial gradient of a Mesoamerican coastal river. River Research and Applications 803: 791-803.

Woodward, G. & A. G. Hildrew, 2002. Food web structure in riverine landscapes. Freshwater Biology 47: 777-798.

2 Carbon sources supporting large river food webs: A review of ecological theories and evidence from stable isotopes

2.1 Abstract

Quantifying the contributions of carbon sources that support food webs in large rivers is an important and growing field of ecological research with implications for future management and rehabilitation. Here I review theoretical concepts and recent empirical evidence that address carbon flow through aquatic food webs in large rivers. The literature reviewed focuses on studies using stable isotope analysis, which is a tested framework for identifying the origin of carbon sources that are assimilated by primary consumers and subsequently transferred through the food web to support higher consumers. Theoretical concepts addressing carbon flow in large river food webs have tended to stress the importance of organic matter originating from different sources, such as floodplains (Flood Pulse Concept), local riparian and aquatic primary producers (Riverine Productivity Model), or leakage from upstream processing of terrestrial organic matter (River Continuum Concept). Recent empirical evidence from a range of studies has highlighted the importance of autochthonous carbon, especially in the form of benthic algae and phytoplankton, to food webs in a variety of large rivers. However, some flexibility is apparent within food webs and several studies have identified a range of secondary carbon sources that can also be consistently important, depending on the temporal and spatial patterns of hydrogeomorphic conditions. The geographic spread of studies addressing carbon flow in large river food webs is steadily increasing, although long term data sets remain sparse. Despite this, opportunities exist to improve our understanding of historical changes in river food webs and to develop predictive models of future responses to environmental change through the use of museum collections and rehabilitation case-studies.

2.2 Introduction

Large rivers play an important role in human societies, providing drinking water, navigable networks for the movement of people and goods, and supporting food webs that sustain economically and culturally valuable fisheries (Allan & Flecker, 1993). Unsurprisingly, large rivers are also amongst the most regulated and altered ecosystems on Earth, with only 35 % of large river systems remaining unfragmented by dams or unaffected by hydrological regulation for flood control, hydro-electricity generation, irrigation or ship movement (Nilsson et al., 2005). Recent estimates indicate that aquatic habitats associated with 65 % of global river discharges are moderately to highly threatened (Vörösmarty et al., 2010). In addition, riverine ecosystems are threatened by species invasions, overharvesting, pollution and climate change (Allan & Flecker, 1993). In recent years, efforts to conserve and restore large river ecosystems have become the focus of a range of disciplines including hydrology, ecology, planning, engineering and management. In order to evaluate the effects of ongoing management activities and potential restoration measures on large river ecosystems, it is essential to have an understanding of the function and structure of riverine food webs and the sources of carbon that sustain productivity at higher trophic levels (Johnson et al., 1995).

Winemiller & Polis (1996) defined a food web as “a network of consumer-resource interactions among a group of organisms, populations, or aggregate trophic units” (see also Woodward & Hildrew, 2002). The most basic of interactions is that of consumption and assimilation into the tissues of other organisms, either through direct predation or through microbial and detrital loops (Winemiller & Polis, 1996; Thorp & Delong, 2002). Consumption can be measured by examining the stomach contents of consumers of interest, and this information can be used to identify direct interactions and classify consumers into functional groupings, e.g. detritivore, herbivore, planktivore, insectivore and piscivore (e.g. Fisher et al., 2001). However, the sole use of dietary analysis for food web studies can be confounded by consumed items being selectively assimilated, an overemphasis of numerically abundant items in the diet (Fry & Sherr, 1989), and by only giving a snapshot of what mobile organisms may be consuming across time and space (Ebner et al., 2009). Furthermore, partial digestion or damage to food items and the consumption of amorphous detritus can hamper accurate identification of consumed material (Fisher et al., 2001; Layman et al., 2005). Accordingly, stable isotope analysis is often used as an integrative technique, which can be used to support dietary analysis and describe a range of food web characteristics (Herwig et al., 2007).

Stable isotope analysis has been applied to investigate a wide range of aquatic ecosystem traits and processes, often using naturally occurring ratios of heavier to lighter carbon and nitrogen isotopes (usually presented as $\delta^{13}C$ and $\delta^{15}N$, respectively), to elucidate trophic position (Vander Zanden & Rasmussen, 1999; Post, 2002), food web interactions (Fisher et al., 2001), fish movements (Rasmussen et al., 2009), fish habitat use (Fry, 2002), seasonal food web patterns (Herwig et al., 2007), the effects of introduced species (Martinez et al., 2001), catchment geochemistry and land use (Chang et al., 2002; Jepsen & Winemiller, 2007; Winemiller et al., 2011), and other human impacts on aquatic ecosystems (Kohzu et al., 2009). One of the most important uses of stable isotope analysis is to identify and quantify patterns of carbon flow through food webs as stable isotopes provide a time integrated measure of energy flow and trophic interactions (Post, 2002). Carbon isotope ratios can be used to differentiate between sources of carbon and to track energy flow through the food web, as $\delta^{13}C$ changes little as a result of trophic transfer (usually < 1 ‰ at each trophic level) (Fry & Sherr, 1989; McCutchan et al., 2003). Nitrogen isotope ratios tend to reflect the number of transfers a carbon source has undertaken (trophic position) and can fractionate by c. 2–4 ‰ with each trophic transfer (Post, 2002; McCutchan et al., 2003). The use of multiple isotopes in unison can strengthen the discrimination of potential food sources, particularly where signatures of one isotope may overlap (France, 1997; Finlay, 2001). Where discrimination is possible, mixing models can be used to estimate feasible contributions of primary carbon sources to higher consumers. These models allow researchers to quantify carbon flow and ultimately determine the source or sources of carbon supporting secondary production. Linear mixing models such as IsoSource (Phillips & Gregg, 2003) have been employed regularly for this purpose, and although unique solutions arising from these models are generally limited to $n+1$ basal carbon sources (where n is the number of isotopes employed), a posteriori aggregations of ecologically similar resources can provide meaningful conclusions regarding resource use by consumers (Phillips et al., 2005). More recently, Bayesian mixing models such as SIAR (Parnell et al., 2010) and MixSiR (Moore & Semmens, 2008) have become available. A strength of these models is that variation associated with estimates of trophic fractionation and isotopic signatures of basal carbon resources, particularly those of aquatic primary producers which often vary in time and space (Boon & Bunn, 1994; Finlay et al., 1999; Hawden et al., 2010), can be incorporated to produce probability estimates of source contributions. Although several assumptions need to be made in order to interpret stable isotope ratios of consumers and to estimate contributions from carbon sources (e.g. regarding tissue turnover, food assimilation and trophic fractionation (see Gannes et al., 1997 and del Rio et al., 2009), when supported by concurrent observational data or detailed literature information they provide powerful tools for elucidating energy flow in food webs.

The logistical challenges of effectively sampling biological communities in large rivers, due to their inherent size, hydrogeomorphic complexity and geographical and temporal variation, mean that ecological knowledge of large rivers is still relatively limited compared with smaller wadeable streams (Sedell et al., 1989). Nevertheless, there have been significant advances in conceptualising pathways of carbon flow in large river ecosystems in recent years (see Thorp et al., 2008) and consequently, a number of studies have tested various large river food web theories in different parts of the world. The aim of this review is to relate recent findings on carbon sources supporting large river food webs to the relevant theoretical concepts accounting for carbon flow in large rivers. I first review knowledge underpinning the development of large river food web theory and then summarise the findings of studies that have tested these theories since publication of the Riverine Ecosystem Synthesis (Thorp et al., 2006). Several definitions exist as to what constitutes a 'large' river or river system. They include rivers of seventh order or greater based on the Strahler concept (Vannote et al., 1980; Johnson et al., 1995) and rivers with a virgin mean annual discharge of ≥ 350 $m^3 s^{-1}$ (Dynesius & Nilsson, 1994; Nilsson et al., 2005). For the purposes of this review, I used both of these definitions as a basis to select relevant studies. Although other techniques are also available for quantifying direct and indirect interactions in food webs, this review focuses on studies which have employed stable isotope analysis techniques, as they provide a tested and consistent framework for estimating the flow of carbon through food webs.

2.3 Spatial and temporal complexity in large rivers

Large rivers are dynamic, multi-dimensional ecosystems with longitudinal, lateral, vertical and temporal dimensions, that can occur as single or multi-branched channels etched into the landscape (Ward, 1989; Power et al., 1995; Thorp et al., 2008). From a lateral perspective, the fast-flowing main and secondary channel habitats can be supplemented by a mosaic of low-flow habitats (e.g. backwaters, side channels, lakes, bays, tributary confluences, lagoons, and littoral zones) whose physical and biological characteristics differ from each other in terms of hydrologic connectivity dictated by flow in the main channel, with subsequent implications for food webs (Schiemer & Hein, 2007; Thorp et al., 2008; Zeug & Winemiller, 2008; Roach et al., 2009a, b). The arrangement and frequency of occurrence of lateral habitats will be determined by the hydrogeomorphic nature of the river and its catchment (e.g. braided vs. canyon reaches, rain vs. snowmelt fed), and can be further influenced by anthropogenic regulation of the flow regime (e.g. dams) and floodplain extent (e.g. dykes). Low-flow lateral habitats can differ from those in the main channel by providing shelter from high current velocities, increased riparian inputs and shading, and temperature and turbidity gradients (Schiemer & Hein, 2007; Thorp et al., 2008). Contributing watercourses provide additional complexity to the riverscape. As well as structuring physical characteristics downstream, tributaries can provide important linkages with, and donate carbon sources from, distant habitats such as lakes, wetlands and headwater streams (Vannote et al., 1980; Kiffney et al., 2006; Rice et al., 2006; Rosales et al., 2007). Within the floodscape, variability of the fluvial regime results in the disconnection and reconnection of a range of lateral habitats such as side arms, billabongs, oxbow and other floodplain lakes, thereby resulting in the generation and dispersal of novel carbon sources (Amoros & Bornette, 2002).

The temporal pattern of interactions between the main channel and lateral habitats can also have significant implications for the relative abundance and importance of carbon sources, and for pathways of carbon flow to the river food web as a whole. Hydraulic retention zones can play an important role in nutrient processing and organic matter production at times of low connectivity with the main channel, providing carbon for food webs within these habitats and also to those downstream through export during connection phases (Schiemer & Hein, 2007; Preiner et al., 2008). As a result, conditions in these habitats can vary seasonally, resulting in temporal changes in the abundance and diversity of predator and prey species, food web structure and primary producers, which are often the carbon sources supporting riverine food chains (Fisher et al., 2001). Increased lateral complexity within the riverscape (including 'terrestrial' habitats such as islands and exposed sand bars) further increases the potential for interaction between the river and floodplain habitats, and can provide important resource subsidies and habitat for aquatic organisms during high flows (Junk et al., 1989; Benke, 2001; Górski et al., 2010). Temporarily inundated habitats can enhance recruitment of both main stem and floodplain fish species during floods and along with more semi-permanent features act as refugia during extreme events of flooding, drought and freezing (Sedell et al., 1990; Górski et al., 2010; Górski et al., 2011a).

2.4 Potential sources of carbon in riverine food-webs

Carbon can enter the food web through multiple pathways, including photosynthesis of atmospheric CO_2 (e.g. emergent aquatic and terrestrial C_3 and C_4 plants), as dissolved inorganic carbon utilised by suspended algae and attached biofilms, and from the processing of methane by chemoautotrophic biofilms. Primary producers then provide basal carbon/energy sources for fuelling food chains and more specifically for incorporation into metazoan consumer food webs.

Potential basal energy sources are often divided into two groups: autochthonous (those formed locally) and allochthonous (those originating from elsewhere). Allochthonous sources of carbon include:

- Processed organic matter from upstream sources, e.g. inputs of processed terrestrial leaf litter from headwater streams and tributary inputs (Vannote et al., 1980; Minshall et al., 1985).
- Terrestrial inputs derived from floodplain interactions (Junk et al., 1989; Tockner et al., 2000), or local riparian and littoral vegetation (Angradi, 1994; Burns & Walker, 2000; Huryn et al., 2001; Zeug & Winemiller, 2008).
- Marine-derived contributions from spawning migrations of anadromous fish (Hicks et al., 2005; Jardine et al., 2009; Syvaranta et al., 2009) and colonies of breeding marine birds, such as petrels (Harding et al., 2004).

- Aged inputs of millennial-aged organic carbon that has been stored in soils and sediments (Caraco et al., 2010), or methane from groundwater incorporated through methanotrophic bacteria (Trimmer et al., 2009).
- Anthropogenic sources, such as sewage inputs (deBruyn & Rasmussen, 2002; deBruyn et al., 2003) and carbon derived from drifting plankton discharged from impoundments, e.g. dams constructed for water reservoirs (Doi et al., 2008) or electricity generation (Angradi, 1994).

Autochthonous sources of carbon in large rivers are more restricted and are typically represented by (i) carbon generated from in-stream primary producers such as phytoplankton (Hamilton et al., 1992; Lewis et al., 2001; Thorp & Delong, 2002), benthic algae (Bunn et al., 2003; Hladyz et al., 2012), biofilms (Burns & Walker, 2000) and macrophytes (Hoeinghaus et al., 2007) and (ii) local algal and phytoplankton carbon sources generated within inundated floodplains and lakes (Delong et al., 2001). In-stream primary production is essentially regulated by the physical properties of the river and its catchment (e.g. discharge, channel form and gradient, fluvial chemistry, velocity, turbulence and turbidity) (Reynolds, 1996).

2.5 Large river carbon flow theory

Several different theories have been developed to account for carbon flow through large river food webs and to stimulate discussion of this topic and other key aspects of large river ecological function. Significant and widely tested models describing energy flow driving biotic communities in large rivers include the River Continuum Concept (Vannote et al., 1980), the Flood Pulse Concept (Junk et al., 1989) and the Riverine Productivity Model (Thorp & Delong, 1994). Each of these models focuses on a different dimension of the riverscape. The River Continuum Concept has a longitudinal perspective describing ecosystem processes from upstream to downstream, whereas the Flood Pulse Concept highlights the importance of energy transfer from lateral floodplains. In contrast, the Riverine Productivity Model emphasises carbon derived from within the river channel itself. More recently, the Riverine Ecosystem Synthesis (Thorp et al., 2006; Thorp et al., 2008) examined the origin and relative importance of potential carbon sources in fuelling riverine ecosystem processes. These and other concepts

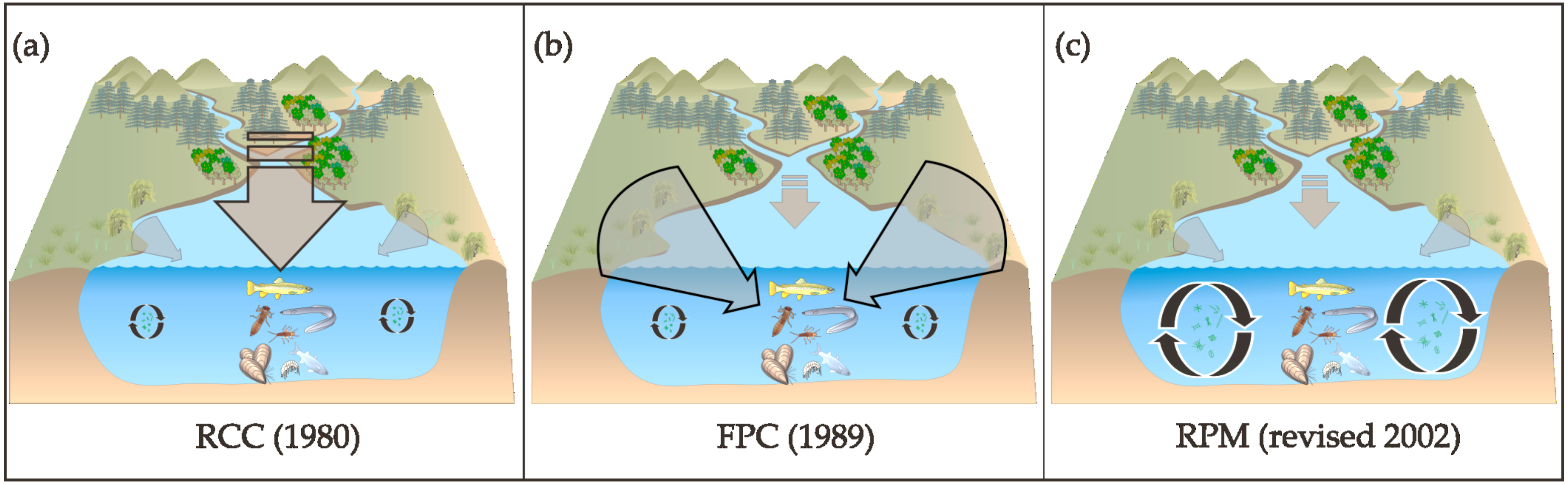


Figure 2.1: Hypothetical river illustrating dominant carbon sources to aquatic food webs as predicted by the three main conceptual models, (a) River Continuum Concept (RCC), (b) Flood Pulse Concept (FPC) and (c) revised Riverine Productivity Model (RPM). Brown arrows represent fine processed organic matter leaked from upstream food webs, grey arrows represent terrestrial floodplain and riparian inputs of carbon and black circular arrows represent autochthonous carbon generated by in-stream algal production. This figure was constructed using images courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

relevant to energy flow in large rivers are discussed in more detail below.

2.5.1 Upstream inputs

In the River Continuum Concept, Vannote et al. (1980) proposed that natural river systems could be viewed as a continuous and predictable gradient from headwaters to their mouths. Variables considered included water temperature, river flow, substrate, riparian influence and the origin of carbon for consumers. A key component of this concept is that biological processes can be predicted by their longitudinal position within the river network. In terms of energy flow in large rivers (> 6th order) the River Continuum Concept proposes that the main source of carbon for organisms will be fine processed organic matter transported from upstream (Fig. 2.1a). Coarse particulate organic matter originating in river headwaters decreases in abundance with increasing distance downstream. In contrast, fine particulate matter generally increases as a result of invertebrate and microbial processing, although tributaries may provide localised inputs of coarse particulate organic matter. Community structure and composition are also predicted to change along a longitudinal gradient in response to the decreasing ratio of coarse particulate organic matter to fine particulate organic matter availability, e.g. dominant invertebrate functional groups are predicted to change from collectors and shredders in headwater streams, to collectors and grazers in the mid-order rivers, to predominantly collectors in large, high-order rivers (Vannote et al., 1980). Local contributions from riparian vegetation and autochthonous primary production are considered less important in large rivers due to their width and turbidity. The River Continuum Concept was further developed by Minshall et al. (1985) to address a broader range of spatial and temporal scales, acknowledging that direct terrestrial inputs from floodplain habitats could be important in some rivers and that available carbon resources could differ with season to provide a varied food base for consumers. For large rivers with seasonally inundated floodplains, Sedell et al. (1989) adapted the longitudinal patterns originally stipulated in the River Continuum Concept to account for floodplain carbon contributions, as addressed by the Flood Pulse Concept described below.

2.5.2 Floodplain inputs

The Flood Pulse Concept proposes that in large rivers with unaltered floodplains and predictable, seasonal flood pulses (e.g. the tropics), aquatic food webs derive a significant amount of their organic carbon from terrestrial sources as a result of floods (Junk et al., 1989) (Fig. 2.1b). In contrast to the River Continuum Concept, this concept asserts that organic material derived during inundation of the floodplain is of higher nutritional value to consumers and easier to assimilate than carbon that had already been processed upstream. The main channel was proposed to act primarily as a transport mechanism for water and suspended matter, whereas the majority of primary and secondary production occurred on the floodplain (Junk et al., 1989; Junk & Wantzen, 2004). In some temperate large rivers, however, many fish species are dependent on fluvial environments and reside in the main channel on a permanent or semi-permanent basis (Dettmers et al., 2001; Galat & Zweimüller, 2001). Importantly, the Flood Pulse Concept highlights the lateral aspect of lowland alluvial rivers and their floodplains, emphasising that they are both parts of the same dynamic system, and that in larger rivers, significant carbon resources can be derived through terrestrial-aquatic exchange mediated by high flows. Although the Flood Pulse Concept was initially restricted to rivers with predictable seasonal flood pulses, Tockner et al. (2000) added the ‘flow pulse’ to account for within-bank expansion and contraction of river flow and associated temperature cycles. For example, flow pulses may increase or decrease riverscape habitat heterogeneity and induce an intermediate degree of connectivity with lateral habitats such as side arms, transporting organic matter and stimulating autochthonous production, depending on the expansion or contraction phase of the pulse. As such, within channel flow pulses may enhance the overall productivity of the floodplain, which in turn can act as both a source and a sink for materials (Tockner et al., 2000). The relative importance of allochthonous and autochthonous organic carbon derived from the floodplain can also vary with the size of the associated river, the extent of the floodplain itself and factors such as water temperature, the duration and volume of the flood or flow pulse, concentrations of transported nutrients and solids (both organic and inorganic) and the origin of flood waters (Tockner et al., 2000).

2.5.3 Internal carbon generation and inshore processing

The Riverine Productivity Model (Thorp & Delong, 1994) contends that previous concepts have underestimated the importance of autochthonous production and local organic inputs from the riparian zone in food webs of large rivers, particularly those with constricted channels and unpredictable flood pulses. Thus, according to this model, several of the predictions of the River Continuum Concept and Flood Pulse Concept are likely to be applicable only in a limited number of situations (e.g. small to medium sized rivers and rivers with predictable seasonal flooding). The original Riverine Productivity Model placed emphasis on the role of carbon from locally generated autochthonous algal and riparian carbon sources, as these were believed to be easier for organisms to assimilate (e.g. more labile), as opposed to processed organic matter transported from upstream, which is often of little nutritional value (Thorp & Delong, 1994). It was proposed that terrestrial carbon derived during predictable seasonal floods, as proposed in the Flood Pulse Concept, may not be applicable to many large rivers, particularly those with aseasonal or cold-water flow patterns (Thorp & Delong, 1994).

Support for the Riverine Productivity Model was provided by a comparison of carbon flow and food web structure between floodplain reaches of the Missouri and Mississippi Rivers and the constrained Ohio River, which were all subjected to a large, unpredicted flood event (Delong et al., 2001). No apparent differences were observed in terms of primary carbon sources, although the flood may have enhanced the productivity of the riverine food web by increasing the availability of important autochthonous carbon sources, e.g., algal production in flooded areas rather than terrestrial carbon released from the floodplain (Delong et al., 2001). Following further research that highlighted the importance of sestonic and benthic algae to riverine food webs, the Riverine Productivity Model was revised (Thorp et al., 1998; Thorp & Delong, 2002). These revisions expanded the applicability of the Riverine Productivity Model to a greater range of channel types and placed greater emphasis on the theoretical importance of autochthonous primary production to overall metazoan productivity through an algal-grazer food pathway, although local riparian inputs are likely to be seasonally important to some species dwelling in littoral habitats (Thorp & Delong, 2002) (Fig. 2.1c). Further support for the role of autochthonous carbon in large river food webs comes from studies of tropical and dry-land Australian rivers. Bunn et al. (2003)

demonstrated that despite the high availability of terrestrial organic matter, a band of filamentous algae provided the major source of carbon to fish and invertebrates in floodplain water bodies (Bunn et al., 2003). Autochthonous algal production is also considered to be the main carbon source fuelling fish production and food webs in tropical river systems of northern Australia (Douglas et al., 2005) and Papua New Guinea (Bunn et al., 1999).

Although it does not describe patterns of ecosystem structure and energy flow in large rivers over large spatial scales, the Inshore Retention Concept (Schiemer et al., 2001a) is important when considering the locations of carbon flow and processing in large rivers. As discussed earlier, lateral habitats are important to many aquatic organisms at base and peak flows, providing refuge from the greater water velocities in the main channel and increasing water retention for processing of material at low flows (Schiemer & Hein, 2007). Depending on the size, longevity of the retention zone, and the duration of water retention within it (varying in scale from seconds and minutes to days and weeks), retention zones can have a high abundance and diversity of algal, invertebrate and fish species (Schiemer et al., 2001a; Schiemer & Hein, 2007). Phytoplankton communities are often enhanced by the slower flow of backwaters, benefiting from main channel nutrient inputs and increased light penetration. As the phytoplankton communities undergo a successional process, energy is transferred to other parts of the food web, either via direct consumption by zooplankton, senescence, or by export back to the main channel (Schiemer et al., 2001a). Smaller retention zones created by changes in shoreline configuration reduce current velocities to levels that benefit in-stream organisms (Schiemer et al., 2001a). Larger retention zones (e.g. backwaters and tributary junctions) provide valuable nursery and foraging habitats for fish (Schiemer et al., 2001a, b; Schiemer & Hein, 2007). These zones are important for main channel ecological functioning and in structurally complex rivers are probably as important as the main channel in terms of supporting productivity (Thorp & Delong 2002).

2.5.4 Inputs from tributaries

Other concepts, such as the Network Dynamics Hypothesis (Benda et al., 2004), have focussed on physical hydrogeomorphic nature of river networks at a landscape scale, providing a framework based on physical heterogeneity and environmental stochasticity as opposed to a mean state within river networks. Important nodes in the river network can be created by connecting tributaries, which can influence water volume and quality, sediment inputs, bed particle size and slope (Rice et al., 2001, 2006), and in turn may create areas of high habitat complexity, biological diversity and productivity (Benda et al., 2004). For example, woody debris, nitrogen, phosphorus, algal biomass, substrate heterogeneity and consumer abundance are often higher within and downstream of tributary junctions (Benda et al., 2004; Kiffney et al., 2006). The degree to which tributaries have an impact on the ecology of main stems can vary with the size and hydrogeomorphology of the two (or more) adjoining rivers (Poole, 2002; Benda et al., 2004). Tributary junctions and confluence zones provide shelter for organisms from high flows in the main stem as well as additional food resources for certain fish and invertebrates, making them important juvenile rearing areas for many species. Tributary junctions typically support a greater diversity of macroinvertebrates and fish species than the main channel, thus contributing to the overall biodiversity of large rivers (Fernandes et al., 2004; Collier & Lill, 2008). Therefore, tributary confluences can be potential hotspots for biological diversity, production, and food web carbon exchange in large river systems.

2.6 Recent developments

The Riverine Ecosystem Synthesis of Thorp et al. (2006), is based around the widely held principles that lotic ecosystems are four dimensional (longitudinal, lateral, vertical, temporal) and multi-threaded facets of the landscape. The Riverine Ecosystem Synthesis has sought to build on previous theories, using empirical evidence that has indicated that certain aspects of them may be applicable in only a limited number of situations (Thorp et al., 2006, 2008). By bringing together elements of ecology, fluvial geomorphology, a terrestrial landscape patch dynamic model, and aspects of other aquatic models, the Riverine Ecosystem Synthesis aims to describe the biocomplexity of rivers and provide a framework for understanding the broad and often complex patterns of temporal, longitudinal and lateral dimensions of river networks that affect trophic complexity and carbon flow (Thorp et al., 2006, 2008). Fundamental to the Riverine Ecosystem Synthesis is the concept of the functional process zone, which can be loosely defined as a fluvial geomorphic unit of scale between a valley and a reach (Thorp et al., 2008). The Riverine Ecosystem Synthesis regards rivers as arrangements of these large hydrogeomorphic patches (e.g. constrained, anabranching, distributary and meandering functional process zones) formed by catchment geomorphology and climate, characteristics that may recur longitudinally along the river network. The type and frequency of riverine habitats can be linked back to the hydrogeomorphic characteristics of the zone in which they occur (Thorp et al., 2008). The distribution, frequency and scale of retention zones, for example, will be determined by the geomorphic and hydrological characters of the functional process zones in which they occur.

The Riverine Ecosystem Synthesis proposes 17 model tenets or hypotheses regarding the biocomplexity of riverine ecosystems. In terms of carbon sources and energy flow supporting large river food webs, Model Tenet 10 of the Riverine Ecosystem Synthesis states that primary production within large rivers will depend on the type of functional process zone and its hydrogeomorphic characteristics (e.g. hydraulic retention, main stem connectivity, geomorphic complexity and potential for lateral interaction). On a mean annual basis, however, and in keeping with the Riverine Productivity Model, autotrophy mediated by an algal-grazer food web should provide the trophic basis for metazoan productivity as a whole, although allochthonous organic matter could still be important during some seasons and for some species (Model Tenet 11). Although acknowledging that allochthonous carbon from floodplain interactions can be important, the Riverine Ecosystem Synthesis hypothesises that most carbon derived from floodplain interactions is dominated by autochthonous algal production, as opposed to decaying terrestrial matter (Model Tenet 12) (Thorp et al., 2008).

2.7 Human modification

Human modification of flow regimes, sediment transport and floodplain interactions can change the spatial and seasonal availability and abundance of certain basal carbon sources, and may reduce the ability of food webs to utilise resources previously important for functions such as reproduction (Thorp et al., 2008). Given that a large proportion of the world’s river systems have been altered in some way by human development (Nilsson et al., 2005), conceptual predictions of carbon sources supporting food webs in ‘natural’ large river systems are difficult to test, although testable hypotheses have been framed to account for this. For example, Ward & Stanford (1983) adapted the River Continuum Concept by introducing the Serial Discontinuity Concept, to account for rivers whose flow is artificially regulated by the construction of dams that form large, deep reservoirs. According to the Serial Discontinuity Concept, dams create discontinuities along the river continuum, causing upstream and downstream shifts in biotic and abiotic processes (Ward & Stanford, 1983). The relative effect on river food webs will also reflect the position and number of dams present in a river system. In certain circumstances, the creation of lentic habitats above dams will increase phytoplankton production, allowing export of a potentially novel planktonic carbon source to downstream food webs as water is discharged (Angradi, 1994; Doi et al., 2008). In braided floodplain rivers, a dampening of flood pulses and increased flow stability could potentially lead to greater subsidies of terrestrial coarse particulate organic matter from riparian vegetation as a result of increased bank stability and tree colonisation (Ward & Stanford, 1995). However, where riparian contributions are linked to floodplain inundation, dampening of flow pulses may lead to no change in allochthonous contributions (Kennedy & Ralston, 2012). The opposite may occur in other types of river systems where decreased sediment loads as a result of settling in dams can lead to increased river bed incision, which reduces connectivity with riparian and lateral habitats (Amoros & Bornette, 2002; Górski et al., 2011b).

Human modifications to large rivers are also likely to change the hydrogeomorphic nature of functional process zones. Flow modifications can lead to the loss of floodplains, shift the timing of flow pulses and reduce the ability of rivers to reshape their structural complexity. In addition, alterations to catchments can change the nature of riparian and water quality characteristics, potentially altering the functional characteristics of functional process zones (Thorp et al., 2006, 2008).

2.8 Recent empirical evidence from large river food webs

Much of our knowledge of carbon flow in large river food webs has come from studies of North and South American rivers, with significant contributions from detailed studies of the Mississippi River (Delong, 2010). Since the publication of the Riverine Ecosystem Synthesis, several studies have tested theories relating to carbon flow in large rivers across a range of climates, hydrologic regimes, watershed geochemistry and anthropogenic impacts, as well as at greater temporal and spatial scales (Table 2.1). Collectively, these studies are helping to test the predictions of the above concepts at a near global scale. A detailed investigation by Delong & Thorp (2006) addressed the composition of transported organic matter in the upper Mississippi River, USA. By separating algal and detrital fractions of transported organic matter, they concluded that the majority of carbon moving from primary to secondary consumers originated from algal sources. Thus, Delong & Thorp (2006) concluded that, in line with the revised Riverine Productivity Model, autochthonous carbon was the major energy source for metazoan food webs in the main channel. They did identify, however, that detrital carbon could be important for a small number of consumers, and stressed the need for future studies to account for temporal variation in the abundance of energy sources and potential seasonal differences in their relative importance to river food webs (Delong & Thorp, 2006). In contrast, Zeug & Winemiller (2008), in a study of the Brazos River, Texas, during a period of high connectivity with oxbow lakes, provided support for the Flood Pulse Concept as C_3 plants contributed significant amounts of terrestrial carbon to both main channel and oxbow lake food webs. Although algal carbon was important to invertebrates and small fish (< 100 mm in length) in oxbow lakes, it was not considered to be important in the main channel.

The spatial context of a river system and its watershed can have a significant effect on the carbon sources and pathways dominating the food web. For example, Hoeinghaus et al. (2007) examined patterns of carbon flow in 10 large river food webs of the upper Paraná River, Brazil, to test hypotheses proposed by the River Continuum Concept, Riverine Productivity Model and Flood Pulse Concept. Overall they concluded that C_3 macrophytes and phytoplankton were the dominant sources of carbon supporting the food webs, although relative contributions varied between landscape type and channel gradient. For example, C_3 macrophytes were the dominant source in low-gradient river food webs, contributing as much as 80 % of carbon assimilated by secondary consumers, whereas phytoplankton was the dominant carbon source within and downstream of reservoirs. Additionally, in high-gradient rivers, although C_3 macrophytes and phytoplankton were still important carbon sources, the importance of C_4 plants and filamentous algae increased by around 40 %. From these results they concluded that the predictions of the Flood Pulse Concept were most appropriate for describing carbon sources and flow in food webs of low-gradient rivers, whereas the Riverine Productivity Model provided the best representation for food webs in high-gradient rivers, reservoirs and downstream of dams (Hoeinghaus et al., 2007).

Jepsen & Winemiller (2007) investigated rivers in Venezuela and found little evidence for terrestrial C_4 grasses being important carbon sources, while a combination of algae and C_3 macrophytes provided the major carbon sources to the sampled food webs. Although isotopic signatures of these latter potential sources were broadly overlapping, several benthivorous grazers did align more closely with algae. They also concluded that basin watershed geochemistry can play a major role in influencing the availability and isotopic composition of basal resources. Herwig et al. (2007) investigated spatial and temporal patterns in food web structure in the upper Mississippi River and, despite some difficulties in clearly differentiating the stable isotope signatures of carbon sources within and between river habitats, concluded that both terrestrial C_3 plant material and in-stream algal production were important sources of carbon to metazoan consumers. Furthermore, they identified a potential seasonal shift in the carbon sources of filter feeding primary consumers towards algal carbon during spring and autumn. Their results also identified that larger consumers may display high levels of trophic omnivory and diet flexibility in large river food webs.

Table 2.1. Summary of geographic features and carbon sources supporting food webs from recent studies of large rivers included in this review. Abbreviations: coarse particulate organic matter (CPOM), Revised Riverine Productivity Model (RPM), Flood Pulse Concept.

Publication	River system	Country	Climate	River type/s	Habitat/s sampled	Dominant carbon sources	Secondary carbon sources	Support for aspects of
Delong & Thorp (2006)	Upper Mississippi River	USA	Temperate	Floodplain	Main channel	Autochthonous transported algal matter		RPM
Herwig et al. (2007)	Upper Mississippi River	USA	Temperate	Floodplain and artificially constrained	Main channel	Benthic algae and phytoplankton	C_3 riparian plants	RPM, FPC, RCC
Hoeinghaus et al. (2007)	Upper Paraná River and tributaries	Brazil	Neotropical	High gradient	Main channel	Phytoplankton and C_3 aquatic macrophytes	Benthic algae, C_3 and C_4 riparian plants	RPM
				Below reservoirs	Main channel	Phytoplankton and C_3 aquatic macrophytes		RPM
				Low gradient	Main channel	C_3 aquatic macrophytes	Phytoplankton (seston)	FPC
Jepsen & Winemiller (2007)	Orinoco River tributaries	Venezuela	Neotropical	Floodplain	Connected lagoons and channel shoreline	Attached algae	C_3 aquatic macrophytes	RPM

Table 2.1 (continued).

Publication	River system	Country	Climate	River type/s	Habitat/s sampled	Dominant carbon sources	Secondary carbon sources	Support for aspects of
Zeug & Winemiller (2008)	Brazos River	USA	Temperate to sub-tropical	Meandering floodplain	Main channel	C_3 riparian plants		FPC
					Oxbow lakes	C_3 riparian plants	Autochthonous algal matter	FPC
Leigh et al. (2010)	Flinders and Gregory Rivers	Australia	Wet-dry tropics	Floodplain	Main channel	Phytoplankton and benthic algae (biofilm)		RPM
Medeiros & Arthington (2010)	Macintyre River	Australia	Dry-land	Floodplain	Floodplain lagoons	Benthic algae and phytoplankton	Riparian plants (CPOM)	RPM
Hunt et al. (2011)	Mitchell River	Australia	Wet-dry tropics	Floodplain	Main channel	Benthic algae	Unidentified floodplain sources	RPM
Reid et al. (2011)	Cooper Creek	Australia	Dry-land	Floodplain	Main channel and billabongs	Benthic algae		RPM
Chapter 4	Waikato River	New Zealand	Temperate	Constrained and unconstrained	Main channel	Benthic algae	C_3 aquatic and riparian plants	RPM

Large Australian dry-land rivers present a potentially very different environment to those described above, and recent evidence from floodplain lagoons of the Macinytre River, a tributary of the Murray-Darling River system, has indicated a strong dependence of fish on autochthonous carbon derived from benthic algae and phytoplankton consumed by zooplankton (Medeiros & Arthington, 2010). However, local riparian inputs were also of some importance in the form of coarse particulate organic matter, leading Medeiros & Arthington (2010) to support the Riverine Productivity Model. The hydrological connectivity of floodplain water bodies can influence the relative importance of basal carbon sources to the food web, with benthic algae being of greater importance in billabongs with higher connectivity to the main channel of the Macintyre River (Reid et al., 2011). Further, investigation into the role of the floodplain of Cooper Creek, which flows into Lake Eyre, revealed that flooding played a significant role in lateral exchanges of carbon (Burford et al., 2008). Benthic algal carbon production in flooded areas also greatly exceeded values recorded previously from permanent waterholes in the same river system. Interestingly, the authors identified that the mortality of fish trapped in waterholes following receding of flood waters provided a carbon pool for subsequent benthic algal production (Burford et al., 2008). Leigh et al. (2010) found that in two rivers of northern Australia's wet-dry tropics, the Flinders and Gregory systems, autochthonous carbon in the form of biofilms and phytoplankton (seston) accounted for over half of the carbon assimilated by macroinvertebrates. In addition, a range of consumers also assimilated local riparian detritus, demonstrating flexibility within the food web to exploit a range of carbon sources through generalist feeding strategies (Leigh et al., 2010). Further evidence from the Mitchell River also indicated the importance of benthic algae as a carbon source for primary and secondary benthic consumers collected from the main channel during the dry season (Hunt et al., 2011). However, more mobile secondary consumers such as fish and large invertebrates had $\delta^{13}C$ signatures that reflected an unidentified external carbon source, which the authors concluded was probably sourced from the Mitchell River floodplain during wet season inundation (Hunt et al., 2011). My own work on the lower Waikato River, a temperate floodplain river in New Zealand, also suggests that benthic algae are likely to be the dominant carbon sources supporting aquatic consumers, and that, as with several of the above studies, contributions from C_3 aquatic and riparian plants are also likely to be important for some consumers during certain seasons (authors' unpublished data).

On the basis of recent work using stable isotope analysis to quantify carbon flow in large river food webs, it would appear that autochthonous sources of carbon in the form of aquatic algae, and to a lesser extent phytoplankton and aquatic macrophytes, provide the dominant carbon sources fuelling large river food webs (Table 2.1, Fig. 2.2). With this in mind, aspects of the Riverine Productivity Model are most commonly supported by recent literature from a range of rivers (Table 2.1). Several of the recent studies reviewed above have pointed out, however, that allochthonous carbon sources can also be important, under certain conditions, in certain habitats (e.g. floodplain water bodies) and for selected consumers. Several studies have also supported the Flood Pulse Concept under certain conditions and in certain riverine habitats. Aspects of each concept could hold true depending on when during flow and climatic cycles studies are undertaken, as has been observed for fish productivity in temperate Australian floodplain rivers (Tonkin et al., 2011).

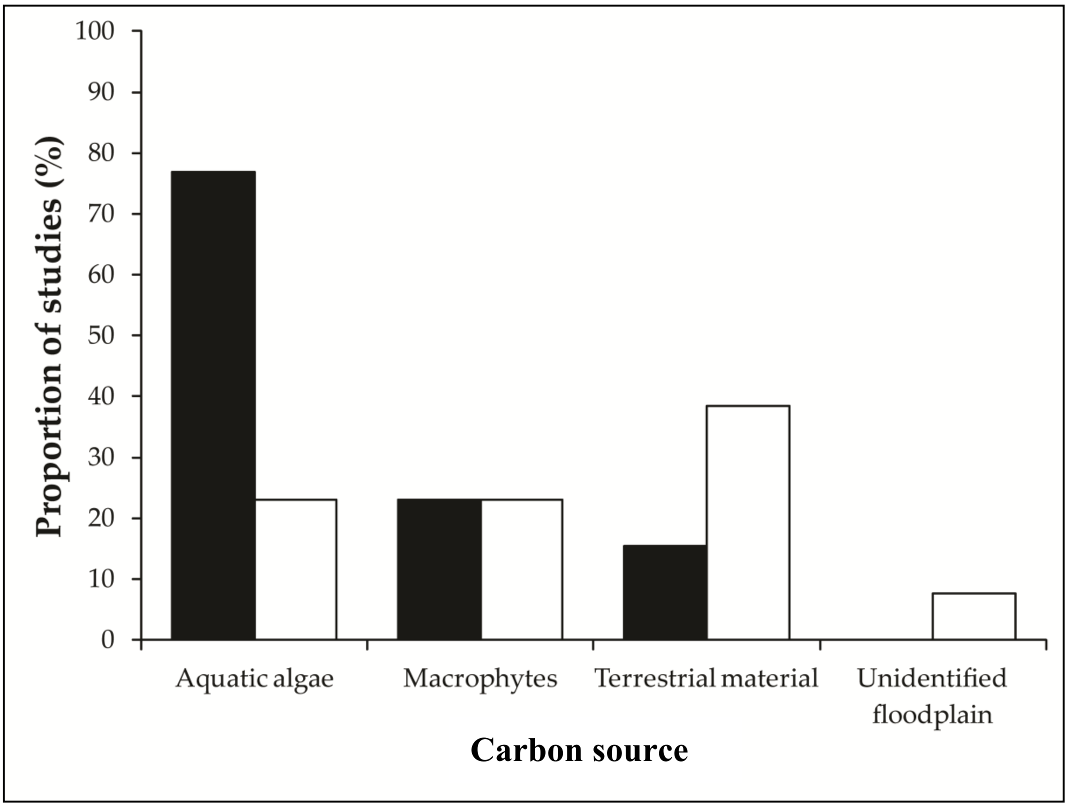


Figure 2.2. Percentage of reviewed studies (n = 13), that identify primary (closed bars) and secondary (open bars) sources of carbon to large river food webs. Note, as some studies identify more than one primary carbon source and others no secondary source, the bars do not sum to 100 %.

Clearly, carbon flow in large river food webs is context dependent, both temporally in terms of flow variability, and spatially in relation to channel characteristics and lateral habitat complexity. Accordingly, the concept of functional process zones (Thorp et al., 2006, 2008) provides a helpful framework for incorporating riverscape heterogeneity into food web models. As addressed in the Riverine Ecosystem Synthesis, carbon sources supporting food webs in large river systems, although predominantly autochthonous in nature (Model Tenet 11), can be influenced by the hydrogeomorphic nature of the river unit or functional process zone (Model Tenet 10). A large proportion of the reviewed studies published since 2005 identify important secondary carbon sources (Table 2.1, Fig. 2.2). The availability, quality and uptake of these secondary carbon sources can vary spatially and temporally within river systems and can have significant effects on energy flow in aquatic food webs (Marcarelli, et al., 2011). Therefore, some flexibility in the utilisation of secondary carbon sources in food webs is likely to be important across a range of flow regimes and lateral complexities in large rivers.

2.9 Future prospects

Isotopes of elements other than carbon and nitrogen can also be employed to study aquatic food webs (Michener & Lajtha, 2007). In some situations alternative isotopes can more clearly distinguish basal carbon resources of different origin (e.g. marine, floodplain, riverine and riparian ecotypes). An increasing number of studies has begun to demonstrate subsidies to stream food webs from riparian vegetation using hydrogen isotopes (e.g. Doucett et al., 2007) and from floodplains to riverine food webs using sulphur isotopes (e.g. Jardine et al., 2011). Furthermore, studies that employ multiple consumer tissue types have the potential to identify carbon contributions over shorter timescales and during important life history phases of organisms such as fish. Using sulphur and carbon isotopes, and muscle, liver and gonadal tissues, Jardine et al. (2011) demonstrated that floodplain food sources were important for short term resource pulses to large fish species as well as providing the energy source for reproductive tissues. Furthermore, studies of fish in temperate lakes have demonstrated that isotopic signatures of liver and muscle tissues respond differently to temporal variation in the signatures of food sources; as liver tissue turns over more rapidly, it tends to represent shorter term changes than white muscle tissue, which tends to reflect assimilation of carbon over extended periods of growth (Perga & Gerdeaux, 2005). When applied alongside traditional dietary analysis and stable isotope techniques, other molecular techniques, such as genetic barcoding of stomach contents (e.g. Hardy et al., 2010) and analysis of fatty acid profiles (e.g. Van den Meersche et al., 2009), may also prove fruitful for better quantifying trophic interactions in large river food webs. Non-lethal sampling methods such as fin clips (e.g. Andvik et al., 2010) could also prove a viable means of assessing temporal changes in isotopic signatures of fish consumers and subsequently carbon flow. Thus, the same individuals may be sampled more than once over a period of time and may enable the identification of food web responses to river rehabilitation measures.

While the accumulation of long-term stable isotope and food web data sets in newly researched rivers will take some time to elucidate critical processes, samples from long-term and museum collections provide a promising avenue for further research on riverine food webs (see Delong & Thorp, 2009). Such collections have been used in lakes to establish long-term changes in isotopic signatures (Perga & Gerdeaux, 2003; Solomon et al., 2008), to estimate historical changes in food web structure (Schmidt et al., 2009) and to identify priorities for food web restoration (Vander Zanden et al., 2003). Where appropriate material has been collected and preserved, such approaches could enable managers and scientists to plan for and predict possible outcomes of future rehabilitation and management decisions, as well as potential impacts of proposed developments, climate change or species introductions. Globally, much effort is being directed at the rehabilitation of rivers and their floodplains, providing opportunities to study aquatic food webs pre- and post-rehabilitation. Studies that quantify carbon flow through aquatic food webs before and after dam removal or floodplain habitat reconnection, for example, could provide valuable insights into how food webs respond to changes in the availability of particular carbon sources resulting from the restoration of more natural flow and floodplain inundation cycles.

Although the geographical coverage of studies has increased in recent years to include a range of continents, types of geochemistry and climatic regimes, the temporal coverage of studies is still generally limited to a single season or annual cycle. In large river systems that have infrequent large-scale flooding, such as Australian dry-land rivers where there may be many years between flood events, food webs may be shaped over periods longer than annual cycles, and important interactions may not be easily identified through stable isotope analysis. Studies that incorporate data collected over extended time periods (potentially up to decades), coupled with studies carried out at shorter time scales, which address hydrogeomorphic units within a river system, will be particularly valuable in unravelling carbon flow in large river food webs. Moreover, restoration initiatives focused on restoring hydrologic connectivity between rivers and their floodplains or other floodscape habitats should allow for the fact that in some cases, changes in the food web structure and carbon flow of the river ecosystem as a whole may take several years to become discernible.

2.10 References

Allan, J. D. & A. S. Flecker, 1993. Biodiversity conservation in running waters. Bioscience 43: 32-43.

Amoros, C. & G. Bornette, 2002. Connectivity and biocomplexity in waterbodies of riverine floodplains. Freshwater Biology 47: 761-776.

Andvik, R. T., J. A. VanDeHey, M. J. Fincel, W. E. French, K. N. Bertrand, S. R. Chipps, R. A. Klumb & B. D. S. Graeb, 2010. Application of non-lethal stable isotope analysis to assess feeding patterns of juvenile pallid sturgeon Scaphirhynchus albus: a comparison of tissue types and sample preservation methods. Journal of Applied Ichthyology 26: 831-835.

Angradi, T. R., 1994. Trophic linkages in the lower Colorado River - Multiple stable-isotope evidence. Journal of the North American Benthological Society 13: 479-495.

Benda, L., N. L. Poff, D. Miller, T. Dunne, G. Reeves, G. Pess & M. Pollock, 2004. The network dynamic hypothesis: how channel networks structure riverine habitats. Bioscience 54: 413-427.

Benke, A. C., 2001. Importance of Flood Regime to Invertebrate Habitat in an Unregulated River-Floodplain Ecosystem. Journal of the North American Benthological Society 20: 225.

Boon, P. I. & S. E. Bunn, 1994. Variations in the stable isotope composition of aquatic plants and their implications for food web analysis. Aquatic botany 48: 99-108.

Bunn, S. E., A. W. Storey & C. Tenakenai, 1999. Energy sources supporting Fly River fish communities. Unpublished report to Ok Tedi Mining Ltd. http: //oktedi.com/news-and-reports/reports/environmental/biology. Accessed November 2011.

Bunn, S. E., P. M. Davies & M. Winning, 2003. Sources of organic carbon supporting the food web of an arid zone floodplain river. Freshwater Biology 48: 619-635.

Burford, M. A., A. J. Cook, C. S. Fellows, S. R. Balcombe & S. E. Bunn, 2008. Sources of carbon fuelling production in an arid floodplain river. Marine and Freshwater Research 59: 224-234.

