Improving conservation of kōwaro

(Canterbury mudfish, *Neochanna burrowsius*)

A thesis submitted in partial fulfilment

of the requirements for the degree of

Master of Science in Ecology

at the

University of Canterbury

by

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2018

Contents

Acknowledgements

Abstract

Global change will likely drive regional shifts in species distribution and localised changes in communities. In aquatic communities, altered drought regimes could be detrimental to the organisms that inhabit affected systems. Furthermore, stress-tolerant species are likely to be more susceptible to these changes, particularly if these species lack the capacity to disperse to new habitats. Kōwaro (Canterbury mudfish, *Neochanna burrowsius*) is a critically endangered stress-tolerant fish largely restricted to isolated populations in agricultural catchments scattered across the Canterbury Plains on South Island, New Zealand. Consequently, knowledge of how kōwaro respond to increased drying intensity and the likely mechanisms associated with these changes could considerably improve conservation efforts for this rare endemic fish. When exposed to two consecutive extreme droughts, a large network of kōwaro populations switched from adult-dominated populations to fry-dominated populations, which indicated a reduction in likely population resilience. Further investigation of kōwaro populations and associated trophic dynamics with stable isotopes along a drying gradient, indicated that drying-prone sites had higher relative abundance of kōwaro fry, which likely led to increased cannibalism by larger kōwaro. Importantly, increased canopy cover was associated with elevated abundance of terrestrial prey entering the aquatic system, with this food resource becoming increasingly important for larger kōwaro. Consequently, increased riparian planting could potentially offset the negative effects of increased drying by facilitating increased survival of larger kōwaro. Therefore, within degraded systems, additional environmental gradients, like the drying and canopy cover effects detected here, likely alter the trophic interactions and population dynamics of stress-tolerant species, providing both challenges and opportunities for their conservation.

Chapter One: Introduction

Global change and the implications for stress-tolerant species

Global change is a multifaceted issue that both directly and indirectly affects biotic and abiotic functioning of ecosystems worldwide (Diaz and Cabido 1997, Sala et al. 2000, Barbour et al. 2010). At local scales, these changes often interact in a synergistic manner, resulting in localised changes to species composition, with species arrival and extirpation occurring simultaneously (Pörtner et al. 2005, Walther et al. 2009, Sorte et al. 2013). At regional scales, this same change may manifest as a distinct shift in the inhabited range or a reduction in abundance, and eventual extinction of the affected species (Adams et al. 2009, Sorte et al. 2013, Travis et al. 2013, Swab et al. 2015). These issues are likely to be more acute for species that persist in already extreme environmental conditions, particularly those with limited capacity to shift to new suitable habitats, because their range is restricted by predation or competition from other species in benign habitats (Harley 2011). Although these species usually have high tolerance of stressful conditions they are likely to be more vulnerable. For example, as climates warm and become more variable and abiotic conditions become more harsh, the available niche space for these species decreases. Such niche contraction may remain until either the environment improves or the other species, which these species negatively interact with, are also forced to alter their own niches. Consequently, global change will likely pose severe implications for the long-term prospects of stress-tolerant species that have narrow realised niches in extreme environments.

The susceptibility of these stress-tolerant species is associated with the trade-off between stress tolerance and competitive dominance, which has been documented in a range of systems (Bestelmeyer 2000, Tessier et al. 2000, Broennimann et al. 2006, Winck et al. 2007, White et al. 2017). Stress tolerance confers the ability to cope with extreme conditions, such as drought, but is synonymous with reduced competitive ability (Liancourt et al. 2005). These stress-tolerant species persist in a 'window of opportunity' whereby competitive exclusion extirpates them from benign

habitats, thereby forcing them into harsh habitats that competitors or predators cannot tolerate (Figure 1.1A). Because of their inability to tolerate competition, the highest levels of population growth are only attainable with isolation, where physical dispersal barriers inhibit competitor access, thus allowing the stress-tolerant species to occupy benign environments (Figure 1.1B).

In freshwater ecosystems, isolation could appear naturally, such as in the upper reaches of a catchment where drought-prone rivers in the lower portions create dispersal barriers, or anthropogenically, due to manipulations of waterways that may separate reaches or change the flow regime. Importantly, in freshwater habitats increased extreme drought frequency from global
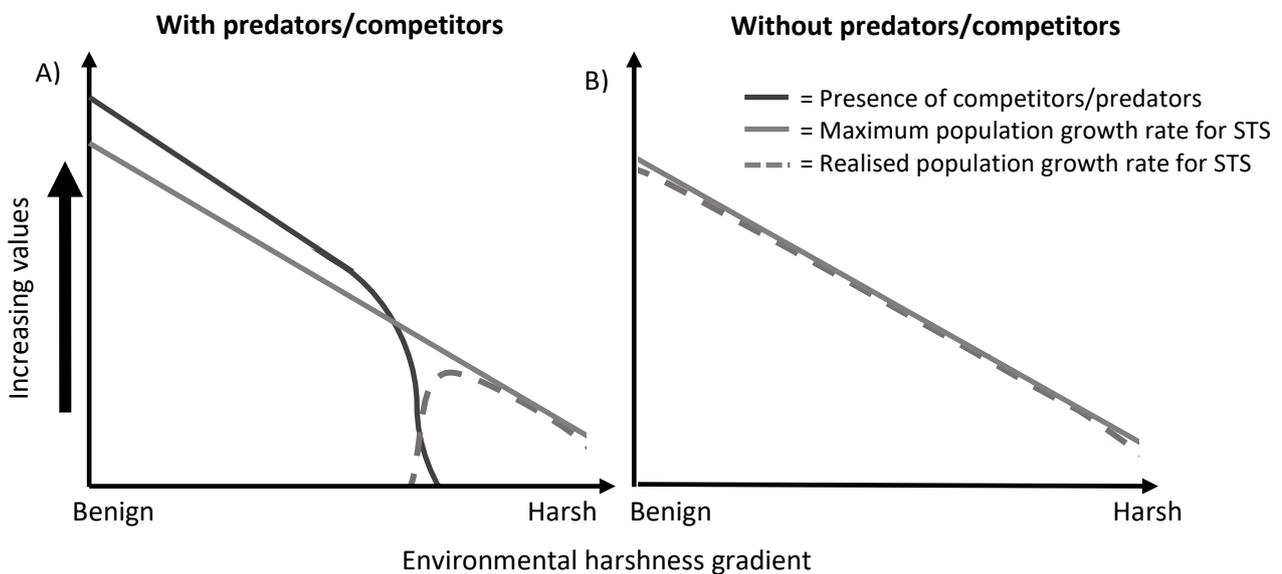
Figure 1.1 Theoretical influence of environment harshness on the population growth rate of a stress-tolerant species [STS] (solid grey) in the presence (A) and absence (B) of predators/ competitors (black). Two extremes are described: A) a predator-accessible population in which predators/competitors are only restricted by environmental conditions (i.e., no dispersal barriers exist), and B) an isolated population where dispersal barriers prevent access by predators/competitors (STS can occupy benign conditions). The presence of predators/competitors will likely restrict the available niche space for STS, which limits the realised population growth rate (dashed line).

warming may make conditions too harsh for species that are already restricted to drought prone habitats, thereby contracting their already limited available niche (White et al. 2016).

When freshwater ecosystems periodically dry, established species and communities can become adapted for this and resilient to its effects (Bond et al. 2008, Vander Vorste et al. 2016). However, the increasing frequency and intensity of droughts driven by global warming are becoming an issue even for stress-tolerant species (Carnicer et al. 2011, Gudmundsson and Seneviratne 2016). Severe drought can affect populations both directly, through reduced survival and fecundity, and indirectly, through changes in the surrounding food web, thereby reducing the likelihood of long-term persistence for a stress-tolerant species (Bond et al. 2008, Clarke et al. 2010, Woodward et al. 2012). These food-web changes may involve the loss of key prey, thereby inducing prey switching behaviour in the stress tolerant species. Under severe conditions this switching could increase the rate of cannibalism by adult fishes, thereby reducing juvenile survival and inhibiting recruitment (Wissinger et al. 1996, Luz-Agostinho et al. 2008). Juveniles may also be less tolerant to the direct physiological stress of droughts compared to adults, thereby limiting juvenile survival and population recruitment further. Therefore, because the relationship between drought severity and survivability is potentially dependent on body size, there is a particular need to evaluate the population dynamics of different sized individuals separately (Nagayama et al. 2009).

The plight of New Zealand's mudfish

New Zealand's mudfish (*Neochanna* spp.) are an example of threatened stress-tolerant species, where a greater understanding is required to stave off the effects of global change (Goodman et al. 2014). These mudfish have specialised in tolerating multiple extreme conditions within waterways, including hypoxia and periodic drying, which is why they presumably thrived in the isolated wetlands that once covered a large portion of New Zealand (Eldon 1979c, Davey et al. 2003). The harsh conditions of these habitats likely excluded other competitively dominant species, that might have otherwise extirpated them (McDowall 2010, White et al. 2015a). However, mudfish are not impervious to these conditions

Figure 1.2 Typical habitat of kōwaro exhibiting large fluctuations in water levels throughout the year. These photos were taken in November (top) and February (bottom), at the same site.

that enable their persistence, and prolonged drought can cause high rates of mudfish mortality (Eldon 1979a, White et al. 2016). This puts mudfish between a rock and a hard place; they require drying to exclude predators and competitors, but at the same time could fall victim to extreme drought.

Mudfish refugia have been unwittingly provided with the creation of small patches of suitable habitat, a consequence of anthropogenic modification of the landscape, whereby some respite from competition is afforded to them by the isolation of these waters (Eldon 1979c, McDowall 1997, Davey et al. 2003, Harding et al. 2007). However, new threats from introduced species and lost connectivity may pose further risks to the long-term persistence of these stress-tolerant fishes (Gleeson et al. 1999, Ling and Willis 2005), with loss of genetic diversity a potential consequence of this lost connectivity (McDowall 1997, Gleeson et al. 1999, Smith 2009). Ideally, the re-establishment of dispersal links between these populations could potentially alleviate these negative effects. However, there is a risk with reconnecting these isolated populations; increased accessibility to predators could undermine the benefits to the mudfish. However, in lieu of physical connections between populations, translocations can work to provide the same functions and benefits without the drawbacks from predator access (Thrimawithana et al. 2013). However, for successful translocations, an understanding of how environmental conditions affect a location's suitability for long-term persistence is required.

Kōwaro (Canterbury mudfish, *N. burrowsius*), in particular, is a prime example of a stress-tolerant species vulnerable to the effect of global change because it persists entirely within the agricultural matrix of the Canterbury Plains. This critically endangered endemic fish has a sporadic distribution within its natural range, wherein inhabitable niche space is limited due to restrictions imposed by both the environment and competitive exclusion by other fishes (Goodman et al. 2014). Their isolation in agricultural streams, many of which periodically dry (Figure 1.2), may afford them niche space that would have otherwise been utilised by other fishes, resulting in a higher realised mudfish population growth rate (Figure 1.1B). For this species, the sparse distribution of contemporary populations precludes physical connections between most populations, indicating the reliance on translocations,

but not just between populations, because they are also utilised to re-establish extirpated populations. However, although translocations have become a key conservation strategy for this endemic species, these have been largely unsuccessful to date (O'Brien and Dunn 2007). This was an overall motivation for this research. I wanted to better understand how drought affects kōwaro populations and the mechanisms through which these changes are manifested, with the hope that such knowledge can be firstly utilised to better understand the processes that lead to extirpation of populations of stress-tolerant species, and secondly, to both improve conservation efforts to safeguard this species and others like it against future risks associated with global change.

Thesis structure and chapter outlines

I have constructed this thesis around two data chapters that I intend to publish as stand-alone papers. Consequently, there is some overlap in the material presented in Chapter Two and Three. References and appendices for all chapters have been combined and can be found at the end of the thesis.

Chapter Two investigates the impact of two consecutive droughts on a large network of interconnected kōwaro populations. This highlights the merit of including an additional size-based metric for monitoring of kōwaro populations. Furthermore, I discuss how the combination of size- and abundance-based metrics potentially provides more information relevant to population resilience.

Chapter Three examines the trophic interactions of kōwaro populations across two core environmental gradients, drying intensity and canopy cover. I show links between the invertebrate communities, the position of kōwaro within the wider community, and size distributions in kōwaro populations.

Chapter Four provides a summary of the research presented in this thesis, showing how the food-web changes described in Chapter Three are likely to be, at least partially, responsible for the catchment-wide changes observed in Chapter Two. Furthermore, I highlight the recommendations for management and put forward other potentially important environmental characteristics influencing kōwaro that need further investigations.

Chapter Two: Shifts in population size structure for a drying-tolerant fish in response to extreme drought

Introduction

Extreme climate-related events will become increasingly important for conservation under a warming climate (Jenkins and Warren 2015, Pacifici et al. 2015, Swab et al. 2015). Consequently, in freshwater systems, changes to drought regimes induced by climate warming will have significant ramifications for organisms, such as fish, that inhabit affected waterways (Morrongiello et al. 2011, Leigh et al. 2015). Moreover, issues that arise from extreme events could potentially be more acute for species that already persist in extreme environmental conditions (Harley 2011), such as stress-tolerant fish species. Tolerance of harsh conditions opens up niche space for stress-tolerant fish when more benign habitat is occupied by competitors and predators (White et al. 2015a). However, because the occupiable niche space of a stress-tolerant species is reduced by increased environmental harshness, and the corresponding shift of predators and competitors in relatively benign habitats will be smaller, or non-existent, there will be an overall reduction in occupiable niche space of the stress-tolerant species compared to other species (Harley 2011). A greater understanding of intraspecific variability of stress-tolerance is likely to improve conservation of stress-tolerant fish because, although these stress-tolerant fish can persist in extreme conditions, their tolerance will not be uniform across all individuals, particularly those of different sizes or life stages.

Natural variation in tolerance to environmental stress occurs between individuals of a species because of multiple underlaying factors, including variable ontogenetic responses to differing environments (Winne and Keck 2005, Fangue et al. 2006, Morrongiello et al. 2013, Grégoir et al. 2017). For example, the partitioning of microhabitats across life history stages and differing needs over those different life history stages means their underlying tolerance will vary (Hakala and Hartman 2004, Penha et al.

2015). Therefore, because these different life history stages could have reactions to environmental stress such as drying, there is often unequal mortality during extreme environmental events.

In freshwater fish, high mortality in smaller individuals, such as young-of-the-year, often occurs during drought because reduced habitat size increases intraspecific competition (Hakala and Hartman 2004, Penha et al. 2015), though this intra-specific competition may also cause uniform mortality across all sizes of fish (White et al. 2016). Similarly, larger individuals can suffer high mortality due to the loss or reduction of lower trophic levels (Winne et al. 2010), or size-dependent physiological constraints (O'Brien 2007). However, the high mortality in larger fish could also result in an increase in the number of fry/juveniles, particularly in cannibalistic species, due to a possible reduction of intraspecific competition or predation that would otherwise reduce fry survival (Dorn and Cook 2015, Katz and Freeman 2015). Therefore, drought could potentially create populations that have undergone stabilising mortality, with the loss of large and small individuals, or exaggerated recruitment, with increased fry survival. Thus, measuring body size-based metrics and abundance to evaluate population responses under drought conditions is likely to be worthwhile.

Metrics that reflect changes in the abundance, body condition and distribution of sizes (Hakala and Hartman 2004, Harding et al. 2007, van Kooten et al. 2010, Katz and Freeman 2015) measure the short-term effects of extreme events like drought. However, because reproductive output is generally disproportionally higher in larger individuals (Eldon 1979a, Venturelli et al. 2010, Beldade et al. 2012, Kindsvater et al. 2012), it may be possible to infer the long-term effects of extreme environmental events, such as changes to reproductive output (Grégoir et al. 2017), by measuring these short-term effects. The loss of larger individuals during droughts could reduce capacity for population growth because of the disproportionally high fecundity of large individuals. This ability for a population, species or community to recover after a disturbance is resilience, with faster post-disturbance recovery equating to higher resilience (Holling 1973). Therefore, body size-based metrics could be used in conjunction with abundance to assess the resilience of populations.

Kōwaro (Canterbury mudfish, *Neochanna burrowsius*) are an example of an stress-tolerant fish species that will likely require increased conservation efforts to ensure persistence in the face of ongoing climate warming. Similar to other mudfish found throughout New Zealand (Gleeson et al. 1999, White et al. 2015a), kōwaro are adapted to live in bodies of water characterised by extreme conditions, such as low dissolved oxygen or periodic drying, that exclude most other fishes (Eldon 1979c); physiological and behavioural adaptations, such as cutaneous gas exchange and air-breathing, enable mudfish survival in extreme conditions (Eldon 1979a, Meredith et al. 1982, O'Brien 2007, Urbina et al. 2014). Despite these stress-tolerant traits, kōwaro are critically endangered and have a fragmented distribution across the Canterbury Plains on South Island, New Zealand (Goodman et al. 2014); a landscape that is predicted to experience increasing drought frequency and intensity because of climate warming (Ministry for the Environment 2016). These extant populations represent the survivors of a historically widespread distribution (Eldon 1979c), which have been impacted by ongoing anthropogenic modifications to the surrounding landscape. This means the kōwaro is an already-threatened stress-tolerant fish that is potentially faced with an increasingly unfavourable environment in a changing landscape. Therefore, investigating how kōwaro populations, particularly their body-size distributions, respond to drought conditions, and whether these size distributions can allow population resilience to be assessed will be particularly useful for conservation efforts.

