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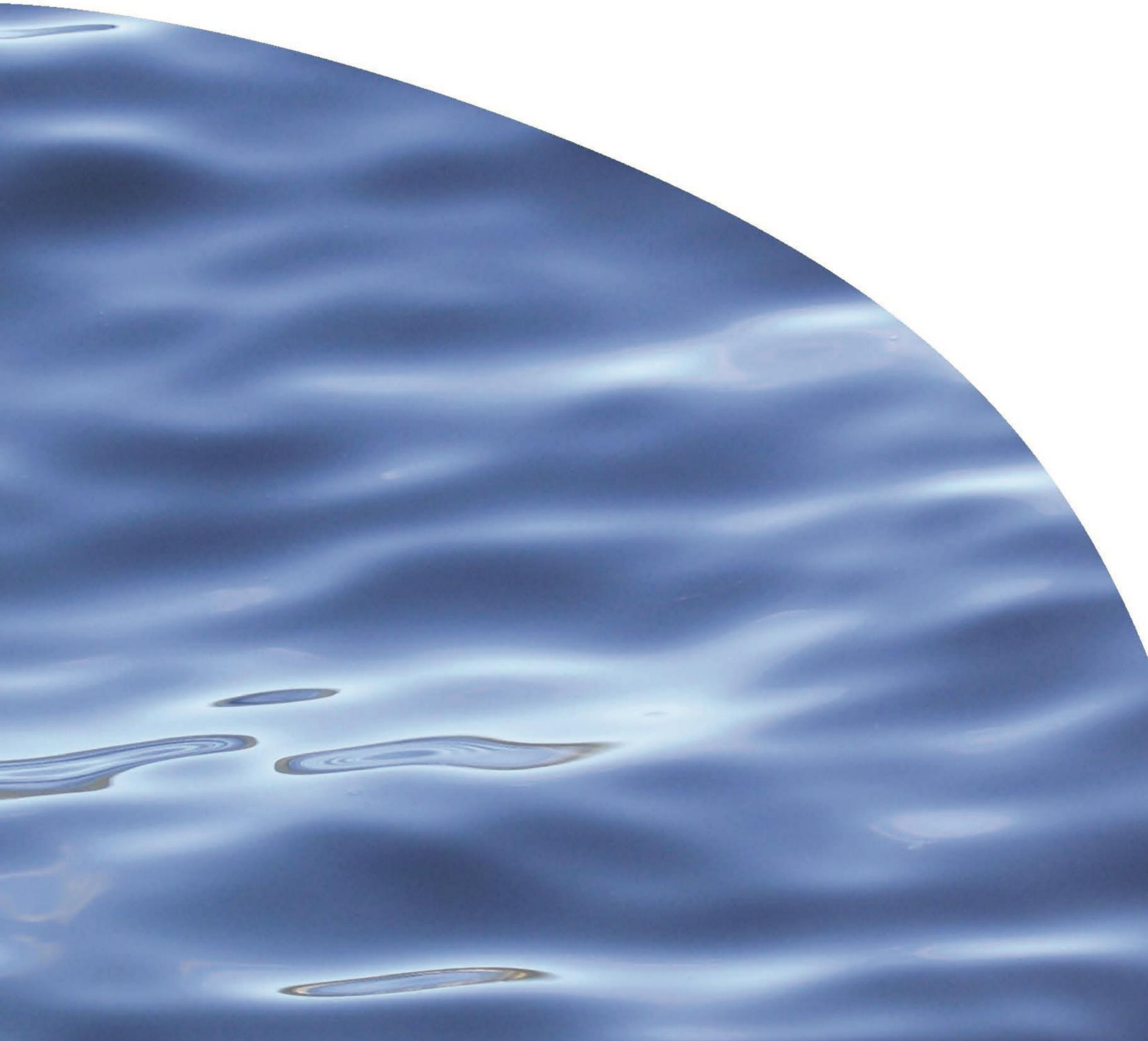
ASSESSING AQUATIC INVERTEBRATE PREY INDICES FOR FISH: TROUT



ASSESSING AQUATIC INVERTEBRATE PREY INDICES FOR FISH: TROUT

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Prepared for Ministry for the Environment

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EXECUTIVE SUMMARY

Indices based on aquatic invertebrate community data are widely used, by regional councils and science providers, to assess the effects of environmental change including inferring effects on higher trophic levels (e.g. fish, birds). However, current indices do not explicitly link change in invertebrate communities to higher trophic levels and there is no science demonstrating relationships between the indices and fish metrics.

We have created fish prey quality indices using an invertebrate traits-based approach to bridge this research and monitoring gap. In this report, we tested our newly-developed fish prey indices (FPIs) for trout, and other existing invertebrate metrics/indices, against trout diet and biomass data to assess their potential for interpreting changes in New Zealand invertebrate communities in respect of effects on fish.

Our results do not provide strong support for the use of our Trout Prey Indices (TPIs) as values-based indicators for trout. We did not find any significant correlations between TPI scores, or the components of the TPIs, and trout biomass or trout diet. We did find some positive correlations, which were encouraging, but they were not statistically significant nor generally consistent among test data sets. However, our testing was limited by available datasets.

Our results also do not provide support for the relevance of existing invertebrate community indices to trout, including the Macroinvertebrate Community Index (MCI), Quantitative MCI and Ephemeroptera, Plecoptera, Trichoptera (EPT) index variants. The recent 2017 amendments to the National Policy Statement for Freshwater Management (NPS-FM) require regional councils to use the MCI as a monitoring tool. Our results suggest MCI would be too coarse for detecting the effects of environmental change on trout (in particular biomass and abundance).