Burns, A. & K. F. Walker, 2000. Biofilms as food for decapods (Atyidae, Palaemonidae) in the River Murray, South Australia. Hydrobiologia 437: 83-90.

Caraco, N., J. E. Bauer, J. J. Cole, S. Petsch & P. Raymond, 2010. Millenial-aged organic carbon subsidies to a modern river food web. Ecology 91: 2385-2393.

Chang, C. C. Y., C. Kendall, S. R. Silva, W. A. Battaglin & D. H. Campbell, 2002. Nitrate stable isotopes: tools for determining nitrate sources among different land uses in the Mississippi River Basin. Canadian Journal of Fisheries and Aquatic Sciences 59: 1874-1885.

Collier, K. J. & A. Lill, 2008. Spatial patterns in the composition of shallow-water macroinvertebrate communities of a large New Zealand river. New Zealand Journal of Marine and Freshwater Research 42: 129-141.

deBruyn, A. M. H. & J. B. Rasmussen, 2002. Quantifying assimilation of sewage-derived organic matter by riverine benthos. Ecological Applications 12: 511-520.

deBruyn, A. M. H., D. J. Marcogliese & J. B. Rasmussen, 2003. The role of sewage in a large river food web. Canadian Journal of Fisheries and Aquatic Sciences 60: 1332-1344.

del Rio, C. M., N. Wolf, S. A. Carleton & L. Z. Gannes, 2009. Isotopic ecology ten years after a call for more laboratory experiments. Biological Reviews 84: 91-111.

Delong, M. D., 2010. Food webs and the Upper Mississippi River: contributions to our understanding of ecosystem function in large rivers. Hydrobiologia 640: 89-101.

Delong, M. D. & J. H. Thorp, 2006. Significance of instream autotrophs in trophic dynamics of the Upper Mississippi River. Oecologia 147: 76-85.

Delong, M. D. & J. H. Thorp, 2009. Mollusc shell periostracum as an alternative to tissue in isotopic studies. Limnology and Oceanography-Methods 7: 436-441.

Delong, M. D., J. H. Thorp, K. S. Greenwood & M. C. Miller, 2001. Responses of consumers and food resources to a high magnitude, unpredicted flood in the upper Mississippi River basin. Regulated Rivers-Research & Management 17: 217-234.

Dettmers, J. M., D. H. Wahl, D. A. Soluk & S. Gutreuter, 2001. Life in the fast lane: fish and foodweb structure in the main channel of large rivers. Journal of the North American Benthological Society 20: 255-265.

Doi, H., K. H. Chang, T. Ando, H. Imai, S. Nakano, A. Kajimoto & I. Katano, 2008. Drifting plankton from a reservoir subsidize downstream food webs and alter community structure. Oecologia 156: 363-371.

Doucett, R. R., J. C. Marks, D. W. Blinn, M. Caron & B. A. Hungate, 2007. Measuring terrestrial subsidies to aquatic food webs using stable isotopes of hydrogen. Ecology 88: 1587-1592.

Douglas, M. M., S. E. Bunn & P. M. Davies, 2005. River and wetland food webs in Australia's wet-dry tropics: general principles and implications for management. Marine and Freshwater Research 56: 329-342.

Dynesius, M. & C. Nilsson, 1994. Fragmentation and flow regulation of river systems in the northern third of the world. Science 266: 753-762.

Ebner, B., R. McAllister & P. Suter, 2009. Effects of sample size on numerical estimates of diel prey consumption in a fish population. New Zealand Journal of Marine and Freshwater Research 43: 579-590.

Fernandes, C. C., J. L. Podos & J. G. Lundberg, 2004. Amazonian ecology: Tributaries enhance the diversity of electric fishes. Science 305: 1960-1962.

Finlay, J. C., 2001. Stable-carbon-isotope ratios of river biota: Implications for energy flow in lotic food webs. Ecology 82: 1052-1064.

Finlay, J. C., M. E. Power & G. Cabana, 1999. Effects of water velocity on algal carbon isotope ratios: Implications for river food web studies. Limnology and Oceanography 44: 1198-1203.

Fisher, S. J., M. L. Brown & D. W. Willis, 2001. Temporal food web variability in an upper Missouri River backwater: energy origination points and transfer mechanisms. Ecology of Freshwater Fish 10: 154-167.

France, R. L., 1997. Stable carbon and nitrogen isotopic evidence for ecotonal coupling between boreal forests and fishes. Ecology of Freshwater Fish 6: 78-83.

Fry, B., 2002. Stable isotopic indicators of habitat use by Mississippi River fish. Journal of the North American Benthological Society 21: 676-685.

Fry, B. & E. B. Sherr, 1989. $\delta^{13}C$ Measurements as indicators of carbon flow in marine and freshwater ecosystems. In Rundel, P. W., J. R. Ehleringer & K. A. Nagy (eds), Stable Isotopes in Ecological Research. Ecological Studies. springer-Verlag, New York, p 196-229.

Galat, D. L. & I. Zweimüller, 2001. Conserving large-river fishes: is the highway analogy an appropriate paradigm? Journal of the North American Benthological Society 20: 266-279.

Gannes, L. Z., D. M. Obrien & C. M. delRio, 1997. Stable isotopes in animal ecology: Assumptions, caveats, and a call for more laboratory experiments. Ecology 78: 1271-1276.

Górski, K., H. V. winter, J. J. De Leeuw, A. E. Minin & L. A. J. Nagelkerke, 2010. Fish spawning in a large temperate floodplain: the role of flooding and temperature. Freshwater Biology 55: 1509-1519.

Górski, K., J. J. De Leeuw, H. V. winter, D. A. Vekhov, A. E. Minin, A. D. Buijse & L. A. J. Nagelkerke, 2011a. Fish recruitment in a large, temperate floodplain: the importance of annual flooding, temperature and habitat complexity. Freshwater Biology 56: 2210-2225.

Górski, K., L. V. van den Bosch, K. E. van de Wolfshaar, H. Middelkoop, L. A. J. Nagelkerke, O. V. Filippov, D. V. Zolotarev, S. V. Yakovlev, A. E. Minin, H. V. winter, J. J. De Leeuw, A. D. Buijse & J. A. J. Verreth, 2011b. Post-damming flow regime development in a large lowland river (Volga, Russian Federation): Implications for floodplain inundation and fisheries. River Research and Applications 28: 1121–1134.

Hadwen, W. L., M. Spears & M. J. Kennard, 2010. Temporal variability of benthic algal $\delta^{13}C$ signatures influences assessments of carbon flows in stream food webs. Hydrobiologia 651: 239-251.

Hamilton, S. K., W. M. Lewis & S. J. Sippel, 1992. Energy sources for aquatic animals in the Orinoco River floodplain: evidence from stable isotopes. Oecologia 89: 324-330.

Harding, J. S., D. J. Hawke, R. N. Holdaway & M. J. winterbourn, 2004. Incorporation of marine-derived nutrients from petrel breeding colonies into stream food webs. Freshwater Biology 49: 576-586.

Hardy, C. M., E. S. Krull, D. M. Hartley & R. L. Oliver, 2010. Carbon source accounting for fish using combined DNA and stable isotope analyses in a regulated lowland river weir pool. Molecular Ecology 19: 197-212.

Herwig, B. R., D. H. Wahl, J. M. Dettmers & D. A. Soluk, 2007. Spatial and temporal patterns in the food web structure of a large floodplain river assessed using stable isotopes. Canadian Journal of Fisheries and Aquatic Sciences 64: 495-508.

Hicks, B. J., M. S. Wipfli, D. W. Lang & M. E. Lang, 2005. Marine-derived nitrogen and carbon in freshwater-riparian food webs of the Copper River Delta, southcentral Alaska. Oecologia 144: 558-569.

Hladyz, S., D. L. Nielsen, P. J. Suter & E. S. Krull, 2012. Temporal variations in organic carbon utilization by consumers in a lowland river. River Research and Applications 28: 513-528.

Hoeinghaus, D. J., K. O. Winemiller & A. A. Agostinho, 2007. Landscape-scale hydrologic characteristics differentiate patterns of carbon flow in large-river food webs. Ecosystems 10: 1019-1033.

Hunt, R. J., T. D. Jardine, S. K. Hamilton & S. E. Bunn, 2012. Temporal and spatial variation in ecosystem metabolism and food web carbon transfer in a wet-dry tropical river. Freshwater Biology 57: 435-450.

Huryn, A. D., R. H. Riley, R. G. Young, C. J. Arbuckle, K. Peacock & G. Lyons, 2001. Temporal shift in contribution of terrestrial organic matter to consumer production in a grassland river. Freshwater Biology 46.

Jardine, T., B. Pusey, S. Hamilton, N. Pettit, P. Davies, M. Douglas, V. Sinnamon, I. Halliday & S. Bunn, 2011. Fish mediate high food web connectivity in the lower reaches of a tropical floodplain river. Oecologia 168: 829-838.

Jardine, T. D., J. M. Roussel, S. C. Mitchell & R. A. Cunjak, 2009. Detecting marine nutrient and organic matter inputs into multiple trophic levels in streams of atlantic Canada and France. American Fisheries Society Symposium 69: 427-445.

Jepsen, D. B. & K. O. Winemiller, 2007. Basin geochemistry and isotopic ratios of fishes and basal production sources in four neotropical rivers. Ecology of Freshwater Fish 16: 267-281.

Johnson, B. L., W. B. Richardson & T. J. Naimo, 1995. Past, present, and future concepts in large river ecology. Bioscience 45: 134-141.

Junk, W. J. & K. M. Wantzen, 2004. The flood pulse concept: new aspects, approaches and applications - an update. Food and Agriculture Organization and Mekong River Commission, FAO Regional Office for Asia and the Pacific.

Junk, W. J., P. B. Bayley & R. E. Sparks, 1989. The flood pulse concept in river-floodplain systems. In Dodge, DP (ed) Proceedings of the International Large River Symposium, Canadian Special Publication of Fisheries and Aquatic Sciences 106: 110-127.

Kennedy, T. A. & B. E. Ralston, 2012. Regulation leads to increases in riparian vegetation, but not direct allochthonous inputs, along the Colorado River in Grand Canyon, Arizona. River Research and Applications 28: 2-12.

Kiffney, P. M., C. M. Greene, J. E. Hall & J. R. Davies, 2006. Tributary streams create serial discontinuities in habitat, biological productivity, and diversity in mainstem rivers. Canadian Journal of Fisheries and Aquatic Sciences 63: 2518-2530.

Kohzu, A., I. Tayasu, C. Yoshimizu, A. Maruyama, Y. Kohmatsu, F. Hyodo, Y. Onoda, A. Igeta, K. Matsui, T. Nakano, E. Wada, T. Nagata & Y. Takemon, 2009. Nitrogen-stable isotopic signatures of basal food items, primary consumers and omnivores in rivers with different levels of human impact. Ecological Research 24: 127-136.

Layman, C. A., K. O. Winemiller & D. A. Arrington, 2005. Describing a species-rich river food web using stable isotopes, stomach contents, and functional experiments. In de Ruiter, P., V. Wolters & J. C. Moore (eds), Dynamic Food Webs: Multispecies assemblages, ecosystem development, and environmental change. Academic Press, p 395-406.

Leigh, C., M. A. Burford, F. Sheldon & S. E. Bunn, 2010. Dynamic stability in dry season food webs within tropical floodplain rivers. Marine and Freshwater Research 61: 357-368.

Lewis, W. M., S. K. Hamilton, M. A. Rodriguez, J. F. Saunders & M. A. Lasi, 2001. Foodweb analysis of the Orinoco floodplain based on production estimates and stable isotope data. Journal of the North American Benthological Society 20: 241-254.

Marcarelli, A., C. Baxter & M. Mineau, 2011. Quantity and quality: unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters. Ecology 92: 1215-1225.

Martinez, P. J., B. M. Johnson & J. D. Hobgood, 2001. Stable isotope signatures of native and nonnative fishes in Upper Colorado River backwaters and ponds. Southwestern Naturalist 46: 311-322.

McCutchan, J. H., W. M. Lewis, C. Kendall & C. C. McGrath, 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102: 378-390.

Medeiros, E. S. F. & A. H. Arthington, 2010. Allochthonous and autochthonous carbon sources for fish in floodplain lagoons of an Australian dryland river. Environmental Biology of Fishes 90: 1-17.

Michener, R. & K. Lajtha, 2007. Introduction. In Michener, R. & K. Lajtha (eds), Stable Isotopes in Ecology and Environmental Science. Ecological Methds and Concepts Series, 2nd edn.

Minshall, G. W., K. W. Cummins, R. C. Petersen, C. E. Cushing, D. A. Bruns, J. Sedell, R. & R. L. Vannote, 1985. Developments in stream ecosystem theory. Canadian Journal of Fisheries and Aquatic Sciences 42: 1045-1055.

Moore, J. W. & B. X. Semmens, 2008. Incorporating uncertainty and prior information into stable isotope mixing models. Ecology Letters 11: 470-480.

Nilsson, C., C. A. Reidy, M. Dynesius & C. Revenga, 2005. Fragmentation and flow regulation of the world's large river systems. Science 308: 405-408.

Parnell, A. C., R. Inger, S. Bearhop & A. L. Jackson, 2010. Source partitioning using stable isotopes: coping with too much variation. PloS one 5: e9672.

Perga, M. E. & D. Gerdeaux, 2003. Using the $\delta^{13}C$ and $\delta^{15}N$ of whitefish scales for retrospective ecological studies: changes in isotope signatures during the restoration of Lake Geneva, 1980-2001. Journal of Fish Biology 63: 1197-1207.

Perga, M. E. & D. Gerdeaux, 2005. 'Are fish what they eat' all year round? Oecologia 144: 598-606.

Phillips, D. L. & J. W. Gregg, 2003. Source partitioning using stable isotopes: coping with too many sources. Oecologia 136: 261-269.

Phillips, D. L., S. D. Newsome & J. W. Gregg, 2005. Combining sources in stable isotope mixing models: alternative methods. Oecologia 144: 520-527.

Poole, G. C., 2002. Fluvial landscape ecology: addressing uniqueness within the river discontinuum. Freshwater Biology 47: 641-660.

Post, D. M., 2002. Using stable isotopes to estimate trophic position: Models, methods, and assumptions. Ecology 83: 703-718.

Power, M. E., A. Sun, G. Parker, W. E. Dietrich & J. T. Wootton, 1995. Hydraulic food-chain models. Bioscience 45: 159-167.

Preiner, S., I. Drozdowski, M. Schagerl, F. Schiemer & T. Hein, 2008. The significance of side-arm connectivity for carbon dynamics of the River Danube, Austria. Freshwater Biology 53: 238-252.

Rasmussen, J. B., V. Trudeau & G. Morinville, 2009. Estimating the scale of fish feeding movements in rivers using delta C-13 signature gradients. Journal of Animal Ecology 78: 674-685.

Reid, M. A., M. D. Delong & M. C. Thoms, 2011. The influence of hydrological connectivity on food web structure in floodplain lakes. River Research and Applications 28: 827–844.

Reynolds, C. S., 1996. Algae. In Petts, G. E. & P. Calow (eds), River Biota: Diversity and Dynamics. Blackwell Science Ltd, Oxford, p 6-26.

Rice, S. P., M. T. Greenwood & C. B. Joyce, 2001. Tributaries, sediment sources, and the longitudinal organisation of macroinvertebrate fauna along river systems. Canadian Journal of Fisheries and Aquatic Sciences 58: 824-840.

Rice, S. P., R. I. Fergusson & T. B. Hoey, 2006. Tributary control of physical heterogeneity and biological diversity at river confluences. Canadian Journal of Fisheries and Aquatic Sciences 63: 2553-2566.

Roach, K. A., J. H. Thorp & M. D. Delong, 2009a. Influence of lateral gradients of hydrologic connectivity on trophic positions of fishes in the Upper Mississippi River. Freshwater Biology 54: 607-620.

Roach, K. A., K. O. Winemiller, C. A. Layman & S. C. Zeug, 2009b. Consistent trophic patterns among fishes in lagoon and channel habitats of a tropical floodplain river: Evidence from stable isotopes. Acta Oecologica-International Journal of Ecology 35: 513-522.

Rosales, J., L. Blanco-Belmonte & C. Bradley, 2007. Hydrogeomorphological and ecological interactions in tropical floodplains: The significance of confluence zones in the Orinoco Basin, Venezuela. In P. J. Wood, D. M.

Hannah & J. P. Sadler (eds), Hydroecology and Ecohydrology: Past, present and future John Wiley & Sons Ltd., Chichester, p 295-316.

Schiemer, F. & T. Hein, 2007. The ecological significance of hydraulic retention zones. In Wood, P. J., D. M. Hannah & J. P. Sadler (eds), Hydroecology and Ecohydrology: Past, present and future. John Wiley & Sons, Ltd, Chichester, p 405-420.

Schiemer, F., H. Keckeis, G. Winkler & L. Flore, 2001a. Large rivers: the relevance of ecotonal structure and hydrological properties for the fish fauna. Large Rivers 12: 487-508.

Schiemer, F., H. Keckeis, W. Reckendorfer & G. Winkler, 2001b. The "inshore retention concept" and its significance for large rivers. Large Rivers 12: 509-516.

Schmidt, S. N., M. J. Vander Zanden & J. F. Kitchell, 2009. Long-term food web change in Lake Superior. Canadian Journal of Fisheries and Aquatic Sciences 66: 2118-2129.

Sedell, J. R., J. E. Richey & F. J. Swanson, The river continuum concept: A basis for the expected ecosystem behaviour of very large rivers? In: Dodge, D. P. (ed) Proceedings of the International Large River Symposium, 1989. Canadian Special Publication of Fisheries and Aquatic Sciences 106. p 49-55.

Sedell, J. R., G. H. Reeves, F. R. Hauer, J. a. Stanford & C. P. Hawkins, 1990. Role of refugia in recovery from disturbances: Modern fragmented and disconnected river systems. Environmental Management 14: 711-724.

Solomon, C. T., S. R. Carpenter, J. A. Rusak & M. J. Vander Zanden, 2008. Long-term variation in isotopic baselines and implications for estimating consumer trophic niches. Canadian Journal of Fisheries and Aquatic Sciences 65: 2191-2200.

Syvaranta, J., J. Cucherousset, D. Kopp, A. Martino, R. Cereghino & F. Santoul, 2009. Contribution of anadromous fish to the diet of European catfish in a large river system. Naturwissenschaften 96: 631-635.

Thorp, J. H. & M. D. Delong, 1994. The riverine productivity model: an heuristic view of carbon sources and organic processing in large river ecosystems. Oikos 70: 305-308.

Thorp, J. H. & M. D. Delong, 2002. Dominance of autochthonous autotrophic carbon in food webs of heterotrophic rivers. Oikos 96: 543-550.

Thorp, J. H., M. C. Thoms & M. D. Delong, 2006. The riverine ecosystem synthesis: Biocomplexity in river networks across space and time. River Research and Applications 22: 123-147.

Thorp, J. H., M. C. Thoms & M. D. Delong, 2008. The Riverine Ecosystem Synthesis: Towards conceptual cohesiveness in river science. Elsevier.

Thorp, J. H., M. D. Delong, K. S. Greenwood & A. F. Casper, 1998. Isotopic analysis of three food web theories in constricted and floodplain regions of a large river. Oecologia 117: 551-563.

Tockner, K., F. Malard & J. V. Ward, 2000. An extension of the flood pulse concept. Hydrological Processes 14: 2861-2883.

Tonkin, Z. D., A. J. King, A. I. Robertson & D. S. L. Ramsey, 2011. Early fish growth varies in response to components of the flow regime in a temperate floodplain river. Freshwater Biology 56: 1769-1782.

Trimmer, M., A. G. Hildrew, M. C. Jackson, J. L. Pretty & J. Grey, 2009. Evidence for the role of methane-derived carbon in a free-flowing, lowland river food web. Limnology and Oceanography 54: 1541-1547.

Van den Meersche, K., P. Van Rijswijk, K. Soetaert & J. J. Middelburg, 2009. Autochthonous and allochthonous contributions to mesozooplankton diet in a tidal river and estuary: Integrating carbon isotope and fatty acid constraints. Limnology and Oceanography 54: 62-74.

Vander Zanden, M. J. & J. B. Rasmussen, 1999. Primary consumer delta C-13 and delta N-15 and the trophic position of aquatic consumers. Ecology 80: 1395-1404.

Vander Zanden, M. J., S. Chandra, B. C. Allen, J. E. Reuter & C. R. Goldman, 2003. Historical food web structure and restoration of native aquatic communities in the Lake Tahoe (California-Nevada) Basin. Ecosystems 6: 274-288.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell & C. E. Cushing, 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37: 130-137.

Vörösmarty, C. J., P. B. McIntyre, M. O. Gessner, D. Dudgeon, A. Prusevich, P. Green, S. Glidden, S. E. Bunn, C. A. Sullivan, C. R. Liermann & P. M. Davies, 2010. Global threats to human water security and river biodiversity. Nature 467: 555-561.

Ward, J. V., 1989. The four-dimensional nature of lotic ecosystems. Journal of the North American Benthological Society 8: 2-8.

Ward, J. V. & J. A. Stanford, 1983. The serial dicontinuity concept of lotic ecosystems. In Fontaine, T. D. & S. M. Bartell (eds), Dynamics of lotic ecosystems. Ann Arbor Scientific Publishers, Ann Arbor, MI, p 29-42.

Ward, J. V. & J. A. Stanford, 1995. The serial discontinuity concept: extending the model to floodplain rivers. Regulated Rivers: Research & Management 10: 159-168.

Winemiller, K. O. & G. A. Polis, 1996. Food webs: What do they tell us about the world? In Polis, G. A. & K. O. Winemiller (eds), Food webs: Integration of Patterns and Dynamics. Chapman and Hall, New York, p 1-22.

Winemiller, K. O., D. J. Hoeinghaus, A. A. Pease, P. C. Esselman, R. L. Honeycutt, D. Gbanaador, E. Carrera & J. Payne, 2011. Stable isotope analysis reveals food web structure and watershed impacts along the fluvial gradient of a Mesoamerican coastal river. River Research and Applications 803: 791-803.

Woodward, G. & A. G. Hildrew, 2002. Food web structure in riverine landscapes. Freshwater Biology 47: 777-798.

Zeug, S. C. & K. O. Winemiller, 2008. Evidence supporting the importance of terrestrial carbon in a large-river food web. Ecology 89: 1733-1743.

3 High intensity data survey and multivariate statistics reveal ecological zones along the longitudinal profile of a large, temperate, lowland river

3.1 Abstract

The importance of environmental heterogeneity and discontinuities in lotic ecosystems is well recognised and continues to underpin studies of hierarchical patch dynamics, geomorphology and landscape ecology. The Riverine Ecosystem Synthesis conceptualises these units as functional process zones which can be important drivers of river food webs and ecological function. The primary aim of this study was to locate and characterise zones of potential ecological importance along the lower Waikato River in North Island, New Zealand, using a combination of (i) high-frequency, along-river water quality measurements collected in four seasons and (ii) river channel morphology data derived from aerial photos. A multivariate hierarchical clustering routine (CLUSTER) was implemented to classify river reaches in an *a priori* unstructured manner (SIMPROF) along the 134-km surveyed distance. ANOSIM was then used to test changes in both water quality and channel character at a greater spatial scale and then to identify zones that represent spatial units for management and to underpin hypothesis development for ecological studies. Channel zones were shaped by the physical complexity and channel character of constituent river reaches. Changes in water clarity, chlorophyll fluorescence and specific conductance described water quality zones, which were driven by tributary inflows in the mid-section of the river tidal cycles in the lower section of the Waikato River. The results highlight the dynamic spatial and temporal properties of these zones which respond over different scales to climatic and hydrological changes.

3.2 Introduction

Rivers are dynamic ecosystems with longitudinal, lateral and vertical dimensions (Ward, 1989; Thorp et al., 2008), that provide a diverse array of habitats across a range of spatial and temporal scales (Power et al., 1995; Woodward & Hildrew, 2002). Large rivers are amongst the most regulated and altered ecosystems on Earth, with only 35% of large river systems remaining un-fragmented by dams or un-affected by hydrological regulation for flood control, hydro-electricity generation, irrigation or ship movements (Dynesius & Nilsson, 1994; Nilsson et al., 2005). Human development has led to changes in river function and character, increasing hydrological extremes, changing sediment transport, and altering channel formation and movement (Elosegi et al., 2010). Understanding the factors that drive longitudinal patterns in the physical and biological functions of rivers, is of particular interest to ecologists (Power & Dietrich, 2002). Consistent trends in river ecosystem function have been identified across a range of river types (Hadwen et al., 2010), and rivers are sometimes viewed as changing along a gradient or continuum (e.g. Vannote et al., 1980). Inputs from major tributaries (Kiffney et al., 2006) and anthropogenic discharges (Varol et al., 2011), as well as impoundments (Ward & Stanford, 1983), may disrupt this continuum and in doing so alter hydrogeomorphic, water quality and food web properties along the fluvial gradient. Interdisciplinary approaches, such as eco-geomorphology, have also revealed hierarchical patterns of physical and biological associations across a range of spatial scales in riverine ecosystems (Thoms & Parsons, 2002; Parsons & Thoms, 2007).

The integration of hierarchical patch dynamics, geomorphology and landscape ecology has expanded scientific perspectives to recognise the importance environmental heterogeneity and discontinuities in lotic ecosystems (Poole, 2002; Winemiller et al., 2010). One approach to conceptualising this is the Riverine Ecosystem Synthesis which proposes recognition of hydrogeomorphic units termed functional process zones, which can be loosely defined as a fluvial geomorphic unit between a valley and a reach in scale (Thorp et al., 2006, 2008). Local riverine habitats and processes are shaped by the hydrology and geology of the zone in which they occur (Thorp et al., 2006, 2008). The distribution, diversity, nature and scale of lateral features, such as retention zones or floodplains, will be determined by the geomorphic and hydrological characters of the catchment and can range from simple single channels to many branches with an array of lateral features. Laterally complex river zones are likely to have a greater array of habitats where abiotic characteristics and biotic function are driven by the frequency, magnitude and duration of main channel flow and flood pulses (Tockner et al., 2000; Schiemer & Hein, 2007; Thorp et al., 2008).

Depending on river typology, lateral connections with floodplains and other waterbodies, particularly in unconstrained river reaches, can also play vital roles for a range of ecosystem functions (Junk et al., 1989). Lateral habitats, such as littoral zones, side arms, tributary confluences, oxbow lakes, lagoons and backwaters (Schiemer & Hein, 2007; Zeug & Winemiller, 2008; Roach et al., 2009a; Roach et al., 2009b), support many aquatic organisms and provide shelter from main channel flows. The nature of flow velocities and water retention in these habitats determines the diversity of biota, and processing of nutrients and organic carbon by plankton before transfer to other parts of the food web (Schiemer et al., 2001a). Smaller retention zones can be created by changes in shoreline configuration, with increasing shoreline complexity (e.g., length, sinuosity) leading to reduced current velocities and longer retention times that benefit littoral organisms (Schiemer et al., 2001a; Schiemer & Hein, 2007). In addition to current velocity and hydraulic retention, these habitats can differ from the main channel and each other in terms of nutrient processing, substrate composition, riparian input and shading, temperature, turbidity and the degree of riverine interaction (Schiemer & Hein, 2007; Thorp et al., 2008). At a larger scale, features like side arms, backwaters and tributary junctions provide important productive habitats for fish growth and recruitment (Schiemer et al., 2001a; Schiemer et al., 2001b; Schiemer & Hein, 2007). The characteristics of retention zones can also change temporally, for example in response to seasonal flows, connectivity and temperatures, leading to changes in physical habitat, water quality, community composition and food web structure (Fisher et al., 2001; Roach et al., 2009a). The diversity, distribution, connectivity and scale of these lateral habitats are therefore important to ecological function, particularly in structurally complex FPZs and river systems (Thorp & Delong, 2002; Schiemer & Hein, 2007).

Water quality in river systems can reflect natural processes related to climate and geology and also anthropogenic disturbances, such as land use, waste water, and channel modifications, the effects of which can be both localised and cumulative (Eyre & Pepperell, 1999; Chang, 2008). Seasonal flow patterns can also affect water quality in that at levels close to base flow, point sources are likely to play a more important role than at high flows when they can become masked by wider catchment effects (Eyre & Pepperell, 1999). Flow variability in river systems, such as that caused by floods, human-induced flow pulses, tidal cycles and tributary inputs, contributes to structuring ecological patterns and communities in lotic systems (Poff & Ward, 1989; Tockner et al., 2000), including the structural properties of food webs (Sabo et al., 2010). Ecological responses to water quality, particularly those in response to anthropogenic stressors and land use, can be reflected in the taxonomic composition and traits of communities of riverine macroinvertebrates (Dolédec et al., 2011; Collier et al., 2012)

Large dams lead to significant downstream changes in ecosystem function, including reduced flow pulses and transported sediments, increased channel incision leading to disconnection of lateral habitats, changes in water temperature and releases of lake-derived plankton (Ward & Stanford, 1983; Amoros & Bornette, 2002; Doi et al., 2008; Górski et al., 2011). The extent of downstream recovery from these effects will be dependent on the magnitude of regulation (Cortez et al., 2012) and the presence of large unregulated downstream tributaries (Stanford & Ward, 2001). Moreover, fluctuations as a result of diurnal hydro-power generation can have impacts on the species richness, abundance and the behaviour of macroinvertebrates and fish (Bunn & Arthington, 2002). Adding to this hydrological complexity, daily water level fluctuations in tidally-influenced freshwater sections of rivers also affect both the morphology of the river channel and biological production, often increasing phytoplankton biomass (Ensign et al., 2012). These sections of river, where water flow is affected by the tidal cycle but remains fresh, can extend upstream for tens of kilometres in smaller coastal rivers (e.g. Ensign et al., 2012) to hundreds of kilometres in larger lowland rivers (e.g. Howarth et al., 1996).

Additional complexity in the main river can be created by adjoining tributaries, with a complex range of associated effects on woody debris abundance, substrate heterogeneity, consumer abundance, water volume, nutrient availability, sediment loading, and bed particle shape and size (Kiffney et al., 2006; Rice et al., 2006), that can in turn create nodes of high habitat complexity, biological diversity and productivity (Benda et al., 2004; Rosales et al., 2007). Contributing watercourses also provide important biological linkages with potentially distant habitats such as lakes, wetlands and headwater streams. The relative impact and extent of discontinuities and complexity in the main river caused by tributary junctions will depend on temporal and spatial flow variability. For example, the distribution and intensity of rainfall in the catchments of large tributaries can mediate the delivery of sediment, allochthonous carbon sources and woody debris to rivers, while high river flows in the main channel can have a dampening effect on tidal cycles and upstream extent of saline intrusion into freshwater sections of lowland rivers (Anderson & Lockaby, 2012).

Understanding the spatial and temporal dynamics of physico-chemically similar sections of a river system underpins the development of management units that can be used to identify management actions that enhance biodiversity and ecological function (Thorp et al., 2006, 2008). The overall aim of this study was to (i) develop a quantitative approach that objectively identified and characterised potential river management zones along a longitudinal gradient punctuated by physicochemical and hydrogeomorphic changes, (ii) compare the patterns identified by different forms of measurement and (iii) investigate the spatial and temporal fidelity of these zones in relation to water quality. To achieve this, I used a combination of water quality measurements and river channel morphology data derived from a boat towed water quality instrument and aerial photos along a continuous 134 km stretch of the lower Waikato River, central North Island, New Zealand. Changes in riverine character that could indicate the presence of zones of ecological importance were tested using a combination of multivariate analyses.

3.3 Methods

3.3.1 Study area

The Waikato River drains a total catchment area of c. 14,443 km^2 (Brown, 2010), c. 13 % of the North Island, New Zealand (Chapman, 1996). The river flows in a roughly northerly direction for around 442 km from its headwaters above Lake Taupo to the Tasman Sea at Port Waikato (Collier et al., 2010). The river is categorised as 7th order and has a mean annual discharge of c.450 m^3 s^{-1} at its mouth (Brown, 2010), conforming to definitions of a large river presented in the literature (Vannote et al., 1980; Dynesius & Nilsson, 1994; Johnson et al., 1995; Nilsson et al., 2005). The river catchment has been significantly altered from its natural state for hydroelectric power generation and flood protection (Chapman, 1996; Collier et al., 2010). The furthest downstream dam forms Lake Karapiro and acts as an effective barrier to the natural movement of aquatic fauna upstream. My study was conducted downstream of this dam, on the lower river, where the channel is low-gradient, falling 22 m over c. 150 km to the sea (Collier et al., 2010); (Fig. 3.1a).

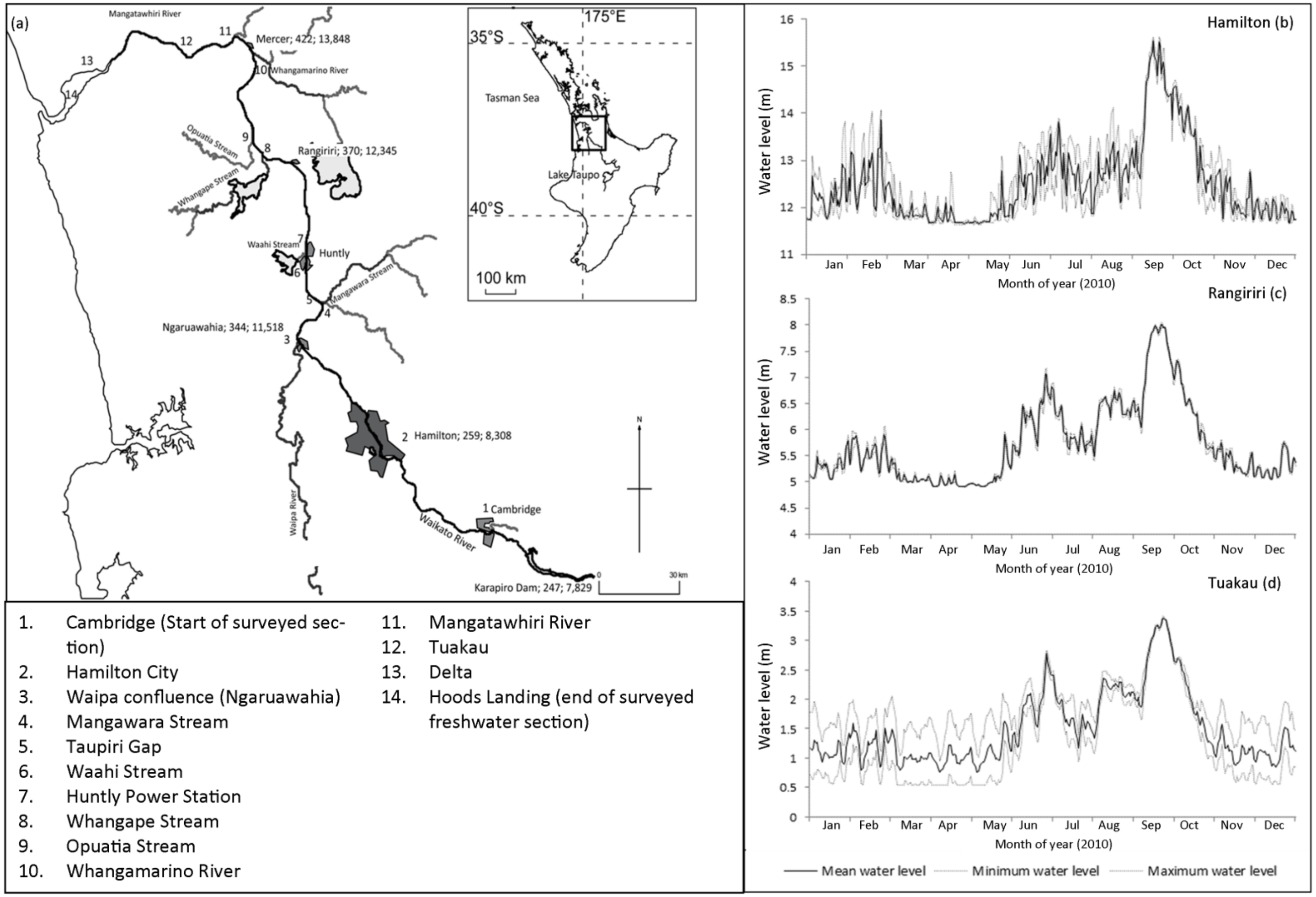


Figure 3.1. (a) Map of lower Waikato River, indicating key locations. Locations followed by numbers indicate mean annual discharge (m^3/s) and catchment area (km^2), respectively (modified from Brown 2010). Mean, maximum and minimum river levels recorded during 2010 at selected Waikato River gauging stations relative to Moturiki mean sea level datum, located at (b) Hamilton, (c) Rangiriri and (d) Tuakau (data courtesy of Waikato Regional Council).

Land use in the catchment is predominantly pastoral (74 %) with only 6 % in native forest, and the river system is highly responsive to rainfall, with large flood flows after heavy rain, usually in winter and spring (Brown, 2010; Collier et al., 2010). Although unimpeded by dams, flooding is regulated by 242 km of stopbanks, 269 floodgates and 69 pump stations, and as a result 47 % (172 km^2) of the original floodplain is now disconnected from the river (Chapman, 1996; Mulholland, 2010; Speirs et al., 2010). The lower river is fed by several major tributaries, including some derived from wetlands and lakes. The largest and most significant tributary to the lower river is the Waipa River, which joins the main stem at Ngaruawahia (Fig. 3.1a). It augments mean river flow by c. 25 % and is largely responsible for flow and flood pulses that occur downstream (Chapman, 1996; Brown, 2010) (Fig. 3.1c).

3.3.2 Physical complexity

Physical complexity was determined for 1-km long reaches using ArcGIS versions 9.3 and 10. River shoreline was digitised from recent aerial photos (Waikato Regional Council), and GIS tools were then used to create a centreline from which perpendicular dividing lines could be located to delineate 1 km reaches (polygons). River channel character was then estimated by calculating five metrics for each 1-km polygon. Mean river width and channel shoreline length (indicative of shoreline complexity) were measured directly from each polygon. The River Channel Complexity Ratio (RCCR) was calculated to reflect lateral complexity within the riverscape as the ratio of total shoreline length of a reach (including side arms and islands) to that of the main channel shoreline length (O'Neill & Thorp, 2011). The percentage of aquatic channel area for each reach was calculated by taking the total polygon area minus the area of lateral features, such as islands and dividing it by the total polygon area, and is expressed as percentage open water.

3.3.3 Water quality survey

Physico-chemical measurements were taken during summer, autumn, winter and spring 2010. Data were collected using a Biofish underwater sensor array (ADM-Elektronik, Germany) towed by boat to collect real time, high frequency data on water quality changes (Hamilton et al., 2010). Surveys were restricted to water that could be safely navigated by boat (e.g. excluding rapids and sand bars), and therefore the upstream starting point was 7 km downstream of Karapiro dam at Cambridge (Fig. 3.1a). Surveys finished at the downstream extent of the delta islands, leading to a total surveyed distance of c. 137 km, although the last 3 km were excluded from analyses due to salt water intrusion downstream of Hoods Landing (Fig. 3.1a). Surveys were completed over three consecutive days, apart from the spring survey when an equipment failure required spatially overlapping surveys on two separate two-day surveys (Cambridge to Huntly and Waipa confluence to Hoods Landing).

Measurements of water clarity (percent light transmittance), chlorophyll fluorescence (measured as relative fluorescence units (RFUs)), water temperature (°C) and specific conductivity (µS/cm) were measured at a depth of 0.5 m using the Biofish. These measurements, and bed depth in the navigable channel (m) measured by an echo sounder attached to the boat, were linked to a GPS reference (Garmin GPSMAP 168 Sounding). Data were automatically recorded to a computer along with longitude and latitude from a global positioning system. During each survey the Biofish was towed at a speed of 7 to 15 km/h, depending on river conditions. On return to the laboratory every 100th Biofish data point was extracted from the data file (c. 25 second intervals), and summarised in ArcGIS for each 1-km reach using the polygon delineation described above. Although downstream distance between points depended on boat speed and direction, the number of points summarised in each km of river reach was in excess of 100. Additional measurements were taken at regular intervals using a conductivity-temperature-depth (CTD) profiler (SBE 19 plus Seabird Electronics), fitted with additional beam transmittance and fluorescence sensors. Measurements from similar depths were then used to calibrate and validate Biofish fluorescence and transmittance readings (McBride et al., 2008; Hamilton et al., 2010).

3.3.4 Data analysis

Multivariate statistical approaches are useful for interpreting and evaluating complex water quality datasets (Vega et al., 1998; Wunderlin et al., 2001; Varol et al., 2011). Statistical analyses were undertaken using Primer 6 with PERMANOVA extension (Version 1.0.3). Prior to use in PRIMER, data were normalised and converted to a Euclidean distance matrix. To identify functionally similar river reaches along the length of the surveyed section of the lower river, CLUSTER analysis was undertaken using group average distance and a SIMPROF analysis was used to identify groups of river reaches with 99 % similar structure. Groups for which the significant split in the CLUSTER dendrogram was at < 1 Euclidean distance unit were deemed to be very closely related and were collapsed into single groups. A one-way SIMPER analysis was then carried using these groups to ascertain the variables responsible for similarities within groups and dissimilarity between groups (cumulatively up to 100 %). The major principal components ordination (PCO) axes which accounted for the most variation in the data (PCO 1 and PCO 2) were selected and plotted to visualise relationships between sites and particular variables, illustrated by vector plots constructed using Spearman correlation coefficients. PCO based on Euclidean distance matrices in Primer are equivalent to principal components analysis (PCA) used elsewhere (Anderson et al., 2008). The two surveys conducted during spring 2010 were also analysed separately due to notable changes in underlying flow conditions during the time between surveys (approximately four weeks).

3.4 Results

3.4.1 Physical complexity

The surveyed section of the lower Waikato River was deepest above, and shallowest below the Waipa confluence (Fig. 3.2a), indicative of the marked shift in catchment geomorphology from a section dominated by ignimbrite walls and steep littoral zones to a sandier bottomed and more open river channel. This was particularly evident around Meremere and in the delta where the channel was often less than 1 m deep and sand bars were common (Fig. 3.2a). Water depth in some tidally influenced reaches was deeper than in some fluvial river reaches downstream of the Waipa River. Mean channel width was generally less above the Waipa, notably between Cambridge and Hamilton, where the river can be narrow (< 10 m) and deep (>5 m) (Fig. 3.2a,b). River width began to increase steadily below the Waipa confluence, with the widest reaches occurring around 5-10 km below Mercer and around the delta which could be >3 km wide (Fig. 3.2a,b). RCCR ratios and mean channel shoreline length ranged from 1.00–6.36 and 2.00–2.63, respectively, and increased markedly once the river passes through a geomorphic constriction known as the Taupiri Gap (Fig. 3.1a & Fig. 3.2c,d).

This highlights the increase in embayments, backwaters, side arms and islands, and a decreasing proportion of open water in the main channel (Fig. 3.2e), particularly in the delta region of the river. Interestingly, the RCCR ratio appeared to decrease in river reaches immediately below major tributary junctions.

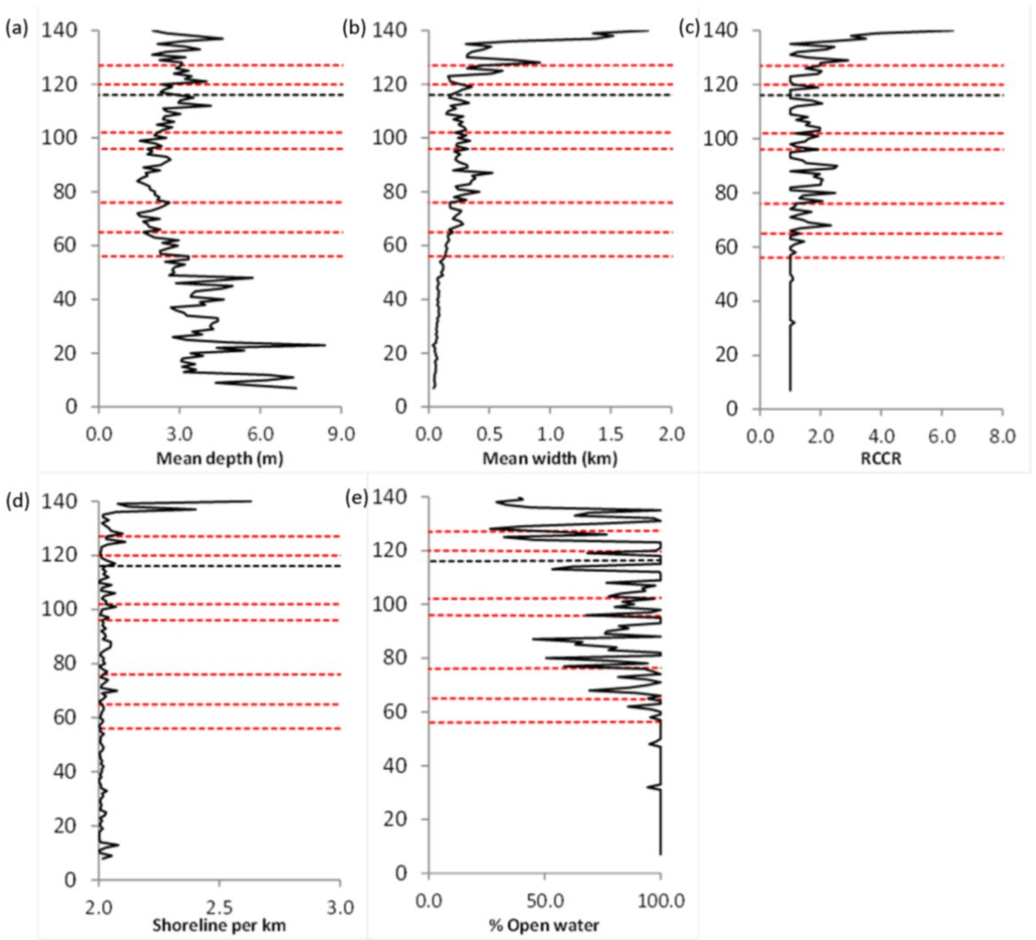


Figure 3.2. Physical parameters, summarised for each river kilometre measured from Karapiro dam. (a) Mean depth measured using a boat mounted transducer, (b) mean width, (c) River channel complexity ratio, (d) channel shoreline per km and (e) percentage open water (b-e calculated using ArcGIS). Dashed red lines represent locations of major tributaries to the lower Waikato Rive. Dashed black line indicates the estimated maximum tidal influence on river levels.

CLUSTER and SIMPROF analyses characterised river reaches into 7 significant cluster groups or types of reach based on the physical variables measured for the surveyed section of the lower river (the characteristics of each cluster group are summarised in Table 3.1). The most common group (P2) accounted for c. 40 % of river reaches and was the dominant reach type in the first 60 km of the lower river. Cluster groups P2 and P3 formed a closely related ‘family’ which characterised 65 % of reaches surveyed (Fig. 3.3a). These two clusters, however, could be differentiated most strongly in terms of mean width and depth, with one being deeper (mean 4 m depth) and narrower (mean 90 m width) and the other typically shallower (mean 2 m depth) and wider (mean 200 m width). Deep (mean 7 m depth), narrow reaches (mean 50 m wide) only occurred above the Waipa confluence, mostly above Hamilton City (within c. 30 km downstream of Karaprio dam), and formed group P1 (Fig. 3.3b).

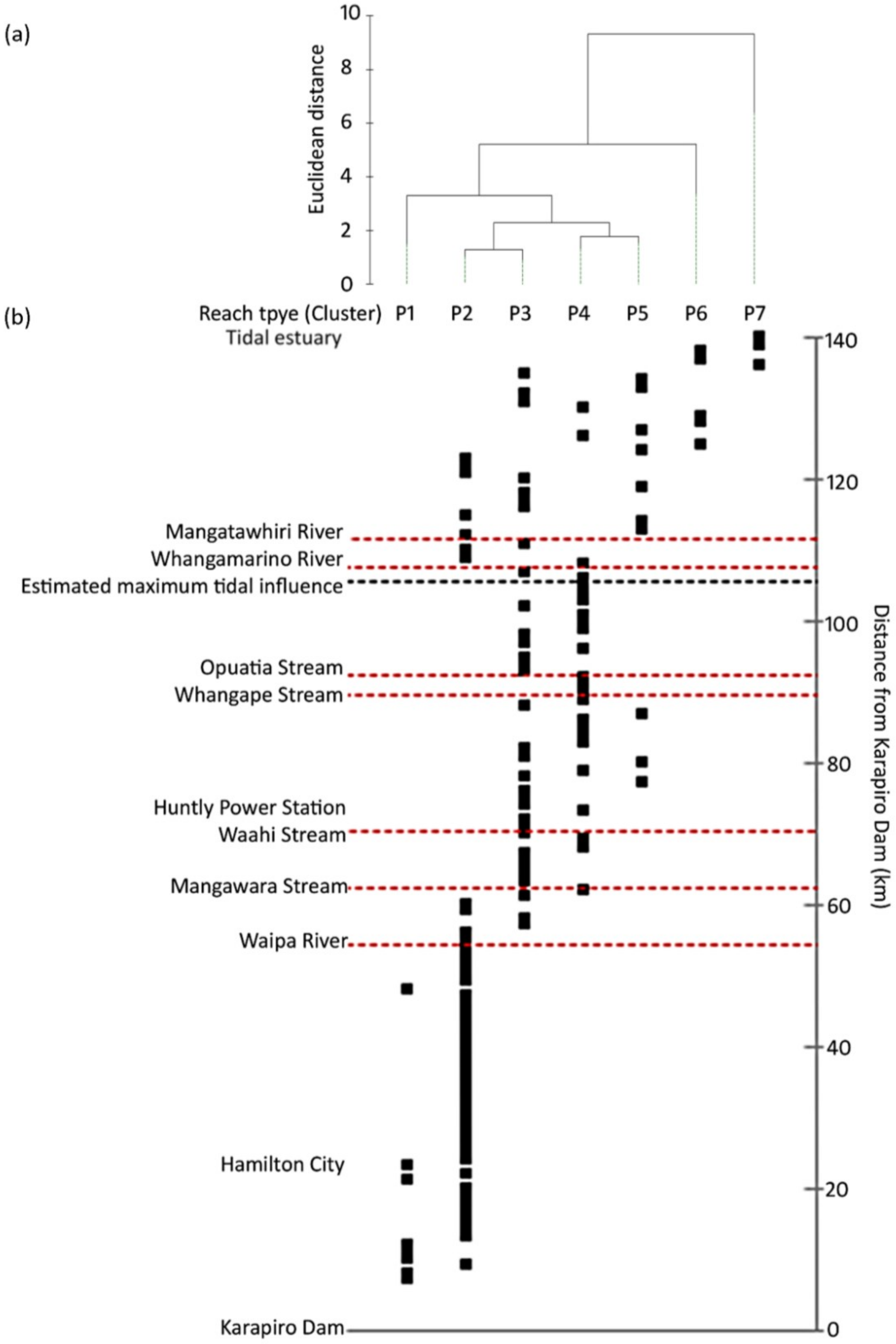


Figure 3.3. (a) Dendrogram of relationships between reach types and (b) spatial arrangement of physical reach types along the surveyed section of the lower Waikato River. See Fig. 3.4 and Table 3.1 for characteristics of each reach type (P1-P7).