I compared kōwaro size distributions between surveys undertaken after periods of high, medium and low drought intensity. I predicted that stabilising mortality, exaggerated recruitment or a mixture of both would occur within these populations during droughts, and I investigated both population abundance and median size to assess the mechanisms of drought-induced population change. Specifically, I predicted that CPUE would either decrease, due to stabilising mortality, or increase, due to exaggerated recruitment. Whereas, I expected that median size would either not change, due to stabilising mortality, or decrease due to exaggerated recruitment.

Methods

Survey overview

I studied a large network of kōwaro-inhabited waterways in the Waianiwaniwa Valley described as an important refuge for kōwaro in a changing landscape and, therefore, significant for the conservation of this endemic freshwater fish (Harding et al. 2007). The Waianiwaniwa River flows from the foothills onto the Canterbury Plains (43°27 S, 171°59 E) and is surrounded by a combination of pastoral agriculture and plantation forestry (Harding et al. 2007). This river system experiences low flows during summer, wherein portions of tributaries and the mainstem dry partially, with close to complete drying possible during extreme droughts.

Kōwaro population densities are difficult to measure, and methods measuring density, such as mark-recapture, although suitable for other mudfish species (White et al. 2015b), have proven unsuccessful with kōwaro (O'Brien 2005). Instead, kōwaro populations were sampled using gee-minnow traps from which catch-per-unit-effort, a measure of relative abundance (Cadwallader 1975, Eldon 1979c, Harding et al. 2007, hereafter CPUE) was calculated. Gee-minnow traps with 3.2 mm mesh were used to trap smaller mudfish, including fry. Traps were not baited because previous mudfish surveys, including those with kōwaro, show that baiting does not affect catch rates (Harding et al. 2007, White et al. 2015b). I used data collected from 2007, 2010 and 2015, which corresponded to periods of high, average and low rainfall respectively, as described below from both previously published and unpublished datasets collected using equivalent methods.

Climate comparison

The rainfall for the six months (July to December) preceding each survey was obtained from a climate station positioned near the bottom of the Waianiwaniwa valley (National Institute of Water and Atmospheric Research 2017). The long-term average for this station was derived from ~60 years of rainfall data (1960-2016), which yielded an average of c. 430 mL of rainfall for these six months. For the survey by Harding et al. (2007), these months had a total rainfall of c. 520 mL, or 21% above

average, so this survey year was referred, hereafter, as 'wet'. For the survey by Gwatkin and McIntosh (2010), these months had a total rainfall of c. 415 mL, or 3% below average, so this survey year was referred, hereafter, to as 'mild'. Whereas, in 2015, these six months had a total rainfall of 290 mL, or 33% below average, so this survey year was referred, hereafter, to as 'drought'. It is important to note that these six months in 2014 experienced the lowest rainfall in the last 60 years, which was c. 240 mL or 44% below average, showing that the Waianiwaniwa Valley experienced two significant droughts in consecutive years in 2014 and 2015.

Kōwaro datasets

The 2007 data were collected from 14 sites which were sampled either once or twice (Harding et al. 2007). These sites were 20-m stream reaches and isolated ponds within which seven un-baited Gee-minnow traps were placed at even distances. Sampling done with baited traps was not used in these analyses. Traps were positioned with a small section of the trap above the water, which would allow mudfish to take gulps of air from the surface should the water start to become hypoxic, and were left overnight and retrieved after c. 24 hours. Trapped kōwaro were anaesthetised with Aqui-S and total body length was measured (to the nearest mm), after which the fish were released once they had recovered. In 2010, this same methodology was applied by Gwatkin and McIntosh (2010) for 29 sites; wherein, most sites sampled in 2007 were resampled and others were added to extend knowledge of mudfish distributions within the Waianiwaniwa Valley. In 2015, I selected sampling sites from those that were sampled during either the 2007 or 2010 surveys. Minimum distance between sites was 400 m to limit the potential for fish to be sampled twice. Although a total of 26 sites were selected for sampling in 2015, the low rainfall resulted in the Waianiwaniwa River receding to become a series of isolated pools, which meant 13 sites were dry and, for those with surface water, 20-m reaches were not feasible. Therefore, the number of traps placed at each site was altered from those used by Harding et al. (2007) and was determined by pool size, with traps set at approximately one per 5–6 m^2 surface area, meaning sites had between three to five traps.

Size class definitions

Mudfish were classified into age-based size classes using information from Eldon (1979a). Pelagic fry were fish up to 40 mm in length, the mean size associated with the behavioural change to a cryptic, nocturnal and largely benthic, habit characteristic of all other life stages. Benthic fry were fish between 40 mm and 59 mm because the latter was the minimum size for year-old fish. Individuals between 60 mm and 89 mm were described as yearlings (year-old fish), and this class was further separated into large and small about the median size of 75 mm to account for hatching time the previous year; large yearlings likely hatched earlier than small yearlings. Adults were fish larger than 90 mm, which Eldon (1979a) specified as being at least two years old. Large and small adults were split about the median size of 120 mm to account for the maximum size attained by females being larger than males. Furthermore, these size classes reflected temporal patterns, being fish produced in the current year (i.e., fry), survived from the previous year (i.e., yearlings), or multiple years (i.e., adults).

Data preparation and analysis

All data analysis was carried out in R, version 3.4.1 (R Core Team 2017). For the 2007 and 2010 data, samples from sites sampled twice had a representative sample constructed that was the average of the two samples, with averaged values for proportions of total fish within each size class, catch-per-unit-effort, and median size.

Catch-per-unit-effort (CPUE), the total number of fish at each site divided by the number of traps used, was calculated for each site in each year. A single-factor ANOVA with rainfall regime as the factor with three levels (wet, mild and drought) was used to analyse the mean CPUE between the three rainfall conditions. For each site within each of the rainfall conditions, the cumulative proportion of total mudfish caught, as a function of length, was calculated both to determine the median size and to visually depict population size structure. This visual depiction of the population size structure allowed inference about the relative proportion of a population of breeding size. A single-factor ANOVA, with the same design as that used for CPUE, with rainfall regime as the factor with three levels (wet, mild and drought) was used to analyse the average median size of mudfish between the three rainfall

conditions. Furthermore, using the size classes described above, all fish caught were classified into their respective classes. The proportion of the total number of fish, and not just the absolute number, was used for classification because a site, or sites, with very low or high CPUE would otherwise exert a large influence on the means for each size class within the different rainfall conditions. A binomial generalised linear model, with a logit link function, was used to predict the proportions of each size class within the different rainfall conditions; wherein, the significance of mudfish size class and rainfall conditions as predictors, for the proportion with each size class, was assessed.

Inferring the resilience of kōwaro populations

To evaluate population status, populations at each site within each year were categorised based on thresholds associated with CPUE-derived abundance and body size distribution that likely reflected aspects of potential population resilience (Figure 2.1A). For CPUE, threshold of six (i.e., six fish per trap) representing the top c. 20% of all CPUE values from the 474 surveys of kōwaro populations sampled with gee-minnow traps and stored within the New Zealand Freshwater Fish Database (National Institute of Water and Atmospheric Research 2016). The threshold for median size was 60 mm because this is the minimum size at which these mudfish can breed (Eldon 1979a), meaning populations with a median size greater than 60 mm will mostly consist of breeding-size individuals. This resilience framework consisted of four categories that ranked those expected to be most to least resilient, as 'excellent', followed by 'good', then 'fair', and finally 'vulnerable' (Figure 2.1A). Populations with excellent resilience consisted of high number of individuals that can breed, which means there is strong capacity for recovery. Whereas, good populations had fewer individuals of breeding size, which equates to a diminished capacity for recovery. Populations with only fair resilience had most individuals not yet able to breed (i.e., median size below 60 mm), and this lack of breeding adults would likely mean the capacity for recovery is small. Finally, vulnerable populations consisted of smaller individuals that were not of breeding size and at low abundance, which equates to a very small capacity for recovery and, consequently, the highest risk of extirpation from further
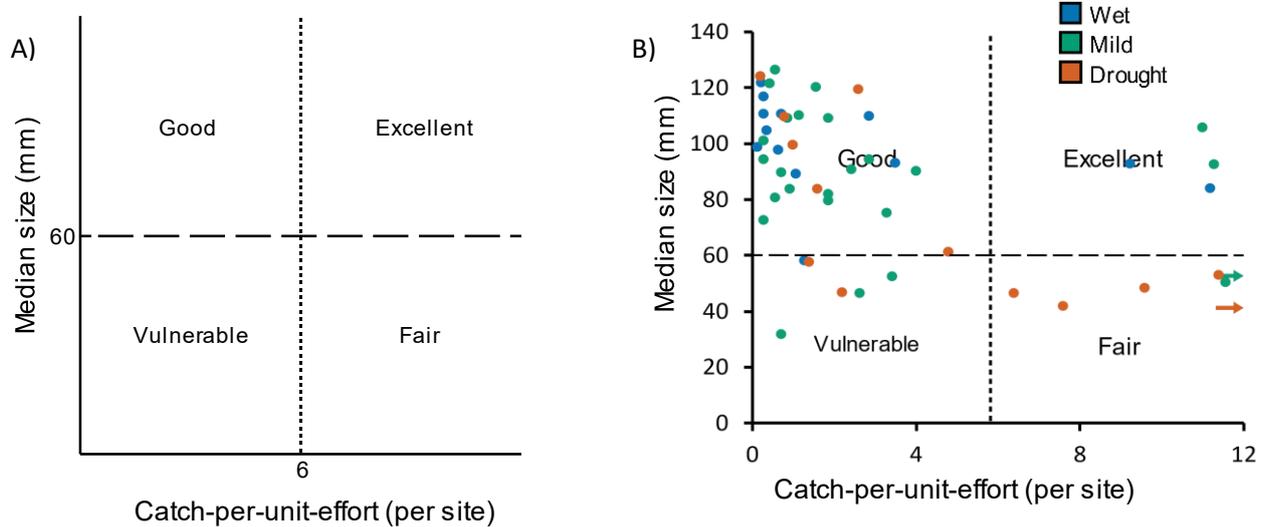
Figure 2.1 A resilience framework (A) for the categorisation of kōwaro populations using median size, a measure of the distribution of sizes, and catch-per-unit-effort (CPUE), a measure of relative abundance, and (B) the kōwaro populations positioned within the framework. The median size threshold of 60 mm (dashed line) denotes the minimum size at which a mudfish reaches maturity, and the CPUE threshold of six (dotted line) denotes the top c. 20% of all CPUE values recorded, within the New Zealand Freshwater Fish Database. These four categories, ranked from most to least resilient, are 'excellent', followed by 'good', then 'fair', and finally 'vulnerable'. The colours represent the wet (blue), mild (green) and drought (orange) rainfall conditions, and arrows indicated extremely high values for CPUE; the green arrow represents a CPUE of ~18, and the orange arrow a CPUE of ~ 28.

drought. A chi-squared test of independence was used to evaluate the relationship between the number of sites within each category and the rainfall regime.

Results

There was no significant difference in kōwaro catch-per-unit-effort (CPUE) between the three different rainfall conditions ($F_{2,49}$ = 2.25, p = 0.116), and populations had mean CPUE values ranging from 3.29 to 5.08 fish per trap, with large 95% confidence intervals, reflecting the high variability in catch rate (Figure 2.2).

In comparison to CPUE, there were significant effects of rainfall conditions on the body size distributions of mudfish ($F_{2,49}$ = 4.08, p = 0.023; Figure 2.3). The wet and mild conditions had similar average median kōwaro size of 95 mm and 89 mm, respectively (± 95% confidence intervals: 84 to 107 and 73 to 106 mm, respectively; Figure 2.3B & D), but under drought conditions the average median kōwaro size was 68 mm ((± 95% confidence interval: 56 to 81 mm; Figure 2.3F).
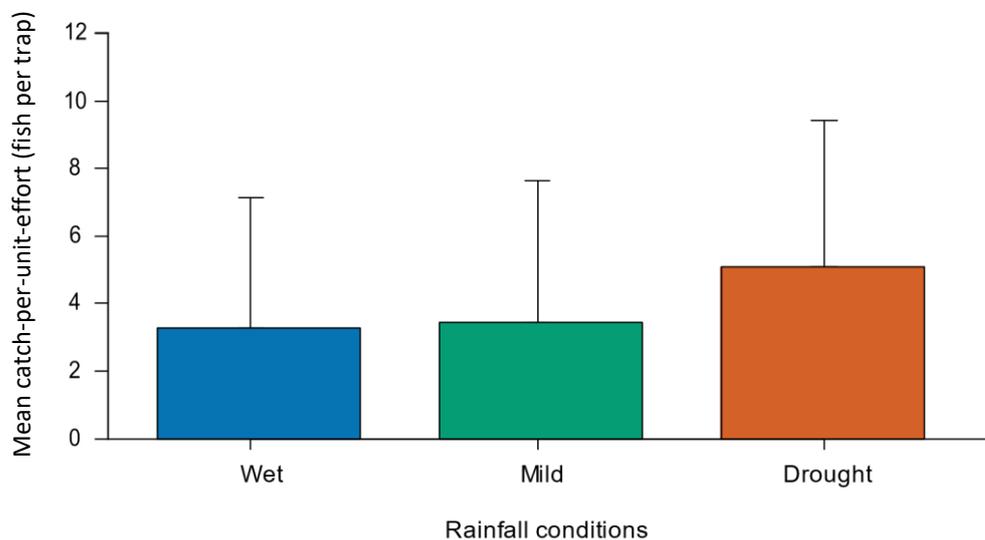
Figure 2.2 Mean catch-per-unit-effort (CPUE) of kōwaro populations surveyed under different rainfall conditions in the Waianiwaniwa Valley. Error bars show the upper value in the 95% confidence interval determined from model fits.
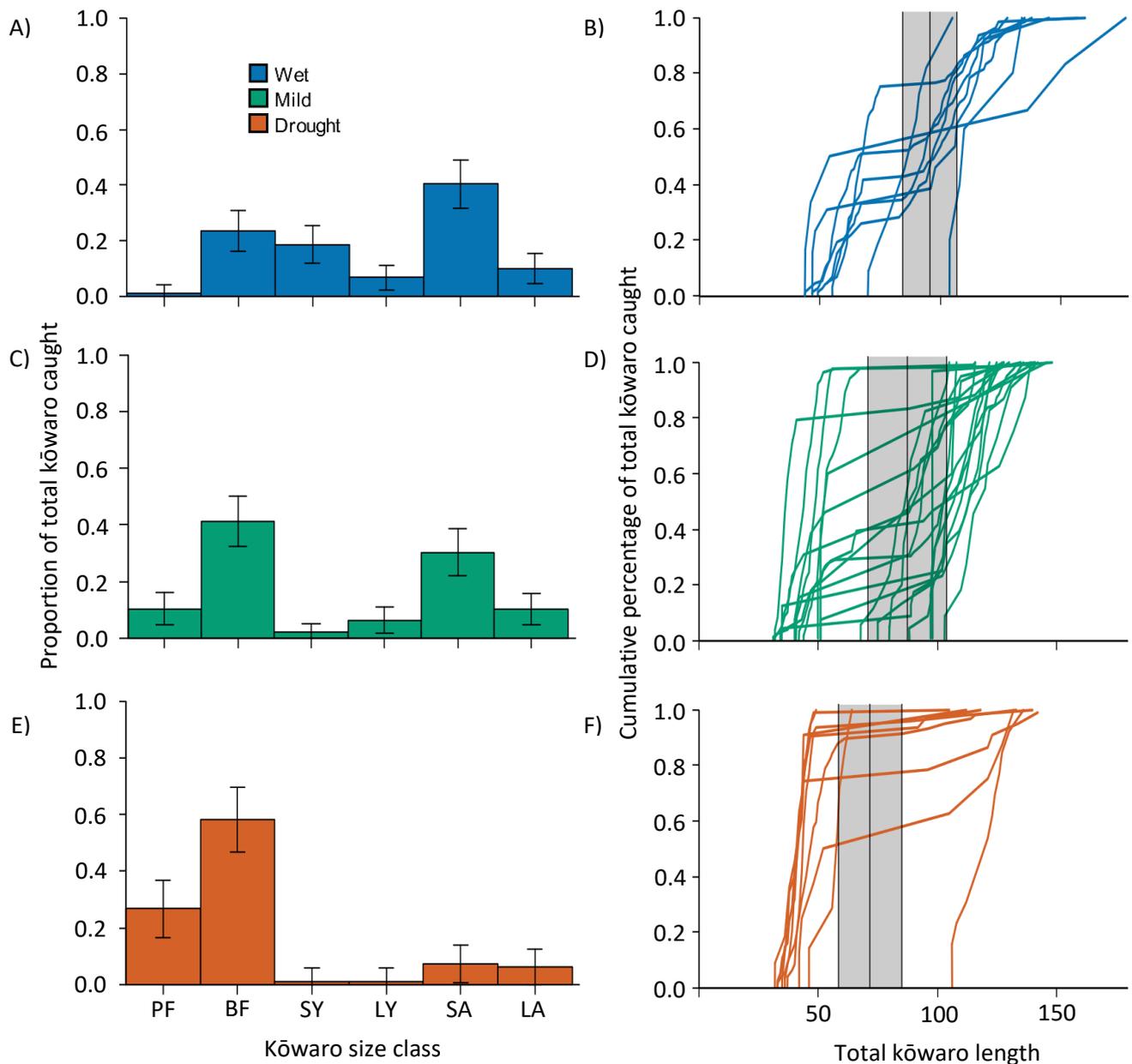
Figure 2.3 Size distributions (A, C & E) and size-based cumulative frequencies (B, D & F) of kōwaro populations under different rainfall conditions. Size classes in A, C & E reading from left to right, are pelagic fry (PF), benthic fry (BF), small yearling (SY), large yearling (LY), small adult (SA), and large adult (LA). Error bars show 95% confidence interval determined from model fits. Line graphs in B, D & F show cumulative proportion distributions for each site that contained at least five mudfish. Grey panels show 95% confidence intervals for median size of kōwaro populations determined from model fits. The colours represent the wet (blue), mild (green) and drought (orange) rainfall conditions.