Our results do provide support for the relevance of total benthic invertebrate community density, and especially biomass, to trout. The sum of EPT taxa and density appear to have some utility, although total community density and biomass is more useful.

Finally, our progress to date provides a useful foundation for further research on FPIs. In this regard we see most promise in more thoroughly testing the correlation of TPI taxon scores with trout diet data. Ideally, targeted research is needed involving concurrently collected benthic and drifting invertebrate data and trout diet data that integrate food availability and fish diet over spatial and temporal scales.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES

1. INTRODUCTION

1.1. Background

Indices based on aquatic invertebrate community data, such as the Macroinvertebrate Community Index (MCI) and EPT[1], are widely used to assess the effects of environmental change in rivers / streams, and they have also been used to infer effects on higher trophic levels (e.g. fish, birds). However, these indices do not explicitly link change in invertebrate communities to higher trophic levels, and, to our knowledge, there is no science demonstrating relationships between the indices and fish metrics in New Zealand.

The core element of environmentally sustainable management under the Resource Management Act 1991 and clarified for regional councils by the National Policy Statement for Freshwater Management (NPS-FM), is to safeguard the life-supporting capacity and ecosystem processes of freshwater ecosystems (cf. RMA s5(2)(b) and NPS-FM Objective B1) (New Zealand Government 2014). This includes invertebrates and fish and the processes that link them. To give effect to environmentally sustainable management under the RMA and NPS-FM, regional councils must set freshwater management objectives and limits to achieve those objectives and monitor to assess the effectiveness of those limits (New Zealand Government 2014). However, freshwater management objectives are often insufficiently measurable, and monitoring inadequately focussed on attributes relevant to instream values, for the effectiveness of water plan limits to be adequately assessed. For example, protection of fish habitat and their food base (aquatic invertebrates) are important considerations when setting instream water quantity and quality limits. Various monitoring tools are available for assessing the consequences of an instream change on fish habitat, e.g. hydraulic-habitat and bioenergetics modelling (Jowett et al. 2008; Hayes et al. 2016) and broad-scale habitat mapping (Holmes et al. 2012, 2016). However, despite demand from regional councils there are currently no monitoring indices/metrics, other than invertebrate abundance and biomass, available for them to interpret changes in invertebrate communities in respect of effects on fish.

Fish prey indices (FPIs) offer interpretation of the quality of benthic invertebrate communities for fish food, potentially adding value to State of the Environment (SOE) and other invertebrate monitoring data. They have the potential to link the quality of macroinvertebrate communities as food to fish growth and abundance.

Development of FPIs can be approached in several ways. The ‘gold standard’ would be the collection of invertebrate benthic, drift and trout diet data from different river types (e.g. spring-fed, lowland, mountain-fed, lake outlet), which could then be used to develop a scoring system that encapsulates food availability versus actual fish diet

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[1] Ephemeroptera, Plecoptera, Trichoptera

using data within the same spatial and temporal scale. However, this research would involve extensive fieldwork and data analysis requiring substantial funding.

Another (cheaper) approach would be to use existing river-specific datasets of benthic, drift and trout diet data to create FPIs. Unfortunately, few datasets exist where invertebrate and fish diet data have been collected concurrently; insufficient data being a major limitation to this method.

Alternatively, FPIs can be created using a traits-based approach whereby invertebrate traits that underpin prey preference by fish can be parameterised (scored) using expert knowledge of invertebrates and information on fish diet from the literature (for trout FPIs) or from targeted diet studies (e.g. Rader 1997). The relevant traits are those such as size, shape, mobility, predator evasion behaviour and drifting that influence the vulnerability and energetic profitability of aquatic invertebrate prey to fish (Ware 1972, 1973; Ringler 1979; Bannon & Ringler 1986; Grubb 2003).

We created our FPIs using the traits-based approach because it was easy to apply, cost-effective, independent of the availability of paired aquatic invertebrate and fish diet datasets and aligned with how we envisaged these indices could be developed.

1.2. Development of Trout Prey Indices

The development of fish prey indices for trout, hereafter termed Trout Prey Indices or TPIs, was initiated through a request from NIWA who were engaged in an Envirolink Tools Grant contract (C01X1304) to review the New Zealand instream plant and nutrient guidelines and develop a decision-making framework (Matheson et al. 2016). There was interest in using TPIs to assist in determining relationships between periphyton and the quality of invertebrates as food for adult trout. Theoretically, FPIs can be developed for any of New Zealand's fish species. Trout provide a good starting point because:

- there is extensive literature and expert knowledge on trout diet and foraging behaviours
- they are New Zealand's most economically and socially valuable freshwater fisheries, and as such, maintenance of these fisheries is commonly a management objective in regional water plans.

In preparation for their report Matheson et al. (2016) made a cursory attempt to develop a TPI based on aquatic invertebrate mode of movement (i.e. swimmer, crawler, burrower, sit and wait predator, sessile) and maximum size, using a list of invertebrates compiled from data collected by Environment Canterbury, Hawke's Bay Regional Council, Greater Wellington Regional Council, Environment Southland, and NIWA (from NIWA's New Zealand Water Quality Network).

We were initially asked to review the Matheson et al. draft TPI. It was apparent that more research was required before the TPI could be applied to benthic invertebrate datasets. We developed the TPI further mainly with Cawthron funding supplemented with a small grant from NIWA's Envirolink Tools Plant Nutrient Guidelines project. The advancements included the addition of the trout prey preference traits (that were categorised for each invertebrate taxon and then multiplied to generate a combined taxon score), and the creation of different versions of the TPI to account for different foraging behaviours used by trout (see Section 2.1 on trout feeding behaviour). We were then able to advance the development of the TPIs further, and test their predictions, in the present project funded by the Ministry for the Environment (MfE) (Contract No. 18502).