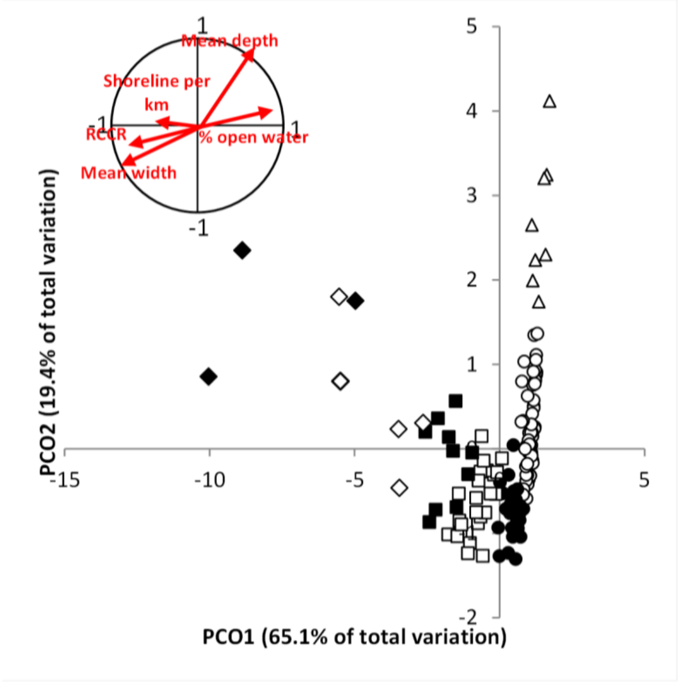
Table 3.1. Mean (±1 SD) of physical river characteristics for clusters identified using SIMPROF routines (see Fig. 3.3). Superscripts denote percentage contribution to group structure 1, 1-10 %; 2, 11-20 %; 3, 21-30 % and so on.

Reach type (Cluster)	n	Mean depth (m)	Mean width (m)	RCCR	Shoreline per km	% open water
P1	8	6.6 (1.0)^{9}	48.6 (11.6)^{1}	1.0 (0.0)^{1}	2.03 (0.02)^{2}	99 (2)^{1}
P2	51	3.5 (0.7)^{9}	92.5 (38.1)^{1}	1.0 (0.0)^{1}	2.01 (0.01)^{1}	100 (1)^{1}
P3	33	2.2 (0.3)^{4}	216.5 (50.1)^{2}	1.1 (0.1)^{2}	2.02 (0.02)^{3}	98 (3)^{1}
P4	24	2.2 (0.5)^{3}	294.7 (48.4)^{1}	1.8 (0.3)^{4}	2.03 (0.02)^{2}	79 (8)^{3}
P5	10	2.8 (0.6)^{3}	412.8 (93.2)^{2}	2.1 (0.2)^{2}	2.04 (0.04)^{4}	57 (9)^{3}
P6	5	3.4 (0.9)^{2}	1027.6 (404.3)^{6}	2.7 (0.7)^{3}	2.06 (0.04)^{1}	33 (5)^{1}
P7	3	2.6 (0.6)^{1}	1287.3 (557.4)^{3}	4.2 (2.0)^{5}	2.46 (0.15)^{3}	41 (3)^{1}
Total	134	3.1 (1.2)	242.2 (270.7)	1.4 (0.7)	2.03 (0.1)	89 (0.2)

Groups P4 to P7 effectively represented increasing frequency and scale of lateral features (e.g. RCCR and shoreline length per km) and also increasing mean width, although mean depth did not follow a longitudinal pattern.

Only two groups were present above the Waipa confluence; 8 deep and narrow river reaches belonging to group P1, which was unique to this section of river, and the remaining 40 reaches belonging to group P2, often uninterrupted for tens of kilometres. P2 also occurred immediately downstream of the Waipa confluence, and occasionally further downstream within the tidal influence, usually in narrow and deep river sections (Fig. 3.3b). In SIMPER analyses these two groups were most strongly characterised (>80 %), by mean river depth with both groups having mean depth >3.5 m (Table 3.1). The analyses identified another five groups which only occurred below the Waipa confluence where the majority of river reaches (55) were represented by two groups - P3 which was characterised by shallow river depths and low lateral complexity, and P4 which was also shallow but had a higher frequency of lateral features (e.g. higher RCCR ratios and river shoreline length). Downstream of the Waipa confluence the occurrence of reach types tended to change more frequently, with fewer and shorter stretches of a single type. This variability increased downstream of the Mangatawhiri confluence, particularly below Tuakau (c. 120 km downstream from Karapiro dam). Six different reach types occurred in the most downstream 20 km surveyed, and of these, two (P6 and P7, represented by a total of 8 river reaches), were only located in the tidally-influenced section, while a third (P5) was rare upstream (Fig. 3.3b). SIMPER analyses indicated that these 3 groups were characterised by high RCCR ratios and high mean width, P7 also had a high shoreline length (Table 3.1).

Investigation of the 5 selected physical complexity measures using Principal Coordinates Ordination (PCO) indicated that the 1st and 2nd axes of the PCO explained a total of 87.5 % of the variation (Fig. 3.4). P1 and P2 reaches generally had little lateral complexity and were deeper than other reach types (Fig. 3.4a). Reaches to the left of the plot (progressively from P5 through P7) reflect increasing river width and lateral complexity metrics (higher RCCR ratios), are shallower and wider, and have a more complex channel with a longer shoreline length (embayments and backwaters) (Fig. 3.4a).



Reach type (Cluster)	Symbol	Description
P1	△	Narrow and deep, low lateral complexity
P2	○	Narrower and deeper than average, low lateral complexity
P3	●	Average width, but shallower than average, low lateral complexity
P4	□	Average width, shallower than average, islands and/or side arms present
P5	■	Above average width, islands and side arms common
P6	◇	Wide, lateral features abundant
P7	◆	Wide, lateral features very abundant, shallower than P6

Figure 3.4. Principal coordinates ordination of reach types identified using CLUSTER and SIMPROF analyses of physical variables, and vector plot of Spearman correlation coefficients. Symbols and descriptions of each reach type are displayed below the plot.

3.4.2 Intensive along river water quality measurements

Measurements of water quality summarised using the same 1-km reaches as above showed both spatial and seasonal patterns. Although somewhat variable down the length of the surveyed stretch of river, some general patterns in chlorophyll fluorescence were discernible. Fluorescence tended to drop immediately below the Waipa River confluence and steadily increase once the river channel became tidally influenced, c. 115 km from Karapiro dam depending on the season (Fig. 3.5). Although similar patterns were observed in each month, an increase in fluorescence was less pronounced downstream of Mercer during August (Fig. 3.5c). Depending on the season, smaller fluctuations in fluorescence were also observed around specific locations, often coinciding with tributary junctions, notably the Mangawara, Whangape and Whangamarino confluences. Overall, transmittance (water clarity) decreased with increasing distance from Karapiro dam (Fig. 3.5). Localised decreases were also evident immediately downstream of tributaries, although these often recovered further downstream. The Waipa River confluence was consistently associated with the largest changes in water clarity, most notably during high flows in winter when low transmittance persisted for the remainder of the survey downstream (Fig. 3.5c).

Water temperature was highest in summer (March) and lowest in winter (August) (Fig. 3.5a,c). At low flows water temperature in the main channel generally decreased downstream of tributary confluences while the opposite was true at high flows (notably the Waipa) (Fig. 3.5c). A localised temperature increase was regularly observed, downstream of Huntly where a thermal power station discharges heated water to the river (Fig. 3.1a and Fig. 3.5). Specific conductivity declined immediately below the Waipa River confluence, reflecting the low-conductivity water from this tributary, with most notable reductions apparent at higher flows (August and May). In contrast, specific conductivity generally increased downstream of the other tributaries (e.g. Mangawara Stream and Whangamarino River). Specific conductivity increased rapidly near the upstream extent of saltwater intrusion, usually around 140 km from Karapiro dam, and for this reason, reaches from 141 – 143 km were not deemed “freshwater” and were excluded from further analysis (see Methods).

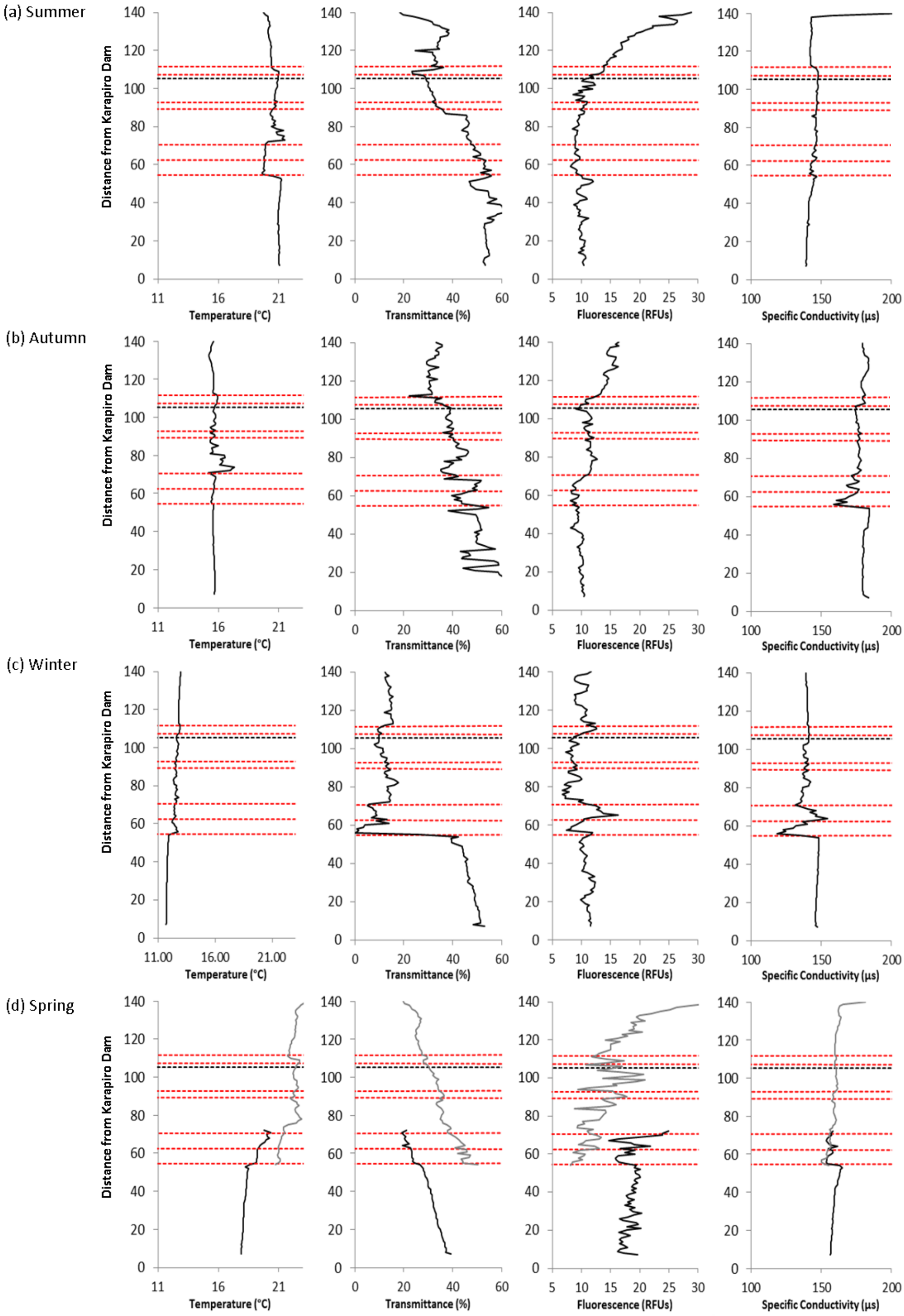


Figure 3.5. Surface water quality measurements collected using the Biofish during (a) summer (March 2010), (b) autumn (May 2010), (c) winter (August 2010) and (d) spring (November (black) / December 2010 (grey)). Dashed red lines represent locations of major tributaries to the lower Waikato Rive. Dashed black line indicates the estimated maximum tidal influence on river levels.

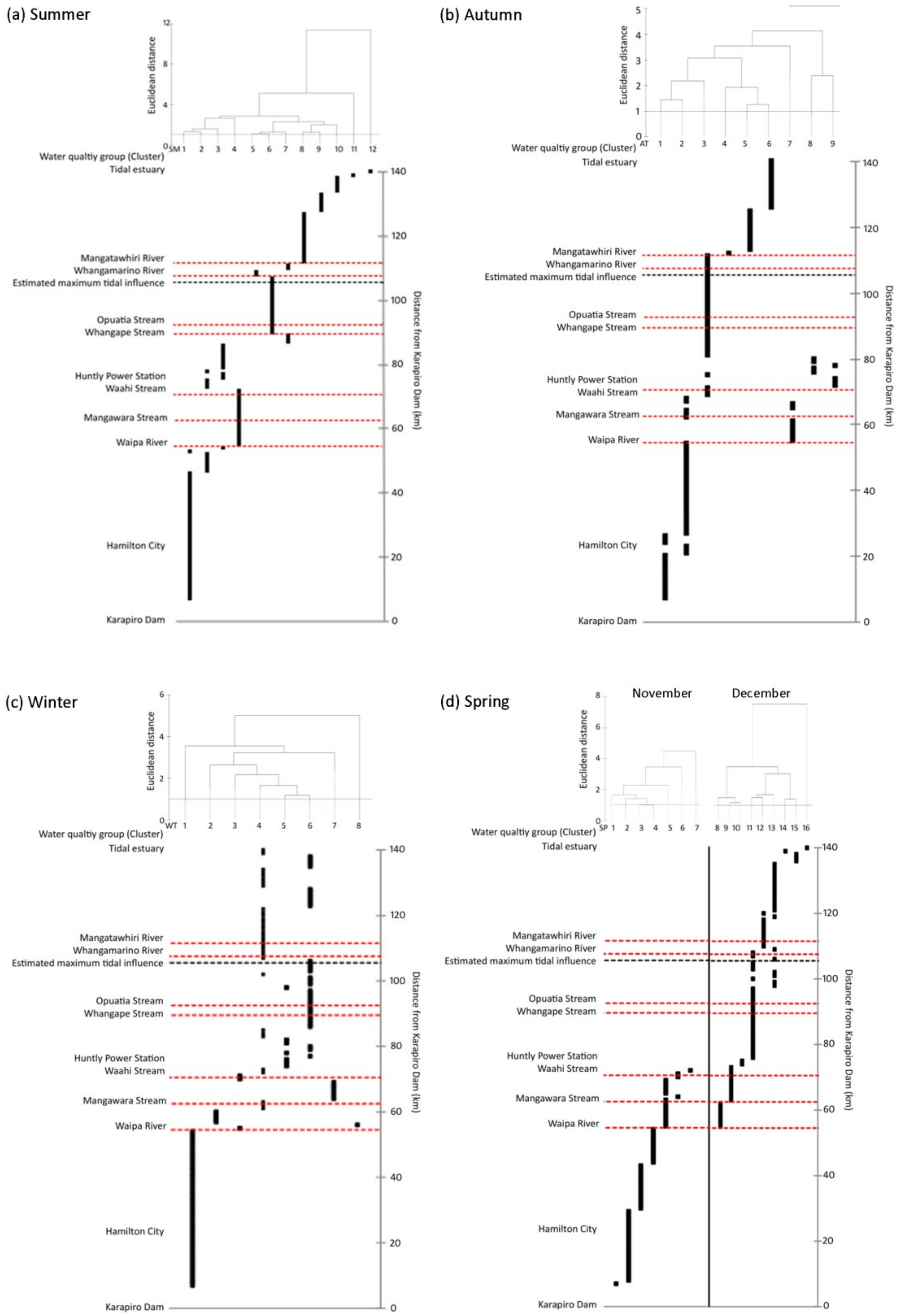


Figure 3.6. Dendrogram and spatial arrangement of significant groups identified by PRIMER SIMPROF and CLUSTER routines for surface water quality measurements collected using the Biofish during (a) summer (March 2010), (b) autumn (May 2010), (c) winter (August 2010) and (d) spring (November/December 2010, separated by black line). Dashed red lines represent locations of major tributaries to the lower Waikato Rive. Dashed black line indicates the estimated maximum tidal influence on river levels.

CLUSTER and SIMPROF analyses of seasonal water quality measurements identified a number of significant water quality reach types (groups) in each sampling month. The number of groups with significant internal structures was 23 in summer, 12 in autumn, 16 in winter and a total of 17 in spring, which when condensed to groups diverging at > 1 Euclidean distance unit final numbers in each group were 12, 9, 8 and 16, respectively (Fig. 3.6, Table 3.2 in supporting information). Cluster groups above the Waipa were generally unique to that part of the river, a pattern supported by the dendrograms in Fig. 3.6a-d whereby clusters above the Waipa confluence were generally more closely related to each other than those below. SIMPER analyses indicated that clusters of river reaches above the Waipa River could generally be distinguished from those immediately below, as they were associated with higher water clarity and specific conductivity (Table 3.2 in supporting information). Although multiple significant clusters often occurred above the Waipa confluence, the Euclidean distance between adjacent reaches and cluster groups was usually less than those observed below the Waipa confluence (Fig. 3.6a,b). However, at lower flows (March and May) some clusters downstream of the Waipa were also closely related to those above, and some water quality reach types occurred both above and below the Waipa confluence. This was most apparent during autumn low flows when the Waipa contributed a smaller relative volume to the main stem flow. At this time, reaches more immediately downstream of the confluence belonged to a distinct cluster group, and the dominant cluster type from above the confluence reappeared further downstream. Conversely, during winter and spring when flows from the Waipa were high, groups above the confluence did not persist downstream (Fig. 3.6c,d).

Cluster groupings were often present downstream of tributary confluences, most notably the Waipa (driven by low water clarity and specific conductance as described above), but also for smaller tributaries such as the Mangawara Stream. Tributary confluences, other than the Waipa tended to belong to groups characterised by increased chlorophyll fluorescence and conductivity (Figs. 6 & 7). Unique groups did exist in the tidal freshwater section of the lower river, generally reflecting higher fluorescence measurements, and the upstream extent of groups unique to the tidally influenced region was greatest at low flows (March and May) (Fig. 3.6a,b). Potential anthropogenic disturbances were also detected, notably at Huntly where sites downstream often grouped separately (Fig. 3.6), driven by higher water temperatures, particularly at low flows (Fig. 3.7).

PCO of seasonal water quality measurements indicated that the 1st and 2nd axes explained between 70 and 90 % of the variation in each season, ranging from c. 40-80 % on the 1st axis and c. 10-30 % on the 2nd axis (Fig. 3.7). The 3rd PCO axis generally explained <10 %, except in autumn when it explained similar variation to the second axis (c. 25 %). In general river reaches above the Waipa confluence grouped away from those below in PCO plots in each season (Figs. 6 & 7), usually due to changes in water clarity. This clustering of points was most pronounced during high winter and spring flows reflecting marked differences in water clarity, as suggested by SIMPER analyses and Spearman correlation coefficients (Fig. 3.7c,d). Reaches immediately below the Waipa confluence also tended to reflect changes in specific conductivity and water temperature, as water from the Waipa mixes with water in the main stem (Fig. 3.5). Except during winter, reach types typical of the tidally influenced section of river grouped away from most of those upstream, apparently due to increasing fluorescence (Fig. 3.7), while specific conductivity at river reach 140 during summer appears to indicate a possible interface between the saline intrusion and freshwater (Fig. 3.7a). The upstream extent of tidal influence on groups varied with flow conditions, and during low autumn flows 2 reaches typically associated with the downstream end of the fluvial section aligned more closely with tidally influenced river reaches (Fig. 3.7b). This indicates that the upstream extent and magnitude of tidal cycle effects on river water quality are likely to vary between seasons in response to flow conditions upstream. During high winter flows, however, there appears to be little effect of the tidal cycle on water quality measurements at the end of the surveyed section of river, 140 km from Karapiro dam. Reaches influenced by higher than average water temperatures were evident at low flows (Fig. 3.7a,b) and belonged to cluster groups immediately downstream of Huntly (Fig. 3.6a,b). Conversely, tributaries appeared to contribute cooler water to the main stem at during summer and autumn (Fig. 3.5).

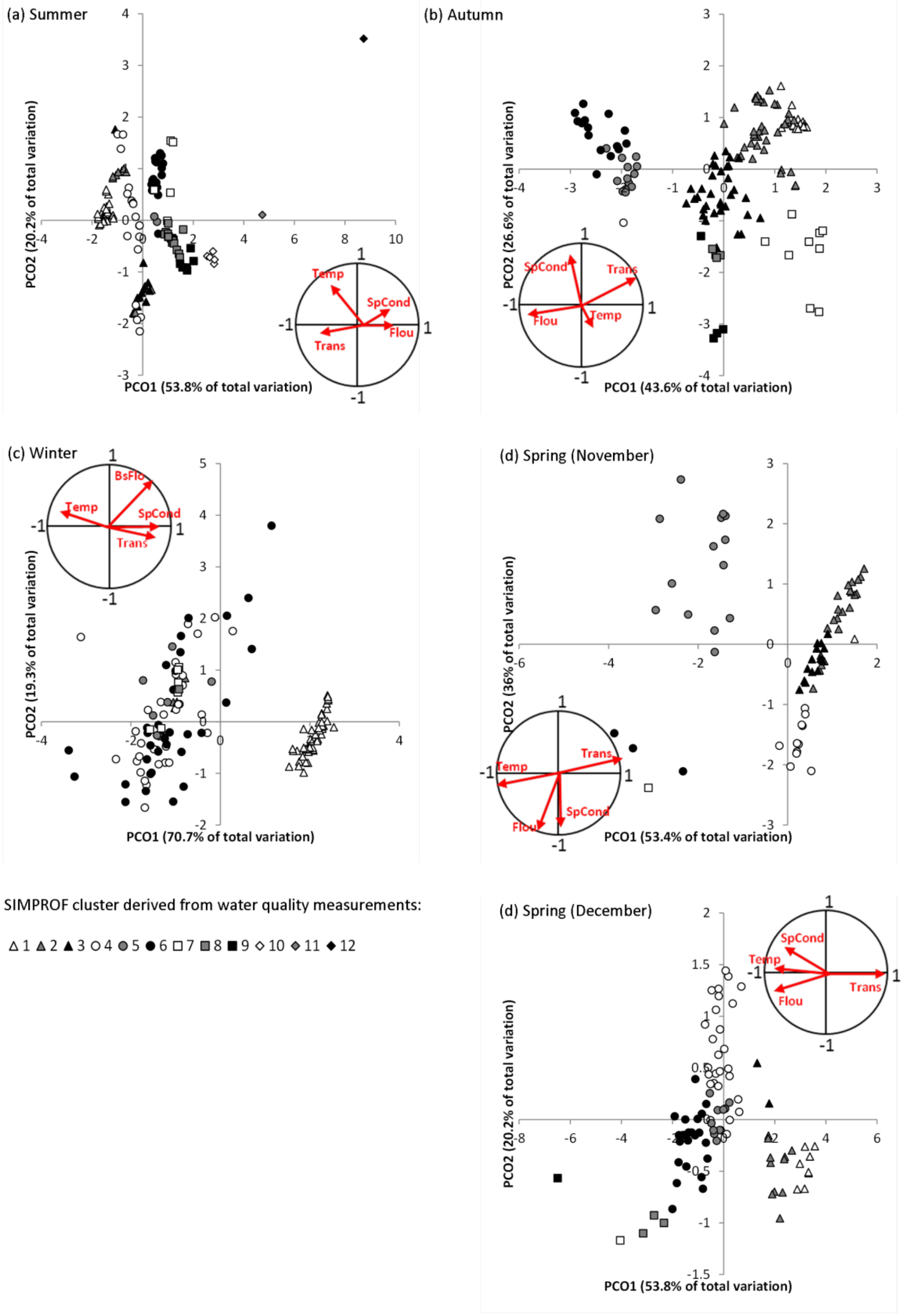


Figure 3.7. Principal coordinates ordination of two most important axes of water quality measurements collected using the Biofish during (a) March, (b) May, (c) August, and the two spring surveys (d) November, and (e) December. Symbols denote groups identified by SIMPROF analyses (up to 14). Inserts represent vector diagrams of Spearman correlation coefficients (red arrows) for water clarity (Trans), specific conductance (SpCond), chlorophyll fluorescence (Flou) and water temperature (Temp).

3.5 Discussion

3.5.1 Identification of zones

Based on this combination of physical complexity and water quality analyses the lower Waikato River can be divided into three physico-chemically distinct zones, although the divisions are not necessarily abrupt and the extent of transition between them can depend on the variables used or season in question. These zones support patterns identified by previous measurements of turbidity and concentrations of nitrogen, phosphorus, water column chlorophyll *a* and dissolved colour (Vant, 2010). Spatial patterns of phytoplankton biomass in the lower Waikato River are also similar to those observed by Lam (1981) in that they peaked in the tidal freshwater section of the river and decreased immediately below the Waipa River.

The first zone identified is c. 54 km in length and extends as far downstream as the Waipa River confluence at Ngaruawahia (Fig. 3.1). Although I did not survey the 6 km immediately below Karapiro dam due to navigation hazards, this zone can likely be expanded to include this stretch of river, as river width and channel shape are similar to those at the upstream end of the surveyed section. This 'constrained' zone is characterised by a deeper than average, generally narrower, steeper-sided channel lacking in lateral complexity (P1 and P2 reach types). Low values for suspended solids in the constrained zone reflect retention of sediment by upstream dams, which has also led to increased bed incision downstream (Hicks & Hill, 2010). Flow variability in this section of river is regulated by the dam (Fig. 3.1a) and high water clarity partly reflects the retention of suspended solids in the hydro lakes (Hicks & Hill, 2010). A second, 'unconstrained' zone is c. 58 km in length and begins at the Waipa confluence and extends to downstream of the Mangatawhiri confluence (Fig. 3.1d) This zone includes the confluences of all six other major tributaries flowing across the former floodplain of the lower river, and is characterised by reduced water clarity, shallow depth (c. 2-3 m), a wide channel (c. 200-500 m), and regular lateral features such as islands and side arms (mostly P3 and P4). Boundaries between strictly fluvial and 'tidal freshwater' zones are likely to be transitional, variable and sometimes indistinct due to the nature and strength of daily tidal cycles, the upstream extent of which may have been increased by channel dredging, and high flow conditions (Fig. 3.1c). The third zone identified is a 'tidal freshwater zone' that is c. 28 km in length and extends to the upper limit of salt water intrusion (140 km downstream from Karapiro dam). Flow in this zone is influenced by daily water level fluctuations as a result of the tidal cycle (Fig. 3.1c), and algal biomass is generally high, likely due to increased water retention times as a result of the tidal cycle which may also have shaped the high lateral complexity, particularly in the delta. This zone has a high diversity of reach types (including representatives of P2-P4), and the channel is generally wide to very wide (often > 1 km width), with lateral features often abundant and becoming increasingly so with distance downstream (P5 to P7) (Fig. 3.3).

3.5.2 Comparison of physical and water quality analyses

Similar patterns were observed for reach types identified in both the physical and water quality analyses, in that reach types above the Waipa confluence tended to be unique and when they did recur below the confluence they tended to be uncommon. In terms of reaches defined by water quality analyses, these persisted only briefly downstream, while physical reach types reappeared briefly over 50 km downstream of the confluence within the extent of the tidal cycle. Similarly, at the downstream end and within the tidally influenced section of the river, particular water quality and physical reach types occurred (Fig. 3.6), while the variety of physical groups was also highest (Fig. 3.3). Where reach types identified in analyses of physical variables did reoccur throughout the river, they tended to reflect the dominant water quality cluster group in water quality analyses, as opposed to those of the same physical group, some distance away. However, given that physical channel and water quality management actions and targets may differ, spatial units (reach types) identified for each of these do not necessarily need to directly coincide from management or research perspectives, although both should be considered in decision making and experimental design.

3.5.3 Effects of tributaries

Significant changes in riverine characteristics, water quality in particular, can be caused by the joining of major tributaries (Rice et al., 2001; Rice et al., 2006; Rice et al., 2008). In my study there was a clear discontinuity between river reaches above and below the confluence of the largest tributary, the 5th order Waipa River, for all water quality measurements taken, particularly at high flows (winter and spring). Depending on the relative flow conditions in the main stem, minor discontinuities were also apparent around smaller tributaries, usually denoted by increased chlorophyll fluorescence or specific conductivity. Lake- and wetland-fed tributaries in particular tended to have localised positive effects on phytoplankton biomass in the main stem, while the Waipa tended to reduce chlorophyll fluorescence. The differential effects of tributaries on main stems, dependent on donor concentration of algae and magnitude of flow, has also been noted by other workers in terms of positive (Neal et al., 2006; Bukaveckas et al., 2011b) or negative (Descy et al., 1987) effects on main stem phytoplankton biomass. Direct human influences were also noted in the present study, in particular associated with the Huntly Power Station which discharges warm water to the river (Rutherford, 2010) and measurably increases water temperature (Fig. 3.5) leading to a significantly distinct group of reaches immediately downstream (Figs. 6 & 7). These smaller discontinuities, however, tended to produce localised clustering of SIMPER-identified groups, and reaches further downstream tended to belong to the predominant group upstream of the minor discontinuity. The distance downstream of tributaries, for which minor discontinuities in water quality measurements were observed in the main channel, will likely depend on flow volumes and velocities of both the contributing source and the receiving main channel (Rice et al., 2001; Rice et al., 2008). Therefore, these localised changes can be considered as ‘noise’ within a given river ‘link’, as defined by Rice et al. (2001) since they do not lead to a significant shift in overall main stem character. Nevertheless, major discontinuities caused by significant tributary contributions of flow and sediment, such as the Waipa confluence in this study, can significantly affect biological community spatial patterns and production (Rice et al., 2001).

3.5.4 Tidal hydrology

Tidal hydrology can be expected to have direct effects on river channel morphology and indirect effects on biological growth and production (Ensign et al., 2012). The effect of tidal cycles was evident on the freshwater section of the lower Waikato River, both in terms of physical complexity and water quality measurements, with clusters in the tidally influenced section of the river generally defined by greater river width, depth and shoreline complexity, and higher than mean seasonal chlorophyll fluorescence. In terms of physical complexity (channel morphology), some reach types (groups) identified in the SIMPROF and CLUSETR analyses occurred in both the fluvial and tidally influenced parts of the river, although the diversity of reach types was highest in the sections of the lower river downstream of the estimated upstream extent of tidal influence (Fig. 3.3b). Similar to studies of smaller coastal rivers, a significant divergence in river morphology began around a third of the way into the tidally influenced freshwater section (Ensign et al., 2012). It is also possible that developments such as channel modification and widening may have led to an increase in the upstream extent of the tidal influence by around 10 km, supported by observations made in the 1960s prior to channel deepening for flood control purposes that suggest historical tidal influence may have previously been closer to Tuakau (120 km from Karapiro Dam) (Van Kampen, 2010). Phytoplankton biomass, for which I used chlorophyll fluorescence as a surrogate, is strongly dependent on fluvial discharge and the residence time available for community development in tidally influenced freshwater sections of rivers (Neal et al., 2006). High biomass often occurs at low flows (Bennett et al., 1986; Schuchardt & Schirmer, 1991) when water travel times can be many times greater than in non-tidal river sections (Ensign et al., 2012). Production is also closely linked to channel form, with broad channels and extensive shallow lateral areas, such as those in the delta, providing favourable light and flow retention conditions for algal growth (Bukaveckas et al., 2011a).

3.5.5 Seasonal patterns

Seasonal patterns of environmental variables such as discharge and temperature play important roles in the ecological function of many large rivers. Substantial increases in sediment loads supplied by major tributaries may occur with seasonal high flows, while high flows in the main channel can also swamp the contributions of smaller tributaries (Boyer et al., 2010). Water temperature also plays an important role in primary production, with increased seasonal temperature and light availability linked to rates of photosynthesis, respiration and metabolism in other large lowland rivers (Descy et al., 1987). In my study and that of Lam (1981), measurements of phytoplankton biomass (chlorophyll fluorescence in my study), was recorded during summer and spring when water temperatures were warmest, particularly in the tidal freshwater zone. The abruptness or transitional nature of boundaries between different hydrological sections of the lower river differed between seasons, likely reflecting seasonal discharge and environmental patterns. The discontinuity between the river sections dominated by clear, dam-fed water of the Waikato River and the Waipa River which contributes significant amounts of flow and sediment at high flows (Chapman, 1996; Brown, 2010), was most distinct during winter and spring (high flows) and less so during summer and autumn (low flows). Tidal cycle fluctuations at Tuakau were greatest during months of lower fluvial flows (Fig. 3.1c), and this is reflected in the transition from fluvial to tidal water quality reach types being shortest and furthest upstream during summer and autumn (Fig. 3.3b), conversely during high winter flows a transition is almost undetectable and daily water level fluctuations were also small (Fig. 3.1c).

3.5.6 Conclusions

Large lowland rivers provide a challenging environment to study, particularly given their potentially large temporal and spatial heterogeneity. As demonstrated here, multivariate statistical approaches and geographic tools such as ArcGIS provide a powerful means for condensing spatially intensive datasets to guide identification of river zones for future ecological management and research. Zones were distinguished by both riverscape features and physico-chemical parameters, although these zones did not necessarily align. Lateral channel complexity and depth played an important role in shaping physical zones, while features such as large tributaries and tidal influences play significant roles in shaping water quality zones. The scale of these zones integrates an ecologically meaningful combination of properties that is likely to shape ecosystem processes such as energy transfer in food webs. The boundaries of these zones may have been different in the past and could change again as a result of ecological improvements to current land and flow management practices. Management objectives should reflect the dynamic spatial and temporal nature of rivers (Elosegi et al., 2010), which can create fuzzy or shifting boundaries between hydrogeomorphic units. The nature of channel complexity can change with flow conditions, and although this study did not address seasonal changes in lateral complexity as many features were derived from aerial photos, future use of satellite images taken during different seasons and flow conditions could be validated and used to quantify temporal variability in physical complexity metrics, which could be of use to river managers as recommended by the authors of the RCCR (O'Neill & Thorp, 2011). My results can also be seen in the context of a developed river, whereby the anthropogenic impacts such as large dams (increased water clarity and incision), thermal power stations (warm discharges), and land clearance for agriculture (suspended sediments and hydrological extremes) can have potentially significant effects on the character of a fluvial system and the composition of contemporary management units.

3.6 References

Amoros, C. & G. Bornette, 2002. Connectivity and biocomplexity in waterbodies of riverine floodplains. Freshwater Biology 47: 761-776.

Anderson, C. J. & B. G. Lockaby, 2012. Seasonal patterns of river connectivity and saltwater intrusion in tidal freshwater forested wetlands. River Research and Applications 28: 814-826.

Anderson, M. J., R. N. Gorley & K. R. Clarke, 2008. PERMANOVA+ for PRIMER: guide to software and statistical methods Primer-e, Plymouth, UK. 214 pp.

Benda, L., N. L. Poff, D. Miller, T. Dunne, G. Reeves, G. Pess & M. Pollock, 2004. The network dynamic hypothesis: how channel networks structure riverine habitats. Bioscience 54: 413-427.

Bennett, J. P., J. W. Woodward & D. J. Shultz, 1986. Effect of discharge on the chlorophyll a distribution in the tidally-influenced Potomac River. Estuaries 9: 250-260.

Boyer, C., P. M. Verhaar, A. G. Roy, P. M. Biron & J. Morin, 2010. Impacts of environmental changes on the hydrology and sedimentary processes at the confluence of St. Lawrence tributaries: potential effects on fluvial ecosystems. Hydrobiologia 647: 163-183.

Brown, E. J., 2010. Flow regime and water use. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, Hamilton, p 29-46.

Bukaveckas, P., L. Barry, M. Beckwith, V. David & B. Lederer, 2011a. Factors determining the location of the chlorophyll maximum and the fate of algal production within the tidal freshwater James River. Estuaries and Coasts 34: 569-582.

Bukaveckas, P., A. MacDonald, A. Aufdenkampe, J. Chick, J. Havel, R. Schultz, T. Angradi, D. Bolgrien, T. Jicha & D. Taylor, 2011b. Phytoplankton abundance and contributions to suspended particulate matter in the Ohio, Upper Mississippi and Missouri Rivers. Aquatic Sciences 73: 419-436.

Bunn, S. E. & A. H. Arthington, 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management 30: 492-507.

Chang, H., 2008. Spatial analysis of water quality trends in the Han River basin, South Korea. Water Research 42: 3285-3304.

Chapman, M. A., 1996. Human impacts on the Waikato river system, New Zealand. GeoJournal 40: 85-99.

Collier, K. J., E. M. Watene-Rawiri & J. D. McCraw, 2010. Geography and history. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, p 1-12.

Collier, K. J., J. E. Clapcott, B. O. David, R. G. Death, D. Kelly, J. R. Leathwick & R. G. Young, 2012. Macroinvertebrate pressure relationships in boatable New Zealand rivers: Influence of underlying environment and sampling substrate. River Research and Applications 29: 645–659.

Cortez, D. P., I. O. Growns, S. M. Mitrovic & R. P. Lim, 2012. Effects of a gradient in river regulation on the longitudinal trends in water quality and benthic algal and macroinvertebrate assemblages in the Hunter River, Australia. Marine and Freshwater Research 63: 494-504.

Descy, J. P., P. Servais, J. S. Smitz, G. Billen & E. Everbecq, 1987. Phytoplankton biomass and production in the river meuse (Belgium). Water Research 21: 1557-1566.

Doi, H., K. H. Chang, T. Ando, H. Imai, S. Nakano, A. Kajimoto & I. Katano, 2008. Drifting plankton from a reservoir subsidize downstream food webs and alter community structure. Oecologia 156: 363-371.

Dolédec, S., N. Phillips & C. Townsend, 2011. Invertebrate community responses to land use at a broad spatial scale: trait and taxonomic measures compared in New Zealand rivers. Freshwater Biology 56: 1670-1688.

Dynesius, M. & C. Nilsson, 1994. Fragmentation and flow regulation of river systems in the northern third of the world. Science 266: 753-762.

Elosegi, A., J. Díez & M. Mutz, 2010. Effects of hydromorphological integrity on biodiversity and functioning of river ecosystems. Hydrobiologia 657: 199-215.

Ensign, S. H., M. W. Doyle & M. F. Piehler, 2012. Tidal geomorphology affects phytoplankton at the transition from forested streams to tidal rivers. Freshwater Biology 57: 2141–2155.

Eyre, B. D. & P. Pepperell, 1999. A spatially intensive approach to water quality monitoring in the Rous River catchment , NSW , Australia. Journal of Environmental Management 56: 97-118.

Fisher, S. J., M. L. Brown & D. W. Willis, 2001. Temporal food web variability in an upper Missouri River backwater: energy origination points and transfer mechanisms. Ecology of Freshwater Fish 10: 154-167.

Górski, K., L. V. van den Bosch, K. E. van de Wolfshaar, H. Middelkoop, L. A. J. Nagelkerke, O. V. Filippov, D. V. Zolotarev, S. V. Yakovlev, A. E. Minin, H. V. winter, J. J. De Leeuw, A. D. Buijse & J. A. J. Verreth, 2011. Post-damming flow regime development in a large lowland river (Volga, Russian Federation): Implications for floodplain inundation and fisheries. River Research and Applications 28: 1121–1134.

Hadwen, W. L., C. S. Fellows, D. P. Westhorpe, G. N. Rees, S. M. Mitrovic, B. Taylor, D. S. Baldwin, E. Silvester & R. Croome, 2010. Longitudinal trends in river functioning: patterns of nutrient and carbon processing in three Australian rivers. River Research and Applications 26: 1129-1152.

Hamilton, D. P., K. R. O'Brien, M. A. Burford, J. D. Brookes & C. G. McBride, 2010. Vertical distributions of chlorphyll in deep, warm monomictic lakes. Aquatic Sciences 72: 295-307.

Hicks, D. M. & R. B. Hill, 2010. Sediment regime: sources, transport and changes in the riverbed. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, Hamilton, p 71-92.

Howarth, R. W., R. Schneider & D. Swaney, 1996. Metabolism and organic carbon fluxes in the tidal freshwater Hudson River. Estuaries and Coasts 19: 848-865.

Johnson, B. L., W. B. Richardson & T. J. Naimo, 1995. Past, present, and future concepts in large river ecology. Bioscience 45: 134-141.

Junk, W. J., P. B. Bayley & R. E. Sparks, 1989. The flood pulse concept in river-floodplain systems. In Dodge, DP (ed) Proceedings of the International Large River Symposium, Canadian Special Publication of Fisheries and Aquatic Sciences 106: 110-127.

Kiffney, P. M., C. M. Greene, J. E. Hall & J. R. Davies, 2006. Tributary streams create serial discontinuities in habitat, biological productivity, and diversity in mainstem rivers. Canadian Journal of Fisheries and Aquatic Sciences 63: 2518-2530.

Lam, C. W. Y., 1981. Ecological studies of phytoplankton in the Waikato River and its catchment. New Zealand Journal of Marine and Freshwater Research 15: 95-103.

McBride, C., D. Hamilton, M. Gibbs, P. White & L. Stewart, 2008. BioFish survey of Lake Taupo, 2006.

Mulholland, W. M., 2010. Box 2.2: History of the lower Waikato Flood Protection Scheme. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, Hamilton, p 16.

Neal, C., J. Hilton, A. J. Wade, M. Neal & H. Wickham, 2006. Chlorophyll-a in the rivers of eastern England. Science of the Total Environment 365: 84-104.

Nilsson, C., C. A. Reidy, M. Dynesius & C. Revenga, 2005. Fragmentation and flow regulation of the world's large river systems. Science 308: 405-408.

O'Neill, B. J. & J. H. Thorp, 2011. A simple channel complexity metric for analyzing river ecosystem responses. River Systems 19: 327-335.

Parsons, M. & M. C. Thoms, 2007. Hierarchical patterns of physical - biological associations in river ecosystems. Geomorphology 89: 127-146.

Poff, N. L. & J. V. Ward, 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. Canadian Journal of Fisheries and Aquatic Sciences 46: 1805-1818.

Poole, G. C., 2002. Fluvial landscape ecology: addressing uniqueness within the river discontinuum. Freshwater Biology 47: 641-660.

Power, M. E. & W. E. Dietrich, 2002. Food webs in river networks. Ecological Research 17: 451-471.

Power, M. E., A. Sun, G. Parker, W. E. Dietrich & J. T. Wootton, 1995. Hydraulic food-chain models. Bioscience 45: 159-167.

Rice, S. P., M. T. Greenwood & C. B. Joyce, 2001. Tributaries, sediment sources, and the longitudinal organisation of macroinvertebrate fauna along river systems. Canadian Journal of Fisheries and Aquatic Sciences 58: 824-840.

Rice, S. P., R. I. Fergusson & T. B. Hoey, 2006. Tributary control of physical heterogeneity and biological diversity at river confluences. Canadian Journal of Fisheries and Aquatic Sciences 63: 2553-2566.

Rice, S. P., P. Kiffney, G. Correigh & G. R. Pess, 2008. The ecological importance of tributaries and confluences. In Rice, S. P., A. G. Roy & B. L. Rhoads (eds), River Confluences, Tributaries and the Fluvial Network. John Wiley & Sons, Ltd., Chichister, p 209-242.

Roach, K. A., J. H. Thorp & M. D. Delong, 2009a. Influence of lateral gradients of hydrologic connectivity on trophic positions of fishes in the Upper Mississippi River. Freshwater Biology 54: 607-620.

Roach, K. A., K. O. Winemiller, C. A. Layman & S. C. Zeug, 2009b. Consistent trophic patterns among fishes in lagoon and channel habitats of a tropical floodplain river: Evidence from stable isotopes. Acta Oecologica-International Journal of Ecology 35: 513-522.

Rosales, J., L. Blanco-Belmonte & C. Bradley, 2007. Hydrogeomorphological and ecological interactions in tropical floodplains: The significance of confluence zones in the Orinoco Basin, Venezuela. In P. J. Wood, D. M. Hannah & J. P. Sadler (eds), Hydroecology and Ecohydrology: Past, present and future John Wiley & Sons Ltd., Chichester, p 295-316.

Rutherford, J. C., 2010. Water temperature and mixing. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, Hamilton, p 47-70.

Sabo, J. L., J. C. Finlay, T. Kennedy & D. M. Post, 2010. The role of discharge variation in scaling of drainage area and food chain length in rivers. Science 330: 965-967.

Schiemer, F. & T. Hein, 2007. The ecological significance of hydraulic retention zones. In Wood, P. J., D. M. Hannah & J. P. Sadler (eds), Hydroecology and Ecohydrology: Past, present and future. John Wiley & Sons, Ltd, Chichester, p 405-420.

Schiemer, F., H. Keckeis, W. Reckendorfer & G. Winkler, 2001a. The "inshore retention concept" and its significance for large rivers. Large Rivers 12: 509-516.

Schiemer, F., H. Keckeis, G. Winkler & L. Flore, 2001b. Large rivers: the relevance of ecotonal structure and hydrological properties for the fish fauna. Large Rivers 12: 487-508.

Schuchardt, B. & M. Schirmer, 1991. Phytoplankton maxima in the tidal freshwater reaches of two coastal plain estuaries. Estuarine, Coastal and Shelf Science 32: 187-206.

Speirs, D. A., D. G. Allen, R. M. Kelleher, M. D. Lake, A. N. Marchant, K. A. Mayes, E. M. Watene-Rawiri & B. J. Wilson, 2010. River management. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, Hamilton, p 13-26.

Stanford, J. A. & J. V. Ward, 2001. Revisting the serial discontinuity concept. Regulated Rivers: Research & Management 17: 303-310.

Thoms, M. C. & M. Parsons, 2002. Eco-geomorphology: an interdisciplinary approach to river science. International Association of Hydrological Sciences, Publication: 113-119.

Thorp, J. H. & M. D. Delong, 2002. Dominance of autochthonous autotrophic carbon in food webs of heterotrophic rivers. Oikos 96: 543-550.

Thorp, J. H., M. C. Thoms & M. D. Delong, 2006. The riverine ecosystem synthesis: Biocomplexity in river networks across space and time. River Research and Applications 22: 123-147.

Thorp, J. H., M. C. Thoms & M. D. Delong, 2008. The Riverine Ecosystem Synthesis: Towards conceptual cohesiveness in river science. Elsevier.

Tockner, K., F. Malard & J. V. Ward, 2000. An extension of the flood pulse concept. Hydrological Processes 14: 2861-2883.

Van Kampen, J., 2010. Flow river flow. Jack Van Kampen, Manukau.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell & C. E. Cushing, 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37: 130-137.

Vant, W. N., 2010. Water quality. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, Hamilton, p 93-114.

Varol, M., B. Gökot, A. Bekleyen & B. Şen, 2011. Water quality assessment and apportionment of pollution sources of Tigris River (Turkey) using multivariate statistical techniques—a case study. River Research and Applications 28: 1428–1438.

Vega, M., R. Pardo, E. Barrado & L. Deban, 1998. Assessment of seasonal and polluting effects on the quality of river water by exploratory data analysis. Water Research 32: 3581-3592.

Ward, J. V., 1989. The four-dimensional nature of lotic ecosystems. Journal of the North American Benthological Society 8: 2-8.

Ward, J. V. & J. A. Stanford, 1983. The serial dicontinuity concept of lotic ecosystems. In Fontaine, T. D. & S. M. Bartell (eds), Dynamics of lotic ecosystems. Ann Arbor Scientific Publishers, Ann Arbor, MI, p 29-42.

