Fish biomass in Taranaki streams in relation to sources and availability of energy

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ABSTRACT

Light and temperature are the principal drivers of ecosystem function influencing nutrient cycling, energy flows, and food web dynamics. Solar irradiance controls stream thermodynamics, and in-stream temperature governs the metabolic rate of stream biota. The loss of riparian vegetation can lead to unpredictable changes in fish biomass due to variations in metabolic requirements and energy availability. In New Zealand, unshaded pasture streams have been shown to support greater fish biomass, leading to questions about supply and demand synchronies and energy sources that support fish biomass under differing light and temperature regimes.

This thesis focuses on the ecological processes in relation to the interactions among stream biota and their physical and chemical environment linking freshwater fish biomass, food web dynamics and energy availability. Using a variety of field assessments, I investigate food web dynamics and characterise energy flow with respect to land use and longitudinal riparian fragmentation in mountainous Taranaki streams, New Zealand. I further analyse the influence of alternative energy sources derived from terrestrial and marine environments and their subsidiary role in supporting fish biomass.

Fish densities and biomasses were five-fold greater in pasture than in forest streams and significant correlations were found with light intensity and water temperature ($p < 0.05$). Body mass to abundance (*M-N*) allometry was similar between land uses, but the effects of increased light and temperature in pasture streams likely resulted in increased abundance for the equivalent body sizes across the entire community.

Stable isotope analyses (SIA) revealed evidence for energetic and functional food web alterations, in response to land use. Changes in food sources were reflected by the transition in physical variables at the forest to pasture boundary. Here, non-predatory invertebrates showed a distinct food dominance transition between land uses, predominantly assimilating leaf litter (77%) in forest and shifting to periphyton (73%) in pasture. Periphyton biomass was significantly greater in pasture streams and was the most important food source for crayfish (*Paranephrops planifrons*), contributing 76% to crayfish diet in forest and 97% to crayfish diet in pasture. This highlights the importance of periphyton for energy transfer to higher trophic levels in streams.

Fish showed a distinct dietary reliance on both crayfish and terrestrial invertebrates in both land uses. Unexpectedly, terrestrial invertebrate inputs were five-fold greater at pasture sites when compared to forest sites ($p < 0.05$). Since terrestrial invertebrates are an important food source consumed by New Zealand fish species, these terrestrially derived food sources may play a significant role in the observed fish biomass. This research highlighted the role of terrestrially derived invertebrates in providing a significant subsidiary energy source, irrespective of land use.

Temperature plays a fundamental role in metabolic rates and energetic requirements of fish, emphasising the importance of temperature-driven changes in supply-demand synchronies. Importantly, summer water temperatures at pasture sites were closer to the thermal preferences of New Zealand fish species. This suggests that higher temperatures increase metabolic scope and food requirements. However, there must be sufficient food supply to compensate for rising metabolic demands of fish.

On a longitudinal scale, Taranaki streams showed localised variations in energy utilisation in response to riparian fragmentation. Non-predatory invertebrates showed a food dominance transition back to allochthonous sources at lower sites, corresponding with greater riparian vegetation cover downstream. Transitions in source dominance were also observed in longfin eel (*Anguilla dieffenbachii*) and shortfin eel (*Anguilla australis*) diets, where the proportional dominance shifted from aquatic invertebrates to terrestrial invertebrates at vegetated downstream sites. These data were more reflective of recent conceptualised models derived from the Riverine Ecosystem Synthesis (RES), rather than the River Continuum Concept (RCC), with localised processes influencing pathways of energy transfer.

There is limited research on the contribution of marine-derived nitrogen (MDN) by diadromous New Zealand fish, which may provide an important subsidiary source of nutrients for stream production. MDN was detected in migratory inanga larvae (*Galaxias maculatus*) and shrimp (*Paratya curvirostris*), with these species showing comparable δ^{15}N that reflected a period of marine residence. The incorporation of MDN was not expressed in the food web, however, most likely due to low densities of inanga and shrimp in the study reaches. High δ^{15}N in inanga shows the potential for MDN to be incorporated into stream food webs where significant seasonal whitebait migrations occur.

This research provides critical insight into the drivers behind fish biomass, highlighting temperature-driven supply and demand synchronies and the importance of resource availability in sustaining New Zealand fish populations.

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CHAPTER I

Thesis introduction

Mount Taranaki National Park forest boundary with privately-owned pasture in foreground. Photo credit: Warrick Powie, January 2020

1.1 | Stream production

Streams have multidimensional components that vary along longitudinal, lateral and vertical axes (Vannote et al., 1980; Miller, 1990; Bravard & Petit, 2009). Longitudinally, streams can vary in habitat complexity, species composition, and water quality following variations in topography and hydrology (Townsend & Hildrew, 1994). Laterally, streams can vary in floodplain characteristics, riparian interactions, and adjacent land use. Vertically, streams can be influenced by the degree of the hyporheic zone, groundwater exchange and aerially via the extent of allochthonous inputs from terrestrial invertebrates and leaf litter (Bravard & Petit, 2009; Wondzell, 2011). Stream networks are cumulative in nature and intrinsically linked through the spatial and temporal connectivity between these dimensions (Erdozain et al., 2021). The relationships between longitudinal, lateral, and vertical dimensions govern stream ecosystem structure and function (Fisher & Likens, 1973; Vannote et al., 1980; Miller, 1990; Bravard & Petit, 2009; Fritz et al., 2018). Stream production studies provide an integrative method by which ecosystem function can be quantified by incorporating measures of energy availability and energy expenditure along a trophic continuum (Cummins, 1974; Dolbeth et al., 2012). Evaluating stream production can provide valuable insight into energy availability and transfer sustaining primary and secondary biomass (Cummins, 1974; Benke, 1993). As described by Benke (1993), secondary production is ‘the most comprehensive representation of population success’ and is the ultimate ‘dynamic variable’ providing an appropriate response variable for many questions relating to ecosystem ecology.

Secondary production can be defined as the accrual of living biomass by consumers over time within a given stream reach (Ivlev, 1945). Freshwater fish biomass represents the expression of energy at the highest trophic level and can provide useful insight into the productive capacity of the stream and ecosystem health (Randall & Mills, 2000; Jones et al., 2003; Moi et al., 2022). Here, freshwater fish biomass is defined as the standing stock that results from the ecological response of fish to the environment (Allen, 1951; Huryn & Benke, 2007; Myers et al., 2018). The biomass of aquatic organisms is regulated by the ratio of available nutrients to biological demand within a system ((Hicks and McCaughan, 1997; Allan et al., 2020; Allen et al., 2021). This ratio is primarily influenced by:

1. Physicochemical factors including light, temperature, dissolved oxygen, pH, conductivity, nitrogen and phosphorus (Valentine-Rose et al., 2007; Finlay, 2011; Myers et al., 2018);
2. Biological factors including inter- and intraspecific competition, predation, recruitment, and food availability (Power et al., 1988; Magoulick, 2000; Ernesto, 2003); and
3. Habitat factors including the composition of riparian margins, stream width, depth, and velocity (Allen et al., 2020).

Variations in the structure and extent of these factors determine the available energy and pathways for energetic transfer within a stream system.

1.1.1 | Ecological theory and energy availability

Ecological theories such as the River Continuum Concept (RCC) integrate the continuum of energy with structural variations in energy flow and biotic composition along longitudinal lotic gradients (Vannote et al., 1980). At the time, the RCC was foundational in stream ecology by describing how the connectivity of a river system from headwaters to sea shapes energy transfer and biotic community compositions. The RCC conceptualises stream headwaters as heavily shaded, which are predicted to receive significant proportions of leaf litter with limited primary production, while downstream, environments are typically less shaded and become more reliant on primary production as stream channels widen (Vannote et al., 1980). Although its relevance has been questioned in some biomes (e.g., Winterbourn et al., 1981), the RCC shaped assumptions of other theoretical concepts defining energy patterns along stream continuums. For example, the Flood Pulse Concept (FPC) evaluated lateral floodplain energetic exchange (Junk et al., 1989), the Hyporheic Corridor Concept (HCC) detailed the hydrological-biological exchange (Stanford & Ward, 1993; Bolton et al., 1998), the Riverine Productivity Model (RPM) highlighted local autochthonous inputs to large rivers (Thorp & Delong, 1994), the Nutrient-Spiralling Concept (NSC) described biological exchange and retention of nutrients (Webster & Pattern, 1979; Webster, 2007), and the Riverine Ecosystem Synthesis (RES) discussed hydrogeomorphic patches along a river continuum representative of functional energy zones (Thorp et al., 2006; Thorp et al., 2008). However, land-use change can influence energy dynamics conceptualised by these theories by altering key physical and biological variables that drive stream production. For example, the removal of forest can lead to elevated light, temperature, and nutrients, which have been associated with enhanced in-stream metabolism (Griffiths et al., 2013; Huryn & Benstead, 2019). These effects can lead to unpredictable changes in energy inputs, aquatic biomass, food web dynamics and the metabolic rates of biota. The question of how abiotic and biotic indices are primarily interrelated in driving secondary production has been poorly addressed (Wild et al., 2022). Further, there is a lack of consistency on how freshwater fish respond energetically to land-use change (e.g., Bilby & Bisson, 1992; Dineen et al., 2007; O'Gorman et al., 2016; Martens, 2019). This is important for management practices intended to restore the productive capacity of native fish.

1.1.2 | Factors affecting energy inputs into streams

Energy availability is a key factor that governs that production of biomass in streams. Energy inputs into stream systems are predominately derived from allochthonous or autochthonous sources. Allochthonous basal sources refer to inputs of terrestrially derived organic matter, while autochthonous sources refer to energy sources derived from primary production (Vannote et al., 1980; Gessner et al., 1999; Tank et al., 2010, Hershey et al., 2017). The riparian zone exerts considerable control of energy exchange and the relative contributions of allochthonous and autochthonous inputs (Kaylor & Warren, 2017). Small streams with dense forest canopies have high shading, leading to changes in key abiotic factors, such as light and temperature. Light and temperature are considered the dominant drivers of stream production, influencing nutrient cycling, energy flows and food web dynamics (e.g., Heffernan & Cohen, 2010; Wootton, 2012; Kaylor et al., 2017; Martens et al., 2019; Huryn & Benstead, 2019).

The levels of incident photosynthetically active radiation (PAR) and thermal radiation are collectively altered by canopy removal, which leads to decreased light attenuation. This consequently increases primary production and algal biomass when compared to the original forested state (Gregory, 1980; Warren et al., 2016; Wootton, 2012; Kaylor & Warren, 2017; Marten, 2019). Significant research has been undertaken overseas to determine the factors that control primary production. For example, early research in Oregon by Gregory (1980), illustrated how additional artificial light increased primary production, while Hill & Dimick (2002), confirmed that periphyton photosynthetic characteristics were primarily the result of altered light levels. More recently, Pacheco et al., (2022), demonstrated how high light intensity, in addition to nutrients, enhanced periphyton biomass. Periphyton is considered the dominant source of basal carbon at the base of the food web and the available biomass is expected to have implications for secondary consumer biomass (Lau et al., 2009; Guo et al., 2016b, Guo et al., 2018).

Periphyton provides a readily accessible source of soluble carbohydrates, while leaf litter requires conditioning by microbial communities to increase resource accessibility (Rounick & Winterbourne, 1983; Lau et al., 2009). When compared to allochthonous inputs of terrestrial leaf litter, periphyton is considered a higher-quality food source for secondary consumers (Torres-Ruiz et al., 2007; Lau et al., 2009; Guo et al., 2021). Moreover, periphyton provides polyunsaturated fatty acids (PUFA), which can enhance energy transfer efficiency and are essential for somatic growth and the reproduction of aquatic organisms (Guo et al., 2016a; Guo et al., 2016b). Recent research on light-exposed biofilms showed enhanced algal fatty acids when compared to dark biofilms (Guo et al., 2021), while nutrient additions increased periphyton carbon content and algal fatty acids (Cashman et al., 2013). Therefore, basal consumers feeding on high-quality food sources will provide high nutritional quality to secondary consumers (Brett & Muller-Navarra, 1997). Increased light has been shown to stimulate both algae and bacterial production rates and temperature enhances enzyme activities, accelerating bacterial leaf litter decomposition (Pope et al., 2020). In forested streams, there is a perceived high dependency on terrestrial leaf litter fuelling the food web due to the limitation in gross primary production (Vannote et al., 1980; Neres-Lima et al., 2016; Allan et al., 2021). In contrast, there is an assumed reliance on primary production in warmer pasture streams (Neres-Lima et al., 2016; Allan et al., 2021).

As a result, the quantitative and qualitative nature of food sources varies depending on the surrounding canopy cover and available light.

One key consideration when evaluating aquatic biomass is the balance between energy sources. In early research, Fisher & Likens (1973), described the dynamics of cross-boundary energy flow and energy balance in Bear Brook, New Hampshire. They found that over 99% of energy derived in Bear Brooks was allochthonous sources of organic matter from the surrounding forest. Evidentially, there is a trade-off between the loss of allochthonous inputs and replacement by autochthonous primary production in pasture streams. However, research argues that autochthonous resources are more important than allochthonous food sources for secondary production (Lau et al., 2009). Others suggest that the overall carbon budget is equal, whether derived from allochthonous and autochthonous sources (Hagen et al., 2010; Neres-Lima et al., 2017). Therefore, resource availability and type can have important implications on food web dynamics and energy flow within a stream system that is not always predictable (Huxel et al., 2002; Lau et al., 2009).

Solar irradiance controls stream thermodynamics, whereby open canopy streams experience elevated thermal radiation driving warmer in-stream temperatures (Rutherford et al., 1997; Roon et al., 2021). Ecological theory emphasises the importance of temperature in energetic regulation (e.g., Metabolic Theory; Brown et al., 2003) through temperature control of energetic requirements and metabolic rates of stream biota (Gillooly et al., 2001; Enquist et al., 2003; Imberger et al., 2008; Demars et al., 2011). Warmer in-stream temperature can enhance nutrient cycling and biochemical reaction rates (Caissie, 2006; Kaushal et al., 2010). Therefore, food supplies must increase to meet metabolic demand to sustain consumers at a higher trophic level in pasture streams (Perkins, 2021). This can lead to changes in the supply and demand synchronies of aquatic biota, influencing the biomass of organisms.

1.2 | Secondary consumer biomass and land-use change

The complex nature of stream food webs and trophic inefficiencies can be distorted by land-use change from forest to pasture. As noted earlier, land-use change can have direct effects on the stream function and production by altering key functioning variables such as light and temperature regimes and the relative importance of allochthonous and autochthonous energy sources (Groom et al., 2011; Kaylor & Warren, 2017; Kaylor et al., 2017; Bideault et al., 2021).

Forest canopy removal has been reported to lead to unpredictable changes in fish biomass. For example, research has shown higher fish densities and biomass under riparian or forested canopy cover (Dineen et al., 2007), while other studies have shown open pasture streams support increased densities and biomass of fish (Bilby & Bisson, 1992; Kaylor & Warren, 2017, Wooten, 2012; O'Gorman et al., 2016; Martens, 2019). The density and biomass of fish species can be altered by land-use change, both positively and negatively, but the underpinning relationships behind the specific environmental drivers of fish biomass are not well understood (Kaylor et al., 2017; Martens, 2019; Wilkinson et al., 2018; Tóth et al., 2019). New Zealand research suggests that native fish biomass increases in open pasture streams, raising questions concerning the energetic resources and physicochemical factors that sustain biomass (Hanchet, 1990; Hicks & McCaughan, 1997; Rowe et al., 1999). Research is required to understand the changes to key environmental metrics and ecological components that influence freshwater fish biomass. This is imperative for developing restoration strategies to sustain freshwater fish populations (Baldigo et al., 2010; Warren et al., 2010; Shirey et al., 2016; Kaylor & Warren, 2017).

1.2.1 | Temperature dependence and secondary consumers

O'Gorman et al. (2017) evaluated the temperature dependence of basal resources and highlighted that resource production was converted to consumers more efficiently as stream temperatures increased. Therefore, if high-quality food supply increases with temperature, there will be sufficient basal resources to sustain larger consumers at higher trophic levels (O'Gorman et al., 2017). However, if increased metabolic rates cause food consumption to exceed supply, this can lead to energetic inefficiency at the highest trophic level (Rall et al., 2010; Vucic-Pestic et al., 2011; Hughes & Grand, 2000). This concept is important as open pasture streams have been shown to support greater biomasses of secondary consumers, both globally (e.g., Bilby & Bisson, 1992; Kaylor & Warren, 2017, O'Gorman et al., 2016; Scrine et al., 2017) and in New Zealand (e.g., Hanchet, 1990; Hicks & McCaughan, 1997; Rowe et al., 1999).

Freshwater fish are ectotherms, so rely directly on specific ranges of water temperature for optimisation of growth, food consumption and metabolic demand. The preferred temperature range for most of the native New Zealand species studied was approximately 16.1°C to 21.8°C for smelt (*Retropinna retropinna*), banded kokopu (*Galaxias fasciatus*), kōaro (*Galaxias brevipinnis*), giant kokopu (*Galaxias argenteus*), inanga (*Galaxias maculatus*), torrentfish (*Cheimarrichthys fosteri*) and bullies (*Gobiomorphus* spp.). Eels (*Anguilla* spp.) were more tolerant of elevated water temperatures, with preferences around 24.4°C for longfin eel (*Anguilla dieffenbachii*) and 26.9°C for shortfin eel (*Anguilla australis*) (Richardson et al., 1994). Ectotherms have a higher productive efficiency than endotherms, meaning that at a given temperature ectotherms can allocate a greater proportion of assimilated food to growth (Humphrey, 1979; Vadeboncoeur & Power, 2017). There are well-established relationships between in-stream temperatures and metabolic rates and the growth of ectotherms (Brown et al., 2004; Perkins, 2022). Therefore, temperature is important for regulating fish growth and biomass in streams (Chisnall & Hicks, 1993; Hicks & McCaughan, 1997; Xu et al., 2010; Myers et al., 2018; Huryn & Benstead, 2019).

1.2.2 | Ecological production paradigms

Compared with typical terrestrial food webs where predator biomass is markedly lower than that of its prey (Elton, 1927), streams can present an inverted pyramid of biomass (Huryn 1996). Counterintuitively, the biomass of consumers exceeds that of the resource meaning production is insufficient, despite simultaneously providing a surplus of prey (Waters, 1988; Vadeboncoeur & Power, 2017). Research in warmer streams has shown such a change in biomass structure, whereby the biomass of higher trophic levels increases with local stream temperature (Hicks & McCaughan, 1997; Wooten, 2012; O'Gorman et al., 2016). These observed patterns conflict with predictions of the Metabolic Theory, where higher biomass–specific respiration at warmer temperatures should decrease the amount of biomass supported by a given amount of energy (Brown et al., 2004; Perkins, 2022). The inverted biomass pyramid was described in New Zealand by Allen (1951) and referred to as Allen's paradox (Hynes, 1970). The phenomenon has long challenged our understanding of stream ecosystem trophic interactions and production and has led to research to explain such aquatic inefficiencies, via sufficient subsidisation from terrestrial carbon (Cole et al., 2011), and variations to the nutritious value of periphyton (Lau et al., 2009; Vadeboncoeur & Power, 2017).

Questions remain around conclusions regarding the inverted pyramid of biomass and energy availability sustaining secondary biomass under differing land uses (Perkins, 2022). Research into these concepts may provide insight into the structure and functioning of fish communities in New Zealand streams.

1.3 | Importance of external subsidies to secondary consumers

1.3.1 | Terrestrial invertebrate subsidies

Although basal energy sources driving secondary production focus on terrestrial leaf litter and in-stream primary production, terrestrial invertebrate subsidies can provide an important alternative energy source for secondary consumers (Felden et al., 2021; Roussel et al., 2021; Burbank et al., 2022). Many ecological theories such as the RCC, the Flood Pulse Concept (Junk et al., 1989), the Riverine Productivity Model (Thorp & Delong, 1994) and the Riverine Ecosystem Synthesis (Thorp et al., 2006; Thorp et al., 2008) help conceptualise energy transfer pathways along a stream-river continuum but few of these explicitly account for terrestrial invertebrate inputs or the migratory nature of diadromous fish. Streams with high riparian cover are expected to increase the availability of terrestrial invertebrates falling into streams. This can lead to significantly greater biomass of terrestrial invertebrate inputs when compared to pasture streams (Edwards & Huryn, 1996). For example, Burbank et al. (2022), found gut contents of silver shiner (*Notropis photogenis*) contained significantly higher proportions of terrestrial invertebrates in sections of streams where riparian vegetation cover was greatest. However, recent research by Benjamin et al. (2022), showed an increase in terrestrial invertebrates when canopy cover was reduced by 50%.

Quantifying the extent to which higher trophic levels utilise these terrestrial invertebrate energy sources would assist in understanding the role of alternative resources in supporting secondary biomass in streams, particularly when primary production is low (Felden et al., 2021). Research to date has suggested that fluxes of terrestrial invertebrates can provide up to half the annual energy budget for fish (Baxter et al., 2005). With overseas research suggesting terrestrial invertebrates provide a critical energetic pathway in subsidising biomass (e.g., Wilson et al., 2014; Brett et al., 2017; Niles & Hartman, 2021), the contribution of terrestrial invertebrates to stream food webs under differing land uses warrants investigation in New Zealand.

1.3.2 | Marine subsidies from migratory fish

A large proportion of New Zealand stream fish communities are diadromous, meaning they migrate between marine and freshwater environments to complete their lifecycle (McDowall, 1993). Migratory fish can alter ecological subsidies through the transport of nutrients across marine-freshwater boundaries. These additional sources from marine-derived nitrogen (MDN) can alter stream production (Gresh et al., 2000; Flecker et al., 2010). The relationship between MDN and freshwater food web dynamics has been well documented overseas, particularly for anadromous species (Garman & Macko, 1998; Gresh et al., 2000; Naiman et al., 2002; Flecker et al., 2010; Wipfli & Baxter, 2010). For example, Hicks et al. (2005) demonstrated how spawning coho salmon enhanced the production of aquatic food webs in the Copper River Delta. Other research has suggested that nutrient subsidies from spawning salmon increase the production of autotrophic biomass (Holtgrieve & Schindler, 2011; Muñoz et al., 2021).

Isotopic analyses have been used to assess energy transformation within marine-freshwater environments by analysing distinct differences in isotopic signature (e.g., Hicks et al., 2005; Fraley et al., 2021). There is a greater proportion of the heavier C and N isotopes in marine organisms when compared to most freshwater and terrestrial organisms (Schindler et al., 2003). This natural isotopic marker allows for the ability to trace marine-derived isotopes in freshwater systems (Finlay & Kendall, 2007). For example, Walters et al. (2009) used stable isotopes analyses to address the influx of marine nitrogen and found increased $\delta^{15}N$ at all trophic levels, coinciding with the spawning of anadromous Alewife (*Alosa pseudoharengus*). Therefore, stable isotope analyses can provide useful insight into the importance of marine-derived nutrients in stream food webs and the energetic exchange between marine-freshwater boundaries. Recruiting inanga (*Galaxias maculatus*), may provide an important food source subsiding fish biomass in New Zealand stream food webs. However, the extent and importance of these marine subsides to New Zealand stream food webs is unknown. Understanding the contribution of marine-derived sources of nutrients in streams may have important implications for whitebait management in New Zealand.

1.4 | Stable isotopes in streams

Stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) provide a powerful tool to characterise, trace resources and delineate food web dynamics in stream food webs (Peterson & Fry, 1987; Hicks, 1997; Vander Zanden et al., 1999; Post, 2002a; Carvalho et al., 2017; Hershey et al., 2017). Stable isotope analyses (SIA) allow for key insight into the resources sustaining aquatic biomass and are useful for tracing energy flow along stream continua. SIA techniques have been widely applied to stream research, proving valuable for determining dietary contributions of food sources to consumers, energy transfer and trophic position (e.g., Reid et al., 2008; Lau et al., 2009; Neres-Lima, 2016). For example, the ratio of the heavy-to-light isotopes $^{15}N/^{14}N$ in tissue in comparison to the atmospheric nitrogen standard can be used to estimate trophic position due to the progressive increase in $\delta^{15}N$ by 3-4‰ with each trophic level (DeNiro & Epstein, 1981; Bowes & Thorp, 2015). This is due to the retention of the heavier isotope and the loss of the lighter isotope during physicochemical processes via excretion and respiration (Macko et al., 1986; Miura & Goto, 2012). Traditionally, bulk stable isotope approaches have been used throughout food web research (Post, 2002b; Fry, 2006). Bulk stable isotope analyses have been widely used as a reliable and cost-effective method to resolve food web dynamics, particularly for higher trophic levels (e.g., freshwater fish). Although there are several benefits to bulk isotope analysis, there are limitations. For example, the interpretation of the isotope values derived from bulk tissue can be confounded by temporal and spatial variations of primary producers (Schmittner & Somes, 2016). To account for this variation, potential basal dietary sources require sampling at appropriate locations and time. Moreover, there is occasionally isotopic overlap across co-occurring dietary resources, with can occur with terrestrial C_3 plants and periphyton. This can make it challenging to determine whether a consumer relies on terrestrial or algal sources of energy (Finlay & Kendall, 2007). Bulk tissue isotope data also requires the assumption that source protein is directly incorporated into consumer protein and some macromolecules can be extensively synthesised by physiological processes (Whiteman et al., 2019). For example, excretion of nitrogen favours the lighter isotope ^{14}N over ^{15}N, leading to consumers retaining ^{15}N and therefore having higher $\delta^{15}N$ values than their food source (Vanderklift et al., 2003). This requires trophic discrimination factors (TDF) to be applied to reflect the isotopic fractionation, but these are often uncertain (Blanke et al., 2017). Compound specific isotope analysis (CSIA) can overcome many of the limitations associated with bulk stable isotope analysis, with the ability to resolve overlapping isotope values of basal sources and refine the link consumers to basal resources (Bowes & Thorp, 2015; Potapov et al., 2019). This novel technique can facilitate adequate separation of food sources by allowing for the separation of actively cycling and refractory basal food sources, thus reducing uncertainty in dietary source estimates and trophic level (Larsen et al., 2013; Magozzi et al., 2021). However, recent research by Chiapella et al. (2021) suggested that the promise provided by CSIA to overcome limitations of bulk isotope analysis may be overstated, underscoring the importance of further experimental investigation. Despite the limitations of bulk isotope analysis, CSIA remains in its infancy with limited use in freshwater systems to-date (Bec et al., 2011; Larsen et al., 2013; Chiapella et al., 2021). High costs and labour-intensive sample preparation and measurement time currently limits the applicability of CSIA (Zhu, 2019).

1.5 | Study location

Mount Taranaki (Taranaki Maunga) provides the ideal study area for ecological research with distinct changes in land use, and streams that have structurally representative catchments and similar species. The mountain is a dormant stratovolcano reaching 2518-m in elevation and is located on the west of the North Island, New Zealand. Mount Taranaki formed through a series of pyroclastic flows and lahars leading to a fan of volcanic conglomerates, breccia and tephra material structuring the unique environment (Neall et al., 1993). Water courses developed channels through easily eroded volcanic formations resulting in streams that flow radially through a forested national park into open pasture environments (TRC, 2011). The original forest of the Taranaki ring plain was cleared in support of farming practices that developed throughout the 1870s to early 1900s. In 1981, the remaining forested environment was protected, leading to a distinct circular forest reserve (TRC, 2011). The abruptness between the forested reserve and to pasture ring plain allows for key functional attributes of stream production to be assessed. Longitudinally, streams are structurally representative and permit comparisons of important energetic concepts in ecological theory to be tested. Taranaki streams further provide a desirable environment to investigate the input of marine-derived nutrients from diadromous fish, where streams abruptly discharge into the Tasman Sea.

Understanding the drivers behind fish biomass under differing land uses can provide useful insight into restoration practices required to maintain stream function and sustain aquatic communities. Furthermore, research in New Zealand is limited with respect to the relative importance and extent that terrestrial invertebrates may be subsiding fish biomass under differing land uses, while the contribution of MDN to New Zealand stream food webs is largely unknown.

1.6 | Thesis aims and objectives

In the previous sections, I describe how differences in land use can affect energy availability, in-stream metabolic rates, and food web dynamics in streams. This thesis focuses on the ecological processes in relation to the drivers and interactions among biota and their physical and chemical environment linking freshwater fish biomass, food web dynamics and their trophic connectivity. Using a range of field assessments and SIA, this thesis addresses four specific objectives relating to secondary biomass.

i) Quantity differences in the abundance and aquatic biomass in native forest and open pasture streams (Chapter 2).

ii) Investigate the drivers accounting for fish biomass in relation to variations in light and temperature regimes, water chemistry, organic matter processing, terrestrial input, periphyton and aquatic invertebrate biomass within native forest and open pasture streams (Chapter 2).

iii) Determine food web structure in forest and pasture streams and delineate sources of energy to consumer diet using stable isotope mixing models. (Chapter 3)

iv) Assess longitudinal variations in aquatic biomass and sources of energy to consumer diet, including large-scale effects of riparian habitat and evaluate the extent of MDN contribution (Chapter 4).

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CHAPTER II

Energy supply and fish biomass increase with forest cover removal in temperate montane streams

Forested stream reach of the Kapoaiaia Stream. Photo credit: Warrick Powie, January 2020.

2.1 | ABSTRACT

Determining the factors that limit fish abundance and biomass is fundamental to understanding the effects of forest removal on stream ecosystems. Energy input from solar irradiance controls stream thermodynamics and is closely linked to in-stream metabolism. Forest canopy cover and riparian vegetation directly influence radiant energy inputs, profoundly altering light and temperature regimes of streams and the availability of allochthonous and autochthonous resources. The removal of riparian vegetation can increase stream temperatures, leading to an increase in both primary production and the metabolic rate of fish but can diminish allochthonous food sources. If allochthonous sources are diminished by forest removal and not compensated by increased autochthonous food supply, the fish biomass response should reduce in open sites due to increased metabolic demand and inadequate food availability. The balance between allochthonous and autochthonous energy sources is critical in evaluating the response of stream fish to conversion from forest to pasture.

I analysed the abundance and biomass of fish in forest and open pasture streams in Mount Taranaki in relation to light and temperature regimes, water quality, organic matter processing, allochthonous input, periphyton biomass and aquatic invertebrate biomass and abundance. Fish abundance was estimated using multiple-pass electrofishing at six paired sites situated 1.5 – 3.5 km apart. A combination of body-mass to abundance (*M-N*) allometries, principal component analyses, correlations, and piecewise Structural Equation Modelling were used to evaluate relationships between components and characterise energy flow.

Fish densities from removal population estimates were greater in pasture ($\bar{x}$ = 60.2 fish 100 m^{-2} ± 21.1 SE) than in forest ($\bar{x}$ = 12.5 fish 100 m^{-2} ± 3.8 SE; paired

t-test $p = 0.002$). Fish biomass of all species combined was five-fold greater in pasture ($\bar{x} = 35.1$ g m^{-2} ± 5.7 SE) than in forest sites ($\bar{x} = 6.6$ g m^{-2} ± 2.0 SE; paired *t*-test $p = 0.002$). Crayfish were abundant at all sites (forest $\bar{x} = 27.5$ crayfish 100 m^{-2} ± 12.7 SE; pasture $\bar{x} = 75.6$ crayfish 100 m^{-2} ± 51.2 SE; paired *t*-test $p = 0.184$), but densities and biomasses were not significantly different between forest and pasture streams (forest $\bar{x} = 1.5$ g m^{-2} ± 0.8 SE; pasture $\bar{x} = 4.9$ g m^{-2} ± 3.8 SE; paired *t*-test $p = 0.142$).

Despite greater community biomass in pasture, body-mass to abundance (*M*-*N*) allometries showed no differences in slope between forest and pasture communities. This could suggest that community structure is functionally similar in forest and pasture streams, but the effects of increased light and temperature in pasture streams caused an increase in body size for the equivalent abundances across the entire community.

Light intensity and water temperature were positively correlated ($p < 0.001$). Periphyton biomass was significantly greater in pasture streams (pasture $\bar{x} = 11.52$ g m^{-2}; forest $\bar{x} = 4.28$ g m^{-2}; $p = 0.007$). Terrestrial invertebrate inputs were five-fold greater at pasture when compared to forest sites (pasture $\bar{x} = 0.72$ g m^{-2} day^{-1}, forest $\bar{x} = 0.14$ g m^{-2} day^{-1}; $p = 0.020$). Terrestrial invertebrates can serve as a critical energetic pathway for sustaining fish populations. Terrestrially derived food sources are expected to have consequences on the observed fish biomass, given their close correlation. Higher water temperatures at pasture sites were closer to the preferred temperatures for New Zealand fish, than at forested sites. This, coupled with more available food sources (both autochthonous and allochthonous) supported greater fish densities and biomasses at pasture sites.

2.2 | INTRODUCTION

Stream production can be measured in terms of change in biomass and is central to the ecology and sustainability of fish assemblages (Myers et al., 2018). The biomass of fish is defined as the standing stock of living mass that accumulates over time. Fish biomass is the physical expression of energy at the highest trophic level and can vary depending on the physiological response of fish through related ecosystem processes. The analysis of freshwater fish biomass can provide unique insight into the energetic functioning of stream systems. Light and temperature drive ecosystem processes and influence nutrient cycling, energy flows and food web dynamics (e.g., Heffernan & Cohen, 2010; Wootton, 2012; Huryn et al., 2014; Kaylor et al., 2017; Martens et al., 2019; Huryn & Benstead., 2019). As freshwater ecosystems have discrete ecosystem boundaries, slight increases in light and temperatures can alter the structure and functioning of freshwater communities (Woodward et al., 2010; Scrine et al., 2017; Bengtsson et al., 2018).

Forest canopy cover and riparian vegetation directly influence light and temperature regimes and the available energy sources within a stream system (Groom et al., 2011, Kaylor et al., 2017). The levels of incident radiation via photosynthetically active radiation (PAR) and thermal radiation are collectively altered by the level of vegetation and stream shading. Elevated PAR due to canopy removal has been shown to increase primary production and algal biomass, which are considered important carbon sources at the base of the food web (Gregory, 1980; Wootton 2012; Warren et al., 2016; Kaylor & Warren, 2017). Canopy removal further increases thermal radiation, driving warmer in-stream temperatures which alters in-stream metabolism (Brown et al., 2004). Warmer in-stream temperatures have been shown to accelerate the organic matter processing rates of streams

(Imberger et al., 2008). Accelerated processing at the detrital energy base can enhance secondary production (Quinn et al., 2000; Hall et al., 2000; Cross et al., 2006; Patrick et al., 2019). However, warmer stream temperatures can increase the metabolic demand of aquatic organisms (Power & Dietrich, 2002; Demars et al., 2011; Huryn et al., 2014). Temperature governs metabolism arising from its effect on biochemical reaction rates (Gillooly et al., 2001). As metabolic processes and growth rates of fish are temperature-dependent, small increases in temperature can increase both fish density and biomass (Xu et al., 2010; Huryn & Benstead, 2019). However, if increased metabolic rates cause food consumption to exceed supply, this can lead to energetic inefficiency, with decreased fish size and abundance (Rall et al*.,* 2010; Vucic-Pestic et al*.,* 2011; Hughes & Grand, 2000; O'Gorman et al., 2016; O'Gorman et al., 2017).

Removal of riparian vegetation caused by land-use change to pasture is likely to offset the balance between allochthonous and autochthonous carbon sources. Allochthonous sources can be significant food sources for secondary production (Lu et al., 2014; Brett et al., 2017). An important consideration is whether the reduction of allochthonous food sources is compensated by increased in-stream primary production with increased light. If allochthonous sources are diminished and not compensated by in-stream food production, fish biomass response could reduce in open sites. This is due to increased metabolic demand and limitations in food availability. However, fish responses to pastoral habitat changes have not been consistently negative. For example, open and pasture streams have shown an increase in density, biomass, and production of fish, both globally (Bilby & Bisson, 1992; Kaylor & Warren, 2017, O'Gorman et al., 2016; Scrine et al., 2017) and in New Zealand (Hanchet, 1990; Chisnall & Hicks, 1993; Hicks & McCaughan, 1997; Rowe et al., 1999). Thus, questions arise around the drivers behind fish biomass given the potential reduction in available allochthonous food sources, in addition to the balance between increased metabolic scope and potentially reduced food supply at open sites.

In forested streams, energetic transfer is predicted to be inefficient and consequently, energy availability is progressively less as body size increases (Brown & Gillooly, 2004; Barneche & Allen, 2018). Therefore, evaluating body-mass to abundance (*M-N*) allometries can provide a key measure of community structure by illustrating how energy flows through food webs (Perkins et al., 2018). These relationships can provide integrated measures of food web structure and energy flow in relation to environmental variables, such as warming of in-stream temperatures (Dossena et al., 2012). The slope of the *M-N* relationship describes the rate of biomass depletion (as a proxy of energy flux) and depends on the community-wide mean predator-prey mass ratio and the trophic efficiency (Kerr & Dickie, 2001; Perkins et al., 2018). In aquatic systems, there is a consistent negative relationship between *M-N* (White et al., 2007; Trebilco et al., 2013), with evidence that warmer streams result in a decrease in mean individual body mass (e.g., Daufresne et al., 2009, Perkins, 2022). These patterns conflict with metabolic scaling theory, that the standing biomass should decrease with temperature, given a fixed supply of resources (Brown et al., 2004). Contrary to the metabolic scaling theory, it is predicted that community *M-N* relationships will result in a less negative slope with increasing temperature. Therefore, greater aquatic community biomass is favoured at warmer pasture sites. However, temperature alone is unlikely the driver of greater community biomass and abundance relationships. To sustain larger prey at warmer temperatures, supply of resources must increase with metabolic demand. Elevated allochthonous subsidies have been shown to serve as a critical energetic pathway allowing for the maintenance of greater aquatic carrying capacities (Huxel et al., 2002; Niles & Hartman, 2021). Allochthonous subsidies have also been predicted to lead to changes in the predicted *M-N* relationships in open stream systems (Dossena et al., 2012; Perkins et al., 2018; Perkins, 2022). For example, if fish in warmer streams are subsidised by terrestrial invertebrate inputs, then the *M-N* scaling is also predicted to be less negative. This is because the abundance of the consumer is greater than can be accounted for by entirely autochthonous inputs (Perkins et al., 2018). Therefore, evaluating changes in *M-N* scaling in forest and pasture streams may provide insight into the energetic functioning of the stream communities in pasture sites.

Fish biomass can be limited by water quality, nutrient availability, and habitat availability. Land-use change from forest to pasture can cause increased levels of fine sediments and alter available nutrients. The riparian zone is considered an important transitional zone between land and stream and riparian planting is a proposed method of mitigating agricultural degradation (Scarsbrook & Halliday, 1999). However, reducing in-stream nutrients has been shown to lead to a reduction in primary productivity, which is a major determinant of the dynamics of higher trophic levels in streams (Gregory, 1980, Gücker et al., 2009). Whilst exceedance of environmental thresholds (e.g., sediment, light, temperature, and nutrients) can be detrimental to fish communities (Jones & Petreman, 2013), canopy removal has shown positive implications for fish production. For example, Riley et al. (2009) found that in open sites, fish were larger and at higher densities, which was positively driven by the growth and abundance of food in the open sites. Streams with areas of dense riparian shaded sections showed low levels of in-stream macrophytes and aquatic invertebrate biomass, consequently reducing both densities and biomasses of fish (Hawkins et al., 1983, O'Grady 1993, Riley et al., 2009). However, fish densities and biomasses can be greater in closed-canopy streams, particularly in summer (Dineen et al., 2007). The underpinning relationships of fish production with shade, temperature and food availability are not always predictable and production following land-use modification is more challenging to quantify (Scott, 2006; Kaylor et al., 2017; Martens et al., 2019; Wilkinson et al., 2018; Tóth et al., 2019; Murdoch et al., 2020). Piecewise Structural Equation Modelling (pSEM) provides the ideal solution to testing hypotheses of energy flow within streams (Lefcheck, 2016). If periphyton is driving consumer biomass through increased light and temperature, then warmer conditions alone would have a positive influence on consumer biomass.

Increased metabolic demand must be matched by increased basal resource availability to sustain higher trophic levels (e.g., Metabolic Theory; Enquist et al., 2003). This is particularly important given that major restoration aims are to restore ecosystem function through whole catchment riparian planting, often to meet increased shading objectives. In a global review, of the 55 completed habitat rehabilitation or enhancement projects targeting in-stream fish production, only 5% demonstrated an increase in fish production, despite 98% achieving specified habitat targets (Smokorowski et al. 1998; Bond & Lake, 2003). If fish biomass is predominately driven by the underlying effects of light and temperature, stream management that encourages dense riparian buffer zones resulting in canopy closure of stream habitats may have unintended detrimental effects on fish dynamics. Understanding the drivers behind fish production is therefore essential for understanding how aquatic species respond to varying levels of modification and determining appropriate restoration strategies for stream fish communities.

This study aims to compare the abundance and biomass of fish in native forest and open pasture sites in Taranaki streams, New Zealand. I investigate the drivers behind fish production in relation to variabilities in light and temperature regimes, water chemistry, organic matter processing, terrestrial input, periphyton and aquatic invertebrate biomass within paired sites. I hypothesise that secondary consumer biomass in forested streams is constrained decreased by metabolic rates and available energy while, secondary biomass in pasture streams benefits from high metabolic rates and available energy (depicted in Figure 2-1).

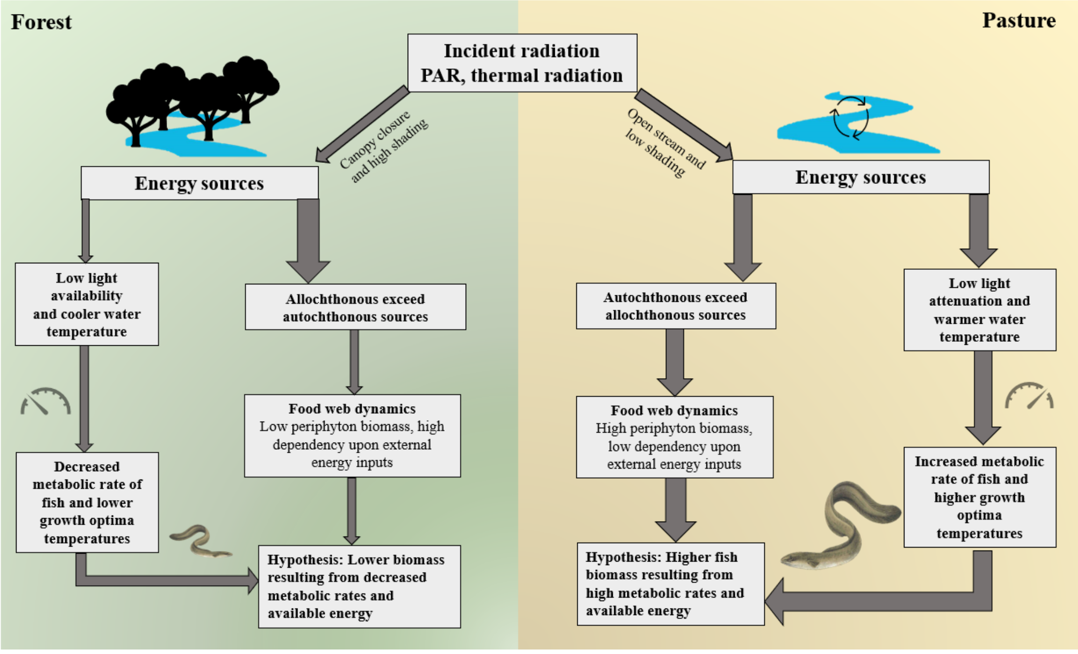


FIGURE 2-1 Conceptual model of energy flows in forest and pasture streams (Hypothesis 1).

2.3 | METHODS

2.3.1 | Study sites

Mount Taranaki is located on the west coast of the North Island, New Zealand. The mountain is a 2518-m high symmetrical volcano with a series of streams that flow radially from native forest around the summit to a surrounding lower-elevation ring plain. Streams that flow through this ring plain are subject to intensive pastoral land use (dairy, sheep and beef farming). Six paired sites were chosen around the mountain, with one of each pair located in shaded native forest and the other located downstream in open pasture (Figure 2-2).

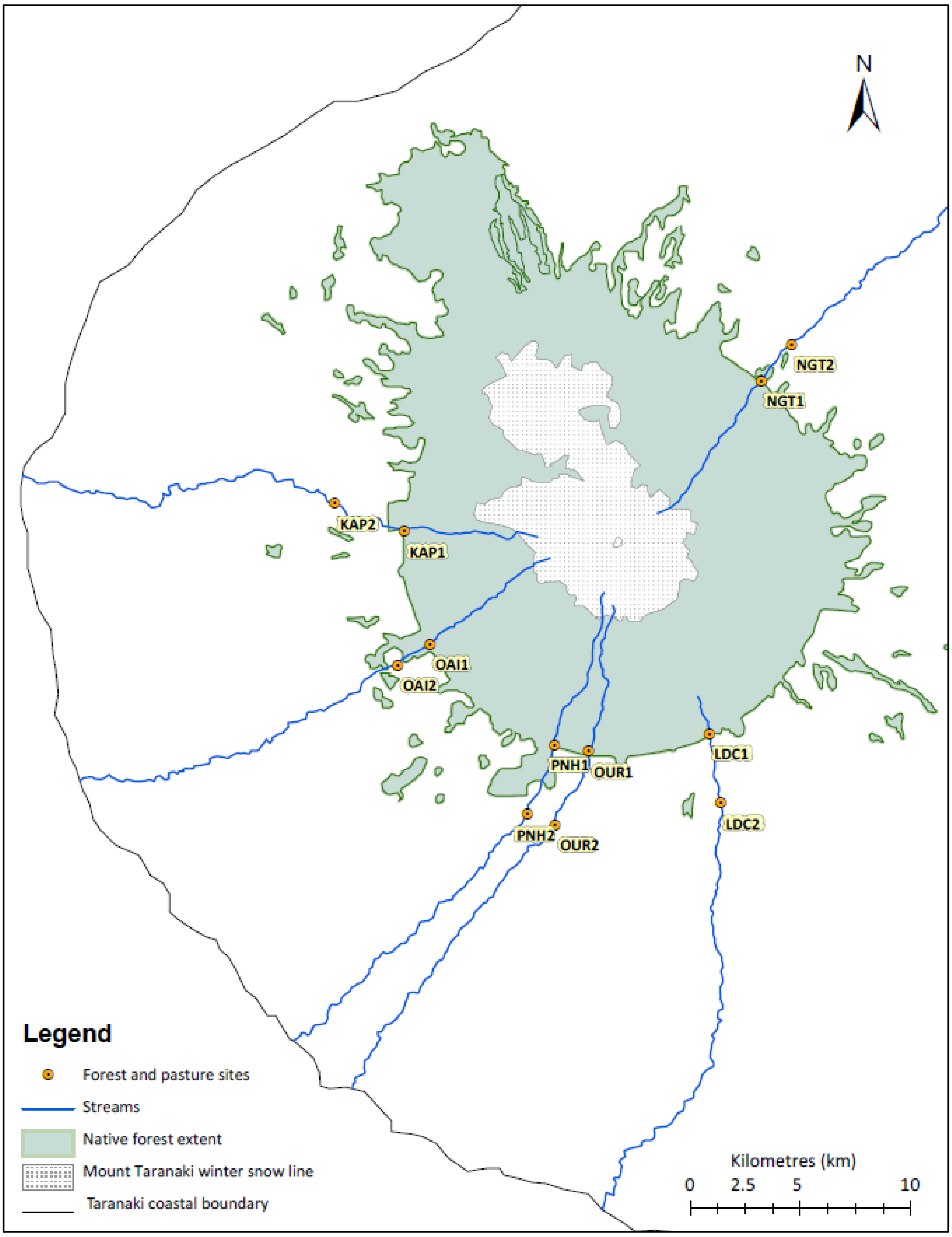


FIGURE 2-2 Location of sites in native forest and pasture streams in the Taranaki Region, North Island, New Zealand. See Table 2-1 for site abbreviations. 1 following site code denotes forest sites; 2 following site code denotes pasture sites.

Paired sites were situated 1.5 km to 3.5 km apart and all had similar physical attributes for substrate, width, depth, flow, catchment size, distance from sea and elevation (Table 2-1). All sites had equal recruitment opportunities as there were no fish passage barriers between the forest and pasture sites. Downstream barriers were investigated prior to the analysis using the fish passage assessment tool (Franklin, 2022) and no downstream barriers were identified. As channel slope and in-stream barriers can influence the recruitment of native fish (McDowall, 1993), homogeneity of slope within and between forest and pasture sites was analysed using ArcGIS Pro and Google Earth Pro (ESRI Inc., 2020; Google Inc, 2021).

2.3.2 | Physical site attributes and water quality

Sampling following the principles in Stream Ecological Valuation (SEV, Storey et al., 2011) were undertaken at 10-m intervals for 50-m reach lengths at each site using cross-sectional measurements in November 2019. Variables of channel geomorphology including stream width, depth, and velocity were undertaken. Percentage stream shade was estimated visually within 5-m intervals at the cross section for each site. In December 2019, a hemispherical camera fitted with a fish-eye lens was used to assess the canopy openness at forest and pasture sites. Five photographs were taken along a transect, with the camera positioned centrally in the stream following protocols detailed in Zhang et al. (2005). Canopy photos were analysed using the imaging software Gap Light Analyzer (GLA) to provide a percentage of mid-canopy openness for forest sites (Frazer et al., 1999). In January 2020, a YSI ProSolo handheld meter was used to measure pH, specific conductivity, and dissolved oxygen. Fifty-mL unfiltered and filtered water samples were also taken at each site and sent to Hills Laboratories Ltd, Hamilton for nitrogen (total nitrogen, total ammoniacal-nitrogen, nitrates and nitrates) and phosphorus analysis (total phosphorus and dissolved reactive phosphorus).

2.3.3 | Light and temperature analysis

Two Onset HOBO Pendant MX2202 light and temperature data loggers were deployed at each site in November 2019. One logger was placed in the water, the second directly adjacent on the stream bank. Continuous annual light and temperature measurements were taken every 15 minutes (November 2019 to November 2020). Mean temperature was calculated for the summer period (December, January, and February) and as annual means for each site.