The objectives of the MfE project were to:

1. Advance the development of provisional TPIs created for two trout foraging strategies (drift feeding and benthic browsing) by defining and scoring component traits that potentially influence the vulnerability and energetic profitability of invertebrate taxa as prey for adult trout.
2. Re-evaluate individual TPI traits and filter them for redundancy.
3. Document the development of the TPIs.
4. Test the TPIs[2] by correlating their invertebrate taxon scores with trout diet data (occurrence and relative abundance of prey in diet).
5. Test the TPIs on two national datasets for which both invertebrate community and trout biomass data were available in the following ways:
    (a) correlating the TPI component trait scores, with trout biomass.
    (b) correlating TPIs (community scores) with existing, commonly used, invertebrate community indices—including MCI and EPT variants.
    (c) compare the correlative performance of the TPIs (community taxon scores) and existing, commonly used, invertebrate community indices/metrics with trout biomass.

In considering how the TPIs would take shape, it was clear that the following factors needed to be considered and, if possible, accounted for:

- feeding strategies that adult trout employ
- features of aquatic invertebrates that influence their prey capture vulnerability and energetic profitability, specific to the trout foraging mode—including taxon life histories, feeding mode, activity and size
- occurrence of aquatic invertebrate taxa in trout diets using information from existing trout stomach content data

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[2] The tested TPIs included those for drift feeding, benthic browsing and a generic version combining drift feeding and benthic browsing.

- how the indices were to be calculated such that they could be easily integrated and applied to existing benthic invertebrate monitoring datasets.

To inform the above factors we relied on our professional invertebrate and salmonid research expertise, angling experience, trout dietary preferences, supporting literature, and reference to existing trout diet datasets.

2. COMPONENTS OF THE TROUT PREY INDICES

2.1. Trout feeding behaviour

There are four foraging modes (strategies) that trout (and native fish) may employ to capture prey (Ware 1972, 1973; Hayes & Hill 2005; Grubb 2003):

a. drift feeding
b. benthic browsing
c. cruise feeding
d. pursuit feeding (confined mainly to capturing fish – but may also include fast-swimming mayflies, e.g. *Nesameletus* and *Oniscigaster*)

When drift-feeding, trout hold station, usually in a velocity refuge near the river bottom, and intercept invertebrates drifting past in the faster water above and to the side of them. Sometimes trout may drift feed more actively, moving about in the water column intercepting prey sequentially; usually in slower flowing locations or when prey are very abundant—such as during insect emergence. Trout employing this method of foraging therefore preferentially select for invertebrates with a high propensity to drift, and that are abundant in the drift. Often trout will feed most voraciously around dusk and dawn, especially the former, as invertebrates with a high propensity to drift are more active then and it is still light enough for trout to see their prey.

When benthic browsing, trout take prey directly from the surface of the substrate. Prey with low mobility are preferentially eaten (e.g. snails and cased caddis). Active prey such as *Deleatidium* mayfly larvae can evade capture by scuttling under the surface of stones.

Cruise feeding is a common strategy employed by trout in still-water environments (e.g. lakes and river backwaters) whereby they actively swim a circuit known as a ‘beat’ searching for prey that are available within the water column or on the water surface.

In rivers, the relative importance of the above foraging modes depends on the gradient and channel morphology. Drift feeding is the predominant foraging mode in moderately- to fast-flowing segments of rivers (Jenkins et al. 1970; Bachman 1984; Hayes & Hill 2005; Fausch 2014; Piccolo et al. 2014). Water velocities and flood disturbance regimes provide unsuitable conditions for proliferation of aquatic macrophytes and benthic invertebrates that have low mobility and are less drift prone (e.g. snails, and cased caddis). In more stable, slower, lower gradient segments in lowland areas, or in low gradient spring-fed rivers, such invertebrates are more common and provide trout with more opportunity to profitably browse prey directly from the riverbed (Hayes & Hill 2005).

The foraging mode employed by trout depends on water velocity[3]. When average cross-sectional water velocity falls below 0.3 m/s, trout switch from drift feeding to active searching for prey (benthic browsing and cruise feeding) and schooling, because drift rates are insufficient for profitable drift feeding (Campbell & Scott 1984; Fausch et al. 1997; Sweka & Hartman 2001). In moderately-flowing rivers a switch to browsing may been 'forced' on trout when low flows result in average water velocity falling below the 0.3 m/s threshold during low flow, with adverse potential adverse consequences on food intake rate for trout. However, in highly productive lowland spring-fed rivers, benthic browsing can be a profitable foraging strategy, because prey that are vulnerable to benthic browsing are more abundant. Note also that trout will undertake benthic browsing when mean column water velocities are greater than 0.3 m/s, probably up to 0.8 m/s when the riverbed is rough enough to shelter foraging trout from the full force of the current, and benthic prey are sufficiently abundant.

An invertebrate prey scoring system needs to take account of trout varying their foraging mode depending on the environmental conditions, i.e. classifying prey according to whether they apply to drift feeding, cruise feeding or benthic browsing modes.

Drift-feeding and benthic-browsing are the two most common foraging strategies trout are likely to use in rivers (Keup 1988; Stolz & Schnell 1991; Hayes & Hill 2005). For this reason, we focused on developing TPIs for these foraging modes. However, because trout are likely to switch foraging strategies throughout the course of a day, we also developed a general TPI by averaging the drift feeding and benthic browsing prey scores.