Winemiller, K. O., A. S. Flecker & D. J. Hoeinghaus, 2010. Patch dynamics and environmental heterogeneity in lotic ecosystems. Journal of the North American Benthological Society 29: 84-99.

Woodward, G. & A. G. Hildrew, 2002. Food web structure in riverine landscapes. Freshwater Biology 47: 777-798.

Wunderlin, D. A., M. D. P. Diaz, M. V. Ame, S. F. Pesce & A. C. Hued, 2001. Pattern recognition techniques for the evaluation of spatial and temporal variations in water quality. A case study: Suquia River basin (Cordoba-Argentina). Water Research 35: 2881-2894.

Zeug, S. C. & K. O. Winemiller, 2008. Evidence supporting the importance of terrestrial carbon in a large-river food web. Ecology 89: 1733-1743.

3.7 Supporting Information

Table 3.2. Summary characteristics of seasonal water quality clusters identified using SIMPROF routines (with a Euclidean distance of >1 between reach types) for summer (SM), autumn (AT), winter (WT) and spring (SP), and presented in Figs. 3.6 and 3.7.

Cluster	n	Temperature (°C)	Specific conductance (µS/cm)	Fluorescence (RFUs)	% Transmittance
SM1	37	20.99 (0.04)	140.33 (0.73)	10.03 (0.54)	55.2 (2.56)
SM2	4	21.14 (0.04)	143.34 (0.92)	9.59 (0.48)	54.19 (0.77)
SM3	6	21.19 (0.01)	144.18 (0.67)	10.68 (1.16)	48.35 (1.39)
SM4	4	21.41 (0.09)	147.05 (0.11)	9.04 (0.24)	45.59 (1.28)
SM5	11	20.6 (0.19)	146.05 (0.84)	9.38 (0.4)	46.9 (3.06)
SM6	18	19.82 (0.1)	144.44 (1.63)	9.01 (0.43)	51.19 (2.51)
SM7	2	21.03 (0.01)	147.94 (0.05)	13.39 (0.44)	23.41 (0.15)
SM8	18	20.79 (0.12)	147.29 (0.44)	10.58 (1.05)	31.16 (1.73)
SM9	5	20.42 (0.13)	146.7 (0.5)	11.69 (1.98)	35.49 (2.1)
SM10	16	20.34 (0.07)	142.62 (0.43)	16.05 (1.35)	32.84 (2.44)
SM11	6	20.16 (0.08)	143.26 (0.22)	20.71 (1.36)	37.06 (1.61)
SM12	5	20.15 (0.06)	142.9 (0.09)	25.36 (1.3)	28.75 (3.64)
SM13	1	19.88 (0)	157.54 (0)	27.2 (0)	19.71 (0)
SM14	1	19.72 (0)	206.66 (0)	28.83 (0)	18.38 (0)
Total	134	20.62 (0.47)	144.22 (6.18)	12.05 (4.52)	43.91 (10.88)

Cluster	n	Temperature (°C)	Specific conductance (µS/cm)	Fluorescence (RFUs)	% Transmittance
AT1	17	15.7 (0.03)	179.99 (1.05)	10.15 (0.23)	60.68 (1.68)
AT2	36	15.6 (0.05)	180.71 (2.52)	9.5 (0.56)	49.32 (3.68)
AT3	35	15.64 (0.22)	176.28 (1.96)	11.06 (0.71)	39.53 (3.26)
AT4	1	15.85 (0)	179.57 (0)	12.81 (0)	22.13 (0)
AT5	13	15.59 (0.03)	180.02 (1.36)	14.03 (0.45)	30.89 (1.09)
AT6	15	15.38 (0.1)	181.92 (1.86)	15.42 (0.69)	32.71 (2.15)
AT7	9	15.52 (0.1)	167.03 (4.33)	8.77 (0.51)	44.69 (3.71)
AT8	4	16.44 (0.12)	177.47 (0.93)	12.08 (0.45)	41.07 (2.05)
AT9	4	16.89 (0.52)	177.37 (1.03)	11.62 (0.16)	35.76 (0.67)
Total	134	15.66 (0.31)	178.41 (4.23)	11.21 (2.12)	43.39 (9.66)

Cluster	n	Temperature (°C)	Specific conductance (µS/cm)	Fluorescence (RFUs)	% Transmittance
WT1	48	11.8 (0.06)	147.23 (0.79)	47.03 (3.28)	10.95 (0.75)
WT2	4	12.54 (0.11)	127.46 (4.35)	2.54 (1.64)	8.22 (0.74)
WT3	3	12.45 (0.15)	134.12 (2.17)	12.29 (11.9)	11.6 (0.81)
WT4	33	12.75 (0.21)	140.11 (2)	13.23 (2.29)	10.58 (0.83)
WT5	7	12.58 (0.15)	138.1 (2.53)	14.63 (1.98)	7.15 (0.35)
WT6	32	12.71 (0.15)	139.09 (1.47)	12.64 (1.75)	8.56 (0.49)
WT7	6	12.47 (0.07)	146.07 (4.84)	8.04 (0.89)	13.47 (1.54)
WT8	1	12.77 (0)	118.7 (0)	0.21 (0)	11.91 (0)
Total	134	12.37 (0.45)	141.9 (5.43)	10.14 (1.61)	24.6 (17.22)

Cluster	n	Temperature (°C)	Specific conductance (µS/cm)	Fluorescence (RFUs)	% Transmittance
SP1	1	17.88 (0)	156.7 (0)	19.59 (0)	39.43 (0)
SP2	22	18 (0.07)	157.64 (0.5)	17.75 (1.27)	35.2 (1.48)
SP3	14	18.2 (0.09)	159.43 (0.44)	18.5 (0.61)	31.56 (0.8)
SP4	11	18.39 (0.1)	162.98 (1.04)	19.45 (0.42)	28.67 (1.05)
SP5	14	19.47 (0.38)	155.25 (1.54)	17.32 (1.53)	22.64 (1.31)
SP6	3	19.93 (0.43)	158.71 (2.62)	23.19 (1.2)	19.42 (0.26)
SP7	1	19.77 (0)	158.57 (0)	24.94 (0)	21.06 (0)
Total	66	18.53 (0.69)	158.45 (2.67)	18.48 (1.86)	29.81 (5.54)

Cluster	n	Temperature (°C)	Specific conductance (µS/cm)	Fluorescence (RFUs)	% Transmittance
SP8	8	21 (0.09)	152.87 (1.9)	9.49 (0.93)	44.96 (1.81)
SP9	11	21.22 (0.17)	156.28 (0.56)	11.74 (1.25)	41.17 (2.44)
SP10	2	21.6 (0.26)	158.33 (0.24)	9.3 (0.08)	38.33 (1.12)
SP11	28	22.44 (0.21)	159.9 (1.08)	13.76 (2.32)	34.03 (2.26)
SP12	10	21.93 (0.12)	160.09 (0.35)	14.02 (1.16)	27.15 (1.44)
SP13	22	22.39 (0.14)	161.54 (1.31)	19.17 (1.83)	27.41 (2.99)
SP14	1	23.06 (0)	165.52 (0)	30.95 (0)	20.4 (0)
SP15	3	22.68 (0.18)	162.59 (0.41)	26.65 (1.73)	22.83 (0.48)
SP16	1	23.24 (0)	181.64 (0)	31.38 (0)	19.72 (0)
Total	87	22.08 (0.59)	159.6 (3.79)	15.27 (4.9)	32.85 (6.92)

4 Spatial and temporal patterns of carbon flow in a temperate large river food web

4.1 Abstract

Using natural abundances of stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes, I quantified spatial and temporal patterns of carbon flow through the main channel food web in the lowland section of New Zealand's longest river, the Waikato River. The study was undertaken with the objective of determining whether the Waikato River conforms to contemporary theoretical concepts regarding carbon flow in large river food webs. Potential organic carbon sources and invertebrate and fish consumers were sampled from three different hydrogeomorphic zones on six occasions, representing a range of seasonal and flow conditions. In line with the predictions of the Riverine Productivity Model and Riverine Ecosystem Synthesis, autochthonous algae and biofilms were the most important basal carbon source contributing to consumer biomass. These were often supported by C_3 aquatic macrophytes and allochthonous C_3 riparian plants. The relative importance of organic carbon sources differed between zones and appeared to change depending on season, presumably in response to water temperature and flow, particularly in the unconstrained zone of the lower river. I also demonstrate that to draw robust conclusions, consideration must be given to quantifying the isotopic signatures of organisms lower in the food web, as these can change significantly between sampling times and hydrogeomorphic zones.

4.2 Introduction

Despite the importance of large rivers to human societies and the pressures imparted on them by development (Allan & Flecker, 1993; Nilsson et al., 2005; Vörösmarty et al., 2010), the understanding of food web processes in these ecosystems is still relatively limited compared with wadeable streams (Sedell et al., 1989). Food webs describe the trophic interactions between consumers and resources associated with the transfer and utilisation of energy (carbon) and nutrients (Woodward & Hildrew, 2002; de Ruiter et al., 2005). They also provide an understanding of the interrelationships between community dynamics, stability and ecosystem function, as well as how these are influenced by environmental change and disturbance (de Ruiter et al., 2005). In recent decades, technological and theoretical developments have led to increased scientific attention directed towards the physical and biological processes which underpin large river ecosystems (see Thorp et al., 2008). Longitudinal patterns in the physical and biological nature of rivers, and the associated changes in ecosystem function and community structure from headwaters to the sea, are of particular interest (Power & Dietrich, 2002). However, the integration of patch dynamics, geomorphology and landscape ecology have expanded the scientific focus beyond a river continuum approach (Winemiller et al., 2010) to include a view of rivers made up of fluvial geomorphic units whose spatial arrangement can be an important driver of river food webs and processes (Thorp et al., 2006, 2008).

Studies that address energy flow through large river food webs are important as they can identify specific habitats and energy sources important for riverine productivity, and can lead to improved management and restoration of lowland floodplain rivers (Johnson et al., 1995; Thorp et al., 2006, 2008). Different organic carbon sources have been ascribed the key role of supporting large river food webs by different concepts. The River Continuum Concept (RCC, Vannote et al., 1980) proposes that the main source of carbon comes from processed organic matter transported from upstream, as the relative availability of carbon from local riparian areas, and algal and macrophyte productivity becomes reduced due to increasing downstream turbidity and channel width of most large rivers. The Flood Pulse Concept (FPC, Junk et al., 1989) emphasises that in large rivers with unaltered floodplains and predictable, seasonal flood pulses (e.g. some tropical rivers), aquatic food webs derive the majority of their organic carbon from terrestrial sources made available by floods (Junk et al., 1989; Junk & Wantzen, 2004). In contrast, the Riverine Productivity Model (RPM, Thorp & Delong, 1994, 2002) emphasises the importance of autochthonous primary production to overall metazoan productivity through an algal-grazer food pathway, across a range of channel types and climates while acknowledging that local riparian inputs are likely to be seasonally important to some species dwelling in littoral habitats (Thorp & Delong., 2002). The Riverine Ecosystem Synthesis (RES, Thorp et al., 2006; Thorp et al., 2008) expands on the RPM such that primary production within large rivers will depend on the hydrogeomorphic characteristics of functional process zones (e.g. hydraulic retention, main stem connectivity, geomorphic complexity and potential for lateral interaction) (Thorp et al., 2006, 2008).

Empirical evidence supporting the significance of different carbon sources to riverine food webs is often based on stable isotope analysis (SIA) (e.g. Thorp et al., 1998; Delong et al., 2001; Zeug et al., 2008) which provides a time-integrated measure of carbon flow and trophic interactions in food webs (Post, 2002). The ratio of ^{13}C to ^{12}C isotopes ($\delta^{13}C$) is used to distinguish between different organic carbon sources (e.g. terrestrial and aquatic plants), and can be used to infer energy flow through food webs (Fry & Sherr, 1989; McCutchan et al., 2003). Meanwhile, the ratio of ^{15}N to ^{14}N isotopes ($\delta^{15}N$) can be used to infer the number of trophic steps between an organism and its diet (Post, 2002; McCutchan et al., 2003). The use of multiple isotopes in unison can strengthen the discrimination between potential food sources, for example where detrital (riparian vegetation) and littoral (benthic algae) $\delta^{13}C$ signatures overlap (France, 1997; Finlay, 2001). The isotopic signatures of potentially important aquatic primary producers, such as phytoplankton and macrophytes, can vary across time (e.g. between seasons) and space (e.g. between fluvial units) (Boon & Bunn, 1994; Doucett et al., 1996). Therefore, capturing the potential variability of primary producer isotopic signatures should be incorporated into research methodologies to enable robust estimates of food web properties in aquatic ecosystems (France, 1995b; McCutchan & Lewis, 2002; Hadwen et al., 2010a). Primary consumers can provide reliable estimates of the isotopic ratios of basal carbon resources, as they tend to integrate both temporal and spatial variation in the isotopic signatures of primary producers (Cabana & Rasmussen, 1996; Vander Zanden & Rasmussen, 1999; Layman et al., 2005).

Knowledge of carbon flow in large river food webs comes mostly from studies of North (e.g. Thorp et al., 1998; Herwig et al., 2007; Delong 2010) and South (e.g. Hoeinghaus et al., 2007; Jepsen & Winemiller 2007) American rivers. In addition, a growing body of research from Australian river systems has provided valuable information on food web properties across a range of arid (e.g. Bunn et al., 2003; Burford et al., 2008; Leigh et al., 2010b) and tropical (e.g. Douglas et al., 2005; Hunt et al., 2011) climates. Temperate southern hemisphere rivers, such as those in parts of southern Australia and New Zealand, have naturally low fish diversity with few piscivorous species and dominance by diadromous life-histories (McDowall 2000). Moreover, several northern hemisphere fish species have become established and proliferate in New Zealand's lowland waterways, although the role that these species play in riverine food webs is not well understood. As a result of development for agriculture the once evergreen riparian zones of lowland New Zealand rivers are now dominated by introduced, deciduous tree species (e.g. *Salix* spp.), typical of many northern hemisphere river systems. Consequently, inputs of allochthonous leaf litter tend to occur as seasonal pulses during autumn, prior to high winter rainfall. These changes, along with development for hydroelectric power generation, flood regulation and enrichment from agricultural runoff, have resulted in a complex array of natural and anthropogenic factors that potentially interact to influence carbon availability and utilisation in aquatic food webs of New Zealand rivers.

The aim of this study was to test predictions about carbon sources supporting large river food webs, from concepts largely developed around large temperate and tropical rivers in the Americas (e.g. the RCC, FPC and RPM), in the context of a large, temperate southern hemisphere river. A growing pool of evidence from studies using SIA across a range of climates and hydrogeomorphologies suggests that autochthonous algal sources are the primary carbon source supporting the majority of metazoan production in large river food webs (see Pingram et al., 2012). Therefore, it was first hypothesised that the majority of carbon fuelling littoral, main-channel food webs would be derived from autochthonous suspended and benthic algae, in line with the revised RPM (Thorp & Delong, 2002). Secondly, I hypothesised that allochthonous riparian carbon contributions would increase in importance in the more hydrogeomorphically complex unconstrained and tidal sections of the lower Waikato River, due to increased interaction with floodplains and other lateral habitats. To address these hypotheses, I (i) used SIA of carbon (δ^{13}C) and nitrogen (δ^{15}N) isotopes to distinguish different potential organic carbon sources; (ii) quantified spatial and temporal differences in stable isotope signatures of basal and consumers in three distinct hydrogeomorphic zones covering the length of the lower Waikato River; and (iii) estimated the relative contributions of sampled carbon sources to consumers in different seasons corresponding to high and low-flow conditions.

4.3 Methods

4.3.1 Study area

The Waikato River is New Zealand's longest river and flows in a roughly northerly direction for c. 442 km from its headwaters above Lake Taupo to the Tasman Sea at Port Waikato (Collier et al., 2010b), draining a catchment of c. 14,443 km^2 (Brown, 2010) equivalent to c. 13 % of the North Island (Chapman, 1996) (Fig. 4.1a). It is a 7th order river, with a mean annual discharge of c. 450 m^3 s^{-1} at the mouth (Brown, 2010), conforming to the various definitions of a large river used elsewhere (Vannote et al., 1980; Dynesius & Nilsson, 1994; Johnson et al., 1995; Nilsson et al., 2005). Eight hydroelectric power dams have been constructed on the upper river with the furthest downstream dam at Lake Karapiro acting as a barrier to the natural movement of aquatic fauna upstream. My study was conducted on the lower Waikato River downstream of Karapiro where the river flows along a low gradient channel, falling c. 22 m over c. 150 km to the sea (Collier et al., 2010b) (Fig. 4.1a). The immediate catchment of the lower Waikato River is dominated by old tertiary sediments with low infiltration rates. As a result, the river system is highly responsive to rainfall, with large peak flood flows after heavy rain and low flows after dry periods (Brown, 2010). Land use is predominantly pastoral (74 %) with approximately 4 and 6 % in exotic forestry and native forest, respectively (Brown, 2010; Collier et al., 2010b).

The lower Waikato River is fed by several major tributaries, the largest and most significant being the Waipa River which augments mean flow by c. 25 % (Fig. 4.1a) and contributes significant amounts of agriculturally derived nutrients and sediment, particularly during winter and spring high flows (Chapman, 1996; Brown, 2010). River flow becomes tidally influenced around Mercer (Fig. 4.1a), although saline intrusion does not usually occur until the downstream edge of the delta (Brown 2003). River velocity above Karapiro dam is now many times slower than prior to dam construction (Hicks & Hill, 2010), leading to a reduction in suspended sediment loads and subsequent increased bed incision in sections of the lower river (Hicks & Hill., 2010). Conversely, chlorophyll *a* concentrations below Karapiro dam are estimated to have increased by more than 300 % from pre-dam conditions as a result of phytoplankton from the lake being discharged in river water (Vant, 2010). Water column turbidity and concentrations of nitrogen, phosphorus, chlorophyll *a* and dissolved colour all increase steadily downstream, with marked increases below the Waipa River confluence, except for chlorophyll *a* which drops initially before also increasing (Vant, 2010). Below Huntly (Fig. 4.1a) the river once possessed an extensive floodplain characterised by peat wetlands and several riverine lakes. Floodplain inundation and interactions with these habitats and are now generally restricted by a flood protection scheme that includes 242 km of stopbanks, 269 floodgates and 69 pump stations, disconnecting 47 % (172 km^2) of the original floodplain (Chapman, 1996; Mulholland, 2010; Speirs et al., 2010).

The riparian zone of the lower Waikato River is dominated by introduced vegetation, primarily crack willow (*Salix fragilis* Linneaus) and alder (*Alnus glutinosa* Linneaus), and pasture for stock grazing (Champion & Clayton., 2010a). Similarly, the aquatic flora is almost exclusively dominated by the exotic macrophytes *Egeria densa* (Planch) and *Ceratophyllum demersum* (Linneaus) (Collier et al., 2008; Champion & Clayton, 2010b). The planktonic algal assemblage is mostly made up of species of green algae, diatoms and blue-green algae, while the zooplankton assemblage is dominated by small-sized rotifers (Hamilton & Duggan, 2010). At present there is no information available on the composition, taxonomy or productivity of phytomicrobenthos in the lower river. Littoral macroinvertebrate faunas are characterised by taxa with a preference for soft, silty bottom sediments, and are characterised by several species of annelids, nematodes, roundworms, ribbonworms, molluscs and midge larvae, with high abundances of the amphipod *Paracalliope fluviatilis* (Thomson) and the diadromous shrimp *Paratya curvirostris* (Heller) (Collier & Lill, 2008; Collier & Hogg, 2010). While several native diadromous fish species primarily use the mainstem as a migratory route to smaller headwater tributaries, others such as grey mullet (*Mugil cephalus* Linnaeus), shortfin eel (*Anguilla australis* Richardson), smelt (*Retropinna retropinna* Richardson), common bully (*Gobiomorphus cotidianus* McDowall), and īnanga (*Galaxias maculatus* Jenyns), are resident as adults in the mainstem of the lower river (David & Speirs, 2010). At least ten introduced fish species are known to be present, and many of these are now widespread and comprise a significant proportion of total fish abundance and biomass, notably, koi carp (*Cyprinus carpio* Linnaeus), rudd (*Scardinius erythrophthalmus* Linnaeus), *Gambusia* (*Gambusia affinis* Baird & Girard), catfish (*Ameiurus nebulosus* Lesueur) and goldfish (*Carassius auratus* Linnaeus) (Hicks et al., 2010).

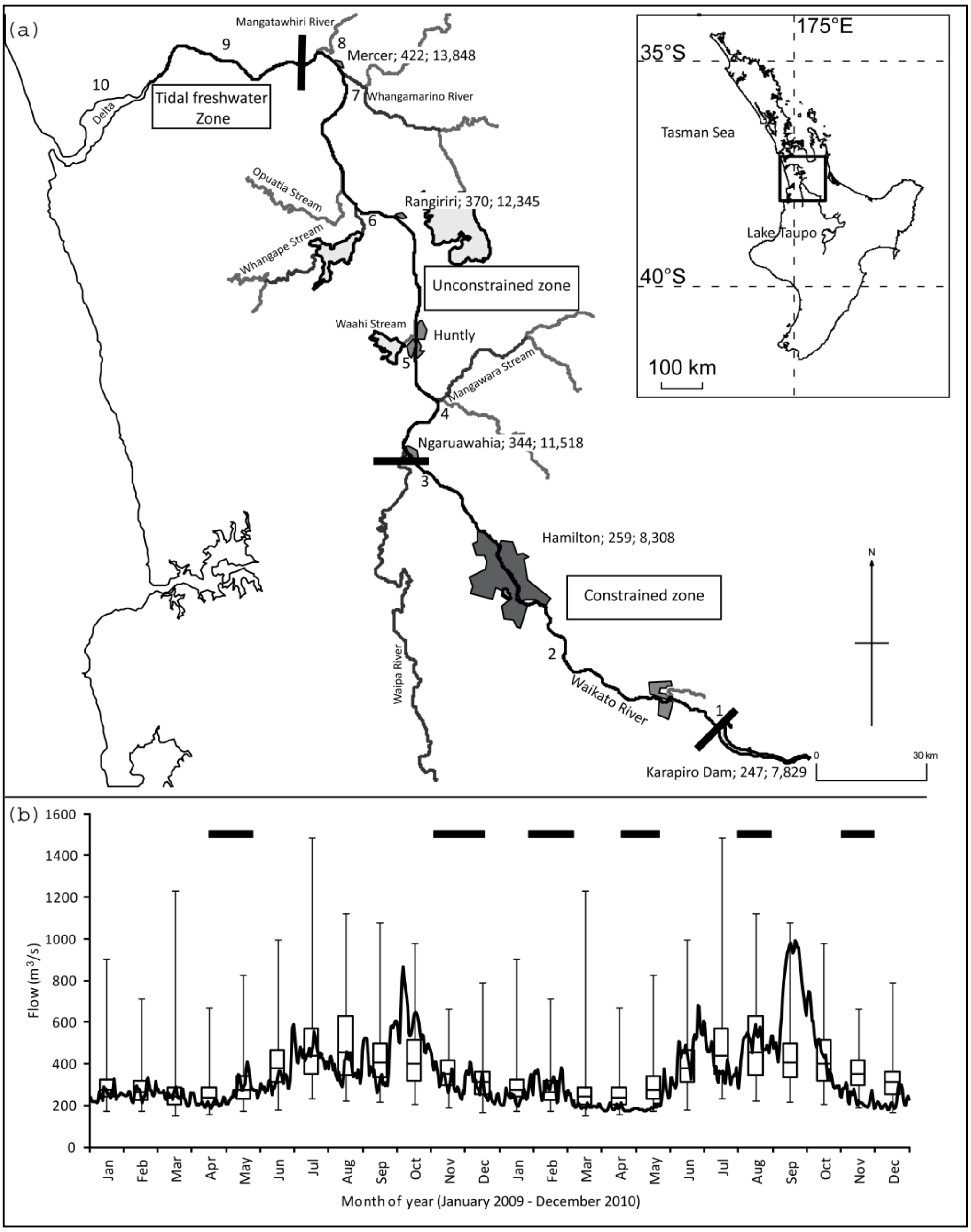


Figure 4.1. (a) Map of lower Waikato River, indicating sampling sites (1-10), river zones and major tributaries. Numbers following locations indicate mean annual discharge (m^3/s) and catchment area (km^2), respectively. The three river zones are identified in boxes with their point of separation shown by lines at right angles to the river. (b) River flow hydrograph at Rangiriri during the study period autumn 2009 – spring 2010 (solid line). Boxes encompass 25th and 75th percentiles with median shown as horizontal line; whiskers represent minimum and maximum of monthly flow data between 1983 and 2008. Thick bars above hydrograph indicate sample collection periods.

4.3.2 Sampling sites

Ten sampling sites were chosen to represent three hydrogeomorphic zones based on existing conditions, modified from Collier & Lill (2008) (Fig. 4.1a). Sites 1-3 were located in the 'constrained zone' (Fig. 4.1a), which extends from Karapiro to above the Waipa River confluence at Ngaruawahia. This zone is characterised by vertical ignimbrite walls, an incised channel with steep littoral zones and occasional more open sections with sand-gravel beaches and extensive willow fringes. Flow in this zone is influenced by releases from the hydroelectric dam at Karapiro, with c. 61 cm (range 2 – 186 cm) mean daily fluctuation at Hamilton during the study period. Owing to the incised nature of the channel, this leads to fluctuating water depth as opposed to wetted width. Sites 4-8 were located above major tributary confluences in the 'unconstrained zone' (Fig. 4.1a), which stretches from the Waipa River confluence to Mercer and is chiefly characterised by inflows from the Waipa and regular contributions from other tributaries; in this zone the river becomes wider, the littoral zone less steep and lateral habitats become more varied. Although flow in this zone is largely dictated by discharges from the Waipa River, particularly during periods of high flow, the frequency and extent of flooding has been reduced as a result of flood protection works. Sites 9 and 10 were located in the 'tidal freshwater zone', which extends downstream from below the Mangatawhiri River at Mercer and is characterised by increasing frequency of mid-channel islands, macrophyte beds, sand bars and an expansive delta. Although no saline intrusion occurs in this zone, water level and velocity fluctuate in response to the tidal cycle, and mean daily water level fluctuation at Tuakau during the study period was c. 63 cm (range 3 – 133 cm). To consistently access littoral habitats that would otherwise be too deeply submerged, sites in the constrained and tidal freshwater zones were sampled during troughs in the daily hydro-dam discharge and tidal elevation cycles, respectively.

4.3.3 Sample collection

Potentially important basal carbon sources of aquatic and terrestrial origin, and invertebrate primary consumers were collected from littoral habitats during November-December 2009 and 2010 (spring), January-February 2010 (summer), April-May 2009 and 2010 (autumn) and July-August 2010 (winter). Sample collections were therefore spread evenly over high and low flow periods (i.e. three representing each flow period). Flows (m^3/s) during the study period were generally within the 25th and 75th percentiles of monthly mean flows averaged over the 25 years (1983 to 2008) since the completion of the Waikato-Waipa flood control scheme (Fig. 4.1b). Sites 9 and 10 were not sampled during autumn 2009. During winter and spring 2010 riparian leaves were not collected due to their absence and few samples of macrophytes and phytomicrobenthos could be collected due to high flows. To accommodate logistical and resource constraints, fish were collected during autumn and spring 2009 towards the end of low and high river flow periods, respectively. Aquatic primary producers and consumers were collected more frequently to better characterise the isotopic signatures of lower trophic levels.

Senescent and recently abscised leaves were collected from riparian willow and alder trees to represent allochthonous inputs. Predominantly young apical shoots were taken where possible from common submerged macrophytes *C. demersum* and *E. densa*, after first ensuring that plants were rooted in place. Macrophyte-entrained material (MEM) was collected by lightly rinsing *E. densa* samples in a bucket of water and passing dislodged material through sieves to collect a 40-250 μm sample. Seston was collected by towing a 40 μm plankton net through the water at each site. The retained sample was stored in an opaque plastic container, and immediately on return to the laboratory was rinsed through a nested array of sieves with the 40-100 μm sample retained to characterise transported phytoplankton. Benthic biofilms and algae were scraped from a range of accessible stable substrates (i.e. woody debris and rocks).

Invertebrates were collected from aquatic macrophytes and submerged substrates (logs, banks) using a sweep net or by searching by hand. Species were selected to represent different feeding guilds; scrapers were represented by the snails *Potamopyrgus antipodarum* (Gray), *Physa acuta* (Draparnaud) and species of *Lymnaea* and *Gyraulus*. Collectors were represented by the crustaceans *P. fluviatilis* and *P. curvirostris*. Predatory invertebrates were represented by damselfly nymph (Odonata). Fish were collected using a combination of boat electric fishing, minnow traps, and hand and fyke nets from in and around littoral habitats, as these provide shelter and feeding habitats for many of the fish species in the lower Waikato River (McDowall 1990; David & Speirs, 2010). Following collection, fish were euthanised in an ice slurry, and as with all other samples were placed on ice immediately in the field. Collected species of fish comprised the pelagic grey mullet and common smelt, the benthic-dwelling common bully and catfish, and the littoral-dwelling īnanga, *Gambusia*, goldfish, and koi carp, and the shortfin eel which was the largest predatory fish caught. Fish for SIA were selected from an intermediate size range, so that wherever possible fish sizes within species were consistent across sites and sampling occasions.

4.3.4 Sample preparation and stable isotope analysis

On return to the laboratory samples were immediately prepared for stable isotope analysis or transferred to a -20 ˚C freezer for later processing. Terrestrial and aquatic plant matter was carefully rinsed in de-ionised water to remove any extraneous material. To verify that seston samples analysed for stable isotope analysis were dominated by phytoplankton subsamples were examined under a 40-100 X magnification, and were typically dominated by diatoms of the genera *Asterionella* and *Aulacoseira* (authors' unpublished data). Biofilm samples were rinsed with distilled water and then inspected under a dissecting microscope to remove invertebrates and large particles of sediment or organic matter. Retained samples typically contained a range of fungi, algae, microorganisms and detritus and are referred to as phytomicrobenthos (after Zeug et al., 2008).

Before being frozen, snails were kept in river water over a 500 µm nylon mesh for 12 hours to evacuate their guts, as evidenced by the fine faecal material that accumulated on the container bottom. Where possible 10-15 snails from each site were pooled for stable isotope analysis. To avoid contamination by carbonates, which can be depleted in $\delta^{13}C$ compared with living tissues, snails were removed from their shells, rather than using a chemical dissolution treatment which can affect $\delta^{15}N$ ratios (Carabel et al., 2006). 50-100 whole *P. fluviatilis* were rinsed with distilled water and pooled. White muscle was extracted and pooled for each site from the tail of up to three *P. curvirostris* with an occipital carapace length > 4 mm to represent adult shrimps (Nichols, 1996). Up to five damselfly nymph were also pooled following removal of their stomachs under a dissecting microscope. Invertebrate tissue samples were pooled to produce sufficient dry tissue to meet the required minimum dry weight of 2 mg for stable isotope analysis. Fish tissue was extracted from the white dorsal muscle which provides a representative isotopic signature and has less variable fractionation than other tissue (Pinnegar & Poluinin, 1999). Individual fish were analysed separately, except where it was not possible to extract sufficient white dorsal muscle from a single small fish (e.g. *Gambusia*), in which case muscle from up to three individuals was pooled. Prior to drying all muscle samples were rinsed in distilled water and inspected for stray scales and bones which were removed.

All samples, except for seston which were freeze-dried in a Dynavac FD12, were transferred to a Contherm drying oven pre-heated to 50 °C, for 48 h. Samples were then ground to a powder and stored at room temperature in airtight containers containing bags of silica crystals. Samples were later weighed into tin cups, usually to specific weights (2-40 mg to nearest 0.01 mg) depending on expected carbon and nitrogen content, and analysed for $\delta^{13}C$ and $\delta^{15}N$ by the Waikato Stable Isotope Unit, University of Waikato, Hamilton, on a Europa Scientific 20/20 isotope ratio mass spectrometer. Stable isotope ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) are expressed as delta (δ) and defined as parts per thousand (‰) relative to the laboratory standard leucine, calibrated relative to atmospheric nitrogen for $\delta^{15}N$ and to Vienna Pee Dee Belemnite for $\delta^{13}C$. The instrument precision was c. 0.3 ‰ for $\delta^{13}C$ and c. 0.5 ‰ for $\delta^{15}N$.

Lipids in tissue samples tend to be 6-8 ‰ more depleted in $\delta^{13}C$ than proteins and carbohydrates, and overall lipid content can differ between organisms, and in response to environmental conditions, potentially introducing significant bias if not accounted for (Post et al., 2007). As some fish and invertebrate samples exceed a C: N ratio of 3.5 (a ratio indicative of significant lipid content) a mathematical correction for lipids was used as recommended by Post et al., (2007), whereby: $\delta^{13}C_{\text{corrected}} = \delta^{13}C_{\text{uncorrected}} - 3.32 + 0.99 \times C:N$. The effect of lipids on consumer tissue $\delta^{13}C$ was validated using 47 representative samples from fish and shrimps. Lipids were removed using the methanol and chloroform method of Folch et al., (1957), as revised by Post & Parkinson (2001) and Arrington et al., (2006). Paired t-tests indicated a significant difference between untreated and lipid free samples ($P<0.01$), and no difference between treated samples and the equation recommended by Post et al., (2007) ($P>0.05$). As plant samples generally exceeded 40 % carbon the equation: $\delta^{13}C_{\text{corrected}} = \delta^{13}C_{\text{uncorrected}} - 5.83 + 0.14 \times \%$ carbon, was applied to all riparian (mean 45.7 % C) and aquatic macrophyte samples (mean 42.4 % C), as also recommended by Post et al., (2007). All presented results, data analysis and mixing models reflect $\delta^{13}C_{\text{corrected}}$ values for consumers and plants.

4.3.5 Data analysis

Statistical analyses were undertaken using PERMANOVA (Version 1.0.3) with Monte Carlo *P* values to explore spatial and temporal changes of $\delta^{13}C$ and $\delta^{15}N$ for each aquatic basal carbon resource and primary consumer (Model: Zone, Time, Zone*time). C_3 riparian vegetation samples were collected at provide representative $\delta^{13}C$ and $\delta^{15}N$ signatures across the study site, so the effect of zone was not tested (Model: Species, Time, Species*time). As the use of $\delta^{13}C$ and $\delta^{15}N$ together can assist in the discrimination of basal organic carbon sources for use in IsoSource, a multivariate test was also undertaken to assess the variability of riparian and aquatic basal isotopic signatures within each zone (Model: Source, Time, Source* time). Where significant differences or effects were evident *post-hoc* pairwise comparisons were undertaken for the appropriate factors.

To estimate contributions of basal carbon sources to consumers during each sample period, a dual isotope, multiple source mixing model was applied to the stable isotope data using IsoSource 1.3.1, which provides a range of feasible solutions based on isotopic mass balance (Phillips & Gregg, 2003). Possible source contributions were modelled at 2 % increments and mass balance tolerance was set at 0.1 and increased to a maximum of 1 until a solution was achieved. Isotopic signatures of consumers tend to be less temporally variable than those of primary producers over time and can lag behind those of their diet, depending on environmental conditions, the rate of tissue turnover and body characteristics of the organism (Perga et al., 2005; McIntyre& Flecker., 2006; Weidel et al., 2011). Annual averages for each organic carbon source used in the IsoSource model were used to account for the isotopic variability of primary producers over time (after Hladyz et al., 2012).

To expand the mixing polygons employed in IsoSource, snail signatures adjusted for trophic fractionation were added to the model in the unconstrained and tidal freshwater zones as an additional benthic carbon source. Scrapers have been used elsewhere to represent epilithic algae in rivers (Finlay, 2001) and this approach has been employed elsewhere to characterise littoral benthic carbon sources (e.g. Post, 2002; Roach et al., 2009a). This approach was deemed appropriate in my study because snail signatures aligned most closely with the $\delta^{13}C$ and $\delta^{15}N$ signatures of phytomicrobenthos, particularly in the constrained zone, and were likely to be assimilating autochthonous material based on the low

C: N ratios of aquatic sources. *E. densa* and *C. demersum* isotope signatures were averaged to provide an overall 'macrophyte' source, due to their closely overlapping signatures, while significant differences in the $\delta^{15}N$ of willow and alder led to them being treated separately in the IsoSource model.

Prior to use in the IsoSource mixing model, consumer isotopic ratios were adjusted to reflect trophic fractionation of their inferred trophic level using the fractionation estimates of McCutchan et al. (2003). Trophic levels were based on available literature information regarding consumer diets (for fish McDowall, 1990, 2000; and for invertebrates winterbourn 2000; Chapman et al., 2011), and stomach contents of fish were identified to support these classifications (authors' unpublished data). Primary consumers (i.e. snails, shrimps, amphipods and grey mullet) were therefore adjusted by 0.4 ‰ and 2.3 ‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. Predatory invertebrates and fish, except for shortfin eels, were adjusted by 0.8 ‰ and 4.6 ‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively, representing their role as secondary consumers. Shortfin eels, which are opportunistic generalists that will eat invertebrates and small fish, were treated as tertiary consumers and adjusted accordingly (i.e. 1.2 ‰ and 6.9 ‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively).

Following the approach recommended by Phillips et al., (2005), sources of similar ecological origin were combined *a posteriori* to represent autochthonous benthic carbon (i.e. phytomicrobenthos and snail proxy), and riparian plants. When interpreting IsoSource outputs it is important to consider the range of feasible solutions (i.e. 1st - 99th percentiles; Phillips & Gregg, 2003), whereby carbon sources with high 1st percentiles can be considered as likely to be important to the species of interest (Benstead et al., 2006) and 1st percentiles >0 are often used to infer assimilation of that carbon source (e.g. Roach et al., 2009b). Carbon sources with the highest 1st percentiles were considered to be the primary carbon source for a particular consumer, while secondary carbon sources were considered to be those with a 1st percentile > 1 but less than that of the primary carbon source.

4.4 Results

4.4.1 Isotopic signatures

Basal carbon sources

Overall, the two riparian tree species (alder and willow) had significantly different $\delta^{13}C$ and $\delta^{15}N$ signatures (Table 4.1). Willow signatures were more depleted in $\delta^{13}C$ (alder mean -28.34 ‰, willow mean -29.24 ‰; F = 6.24, $P < 0.05$; Fig. 4.2a) and more enriched in $\delta^{15}N$ (alder mean -1.46 ‰, willow mean 6.94 ‰; F = 614.22, $P < 0.01$). There was also a significant interaction between species and season (F = 3.77, $P < 0.05$), and pairwise comparisons across time for each species indicated that willow leaves differed between spring and other times, while comparisons between the two species indicated a significant difference in autumn. The low $\delta^{15}N$ values of alder likely reflect endophytic nitrogen fixation (Kohl & Shearer, 1980) and alder leaves were generally higher in nitrogen content as reflected by their lower C: N percentage ratios (alder mean 16.24, willow mean 27.32; F = 18.95, $P < 0.01$), with ratios lowest for both species during spring 2009. Aquatic macrophytes had the highest $\delta^{15}N$ values of the sampled organic carbon sources. There was no significant effect of zone or sample time on $\delta^{13}C$ or $\delta^{15}N$ signatures of *C. demersum* and *E. densa* ($P > 0.05$; Table 4.1). Macrophyte samples could be highly variable within each zone during a single sampling occasion, possibly due to localised environmental conditions, with standard errors > 2 delta units in some cases for both $\delta^{13}C$ and $\delta^{15}N$ (Figs. 2b and 2c), although annual variability was generally lower.

Seston samples collected from the constrained zone during winter were the most depleted carbon source, with mean $\delta^{13}C$ of -33.80 ‰, while the most enriched seston samples were also effect on $\delta^{13}C$ values for both sample time (F = 52.50, $P < 0.01$) and zone (F = 7.63, $P < 0.01$), as well as an interaction of time and zone (F = 3.56, $P < 0.05$). $\delta^{13}C$ of seston in the tidal freshwater zone was significantly different to that from the other two zones, while significant differences occurred between sample times, notably for summer and winter which were the most different to other sample times in pairwise comparisons. Pairwise comparison of the interaction effect indicated that seston $\delta^{13}C$ in the tidal freshwater zone was most likely to differ from the other two zones during spring,

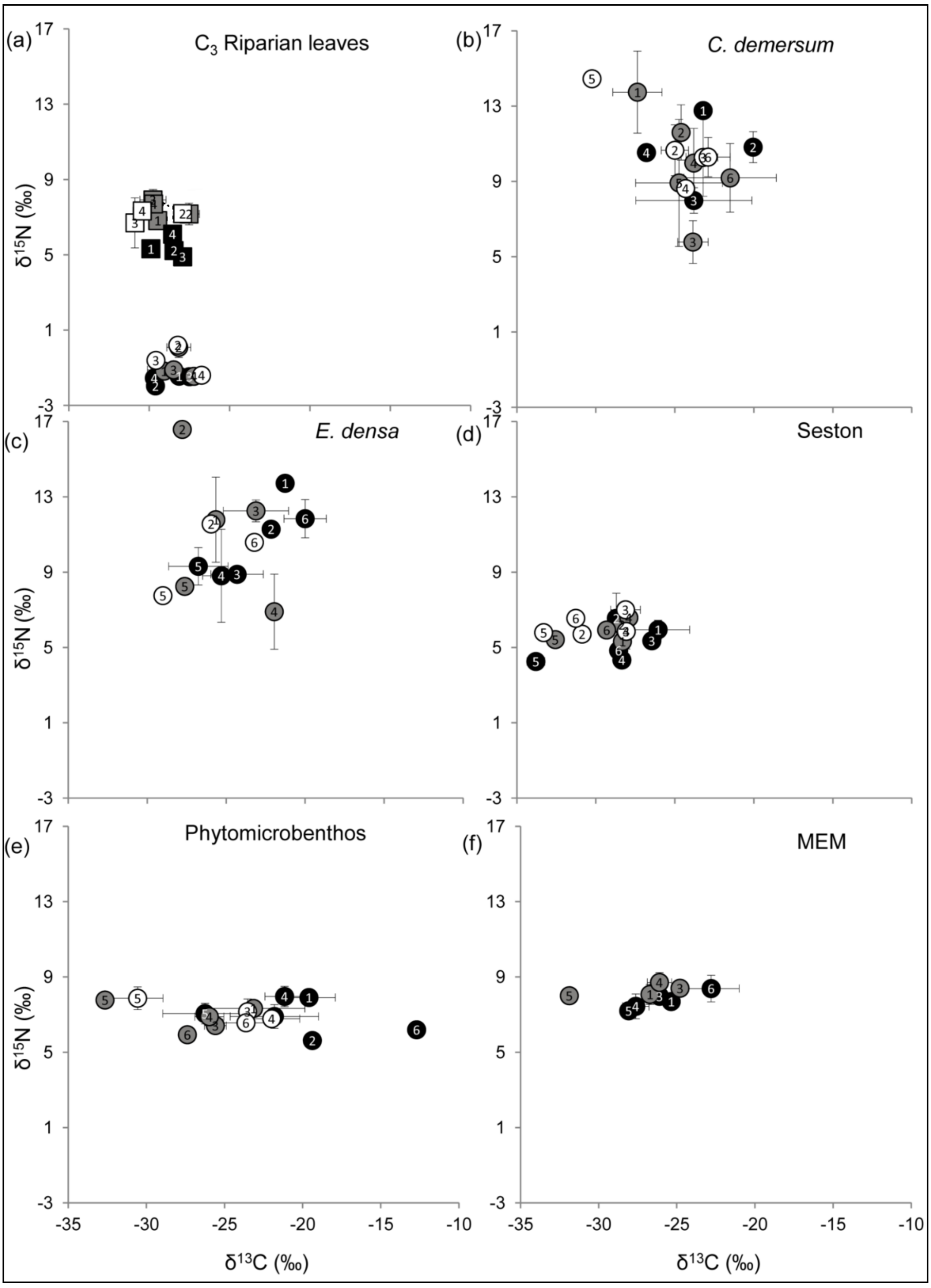


Figure 4.2. Mean $\delta^{13}C$ and $\delta^{15}N$ ratios of basal organic carbon sources collected from the lower Waikato River: (a) willow (squares) and alder (circles) riparian tree leaves, the aquatic macrophytes (b) *Ceratophyllum demersum* and (c) *Egeria densa,* (d) seston suspended in the water column, (e) phytomicrobenthos attached to hard substrates, and (f) macrophyte-entrained material (MEM) comprising mostly fine organic matter. Black symbols denote samples collected from the constrained zone, grey symbols the unconstrained zone and white symbols the tidal freshwater zone. Bars represent ±1 SE. Numbers denote sample period: 1, autumn 2009; 2, spring 2009; 3, summer 2010; 4, autumn 2010; 5, winter 2010; and 6, spring 2010.

Table 4.1. PERMANOVA F-ratios for $\delta^{13}C$ and $\delta^{15}N$ comparisons of basal organic carbon sources between zones and sampling times. * and ** denote P <0.05 and P <0.01, respectively.

	Organic carbon source	Zone	Time	Zone*time	Species	Species* time
$\delta^{13}C$	Riparian		1.73		6.24*	3.77*
	E. densa	2.01	3.33	2.14		
	C. demersum	0.57	1.39	0.84		
	Seston	7.63**	52.50**	3.56**		
	Phytomicrobenthos	8.63**	4.02*	0.85		
	MEM	0.46	6.04*	2.02		
$\delta^{15}N$	Riparian		0.69		614.22**	1.04
	E. densa	0.41	2.34	0.68		
	C. demersum	0.49	1.33	0.45		
	Seston	7.31**	2.25	3.03**		
	Phytomicrobenthos	0.36	1.75	0.63		
	MEM	2.2	0.51	0.23		

while the constrained and unconstrained zones differed during summer 2010 (all $P < 0.05$).

Values of $\delta^{15}N$ differed significantly with zone (F = 7.31, P <0.01), and the constrained reach was different to both the tidal and unconstrained reaches in pairwise comparisons (both P <0.01). Seston $\delta^{15}N$ signatures differed both within each zone between seasons, and between zones during some seasons (zone*time interaction F = 3.03, P <0.01). High seasonal variability of seston $\delta^{15}N$ signatures was most evident within the unconstrained reach (Fig. 4.2d), where several sample times were statistically different (P <0.05). Differences between zones during particular seasons were most notable in winter, when the constrained zone differed from both unconstrained (P <0.01) and tidal (P <0.05) zones, and during spring 2010 when all zones were different to each other (all P <0.05). Typically, the C: N ratios of seston were generally lowest in the constrained zone (mean 7.09), highest in the unconstrained zone (9.31), and intermediate in the tidal freshwater zone (8.47).

Mean $\delta^{13}C$ values for phytomicrobenthos ranged from -12.71 ‰ during spring 2010 in the constrained zone to -32.65 ‰ in the unconstrained zone during winter. Values were generally more depleted in the unconstrained zone than in the constrained or tidal freshwater zones (Fig. 4.2e). Phytomicrobenthos $\delta^{13}C$

signatures were significantly different between zones (F = 8.63, *P* <0.01) and sample times (F = 4.02, *P* <0.05) and pairwise comparisons indicated that each zone was different (all *P* <0.05). As with seston, samples collected during winter 2010 were the most depleted (Fig. 4.2e) and statistically different to other sampling times. No effects of zone or sample time were observed for $\delta^{15}N$ signatures of phytomicrobenthos (Table 4.1). MEM samples were not collected from the tidal section of the river and no difference was observed between the constrained and unconstrained zones for either isotope (Table 4.1).