2.3.4 | Organic matter processing

Organic matter processing was estimated by wood break-down (measured as mass loss) by deploying five groups of birch wood sticks at each site across the stream width attached by heavy-duty fishing nylon. The sticks were left in the stream for an incubation period of 30 days in December 2019. The dry weight of sticks before and after incubation was measured in the laboratory. Additionally, five leaf-filled mesh bags containing 10 g of black alder (*Alnus glutinosa*) leaves were threaded 50-cm apart across the stream width using fishing nylon. Alder leaves were chosen as they represent an intermediate breakdown rate suitable for mass loss analysis for a 30-day incubation period (k day^{-1} = 0.0103 to 0.0216, 24% mass loss after 28 days: Hicks & Laboyrie, 1999). The dry weight of leaves and sticks before and after incubation were measured in the laboratory. Leaf and stick mass-loss rates were determined using degree days as a variable of time (Petersen & Cummings, 1974; Equation 1).

$$k = \frac{\ln(w_0) - \ln(w_t)}{t} \qquad \text{Equation 1,}$$

where W_0 is leaf dry weight at time 0 and W_t is the leaf dry weight at time t, and t is the incubation time in days.

2.3.5 | Allochthonous and autochthonous sampling

2.3.5.1 | Autochthonous inputs

Periphyton was sampled in January 2020 from five randomly selected cobbles (20 – 25 cm) using the quantitative Method QM-1b (Biggs & Kilroy, 2000). A 15-cm diameter ring was placed centrally on the rock and periphyton was scraped within the ring and pipetted into a container. Samples of periphyton were frozen in the field. The AFDW of periphyton at each site was determined by drying the samples for at least 24 h at 40°C, weighing and ashing for 4 h at 400°C, and then re-weighing.

Aquatic invertebrates were sampled in January 2020 using a 0.1-m^2 area, 500-µm mesh Surber sampler, following the quantitative protocol C3 for hard-bottomed streams detailed in Stark et al. (2001). Four samples of aquatic invertebrates were pooled to measure biomass. Aquatic invertebrates were frozen onsite rather than using ethanol as a preservative, to account for weight loss known to affect biomass samples (Stark et al., 2001). Aquatic invertebrates were identified to species level, where possible, using a dissecting microscope, counted and lengths recorded. The cases of caddisfly and shells of snails (*Potamopyrgus antipodarum* and *Physa*) were removed for a direct estimate of consumable biomass. Aquatic invertebrates grouped by species and dried at 40°C for at least 48 h to a constant weight and the subsequent biomass was calculated.

2.3.5.2 | Allochthonous inputs

To capture terrestrially derived organic matter and invertebrates entering the stream system, four 5-L buckets were dug approximately 20 cm into the stream bank. Two were situated on the left bank and two were situated on the right bank, at each site. Each bucket contained 5 cm of water combined with 10 mL of 4% formalin to prevent decay, whilst allowing for accurate biomass assessments (Manson & Macdonald, 1982; Stark et al., 2001). Buckets were left for a period of 30 days during December 2019 and January 2020 to capture autochthonous input. Terrestrial invertebrates were identified to genus level and counted. Terrestrial vegetation and invertebrates were dried at 40°C for at least 48 h to a constant weight and the subsequent biomass was calculated.

2.3.6 | Fish and crayfish

Fish and crayfish populations were sampled using multiple-pass electrofishing at each site from 20 January 2020 to 31 January 2020. Each reach was blocked with a 5-mm mesh net downstream, and 20 m of stream reach was fished in a downstream direction at each site until there was a reduction in fish between passes, following the depletion method (White et al., 1982). Fish from each pass were identified to species, then counted and their total length measured for eels, lamprey, and bullies. For other fish, fork length was defined as the distance from the snout tip to the fork of the tail. The length of crayfish was measured by carapace length from rear of the eye socket to the end of the external body shell (carapace). Population estimates were considered reliable when numbers caught in the second pass did not exceed that caught in the first pass. In the few instances when the second pass was greater than the first pass, for example, for some estimates of crayfish, a third pass was undertaken and occasionally a fourth.

2.3.7 | Statistical analysis

The weight of fish was calculated from the length-weight relationship using the parameters of length-weight relationships of fish species in New Zealand determined by Jellyman et al. (2013) and applying Equation 2.

$$W = aL^b, \qquad \text{Equation 2,}$$

where W = weight in g and L = length in mm, and a and b are constants for each species.

The population estimate was derived from the number of fish and crayfish at each site and estimated using the Carle and Strub maximum weighted likelihood method in the statistical program R, FSA package (Carle & Strub, 1978; Ogle et al., 2021).

Fish density was calculated using the population estimate divided by the total area fished. Biomass was then calculated using the density of fish and the mean fish weight by species for each land use, while areal biomass was determined from the fish biomass for each species divided by the area fished.

To account for the paired-site study design, differences between means of variables for forest and pasture sites were examined with paired *t*-tests to determine significant differences using TIBCO Statistica 13.5 software (TIBCO Software, 2018). To meet the parametric assumptions of *t*-test, the data was log transformed. Spearman correlation coefficients on non-transformed data were calculated to determine the relationship between variables, while scatterplots were presented to visualise relationships between variables.

To determine the response levels for biotic and environmental variables, a principal component analysis (PCA) ordination plot was generated using the Vegan package in the statistical programme R version 3.1.3 (R Development Core Team, 2020). Variables strongly correlated (Spearman correlation, $r > 0.90$) were excluded from the analysis. PCA was performed on standardised environmental and biological data.

Body mass (*M*) and abundance (*N*) relationships for stream invertebrates, crayfish and fish were constructed following methodology described in Perkins et al. (2018). *M*-*N* relationships were derived following logarithmic ($\log_{10}$) transform of mean body mass and the total abundance for each functional group (stream invertebrates, crayfish and fish) at each site for pasture streams ($n = 18$) and forest streams ($n = 18$). Samples were undertaken during the summer period and provide only a snapshot of community structure.

Piecewise structural equation models (pSEM) were constructed to test the strength of connections of biological with physical variables. Low sample size can be problematic with traditional SEM, but pSEM can account for sample size limitations by constructing a series of linear models and 'piecing' them together (Lefcheck, 2016). This makes pSEM a useful statistical technique given the low sample size ($n = 12$). All variables were standardised prior to running the analysis to meet the model assumptions and permit comparable measurements between predictors. Centring and standardisation of input variables allows improvement of the interpretability of regression coefficients (Schielzeth, 2010). Models were structured using the 'lme' function in the 'nlme' package within the statistical programme R version 3.1.3 (R Development Core Team, 2020). The variance inflation factors (VIF) were calculated to assess the collinearity of the predictors in the component model with a cut of ≥ 5. If predictor variables presented collinearity, the highly correlated predictor were removed from the model to prevent erroneous results and avoid violation of model assumptions. Paired sites were expected to be subject to common influences such as similar disturbance regimes and potential fish barriers downstream. To account for the paired study design, a nested random effect of 'Stream' was used to account for the common influences within each paired site (i.e., =~1|Stream). Correlated error terms were specified in the model to determine shared relationships with underlying drivers that may not be otherwise determined in the pSEM. They describe the relationship among variables that are not presumed to be casual or unidirectional (Lefcheck, 2016). Fishers *C* test was used to determine the appropriateness of the model ($p > 0.05$). Marginal and conditional R^2 values were computed according to Nakagawa & Schielzeth (2013).

2.4 | RESULTS

2.4.1 | Physical variables

There were no significant differences between forest and pasture sites for distance from sea catchment area ($p = 0.109$), area fished ($p = 0.775$), stream width ($p = 0.773$), mean water depth ($p = 0.179$) allowing for direct comparisons of fish biomass across forest and pasture sites (Table 2-1). However, elevation between forest and pasture sites showed a significant difference ($p < 0.001$) as forest sites were upstream of the pasture sites. Elevation was controlled for by ensuring there were no physical barriers to fish passage between forest and pasture sites. There were marginally significant differences between slope ($p = 0.034$) and mean water column velocity ($p = 0.044$). Mean channel slope ranged between 2.74% and 4.30% for pasture and 3.74% and 4.78% in forested sites and were marginally higher in forest than pasture sites ($p = 0.034$; Table 2-1).

Abiotic variables including light, temperature, stream shade, mid-canopy openness and dissolved oxygen were greater in pasture and were statistically different between land uses (Table 2-1; Table 2-2). Water quality variables including specific conductivity, pH, total nitrogen, and total phosphorus were similar among land uses and presented no significant differences between forest and pasture sites, albeit for dissolved oxygen. Total nitrogen at LDC2 showed elevated nitrogen in comparison to other sites (Table 2-1). The mean summer water temperatures were 11.2°C–14.9°C at forest sites and 14.2°C–16.9°C at pasture sites, with a mean 3.1°C difference between land use (p = 0.006). The lowest summer water temperature was recorded at OUR1, while the warmest summer water temperature were recorded at PNH2 and OAI2. Annual water temperatures ranged between 9.1°C–10.2°C for forest and 10.6°C–13.8°C for pasture, with a mean annual difference of 2.2°C between land use (p = 0.003; Table 2-2). There was a strong positive relationship with the annual air temperature and the annual water temperature (r^2= 0.667; Figure 2-3A). All water and air temperatures, in addition to in-stream and bank light, showed significant differences between forest and pasture sites ($p < 0.05$). The mean annual in-stream and bank light intensity were positively correlated with water temperatures (r = 0.635; r =0.796; Appendix 2-1). Forest sites had both the lowest mean light intensities and water temperatures (Table 2-2). The relationship between temperatures and light intensities for both summer and annual means showed significant correlations ($p < 0.05$; Appendix 2-1).

TABLE 2-1 Physical site characteristics and water quality taken in January 2020 includes means and paired *t*-tests for variables between native forest and pasture streams in the Taranaki Region, New Zealand. Statistically significant differences ($p < 0.05$) are marked in bold.

Land-use and stream	**Stream code**	**Elevation (m ASL)**	**Distance from sea (km)**	**Mean slope (%)**	**Catchment area (km^2)**	**Area fished (m^2)**	**Mean water width (m)**	**Mean depth (m)**	**Mean water column velocity ($m\ s^{-1}$)**	**pH**	**Specific conductivity ($\mu S\ cm^{-1}$)**	**Dissolved oxygen (%)**	**Total nitrogen ($g\ m^{-3}$)**	**Total phosphorus ($g\ m^{-3}$)**
Forest														
Kapoaiaia	KAP1	400	22.6	4.78	5.84	61	3.04	0.27	0.65	7.4	91.9	100.0	0.16	0.01
Little Dunns Creek	LDC1	475	29.2	4.56	2.48	63	3.14	0.22	0.54	7.9	102.8	99.2	0.13	0.02
Ngatoro	NGT1	458	46.3	3.74	4.45	118	5.88	0.26	0.58	8.6	64.3	100.5	0.11	0.05
Oaonui	OAI1	375	20.6	3.76	6.62	118	5.92	0.24	0.76	8.5	106.4	101.5	0.11	0.06
Ouri	OUR1	425	22.1	4.28	6.03	99	4.94	0.19	0.58	7.3	89.6	100.8	0.23	0.05
Punehu	PNH1	399	21.8	4.40	9.15	83	4.14	0.24	0.81	7.1	85.8	101.2	0.23	0.05
Pasture														
Kapoaiaia	KAP2	257	19.3	4.30	8.53	119	5.96	0.26	0.68	8.5	112.7	109.2	0.18	0.04
Little Dunns Creek	LDC2	362	26.1	3.08	3.49	58	2.90	0.26	0.60	9.0	122.7	104.2	0.84	0.03
Ngatoro	NGT2	370	44.2	3.24	5.02	91	4.54	0.29	0.68	8.0	55.3	102.2	0.15	0.04
Oaonui	OAI2	294	18.9	2.74	6.64	105	5.24	0.21	0.72	10.3	120.4	104.0	0.11	0.07
Ouri	OUR2	297	18.6	4.28	6.03	85	4.24	0.25	0.71	7.6	97.0	105.8	0.18	0.04
Punehu	PNH2	294	18.5	4.00	9.15	101	5.04	0.30	0.94	7.6	98.3	105.1	0.11	0.03
Mean in forest		422	27.1	4.25	5.76	90	4.51	0.24	0.65	7.8	90.1	100.5	0.16	0.040
Mean in pasture		306	24.3	3.61	6.48	93	4.65	0.26	0.72	8.5	101.1	105.1	0.26	0.040
Paired *t*-test; *p* value		**<0.001**	**0.002**	**0.034**	0.109	0.775	0.773	0.179	0.044	**0.078**	0.129	**0.008**	0.571	0.534

TABLE 2-2 Water and air temperature, in-stream and bank light intensities, stream shading estimates and mid-stream canopy openness for native forest and pasture streams in the Taranaki Region, New Zealand. Data for temperature and light show means for summer (December 2019, January, and February 2020) and annual (November 2019 to November 2020) and includes means and paired *t*-test. Statistically significant ($p < 0.05$) outcomes are marked in bold.

Land use and stream	**Mean annual water temperature (°C)**	**Mean summer water temperature (°C)**	**Mean annual air temperature (°C)**	**Mean summer air temperature (°C)**	**Mean annual in-stream light intensity (μmol m^{-2} s^{-1})**	**Mean summer in-stream light intensity (μmol m^{-2} s^{-1})**	**Mean annual bank light intensity (μmol m^{-2} s^{-1})**	**Mean summer bank light intensity (μmol m^{-2} s^{-1})**	**Stream shading (%)**	**Mid-stream canopy openness (%)**
Forest										
Kapoaiaia	10.2	12.6	10.5	13.9	0.5	1.1	2.2	4.9	81	11.20
Little Dunns Creek	9.2	11.9	9.8	13.8	4.8	7.6	3.1	5.6	94	5.14
Ngatoro	9.5	13.9	10.4	15.0	10.4	26.3	6.4	19.3	75	19.77
Oaonui	10.2	14.9	10.9	15.2	45.0	104.0	14.1	35.4	78	22.26
Ouri	9.1	11.2	9.7	13.5	2.7	6.3	2.9	6.2	80	6.23
Punehu	9.2	13.0	10.4	13.0	25.4	45.6	6.0	9.1	58	44.74
Pasture										
Kapoaiaia	13.8	16.8	15.5	23.0	145.7	168.9	190.3	389.6	7	99.80
Little Dunns Creek	12.1	15.7	12.7	19.8	50.1	96.0	102.8	233.4	36	95.30
Ngatoro	10.6	14.2	14.7	22.7	87.3	336.4	270.8	460.1	15	99.30
Oaonui	11.2	16.9	14.9	22.3	27.9	56.9	190.0	307.7	8	98.90
Ouri	11.5	15.4	13.9	20.0	118.9	254.8	80.5	197.5	5	98.20
Punehu	11.2	16.9	14.5	20.2	49.8	189.5	132.6	226.6	9	99.80
Mean in forest	9.6	12.9	10.3	14.1	14.8	31.8	5.8	13.4	78	18.22
Mean in pasture	11.7	16.0	14.4	21.3	80.0	183.8	161.2	302.5	13.3	98.6
Paired *t*- test; *p* value	**0.003**	**0.006**	**<0.001**	**<0.001**	**0.046**	**0.027**	**<0.001**	**<0.001**	**0.001**	**0.002**

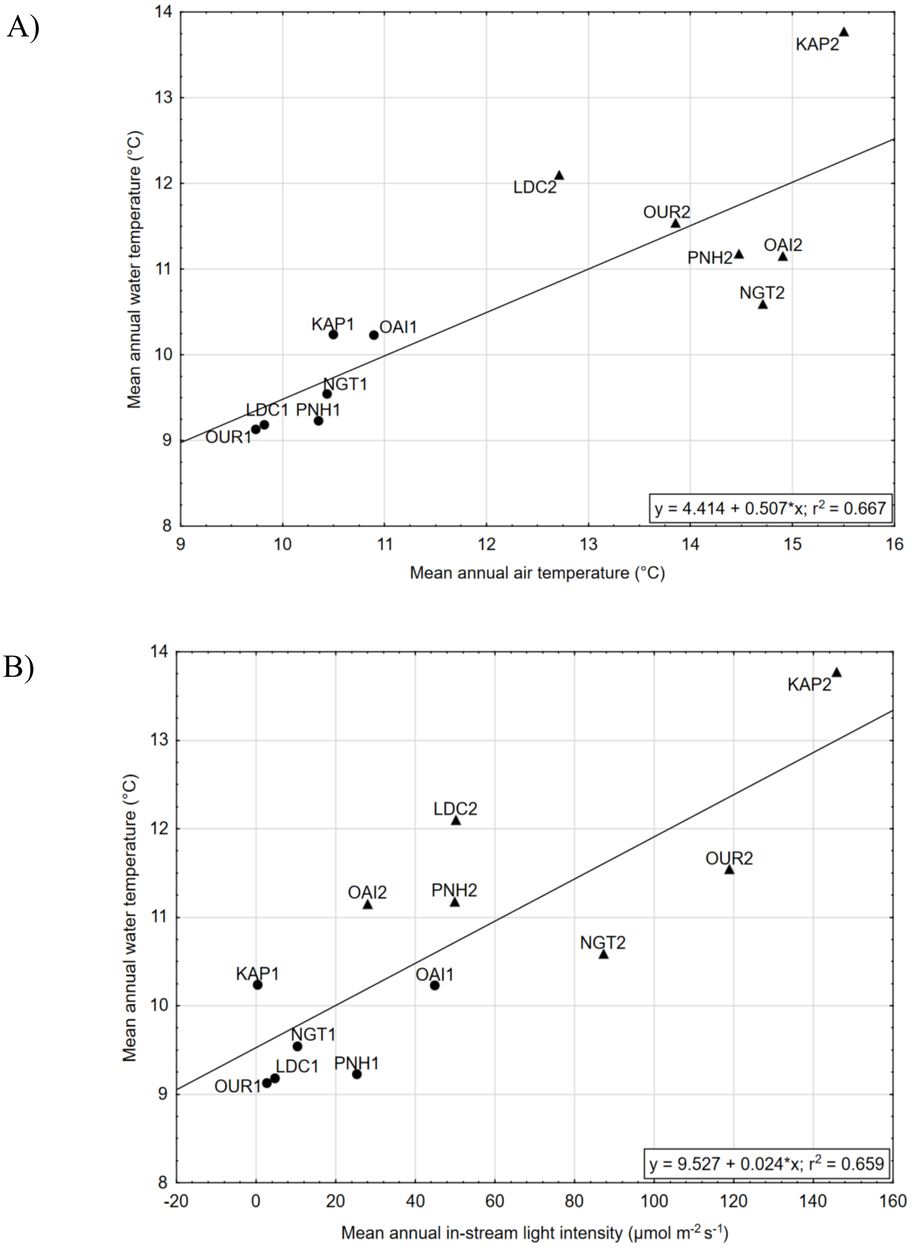


FIGURE 2-3 Variability of A) mean annual water temperature against mean annual air temperature and B) mean annual water temperature against mean annual in-stream light intensity. *n* = 12 for each plot. See Table 2-1 for site abbreviations. Forest (site code 1) are denoted by circles; Pasture (site code 2) are denoted by triangles.

2.4.2 | Aquatic biomass and densities and land use

2.4.2.1 | Autochthonous and aquatic invertebrate biomass

Periphyton biomass was greater in pasture ($\bar{x}$ = 11.52 g m^{-2}) than forest ($\bar{x}$ = 4.28 g m^{-2}; *p* = 0.007), but results were variable between sites (Table 2-3; Table 2-4). Both aquatic invertebrate biomass and densities were greater in pasture (*p* > 0.003) (Table 2-3; Table 2-4). Aquatic invertebrate species were largely consistent across land uses and dominantly included the mayflies (*Deleatidium, Coloburiscus, Nesameletus, Zephlebia*)*;* stoneflies (S*tenoperla, Zealandoperla and Zelandobius*)*;* Dobsonfly (*Archichauliodes*); Trichoptera (*Aoteapsyche, Orthopsyche, Hydrobiosis, Pycnocrentrodes, Beraeoptera*). Snail species including *Potamopyrgus antipodarum* and *Physa*, were more prominent in pasture sites.

2.4.2.2 | Allochthonous biomass

Rates of allochthonous sources differed between vegetation input and invertebrate input and showed inverse relationships with land use (Figure 2-3; Table 2-3; Table 2-4). Vegetation input was not statistically significant between forest and pastures sites (pasture $\bar{x}$ = 1.15 g m^{-2} day^{-1}, forest $\bar{x}$ = 2.67 g m^{-2} day^{-1}; *p* = 0.124). However, inputs of terrestrial invertebrates were higher in the pasture (pasture $\bar{x}$ =0.72 g m^{-2} day^{-1}, forest $\bar{x}$ =0.14 g m^{-2} day^{-1}; *p* = 0.020) (Table 2-3; Table 2-4). Terrestrial invertebrate species found included Diptera (flies), Culicidae (mosquitoes), Araneae (spiders), Formicidae (ants), Anthropila (bees), *Vespula* (wasps), Cicadoidea (cicadas), Diplopoda (millipedes), Caelifera (grasshopper) and Coleoptera (beetles). More terrestrial insects were caught in pasture (*n* = 387) than in forest (*n* = 58) with a total 445 individuals caught at all sites. Pasture sites contained significantly more bees, wasps, flies, and beetles. Notably *Stethaspis* sp. (Melolonthinae) beetles were dominant at pasture sites. Total biomass of allochthonous sources (combined terrestrial invertebrates and vegetation input) showed no difference between the forest and pasture sites (p = 0.373; Figure 2-4C).

TABLE 2-3 Autochthonous (periphyton and aquatic invertebrate biomass) and allochthonous (vegetation and terrestrial invertebrate input over 30 days) results at forest and pasture sites, in Taranaki New Zealand. All weights are dry mass.

Land use	**Site**	**Periphyton biomass ($g\ m^{-2}$)**	**Aquatic invertebrate biomass ($g\ m^{-2}$)**	**Total vegetation input ($g\ m^{-2}\ day^{-1}$)**	**Total terrestrial invertebrate input ($g\ m^{-2}\ day^{-1}$)**
Forest	KAP1	1.21	0.96	1.07	0.058
Forest	LDC1	5.78	0.57	0.92	0.054
Forest	NGT1	1.72	0.49	4.44	0.045
Forest	OAI1	9.60	0.40	5.31	0.024
Forest	OUR1	0.81	1.05	2.05	0.571
Forest	PNH1	6.53	0.60	2.27	0.093
Pasture	KAP2	8.48	3.04	1.10	1.303
Pasture	LDC2	22.16	5.10	3.78	0.930
Pasture	NGT2	3.65	1.73	1.15	0.586
Pasture	OAI2	23.64	1.68	0.57	0.865
Pasture	OUR2	1.75	1.88	0.16	0.312
Pasture	PNH2	9.44	1.60	0.10	0.335

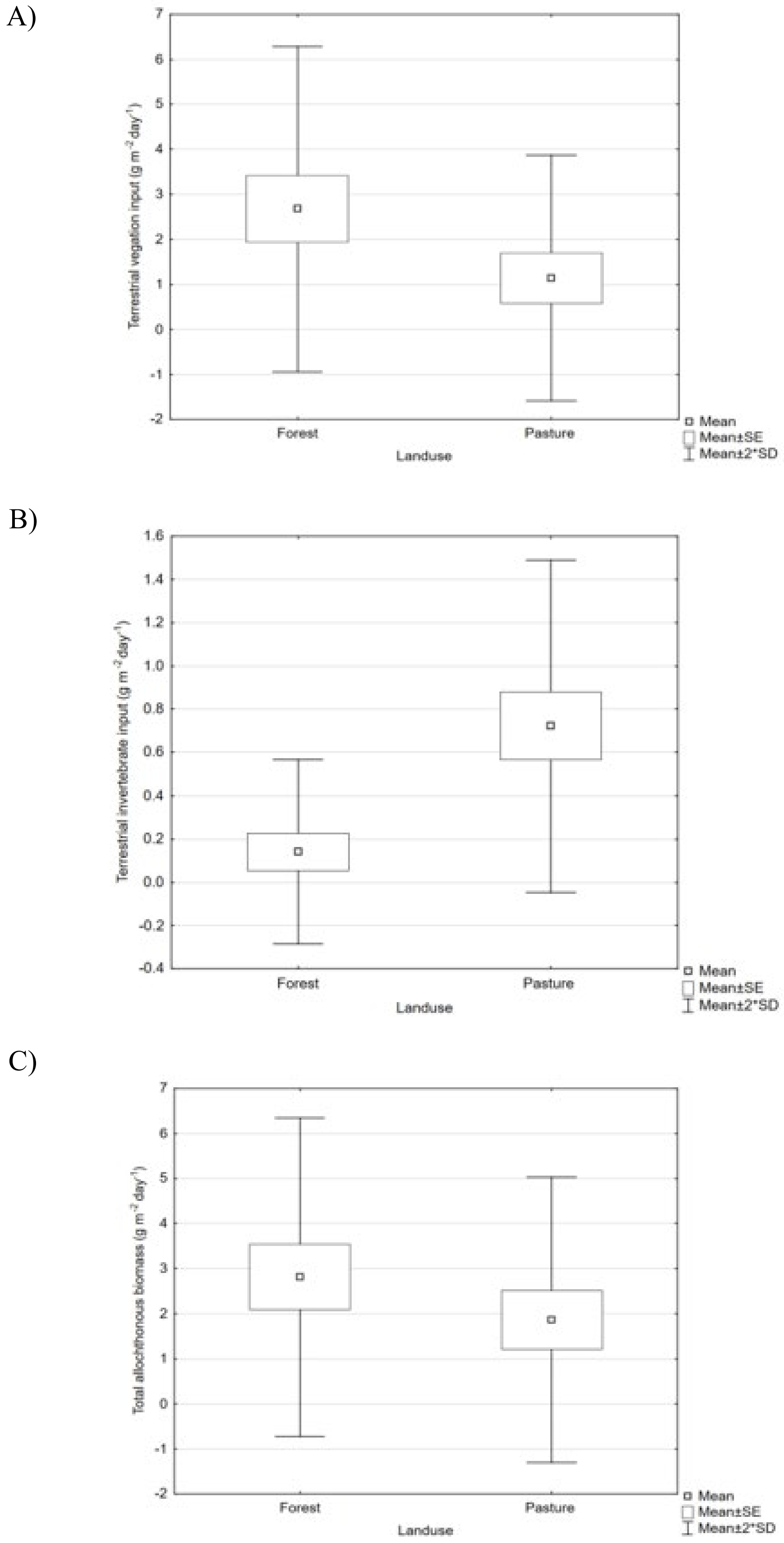


FIGURE 2-4 Mean terrestrial input over 30 days at forest and pasture sites showing A) vegetative inputs, B) invertebrate inputs, and C) total allochthonous inputs (invertebrates and vegetation).

2.4.2.3 | Organic matter processing

Decomposition rates of organic matter were higher in pasture (leaf mass loss $\bar{x} = 0.084$ *k* day^{-1} in pasture, $\bar{x} = 0.042$ *k* day^{-1} in forest; stick mass loss $\bar{x} = 0.005$ *k* day^{-1} in pasture, forest $\bar{x} = 0.003$ *k* day^{-1}; $p < 0.001$) (Table 2-4).

TABLE 2-4 Mean, standard error and paired *t*-test for measured variables in January 2020 and November 2019 to November 2020 at forest and pasture streams in the Taranaki Region, New Zealand. Statistically significant differences ($p < 0.05$) are marked in bold.

Variable	**Forest (Mean ± SE)**	**Pasture (Mean ± SE)**	**Paired *t*-test;**
Aquatic invertebrate density (individuals m^{-2})	253.3 ± 56.7	900.8 ± 51.4	**0.003**
Aquatic invertebrate biomass (g m^{-2})	0.67 ± 0.12	2.50 ± 0.56	**0.002**
Periphyton biomass (g m^{-2})	4.28 ± 1.46	11.52 ± 3.79	**0.007**
Mean leaf bag mass-loss rate (*k* day^{-1})	0.042 ± 0.006	0.084 ± 0.012	**<0.001**
Mean stick mass-loss rate (*k* day^{-1})	0.0026 ± 0.0001	0.0049 ± 0.0003	**0.001**
Terrestrial vegetation input (g m^{-2} day^{-1})	2.67 ± 0.74	1.14 ± 0.56	0.124
Terrestrial invertebrate input (g m^{-2} day^{-1})	0.14 ± 0.09	0.72 ± 0.16	**0.020**

2.4.2.4 | Fish and crayfish biomasses and densities

Pasture sites had more fish ($n = 371$) than forest ($n = 70$) (Table 2-5). A wide range of fish species were caught, including brown trout (*Salmo trutta*), redfin bully (*Gobiomorphus huttoni*), bluegill bully (*Gobiomorphus hubbsi*), kōaro (*Galaxias brevipinnis*), shortjaw kokopu (*Galaxias postvectis*), lamprey (*Geotria australis*), longfin eel (*Anguilla dieffenbachii*) and shortfin eel (*Anguilla australis*). Kōaro were only found at forest sites, while lamprey, bluegill bully and shortjaw kokopu were found at a single pasture site. Shortfin eels occurred at two of the six forest sites and five of the six pasture sites (Table 2-5).

TABLE 2-5 Removal population estimates of fish and crayfish abundance in 20-m stream reaches in native forest and open pasture streams in the Taranaki region, New Zealand. Forest and pasture means are shown in bold. Blanks indicate species not caught.

	Removal population estimate (number of individuals)									
Land-use and stream	**Longfin eel**	**Shortfin eel**	**Redfin bully**	**Kōaro**	**Brown trout**	**Shortjaw kokopu**	**Bluegill bully**	**Lamprey**	**Total fish**	**Total crayfish**
Forest										
Kapoaiaia	5	1	2		1				9	10
Little Dunns Creek	2								2	54
Ngatoro	4								4	17
Oaonui	1	1	23	6					31	3
Ouri	1			4	3				8	38
Punehu	5		6	3	2				16	6
Pasture										
Kapoaiaia	35	43	58					1	137	20
Little Dunns Creek	16	4							20	190
Ngatoro	12								12	56
Oaonui	38	10	89			3	2		142	4
Ouri	17	1			2				20	33
Punehu	25	10	5						40	5
Total in forest	**18**	**2**	**31**	**13**	**6**	**0**	**0**	**0**	**70**	**128**
Total in pasture	**143**	**68**	**152**	**0**	**2**	**3**	**2**	**1**	**371**	**308**

Mean densities of fish were greater in pasture streams than in forest (60.2 individuals 100 m^{-2} ± 21.1 SE in pasture, 12.5 individuals 100 m^{-2} ± 3.8 SE in forest; $p = 0.002$). Mean crayfish densities did not differ between land uses ($p = 0.184$; 75.6 individuals 100 m^{-2} ± 51.2 SE in pasture, 27.5 individuals 100 m^{-2} ± 12.7 SE in forest) (Table 2-6). However, population estimates of crayfish had wider confidence intervals (mean $n = 36$; 95% CI = 39.91) than fish species (i.e., longfin eels (mean $n = 13$; 95% CI = 5.47); kōaro (mean $n = 4$; 95% CI = 0.80) suggesting that crayfish populations estimates were less reliable.

TABLE 2-6 Density of fish and crayfish in forest and pasture streams in the Taranaki region, New Zealand. Forest and pasture mean ± standard deviation and significant *p* values ($p < 0.05$) are shown in bold.

	Density (number 100 m^{-2})									
Land-use and stream	**Longfin eel**	**Shortfin eel**	**Redfin bully**	**Kōaro**	**Brown trout**	**Shortjaw kokopu**	**Bluegill bully**	**Lamprey**	**Total fish density**	**Total crayfish**
Forest										
Kapoaiaia	8.22	1.64	3.29	0.00	1.60	0.00	0.00	0.00	14.76	16.45
Little Dunns Creek	3.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.18	85.99
Ngatoro	3.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.40	14.46
Oaonui	0.84	0.84	19.43	5.07	0.00	0.00	0.00	0.00	26.18	2.53
Ouri	1.01	0.00	0.00	4.05	3.00	0.00	0.00	0.00	8.06	38.46
Punehu	6.04	0.00	7.25	3.62	2.40	0.00	0.00	0.00	19.31	7.25
Pasture										
Kapoaiaia	29.36	36.07	48.66	0.00	0.00	0.00	0.00	0.84	114.93	16.78
Little Dunns Creek	27.59	6.90	0.00	0.00	0.00	0.00	0.00	0.00	34.48	327.59
Ngatoro	13.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	13.22	61.67
Oaonui	36.26	9.54	84.92	0.00	0.00	2.86	1.91	0.00	135.50	3.82
Ouri	20.05	1.18	0.00	0.00	2.40	0.00	0.00	0.00	23.63	38.92
Punehu	24.80	9.92	4.96	0.00	0.00	0.00	0.00	0.00	39.68	4.96
Mean in forest	3.78	0.41	4.99	2.12	3.56	0.00	0.00	0.00	**12.48 ± 3.8**	**27.52 ± 12.7**
Mean in pasture	25.21	10.60	23.09	0.00	0.40	0.48	0.32	0.14	**60.24 ± 21.1**	**75.62 ± 51.1**
Paired *t* test; *p* value									**0.002**	0.184

Fish biomass in pasture sites ($\bar{x}$ =35.1 g m^{-2} ± 5.7 SE) was five times greater than in forest sites ($\bar{x}$ = 6.6 g m^{-2} ± 2.0 SE; p = 0.002) (Figure 2-5; Table 2-7). Longfin eels were found at all sites and dominated the fish biomass ($\bar{x}$ = 32 g m^{-2} in pasture, $\bar{x}$ = 4.7 g m^{-2} in forest). Crayfish were abundant at all sites with biomasses ranged from 0.1–23.5 g m^{-2} and were not different between land uses (p = 0.274; Table 2-7).

TABLE 2-7 Areal biomass of fish and crayfish in forest and pasture streams in the Taranaki Region, New Zealand. Forest and pasture mean ± standard deviation and significant *p* values ($p < 0.05$) are shown in bold. Paired *t*-tests were conducted on log-transformed data.

	Areal biomass (g m^{-2})									
Land-use and stream	**Longfin eel**	**Shortfin eel**	**Redfin bully**	**Kōaro**	**Brown trout**	**Shortjaw kokopu**	**Bluegill bully**	**Lamprey**	**Total fish biomass**	**Total crayfish**
Forest										
Kapoaiaia	12.37	0.09	0.40	0.00	1.63	0.00	0.00	0.00	14.48	1.06
Little Dunns Creek	4.64	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.64	5.35
Ngatoro	2.65	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.65	0.48
Oaonui	0.65	0.02	1.20	1.35	0.00	0.00	0.00	0.00	3.23	0.08
Ouri	0.94	0.00	0.00	1.29	1.85	0.00	0.00	0.00	4.08	1.52
Punehu	6.67	0.00	0.64	1.38	1.76	0.00	0.00	0.00	10.45	0.34
Pasture										
Kapoaiaia	27.91	1.25	1.99	0.00	0.00	0.00	0.00	0.01	31.16	0.59
Little Dunns Creek	53.88	0.49	0.00	0.00	0.00	0.00	0.00	0.00	54.37	23.47
Ngatoro	16.49	0.00	0.00	0.00	0.00	0.00	0.00	0.00	16.49	2.82
Oaonui	39.20	0.38	3.95	0.00	0.00	4.77	0.06	0.00	48.35	0.15
Ouri	26.78	0.06	0.00	0.00	4.89	0.00	0.00	0.00	31.73	1.91
Punehu	27.87	0.41	0.24	0.00	0.00	0.00	0.00	0.00	28.52	0.20
Mean in forest	4.65	0.02	0.37	0.67	0.87	0.00	0.00	0.00	**6.59 ± 2.0**	**1.47 ± 0.8**
Mean in pasture	32.02	0.43	1.03	0.00	0.81	0.79	0.01	0.00	**35.10 ± 5.7**	**4.86 ± 3.8**
Paired *t* test; *p* value									**0.002**	0.274

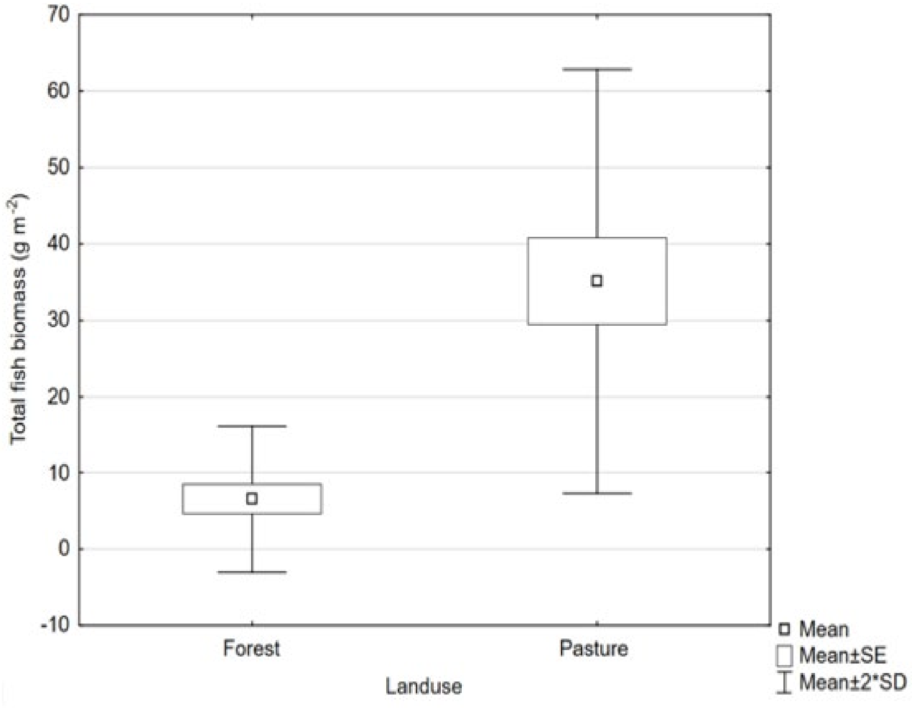


FIGURE 2-5 Mean of fish biomass in native forest and pasture streams in the Taranaki region, New Zealand. $n = 6$ for each land use.

2.4.3 | Relationships between variables land use

2.4.3.1 | Abundance and body mass relationships

The relationship between mean body size (*M*) at abundance (*N*) (*M-N* relationship) demonstrated similar negative slopes in both forest and pasture streams. Despite the greater body mass and abundance of aquatic invertebrates and fish in pasture streams, the *M-N* slopes were very similar for both land uses.

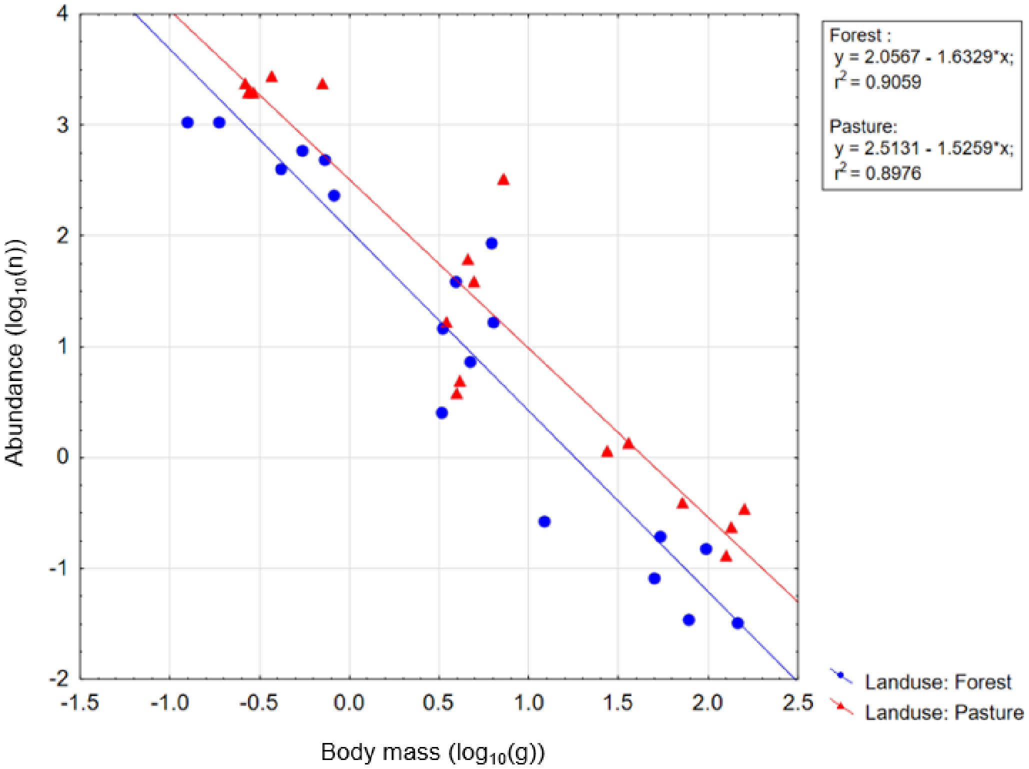


FIGURE 2-6 Relationships between body mass (*M*) and abundance (*N*) at forest and pasture sites in Taranaki streams. *M-N* relationships were derived following logarithmic ($\log_{10}$) transform of mean body mass and the total abundance for each functional group (stream invertebrates, crayfish and fish) at each site for pasture and forest streams. Abundance declines with increasing body mass typically observed in aquatic systems.

2.4.3.2 | Biotic and environmental relationships

The PCA plot of biotic and environmental variables indicated the 53% of variance was explained in PC1, while 21% of variance was explained in PC2

(Figure 2-7). Stream shade represented the most explanatory power at forested sites and was contrasted by mean annual temperature and mean annual light intensities. Fish biomass, aquatic invertebrate biomass and temperature pointed towards the same direction, suggesting both explained similar variation. Periphyton biomass indicated in a similar direction with annual in-stream light intensity and pH, while crayfish biomass had no distinct relationships with the physical variables (Figure 2-7).

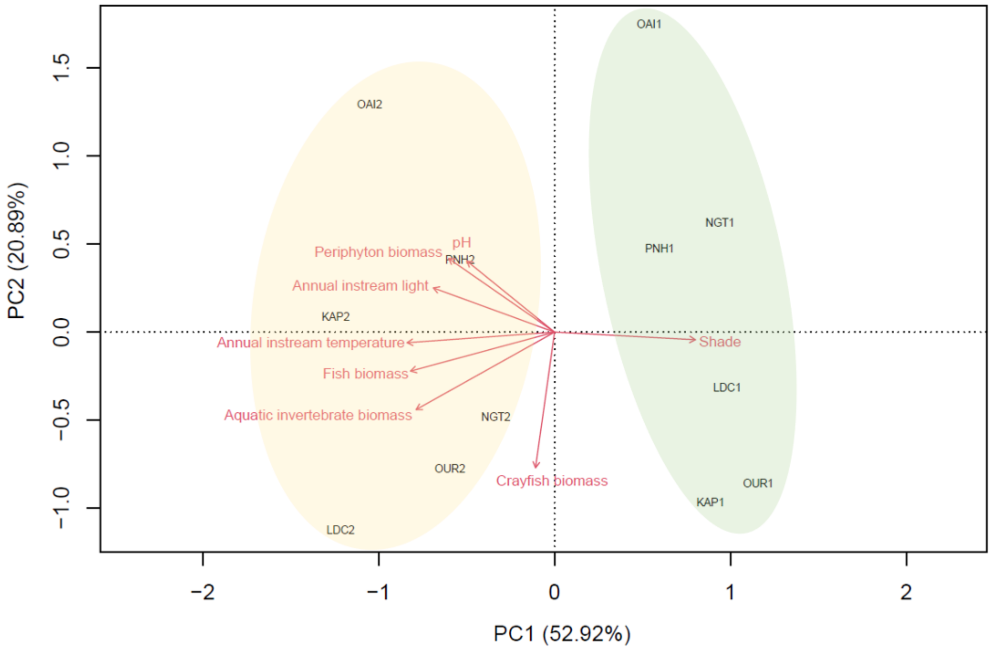


FIGURE 2-7 Principal component analysis ordination plot for biotic and environmental variables for forest and pasture streams. PC1 explains 53% of variance and PC2 explains 21% of variance. Each vector points in the direction of the steepest increase of values. Forested sites are grouped in green and pasture sites are grouped in yellow.

2.4.3.3 | Correlations between biotic and abiotic variables

Periphyton biomass showed positive correlations with fish density ($r = 0.762$), summer water temperature ($r = 0.753$), annual bank light intensity ($r = 0.580$), pH ($r = 0.616$) and specific conductivity ($r = 0.755$) (Table 2-8; Figure 2-

8). Aquatic invertebrate densities presented positive correlations with mean annual and summer water and air temperature (*r* > 0.760), annual and summer in-stream and bank light intensities (*r* > 0.704). A positive correlation was also evident with stick mass loss (*r* = 0.585) (Table 2-8). Aquatic invertebrate biomass showed positive correlations with annual water temperature (*r* = 0.797), annual and summer air temperature (*r* > 0.643), bank light intensities (*r* > 0.622), leaf and stick mass loss (*r* > 0.671) and dissolved oxygen (*r* = 0.762). Both aquatic invertebrate biomass and densities showed negative correlations with shade (*r* > -0.713) (Table 2-8). Overall, annual water temperature showed the strongest significant positive correlations with invertebrate densities and biomass (Figure 2-8).

TABLE 2-8 Spearman rank correlations between physical variables and aquatic invertebrate density, aquatic invertebrate biomass and periphyton biomass, measured in 2019 and 2020, in streams in the Taranaki Region, New Zealand. Variables that presented no significant correlations have been omitted from the table. Bold figures indicate significant correlations ($p < 0.05$).

Variables	**Periphyton biomass (g m^{-2})**	**Aquatic invertebrate density (number m^{-2})**	**Aquatic invertebrate biomass (g m^{-2})**
Mean annual water temperature (°C)	0.490	**0.911**	**0.797**
Mean summer water temperature (°C)	**0.753**	**0.782**	0.543
Mean annual air temperature (°C)	0.538	**0.844**	**0.658**
Mean summer air temperature (°C)	0.448	**0.760**	**0.643**
Mean annual in-stream light intensity (µmol m^{-2} s^{-1})	0.455	**0.862**	**0.685**
Mean summer in-stream light intensity (µmol m^{-2} s^{-1})	0.399	**0.704**	0.517
Mean annual bank light intensity (µmol m^{-2} s^{-1})	**0.580**	**0.771**	**0.622**
Mean summer bank light intensity (µmol m^{-2} s^{-1})	0.559	**0.813**	**0.678**
Stream shade (%)	-0.399	**-0.855**	**-0.713**
Mean leaf bag mass loss (*k* day^{-1})	-0.245	0.473	**0.671**
Mean stick mass loss (*k* day^{-1})	0.266	**0.585**	**0.790**
pH	**0.616**	0.360	0.210
Specific conductivity (µS cm^{-1})	**0.755**	0.497	0.357
Dissolved oxygen (%)	0.497	**0.921**	**0.762**

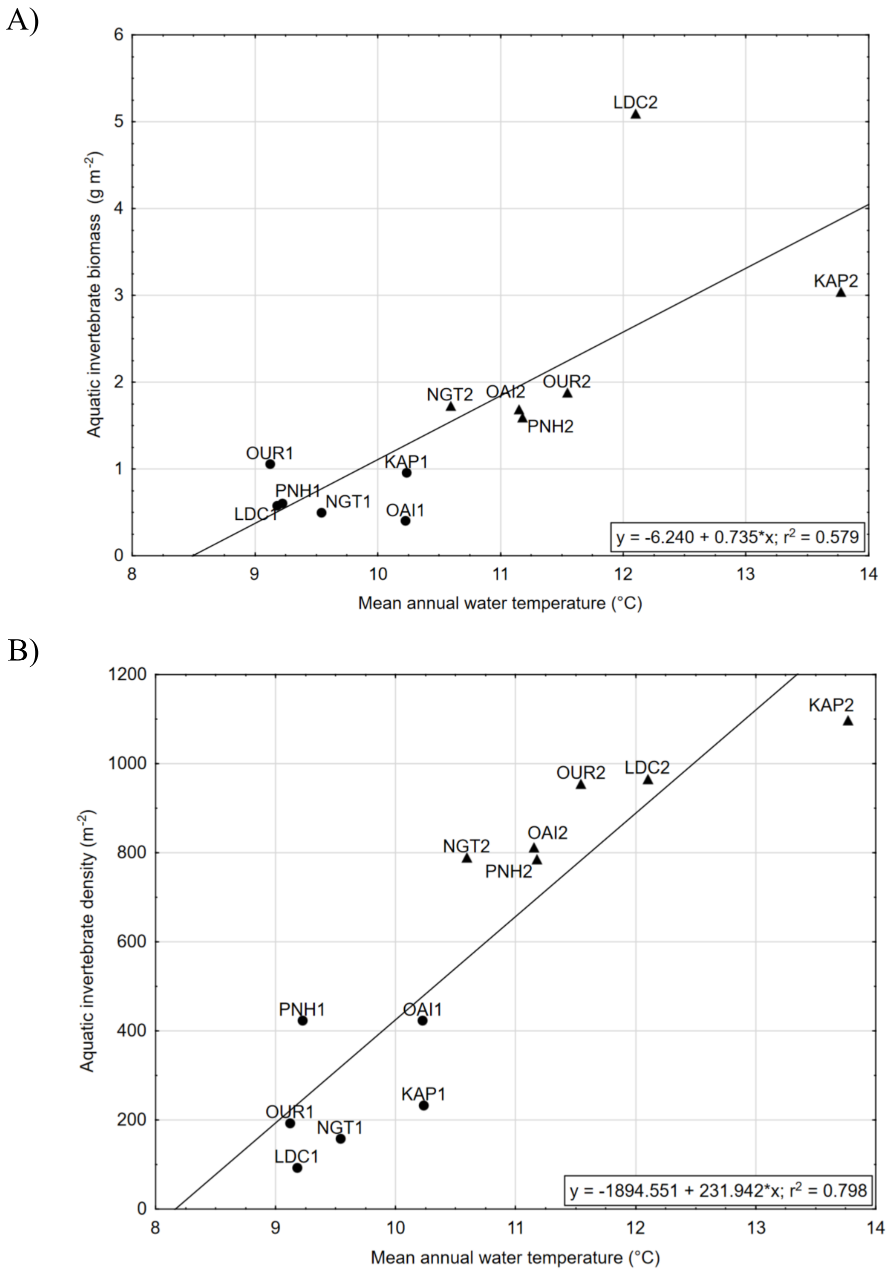


FIGURE 2-8 Variability and Spearman correlations of A) aquatic invertebrate biomass and mean annual water temperature, B) aquatic invertebrate density and annual water temperature. See Table 2-1 for site abreviations. Forest (site code 1) are denoted by circles; pasture (site code 2) are denoted by triangles.