The significant difference in median kōwaro sizes was associated will obvious changes in cumulative proportion of mudfish caught at a site as a function of length. Populations sampled in the wet conditions contained mudfish across a range of sizes (Figure 4B) and populations sampled in mild conditions also had a mix of both large and small mudfish (Figure 4D). However, the variability between populations became more pronounced under mild conditions, with some sites containing fry-dominated populations, while others contained adult-dominated populations (Figure 4D). Furthermore, under drought conditions, the overall body size distribution pattern was noticeably different from the wet and mild surveys, with fry-dominated populations being more common, although one adult-dominated population was still present (Figure 4F). Noticeably under drought, there was no population that contained both adults and fry in similar proportions as had occurred in wet and mild conditions.

Classifying kōwaro into specific size classes revealed there was a significant interaction between rainfall condition and size class affecting kōwaro relative abundance ($F_{10,294} = 2.79$, $p = 0.002$), which meant the effect of drought depended on kōwaro size. The size distributions of kōwaro caught in the wet and mild conditions looked similar (Figure 4A & C), with bimodal distributions indicating relatively equal proportions of fry and adults. In comparison, the size distribution of kōwaro caught under drought conditions was unimodal (Figure 4E), with a right-skew indicating a severe reduction in all mudfish larger than 60 mm (i.e., individuals at least one year old). Consequently, under drought, fry (i.e., mudfish shorter than 60 mm) represented c. 85% of the population compared to c. 20% in the wet or mild conditions. Thus, any kōwaro greater than 60 mm was negatively affected by drought (i.e., their proportions decreased), but kōwaro less than 60 mm were positively affected by drought (i.e., their proportions increased).

Combining CPUE and median size into a population resilience framework revealed the number of populations within each category and rainfall conditions were not independent ($\chi^2 = 13.65$, df = 6, $p = 0.034$). The overall trend was a move from populations classified as having good and excellent

resilience in wet conditions, to populations with fair and vulnerable resilience in drought conditions, with the populations occupying an intermediary space in mild conditions (Figure 2.1B). This change occurred because the populations surveyed in wet conditions were generally categorised as 'good', with a couple falling into the excellent category. Populations surveyed in mild conditions were, again, centred in the good category, but some had fallen into the fair and vulnerable categories. However, under drought conditions, populations were completely lacking from the excellent category and the majority fell below the 60-mm body size threshold.

Discussion

Stress-tolerant fish species are potentially going to be faced with smaller occupiable habitats in environments becoming harsher due to climate warming (Harley 2011, Morrongiello et al. 2011, Leigh et al. 2015). For already threatened stress-tolerant species, such as the kōwaro, an increase in frequency of extreme events, like the consecutive drought years I studied here, could be detrimental to their ongoing persistence. This highlights the need for improved understanding of how these stress-tolerant species respond to extreme events, the population-level changes these events induce and how they might affect population resilience. I aimed to assess the effect of drought conditions on two aspects of kōwaro populations, their body size distributions and abundance, and to investigate the potential of using these two metrics to infer information about a population's resilience. Drought conditions caused no change in catch-per-unit-effort (CPUE), and a significant decline in the median size, which was caused by the loss of large reproductively-active adults and an increase in the amount of smaller immature fry. I argue below, this loss in reproductive potential possibly caused a reduction in the likely resilience of kōwaro populations due to the consecutive droughts.

The decline of the large reproductive adults I observed was probably the first change caused by drought conditions, possibly driven by three potential causes: behaviour, physiology and changes to intraspecific interactions. Firstly, kōwaro adults may have moved or altered their behaviour in response to drought conditions (O'Brien 2007, Urbina et al. 2014), so that our sampling did not detect

them. However, another sampling post-drought, when high-water conditions had returned confirmed that adults had probably died and were not missed with sampling during the drought because few adults were caught in subsequent sampling (CG. Meijer unpubl. data), thus ruling out behaviour as a potential cause for the observed pattern. The second potential mechanism involves size-dependent kōwaro physiology. Stagnating waters during low flow events contained decreasing levels of dissolved oxygen and the capacity for a kōwaro to tolerate this change may depend on their body size. The ability for kōwaro to get sufficient oxygen to vital organs likely decreases as size of the individual increases (Eldon 1979a, O'Brien 2007, Urbina et al. 2014), with one study identifying the highest mortality of kōwaro from excavated drought refugia being suffered by both the largest and smallest individuals (O'Brien 2007). Therefore, size-dependent physiology provides a plausible explanation for the loss of adults observed in during the drought. The final potential mechanism is the reduction in habitat size that occurred during drought, with smaller habitats leading to decreased prey availability and higher densities of kōwaro, and consequently, increased competition for these diminished resources (Winne et al. 2010, Katz and Freeman 2015, White et al. 2016). The decrease in prey availability would likely negatively affect the largest individuals at the top of the food chain the most (Winne et al. 2010). Thus, the loss of large kōwaro was potentially caused by the combination of physiological constraints and increased intra-specific interactions.

These mechanisms likely underpinning the loss of large kōwaro provided little insight into why the proportions of fry increased under drought conditions, however. This population change was not consistent with two previous studies, including one on kōwaro that identified high mortality of small and large individuals found in drought refugia (O'Brien 2007), and another with harsh low flow conditions resulting in high mortality in juveniles of a wetland-inhabiting fish (Penha et al. 2015). However, I would argue that this difference is because these studies covered one-off events, the loss of smaller individuals occurring concurrently with the loss of adults or with no loss of adults, respectively. The increase in fry abundance in my study is like results described in two systems involving strong intra-specific competition. Firstly, in a fluvial river system studied by Katz and

Freeman (2015), which indicated increased survival of young-of-the-year during periods of low water levels. Secondly, in a wetland system studied by Dorn and Cook (2015), indicated that loss of large fish, during low-flow events, corresponded with an increase in crayfish abundance. Furthermore, these studies described a two-step process with the release from intra-specific competition and predation occurring prior to the increase in survival. Collectively, these results support two conclusions. Firstly, that adult kōwaro, which likely represent the top of the food chain in most kōwaro-inhabited waterways (Chapter Three), potentially limit the survival of kōwaro fry through cannibalism and resource competition, and secondly, the loss of kōwaro adults likely occurred prior to the increase in abundance of kōwaro fry.

I had initially predicted the loss of kōwaro adults in two scenarios for population change under drought conditions, where either stabilising mortality, involving equal losses of large and small kōwaro, or exaggerated recruitment with losses of large kōwaro and their replacement with numerous fry, to occur during drought. Interestingly, both scenarios may have occurred within kōwaro populations due to the consecutive droughts. During the first extreme drought, stabilising mortality likely occurred because, in populations surveyed during drought conditions, small adults were the only size class (other than fry) with a proportion statistically different from zero. Furthermore, during the first drought, most of these small adults would have been within the intermediate sizes that appear to have the highest survival likelihood based on previous studies (O'Brien 2007). This would create the unimodal pattern of kōwaro body size expected from stabilising mortality, with the remnants of this stabilising mortality still visible a year later in the proportions of yearling and large adult kōwaro I observed. This scenario may then have created an environment for increased fry survival during the second drought, where these remaining adults were still able to produce large numbers of fry. This could explain the increased proportions of fry during drought conditions as well as the significant decrease in median size. However, the lack of a definitive change in CPUE means that whilst some recruitment occurred, this was not exaggerated recruitment, which would cause a significant increase in CPUE, as predicted. Therefore, either the low numbers of larger kōwaro present could still have

restricted fry survival or the recruitment was limited by the reduced numbers of reproductively capable adult kōwaro left after two consecutive droughts.

This loss of large kōwaro and increase in abundance of kōwaro fry were measured independently with catch-per-unit-effort (CPUE) and median size. However, the combination of these metrics potentially provides the platform for creating a framework to infer changes to population resilience, a possible long-term effect of drought. The link between kōwaro size and reproductive capabilities, with larger fish contributing disproportionally more to reproduction, facilitated the use of kōwaro median size for drawing inferences regarding the likely reproductive potential of a population. With the addition of CPUE as a measure of abundance, it was expected that kōwaro populations containing abundant large adults would have the highest reproductive capabilities, and populations containing only a few small fry would have the lowest capabilities for reproduction. Consequently, a change in likely population resilience was observed under different rainfall conditions, with a tendency for populations to change from having with potentially high resilience during wet conditions to having potentially low resilience during drought conditions. This suggests using a resilience framework such as this to compare populations both during and after extreme events will be useful. Moreover, from a monitoring point of view, measuring median size is likely more insightful than just CPUE to identify populations changes associated with extreme events.

The positioning of kōwaro populations in the river network, as well as within this resilience framework provides useful information about their response to drought. During drought conditions, most populations were fry-dominated with CPUE values ranging from approximately 2 to 28 fish per trap, though there were also adult-dominated populations with CPUE values that ranged from approximately 1 to 3 fish per trap. These differences in population median size and CPUE, when sampled within the same survey, likely reflected the underlying differences in environmental stress between sites. During drought conditions, the adult-dominated populations were found in large pools along the mainstem where these pools also contained large numbers of upland bullies (*Gobiomorphus*

breviceps). Whereas, the fry-dominated populations were found in small pools along the tributaries, separated from the mainstem by dry sections of streambed. This situation created a spatial pattern like that described for populations of another native New Zealand galaxiid (*Galaxias vulgaris*), driven by unfavourable interactions with an introduced trout (Woodford and McIntosh 2010). Therefore, this suggests that these tributary populations likely provide the fry that disperse downstream during high-flow periods to replenish adult-dominated populations along the more-permanent portions of the mainstem, potentially creating a source-sink metapopulation dynamic between kōwaro populations within this river system.

Overall, these populations with a few adults and many fry reflect kōwaro life history, where large population declines followed by recovery occurring within a system of many inter-connected populations. These fish mature early and invest significant resources into reproduction (Eldon 1979a), likely maximising their chances to persist through harsh events, such as drought. A small number of surviving adults in isolated refugia could potentially yield numerous fry and juveniles. These offspring likely utilise the end of the drought, when water levels begin to rise, to spread across the landscape to potentially recolonise those populations that were extirpated during harsh conditions. Their early maturity allows these new colonists to reproduce the following spring and potentially form large populations in bodies of water where kōwaro had died just one year before. This would create a pattern of population colonisation, followed by growth, then decline, and potentially extirpation, during harsh periods, only for recolonisation and growth to occur again, with this cycle producing a characteristic 'boom and bust' trend.

These 'boom and bust' cycles are an intrinsic part of living in extreme events, where these stress-tolerant species experience population growth and expansion during less-harsh conditions, to facilitate their persistence through extreme events (Bunn et al. 2006, Arthington and Balcombe 2011). However, the likely effects of fragmentation and isolation of stress-tolerant species populations (Perkin et al. 2015), as has occurred with kōwaro, with the additional impact of climate warming

(Jenkins and Warren 2015, Pacifici et al. 2015, Swab et al. 2015), mean the adverse effects experienced by stress-tolerant fish are likely to become increasingly detrimental to their ongoing survival. I have demonstrated that measuring just abundance is likely insufficient to accurately monitor stress-tolerant fish and with the addition of a size-based metric, such as median size, more insightful measurements could be made. Furthermore, the combination of these metrics will be useful if used in a population resilience framework that allows possible long-term impacts of extreme events to be inferred and appropriate conservation action to be taken.

Chapter Three: Drying intensity in degraded waterways drives changes in the trophic interactions of rare kōwaro (Canterbury mudfish)

Introduction

Anthropogenic degradation of local environments, such as habitat manipulation for repurposing of land (e.g., for agriculture and forestry) and species introductions, can have drastic consequences on communities, with the loss of sensitive species and the increase of more-tolerant species (Violin et al. 2011, Mantyka-pringle et al. 2012, Havel et al. 2015, Muylaert et al. 2016, Boeckman and Whiteman 2017, Hempson et al. 2017). Furthermore, changes to species abundance and composition occurs across environmental gradients, with these changes from both degradation and environmental gradients altering trophic interactions within communities (Albouy et al. 2014, Brose et al. 2017). Knowledge of these changes in trophic interactions between species will likely be useful for conservation strategies (Gray et al. 2014), particularly for rare species requiring efficient management because these species generally lack the population reserves for failed conservation attempts. Therefore, an understanding of trophic interactions and how they change along environmental gradients would likely improve conservation of rare species restricted to degraded systems.

Top predators are likely to be the most sensitive to environmental changes because they are susceptible to small changes at lower trophic levels, which then potentially propagate throughout the community (Dobson et al. 2006, Estes et al. 2011). In situations where top predators persist in the face of environmental change, it is likely that their trophic interactions will have changed due to alterations in the prey communities (Solomon 1949, Holling 1965, Hempson et al. 2017, Zeug et al. 2017). The effects of environmental change can also be reflected in alterations to the size distribution of top predator populations (Katz and Freeman 2015, Penha et al. 2015), which would likely be more

pronounced if predators have ontogenetic differences in prey choice (Arim et al. 2010, Dodrill et al. 2016, Usui et al. 2018). Therefore, investigating the effects of environmental change on trophic interactions of top predators would require distinction between different sizes classes to account for ontogenetic changes in diet composition.

In aquatic systems, trophic structure and top predators are particularly sensitive to drying gradients (McHugh et al. 2015), with altered habitat size (Pace et al. 2000, McHugh et al. 2010) and associated changes in prey abundances (Brooks 2000, Tarr et al. 2005, Stewart and Downing 2008) likely driving these changes. Consequently, drying of aquatic environments potentially limits persistence of top predators in drought-prone habitats (Bogan and Lytle 2011, Greig et al. 2013, Dorn and Cook 2015, McHugh et al. 2015), with environmental conditions, such as willow coverage (Marttila et al. 2018), that amplify drying likely further restricting top predators. However, by providing alternative energy sources at both basal and intermediate levels to adjacent aquatic communities, subsidies from terrestrial ecosystems may offset some effects of stressors in aquatic ecosystems (Cloe and Garman 1996, Nakano et al. 1999, Eros et al. 2012). Therefore, understanding how multiple stressors affect trophic interactions in aquatic food webs, and the potential for these to be offset by terrestrial subsidies will be important for the conservation of top predators in degraded systems.

Kōwaro (Canterbury mudfish, *Neochanna burrowsius*) is a fish which is the top predator in degraded agricultural streams and pools, many of which also periodically dry during summer months (Eldon 1979c, Harding et al. 2007) and are surrounded by various sorts of riparian vegetation. Furthermore, kōwaro is a critically endangered endemic species, with the surviving populations becoming increasingly fragmented and isolated (Eldon 1979a, Goodman et al. 2014). Thus, investigating how trophic interactions in kōwaro communities change along a gradient of drying intensity, and additionally investigating how canopy cover might influence these effects, within an already-degraded environment could considerably help management and conservation efforts for this species.

I investigated the potential effects of drying intensity and canopy cover on kōwaro by comparing the trophic interactions associated with kōwaro populations across two river networks. These locations, situated within an agricultural landscape with underlying variation in drying intensity and canopy cover, were used to test the importance of these two environmental gradients on kōwaro in already-degraded river systems. I predicted that the drying and canopy cover gradients would drive changes in overall community isotope biplots of nitrogen and carbon, because isotope ratios of nitrogen, $N^{15}:N^{14}$ and carbon, $C^{13}:C^{12}$ summarise trophic pathways in an ecosystem (e.g., Vander Zanden et al. 1999). Subsequently, I predicted changes in the isotopic signatures of kōwaro, due to underlying alterations to their trophic interactions. I also predicted that drying intensity would negatively affect kōwaro, but could possibly be offset by terrestrial subsidies in locations with tree canopy cover. Furthermore, in Chapter Two, I described a drought-induced switch to fry-dominated populations, with one potential mechanism being changes to invertebrate communities. Thus, I also predicted drying intensity and canopy cover would change size distributions within the kōwaro populations, and that this would be associated with altered invertebrate communities.