Primary consumers

Snails were the primary consumers with the most enriched $\delta^{13}C$ signatures (Fig. 4.3a, mean -22.58 ± 0.41 SE), while the shrimp *P. curvirostris* had the most enriched $\delta^{15}N$ signature (Fig. 4.3c, mean 12.1 ± 0.09 SE). Significant effects of zone and time were observed for $\delta^{13}C$ signatures of *P. fluviatilis* (zone: F = 8.60, *P* <0.01; time: F = 3.90, *P* <0.05) and snails (zone: F = 7.46, *P* <0.01; time: F = 3.59, *P* <0.05). Subsequent pairwise comparisons indicated that *P. fluviatilis* samples collected in summer 2010 and snails

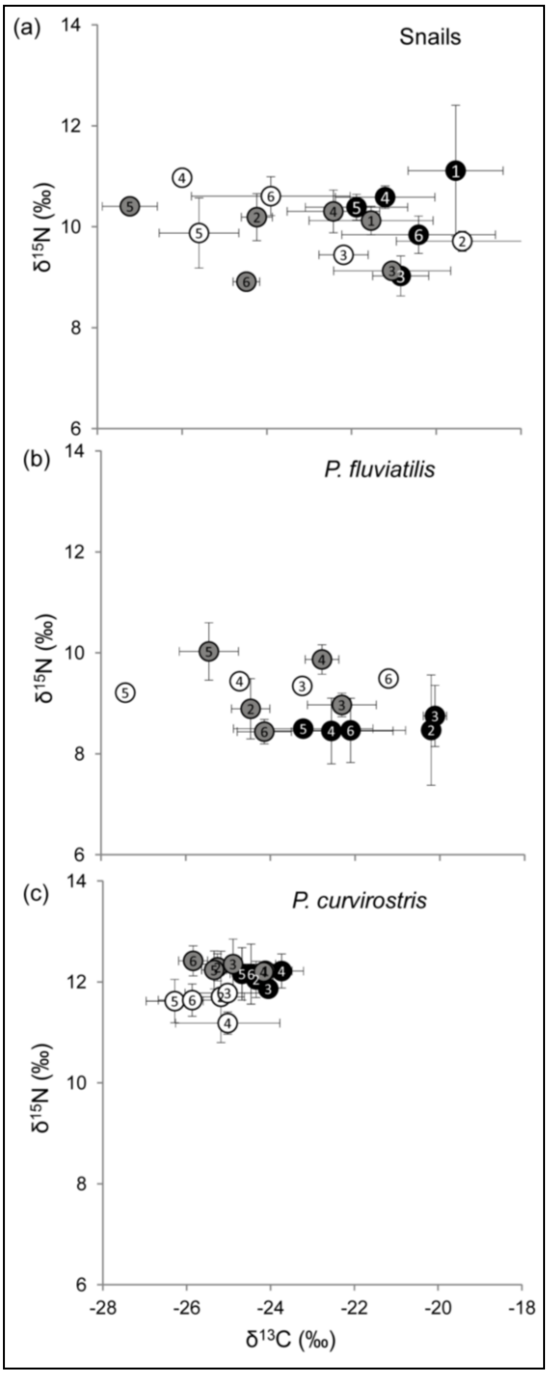


Figure 4.3. Mean $\delta^{13}C$ and $\delta^{15}N$ ratios of primary consumers: (a) snails (mainly Potamopyrgus antipodarum and Physa acuta), (b) *Paracalliope fluviatilis*, and (c) *Paratya curvirostris*. Numbers denote sample period (see Fig. 2). Black symbols denote samples collected from the constrained zone, grey symbols the unconstrained zone and white symbols the tidal freshwater zone. Bars represent ±1 SE. Numbers denote sample period: 1, autumn 2009; 2, spring 2009; 3, summer 2010; 4, autumn 2010; 5, winter 2010; and 6, spring 2010.

collected during winter 2010 were different from those collected at other times. In addition, $\delta^{13}C$ signatures of both *P. fluviatilis* and snails in the constrained zone were significantly different to those collected in the unconstrained zone, reflecting the more enriched values of samples from above the Waipa confluence, and were also different (*P* <0.05) between the unconstrained and tidal freshwater zones (Figs 3a and 3b). $\delta^{13}C$ signatures of *P. curvirostris* were similar throughout the lower Waikato River (Fig 3c), however, $\delta^{15}N$ signatures differed between zones (F = 4.23, *P* <0.05) and significant pairwise differences occurred between the unconstrained and tidal freshwater zones (*P* <0.05). Only snail $\delta^{15}N$ signatures appeared to be significantly different between sample times (F = 4.39, *P* <0.01), particularly between summer 2010 and all other dates in pairwise comparisons. Mean $\delta^{13}C$ and $\delta^{15}N$ ratios for grey mullet, were similar between season and zone, although some variation amongst individual fish was evident (Fig. 4.4).

Secondary and tertiary consumers

The $\delta^{13}C$ and $\delta^{15}N$ signatures of predatory fish were between c. -27 ‰ to -21 ‰ and c. 11 ‰ to 14 ‰ respectively. Although common bully was the only fish species to show a statistically significant seasonal difference of $\delta^{13}C$ and $\delta^{15}N$ (F = 3.73, *P* <0.05), values for fish consumers appeared to be slightly more depleted in spring (high flows) compared to autumn (low flows) (Fig. 4.4a-e). Common bully and smelt had similar $\delta^{13}C$ and $\delta^{15}N$ values, as did *Gambusia* and īnanga although inanga more variable in $\delta^{13}C$ and $\delta^{15}N$ between zones and seasons (Fig. 4.4). Shortfin eel, the top predator, also had $\delta^{15}N$ values similar to the other fish consumers but was generally more depleted in $\delta^{13}C$. Goldfish from the constrained and unconstrained zones had similar $\delta^{13}C$ values during autumn; however, in spring goldfish in the unconstrained zone was the most depleted fish species (mean -27.08 ‰) and also had consistently higher $\delta^{15}N$ values than other consumers. Damselfly nymphs generally had lower $\delta^{15}N$ values than fish consumers and appeared to have more variable $\delta^{13}C$ signatures than predatory fish (Fig. 4.4).

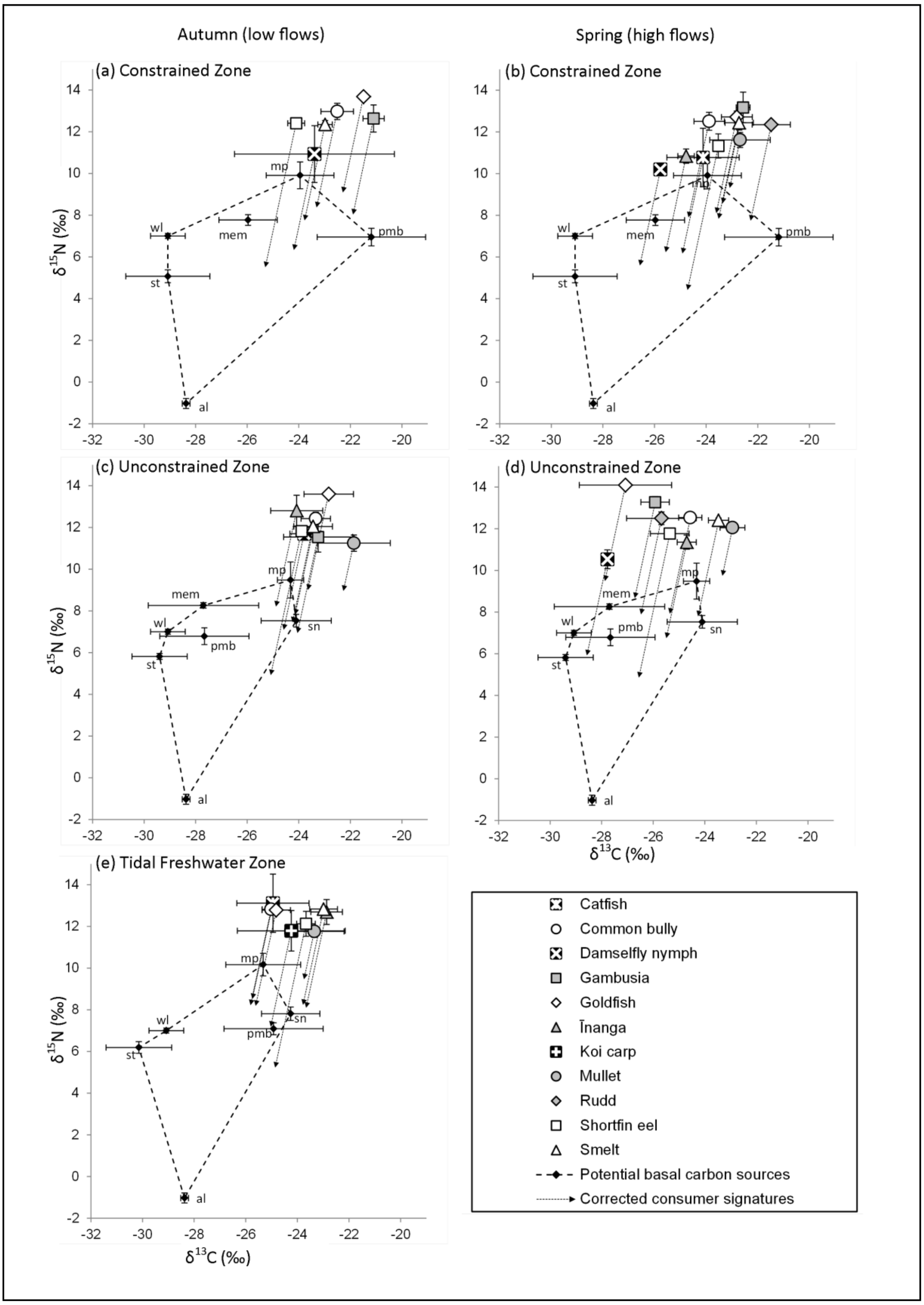


Figure 4.4. Mean $\delta^{13}C$ and $\delta^{15}N$ ratios of predatory consumers and grey mullet collected from: the constrained zone during (a) autumn and (b) spring, the unconstrained zone in (c) autumn and (d) spring, and (e) from the tidal freshwater zone in spring. Bars represent ±1 S.E. Labels indicate unadjusted carbon sources used in the IsoSource mixing models: willow (wl) and alder (al) leaves, macrophytes (mp), seston (st), phytomicrobenthos (pmb), macrophyte-entrained material (mem) and the adjusted snail signatures (sn).

4.4.2 Mixing model carbon source contributions

Carbon sources

Organic carbon sources used in the mixing models had typically distinct $\delta^{13}C$ and $\delta^{15}N$ signatures within each of the three zones (constrained zone F = 59.69, *P* <0.01; unconstrained zone F = 45.34, *P* <0.01; tidal freshwater zone F = 75.20, *P* <0.01). Subsequent *post hoc* comparisons indicated that the macrophytes *C. demersum* and *E. densa* were similar in all zones and occasionally overlapped with phytomicrobenthos and MEM signatures. The use of multiple isotopes improved the discrimination of different carbon sources, such that where they had overlapping ranges of $\delta^{13}C$ they differed in their $\delta^{15}N$ signatures and vice versa (Fig. 4.4). C: N ratios can be indicative of the origin of material, with terrestrial sources usually having higher ratios compared to aquatic sources (Delong et al., 2001; Zeug et al., 2008; Hladyz et al., 2012), and in this study terrestrial sources (willow leaves 27.32 ± 2.07 SE; alder leaves 16.24 ± 0.69 SE) were approximately two to three times those of aquatic sources (macrophytes 9.13 ± 0.15 SE; seston 8.50 ± 0.21 SE; phytomicrobenthos 8.47 ± 0.20 SE; MEM 7.63 ± 0.25 SE).

Primary consumers

Outputs of mixing models indicating possible solutions showed that phytomicrobenthos was the primary carbon source for snails, particularly in the constrained zone (Table 4.2). In addition to phytomicrobenthos, snails appeared to utilise carbon of macrophyte and riparian origins at various times in all zones. Where solutions could be generated, *P. fluviatilis* biomass was consistently dominated by autochthonous benthic carbon in all zones, with smaller contributions from C_3 riparian and aquatic plants (Table 4.2). In contrast, IsoSource outputs indicated that *P. curvirostris* biomass was dominated by C_3 macrophyte-derived carbon with secondary contributions from C_3 riparian vegetation, MEM and autochthonous benthic carbon (Table 4.2).

Although tolerance limits of up to 1 ‰ were used to generate solutions in IsoSource, these are likely to reflect instances where consumer signatures were outside of the range of annual mean carbon signatures and may therefore affect conclusions drawn about trophic connections (see Hadwen et al., 2010a). For solutions within a more conservative mass balance tolerance of 0.5 ‰, however, a limit used in other studies of large river food webs (e.g. Hoeinghaus et al., 2007), both snail and *P. fluviatilis* $\delta^{13}C$ signatures were generally higher than the annual mean used in the analysis and were more similar to phytomicrobenthos from the same time of collection (Figs. 2 and 3). The percentage of solutions possible within a mass balance tolerance of 0.5 ‰ for snails and *P. fluviatilis* was highest in the constrained zone (70 %) and decreased to 40 % in the unconstrained and tidal freshwater zones. For *P. curvirostris*, solutions within a 0.5 ‰ tolerance were possible in all but one instance (Table 4.2), and this was likely due to the high mean $\delta^{15}N$ signature of *P. curvirostris* in that season.

No IsoSource solutions were possible for grey mullet samples collected during autumn 2009 as their mean $\delta^{13}C$ values were too enriched to fit within the range annual means of carbon sources. Solutions for grey mullet collected in spring 2009, showed that significant (1st percentile greater than 1 %) contributions were made by aquatic macrophytes, probably consumed as detritus (Wells, 1984; David & Speirs, 2010), and autochthonous benthic carbon which appeared to increase in significance in a downstream direction (Table 4.3). As with snails and *P. fluviatilis*, mullet collected downstream of the Waipa River required tolerances of more than 0.5 ‰ to generate a solution in IsoSource using the annual mean signatures of organic carbon sources.

Table 4.2. 50th percentile carbon contributions to primary consumer biomass estimated using IsoSource. 1st to 99th percentiles are displayed in parentheses. Values in bold indicate carbon sources with a 1st percentile proportion contribution greater than 1 %. 'ns' indicates that no solution was possible in IsoSource within a maximum mass balance tolerance of 1.

Species	*Zone*	*Sample Time*	*Riparian*	*Macrophyte*	*Seston*	*Autochthonous benthic carbon*	*MEM*	*Tolerance*
Snails	Constrained	autumn 2009	ns	ns	ns	ns	ns	ns
		summer 2010	**2 (2-2)**	0 (0-0)	0 (0-0)	**98 (98-98)**	0 (0-0)	0.1
		autumn 2010	0 (0-0)	**30 (28-32)**	0 (0-0)	**70 (68-70)**	0 (0-2)	0.5
		winter 2010	0 (0-2)	**36 (36-40)**	0 (0-0)	**62 (60-64)**	0 (0-4)	0.1
		spring 2010	0 (0-0)	**4 (4-4)**	0 (0-0)	**96 (96-96)**	0 (0-0)	0.5
	Unconstrained	autumn 2009	ns	ns	ns	ns	ns	ns
		spring 2009	**12 (12-14)**	**86 (84-86)**	0 (0-2)	0 (0-4)	0 (0-0)	0.8
		summer 2010	ns	ns	ns	ns	ns	ns
		autumn 2010	ns	ns	ns	ns	ns	ns
		winter 2010	8 (0-33)	8 (0-18)	2 (0-14)	4 (0-16)	**74 (48-93)**	0.1
		spring 2010	**24 (22-26)**	**74 (74-76)**	0 (0-2)	1 (0-4)	0 (0-2)	0.9
	Tidal	spring 2009	ns	ns	ns	ns	ns	ns
		summer 2010	ns	ns	ns	ns	ns	ns
		autumn 2010	16 (0-32)	**62 (50-74)**	10 (0-24)	10 (0-21)	0 (0-0)	0.1
		winter 2010	16 (0-26)	**36 (16-73)**	6 (0-18)	**42 (4-62)**	0 (0-0)	0.1
		spring 2010	0 (0-0)	**19 (18-20)**	0 (0-0)	**81 (80-82)**	0 (0-0)	0.8
Paracalliope fluviatilis	Constrained	spring 2009	1 (0-2)	0 (0-2)	0 (0-2)	**98 (96-100)**	0 (0-2)	0.8
		summer 2010	0 (0-0)	0 (0-0)	0 (0-0)	**100 (100-100)**	0 (0-0)	0.7
		autumn 2010	**14 (6-22)**	4 (0-18)	4 (0-16)	**72 (64-78)**	4 (0-16)	0.1
		winter 2010	**16 (4-29)**	6 (0-28)	6 (0-24)	**60 (48-68)**	6 (0-28)	0.1
		spring 2010	**12 (8-18)**	2 (0-12)	2 (0-10)	**80 (74-82)**	2 (0-10)	0.1
	Unconstrained	spring 2009	**14 (10-18)**	6 (0-26)	0 (0-6)	**78 (56-88)**	0 (0-6)	0.1
		summer 2010	0 (0-2)	8 (0-31)	0 (0-1)	**90 (69-100)**	0 (0-2)	1.5
		autumn 2010	0 (0-0)	13 (0-36)	0 (0-0)	**87 (64-100)**	0 (0-2)	1
		winter 2010	10 (0-30)	**34 (4-64)**	6 (0-24)	**38 (4-66)**	10 (0-36)	0.1
		spring 2010	**14 (14-14)**	0 (0-0)	0 (0-0)	**86 (86-86)**	0 (0-0)	0.2

Table 4.2 (continued).

Species	*Zone*	*Sample Time*	*Riparian*	*Macrophyte*	*Seston*	*Autochthonous benthic carbon*	*MEM*	*Tolerance*
	Tidal	spring 2009	ns	ns	ns	ns	ns	ns
		summer 2010	0 (0-2)	0 (0-0)	0 (0-0)	**100 (98-100)**	0 (0-0)	0.7
		autumn 2010	10 (0-18)	6 (0-24)	2 (0-10)	**82 (62-94)**	0 (0-0)	0.1
		winter 2010	**34 (2-72)**	12 (0-36)	30 (0-56)	**24 (2-38)**	0 (0-0)	0.1
		spring 2010	ns	ns	ns	ns	ns	ns
Paratya curvirostris	Constrained	spring 2009	**8 (3-14)**	**86 (81-90)**	2 (0-7)	0 (0-2)	2 (0-15)	0.3
		summer 2010	6 (0-11)	**86 (81-92)**	2 (0-8)	0 (0-2)	4 (0-17)	0.1
		autumn 2010	**2 (2-2)**	**98 (98-98)**	0 (0-0)	0 (0-0)	0 (0-0)	0.3
		winter 2010	**10 (4-17)**	**83 (78-86)**	2 (0-7)	0 (0-2)	4 (0-15)	0.5
		spring 2010	**10 (4-14)**	**86 (82-88)**	0 (0-4)	0 (0-2)	3 (0-12)	0.4
	Unconstrained	autumn 2009	0 (0-2)	**98 (96-100)**	0 (0-0)	0 (0-2)	0 (0-4)	0.5
		spring 2009	2 (0-7)	**82 (78-86)**	0 (0-2)	2 (0-4)	**14 (6-21)**	0.3
		summer 2010	1 (0-2)	**91 (90-92)**	0 (0-0)	0 (0-0)	**8 (6-10)**	0.2
		autumn 2010	0 (0-2)	**97 (94-100)**	0 (0-2)	0 (0-4)	1 (0-6)	0.3
		winter 2010	2 (0-11)	**80 (74-85)**	0 (0-4)	2 (0-6)	**16 (5-25)**	0.3
		spring 2010	0 (0-0)	**72 (72-72)**	0 (0-0)	0 (0-0)	**28 (28-28)**	0.6
	Tidal	spring 2009	6 (0-12)	**78 (70-90)**	2 (0-10)	**14 (2-20)**	0 (0-0)	0.1
		summer 2010	4 (0-8)	**78 (72-90)**	2 (0-6)	**16 (4-22)**	0 (0-0)	0.1
		autumn 2010	6 (0-12)	**60 (48-76)**	2 (0-10)	**32 (14-40)**	0 (0-0)	0.1
		winter 2010	13 (0-32)	**72 (68-74)**	15 (0-26)	0 (0-2)	0 (0-0)	0.1
		spring 2010	12 (0-26)	**76 (70-80)**	10 (0-20)	2 (0-6)	0 (0-0)	0.1
Mullet	Constrained	spring 2009	0 (0-0)	**75 (74-76)**	0 (0-0)	**25 (24-26)**	0 (0-0)	0.2
	Unconstrained	autumn 2009	ns	ns	ns	ns	ns	ns
		spring 2009	0 (0-0)	**72 (63-99)**	0 (0-0)	**28 (1-36)**	0 (0-2)	1
	Tidal	spring 2009	0 (0-0)	**34 (32-34)**	0 (0-0)	**66 (66-68)**	0 (0-0)	0.9

Secondary and tertiary consumers

Autochthonous benthic carbon (represented by combined phytomicrobenthos and adjusted snail contributions from IsoSource outputs) was important for all predatory consumers in both autumn and spring 2009 (1st percentile >1 %). The 50th percentile contributions ranged from 22–100 % and were generally higher in autumn 2009 (Table 4.3). Autochthonous benthic carbon was most important to common smelt biomass, contributing 40-100 % of its carbon, particularly in the unconstrained zone. Aquatic macrophytes appeared to be the next most important carbon source assimilated by secondary consumers, with 50th percentiles ranging from 1–73 %. Terrestrial carbon increased in importance during spring, particularly for large mobile consumers such as shortfin eels. Contributions from autochthonous benthic carbon were generally greater for fish collected in the unconstrained zone during autumn 2009, while during spring 2009 potential contributions from terrestrial, seston and MEM sources increased in both constrained and unconstrained zones (Table 4.3). In both these zones, predatory damselfly nymphs mostly assimilated carbon which was ultimately of autochthonous benthic origin during autumn 2009 and terrestrial origin during spring 2009. It appeared that contributions from autochthonous benthic carbon increased, and those from macrophytes decreased, in a downstream direction for a range of fish species, notably common bully, *Gambusia* and common smelt (Table 4.3). MEM also increased in importance during spring, particularly for goldfish and *Gambusia* for which it contributed around 70 % of carbon (Table 4.3). Interestingly, seston appeared to contribute little to the sampled fish biomass and there was no fish species for which the recorded 1st percentile values were greater than zero.

Table 4.3. 50th percentile carbon contributions to predatory consumer biomass estimated using IsoSource. 1st to 99th percentiles are displayed in parentheses. Values in bold indicate carbon sources with a 1st percentile proportion contribution greater than 1 %. 'ns' indicates that no solution was possible in IsoSource within a maximum mass balance tolerance of 1.

Species	*Zone*	*Flow*	*Riparian*	*Macrophyte*	*Seston*	*Autochthonous benthic carbon*	*MEM*	*Tolerance*
Common Smelt	Constrained	Low	8 (0-22)	**34 (14-56)**	4 (0-16)	**40 (28-50)**	10 (0-42)	0.1
		High	6 (0-18)	**34 (19-54)**	4 (0-14)	**44 (34-52)**	8 (0-35)	0.1
	Unconstrained	Low	2 (0-4)	2 (0-17)	0 (0-4)	**94 (79-100)**	0 (0-4)	0.1
		High	0 (0-4)	**16 (8-33)**	0 (0-4)	**82 (63-89)**	0 (0-6)	0.1
	Tidal	High	0 (0-0)	0 (0-0)	0 (0-0)	**100 (100-100)**	0 (0-0)	0.5
Common bully	Constrained	Low	4 (0-10)	**50 (40-62)**	2 (0-8)	**38 (32-44)**	4 (0-21)	0.1
		High	12 (0-30)	**42 (16-72)**	6 (0-24)	**22 (6-34)**	14 (0-56)	0.1
	Unconstrained	Low	0 (0-2)	**16 (10-24)**	0 (0-2)	**84 (74-90)**	0 (0-2)	0.1
		High	8 (0-22)	**40 (14-74)**	4 (0-18)	**40 (4-64)**	6 (0-28)	0.1
	Tidal	High	12 (0-24)	**42 (26-74)**	6 (0-18)	**38 (8-50)**	0 (0-0)	0.1
Īnanga	Constrained	High	**26 (2-50)**	14 (0-56)	12 (0-46)	**26 (2-42)**	14 (0-56)	0.1
	Unconstrained	Low	6 (0-14)	**46 (28-82)**	2 (0-10)	**42 (6-58)**	4 (0-16)	0.1
		High	**16 (6-28)**	14 (0-64)	4 (0-18)	**60 (8-84)**	4 (0-20)	0.1
	Tidal	High	0 (0-0)	0 (0-0)	0 (0-0)	**100 (100-100)**	0 (0-0)	0.6
Gambusia	Constrained	Low	2 (0-12)	**20 (6-44)**	2 (0-8)	**68 (52-84)**	4 (0-22)	0.8
		High	4 (0-9)	**56 (48-67)**	2 (0-7)	**34 (28-38)**	4 (0-18)	0.1
	Unconstrained	Low	**4 (4-4)**	0 (0-2)	0 (0-0)	**94 (94-96)**	0 (0-2)	0.1
		High	2 (0-8)	**30 (26-34)**	0 (0-2)	0 (0-2)	**66 (58-74)**	0.1
Goldfish	Constrained	Low	0 (0-0)	**56 (56-56)**	0 (0-0)	**44 (44-44)**	0 (0-0)	0.6
		High	6 (0-16)	**44 (30-60)**	2 (0-12)	**38 (28-44)**	8 (0-32)	0.1
	Unconstrained	Low	0 (0-2)	**57 (40-98)**	0 (0-2)	**42 (2-58)**	0 (0-4)	0.8
		High	0 (0-6)	**24 (20-26)**	0 (0-2)	0 (0-4)	**74 (68-80)**	0.9
	Tidal	High	10 (0-22)	**40 (24-68)**	4 (0-16)	**44 (18-56)**	0 (0-0)	0.1

Table 4.3 (continued).

Species	*Zone*	*Flow*	*Riparian*	*Macrophyte*	*Seston*	*Autochthonous benthic carbon*	*MEM*	*Tolerance*
Damselfly nymph	Constrained	Low	**18 (2-34)**	10 (0-38)	8 (0-32)	**50 (34-62)**	10 (0-38)	0.1
		High	**34 (8-62)**	12 (0-42)	16 (0-56)	12 (0-30)	16 (0-62)	0.1
	Unconstrained	Low	**8 (4-12)**	6 (0-26)	0 (0-6)	**84 (62-94)**	0 (0-6)	0.1
		High	**32 (4-84)**	2 (0-12)	40 (0-74)	12 (0-36)	8 (0-32)	0.1
Shortfin eel	Constrained	Low	**30 (12-48)**	10 (0-42)	10 (0-38)	**32 (14-46)**	10 (0-42)	0.1
		High	**38 (28-46)**	4 (0-20)	4 (0-18)	**46 (36-52)**	4 (0-20)	0.1
	Unconstrained	Low	**28 (28-30)**	2 (0-4)	0 (0-0)	**70 (66-72)**	0 (0-2)	0.3
		High	**38 (28-52)**	14 (0-44)	4 (0-20)	**36 (2-62)**	4 (0-22)	0.1
	Tidal	High	**24 (22-26)**	0 (0-4)	0 (0-0)	**76 (72-78)**	0 (0-0)	0.5
Koi	Tidal	High	8 (0-16)	6 (0-22)	2 (0-8)	**84 (64-96)**	0 (0-0)	0.1
Rudd	Constrained	High	10 (0-22)	**26 (6-50)**	4 (0-18)	**46 (34-56)**	10 (0-44)	0.1
	Unconstrained	High	12 (0-46)	**28 (6-44)**	4 (0-22)	12 (0-30)	**40 (2-70)**	0.1
Catfish	Constrained	High	**22 (4-42)**	12 (0-46)	10 (0-40)	**38 (18-52)**	12 (0-46)	0.1
	Tidal	High	12 (0-22)	**50 (38-78)**	6 (0-16)	**32 (8-44)**	0 (0-0)	0.1

4.5 Discussion

4.5.1 Carbon flow

Carbon sources supporting the food web

Autochthonous benthic carbon (phytomicrobenthos, made up of biofilms and algae), appeared to be the main organic carbon source underpinning secondary production in this large, temperate, southern hemisphere river, and was an important source (1st percentile contribution > 1 %) in 32 of the 38 IsoSource mixing models for predatory species (Table 4.2; Fig. 4.5). This finding is consistent with studies of continental large rivers such as the Mississippi and Ohio (Thorp et al., 1998; Delong et al., 2001; Delong & Thorp., 2006; Herwig et al., 2007), large neotropical river systems such as the Paraná and Orinoco (Hoeinghaus et al., 2007; Jepsen & Winemiller 2007), and large Australian rivers where algae (particularly benthic forms) provide important carbon resources to riverine food webs across a range of dry (Bunn et al., 2003; Medeiros & Arthington, 2010; Reid et al., 2011), tropical (Douglas et al., 2005; Leigh et al., 2010b; Hunt et al., 2011), and temperate (Hadwen et al., 2010b; Hladyz et al., 2012) climates.

I had hypothesised that algal carbon of both suspended and benthic origin would provide the bulk of carbon supporting consumers sampled from littoral habitats, following predictions of the revised RPM (Thorp & delong, 2002). Unlike studies elsewhere that have demonstrated the importance of phytoplankton (seston) to food webs downstream of large reservoirs (Angradi, 1994; Hoeinghaus et al., 2007; Doi et al., 2008), I found little evidence for transported phytoplankton (seston) playing a major trophic role during the study period in the three hydrogeomorphic river zones sampled. The low estimated contribution of phytoplankton likely reflects the fact that the littoral macroinvertebrate community is dominated by species that graze from surfaces (e.g. snails) or collect deposited organic material (e.g. amphipods), as opposed to filtering collectors such as Hydropsychidae caddis larvae which occur in faster-flowing mid-channel habitats, particularly in the constrained zone of the lower Waikato River (Collier & Hogg, 2010). The main location for carbon transfer to consumers in large rivers such as the Waikato is likely to be in littoral zones which offer areas of reduced water velocity, complex habitats such as those provided by wood and aquatic plants, and interactions with marginal and terrestrial riparian vegetation (after Schiemer et al., 2001).

Secondary carbon sources

Carbon sources making valuable secondary contributions to food webs in large river systems are also regularly reported in the literature (Pingram et al., 2012). The availability, quality and uptake of these carbon subsidies can vary spatially and temporally within river systems and can affect food web processes, including trophic energy and carbon flow (Marcarelli et al., 2011). In my study, secondary carbon sources contributing to consumer biomass were largely derived from C_3 aquatic and riparian plants (Fig. 4.5). In line with other studies, it would appear that large river food webs can incorporate a variety of carbon sources depending on the consumer species present, and the environmental and hydrogeomorphic nature of the river zone in question (Thorp et al., 2006; Hoeinghaus et al., 2007). C_3 aquatic macrophytes (the exotic *C. demersum* and *E. densa*) made notable carbon contributions to both invertebrate and fish consumers, in particular to the detritivorous shrimp *P. curvirostris* and grey mullet. Both of these consumer species are likely to play significant ecological roles in the lower Waikato River as they collect fine material (MEM), including macrophyte detritus, algae deposited or growing on aquatic macrophytes and other surfaces (e.g. logs and riprap) (David & Speirs, 2010; Chapman et al., 2011). *P. curvirostris* can be abundant along river edges where individuals are known to aggregate and feed during migration (Nichols, 1996; Chapman et al., 2011), while grey mullet often reach large sizes, are abundant and range widely in the lower river, potentially filtering 100s of 1000s of tonnes of material every year (Wells, 1984; Hicks et al., 2005; David & Speirs, 2010). The flow of macrophyte derived carbon to other secondary consumers was evident in the constrained zone, and could be facilitated through the consumption of decaying plant detritus by primary consumers (e.g. grey mullet, Wells, 1984; and *P. curvirostris*, winterbourn 2000) or via a decomposer food web pathway (Thorp & Delong, 2002). C_3 aquatic macrophytes have been demonstrated to be potentially important carbon sources for secondary production in low-gradient, floodplain and below-reservoir sections of other large rivers (Hoeinghaus et al., 2007), often in conjunction with benthic algae (Jepsen & Winemiller 2007).

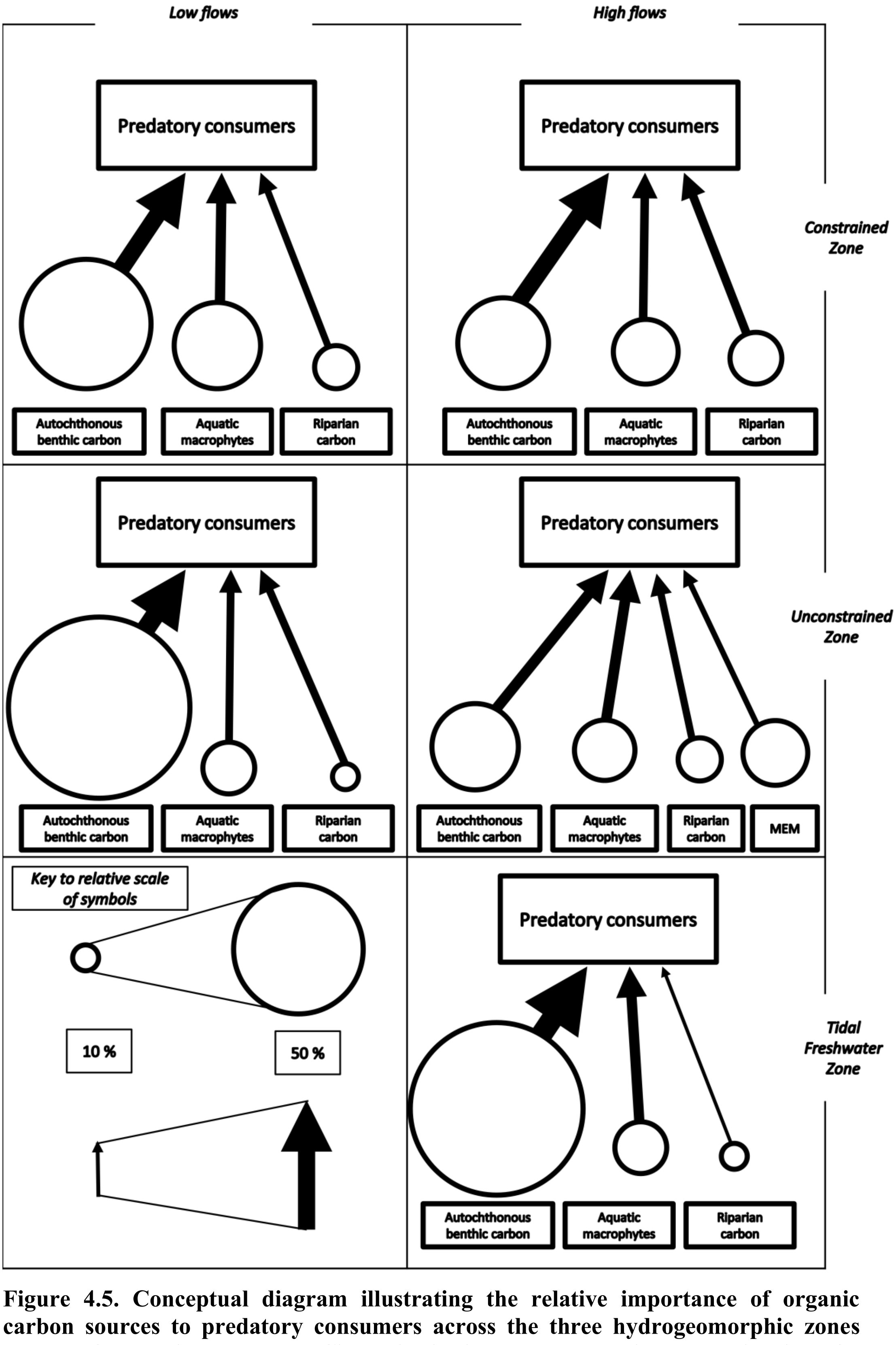


Figure 4.5. Conceptual diagram illustrating the relative importance of organic carbon sources to predatory consumers across the three hydrogeomorphic zones and two flow periods sampled. Circle size indicates the mean likely contribution of a source to predatory consumers (i.e. mean of IsoSource 50th percentiles). Arrow thickness indicates the percentage of sampled consumers for which a particular carbon source is likely to be important. Only carbon sources which recorded IsoSource 1st percentiles of >1 % are included in the diagram.

Allochthonous carbon from C_3 riparian plants was important for some secondary consumers, including catfish, īnanga, damselfly nymph, and in particular shortfin eel for which it contributed around 30 % of assimilated carbon. Only limited support for the original FPC was apparent during this study in terms of terrestrial floodplain carbon being the primary carbon source supporting the food web. In other temperate floodplains autochthonous algal production in wetted areas, rather than terrestrial sources, has been demonstrated to provide the majority of carbon to secondary consumers during extended flooding (Delong et al., 2001). Flooding in the lower Waikato River can occur during warmer seasons contributing to enhanced zooplankton abundance in the river and floodplain water bodies (K. Gorski, University of Waikato, unpubl. data). Accordingly floodplain contributions will ultimately be determined by the duration, extent, sequence, and seasonal timing of floods (Thorp et al., 2008; Leigh et al., 2010a).

Contributions from riparian carbon were generally greatest in the constrained zone of the lower Waikato River, even following periods of low flow (Fig. 4.5). This may reflect the steep and fast-flowing littoral zones present in much of the constrained zone which limit the habitat available for some of the sampled consumer species. In addition, water levels in the constrained zone fluctuate regularly due to hydropower generation, potentially making riparian food sources available to more mobile aquatic consumers during periodic wetting of shore zones. Shortfin eel and īnanga are known to feed directly on terrestrial invertebrates in small pastoral and forested streams elsewhere in the lower Waikato River catchment and New Zealand (McDowall et al., 1996; Hicks, 1997). My results suggest that, for fish species capable of exploiting the interface between riparian and aquatic habitats along edges of large rivers, riparian carbon is likely to enter the food web via the consumption of terrestrial invertebrates which can provide significant, direct and high quality resource subsides to fish in temperate rivers, particularly during periods of high plant growth and low aquatic macroinvertebrate abundance (Baxter et al., 2005; Wipfli & Baxter, 2010). Their incorporation into aquatic food webs can be mediated either by falling from the riparian zone, (Cloe III & Garman, 1996), or during lateral inundation of riparian and floodplain habitats when fish often respond rapidly to terrestrial invertebrates caught in inundated areas (Wantzen et al., 2002).

Temporal and spatial variability

The relative importance of organic carbon sources to consumers can change depending on the availability and accessibility of particular organic carbon sources to the food web, such as through upstream releases of plankton from lakes and dams, inputs of autumnal leaf litter, access to the riparian zone and floodplain during high flows, and inputs of particulate organic matter derived from tributaries and receding flood waters (Thorp et al., 2008). Generally, IsoSource estimates indicated that autochthonous benthic carbon was likely to be the most important carbon source for the primary consumers snails and *P. fluviatilis*, particularly in the constrained zone, where their isotopic signatures aligned closely with those of phytomicrobenthos. Fewer solutions were possible when using a reasonable maximum mass balance tolerance in IsoSource (0.5 ‰) downstream of the Waipa confluence for several snail and *P. fluviatilis* samples, where $\delta^{13}C$ values were too enriched to fit with a mixing polygon made up of basal carbon source annual means. It is possible that during some seasons the isotopic signatures of primary consumers could respond more rapidly and reflect changes in phytomicrobenthos signatures at a shorter time scale, compared to the annual means employed in the mixing models. Further, as phytomicrobenthos can comprise a range of living and detrital carbon components, the relative proportion of which can change with flow conditions, the isotopic signature of phytomicrobenthos may not accurately reflect what is ingested and assimilated by primary consumers if they preferentially select for certain components, a problem identified in other isotopic studies of riverine food webs (Delong et al., 2001; Hamilton et al., 2004; Delong & Thorp, 2006). While the use of annual means for each zone in mixing models may not accurately reflect close seasonal relationships between primary consumers and basal carbon sources, it does provide a consistent approach for addressing tissue turnover in consumers (Zeug & Winemiller, 2008; Hladyz et al., 2012).

High levels of suspended sediment can reduce the availability and quality of benthic algal food sources to primary consumers (Broekhuizen et al., 2001). This potentially explains the reduced contributions of autochthonous benthic carbon to higher consumers during winter and spring in the unconstrained zone (Fig. 4.5), which is subject to large inputs of cooler, sediment-laden water from the Waipa River at high flows. Autochthonous benthic carbon (phytomicrobenthos or the snail proxy) was consistently important for secondary and tertiary consumers in all zones and both flow periods (Tables 1 & 2; Fig. 4.5), often appearing to increase in a downstream direction, particularly after low autumn flows. For example, common smelt 50th percentile values increased from 40 to 79 % between the constrained and unconstrained zones, while those of C_3 macrophytes decreased from 14 to 0 %. Similar to my study, consistent utilisation of autochthonous algal carbon by food webs sampled along longitudinal gradients was identified in three Australian rivers with contrasting climatic and flow regimes sampled concurrently during low flows (Hadwen et al., 2010b). Potentially important contributions from other carbon sources (e.g. aquatic macrophytes, MEM and riparian vegetation) increased in the lower Waikato River during high spring flows (Fig. 4.5), when 50th and 99th percentiles of seston and also increased, notably in the unconstrained zone.

4.5.2 Isotopic signatures

Basal carbon sources

Isotopic ratios of C_3 riparian vegetation were within the range of values reported from other temperate and lowland river systems from both the northern and southern hemispheres (e.g. Thorp et al., 1998; Herwig et al., 2007; Hladyz et al., 2012) and from elsewhere in the Waikato catchment (Hicks, 1997). The elevated $\delta^{15}N$ values of aquatic macrophytes are also consistent with those reported from other large rivers (e.g. Thorp et al., 1998) and from previous studies of the lower Waikato River (e.g. West, 2007). The $\delta^{13}C$ signature of the dissolved inorganic carbon pool, and environmental variables such as flow velocity, temperature and water turbidity, can drive changes in the $\delta^{13}C$ signatures of primary producers, such as phytoplankton (seston) and phytomicrobenthos in rivers (France, 1995a; Finlay et al., 1999; Finlay, 2001). These factors can also change according to season, catchment area and the presence of wetlands in the catchment (Rounick & James, 1984; Finlay, 2001; Finlay et al., 2002), contributing to the temporal and spatial variability seen in the present study and other temperate and lowland river systems (Herwig et al., 2007; Hladyz et al., 2012). A notable shift in the $\delta^{13}C$ signature of dissolved inorganic carbon occurs directly downstream of the Waipa River confluence, where it becomes depleted by around 3 ‰ (Fitzgerald, 1996). Accordingly, mean $\delta^{13}C$ signatures of seston and phytomicrobenthos in each zone were most depleted during periods of low temperature and high flow (i.e. winter

2010), while at other times $\delta^{13}C$ signatures of seston and phytomicrobenthos were most depleted in the unconstrained and tidal freshwater zones where the river catchment includes several major wetlands. On sampling occasions when the isotopic signatures of seston in the tidal freshwater zone differed from other zones, it was more depleted in $\delta^{13}C$ and enriched in $\delta^{15}N$. A similar pattern has been observed for $\delta^{15}N$ in other freshwater tidal rivers where increasing values were associated with greater levels of human development in the watershed, particularly for agriculture (Chang et al., 2002; Anderson & Cabana., 2005; Winemiller et al., 2011). In this study, a similar pattern was observed for seston which was significantly enriched in $\delta^{15}N$ downstream of the Waipa River confluence, which contributes a large amount of agriculturally derived sediment and nutrients to the lower Waikato river, especially at high flows (Hicks & Hill, 2010; Vant, 2010).

Primary consumers

In general $\delta^{13}C$ and $\delta^{15}N$ signatures of primary invertebrate consumers were less variable than those of the basal carbon resources. The isotopic signatures of snails and amphipods showed similar spatial responses associated with the Waipa inflow, tending to be enriched in $\delta^{13}C$ in the constrained zone compared with the unconstrained and tidal zones. Additionally, $\delta^{13}C$ signatures of both snails and *P. fluviatilis* changed seasonally, particularly during periods of high flow and lower water temperatures (i.e. winter and spring). This was likely in response to isotopic changes of key food items (i.e. phytomicrobenthos). Snails and *P. fluviatilis* were sometimes more enriched in $\delta^{13}C$ than phytomicrobenthos, their most probable food source. This was likely a result of changes in the relative composition of phytomicrobenthos with seasonal episodes of high terrestrial runoff increasing the inorganic content and leading to selective assimilation by primary consumers (del Giorgio & France, 1996). It has been suggested that lower invertebrate densities below the Waipa confluence during winter and spring may be a result of less suitable flow and growth conditions (Collier et al., 2011), particularly for *P. antipodarum* whose growth and food assimilation are adversely affected by high sediment to food ratios (Broekhuizen et al., 2001). The other crustacean collector sampled, the shrimp *P. curvirostris,* consistently aligned with the isotopic signatures of aquatic macrophytes (Fig. 4.2b & c, Fig. 4.3c) and these tend to be an important littoral feeding habitat in all zones for this species.

Secondary and tertiary consumers

Both marked seasonal shifts (Hladyz et al., 2012) and low intra-annual variability (Herwig et al., 2007) in the isotopic signatures of higher consumers have been documented in river systems. The isotopic signatures of fish species collected in this study generally showed a similar pattern to those of aquatic basal carbon resources, as they were more depleted in $\delta^{13}C$ during spring (after high flows) than in autumn (after lower flows), although only common bully were significantly different in $\delta^{13}C$ and $\delta^{15}N$ between seasons. Goldfish and *Gambusia* were the most enriched in $\delta^{15}N$, while the predatory shortfin eel was generally less enriched. Shortfin eels, however, appear to assimilate significant amounts of carbon from riparian sources which generally had lower $\delta^{15}N$ signatures than aquatic carbon sources. The lower $\delta^{15}N$ signatures for eels likely reflects their opportunistic ability to exploit local riparian habitats for feeding when they become inundated (Jellyman 1989), and possibly a degree of trophic omnivory. Damselfly nymphs had lower and often variable $\delta^{15}N$ signatures compared to fish, potentially reflecting (i) the prey assemblage present in a particular mesohabitat from which the nymphs were collected (e.g. aquatic macrophytes, woody debris), which could change between sampling sites and times, (ii) potential differences in dietary preferences of smaller and larger nymphs, or (iii) some degree of trophic omnivory.

4.5.3 Conclusions

This study indicates that autochthonous benthic carbon was the major energy source supporting littoral food webs in this large, temperate southern hemisphere river. This is similar to studies from other biomes (see Pingram et al., 2012 for review), and supports aspects of both the original and revised RPM (Thorp & Delong, 1994, 2002). Carbon subsidies from riparian plants may have come from a combination of autumnal leaf fall, terrestrial invertebrates falling into the water, mobilisation of stored organic matter during flow pulses, or from consumers moving into inundated riparian areas during high flows as proposed by the FPC (Junk et al., 1989). Although longitudinal patterns were observed, my results provide little support for the prediction of the RCC that processed organic matter from upstream provide the main carbon source for food webs in large rivers (Vannote et al., 1980). The upper Waikato River is regulated by hydroelectric dams and processed organic matter originating from higher in the catchment is likely to settle in the hydro-lakes (Ward & Stanford, 1983). Contrary to my expectations, contributions of autochthonous benthic carbon were high overall for more mobile consumers (e.g. shortfin eel, common smelt and grey mullet) in the unconstrained and tidal freshwater zones, despite the array of lateral habitats and potential for carbon exchange with the riparian zone. The relative importance of secondary carbon sources changed temporally during the study period, appearing to increase following high flows (Fig. 4.5), possibly as a result of increased availability to terrestrial carbon (e.g. riparian leaf fall from the preceding autumn) or reduced palatability of phytomicrobenthos in the unconstrained zone (e.g. from high sediment loads during winter).

Variation in the isotopic ratios of organic carbon sources and primary consumers in this study reinforces the importance of quantifying spatial and temporal patterns to enable robust conclusions to be drawn regarding carbon flow in riverine food webs (Hladyz et al., 2012). Future studies employing SIA that address assimilation and trophic fractionation of food sources by consumers at different growth rates, size classes, tissues types, and seasonal and flow cycles, similar to Perga & Gerdeaux (2005) and Jardine et al. (2011), should prove valuable in unravelling carbon transfer in temperate river systems. At a local scale, my work provides a basis for assessing possible food web changes resulting from future rehabilitation of the lower Waikato River, particularly with regard to broad scale catchment management and localised reconnection of lateral habitats. Furthermore, for temperate floodplain rivers with similar morphological characteristics to the lower Waikato River, my study emphasises that food web properties, such as carbon flow can be driven by the nature of the hydrogeomorphic zone in line with the RES (Thorp et al., 2006, 2008), particularly where lateral and longitudinal linkages, and daily water level fluctuations potentially influence the availability of carbon subsidies from lateral habitats and the riparian zone.

4.6 References

Allan, J. D. & A. S. Flecker, 1993. Biodiversity conservation in running waters. Bioscience 43: 32-43.

Anderson, C. & G. Cabana, 2005. delta N-15 in riverine food webs: effects of N inputs from agricultural watersheds. Canadian Journal of Fisheries and Aquatic Sciences 62: 333-340.

Angradi, T. R., 1994. Trophic linkages in the lower Colorado River - Multiple stable-isotope evidence. Journal of the North American Benthological Society 13: 479-495.

Arrington, D. A., B. K. Davidson, K. O. Winemiller & C. A. Layman, 2006. Influence of life history and seasonal hydrology on lipid storage in three neotropical fish species. Journal of Fish Biology 68: 1347-1361.

Baxter, C. V., K. D. Fausch & W. Carl Saunders, 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology 50: 201-220.

Benstead, J. P., J. G. March, B. Fry, K. C. Ewel & C. M. Pringle, 2006. Testing isosource: stable isotope analysis of a tropical fishery with diverse organic matter sources. Ecology 87: 326-333.

Boon, P. I. & S. E. Bunn, 1994. Variations in the stable isotope composition of aquatic plants and their implications for food web analysis. Aquatic botany 48: 99-108.

Broekhuizen, N., S. Parkyn & D. Miller, 2001. Fine sediment effects on feeding and growth in the invertebrate grazers *Potamopyrgus antipodarum* (Gastropoda, Hydrobiidae) and *Deleatidium* sp. (Ephemeroptera, Leptophlebiidae). Hydrobiologia 457: 125-132.

Brown, E. J., 2003. Hydraulic travel time of major Waikato rivers. Environment Waikato Technical Report 2003/02. Environment Waikato, Hamilton.

Brown, E. J., 2010. Flow regime and water use. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, Hamilton, 29-46.

Bunn, S. E., P. M. Davies & M. Winning, 2003. Sources of organic carbon supporting the food web of an arid zone floodplain river. Freshwater Biology 48: 619-635.

Burford, M. A., A. J. Cook, C. S. Fellows, S. R. Balcombe & S. E. Bunn, 2008. Sources of carbon fuelling production in an arid floodplain river. Marine and Freshwater Research 59: 224-234.