2.2. Defining invertebrate prey traits

The key features of invertebrates that influence their suitability for trout prey are:

a. likelihood of being detected and captured by trout—in the drift or on the substrate
b. size (length)
c. activity/movement
d. energetic value of prey to fish (digestibility).

For trout to consume invertebrates, the prey must be accessible (available) to trout in the habitats that trout occupy. Furthermore, the likelihood of trout detecting and capturing an individual invertebrate, whether it be in the water column or on the benthos, must be relatively high. Linked to this is the attack response of trout to prey,

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[3] Water velocity also plays an important role in determining what aquatic invertebrates are available. While *Deleatidium* is an important prey for trout in a moderate to fast-flowing rivers, it is less important in slow, weedy lowland rivers or backwaters. The converse is true for invertebrates commonly found in still-water environments e.g. water boatman, dragonflies and damselflies.

which is stimulated by prey movement, i.e. whether invertebrates actively crawl or drift, swim and wriggle. This renders moderately active prey in the water column or on the substrate more vulnerable to trout (Ware 1973). Movement by prey will also attract the attention of benthic-browsing trout. However, active prey are also more likely to evade capture by escaping to refuge cover (under stones), which is closest and more abundant on the river bed. So, some movement, but limited ability for evasive manoeuvre would render benthic prey most vulnerable to detection and capture by trout.

Trout preferentially feed on large invertebrates but may select for smaller invertebrates when they are abundant (because of search image conditioning to abundant prey) (Ware 1972; Ringler 1979)). Prey capture by trout is restricted to a subset of prey falling within maximum and minimum prey sizes that are limited by mouth gape and gill raker spacing, respectively (small prey escape through the trout's gill rakers) (Wankowski 1979; Bannon & Ringler 1986). Wankowski (1979) provides equations relating minimum and maximum prey length to trout length. The energetic value of prey to trout is also size related; large prey are preferred because they offer greater energy return for foraging effort.

The indices we have developed are based on the feeding habits of adult trout in New Zealand gravel-bed rivers (i.e. typically trout > 30 cm). For each invertebrate feature (trait) listed at the beginning of this section we assigned categories. The lowest category scores equated to low prey quality for adult trout and highest to best prey quality. The cut-off points between categories were guided by the range of possible values, identified through a literature review, as well as expert opinion. An explanation of each trait and the categories is provided below.

2.2.1. *Likelihood of prey detection and capture*

Drift-feeding trout

The likelihood of a drift-feeding trout detecting and capturing an invertebrate prey taxon in the drift will depend on whether the invertebrate is drift prone, when it drifts (i.e. time of day), and whether it is drifting in the vicinity of a feeding trout such that the trout is able to detect it.

Note that our definition of likelihood of prey detection and capture (for drift feeding and benthic browsing) is independent of the abundance of taxa. Only those features that contribute to an individual of a taxon being vulnerable to capture by trout are considered. This overlooks the effect of abundance on selective prey detection by trout, whereby trout develop a search image for abundant prey (Ringer 1979).

Invertebrate drift can be broadly classified into two categories—passive and active drift (often termed behavioral drift). Passive drift occurs when an invertebrate has been unintentionally dislodged (i.e. entrained and carried by the current). An actively drifting animal is in the water column intentionally (e.g. moving to better habitat conditions, emerging through the water column, predator evasion) (Rader 1997; Naman et al. 2016).

Exposure to currents, over space and time, sufficient to entrain invertebrates into the water column and keep them in suspension, was the main consideration for the likelihood of prey detection and capture trait. This included consideration of whether taxa frequent erosional habitats with moderate to strong currents, and the frequency of exposure. Those taxa that live in permanently wetted, erosional habitats are exposed to risk of entrainment and drift all the time. However, taxa that inhabit slow, depositional habitats (e.g. in margins and pools) have a lower likelihood of drifting than those exposed to fast currents. Others sometimes live beyond the margins of the baseflow-channel but are exposed to entraining currents occasionally (e.g. *Archichauliodes*). As a river widens with increasing flow and the habitat of these taxa is inundated, they become available to drift then and on subsequent receding flow.

The probability of an invertebrate being entrained and staying in the water column long enough for a trout to detect it will depend on the invertebrate’s resistance and resilience (ability to settle) to drifting (Hayes et al. 2018). For example, Simulidae (sandfly) larvae can cling to the surfaces of rocks exposed to the water current using a specialised circlet of small hooks. They will frequently drift when confronted by predators, using a silk thread attached to the substrate as a lifeline to partially resist being washed away (Reidelbach & Keil 1990). The propensity of leptophlebiid mayflies to drift is governed by other factors, interacting with the force of the current. They have dorso-ventrally flattened bodies that allow them to withstand current, but they frequent habitats in moderate to fast-flowing currents—and they are highly active, scuttling over exposed rock surfaces as they graze. When they are entrained into the drift, leptophlebiids can limit the time they are exposed in the drift by swimming back to the river bed. While more sessile invertebrates, such as snails and cased caddisflies, have some ability to resist moderate currents by clinging to the substrate, their bulk creates drag, making them vulnerable to displacement. Although they may sink faster than a leptophlebiid mayflies, they have little control over when and where they can settle because they can’t swim (Otto & Sjostrom 1986). Rader (1997) considered that the propensity of an invertebrate to drift should be affected by its mobility, with the likelihood of dislodgement descending from swimmer>crawler>attached>sessile. But, as reasoned above, mobility (activity) is only one factor that influences how drift prone a taxon is.