Rates of stick decomposition showed correlations with temperature and light ($r > 0.634$). However, leaf decomposition showed no significant correlations with temperature or light, despite, showing significant negative correlations with shade (*r* = -0.654). Both measures of decomposition showed positive correlations dissolved oxygen (*r* > 0.601) (Appendix 2-3).

Fish biomass and densities showed similar correlations and were strongly correlated with summer and annual water temperature. Fish density correlated with 12 variables, showing positive correlations with summer and annual water and air temperatures (*r* > 0.636), annual in-stream light intensity (*r* = 0.580), summer and annual bank light intensity (*r* =0.622), aquatic invertebrate densities (*r* = 0.806), periphyton biomass (*r* =0.762), specific conductivity (*r* = 0.685), dissolved oxygen (*r* =0.797) and a negative correlation with shade (*r* = -0.706) (Table 2-9). Areal fish biomass correlated with 13 variables, showing positive correlations with summer and annual water and air temperatures (*r* > 0.678), annual in-stream light intensity (*r* =0.601), annual and summer bank light intensities (*r* > 0.594), aquatic invertebrate density and biomass (*r* > 0.851), terrestrial invertebrate input (*r* = 0.776), dissolved oxygen (*r* = 0.727) and negatively with stream shade (*r* = -0.713) (Figure 2-9; Table 2-8). Crayfish biomass showed no correlations with variables albeit total nitrogen (*r* = 0.586). However, this was largely driven by a single outlier at LDC2 (Table 2-9).

TABLE 2-9 Spearman rank correlation of fish biomass, fish densities and crayfish biomass against all variables assessed. Variables that presented no significant correlations have been omitted from the table. Statistically significant differences ($p < 0.05$) are marked in bold. Additional correlations are available in Appendix 2-1 and 2-3.

Variables	**Density of fish (number 100 m^{-2})**	**Areal fish biomass (g m^{-2})**	**Crayfish biomass (g m^{-2})**
Mean annual water temperature (°C)	**0.762**	**0.825**	0.063
Mean summer water temperature (°C)	**0.890**	**0.697**	-0.354
Mean annual air temperature (°C)	**0.785**	**0.678**	-0.193
Mean summer air temperature (°C)	**0.636**	**0.715**	-0.070
Mean annual in-stream light intensity (µmol m^{-2} s^{-1})	**0.580**	**0.601**	0.077
Mean annual bank light intensity (µmol m^{-2} s^{-1})	**0.622**	**0.594**	-0.084
Mean summer bank light intensity (µmol m^{-2} s^{-1})	**0.629**	**0.615**	-0.042
Stream shade (%)	**-0.706**	**-0.713**	0.140
Mean stick mass-loss (k day^{-1})	0.396	**0.727**	0.371
Aquatic invertebrate density (individuals m^{-2})	**0.806**	**0.851**	0.046
Aquatic invertebrate biomass (g m^{-2})	0.531	**0.888**	0.441
Periphyton biomass (g m^{-2})	**0.762**	0.510	-0.343
Terrestrial invertebrate input (g m^{-2} day^{-1})	0.566	**0.776**	0.266
Specific conductivity (µS cm^{-1})	**0.685**	0.559	-0.070
Dissolved oxygen (%)	**0.797**	**0.727**	-0.098
Total nitrogen (g m^{-3})	-0.054	0.296	**0.586**

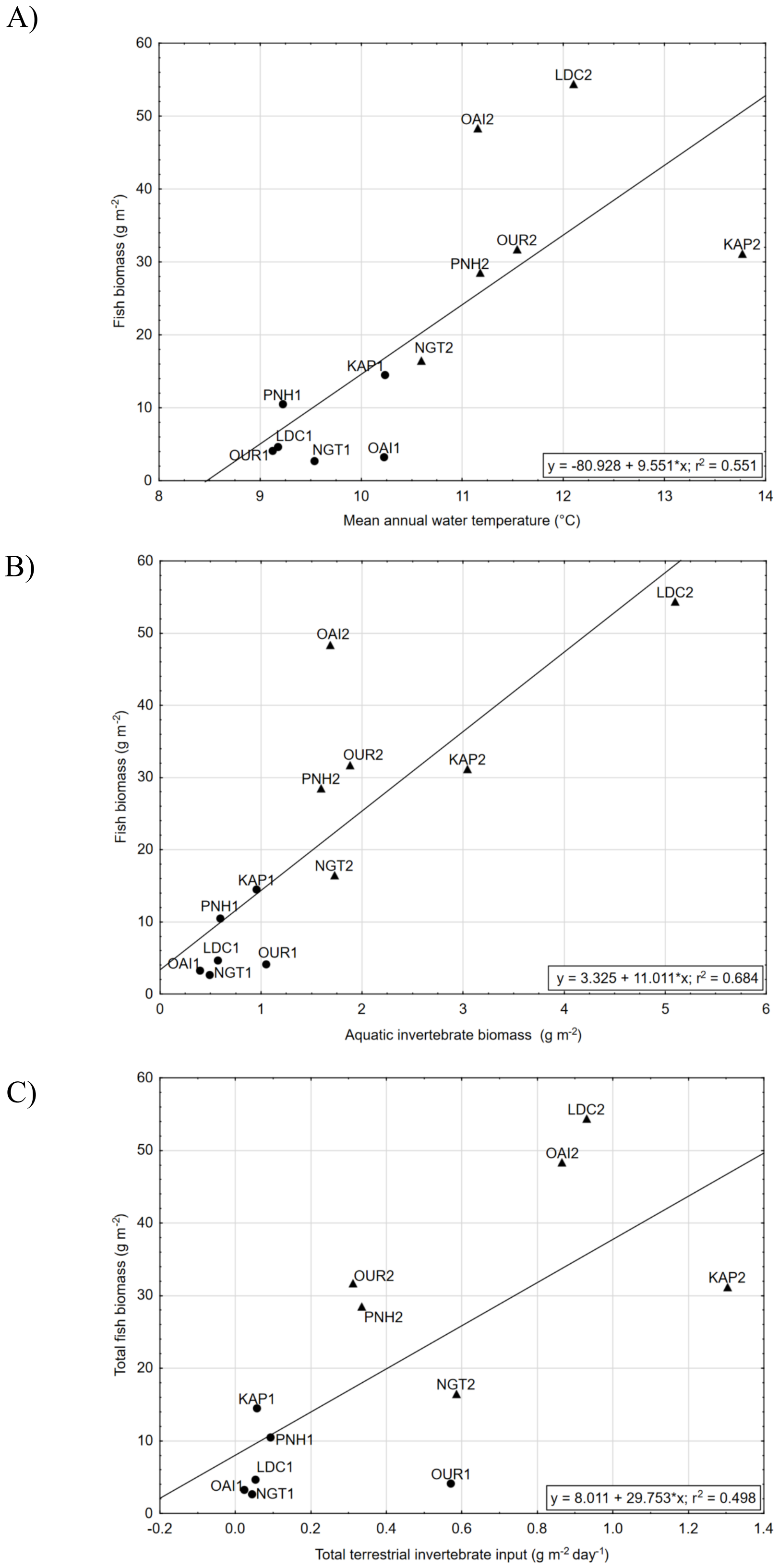


FIGURE 2-9 Fish biomass against A) mean annual temperature, B) aquatic invertebrate biomass and C) terrestrial invertebrate input in the Taranaki Region, North Island, New Zealand. See Table 2-1 for site abbreviations. Forest sites are denoted by circles; pasture sites are denoted by triangles.

2.4.3.4 Community biomass pSEM

Piecewise SEM was used to test the energy flow hypothesis within Taranaki Streams. Three models were compared using the three light measurements (stream shade, annual in-stream light intensity and annual bank light intensities). The AIC and BIC values were lowest for both annual in-stream light intensities and bank light intensities indicative of a better model fit (AIC < 48.0; BIC < 59.0) (Appendix 2-4). Annual in-stream light intensity was selected in the model as the measurement presented the lowest AIC and BIC values. Fishers *C* test indicated the piecewise SEM model structure was appropriate for the biomass data (Fishers *C* test p = 0.949). Model results showed a significant positive relationship with annual bank light intensity and water temperature ($p < 0.001$). Periphyton showed a non-significant positive effect on aquatic invertebrate biomass and a non-significant negative effect on crayfish biomass. There were positive effects between aquatic invertebrate biomass and crayfish biomass, which were marginally significant (p = 0.060). While aquatic invertebrate biomass showed significant positive effects on fish biomass (p = 0.004). Marginal R^2 was high fish biomass ($mR^2 > 0.70$) and low for crayfish biomass, periphyton biomass and aquatic invertebrate ($mR^2 < 0.24$). Conditional R^2 was identical for both fish biomass and aquatic invertebrate biomass and 0.24 higher for annual water temperature. This suggests the fixed effects within the model explained the variance for fish, aquatic invertebrate biomass and annual water temperature and spatial influences captured by the random effect of stream did not significantly add to the explanatory power. However, the conditional R^2 was greater than marginal R^2 for all other variables, suggesting that including stream as a random effect improved the explanatory power for periphyton and crayfish biomass (Figure 2-10; Table 2-10).

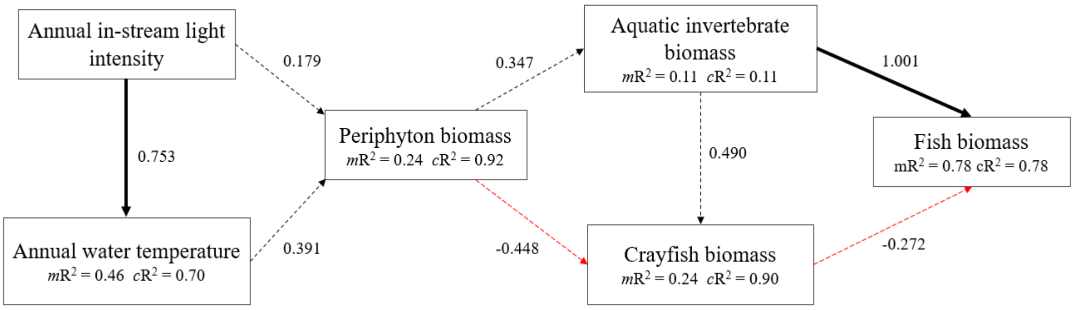


FIGURE 2-10 Piecewise Structural Equation Modelling results of aquatic biomass inter-relationships in Taranaki streams. Solid arrows indicate a significant effect and dashed arrows indicate a non-significant effect. Marginal R^2 (mR^2) and conditional R^2 (cR^2) are reported for endogenous variables and standardised parameter estimates are reported for significant model pathways.

Correlated error terms were specified in the model and showed a significant positive corelated error with bank light intensity and aquatic invertebrate biomass. This suggests that this relationship is assumed to be positively shared by an underlying driver. While not significant, temperature presented a negative correlated error with fish biomass (Table 2-10).

TABLE 2-10 Standardised component model results from piecewise SEM for fish biomass, summer water temperature, crayfish biomass, periphyton biomass and aquatic invertebrate biomass as endogenous variables from 12 sampling reaches in Taranaki streams. Significant results are in bold ($p < 0.05$). Fishers *C* test = 0.715 $p = 0.949$ suggests model is a good fit. AIC = 46.72; BIC =57.86 provided the best model when compared with other light estimates (stream shade and in-stream light intensity). Correlated error terms are indicative of relationships not presumed to be causal or unidirectional. Significant relationships are marked in bold. Marginal R^2 (mR^2) provides the variance explained by fixed effects and conditional R^2 (cR^2) explains the variance explained by both fixed effects and the random effect of 'stream'.

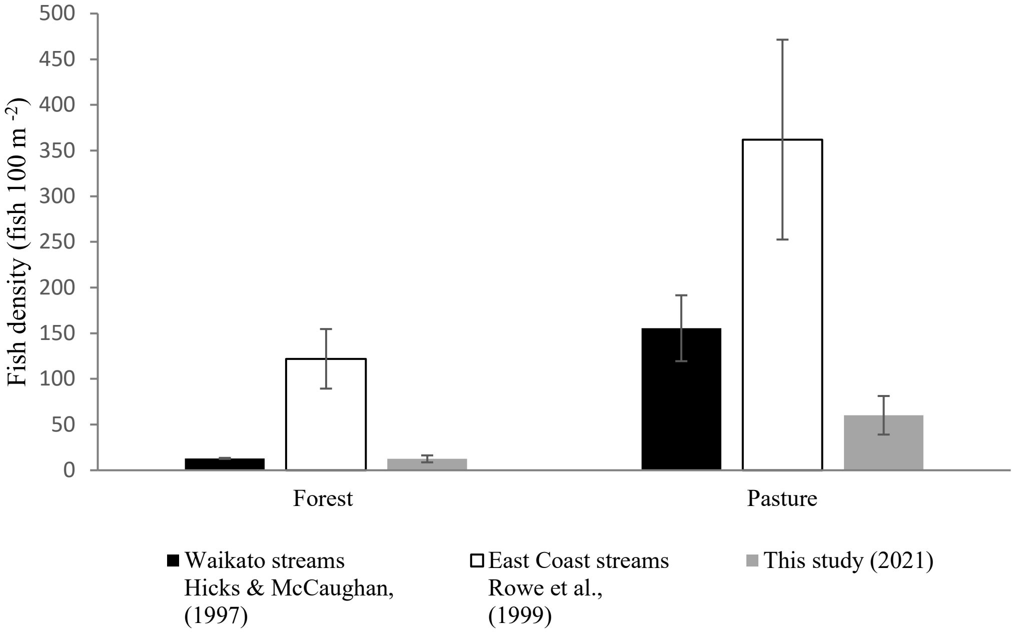
Component model	$m\mathrm{R}^2$	$c\mathrm{R}^2$	Predictor	Parameter estimate	Standard error	p-value
Fish biomass (g m^{-2})	0.78	0.78	Crayfish biomass (g m^{-2})	-0.272	0.164	0.172
Fish biomass (g m^{-2})			Aquatic invertebrate biomass (g m^{-2})	1.001	0.164	**0.004**
Annual water temperature (°C)	0.66	0.89	Annual in-stream light intensity (μmol m^{-2} s^{-1})	0.753	0.190	**0.011**
Crayfish biomass (g m^{-2})	0.24	0.90	Aquatic invertebrate biomass (g m^{-2})	0.490	0.188	0.060
Crayfish biomass (g m^{-2})			Periphyton biomass (g m^{-2})	-0.448	0.299	0.209
Periphyton biomass (g m^{-2})	0.24	0.92	Annual water temperature (°C)	0.391	0.202	0.126
Periphyton biomass (g m^{-2})			Annual in-stream light intensity (μmol m^{-2} s^{-1})	0.179	0.190	0.399
Aquatic invertebrate biomass (g m^{-2})	0.11	0.11	Periphyton biomass (g m^{-2})	0.347	0.297	0.295
Correlated error terms						
Aquatic invertebrate biomass (g m^{-2})			Annual in-stream light intensity (μmol m^{-2} s^{-1})	0.284		0.199
Aquatic invertebrate biomass (g m^{-2})			Annual water temperature (°C)	0.714		**0.007**
Fish biomass (g m^{-2})			Annual water temperature (°C)	0.025		0.471
Fish biomass (g m^{-2})			Periphyton biomass (g m^{-2})	0.036		0.458
Crayfish biomass (g m^{-2})			Annual water temperature (°C)	-0.367		0.134

2.5 | DISCUSSION

2.5.1 | Fish biomass and land use

Carbon sources in stream ecosystems can be viewed as a combination of allochthonous and autochthonous inputs. The balance between the two is constrained by overhanging riparian vegetation and light availability. This leads to the assumption that allochthonous inputs should dominate shaded forest sites, while autochthonous inputs should dominate open sites via in-stream primary production. Therefore, if allochthonous sources are diminished and not compensated by in-stream food supply, fish biomass response would reduce in open sites, due to increased metabolic demand and limitations in food availability (Huxel et al., 2002). However, fish biomass and densities were five times greater in pasture (60.2 individuals 100 m^{-2} and biomass $\bar{x} = 35.1$ g m^{-2}) than in forest (12.5 individuals 100 m^{-2} and biomass $\bar{x} = 6.6$ g m^{-2}), consistent with other land-use based studies (Hopkins, 1971; Rowe et al., 1999; Hicks & McCaughan, 1997; Miserendino et al., 2011; Myers et al., 2018). Results coincide with other New Zealand studies that demonstrate pasture streams have considerably increased fish biomass than forest streams (Figure 2-11) (Hopkins, 1971; Hicks & McCaughan, 1997, Rowe et al., 1999). A key assumption of this study is that there are no barriers between forest and pasture sites. Site pairs showed similar species upstream to downstream and no barriers between forest and pasture sites, therefore fish biomass differences were caused by energy availability rather than barriers to migration.

A) Density



B) Biomass

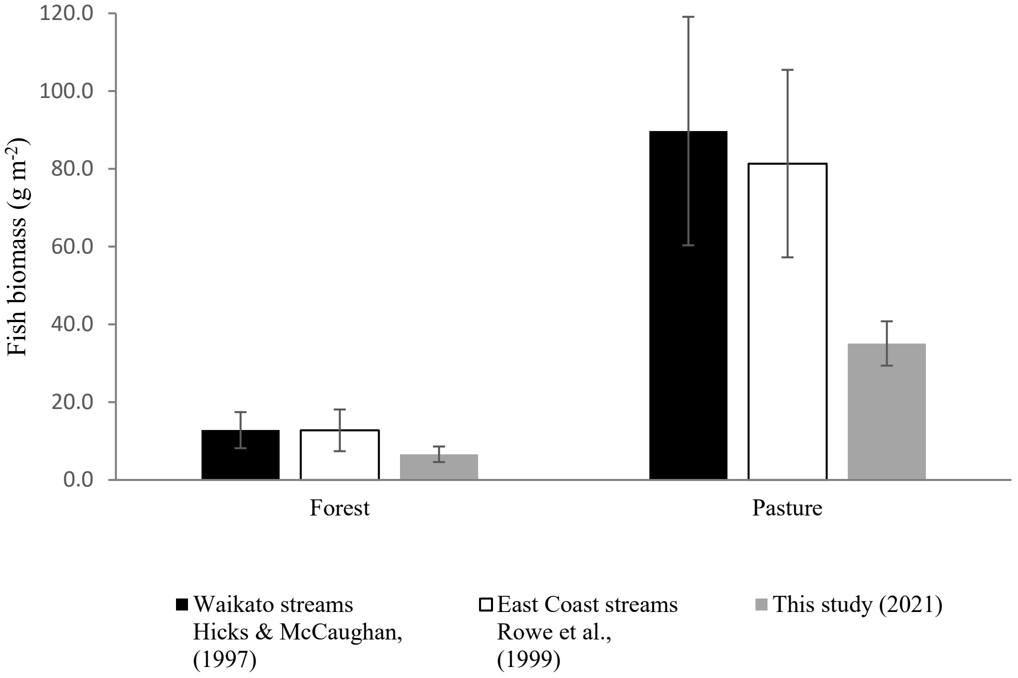


FIGURE 2-11 Fish A) densities and B) biomasses in forest and pasture streams in Waikato, Taranaki and East Coast streams in North Island, New Zealand.

2.5.2 | Light and temperature

Ecological theory examines the importance of energy in stream systems in supporting secondary biomass and emphasises the significance of light and temperature in energetic regulation (e.g., Metabolic Theory; Enquist et al., 2003). Light and water temperature in Taranaki streams were positively correlated ($r > 0.727$; $p < 0.05$). Further, annual in-stream light intensity presented significant positive effects on water temperature in the pSEM (Parameter Estimate = 0.753; $p < 0.05$) These results strengthen known relationships between light and temperature (e.g., Groom et al., 2011, Kaylor & Warren, 2017; Roon et al., 2021). In essence, in-stream light intensities are driving warmer water temperatures at pasture sites. These relationships are consistent with Roon et al. (2021), where increased light intensity shifted thermal regimes by increasing maximum temperatures and thermal variability due to reduced riparian vegetation. The proximity between forest and pasture sites (1.5 km to 3.5 km) indicate how temperature can fluctuate on average 3.1°C in summer and 2.2°C annually, over a relatively small spatial extent. These data support the concept that localised increases in light and temperatures can alter the structure and functioning of freshwater communities (Woodward et al., 2010; Scrine et al., 2017, Bengtsson et al., 2018).

2.5.3 | Autochthonous biomass

Pasture streams have more available light and are often associated with greater gross primary production and periphyton biomass than forest streams (Gregory, 1980; Kiffney et al., 2004; Wootton, 2012; Kaylor & Warren, 2017). Ecological theory suggests the relationship with consumer biomass and densities may be associated with increased autochthonous resources, which are often correlated with less canopy cover (Vannote et al., 1980; Kiffney & Roni, 2007). Increases in autochthonous production can indirectly support greater densities of higher trophic level through energetic transfer (Hannesdóttir et al., 2013). For example, Wilzbach et al. (2005) speculated that the higher densities of yearling cutthroat and rainbow trout found in open stream reaches was due to increased prey availability, driven by higher primary productivity. This concept of higher primary production in open streams has been largely supported by literature (Gregory, 1980; Bilby & Bisson, 1992; Wootton, 2012; Kaylor & Warren, 2017). In Taranaki, periphyton biomass was greater in pasture and significantly different between land uses ($p < 0.01$). However, periphyton biomass showed no correlations with light, despite well established relationships (Hill & Knight, 1988; Hill et al., 1995). The pSEM suggested light availability had a positive effect on periphyton biomass, albeit not significant. Results may be attributed to the episodic nature of Taranaki streams. The level of disturbance and velocities often experienced by these streams may be underlying in our periphyton results (Biggs et al., 1999; Canning et al., 2018). With marginal significant differences between stream velocities at forest and pasture sites, it is also plausible that sampling strength was not enough to capture the variability of periphyton in these streams (Baulch et al., 2009). Periphyton provides a high-quality, easily assimilated source of nutrition and is considered a major dietary constituent in supporting non-predatory aquatic invertebrates and crayfish (Guo et al., 2016a; Guo et al., 2016b; Guo et al., 2017; Brett et al., 2017). Aquatic invertebrates can exhibit profound grazing pressure on periphyton. This can cause a reduction in biomass but consequently lead to higher turnover rates (Lamberti & Resh, 1983). Although periphyton has a small biomass, it remains the trophic foundation in most stream systems because of its high production

(Vadeboncoeur & Power, 2017). Grazing pressures exerted on periphyton by consumers may be primarily responsible for the variability in the results, particularly as aquatic invertebrate biomass was significantly greater in pasture. The pSEM did show periphyton biomass had a non-significant positive effect on aquatic invertebrate biomass, and a non-significant negative effect on crayfish biomass. However, resource quality may substantially change between land uses due to light and nutrient availability, irrespective of basal biomass (Cashman et al., 2013). Results could be due to insufficient basal sampling, grazing pressures exerted by aquatic invertebrate communities, or that resource quality is markedly different between sites (Guo et al., 2016a, Guo et al., 2016b).

2.5.4 | Invertebrate consumer biomass

Pasture streams in Taranaki supported more aquatic invertebrate densities and biomasses when compared to forest ($p < 0.05$). These data were positively correlated with light and temperature, while presenting a negative correlation with shade. Results are consistent with Scarsbrook and Halliday (1999) and Scrine et al. (2017), where warmer streams supported higher aquatic invertebrate densities and biomasses. Abiotic factors may be primarily responsible for the aquatic invertebrate and biomasses. For example, less canopy cover has been associated with increased invertebrate densities (Quinn et al., 1997). Bank light intensities showed a significant correlation with both aquatic invertebrates and fish densities and biomasses ($r > 0.594$; $p < 0.05$). However, studies have suggested this may be attributed to habitat availability. For example, Miserendino et al. (2011) suggested that pasture sites support richer communities and biomasses of aquatic invertebrates and fish by the provision of stream edge habitat. As in-stream habitat conditions were parallel at forest and pasture sites, it is more likely that temperature and light are primary drivers of biomass accrual, given the strong correlations.

A correlated error was specified in the pSEM between aquatic invertebrate biomass and annual water temperature. This was indicative of a significant positive relationship ($p = 0.007$), which suggested the same underlying driver was positively shared between the two variables. Water temperature alone is unlikely to have a direct causal effect on aquatic invertebrate biomass and the underlying shared variable is likely light availability. A realistic scenario is periphyton quality increases with light, resulting in greater quality of fine particulate organic matter (FPOM) leading to increased standing consumer biomass. However, these attributes were unquantified in the model, therefore the correlated error term could suggest energy transference is not well characterised. It is likely that these abiotic factors, in addition to adequate habitat and food quality, are important controlling factors.

Water quality can be an important abiotic factor in driving secondary biomass and assemblage (Paredes del Puerto et al., 2021). However, results suggest that water quality showed limited correlations with fish. Correlations with fish biomass and their densities were only present with dissolved oxygen ($r = 0.727$; $r = 0.797$, respectively). These results are consistent with Casatti et al. (2006) and Kwak & Waters, (1997) where limited correlations were found with water quality and fish densities and biomasses. Kwak & Waters, (1997) suggested that factors other than water quality limit fish density and biomass. In this study, fish biomass and density were strongly influenced by the relationship between light intensity and temperature. Subsequent measurements of light availability via percentage shade strengthens these results. Whereby, as the level of shading is increased, there is a corresponding negative relationship with fish biomass and densities ($r > -0.706$; $p < 0.05$). Results align with overseas research where shading caused by riparian cover resulted in lower densities and biomasses of fish when compared to open sites (Kiffney & Roni, 2007; Riley et al., 2009). Kaylor et al. (2017) found that 84% of fish biomass was explained by canopy openness. The consistency with these abiotic factors (light, shade, temperature) and fish biomass collectively suggest that fish biomass is strongly driven by the levels of light and temperature. This is likely a product of the influence on lower trophic levels. The importance of light and temperature as a key factors fuelling secondary biomass is remarked in this study.

Surprisingly, crayfish showed no significant differences in densities or biomasses between land use ($p > 0.05$). This was consistent with biomass and density results in the Waikato, where crayfish maintained similar biomasses in native forest and pasture (Parkyn et al., 2002). Our results did not indicate any correlations with crayfish and variables assessed, albeit total nitrogen, which was largely driven by an outlier at LDC2. The lack of relationships may have been a product of the crayfish population estimates, where electrofishing may be under-representative of crayfish populations. This was owing to instances of insufficient crayfish reductions between each sample-pass. Crayfish can be an important food source for fish and are considered to control energy flow by serving as conduits of energy to higher trophic levels (Nyström, 2002; Davic, 2003). Therefore, the availability of crayfish was expected to have a strong control on fish biomass. The lack of correlation and the marginal negative effect between crayfish biomass and fish biomass was not expected. Predation can be an important regulatory factor in community structure (Ruetz et al., 2002). Research on the crayfish-eel interactions suggest eels have a reciprocal control on crayfish through predation (Aquiloni et al., 2010, Reynolds, 2011). Results could suggest feeding pressures exerted by high densities of eels may have controlled crayfish biomass at pasture sites. Top-down control cascades have been observed in New Zealand streams (McIntosh & Townsend, 1996). Fish in Taranaki streams may be exerting strong top-down controls on crayfish biomass resulting in the observed variability (Ruetz et al., 2002). However, fish gape limitations could also be a controlling factor. For example, studies have shown that predatory fish were only able to feed upon juvenile crayfish due to gape-limitation (Dorn et al., 1999; Musseau et al., 2015). Therefore, larger fish in pasture streams have greater gape ability and may be feeding on larger crayfish resulting in the observed negative interaction.

2.5.5 | Allochthonous inputs

The assumption is that forest canopy cover represents higher rates of allochthonous inputs of terrestrial subsidies, and these rates compensate for the observed loss of basal production (e.g., Vannote et al., 1980; Canning et al., 2018; Felden et al., 2021; Roussel et al., 2020, Niles & Hartman, 2021). The results of this study suggest that whilst forested areas provide an important diverse source of allochthonous vegetative material, the quantity of vegetative input in summer is comparable to that of pasture streams ($p = 0.124$). However, the input of vegetation at the pasture is perhaps seasonal and as this study was undertaken during the summer, the input of grass seed is likely to be seasonally higher. Therefore, caution should be taken with observed vegetation input. Acknowledging that the nutritional quality of vegetative allochthonous sources may be less in pasture (Lu et al., 2014). Theoretical explorations of low nutritional quality food sources suggest that low to moderate allochthonous inputs relative to autochthonous inputs can stabilise autochthonous based communities (Huxel et al., 2002). This was evident in Canning et al. (2018) where no differences were evident in trophic network structure, stability, or temporal variability of aquatic invertebrates in Mount Taranaki, irrespective of the energy source.

It is further important to consider the level of terrestrial-derived invertebrate sources were not constrained when compared to forested streams. This is consistent with Albertson et al. (2018) where greater abundances of terrestrial invertebrates were found in meadow habitat. Recent research suggests that terrestrial invertebrates serve as critical energetic pathway for sustaining fish populations (Niles & Hartman, 2021). Since terrestrial invertebrates are an important food source consumed by New Zealand fish species, these terrestrially derived food sources may play a significant role in the observed fish biomass (Edwards & Huryn, 1996; Niles & Hartman, 2021). The loss of allochthonous energy inputs in pasture streams may not be necessarily compensated by elevated autochthonous energy, but rather enhanced by allochthonous invertebrate food sources for fish.

As allochthonous inputs provide an alternative energy supply to temporally variable autochthonous production, these sources can maintain greater aquatic invertebrate and fish population carrying capacities (Huxel et al., 2002). The additional input of terrestrial invertebrates and elevated temperatures in pasture streams were predicted to show a less negative slope (Perkins et al., 2018; Perkins, 2022). However, *M-N* slopes were not consistent with those predicted by Perkins et al. (2018). Although forested streams showed consistently lower biomasses of aquatic invertebrates and fish, there were no differences between *M-N* slopes. This could suggest that community structure is functionally similar in forest and pasture streams, but the effects of increased light and temperature in pasture streams caused an increase in body size for the equivalent abundances across the entire community. Yet, the data did not contain *M-N* relationships for primary producers, which could have implications on slope structure (Perkins, 2022).

2.5.6 | Food production and metabolic rates

Food production and synchronies between consumer metabolic rates and temperature are often a secondary goal to improving habitat. However, both should be considered as important for predicting successful outcomes for fish (Naiman et al., 2012, Albertson et al., 2017). For example, Huryn et al. (2019) illustrated the importance of light and temperature on Alaskan food webs demonstrating the fundamental role of light-temperature synchrony in matching the energy supply and demand. Results suggest that water temperature plays a significant role in predicting the in-stream food supply and the subsequent biomass of fish. The reduction of temperature due to shading can result in significant changes to the food web-structure and supply (Naiman et al., 2012). O'Gorman et al. (2017) showed the temperature dependence of basal resources and highlighted that resource production was converted to consumer more efficiently as stream temperatures increased. Moreover, if food supply increases with temperature to compensate rising metabolic demands of primary producers, there will be sufficient basal resources to sustain larger consumers at higher trophic positions (O'Gorman et al., 2017). Organic matter processing rates are expected to increase with warmer in-stream temperatures consistent with metabolic scope (Enquist et al., 2003; Imberger et al., 2008; Demars et al., 2011). Pasture sites exceeded rates of decomposition at the forest sites ($p < 0.05$). Enhanced detrital processing can enhance secondary production (Cross et al., 2006). This energetic concept is applicable to higher trophic levels where supply-demand synchronies may be evident in freshwater fish. For example, the biomass and growth rates of eels in forest streams have been shown to be substantially less than in pastoral streams in the same catchment (Chisnall & Hicks, 1993). Jellyman (1997) suggested that food availability alone is unlikely to limit the growth and biomass of eels and concluded cool temperatures inhibit growth and activity. As fish are ectotherms, they cannot regulate their temperature, meaning they rely directly on the surrounding environmental temperature for optimisation of growth, food consumption and metabolic demand. The preferential thermal range for native New Zealand species is approximately 16.1°C to 21.8°C for smelt, banded kokopu, kōaro, giant kokopu, inanga, torrent fish and bullies. Eels are more tolerant, at around 24.4°C for longfin eels and 26.9°C for shortfin eels (Richardson et al., 1994). The mean summer water temperatures in pasture were between 14.2°C — 16.9°C, with a maximum of 22.1°C. This suggests that pasture sites in Taranaki are closer to preferred temperature ranges for New Zealand native fish. With forest summer water temperatures ranging between 11.2°C — 14.9°C, the warmest period is below the preferred thermal range and is presumably too cold for optimum growth (Graynoth & Taylor, 2000). The required metabolic demand, in conjunction to limited food, could explain the decrease in fish biomass at these forest sites. With more available rich food sources for fish, these open pasture sites may inevitably support larger fish communities and biomasses. Therefore, energetic supply-demand synchronies are critical considerations to biotic function.

2.5.7 | Implications for restoration and management of freshwater fish

Biomass is an important metric and can provide insight into the ecosystem function and energic production within a stream system. For example, Dolbeth et al. (2012) emphasised how secondary production provides a more integrative tool for assessment of ecosystem function. However, it is often overlooked in restoration approaches, perhaps due to the time-consuming nature of sampling and associated cost. Typical restoration approaches assume that rehabilitation of physical habitat restores ecological function and processes (Roni et al., 2008; Wipfli & Baxter, 2010; Albertson et al., 2018). These have not supported an increase in subsequent fish abundance and biomass (Riley et al., 2009; Stewart et al., 2009; Whiteway et al., 2010). This emphasises the concept that restoring physical habitat may have minimal effect on stream communities, particularly if productivity at lower trophic levels is limited and below the metabolic demand of the fish (Kiffney & Roni, 2007). This key link between temperature, light and process variables and the subsequent relationship with fish biomass is evident within the results of this study. With these results reflective of other studies globally and within New Zealand, it is an important consideration that decreasing the light and in-stream temperature as a function of riparian restoration can have implications on the abundance and biomass of secondary sources that contribute to freshwater fish diet. The interactive effects observed in this study suggest that modification to temperature regimes may have important consequences on ecosystem function and community structure by alterations to energy flows and food web dynamics. Higher rates of decomposition of organic material are observed at the pasture sites ($p < 0.05$), which were strongly correlated with warmer temperatures. We gather from these results that the metabolic scope is often greater in open and warmer streams (Quinn et al., 1997; Young & Huryn, 1999). However, in this study metabolic demand of fish is likely sustained by the observed larger food supply (aquatic and terrestrial invertebrates) and temperatures that fall within growth optima for New Zealand fish in the pasture sites (Richardson et al., 1994; Graynoth & Taylor, 2000).

These results may have implications for stream restoration that involves planting dense tree cover in riparian margins driving closed canopies. The importance of light and temperature as the fundamental drivers behind fish biomass should be considered during restorative stream practices. However, it is important to acknowledge that exceedance of these environmental thresholds (light and temperature) can have negative consequences for fish biomass (Dorst et al., 2019). For example, if rising metabolic demands are not met by increased resource supply, temperature could have a negative effect on fish biomass. Understanding species present and thermal tolerances for metabolic function, in addition to food supply and temperature regimes is essential for successful restoration and management of freshwater fish.

2.5.8 | Study limitations and future research

Allen (1951) modelled the production budget for trout in the Horokiwi Stream, New Zealand. This early research suggested that the secondary production of aquatic invertebrates was insufficient to support the trout biomass, even though the invertebrate community did not reduce over time. This phenomenon has been termed Allen's paradox (Allen, 1951), which has been as a confounding issue in aquatic ecology. Further research into Allen's Paradox by Huryn (1996) included the terrestrial invertebrate input and discovered that these sources are approximately equal to the respiration requirements of trout. For example, the production to biomass (P:B) ratio was 6.88 for aquatic invertebrates, while trout P:D ratio was 1.0, suggesting that prey are much more productive than trout. When all the total available prey for consumption were considered, prey production to trout demand were numerically equal. Huryn (1996) concluded that there was enough surplus production to support the ongoing abundance of aquatic invertebrates. In order to explicitly address the energy production dynamics and address the concepts of Allen's Paradox in Taranaki forest and pasture streams, modelling of energy fluxes is required. Bioenergetic modelling would have benefited this research by inferring the relationship between energy requirements (respiration and production) and energy transfer between trophic levels. Future research should allow for a definitive exploration of energy production to address energetic inefficiencies in forest compared to pasture streams.

Limitations to this study is that there was no manipulation of the key variables (shade and temperatures) within both the forest and pasture sites, therefore we cannot explicitly link pattern with process. Future studies should investigate the effects of a reduction in light and temperature following riparian planting on fish biomass in New Zealand.

2.6 | CONCLUSION

Food production and consumer metabolic scope synchronies are important aspects in understanding the drivers of aquatic biomass. In line with energetic theory, if autochthonous sources do not compensate for the loss of allochthonous sources to meet rising metabolic demands of consumers, the biomass of highest trophic level is expected to lower in open sites. However, pasture streams showed a five-fold increase in fish biomass when compared to forest streams in Taranaki. Water temperature and light availability play a pivotal role in predicting the in-stream food supply required to support the subsequent biomass of fish. The availability of autochthonous sources differed significantly between forest and pasture sites. This study demonstrates that the levels of allochthonous input (terrestrially derived invertebrates and vegetation) at forested streams can be comparable to pasture streams. Terrestrially derived food sources are expected to have consequences on the observed fish biomass, given their close correlation. Results suggest that allochthonous energy inputs are not necessarily compensated by autochthonous energy inputs, but rather enhanced by additional allochthonous invertebrate sources in pasture streams. However, cool temperatures inhibit fish metabolic activity and movement, so food availability alone is unlikely to limit the growth and biomass of fish (Jellyman, 1997). The warmest period at forest sites were below the preferred temperatures for New Zealand fish, especially eels (Richardson et al., 1994; Graynoth & Taylor, 2000). Therefore, the required metabolic demand, in conjunction to limited food could explain the decrease in fish biomass at these forest sites. This coupled with more available food sources are likely sustaining greater fish biomass. These energetic supply-demand synchronies are temperature-dependent and are considered important factors in controlling fish biomass.

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2.8 | APPENDIX

APPENDIX 2-1 Spearman rank correlations of mean annual and summer temperatures and light intensities in forest and pasture sites in the Taranaki Region, New Zealand. Annual = November 2019 to November 2020) and summer = December 2019, January and February 2020.

Variables	**Mean annual water temperature (°C)**	**Mean annual air temperature (°C)**	**Mean annual in-stream light intensity (μmol m^{-2} s^{-1})**	**Mean annual bank light intensity (μmol m^{-2} s^{-1})**
Mean annual water temperature (°C)	1.000	**0.858**	**0.811**	**0.727**
Mean annual air temperature (°C)	**0.858**	1.000	**0.788**	**0.900**
Mean annual in-stream light intensity (µmol m-2 s-1)	**0.811**	**0.788**	1.000	**0.853**
Mean annual bank light intensity (µmol m-2 s-1)	**0.727**	**0.900**	**0.853**	1.000

APPENDIX 2-2 Lineal biomass of fish and crayfish in forest and open pasture streams in the Taranaki Region, New Zealand. Forest and pasture means are shown in bold.

	Lineal biomass (g m^{-1})									
Land-use and stream	**Longfin eel**	**Shortfin eel**	**Redfin bully**	**Koaro**	**Brown trout**	**Shortjaw kokopu**	**Bluegill bully**	**Lamprey**	**Total fish biomass**	**Total crayfish biomass**
Forest										
Kapoaiaia	37.61	0.26	1.20	0.00	4.96	0.00	0.00	0.00	44.03	3.21
Little Dunns Creek	14.57	0.00	0.00	0.00	0.00	0.00	0.00	0.00	14.57	16.79
Ngatoro	15.56	0.00	0.00	0.00	0.00	0.00	0.00	0.00	15.56	2.82
Oaonui	3.86	0.14	7.10	8.00	0.00	0.00	0.00	0.00	19.09	0.49
Ouri	4.63	0.00	0.00	6.39	9.15	0.00	0.00	0.00	20.17	7.51
Punehu	27.62	0.00	2.65	5.72	7.28	0.00	0.00	0.00	43.26	1.41
Pasture										
Kapoaiaia	166.32	7.46	11.86	0.00	0.00	0.00	0.00	0.05	185.69	3.49
Little Dunns Creek	156.26	1.43	0.00	0.00	0.00	0.00	0.00	0.00	157.68	68.08
Ngatoro	74.86	0.00	0.00	0.00	0.00	0.00	0.00	0.00	74.86	12.82
Oaonui	205.39	1.97	20.70	0.00	0.00	24.99	0.32	0.00	253.36	0.79
Ouri	113.55	0.24	0.00	0.00	20.73	0.00	0.00	0.00	134.52	8.09
Punehu	140.49	2.05	1.21	0.00	0.00	0.00	0.00	0.00	143.75	1.03
Mean in forest	**17.31**	**0.07**	**1.82**	**3.35**	**3.56**	**0.00**	**0.00**	**0.00**	**26.11**	**5.37**
Mean in pasture	**142.81**	**2.19**	**5.63**	**0.00**	**3.45**	**4.16**	**0.05**	**0.01**	**158.31**	**15.72**

APPENDIX 2-3 Spearman rank correlations between mean rates for birch sticks and alder leaves with variables assessed during November 2019 to November 2020 and January 2020 at streams in the Taranaki Region, New Zealand. Statistically significant differences (*p* <0.05) are marked in bold.

Variables	**Mean leaf bag mass-loss (k day^{-1})**	**Mean stick mass-loss (k day^{-1})**
Mean annual water temperature (°C)	0.545	**0.636**
Mean summer water temperature (°C)	0.291	**0.588**
Mean annual air temperature (°C)	0.371	0.560
Mean summer air temperature (°C)	0.455	**0.636**
Mean annual in-stream light intensity (μmol m^{-2} s^{-1})	**0.587**	0.573
Mean summer in-stream light intensity (μmol m^{-2} s^{-1})	**0.587**	**0.587**
Mean annual bank light intensity (μmol m^{-2} s^{-1})	0.413	**0.650**
Mean summer bank light intensity (μmol m^{-2} s^{-1})	0.420	**0.650**
Stream shade (%)	**-0.580**	**-0.615**
Mid-stream canopy openness (%)	**0.657**	**0.860**
Aquatic invertebrate density (individuals m^{-2})	0.473	**0.585**
Aquatic invertebrate biomass (g m^{-2})	**0.671**	**0.790**
Periphyton biomass (g m^{-2})	-0.245	0.266
pH	-0.182	0.259
Specific conductivity (μS cm^{-1})	-0.210	0.231
Dissolved oxygen (%)	**0.601**	**0.643**
Total nitrogen (g m^{-3})	0.307	0.096
Total phosphorus (g m^{-3})	-0.406	-0.280

APPENDIX 2-4 Comparison of model AIC and BIC values for various light measurements.

Model type	**AIC**	**BIC**	**Fisher's *C* test**	***p* value**
Stream shade (%)	51.15	62.30	5.15	0.273
Annual instream light intensity (μmol m^{-2} s^{-1})	46.72	57.87	0.72	0.949
Annual bank light intensity (μmol m^{-2} s^{-1})	47.49	58.62	1.49	0.829

CHAPTER III

Trophic dynamics and the importance of terrestrial invertebrate subsidies in forest and pasture streams on Mount Taranaki, New Zealand

Bluegill bully (*Gobiomorphus hubbsi*) caught at pasture site of the Oaonui Stream, January 2020

3.1 | ABSTRACT

The contributions of allochthonous and autochthonous carbon sources are an important currency of energy in stream food webs. Land-use change from forest to pasture directly influences available energy sources in streams by reducing allochthonous inputs from riparian vegetation and light attenuation that fuels autotrophs. The extent of riparian vegetation can therefore indirectly regulate stream fish biomass by controlling allochthonous and autochthonous contributions to secondary production. Unshaded pasture streams have been shown to support greater fish biomass in Taranaki, leading to questions about which energy source provides the greater subsidy to fish biomass. Understanding how food web and energy dynamics differ in forest and pasture streams should provide insight into the underlying mechanisms behind changes in fish biomass.

Stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) and Bayesian mixing models were used to identify the relative importance of source type, and the proportional contribution of energy to consumer biomass at six paired sites in forest and pasture streams in Taranaki, North Island, New Zealand. Trophic structure was similar between forest and pasture sites, irrespective of resource availability and land use. Energetic sources assimilated by fish did not vary significantly between land uses and showed a distinct reliance on crayfish (*Paranephrops planifrons*; 41% in forest and 51% in pasture) and terrestrial invertebrates (48% in forest and 45% in pasture). Results suggest that crayfish provide an important intermediary source of energy to fish in Taranaki streams. Generally, periphyton was the most important source of nutrition for crayfish, in both forest (76%) and pasture (97%) streams. Aquatic invertebrates did not appear to contribute significantly to fish and crayfish diets. However, non-predatory stream invertebrates (excluding crayfish) showed a

distinct transition in sources of carbon assimilated between land uses, with forest stream invertebrates obtaining 77% of their nutrition from available leaf litter, shifting to dominance by periphyton (73%) in pasture streams ($p < 0.05$). This study highlighted the important roles of crayfish and terrestrially derived invertebrates in mediating the transfer of energy that sustains secondary consumer biomass in Taranaki streams, irrespective of land use.

3.2 | INTRODUCTION

Land-use change from forest to pasture directly influences available energy sources within stream systems (e.g., Heffernan & Cohen, 2010; Wootton, 2012; Kaylor et al., 2017; Martens et al., 2019; Huryn & Benstead, 2019). The removal of canopy cover has been related to changes in community composition, metabolic stream scope and the supply of allochthonous (terrestrially derived energy sources) and autochthonous food sources (in-stream derived energy sources) (Edwards & Huryn, 1996; Thompson & Townsend, 2004). Various ecological concepts emphasise the significance of organic matter derived from autochthonous (in-stream derived energy sources) and allochthonous sources (terrestrially derived energy sources) in unmodified stream systems. For example, the River Continuum Concept (Vannote et al., 1980), the Flood Pulse Concept (Junk et al., 1989), the Riverine Productivity Model (Thorp & Delong, 1994) and the Riverine Ecosystem Synthesis (Thorp et al., 2006; Thorp et al., 2008) all illustrate the importance of autochthonous and allochthonous resources in subsidising biomass (Felden et al., 2021).

Pasture streams are considered more productive than forested streams and generally support greater fish biomass (e.g., Bilby & Bisson, 1992; Chisnall & Hicks, 1993; Hicks & McCaughan, 1997; Kaylor & Warren, 2017; O'Gorman et al., 2016; Scrine et al., 2017). The assumption is that pasture streams have higher basal autochthonous production, capable of energetically sustaining the observed fish biomass, leading to longer food chain lengths (Pimm, 1982). Maximum trophic position (MTP) is a measure of food chain length defined by the trophic position of the top trophic consumer (Post et al., 2000; Post, 2002b). Isotopic analysis of trophic position allows for detection of subtle changes in food chain length by integrating the assimilation of energy to the highest trophic level (Post, 2002a). The productivity hypothesis (Pimm, 1982) proposes that food chain length should be longer where there is greater basal production due to energetic inefficiencies and depletion of energy at each trophic transfer (Post, 2000b; Thompson & Townsend, 2004). Thus, questions arise around the available energy sources and potential energetic inefficiencies in pasture streams that support greater fish biomass.

Energy in stream food webs can be perceived by the type and contribution of carbon, which varies depending on physical and biogeochemical stream attributes (Vannote et al., 1980; Hall, 2016). There are two dominant forms of basal carbon that contribute to consumer biomass. These consist of terrestrial allochthonous material entering the stream and internal autochthonous sources of periphyton (Allan et al., 2021; Roussel et al., 2021). The contribution of autochthonous and allochthonous sources to secondary production are an important currency of energy transfer in stream food webs (Allan et al., 2021). Allochthonous and autochthonous food sources occupy the lowest trophic level, but the relative importance of these energy sources to the food web can vary significantly within streams (Hershey et al., 2017).

In forested streams, gross primary production is assumed to be limited by shade. Organic inputs from terrestrial inputs can provide the dominant source of carbon (C) for aquatic consumers (Neres-Lima et al., 2016; Roussel et al., 2021; Allan et al., 2021). Overseas, leaf fall from deciduous forest canopies has been shown to provide up to eight times more carbon than that derived from aquatic primary production (Webster & Meyer, 1997; Roussel et al., 2021). However, New Zealand native trees are mostly evergreen so seasonally pulsed inputs of allochthonous carbon are generally not observed. For example, annual stream leaf litter fall rates in deciduous-mixed evergreen forest in the Northern Hemisphere are estimated around 716 g m^{-2} yr^{-1} in Denmark (Iversen et al., 1982), 700 g m^{-2} yr^{-1}

in Germany (Benfield, 1997), and 715 g m^{-2} yr^{-1} in Spain (Pozo et al., 1997; Abelho, 2001), while New Zealand annual stream native leaf litter fall rates have been estimated at 338 g m^{-2} yr^{-1} (Scarsbrook et al., 2001). Therefore, a greater understanding of the relative importance of allochthonous sources and their contribution to consumer biomass is important in New Zealand stream systems.

The removal of canopy cover both exacerbates light availability driving periphyton biomass and reduces sources of allochthonous vegetation. Pasture streams have higher light availability and greater gross primary production and periphyton biomass (Gregory, 1980; Kiffney et al., 2004; Wootton, 2012; Kaylor & Warren, 2017). Periphyton is easily assimilated and considered a higher quality food source than leaves, supporting the general conclusion that algae production is the dominant food source in stream food webs (Brett et al., 2017). Food quality is a key regulatory factor in the efficiency of energy flow through stream ecosystems (Torres-Ruiz et al., 2007; Lau et al., 2009; Guo et al., 2016a; Guo et al., 2016b). However, allochthonous and autochthonous sources differ in their nutritional quality for aquatic invertebrates (Cross et al., 2005; Lau et al., 2009; Guo et al., 2018). Nutritional quality is important as aquatic invertebrates can link the energy transfer from food sources to higher trophic levels (Sushchik et al., 2006). Crayfish are a dominant food source for fish in streams and may provide an important subsidiary link in transferring energy through the food web. Crayfish are polytrophic organisms, providing dual functional roles as both detritivores and carnivores (Parkyn et al., 2001; Reynolds et al., 2013). They provide a multipath energetic role in aquatic systems encapsulating energy that may not be readily available to higher trophic levels. Analysing the origins and availability of food sources to intermediary trophic levels will assist in the understanding of the regulation of fish biomass in stream systems.