Cabana, G. & J. B. Rasmussen, 1996. Comparison of aquatic food chains using nitrogen isotopes. Proceedings of the National Academy of Sciences of the United States of America 93: 10844-10847.

Carabel, S., E. Godinez-Dominguez, P. Verisimo, L. Fernandez & J. Freire, 2006. An assessment of sample processing methods for stable isotope analyses of marine food webs. Journal of Experimental Marine Biology and Ecology 336: 254-261.

Champion, P. D. & J. S. Clayton, 2010a. Box 14.1: Riparian vegetation. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, 268.

Champion, P. D. & J. S. Clayton, 2010b. Native macrophytes and aquatic weeds. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, 153-172.

Chang, C. C. Y., C. Kendall, S. R. Silva, W. A. Battaglin & D. H. Campbell, 2002. Nitrate stable isotopes: tools for determining nitrate sources among different land uses in the Mississippi River Basin. Canadian Journal of Fisheries and Aquatic Sciences 59: 1874-1885.

Chapman, M. A., 1996. Human impacts on the Waikato river system, New Zealand. GeoJournal 40: 85-99.

Chapman, M. A., M. H. Lewis & M. J. winterbourn, 2011. Guide to the freshwater Crustacea of New Zealand. New Zealand Freshwater Sciences Society, Chrsitchurch.

Cloe III, W. & G. Garman, 1996. The energetic importance of terrestrial arthropod inputs to three warm-water streams. Freshwater Biology 36: 104-114.

Collier, K. J. & A. Lill, 2008. Spatial patterns in the composition of shallow-water macroinvertebrate communities of a large New Zealand river. New Zealand Journal of Marine and Freshwater Research 42: 129-141.

Collier, K. J. & I. D. Hogg, 2010. Macroinvertebrates. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the

Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, Hamilton, 175-192.

Collier, K. J., E. M. Watene-Rawiri & J. D. McCraw, 2010b. Geography and history. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, 1-12.

Collier, K. J., M. P. Hamer & M. W. Davenport, 2011. Artificial substrate monitoring of macroinvertebrates in the Waikato River: 25 years on. Waikato Regional Council Technical Report 2011/25. Waikato Regional Council, Hamilton.

David, B. O. & D. A. Speirs, 2010. Native fish. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, 193-208.

de Ruiter, P. C., V. Wolters & J. C. Moore, 2005. Dynamic foodwebs. In de Ruiter, P. C., V. Wolters & J. C. Moore (eds), Dynamic Food Webs: Multispecies assemblages, ecosystem development and environmental change. Academic Press, 3-9.

del Giorgio, P. A. & R. L. France, 1996. Ecosystem-specific patterns in the relationship between zooplankton and POM or microplankton $\delta^{13}C$. Limnology 41: 359-365.

Delong, M. D., 2010. Food webs and the Upper Mississippi River: contributions to our understanding of ecosystem function in large rivers. Hydrobiologia 640: 89-101.

Delong, M. D. & J. H. Thorp, 2006. Significance of instream autotrophs in trophic dynamics of the Upper Mississippi River. Oecologia 147: 76-85.

Delong, M. D., J. H. Thorp, K. S. Greenwood & M. C. Miller, 2001. Responses of consumers and food resources to a high magnitude, unpredicted flood in the upper Mississippi River basin. Regulated Rivers-Research & Management 17: 217-234.

Doi, H., K. H. Chang, T. Ando, H. Imai, S. Nakano, A. Kajimoto & I. Katano, 2008. Drifting plankton from a reservoir subsidize downstream food webs and alter community structure. Oecologia 156: 363-371.

Doucett, R. R., D. R. Barton, K. R. a. Guiguer, G. Power & R. J. Drimmie, 1996. Comment: Critical examination of stable isotope analysis as a means for tracing carbon pathways in stream ecosystems. Canadian Journal of Fisheries and Aquatic Sciences 53: 1913-1915.

Douglas, M. M., S. E. Bunn & P. M. Davies, 2005. River and wetland food webs in Australia's wet-dry tropics: general principles and implications for management. Marine and Freshwater Research 56: 329-342.

Dynesius, M. & C. Nilsson, 1994. Fragmentation and flow regulation of river systems in the northern third of the world. Science 266: 753-762.

Finlay, J. C., 2001. Stable-carbon-isotope ratios of river biota: Implications for energy flow in lotic food webs. Ecology 82: 1052-1064.

Finlay, J. C., M. E. Power & G. Cabana, 1999. Effects of water velocity on algal carbon isotope ratios: Implications for river food web studies. Limnology and Oceanography 44: 1198-1203.

Finlay, J. C., S. Khandwala & M. E. Power, 2002. Spatial scales of carbon flow in a river food web. Ecology 83: 1845-1859.

Fitzgerald, J. M., 1996. Carbon-13 and oxegyn-18 isotope geochemistry of the Waikato River. MSc Thesis, University of Waikato.

Folch, J., M. Lees, G. Sloane-Stanley & others, 1957. A simple method for the isolation and purification of total lipids from animal tissues. Journal of Biological Chemistry 226: 497-509.

France, R., 1995a. Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. Marine Ecology Progress Series 124: 307-312.

France, R., 1995b. Stable Nitrogen Isotopes in Fish: Literature Synthesis on the Influence of Ecotonal Coupling. Estuarine, Coastal and Shelf Science 41: 737-742.

France, R. L., 1997. Stable carbon and nitrogen isotopic evidence for ecotonal coupling between boreal forests and fishes. Ecology of Freshwater Fish 6: 78-83.

Fry, B. & E. B. Sherr, 1989. $\delta^{13}C$ Measurements as indicators of carbon flow in marine and freshwater ecosystems. In Rundel, P. W., J. R. Ehleringer & K. A. Nagy (eds), Stable Isotopes in Ecological Research. Ecological Studies. springer-Verlag, New York, 196-229.

Hadwen, W. L., M. Spears & M. J. Kennard, 2010a. Temporal variability of benthic algal $\delta^{13}C$ signatures influences assessments of carbon flows in stream food webs. Hydrobiologia 651: 239-251.

Hadwen, W. L., C. S. Fellows, D. P. Westhorpe, G. N. Rees, S. M. Mitrovic, B. Taylor, D. S. Baldwin, E. Silvester & R. Croome, 2010b. Longitudinal trends in river functioning: patterns of nutrient and carbon processing in three Australian rivers. River Research and Applications 26: 1129-1152.

Hamilton, D. P. & I. C. Duggan, 2010. Plankton. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, 117-131.

Hamilton, S. K., J. L. Tank, D. F. Raikow, E. R. Siler, N. J. Dorn & N. E. Leonard, 2004. The role of instream vs allochthonous N in stream food webs: modeling the results of an isotope addition experiment. Journal of the North American Benthological Society 23: 429-448.

Herwig, B. R., D. H. Wahl, J. M. Dettmers & D. A. Soluk, 2007. Spatial and temporal patterns in the food web structure of a large floodplain river assessed using stable isotopes. Canadian Journal of Fisheries and Aquatic Sciences 64: 495-508.

Hicks, B. J., 1997. Food webs in forest and pasture streams in the Waikato region, New Zealand: A study based on analyses of stable isotopes of carbon and nitrogen, and fish gut contents. New Zealand Journal of Marine and Freshwater Research 31: 651-664.

Hicks, B. J., N. Ling & B. J. Wilson, 2010a. Introduced fish. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, 209-228.

Hicks, B. J., N. Ling, M. W. Osborne, D. G. Bell & A. Ring, 2005. Boat electrofishing survey of the lower Waikato River and its tributaries. CBER contract report no. 39. University of Waikato, Hamilton.

Hicks, D. M. & R. B. Hill, 2010b. Sediment regime: sources, transport and changes in the riverbed. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, Hamilton, 71-92.

Hladyz, S., D. L. Nielsen, P. J. Suter & E. S. Krull, 2012. Temporal variations in organic carbon utilization by consumers in a lowland river. River Research and Applications 28: 513-528.

Hoeinghaus, D. J., K. O. Winemiller & A. A. Agostinho, 2007. Landscape-scale hydrologic characteristics differentiate patterns of carbon flow in large-river food webs. Ecosystems 10: 1019-1033.

Hunt, R. J., T. D. Jardine, S. K. Hamilton & S. E. Bunn, 2011. Temporal and spatial variation in ecosystem metabolism and food web carbon transfer in a wet-dry tropical river. Freshwater Biology 57: 435-450.

Jardine, T., B. Pusey, S. Hamilton, N. Pettit, P. Davies, M. Douglas, V. Sinnamon, I. Halliday & S. Bunn, 2011. Fish mediate high food web connectivity in the lower reaches of a tropical floodplain river. Oecologia 168: 829-838.

Jellyman, D. J., 1989. Diet of two species of freshwater eel (Anguilla spp.) in Lake Pounui, New Zealand. New Zealand Journal of Marine and Freshwater Research 23: 1-10.

Jepsen, D. B. & K. O. Winemiller, 2007. Basin geochemistry and isotopic ratios of fishes and basal production sources in four neotropical rivers. Ecology of Freshwater Fish 16: 267-281.

Johnson, B. L., W. B. Richardson & T. J. Naimo, 1995. Past, Present, and Future Concepts in Large River Ecology. Bioscience 45: 134-141.

Junk, W. J. & K. M. Wantzen, 2004. The flood pulse concept: new aspects, approaches and applications - an update. Food and Agriculture Organization and Mekong River Commission, FAO Regional Office for Asia and the Pacific.

Junk, W.J., P.B. Bayley, & R.E.Sparks, 1989. The flood pulse concept in river-floodplain systems. In: D.P. Dodge (ed), Proceedings of the International Large River Symposium, Canadian Special Publication of Fisheries and Aquatic Sciences 106: 110-127.

Kohl, D. H. & G. Shearer, 1980. Isotopic fractionation associated with symbiotic N2 fixation and uptake of NO3− by plants. Plant Physiology 66: 51-56.

Layman, C. A., K. O. Winemiller & D. A. Arrington, 2005. Describing a species-rich river food web using stable isotopes, stomach contents, and functional experiments. In de Ruiter, P., V. Wolters & J. C. Moore (eds), Dynamic Food Webs: Multispecies assemblages, ecosystem development, and environmental change. Academic Press, 395-406.

Leigh, C., F. Sheldon, R. T. Kingsford & A. H. Arthington, 2010a. Sequential floods drive'booms' and wetland persistence in dryland rivers: a synthesis. Marine and Freshwater Research 61: 896-908.

Leigh, C., M. A. Burford, F. Sheldon & S. E. Bunn, 2010b. Dynamic stability in dry season food webs within tropical floodplain rivers. Marine and Freshwater Research 61: 357-368.

Marcarelli, A., C. Baxter & M. Mineau, 2011. Quantity and quality: unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters. Ecology 92: 1215-1225.

McCutchan, J. H., W. M. Lewis, C. Kendall & C. C. McGrath, 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102: 378-390.

McCutchan Jr, J. H. & W. M. Lewis Jr, 2002. Seasonal variation in stable isotope ratios of stream algae. Internationale Vereinigung fur Theoretische und Angewandte Limnologie Verhandlungen 27: 3304-3307.

McDowall, R. M., 1990. New Zealand freshwater fishes: a natural history and guide. Heinemann Reed, Auckland.

McDowall, R. M., 2000. The reed field guide to fishes of New Zealand. Reed Books, Auckland.

McDowall, R. M., M. R. Main, D. W. West & G. L. Lyon, 1996. Terrestrial and benthic foods in the diet of the shortjawed kokopu, Galaxias postvectis Clarke (Teleostei: Galaxiidae). New Zealand Journal of Marine and Freshwater Research 30: 257-269.

McIntyre, P. B. & A. S. Flecker, 2006. Rapid turnover of tissue nitrogen of primary consumers in tropical freshwaters. Oecologia 148: 12-21.

Medeiros, E. S. F. & A. H. Arthington, 2010. Allochthonous and autochthonous carbon sources for fish in floodplain lagoons of an Australian dryland river. Environmental Biology of Fishes 90: 1-17.

Mulholland, W. M., 2010. Box 2.2: History of the lower Waikato Flood Protection Scheme. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, Hamilton, 16.

Nichols, S. N., 1996. Studies on the freshwater shrimp *Paratya curvirostris* (Heller, 1862) in the Waikato River. MSc Thesis, University of Waikato.

Nilsson, C., C. A. Reidy, M. Dynesius & C. Revenga, 2005. Fragmentation and flow regulation of the world's large river systems. Science 308: 405-408.

Perga, M. E. & D. Gerdeaux, 2005. 'Are fish what they eat' all year round? Oecologia 144: 598-606.

Phillips, D. L. & J. W. Gregg, 2003. Source partitioning using stable isotopes: coping with too many sources. Oecologia 136: 261-269.

Phillips, D. L., S. D. Newsome & J. W. Gregg, 2005. Combining sources in stable isotope mixing models: alternative methods. Oecologia 144: 520-527.

Pingram, M. A., K. J. Collier, D. P. Hamilton, B. O. David & B. J. Hicks, 2012. Carbon sources supporting large river food webs: A review of ecological theories and evidence from stable isotopes. Freshwater Reviews 5: 85-103.

Pinnegar, J. K. & N. V. C. Polunin, 1999. Differential fractionation of $\delta^{13}C$ and $\delta^{15}N$ among fish tissue: implication for the study of trophic interactions. Functional Ecology 13: 225-231.

Post, D. M., 2002. Using stable isotopes to estimate trophic position: Models, methods, and assumptions. Ecology 83: 703-718.

Post, D. M., C. A. Layman, D. A. Arrington, G. Takimoto, J. Quattrochi & C. G. Montana, 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analysis. Oecologia 152: 179-189.

Post, J. R. & E. A. Parkinson, 2001. Energy allocation strategy in young fish: Allometry and Survival. Ecology 82: 1040.

Power, M. E. & W. E. Dietrich, 2002. Food webs in river networks. Ecological Research 17: 451-471.

Reid, M. A., M. D. Delong & M. C. Thoms, 2011. The influence of hydrological connectivity on food web structure in floodplain lakes. River Research and Applications 28: 827–844.

Roach, K. A., J. H. Thorp & M. D. Delong, 2009a. Influence of lateral gradients of hydrologic connectivity on trophic positions of fishes in the Upper Mississippi River. Freshwater Biology 54: 607-620.

Roach, K. A., K. O. Winemiller, C. A. Layman & S. C. Zeug, 2009b. Consistent trophic patterns among fishes in lagoon and channel habitats of a tropical floodplain river: Evidence from stable isotopes. Acta Oecologica-International Journal of Ecology 35: 513-522.

Rounick, J. S. & M. R. James, 1984. Goethermal and cold springs faunas: inorganic carbon sources affect isotope values. Limnology and Oceanography 29: 386-389.

Schiemer, F., H. Keckeis, W. Reckendorfer & G. Winkler, 2001. The "inshore retention concept" and its significance for large rivers. Large Rivers 12: 509-516.

Sedell, J. R., J. E. Richey & F. J. Swanson, The river continuum concept: A basis for the expected ecosystem behaviour of very large rivers? In: Dodge, D. P. (ed) Proceedings of the International Large River Symposium, 1989. Canadian Special Publication of Fisheries and Aquatic Sciences 106. p 49-55.

Speirs, D. A., D. G. Allen, R. M. Kelleher, M. D. Lake, A. N. Marchant, K. A. Mayes, E. M. Watene-Rawiri & B. J. Wilson, 2010. River management. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, Hamilton, 13-26.

Thorp, J. H. & M. D. Delong, 1994. The riverine productivity model: an heuristic view of carbon sources and organic processing in large river ecosystems. Oikos 70: 305-308.

Thorp, J. H. & M. D. Delong, 2002. Dominance of autochthonous autotrophic carbon in food webs of heterotrophic rivers. Oikos 96: 543-550.

Thorp, J. H., M. C. Thoms & M. D. Delong, 2006. The riverine ecosystem synthesis: Biocomplexity in river networks across space and time. River Research and Applications 22: 123-147.

Thorp, J. H., M. C. Thoms & M. D. Delong, 2008. The Riverine Ecosystem Synthesis: Towards conceptual cohesiveness in river science. Elsevier.

Thorp, J. H., M. D. Delong, K. S. Greenwood & A. F. Casper, 1998. Isotopic analysis of three food web theories in constricted and floodplain regions of a large river. Oecologia 117: 551-563.

Vander Zanden, M. J. & J. B. Rasmussen, 1999. Primary consumer delta C-13 and delta N-15 and the trophic position of aquatic consumers. Ecology 80: 1395-1404.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell & C. E. Cushing, 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37: 130-137.

Vant, W. N., 2010. Water Quality. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, Hamilton, 93-114.

Vörösmarty, C. J., P. B. McIntyre, M. O. Gessner, D. Dudgeon, A. Prusevich, P. Green, S. Glidden, S. E. Bunn, C. A. Sullivan, C. R. Liermann & P. M. Davies, 2010. Global threats to human water security and river biodiversity. Nature 467: 555-561.

Wantzen, K. M., F. D. Machado, M. Voss, H. Boriss & W. J. Junk, 2002. Seasonal isotopic shifts in fish of the Pantanal wetland, Brazil. Aquatic Sciences 64: 239-251.

Ward, J. V. & J. A. Stanford, 1983. The serial dicontinuity concept of lotic ecosystems. In Fontaine, T. D. & S. M. Bartell (eds), Dynamics of lotic ecosystems. Ann Arbor Scientific Publishers, Ann Arbor, MI, 29-42.

Weidel, B. C., S. R. Carpenter, J. F. Kitchell & M. J. Vander Zanden, 2011. Rates and components of carbon turnover in fish muscle: insights from bioenergetics models and a whole-lake ^{13}C addition. Canadian Journal of Fisheries and Aquatic Sciences 68: 387-399.

Wells, R. D. S., 1984. The food of the grey mullet (*Mugil cephalus* L.) in Lake Waahi and the Waikato River at Huntly. New Zealand Journal of Marine and Freshwater Research 18: 13-19.

West, D. W., 2007. Responses of wild freshwater fish to anthropogenic stressors in the Waikato River of New Zealand. PhD Thesis, University of Waikato.

Winemiller, K. O., A. S. Flecker & D. J. Hoeinghaus, 2010. Patch dynamics and environmental heterogeneity in lotic ecosystems. Journal of the North American Benthological Society 29: 84-99.

Winemiller, K. O., D. J. Hoeinghaus, A. A. Pease, P. C. Esselman, R. L. Honeycutt, D. Gbanaador, E. Carrera & J. Payne, 2011. Stable isotope analysis reveals food web structure and watershed impacts along the fluvial gradient of a Mesoamerican coastal river. River Research and Applications 803: 791-803.

Winterbourn, M. J., 2000. Feeding ecology. In Collier, K. J. & M. J. winterbourn (eds), New Zealand stream invertebrates: ecology and implications for management. New Zealand Limnological Scoiety, Hamilton, 100-156.

Wipfli, M. S. & C. V. Baxter, 2010. Linking ecosystems, food webs, and fish production: subsidies in salmonid watersheds. Fisheries 35: 373-387.

Woodward, G. & A. G. Hildrew, 2002. Food web structure in riverine landscapes. Freshwater Biology 47: 777-798.

Zeug, S. C. & K. O. Winemiller, 2008. Evidence supporting the importance of terrestrial carbon in a large-river food web. Ecology 89: 1733-1743.

5 Trophic patterns and carbon flow in main stem and tributary junction habitats in a large temperate riverscape

5.1 Abstract

Tributary confluences can be hotspots for biological production and provide novel carbon sources from donor sub-catchments in large river systems. In this study littoral food webs and water quality were compared between two main stem habitats (constrained and unconstrained hydrogeomorphic zones) and tributary junctions representing those fed by streams, lakes and wetlands feeding the lowland section of New Zealand's longest river, the Waikato River. Samples were collected to represent seasonal low flows during summer and autumn, when these habitats were likely to be most different. Natural abundances of stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes were then used to estimate carbon flow through food webs and also to estimate measures of trophic structure. Trophic pathways were also tested using analysis of fish stomach contents. To estimate carbon flow and trophic metrics the Bayesian statistics R package Stable Isotope Analysis in R (SIAR) was used. Despite marked differences in water quality between main stem and tributary junctions, littoral food webs were similar. SIAR mixing models indicated that autochthonous benthic carbon was the most important source to littoral food webs in all habitats. Trophic position of fish species collected in both main stem and tributary junction habitats were generally similar, as were fish stomach contents and community metrics estimated using stable isotope signatures and SIAR. This study demonstrates that while permanently connected habitats such as tributary junctions may add to the lateral complexity of the riverscape, they do not necessarily contribute to food web complexity. In this instance, tributary junctions tended to be steep-sided and complex littoral habitats such woody debris and macrophytes were typically rare, potentially limiting food web complexity. Management actions to improve water quality and structural habitat complexity within these junctions may provide better habitat for freshwater fish species and aid the rehabilitation of this large river system.

5.2 Introduction

Food web analysis provides a powerful approach to represent and describe trophic interactions and energy flow in a way that allows comparisons amongst spatial units (de Ruiter et al., 2005; Thompson et al., 2012). Understanding the structure and function of food webs is vital for developing predictions regarding the interrelationships between community dynamics, stability and ecosystem function in riverine systems, and how these are influenced by management actions and environmental change or disturbance (de Ruiter et al., 2005). Although the integration of patch dynamics, geomorphology and landscape ecology has expanded the scientific focus beyond a river continuum approach (Winemiller et al., 2010), freshwater food webs are still typically investigated at small spatial scales (Thompson et al., 2012). The need to take a landscape approach when studying the structure of food webs in large rivers has been recognised and there is now an increasing effort to incorporate broader landscape scale influences into riverine food web studies (Hoeinghaus et al., 2007; Jepsen & Winemiller, 2007; Thompson et al., 2012).

Tributary confluences can be hotspots for biological production and provide novel carbon sources from donor sub-catchments in large river systems. These junctions between the main stem and contributing watercourses, and immediately downstream are often areas of high habitat complexity that influence biological diversity and productivity due to higher substrate heterogeneity and abundance of woody debris, nutrients, and algal and consumer biomass (Kiffney et al., 2006), as articulated in the Network Dynamics Hypothesis (Benda, 2004). These factors are often determined by catchment land use and hydrological features such as lakes, wetlands, and agricultural areas, which can contribute different forms, combinations and amounts of carbon, nutrients, and sediment (Vannote et al., 1980; Kiffney et al., 2006; Rice et al., 2006; Rosales et al., 2007). Tributary junctions can also provide refugia for aquatic flora and fauna from higher flow velocities in the main stem, and as a result can support a greater diversity of macroinvertebrates and fish species than the main channel, contributing to the overall biodiversity in large river systems (Fernandes et al., 2004; Collier & Lill, 2008). Variation in flow velocities between habitats can also facilitate fundamental food web properties such as food chain length (Sabo et al., 2010).

Stable isotope analysis can provide a time-integrated measure of energy flow in aquatic food webs (see Chapter 2 and Post, 2002a; Pingram et al., 2012b) Trophic interactions are often quantified using the linear IsoSource mixing model (Phillips & Gregg, 2003; Phillips et al., 2005), which in turn allows exploration of spatial and temporal variation of food webs in river systems (e.g. Roach et al., 2009b; Hladyz et al., 2012; Pingram et al., 2012a). More recently, Bayesian probability models, such as MixSir (Moore & Semmens, 2008) and Stable Isotope Analysis in R (SIAR; Parnell et al., 2010) have become increasingly used to estimate carbon flow and other trophic metrics (e.g. Jackson et al., 2012). Trophic position, for example, is a useful metric of food web structure that can be estimated using δ^{15}N values. Other metrics of community and individual trophic variability have also been developed using the 2-dimensionl arrangement of δ^{13}C and δ^{15}N values (Layman et al., 2007b; Layman et al., 2007a; Layman et al., 2011), and these metrics are also readily calculated in computer packages such as SIAR (Jackson et al., 2011). Both stable isotope and dietary analyses can be used together to identify trophic interactions and quantify energy flow in aquatic food webs, although each method has weaknesses which can be alleviated and conclusions strengthened by using them in unison (Davis et al., 2012; Thompson et al., 2012).

The main objective of this chapter was to determine differences in trophic structure and energy flow between main stem and tributary junction habitats within the riverscape of the lower Waikato River. Tributary junctions are an important aspect of the ecology of the lower Waikato River riverscape, providing off-channel habitats that are characterised by their own catchment processes, such as agricultural land use, riverine lakes and flood control. Therefore, a better understanding of the ecological function of tributary confluences compared to the main stem has the potential to provide useful information for environmental restoration efforts undertaken in the lower Waikato River catchment generally. It was hypothesised that energy sources supporting fish production would differ between main stem and tributary junction sites, reflecting their catchment sources, particularly for lake-fed tributaries which would be expected to reflect seston exported from lakes upstream, and stream- and wetland-fed tributaries where a greater contribution of terrestrially derived carbon would be expected. Trophic structure was also expected to respond to differences in water quality characteristics. Stable isotope signatures of basal organic carbon sources and consumers in two hydrogeomorphic zones and six tributary confluences were quantified at low flows when tributary effects were considered least likely to be swamped by higher main stem flows. Carbon flow and trophic structure were then characterised using stable isotope analysis coupled with and dietary analysis of fish consumers.

5.3 Methods

5.3.1 Study area

The 7th order Waikato River flows in a roughly northerly direction for around 442 km from its headwaters above Lake Taupo to the Tasman Sea at Port Waikato (Collier et al., 2010) (Fig. 5.1). It drains a total catchment area of c. 14,443 km^2, and has a mean annual discharge of c. 450 $m^3 s^{-1}$ at the mouth (Brown, 2010). The river catchment has been significantly altered from its natural state, mostly for agriculture and forestry, as well as some urban development. Eight hydroelectric power dams have been constructed on the upper river and the furthest downstream dam forms Lake Karapiro which acts effectively as a barrier to the natural movement of aquatic fauna upstream. This study was conducted downstream of this final dam where the river flows along a low gradient channel, falling 22 m over c. 150 km to the sea (Collier et al., 2010) (Fig. 5.1). The lower Waikato River is fed by several major tributaries, the largest and most significant being the Waipa River, which augments mean flow by c. 25 % (Fig. 5.1) and contributes large loads of agriculturally-derived nutrients and sediment, particularly during high discharges in winter and spring (Chapman, 1996; Brown, 2010). Below this confluence six other major tributaries (> 4th order) feed the river and are fed by predominantly lakes, wetlands or stream runoff, all of which are in largely pastoral catchments (Fig. 5.1, Table 5.1).

The riparian zone, including in and around tributary junctions, of the lower Waikato River, is dominated by introduced vegetation, primarily crack willow (*Salix fragilis*) and alder (*Alnus glutinosa*), and pasture for stock grazing (Champion & Clayton, 2010a). The submerged aquatic flora is almost exclusively dominated by the exotic macrophytes *Egeria densa* and *Ceratophyllum demersum*, while other introduced species such as *Iris pseudocorus* and *Glyceria maxima* grow along river margins, and the sprawling emergent *Ludwigia peplodies* and *Myriophyllum aquaticum* are present along slow-flowing edges, particularly in tributary junctions (Collier & Lill, 2008; Champion & Clayton, 2010b). The planktonic algal assemblage is mostly made up of species of chlorophytes, diatoms and cyanobacteria, while the zooplankton assemblage in the main stem is dominated by small-sized rotifers (Hamilton & Duggan, 2010), although tributaries can deliver novel zooplankton communities to the main stem (Górski et al., 2013). At present there is no information available in the lower Waikato River and its tributaries on the composition, taxonomy or productivity of benthic biofilms, which can contain fungi, algae, microorganisms and detritus (collectively referred to as phytomicrobenthos after Zeug & Winemiller, 2008). . The littoral macroinvertebrate fauna is characterised by taxa with a preference for soft, silty sediments, including several species of worm (annelids, nematodes, roundworms, and ribbonworms), molluscs and midge larvae, and high abundances of the amphipod *Paracalliope fluviatilis* and the diadromous shrimp *Paratya curvirostris* along littoral margins (Collier & Lill, 2008).

Several native diadromous native fish species use the main stem primarily as a migratory route to smaller headwater tributaries, while others, including grey mullet (*Mugil cephalus*), shortfin eel (*Anguilla australis*), smelt (*Retropinna retropinna*), common bully (*Gobiomorphus cotidianus*) and īnanga (*Galaxias maculatus*), are resident as adults in the main stem (David & Speirs, 2010). At least ten introduced fish species are known to be present in the river and its tributaries, and many of these are now widespread and comprise a significant proportion of total fish abundance and biomass (Hicks et al., 2010), notably, koi carp (*Cyprinus carpio*), rudd (*Scardinius erythrophthalmus*), gambusia (*Gambusia affinis*), catfish (*Ameiurus nebulosus*) and goldfish (*Carassius auratus*) (Hicks et al., 2010). These common fish species are generally found in both main stem and tributary junction habitats.

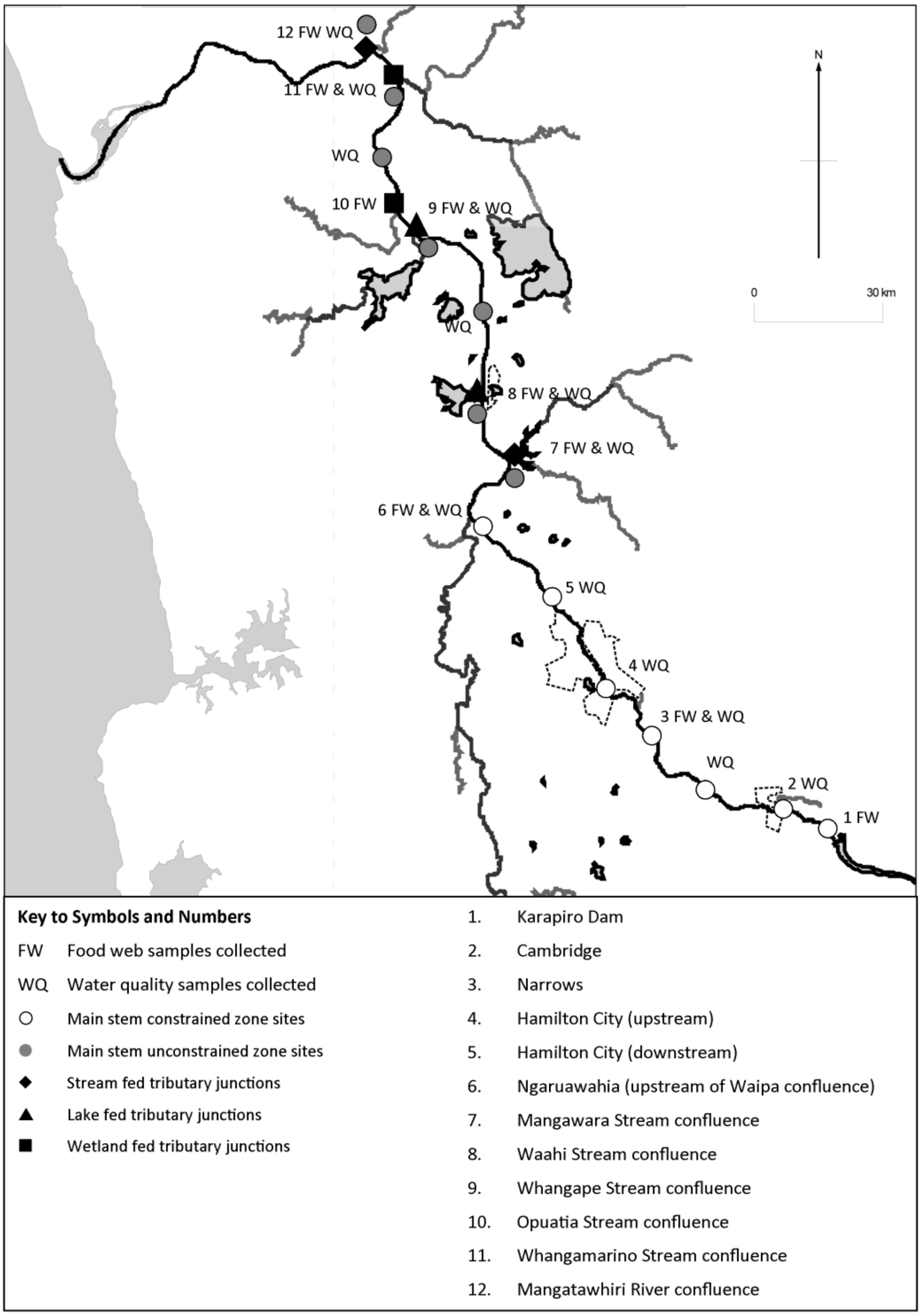


Figure 5.1. Map of lower Waikato River, indicating water quality and food web sampling locations.

5.3.2 Water quality sampling

Water quality measurements and samples were collected during March (summer) and May (autumn) 2010 from sites in the constrained and unconstrained zone of the lower Waikato River, and from within six major tributary junctions (Fig. 5.1).

Tributary habitats were categorised by their dominant source, i.e. riverine lakes (Waahi and Whangape), wetlands (Opuatia and Whangamarino) and runoff-fed streams (Mangawara and Mangatawhiri; for site locations and details see Fig. 5.1 and Table 5.1, respectively). When near tributaries, main stem samples were collected 200 – 400 m above confluences. Samples from tributary junctions were collected 100 – 200 m from the main river, except Waahi stream where samples were collected as far upstream as the flood gates (Fig. 5.1).

Water quality measurements were taken with a conductivity-temperature-depth (CTD) profiler (SBE 19 plus Seabird Electronics), fitted with additional dissolved oxygen (DO) and beam transmittance sensors. To characterise the surface waters, measurements were summarised in the same way as those used to calibrate Biofish measurements presented in Chapter 3. Beam transmittance was corrected to total beam attenuation coefficient (m^{-1}) using the equation: $c = \left(\frac{1}{z}\right) \times In\ (beam\ transmission)$. Surface water samples (c. 30 – 50 cm depth) were also collected to measure chlorophyll a (chl a), suspended solids and coloured dissolved organic matter (CDOM).

Concentrations of chl a ($\mu g\ l^{-1}$) were determined by filtering a known volume of water (usually 30 – 60 ml) through an Advantec GC-50 glass fibre filter. The filter paper was then folded, wrapped in tin foil and placed on ice to prevent light and heat exposure. On return to the laboratory this sample was frozen. Pigments were later extracted using 90 % buffered acetone and fluorescence measured using a 10-AU Fluorometer (Turner Designs), with phaeophytin corrected using acidification (Arrar & Collins, 1997). Total suspended solids (TSS), inorganic suspended solids (ISS), and total volatile solids (TVS) concentrations ($mg\ l^{-1}$) were determined using gravimetric methods, the drying and combustion of filters (Eaton & Franson, 2005). Briefly, sufficient water to produce 2.5 to 200 mg dried residue (generally 1 to 2 l) was collected in opaque plastic bottles and placed on ice in the field. On return to the laboratory (within 24 h) samples were filtered onto pre-weighed (± 0.1 mg), pre-combusted (550 °C) Advantec GC-50 glass fibre filters using a Gast vacuum pump. Filters were dried at 105°C for 4 h, cooled to room temperature and then re-weighed. The drying and weighing process was then repeated to ensure a constant weight (TSS). To determine ISS and TVS, filters were placed were ashed at 550 °C for 4 h, and then weighed as before.

To estimate coloured dissolved organic matter or yellow substance (CDOM) remaining unfiltered water was filtered through an Advantec 0.2 µm membrane filter, and absorbance was measured across a spectrum from 260 to 700 nm at 1 nm intervals using an optical glass cuvette with a 40 mm path length. A cuvette containing Milli-Q deionised water was used as a baseline, and this sample was reset every 4th occasion to account for any potential drift or variation in the lamps. CDOM absorption coefficients, aλ (natural log base), were calculated from the measured absorbance, Dλ, using equations in Davies-Colley and Vant (1987). Absorption coefficients were then corrected for backscatter of small particles and colloids which pass through filters, assuming that at a long wavelength (i.e. 700 nm) all measured absorption was essentially due to scattering (after Bricaud et al., 1981; Davies-Colley & Vant, 1987; Keith, 2002). The corrected absorption coefficient was then calculated at 440 nm (a_{440}) (after Davies-Colley & Vant, 1987; Kostoglidis et al., 2005) and at 340 nm (a_{340}) as this wavelength can be measured with greater precision due to higher absorbance in the infra-red region of the spectrum (Davies-Colley & Vant, 1987). Similar to other studies (e.g. Davies-Colley & Vant, 1987), a_{340} and a_{440} both showed similar patterns so only a_{440} is reported here.

5.3.3 Food web sampling

Potentially important basal carbon sources of aquatic and terrestrial origin, and invertebrate primary consumers were initially collected from littoral habitats of main river and tributary junction sites at low flows during April – May 2009; additional samples were collected during January - February (summer), and April – May 2010 (autumn) to better describe lower trophic levels. Sample collections were made during periods of low discharge, when the ability to discriminate between processes in tributary junctions and the main stem was likely to be enhanced. Fish were collected during autumn 2009 towards the end of a seasonal low flow period which should have allowed sufficient time for fish growth and muscle tissue turnover to reflect the isotopic signatures of their food sources consumed during the summer growth period (Perga & Gerdeaux, 2005). Aquatic primary producers and consumers were collected more frequently to better characterise variability in isotopic signatures of lower trophic levels.

Senescent and recently abscised leaves were collected from riparian willow and alder trees to represent allochthonous inputs. Predominantly young apical shoots were taken where possible from the common submerged macrophytes *C. demersum* and *E. densa*, after first ensuring that plants were rooted in place. Seston was collected by towing a 40 µm plankton net through the water at each site. The retained sample was stored in an opaque plastic container, and immediately on return to the laboratory was rinsed through a nested array of sieves, with the 40 – 100 µm sample retained to characterise transported phytoplankton. Benthic biofilms and algae (phytomicrobenthos) were scraped from a range of accessible stable substrates (i.e. woody debris and rocks). To provide an additional measure of aquatic benthic carbon sources, scrapers (snails) were collected from aquatic macrophytes and submerged substrates (logs, banks) using a sweep net (500 µm mesh) or by searching by hand. Snail species were generally a mix of *Potamopyrgus antipodarum*, *Physa acuta* and species from the genera *Lymnaea* and *Gyraulus*.

Fish were collected using a combination of boat electric fishing, minnow traps, and hand and fyke nets from in and around littoral habitats, as these provide shelter and feeding areas for many of the fish species in the lower Waikato River (McDowall 1990; David et al. 2010). Following collection, fish were euthanised in an ice slurry, and kept on ice until return to the laboratory, as were all other samples. Collected species of fish comprised the pelagic grey mullet and common smelt, the benthic-dwelling common bully and catfish, and the littoral-dwelling īnanga, gambusia, goldfish, and koi carp, and the widespread shortfin eel. Fish for SIA were selected from an intermediate size range, so that wherever possible fish sizes within species were consistent across sites and sampling occasions.

5.3.4 Sample preparation and stable isotope analysis

On return to the laboratory, samples were immediately prepared for stable isotope analysis or transferred to a -20 °C freezer for later processing. Terrestrial and aquatic plant matter was carefully rinsed in deionised water to remove any extraneous material. Sub-samples of seston were examined under 40 – 100 X magnification, and were typically dominated by diatoms of the genera *Asterionella* and *Aulacoseira* in riverine sites, while tributary junction samples often contained greater amounts of terrestrial detritus (authors' unpublished data).

Phytoplankton communities can also contain cyanobacteria, particularly in tributaries (Hamilton & Duggan, 2010). Phytomicrobenthos samples were rinsed with distilled water and then inspected under a dissecting microscope to remove invertebrates and large particles of sediment or organic matter.

Before being frozen, snails were kept in river water over a 500 μm nylon mesh for 12 h to evacuate their guts, as evidenced by the fine faecal material that accumulated on the container bottom. Where possible, muscle tissue from 10 – 15 snails from each site was pooled to produce sufficient material to meet the required minimum dry weight of 2 mg for stable isotope analysis. To avoid contamination by carbonates, which can be depleted in $\delta^{13}C$ compared with living tissues, snails were removed from their shells, rather than using a chemical dissolution treatment which can affect $\delta^{15}N$ ratios (Carabel et al. 2006). Fish tissue was extracted from the white dorsal muscle, which provides a representative isotopic signature and has less variable fractionation than other tissue (Pinnegar et al. 1999). Individual fish were analysed separately, except where it was not possible to extract sufficient white dorsal muscle from a single small fish (e.g. gambusia), in which case muscle from up to three individuals was pooled. Prior to drying, all muscle samples were rinsed in distilled water and inspected for stray scales and bones which were removed.

All samples, except for seston which was freeze-dried in a Dynavac FD12, were transferred to a Contherm drying oven pre-heated to 50 °C, for 48 h. Samples were then ground to a powder and stored at room temperature in air-tight containers containing bags of silica crystals. Samples were later weighed into tin cups, usually to specific weights (2 – 40 mg to nearest 0.01 mg) depending on expected carbon and nitrogen content, and analysed for $\delta^{13}C$ and $\delta^{15}N$ by the Waikato Stable Isotope Unit, University of Waikato, Hamilton, on a Europa Scientific 20/20 isotope ratio mass spectrometer. Stable isotope ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) are expressed as delta (δ) and defined as parts per thousand (‰) relative to the laboratory standard leucine, calibrated relative to atmospheric nitrogen for $\delta^{15}N$ and to Vienna Pee Dee Belemnite for $\delta^{13}C$. The instrument precision was c. 0.3 ‰ for $\delta^{13}C$ and c. 0.5 ‰ for $\delta^{15}N$. All data analysis and mixing models were undertaken using corrected $\delta^{13}C$ values for consumers and plants. $\delta^{13}C$ corrections were undertaken using the equations in Post et al. (2007), which were validated for fish muscle (see Chapter 4 and Pingram et al., 2012a)

5.3.5 Dietary analysis

To identify direct food web linkages (i.e. predation) the stomachs of fish used for stable isotope analysis and some additional fish collected simultaneously were examined under a dissecting microscope using 10 – 63 X magnification, and the contents were identified and recorded to the highest taxonomic level possible. The species used were selected to represent a range of feeding guilds. Results for four species (the native common bully, smelt and shortfin eel, and the introduced gambusia) that were collected in each habitat and for which contents could be successfully identified were then expressed as the percentage occurrence of food items in stomachs of each fish species (i.e. percentage of fish containing a particular item), excluding empty stomachs and those containing nothing identifiable (Hynes, 1950).

5.3.6 Statistical analysis

Statistical analyses were undertaken using Primer 6 and PERMANOVA extension (Version 1.0.3) with Monte Carlo *P* values where appropriate. Where significant differences or effects were evident *post-hoc* pairwise comparisons were undertaken for the appropriate factors. Water quality measurements were normalised and converted to a Euclidean distance matrix. To explore spatial differences of water quality characteristics between main stem and tributary confluence sites, principal components ordination (PCO) was applied to chl *a*, ISS, TVS, the total beam attenuation coefficient (c), temperature, CDOM (a_{440}) and % dissolved oxygen saturation.

Spatial differences of $\delta^{13}C$ and $\delta^{15}N$ were tested for each aquatic basal carbon resource and fish species collected in each of the five habitat types (constrained and unconstrained zones, and stream, lake and wetland-fed tributary junctions). Although two species of aquatic macrophyte were collected in this study, *C. demersum* (main stem and tributary junctions) and *E. densa* (main stem), they were treated as a single basal resource ‘type’ in analyses following the results of species comparisons presented Chapter 4 and Pingram et al. (2012a). Willow and alder leaves were collected to provide representative $\delta^{13}C$ and $\delta^{15}N$ signatures for each plant across the study area, therefore these were not included in analyses between sites (see Chapter 4 for species comparisons of willow and alder leaves).

Carbon signatures of grey mullet were often notably enriched in δ^{13}C compared to the primary producers sampled (up to c. 10 ‰, Fig. 5.3), particularly for samples collected in tributary junctions where fish tended to be smaller (<250 mm in length). Grey mullet (usually younger fish) tend to migrate upstream from more estuarine habitats at this time of year (McDowall, 1990, 2000), and their signatures were similar to those for seagrass previously recorded from the nearby Raglan Harbour estuary (Hailes, 2006). Therefore, their signatures may reflect fish which have only recently occupied freshwater habitats and whose tissue is yet to turnover to reflect the isotopic signatures of freshwater carbon sources. For this reason grey mullet was excluded from further analyses of energy flow and trophic structure.

5.3.7 Calculation of food web properties and metrics

SIAR was used to estimate contributions of basal carbon sources (Parnell et al., 2010) because it (i) provides highest density region estimates of likelihoods of contributions (HDRs) and (ii) allows the incorporation of variability of consumers, basal resource signatures and trophic enrichment factors. Trophic enrichment factors were based on the estimates of McCutchan et al. (2003), whereby consumer δ^{13}C values were adjusted by 0.4 ‰ (SD 0.17) and δ^{15}N values by 2.3 ‰ (SD 0.4) per trophic level. Trophic enrichment factors for fish other than shortfin eel and catfish were set at 0.8 ‰ (SD 0.34) and 4.6 ‰ (SD 0.8), for δ^{13}C and δ^{15}N, respectively, to reflect two trophic steps. Trophic enrichment factors for shortfin eel and catfish were set higher at 1 ‰ (SD 0.43) and 5.75 ‰ (SD 1), for δ^{13}C and δ^{15}N respectively, to reflect the regular occurrence of small fish in eel stomachs (2.5 steps). In addition to stomach contents, these enrichment factors were supported by other published information regarding fish diets in New Zealand waters (e.g. McDowall, 1990, 2000).

All mixing models were run using habitat specific means of aquatic basal resources (i.e. constrained, unconstrained, lake, wetland, and stream) (Fig. 5.3). As with Chapter 4, snail signatures assigned an appropriate trophic enrichment factor were added as an additional benthic carbon representative to expand the range of sources in mixing models. Scrapers have been used successfully elsewhere to represent epilithic algae in rivers (Finlay, 2001), and as snails feed on a range of periphyton and detritus this approach was employed to provide an integrator of littoral benthic carbon sources (e.g. Post, 2002b; Roach et al., 2009a). *E. densa* and *C. demersum* isotope signatures were averaged together to provide a 'macrophyte' value due to their statistically similar signatures (see Chapter 4 and Pingram et al., 2012a). Due to significant differences in the δ^{15}N of willow and alder these were used separately in mixing models (see Chapter 4 and Pingram et al., 2012a). Following the approach of Phillips et al. (2005), which can also be applied to the outputs of IsoSource mixing models (see Chapter 4), sources of similar ecological origin were combined *a posteriori* following model runs but prior to HDR calculations, to represent autochthonous benthic carbon (i.e. phytomicrobenthos and snail proxy), and riparian plants (willow and alder leaves). Similar to interpreting IsoSource outputs (Phillips & Gregg, 2003), as used in Chapter 4, it is important to consider the range of feasible solutions in SIAR. When interpreting IsoSource results carbon sources with high 1st percentiles are often considered as likely to be important to the species of interest (Benstead et al., 2006) and 1st percentiles >0 are often used to infer assimilation of that carbon source (e.g. Roach et al., 2009b). A similar approach was applied to SIAR results in this study whereby sources that had low 95 % HDR of ≥1 % were considered to indicate that a carbon source was likely to be assimilated by a consumer (following Parnell et al., 2010).

Trophic position (TP) for predatory consumers was estimated using the equation $\mathrm{TP} = \lambda + (\delta^{15}\mathrm{N}_{\mathrm{consumer}} - \delta^{15}\mathrm{N}_{\mathrm{reference}})/\mathrm{F}$ (Vander Zanden & Rasmussen, 1999). Whereby, λ was 1, F was the estimated δ^{15}N fractionation between trophic levels, in this case 2.3 ‰ (McCutchan et al., 2003), and $\delta^{15}\mathrm{N}_{\mathrm{reference}}$ was calculated for each habitat as the mean of riparian plants (collected from all sites), seston, phytomicrobenthos and aquatic macrophytes (collected from each habitat). Layman et al. (2007b) proposed metrics employing stable isotope ratios of δ^{13}C and δ^{15}N, which use the range and distribution of data points in 2-dimensional space to generate useful information. The proposed metrics are:

i. Nitrogen range (NR) - the range of δ^{15}N values which provides information on the trophic the range of δ^{15}N of a community or species;
ii. Carbon range (CR) - the range of δ^{13}C values which provides an estimate of the diversity of basal resources utilised by the community and their δ^{13}C signatures;

iii. Trophic area (TA) - the total area of the convex hull encompassing the data points in bi-plot space giving an indication of niche width of a community of species;

iv. Mean distance to centroid (CD) - the average Euclidean distance to the $\delta^{13}C$ – $\delta^{15}N$ centroid, where the centroid is the mean $\delta^{13}C$ and $\delta^{15}N$ values for the food web or species. This metric provides additional information on trophic diversity and species spacing, and is less sensitive to outliers than TA;

v. Mean nearest neighbour distance (MNND) - the average Euclidean distance between nearest neighbours provides a measure of the density and clustering of species within the community;

vi. Standard deviation of nearest neighbour distance (SDNND) - provides a measure of the evenness of spatial density and species packing (trophic evenness) which is less affected by sample size than MNND.