Time of day is another factor to consider in respect of invertebrate prey traits especially for invertebrates that actively drift. Invertebrates entrained in the drift during the day and at dawn and dusk are most easily detected and captured by drift-feeding trout (Rader 1997; Naman et al. 2016). Beyond the daylight hours a trout’s ability to visually detect prey and forage efficiently decreases. Dusk and dawn peaks in invertebrate drift activity have been well documented, and often these peaks relate to a life history activity such as the emergence of insects through the water column towards the terrestrial adult phase (Naman et al. 2016).

When considering trait features for the likelihood of prey detection and capture we concentrated on drifting activity that would occur over median to low flows (i.e. the lower limb of flow recessions). This range includes baseflows that correspond to when regional councils sample benthic invertebrates, and which are clear enough for trout to visually drift feed. All of the features that we considered when categorising invertebrates under the likelihood of prey detection and capture trait are listed below:

- Functional feeding group: whether a taxon is a grazer/browser/algal piercer (more likely to be found on the surface of rocks where periphyton grows), collector/gatherer (likely to inhabit backwaters where detritus collects), or predator (more likely to be found under rocks searching for prey).
- Diel activity: whether a taxon is predominately diurnally or nocturnally active (e.g. day active invertebrates such as the common mayfly *Deleatidium* have higher likelihood of being encountered by visually-feeding trout than predominately nocturnal invertebrates such as the predaceous mayfly *Ameletopsis*).
- Habitat preference: whether a taxon is found in fast or slow currents. Some invertebrates prefer fast currents (riffles and cascades) but are not generally drift prone (e.g. the fly larvae Blephariceridae, which uses suction to cling to rocks), whereas others preferring moderate to fast currents are more drift prone (e.g. the net-spinning caddis *Aoteapsyche*, which builds a stone dwelling for protection but otherwise has limited ability to attach itself to the substrate). Some invertebrates inhabit slow-flowing backwaters in rivers and may only occasionally be susceptible to drifting if accidently caught up in faster currents (e.g. backswimmers (*Sigara*) or diving beetles (Dytiscidae)).
- Feeding activity: whether a taxon actively forages on substrate surfaces exposed to moderate to fast currents (e.g. *Deleatidium* is entrainment-prone because it forages on rock surfaces in moderate–fast currents, whereas cased caddisflies such as *Helicopsyche* are less entrainment-prone because they inhabit crevices on the underside of rocks).
- Settling and swimming ability: the degree to which a taxon’s exposure in the drift is limited by settling speed and/or active return to the river bed (e.g. the mayfly *Nesameletus* has good swimming ability, other taxa have only moderate swimming ability and settling speed (e.g. free-living caddis), and others have no active swimming ability but fast settling speed owing to body weight and shape (e.g. cased caddisflies).

The above traits consider activity and body features that affect the propensity of taxa to drift, influencing their vulnerability to detection and capture by drift-feeding trout (Keup 1988; Rader 1997; Naman et al. 2016). The categories for the likelihood of prey detection and capture trait ranged from 0 (don't occur in water column or on surface) to 5 (often in water column or on water surface) (Appendix 1). Assignment of invertebrates to the categories was based largely on expert opinion backed by published and unpublished data (e.g. Cawthron unpublished data; McLeod 1998; Collier & Winterbourn 2000).

Benthic-feeding trout

Benthic feeding by trout is most likely in depositional, slow-flowing or still habitats (pools and backwaters), where currents are not great enough to entrain invertebrates from the river bed (Campbell & Scott 1984; Fausch et al. 1997; Nakano et al. 1999; Hayes & Hill 2005). Invertebrates that scurry around on the surface of the substrate will be more exposed to trout than prey that live in substrate interstices. Invertebrates with low mobility but which occur on the surface of the substrate will be available to benthic-browsing trout (e.g. the snail *Potamopyrgus*, or cased caddis *Olinga*). More mobile taxa, with predation escape responses, although present on the surface of stones, presumably can evade capture.

The categories for the likelihood of prey detection and capture trait for benthic feeding ranged from 0 (not found on substrate surface) to 2 (often found on substrate surface) (Appendix 1).

2.2.2. Invertebrate length

Invertebrate length (usually recorded as body length (mm) and excluding the cerci (tail)) is a key feature in prey selection by trout (Ware 1972; Ringler 1979). The ingestion of invertebrates is mouth-gape limited for small (juvenile) trout, but not for large (adult) trout—with the exception of large freshwater crayfish prey. For this reason, small trout are less subject to growth limitation than large trout i.e. as juveniles grow they can ingest larger prey items (Hayes et al. 2000). On the other hand, the growth of large trout (> about 30 cm) is limited by the availability of large prey items, especially large invertebrates, given that invertebrates are usually the main prey source in the middle to upper reaches of New Zealand rivers. The larger the trout the larger the food items required to provide a greater energy return for maintaining metabolism and growth (Ringler 1979). The optimal prey size for growth is c. 0.115 x trout fork length (Wankowski 1979). Since invertebrates > 20 mm are rare, it follows that the growth of trout > 30 cm is likely to limited by invertebrate prey size and growth will be increasingly limited the larger the trout.

Our invertebrate taxon size classes were based on the body lengths of late instar larvae. Using published literature[4] and our own unpublished data, we determined the maximum length that each invertebrate taxon could attain and categorised them into the appropriate 3-mm size class. By choosing 3-mm length classes we minimised the number of length categories while maintaining reasonable resolution. A 30-cm trout is

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[4] Winterbourn (1973); Cowley (1978); Rowe (1987); McLellan (1991,1993,1998); Towns & Peters (1996); Smith (2001); Winterbourn et al. (2006); Chapman et al. (2011).

unlikely to retain invertebrates less than 3-mm within its gill rakers (based on Wankowski's 1979 equation). Although adult trout may not always ignore smaller prey, we assigned a 0 to the lowest length category (0-3 mm invertebrate body length), because the quality of a prey item this small would be negligible to a large trout. The length trait comprised eleven 3-mm size classes ranging from 0 to ≤ 3 mm through to > 30 mm (Appendix 1).