While the contribution of basal allochthonous and autochthonous sources are considered important for the propagation of energy to higher trophic levels, allochthonous sources of terrestrial invertebrates that fall into the water have received little attention in stream food webs and are largely under studied (Baxter et al., 2005; Menninger et al., 2008; Felden et al., 2021; Roussel et al., 2021). Knowing the extent to which higher trophic levels utilise these energy sources would assist in understanding the role of alternative resources in supporting biomass in streams, particularly when primary production is lacking (Felden et al., 2021). Although pasture streams in Taranaki have been found to support significantly higher input rates of terrestrially-derived invertebrates when compared to forest streams (Chapter 2), their proportional contribution to secondary consumers in Taranaki is unknown. Terrestrial invertebrates are a known food source for fish and crayfish and determining the subsidiary role to consumer diet at different land uses may provide insight to direct energy sources supporting fish biomass (Parkyn et al., 2001; Albertson et al., 2018).

Understanding the differences in energy availability and source contribution between forest and pasture streams can providing insight into the underlying mechanisms behind changes in fish biomass. The aim of this research was to i) determine food web structure in forest and pasture streams and ii) delineate sources of energy fuelling consumer nutrition using stable isotope mixing models. I hypothesised that:

i) Increased food availability in pasture streams (Chapter 2) will increase food-chain length.

ii) In response to light availability, periphyton will contribute more carbon than leaf litter and provide a significant source contribution to intermediate trophic levels in pasture streams than in forest streams.

iii) Terrestrial invertebrates will provide an important subsidiary source of carbon to secondary consumers in direct relation to riparian vegetation cover.

3.3 | METHODS

Mount Taranaki (Taranaki Maunga) is located on the west coast of the North Island, New Zealand. The mountain is a 2,518-m high symmetrical volcano with a series of streams that flow radially from native forest around the summit to the surrounding Taranaki ring plain. Streams that flow through this ring plain are subject to intensive pastoral land use (dairy, sheep and beef farming). Six paired sites were chosen around the mountain, with one of each pair located in shaded native forest and the other located 1.5 km to 3.5 km downstream in open pasture (Figure 3-1). Paired sites all had similar physical attributes of substrate, width, depth, flow, catchment size, distance from sea and elevation (Chapter 2). To ensure the same fish species were represented at each site, historical records of fish species present were obtained using the New Zealand Freshwater Fish Database (Crow, 2017).

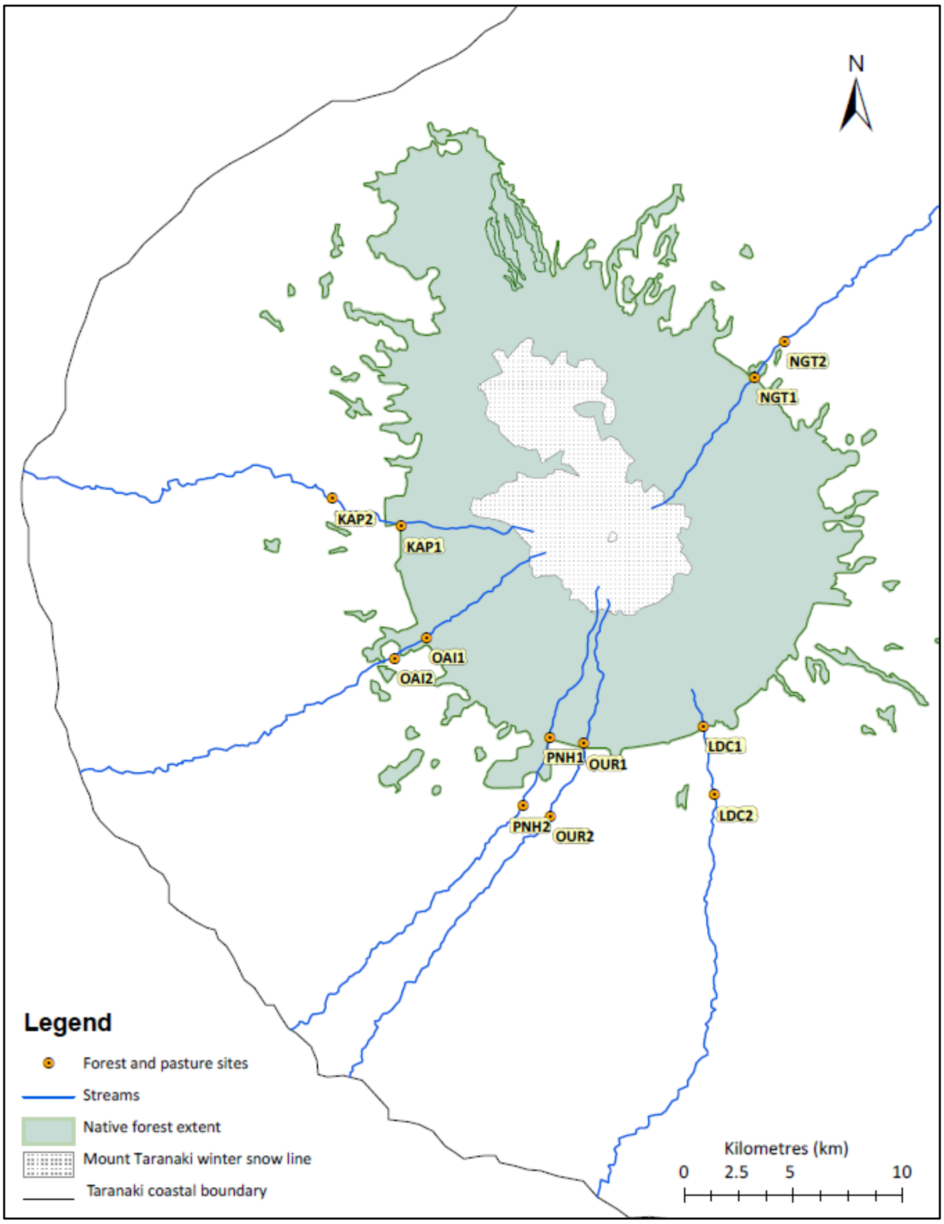


FIGURE 3-1 Location of paired sites in native forest and pasture streams in the Taranaki Region, North Island, New Zealand. See Table 2-1 for site abbreviations. 1 following site code denotes forest sites; 2 following site code denotes pasture sites.

3.3.1 | Autochthonous sampling and preparation

Periphyton was sampled in January 2020 from five randomly selected cobbles (20–25 cm) following the quantitative Method QM-1b (Biggs & Kilroy, 2000). A 15-cm diameter ring was placed centrally on the rock and periphyton was scraped within the ring and pipetted into a container. One pooled sample per site of periphyton was frozen in the field for stable isotope analysis. The stable isotope samples were later dried for a minimum of 48 h at 40°C, and ground to a fine, homogenous powder.

Aquatic invertebrates were sampled in January 2020 using a 0.1 m^2-area, 500µm-mesh Surber sampler, following the quantitative protocol C3 for hard-bottomed streams detailed in Stark et al. (2001). Aquatic invertebrates were frozen onsite rather than using ethanol as a preservative as ethanol is known to result in increased $\delta^{13}C$ values (Hogsden & McHugh, 2017). Aquatic invertebrates were identified to species level, where possible, using a dissecting microscope and counted. The cases of caddisflies and snails (*Potamopyrgus antipodarum* and *Physa*) were removed to account for known carbon discrepancies in shell and animal tissue (Hicks, 1997). Aquatic invertebrates were dried at 40°C for at least 48 h to a constant weight. Whole body samples and tissue for each species were ground to a fine, homogenous powder by using a mortar and pestle and each species processed separately.

3.3.2 | Allochthonous sampling and preparation

To capture terrestrially derived organic matter, and invertebrates entering the stream system, four 5-L buckets were dug approximately 20 cm into the stream bank. Two were situated on the left bank and two were situated on the right bank at each site. Each bucket contained 5 cm of water combined with 10 ml of 4% formalin to prevent decay (Manson & Macdonald, 1982; Stark et al., 2001). Formalin has been proven to not alter the isotopic signatures of invertebrates (Rennie et al., 2012; Willert et al., 2020). Buckets were left for a period of 30 days during December 2019 and January 2020 to capture autochthonous input. Terrestrial invertebrates collected were identified to genus level and counted. Terrestrial vegetation and invertebrates were then oven dried at 40°C for at least 48 h to a constant weight. Whole body samples, tissue of larger individuals (>10 mm long) and leaf litter were ground individually to a fine, homogenous power.

3.3.3 | Fish and crayfish

Fish and crayfish populations were sampled using multiple-pass electrofishing at each site between 20 January 2020 and 31 January 2020 following fish sampling protocols (Joy et al., 2013). At each site, a 20 m reach was blocked with a 5-mm mesh net downstream, and the reach was fished in a downstream direction until there was a reduction in fish numbers, following the removal method (White et al., 1982). Fish from each pass were identified to species, counted and their total lengths measured.

A maximum of five eels and crayfish were taken from each site, in addition to non-lethal fin clips from other eels and fish species (> 200 mm in length) for isotope analysis. All samples were frozen in-field prior to laboratory analysis. Fish fin clips and the white muscle from eels were oven dried for at least 48 h at 40°C to a constant weight. Muscle from crayfish tails was removed from the exoskeleton and oven dried at 40°C for at least 48 h. All samples of fin and muscle tissue were homogenized into a fine power. As eels were found at all sites, rapid analyses of gut content using presence/absence analysis of sources was undertaken.

3.3.4 | Stable isotope analysis

Individual homogenous samples (n = 422; Appendix 3-1) were weighed to 1.5 mg and placed into silver tin capsules (4.0 x 6.0 mm). The samples were analysed using a Europa Scientific Tracermass mass spectrometer with a precision of c. 0.1‰ ^{13}C and 0.3‰ for ^{15}N at the Waikato Stable Isotope unit (WSIU). Ratios of ^{13}C/^{12}C and ^{15}N/^{14}N were expressed relative to standards in equation 1 below:

Equation 1 $$\delta X = \left[\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right] x\, 1000,$$

where X = ^{13}C or ^{15}N, and R = ^{13}C/^{12}C or ^{15}N/^{14}N. The ratio of ^{13}C to ^{12}C was compared to the PDB standard, for which R standard = 1.1237 atom % ^{13}C (Craig, 1957). For ^{15}N/^{14}N, N_2 in air was used as the standard, and R standard = 0.3663 atom % ^{15}N (Mariotti, 1983).

Fish fin tissue provide comparable δ^{13}C and δ^{15}N signatures to fish muscle, therefore, no conversion correction was applied to fish fin tissue (McIntosh & Reid, 2021). Lipids were not chemically extracted from the samples. The assumption of mathematical lipid correction after analysis has been subject to criticism, with literature proposing that lipids bias diet reconstructions using stable isotopes and should be accounted for prior to analysis in food web mixing models (Arostegui, 2019). The purpose of lipid correction is to account for the decrease in δ^{13}C caused by de novo lipid synthesis (McConnaughey & McRoy, 1979; Sweeting et al., 2006; Post et al., 2007; Logan et al., 2008; Hoffman et al., 2015). However, corrections of benthic invertebrates for the application of Bayesian mixing models should be avoided to reduce bias within the model (Silberberger et al., 2021). Lipid correction has therefore been applied only to fish and crayfish samples with a C:N ratio of $\geq$ 3.5 with no correction for aquatic invertebrates, terrestrial invertebrates, leaf litter or periphyton (Post et al., 2007).

Dual stable isotope biplots were generated using the ‘ggplot’ function in the statistical programme R. Land-use and site-specific plots were produced to provide a visual representation of the food web and included fish, crayfish, aquatic invertebrates, terrestrial invertebrates, periphyton and leaf litter. Aquatic invertebrates were grouped into functional feeding groups that best represent their feeding guilds (following Ryder & Scott, (1998) as detailed in Manaaki Whenua (1996-2022); Appendix 3-2).

3.3.5 | Statistical analysis

Food chain length was calculated as maximum trophic position (MTP) of the top predator (i.e., eels; Hicks, 1997) using equation 2 below (Post, 2002a; Quezada-Romegialli et al., 2018).

Equation 2 $$\delta^{15}N_{eel} = \Delta N\ (TP + \lambda + \alpha\ (\delta^{15}N_{baseline1} + \delta^{15}N_{baseline2}) - \delta^{15}N_{baseline2,}$$

where ΔN is the trophic discrimination factor (TDF). λ is the TP of the baseline (λ=1). Trophic discrimination factors (TDF) of 0.4 ± 1.3 ‰ for C and 3.4 ± 0.9 ‰ for N were used in the model (Post, 2002a, Quezada-Romegialli et al., 2018).

TP of eels was calculated using a Bayesian model in the tRophicPosition package in R (Quezada-Romegialli et al., 2018). Estimates of TP reflect the available energy within the food web (Post et al., 2002b). The dual baseline approach was used to discriminate among leaf litter (baseline 1) and periphyton (baseline 2) in the model. The dual baseline equations are summarised below in Equation 3 (Vander Zanden et al., 1997; Quezada-Romegialli et al., 2018):

Equation 3 $$\alpha = (((\delta^{13}C_{baseline2} - (\delta^{13}C_{consumer} + \Delta C)) / (TP - \lambda\ ))/(\delta^{13}C_{baseline\ 2} + \delta^{13}C_{baseline\ 1})$$

Where, baseline 1 is leaf litter and baseline 2 is periphyton. TP is the trophic position and λ is the TP of the baseline (λ=1).

Markov Chain Monte Carlo (MCMC) simulations were set to 10,000 interactions with a burn in of 10,000. Gelman diagnostics were close to one and indicated that model convergence was achieved (Gelman & Rubin, 1992; Quezada-Romegialli et al., 2018). Pairwise comparisons of posterior estimates of trophic position of eels in forest and pasture streams was performed in the tRophicPosition package in R (Quezada-Romegialli et al., 2018).

Bayesian stable isotope mixing models were used to determine the dietary contribution of food sources to fish, crayfish and non-predatory aquatic invertebrates in forest and pasture streams using the MixSIAR package in R (Stock et al., 2018). Non-predatory aquatic invertebrates were defined by excluding aquatic invertebrates that feed on other aquatic invertebrates such as *Hydrobiosis, Archichauliodes*, *Stenoperla* and *Ameletopsis*. Aquatic invertebrates as a food source were grouped within each land-use group to reduce the number sources for mixing models. This also avoided the issue of saturated food sources but still ensured functional significance within each fish and crayfish model (*sensu* Phillips et al., 2005). The data were normalised by subtracting the lowest δ^{13}C (−28.75‰) and δ^{15}N (−0.26‰) for each food web component. Normalisation accounted for the observed magnitude of δ^{15}N between forest and pasture food webs, while maintaining the relative differences between food-web components (Appendix 3-3). This approach allowed the mixing model to run on a common scale for land-use and site-specific comparisons.

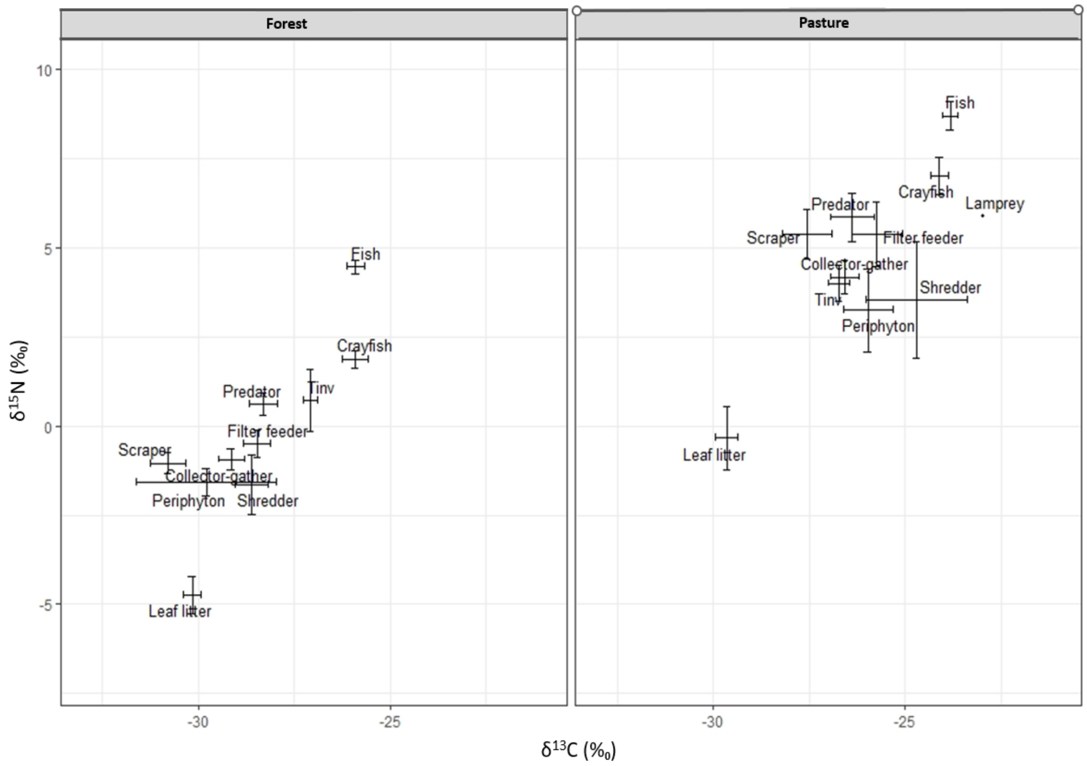
Consumable sources were defined in the mixing model as the lower trophic positions analysed from the dual isotope plot outputs of trophic food web. For fish, consumable sources included aquatic and terrestrial invertebrates and crayfish. For crayfish, consumable sources included periphyton, leaf litter, aquatic invertebrates and terrestrial invertebrates. Non-predatory aquatic invertebrates were analysed to evaluate known consumed basal sources of leaf litter and periphyton at each land use and site. Land use and site models were run using the JAGS 4.3.0 (2017) model using Markov Chain Monte Carlo (MCMC) simulations with a chain length of 100,000 and burn length of 50,000 for each model. Geweke diagnostics for convergence were run for all models to determine suitability of burn-in period were appropriate for each mixing model. The Gelman diagnostics were all close to one for all models indicating adequate Markov Chain Monte Carlo (MCMC) convergence (Gelman & Rubin, 1992). Mann-Whitney *U* test were performed in Statistica (TIBCO Software, 2018) to determine the significant differences between source contributions in forest and pasture streams.

3.4 | RESULTS

3.4.1 | Forest and pasture food web dynamics

Prior to normalisation, $\delta^{15}N$ in pasture streams was approximately 7.0‰ greater for all food web components than in pasture streams (Figure 3-2). Basal sources of leaf litter and periphyton were lower in $\delta^{13}C$ for both forest and pasture sites. Fish being the top consumers showed the highest $\delta^{15}N$ values. The increase in $\delta^{13}C$ between leaf litter and fish was greater in forest streams at 5.8‰ on average (−30.2 to −25.9‰) when compared to pasture at 4.3‰ (−29.6 to −23.8‰), as was the increase in $\delta^{13}C$ between periphyton and fish (mean 3.9‰; (−29.8 to −25.9‰) and 2.2‰ (−26.0 to −23.8‰), respectively). The trophic length defined by the difference in $\delta^{15}N$ was the same in forest (9.2‰ (leaf litter −4.7 to 4.5‰) and 9.0‰ (leaf litter −0.3 to 8.7‰)), whereas the differences between $\delta^{15}N$ between periphyton and fish was greater in pasture 6.1‰ (−1.6 to 4.5‰) than forest 5.4‰ (3.3 to 8.7‰).

A) Non-normalised



B) Normalised

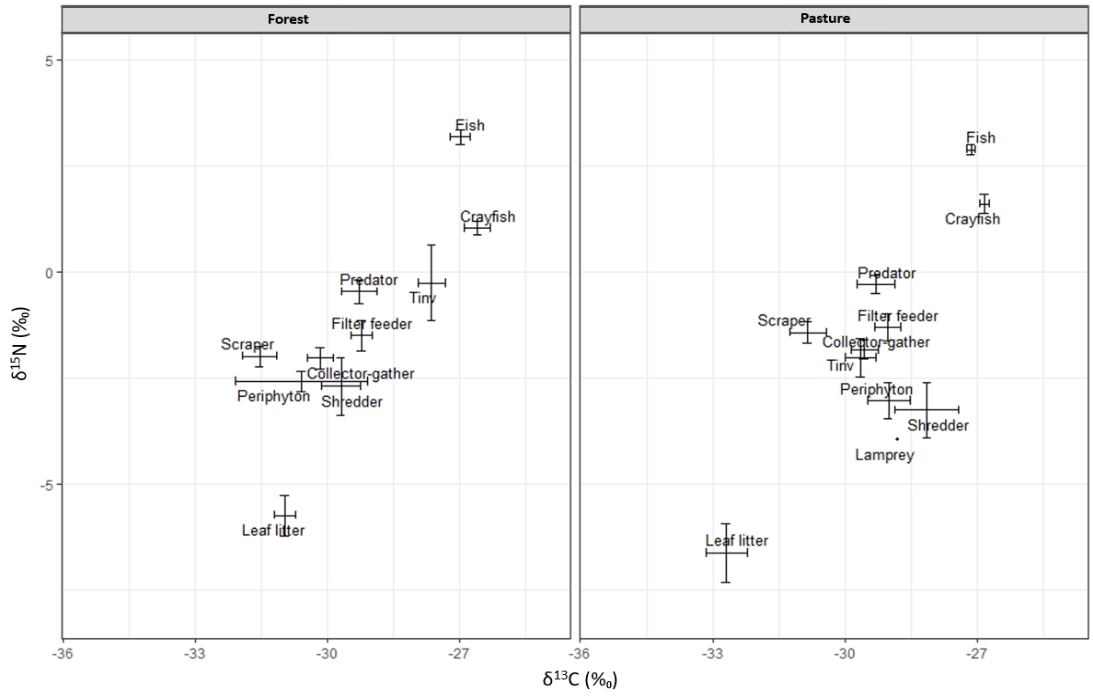
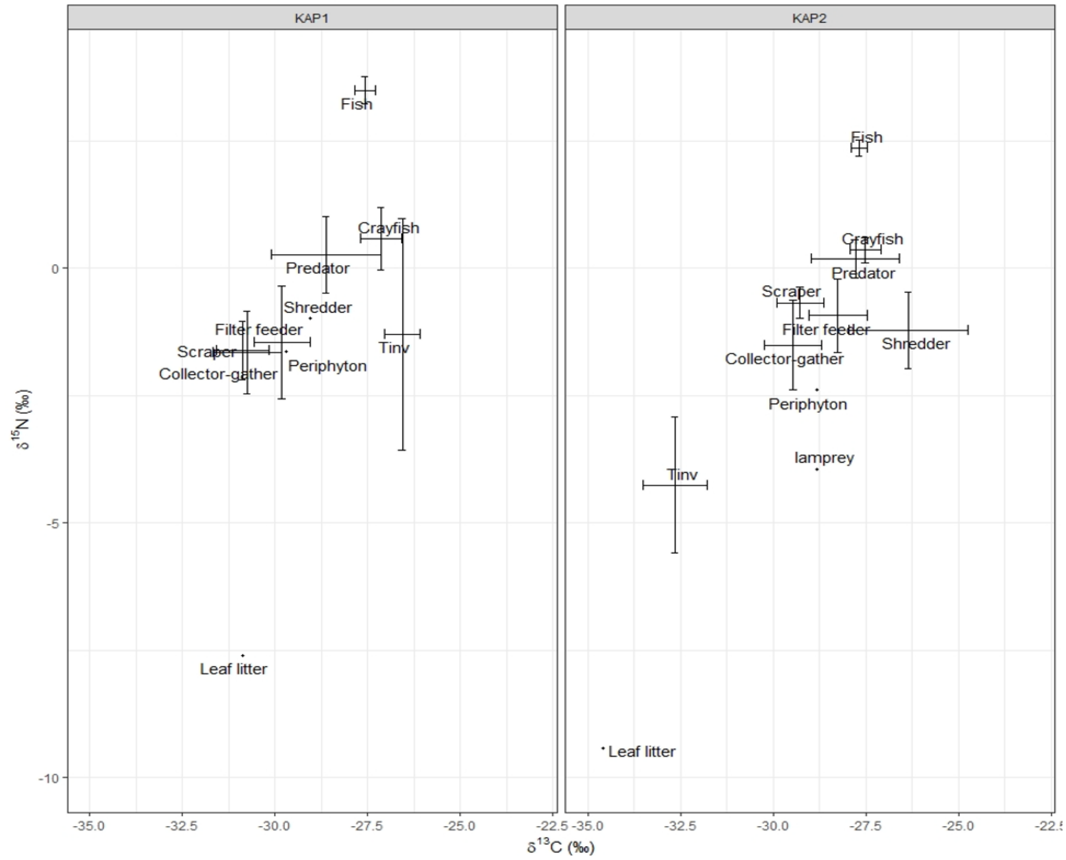


FIGURE 3-2 Dual isotope plot of A) non-normalised and B) normalised means of $\delta^{13}C$ and $\delta^{15}N$ across individual functional feeding groups in grouped forest and pasture streams in Taranaki, New Zealand. Fish $\delta^{13}C$ values have been lipid corrected using equation 3 of Post et al. (2007). Error bars are 1 standard error. tinv = terrestrial invertebrates.

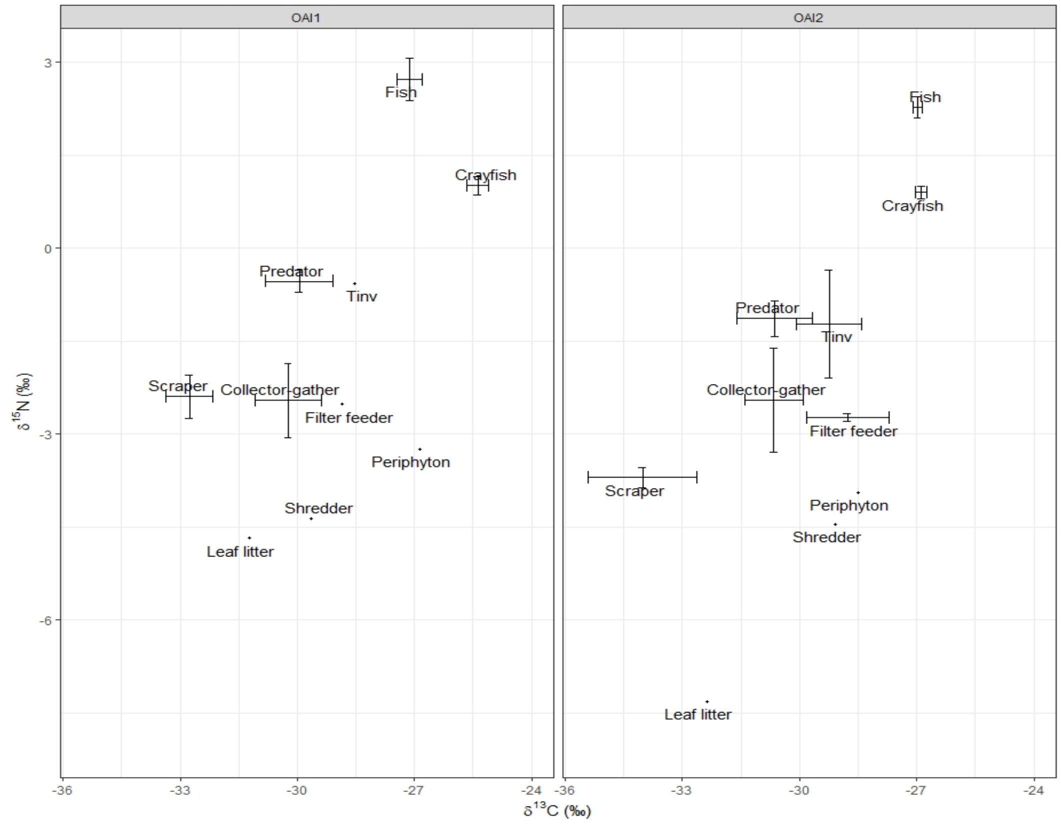
3.4.2 | Site-specific food web structure

The site-specific isotope biplots allowed for an assessment of variability within the data. Individual normalised site food web dynamics showed similar food web structure between forest and pasture sites (Figure 3-3). Although fish were at the top of the food web at all sites, mean crayfish $\delta^{13}C$ and $\delta^{15}N$ were close to mean fish $\delta^{13}C$ and $\delta^{15}N$ values, at sites KAP2, OAI2, PNH1 and PNH2. Fish had higher $\delta^{15}N$ values at site OUR2 when compared to site OUR1. Periphyton had higher $\delta^{13}C$ values at LDC1 when compared to other sites. No distinct differentiation in food structure was evident between forest and pasture sites and food web components. Mean predatory invertebrates $\delta^{13}C$ and $\delta^{15}N$ were close to crayfish for KAP1, KAP2 and NGT1. Generally, aquatic invertebrate functional feeding groups and terrestrial invertebrates showed site specific variation, indicative of variability within the data (Figure 3-3 A, B, C, D, E, F).

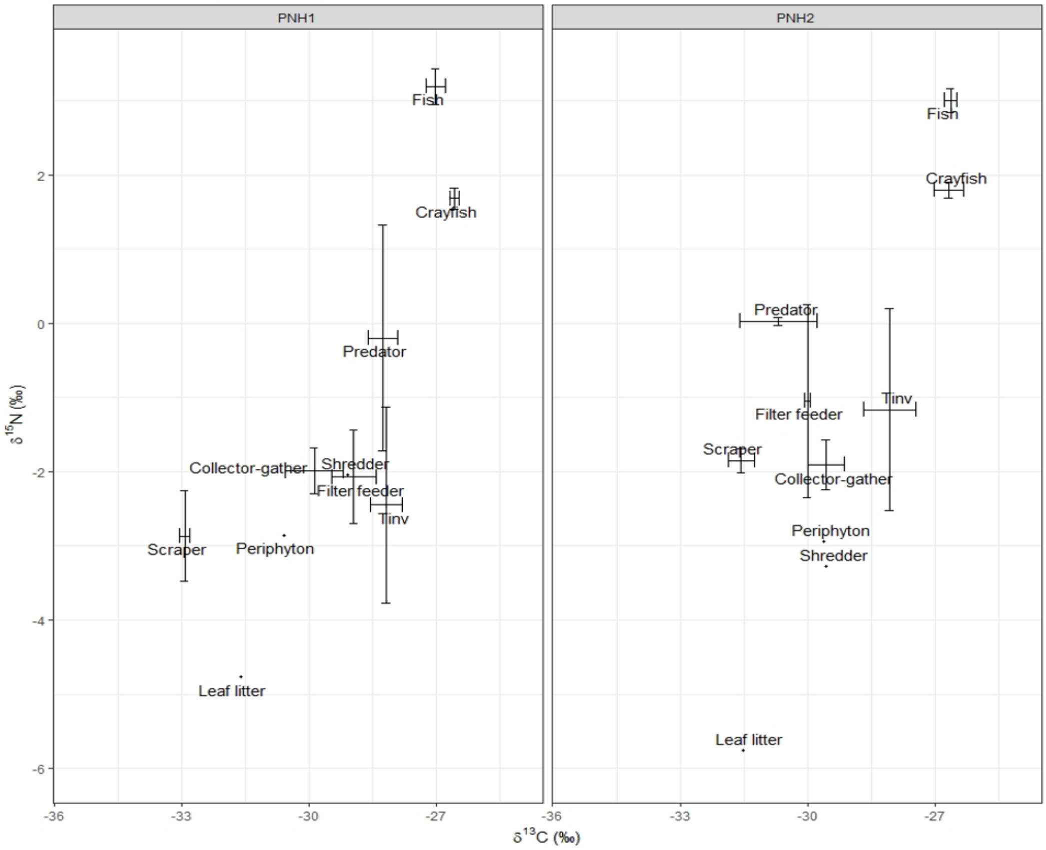
A) Kapoaiaia (KAP)



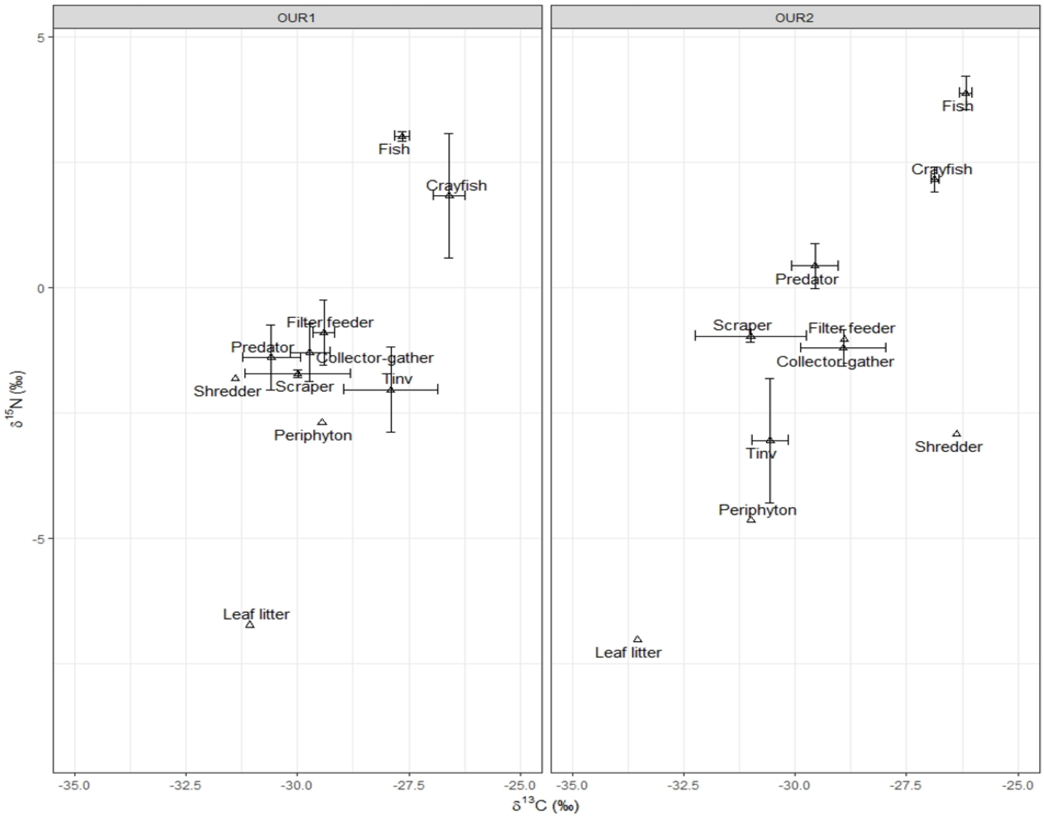
B) Oaonui (OAI)



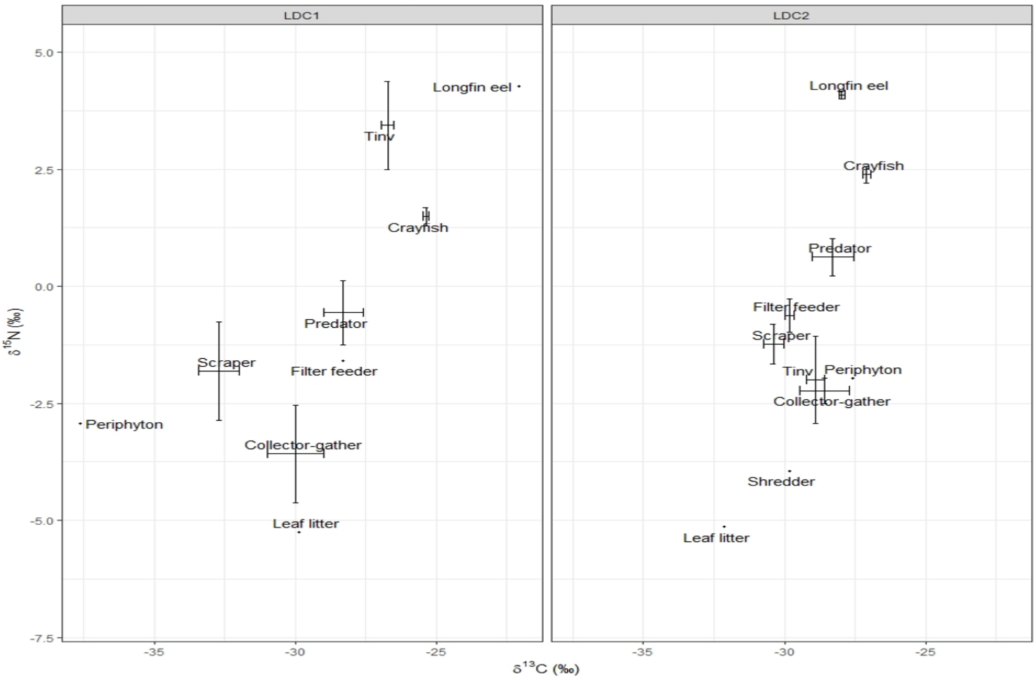
C) Punehu (PNH)



D) Ouri (OUR)



E) Little Duns Creek (LDC)



F) Ngatoro (NGT)

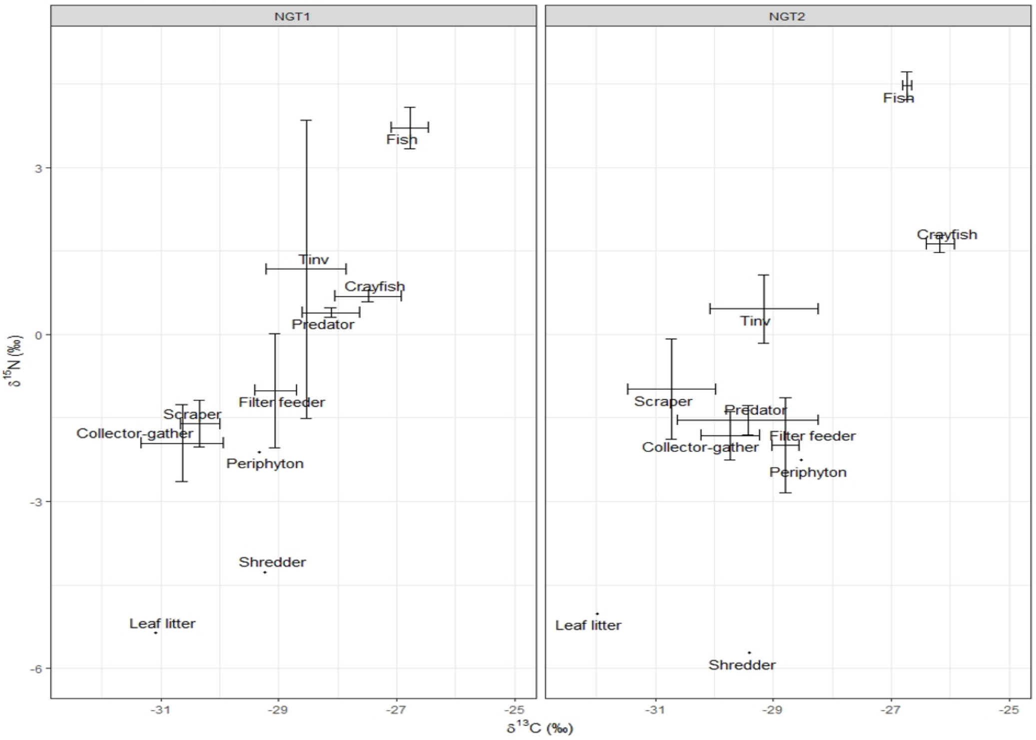


FIGURE 3-3 Means for fish and crayfish, normalised by subtracting the lowest δ^{13}C and δ^{15}N means by site A) Kapoaiaia B) Oaonui C) Punehu D) Ouri E) Little Dunns Creek F) Ngatoro for all items. This preserves the relative differences across each food web. Error bars are 1 SE. tinv = terrestrial invertebrates.

3.4.3 | Maximum trophic position of eels

Maximum trophic position of eels was similar between streams modelled at 4.1 in forest and 4.0 in pasture (Figure 3-4; Appendix 3-4), implying that there were four trophic steps in both land uses. Pairwise comparisons show no significant difference between maximum trophic position at forest and pasture streams ($p > 0.05$).

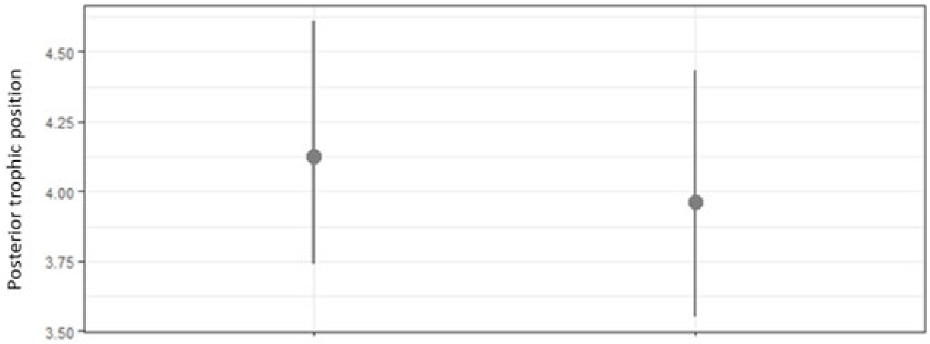


FIGURE 3-4 Maximum trophic position posterior plot of eels in forest and pasture. Bars show 95% credible interval of each posterior trophic position.

3.4.4 | Proportional contribution to fish

The Bayesian mixing models illustrate distinct dietary support for fish by crayfish, terrestrial invertebrates and aquatic invertebrates at both forest and pasture sites (Figure 3-5). Despite more variability in food groups in forest streams, there were no differences between food sources between land uses (Figure 3-5; Figure 3-6). Crayfish were proportionally dominant on average at 51%, closely followed by terrestrial invertebrates at 45% contribution to fish diet in pasture (Table 3-1). In forest, the proportional contribution of terrestrial invertebrates was 49% and crayfish contributed marginally less to fish diet at 41%. Low contributions of aquatic invertebrates were observed at both forest (11%) and pasture (<1%) streams. No statistical differences were found between dietary sources to fish at forest and pasture streams (*p* > 0.05; Figure 3-6; Table 3-1).

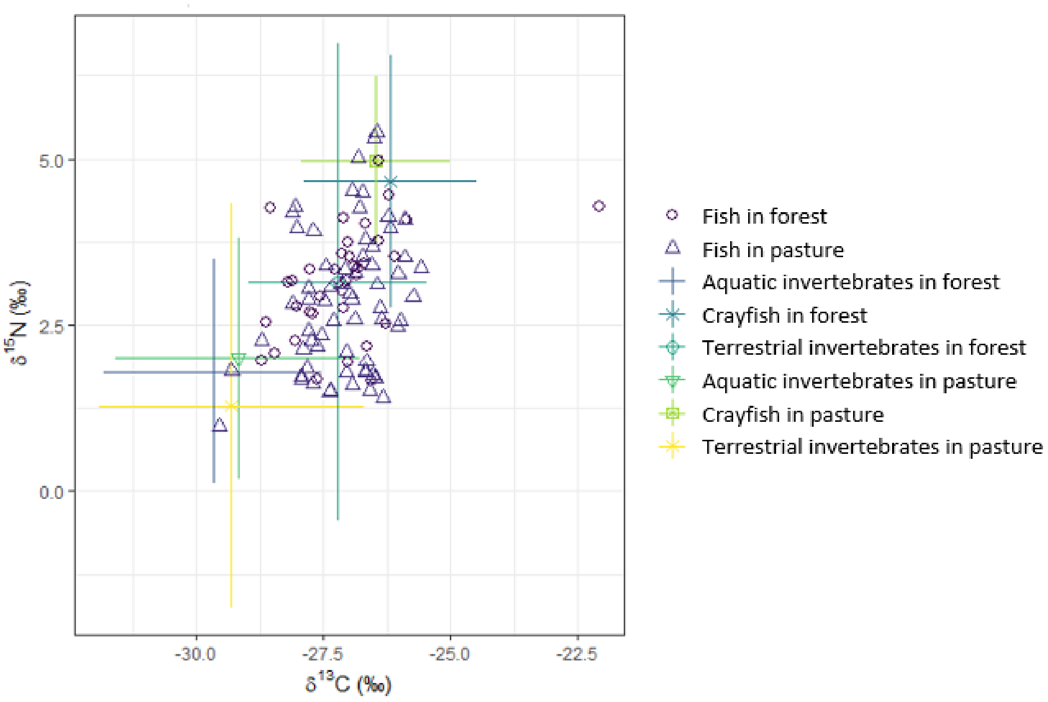
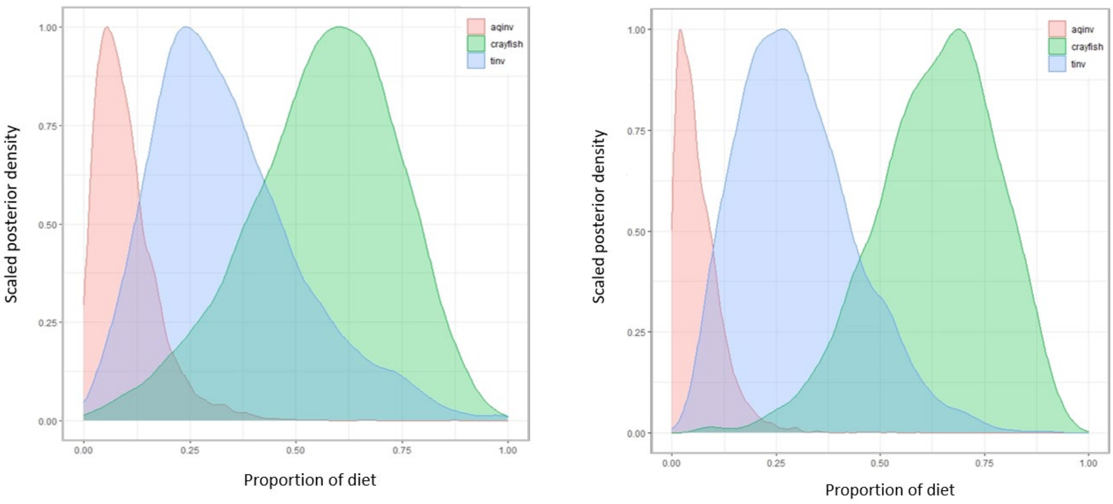


FIGURE 3-5 Dual isotope plot of fish as consumers and their potential food sources (aquatic invertebrates, crayfish, and terrestrial invertebrates) in forest and pasture streams in Taranaki, New Zealand, showing that adjusted food sources encompass the consumers. Trophic discrimination factors (0.4‰ for $\delta^{13}C$ and 3.4‰ for $\delta^{15}N$) have been added to the means for food sources. Error bars are 1 SD, while symbols represent the mean potential food sources for fish in each land use.


A) Forest

B) Pasture

FIGURE 3-6 Posterior probability distributions of proportional contributions of aquatic invertebrates (aqinv), crayfish (crayfish) and terrestrial invertebrates (tinv) food sources for fish in A) forest and B) pasture streams in Taranaki, New Zealand.

Site-specific Bayesian mixing models of food sources for fish all showed a greater proportional contribution of crayfish and terrestrial invertebrates compared to aquatic invertebrates (Table 3-1). All forest sites indicated crayfish were the dominant food source, except for OAI1, where terrestrial invertebrates showed a proportionally higher contribution to fish diet (72%). LDC1 forest and NGT2 pasture sites showed that crayfish contributed >85% to fish diet. Four of the six pasture sites showed higher proportional contributions of crayfish when compared to other potential food sources. However, KAP2 and OAI2 showed >50% dietary contribution by terrestrial invertebrates. OUR1 showed the highest contribution of aquatic invertebrates when compared to other sites. Source contributions were similar at OUR1, showing no variation between crayfish (37%), terrestrial invertebrates (30%) and aquatic invertebrates (33%) (Table 3-1).

TABLE 3-1 Proportional contribution to fish diet at individual sites in Taranaki, New Zealand (mean ± standard deviation). Sources include crayfish, terrestrial invertebrates, and aquatic invertebrates. Dominant source contributions are shown in bold.

Source		**Crayfish**	**Terrestrial invertebrates**	**Aquatic invertebrates**
Land use	**Site**	Mean ± SD	Mean ± SD	Mean ± SD
Forest	KAP1	**0.481 ± 0.12**	0.352 ± 0.13	0.167 ± 0.08
Forest	LDC1	**0.871 ± 0.32**	0.101 ± 0.31	0.028 ± 0.03
Forest	NGT1	**0.586 ± 0.16**	0.296 ± 0.18	0.118 ± 0.08
Forest	OAI1	0.199 ± 0.11	0.720 ± 0.13	0.081 ± 0.07
Forest	OUR1	**0.369 ± 0.09**	0.303 ± 0.13	0.327 ± 0.10
Forest	PNH1	0.420 ± 0.12	**0.453 ± 0.15**	0.127 ± 0.08
Pasture	KAP2	0.375 ± 0.07	**0.504 ± 0.08**	0.121 ± 0.09
Pasture	LDC2	**0.689 ± 0.09**	0.150 ± 0.09	0.161 ± 0.12
Pasture	NGT2	**0.857 ± 0.03**	0.098 ± 0.05	0.045 ± 0.05
Pasture	OAI2	0.415 ± 0.06	**0.547 ± 0.06**	0.038 ± 0.03
Pasture	OUR2	**0.779 ± 0.07**	0.197 ± 0.07	0.024 ± 0.02
Pasture	PNH2	**0.581 ± 0.07**	0.368 ± 0.07	0.050 ± 0.05
Forest		0.409 ± 0.12	0.485 ± 0.15	0.106 ± 0.07
Pasture		0.512 ± 0.05	0.450 ± 0.06	0.038 ± 0.06
Mann-Whitney *U* Test		0.230	0.471	0.810

3.4.5 | Proportional contribution to eels

The gut content analyses of eels in forest and pasture sites showed remnants of crayfish, and terrestrial and aquatic invertebrates at both land uses (Table 3-2). Caddisfly cases and snail shells were found in the gut across eels at both forest and pasture. Remnants of Anostostomatidae sp. and Anisoptera sp. were present in gut contents of eels in a single forest site. Eel guts from pasture sites contained a wide range of terrestrial invertebrates, notably exoskeletons of *Stethaspis* sp. (Melolonthinae). However, there were no distinct differences in source contributions between forest and pasture sites (Table 3-2).