Jackson et al. (2011) have further advanced the quantification of these metrics using Bayesian statistics to generate probability statistics that enable further comparison between communities. Therefore, in this study the R package SIAR (Parnell et al., 2010) was employed using the siber.hull.metrics function and 10000 iterations to generate Bayesian probability estimates based on species means of the metrics proposed by Layman et al. (2007b) and denoted by the subscript ‘$_b$’ (after Jackson et al., 2012). TA_b, NR_b, CR_b were selected in this study to provide general descriptors of sampled food webs, while CD_b and $SDNND_b$ are also presented as these are less sensitive to sample size.

5.4 Results

5.4.1 Water quality

Analysis of variables measured to characterise water quality in the different habitats indicates clear differences between main stem riverine sites and tributary confluence sites. On average chl *a* was highest in lake-fed tributaries and was generally lower in the main stem than in the slower flowing tributaries (Table 5.1). Beam attenuation was markedly less in the main stem of the lower river than in tributary confluences, and this difference was most pronounced in lake-fed tributaries where beam attenuation was high and light transmittance was close to zero (Table 5.1). Tributary habitats also had higher TSS concentrations, which was generally dominated by the inorganic fraction (by weight). Lake-fed tributaries, particularly Whangape Stream, had higher organic content than the other tributary types (Table 5.1), likely a result of high phytoplankton biomass. Coloured dissolved organic matter was also higher in tributaries, especially in the Mangawara Stream (Table 5.1, Fig. 5.2). Specific conductance was lower in the main stem compared to tributary junctions (Table 5.1). Dissolved oxygen was generally higher in the main stem than in tributary junctions, except for the Whangape Stream (Table 5.1), while water temperature was slightly lower in stream- and lake-fed tributaries (Table 5.1). Tributary confluences could generally be differentiated from river sites in the PCO analysis (Fig. 5.2). Two groupings also appeared for river sites and these appeared to be related to water temperature differences between summer and autumn samples.

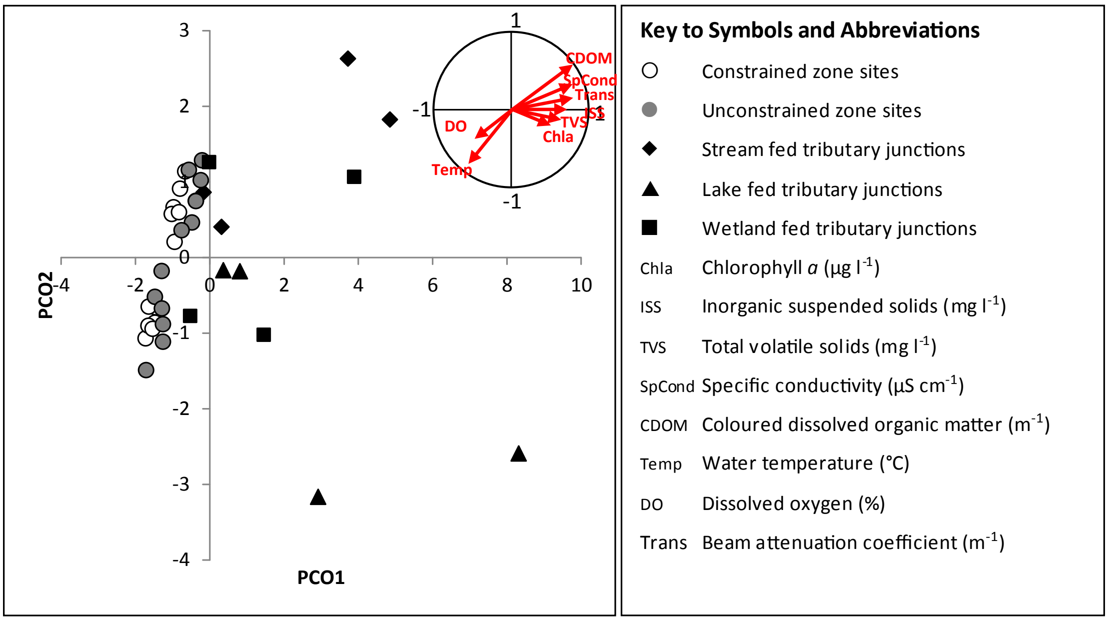


Figure 5.2. Principal coordinates ordination (PCO) and vector diagram of Spearman co-efficients for water quality variables for riverine and tributary junction sites.

Table 5.1. Water quality measurements for riverine sites and tributary junction sites (grouped by habitat; mean ± standard deviation). '-' indicates that no data was collected.

Habitat	Zone or tributary	Catchment area (km^2)	Chlorophyll *a* ($\mu g\ l^{-1}$)	Total suspended solids ($mg\ l^{-1}$)	Inorganic suspended solids ($mg\ l^{-1}$)	Total volatile solids ($mg\ l^{-1}$)	Coloured dissolved organic matter absorption at 440 nm (m^{-1})	Dissolved oxygen %	Temperature (°C)	Beam attenuation (m^{-1})	Specific conductance ($\mu S\ cm^{-1}$)
Riverine	Constrained Zone	-	6.6 ±0.3	3.2 ±0.2	2.8 ±0.2	0.4 ±0.1	0.8 ±0.1	69.2 ±1.1	18.1 ±0.9	2.5 ±0.6	169 ±3.3
Riverine	Unconstrained Zone	-	7.2 ±0.5	7 ±0.5	5.9 ±0.4	1.1 ±0.2	1.1 ±0.2	68.3 ±1.6	17.6 ±0.7	3.7 ±0.6	169.5 ±2
Stream	Overall		9.6 ±1.8	26.8 ±7.3	22.3 ±6	4.5 ±1.5	3.3 ±1	51.8 ±7.5	16.1 ±0.9	20.0 ±13.6	202.8 ±19.2
	Mangawara Stream	182	12.6	37.7	30.8	6.9	4.9	41.7	15.9	30.8	235.2
	Mangatawhiri River	602	6.5	15.8	13.8	2	1.6	61.9	16.4	9.3	170.3
Lake	Overall		52.3 ±17.3	45.1 ±23.1	35.3 ±19.1	9.8 ±4.2	2.1 ±0.3	72.7 ±13.1	16.8 ±2.2	35.5 ±2.0	246.2 ±8.8
	Waahi Stream	94	23.3	21.7	17.1	4.6	1.9	-	-	-	-
	Whangape Stream	347	81.4	68.5	53.5	15	2.3	72.7	16.8	35.5 ±2.0	246.2
Wetland	Overall		24.5 ±11.3	15.5 ±4.4	12.5 ±3.6	2.9 ±1.1	1.4 ±0.4	57.3 ±3.6	17.8 ±1.5	11.8 ±5.9	243.7 ±45.6
	Opuatia Stream	213	14.5	18.8	16.3	2.5	1.4	59.7	17.8	13.7	201.5
	Whangamarino River	800	34.4	12.1	8.7	3.3	1.3	55	17.8	9.9	286

5.4.2 Isotopic signatures

Both the δ^{15}N and δ^{13}C signatures of aquatic basal resources (seston, phytomicrobenthos and macrophytes) differed between some habitats. The mean δ^{13}C signature of phytomicrobenthos collected from the constrained zone was significantly enriched compared with all other habitats (Table 5.2), except stream-fed tributaries (*P*=0.08). For δ^{15}N, phytomicrobenthos from lake-fed tributaries had significantly lower values than all other habitats (Table 5.2), except wetland-fed tributaries (*P*=0.07). As with phytomicrobenthos, seston δ^{15}N signatures tended to be lowest in lake-fed tributary junctions (Table 5.2, Fig. 5.3), although this difference was only significant between lake and river sites (Table 5.2). Seston δ^{13}C appeared to be most enriched in stream- and lake-fed tributary junctions, particularly compared to the unconstrained zone (Table 5.2). The range of isotopic signatures of aquatic macrophytes was variable across all sites, particularly for δ^{15}N. Although there was no statistically significant effect of habitat on macrophyte δ^{15}N, there was for δ^{13}C signatures which were significantly more enriched in lake-fed tributaries compared to all other habitats (Table 5.2). As presented in Chapter 3 and Pingram et al. (2012a), senesced alder and willow leaves have significantly different δ^{15}N signatures, by c. 8 ‰ on average (Fig. 5.3).

Table 5.2. PERMANOVA F-ratios for comparisons between habitats of mean δ^{13}C and δ^{15}N isotope signatures of aquatic basal carbon sources. Letters in 'superscript' indicate significant differences between habitats in pairwise comparisons (*P*<0.05) for each basal carbon source (row). ** indicates a significant effect of habitat in PERMANOVA analyses of *P*<0.01. Values in parentheses are (± 1 standard deviation).

Aquatic basal carbon sources	**Pseudo-*F***	**Mean**				
		Constrained Zone	Unconstrained Zone	Stream	Lake	Wetland
δ^{13}C						
Phytomicrobenthos	4.97**	-21.1 ± 3.8 ^{abc}	-25.2 ± 2.4 ^{a}	-24.4 ± 3.3	-25.6 ± 1.2 ^{b}	-26 ± 2 ^{c}
Seston	5.04**	-27.7 ± 2.4 ^{a}	-28.1 ± 0.5 ^{abc}	-26.7 ± 2.0 ^{b}	-25.6 ± 1.6 ^{cd}	-28 ± 0.8 ^{d}
Macrophytes	7.23**	-24.3 ± 2.6 ^{a}	-24.5 ± 2.7 ^{b}	-27.9 ^{c}	-17.6 ± 1.5 ^{abcd}	-24.2 ± 1.7 ^{d}
δ^{15}N						
Phytomicrobenthos	6.22**	7.5 ± 1.1 ^{a}	6.8 ± 0.6 ^{a}	8.3 ± 2 ^{cd}	5.2 ± 1.5 ^{abc}	6.4 ± 1 ^{d}
Seston	4.30**	5.0 ± 0.9 ^{a}	5.9 ± 0.7 ^{ab}	5.5 ± 1.7	3.2 ± 2.4 ^{b}	5.5 ± 1.8
Macrophytes	1.65	9.7 ± 2.9	9.7 ± 4.6	12.3	4.9 ± 2.8	7.2 ± 3.7

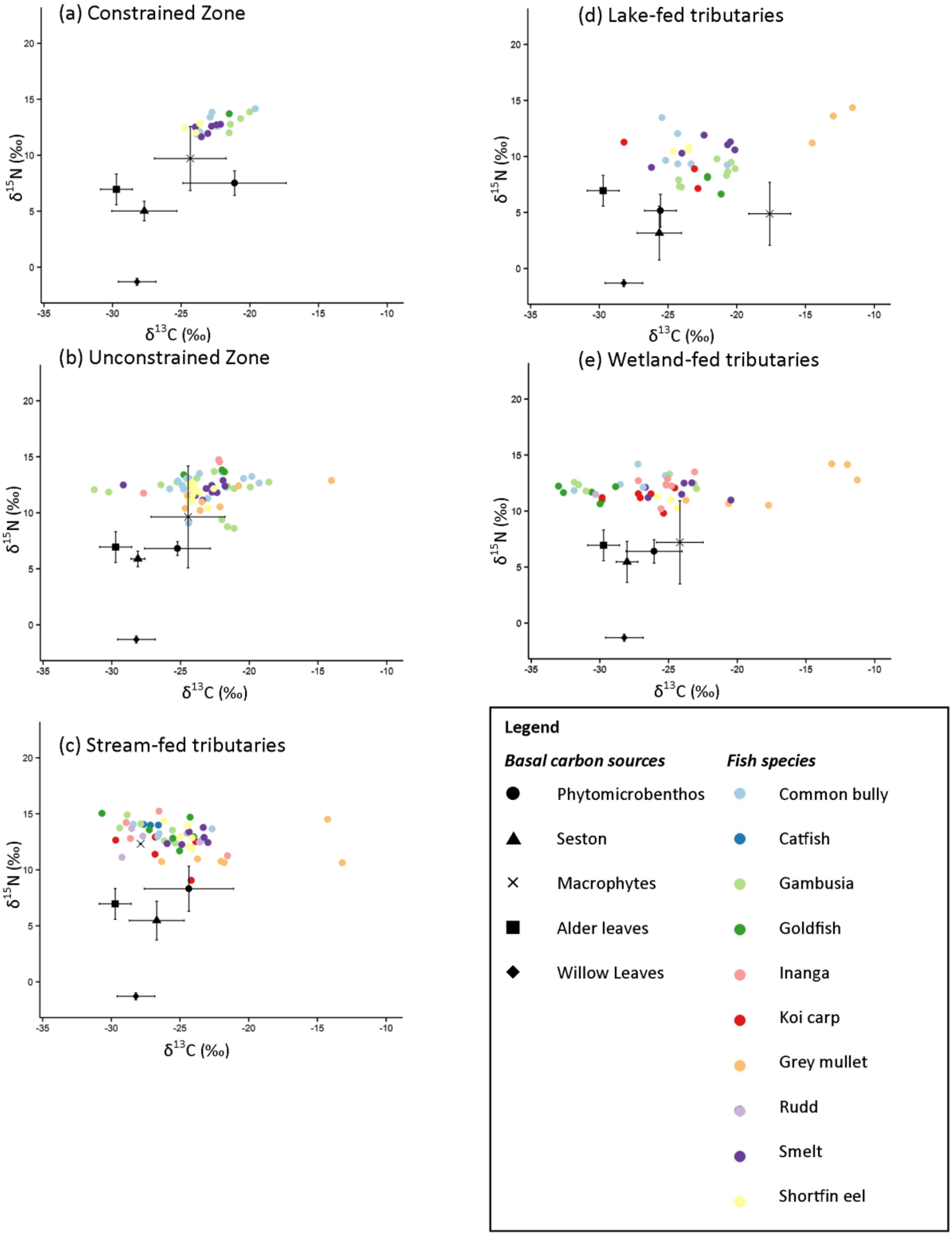


Figure 5.3. $\delta^{13}C$ and $\delta^{15}N$ ratios of basal organic carbon sources and secondary fish consumers collected from the lower Waikato River and tributary junctions. (a) constrained zone (b) unconstrained zone (c) stream-fed tributaries (d) lake-fed tributaries, and (e) wetland-fed tributaries. Black symbols denote mean basal organic carbon sources. Bars represent ±1 SD.

Isotopic signatures of fish collected also differed between habitats, for both $\delta^{13}C$ (common bully, gambusia and goldfish) and $\delta^{15}N$ (common bully, smelt, gambusia, goldfish and shortfin eel) (Table 5.3, Fig. 5.3). Both $\delta^{13}C$ and $\delta^{15}N$

signatures were similar between fish collected in the constrained and unconstrained zones. Fish collected in wetland-fed tributaries tended to be more depleted in $\delta^{13}C$, although this was not always significant. Fish from lake-fed tributaries tended to have lower $\delta^{15}N$ values, while smelt and shortfin eel tended to have similar signatures regardless of habitat, although $\delta^{15}N$ signatures differed between riverine and tributary junctions (Table 5.3).

Table 5.3. PERMANOVA F-ratios for comparisons between habitats of mean $\delta^{13}C$ and $\delta^{15}N$ isotope signatures of common fish species collected from each habitat. Letters in 'superscript' indicate significant differences between habitats in pairwise comparisons (*P*<0.05) for each row (fish species). ** indicates a significant effect of habitat in PERMANOVA analyses of *P*<0.01. Values in parentheses are (± 1 standard deviation).

Secondary fish consumers	**Pseudo-*F***	**Mean**				
		Constrained Zone	Unconstrained Zone	Stream	Lake	Wetland
$\delta^{13}C$						
Common Bully	6.04**	-22.5 ± 1.5^{ab}	-23.3 ± 2.1^{cd}	-25.5 ± 2.2^{ac}	-23.9 ± 1.7^{e}	-27.5 ± 2.5^{bde}
Smelt	0.97	-20.9 ± 0.7	-23.4 ± 3.7	-27.2 ± 1.7	-22 ± 1.8	-27.6 ± 4.3
Gambusia	5.32**	-23 ± 0.7^{ab}	-23.4 ± 2.3^{cd}	-24.1 ± 1.2^{ace}	-22.3 ± 2.4^{ef}	-24.1 ± 2.3^{bdf}
Goldfish	16.53**	-21.5^{ab}	-22.8 ± 1.7^{c}	-26.1 ± 2.5^{d}	-21.8 ± 0.6^{acd}	-30.8 ± 1.7^{acd}
Shortfin eel	2.83	-24.1 ± 0.6	-23.9 ± 0.6	-24.7 ± 0.8	-23.9 ± 0.6	-25 ± 0.8
$\delta^{15}N$						
Common Bully	5.30**	13 ± 1^{a}	12.4 ± 1.2^{b}	13.2 ± 0.6^{c}	10.5 ± 1.8^{abcd}	12.6 ± 0.9^{d}
Smelt	8.90**	13 ± 0.8^{a}	11.7 ± 1.6^{b}	13.5 ± 0.9^{bc}	8.4 ± 0.9^{bc}	12.4 ± 0.5^{c}
Gambusia	20.01**	12.3 ± 0.5^{a}	12 ± 0.5^{b}	12.8 ± 0.6^{bc}	10.7 ± 1.0^{ab}	11.8 ± 0.7^{ac}
Goldfish	24.90**	13.7^{a}	13.6 ± 0.2^{b}	13.5 ± 1.3^{c}	7.6 ± 0.9^{abc}	11.5 ± 0.6^{abc}
Shortfin eel	8.42**	12.4 ± 0.4^{ab}	11.8 ± 0.7^{cd}	13 ± 1.0^{cd}	10.6 ± 0.2^{ac}	10.8 ± 0.5^{bd}

Diet analysis

Aquatic macroinvertebrates were recorded from most of the fish stomachs examined (Table 5.4). Collector/gatherer taxa were present in over half of all stomachs examined and in over 75 % of both common bully and smelt samples (Table 5.4). Zooplankton (mixture of copepods and cladocerans) were the next most common food item in the stomachs of these two fish species. The collector/gatherer group was dominated by the amphipod *P. fluviatilis*, which can readily be collected from a wide range of benthic and plant surfaces including macrophytes, emergent littoral vegetation such as *Glyceria*, amongst willow roots, and rocks and logs covered in filamentous algae, bryophytes or bryozoans

Table 5.4. Percentage occurrence of identifiable dietary items recorded from common fish species.

Species	**Habitat**	**N**	**Empty**	**Miscellaneous**		**Aquatic Invertebrates**								**Terrestrial invertebrates**	**Unidentified Invertebrates**	**Fish**
				Algae	Sediment and detritus	Scrapers	Zoo-plankton	Shredder/ Collector	Collector/ Filterer	Piercers	Collector/ Gatherer	Mites, flatworms and leaches	Large predatory invertebrates			
Bully	**Total**	**41**	**6**	**3**	**9**	**23**	**43**	**0**	**14**	**29**	**77**	**3**	**3**	**0**	**3**	**6**
	Constrained	6	0	0	0	50	50	0	50	33	67	17	0	0	0	0
	Unconstrained	17	2	7	7	27	40	0	0	27	87	0	7	0	7	7
	Stream	6	0	0	17	0	33	0	0	17	50	0	0	0	0	17
	Lake	6	2	0	0	0	25	0	50	0	75	0	0	0	0	0
	Wetland	6	2	0	25	25	75	0	0	75	100	0	0	0	0	0
Smelt	**Total**	**27**	**7**	**20**	**20**	**0**	**30**	**0**	**15**	**5**	**75**	**20**	**20**	**30**	**0**	**0**
	Constrained	3	1	50	0	0	50	0	100	0	100	50	0	0	0	0
	Unconstrained	9	0	11	44	0	22	0	11	11	89	11	33	44	0	0
	Stream	6	2	25	0	0	25	0	0	0	75	25	25	25	0	0
	Lake	6	2	25	0	0	50	0	0	0	50	25	0	0	0	0
	Wetland	3	2	0	0	0	0	0	0	0	0	0	0	100	0	0
Gambusia	**Total**	**41**	**4**	**0**	**3**	**0**	**43**	**0**	**65**	**3**	**35**	**5**	**0**	**35**	**8**	**0**
	Constrained	3	0	0	0	0	33	0	100	0	33	0	0	0	33	0
	Unconstrained	18	1	0	0	0	35	0	65	6	29	12	0	41	12	0
	Stream	6	1	0	0	0	20	0	100	0	60	0	0	0	0	0
	Lake	8	0	0	0	0	88	0	25	0	38	0	0	38	0	0
	Wetland	6	2	0	25	0	25	0	75	0	25	0	0	75	0	0
Shortfin eel	**Total**	**32**	**7**	**0**	**24**	**24**	**0**	**4**	**0**	**4**	**28**	**0**	**12**	**36**	**8**	**24**
	Constrained	4	2	0	50	50	0	0	0	50	100	0	0	50	0	50
	Unconstrained	12	1	0	9	45	0	9	0	0	27	0	18	45	0	0
	Stream	9	2	0	29	0	0	0	0	0	14	0	0	29	29	57
	Lake	4	1	0	33	0	0	0	0	0	0	0	0	33	0	33
	Wetland	3	1	0	50	0	0	0	0	0	50	0	50	0	0	0
All	**Total**	**141**	**24**	**4**	**12**	**12**	**32**	**1**	**27**	**11**	**53**	**6**	**7**	**24**	**5**	**7**

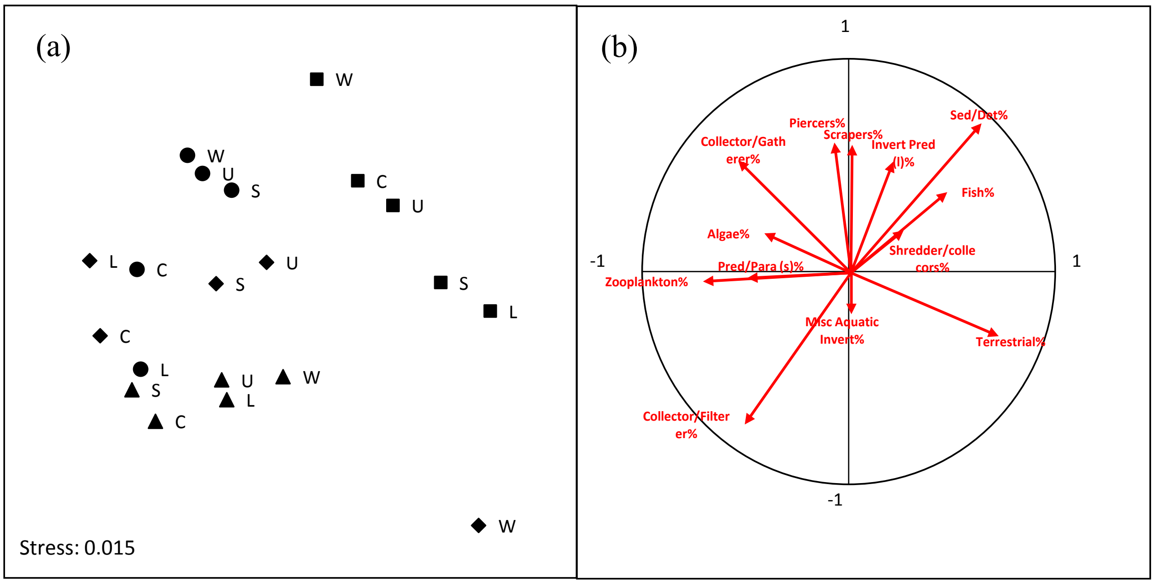


Figure 5.4. (a) MDS and (b) vector plot of percentage occurrence of dietary items in stomachs of common bully (●), smelt (◆), gambusia (▲) and shortfin eel (■), collected from constrained (C) and unconstrained zones (U), and from stream-fed (S), lake-fed (L) and wetland-fed (W) tributary junctions.

(pers. obs. and Collier & Lill, 2008). Remains of other collector/gatherer taxa were represented in stomach contents by insect larvae, emerging or winged adult life stages, and also the shrimp *P. curvirostris*, which was detected in shortfin eel stomachs (Table 5.4).

Other food items of note that occurred regularly were scrapers (snails) and piercers (axe- and purse-head caddis) in bully stomachs, and small invertebrate predators (flatworms, leeches and mites) in smelt and gambusia. Scrapers (snails), collector-gatherers (mostly *P. fluviatilis*), terrestrial invertebrates and small fish each occurred in around 25 % of eel stomachs. Zooplankton were mostly found in fish stomachs from tributary habitats and typically comprised a mix of ostracods, copepods, and some cladocerans. Scrapers (snails) were most commonly found in bully and eel stomachs. Trichopterans (mostly from the families Hyropsychidae and Hydroptilidae) and dipterans (mostly members of the family Chironomidae) were recorded as larvae, emerging and adult individuals, especially in smelt. Terrestrial invertebrates occurred in around 25 % of all fish stomachs, ranging from c. 30 % for gambusia, smelt and shortfin eel to 0 % for common bully (Table 5.4). Terrestrial food items included a range of functional groups, including earthworms, slugs, bees and wasps. Other than for smelt collected from wetlands, for which there was only a single stomach containing dietary items, fish species tended to plot more closely by species than habitat, particularly for shortfin eels and gambusia (Fig. 5.4). The species plotted in Fig. 5.4 also illustrate the possible trophic omnivory of species such as shortfin eel.

5.4.3 Carbon flow - SIAR

Autochthonous benthic carbon was consistently important, contributing to between 26 and 58 % of consumer biomass on average for all of the fish sampled in all habitats (Table 5.5). It is also worth noting that autochthonous benthic carbon was also the most likely source to contribute more than 10 % of carbon to fish species at low HDRs and mean values. Riparian carbon was the next most important carbon source, making significant contributions to all species (i.e. low 95 % HDR ≥0.01 proportional contribution), except gambusia sampled from the constrained zone (Table 5.5). Macrophytes were also important, contributing to consumer biomass for around half of the species sampled, while seston had no model outputs with low 95 % HDR values greater than 0.5 %. For consumers sampled from both riverine and tributary junctions, mean contributions of benthic carbon were generally higher in the constrained and unconstrained zones than in tributary junctions, although HDRs of probability estimates could overlap due to wide ranges (Table 5.5). Some differences also appear to exist between tributary junctions for some fish species, with common bully, smelt, goldfish and shortfin eel collected in stream-fed habitats all having lower mean riparian contributions than lake- and wetland-fed tributary junctions. For species such as koi carp and rudd, however, contributions of riparian carbon were very similar between tributary habitats. Autochthonous benthic carbon contributions were similar for fish collected in each of the tributary habitats, except for smelt which had noticeably lower mean contribution in lake-fed tributaries.

Table 5.5. Mean proportion carbon contributions to primary consumer biomass estimated using SIAR. 95 % highest density regions are displayed in parentheses. Values in bold indicate carbon sources with a 95 % low highest density region proportion contribution greater than or equal to 0.01. '*' indicates species that had trophic enrichment factors set for 2.5 trophic steps in mixing models.

Species	Habitat	Benthic	Macrophyte	Seston	Riparian
Bully	Constrained zone	**0.49 (0.29-0.69)**	**0.28 (0.07-0.48)**	0.08 (0-0.21)	**0.15 (0.01-0.3)**
	Unconstrained zone	**0.53 (0.32-0.74)**	**0.25 (0.09-0.39)**	0.09 (0-0.23)	**0.13 (0.01-0.28)**
	Stream	**0.39 (0.15-0.62)**	**0.29 (0.13-0.44)**	0.13 (0-0.28)	**0.2 (0.03-0.36)**
	Lake	**0.35 (0.08-0.59)**	**0.19 (0.03-0.34)**	0.15 (0-0.31)	**0.31 (0.11-0.51)**
	Wetland	**0.31 (0.06-0.55)**	0.19 (0-0.37)	0.17 (0-0.35)	**0.32 (0.07-0.57)**
Smelt	Constrained zone	**0.49 (0.32-0.65)**	**0.21 (0.04-0.37)**	0.11 (0-0.25)	**0.19 (0.04-0.34)**
	Unconstrained zone	**0.58 (0.33-0.83)**	**0.14 (0.01-0.27)**	0.11 (0-0.27)	**0.16 (0.01-0.33)**
	Stream	**0.49 (0.23-0.77)**	**0.21 (0.03-0.36)**	0.14 (0-0.3)	**0.16 (0.01-0.32)**
	Lake	**0.33 (0.07-0.57)**	**0.27 (0.07-0.46)**	0.12 (0-0.28)	**0.28 (0.06-0.49)**
	Wetland	**0.44 (0.2-0.7)**	**0.21 (0.01-0.37)**	0.13 (0-0.29)	**0.22 (0.03-0.41)**
Gambusia	Constrained zone	**0.57 (0.3-0.83)**	**0.23 (0.01-0.41)**	0.08 (0-0.22)	0.13 (0.00-0.30)
	Unconstrained zone	**0.43 (0.19-0.68)**	**0.24 (0.04-0.4)**	0.14 (0-0.3)	**0.20 (0.03-0.38)**
	Stream	**0.3 (0.06-0.53)**	**0.33 (0.15-0.52)**	0.12 (0-0.29)	**0.25 (0.04-0.45)**
	Lake	**0.36 (0.12-0.6)**	**0.27 (0.12-0.42)**	0.15 (0-0.31)	**0.21 (0.04-0.4)**
	Wetland	**0.34 (0.08-0.59)**	**0.21 (0.01-0.38)**	0.16 (0-0.33)	**0.29 (0.05-0.52)**
Goldfish	Constrained zone	**0.46 (0.21-0.72)**	**0.3 (0.08-0.52)**	0.09 (0-0.23)	**0.14 (0.01-0.29)**
	Unconstrained zone	**0.41 (0.14-0.67)**	**0.24 (0.01-0.42)**	0.13 (0-0.3)	**0.23 (0.02-0.43)**
	Stream	**0.38 (0.13-0.62)**	**0.27 (0.08-0.46)**	0.13 (0-0.3)	**0.22 (0.03-0.41)**
	Lake	**0.33 (0.09-0.56)**	**0.27 (0.05-0.46)**	0.16 (0-0.32)	**0.24 (0.03-0.46)**
	Wetland	**0.35 (0.08-0.6)**	0.16 (0-0.31)	0.17 (0-0.35)	**0.32 (0.06-0.56)**
Inanga	Unconstrained zone	**0.39 (0.15-0.63)**	**0.25 (0.03-0.44)**	0.14 (0-0.3)	**0.22 (0.03-0.41)**
	Stream	**0.36 (0.11-0.6)**	**0.22 (0.02-0.4)**	0.15 (0-0.32)	**0.27 (0.05-0.47)**
	Wetland	**0.36 (0.14-0.58)**	**0.23 (0.01-0.41)**	0.15 (0-0.31)	**0.26 (0.05-0.44)**
Koi	Stream	**0.34 (0.11-0.57)**	**0.18 (0.01-0.32)**	0.17 (0-0.33)	**0.31 (0.11-0.51)**
	Lake	**0.34 (0.08-0.57)**	0.16 (0-0.31)	0.17 (0-0.33)	**0.33 (0.09-0.56)**
	Wetland	**0.34 (0.1-0.57)**	0.14 (0-0.29)	0.19 (0-0.36)	**0.33 (0.1-0.55)**
Rudd	Stream	**0.35 (0.1-0.59)**	**0.23 (0.06-0.4)**	0.16 (0-0.32)	**0.26 (0.06-0.45)**
	Wetland	**0.53 (0.28-0.8)**	0.08 (0-0.23)	0.13 (0-0.31)	**0.26 (0.02-0.51)**
Shortfin eel*	Constrained zone	**0.36 (0.18-0.54)**	**0.17 (0.01-0.31)**	0.17 (0-0.32)	**0.3 (0.11-0.48)**
	Unconstrained zone	**0.52 (0.37-0.68)**	0.11 (0-0.22)	0.14 (0-0.29)	**0.22 (0.1-0.36)**
	Stream	**0.48 (0.26-0.7)**	0.13 (0-0.26)	0.18 (0-0.35)	**0.21 (0.05-0.37)**
	Lake	**0.36 (0.12-0.6)**	**0.17 (0.03-0.29)**	0.15 (0-0.3)	**0.32 (0.13-0.5)**
	Wetland	**0.35 (0.14-0.55)**	0.16 (0-0.3)	0.16 (0-0.31)	**0.33 (0.14-0.53)**
Catfish*	Stream	**0.26 (0.04-0.49)**	**0.29 (0.09-0.49)**	0.14 (0-0.3)	**0.32 (0.1-0.52)**

5.4.4 Food web metrics

Generally there was little difference between the trophic position of fish collected from different habitats using a baseline $\delta^{15}N$ calculated from the mean stable isotope signatures of basal resources. Mean trophic position of secondary fish consumers ranged from 3.5 (shortfin eel) to 4.2 (goldfish) in the main stem, and from 3.2 (koi carp) and 3.9 (catfish) for tributary junctions. Trophic position was generally similar between species collected from each habitat, with very few significant differences in PERMANOVA pairwise comparisons (Fig. 5.5). Mean trophic area (encompassed by convex hulls of mean $\delta^{13}C$ and $\delta^{15}N$ of species) estimated in SIBER was higher for fish communities collected from tributaries (Stream 6.0, Lake 7.3, Wetland 12.8) than in either the constrained (4.0) or unconstrained (2.5) zones.

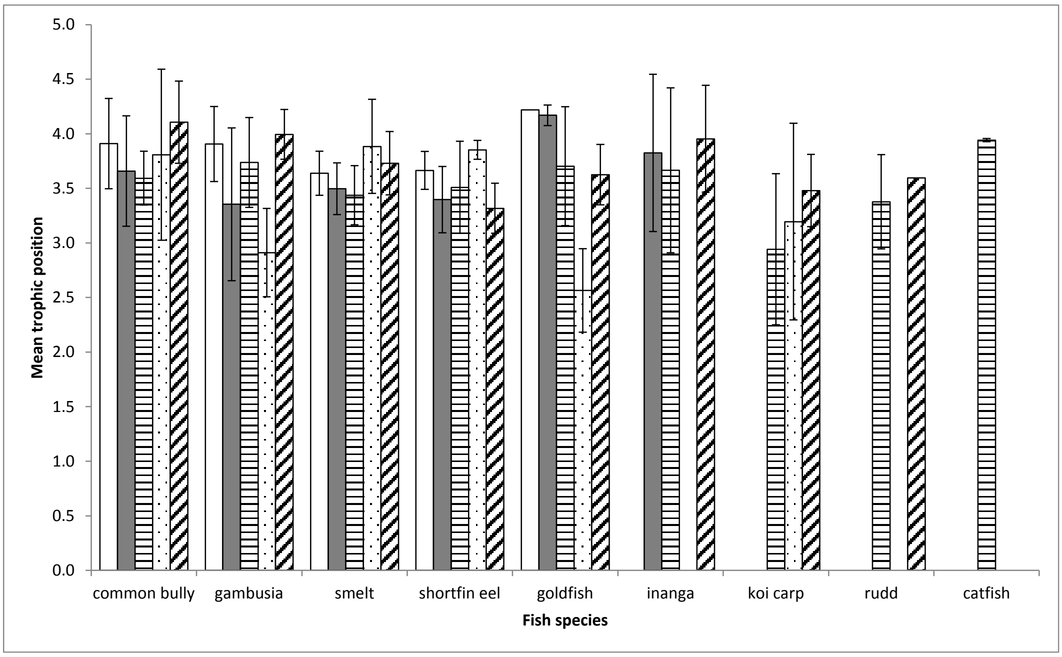


Figure 5.5. Mean trophic position of fish consumers collected from riverine constrained (☐) and unconstrained (■) zone sites, stream-fed (▤), lake-fed (⬚), and wetland-fed (▨) tributary junction sites

Mean Bayesian probability estimates of TA_b were higher in tributary junctions than main stem habitats, however 95 % HDRs did overlap and a greater range of species was collected from tributary junctions (Fig. 5.6). Both CR_b and NR_b were lowest in the unconstrained zone, although as with TA_b the estimates of these were likely to overlap with other habitats. It is also worth reiterating that SIBER community metrics were calculated using species means, therefore where species had wide ranging $\delta^{13}C$ or $\delta^{15}N$ values, such as smelt and gambusia in the unconstrained zone (Table 5.3), some variability in bi-plot space may be lost and metrics underestimated. Measures of trophic diversity (CD_b) and evenness ($SDNND_b$) were also similar between tributary junctions of different habitats and the two riverine zones, however tributary confluences all had higher mean values than the unconstrained zone (Fig. 5.6).

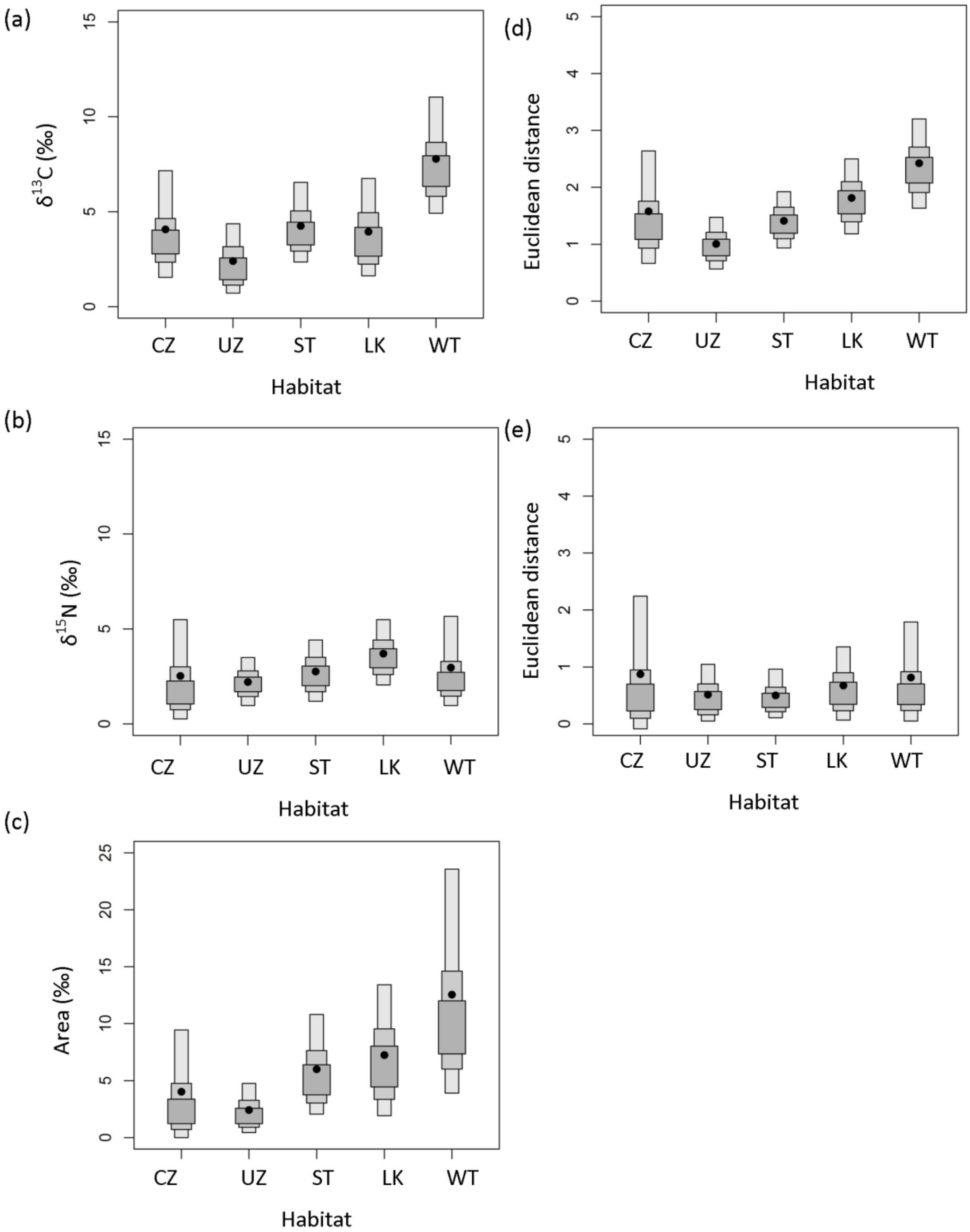


Figure 5.6. Comparison of fish communities in the constrained (CZ) and unconstrained (UZ) zones, and stream-fed (ST), lake-fed (LK) and wetland-fed (WT) tributary junctions. Using Bayesian estimates of (a) carbon range, (b) nitrogen range, (c) total convex hull area, (d) mean distance to centroid, and (e) standard deviation to nearest neighbour. Dots indicate mean values, and boxes indicate 50, 75, and 95 % highest density region estimates based on species means.

5.5 Discussion

5.5.1 Carbon flow

Autochthonous benthic carbon (phytomicrobenthos) was consistently important to all of the selected species in each of the habitats. This supports findings from contrasting hydrogeomorphic zones in the lower Waikato River estimated using IsoSource (Chapter 4 Pingram et al., 2012a). This pathway is likely facilitated through benthic invertebrate collector/gatherer, scraper and piercer taxa, as evidenced by fish stomach contents. Nevertheless, mean contributions of benthic carbon were often slightly higher in riverine sites for several species (e.g. smelt, bullies, gambusia). Compared to the main stem, mean riparian carbon contributions appeared to increase in importance in tributary confluences, particularly those sourced from wetlands. This difference possibly reflects narrower channel width and slower flows in tributary junctions, and a greater proportion of the channel being littoral zone and allowing for greater contribution and local processing of riparian leaves and organic matter. Similar pathways appear to operate across the range of habitats sampled as evidenced by dietary analysis, with collector/gatherer and riparian invertebrate taxa important across all habitats. Submerged macrophytes also appear to be a relatively important carbon source to some consumers, although they were far less common in tributary confluences than the main stem, particularly in stream-fed tributaries where only a single sample was collected. The paucity of macrophytes in tributaries possibly reflects a combination of steep-sided banks, low light transmittance through water, and more extensive riparian shading due to narrower channel width. Because of these factors it is possible that estimates of macrophyte contributions could be over-estimated in some habitats, particularly stream-fed tributaries. Aquatic macrophytes do, however, provide important habitat structure and surfaces for periphyton production in riverine and floodplain ecosystems (Winemiller & Jepsen, 1998), and may therefore be disproportionately important as sites for carbon transfer compared with their occurrence in tributary junctions.

Potential pathways for riparian carbon to enter aquatic food webs and contribute to fish biomass include ingestion of terrestrial invertebrates and the local processing of terrestrial matter by primary consumers. Except for common bully, the fish dietary analyses provide compelling evidence that terrestrial invertebrates are more commonly consumed by fish taxa in tributary junctions, although a larger sample size would help to further elucidate the significance of this pathway. New Zealand native fish are known to feed directly on terrestrial invertebrates in small pastoral and forested streams elsewhere in the lower Waikato River catchment and New Zealand (McDowall et al., 1996; Hicks, 1997). The consumption of terrestrial invertebrates can be facilitated by invertebrates falling from vegetation in local riparian zones (Cloe III & Garman, 1996). Terrestrial invertebrates can provide a high quality food source to fish in temperate rivers, particularly during periods of high plant growth and low aquatic macroinvertebrate abundance (Baxter et al., 2005; Wipfli & Baxter, 2010). The widespread shrimp collector-gatherer *P. curvirostris* had $\delta^{13}C$ signatures similar to terrestrial vegetation in both wetland and stream habitats (Author's unpub. data), potentially supporting the connection of terrestrial organic matter (riparian and/or wetland/land discharged detritus) and aquatic food webs in tributary junctions.

Lake-derived seston was initially expected to be an important carbon source for fish in lake-fed tributary junctions, particularly as these outflows contain high phytoplankton biomass and also large-bodied zooplankton under some flow conditions (Gorski et al., 2013). Lakes such as Whangape and Waahi, however, can be subject to blooms of toxic cyanobacteria (Ryan et al., 2003), which is a relatively poor-quality food source (Lampert, 1987; Schmidt & Jonasdottir, 1997). High chlorophyll *a* was evident at low flows, and seston had low $\delta^{15}N$ during the low-flow period, possibly reflecting nitrogen-fixation by some cyanobacteria species (Wolk et al., 1976; Berman-Frank et al., 2003).

5.5.2 Trophic structure

Average trophic position of selected consumers collected from each habitat was generally similar. While some studies have identified differences between the trophic structure of main stem and off-channel habitats in other large rivers, others have observed little or no difference. Consistent trophic positions were observed for species collected from both lagoon and channel habitats in the Cinaruco River, Venezuala (Roach et al., 2009b), whereas studies from temperate systems have recorded differences between the trophic positions of fish between main channel and various off channel habitats such as disconnected oxbow lakes (Zeug & Winemiller, 2008). These relative differences between off channel habitats in the riverscape are linked to the frequency and duration of connectivity with the main channel (Zeug & Winemiller, 2008; Reid et al., 2011). In this study sampling sites were permanently connected to the main stem at low flows, although water from the main stem generally only enters these junctions when main stem flows are high, and under some circumstances water from the main stem can travel up to hundreds of metres upstream of the confluence (Pers. Obs.). Consistent trophic positions for fish collected in both main stem and tributary junctions are also supported here by dietary analyses which generally indicated similar dietary niches between habitats for individual fish species (Fig. 5.4), although there appeared to be subtle differences in carbon flow (Table 5.5). The similarity of shortfin eel diets amongst habitats was also observed in a study undertaken in Lake Pounui, Wairarapa, New Zealand (Jellyman, 1989). Community metrics (Layman et al., 2007b; Jackson et al., 2011) of food web and trophic structure were also very similar between tributary junctions and the main stem in this study. Although a greater variety of species were collected from tributary junctions, similar fish assemblages occur in both the main stem and tributaries (Hicks et al., 2005). Species that could be considered to be largely piscivorous and potentially occupy higher trophic positions than the collected species include trout (*Salmo trutta* and *Onchorhynchus mykiss*), perch (*Perca fluviatilis*) and longfin eel (*Anguilla dieffenbachii)*, however none of these species was captured at low flows. This suggests that either food chain length in the lower Waikato River is generally shorter, with a greater degree of trophic omnivory than other river systems, or these consumers are relatively rare.

5.5.3 Water quality and isotopic signatures

As expected, main stem and tributary confluences in the lower Waikato River clearly differ with regard to their water quality characteristics, with potentially significant impacts on food web processes (Henley et al., 2000). Although the differences between tributary junctions and the main stem in terms of carbon flow and trophic structure appear to be small, the effect on stable isotope signatures of carbon and nitrogen was more pronounced, highlighting the importance of using appropriately sourced basal signatures when comparing habitats (Boon & Bunn, 1994; Jepsen & Winemiller, 2007). The available dissolved inorganic carbon pool, and environmental variables such as flow velocity, temperature and water turbidity, can drive changes in the $\delta^{13}C$ and $\delta^{15}N$ signatures of primary producers such as phytoplankton (seston) and phytomicrobenthos in rivers (France, 1995; Finlay et al., 1999; Finlay, 2001). Phytomicrobenthos $\delta^{13}C$ signatures were highest downstream of the Waipa river confluence and in tributary junctions, reflecting increased human modifications to the catchment, particularly the area developed for agriculture, and also the presence of wetlands, which can affect $\delta^{13}C$ and $\delta^{15}N$ signatures of primary producers (Rounick & James, 1984; Finlay, 2001; Chang et al., 2002; Finlay et al., 2002; Anderson & Cabana, 2005; Winemiller et al., 2011).

Factors such as water clarity and nutrient concentrations can also affect primary aquatic production with potential impacts on carbon flow to secondary consumers (Jepsen & Winemiller, 2007). Carbon uptake by aquatic plants can be influenced by the availability and demand for CO_2 and HCO_3^-, pushing macrophyte $\delta^{13}C$ closer to that of the dissolved pool of the waterbody (Smith & Walker, 1980). This is likely reflected in $\delta^{13}C$ signatures of macrophytes from lake-fed tributary junctions, which were markedly lower than other sites (Table 5.2), and these sites also had high chl *a* (Table 5.1). As observed here, McCabe (1985) identified that aquatic macrophytes in shallow Waikato lakes could be markedly enriched in $\delta^{13}C$ compared to phytoplankton, implying that aquatic macrophytes in lake-fed tributary junctions discriminate less against ^{13}C than phytoplankton.

Isotopic signatures of fish can also show site specificity as a result of the environmental factors affecting the isotopic signatures of food resources (Jepsen & Winemiller, 2007). My study indicated that fish may utilise similar resources whose signatures differ, thereby appearing isotopically distinct between some habitats, with potential applications in identifying fish movements and subsidies throughout the riverscape. Fish movements between the main stem and tributary junctions can also occur as these habitats are connected year-round, and this may explain the similarity of $\delta^{13}C$ signatures amongst some habitats for some fish species. Movement in and out of floodplain habitats for both smelt and shortfin eel in the lower Waikato River was recorded by Gorski et al. (2012). In my study, both eels and smelt had similar mean $\delta^{13}C$ signatures between habitats; in the case of smelt there was often substantial variability around mean values, also suggesting that some dietary or ontogenetic specialisation may occur between individuals of the same species.

Although not addressed in this study ontogenetic shifts in fish diet, due to changes in behaviour or gape size, can also lead to variation within species isotopic signatures (Davis et al., 2012). Feeding behaviour between individuals of the same species within a population can also be reflected by wide-ranging isotopic variation when individual diet specialisation occurs amongst a generalist population (Araújo et al., 2007; Layman & Allgeier, 2012). It is also possible that some fish signatures may reflect specialisation for a trophic pathway derived from an unsampled carbon source or, in the case of goldfish, possible excretion of alcohols which can synthesise lipids under anoxic conditions (van Raaij et al., 1994).