We also considered invertebrate area (mm^2) as a substitute to the invertebrate length trait. Area (width x length) is arguably a more relevant trait than prey length in relation to what a trout actually perceives when feeding. However, area did not perform better than length when we tested prey traits by correlation with trout diet and biomass data so we retained taxon length over area for the TPIs.

2.2.3. Invertebrate activity

The activity trait was based on invertebrate behaviours that would attract the attention of trout and instigate a predatory strike. Two invertebrate activity traits were assessed in the development of the TPIs for drift feeding (invertebrate movement and emergence activity) and one for benthic browsing (invertebrate movement).

Invertebrate movement (in the drift and on the benthos)

Prey movement is well known to attract the attention of trout and induce a predatory strike; a fact employed by anglers to catch salmonids with lures (Ware 1973; Grubb 2003; Hayes & Hill 2005). Few drifting invertebrate taxa can move fast enough to evade capture by trout, with the possible exception of the swimming mayflies *Nesamaletus* and *Oniscigaster*. So, movement by drifting taxa almost universally will increase the likelihood of prey detection and capture. Low to moderate movement capability would positively contribute to detection and capture of benthic prey by trout. However, high movement capability by benthic invertebrates on the substrate will contribute negatively to prey capture success, owing to predator evasion.

We categorised drifting invertebrate movement from 1 (low/feeble movements in the water column) to 5 (active swimmers, erratic wigglers). For benthic invertebrate movement our categories were: 1 (fast crawlers and swimmers), 2 (slow crawlers/wrigglers) and 3 (medium crawlers/wrigglers) (Appendix 1). The prey movement ranking for benthic foraging did not follow an ascending order of movement, because fast crawlers and swimmers are likely to evade capture by trout. Hence, we ranked these taxa lowest in respect of movement invoking predatory strike and successful capture by trout.

Assignment of invertebrates to the categories was based largely on expert opinion.

Emergence behavior (drift-feeding)

Emergence behavior was used to classify emerging insect nymphs with respect to their occurrence in the drift and exposure to trout predation. Many taxa that are unavailable as nymphs can be important prey if they enter the drift to emerge through the water surface (Marsh 1983; Marinaro 1988; Rader 1997; Stolz & Schnell 1991). Moreover, emergence in this manner enhances the quality of normally drift-prone taxa as trout prey. This trait has two categories: 1 (doesn't emerge through water column) and 2 (does emerge through water column). Assignment of invertebrates to the categories was based on expert opinion and, where possible, the literature (e.g. Smith & Storey (2018)).

2.2.4. Energetic value of invertebrate prey to trout

For a trout to grow, its energy intake must exceed energy expenditure (Elliott 1994). This is the energetic reason for trout preferring large prey, these offer a greater energy reward for foraging (swimming) effort (Bannon & Ringler 1986). The energy required for a drift-feeding adult trout to capture a small fly larva from the drift in moderate to swift currents may outweigh the energy gained from the prey. The energetic balance of foraging on small prey will be different for benthic-browsing trout. This foraging behavior is more common in slower water, where energy intake from foraging on small invertebrates may outweigh costs, especially when prey are abundant. Nevertheless, the principle of greater energy reward for foraging effort also applies to benthic browsing fish. Hence, comparatively large prey such as a free-living caddis and *Archichauliodes* will be preferred.

The primary size- and energy-related feature that we considered was taxon maximum length, as described above (Section 2.2.2). We also investigated a secondary feature in an attempt to better index invertebrate weight and energy content, namely digestibility.

Digestibility: relative proportion of digestible material

Invertebrates vary in their energy value to fish depending on the proportion of the body composed of indigestible chiton or shell (calcium carbonate) (Elliott 1976). Furthermore, the more space taken up in a fish gut by indigestible material the less space for more energy dense prey. For example, a trout feeding exclusively on the heavily armoured snail *Potamopyrgus* will gain much less energy overall from their diet than if feeding on midge larvae or worms (McCarter 1986). The categories for this trait ranged from 1 (low level of digestible material) to 5 (high level of digestible material). Assignment of invertebrates to the categories was based on expert opinion.

3. CALCULATION OF TROUT PREY INDICES

3.1. Development of invertebrate taxon TPI scores

In Section 2.2 we described the invertebrate prey traits and their component categories. Using the list of invertebrate names supplied by NIWA[5], we assigned each taxon a category under each trait. Individual taxon TPI scores (i.e. scores for each invertebrate) were then calculated by multiplying the category scores among all traits. The combined scores were normalised, by dividing by the maximum, and then scaled so they ranged from 0 (low prey quality) to 10 (high prey quality). The scaled, normalised taxon scores are listed in Appendix 2.

As mentioned in Section 2.1 we also developed a set of general (combined) taxon TPI scores. We did this by averaging the drift feeding and benthic browsing prey scores for each taxon listed in Appendix 2.

3.2. Initial use of taxon TPI scores (Matheson et al.)

An earlier set of provisional taxon TPI scores were used by Matheson et al. (2016) to assess the effects of periphyton on the quality and quantity (density) of invertebrates for adult trout. They calculated drift-feeding scores (DFS) and benthic browsing scores (BBS) using the following equations:

DFS = [Σ(n individuals[6] x drift feeding score for each taxon)]/10
BBS = [Σ(n individuals x benthic browsing score for each taxon)]/10

where 'n individuals' represents the number of individuals of a given taxon in the sample.