TABLE 3-2 Invertebrate groups found in gut contents of eels in forest and pasture streams in Taranaki. 1 indicates the presence in gut, 0 indicates absence in gut). * = terrestrial invertebrate.

Observation	Common name	Structure identified	Forest	Pasture
Paranephrops planifrons	Crayfish	Whole and pincers	1	1
Ephemeroptera	Mayflies	Whole	1	1
Plecoptera	Stoneflies	Whole	1	1
Pycnocentrodes	Stony cased caddisfly	Case	1	1
Beraeoptera	Smooth cased caddisfly	Case	1	1
Potamopyrgus	Mud snails	Shell	1	1
Archichauliodes diversus	Dobsonfly*	Body plates and adult wing	1	1
Anostostomatidae	Weta*	Leg	1	0
Anisoptera	Dragonfly*	Wing	0	1
Melolonthinae *Stethaspis* sp.	Green beetle*	Outer shell	0	1
Diptera	Flies*	Whole	1	1
Coleoptera	Beetles*	Outer shell	0	1

Bayesian mixing models for eel diet also indicated no variations in source contributions between land uses, with a strong tendency towards crayfish at both forest and pasture streams (Figure 3-7; Appendix 3-5). However, there was a clearer tendency to reliance on both crayfish and terrestrial invertebrates in pasture streams, where the range of contributions was narrower (Figure 3-7). Overall, crayfish contributed around 64% of eel diet in forest and 54% in pasture. Terrestrial invertebrates contribute less to forest eel diet at 24% when compared to pasture at 37%. Both land uses show low contributions of aquatic invertebrates in forest (12%) and pasture (<1%) (Figure 3-7; Appendix 3-5).

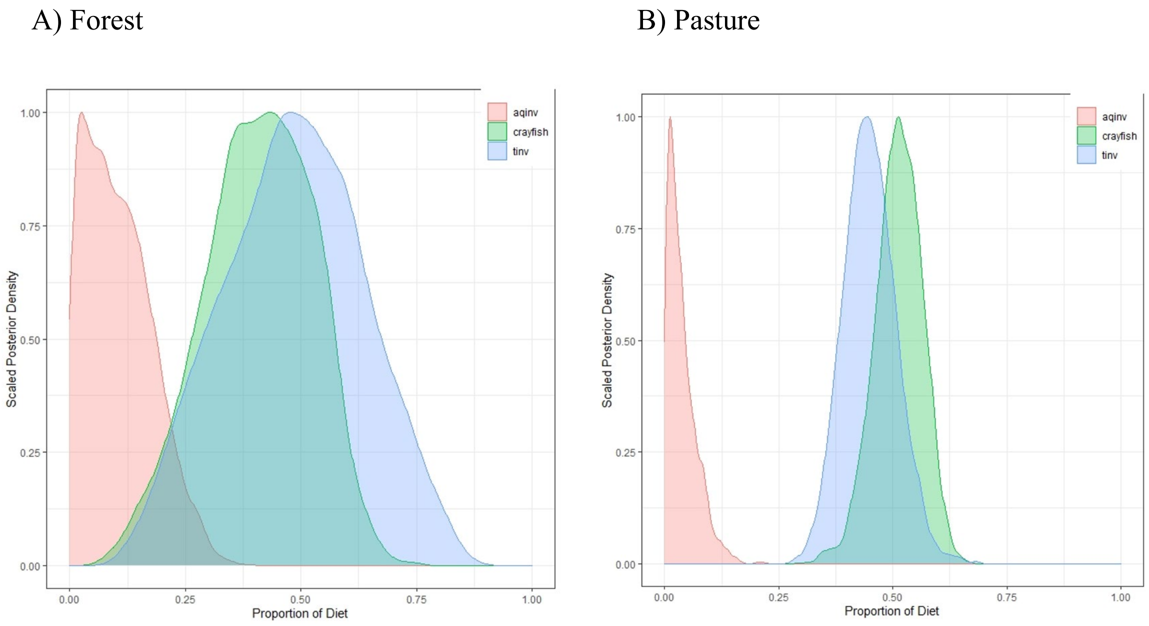


FIGURE 3-7 Posterior probability distributions of proportional contributions of aquatic invertebrates (aqinv), crayfish (crayfish) and terrestrial invertebrates (tinv) food sources for eels in A) forest and B) pasture streams in Taranaki, New Zealand.

3.4.6 | Proportional contribution to crayfish

The dual isotope plot of normalised crayfish isotope data showed no distinct differentiation between forest and pasture sites (Figure 3-8). Potential consumable sources for crayfish were aquatic invertebrates, terrestrial invertebrates, periphyton and leaf litter. Crayfish isotope data overlapped with sources of periphyton and terrestrial invertebrates in forest while, crayfish in pasture also show distinct overlaps with periphyton and limited overlaps between other food sources (Figure 3-8).

Bayesian mixing models illustrate distinct dietary support from periphyton in both forest and pasture (Figure 3-9; Table 3-3). The dietary contribution predicted by the Bayesian mixing model suggests periphyton contributed 76% to crayfish diet in forest and 97% of crayfish diet in pasture. Terrestrial invertebrates show a 20% contribution to crayfish diet in forest.

Site-specific Bayesian mixing models for crayfish diet showed a significant tendency towards periphyton at both forest and pasture sites. Periphyton contributed >95% to crayfish nutrition in pasture streams on average, compared to forest streams (76%), where periphyton contributions were less and more variable among sites (22% to 84%). Site OUR1 showed much less contribution of periphyton with strong tendencies towards terrestrial invertebrates (Table 3-3). This may have led to the observed skewness in diet evident in the land-use Bayesian mixing model (Figure 3-8). Aquatic invertebrates were not strongly represented in crayfish nutrition for either forest or pasture sites, however, they contributed significantly more to crayfish in forest than pasture ($p < 0.05$). Leaf litter appeared to make little direct contribution to crayfish nutrition in pasture streams, but it did make a small contribution in forest streams. Significant differences ($p < 0.05$) were found for all potential dietary sources between forest and pasture sites (Table 3-3). However, there were no nutritional differences between food sources at different land uses with periphyton significantly contributing to crayfish at both forest and pasture streams.

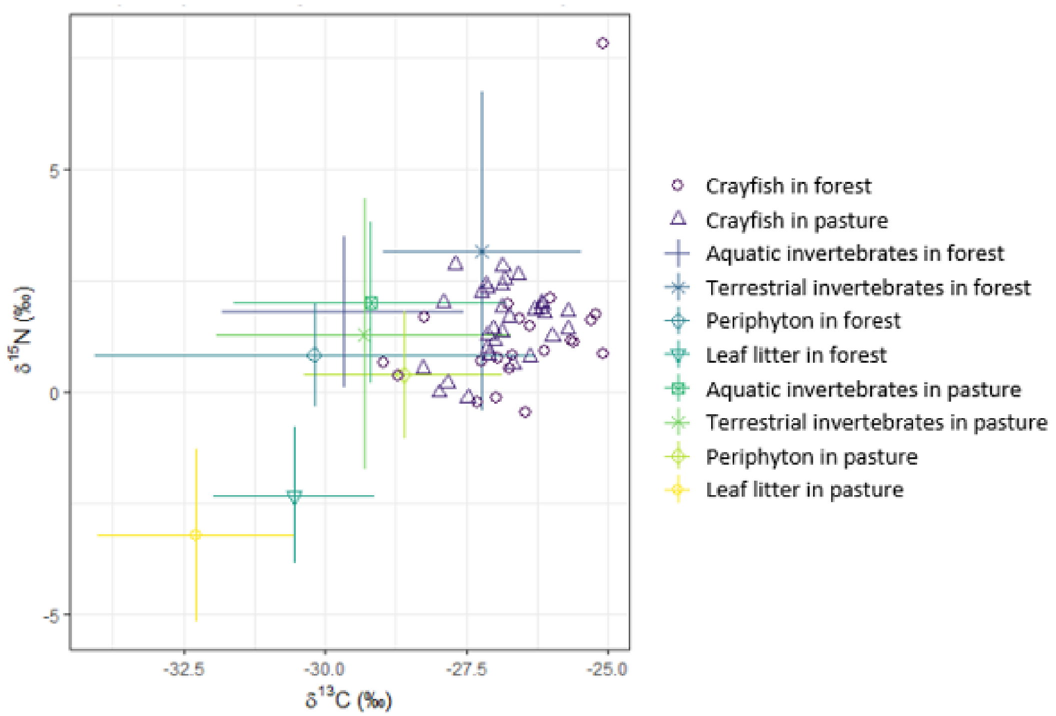


FIGURE 3-8 Dual isotope plot of normalised crayfish as consumers and their potential food sources (aquatic invertebrates, terrestrial invertebrates, periphyton and leaf litter) in forest and pasture streams in Taranaki, New Zealand, showing that adjusted food sources encompass the majority of consumers. Trophic discrimination factors (0.4‰ for $\delta^{13}C$ and 3.4‰ for $\delta^{15}N$) has been added to the means for food sources. Error bars are 1 SD, while symbols represent the mean potential food sources for crayfish in each land use.

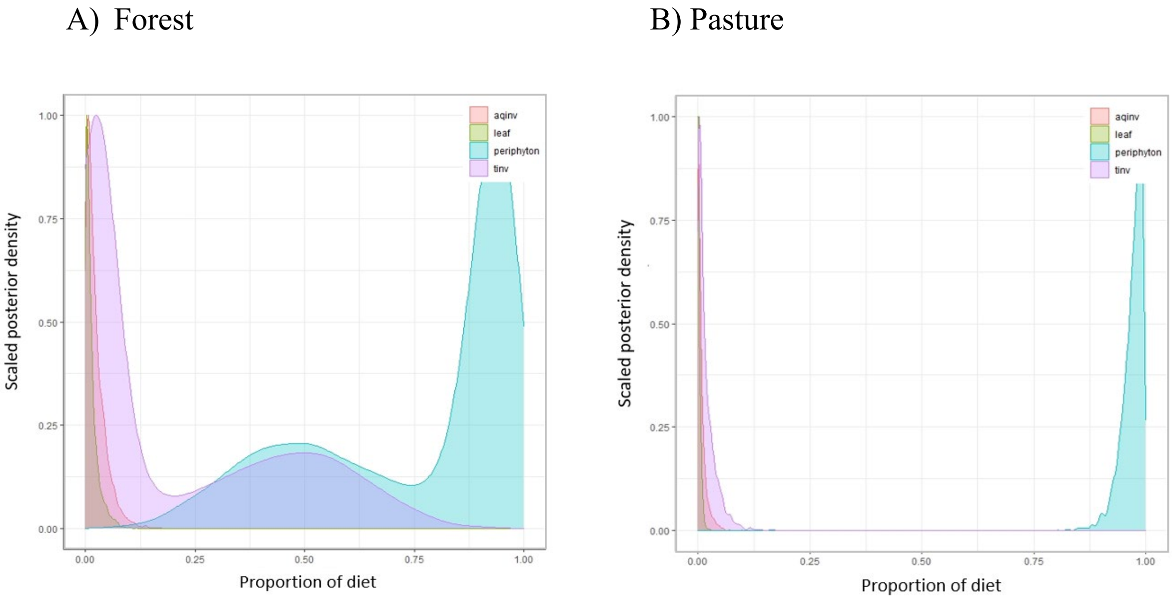


FIGURE 3-9 Proportional contributions of aquatic invertebrates (aqinv), leaf litter, periphyton and terrestrial invertebrates (tinv) for crayfish nutrition in A) forest and B) pasture streams in Taranaki, New Zealand.

TABLE 3-3 Proportional contribution to crayfish at individual sites in Taranaki, New Zealand (mean ± standard deviation). Sources include aquatic invertebrates, leaf litter, periphyton and terrestrial invertebrates. Dominant source contributions and Mann-Whitney *U* significant differences between contributions and are marked in bold.

Source		**Periphyton**	**Leaf litter**	**Aquatic invertebrates**	**Terrestrial invertebrates**
Land use	**Site**	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD
Forest	KAP1	**0.725 ± 0.13**	0.026 ± 0.03	0.018 ± 0.02	0.230 ± 0.13
Forest	LDC1	**0.833 ± 0.12**	0.014 ± 0.02	0.013 ± 0.02	0.141 ± 0.12
Forest	NGT1	**0.827 ± 0.12**	0.055 ± 0.07	0.020 ± 0.03	0.098 ± 0.01
Forest	OAI1	**0.844 ± 0.14**	0.016 ± 0.02	0.012 ± 0.02	0.128 ± 0.13
Forest	OUR1	0.217 ± 0.14	0.015 ± 0.02	0.012 ± 0.02	**0.756 ± 0.14**
Forest	PNH1	**0.684 ± 0.21**	0.024 ± 0.03	0.023 ± 0.03	0.268 ± 0.21
Pasture	KAP2	**0.917 ± 0.07**	0.011 ± 0.02	0.007 ± 0.01	0.065 ± 0.07
Pasture	LDC2	**0.955 ± 0.06**	0.004 ± 0.02	0.009 ± 0.02	0.032 ± 0.05
Pasture	NGT2	**0.984 ± 0.02**	0.002 ± 0.003	0.003 ± 0.01	0.011 ± 0.02
Pasture	OAI2	**0.966 ± 0.03**	0.004 ± 0.01	0.004 ± 0.01	0.025 ± 0.02
Pasture	OUR2	**0.966 ± 0.04**	0.003 ± 0.01	0.006 ± 0.01	0.024 ± 0.04
Pasture	PNH2	**0.975 ± 0.03**	0.003 ± 0.004	0.004 ± 0.01	0.018 ± 0.03
Forest		0.760 ± 0.24	0.014 ± 0.02	0.024 ± 0.02	0.202 ± 0.24
Pasture		0.970 ± 0.02	0.003 ± 0.01	0.008 ± 0.01	0.019 ± 0.02
Mann-Whitney *U* Test		**0.005**	**0.005**	**0.005**	**0.005**

3.4.7 | Proportional contribution to non-predatory aquatic invertebrates

No distinct differentiation was evident in isotopic space between non-predatory aquatic invertebrates in forest and pasture streams, although variability between invertebrates appeared greater in pasture streams, where some had higher $\delta^{13}C$ values (Figure 3-10). Mean consumable sources for non-predatory aquatic invertebrates showed isotopic overlaps with leaf litter and periphyton for both forest and pasture. However, leaf litter in pasture was less distinct than periphyton (Figure 3-10).

Bayesian mixing models show distinct land-use differences in food sources for non-predatory aquatic invertebrates (Figure 3-11). The dominant food source of non-predatory aquatic invertebrates was leaf litter, contributing an estimated 77% of nutrition in forest streams, whereas periphyton accounted for 73% of nutrition in pasture (Figure 3-11; Table 3-4). Site-specific Bayesian modelling confirmed this pattern. Leaf litter was the dominant food source for non-predatory aquatic invertebrates for all sites in forest (>72%), whereas periphyton was the dominant food source at pasture sites, except at OAI2, where leaf litter contributed around 80% to non-predatory aquatic invertebrate diet. Significant differences were present between leaf litter and periphyton contributions to non-predatory aquatic invertebrates at forest and pasture sites ($p < 0.05$) (Table 3-4).

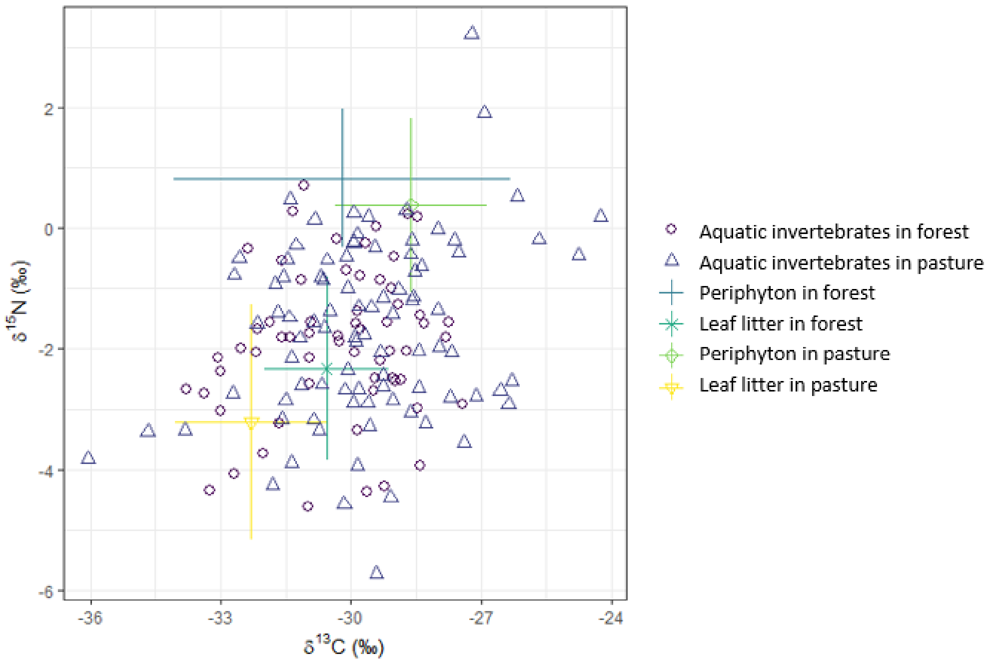


FIGURE 3-10 Dual isotope plot of non-predatory aquatic invertebrates as consumers and their food sources (periphyton and leaf litter) in forest and pasture streams in Taranaki, New Zealand, showing that adjusted food sources encompass the majority of consumers. Trophic discrimination factors (0.4‰ for $\delta^{13}C$ and 3.4‰ for $\delta^{15}N$) has been added to the means for food sources. Error bars are 1 SD, while symbols represent the mean potential food sources for non-predatory invertebrates in each land use.

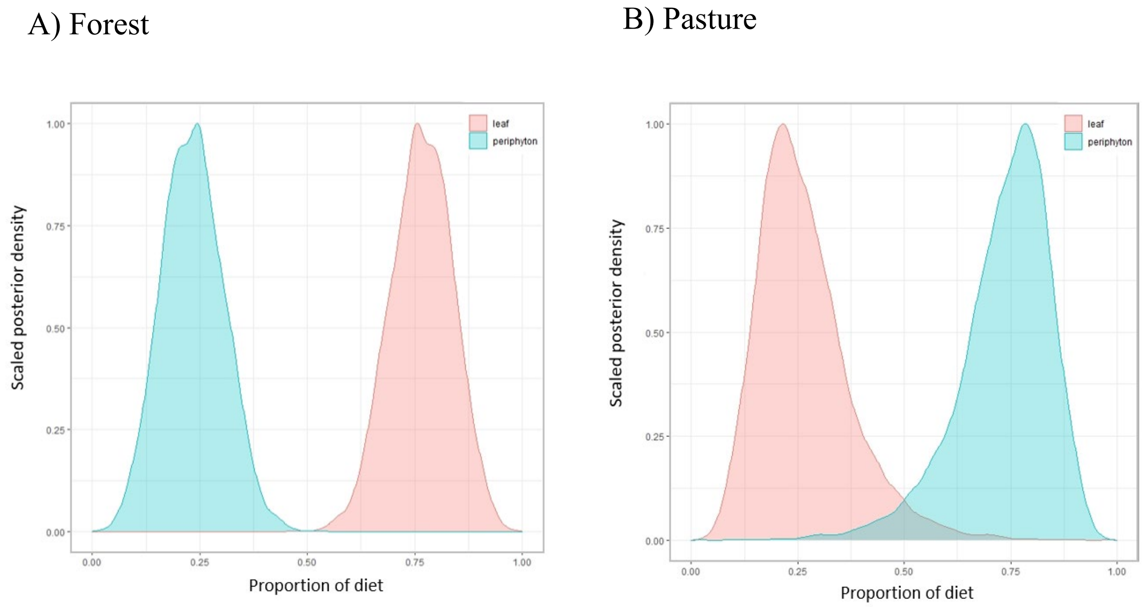


FIGURE 3-11 Proportional contributions of periphyton and leaf litter food sources for non -predatory aquatic invertebrates in forest (A) and pasture (B) streams in Taranaki, New Zealand.

TABLE 3-4 Proportional contribution to non-predatory aquatic invertebrates individual sites and between land uses in Taranaki, New Zealand. Sources include leaf litter and periphyton (mean ± standard deviation). Dominant source contributions and Mann-Whitney *U* significant differences between forest and pasture sources are marked in bold.

Source		**Periphyton**	**Leaf litter**
Land use	**Site**	Mean ± SD	Mean ± SD
Forest	KAP1	0.217 ± 0.09	**0.783 ± 0.09**
Forest	LDC1	0.091 ± 0.07	**0.909 ± 0.07**
Forest	NGT1	0.172 ± 0.10	**0.828 ± 0.10**
Forest	OAI1	0.075 ± 0.06	**0.925 ± 0.06**
Forest	OUR1	0.282 ± 0.11	**0.718 ± 0.11**
Forest	PNH1	0.137 ± 0.09	**0.863 ± 0.09**
Pasture	KAP2	**0.850 ± 0.08**	0.150 ± 0.08
Pasture	LDC2	**0.691 ± 0.11**	0.309 ± 0.11
Pasture	NGT2	**0.581 ± 0.14**	0.419 ± 0.14
Pasture	OAI2	**0.198 ± 0.12**	0.802 ± 0.12
Pasture	OUR2	**0.825 ± 0.09**	0.175 ± 0.09
Pasture	PNH2	**0.614 ± 0.13**	0.386 ± 0.13
Forest		0.234 ± 0.07	0.766 ± 0.07
Pasture		0.734 ± 0.11	0.266 ± 0.11
Mann-Whitney *U* Test		**0.013**	**0.013**

3.5 | DISCUSSION

3.5.1 | Trophic position and food web dynamics

Maximum trophic position was expected to be higher in pasture, consistent with the greater biomass of resources found in pasture streams (Hypothesis I: Chapter 2). However, trophic position of eels was similar between forest and pasture sites, irrespective of resource availability. These results are not consistent with the Productivity Hypothesis (Pimm, 1982), where food chain length is proposed to increase with basal production due to a depletion of available energy at each trophic transfer (Post et al., 2000; Thompson & Townsend, 2004). While basal productivity may be higher in pasture streams, the Productivity Hypotheses does not consider allochthonous energy sources in sustaining productivity of higher trophic levels (Pimm, 1982). As the physical attributes (width and depth) at forest and pasture streams were similar (Chapter 2), these results may be more consistent with findings in Post et al. (2000) where ecosystem size and not resource availability determine food chain length. These food web dynamics were consistent with Canning et al. (2019) who found no differences in aquatic invertebrate trophic network structure in open and forested stream in Taranaki.

While forest and pasture food webs were structurally similar, there was a distinct increase in $\delta^{15}N$ at pasture sites leading to an increase of all food web components approximately by 7.0‰, compared to forest. This increase was probably caused by soil nitrogen dynamics propagating up the food web through N-plant fixation (Stevenson et al., 2010; Mudge et al., 2013). Research on New Zealand soils confirm the general increase of $\delta^{15}N$ in areas of intensive pastoral management associated with greater N inputs and isotope fractionation loss (Mudge et al., 2013). Normalisation of the data permitted the direct comparison of magnitude of $\delta^{15}N$ enrichment, while retaining the compartmental structure to compare energy sources between forest and pasture sites independent of anthropogenic inputs.

3.5.2 | Proportional contribution of sources to fish diet

Comparisons between fish and their potential food sources illustrate the distinct nutritional support provided by crayfish and terrestrial invertebrates under both land uses. These findings indicate that crayfish, in particular, are a major contributor to fish biomass, irrespective of land use. Crayfish are known as a “keystone” species, meaning they exert strong controls on the stream food web structure and functioning (Davic, 2003; Reynolds et al., 2013; Wood et al., 2016), notably by serving as conduits of energy to higher trophic levels (Nyström, 2002; Davic, 2003). The availability of crayfish is likely to have a strong control on fish biomass and this relationship is not confined to land use (Chapter 2). Research on crayfish-eel interactions suggest eels play a reciprocal control on crayfish populations through predation (Aquiloni et al., 2010, Reynolds, 2011). The feeding pressures exerted by eels is evidenced by the proportional contribution to eel diet at forest and pasture sites (> 50%). Aquiloni et al. (2010) investigated the predation rate of *Anguilla anguilla* in relation to crayfish size-class and found predation rate was similar among all crayfish size-class ranges. Feeding pressures, coupled with no preferential prey size range may explain why there is no distinct variation between crayfish biomass between land uses (Chapter 2).

It is often assumed that riparian vegetation provides higher rates of allochthonous inputs of terrestrial subsidies to streams, and that these rates compensate for the observed reduction of basal autotrophic production (e.g., Vannote et al., 1980; Canning et al., 2019; Felden et al., 2021; Roussel et al., 2021, Niles & Hartman, 2021). This study demonstrated that terrestrially derived invertebrates represented a significant energetic subsidy to fish diet in both land uses. Terrestrial inputs of invertebrates are considered a high-quality food resource for fish (Wilson et al., 2014; Brett et al., 2017). Around 45% of fish nutrition in pasture and 48% of fish diet in forest streams was attributed to allochthonous sources of invertebrates. This is consistent with overseas tropical stream systems, where terrestrial invertebrates accounted for half of the diet of the dominant fish species (Small et al., 2013). Recent research suggests that terrestrial invertebrates provide a critical energetic pathway for sustaining fish populations (Niles &

Hartman, 2021) and results suggests that this is consistent irrespective of land use. However, pasture streams in Taranaki support significantly more fish biomass than forest (Chapter 2) and it is possible that fish are largely sustained by the availability of allochthonous and autochthonous food sources in these systems.

Although remnants of aquatic invertebrates were present in guts of fish, they did not represent a significant food source for fish in Taranaki streams. This was unexpected given the correlation between aquatic invertebrate biomass and fish biomass (Chapter 2). No differences were apparent in eel gut contents between forest and pasture streams. This supports the concept that source quality over quantity is perhaps more important in sustaining higher trophic level (Guo et al., 2016a; Guo et al., 2016b).

In-stream temperatures are considered a major factor affecting fish metabolism and required energetic demand (Volkoff & Rønnestad, 2020). Temperatures outside the metabolic scope of certain fish species may result in acute changes in feeding behaviour (Watz et al., 2014; Volkoff, & Rønnestad, 2020). Fish showed an even dependency on each potential food source at OUR1. This forest site had the coldest in-stream temperatures (9.1°C mean annual temperature and 11.2°C mean summer temperature). Results suggest that low average in-stream temperatures may have resulted in more generalist feeding behaviours, where fish exploit a range of available food sources to meet energetic demand (see Chapter 2).

3.5.3 | Proportional contribution of sources to crayfish diet

As discussed above, crayfish were a significant food source for fish at both land uses and likely provide an important intermediary source of energy transfer to fish in Taranaki streams, underscoring the importance of sustaining energy sources for crayfish populations. Crayfish in streams under both land uses showed distinct nutritional support from periphyton, particularly in pasture, where they were almost entirely sustained by periphyton (> 90%). Periphyton is considered to have little structural carbon and is more palatable when compared to leaf litter (Brett et al., 2017). It is likely that crayfish preferentially consume periphyton over other available food sources, due to its higher nutritional value (Sushchik et al., 2006; Guo et al., 2018). Results differed from Parkyn et al. (2001), where crayfish in Waikato streams incorporated energy from both aquatic invertebrates and leaf detritus. They suggested that local habitat and resource availability may alter nutrition selection of crayfish.

The contribution of periphyton to crayfish diet was less and more variable in forested sites, again notably at OUR1, where consumption of terrestrial invertebrates was implicated as the primary means of energetic transfer. In addition to having the coldest in-stream temperatures, OUR1 also had the lowest periphyton biomass, and the second lowest in-stream light intensities of all sites (Chapter 2). Research has shown that algae PUFA is strongly influenced by light and temperature (Guschina & Hardwood, 2009), with high light intensities required for the synthesis of saturated algal fatty acids (Cashman et al., 2013; Guo et al., 2016a). It is possible that the quantities and quality of available periphyton was not sufficient to energetically support crayfish as a sole food source at OUR1, given it was marginally colder in other forested sites (Chapter 2). Notably, this site also had the highest rates of terrestrial invertebrate input of all forested sites (0.58 g m^{-2} day^{-1}; Chapter 2), highlighting the importance of terrestrially derived invertebrates as an alternative food source where crayfish may not be sustained solely by autochthonous basal sources.

3.5.4 | Proportional contribution of sources to non-predatory aquatic invertebrate diet

Although aquatic invertebrates can link the energy transfer from periphyton and leaf litter to upper trophic levels (Guo et al., 2016b), non-predatory aquatic invertebrates in this research showed low contributions, in comparison to other food sources for both crayfish and fish. Nevertheless, there were distinct isotopic transitions between land uses, whereby aquatic invertebrates predominantly acquired more carbon from available leaf litter (77%) over periphyton in forest, shifting to periphyton (73%) over leaf litter ($p < 0.05$) in pasture streams. This suggests that periphyton contributed more carbon than leaf litter for intermediate trophic levels in response to light availability. The feeding pressures and interspecific food competition between crayfish and non-predatory aquatic invertebrates may have resulted in observed variability in periphyton biomass between sites (Chapter 2).

Stable isotopes provide a time-integrated measure of nutritional history and although $\delta^{13}C$ and $\delta^{15}N$ of consumers can change in response to dietary shifts (Sakano et al., 2005; Busst & Britton, 2018), the rate of this turnover can be influenced by seasonal factors, such as temperature (Perga & Gerdeaux, 2003; Hicks et al., 2021). Future research is required to understand seasonal variability in terrestrial and aquatic contributions to stream food webs under distinct land uses, particularly in relation to key life-history events such as fish spawning and migration.

3.5.5 | Study limitations

Stable isotope mixing models have provided a powerful means of analysing the contribution of food sources to consumers (Osada et al., 2021), however, there are limitations to the use and interpretation of these models. For example, Fry (2013), discussed several limitations of using stable isotope mixing models and reviewed approaches to solving underdetermined systems. Underdetermined systems originate when the number of sources is greater than the number of isotopes, or sources fall on the same line within the 'mixing space.' This can lead to uncertainty in model outputs (Parnell et al., 2010; Osada et al., 2021). Upon rebuttal, Semmens et al. (2013) stated that Fry (2013) inaccurately characterised the statistics and interpretation of outputs from more recent Bayesian mixing model tool, such as MixSIAR. In the case of this research, basal sources and combined invertebrate sources presented a high level of variability within sites. This can result in difficulties in interpreting outcomes of actual differences in food groups between forest and pasture sites (Phillips et al., 2014). The site-specific modelling of contributions to fish, crayfish and non-predatory invertebrates reflected similar model outputs to the land-use model, suggesting the variability of basal and aquatic invertebrate food sources did not alter the land use model outcomes.

The variability in sources may be attributed to the use of bulk stable isotope analysis used in this study. Variance in isotopic compositions from bulk isotope analyses can reflect effects from 1) spatial and temporal isotopic variation of basal sources (Schmittner & Somes, 2016), 2) trophic effects from changes in diet and trophic level, and 3) physiological effects from consumer turnover rates and the extent that macromolecules are synthesized (Newsome et al., 2014; Wang et al., 2019). Ecological applications have demonstrated that variation in basal isotope values can produce misleading results when using bulk tissue isotope analysis, which can be resolved with compound specific isotope analyses (CSIA) (Magozzi et al., 2021). CSIA allows for the separation of actively cycling and refractory basal food sources and may facilitate adequate separation of food sources (Whiteman et al., 2019). To accurately overcome the issues discussed above, future research addressing land use variation in source contributions to consumers in streams should consider using CSIA.

A further limitation of this research is that crayfish did not fall within the mixing polygons, therefore, caution should be taken when interpreting model outputs. It is possible that the TDFs did not accurately reflect the difference between the stable isotope ratio of crayfish to its food source, or that all food sources were not quantified in the model. The TDF is a critical parameter used for estimation of food source contributions, and multiple factors can affect the TDFs including food quality, metabolic date, developmental stage, body mass and sex (Bastos et al., 2017). Knowledge of the food sources assimilated into the consumer tissue is a requirement for accurate mixing model outputs. As crayfish are well known for cannibalism by feeding on their smaller counterparts, this food source was not quantified in our model. As a result, the implication of smaller crayfish as a food source reduces the interpretability of model outputs. Research by He et al. (2021) on freshwater crayfish *Procambarus clarkii*, indicated that TDFs were δ^{13}C of -1.98‰ and δ^{15}N of 5.14‰, thus greatly exceeding the variation range of standard TDFs for aquatic animals (Post, 2002). Future research on appropriate TDFs is required to accurately reflect mechanisms of omnivory and cannibalism for New Zealand freshwater crayfish.

3.6 | CONCLUSION

This study showed that trophic structure was similar between forest and pasture sites, irrespective of resource availability and land use. Despite greater proportional biomass found in pasture streams, energy transfer pathways to fish did not vary significantly between land uses, with crayfish and terrestrial invertebrates the dominant food source supporting fish biomass in forest and pasture streams. Results suggest that crayfish may provide an important intermediate source of energy to fish in Taranaki aquatic systems, mediated by the consumption of periphyton. Further, the importance of terrestrially derived invertebrates as a distinct source of nutrition for both crayfish and fish were evident in both forest and pasture streams, particularly at one site with low water temperature. This finding supports recent literature addressing the importance of terrestrially derived invertebrates as a potential alternative food source for fish and crayfish (Brett et al., 2017; Niles & Hartman, 2021), particularly in instances where fish and crayfish may not be sustained solely by autochthonous energy sources. However, further research would be useful to incorporate seasonal changes in terrestrial contributions to forest and pasture sites to determine whether terrestrial invertebrate subsidies are important year-round. Aquatic invertebrates were the only source that showed distinct differences between forest and pasture sites, but they did not significantly contribute to secondary consumers biomass within alternative land uses. Generally, periphyton was the most important basal food source and may support the concept that quality over quantity is the most important attribute contributing towards secondary biomass. Future research could also consider the use of CSIA to address the issues of variation in basal and aquatic invertebrate isotope values observed in this study.

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3.8 | APPENDIX

APPENDIX 3-1 Number of isotopic analyses undertaken for each food web component. Lamprey were depauperate and not analysed in the Bayesian mixing model.

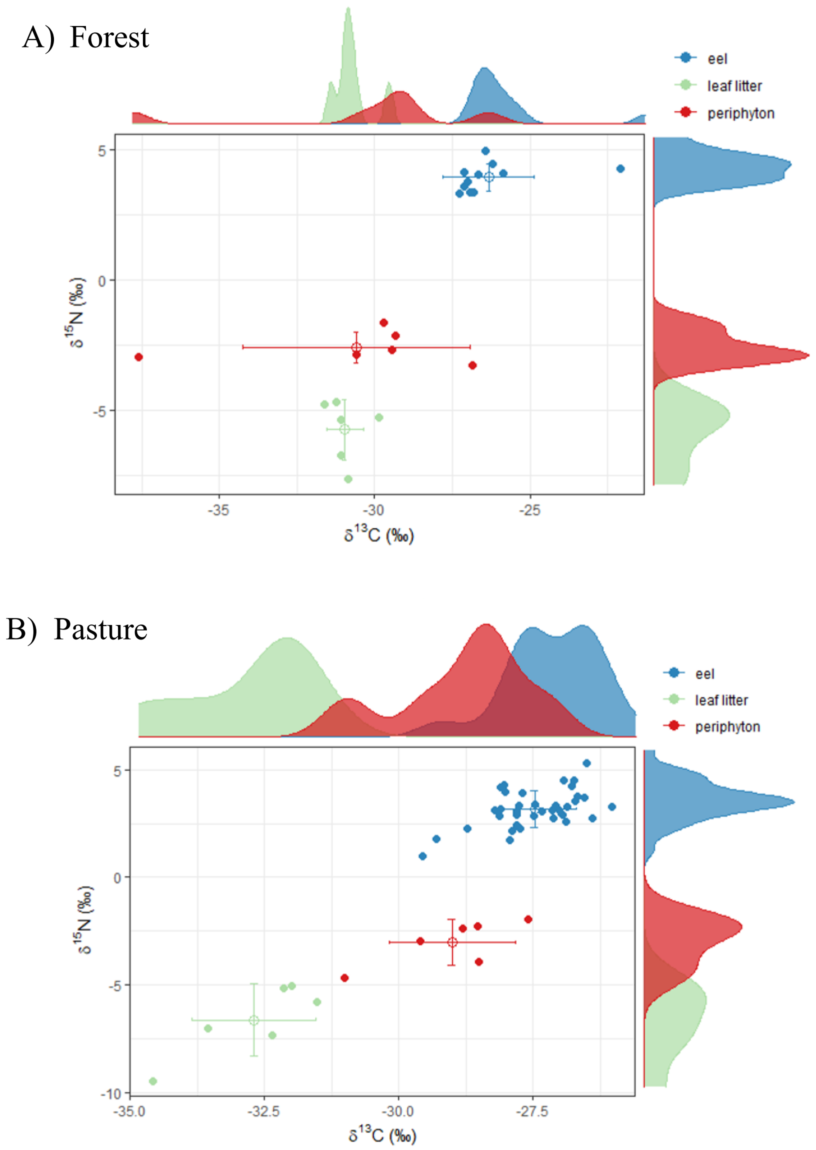
Land use	Aquatic invertebrates	Crayfish	Fish	Lamprey	Leaf litter	Periphyton	Terrestrial invertebrates
Forest	78	16	29	0	6	6	15
Pasture	111	37	70	1	6	6	41

APPENDIX 3-2 Functional feeding groups of aquatic invertebrates sampled in Kapoaiaia, Oaonui, Punehu, Ouri, Little Dunns Creek and Ngatoro Streams, Mount Taranaki. Abbreviation 'npinv' represents non-predatory aquatic invertebrates and 'pinv' represents predatory aquatic invertebrates.

Order or family	Common name	Genus	Functional feeding group	Group
Ephemeroptera	Mayfly	*Deleatidium*	Scraper	npinv
Ephemeroptera	Mayfly	*Nesameletus*	Scraper	npinv
Ephemeroptera	Mayfly	*Rallidens*	Scraper	npinv
Ephemeroptera	Mayfly	*Coloburiscus*	Filter feeder	npinv
Ephemeroptera	Mayfly	*Ichthybotus*	Collector-gatherer	npinv
Ephemeroptera	Mayfly	*Ameletopsis*	Predator	pinv
Ephemeroptera	Mayfly	*Zephlebia*	Scraper	npinv
Ephemeroptera	Mayfly	*Neozephlebia*	Scraper	npinv
Ephemeroptera	Mayfly	*Austroclima*	Scraper	npinv
Ephemeroptera	Mayfly	*Acanthophlebia*	Scraper	npinv
Plecoptera	Stonefly	*Stenoperla*	Predator	pinv
Plecoptera	Stonefly	*Austroperla*	Collector-gather	npinv
Plecoptera	Stonefly	*Megaleptoperla*	Collector-gather	npinv
Plecoptera	Stonefly	*Zelandoperla*	Collector-gather	npinv
Plecoptera	Stonefly	*Zelandobius*	Collector-gather	npinv
Plecoptera	Stonefly	*Acroperla*	Collector-gather	npinv
Megaloptera	Dobsonfly	*Archichauliodes*	Predator	pinv
Trichoptera	Caddisfly	*Orthopsyche*	Filter feeder	npinv
Trichoptera	Caddisfly	*Aoteapsyche*	Filter feeder	npinv
Trichoptera	Caddisfly	*Hydrochorema*	Predator	pinv
Trichoptera	Caddisfly	*Hydrobiosis*	Predator	pinv
Trichoptera	Caddisfly	*Costachorema*	Predator	pinv
Trichoptera	Caddisfly	*Edpercivalia*	Predator	pinv
Trichoptera	Caddisfly	*Polyplectropus*	Filter feeder	npinv
Trichoptera	Caddisfly	*Plectrocnemia*	Filter feeder	npinv
Trichoptera	Caddisfly	*Hydrobiosella*	Predator	npinv
Trichoptera	Caddisfly	*Helicopsyche*	Collector-gather	npinv
Trichoptera	Caddisfly	*Pycnocentrodes*	Collector-gather	npinv
Trichoptera	Caddisfly	*Beraeoptera*	Collector-gather	npinv
Trichoptera	Caddisfly	*Confluens*	Collector-gather	npinv
Trichoptera	Caddisfly	*Pycnocentria*	Collector-gather	npinv
Trichoptera	Caddisfly	*Olinga*	Collector-gather	npinv
Trichoptera	Caddisfly	*Triplectides*	Shredder	npinv
Trichoptera	Caddisfly	*Pycnocentrella*	Collector-gather	npinv
Tipulidae	Crane fly	*Aphrophila*	Shredder	npinv
Tipulidae	Crane fly	*Limonia*	Shredder	npinv
Coleoptera	Beetle	Elmidae	Collector-gather	npinv
Coleoptera	Beetle	Hydraenidae	Collector-gather	npinv
Coleoptera	Water scavenger beetle	Hydrophilidae	Predator	pinv
Mollusca	Snail	*Potamopyrgus*	Scraper	npinv
Mollusca	Snail	*Physa*	Scraper	npinv
Mollusca	Freshwater limpet	*Ferrissia*	Scraper	npinv
Diptera	Chromomid midge	*Maoridiamesa*	Collector-gather	npinv
Diptera	Chromomid midge	*Polypedilum*	Collector-gather	npinv
Diptera	Chromomid midge	*Chironomus*	Collector-gather	npinv
Diptera	Diptera	*Nothodixa* (Dixidae)	Filter feeder	npinv
Diptera	Diptera	*Austrosimulium*	Filter feeder	npinv
Amphipod	Talitridae	Talitridae	Shredder	npinv

APPENDIX 3-3 Normalisation of food web components. The data was normalised by subtracting the lowest $\delta^{13}C$ (-28.75‰) and $\delta^{15}N$ (-0.26‰) for each food web component. Normalisation accounted for the observed magnitude between forest and pasture food webs, while maintaining the relative differences between food-web components.

Site	N	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$ ajusted	$\delta^{13}C$ adjustment	$\delta^{15}N$ ajusted	$\delta^{15}N$ adjustment
KAP1	29	-28.75	1.52	0.00	-28.75	-1.79	-0.26
KAP2	53	-22.92	9.58	-5.83	-28.75	-9.84	-0.26
LDC1	17	-29.35	0.49	0.60	-28.75	-0.75	-0.26
LDC2	38	-26.97	6.81	-1.78	-28.75	-7.08	-0.26
NGT1	24	-27.62	-0.26	-1.13	-28.75	0.00	-0.26
NGT2	36	-27.14	3.23	-1.61	-28.75	-3.49	-0.26
OAI1	29	-26.90	1.84	-1.85	-28.75	-2.11	-0.26
OAI2	54	-26.19	3.22	-2.55	-28.75	-3.48	-0.26
OUR1	36	-27.45	0.55	-1.30	-28.75	-0.82	-0.26
OUR2	40	-24.97	8.35	-3.78	-28.75	-8.61	-0.26
PNH1	31	-27.66	0.24	-1.08	-28.75	-0.51	-0.26
PNH2	35	-26.04	4.91	-2.70	-28.75	-5.18	-0.26



APPENDIX 3-4 Summary dual isotope plot generated in tRophicPosition showing food chain length derived from normalised mean baselines of periphyton and leaf litter compared to eels as top consumers in A) forest and B) pasture streams in Taranaki, New Zealand.

APPENDIX 3-5 Proportional contribution to eel diet at individual sites in Taranaki, New Zealand (mean ± standard deviation). Sources include crayfish, terrestrial invertebrates, and aquatic invertebrates.

	Crayfish	**Terrestrial invertebrates**	**Aquatic invertebrates**
Land use	Mean ± SD	Mean ± SD	Mean ± SD
Forest	0.637 ± 0.11	0.240 ± 0.13	0.122 ± 0.01
Pasture	0.536 ± 0.05	0.373 ± 0.07	0.009 ± 0.08

CHAPTER IV

Longitudinal energy sources, food web dynamics, and fish biomass in mountainous New Zealand streams

Torrentfish (*Cheimarrichthys fosteri*) caught in the Ouri Stream, November 2020

4.1 | ABSTRACT

Stream ecosystems are often conceptualised by models that reflect variations in energy flow along a longitudinal gradient. Stable isotope techniques and Bayesian mixing models were used to evaluate the proportional contribution of allochthonous and autochthonous food sources to trophic levels in three mountainous streams in Taranaki, New Zealand. Changes in longitudinal aquatic biomass and food web dynamics were evaluated to address variations in energy resources with respect to riparian fragmentation.

Taranaki streams showed abrupt changes in response to riparian vegetation rather than gradual longitudinal transitions from allochthonous to autochthonous energy sources. Study streams showed that non-predatory invertebrates favoured leaf litter at the forested boundary but transitioned to periphyton downstream at pasture-dominated sites. The abrupt transition in physical variables at the upstream forest to pasture boundary showed distinct evidence for energetic and functional food web alterations in response to land use. However, non-predatory invertebrates showed a food dominance transition back to allochthonous sources in response to greater riparian vegetation cover at downstream sites. Proportional dietary source transitions were also observed in eel diet, where dominance shifted from aquatic invertebrates to terrestrial invertebrates at vegetated downstream sites. These results reflect more recent conceptualised models derived from the Riverine Ecosystem Synthesis with respect to complexity of patchy riparian dynamics. Marine-derived nitrogen (MDN) was detected in migratory inanga larvae (*Galaxias maculatus*) and shrimp (*Paratya curvirostris*), with these species having comparable $\delta^{15}N$ to resident stream fish at higher trophic levels. The incorporation of MDN was not expressed in higher trophic levels, most likely due to low densities

of inanga and shrimp in the study reaches. This research highlights the importance of riparian shading for the control of physical attributes and food webs along stream continua.

4.2 | INTRODUCTION

Energy sources fuelling stream ecosystems vary with respect to longitudinal, lateral, vertical, and temporal dimensions (Vannote et al., 1980; Miller, 1990; Bravard & Petit, 2009). The connectivity between freshwater, terrestrial and marine realms embodies the nature and extent of energetic resources that support stream fish biomass (Polis et al., 1997). The transportation of external resources across terrestrial and marine landscapes can increase biomass within recipient food webs, beyond what is supported by in-situ production (Muñoz et al., 2021). Therefore, the connectivity across landscapes is paramount for ecological function and resource availability subsidising biomass in streams (Vannote et al., 1980; Hood et al., 2019; Walsh et al., 2020).

The level of connectivity between landscapes and subsequent energy sources can be variable along a longitudinal stream gradient, and several theories have been proposed to account for this. Notably, the River Continuum Concept (RCC) provided foundational theory that has shaped traditional thinking of energetic patterns along stream continua. A key principle of the RCC is the transition of energy from upstream processing to downstream environments, whereby downstream communities capitalise on upstream processing inefficiencies (Vannote et al., 1980). This is assumed to result in predicable downstream changes in community composition and food web structure (Vannote et al., 1980; Hette-Tronquart et al., 2002). However, the RCC has been criticised for its inability to differentiate between natural and land-use discontinuities along longitudinal gradients (Perry & Schaeffer, 1987; Doretto et al., 2020), and its failure to account for energy inputs across novel ecosystem boundaries such as marine-freshwater environments (Doretto et al., 2020). The RCC set a precedent for the development of ecosystem theories predicting how physical, chemical, and biological processes drive energy dynamics along stream continua. For example, the Flood Pulse Concept (FPC) proposed lateral floodplain energetic exchange during periodic flood events (Junk et al., 1989), the Riverine Productivity Model (RPM) highlighted local autochthonous energy generation along the edges of large rivers (Thorp & Delong, 1994). Further, the Nutrient Spiralling Concept (NSC) described biological exchange and retention of nutrients (Webster & Patten, 1979; Webster, (2007) and some tenets of the Riverine Ecosystem Synthesis (RES) incorporated hydrogeomorphic patches along a river continuum representative of functional process zones (Thorp et al., 2006; Thorp et al., 2008). The range of stream ecological concepts relating to energy flow emphasises the complexity of delineating consistent stream patterns both within catchments and across regions.

Stream ecosystems can differ significantly across longitudinal gradients, particularly when the level of connectivity between terrestrial-freshwater environments is fragmented (Thorp et al., 2006; Baruch et al., 2021). Longitudinally, streams can flow through patches of vegetation that can lead to localised alterations in the food web and in-stream processing of coarse particulate carbon subsidies, that are not accounted for within the RCC (Lake et al., 2007; Larsen et al., 2019; Doretto et al., 2020). This is important as fragmented continuum-based processes can influence the concentration of macronutrients and system metabolism (Collins et al., 2018), and intermittent fluxes of external subsides due to the proximal vegetative environment, of which can directly affect the biomass of higher trophic levels (Niles & Hartman, 2021).

Streams draining Mount Taranaki in New Zealand's North Island present a unique environment with abrupt physical transitional zones from native forest to pasture and fragmented riparian vegetation along stream continua (Clarkson et al., 2018). These mountainous streams provide the opportunity to test predictions of longitudinal changes in energy sources and food web structure, based on the RCC and RPM. The importance of evaluating the complete headwater-to-sea gradients is paramount when evaluating predictions of the RCC and the relative contribution of allochthonous and autochthonous sources (Hayden et al., 2016). Although autochthonous sources have been shown to increase along a longitudinal gradient (e.g., Finlay, 2001; Rosi-Marshall & Wallace, 2002), research is increasingly challenging the energetic concepts derived from ecological models in modified stream continuums (e.g., Rosi-Marshall et al., 2016; Brett et al., 2017; Erdozain et al., 2021). For example, Winterbourn et al. (1981), initially raised the hypothesis of whether New Zealand streams can be conceptualised by the RCC, due to inconsistencies with functional traits of aquatic invertebrates and physical attributes when compared to North American Streams, where concepts of the RCC originated. These questions remain prevalent, with recent research suggesting empirical evidence in support of the RCC and other conceptualised models is somewhat lacking (Erdozain et al., 2021).

Stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) provide a powerful tool to characterise and trace resources in stream food webs (Peterson & Fry, 1987; Vander Zanden et al., 1999; Post, 2002; De Carvalho et al., 2017; Hershey et al., 2017). The approaches in analysing stable isotopic data have advanced in recent years (e.g., Phillips et al., 2014; Stock et al., 2018), and have the potential to address such ecological theories in a novel light. Isotopic mixing models can provide insight into the utilisation of food resources by consumers and reflect the structure and functioning of aquatic food webs (Wang et al., 2021). Addressing the proportional contribution of resources to trophic levels may provide insight into the longitudinal transformation of energy predicted by ecological concepts (Finlay & Kendall, 2007). The RCC predicts that downstream communities should capitalise on upstream processing efficiencies (Vannote et al., 1980). In accordance with the RCC, aquatic invertebrate food source dominance should gradually transition from leaf litter to periphyton along a longitudinal gradient reflected in isotopic data (Figure 4-1).

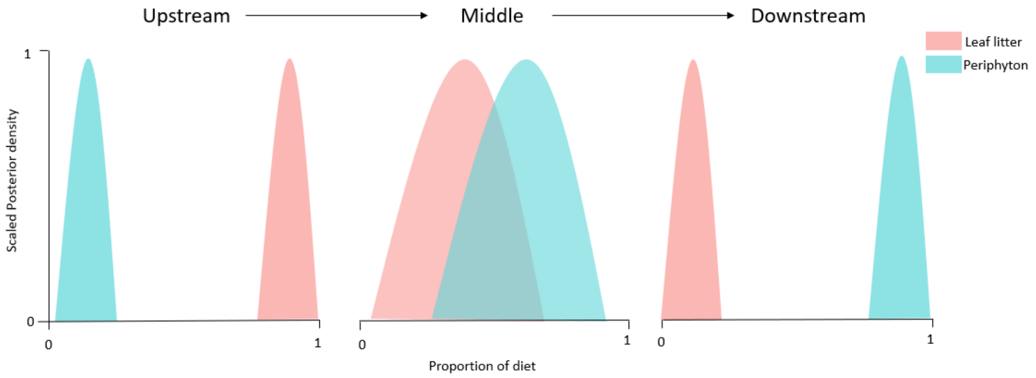


FIGURE 4-1 Conceptual model of proportional food source (leaf litter and periphyton) contributions to non-predatory aquatic invertebrate nutrition given predictions from the River Continuum Concept along a longitudinal gradient (RCC; Vannote et al., 1980). The RCC suggests transition of energy from upstream processing to downstream environments (Vannote et al., 1980), whereby downstream communities capitalise on upstream processing inefficiencies leading to a gradual transition of allochthonous (leaf litter) to autochthonous food sources (periphyton).

As autochthonous sources increase downstream with reducing shade, food chain length should increase (Post et al., 2000; Thompson & Townsend, 2004). For example, the Productivity Hypothesis (Pimm, 1982) proposes that streams with higher basal autochthonous production energetically sustain the higher trophic levels, leading to longer food chain lengths. Maximum trophic position (MTP) is an indicator of food chain length and can be derived from stable isotopes (Post, 2000). Isotopic analysis of trophic position allow for detection of subtle changes in food chain length by integrating the assimilation of energy to the highest trophic level (Post et al., 2002). An expected hypothesis is that maximum trophic position will increase downstream in-line with the RCC and the productivity hypothesis.

The RCC predicts that streams progressively widen leading to less canopy cover with increased primary production and warmer in-stream temperature downstream (Vannote et al., 1980). Warmer in-stream temperatures may increase organic matter decomposition rates (Chapter 2; Enquist et al., 2003; Demars et al., 2011). Enhanced rates of primary production and decomposition can accelerate stream N-uptake promoting isotopic fractionation of periphyton with higher $\delta^{15}N$ than forested streams (Ishikawa et al., 2018; Machado-Silva et al., 2022). Machado-Silva et al. (2022) determined that periphyton tend to assimilate more ^{15}N in high-light environments and concluded that forest removal elevates values of $\delta^{15}N$ of stream ecological components. Moreover, some pasture soils in New Zealand have illustrated a clear increase of $\delta^{15}N$ in response to intensified pastoral agriculture. This has been attributed to soil nitrogen dynamics propagating up the food web through plant fixation (Stevenson et al., 2010; Mudge et al., 2013). Taranaki streams present a distinct gradient from heavily dominated forest to open pasture and provide a unique opportunity to evaluate the longitudinal increases in $\delta^{15}N$. Isotopically, a gradual longitudinal increase in $\delta^{15}N$ reflected by the food web is expected, owning to enhanced primary production (Machado-Silva et al., 2022), increased catchment nitrogen losses (Stevenson et al., 2010; Mudge et al., 2013), sequential in-stream processing in lower reaches (Finlay & Kendall, 2007; Webster, 2007) and the incorporation of marine-derived nutrients (Schindler et al., 2003).

While the RCC conceptualises energy transfer in stream systems with respect to upstream-downstream relationships, streams that support diadromous fish represent potential energy transfer from a downstream-to-upstream direction.

Migratory fish can alter ecological subsidies at certain times of the year through the transport of nutrients across marine-freshwater boundaries, providing a pulsed influx of marine-derived nitrogen (MDN) that can alter stream production (Gresh et al., 2000; Flecker et al., 2010). This key link between marine and freshwater food webs has been well documented overseas, particularly for anadromous species (Kline et al., 1997; Garman & Macko, 1998; Gresh et al., 2000; Hicks et al., 2005; Flecker et al., 2010; Wipfli & Baxter, 2010). The incorporation of marine-derived nutrients has been shown to be incorporated into all freshwater trophic levels (Bilby et al., 1996; Chaloner et al., 2002) as well as to the adjacent terrestrial food web (Bilby et al., 1996; Ben-David et al., 1998; Rammell et al., 2021). Though traditional stream ecological theory does not acknowledge inverse downstream-to-upstream relationships, these data highlight the role MDN may play in stream food webs and supporting secondary biomass. However, there has been limited research on the contribution of MDN by diadromous New Zealand fish, which migrate between freshwater and marine environments to complete their lifecycle (McDowall, 1995).

For many migratory species, the dispersal potential is associated with the ability to transition through habitat boundaries (Cadenasso et al., 2003). For example, streams can cease with an abrupt salinity transition to marine systems, whereas others present a more gradual transition via coastal embayments (Kaemingk et al., 2019). Abrupt transitions may influence the extent of MDN permissible from diadromous fish transitioning into freshwater environments. Recent research on recruiting inanga (*Galaxias maculatus*) in New Zealand estuaries showed larger embayments had higher δ^{15}N and δ^{13}C values with lower biomass than fish recruiting to rivers with abrupt marine-freshwater transitional zones (Kaemingk et al., 2019). Short, incised estuaries are a feature of the Taranaki ring plain, but the longitudinal extent of marine nutrient input from diadromous fish to stream food webs is unknown. While the magnitude of whitebait recruitment may not be comparable to overseas salmon recruitment in biomass, the physical attributes of short, incised estuaries may influence extent of marine-derived nitrogen contribution.

There are several influential factors that may drive energy resources and isotopic variation that challenges conventional thinking behind ecological concepts such as the RCC. This study uses stable isotope analyses (SIA) to investigate energy transfer pathways in Mount Taranaki streams with various scales of riparian fragmentation and considers the large-scale effects of riparian habitat to stream food webs and longitudinal aquatic biomass. Further, the link of marine contribution to stream food webs is explored with the hypotheses that:

i. $\delta^{15}N$ will gradually increase from upstream to downstream independent of riparian fragmentation.
ii. Proportional contribution of resource type to consumer diet will change longitudinally from allochthonous to autochthonous sources consistent with energy dynamics resulting from riparian removal.
iii. Food chain length will increase downstream in response to increased food source availability.
iv. Marine nitrogen from shrimp and native diadromous fish will contribute to the stream food web leading to an increase in $\delta^{15}N$ at lower sites.

4.3 | METHODS

4.3.1 | Study sites

Seventeen sites in Mount Taranaki streams, were chosen within the Kapoaiaia (KAP; *n*=6), Oaonui (OAI; *n*=6) and Ouri (OUR; *n*=5) streams (Figure 4-2). Sites were evenly distributed along each stream and situated approximately 4 km apart following a longitudinal sequence. Longitudinal sites are a continuation of the 'paired' forest and pasture sites from KAP, OAI and OUR sampled in January 2020 (Chapter 2). Sites with codes 3, 4, 5 and 6 were sampled in November 2020 (Figure 4-2; Appendix 4-1). All streams are 4th order, which are expected to have predominately autochthonous energy sources (Vannote et al., 1980; Allan et al., 2021).

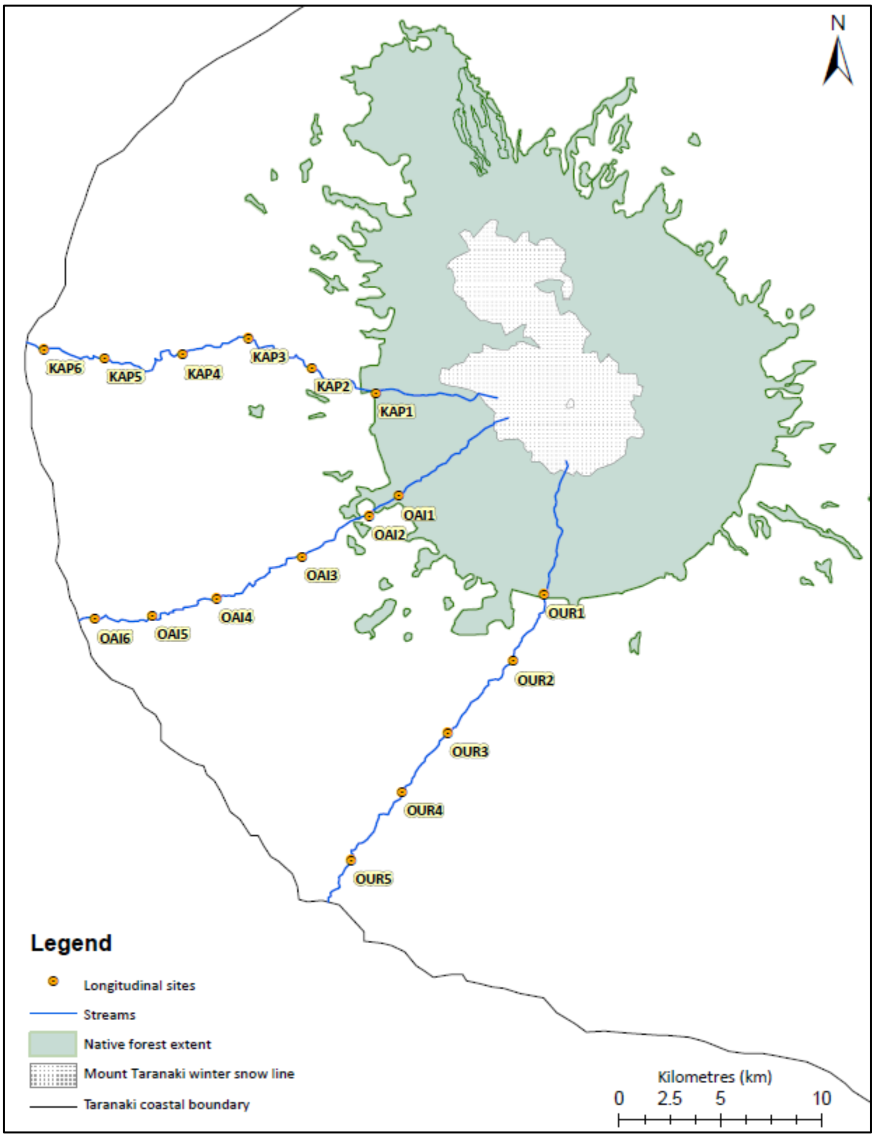


FIGURE 4-2 Location of longitudinal sites in the Kapoaiaia (KAP), Oaonui (OAI) and Ouri (OUR) streams in the Taranaki Region, North Island, New Zealand.

4.3.2 | Physical site attributes and water quality

Two Onset HOBO Pendant MX2202 light and temperature data loggers were deployed at each site (site codes 1 and 2) in November 2019 (Chapter 2) and November 2020 (site codes 3, 4, 5 and 6). One logger was placed in the water and a second logger was placed directly adjacent on the stream bank. Continuous annual light and temperature measurements were taken every 15 minutes. Mean temperature was calculated for the summer period (December, January, and February) for each site.

Sampling following the principles in Stream Ecological Valuation (SEV, Storey et al., 2011) were undertaken at 10-m intervals for 50-m reach lengths at each site using cross-sectional measurements. Variables of channel geomorphology including average stream wetted width and depth were undertaken. Percentage stream shade derived from vegetation and topological features was estimated visually within 5-m intervals at cross section for each site. A YSI ProSolo hand-held meter was used to measure pH, specific conductivity, and dissolved oxygen. Unfiltered and filtered 50-mL water samples were also taken at each site and sent to Hills Laboratories Ltd, Hamilton for nitrogen and phosphorus analysis. The New Zealand Freshwater Fish Database Assistant was used to determine distance of sites from the sea, elevation, and the mean annual water flow at each site using the River Environment Classification 1 dataset.

Contiguous stream riparian margins were mapped, and the area of vegetation estimated using ArcGIS (ESRI Inc., 2020). The contiguous vegetation extent 50 m upstream and 50 m downstream of the site (representative of a 100 m reach) was also estimated using ArcGIS to provide context to the locality of riparian vegetation at sampled sites. To represent the vegetation surrounding forested sites, a 50-m buffer width was specified within a 100-m stream reach surrounding each site to give a maximum vegetated extent of 50 x 100 = 5,000 m^2 (Figure 4-2). Spearman rank correlations between physical and biological variables (see Section 2.3.7) were undertaken in using TIBCO Statistica 13.5 software (TIBCO Software, 2018).

4.3.3 | In-stream biotic sampling

Periphyton was sampled from five randomly selected cobbles (20 – 25 cm) using the quantitative Method QM- 1b (Biggs & Kilroy, 2000). A 15-cm diameter ring was placed centrally on the rock and periphyton within the ring was scraped and pipetted into a container. A combined sample of periphyton from each site was placed on ice in the field for stable isotope analysis. The stable isotope samples were later dried for a minimum of 48 h at 40°C, and ground to a fine, homogenous powder.

Aquatic invertebrates were sampled using a 0.1-m^2 area, 500-µm mesh Surber sampler following the quantitative protocol C3 for hard-bottomed streams detailed in Stark et al. (2001). Four samples were taken and pooled for analysis. Aquatic invertebrates were frozen on site rather than using ethanol as a preservative as ethanol is known to increase δ^{13}C values (Hogsden & McHugh, 2017). Aquatic invertebrates were identified to species level, where possible, using a dissecting microscope and counted and sorted into functional feeding groups (following Ryder & Scott, (1998) as detailed in Manaaki Whenua (1996-2022); Appendix 4-2). The cases of caddisflies and snails (*Potamopyrgus antipodarum* and *Physa*) were removed to account for known carbon discrepancies in shell and animal tissue (Hicks, 1997). Terrestrial invertebrates at Sites 1 and Sites 2 were sampled following protocols described in Chapter 3. At site codes '4', '5' and '6', overhanging riparian vegetation and tall grasses within the 20-m site reach was disturbed using a sweep-net to capture a representative sample of stream-side terrestrial invertebrates for isotope analysis at each site. Aquatic and terrestrial invertebrates were dried at 40°C for at least 48 h to a constant weight. Whole body samples and tissue for each species were ground to a fine homogenous powder, each species was processed separately.

Fish and crayfish (*Paranephrops planifrons*) populations were sampled along a 20-m stream reaches using multiple-pass electrofishing at paired sites (site codes 1 and 2) in January 2020 (Chapter 2), and single-pass fishing at other sites in November 2020. Multiple-pass fishing requires considerable sampling effort, particularly when evaluating longitudinal sequences, as streams progressively deepen and widen downstream (Reynolds et al., 2003; Kauth et al., 2019). Jowett & Richardson (1996) compared first-pass catches with multiple-pass population estimates and reported no differences in capture probability. At the paired upper sites, each reach was blocked with a 5-mm mesh net downstream that was 20-m long and 2-m deep and fished in a downstream direction until there was a reduction in fish between passes (White et al., 1982). All fish were identified to species, counted, and their total lengths measured. A population estimate was derived from the number of fish and crayfish captured at each site and estimated using the Carle and Strub maximum weighted likelihood method in the statistical program R, FSA package (Carle & Strub, 1978; Ogle et al., 2021).

Taranaki stream regression models were generated to produce population estimates for each fish species derived from the first-pass estimates (Chapter 2; Carl & Strub, 1978) ($r^2_{\mathrm{adj}} = 0.964$; $p < 0.001$; Figure 4-3):

fish population estimate = 1.073 x (fish first-pass count)$^{1.131}$ Equation 1.

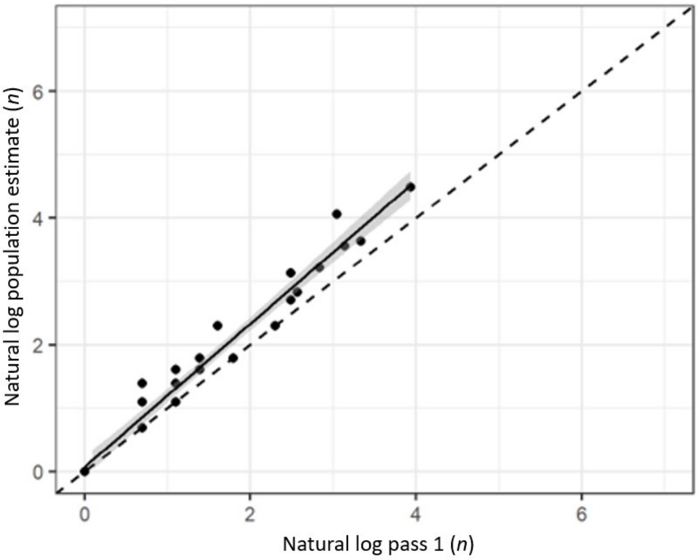


FIGURE 4-3 Regression of fish population estimates against first-pass counts from paired sites in Taranaki streams, New Zealand. Dotted line represents 1:1 relationship. Shading represents 95% confidence limits. *n* represents the total count of fish.

A separate model was generated for crayfish ($r^2_{\text{adj}} = 0.925$; $p < 0.001$; Figure 4-4): crayfish population estimate = 1.751 x (crayfish first-pass count)$^{1.047}$ Equation 2.

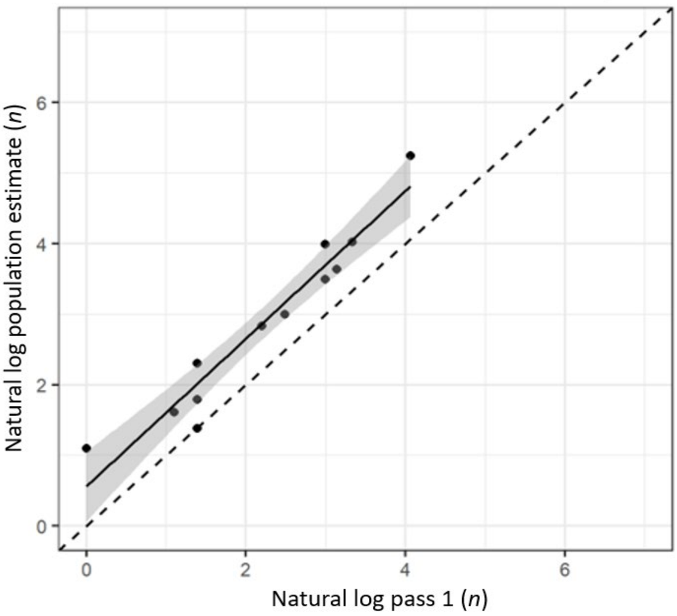


FIGURE 4-4 Regression for crayfish population estimate derived from the first-pass from upstream sites in Taranaki streams, New Zealand. Dotted line represents 1:1 relationship. Shading represents 95% confidence limits. *n* represents the total count of crayfish.

Fish density was calculated using the population estimate divided by the total area fished. The subsequent biomass was then calculated by multiplying the density of fish by the mean fish weight by species for each land use at paired sites (site codes 1 and 2) and dividing each species by the area fished (Chapter 2). For downstream sites (site codes 4, 5 and 6), biomass was calculated by multiplying the density of fish by mean fish weight for each species and site. More individuals were caught at the longitudinal sites, permitting a site-specific species mean to calculate fish biomass at longitudinal sites (Appendix 4-3).

A maximum of five crayfish and shrimp were taken from each site, in addition to non-lethal fin clips from fish species (> 200 mm) for isotope analysis. All samples were frozen prior to laboratory analysis. Muscle tissue from crayfish and shrimp tails were removed from the exoskeleton. Fin clips and tissue were oven dried at 40°C for at least 48 h. All samples of animal tissue and plant tissue were homogenised by using a mortar and pestle.

4.3.4 | Stable isotope analysis

Individual homogenous samples (n = 402) were weighed to 1.5 mg and placed into tin capsules (4.0 x 6.0 mm). Samples with site codes 1 and 2 were analysed using a Europa Scientific Tracermass mass spectrometer with a precision of c. 0.1‰ ^{13}C and 0.3‰ for ^{15}N at the Waikato Stable Isotope unit (WSIU). Samples 3, 4, 5 and 6 were analysed at the Centre of Stable Isotope Biogeochemistry Berkely (CSIB) in California due to the closure of the WSIU. These data were analysed using a CHNOS Elemental Analyzer coupled with a IsoPrime 100 mass spectrometer with the same precision of c. 0.1% ^{13}C and 0.3% for ^{15}N. Ratios of ^{13}C/^{12}C and ^{15}N/^{14}N were expressed relative to standards with the equation below:

$$\delta X = \left[\frac{R_{\mathrm{sample}}}{R_{\mathrm{standard}}} - 1 \right] \mathrm{x}\, 1000,$$

where X = ^{13}C or ^{15}N, and R = ^{13}C/^{12}C or ^{15}N/^{14}N. The ratio of ^{13}C to ^{12}C was compared to the PDB standard, for which R_{standard} = 1.1237 atom % ^{13}C (Craig, 1957). For ^{15}N/^{14}N, N_2 in air was used as the standard, and R_{standard} = 0.3663 atom % ^{15}N (Mariotti, 1983).

Fish fin tissue provide comparable δ^{13}C and δ^{15}N signatures to fish muscle, therefore, no conversion correction was applied to fish fin tissue (McIntosh & Reid, 2021). Lipids were not chemically extracted from the samples, so a lipid correction was applied to fish with a C:N ratio of ≥ 3.5 to account for the decrease in δ^{13}C caused by lipid content (McConnaughey & McRoy, 1979; Sweeting et al., 2006; Post & Takimoto, 2007; Logan et al., 2008; Hoffman et al., 2015; Hicks et al., 2021). Corrections of benthic invertebrates for the application of Bayesian mixing models were avoided to reduce bias within the model and no correction was applied to leaf litter or periphyton (Post et al., 2007; Arostegui et al., 2019; Silberberger et al., 2021). Dual isotope plots were produced using the statistical programme R studio to visualise the food web structure at stream sites in a longitudinal sequence.

4.3.4.1 | Food chain length

Food chain length was calculated as the number of trophic steps from the basal resources to the top predator (i.e., eels; Hicks, 1997), which can be summarised as maximum trophic position (MTP) in a food web (Post et al., 2002). MTP was calculated using a Bayesian model in the tRophicPositon package in R (Quezada-Romegialli et al., 2018). The dual baseline approach was used to discriminate among leaf litter (baseline 1) and periphyton (baseline 2) in the model.

The maximum trophic position (MTP) and dual baseline equation are summarised below (Vander Zanden et al., 1999; Post et al., 2002; Quezada-Romegialli et al., 2018):

$$\delta^{15}N = \Delta N\ (MTP + \lambda + \alpha\ (\delta^{15}N_{baseline1} + \delta^{15}N_{baseline2}) - \delta^{15}N_{baseline2}, \qquad \text{Equation 3}$$

where $\alpha = ((\delta^{13}C_{baseline2} - (\delta^{13}C_{consumer} + \Delta C))\ /\ (MTP - \lambda))\ (\delta^{13}C_{baseline2} + \delta^{13}C_{baseline1})$, and λ is the trophic position (TP) of the baseline (λ=1), and, ΔN represents average trophic increase in $\delta^{15}N$ per trophic step (3.4‰), and ΔC is the average trophic increase in $\delta^{13}C$ per trophic step (0.4‰).

Trophic discrimination factors (TDF) of 0.4 ± 1.3 ‰ for $\delta^{13}C$ and 3.4 ± 0.9 ‰ for $\delta^{15}N$ were used in the model (Post, 2002; Quezada-Romegialli et al., 2018). Markov Chain-Monte Carlo (MCMC) simulations were set to 10,000 interactions with a burn in of 10,000. Gelman diagnostics were close to 1 and indicated that model convergence was achieved (Gelman & Rubin, 1992; Quezada-Romegialli et al., 2018).

4.3.4.2 | Isotope mixing model

Consumable food sources were defined in the mixing model as the lower trophic positions analysed from the isotopic biplots. Longfin eels (*Anguilla dieffenbachii*) and shortfin eels (*Anguilla australis*) represent the top consumers in New Zealand streams and were combined in the isotopic dietary analysis (Hicks, 1997). For eels, consumable sources included aquatic and terrestrial invertebrates and combined crayfish and shrimp (*Paratya curvirostris*). To avoid the problem of saturated food sources (*sensu* Phillips et al., 2005), food sources were grouped by related source type into Forest (site 1), Pasture upper (site 2 and site 3) and Pasture lower (site 4, 5 and 6) for each individual stream. Aquatic invertebrates within each land-use group represented similar isotopic source signatures as shown by the isotopic biplots to ensure functional significance within each model (Phillips et al., 2005). In instances where crayfish and terrestrial invertebrates were not caught or where low sample size occurred, grouping by location within each stream allowed for a representative mean of each food source type and allowed for a complete crustacean trophic group.

Predatory aquatic invertebrates were restricted to *Hydrobiosis, Archichauliodes*, *Stenoperla* and *Ameletopsis* (Appendix 4-2). Non-predatory aquatic invertebrates represent an intermediary food source so were analysed to evaluate consumed basal sources of leaf litter and periphyton at each land use and site. Trophic discrimination factors (TDF) of 0.4 ± 1.3 ‰ for C and 3.4 ± 0.9 ‰ for N was applied to address dietary contributions for consumers (Post, 2002; Quezada-Romegialli et al., 2018).

Longitudinal site models were run using the JAGS 4.3.0 (2017) model using Markov Chain Monte Carlo (MCMC) simulations with a chain length of 100,000 and burn length of 50,000 for each model. Geweke and Gelman diagnostics (convergence diagnostic) were run for all models to determine suitability of burn-in period were appropriate for each mixing model. The Geweke diagnostics were within the 5% outside ± 1.96 range in each chain, while Gelman diagnostics were all close to 1 for all models indicating adequate MCMC convergence (Gelman & Rubin, 1992).

4.4 | RESULTS

4.4.1 | Physical site attributes

The Oaonui Stream had the largest catchment area (38.3 km^2) and the Kapoaiaia Stream the smallest (19.3 km^2) (Table 1). Kapoaiaia and Ouri streams represented similar catchment size. However, mean annual flow was lowest at the Ouri Stream, when compared to both Kapoaiaia and Oaonui streams. Overall, the Oaonui Stream showed the highest mean annual flows (1.26 $m^3 s^{-1}$), consistent with larger catchment area. The mean water width increased marginally from upstream to downstream at all sites, however stream widths were widest at mid-elevations for all streams (Table 4-1).

pH was circumneutral (6.5–7.5) at lower sites but more alkaline (pH > 8) at several upper sites, notably in the Oaonui Stream (Table 4-1). pH showed an increase with elevation (r = 0.515), while specific conductivity decreased with elevation across sites (r = -0.574) (Table 4-3). Dissolved oxygen was 100.0-109.2% saturated across all sites and was inversely related to stream shade (Table 4-1; Table 4-2). Total nitrogen (TN) was highest at lower elevations for all streams but otherwise showed no trends. Total phosphorus (TP) values were low with no longitudinal trends. The highest readings of TN and TP were recorded at KAP6 (2.30 g m^{-3} and 0.17 g m^{-3}, respectively), where the site was adjacent to an effluent pond, suggesting nutrient leakage from the pond (Table 4-1).

TABLE 4-1 Physical attributes taken during December 2019, 2020, January, and February 2020 and 2021 for Kapoaiaia, Oaonui and Ouri streams in the Taranaki Region, New Zealand. Mean annual flow at each site was determined using the River Environment Classification 1 dataset.

Stream	Site	Elevation (m)	Distance from sea (km)	Catchment area (km^2)	Mean annual flow (m^3s^{-1})	Mean water width (m)	Mean depth (m)	pH	Specific conductivity ($\mu S\ cm^{-1}$)	Dissolved oxygen (%)	Total nitrogen ($g\ m^{-3}$)	Total phosphorus ($g\ m^{-3}$)
Kapoaiaia	KAP1	400	22.6	5.8	0.54	3.04	0.27	7.4	91.9	100.0	0.16	0.009
	KAP2	257	19.3	8.5	0.68	5.96	0.26	8.5	112.7	109.2	0.18	0.038
	KAP3	186	14.4	12.7	0.87	8.42	0.30	8.1	77.5	100.6	0.17	0.039
	KAP4	131	10.2	15.3	0.94	9.94	0.28	8.3	86.4	101.7	0.31	0.033
	KAP5	70	5.6	19.3	1.02	7.74	0.31	6.9	93.3	101.3	0.14	0.077
	KAP6	12	0.8	19.3	1.02	7.12	0.57	6.9	127.3	100.9	2.30	0.166
Oaonui	OAI1	375	20.6	6.6	0.42	5.92	0.24	8.5	106.4	101.5	0.11	0.060
	OAI2	294	18.9	6.6	0.51	5.24	0.21	10.3	120.4	104.0	0.11	0.067
	OAI3	225	16.4	11.2	0.72	7.14	0.31	6.8	154.5	100.9	0.11	0.045
	OAI4	132	12	17.1	0.85	6.08	0.28	6.9	212.5	103.8	0.42	0.028
	OAI5	41	4.3	30.8	1.14	7.96	0.40	6.9	215.9	106.2	0.39	0.016
	OAI6	8	0.7	38.3	1.26	4.20	0.29	7.2	228.5	107.5	0.55	0.019
Ouri	OUR1	425	22.1	6.0	0.45	4.94	0.19	7.3	89.6	100.8	0.23	0.053
	OUR2	297	18.6	6.0	0.45	4.24	0.25	7.6	97.0	105.8	0.18	0.037
	OUR3	175	12.5	9.9	0.55	6.28	0.38	6.7	130.1	105.3	0.26	0.018
	OUR4	109	8.1	12.4	0.59	4.06	0.62	6.7	150.3	100.7	0.30	0.089
	OUR5	35	2.3	20.9	0.69	5.84	0.25	6.8	194.7	102.4	0.97	0.027

4.4.1.1 | Riparian vegetation

Surrounding contiguous vegetation at the Kapoaiaia, Oaonui and Ouri stream sites represented a mix of native and exotic vegetation, including native riparian planting and remnant native bush (e.g., tawa (*Beilschmiedia tawa*), kohekohe (*Didymocheton spectabilis*), rewarewa (*Knightia excelsa*), hinau (*Elaeocarpus dentatus*) and mixed podocarp species; Taranaki Regional Council, n.d; Singers & Rogers, 2014). Mapped stream-bank vegetation (mixed native and exotic forest and scrub) indicated the Ouri Stream had the largest extents of surrounding vegetation (estimated as 50.8 ha) with vegetation extents increasing towards the coast at OUR4 and OUR5. In comparison to other streams, the Ouri Stream had the least fragmented vegetation and showed the highest extent of riparian vegetation downstream around OUR5 (4067 m^2; Table 4-2). Longitudinally, Oaonui Stream had the most fragmented vegetation, showing the lowest riparian vegetation (estimated as 18.9 ha) and the lowest proportional riparian vegetation surrounding sites (Table 4-2). Estimated proportion of stream vegetation at Kapoaiaia Stream was 42.3 ha, although vegetation was distinctly fragmented with broader riparian vegetation bands located at mid elevations (Figure 4-5; Table 4-2). The riparian vegetation extent was comparable to the Ouri Stream, probably because of the sinuosity of the Kapoaiaia Stream (Figure 4-5).

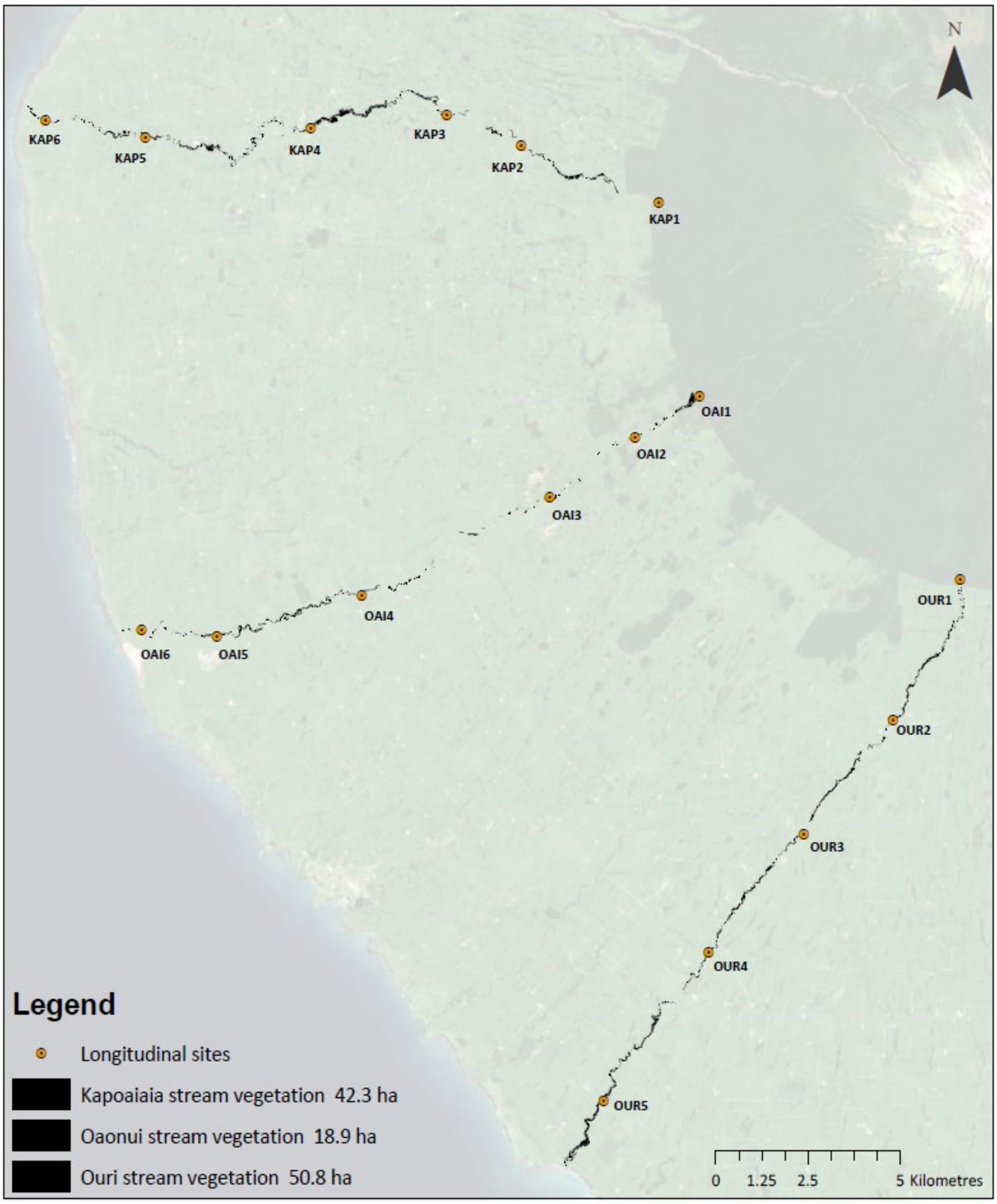


FIGURE 4-5 Mapped stream vegetation (native and exotic forest and scrub) at the Kapoaiaia, Oaonui and Ouri streams and estimated area (ha) calculated in ArcGIS. Service credit layer; Eagle Technology, Land information New Zealand. Projection NZGD 2000 New Zealand Transverse Mercator.

4.4.1.2 | Water temperature and light availability

Mean water and air temperature gradually increased downstream, resulting in a significant correlation between these variables (*r* = 0.708) (Table 4-2; Table 4-3). The Oaonui Stream showed relatively low mean temperatures, despite longitudinal vegetation fragmentation (Table 4-2; Figure 4-5). Mean summer water temperatures were inversely related to elevation and estimated riparian vegetation (Table 4-2; Table 4-3).

Stream shade was consistent with summer bank light intensities and negatively correlated with mean summer water temperature (*r* = -0.579), mean summer air temperature (*r* = -0.755), mean summer bank light intensity (*r* = -0.765) (Table 4-3). Mean summer water temperature was correlated with estimated riparian vegetation (*r* = -0.592), mean summer air temperature (*r* = 0.708), mean summer bank light intensity (*r* = 0.625) (Table 4-3).

TABLE 4-2 Water and air temperature, in-stream and bank light intensities, stream shading estimates at longitudinal sites in the Kapoaiaia, Oaonui and Ouri streams in the Taranaki Region, New Zealand. Data for temperature and light show means for summer (December, January, and February). Vegetation within 50 m upstream and 50 m downstream of each site and 25 m each side was estimated using ArcGIS.

Stream	**Site**	**Mean summer water temperature (°C)**	**Mean summer air temperature (°C)**	**Mean summer instream light intensity PAR (μmol m^{-2} s^{-1})**	**Mean summer bank light intensity PAR (μmol m^{-2} s^{-1})**	**Stream shade (%)**	**Estimated contiguous vegetation within 100m proximity of site (m^2)**
Kapoaiaia	KAP1	12.6	13.9	1.1	4.9	81	5000
	KAP2	16.8	23.0	168.9	389.6	7	6
	KAP3	15.9	16.8	56.7	60.6	5	76
	KAP4	16.4	17.5	77.1	44.6	20	2375
	KAP5	17.8	19.6	21.3	249.1	8	169
	KAP6	18.0	19.1	105.7	58.5	10	31
Oaonui	OAI1	14.9	15.2	104.0	35.4	78	5000
	OAI2	16.9	22.3	56.9	307.7	8	9
	OAI3	15.9	15.9	88.0	38.9	10	166
	OAI4	15.4	16.0	9.6	14.5	40	2201
	OAI5	15.8	16.4	98.2	61.2	10	59
	OAI6	17.9	19.5	72.2	216.9	2	7
Ouri	OUR1	11.2	13.5	6.3	6.2	80	5000
	OUR2	15.4	20.0	254.8	197.5	2	20
	OUR3	14.9	17.4	16.7	91.7	15	86
	OUR4	16.5	16.8	126.7	42.6	18	1791
	OUR5	16.1	16.9	38.5	98.4	45	4067

TABLE 4-3 Spearman rank correlation of physical site attributes at longitudinal sites in the Kapoaiaia, Oaonui and Ouri streams on Mount Taranaki, New Zealand. Statistically significant differences ($p < 0.05$) are marked in bold. Estimated riparian vegetation is the vegetation within 50 m upstream and downstream of the site.

	Elevation	**Mean summer water temperature (°C)**	**Mean summer air temperature (°C)**	**Mean summer in-stream light intensity (µmol m^{-2} s^{-1})**	**Mean summer bank light intensity (µmol m^{-2} s^{-1})**	**Stream shade (%)**	**Estimated riparian vegetation (m^2)**	**pH**	**Specific conductivity (µS cm^{-1})**	**Dissolved oxygen (%)**	**Total nitrogen (g m^{-3})**	**Total phosphorus (g m^{-3})**
Elevation	1.000	**-0.657**	-0.319	-0.145	-0.341	0.279	0.295	**0.515**	**-0.574**	-0.242	**-0.713**	0.042
Mean summer water temperature (°C)	**-0.657**	1.000	**0.708**	0.426	**0.625**	**-0.579**	**-0.592**	0.014	0.235	0.216	0.222	0.439
Mean summer air temperature (°C)	-0.319	**0.708**	1.000	0.422	**0.909**	**-0.755**	**-0.776**	0.256	0.022	**0.586**	0.079	0.169
Mean summer in-stream light intensity (µmol m^{-2} s^{-1})	-0.145	0.426	0.422	1.000	0.336	-0.476	**-0.511**	0.159	0.145	0.325	0.028	0.350
Mean summer bank light intensity (µmol m^{-2} s^{-1})	-0.341	**0.625**	**0.909**	0.336	1.000	**-0.765**	**-0.769**	0.167	0.162	**0.668**	0.012	0.047
Stream shade (%)	0.279	**-0.579**	**-0.755**	-0.476	**-0.765**	1.000	**0.901**	-0.175	-0.100	-0.469	0.059	-0.127
Estimated riparian vegetation (m^2)	0.295	**-0.592**	**-0.776**	**-0.511**	**-0.769**	**0.901**	1.000	-0.159	-0.290	**-0.617**	-0.087	-0.052
pH	**0.515**	0.014	0.256	0.159	0.167	-0.175	-0.159	1.000	**-0.552**	0.143	-0.429	0.093
Specific conductivity (µS cm^{-1})	**-0.574**	0.235	0.022	0.145	0.162	-0.100	-0.290	**-0.552**	1.000	**0.492**	0.472	-0.252
Dissolved oxygen (%)	-0.242	0.216	**0.586**	0.325	**0.668**	-0.469	**-0.617**	0.143	**0.492**	1.000	0.248	-0.373
Total nitrogen (g m^{-3})	**-0.713**	0.222	0.079	0.028	0.012	0.059	-0.087	-0.429	0.472	0.248	1.000	-0.274
Total phosphorus (g m^{-3})	0.042	0.439	0.169	0.350	0.047	-0.127	-0.052	0.093	-0.252	-0.373	-0.274	1.000

4.4.2 | Aquatic biomasses and densities

Ten species of fish were caught and included longfin eel and shortfin eel, redfin bully (*Gobiomorphus huttoni*), lamprey (*Geotria australis*), brown trout (*Salmo trutta*), shortjaw kokopu (*Galaxias postvectis*), bluegill bully (*Gobiomorphus hubbsi*), kōaro (*Galaxias brevipinnis*), inanga (*Galaxias maculatus*) and torrentfish (*Cheimarrichthys fosteri*). Longfin eels produced the highest densities and biomasses in all streams (Table 4-4; Table 4-5). Redfin bullies were present at all sites in the Kapoaiaia and Oaonui streams and the species was only present at the lowest sites of the Ouri Stream. However, OUR5 had comparably higher densities than both Kapoaiaia and Oaonui streams (Table 4-4; Table 4-5).

Crayfish densities and biomasses declined downstream in both the Kapoaiaia and Oaonui streams, with some sites on the lower reaches yielding no crayfish (Table 4-4; Table 4-6). Ouri Stream had the highest densities and biomasses of crayfish when compared to Kapoaiaia and Oaonui streams. Although no crayfish were caught at sites closest to the coast in the Kapoaiaia and Oaonui streams, crayfish presence has been recorded at downstream sites of all streams (Crow, 2017), so was likely an artefact of our sampling (Table 4-4; Table 4-6).

TABLE 4-4 Density of fish and crayfish at longitudinal sites in streams in the Taranaki region, New Zealand. Total fish and crayfish densities are shown in bold.

	Density (number 100 m^{-2})											
Site	**Longfin eel**	**Shortfin eel**	**Redfin bully**	**Lamprey**	**Brown trout**	**Shortjaw kokopu**	**Bluegill bully**	**Kōaro**	**Inanga**	**Torrentfish**	**Total fish**	**Crayfish**
KAP1	8.2	1.6	3.3	0.0	1.6	0.0	0.0	0.0	0.0	0.0	**14.8**	**16.4**
KAP2	29.4	36.1	48.7	0.8	0.0	0.0	0.0	0.0	0.0	0.0	**114.9**	**16.8**
KAP3	54.4	62.9	22.1	3.1	1.4	0.0	0.0	0.0	0.0	0.0	**143.8**	**84.9**
KAP4	135.1	25.3	78.8	1.2	0.0	0.0	0.0	0.0	0.0	0.0	**240.4**	**37.5**
KAP5	68.4	113.9	39.9	5.3	0.0	0.0	0.0	0.0	0.7	0.0	**228.2**	**12.6**
KAP6	61.1	61.1	35.9	12.7	0.0	0.0	0.0	0.0	0.0	0.0	**170.8**	**0.0**
OAI1	0.8	0.8	19.4	0.0	0.0	0.0	0.0	5.1	0.0	0.0	**26.2**	**2.5**
OAI2	36.3	9.5	84.9	0.0	0.0	2.9	1.9	0.0	0.0	0.0	**135.5**	**3.8**
OAI3	77.1	117.3	23.5	1.6	1.6	0.0	0.0	0.0	0.0	0.0	**221.2**	**69.1**
OAI4	83.7	21.7	14.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	**120.1**	**0.0**
OAI5	120.4	93.0	28.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	**242.2**	**0.0**
OAI6	98.5	204.9	4.0	0.0	0.0	0.0	0.0	0.0	6.3	0.0	**313.7**	**0.0**
OUR1	1.0	0.0	0.0	0.0	3.0	0.0	0.0	4.1	0.0	0.0	**8.1**	**38.5**
OUR2	20.0	1.2	0.0	0.0	2.4	0.0	0.0	0.0	0.0	0.0	**23.6**	**38.9**
OUR3	132.4	12.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.5	**146.8**	**135.2**
OUR4	41.3	10.0	17.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	**69.2**	**102.6**
OUR5	80.9	15.5	113.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	**209.8**	**36.4**

TABLE 4-5 Areal biomass of fish at longitudinal sites in streams.

	Areal biomass (g m^{-2})									
Site	**Longfin eel**	**Shortfin eel**	**Redfin bully**	**Lamprey**	**Brown trout**	**Shortjaw kokopu**	**Bluegill bully**	**Kōaro**	**Inanga**	**Torrentfish**
KAP1	12.37	0.09	0.40	0.00	1.63	0.00	0.00	0.00	0.00	0.00
KAP2	27.91	1.25	1.99	0.01	0.00	0.00	0.00	0.00	0.00	0.00
KAP3	8.22	3.84	0.45	0.03	0.01	0.00	0.00	0.00	0.00	0.00
KAP4	24.01	0.96	1.67	0.01	0.00	0.00	0.00	0.00	0.00	0.00
KAP5	139.02	5.75	0.65	0.05	0.00	0.00	0.00	0.00	0.03	0.00
KAP6	75.24	6.38	0.48	0.13	0.00	0.00	0.00	0.00	0.00	0.00
OAI1	0.65	0.02	1.20	0.00	0.00	0.00	0.00	1.35	0.00	0.00
OAI2	39.20	0.38	3.95	0.00	0.00	4.77	0.06	0.00	0.00	0.00
OAI3	9.71	4.35	0.27	0.00	0.01	0.00	0.00	0.00	0.00	0.00
OAI4	5.77	0.44	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00
OAI5	8.35	8.66	0.41	0.00	0.00	0.00	0.00	0.00	0.01	0.00
OAI6	723.79	50.53	0.06	0.00	0.00	0.00	0.00	0.00	0.09	0.00
OUR1	0.94	0.00	0.00	0.00	1.85	0.00	0.00	1.29	0.00	0.00
OUR2	26.78	0.06	0.00	0.00	4.89	0.00	0.00	0.00	0.00	0.00
OUR3	121.37	0.46	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.61
OUR4	102.47	2.03	1.31	0.00	0.00	0.00	0.00	0.00	0.00	0.00
OUR5	68.49	0.59	3.66	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Total fish biomass was greatest in the Oaonui Stream, largely due to the significant increase in fish biomass at OAI6 (Table 4-6). Both the Kapoaiaia and Oaonui streams had increased total fish biomass at sites closest to the coast, while the Ouri Stream showed the highest biomass at mid-stream sites (OUR3 and OUR4) and a decrease at the site closest to the coast (OUR5) (Table 4-6).

Aquatic invertebrate biomass increased with decreasing elevation (Table 4-6). Periphyton biomass also increased downstream, but there was considerable variability within the data. Despite similar longitudinal trends between periphyton and invertebrate biomasses, there were no significant correlations (*r* = 0.311; Table 4-7).

TABLE 4-6 Total periphyton, aquatic invertebrate, crayfish, and fish biomasses at longitudinal stream sites in Taranaki. Periphyton and aquatic invertebrate biomasses are based on pooled samples at each site.

Site	Fish biomass (g m^{-2})	Crayfish biomass (g m^{-2})	Aquatic invertebrate biomass (g m^{-2})	Periphyton biomass (g m^{-2})
KAP1	14.48	1.06	0.96	1.21
KAP2	31.16	0.59	3.04	8.48
KAP3	12.55	2.15	9.18	9.79
KAP4	26.66	0.64	4.80	8.17
KAP5	145.51	0.62	10.28	10.03
KAP6	82.23	0.00	7.32	15.12
OAI1	3.23	0.08	0.40	9.60
OAI2	48.35	0.15	1.68	23.64
OAI3	14.35	2.13	2.88	6.00
OAI4	6.30	0.00	2.64	5.45
OAI5	17.43	0.00	3.98	6.75
OAI6	774.47	0.00	8.13	5.88
OUR1	4.08	1.52	1.05	0.81
OUR2	31.73	1.91	1.88	1.75
OUR3	122.44	2.80	3.63	3.91
OUR4	105.82	6.30	6.03	6.67
OUR5	72.73	1.20	7.22	7.41

Fish biomass, aquatic invertebrate biomass and periphyton biomass were significantly correlated with water temperature for longitudinal sites (Table 4-7). Other significant correlations between aquatic invertebrate biomass included elevation (*r* = -0.831) and fish biomass (*r* = 0.615). Periphyton biomass was significantly correlated with total phosphorus (*r* = 0.561) (Table 4-6; Table 4-7), suggesting that phosphorus increased periphyton biomass. No significant correlations were found with crayfish biomass (Table 4-7).