5.5.4 Conclusions

The conclusion that autochthonous benthic carbon is the major energy source supporting littoral food webs in the main stem of the lower Waikato River is in general accordance with the findings of Chapter 4, for which results were derived using IsoSource. SIAR estimates of carbon flow do, however, indicate that contributions of riparian carbon to aquatic food webs may occur to a greater extent than previously suggested, particularly in tributary junctions. Organic terrestrial carbon may have come from a combination of riparian leaf fall processed instream by invertebrates, terrestrial invertebrates falling into the water, or, in the case of tributary junctions, particulate organic matter discharged from stream- and wetland-derived catchments. As with carbon flow, other measurements of trophic structure and linkages (trophic position, dietary analysis, and SIBER metrics) were similar between the main stem and tributary junctions, for both individual fish species and community trophic metrics, despite significant differences in water quality. This similarity between habitats is likely linked to the fact that similar fish assemblages occupy each habitat and, as indicated by dietary analyses, they feed on similar taxa regardless of habitat. It is also probable that as tributary junctions are permanently connected to the main stem some species may regularly move in and out of tributary junctions and assimilate carbon from a range of locations within the river. Alternatively, the poor water quality and simple habitat structure of tributary junctions could be limiting the development of more complex food webs in these off-channel habitats. More complex food webs may therefore be restricted to lateral habitats where aquatic macrophytes and woody debris are more common. Enhancing the habitat complexity within tributary junctions would allow the development of more complex macroinvertebrate communities and feeding interactions in these lateral habitats (Warfe & Barmuta, 2004; Warfe & Barmuta, 2006). Improving water quality will likely improve the foraging opportunities and effectiveness for visual predators (Rowe & Dean, 1998; Utne-Palm, 2002), but consideration will need to be given to the movements of pest fish species in and out of these habitats for key parts of their life cycles (Daniel et al., 2011; Górski et al., 2012), and also their direct roles in shaping water quality and in stream habitats (Hicks et al., 2010). Rehabilitation measures will likely need to range in scale from local habitat manipulations or fish exclusions to catchment wide changes to land and water management.

5.6 References

Anderson, C. & G. Cabana, 2005. delta N-15 in riverine food webs: effects of N inputs from agricultural watersheds. Canadian Journal of Fisheries and Aquatic Sciences 62: 333-340.

Araújo, M. S., D. I. Bolnick, G. Machado, A. A. Giaretta & S. F. dos Reis, 2007. Using $\delta^{13}C$ stable isotopes to quantify individual-level diet variation. Oecologia 152: 643-654.

Arrar, E. J. & G. B. Collins, 1997. Method 445.0, In Vitro Determination of Chlorophyll *a* and Pheophytin *a* in Marine and Freshwater Algae by Fluorescence, Revision 1.2. U.S. Environmental Protection Agency, Cincinnati, Ohio.

Baxter, C. V., K. D. Fausch & W. Carl Saunders, 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology 50: 201-220.

Benstead, J. P., J. G. March, B. Fry, K. C. Ewel & C. M. Pringle, 2006. Testing isosource: stable isotope analysis of a tropical fishery with diverse organic matter sources. Ecology 87: 326-333.

Berman-Frank, I., P. Lundgren & P. Falkowski, 2003. Nitrogen fixation and photosynthetic oxygen evolution in cyanobacteria. Research in microbiology 154: 157-164.

Boon, P. I. & S. E. Bunn, 1994. Variations in the stable isotope composition of aquatic plants and their implications for food web analysis. Aquatic botany 48: 99-108.

Bricaud, A., A. Morel & L. Prieur, 1981. Absorption by dissolved organic matter of the sea (yellow substance) in the UV and visible domains. Limnology and Oceanography 26: 43-53.

Brown, E. J., 2010. Flow regime and water use. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, Hamilton, p 29-46.

Champion, P. D. & J. S. Clayton, 2010a. Box 14.1: Riparian vegetation. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, p 268.

Champion, P. D. & J. S. Clayton, 2010b. Native macrophytes and aquatic weeds. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, p 153-172.

Chang, C. C. Y., C. Kendall, S. R. Silva, W. A. Battaglin & D. H. Campbell, 2002. Nitrate stable isotopes: tools for determining nitrate sources among different land uses in the Mississippi River Basin. Canadian Journal of Fisheries and Aquatic Sciences 59: 1874-1885.

Chapman, M. A., 1996. Human impacts on the Waikato river system, New Zealand. GeoJournal 40: 85-99.

Cloe III, W. & G. Garman, 1996. The energetic importance of terrestrial arthropod inputs to three warm-water streams. Freshwater Biology 36: 104-114.

Collier, K. J. & A. Lill, 2008. Spatial patterns in the composition of shallow-water macroinvertebrate communities of a large New Zealand river. New Zealand Journal of Marine and Freshwater Research 42: 129-141.

Collier, K. J., E. M. Watene-Rawiri & J. D. McCraw, 2010. Geography and history. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, p 1-12.

Daniel, A. J., B. J. Hicks, N. Ling & B. O. David, 2011. Movements of radio-and acoustic-tagged adult koi carp in the Waikato River, New Zealand. North American Journal of Fisheries Management 31: 352-362.

David, B. O. & D. A. Speirs, 2010. Native fish. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, p 193-208.

Davies-Colley, R. J. & W. N. Vant, 1987. Absorption of light by yellow substance in freshwater lakes. Limnology and Oceanography 32: 416-425.

Davis, A. M., M. L. Blanchette, B. J. Pusey, T. D. Jardine & R. G. Pearson, 2012. Gut content and stable isotope analyses provide complementary understanding of ontogenetic dietary shifts and trophic relationships among fishes in a tropical river. Freshwater Biology 57: 2156-2172.

de Ruiter, P. C., V. Wolters & J. C. Moore, 2005. Dynamic food webs. In de Ruiter, P. C., V. Wolters & J. C. Moore (eds), Dynamic Food Webs: Multispecies assemblages, ecosystem development and environmental change. Academic Press, p 3-9.

Eaton, A. D. & M. A. H. Franson, 2005. Standard methods for the examination of water & wastewater. American Public Health Association, Washington, DC.

Fernandes, C. C., J. L. Podos & J. G. Lundberg, 2004. Amazonian ecology: Tributaries enhance the diversity of electric fishes. Science 305: 1960-1962.

Finlay, J. C., 2001. Stable-carbon-isotope ratios of river biota: Implications for energy flow in lotic food webs. Ecology 82: 1052-1064.

Finlay, J. C., M. E. Power & G. Cabana, 1999. Effects of water velocity on algal carbon isotope ratios: Implications for river food web studies. Limnology and Oceanography 44: 1198-1203.

Finlay, J. C., S. Khandwala & M. E. Power, 2002. Spatial scales of carbon flow in a river food web. Ecology 83: 1845-1859.

France, R., 1995. Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. Marine ecology progress series Oldendorf 124: 307-312.

Górski, K., K. J. Collier, D. P. Hamilton & B. J. Hicks, 2012. Effects of flow on lateral interactions of fish and shrimps with off-channel habitats in a large river-floodplain system. Hydrobiologia. doi:10.1007/s10750-012-1352-1.

Górski, K., K. J. Collier, I. C. Duggan, C. M. Taylor & D. P. Hamilton, 2013. Connectivity and complexity of floodplain habitats govern zooplankton dynamics in a large temperate river system. Freshwater Biology 58: 1458–1470.

Hailes, S. F., 2006. Contribution of seagrass (*Zostera muelleri*) to estuarine food webs revealed by carbon and nitrogen stable isotope analysis. University of Waikato.

Hamilton, D. P. & I. C. Duggan, 2010. Plankton. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, p 117-131.

Henley, W. F., M. A. Patterson, R. J. Neves & A. D. Lemly, 2000. Effects of sedimentation and turbidity on lotic food webs: a concise review for natural resource managers. Reviews in Fisheries Science 8: 125-139.

Hicks, B. J., 1997. Food webs in forest and pasture streams in the Waikato region, New Zealand: A study based on analyses of stable isotopes of carbon and nitrogen, and fish gut contents. New Zealand Journal of Marine and Freshwater Research 31: 651-664.

Hicks, B. J., N. Ling & B. J. Wilson, 2010. Introduced fish. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, p 209-228.

Hicks, B. J., N. Ling, M. W. Osborne, D. G. Bell & A. Ring, 2005. Boat electrofishing survey of the lower Waikato River and its tributaries. CBER contract report no. 39. University of Waikato, Hamilton.

Hladyz, S., D. L. Nielsen, P. J. Suter & E. S. Krull, 2012. Temporal variations in organic carbon utilization by consumers in a lowland river. River Research and Applications 28: 513-528.

Hoeinghaus, D. J., K. O. Winemiller & A. A. Agostinho, 2007. Landscape-scale hydrologic characteristics differentiate patterns of carbon flow in large-river food webs. Ecosystems 10: 1019-1033.

Hynes, H. B. N., 1950. The food of the fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitus*), with a review of methods used in studies of the food of fishes. Journal of Animal Ecology 19: 36-58.

Jackson, A. L., R. Inger, A. C. Parnell & S. Bearhop, 2011. Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R. The Journal of animal ecology 80: 595-602.

Jackson, M. C., I. Donohue, A. L. Jackson, J. R. Britton, D. M. Harper & J. Grey, 2012. Population-level metrics of trophic structure based on stable isotopes and their application to invasion ecology. PloS one 7: e31757.

Jellyman, D. J., 1989. Diet of two species of freshwater eel (Anguilla spp.) in Lake Pounui, New Zealand. New Zealand Journal of Marine and Freshwater Research 23: 1-10.

Jepsen, D. B. & K. O. Winemiller, 2007. Basin geochemistry and isotopic ratios of fishes and basal production sources in four neotropical rivers. Ecology of Freshwater Fish 16: 267-281.

Keith, D., 2002. Spatial and temporal distribution of coloured dissolved organic matter (CDOM) in Narragansett Bay, Rhode Island: Implications for phytoplankton in coastal waters. Estuarine, Coastal and Shelf Science 55: 705-717.

Kiffney, P. M., C. M. Greene, J. E. Hall & J. R. Davies, 2006. Tributary streams create serial discontinuities in habitat, biological productivity, and diversity in mainstem rivers. Canadian Journal of Fisheries and Aquatic Sciences 63: 2518-2530.

Kostoglidis, A., C. B. Pattiaratchi & D. P. Hamilton, 2005. CDOM and its contribution to the underwater light climate of a shallow, microtidal estuary in south-western Australia. Estuarine Coastal and Shelf Science 63: 469-477.

Lampert, W., 1987. Laboratory studies on zooplankton-cyanobacteria interactions. New Zealand Journal of Marine and Freshwater Research 21: 483-490.

Layman, C. A. & J. E. Allgeier, 2012. Characterizing trophic ecology of generalist consumers: a case study of the invasive lionfish in The Bahamas. Marine Ecology Progress Series 448: 131-141.

Layman, C. a., J. P. Quattrochi, C. M. Peyer & J. E. Allgeier, 2007a. Niche width collapse in a resilient top predator following ecosystem fragmentation. Ecology Letters 10: 937-944.

Layman, C. A., D. A. Arrington, C. G. Montana & D. M. Post, 2007b. Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology 88: 42-48.

Layman, C. A., M. S. Araujo, R. Boucek, C. M. Hammerschlag-Peyer, E. Harrison, Z. R. Jud, P. Matich, A. E. Rosenblatt, J. J. Vaudo, L. A. Yeager, D. M. Post & S. Bearhop, 2011. Applying stable isotopes to examine food-web structure: an overview of analytical tools. Biological Reviews 87: 545-562.

McCabe, B., 1985. The dynamics of ^{13}C in several New Zealand lakes. PhD Thesis, University of Waikato.

McCutchan, J. H., W. M. Lewis, C. Kendall & C. C. McGrath, 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102: 378-390.

McDowall, R. M., 1990. New Zealand freshwater fishes: a natural history and guide. Heinemann Reed, Auckland.

McDowall, R. M., 2000. The Reed field guide to fishes of New Zealand. Reed Books, Auckland.

McDowall, R. M., M. R. Main, D. W. West & G. L. Lyon, 1996. Terrestrial and benthic foods in the diet of the shortjawed kokopu, Galaxias postvectis Clarke (Teleostei: Galaxiidae). New Zealand Journal of Marine and Freshwater Research 30: 257-269.

Moore, J. W. & B. X. Semmens, 2008. Incorporating uncertainty and prior information into stable isotope mixing models. Ecology Letters 11: 470-480.

Parnell, A. C., R. Inger, S. Bearhop & A. L. Jackson, 2010. Source partitioning using stable isotopes: coping with too much variation. PloS one 5: e9672.

Perga, M. E. & D. Gerdeaux, 2005. 'Are fish what they eat' all year round? Oecologia 144: 598-606.

Phillips, D. L. & J. W. Gregg, 2003. Source partitioning using stable isotopes: coping with too many sources. Oecologia 136: 261-269.

Phillips, D. L., S. D. Newsome & J. W. Gregg, 2005. Combining sources in stable isotope mixing models: alternative methods. Oecologia 144: 520-527.

Pingram, M. A., K. J. Collier, D. P. Hamilton, B. J. Hicks & B. O. David, 2012a. Spatial and temporal patterns of carbon flow in a temperate, large river food web. Hydrobiologia. doi:10.1007/s10750-012-1408-2.

Pingram, M. A., K. J. Collier, D. P. Hamilton, B. O. David & B. J. Hicks, 2012b. Carbon sources supporting large river food webs: a review of ecological theories and evidence from stable isotopes. Freshwater Reviews 5: 85-103.

Post, D. M., 2002a. The long and short of food-chain length. Trends in Ecology & Evolution 17: 269-277.

Post, D. M., 2002b. Using stable isotopes to estimate trophic position: Models, methods, and assumptions. Ecology 83: 703-718.

Post, D. M., C. A. Layman, D. A. Arrington, G. Takimoto, J. Quattrochi & C. G. Montana, 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analysis. Oecologia 152: 179-189.

Reid, M. A., M. D. Delong & M. C. Thoms, 2011. The influence of hydrological connectivity on food web structure in floodplain lakes. River Research and Applications 28: 827–844.

Rice, S. P., R. I. Fergusson & T. B. Hoey, 2006. Tributary control of physical heterogeneity and biological diversity at river confluences. Canadian Journal of Fisheries and Aquatic Sciences 63: 2553-2566.

Roach, K. A., J. H. Thorp & M. D. Delong, 2009a. Influence of lateral gradients of hydrologic connectivity on trophic positions of fishes in the Upper Mississippi River. Freshwater Biology 54: 607-620.

Roach, K. A., K. O. Winemiller, C. A. Layman & S. C. Zeug, 2009b. Consistent trophic patterns among fishes in lagoon and channel habitats of a tropical floodplain river: Evidence from stable isotopes. Acta Oecologica-International Journal of Ecology 35: 513-522.

Rosales, J., L. Blanco-Belmonte & C. Bradley, 2007. Hydrogeomorphological and ecological interactions in tropical floodplains: The significance of confluence zones in the Orinoco Basin, Venezuela. In P. J. Wood, D. M. Hannah & J. P. Sadler (eds), Hydroecology and Ecohydrology: Past, present and future John Wiley & Sons Ltd., Chichester, p 295-316.

Rounick, J. S. & M. R. James, 1984. Goethermal and cold springs faunas: inorganic carbon sources affect isotope values. Limnology and Oceanography 29: 386-389.

Rowe, D. K. & T. L. Dean, 1998. Effects of turbidity on the feeding ability of the juvenile migrant stage of six New Zealand freshwater fish species. New Zealand Journal of Marine and Freshwater Research 32: 21-29.

Ryan, E., D. Hamilton & G. Barnes, 2003. Recent occurrence of Cylindrospermopsis raciborskii in Waikato lakes of New Zealand. New Zealand Journal of Marine and Freshwater Research 37: 829-836.

Sabo, J. L., J. C. Finlay, T. Kennedy & D. M. Post, 2010. The role of discharge variation in scaling of drainage area and food chain length in rivers. Science 330: 965-967.

Schmidt, K. & S. Jonasdottir, 1997. Nutritional quality of two cyanobacteria: How rich is' poor'food? Marine Ecology-Progress Series 151: 1-10.

Smith, F. A. & N. A. Walker, 1980. Effects of unstirred layers in relation to assimilation of CO_2 and HCO_3 - and to carbon isotopic discrimination. New Phytologist 86: 245-259.

Thompson, R. M., J. A. Dunne & G. U. Y. Woodward, 2012. Freshwater food webs: towards a more fundamental understanding of biodiversity and community dynamics. Freshwater Biology 57: 1329-1341.

Utne-Palm, a. C., 2002. Visual feeding of fish in a turbid environment: Physical and behavioural aspects. Marine and Freshwater Behaviour and Physiology 35: 111-128.

van Raaij, M., G. van den Thillart & A. Addink, 1994. Metabolism of 1-14C-acetate and 1-14C-leucine by anoxic goldfish, (*Carasslus auratus* L.): Evidence for anaerobic lipid synthesis. Physiological zoology 67: 673-692.

Vander Zanden, M. J. & J. B. Rasmussen, 1999. Primary consumer delta C-13 and delta N-15 and the trophic position of aquatic consumers. Ecology 80: 1395-1404.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell & C. E. Cushing, 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37: 130-137.

Warfe, D. M. & L. A. Barmuta, 2004. Habitat structural complexity mediates the foraging success of multiple predator species. Oecologia 141: 171-178.

Warfe, D. M. & L. A. Barmuta, 2006. Habitat structural complexity mediates food web dynamics in a freshwater macrophyte community. Oecologia 150: 141-154.

Winemiller, K. O. & D. B. Jepsen, Effects of seasonality and fish movement on tropical river food webs. In: Annual Symposium of the Fisheries-Society-of-the-British-Isles on Tropical Fish Biology, Southampton, England, Jul 13-16 1998. Academic Press Ltd, p 267-296.

Winemiller, K. O., A. S. Flecker & D. J. Hoeinghaus, 2010. Patch dynamics and environmental heterogeneity in lotic ecosystems. Journal of the North American Benthological Society 29: 84-99.

Winemiller, K. O., D. J. Hoeinghaus, A. A. Pease, P. C. Esselman, R. L. Honeycutt, D. Gbanaador, E. Carrera & J. Payne, 2011. Stable isotope analysis reveals food web structure and watershed impacts along the fluvial gradient of a Mesoamerican coastal river. River Research and Applications 803: 791-803.

Wipfli, M. S. & C. V. Baxter, 2010. Linking ecosystems, food webs, and fish production: subsidies in salmonid watersheds. Fisheries 35: 373-387.

Wolk, C. P., J. Thomas, P. W. Shaffer, S. M. Austin & a. Galonsky, 1976. Pathway of nitrogen metabolism after fixation of 13N-labeled nitrogen gas by the cyanobacterium, Anabaena cylindrica. The Journal of Biological Chemistry 251: 5027-5034.

Zeug, S. C. & K. O. Winemiller, 2008. Evidence supporting the importance of terrestrial carbon in a large-river food web. Ecology 89: 1733-1743.

6 General discussion

6.1 Overview

This thesis has contributed to the theory and improved understanding of processes affecting large river food webs, particularly with regard to sources of energy fuelling production, carbon flow sustaining secondary consumers and the role played by lateral habitats and hydrogeomorphic zones in shaping trophic processes. The results also help fill a knowledge gap in food web dynamics in large rivers in temperate regions of the southern hemisphere. By using the lower Waikato River as a model system, my study has also provided information that will be useful for defining future research and management actions to aid the rehabilitation of this riverscape, including lateral margins and tributaries, and their biological communities.

6.2 Synthesis

6.2.1 Carbon flow in large rivers

The production base supporting aquatic food webs in large rivers has been advanced greatly through the use of stable isotopes. Estimates of carbon transfer through the food web from basal organic resources up to higher secondary consumers can be derived using stable isotope mixing models. Recent work using stable isotope analysis to quantify carbon flow in large river food webs appears to mostly support aspects of the Riverine Productivity Model (Thorp & Delong, 1994, 2002). The literature review presented in Chapter 2 clearly demonstrated the importance of autochthonous carbon, especially in the form of benthic algae and phytoplankton, to food webs in large rivers studied across a wide range of climates and geographic regions. The review also highlighted that secondary carbon sources, particularly those from terrestrial riparian plants, can be important across a range of climates (temperate to neotropical) and channel types (constrained and floodplain). Although little support was found for the River Continuum Concept predictions for large-river carbon flow in the review, there was possible support for Flood Pulse Concept (Junk et al., 1989), with allochthonous carbon sources being important under certain conditions and in certain habitats (e.g. floodplain water bodies) for selected consumers.

Clearly, carbon flow in large river food webs is context dependent, both temporally with seasonal pulses of flow and riparian inputs, and spatially in relation to channel characteristics and lateral habitat complexity. Accordingly, the concept of functional process zones (Thorp et al., 2006, 2008), whereby primary productivity can vary throughout the riverine landscape depending on the hydro-geomorphological character of the zone in which it is generated, provides a helpful framework for incorporating riverscape heterogeneity into food web studies. Thus, although autochthonous carbon is expected to provide the trophic basis for the majority of secondary production based on my review of large rivers, contributions of allochthonous organic carbon can be expected to be important to some species in some habitats and in some seasons (Thorp et al., 2006, 2008). The main location for carbon transfer to consumers in large rivers such as the Waikato is likely to be in littoral and nearshore zones that offer (i) areas of reduced water velocity, (ii) increased habitat complexity, such as that provided by wood and aquatic plants, (iii) direct interaction with marginal and terrestrial riparian vegetation, and (iv) are often where a large proportion of carbon processing by invertebrates occurs (after Thorp & Delong, 1994; Schiemer et al., 2001).

This thesis therefore provides support for both the Riverine Productivity Model (Thorp & Delong, 1994, 2002) and some tenets of the Riverine Ecosystem Synthesis (Thorp et al., 2006, 2008) (see Chapters 4 and 5). Benthic algae (phytomicrobenthos) were the dominant basal carbon resource supporting littoral food webs in the lower Waikato River, irrespective of hydrogeomorphic zone and lateral habitat complexity, supporting Hypothesis 1 that littoral, main-channel food webs in the lower Waikato River would be derived from autochthonous algal carbon. I found little evidence for transported phytoplankton (seston) playing a major trophic role during the study period in the three hydrogeomorphic river zones or tributary junctions sampled. This is in contrast to studies elsewhere that have demonstrated the importance of phytoplankton (seston) to food webs downstream of large reservoirs (Angradi, 1994; Hoeinghaus et al., 2007; Doi et al., 2008). The low estimated contribution of phytoplankton likely reflects the fact that the littoral macroinvertebrate community is dominated by species that graze from surfaces (e.g. snails) or collect deposited organic material (e.g. amphipods), as opposed to filtering collectors such as Hydropsychidae caddis larvae which occur on hard substrates in faster-flowing mid-channel habitats of the lower Waikato River (Collier & Hogg, 2010).

Terrestrial carbon was identified as an important secondary carbon source in Chapters 4 and 5. One pathway for riparian carbon to enter the food web is through the consumption of terrestrial invertebrates, as evidenced in fish stomachs in Chapter 5. This pathway can provide significant direct and high quality resource subsidies to fish in temperate rivers, particularly during periods of high plant growth and low aquatic macroinvertebrate abundance (Baxter et al., 2005; Wipfli & Baxter, 2010). Their incorporation into aquatic food webs can be mediated either by falling from riparian vegetation (Cloe III & Garman, 1996), or during inundation of riparian and floodplain habitats when fish often respond rapidly to terrestrial invertebrates caught in inundated areas (Wantzen et al., 2002).

Unlike in some large rivers, stable isotope mixing models indicated that aquatic macrophytes (the exotic *Ceratophyllum demersum* and *Egeria densa*) appeared to provide potentially large amounts of organic carbon to consumers, notably to the shrimp *Paratya curvirostris*, but also to snails and some fish. Macrophytes provide additional habitat and enhance structural complexity in the photic zone of many large rivers, including the lower Waikato River. They offer complex habitats for consumers to occupy and facilitate the growth of periphyton on stable surfaces as well as the entrainment of suspended particulate carbon (Carpenter & Lodge, 1986). In this thesis, fish and invertebrates were often collected from amongst macrophyte beds along littoral areas of the lower river. Aquatic macrophytes are important feeding and refuge habitats for primary consumers such as *P. curvirostris* and the grey mullet (*Mugil cephalus*), which can filter entrained material and detritus from such substrates (Wells, 1984). Further, both rudd (*Scardinius erythrophthalmus*) and goldfish (*Carassius auratus*) are known to consume macrophytes in New Zealand (McDowall, 1990, 2000; Lake et al., 2002) and larvae of the aquatic moth (*Hygraula nitens*) were observed feeding on *C. demersum* plants growing in the lower Waikato River during my study (Pers. Obs.). In addition, the stable isotope signatures of *P. curvirotris* closely aligned with those of macrophytes in the main stem, suggesting that they may be incorporating carbon of macrophyte origin. IsoSource mixing models provided further evidence of the close relationship of *P. curvirotris* to macrophytes (see Chapter 4). Alternatively, the importance of macrophytes to food webs could be overestimated due to the variability of their isotopic signatures leading to overlap with other potential carbon sources. In addition, the validity of including them in mixing models could also be questioned if no pathway actually exists. However, it is my opinion that it is more prudent to include them in the absence of compelling evidence to the contrary, presenting an opportunity for further more detailed identification of specific trophic pathways in subsequent research.

6.2.2 The role of hydrogeomorphic zones in determining carbon flow

Chapter 3 used a combination of high intensity monitoring and channel characteristics mapped at 1-km segments to identify potential zones along the lower Waikato River that could be utilised in food web comparisons. The resulting clusters of physico-chemical and morphological descriptors led to identification of three zones that were used to test hypotheses regarding spatial and temporal patterns of carbon flow in Chapter 4. These zones were shaped by the physical complexity and channel character of constituent river reaches, and shifts, sometimes transitional, of physico-chemical variables. Changes in water clarity, chlorophyll fluorescence and specific conductance were driven by tributary inflows, and chlorophyll fluorescence increased in the tidal freshwater section of the lower Waikato River.

Highly spatially resolved measurements, in this case water quality, highlighted that properties and junctures between these zones could be temporally dynamic in response to flow. Derived using aspects of channel complexity and water quality, the zones identified reflect catchment processes that are similar to those used to delineate physically-based functional process zones of the Riverine Ecosystem Synthesis, and they are similar in scale. Based on the combination of physical complexity and water quality analyses, three possible zones, ranging in length from 28 to 58 km, were identified for investigating differences in trophic patterns along the lower Waikato River. These zones support patterns identified by previous measurements of turbidity and concentrations of nitrogen, phosphorus, water column chlorophyll *a* and dissolved colour (Vant, 2010). Furthermore, spatial patterns of phytoplankton biomass in the lower river are similar to those observed by Lam (1981) in that they peaked in the tidal freshwater section of the river and decreased immediately below the Waipa River.

A constrained zone above the Waipa River confluence at Ngaruawahia was characterised by a deeper than average, generally narrower, and steeper-sided channel. Flow variability in this zone was regulated by the dam at Karapiro which also contributes to relatively high water clarity by detaining sediments. I predicted that autochthonous algal carbon would dominate food web carbon flow in this zone due to the lack of lateral complexity and high water clarity, enabling more extensive algal growth. Two zones were identified below the Waipa river confluence, an unconstrained and a tidal zone. The unconstrained zone was characterised by reduced water clarity and depth, and increasing channel width as well as regular lateral features such as islands and side arms. This zone also included confluences of six other major tributaries flowing across the former floodplain of the lower river. Boundaries between strictly fluvial and tidal zones in lowland rivers are likely to be transitional, variable and sometimes indistinct due to the nature and strength of daily tidal cycles. However, a tidal freshwater zone was evident in the Waikato River downstream, characterised by increases in phytoplankton biomass, likely as a result of greater water retention time associated with tidal influx. This zone was also characterised by high lateral complexity in the form of an expansive delta in its lower reaches.

Using a boat-towed multi-instrument device (Biofish) it was possible to detect localised changes in river water quality, such as discontinuities in water clarity, chlorophyll fluorescence and conductivity associated with major tributaries and shifts in temperature that resulted from Huntly Power station cooling water discharge. This approach yielded high resolution information on water quality changes and inputs, as well as subsequent changes in downstream characteristics. These changes may otherwise have been overlooked by sampling at selected stations only, which may lead to an over representation of longitudinal patterns at the expense of localised and within-zone variability (Belle & Hughes, 1983). The value of multivariate statistical approaches for condensing, interpreting and evaluating complex water quality datasets (Vega et al., 1998; Wunderlin et al., 2001; Varol et al., 2011), is also highlighted here, allowing both longitudinal patterns and discontinuities to be resolved in this study.

I predicted that in both the unconstrained and tidal zones the increase in lateral complexity and discharge from streams and wetlands would increase the importance of allochthonous carbon to littoral food webs, and that increases in seston in the tidal freshwater zone should also become more important. In contrast to this prediction the carbon flow results presented in Chapters 4 and 5 underscore the importance of autochthonous benthic carbon to constrained and unconstrained zone food webs along the lower Waikato River main stem at both low and high flows, and also in the tidal freshwater zone at high flows. This provides equivocal support for the Riverine Productivity Model and supports tenets 10 and 11 of the Riverine Ecosystem Synthesis, in that while aspects of primary production may differ between zones of different hydrogeomorphic character, autochthonous carbon remains the main carbon source supporting aquatic food webs overall.

6.2.3 Tributary confluences

Tributary confluences can lead to potential hotspots for biological production and food web carbon flow in large river systems (Fernandes et al., 2004). These junctions provide areas of differing habitat complexity, food resources, flow velocity and water quality compared with the main stem, leading to high diversity of macroinvertebrates and fish species and contributing to trophic complexity in large river systems (Collier & Lill, 2008; Rice et al., 2008). Tributaries also represent donor systems to large river food webs through the input of novel carbon representative of the catchments that the tributaries drain, such as riverine lakes, wetlands and stream-fed catchments (Vannote et al., 1980; Kiffney et al., 2006; Rice et al., 2006; Rosales et al., 2007). In Chapter 5, I compared food webs in the river main stem with tributary junctions fed by lakes, streams and wetlands to assess whether these habitats increased trophic complexity in the lower Waikato River riverscape. Although there did appear to be a greater contribution of riparian carbon to food webs in and tributary junctions for fish consumers, there appeared to be little difference food webs sampled from different habitats (riverine zones and tributary junctions). Therefore providing little evidence for the second part of Hypothesis 2 or Hypothesis 3, that food web structure would differ between hydrogeomorphically distinct sections of river and that lateral habitats would add to overall food web complexity.

The similarities in carbon flow and consumer trophic position between main stem and tributary junction habitats may reflect the similarities in fish assemblages, with the majority of species being present in both habitat types (Hicks et al., 2005). Aquatic macrophytes are common in nearshore areas of the mainstem, however they tended to be less abundant in tributary junctions, likely as a result of the steep sided nature of these sites and low light transmittance that prevented the development of macrophyte beds. Therefore, despite a reduction in flow velocities, a lack of complex structural habitats may limit the development of more complex macroinvertebrate communities and feeding interactions in these lateral habitats (Warfe & Barmuta, 2004; Warfe & Barmuta, 2006). Low water quality (particularly light transmittance) in tributary junctions can also affect the foraging opportunities, ability and effectiveness of visual predators (Rowe & Dean, 1998; Utne-Palm, 2002).

It is probable that some fish species regularly move between main stem and tributary junction habitats (Górski et al., 2012); if they were to forage in both habitats their $\delta^{13}C$ and $\delta^{15}N$ signatures may become intermediate between habitats, thereby potentially affecting habitat-based measures of trophic structure derived using stable isotopes. However, even relatively sessile and sedentary species such as common bully appeared to occupy similar trophic position in the food web in both main stem and tributary junction sites, despite often having different stable isotope signatures. This reinforces the importance of quantifying spatial differences in stable isotope signatures of both basal carbon resources and consumers. Carbon flow and trophic structure may not differ markedly between habitats despite differences in isotopic signatures, in part because signatures may vary between sites and reflect the effect of local geochemistry and land-use (Jepsen & Winemiller, 2007; Winemiller et al., 2011; Hladyz et al., 2012).

6.3 Recommendations

6.3.1 Management

A range of management recommendations for the lower Waikato River can be derived from this body of work. While autochthonous carbon is the major source supporting littoral food webs in the lower Waikato River, secondary sources or subsidies can play an important role in shaping food web characteristics and ecosystem processes (Marcarelli et al., 2011). Both the dominant riparian (*Salix fragilis* and *Alnus glutinosa*) and aquatic (*C. demersum* and *E. densa*) vegetation along the lower Waikato River have been introduced to New Zealand, and as such would not have been available as habitat or potential carbon sources to aquatic food webs pre-European colonisation. Added to this, a suite of exotic fish and a range of major hydrogeomorphic alterations make it difficult to picture what historical food webs and carbon flow would have looked like in the Waikato River and what a 'restored' food web should resemble.

The use of studies employing museum collections and stable isotope analysis to reconstruct historical food webs, such as those discussed in Chapter 2, could provide valuable insights and help set restoration goals for food webs in the Waikato River. However, consideration would need to be given to the changed physical nature of the catchment, the channel and drivers of flow patterns, as well as changes in the relative availability of carbon sources. Exotic species of both plants and animals, such as koi carp and *C. demersum*, may have filled niches previously vacant or those niches created by human modifications to the river (McDowall, 1990; Ling, 2004), while for native species these changes may have led to contractions or expansions in niche width and changes in the trophic position of species (Layman et al., 2007). A significant reduction in the annual whitebait (Galaxiidae) catch (Howard-Williams et al., 2010), may also have led to a decline in marine or estuarine subsidies to freshwater food webs throughout the lower Waikato River and its tributaries. Furthermore, massive changes to the lateral complexity of the lower Waikato River, its floodplain habitats and water quality may have reduced the abundance of some species (David & Speirs, 2010). Preventing further invasion of food webs by exotic plant and animal species, and actively controlling established species, especially those that can lead to major changes in ecosystem quality, such as koi carp, will also be essential in restoring riverine food webs and enhancing native species.

The results presented in Chapter 5 indicate that, while lateral features, in this case tributary junctions, may add to the lateral complexity of the riverscape as a whole, in themselves they may contribute little to overall food web complexity of the riverscape. I hypothesise that this is due to lower water quality and reduced structural complexity (e.g. littoral zones) in these habitats. Therefore management actions that improve the water quality and structural habitat complexity within these junctions may provide improved habitats to support greater food web complexity and potentially longer food chains. A wider consideration for restoration measures is that some exotic species, such as koi carp, which are known to move in and out of lateral habitats for foraging and reproduction and have been implicated in reduced water quality in lateral habitats (Daniel et al., 2011; Ginders, 2011; Górski et al., 2012), will need to be actively excluded or managed to achieve desired outcomes for native fish, invertebrates and plants.

6.3.2 Future research

This research highlights possible avenues for future food web research that would further improve our understanding of large river food webs. The between-habitat isotopic variation of some fish species has the potential to allow the quantification of movement between habitats (Durbec et al., 2010), and potentially to quantify the contributions of diadromous species to freshwater food webs on a seasonal scale (Walters et al., 2009). The use of isotopes of other elements such as sulphur or hydrogen has the potential to better distinguish between floodplain, marine and freshwater derived carbon (Doucett et al., 2007; Jardine et al., 2011). This may also allow sources supporting key life-cycle stages, such as reproduction, to be distinguished from those supporting biomass (Jardine et al., 2011). Using isotopes and dietary analysis to identify ontogenetic shifts in resource use, trophic position (Davis et al., 2012), and niche width within species (Davis et al., 2012; Jackson et al., 2012), could be important for further elucidating trophic patterns and linkages in food webs, with potential implications for species management. Otolith microchemistry using multiple trace elements provides another potentially valuable method to identify and quantify fish movements between habitats, and also larger migrations such as those undertaken by diadromous fishes (Hicks et al. 2010; Blair & Hicks 2012).

In hindsight, invertebrates were probably under-sampled in this study in terms of the number of species and functional guilds, and a greater number and variety of samples may have illustrated more direct linkages between food web components. Detailed studies employing functional metrics of invertebrate communities can also shed light on important food web and ecosystem processes (Merritt et al., 2002; Cummins et al., 2005), with implications for assessing the success of restoration initiatives (Paillex et al., 2007; Paillex et al., 2009). Terrestrial invertebrates were not sampled in this study and ascertaining their signatures would help to better resolve the likely pathway of terrestrial carbon contributions to aquatic food webs in lateral margins of the lower river. Other pathways that could be better resolved using stable isotope analysis include those related to macrophyte-derived carbon which, as discussed above, is often unimportant in northern hemisphere rivers. Secondly, determining if sestonic carbon plays a role in food webs found in faster flowing habitats could be investigated by sampling invertebrates from mid-channel habitats of the lower

Waikato River. Further investigations of key species to elucidate the balance of generalist and specialist individuals within populations would help to better understand the resource use overlap and potential food web effects of exotic and native fish species (Layman & Allgeier, 2012). All of these potential studies using stable isotope analysis would benefit from estimates of tissue turnover rates and isotopic fractionation under different conditions of environmental stress and food availability (e.g. Perga & Gerdeaux, 2005). While addressing these detailed aspects of stable isotope ecology may not alter overall conclusions regarding carbon flow, they would help to increase certainty around estimates of carbon flow and identify key food web linkages between organisms.

6.4 References

Angradi, T. R., 1994. Trophic linkages in the lower Colorado River - Multiple stable-isotope evidence. Journal of the North American Benthological Society 13: 479-495.

Baxter, C. V., K. D. Fausch & W. Carl Saunders, 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology 50: 201-220.

Belle, G. v. & J. Hughes, 1983. Monitoring for water quality: fixed stations versus intensive surveys. Journal WPCF (Water Pollution Control Federation) 55: 400-404.

Carpenter, S. & D. Lodge, 1986. Effects of submersed macrophytes on ecosystem processes. Aquatic botany 26: 341-370.

Cloe III, W. & G. Garman, 1996. The energetic importance of terrestrial arthropod inputs to three warm-water streams. Freshwater Biology 36: 104-114.

Collier, K. J. & A. Lill, 2008. Spatial patterns in the composition of shallow-water macroinvertebrate communities of a large New Zealand river. New Zealand Journal of Marine and Freshwater Research 42: 129-141.

Collier, K. J. & I. D. Hogg, 2010. Macroinvertebrates. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, Hamilton, 175-192.

Cummins, K. W., R. W. Merritt & P. C. N. Andrade, 2005. The use of invertebrate functional groups to characterize ecosystem attributes in selected streams and rivers in south Brazil. Studies on Neotropical Fauna and Environment 40: 69-89.

Daniel, A. J., B. J. Hicks, N. Ling & B. O. David, 2011. Movements of radio-and acoustic-tagged adult koi carp in the Waikato River, New Zealand. North American Journal of Fisheries Management 31: 352-362.

David, B. O. & D. A. Speirs, 2010. Native fish. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, p 193-208.

Davis, A. M., M. L. Blanchette, B. J. Pusey, T. D. Jardine & R. G. Pearson, 2012. Gut content and stable isotope analyses provide complementary understanding of ontogenetic dietary shifts and trophic relationships among fishes in a tropical river. Freshwater Biology 57: 2156-2172.

Doi, H., K. H. Chang, T. Ando, H. Imai, S. Nakano, A. Kajimoto & I. Katano, 2008. Drifting plankton from a reservoir subsidize downstream food webs and alter community structure. Oecologia 156: 363-371.

Doucett, R. R., J. C. Marks, D. W. Blinn, M. Caron & B. A. Hungate, 2007. Measuring terrestrial subsidies to aquatic food webs using stable isotopes of hydrogen. Ecology 88: 1587-1592.

Durbec, M., L. Cavalli, J. Grey, R. Chappaz & B. Nguyen The, 2010. The use of stable isotopes to trace small-scale movments by small fish species. Hydrobiologia 641: 23-31.

Fernandes, C. C., J. L. Podos & J. G. Lundberg, 2004. Amazonian ecology: Tributaries enhance the diversity of electric fishes. Science 305: 1960-1962.

Ginders, M. A., 2011. The influence of connectivity on the functional role of a natural and re-constructed side-arm in the lower Waikato River. MSc Thesis, University of Waikato.

Górski, K., K. J. Collier, D. P. Hamilton & B. J. Hicks, 2012. Effects of flow on lateral interactions of fish and shrimps with off-channel habitats in a large river-floodplain system. Hydrobiologia. doi:10.1007/s10750-012-1352-1.

Hicks, B. J., N. Ling, M. W. Osborne, D. G. Bell & A. Ring, 2005. Boat electrofishing survey of the lower Waikato River and its tributaries. CBER contract report no.39. University of Waikato, Hamilton.

Hladyz, S., D. L. Nielsen, P. J. Suter & E. S. Krull, 2012. Temporal variations in organic carbon utilization by consumers in a lowland river. River Research and Applications 28: 513-528.

Hoeinghaus, D. J., K. O. Winemiller & A. A. Agostinho, 2007. Landscape-scale hydrologic characteristics differentiate patterns of carbon flow in large-river food webs. Ecosystems 10: 1019-1033.

Howard-Williams, C., W. N. Vant, K. J. Collier & D. P. Hamilton, 2010. The River: past, present and future. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest River. Waikato Regional Council, Hamilton, p 283-292.

Jackson, M. C., I. Donohue, A. L. Jackson, J. R. Britton, D. M. Harper & J. Grey, 2012. Population-level metrics of trophic structure based on stable isotopes and their application to invasion ecology. PloS one 7: e31757.

Jardine, T., B. Pusey, S. Hamilton, N. Pettit, P. Davies, M. Douglas, V. Sinnamon, I. Halliday & S. Bunn, 2011. Fish mediate high food web connectivity in the lower reaches of a tropical floodplain river. Oecologia 168: 829-838.

Jepsen, D. B. & K. O. Winemiller, 2007. Basin geochemistry and isotopic ratios of fishes and basal production sources in four neotropical rivers. Ecology of Freshwater Fish 16: 267-281.

Junk, W. J., P. B. Bayley & R. E. Sparks, 1989. The flood pulse concept in river-floodplain systems. In Dodge, DP (ed) Proceedings of the International Large River Symposium, Canadian Special Publication of Fisheries and Aquatic Sciences 106: 110-127.

Kiffney, P. M., C. M. Greene, J. E. Hall & J. R. Davies, 2006. Tributary streams create serial discontinuities in habitat, biological productivity, and diversity in mainstem rivers. Canadian Journal of Fisheries and Aquatic Sciences 63: 2518-2530.

Lake, M. D., B. J. Hicks, R. D. S. Wells & T. M. Dugdale, 2002. Consumption of submerged aquatic macrophytes by rudd (*Scardinius erythrophthalmus* L.) in New Zealand. Hydrobiologia 470: 13-22.

Lam, C. W. Y., 1981. Ecological studies of phytoplankton in the Waikato River and its catchment. New Zealand Journal of Marine and Freshwater Research 15: 95-103.

Layman, C. A. & J. E. Allgeier, 2012. Characterizing trophic ecology of generalist consumers: a case study of the invasive lionfish in The Bahamas. Marine Ecology Progress Series 448: 131-141.

Layman, C. a., J. P. Quattrochi, C. M. Peyer & J. E. Allgeier, 2007. Niche width collapse in a resilient top predator following ecosystem fragmentation. Ecology Letters 10: 937-944.

Ling, N., 2004. *Gambusia* in New Zealand: really bad or just misunderstood? New Zealand Journal of Marine and Freshwater Research 38: 473-480.

Marcarelli, A., C. Baxter & M. Mineau, 2011. Quantity and quality: unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters. Ecology 92: 1215-1225.

McDowall, R. M., 1990. New Zealand freshwater fishes: a natural history and guide. Heinemann Reed, Auckland.

McDowall, R. M., 2000. The Reed field guide to fishes of New Zealand. Reed Books, Auckland.

Merritt, R. W., K. W. Cummins, M. B. Berg, J. A. Novak, M. J. Higgins, K. J. Wessell & J. L. Lessard, 2002. Development and application of a macroinvertebrate functional-group approach in the bioassessment of remnant river oxbows in southwest Florida. Journal of the North American Benthological Society 21: 290-310.

Paillex, A., E. Castella & G. Carron, 2007. Aquatic macroinvertebrate response along a gradient of lateral connectivity in river floodplain channels. Journal of the North American Benthological Society 26: 779-796.

Paillex, A., S. Doledec, E. Castella & S. Merigoux, 2009. Large river floodplain restoration: predicting species richness and trait responses to the restoration of hydrological connectivity. Journal of Applied Ecology 46: 250-258.

Perga, M. E. & D. Gerdeaux, 2005. 'Are fish what they eat' all year round? Oecologia 144: 598-606.

Rice, S. P., R. I. Fergusson & T. B. Hoey, 2006. Tributary control of physical heterogeneity and biological diversity at river confluences. Canadian Journal of Fisheries and Aquatic Sciences 63: 2553-2566.

Rice, S. P., P. Kiffney, G. Correigh & G. R. Pess, 2008. The ecological importance of tributaries and confluences. In Rice, S. P., A. G. Roy & B. L.

Rhoads (eds), River Confluences, Tributaries and the Fluvial Network. John Wiley & Sons, Ltd., Chichister, p 209-242.

Rosales, J., L. Blanco-Belmonte & C. Bradley, 2007. Hydrogeomorphological and ecological interactions in tropical floodplains: The significance of confluence zones in the Orinoco Basin, Venezuela. In P. J. Wood, D. M. Hannah & J. P. Sadler (eds), Hydroecology and Ecohydrology: Past, present and future John Wiley & Sons Ltd., Chichester, p 295-316.

Rowe, D. K. & T. L. Dean, 1998. Effects of turbidity on the feeding ability of the juvenile migrant stage of six New Zealand freshwater fish species. New Zealand Journal of Marine and Freshwater Research 32: 21-29.

Schiemer, F., H. Keckeis, W. Reckendorfer & G. Winkler, 2001. The "inshore retention concept" and its significance for large rivers. Large Rivers 12: 509-516.

Thorp, J. H. & M. D. Delong, 1994. The riverine productivity model: an heuristic view of carbon sources and organic processing in large river ecosystems. Oikos 70: 305-308.

Thorp, J. H. & M. D. Delong, 2002. Dominance of autochthonous autotrophic carbon in food webs of heterotrophic rivers. Oikos 96: 543-550.

Thorp, J. H., M. C. Thoms & M. D. Delong, 2006. The riverine ecosystem synthesis: Biocomplexity in river networks across space and time. River Research and Applications 22: 123-147.

Thorp, J. H., M. C. Thoms & M. D. Delong, 2008. The Riverine Ecosystem Synthesis: Towards conceptual cohesiveness in river science. Elsevier.

Utne-Palm, a. C., 2002. Visual feeding of fish in a turbid environment: Physical and behavioural aspects. Marine and Freshwater Behaviour and Physiology 35: 111-128.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell & C. E. Cushing, 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37: 130-137.

Vant, W. N., 2010. Water quality. In Collier, K. J., D. P. Hamilton, W. N. Vant & C. Howard-Williams (eds), The Waters of the Waikato: Ecology of New Zealand's longest river. Waikato Regional Council, Hamilton, p 93-114.

Varol, M., B. Gökot, A. Bekleyen & B. Şen, 2011. Water quality assessment and apportionment of pollution sources of Tigris River (Turkey) using multivariate statistical techniques—a case study. River Research and Applications 28: 1428–1438.

Vega, M., R. Pardo, E. Barrado & L. Deban, 1998. Assessment of seasonal and polluting effects on the quality of river water by exploratory data analysis. Water Research 32: 3581-3592.

Walters, A. W., R. T. Barnes & D. M. Post, 2009. Anadromous alewives (*Alosa pseudoharengus*) contribute marine-derived nutrients to coastal stream food webs. Canadian Journal of Fisheries and Aquatic Sciences 66: 439-448.

Wantzen, K. M., F. D. Machado, M. Voss, H. Boriss & W. J. Junk, 2002. Seasonal isotopic shifts in fish of the Pantanal wetland, Brazil. Aquatic Sciences 64: 239-251.

Warfe, D. M. & L. A. Barmuta, 2004. Habitat structural complexity mediates the foraging success of multiple predator species. Oecologia 141: 171-178.

Warfe, D. M. & L. A. Barmuta, 2006. Habitat structural complexity mediates food web dynamics in a freshwater macrophyte community. Oecologia 150: 141-154.

Wells, R. D. S., 1984. The food of the grey mullet (*Mugil cephalus* L.) in Lake Waahi and the Waikato River at Huntly. New Zealand Journal of Marine and Freshwater Research 18: 13-19.

Winemiller, K. O., D. J. Hoeinghaus, A. A. Pease, P. C. Esselman, R. L. Honeycutt, D. Gbanaador, E. Carrera & J. Payne, 2011. Stable isotope analysis reveals food web structure and watershed impacts along the fluvial gradient of a Mesoamerican coastal river. River Research and Applications 803: 791-803.

Wipfli, M. S. & C. V. Baxter, 2010. Linking ecosystems, food webs, and fish production: subsidies in salmonid watersheds. Fisheries 35: 373-387.

Wunderlin, D. A., M. D. P. Diaz, M. V. Ame, S. F. Pesce & A. C. Hued, 2001. Pattern recognition techniques for the evaluation of spatial and temporal variations in water quality. A case study: Suquia River basin (Cordoba-Argentina). Water Research 35: 2881-2894.