Methods

Field survey

I studied 17 kōwaro populations along the Waianiwaniwa River and seven along the Hororata River within the wider Selwyn River catchment on South Island, New Zealand. These sites were a combination of in-stream pools or runs and isolated oxbows, all situated within a matrix of agricultural land-use, with some Waianiwaniwa sites also associated with mining run-off. These sites were visited four times between October 2016 and March 2017 to sample the entire fish community present, with between three and five gee-minnow traps (~5–6 m^2 surface area per trap) set at equal spacing along wetted perimeters and left for up to 24 hours overnight. A suite of environmental characteristics were recorded at each site to investigate how drying intensity and canopy cover correlated with general conditions. Specifically, during the four trapping periods, I measured canopy cover with a

densiometer, and visually estimated the cover of riparian plants, aquatic vegetation, wood debris, livestock intrusion and overhanging vegetation. I characterised substrate conditions with a Wolman pebble count and visually estimated silt cover. I measured dissolved oxygen, pH and specific conductivity adjacent to each trap with probes(YSI 63 and Ecosense ODO200 probes), with a mean value calculated for each visit. Finally, changes in habitat size were tracked throughout the survey with four additional site visits. During the eight total site visits, wetted width, length and depth were recorded to estimate habitat size, and were related to stage height measurements from loggers (Tru-track WT-HR 1000), placed in mid-depth positions at 18 sites, that continuously recorded pool depth. Sites without loggers had depths correlated to nearest logger instead.

Tissue collection for isotopes

Trophic interactions can be confirmed through quantitative analysis of predator-prey interactions, for example through examination of stomach contents or foraging behaviour (Preisser et al. 2005, McClain-Counts et al. 2017). However, when a species is threatened like kōwaro, non-invasive and time-efficient methods would preferably be used. Therefore, because these trophic interactions can be inferred using isotope ratios of nitrogen, $N^{15}:N^{14}$ and carbon, $C^{13}:C^{12}$ (Vander Zanden et al. 1999, Pinnegar and Polunin 2000, Finlay 2001, McNabb et al. 2001, Layman et al. 2012), and these can be collected with non-lethal methods such as fin clips, I used stable isotope analysis tools in this study.

To build representations of local food webs, I collected samples from all trophic groups present at each location, including fish, aquatic invertebrates, aquatic basal resources (plants and detritus), and potential terrestrial food sources. Tissue needed for isotopes was collected during the first two fish-trapping visits, with fish selected from those caught using gee-minnow traps. Up to nine individuals of Canterbury galaxias (*Galaxias vulgaris*) and upland bully (*Gobiomorphus breviceps*) were euthanised per site, but fin clips were taken from kōwaro, with only 15 euthanised from randomly chosen sites to construct a regression between fin and muscle tissue isotope ratios. In addition, three one-metre sweeps were made with a 500-μm tri-net to collect the aquatic invertebrate community, and between two to four floating pan traps, filled with a small amount of surfactant and water, placed at four-metre

intervals along the reach were left for 24 hours to collect samples of terrestrial and flying invertebrates that fell into the water. Detritus and leaf packs were collected by scooping up benthic material, and plants were hand-picked. All samples were stored at -20 °C until processing.

Isotope sample preparation and analysis

In the laboratory invertebrate samples were sorted to the smallest identifiable taxonomic level using a dissecting microscope and identified using the keys of Winterbourn et al. (2006), and the online keys provided by Landcare Research - Manaaki Whenua (2018) and Tofilski (2013). The detritus, leaf pack and plant samples were checked under the microscope and entrained animals removed. Dorsal muscle tissue from the euthanised kōwaro, Canterbury galaxias and upland bullies was extracted by peeling the skin away to expose muscle alongside the backbone, and kōwaro stomach contents were extracted. Tissue samples were dried for three days at 50 °C, weighed and ground into a fine power using a mortar and pestle, with portions of these powder samples sealed in tin capsules (1 mg for fish and invertebrates, and 2-3 mg for plants, detritus and leaf packs), using methodology adapted from Hogsden and McHugh (2016). To achieve sufficient sample weight, the kōwaro fin clips collected in the field needed to be aggregated. To do this fish were combined into groups of three similar sized individuals. Prepared tin capsules were sent to the University of California Davis Stable Isotope Facility for analysis (PDZ Europa 20-20 isotope ratio mass spectrometer). Results were expressed in per mille delta notation [i.e., $\delta^{15}N$ or $\delta^{13}C = (R_{sample} / R_{standard} - 1) \times 1000$, where $R = {}^{13}C{:}^{12}C$ or ${}^{15}N{:}^{14}N$] relative to laboratory standards (bovine liver, glutamic acid, enriched alanine, alfalfa and nylon 6). Analytical error associated with our sample analysis was between 0.05 and 0.08 ‰ for $\delta^{13}C$ and between 0.04 and 0.10 ‰ for $\delta^{15}N$.

Because these samples were stored at -20 °C for up to 6 months, I lipid-corrected the carbon isotope values (see Hogsden and McHugh 2016). Using Post et al. (2007), I corrected aquatic animals with the formula $\Delta\delta^{13}C = -3.32 + 0.99 \times C{:}N$, terrestrial animals with the formula $\Delta\delta^{13}C = -3.44 + 1.00 \times C{:}N$, and plants, detritus and leaf packs with the formula $\Delta\delta^{13}C = -3.02 + 0.09 \times \%\ Carbon$. After this, the isotopic values for kōwaro fin clips were corrected with the fin tissue to muscle tissue regression, with $\delta^{13}C_{muscle}$

$= 0.934 \times \delta^{13}C_{fin} - 2.160$ ($F_{1,13} = 1416$, $p < 0.001$; Appendix A) and $\delta^{15}N_{muscle} = 0.877 \times \delta^{15}N_{fin} + 1.524$ ($F_{1,13} = 993$, $p < 0.001$; Appendix A).

Kōwaro stomachs were dissected under a microscope, with any distinguishable invertebrates counted and identified using the keys previously used for isotope sample sorting (Winterbourn et al. 2006, Tofilski 2013, Landcare Research - Manaaki Whenua 2018). Diptera larvae, such as Chironomidae, were counted from the number of heads identified, whereas the number of adult Diptera were estimated from the number of pairs of similar wings.

Abiotic data preparation

Using the depth information extracted from stage height loggers, which were calibrated with the measurements of water depth taken during site visits, I calculated the coefficient of variation for water depth at each site. Coefficient of variation was used because it reflected the heterogeneity in pool habitats, particularly in relation to disturbance and habitat drying (Covich et al. 1996). The relationship between drying intensity (using the coefficient of variation for water depth as a proxy) and canopy cover, was examined to ensure that these were not correlated. Similarly, I evaluated multicollinearity of other environmental characteristics with drying intensity or canopy cover. Sites experiencing high drying intensity were generally characterised with lower flows, lower dissolved oxygen content, higher sedimentation and increased macrophyte coverage, particularly the floating plants *Azolla filiculoides* and *Lemna minor* (Appendix B). Increased canopy cover was generally associated with decreased riparian cover, decreased overhanging vegetation cover and increased accumulated woody debris (Appendix B).

Isotope biplot analysis

All data analyses were carried out in R, version 3.4.1 (R Core Team 2017). Sites were divided into four categories based on the combination of drying intensity and canopy cover, with thresholds of 0.5 and 45 used for drying intensity and canopy cover, respectively, because these values were approximately the mean values across all sites (Figure 3.1). However, there were only two sites in the high drying

intensity and low canopy cover category. Therefore, drying intensity was treated as a categorical variable in analyses with two levels (high and low) and canopy cover a continuous variable to ensure canopy cover ranged from 0% to ~100% in both levels of drying intensity.

For each combination of drying intensity and canopy cover, except for high drying intensity and low canopy cover category (due to low replication), aggregated biplots were made with the overall mean and standard deviation values for each taxon found within the combination of conditions. Using the 'SIAR' package (Parnell et al. 2010), I compared the three combinations of drying intensity and canopy cover using the aggregated isotope biplots. With each site used as a replicate within a category, I investigated with one-way ANOVAs if the biplots differed in any of the metrics proposed by Layman et al. (2007), where a significant difference would likely mean a change in the community food web property. These metrics were the range of nitrogen values (a measure of diversity in trophic position), the range of carbon values (a measure of niche diversity in basal resources), the total isotopic area enclosed within the biplot (a measure of total niche space), mean distance to centre of biplot (a measure of the degree of trophic diversity), mean distance to nearest neighbour (a measure of species packing) and standard deviation of the distance to nearest neighbour (a measure of evenness of species packing) (Layman et al. 2007), but I also included the mean $\delta^{15}N$ and $\delta^{13}C$ values to test for whole-community shifts in isotope positioning.

Kōwaro diet composition

I also investigated how drying intensity and canopy cover influenced changes in kōwaro diet by constructing separate linear models for nitrogen and carbon isotope values, with body length, canopy cover and drying intensity used as predictors; their interactions were not significant, and were removed from models. All three predictors were used for these kōwaro isotope models because body size was not correlated with drying intensity or canopy cover (Appendix D). With the 'effects' package (Fox 2003), I extracted the independent effects of each predictor to create partial plots, and, because my data were unbalanced, I tested their independent contributions by creating models with each predictor entered last (using type III sums of squares). Due to the underlying differences in $\delta^{13}C$ values

between freshwater sources (usually between -34 and -27 ‰, Hamilton and Lewis 1992, Hellings et al. 1999) and terrestrial sources (generally between -29 and -21 ‰, Peterson and Fry 1987, Kendall et al. 2001), changes in $\delta^{13}C$ values likely indicate variations in diet reflecting the relative contributions of food from those environmental sources.

Five taxa were common in the stomach contents across kōwaro of different sizes, and consequently analyses focused on these prey taxa. Common aquatic prey were combined (microcrustacea, Chironomidae larvae and other Diptera larvae), but adult Chironomidae were kept separate from other adult Diptera because the former had aquatic-derived isotopic values and the latter had terrestrial-derived values. Using generalised linear models for proportion data, with a quasibinomial distribution due to overdispersion, and quasipoisson distribution for biomass data (rounded to the nearest integer) that was overdispersed, I tested the effect of drying intensity and canopy cover on the relative abundance and total biomass of the aquatic prey taxa, adult Chironomidae and other adult Diptera. The significance of the independent effects of drying intensity and canopy cover were tested when entered in the model last, like the type III tests above, with the non-significant interaction term removed.

Changes within kōwaro populations

Using size-based age information (Chapter Two; Eldon 1979a), I separated the kōwaro populations into fry, yearlings and adults. Fry were the individuals up to 60 mm in length and were likely to be less than one year old, yearlings were all individuals with a body length between 61 and 90 mm and likely between one and two years of age, and adults were all kōwaro that were larger than 91 mm long and likely to be at least two years old. The proportion of each size class within the whole population was evaluated with a generalised linear model for proportion data, with a quasibinomial distribution due to overdispersion, using drying intensity and canopy cover as predictors (non-significant interaction was removed). Finally, I used the ratio of kōwaro fry to other larger kōwaro as a proxy for a population's resilience following Chapter Two. A ratio less than 1:1 would mean that within-population replacement was likely limited, whereas a ratio greater than 1:1 meant there was a greater

underlying potential for population growth. To investigate the effects of drying intensity and canopy cover on these ratios, a generalised linear model, with a quasipoisson distribution was used because the data were derived from averaged integers was used, and the interaction term was removed because it was not significant.

The final step was to investigate the link between the invertebrate community and the size distribution within the kōwaro populations. I focused on the three groupings identified for the invertebrate analysis (aquatic prey taxa, adult Chironomidae and other adult Diptera) because the first two represented all prey taxa found in the stomach contents of smaller-sized kōwaro, and the last group also represented important prey, but only for larger-sized kōwaro. Using generalised linear models for proportion data, with a quasibinomial distribution due to overdispersion, I separately evaluated the effects of both biomass and relative abundance of the groups on the proportion of kōwaro that were within the 'fry' size class.

Results

Kōwaro habitat conditions

Water chemistry differed between sites, with varied levels of dissolved oxygen and generally elevated specific conductivity (Appendix B). Moreover, during the summer low flow period, with the decrease in habitat size, all sites exhibited decreased dissolved oxygen (<5 mg/L) due to stagnating water. Generally, these sites also exhibited high sediment cover and some level of bank slumping. Finally, the aquatic invertebrate communities were depauperate and were generally dominated by Coleoptera, Mollusca, microcrustacea and Diptera larvae, which supported the notion that these were degraded aquatic habitats.

Kōwaro diets

Comparing the stomach contents of kōwaro revealed that larger kōwaro consumed a wider range of prey items, but across all individuals there was core diet that consisted of microcrustacea, aquatic Diptera larvae, Chironomidae flies and Diptera flies (Table 3.1).
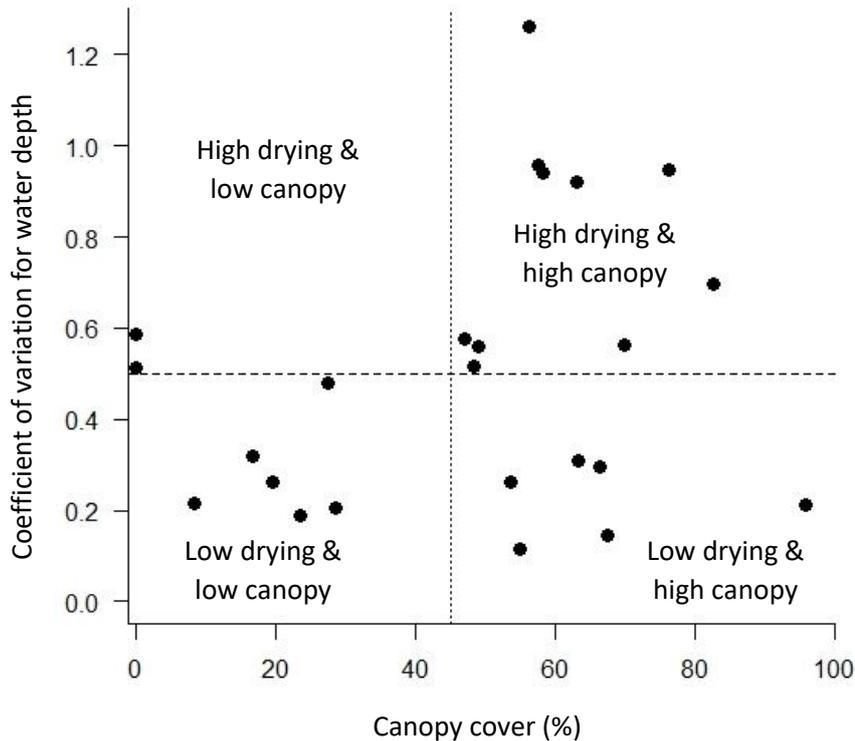
Figure 3.1 The spread of sampled locations containing kōwaro populations based on their variability in water depth and canopy cover. The threshold for high versus low variability in water depth (0.5, dashed line) and the threshold for canopy cover (45%, dotted line) were chosen because they were approximately equal to the respective means for these variables across all sites.

Community isotope biplots

Evaluating the community-wide isotope biplots across the gradients of drying intensity and canopy cover (Figure 3.2), revealed no significant differences in any of the general isotope metrics or mean isotope values (Appendix C). This result did not alter with different combinations of communities, for example, removing the primary producers from the community did not alter this pattern or focusing solely on predatory taxa, yielded no significant difference among groups. However, across the three categories there was a general pattern of kōwaro positions in biplots matching the position of their prey indicated by stomach contents. In isotope biplots, fry were positioned above common aquatic prey and larger kōwaro were aligned such that they appeared to be consuming larger amounts of terrestrial-derived prey

Table 3.1 Stomach contents of kōwaro organised by the length of kōwaro and also including capture location and the drying intensity of that site. Note the increasing variety of prey taxa with increasing kōwaro body size. Cladocera, Ostracoda and Copepoda were group together into microcrustacea, and aquatic Diptera larvae were grouped together except for Chironomidae, because the latter represented the most common prey taxon identified in kōwaro stomachs. Adult Diptera, with terrestrial larvae, belonged to a wide range of families, including Psychodidae, Cecidomyiidae, Lonchopteridae, Chloropidae, Agromyzidae and Anthomyzidae. Adult Chironomidae were also identified and kept separate because this family have aquatic larvae. See Appendix B for coordinates of locations.