TABLE 4-7 Spearman rank correlation of physical site attributes an aquatic biomass for longitudinal sites in Kapoaiaia, Oaonui and Ouri streams on Mount Taranaki, New Zealand. Only variables with significant correlations are presented. Statistically significant differences ($p < 0.05$) are marked in bold.

	Fish biomass (g m^{-2})	**Crayfish biomass (g m^{-2})**	**Aquatic invertebrate biomass (g m^{-2})**	**Periphyton biomass (g m^{-2})**
Elevation	**-0.637**	0.319	**-0.831**	-0.316
Mean summer water temperature (ºC)	**0.654**	-0.327	**0.662**	**0.679**
Mean summer air temperature (ºC)	**0.669**	-0.160	0.409	0.475
Mean summer bank light intensity (µmol m^{-2} s^{-}	**0.654**	-0.132	0.436	0.456
Total phosphorus (g m^{-3})	0.054	0.068	0.120	**0.561**
Aquatic invertebrate biomass (g m^{-2})	**0.668**	0.014	1.000	0.311
Fish biomass (g m^{-2})	1.000	0.027	**0.615**	0.181

4.4.2.1 | Proportion of aquatic invertebrate functional feeding groups

The most common functional feeding types of macroinvertebrates in New Zealand are collector-gathers, filter feeders, scrapers, predators, and shredders. Shredder species present in Taranaki streams included *Triplectides*, *Limonia* and species of amphipods (Talitridae) (Appendix 4-2). All streams had a low proportion of shedders, especially in the Oaonui Stream. Predators were proportionally consistent across sites but were < 10% of the total number of individuals in each stream and were largely absent from sites closest to the coast. All streams showed an increasing proportion of collector-gatherers from forest to pasture. The Kapoaiaia Stream had a distinct longitudinal reduction in the proportion of filter feeding types, transitioning towards a scraper and collector-gathering community downstream (Figure 4-6).

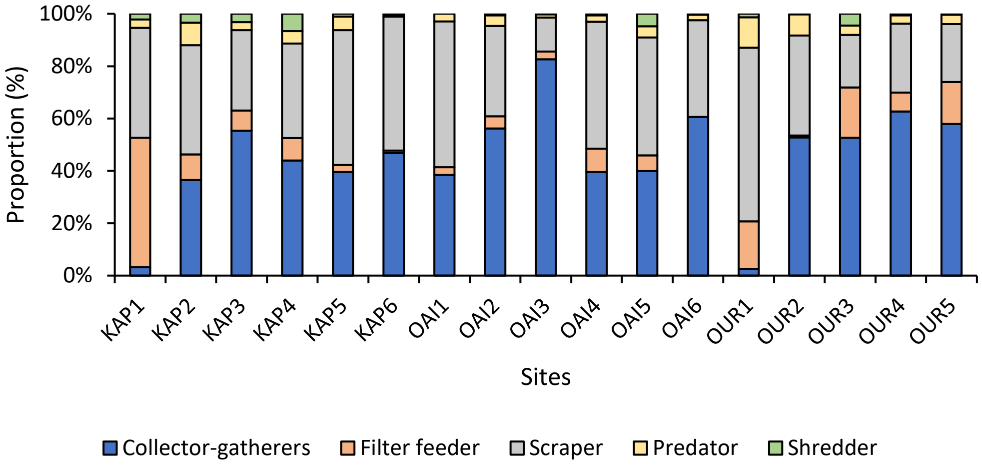


FIGURE 4-6 Proportions of functional feeding groups present at longitudinal sites in the Kapoaiaia (KAP), Oaonui (OAI) and Ouri (OUR) streams, Taranaki, New Zealand. Site numbers run from upstream (1) to downstream (5 or 6).

4.4.3 | Longitudinal isotopic variation

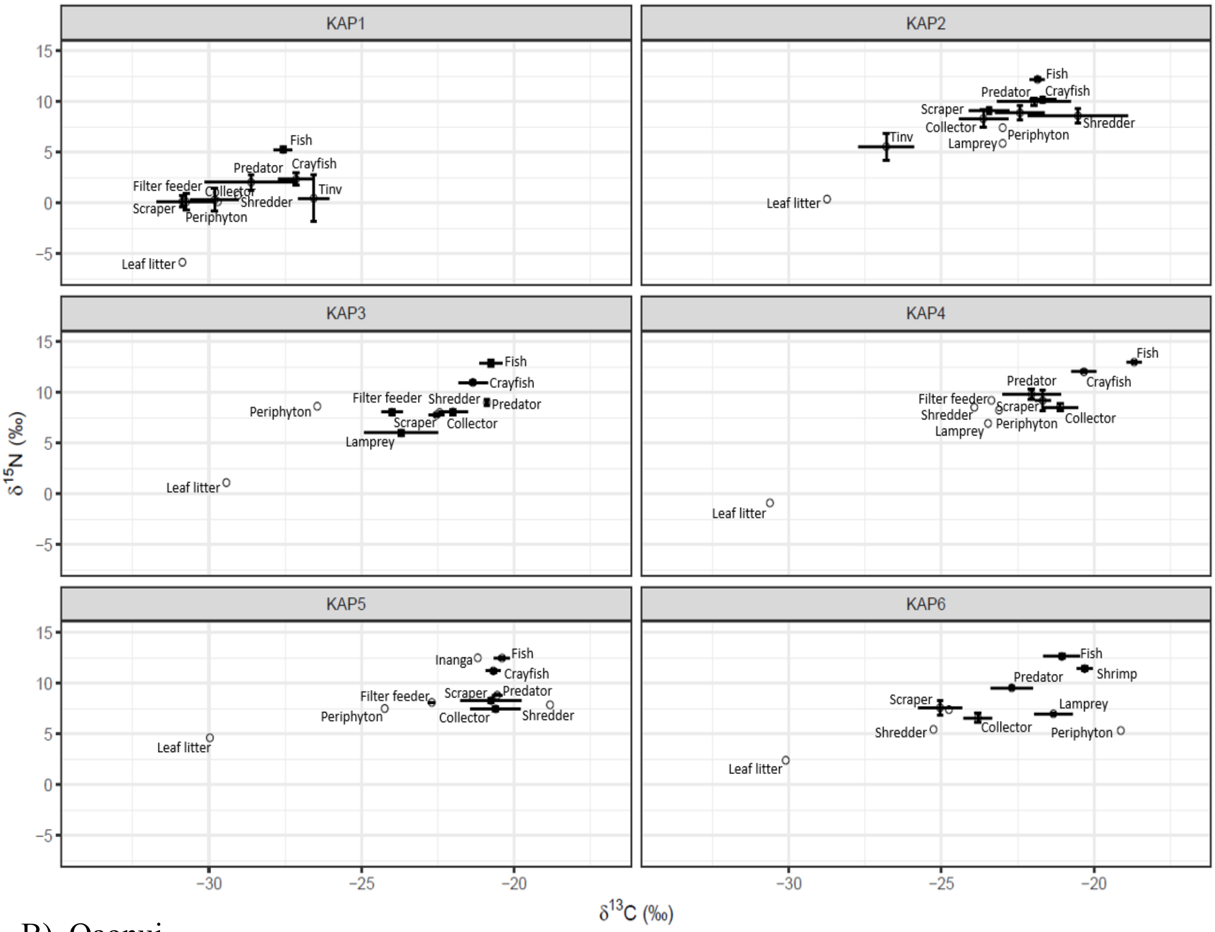
The dual isotope plots showed a distinct increase in δ^{15}N from forest sites to longitudinal pasture sites (Figure 4-7). All food web components were higher in δ^{15}N from sites 1 to 2 on average by 6.8‰ in the Kapoaiaia stream, and 6.4‰ at Ouri but only marginally at Oaonui (0.5‰). However, this trend was not apparent longitudinally whereby, downstream of sites '3', δ^{15}N enrichment was no greater than an average 1.2‰ between sites for all food web components. Basal sources of leaf litter and periphyton were lower in δ^{13}C for all sites (Figure 4-7). Periphyton in the Ouri Stream was more negative in δ^{13}C and progressively became more negative longitudinally from OUR1 (-28.15‰) to OUR5 (-29.71‰), while mean δ^{13}C of periphyton in Kapoaiaia and Oaonui streams became progressively more positive (KAP1 -29.71‰ to KAP6 -19.14‰; OAI1 -25.00‰ to OAI6 -21.85‰).

$\delta^{13}C$ values of leaf litter were consistently less than periphyton for all sites, except OUR4 (Figure 4-7).

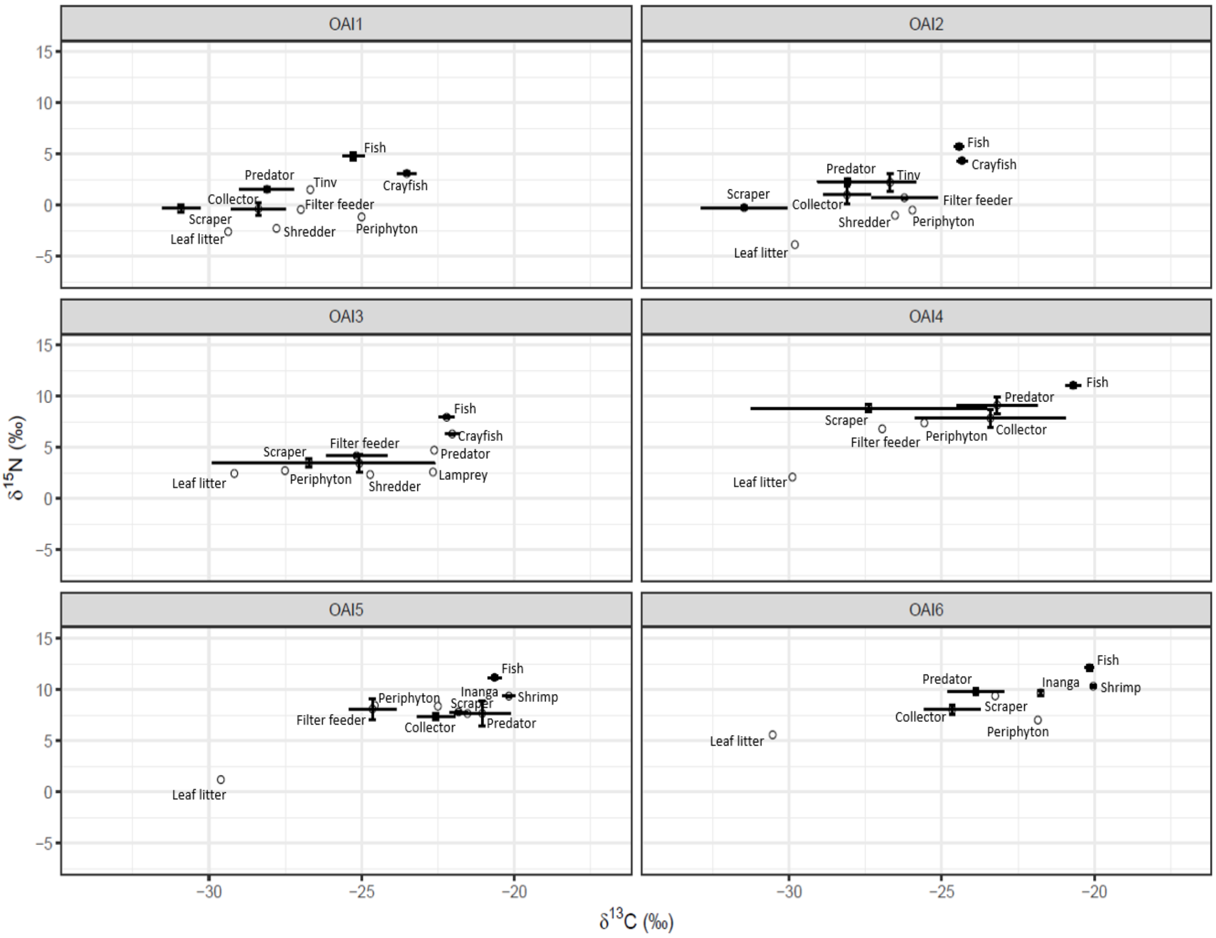
Non-predatory aquatic invertebrates (shredders, scrapers, filter-feeders, and collector-gatherers) showed similar isotopic values within each site, with large variation among functional feeding groups. Shredders were depauperate throughout and often represented by a single isotope sample. In general, predatory invertebrates showed an increase in $\delta^{13}C$ and $\delta^{15}N$ at all sites and situated closer to high trophic levels e.g., crayfish.

Fish (excluding inanga larvae and lamprey ammocetes) represented the highest trophic level and showed distinct increase of $\delta^{15}N$ from forested sites to pasture. However, fish showed no further longitudinal increase of $\delta^{15}N$ or distinct variation in $\delta^{13}C$ between sites. Lamprey ammocetes were caught throughout the Kapoaiaia Stream and at a single site at OAI3. All showed similar $\delta^{13}C$ and $\delta^{15}N$ values to periphyton. Shrimp and inanga larvae were only caught at lower sites and were not found at elevations greater than 110 m and 8 km from the sea; they showed similar $\delta^{13}C$ and $\delta^{15}N$ values to fish that were from higher trophic levels (Figure 4-7).

A) Kapoaiaia



B) Oaonui



B) Ouri

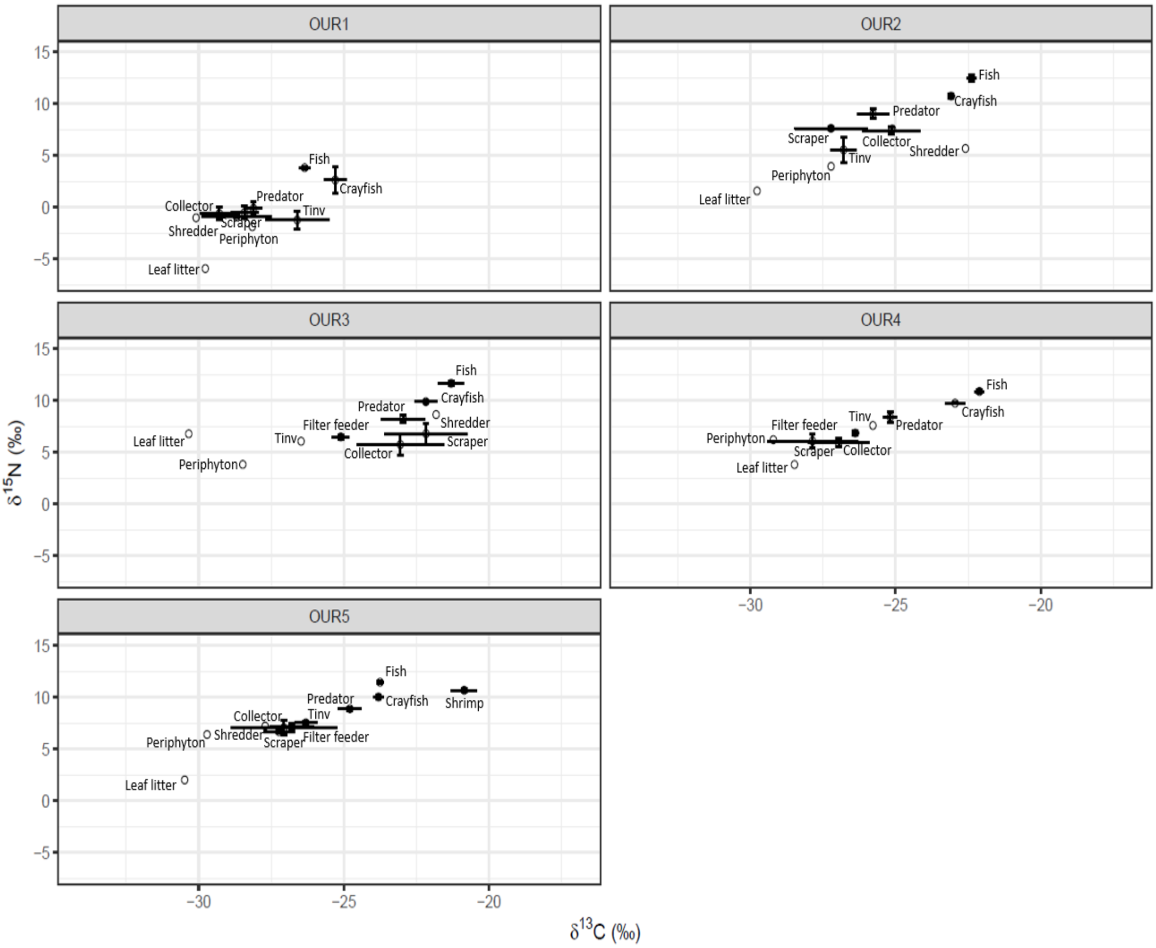


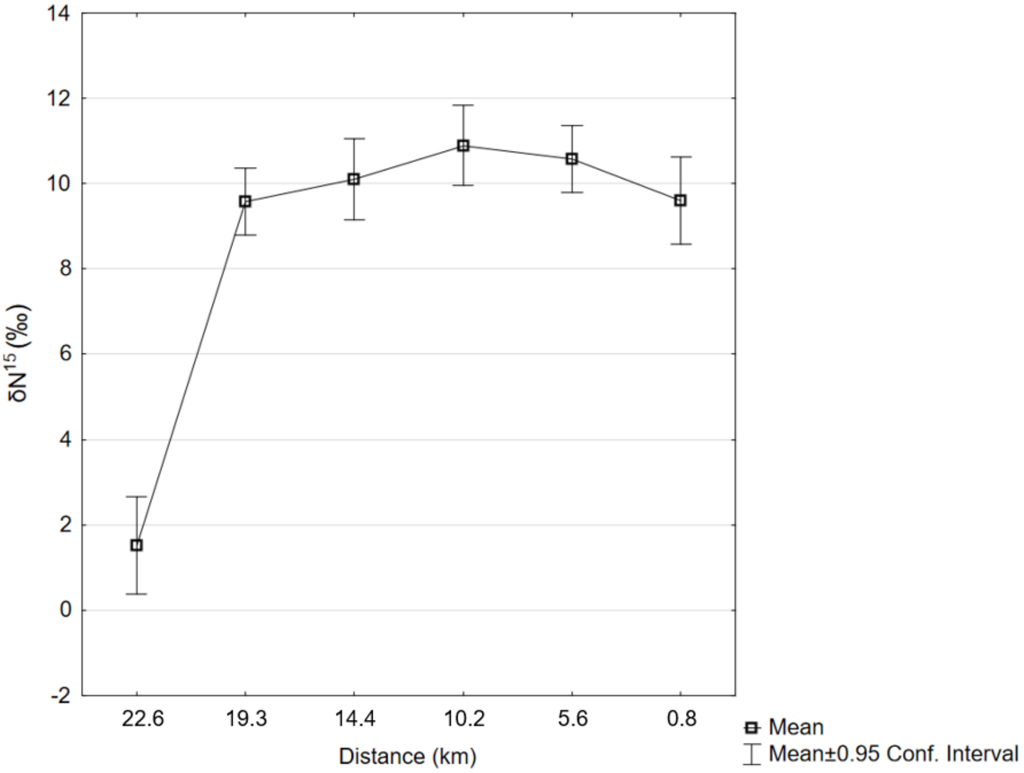
FIGURE 4-7 Mean $\delta^{13}C$ and $\delta^{15}N$ dual isotope plot of stream components at streams A) Kapoaiaia (KAP), B) Oaonui (OAI) and C) Ouri (OUR) along a longitudinal sequence. Fish represent all species caught excluding Inanga and lamprey ammocetes. Inanga whitebait and shrimp represent known sources of marine-derived nitrogen, while lamprey ammocetes as detritovores represent basal resources. Abbreviation ‘Tinv’ and ‘Collector’ represents terrestrial invertebrates and collector-gatherers, respectively. Error bars are 1 SE.

Mean $\delta^{15}N$ of all stream components show a weak negative correlation with shade and a significant weak positive correlation with temperature ($p < 0.05$). Distance from sea presented the strongest negative correlation with Mean $\delta^{15}N$ of all stream components suggesting that $\delta^{15}N$ increases with closer proximity to the coast (Table 4-8). This relationship was emphasized by the means plot, whereby, all streams show increasing $\delta^{15}N$ with distance from sea. Kapoaiaia Stream showed a sharp increase in $\delta^{15}N$ from 22.6 km (KAP1) to 19.3 km (KAP2) where $\delta^{15}N$ values then remained steady at approximately 9.8‰ to 11.0‰ with declining distance. Ouri Stream showed a similar relationship with a sharp increase in $\delta^{15}N$ from 22.1 km (OUR1) to 18.6 km (OUR2) leading to a gradual increase with distance from sea. Oaonui Stream showed consistent sharp increases with $\delta^{15}N$ and distance from sea, with $\delta^{15}N$ peaking mid-stream at 12.0 km (Figure 4-8).

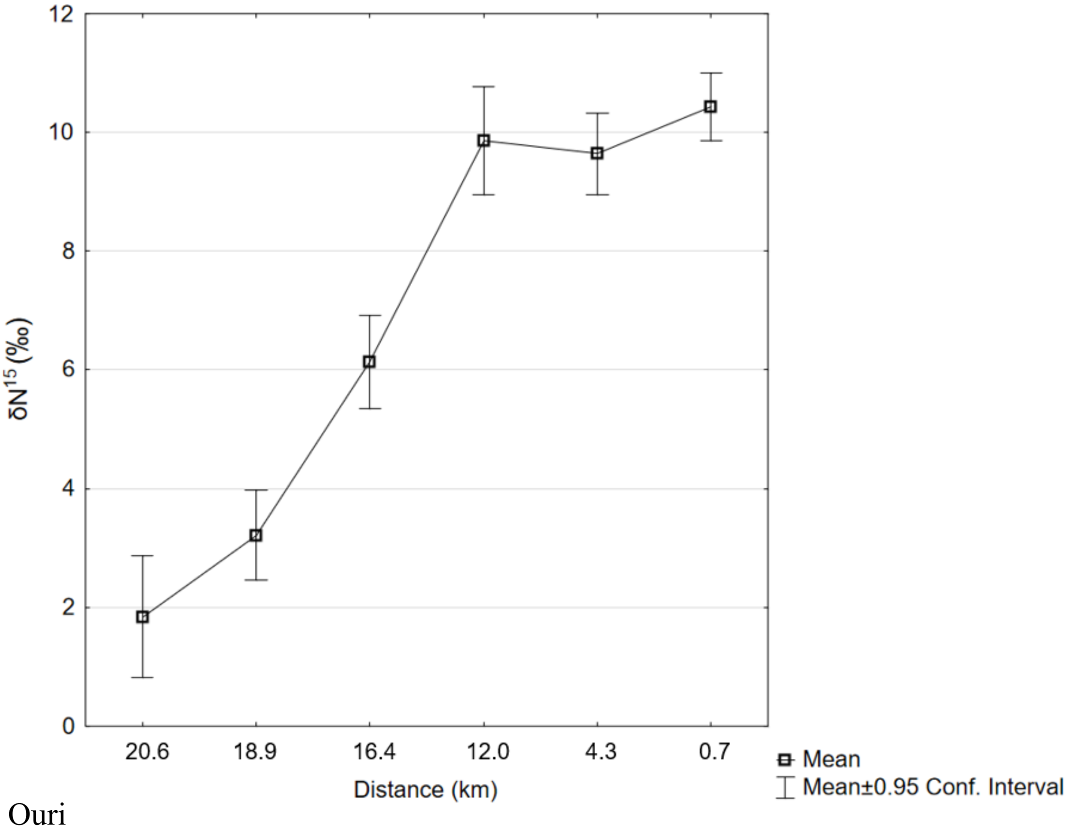
TABLE 4-8 Spearman rank correlation of mean $\delta^{15}N$ of all stream components with shade, temperature, and distance from sea for all streams combined and individually for Kapoaiaia, Oaonui and Ouri streams. Abbreviation SD is standard deviation. All correlations show statistically significant differences ($p < 0.05$) and are marked in bold.

	Variable	Mean	SD	Shade (%)	Temperature (°C)	Distance from sea (km)
All streams	δN^{15}	7.73	4.24	**-0.310**	**0.335**	**-0.534**
Kapoaiaia	δN^{15}	9.05	4.03	**-0.242**	**0.259**	**-0.348**
Oaonui	δN^{15}	6.71	4.10	**-0.183**	**0.132**	**-0.800**
Ouri	δN^{15}	7.30	4.25	**-0.384**	**0.465**	**-0.523**

A) Kapoaiaia



B) Oaonui



C) Ouri

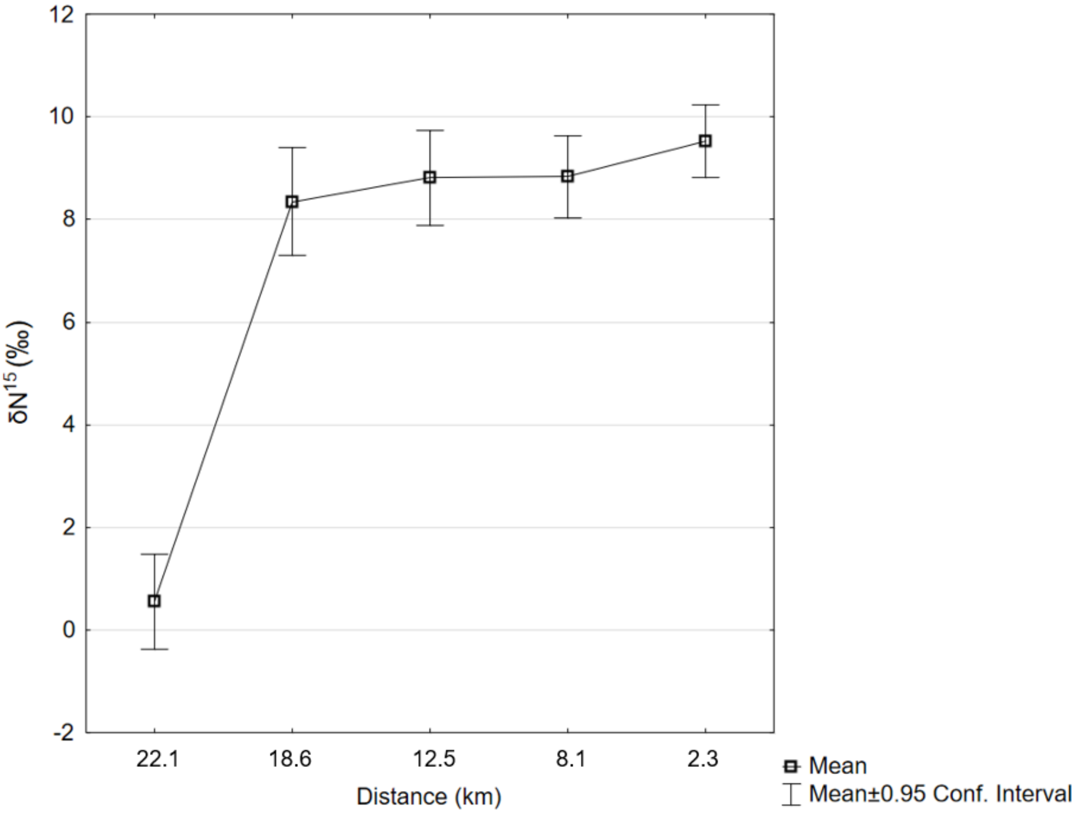


FIGURE 4-8 Means distribution plot of mean δ^{15}N of all stream components for A) Kapoaiaia B) Oaonui and C) Ouri streams.

4.4.3.1 | Proportional contribution to non-predatory aquatic invertebrate diet

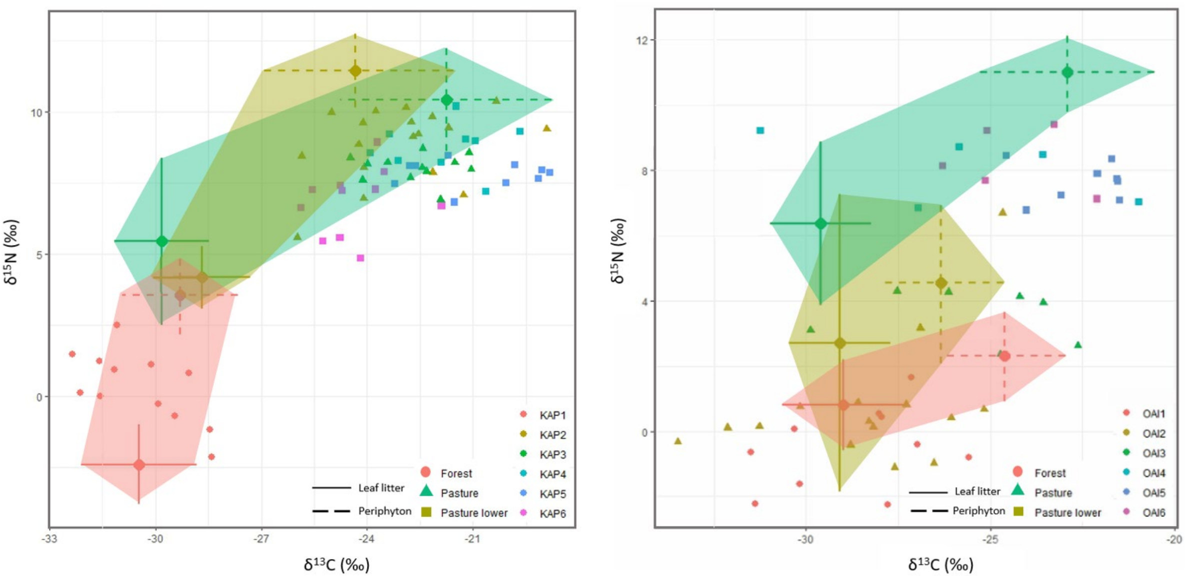
The dual isotope plots showed differentiation between non-predatory aquatic invertebrates in forest and longitudinal pasture sites in the Kapoaiaia Stream. Leaf litter and periphyton mean $\delta^{15}N$ and $\delta^{13}C$ were similar between longitudinal pasture sites and showed that periphyton were the dominant basal source at pasture sites (Figure 4-9; Appendix 4-4). There was a transition in basal food dominance from leaf litter in forest site (54%) to periphyton in pasture sites (>80%). However, there was a marginal increase in the utilisation of leaf litter at KAP6 to 30% (Table 4-9).

In the Oaonui Stream, non-predatory invertebrates showed a gradual longitudinal increase in $\delta^{15}N$ and $\delta^{13}C$. OAI5 and OAI6 showed similar $\delta^{15}N$ and $\delta^{13}C$ values to KAP5 and KAP6, but mean $\delta^{15}N$ and $\delta^{13}C$ were more variable than the Kapoaiaia Stream (Figure 4-9). Leaf litter was the dominant food source at OAI1 (74%) and OAI2 (72%), transitioning to periphyton downstream. Leaf litter remained the prevalent carbon source throughout the Oaonui Stream (Table 4-9).

Non-predatory invertebrates in the Ouri Stream showed an increase in $\delta^{15}N$ from forest to longitudinal pasture sites, unlike the Kapoaiaia and Oaonui streams, which showed no decrease in $\delta^{13}C$, except for a few individuals at OUR2 and OUR3. This trend was further evidenced by mean $\delta^{15}N$ and $\delta^{13}C$ values. Non-predatory invertebrates in the Ouri Stream showed proportional differences in food sources when compared to the Kapoaiaia and Oaonui streams. For example, leaf litter and periphyton contributed evenly to non-predatory invertebrates at forest sites and showed a transition to periphyton at OUR2 (96%) and OUR3 (94%). However, leaf litter was the dominant food source at OUR4 (83%) and OUR5 (63%) consistent with the level of stream shading (Table 4-9, Figure 4-9).

A) Kapoaiaia

B) Oaonui



C) Ouri

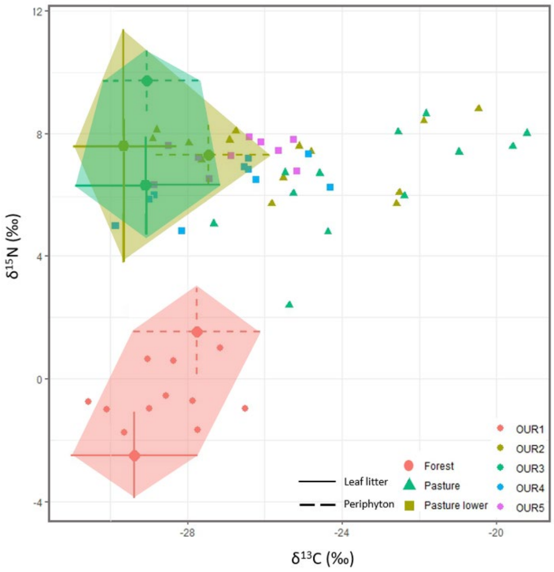


FIGURE 4-9 Dual isotope plot of non-predatory invertebrates as consumers and basal carbon sources (leaf litter and periphyton) in the A) Kapoaiaia, B) Oaonui and C) Ouri streams in Taranaki, New Zealand, showing that adjusted food sources encompass the majority of consumers, expect for some individuals in pasture sites of the Ouri Stream. Trophic discrimination factors (0.4‰ for $\delta^{13}C$ and 3.4‰ for $\delta^{15}N$) has been added to the means for food sources. Larger symbols are site means and error bars are 1 SD. Straight lines represent mean leaf litter and dashed lines represent mean periphyton in forest (site 1), pasture (site 2 and 3), and pasture lower (site 4, 5 and 6).

TABLE 4-9 Proportional contribution to non-predatory aquatic invertebrate diet at Ouri sites in Taranaki, New Zealand (mean ± standard deviation). Sources include leaf litter and periphyton. Dominant source contributions are marked in bold.

Stream	**Site**	**Leaf litter** Mean ± SD	**Periphyton** Mean ± SD
Kapoaiaia	KAP1	**0.54 ± 0.12**	0.46 ± 0.12
	KAP2	0.15 ± 0.12	**0.85 ± 0.08**
	KAP3	0.18 ± 0.09	**0.82 ± 0.09**
	KAP4	0.10 ± 0.05	**0.90 ± 0.05**
	KAP5	0.08 ± 0.05	**0.92 ± 0.05**
	KAP6	0.30 ± 0.06	**0.70 ± 0.06**
Oaonui	OAI1	**0.74 ± 0.14**	0.26 ± 0.14
	OAI2	**0.72 ± 0.16**	0.28 ± 0.16
	OAI3	0.19 ± 0.12	**0.81 ±0.12**
	OAI4	0.40 ± 0.11	**0.60 ± 0.11**
	OAI5	0.38 ± 0.12	**0.62 ± 0.12**
	OAI6	0.35 ± 0.11	**0.65 ± 0.11**
Ouri	OUR1	0.46 ± 0.12	**0.54 ± 0.12**
	OUR2	0.04 ± 0.04	**0.96 ± 0.04**
	OUR3	0.06 ± 0.07	**0.94 ± 0.07**
	OUR4	**0.83 ± 0.10**	0.17 ± 0.11
	OUR5	**0.63 ± 0.11**	0.37 ± 0.11

4.4.3.2 | Proportional contribution to eel diet

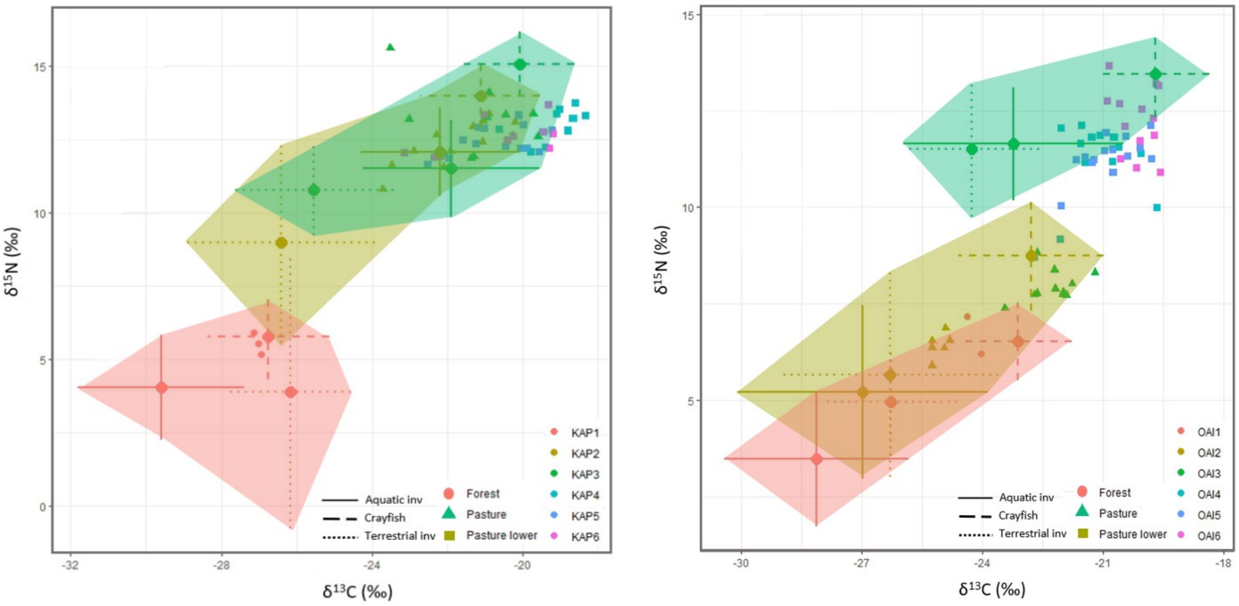
Bayesian mixing model biplots show an increase in $\delta^{15}N$ and reduction in $\delta^{13}C$ from forest sites to longitudinal pasture sites for eels in all streams (Figure 4-10). Functionally, eels in the Kapoaiaia Stream forest sites showed a tendency towards consuming crayfish and terrestrial invertebrates, while in pasture sites eels appeared to be less dependent on terrestrial invertebrates and more dependent on crayfish and aquatic invertebrates (Figure 4-10). The proportional contribution of terrestrial invertebrates was slightly higher at KAP1 (4%), transitionally becoming less dominant downstream at KAP6 (1%). Crayfish were the dominant assimilated resource at KAP1, gradually becoming less dominant downstream. Aquatic invertebrates were proportionally dominant longitudinally from KAP2, representing up to 70% of eel diet at KAP2, KAP4, KAP5 and KAP6. However, this trend was not evident at KAP3, where crayfish were the proportionally dominant source (59%) (Table 4-10).

The dual isotope plot for the Oaonui Stream showed functional differences to the Kapoaiaia Stream, despite comparable evidence of an increase in $\delta^{15}N$ and a decrease in $\delta^{13}C$ (Figure 4-10). Crayfish and terrestrial invertebrates showed dietary dominance for eels throughout the longitudinal sequence and no distinct longitudinal food source transition was evident with elevation. Crayfish were the dominant food source at OAI1, OAI2, OAI3 and OAI6 representing >40% of eel diet, similar to the percentage contributed by terrestrial invertebrates at sites OAI4 and OAI5. There appeared to be no significant reliance on aquatic invertebrates at longitudinal sites on the Oaonui Stream (Table 4-10). Overall, Oaonui Stream had the highest mean eel biomass (142.0 g m^{-2}), with eels predominantly assimilating carbon from crayfish and terrestrial invertebrates.

The dual isotope plot for eels in the Ouri Stream show concurrent evidence of increased $\delta^{15}N$ and decreased $\delta^{13}C$ (Figure 4-10). However, Bayesian mixing models for eels present in the Ouri Stream illustrate a unique transitional dominance from aquatic invertebrates towards terrestrial invertebrates at lower sites (>45 %). These data correspond with shading and estimates of riparian vegetation extents present at these lower sites (Figure 4-10). Crayfish and aquatic invertebrates were the dominant source of nutrition at sites OUR1, OUR2 and OUR3 at >38% (Table 4-10).

A) Kapoaiaia

B) Oaonui



C) Ouri

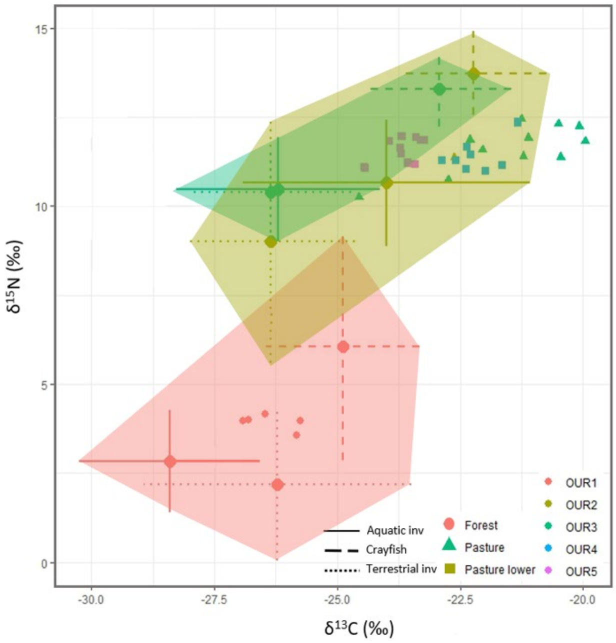


FIGURE 4-10 Dual isotope plot of eels as consumers and their potential food sources (aquatic invertebrates, crayfish, and terrestrial invertebrates) in A) Kapoaiaia, B) Oaonui and C) Ouri streams in Taranaki, New Zealand, showing that adjusted food sources encompass the majority of consumers. Trophic discrimination factors (0.4‰ for δ^{13}C and 3.4‰ for δ^{15}N) have been added to the means for food sources. Larger symbols are site means and error bars are 1 SD. Straight lines represent mean aquatic invertebrates, dashed lines represent mean crayfish and dotted lined represent mean terrestrial invertebrates in forest (site 1), pasture (site 1 and 2), and pasture lower (site 4, 5 and 6).

TABLE 4-10 Proportional contributions to eel diet in streams in Taranaki, New Zealand (mean ± standard deviation). Sources include crayfish, terrestrial invertebrates, and aquatic invertebrates. Dominant source contributions are marked in bold. Crayfish and shrimp were combined to account for low densities of crayfish at OAI4, OAI5, OAI6 and KAP6 (Section 4.3.4.2).

		Crayfish	**Terrestrial invertebrates**	**Aquatic invertebrates**
Stream	**Site**	Mean ± SD	Mean ± SD	Mean ± SD
Kapoaiaia	KAP1	**0.60 ± 0.14**	0.04 ± 0.05	0.36 ± 0.14
	KAP2	0.24 ± 0.15	0.03 ± 0.04	**0.73 ± 0.17**
	KAP3	**0.59 ± 0.30**	0.01 ± 0.02	0.40 ± 0.31
	KAP4	0.38 ± 0.08	0.01 ± 0.01	**0.62 ± 0.08**
	KAP5	0.27 ± 0.06	0.02 ± 0.02	**0.71 ± 0.07**
	KAP6	0.27 ± 0.07	0.01 ± 0.02	**0.72 ± 0.07**
Oaonui	OAI1	**0.70 ± 0.04**	0.26 ± 0.12	0.05 ± 0.04
	OAI2	**0.40 ± 0.08**	**0.40 ± 0.17**	0.21 ± 0.16
	OAI3	**0.93 ± 0.05**	0.05 ± 0.04	0.02 ± 0.03
	OAI4	0.36 ± 0.15	**0.61 ± 0.15**	0.03 ± 0.05
	OAI5	0.35 ± 0.15	**0.63 ± 0.15**	0.02 ± 0.03
	OAI6	**0.67 ± 0.11**	0.32 ± 0.11	0.01 ± 0.01
Ouri	OUR1	0.35 ± 0.11	0.27 ± 0.13	**0.38 ± 0.13**
	OUR2	0.27 ± 0.17	0.13 ± 0.13	**0.60 ± 0.23**
	OUR3	0.28 ± 0.09	0.05 ± 0.05	**0.68 ± 0.11**
	OUR4	0.34 ± 0.09	**0.56 ± 0.20**	0.11 ± 0.19
	OUR5	0.38 ± 0.07	**0.45 ± 0.15**	0.17 ± 0.14

4.4.3.3 | Trophic position of eels

Maximum trophic positions (MTP) of eels showed no distinct differences between sites (Figure 4-11; Appendix 4-5). Eel trophic position ranged between 4.8 and 5.6 for Kapoaiaia sites, with the lowest MTP at KAP2 and the highest MTP at KAP3. Limited variation was evident for eel trophic position between Oaonui sites ranging between 5.4 and 5.7. Ouri sites showed the highest modelled MTP at OUR2 (5.8) with some indication of longitudinal decline with the lowest modelled MTP at OUR4 (4.4). However, Ouri MTP was still within the range of Kapoaiaia and Oaonui. At sites where crayfish were the proportionally dominant source, the MTP was slightly higher ranging between 5.4 to 5.7, while at sites where terrestrial invertebrate dominated, MTP ranged from 4.8 to 5.5 (Table 4-11; Figure 4-11).

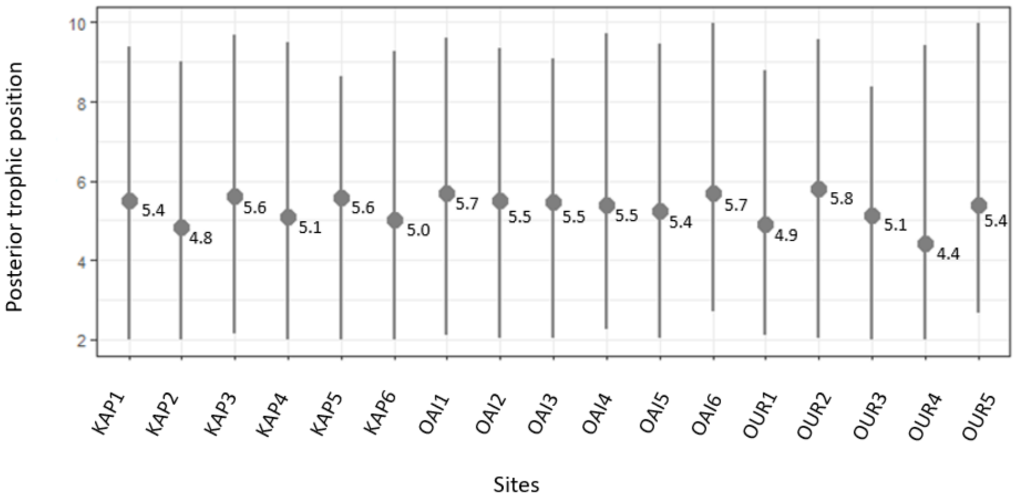


FIGURE 4-11 Maximum trophic position posterior plot of eels in longitudinal sites in Kapoaiaia (KAP), Oaonui (OAI) and Ouri (OUR) streams in Taranaki, New Zealand. Site numbers run from upstream (1) to downstream. Bars show 95% credible intervals of each posterior trophic position.

4.5 | DISCUSSION

4.5.1 | Longitudinal physical and isotopic variations

The RCC predicts a series of longitudinal changes in physical variables leading to a continuum of biotic adjustments (Vannote et al., 1980). These physical changes broadly include stream size and canopy cover, which subsequently influences light attenuation, in-stream water temperature regimes and basal resource availability (Vannote et al., 1980; Doretto et al., 2020). The study streams in Taranaki experienced abrupt changes from forest canopy cover to open pasture leading to distinct shift in light and temperature regimes, and corresponding availability of allochthonous and autochthonous energy sources (Chapter 2).

Generally, mean summer air temperatures and water temperatures increased downstream in all streams. However, streams differed in the longitudinal extent of forest and scrub riparian vegetation, with the Kapoaiaia and Oaonui streams experiencing more fragmented riparian environments. The level of riparian fragmentation can lead to localised variations in the incorporation of terrestrial matter into the food web, in response to altered light and temperature regimes (Wootton, 2012; Warren et al., 2016). This was clearly illustrated at lower sites in the Ouri Stream, where the highest riparian vegetation extents likely resulted in decreased mean summer air temperature of around 3.1°C along a downstream gradient. These results are consistent with those of Kalny et al. (2017), who found air temperature at shaded reaches were around 4°C lower than in unshaded reaches in the alpine River Pinka, Austria. In the present study, mean summer air temperature decreased with elevated riparian planting and was strongly correlated with water temperature ($r = 0.708$). Air temperatures have been found to be the most sensitive parameters controlling stream temperatures (Du et al., 2020), and potentially contributed to lower fish biomass at OUR5, consistent with findings in Chapter 2.

Ecological theory predicts photosynthesis within heavily shaded streams is low, while larger streams with elevated solar energy have high autotrophic production (Vannote et al., 1980; Power, 1992; Hill et al., 1995). The RCC predicts that autochthonous production is greatest downstream, driven by the physical widening of stream and the loss of canopy cover (Vannote et al., 1980). Despite periphyton biomass increasing downstream, the lack of longitudinal variation in physical variables (width, depth and riparian vegetation) suggests predictions from the RCC are partially true in Taranaki streams. Maximum summer water temperatures were distinctly lower when compared to forest sites of the Kapoaiaia and Oaonui streams. Periphyton biomass showed an increasing longitudinal trend with decreasing elevation, expect for OAI2. This site had the lowest mean depths and highest pH and TP concentration in that stream, which are known to have influences of periphyton biomass (Hill & Fanta, 2008; Bray et al., 2008). These data are largely consistent with trends predicted by the RCC, but it is evident that localised physical and biochemical effects may have been driving results.

Longitudinally, the Ouri Stream showed similar periphyton $\delta^{13}C$ values upstream to downstream and were comparably more negative (OUR5, -29.71‰) than most downstream sites in the Kapoaiaia (KAP6, -19.12‰) and Oaonui streams (OAI6, -21.85‰). The slight increase in $\delta^{13}C$ at the Kapoaiaia Stream may be attributed to the effluent pond located in direct proximity to the site (Ulseth & Hershey, 2005; Northington & Hershey, 2006). However, this general trend is more likely related to less stream vegetation fragmentation along the stream catchment. Machano-Silva et al. (2022), showed $\delta^{13}C$ values can be more negative in streams with forested catchments when compared to streams with less canopy shading, corresponding with Taranaki streams. This is consistent with Finlay (2004), where periphyton was lower in $\delta^{13}C$ in unproductive smaller tributaries than more productive sites downstream.