Matheson et al. also calculated variants of the DFS and BBS focusing on high quality prey. These were reported with the somewhat confusing labels 'drift count (DC)' and 'benthic count (BC)'. They are better thought of as $\mathrm{DFS}_{\mathrm{hi}}$ and $\mathrm{BBS}_{\mathrm{hi}}$. They were calculated as follows:

DC = Σ(n individuals for all taxa with drift feeding score ≥ 5)
BC = Σ(n individuals for all taxa with benthic browsing score ≥ 5).

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[5] Described in Section 1.2

[6] It was not clear from the Matheson et al. report whether densities had been standardised to area before calculation of DFS and BBS.

3.3. Calculation of community TPI (equations for TPI and QTPI)

The equations that we used to calculate the community TPI and QTPI scores are based on the MCI and QMCI equations developed by Stark (1985, 1993). A TPI community score is generated by summing the taxon scores present in a sample, dividing the sum by the number of scoring taxa, then multiplying by a scaling factor of 20. This theoretically generates a range of community scores of 0 to 200.

$$Site\ TPI = \frac{site\ score}{number\ of\ scoring\ taxa} \times 20$$

The community QTPI is calculated using the following equation

$$Site\ QTPI = \sum_{i=1}^{S} \frac{n_i \times a_i}{N}$$

Where:

n_i is the number of individuals in the *i*th scoring taxon
a_i is the prey score for the *i*th taxon
N is the total number of individuals in the sample.

It should be noted that like the QMCI, QTPI community scores do not account for the densities or biomass of invertebrates in a sample. They account only for the *relative* abundance of animals (i.e. that there are proportionally more taxon A than taxon B in a sample, not the actual abundances of A and B). This makes the QTPI an index of prey quality, not prey quantity or quality plus quantity. Conversely, the DFS and BBS indices calculated by Matheson et al. (2016) incorporate invertebrate density (prey quantity), meaning that they are indicators of prey quality and quantity.

4. TESTING TAXON TPI SCORES AGAINST TROUT DIET DATA

Trout diet analysis can provide information on:

- the feeding strategy a trout has employed (e.g. a river trout with a stomach full of snails has most likely been benthic-browsing)
- the relative importance of invertebrates as trout prey
- prey size (length) range and structure
- the prey available to trout at the time (e.g. how availability of prey can vary seasonally).

We collated trout diet data collected from studies undertaken by Cawthron (unpublished data from the Maruia River) and Witherow and Scott (1984) (Mataura River). Because our TPIs are based on the aquatic invertebrate component of the trout diet data we removed the terrestrial invertebrates (including aquatic adults) from the datasets.

We found Ephemeroptera (mayflies) and Trichoptera taxa were major components of the aquatic invertebrate trout diets, followed by Diptera (flies)[7] and Mollusca (snails) (Appendix 3). This indicates that the trout were mainly drift-feeding, thus we expected our drift feeding TPI would be most closely related to trout diet indices/metrics calculated from these data.

To examine the correlative performance of the taxon TPI scores with the trout diet data, we calculated two trout diet metrics: 1) the occurrence of prey in the trout diet (PreyOccur), and 2) the proportion of each prey item in the diet (PropPreyDiet). These metrics were calculated on adult brown trout aquatic invertebrate diet data collected only from the Maruia River (*n* = 25 trout stomachs collected over summer) (K Shearer, unpublished data). We also examined correlation between MCI taxon scores and the trout diet metrics.

The analysis was undertaken with R (R Core Team 2017, version 3.4.1), with the correlation between trout diet and the TPI indices examined using the Spearman rank correlation test.

The drift feeding taxon scores (Taxon_DF) had the strongest correlation with the trout diet metrics PreyOccur and PropPreyDiet, followed by the combined drift and benthic feeding taxon scores (Taxon_combined (i.e. for drift feeding and benthic browsing)

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[7] Fewer Diptera were found in the trout stomach contents examined by Witherow and Scott (1984) than the Cawthron dataset (Appendix 3). Dipterans are among the most difficult of the aquatic insect orders for aquatic entomologists to learn and be able to identify to a low taxonomic resolution. Moreover, most Diptera are delicate so they fragment rapidly in trout stomachs making taxonomic identification challenging. It is highly likely that unless the invertebrates in Witherow and Scott's report were identified by a trained taxonomist some dipteran taxon may have been overlooked.

(Table 1). Significant correlations were found only between predictor variables, the result of autocorrelation.

Table 1. Spearman's rank correlation coefficients for taxon TPI scores and MCI compared with two trout diet metrics for the Maruia brown trout diet data. Significant correlation coefficients ($p < 0.05$) are italicised and shaded grey. Taxon_DF and Taxon_BB represent taxon scores for drift feeding and benthic feeding. Taxon_combined represents the average of drift-feeding and benthic-feeding taxon scores.

	Taxon_DF	**Taxon_BB**	**Taxon_combined**	**MCI**	**PreyOccur**
Taxon_BB	*0.58*				
Taxon_combined	*0.84*	*0.87*			
MCI	0.10	0.19	0.17		
PreyOccur	0.13	0.07	0.04	0.17	
PropPreyDiet	0.22	-0.04	0.08	0.13	*0.74*

The MCI taxon scores had a slightly stronger relationship with PreyOccur than Taxon_DF, but weaker correlation with PropPreyDiet than Taxon_DF (Table 1).