Location code	Drying intensity	Length (mm)	Chironomidae larvae	Microcrustacea	Other Diptera larvae	Adult Chironomidae	Adult Diptera	Coleoptera larvae	Hemiptera	Odonata
W13	High	27	1	24	-	-	-	-	-	-
W1	Low	29	8	33	-	-	-	-	-	-
W7	High	35	1	68	-	-	-	-	-	-
W19	High	36	12	15	-	-	-	-	-	-
H4	High	38	7	42	2	1	-	-	-	-
H8	Low	41	7	24	-	3	1	-	-	-
W9	High	46	2	12	4	1	-	-	-	-
W8	High	47	13	91	3	2	-	-	-	-
W16	High	58	5	27	3	-	2	-	-	-
H7	Low	68	4	-	-	4	-	1	-	-
H7	Low	73	8	83	-	3	1	-	-	-
W3	Low	75	1	18	6	-	2	-	-	-
H7	Low	81	4	-	3	-	4	1	-	-
W5	Low	92	5	12	1	2	6	1	1	-
W5	Low	104	1	18	1	3	4	-	1	1
W9	High	115	13	34	6	5	2	-	2	-

Increasing kōwaro body size →
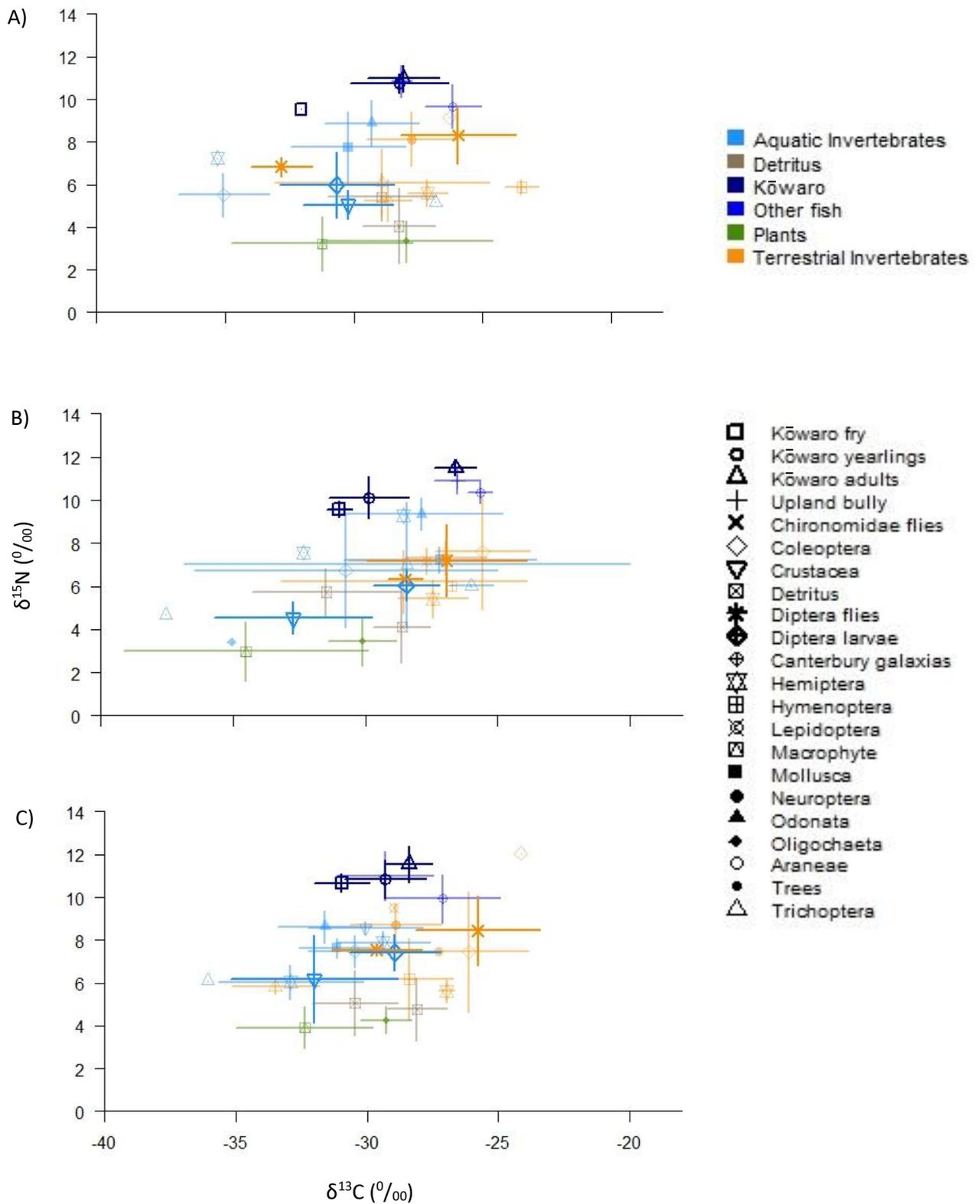
Figure 3.2 Biplots of δ¹⁵N and δ¹³C isotope values for each taxon grouping (symbols), with emphasis on the kōwaro (bold) and the most common prey taxa in their stomachs (darker symbols) and grouped based on drying intensity and canopy cover, with (A) low drying with low canopy cover site, (B) low drying with high canopy covers sites, and (C) high drying with

high canopy cover sites. The position of each point indicates the mean for that taxon grouping for sites in that category, and the error bars indicate the standard deviation for sites in that category. Colours indicate how tissue samples were collected; light blue, aquatic invertebrates sampled with in-stream sweeps; brown, detritus picked from the benthos; purple, mudfish, most of whom were fin clipped; dark blue, co-occurring fish; green, plants and macrophytes; and orange, terrestrial and flying invertebrates that were caught in floating pan traps.
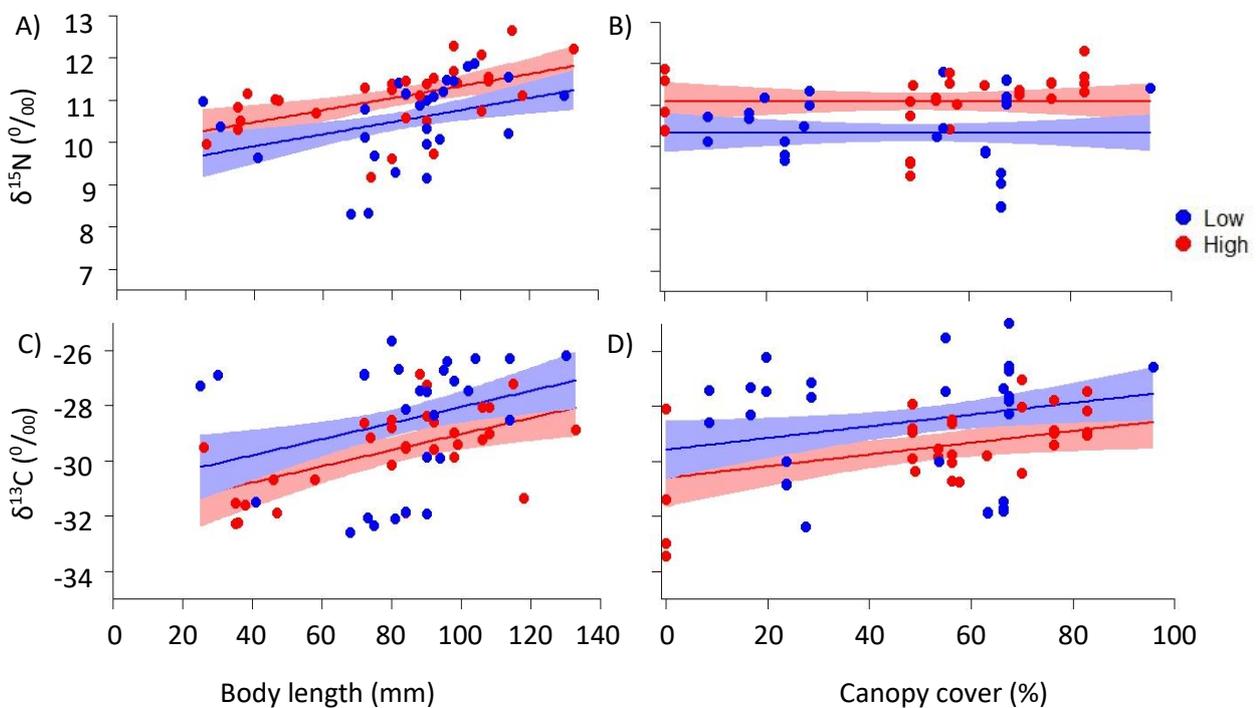
Figure 3.3 Partial plots created from the linear models predicting kōwaro δ^{15}N (A & B) and δ^{13}C (C & D) isotope values based on drying intensity (colours), kōwaro body length (A & C) and canopy cover (B & D). The lines and shaded bands represent the model output and 95% confidence intervals, respectively, with horizontal lines plotted at treatment means when the effect of the continuous predictor (x-axis) was not significant. Each point represents an isotope sample made by combining the fin clips of three kōwaro together.

Table 3.2 Analysis of variance tables for linear models predicting kōwaro body tissue δ^{15}N and δ^{13}C isotope values with drying intensity, kōwaro body length and canopy cover as predictor variables.

Source	Df	Mean squares	F value	p-value
Kōwaro δ^{15}N values				
Length	1	7.72	11.91	0.001
Canopy cover	1	0.55	0.85	0.361
Drying intensity	1	4.67	7.20	0.009
Residual	55	0.65		
Kōwaro δ^{13}C values				
Length	1	32.20	9.93	0.003
Canopy cover	1	16.70	5.15	0.027
Drying intensity	1	13.90	4.29	0.043
Residual	55	3.24		

items (Figure 3.2). Consequently, diet looked to be changing with kōwaro size, reflecting ontogenetic shifts in prey composition. Furthermore, the position of kōwaro within the isotope biplots differed along the environmental gradients of drying intensity and canopy cover. Therefore, visual examination of the biplots suggests that kōwaro δ^{13}C and δ^{15}N values were potentially changing with body size as well as across these environmental gradients, indicating a likely change in their trophic interactions.

Kōwaro trophic interactions

Quantitative analysis of kōwaro isotopes did indeed indicate their trophic indications were changing. Higher drying intensity significantly increased δ^{15}N values ($F_{1,55}$ = 7.20 p = 0.009; Table 3.2). There was also a significant relationship between δ^{15}N and body length ($F_{1,55}$ = 11.91, p = 0.001; Figure 3.3A), but there was no effect of canopy cover on δ^{15}N ($F_{1,55}$ = 0.85, p = 0.361; Figure 3.3B). In comparison, all three predictors (body size, drying intensity and canopy cover) significantly affected δ^{13}C values in kōwaro.
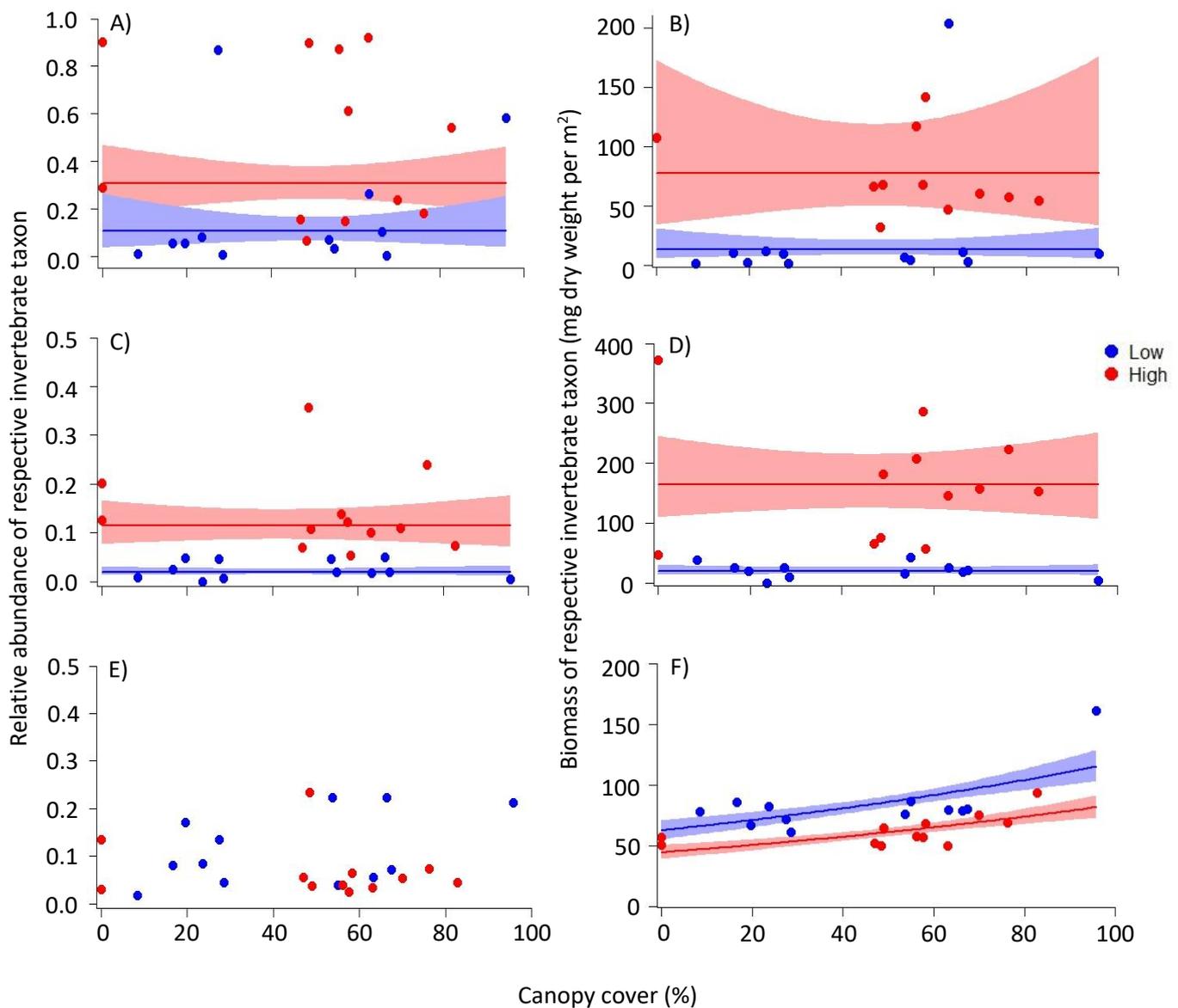
Figure 3.4 The effect of drying intensity (colours) and canopy cover on the proportions and biomass of common aquatic prey taxa (A & B), adult Chironomidae (C & D), and terrestrial adult Diptera (E & F). The proportions and biomass were predicted with quasibinomial and quasipoisson generalised linear models, respectively. The lines and shaded bands represent the model output and 95% confidence intervals, respectively, with horizontal lines plotted at treatment means when the effect of canopy cover was not significant.

Increased drying intensity significantly decreased $\delta^{13}C$ values ($F_{1,55}$ = 4.29, p = 0.043; Table 3.2). There was a significant relationship between $\delta^{13}C$ and body length ($F_{1,55}$ = 9.93, p = 0.003; Figure 3.3C), and between $\delta^{13}C$ and canopy cover ($F_{1,55}$ = 5.15, p = 0.027; Figure 3.3D). Therefore, this suggested that kōwaro likely changed their diet with altered drying intensity and canopy cover.

Table 3.3 The analysis of variance tables for generalised linear models, quasibinomial for relative abundance and quasipoisson for biomass, predicting invertebrate communities in kōwaro habitats based on drying intensity and canopy cover. The significance of each parameter was determined when entered into the model last.

	Df	Deviance	Residual Df	Residual deviance	F value	p-value
Relative abundance of aquatic prey taxa (microcrustacea and Diptera larvae)						
NULL			23	1793.3		
Canopy cover	1	0.30	21	1437.3	0.004	0.949
Drying intensity	1	355.0	21	1437.3	5.12	0.034
Biomass of aquatic prey taxa (microcrustacea and Diptera larvae)						
NULL			23	1255.3		
Canopy cover	1	0.02	21	883.2	<0.001	0.988
Drying intensity	1	366.0	21	883.2	4.51	0.046
Relative abundance of adult Chironomidae						
NULL			23	2091.6		
Canopy cover	1	53.8	21	513.0	1.96	0.176
Drying intensity	1	1550.0	21	513.0	56.40	<0.001
Biomass of adult Chironomidae						
NULL			23	2284.2		
Canopy cover	1	10.4	21	741.8	0.32	0.578
Drying intensity	1	1540.0	21	741.8	46.90	<0.001
Relative abundance of other adult Diptera flies						
NULL			23	992.4		
Canopy cover	1	147.0	21	785.3	2.94	0.101
Drying intensity	1	127.0	21	785.3	2.53	0.126
Biomass of other adult Diptera flies						
NULL			23	137.8		
Canopy cover	1	44.4	21	54.3	16.61	<0.001
Drying intensity	1	50.1	21	54.3	18.78	<0.001

Kōwaro prey communities

The proportion of aquatic prey taxa (i.e., microcrustacea and aquatic Diptera larvae) in aquatic invertebrate communities increased significantly with higher drying intensity ($F_{1,21}$ = 5.12, p = 0.034; Table 3.3). This was consistent with these aquatic prey taxa having significantly higher biomass in drying-prone sites ($F_{1,21}$ = 4.51, p = 0.046). However, there was no relationship between the proportion of aquatic prey, or their biomass, and canopy cover ($F_{1,21}$ = 0.004, p = 0.949; Figure 3.4A and $F_{1,21}$ = 0.001, p = 0.988; Figure 3.4B; respectively). Overall, a similar pattern was observed for adult Chironomidae, with the relative abundance and total biomass of these flies, increasing with drying intensity ($F_{1,21}$ = 56.4, p <0.001 and $F_{1,21}$ = 46.9, p <0.001; respectively), but there was no relationship between the proportion of these flies, or their biomass, and canopy cover ($F_{1,21}$ = 1.96, p = 0.176; Figure 3.4C and $F_{1,21}$ = 0.32, p = 0.578; Figure 3.4D; respectively). In contrast, however, the proportions of other adult Diptera did not differ with either drying intensity ($F_{1,21}$ = 2.53, p = 0.126; Figure 3.4E) or canopy cover ($F_{1,21}$ = 2.94, p = 0.101), but biomass decreased with drying intensity ($F_{1,21}$ = 18.8, p <0.001; Figure 3.4F) and increased with canopy cover ($F_{1,21}$ = 16.6, p <0.001). Thus, the additional environmental gradients of drying intensity and canopy cover were important in determining the composition of invertebrate prey available for kōwaro.