The RCC predicts that streams progressively widen leading to less canopy cover with increased primary production and warmer in-stream temperatures downstream (Vannote et al., 1980; Enquist et al., 2003; Demars et al., 2011). Elevated temperatures can lead to enhanced rates of primary production and decomposition that can accelerate stream N uptake, promoting isotopic fractionation of periphyton with higher $\delta^{15}N$ than forested streams (Ishikawa et al., 2018; Machado-Silva et al., 2022). Therefore, a gradual increase in $\delta^{15}N$ longitudinally from upstream to downstream for all food web components was anticipated. There was a sharp increase in mean $\delta^{15}N$ of all stream components from upstream forest to pasture sites, followed by a general increase in $\delta^{15}N$ towards the coast longitudinally in all streams. However, this was not influenced by marine-derived nitrogen inputs. The distinct increase from forest to pasture was consistent with increased $\delta^{15}N$ found in deforested streams by Machado-Silva et al. (2022). Isotopically, there was limited evidence of any further increase in $\delta^{15}N$ at the most downstream sites, contrary to Hypothesis I that $\delta^{15}N$ would gradually increase from upstream to downstream independent of riparian fragmentation. Results suggest that abrupt transitions from forest canopy cover to open pasture are sufficient to elicit distinct variation in $\delta^{15}N$ on stream continua.

4.5.2 | Longitudinal changes in non-predatory invertebrate diet

The RCC predicts there is a transition of energy from upstream processing to downstream environments, whereby terrestrial leakage from upstream processing results in longitudinal changes in food web structure (Vannote et al., 1980; Hette-Tronquart et al., 2016). Generally, non-predatory invertebrates were expected to show a gradual longitudinal transition from a proportional dominance of allochthonous carbon (leaf litter) to autochthonous carbon (periphyton), in support of the RCC (conceptualised in Figure 4-1). All streams showed that non-predatory invertebrates favoured leaf litter at the forested boundary and transitioned to periphyton downstream.

It was predicted that non-predatory aquatic invertebrates would show a gradual longitudinal transition from leaf litter to periphyton reflective of upstream processing inefficiencies described in the RCC (Hypothesis II). There was no evidence from stable isotopes of downstream non-predatory invertebrates capitalising on upstream processing inefficiencies, but rather localised variation related to the composition of riparian vegetation. For example, non-predatory invertebrates in the Ouri Stream showed a distinct food dominance transition back to leaf litter at lower sites, where riparian vegetation increased 5 km from the coastline. These data are consistent with findings by Erdozain et al. (2021) where stream replanting following deforestation are shown to alter food web dynamics along stream continua. While the RCC predicts there is a gradual transition of energy sources from upstream to downstream in response key physical, chemical, and biological attributes, this was only partially true for Taranaki streams. The abrupt variations in physical variables interrupted the expected longitudinal transition from allochthonous to autochthonous energy sources fuelling secondary production.

The Riverine Ecosystem Synthesis (RES) realises the complexity of patchy riparian dynamic within river networks (Thorp et al., 2006). While tenets of the RES are largely applicable to large rivers, the assumptions on which they are based are somewhat applicable to Taranaki streams. For example, allochthonous material may be important in functional process zones (FPZ). These zones are characterised by intermitted changes in the local riparian environment, rather than the position along a longitudinal gradient, at least for the 4th-order Taranaki streams studied. It is assumed that the transitions in food dominance at OUR4 and OUR5 was likely a result of local conditions of riparian shading, allochthonous inputs, light and temperature regimes.

The lack of gradual transitions in resource dominance may have been due to a lack of longitudinal physical (width and depth), chemical (pH, TN and TP) and biological (aquatic invertebrate functional feeding groups) variation in Taranaki. This may have led to limited functional and energetic dynamics predicted by the RCC, which encompasses river systems up to order 12 (Doretto et al., 2020). Results are in support of early issues raised by Winterbourn et al. (1981), whereby firstly, there was no predictable change in functional feeding group composition in Taranaki streams and secondly shredder feeding types were significantly underrepresented. This may have been caused by the discontinuities of physical, chemical, and biological attributes and limited patterns with aquatic invertebrate functional traits in Taranaki streams (Winterbourn et al., 1981).

4.5.3 | Longitudinal variations in eel diet

Dominant energy sources for eels were generally consistent among sites, but there were different patterns within each stream. In the Kapoaiaia Stream, crayfish and aquatic invertebrates dominated eel diet, whereas in Oaonui Stream, crayfish and terrestrial invertebrates dominated. In the Ouri Stream, aquatic invertebrates and terrestrial invertebrates dominated eel diet. However, eels did show a transition of food sources to dominantly consuming terrestrial invertebrates at OUR4 and OUR5 (>45%). These sites exhibited greater riparian vegetation extents and lower water temperatures when compared to upstream sites of the Ouri Stream. These localised resource transitions may be related to the extent of riparian vegetation or indirectly by temperature-driven changes to resource supply. A plausible scenario is that eels may be foraging terrestrial invertebrates at these sites to meet energetic demand (e.g., Saunders & Fausch, 2012; Akbaripasand et al., 2014) or that there is a greater supply of terrestrial invertebrates at these sites. However, evidence of terrestrial invertebrate food dominance was evident longitudinally within the Oaonui Stream, irrespective of significant fragmentation of vegetation. Recent research suggests that terrestrial invertebrates provide critical energetic pathway for sustaining fish populations (Niles & Hartman, 2021) and may provide a significant food source to higher trophic levels, irrespective of proximal land use and fragmentation. A further scenario, is that densely forested sites act as a biological net, intercepting terrestrial invertebrates from entering or falling into the stream system, particularly during high flood events. This may explain the terrestrial invertebrate food dominance in the Oaonui Stream, and the higher rates of terrestrial invertebrate inputs found in pasture sites when compared to forest (Chapter 2).

Generally, crayfish were the dominant food source across Oaonui Stream with minimal dependence on aquatic invertebrates. The Oaonui Stream also had the highest biomass of eels, thus the quality and source of food available, in addition to temperature-energetic balance, may be driving the observed higher fish biomass (Gillooly et al., 2001). With varying levels of vegetation fragmentation, streams were expected to show slight differences in food web structure. Despite the assumptions RCC and productivity hypothesis, there was no distinct longitudinal pattern of food dominance at the highest predatory level.

4.5.4 | Food chain length and eel trophic position

Aquatic invertebrates can be important conduits of energy, linking high quality algae to higher trophic levels. The food dominance derived from aquatic invertebrates is expected to influence biomass of higher trophic levels (Sushchik et al., 2006). In particular, allochthonous and autochthonous sources differ in their nutritional quality for aquatic invertebrates and crayfish (Lau et al., 2009; Cross et al., 2013; Guo et al., 2018). Therefore, food dominance transitions, such as those evidenced in OUR4 and OUR5, should result in discrete food web changes at higher trophic levels (Lau et al., 2009; Allan et al., 2021). Consistent with the Productivity Hypothesis, the food chain length can be expected to vary at these sites, whereby higher basal autochthonous production energetically sustains the higher trophic levels, leading to longer food chain lengths (Pimm, 1982; Hypothesis III). There was partial evidence of the Productivity Hypothesis as food chain length was shorter at OUR4 (4.4 trophic steps). This could suggest that resource availability was limiting at OUR4 or due to the 'omnivory mechanism' resulting from changes to the degree of trophic omnivory (Post, 2002; Post & Takimoto, 2007). Omnivory refers to consumption of both plant and animal tissue, which can be typical of crayfish diet (Parkyn et al., 2001; Williams & Martinez, 2004). Despite variations in trophic position where crayfish were the proportionally dominant food source, maximum food chain length was similar across sites and did not show any longitudinal trend between sites or among streams. This suggests that longitudinally these 4th-order streams are functionally similar from an upstream to downstream continuum and the availability of food sources results in only marginal variations to food chain length (Post, 2002; Post & Takimoto, 2007).

4.5.5 | Marine-derived nutrients

Streams that support diadromous fish represent potential energy transfer from a downstream-upstream direction, which can enhance stream production (Gresh et al., 2000; Flecker et al., 2010). It was hypothesised that the contribution of marine nitrogen from New Zealand diadromous fish will be evident in the stream food web leading to a distinct increase in $\delta^{15}N$ at lower sites. However, there were limited longitudinal differences in food web architecture, albeit the addition of shrimp and inanga at downstream sites. Taranaki streams did show the presence of marine-derived nitrogen in inanga larvae and shrimp, where these species had $\delta^{15}N$ comparable to the highest trophic predator (eels). However, there was no evidence of incorporation of marine nitrogen into higher trophic levels in the stream food web (Hypothesis IV).

Juvenile migratory fish are considered important conduits of MDN and can provide an important seasonal subsidiary to annual energy and nutrient budgets (Garman & Macko, 1998). An assumed explanation for these results in Taranaki streams is that the relative biomass of shrimp and inanga was not significant enough to be comparable to biomass of salmon migrations overseas, where MDN contributes significantly to secondary production (e.g., Hicks et al., 2005; Holtgrieve & Schindler, 2011). Galaxiid species are subject to intensive fisheries during whitebait recruitment in spring (September to November) (Baker et al., 2018). Further research is required in New Zealand streams, particularly where significant seasonal whitebait migrations are known to occur, to test the generality of MDN (e.g., as observed in the Waikato River; West et al., 2022). Furthermore, as this study was undertaken during the summer period, further assessments are required to evaluate trophic linkages between basal resources, invertebrates, and fish to achieve a better understanding of seasonal food web structure and dynamics.

4.5.6 | Study limitations

Systems with low number of sources with high variability within sources present a prevalent issue for the interpretation of isotope mixing model outputs (Phillips & Gregg, 2001; Parnell et al., 2010; Fry, 2013). In the case of this research, basal sources presented large variability within sites, which can lead to uncertainty in the interpretation of mixing model outputs. It is important to consider that combining related sources with high variability may lead to biases in mixing model estimates (Phillips et al., 2014). Sources with high variability and extensive overlap make it difficult to distinguish between source contribution to consumer (Finlay & Kendall, 2007). While combining aquatic invertebrates still represented biological meaning (*sensu*, Phillips, 2004), sources with large isotope variation can imply that each individual source contributes equally, resulting in unreliable model outputs (Phillips et al., 2014). The variability in sources can arise from using bulk isotope analyses and may be attributed to the several factors including 1) spatial and temporal isotopic variation (Schmittner & Somes, 2016), 2) low sample size of sources resulting in both within and among sites variability (Rosenfeld et al., 1992), 3) dietary changes and trophic level shifts, and 4) variations in routing of dietary proteins and lipids to the consumer tissue (Newsome et al., 2014; Wang et al., 2019). The analysis of structural compounds within tissue (e.g., amino acids) using Compound Specific Isotope Analysis (CSIA) can reduce the variability within isotope data and resolve issues arising of bulk isotope analysis (Bowes & Thorp, 2015; Whiteman et al., 2019). CSIA can facilitate adequate separation of food sources by allowing for the separation of actively cycling and refractory basal food sources, reducing uncertainty in estimates of dietary source and trophic level (Larsen et al., 2013; Magozzi et al., 2021). CSIA may accurately overcome the issue of source variability and aid interpretation of longitudinal variation in source contributions to stream consumers.

A key consumer that has been excluded from the analysis is crayfish because sources did not fall within the mixing polygons. It is possible that the TDFs did not accurately reflect the difference between the stable isotope ratio of crayfish to its food source or that all food sources were not quantified in the model. Knowledge of the food sources assimilated into the consumer tissue is a requirement for accurate mixing model outputs. As discussed above, the lack of precision in the mixing polygons may also be an outcome of the bulk isotope analysis which could be resolved with CSIA. As crayfish form a key component of stream food webs, future research should consider CSIA to address how source allocation changes longitudinally.

4.6 | CONCLUSION

Conceptualised predictions of energy flow derived by the RCC were evaluated on three mountainous streams on Mount Taranaki, North Island, New Zealand. While these streams partially reflected conceptualised models based on the RCC, they did not show a gradual longitudinal transition from allochthonous to autochthonous energy sources. There was no evidence of downstream non-predatory invertebrate communities capitalising on upstream processing inefficiencies but rather their energy uptake appeared to respond to distinct localised variation in the Ouri Stream. These findings are more reflective of more recent conceptualised models derived from the Riverine Ecosystem Synthesis with localised processes influencing pathways of energy transfer.

Non-predatory invertebrates derived their nutrition predominantly from leaf litter at the forested boundary distinctly transitioning to periphyton dominance downstream. The abrupt transition in physical variables at the forest to pasture boundary showed the strongest evidence for energetic and functional responses in food webs to alterations in energy supply. Despite summer in-stream temperatures increasing longitudinally, there was no corresponding changes in proportional dominance of food sources to the highest trophic level.

While evidence of marine-derived nitrogen sources was presented, the incorporation of MDN was not expressed in the food web. However, these data hold promise for the importance of marine-derived nutrients in freshwater systems that sustain significant whitebait runs elsewhere in New Zealand.

4.7 | REFERENCES

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4.8 | APPENDIX

APPENDIX 4-1 Duration, month and year of physical and biological variables sampled in the Kapoaiaia, Oaonui and Ouri streams, Mount Taranaki, New Zealand. Sampling for fish and crayfish populations of downstream sites = 3, 4, 5 and 6 occurred in November (late spring) to facilitate the capture of migratory whitebait (galaxiids) and potential incorporation of MDN into the food web.

Sample	Month	Year	Site code
Light and temperature	December, January, and February	2019 to 2020	1,2
Light and temperature	December, January, and February	2020 to 2021	3,4,5,6
Stream Ecological Valuation	December	2019	1,2
Stream Ecological Valuation	December	2020	3,4,5,6
Periphyton biomass	January	2020	1,2
Periphyton biomass	November	2020	3,4,5,6
Aquatic and terrestrial invertebrates	January	2020	1,2
Aquatic and terrestrial invertebrates	November	2020	3,4,5,6
Fish and crayfish populations	January	2020	1,2
Fish and crayfish populations	November	2020	3,4,5,6

APPENDIX 4-2 Functional feeding groups of aquatic invertebrates sampled in Kapoaiaia, Oaonui and Ouri streams, Mount Taranaki, New Zealand. Abbreviation 'npinv' represents non-predatory aquatic invertebrates and 'pinv' represents predatory aquatic invertebrates.

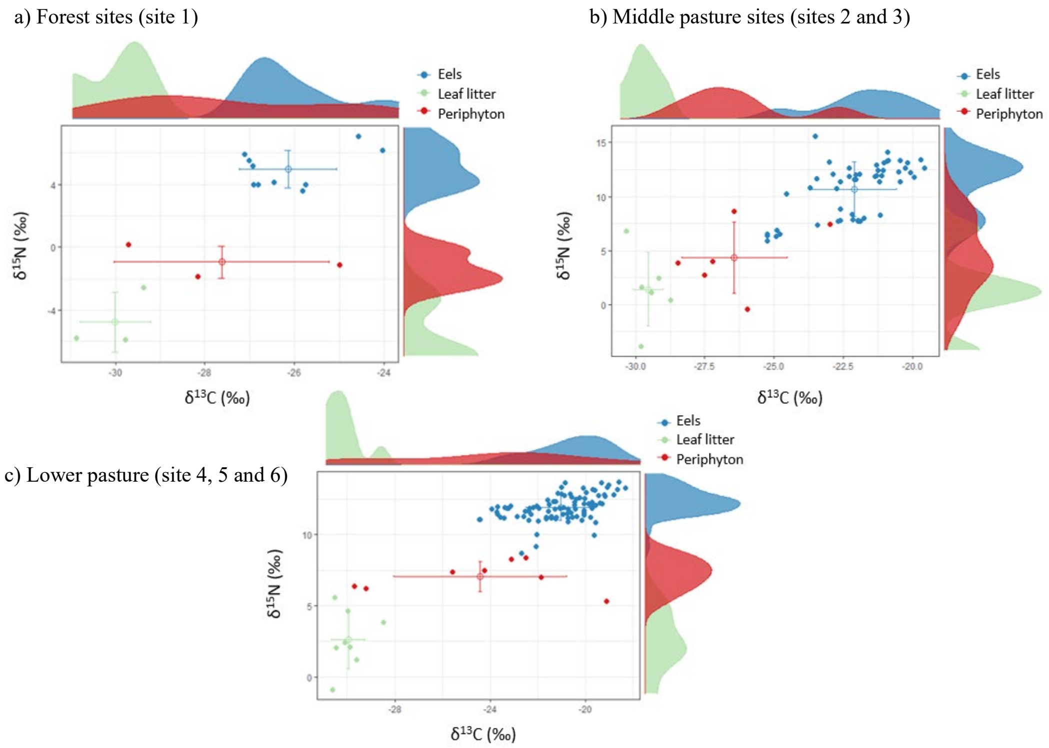
Order or family	**Common name**	**Genus**	**Functional feeding group**	**Group**
Ephemeroptera	Mayfly	*Deleatidium*	Scraper	npinv
Ephemeroptera	Mayfly	*Nesameletus*	Scraper	npinv
Ephemeroptera	Mayfly	*Rallidens*	Scraper	npinv
Ephemeroptera	Mayfly	*Coloburiscus*	Filter feeder	npinv
Ephemeroptera	Mayfly	*Ichthybotus*	Collector-gatherer	npinv
Ephemeroptera	Mayfly	*Ameletopsis*	Predator	pinv
Ephemeroptera	Mayfly	*Zephlebia*	Scraper	npinv
Ephemeroptera	Mayfly	*Neozephlebia*	Scraper	npinv
Ephemeroptera	Mayfly	*Austroclima*	Scraper	npinv
Ephemeroptera	Mayfly	*Acanthophlebia*	Scraper	npinv
Plecoptera	Stonefly	*Stenoperla*	Predator	pinv
Plecoptera	Stonefly	*Austroperla*	Collector-gather	npinv
Plecoptera	Stonefly	*Megaleptoperla*	Collector-gather	npinv
Plecoptera	Stonefly	*Zelandoperla*	Collector-gather	npinv
Plecoptera	Stonefly	*Zelandobius*	Collector-gather	npinv
Plecoptera	Stonefly	*Acroperla*	Collector-gather	npinv
Megaloptera	Dobsonfly	*Archichauliodes*	Predator	pinv
Trichoptera	Caddisfly	*Orthopsyche*	Filter feeder	npinv
Trichoptera	Caddisfly	*Aoteapsyche*	Filter feeder	npinv
Trichoptera	Caddisfly	*Hydrochorema*	Predator	pinv
Trichoptera	Caddisfly	*Hydrobiosis*	Predator	pinv
Trichoptera	Caddisfly	*Costachorema*	Predator	pinv
Trichoptera	Caddisfly	*Edpercivalia*	Predator	pinv
Trichoptera	Caddisfly	*Polyplectropus*	Filter feeder	npinv
Trichoptera	Caddisfly	*Plectrocnemia*	Filter feeder	npinv
Trichoptera	Caddisfly	*Hydrobiosella*	Predator	npinv
Trichoptera	Caddisfly	*Helicopsyche*	Collector-gather	npinv
Trichoptera	Caddisfly	*Pycnocentrodes*	Collector-gather	npinv
Trichoptera	Caddisfly	*Beraeoptera*	Collector-gather	npinv
Trichoptera	Caddisfly	*Confluens*	Collector-gather	npinv
Trichoptera	Caddisfly	*Pycnocentria*	Collector-gather	npinv
Trichoptera	Caddisfly	*Olinga*	Collector-gather	npinv
Trichoptera	Caddisfly	*Triplectides*	Shredder	npinv
Trichoptera	Caddisfly	*Pycnocentrella*	Collector-gather	npinv
Tipulidae	Crane fly	*Aphrophila*	Shredder	npinv
Tipulidae	Crane fly	*Limonia*	Shredder	npinv
Coleoptera	Beetle	Elmidae	Collector-gather	npinv
Coleoptera	Beetle	Hydraenidae	Collector-gather	npinv
Coleoptera	Water scavenger beetle	Hydrophilidae	Predator	pinv
Mollusca	Snail	*Potamopyrgus*	Scraper	npinv
Mollusca	Snail	*Physa*	Scraper	npinv
Mollusca	Freshwater limpet	*Ferrissia*	Scraper	npinv
Diptera	Chiromomid midge	*Maoridiamesa*	Collector-gather	npinv
Diptera	Chiromomid midge	*Polypedilum*	Collector-gather	npinv
Diptera	Chiromomid midge	*Chironomus*	Collector-gather	npinv
Diptera	Diptera	*Nothodixa* (Dixidae)	Filter feeder	npinv
Diptera	Diptera	*Austrosimulium*	Filter feeder	npinv
Amphipod	Talitridae	Talitridae	Shredder	npinv

APPENDIX 4-3 Population estimates of fish and crayfish abundance in 20-m stream reaches at longitudinal sites in streams in the Taranaki region, New Zealand. Total fish and crayfish estimates are shown in bold. Blank cells indicate species not caught.

	Population estimate (number of individuals)											
Site	**Longfin eel**	**Shortfin eel**	**Redfin bully**	**Lamprey**	**Brown trout**	**Shortjaw kokopu**	**Bluegill bully**	**Koaro**	**Inanga**	**Torrentfish**	**Total fish**	**Crayfish**
KAP1	5	1	2		1						**10**	**10**
KAP2	35	43	58	1							**137**	**20**
KAP3	92	106	37	5	2						**242**	**143**
KAP4	269	50	157	2							**478**	**75**
KAP5	106	176	62	8					1		**353**	**20**
KAP6	70	70	41	15							**195**	
OAI1	1	1	23					6			**31**	**3**
OAI2	38	10	89			3	2				**142**	**4**
OAI3	110	168	34	2	2						**316**	
OAI4	102	26	18								**146**	
OAI5	192	148	45						1		**386**	
OAI6	58	121	2						4		**184**	
OUR1	1				3			4			**8**	**38**
OUR2	17	1			2						**20**	**33**
OUR3	125	11								2	**138**	
OUR4	34	8	15								**56**	
OUR5	76	15	106								**196**	

APPENDIX 4-4 Mean $\delta^{13}C$ and $\delta^{15}N$ of leaf litter and periphyton as consumable sources for non-predatory invertebrates in grouped forest (=1), pasture (= 2 and 3) and pasture lower (=3 and 4) in the Kapoaiaia, Oaonui and Ouri streams, Taranaki, New Zealand.

Site	**Source**	**Location**	**Mean $\delta^{13}C$**	**Mean $\delta^{15}N$**
Kapoaiaia	Leaf litter	Forest upper	-30.87	-5.81
Kapoaiaia	Leaf litter	Pasture middle	-29.09	0.77
Kapoaiaia	Leaf litter	Pasture lower	-30.23	2.04
Oaonui	Leaf litter	Forest upper	-29.40	-2.60
Oaonui	Leaf litter	Pasture middle	-29.49	-0.69
Oaonui	Leaf litter	Pasture lower	-30.01	2.96
Ouri	Leaf litter	Forest upper	-29.77	-5.90
Ouri	Leaf litter	Pasture middle	-30.06	4.19
Ouri	Leaf litter	Pasture lower	-29.48	2.92
Kapoaiaia	Periphyton	Forest upper	-29.71	0.15
Kapoaiaia	Periphyton	Pasture middle	-24.72	8.04
Kapoaiaia	Periphyton	Pasture lower	-22.16	7.03
Oaonui	Periphyton	Forest upper	-25.00	-1.10
Oaonui	Periphyton	Pasture middle	-26.73	1.14
Oaonui	Periphyton	Pasture lower	-23.31	7.61
Ouri	Periphyton	Forest upper	-28.15	-1.86
Ouri	Periphyton	Pasture middle	-27.85	3.90
Ouri	Periphyton	Pasture lower	-29.46	6.31



a) Forest sites (site 1)

b) Middle pasture sites (sites 2 and 3)

c) Lower pasture (site 4, 5 and 6)

APPENDIX 4-5 Grouped dual isotope plot generated in tRophicPosition showing food chain length derived from mean baselines of periphyton and leaf litter samples compared to eels as top consumers at grouped longitudinal sites in Mount Taranaki, New Zealand.

CHAPTER V

Fish biomass and energy sources in Taranaki streams: a synthesis

Longfin eel (*Anguilla dieffenbachii*), 271 mm long from Kapoaiaia Stream caught in January 2020

5.1 | Principal drivers of stream ecosystem function

Light and temperature are the major drivers of ecosystem function, influencing nutrient cycling, energy flows and food web dynamics (e.g., Kaylor et al., 2017; Jones et al., 2017; Martens et al., 2019; Huryn & Benstead, 2019). Modification to these processes through riparian disturbance or removal can increase light and temperature, changing energy availability, metabolic demand, and food web dynamics. Comparative evaluations of energy availability under differing light and temperature regimes provides insight into the effects of land-use change on ecological functioning. Forest canopy removal can lead to unpredictable changes in fish biomass. For example, research has shown higher fish densities and biomass under riparian or forested canopy cover (Dineen et al., 2007), while other studies have shown open pasture streams support increased densities and biomass of fish (Bilby & Bisson, 1992; Kaylor & Warren, 2017, Wooten, 2012; O'Gorman et al., 2017; Martens, 2019). In New Zealand, native fish biomass increases in open pasture streams, raising questions about the available energy resources and physicochemical factors that sustain biomass (Hanchet, 1990; Hicks & McCaughan, 1997; Rowe et al., 1999). Temperature structures freshwater communities, by influencing energy flows and the metabolic rates of fish species (Wehrly et al., 2003; Gebrekiros, 2016; Perkins, 2022). Understanding energy flow in streams can assist with determining what drives fish biomass and can provide important insight into the management of freshwater fish in New Zealand. The aim of this thesis was to identify the factors influencing fish biomass under differing land uses in Taranaki.

The objectives of this research were to:

i) Compare fish biomass in forest and pasture streams and temperature-driven changes to the availability of energy.

ii) Investigate the drivers behind fish biomass in relation to light and temperature regimes, water chemistry, organic matter processing, terrestrial input, periphyton and aquatic invertebrate biomass.

iii) Analyse food web structure in forest and pasture streams and delineate sources of energy to consumer diet to provide insight into the underlying mechanisms behind changes in fish biomass.

iv) Investigate energy transfer pathways in Mount Taranaki streams with various scales of riparian fragmentation and address the link of marine contribution to stream food webs using stable isotope analyses.

This synthesis focusses on key findings from each research chapter and aims to address the concept of the costs and benefits of increased temperature against available resources on fish biomass.

5.2 | Fish biomass is greater in pasture than forest

Fish biomass was greater in pasture streams than in forested streams in Taranaki (Chapter 2), consistent with earlier research in New Zealand (Hopkins, 1971; Hicks & McCaughan, 1997, Rowe et al., 1999). Forest and pasture streams in Taranaki presented an inverted pyramid of biomass, which are typically characteristic of stream systems (Allen, 1951; Huryn, 1996; Vadeboncoeur & Power, 2017) (Table 5-1). Inverted pyramids of biomass suggest that there is insufficient energy provided by the preceding trophic level, when assuming conventional pyramid dynamics (Elton, 1927). Inverted patterns conflict with predictions of the Metabolic Theory, where higher biomass–specific respiration at warmer temperatures should decrease the amount of biomass supported by a given amount of energy (Brown et al., 2004; Perkins, 2022). Previous research challenged this phenomenon concluding that the subsidisation of terrestrial carbon can sustain aquatic communities (Cole et al., 2011).

TABLE 5-1 Total available biomass in forest and pasture streams in Taranaki New Zealand.

Trophic level		**Forest**	**Pasture**
		Total biomass (g m^{-2})	Total biomass (g m^{-2})
4	Fish	39.5	210.6
3	Crayfish	8.8	29.1
2	Aquatic invertebrates	4.9	19.4
1	Periphyton	25.7	69.7

5.3 | Input of terrestrial invertebrates in pasture and forest streams

Streams with high riparian cover are expected to increase the availability of terrestrial invertebrates falling into streams (Edwards & Huryn, 1996). The greater input of terrestrial invertebrates in pasture streams was an unexpected result considering the absence of riparian vegetation around pasture sites (Chapter 2). Terrestrially derived invertebrates were a distinct source of nutrition for both crayfish and fish (Chapter 3). Since terrestrial invertebrates are an important food source consumed by New Zealand fish species, these terrestrially derived food sources may play a significant role in the observed fish biomass (Edwards & Huryn, 1996; Hicks & McCaughan, 1997; Niles & Hartman, 2021). This supports the concept that terrestrially derived invertebrates serve as an alternative food source for fish and may be important in instances where secondary consumers may not be solely sustained by aquatic invertebrates (Brett et al., 2017; Niles & Hartman, 2021; Benjamin et al., 2022). In pasture streams, allochthonous energy inputs may not necessarily be compensated by autochthonous energy inputs but enhanced by additional allochthonous invertebrate sources.

5.4 | Utilisation of periphyton by intermediate consumers

The utilisation of periphyton by intermediate consumers (non-predatory aquatic invertebrates and crayfish) was highlighted in this research (Chapter 3). In Taranaki streams, water temperature and light availability played a pivotal role in predicting the in-stream food supply required to support the subsequent biomass of fish (Chapter 2). Periphyton provides a readily accessible source of soluble carbohydrates (Guo et al., 2016; Brett et al., 2017; Lau et al., 2009), and the availability of autochthonous carbon sources was predicted to drive energy flow in Taranaki systems. Periphyton biomass was significantly greater in pasture than in forest ($p < 0.05$), but showed considerable variability between sites. No significant relationships were found between periphyton and aquatic invertebrates or crayfish biomass (Chapter 2). This could be due to insufficient periphyton sampling, however, the variability in sampled periphyton may also be attributed to grazing by consumers (Lamberti & Resh, 1983; Vadeboncoeur & Power, 2017). Aquatic invertebrates can present a profound grazing pressure on periphyton, reducing periphyton biomass and leading to higher turnover rates (Lamberti & Resh, 1983). Vadeboncoeur & Power (2017) argue that only a small fraction of carbon pool is represented in algae biomass because algae forms the trophic foundation in streams. Therefore the inverted pyramid of biomass (Elton, 1927; Allen, 1951) can be confounded by intense resource consumption. This scenario is supported by Chapter 3, where periphyton was the dominant source of nutrition for non-predatory aquatic invertebrates and crayfish. Crayfish distinctly assimilated periphyton irrespective of land use, suggesting that periphyton was the dominant source of nutrition for crayfish (Chapter 3). Non-predatory invertebrates showed a food dominance transition from leaf litter to periphyton at the forest to pasture boundary in all streams, suggesting non-predatory aquatic invertebrates relied on periphyton in pasture sites (Chapter 3; Chapter 4). To support both crayfish and aquatic invertebrate communities, there must be sufficient periphyton biomass production in pasture streams. On a chemical level, the stable isotope analyses (SIA) verify the importance of periphyton for energy transfer to higher trophic levels in stream systems (Chapter 3; Chapter 4).

5.5 | Functional differences between forest and pasture sites

There were limited functional differences between forest and pasture sites and both maximum trophic position and body mass (*M*) to abundance (*N*) relationships were similar between sites (Chapter 2; Chapter 3). This suggests that while fish biomass was greater in pasture streams, the foundations of food web structure in forest and pasture streams were largely similar. This implies that fish biomass is driven by the higher biomasses of available resources in pasture streams. However, food availability alone is unlikely to limit the growth and biomass of fish (Jellyman, 1997). Warmer temperatures can increase metabolic demand of aquatic organisms leading to increased biochemical reaction rates (Gillooly et al., 2001; Power & Dietrich, 2002; Demars et al., 2011; Huryn & Benstead, 2019). Organic matter processing in pasture streams exceeded rates of decomposition at forest streams, indicative of accelerated processing in pasture streams (Chapter 2). As discussed above, the observed patterns in fish biomass conflict with predictions of the Metabolic Theory, where warmer temperatures should decrease the amount of biomass supported by a given amount of energy (Brown et al., 2004; Perkins, 2022). Therefore, if increased metabolic rates lead food consumption to exceed supply, this can lead to energetic inefficiency, resulting in decreased biomass and abundance (Rall et al*.,* 2010; Vucic-Pestic et al*.,* 2011; Hughes & Grand, 2000; O'Gorman et al., 2017). This emphasises the importance of temperature-driven changes in supply-demand synchronies in fish population dynamics. Importantly, forest and pasture streams in Taranaki, were below the optimum thermal range of native New Zealand fishes (Chapter 2). Preferred temperatures are 24°C for longfin eels and 27°C for shortfin eels following acclimation at 15°C (Richardson et al., 1994). This suggests that fish have metabolic scope to increase food intake in response to higher temperatures, but the required metabolic demand, in conjunction to limited food availability could explain the decrease in fish biomass at forest sites.

5.6 | Eel bioenergetics

Energetic supply-demand synchronies are considered important factors in controlling fish biomass. Graynoth & Taylor (2000) examined the daily maximum food consumption of eels required for growth under temperatures between 8.9°C to 20.0°C and showed that eel growth ceased at and below 8.9°C. Longfin (*Anguilla dieffenbachii*) and shortfin eels (*Anguilla australis*) accounted for 66% of the total fish biomass in forest and 94% of in pasture (Chapter 2). Equations derived from Graynoth & Taylor (2000) can be used to evaluate the maximum rations shortfin eels require for growth in Taranaki streams (Graynoth & Taylor (2000); Equation 1).

$$R_{\max} = 0.306T - 2.74 \ (r^2 = 0.83) \qquad \text{Equation 1}$$

Assuming that food supply is constant, the maximum amount of food required for growth in pasture streams based on mean annual water temperature, was 4.5 times greater than the maximum amount required for shortfin eels in forest streams (Table 5-2). This is equivalent to the fish biomass difference between forest and pasture streams in Chapter 2, suggesting that temperature controls the growth rate of eels, rather than food availability. Huryn's (1996) reasoning for the inverted pyramid of biomass in streams, is that fish can consume a large proportion of benthic prey production (> 80%), which implies that invertebrate biomass does not accurately reflect energy flux from prey (i.e., secondary production). Measured aquatic invertebrate biomass can be interpreted as surplus production, so eel growth in Taranaki mountain streams is unlikely to be limited by food resources. Metabolic rates increase with temperature and thus the requirement for nutrition increases. While Graynoth & Taylor (2000) evaluated food consumption in the laboratory, their finding are largely consistent with eel-based fish biomass studies given a constant supply of food and studies that summarise growth in the field (Jellyman, 1997; Hicks & McCaughan, 1997). Temperatures were below 8.9°C for an average of 38% of the year in forest streams and 13% of the year in pasture, the temperature at which eel growth was assumed to cease (Graynoth & Taylor, 2000) (Table 5-2). With mean temperatures ranging between 9.1°C to 10.2°C and under 8.9°C for a large proportion of the year, it is likely that the temperatures in forested sites were limiting the growth of New Zealand shortfin eels, irrespective of available resources at these sites. This may explain the absence of shortfin eel at the majority of forested sites.

TABLE 5-2 The relationship of modelled maximum ration ($R_{\max}$) in percent of wet body mass (w) per day to mean annual water temperature. Derived from equation 10 (Graynoth & Taylor, 2000).

Land use	Location	Site	Mean annual water temperature (°C)	$R_{\max}$ (w day^{-1})
Forest	Kapoaiaia	KAP1	10.2	0.381
Forest	Little Dunns Creek	LDC1	9.2	0.075
Forest	Ngatoro	NGT1	9.5	0.167
Forest	Oaonui	OAI1	10.2	0.381
Forest	Ouri	OUR1	9.1	0.045
Forest	Punehu	PNH1	9.2	0.075
Pasture	Kapoaiaia	KAP2	13.8	1.483
Pasture	Little Dunns Creek	LDC2	12.1	0.963
Pasture	Ngatoro	NGT2	10.6	0.504
Pasture	Oaonui	OAI2	11.2	0.687
Pasture	Ouri	OUR2	11.5	0.779
Pasture	Punehu	PNH2	11.2	0.687
	Mean in forest		9.57	0.187
	Mean in pasture		11.73	0.850
	Pasture/Forest			4.540

TABLE 5-3 Total weeks and the percentage of time below 8.9°C in forest and pasture sites in Taranaki, New Zealand. At temperatures at and below 8.9°C, shortfin eels are predicted to cease growth (Graynoth & Taylor, 2000).

Landuse	Site	Weeks below 9°C	% time below 9°C
Forest	KAP1	21	40.38
Forest	LDC1	14	26.92
Forest	NGT1	25	48.08
Forest	OAI1	15	28.85
Forest	OUR1	24	46.15
Forest	PNH1	21	40.38
Pasture	KAP2	0	0.00
Pasture	LDC2	6	11.54
Pasture	NGT2	12	23.08
Pasture	OAI2	8	15.38
Pasture	OUR2	10	19.23
Pasture	PNH2	6	11.54
Mean in forest		20	38.46
Mean in pasture		7	13.46

5.7 | Changes in feeding behaviour

Temperatures outside the thermal range of certain fish species may result in acute changes in feeding behaviour. Fish at the coldest site (OUR1) showed an even dependency on each potential food source (aquatic invertebrates, terrestrial invertebrates, and crayfish; Chapter 3). The balance between energy availability and energy requirements of fish is an important concept that supports why fish biomass is greater in pasture. Pasture streams support more fish due to the availability of nutritional sources that counterbalance metabolic requirements. This counterbalance between supply-demand synchronies is an important consideration in aquatic biomass research. Moreover, the alternative subsidy of terrestrial invertebrates likely provide an important additional source of nutrition.

The effects of riparian cover can have distinct influences on energy availability by altering the extent of allochthonous and autochthonous sources. Ecological theory describes the changes in energy availability on a longitudinal scale, and longitudinal food web dynamics changed with respect to riparian vegetation (Chapter 4). The abrupt transition in physical variables at the upstream forest to pasture boundary showed distinct evidence for energetic and functional food web alterations, in response to land use. Non-predatory invertebrates transitioned back to allochthonous sources at lower sites of the Ouri Stream, corresponding to greater riparian vegetation cover at downstream sites. Furthermore, high stream shade was associated with lower in-stream temperatures and a reduction in fish biomass at OUR5 (Chapter 4). This highlights the proximal effect that surrounding riparian cover can have on the functional food web dynamics. Similarly, eels showed a proportional transition in food dominance from aquatic invertebrates to terrestrial invertebrates at vegetated sites downstream. This transition may represent the importance of terrestrial invertebrate subsidies in supporting higher trophic positions. This research highlighted the importance of longitudinal discontinuities with respect to physical, chemical, and biological attributes for food webs along stream continua.

Energy sources in New Zealand systems are often viewed with respect to upstream to downstream relationships along a stream continuum. However, streams that support diadromous fish can represent energy transfer from a downstream-upstream relationship. There has been limited research in New Zealand regarding the incorporation of marine-derived nitrogen (MDN) from migratory juvenile fish and the effects this contribution may have to the production of the stream system. The incorporation of MDN was not seen in top consumers in the food web, most likely due to low densities of migratory fauna (inanga and shrimp) in the study reaches (Chapter 3). However, $\delta^{15}N$ and $\delta^{13}C$ values in both shrimp and inanga larvae were indicative of their marine origins and shows the potential for MDN to be incorporated into stream food webs where significant abundance of shrimp, whitebait and common smelt are known to occur (e.g., the Waikato River below Lake Karapiro; West et al., 2022).

5.8 | Restoration management and policy

The importance of understanding how temperature influences both food availability and metabolic rates of fish is important to sustain and manage stream fish populations in New Zealand. Recent research emphasises how secondary production provides a more integrative tool for assessment of ecosystem function (Dolbeth et al., 2012). For example, Cummins et al. (2022), provides methodology for rapid estimates of aquatic invertebrate biomass by functional feeding group with the intention of accurately characterising the environmental conditions of a stream ecosystem. They suggest that these assessments integrate space and time conditions in a stream reach, while reflecting the availability of food resources (Cummins et al., 2022). These types of analyses can provide insight into the stream ecosystem condition that is imperative for successful management and restoration of stream habitat.

Many restoration initiatives assume that rehabilitation of physical habitat restores ecological function and processes (Bond & Lake, 2007). However, restoration failures with respect to biotic responses have been well documented (Palmer et al., 2010). For example, Nilsson et al. (2015), found that restored Finnish and Swedish streams showed a consistent increase in channel complexity and retention capacity, but biotic responses were weak or absent, despite meeting habitat requirements of target fish. In New Zealand, research has suggested that biotic interactions with resource availability form an integral role in structuring freshwater communities; however, these interactions are rarely considered during stream restoration practices (White et al., 2021; Barrett et al., 2021). This research highlights key findings with respect to temperature-supply synchronies that may have important implications on the management of freshwater fish populations in New Zealand.

The goal of many overseas management policies related to stream restoration is to achieve “no-net-loss” of the productive capacity of fish habitat (Jones et al., 2003). The Canadian policy for management of fish habitat defines the productive capacity as “The maximum natural capability of habitats to produce healthy fish or to support or produce aquatic organisms upon which fish depend” (Department of Fisheries and Oceans, 1986; Jones et al., 2003). While such policy goals are not explicit for New Zealand stream systems, there is much to be gained by evaluating fish biomass. The NPS-FM defines a healthy freshwater ecosystem as “one in which ecological processes are maintained, there is a range and diversity of indigenous flora and fauna and there is a resilience to change” (NPS-FM, 2020). The NPS-FM framework identifies five core biophysical components that contribute to freshwater ecosystem health and include aquatic life, physical habitat, water quality, water quantity and ecological processes (Clapcott et al., 2018). Evaluating fish biomass can assist with unravelling the major drivers of ecosystem functioning (Woodward et al., 2021). Fish biomass integrates these five biophysical components denoted in the NPS-FM, and the analysis of freshwater fish biomass can provide useful indication by which ecological gains and losses of function could be quantified. Ultimately, analyses of fish biomass should be incorporated into management strategies and inform future research recommendations that may provide essential insight into stream functioning of New Zealand streams.

5.9 Study limitations and future research

5.9.1 | Stable isotope analyses

Bulk stable isotope analyses have been widely used as a reliable and cost-effective method to resolve food web dynamics (Peterson & Fry, 1987; Hicks, 1997; Vander Zanden et al., 1999). This research largely focused on the use of bulk stable isotope analyses as it provides a powerful tool for assessing dietary components, energy transfer and trophic position (e.g., Post, 2002; Reid et al., 2008; Neres-Lima et al., 2016). Although there are several benefits to bulk isotope analysis, there are limitations. For example, sources with high variability and extensive overlap across co-occurring dietary resources can lead to challenges in distinguishing between source contribution to consumer (Finlay & Kendall, 2007; Whiteman et al., 2019). High variability and isotopic overlap was observed within grouped functional feeding groups of aquatic invertebrates in both Chapter 3 and Chapter 4. This isotopic overlap can lead to uncertainty in the interpretation of stable isotope mixing model outputs (Phillips & Gregg, 2001; Parnell et al., 2010; Fry, 2013). Therefore, caution is required in interpreting results for dietary sources to consumers at higher trophic levels (e.g., crayfish and fish) in Chapter 3 and Chapter 4.

Emerging techniques such as compound specific isotope analyses (CSIA) can overcome many of the limitations associated with bulk stable isotope analysis (Bowes & Thorp, 2015). The analysis of structural compounds within tissue (e.g., amino acids) using CISA can reduce variability and resolve overlapping values of sources via high resolution isotope data (Whiteman et al., 2017; Blanke et al., 2021). In this approach, the monomers that comprise a macromolecule (such as amino acids in protein or fatty acids) are measured (Whiteman et al., 2019). Because amino acids carry a unique isotopic signature resulting from fractionation processes, the trophic position of a consumer can be determined from the $\delta^{15}N$ value of a source and trophic amino acid pair within the same organism. without the need to measure the $\delta^{15}N$ value of all resources (Whiteman et al., 2019). This allows for the separation of two isotopic changes concerning diet resources and trophic shift within a single species enabling research to accurately link consumers to food sources (Gangné et al., 2018; Choi et al., 2020;). For example, Bowes & Thorp, (2015) demonstrated that CSIA using amino acids more accurately determined food web relations (trophic position and food chain length) with significantly less variability around mean values at each trophic level. Although CSIA may serve as a more informative tracer over bulk isotope analysis, its use in freshwater systems to-date is limited (Bec et al., 2011, Larsen et al., 2013, Chiapella et al., 2021). Recent research has suggested that the approach may overstate the ability to overcome limitations of bulk isotope analyses in aquatic systems (Chiapella et al., 2021). Further technical refinement is required, particularly for trophic position estimates that rely on accurate offset vales between the trophic and source $\delta^{15}N$ values of stream primary producers and assign accurate trophic discrimination factors (TDFs) (Whiteman et al., 2019). While CSIA holds promise in overcoming certain limitations of bulk isotope analysis, there is a significant amount of future research required using CSIA in stream systems.

5.9.2 | Trophic discrimination factors

Bulk tissue isotope analyses assume that source protein is directly incorporated into consumer protein and require trophic discrimination factors (TDF) to reflect the offset from isotopic fractionation (Whiteman et al., 2019). The accurate application of TDF is essential for the reliable estimation of food source contribution to consumers (Bastos et al., 2017). Commonly applied TDFs of 0.4 ± 1.3 ‰ for C and 3.4 ± 0.9 ‰ for N were used in the Bayesian isotope mixing models in this research (Post, 2002a, Quezada-Romegialli et al., 2018). However, physiological processes and dietary shifts in different consumers can lead to significant variation in TDFs causing uncertainty in mixing model outputs (Blanke et al., 2017). For example, research by He et al. (2021) on freshwater crayfish *Procambarus clarkii* showed TDFs were δ^{13}C of -1.98‰ and δ^{15}N of 5.14‰, thus greatly exceeding the range of standard TDFs indicated by Post (2002). The application of standard TDFs may have been an issue for crayfish in Chapter 3 and Chapter 4, as known food sources often did not fall within the 'mixing polygon'. New Zealand crayfish are known omnivorous, with juvenile crayfish susceptible to cannibalism (Usio & Townsend, 2000; Parkyn et al., 2001). Standard TDFs may not accurately offset the change in isotope values of New Zealand crayfish and their food sources. Glutamic acid-phenylalanine TDF ($\mathrm{TDF_{AA}}$) used in CSIA is considered less sensitive to error, as the $\mathrm{TDF_{AA}}$ between the consumer and source amino acid is less variable than bulk tissue TDF estimates (Chikaraishi et al., 2009). This suggests that CSIA may provide the technical refinement required to accurately characterise source contributions to New Zealand crayfish. However, to date, no laboratory studies have estimated TDFs for amino acids for freshwater taxa (Blanke et al., 2021). Future research is required to determine appropriate TDFs that accurately reflect mechanisms of omnivory and cannibalism for New Zealand freshwater crayfish.

5.9.3 | Seasonal limitations

A secondary source of uncertainty when using bulk isotope analyses can arise from temporal and spatial variations of primary producers. Isotopic overlap is known to occur with C_3 terrestrial vegetation and algae, meaning the interpretation of the isotope values derived from bulk tissue can be confounded (Finlay, 2001). However, there was insufficient replication of leaf litter and periphyton in this study to infer potential isotopic overlap and seasonal variability. Future research should consider using CSIA techniques and seasonal sampling of potential basal dietary sources to address these issues.

A key finding of this research is the importance of terrestrial invertebrates as an alternative source of nutrition for fish in Taranaki streams (Chapter 2 and Chapter 3). The higher input of terrestrial invertebrates may also be attributed to season. Consequently, terrestrial invertebrates may provide important seasonal influx of alternative subsidies in Taranaki pasture streams (Kawaguchi & Nakano, 2001; Burbank et al., 2022). Understanding the extent to which seasonal invertebrate inputs may be subsiding consumer biomass is important, particularly given food webs fuelled by multiple energy sources may be more resilient to anthropogenic modification (Benjamin et al., 2022). The proportional contribution of terrestrial derived sources to fish over a seasonal basis warrants further investigation in New Zealand streams.

5.9.4 | Marine-derived nitrogen

While bulk stable isotope analyses showed the presence of marine-derived nitrogen (MDN) in inanga larvae, MDN was not expressed to higher trophic levels (Chapter 4). CSIA may yield higher accuracy and provide the technical refinement required to detect MDN contribution to stream food webs. Further the low densities of migratory juvenile galaxiids, likely contributed to the lack of MDN contribution in Taranaki Streams. This highlights the need for further analysis of MDN where significant juvenile galaxiid migrations are known to occur. The application of

CSIA techniques may provide the accuracy required to assess the MDN contribution to New Zealand stream food webs (Pilecky et al., 2022). Greater knowledge of the role migratory fish may play in contributing MDN to the annual nutrient budgets would provide insight into the management and sustainability of fish populations and may have future implications on whitebait fisheries in New Zealand.

5.9.5 | Energy and fish biomass response following restoration

This research highlighted the effects heavily shaded vegetation cover has on temperature and consequently supply-demand synchronies of fish. Little is known regarding how fish biomass and energy availability varies following restoration in New Zealand. Questions persist about the response of fish biomass to young riparian planting (1 to 5 years) and mature riparian planting (> 15 years). Overseas research has shown a reduction in fish biomass following restoration efforts (Zalewski et al., 2001; Kaylor & Warren, 2018). It may be plausible that whole stream riparian planting towards closed canopy environments (> 90% stream cover) may limit the productive capacity of the stream. Future research should focus on light and temperature regimes, resource availability, the fish species present and their relative biomass over various temporal scales of riparian planting. These data would provide valuable information regarding success of restorative efforts on fish communities.

5.10| CONCLUSION

Freshwater fish biomass is the expression of accumulated energy at the highest trophic level and can provide useful insights into the productive capacity of the stream and ecosystem health (Randall & Mills, 2000; Jones et al., 2003; Moi et al., 2022). The loss of riparian cover can have profound influences on light and temperature regimes and the availability of allochthonous and autochthonous resources. Research has shown this can lead to unpredictable changes in fish biomass. However, fish in Taranaki presented a five-fold increase in fish biomass in pasture streams, leading to key questions around the functioning of these pasture streams. This thesis aimed to identify the causes of greater fish biomass in pasture sites and highlights the importance of evaluating both energy availability and metabolic requirements of fish. The balance between available resources compared to the metabolic scope of fish is paramount to sustainable fish biomass. In this study, pasture streams can have greater allochthonous inputs of terrestrial invertebrates that provide an important additional resource for fish.

The benefits of undertaking fish biomass assessments could provide insight into the ecological function reflecting the metabolic functioning of a stream, food availability and energy flow. These results have implications for stream restoration that involves planting dense tree cover in riparian margins without considering the species present, their thermal tolerances and the extent and quality of food. The importance of light and temperature as the fundamental driver behind fish biomass should be considered during restorative stream practices. Future analyses should apply emerging isotope techniques such as CSIA with a focus on the supply-demand synchronies of target fish and energy availability.

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