Changes within kōwaro populations

Kōwaro responded to drying intensity and canopy cover differently, depending upon their size. The number of kōwaro fry, as a proportion of total kōwaro caught, increased significantly with drying intensity ($F_{1,21}$ = 59.3, p <0.001; Table 3.4) and decreased with canopy cover ($F_{1,21}$ = 5.62, p = 0.027; Figure 3.5A). In contrast, the proportions of kōwaro yearlings decreased with higher drying intensity ($F_{1,21}$ = 23.8, p <0.001) and did not change with canopy cover ($F_{1,21}$ = 0.014, p = 0.905; Figure 3.5B). In comparison, the proportions of kōwaro adults did not differ with drying intensity ($F_{1,21}$ = 3.11, p = 0.092), but did increase with canopy cover ($F_{1,21}$ = 5.60, p = 0.028; Figure 3.5C). The ratio of kōwaro fry to those in larger size classes increased significantly with drying intensity ($F_{1,21}$ = 18.6, p <0.001; Table

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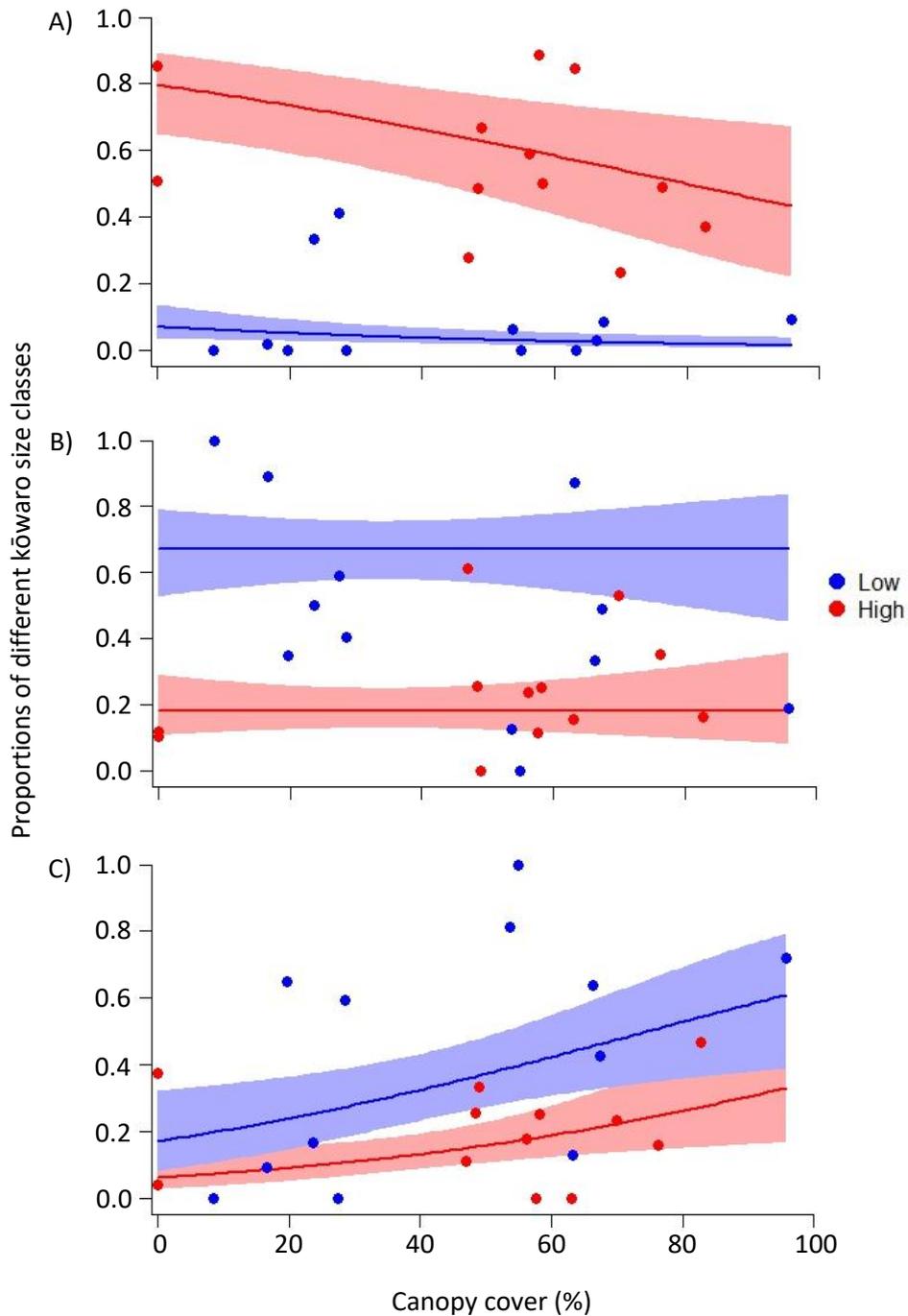
Figure 3.5 The proportions of fry (A), yearling (B) and adult (C) kōwaro in sites across the gradients of drying intensity and canopy cover, using quasibinomial generalised linear models. The lines and shaded bands represent the model output and 95% confidence intervals, respectively, with horizontal lines plotted at treatment means when the effect of canopy cover was not significant.

3.4), but there was no relationship between these ratios and canopy cover ($F_{1,21}$ = 1.07, p = 0.312; Figure 3.6). Therefore, this suggested that the different kōwaro size classes potentially have different habitat requirements.

The proportion of kōwaro fry increased significantly with the combined biomass of the aquatic prey taxa and the biomass of adult Chironomidae ($F_{1,22}$ = 5.67, p = 0.026; Figure 3.7A and $F_{1,22}$ = 73.2, p <0.001; Figure 3.7B; respectively). However, there was no relationship between the proportion of kōwaro fry and the biomass of other adult Diptera ($F_{1,22}$ = 0.165, p = 0.256; Figure 3.7C). This indicated that changes in the invertebrate community could be responsible for driving changes in aspects of kōwaro population.
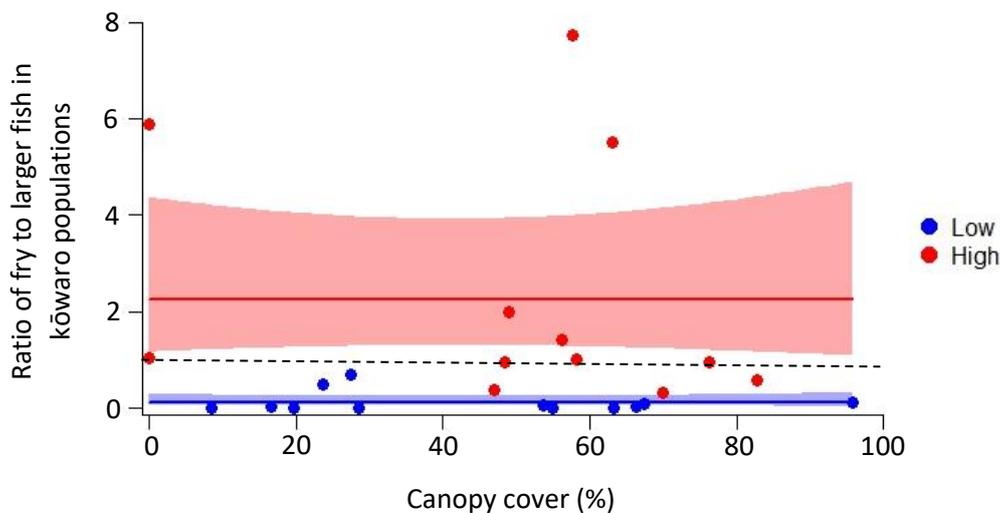
Figure 3.6 The ratio of fry to larger fish in kōwaro populations predicted with a quasipoisson generalised linear model using drying intensity (colours) and canopy cover as predictors. The dashed line represents a population that has one fry present for each mature kōwaro (i.e., a ratio of 1:1). The coloured lines and shaded bands represent the model output and 95% confidence intervals, respectively, with horizontal lines plotted at treatment means because canopy cover was not significant.

Discussion

Communities in degraded systems have likely already undergone significant alterations in species identity and abundance due to changes in environmental conditions (Violin et al. 2011, Muylaert et al. 2016, Boeckman and Whiteman 2017). However, within degraded systems, there may be further alterations to communities along additional environmental gradients, such as drying intensity in aquatic systems. Subsequently, these degraded systems may not uniformly support top predators like fish, though additional external conditions, such as changes in vegetative canopy cover, may alleviate some of the negative effects of drying. For already-threatened taxa, such as kōwaro, an understanding of how they, and the wider community, respond to such environmental gradients could considerably assist conservation efforts. My results indicated no change in the community-wide isotope biplots, with no differences induced by altered drying intensity or canopy cover, suggesting that these overall properties of these communities were likely resilient to environmental changes. However, both drying intensity and canopy cover significantly affected the position of kōwaro, an important top predator, within the wider food web, with changes in the abundance of key prey taxa potentially responsible. Interestingly, the presence of riparian canopy may have offset some of the changes in trophic interactions caused by increased drying intensity. This was indicated by a positive relation between canopy cover and the proportion of adult kōwaro within the local population.

Drying intensity and canopy cover did not exert an overall change on the food webs of these degraded waterways. This suggests that the trophic interactions of these agricultural streams are inherently resilient to further environmental change, which is congruent with other studies on similarly degraded systems (Nyström et al. 2012, Ward-Campbell et al. 2017). This resilience in degraded communities is likely linked to environmental change causing differences in abundance and community composition, rather than the complete loss of trophic links (Dodson et al. 2005). This suggests that linking isotopic values with changes in abundance using proportion-weighted metrics, such as isotopic divergence and dispersion as proposed by Cucherousset and Villéger (2015), may detect internal alterations within

Table 3.4 The analysis of variance tables for generalised linear models, quasibinomial for proportions and quasipoisson for the ratios, predicting the proportions of different size class kōwaro and the ratio of fry to larger fish, with drying intensity and canopy cover as predictors. The significance of each parameter was determined when entered into the model last.

	Df	Deviance	Residual Df	Residual deviance	F value	p-value
Proportion of fry-sized kōwaro (individuals up to 60 mm long)						
NULL			23	96.7		
Canopy cover	1	6.50	21	20.1	5.62	0.027
Drying intensity	1	68.5	21	20.1	59.29	<0.001
Proportion of yearling-sized kōwaro (individuals between 61 and 90 mm long)						
NULL			23	68.4		
Canopy cover	1	0.022	21	31.5	0.014	0.905
Drying intensity	1	36.8	21	31.5	23.80	<0.001
Proportion of adult-sized kōwaro (individuals more than 91 mm long)						
NULL			23	42.1		
Canopy cover	1	8.54	21	28.4	5.60	0.028
Drying intensity	1	4.74	21	28.4	3.11	0.092
Ratio of kōwaro fry to larger individuals						
NULL			23	58.2		
Canopy cover	1	1.73	21	27.9	1.07	0.312
Drying intensity	1	29.9	21	27.9	18.60	<0.001

communities. However, degraded systems potentially rely on strong cross-system links with the surrounding environment (e.g., Giling et al. 2015). Subsequently, creating a complete representation of weighted trophic interactions within communities would require inclusion of all incorporated components (i.e., the fish, and aquatic and terrestrial invertebrates) with a standardisable sampling methodology. However, this is not always practical or achievable. For example, I generated catch-per-unit-effort for fish, biomass per m^2 for aquatic invertebrates, and biomass per m^2 per ~24 hours for terrestrial and flying invertebrates, which were not able to be standardised across the different organism groups. These complications mean whole-community metrics for trophic interactions may have limited usefulness in studies of already-degraded systems such as mine. However, studying top predators is more feasible and may be more insightful.
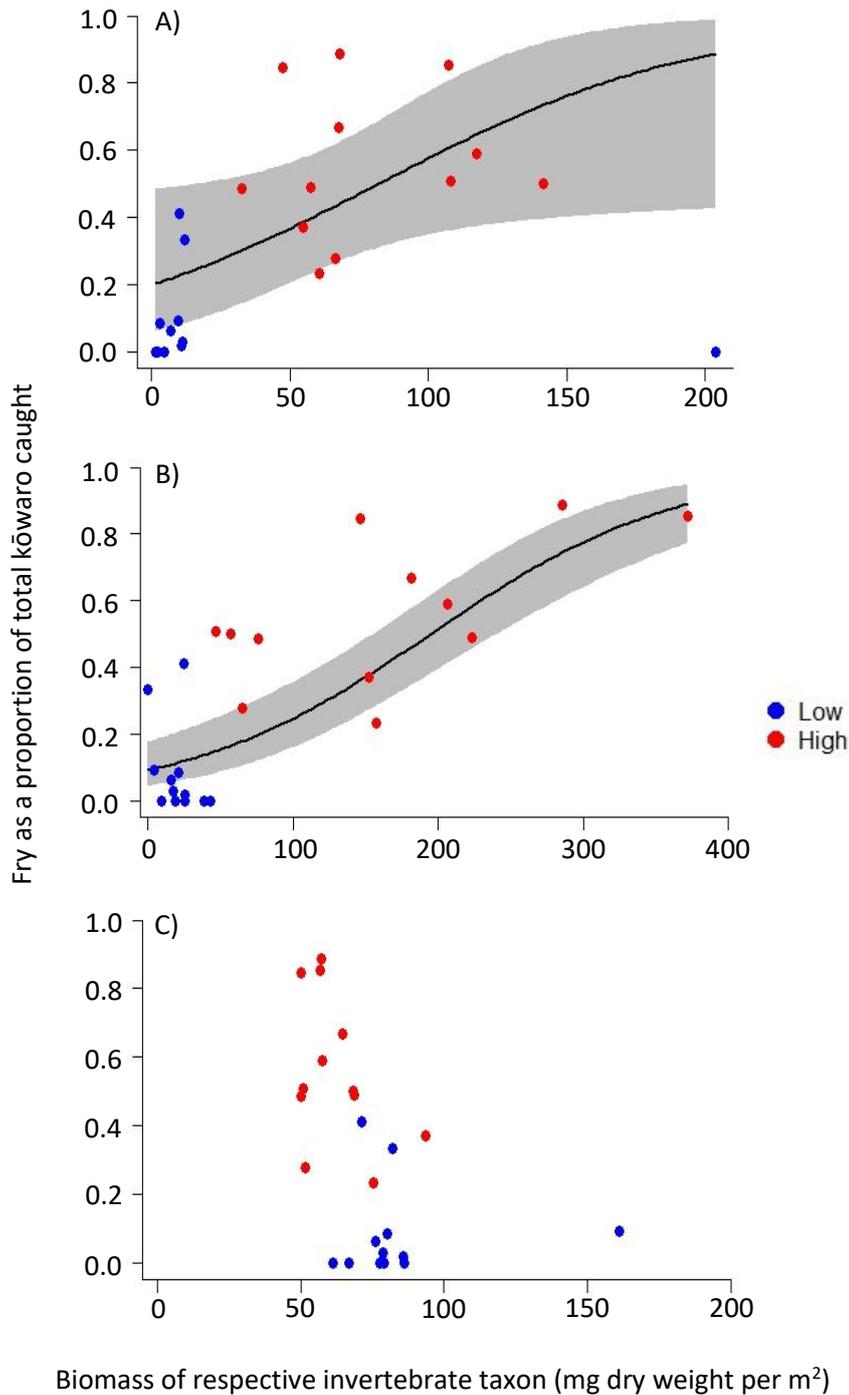
**Figure 3.7** Kōwaro fry as a proportion of all kōwaro caught in relation to biomass of (A) microcrustacea and Diptera larvae (A), adult Chironomidae (B) and terrestrial-based adult Diptera (C) across both drying intensities (colours). The lines and shaded bands represent the model output and 95% confidence intervals, respectively, with the absence of these indicating a non-significant relationship.

The increase in kōwaro δ^{15}N with larger kōwaro body size, independent of drying intensity and canopy cover, suggests that larger kōwaro were feeding on prey at higher trophic levels. This was consistent with kōwaro stomach content analysis where larger individuals included predatory invertebrates, such as beetle larvae and damselflies, in their diet. These sorts of relationships are consistently found across food webs where body size is correlated to trophic position because of gape-limited prey selection (i.e., Shine 1991, Cohen et al. 1993, Scharf et al. 2000). However, the trophic difference was not large, with the predicted model difference of ~1.3 ‰ between the largest and smallest kōwaro considerably less than the ~3.4 ‰ change typically described as a gain of one trophic level (see Post 2002). This also fits with the presence of some prey taxa, such as microcrustacea and Diptera larvae, in the stomach contents of kōwaro across a wide range in body size. Therefore, most prey were probably used by kōwaro of all sizes.

Increases in kōwaro body size were also independently correlated with an increase in their δ^{13}C signature, with a difference of ~2.1 ‰. This difference is considerably more than the ~0.4 ‰ change in δ^{13}C values typically associated with the fractionation that occurs with a gain of one trophic level (see Post 2002). Consequently, the larger kōwaro likely had an increased proportion of terrestrial-based prey in their diet. This finding matched the increased proportions of terrestrially-derived adult Diptera found in the stomach contents in larger kōwaro. Therefore, my results indicate there is likely a shift in kōwaro diet, where their feeding becomes more terrestrially-focused with age. Moreover, grouping isotope samples into body size classes, rather than one amalgamated sample, is more informative for species that display ontogenetic variation in diet, such as kōwaro.

In addition to the increase in δ^{15}N with increasing kōwaro body size, there was also an independent effect of drying intensity on the δ^{15}N signature of kōwaro. Higher drying intensity increased kōwaro δ^{15}N values by ~0.6 ‰. This change could have been caused by elevated δ^{15}N values in basal resources, changes in the consumption of prey reflecting changes to trophic omnivory, or self-metabolising by kōwaro during fasting periods caused by drying (Hobson et al. 1993, Hobson and Welch 1995, Vander

Zanden et al. 1999). An elevation in basal $\delta^{15}N$ values would have lifted the community $\delta^{15}N$ values, but there was no change detected across drying intensity or canopy. Subsequently, there was no change in basal $\delta^{15}N$ values, ruling this potential mechanism out. A change in the relative consumption of prey is plausible, but the only confirmed prey taxa (i.e., identified in stomach contents) that increased with drying intensity were microcrustacea, aquatic Diptera larvae, and adult Chironomidae, and these all had relatively lower $\delta^{15}N$ values compared to other prey. Consequently, an increase in consumption of these taxa would likely decrease $\delta^{15}N$ values, not increase them. However, there was an increase in the relative abundance of kōwaro fry with drying intensity, with the $\delta^{15}N$ values of these kōwaro fry noticeably higher than other identified prey taxa. Thus, it is possible that increased cannibalism was potentially responsible for the overall increase of kōwaro $\delta^{15}N$ values. Occurrence of cannibalism within kōwaro populations has been previously suggested (Cadwallader 1975, Eldon 1979b), and is likely associated with decreasing habitat size during periods of low flow. These conditions coincide with low abundances of typical invertebrate prey and increasing relative density of pelagic fry, potentially providing a readily available alternative prey source for adults which would have had a relatively higher $\delta^{15}N$. However, this seems unlikely to explain the elevated $\delta^{15}N$ values of smaller yearling kōwaro, which were likely gape-limited, thereby probably restricting increased intra-guild predation via cannibalism to larger kōwaro. This potentially indicates self-metabolism was also an important contributor, whereby kōwaro must survive on internal reserves during dry periods, with this use of body tissue potentially elevating the $\delta^{15}N$ in remaining tissue. Therefore, dry periods during summer months probably have a direct effect on kōwaro $\delta^{15}N$ values, through the process of torpor and changes in trophic omnivory associated with cannibalism.

Increased drying intensity was also associated with an independent decrease of ~1.0 ‰ in $\delta^{13}C$ values in kōwaro. This change reflected a likely increase in consumption of aquatic prey, which is supported by the increase in abundance of common aquatic prey (i.e., microcrustacea and Diptera larvae) in sites with high drying intensity. However, the $\delta^{13}C$ values for aquatic invertebrates and kōwaro fry are similar, so increased cannibalism would also likely cause a decrease in kōwaro $\delta^{13}C$ values. Therefore,

the decrease in kōwaro δ^{13}C values is likely due to a combination of increased consumption of aquatic invertebrates by smaller kōwaro and the cannibalism of kōwaro fry by larger adults.

Compared to the effects of kōwaro body size and drying intensity on both kōwaro δ^{15}N and δ^{13}C signatures, only kōwaro δ^{13}C values differed with canopy cover. The likely reason is that canopy cover significantly affected the abundance of terrestrial adult Diptera, and this taxon had similar δ^{15}N values and distinctly higher δ^{13}C values compared to other common prey taxa. Thus, an increase in terrestrial prey abundance would likely have had little effect on kōwaro δ^{15}N values, but would have likely increased δ^{13}C values of kōwaro that were eating more of them. Therefore, these results suggest the increased abundance of certain terrestrial prey associated with increased canopy cover are utilised by kōwaro.

Aside from the changes in kōwaro isotopes, the gradients of drying intensity and canopy cover were also associated with altered kōwaro size distributions. Importantly, the changes associated with increased drying intensity, (i.e., fry-dominated populations), were the same as those identified in the catchment-wide surveys across different rainfall condition (Chapter 2), indicating consistent effects of drying on kōwaro population size structure. Sites with high drying intensity also had higher abundance of common aquatic prey (microcrustacea and Diptera larvae) and adult Chironomidae. Moreover, across all sites, there was a positive relationship between the abundance of these prey taxa and the relative abundance of kōwaro fry. This association is also supported by kōwaro stomach content analysis, with these invertebrate taxa comprising the entire breadth of prey taxa identified in the stomachs of small kōwaro. This relationship between fry abundance increasing and higher prey abundance, is consistent across multiple systems (Dickey-Collas et al. 1996, Hyatt et al. 2011). Furthermore, there was a correlation between high drying intensity and coverage of aquatic and overhanging riparian vegetation (Appendix B), with high coverage of this vegetation likely important for egg-deposition and sheltering newly-hatched fry (O'Brien 2005). Therefore, the sites with high

drying intensity likely provided the kōwaro fry with both food and shelter, at least until habits began to dry.

These conditions associated with high drying intensity (i.e., food and shelter) likely facilitated both increased egg and post-hatching fry survival. Like other species of fish (Hilderbrand 2003, Tschaplinski and Pike 2017), higher survival of kōwaro fry is likely important for ongoing persistence of kōwaro populations. Consequently, the increased fry abundance with higher drying intensity indicates increased population growth potential, but ultimate survival of fry is probably low due to loss of surface water that occurred at multiple sites with high drying intensity (Eldon et al. 1978, O'Brien 2007). Furthermore, because low drying intensity was associated with diminished relative abundance of kōwaro fry, it is likely these populations in permanent sites are not self-maintaining and require continual immigration of fry from those drying-prone locations. Therefore, long-term persistence of kōwaro populations is likely enabled by high post-hatching survival of kōwaro fry in drying-prone locations, but these highly productive kōwaro populations are potentially at risk from changes to drought regimes.

My results highlight the importance of riparian management in the conservation of top predators, such as fish, of degraded waterways, particularly those that undergo periodic drying. Increased riparian canopy cover is synonymous with increased terrestrial subsidies to aquatic systems (Cloe and Garman 1996, Nakano et al. 1999, Eros et al. 2012). The larger fish were positively associated with canopy cover, which suggested the potential of increasing riparian canopy cover to improve likelihood of long-term persistence for top predators. However, most sites were dominated by willows, which could be exacerbating drying of aquatic habitats (Chapter Four; Marttila et al. 2018). Consequently, there is potential that some benefits of high canopy cover are overshadowed by the potentially elevated drying intensity. Therefore, integrated management that incorporates the restoration of riparian margins, potentially including the replacement of willows with species that extract less water

from aquatic habitats, will likely improve the capacity for conserving species that persist in degraded systems.

Overall, drying intensity and canopy cover significantly impacted the trophic interactions of the top predators, kōwaro, in this degraded system. The diet of top predators, within these agricultural streams, comprised largely of readily available and highly abundant prey with limited specialisation, which is like the diets of top predators described in other impacted ecosystems (Hajisamae et al. 2003, Villéger et al. 2010). Furthermore, increased drying intensity likely contributed to increased intra-guild predation and cannibalism by top predators, which was likely associated with constrained habitat size and low abundance of other prey during low-flow periods. However, increased canopy cover was associated with subsidies of alternative prey sources for top predators, potentially offsetting the loss of prey in drying-prone sites. Therefore, top predators of degraded systems are still sensitive to changes along additional environmental gradients, such as drying, with altered trophic interactions potentially affecting long-term population survival.

Chapter Four: Discussion

Conservation implications and future directions

Stress-tolerant species are likely to experience contractions of inhabitable niche space because of global change, particularly for species that have limited capacity for dispersal into new habitats (Harley 2011). Species that are already threatened, such as kōwaro, are likely at higher risk because they already have diminished capacity to withstand further change. However, we know very little about how kōwaro, a drying-tolerant fish, may respond to increased drying intensity, such as extreme droughts. I aimed to investigate the effect of drought on kōwaro and changes to trophic interactions through drought-induced effects. The first survey-based chapter indicated that exposure to two consecutive extreme droughts, triggered a catchment-wide switch in the size distributions within populations (Chapter Two). A subsequent survey indicated that, within these agricultural streams, changes in drying intensity and canopy cover had likely no effect on overall trophic interactions (based on isotope biplots), but they did significantly impact the trophic position of kōwaro and the invertebrates they use as food (Chapter Three). Furthermore, the altered invertebrate communities were linked to changes in the size distributions within kōwaro populations. Therefore, with similar changes in kōwaro size distributions under drought conditions and along a drying gradient, these results provide evidence that the some of the drought-induced changes (Chapter Two) were potentially linked to alterations to the invertebrate community and altered trophic interactions.

In Chapter Two, I described a catchment-wide switch from adult-dominated populations to fry-dominated populations during drought conditions. This change was poorly described by catch-per-unit-effort (CPUE) because of inherent variability between populations, even during wet and mild years. By comparison, median size, which was more sensitive to changes within a population, provided a quick way to infer information regarding the distribution of sizes within a population. Furthermore, the combination of CPUE and median size was used as a basis to construct a rudimentary framework

to infer the likelihood of a population's future persistence (i.e., resilience). This resilience framework could be applied to the other *Neochanna* spp. in New Zealand with species-specific thresholds. Moreover, this framework may work for other fishes, both in New Zealand and beyond, using a combination of abundance- and sized-based metrics. Therefore, I recommend the inclusion of median size as a monitoring tool in conservation efforts targeting New Zealand's threatened fishes, such as kōwaro, and the use of a resilience framework where populations can be objectively compared to assess relative risk.

The risk of livestock intrusion

The populations changes observed in kōwaro were not consistent across all sites under drought conditions, with those sites situated in the smaller, less-permanent tributaries generally containing juvenile-dominated populations, but the larger pools along the mainstem contained adult-dominated populations (Chapter Two). Furthermore, in Chapter Three, with populations along a gradient of high drying intensity, I describe the same trend where sites with high drying intensity were associated with higher proportions of kōwaro fry. However, the relative abundance of kōwaro fry was variable within the high drying intensity category. This variability may be explained by the in-stream and marginal plant cover. The relative abundance of fry was positively associated with aquatic vegetation ($F_{1,10}$ = 3.64, p = 0.086; Figure 4.1A) and overhanging vegetation ($F_{1,10}$ = 6.36, p = 0.029; Figure 4.1A), with these plants likely serving as both egg deposition sites and shelter for newly-hatched pelagic kōwaro larvae (Figure 4.2). However, most sites in this study were exposed to some level of intrusion by livestock, and to classify the level of livestock intrusion at each site, I spilt the wetted perimeter into five metre sections and visually estimated the proportion of riparian area in each section that had signs of livestock intrusion, including hoof prints, eaten grass, turned over soil, and, on a couple of occasions, approximately 20 cows standing in the stream (Figure 4.3). Moreover, the level of estimated intrusion by livestock was negatively correlated with both aquatic vegetation ($F_{1,10}$ = 2.89, p = 0.120; Figure 4.1B) and overhanging vegetation ($F_{1,10}$ = 6.64, p = 0.028; Figure 4.1B). This, therefore,

suggests there is potentially a negative relationship between allowing livestock access into the stream and the capacity of kōwaro populations to produce sufficient recruits long-term. This relationship requires further investigation, particularly because the current distribution of kōwaro is restricted mainly to agricultural streams, like the populations surveyed during my research.
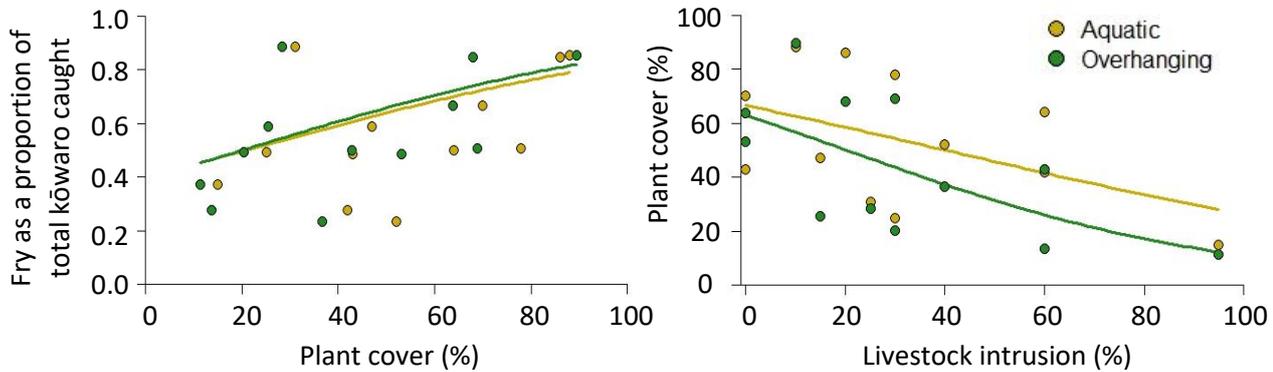
Figure 4.1 The relationship between (A) plant cover and proportion of fry within kōwaro populations and (B) estimated livestock intrusion and plant cover, for two types of vegetation (colours). The lines represent the predicted model relationships from generalised linear models with quasibinomial distributions, with fry proportion and plant cover predicted by plant cover and livestock intrusion, respectively.

Willows: The good, the bad, and the unknown

In Chapter Three, I investigated canopy cover as an environmental gradient that could have the potential to alleviate the negative effects of increased drying intensity. The results indicated that increased canopy cover was associated with elevated amounts of some terrestrial invertebrate taxa falling into the water, where they were likely to be consumed by kōwaro. The increase in alternative prey would be most beneficial during periods of reduced in-stream prey, such as summer low flow periods, when the elevated levels of terrestrial invertebrates falling into the stream could potentially facilitate increased chances of survival of top predators (Chapter Three). Furthermore, there is potential for the higher levels of shading provided by canopy cover to limit temperature fluctuations and, consequently, mitigate water loss during the low-rainfall summer months. Therefore, I was

Figure 4.2 Instream and overhanging riparian plants are likely to be important for kōwaro fry. These photos highlight this relationship with the highest kōwaro catch-per-unit-effort for one sampling (~78 fish per trap) occurring at a site with high plant cover (top) and a small group of kōwaro fry hiding under overhanging riparian vegetation in response to a potential threat (bottom), such as the shadow of a photographer.

Figure 4.3 Livestock intrusion into kōwaro-inhabited waterways was indicated by various signs, including hoof prints left in riparian and intermittently-wetted areas (above), and the erosion of stream banks due to repeated stream crossings by livestock (below).
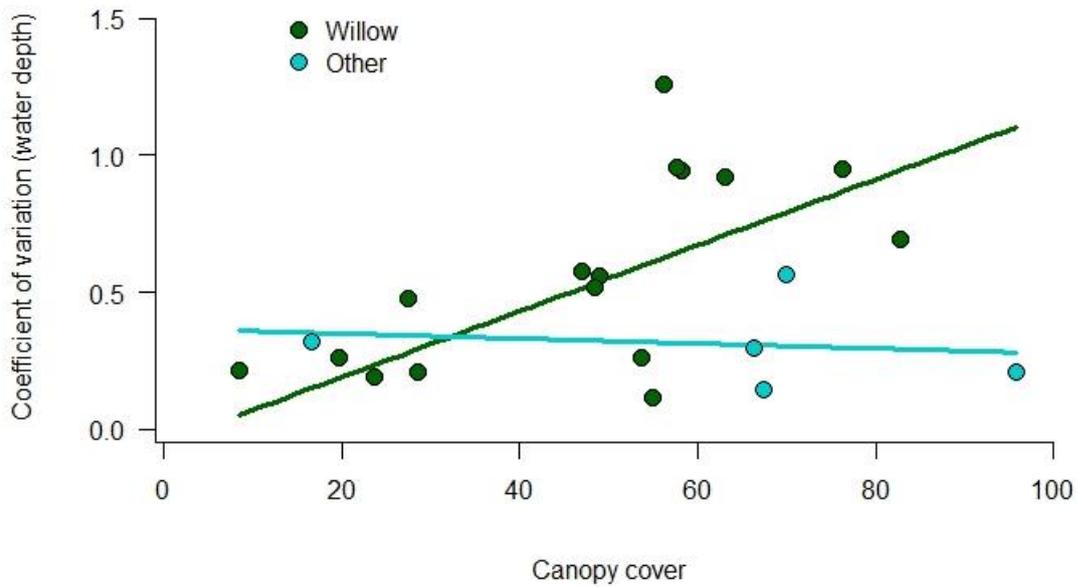
Figure 4.4 Relationship between canopy cover and coefficient of variation for water depth for different tree species (Colours). The lines represent the output from a linear model with an interaction of canopy cover and tree species.

puzzled why the largest coefficients of variation in water depth, which represents the strongest drying intensity, were associated with high canopy cover (Chapter Three, Figure 3.1). These agricultural streams are largely dominated by numerous willows, which have been previously identified as having potential to magnify the rate of water loss from streams (Marttila et al. 2018). This amplification of water loss is particularly important during summer low flow periods, when the presence of willows could potentially decrease the length of time streams have flowing water or any surface water at all. Consequently, the presence of willows could potentially exaggerate drought severity and duration. Reconstructing the relationship between drying intensity and canopy cover, with sites classified based on dominant tree type, showed that the highest drying intensities were indeed associated with high willow canopy (Figure 4.4). Using a linear model with canopy cover and tree type as predictors indicated that there was potentially an interaction between these predictors. Furthermore, after removing the potentially misleading sites (i.e., the no canopy sites downstream of large willow coverage and willow-dominated springs), this interaction was almost significant ($F_{1,17} = 4.29$, $p = 0.054$; Figure 4.4). Consequently, I believe this is an area of interest that requires further investigation

because the presence of willows could be detrimental to the persistence of kōwaro, outweighing any added benefits of increased canopy cover. Therefore, I suggest that native riparian plantings, particularly with increased canopy cover, could not only buffer the in-stream environment from the surrounding landscape, but also, facilitate increased survival during summer low flows, particularly for predatory fishes.

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Appendix A: Kōwaro fin to muscle isotope regressions
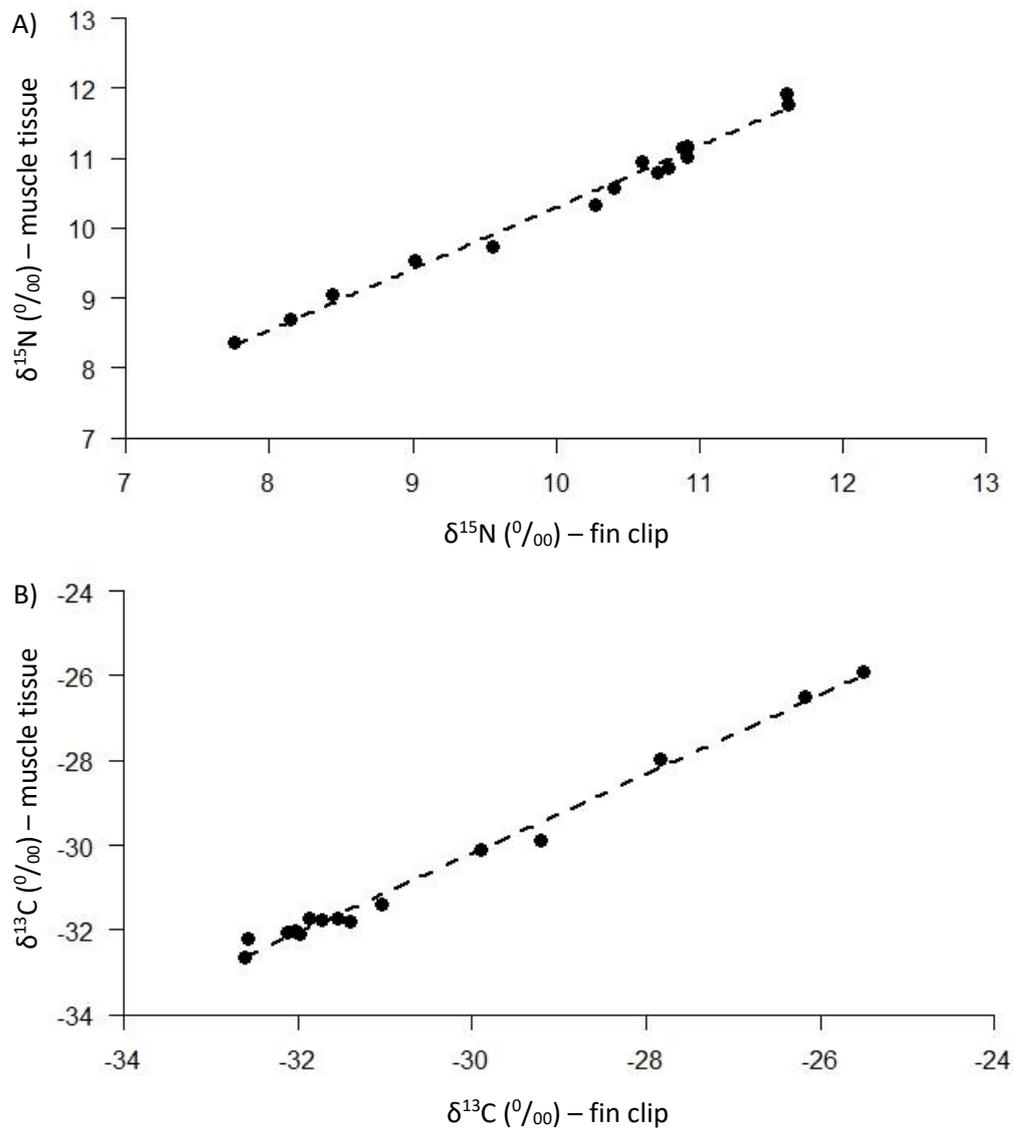
Figure 1 Relationships between the (A) δ^{15}N and (B) δ^{13}C isotopes from tissues from kōwaro,

showing the regression relationship (dotted line) that was used to correct the isotope values for fin

clipped kōwaro to an estimate of the muscle tissue equivalent. Regression equations were: (A)

δ^{15}N$_{muscle}$ = 0.877 x δ^{15}N$_{fin}$ + 1.524 and (B) δ^{13}C$_{muscle}$ = 0.934 x δ^{13}C$_{fin}$ - 2.160.

Appendix B: Population and environmental data from food web survey

Table 1 Population and environmental data collected from October 2016 – March 2017, providing site location, and kōwaro population catch-per-unit-effort and median size, core environmental gradients used in the food web analysis, and finally the water chemistry (the mean values across all probe readings at each site is provided).

Site code	Coordinates		Kōwaro catch-per-unit-effort				Kōwaro size distribution	Core environmental gradients			Dissolved oxygen		Acidity	Specific conductivity
	South	East	Fry	Yearlings	Adults	Total	Median size (mm)	Drying intensity	C.V. (depth)	Canopy cover	mg/L	% saturation	pH	µS/cm @ 25 ℃
W1	-43.424559	171.927123	0	0	0.8	0.8	122.3	Low	0.115	55	10.3	85.7	7.0	150.3
W2	-43.419581	171.947222	0.375	0.75	2.875	4	96.3	Low	0.211	95.75	9.4	86.9	6.9	146.9
W3	-43.419833	171.966439	0	5.875	0.875	6.75	81.5	Low	0.308	63.25	2.0	18.7	6.6	335.5
W4	-43.420741	171.974491	0.1	0.2	1.3	1.6	102.8	Low	0.261	53.75	9.7	89.8	7.0	180.4
W5	-43.426134	171.986225	0.4	2.3	2	4.7	89.5	Low	0.146	67.5	8.5	78.1	7.0	160.7
W6	-43.426070	171.970073	33.75	4.125	1.625	39.5	74	High	0.512	0	8.7	87.1	7.3	190.2
W7	-43.429558	171.976293	10.8	1.4	0	12.2	46.3	High	0.956	57.6	5.8	57.8	6.9	175.4
W8	-43.430464	171.982052	1	0.4	0.3	1.7	66.5	High	1.26	56.2	5.5	51.8	6.9	175.5
W9	-43.431281	171.984839	2.3	1	2.9	6.2	80.5	High	0.695	82.75	7.1	67.1	7.0	163.9
W11	-43.446880	171.942030	0.333	0	0.167	0.5	91.25	High	0.561	49	7.5	70.3	6.7	188.5
W12	-43.444813	171.946094	0	0.833	0	0.833	76.6	Low	0.215	8.5	8.1	75.0	7.2	235.1
W13	-43.446943	171.971776	1.7	0.9	0.9	3.5	64.5	High	0.517	48.4	6.7	68.5	6.5	289.5
W14	-43.451917	171.974489	0	0.7	1.3	2	92.8	Low	0.263	19.6	8.6	83.5	7.0	169.9
W15	-43.457517	171.973080	0	1.7	2.5	4.2	93.3	Low	0.206	28.6	8.9	86.5	6.9	168.8
W16	-43.453225	171.961750	3.5	2.5	1.125	7.125	67.3	High	0.947	76.25	5.6	55.9	6.5	566.7
W17	-43.455256	171.958098	0.5	24.25	2.5	27.25	82.5	Low	0.320	16.67	6.6	63.2	6.7	232.3
W18	-43.465636	171.975770	0.625	1.375	0.25	2.25	74.2	High	0.575	47	6.6	62.1	6.4	326.2
W19	-43.471539	171.976965	1.5	3.4	1.5	6.4	83.7	High	0.563	70	4.5	42.9	6.5	219.4
H1	-43.537155	171.943153	0.8	0.4	0.4	1.6	93.5	High	0.941	58.25	8.1	64.9	6.5	83.7
H2	-43.541400	171.946223	0.7	1	0	1.7	66.3	Low	0.479	27.5	5.9	53.3	6.3	86.0
H3	-43.543143	171.954136	1.833	0.333	0	2.166	56.8	High	0.921	63	3.3	30.3	6.5	93.5
H4	-43.549702	171.975833	3.75	0.875	2.75	7.375	86.8	High	0.587	0	7.9	75.1	6.7	154.3
H7	-43.568348	172.020618	0.1	1.1	2.1	3.3	94.3	Low	0.296	66.4	9.0	82.2	6.8	200.9
H8	-43.573482	172.017747	0.2	0.3	0.1	0.6	104.3	Low	0.190	23.6	9.9	85.9	6.7	113.9

Appendix B (continued)

Table 2 Population and environmental data collected from October 2016 – March 2017, providing percent covers to describe riparian and in-stream conditions, and substrate values to describe the stream benthos, the maximum and minimum habitat size that was achieved during the length of this survey, and the mean flow levels, with a measure of likely stream disturbance (Pfankuch index).

Site code	Percent cover					Substrate		Maximum habitat size			Minimum habitat size			Flow	Disturbance
	Aquatic vegetation	Riparian	Wood debris	Livestock damage	Overhanging vegetation	% Silt	Average size (mm)	Width (m)	Length (m)	Depth (m)	Width (m)	Length (m)	Depth (m)	Cumecs (m^3s^{-1})	Pfankuch index
W1	64	95.0	20.0	60	42.9	75	5.17	8.75	9.5	48.12	7.15	9.17	41.28	0.009	80.0
W2	56	8.0	1.0	0	56.8	80	6.94	3.08	20	36.88	2.06	20	22.32	0.028	82.0
W3	86	80.0	80.0	20	68	100	0.01	7.62	15.8	39.36	7.6	13.3	18.2	0	62.0
W4	78	100.0	40.0	30	68.9	100	0.01	3.48	20	25.2	2.32	20	18.52	0.013	62.0
W5	30	95.0	20.0	45	14.6	70	13.07	5.62	20	48.04	4.81	20	35.68	0.116	75.0
W6	50	100.0	0.0	75	26.8	100	0.01	10.27	13.65	39.96	7.5	8.7	8.36	0.005	62.0
W7	2	95.0	40.0	5	8.8	100	0.01	7.44	20	42.4	0	0	0	0.008	76.0
W8	0	98.0	70.0	100	0	100	0.01	5.76	20	61.68	0	0	0	0.015	69.0
W9	30	75.0	55.0	30	37	100	0.01	7.66	20	34.08	0	0	0	0.014	59.0
W11	35	95.0	40.0	80	12	100	0.01	9.26	11.4	13.6	0.9	6.8	2.08	0	73.0
W12	88	80.0	10.0	10	89.5	10	51.02	4.38	9.43	72.24	5.1	9.8	46.6	0.079	74.0
W13	31	83.0	25.0	25	28.4	45	48.52	9.1	20	44.76	6	18	3.4	0.004	76.0
W14	47	90.0	5.0	15	25.5	40	16.04	5.8	26.3	40.18	4.42	16.85	27.4	0.110	78.0
W15	15	80.0	35.0	95	11.3	50	9.56	7.66	20	64.92	7.58	20	35.68	0.120	76.0
W16	70	85.0	25.0	0	63.8	100	0.01	3.74	20	50.12	0	0	0	0.004	71.0
W17	0	0.0	15.0	0	25.5	30	24.03	2.78	7	46.53	3.8	4.5	17.96	0.010	73.0
W18	43	80.0	10.0	0	53.2	65	6.37	1.65	20	27.4	0.55	1.8	5.12	0.004	86.0
W19	8	80.0	15.0	35	18.2	100	0.01	3.54	20	38.08	0	0	0	0.003	80.0
H1	25	98.0	10.0	55	12.4	90	0.69	22.76	34.46	57.72	0	0	0	0	53.0
H2	25	100.0	2.0	30	20.3	85	2.08	10.86	13.53	33.2	11.23	15.9	31.4	0.006	68.0
H3	5	75.0	50.0	25	14.8	95	0.44	4.64	15.9	15.28	3	6.9	5.56	0	68.0
H4	42	100.0	0.0	60	13.6	80	3.96	4.55	22	31.4	0	0	0	0.032	55.0
H7	52	85.0	15.0	40	36.7	20	23.52	3.78	25	34.24	2.5	25	19.88	0.232	56.0
H8	64	60.0	5.0	60	42.9	90	7.09	8.68	15.5	34.56	6.88	15.5	26.12	0.108	64.0

Appendix C: Whole-community isotope metrics

Table 1 The analysis of variance tables for the ANOVAs comparing the whole-community isotope metrics provided in Layman et al. (2007), as well as the centroid values for δ^{15}N and δ^{13}C, between the different combinations of high and low drying intensity and canopy cover (i.e., the categories provided in Figure 3.1).

Source	Df	Mean squares	F value	p-value
Range of δ^{15}N values				
Category	2	0.142	0.014	0.924
Residual	19	1.80		
Range of δ^{13}C values				
Category	2	16.14	2.81	0.085
Residual	19	5.75		
Total isotope hull area				
Category	2	300.0	1.04	0.373
Residual	19	289.0		
Mean distance from centroid				
Category	2	0.109	0.706	0.506
Residual	19	0.154		
Mean distance to nearest neighbour				
Category	2	0.157	3.02	0.073
Residual	19	0.052		
Standard deviation of distance to nearest neighbour				
Category	2	0.103	1.49	0.250
Residual	19	0.067		
Centroid of isotopic signatures - δ^{15}N values				
Category	2	0.647	1.53	0.242
Residual	19	0.424		
Centroid of isotopic signatures - δ^{13}C values				
Category	2	0.644	0.405	0.672
Residual	19	1.58		

Appendix D: Correlation of kōwaro body size with canopy cover and variability in water depth
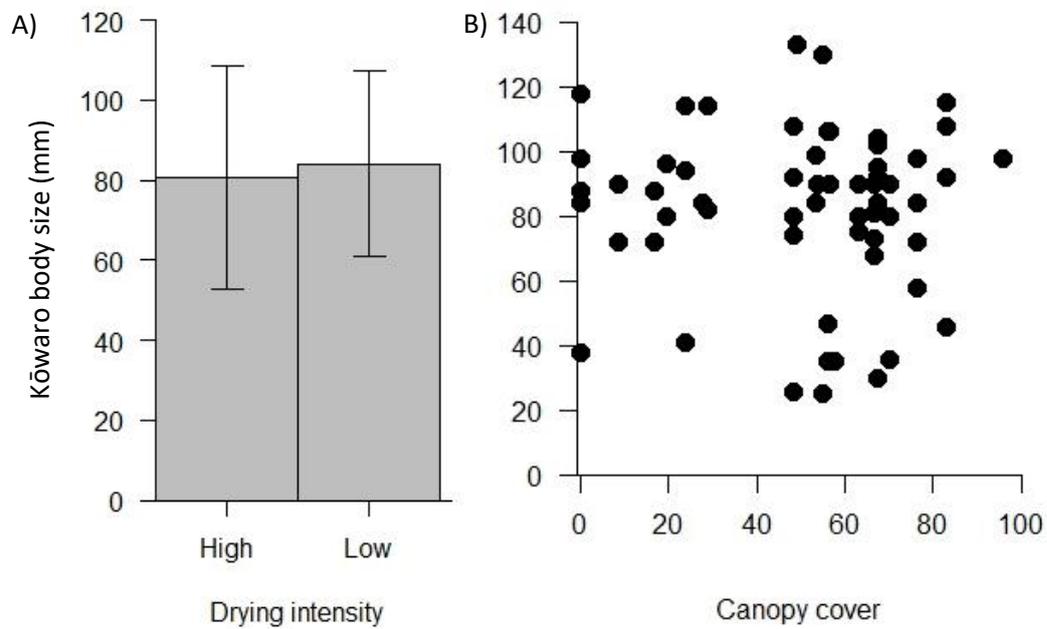

Figure 1 Relationship between the body size of fin clipped kōwaro and (A) the variability in water depth and (B) canopy cover, showing that the size of the fin clipped kōwaro was not correlated with either of the main environmental gradients.