5. TESTING COMMUNITY TPI SCORES AGAINST TROUT BIOMASS DATA

Fish biomass is known to be influenced by the **quantity** of invertebrates (e.g. invertebrate community biomass and density) (Jowett 1992; Jellyman et al. 2013). We hypothesised that it also ought to be influenced by the **quality** of an invertebrate community as fish food (i.e. as indexed by our taxon TPIs). An understanding of the relative sensitivity of fish populations to both the quality and quantity of food supply is necessary for assessing the likely effects on fish of changes in invertebrate community structure and abundance.

As part of the testing process for our indices, we tested the sensitivity of the community TPIs, and their component trait scores, and other invertebrate indices/metrics (MCI, EPT taxa, community density and biomass) to trout population biomass using two existing paired invertebrate-trout national datasets. The first dataset was from 37 rivers sampled by NIWA in the late 1980s ('100 rivers survey'[8]), and the second from 23 rivers sampled by Cawthron in 2014/15 in a MBIE-funded Cumulative Effects research Programme (CEP) assessing the response of trout populations to stressor gradients. The datasets were tested independently because the NIWA data were collected from medium/large rivers throughout New Zealand by single-pass drift diving, whereas the Cawthron data were collected mainly from smaller rivers by multi-pass electro-fishing (see Table 2). The CEP sampling method allowed populations in the study reaches to be accurately estimated by the depletion method (Carle & Strub 1978; Ogle 2016), whereas the NIWA sampling method allowed estimation of only relative abundance, with unknown reach-specific error in the proportion of the population seen by divers.

The fish density and biomass estimates were based on sampling of one reach per river for the 100 rivers data set and one reach for the CEP data. The benthic invertebrate metrics/indices from the 100 rivers study were based on one pooled sample (from 7 Surber samples) from runs in one reach per river. The invertebrate indices from the CEP study were based on one pooled sample (from 3 Surber samples) from runs in one reach per river.

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[8] See NZ Journal of Marine and Freshwater Research special issue '100 rivers' 24(3) 1990. It should be noted that 43 of a total of 88 rivers sampled by NIWA contained paired invertebrate-trout data. However, we found a discrepancy in the invertebrate abundance data supplied to us—apparently due to some taxa being lost from the dataset provided to us (J Quinn, pers. comm.). To account for this when calculating our invertebrate indices, we excluded any rivers for which the discrepancy between our calculated abundances (based on the sum abundances of individual taxa) and the site sum provided in the '100 rivers' dataset differed by more than 5%. This reduced the final sample size down to 37 rivers. We assumed that discrepancies less than 5% would at worst be due to only one taxon missing from the '100 rivers' dataset, which we deemed acceptable error for the data analysis.

Table 2. Mean annual and mean annual low flow (MALF) ranges for rivers in the NIWA '100 rivers' and Cawthron Cumulative Effects Programme datasets.

	Mean (m^3/s)	**MALF (m^3/s)**
'100 rivers'	1.29 – 90.81	0.45 – 21.55
CEP [a]	0.27 – 10.53	0.05 – 1.47

[a] The rivers in the CEP dataset did not have flow gauging stations on them so the mean flow and MALF ranges were predictions from catchment precipitation–flow models (Booker & Woods 2014).

We first assessed the correlative performance of the TPI traits individually to trout biomass. For each trait we calculated a TPI and QTPI 'community trait' score using the TPI and site QTPI equations shown in Section 3.3 (i.e. these community TPI and QTPI scores were based on single-trait scores instead of the individual taxon scores that are calculated from the trait scores combined). We hypothesised the following for the various prey traits being tested:

- The likelihood of a prey being detected and captured will positively correlate with trout biomass.
- Taxon (maximum) length will positively correlate with trout biomass, because adult trout prefer large invertebrates for energetic profitability. We expected this trait to have the strongest correlation with trout biomass.
- Prey movement in the drift and on the benthos will positively correlate with trout biomass, because movement enhances prey detection and triggers predation response by trout.
- Emergence via drifting will positively correlate with fish biomass.
- The digestibility trait would be weakly correlated with trout biomass relative to prey length, prey size being the main determinant of energy value to trout. The digestibility feature is unlikely to directly influence a trout's decision to intercept and capture an invertebrate prey item.

We then calculated and compared the performance of the community TPIs (i.e. based on taxon TPI scores) with those of existing macroinvertebrate metrics/indices in correlating with trout biomass. We hypothesised that the TPIs will positively correlate with trout biomass, because they are based on traits that render invertebrates vulnerable to trout predation. In comparison, we hypothesised that the MCI and EPT-taxa indices will negatively correlate with trout biomass because trout biomass initially increases with nitrogen concentration (Jonsson et al. 2011; Denne et al. 2013) and invertebrate biomass (subsidy response) whereas MCI and proportion of EPT taxa fall steeply as nitrogen concentration increases (Wagenhoff et al. 2017).

Finally, we used regression analysis to investigate further the relationship between trout biomass and invertebrate metrics/indices that showed potential for explaining variation in fish biomass. All analyses were undertaken with R (R Core Team 2017, version 3.4.1). Correlation between trout biomass and the various invertebrate traits, indices and metrics was again examined with the Spearman rank correlation test. Definitions of acronyms representing the various traits, indices and metrics are provided in Table 3. Regression analyses were undertaken to determine the proportion of variation in fish biomass explained by the invertebrate trait, index or metric shown in Table 3. Variables were square-root transformed before undertaking the regression if they did not meet the requirements for normality and homogeneity of variance.

Table 3. Definition of the predictor variables used in the invertebrate trait/index/metric–fish biomass analyses.

Invertebrate prey traits	
Length	Maximum taxon length (mm)
Digestibility	Index of the proportion of an invertebrate's body composed of indigestible chiton or calcium carbonate
LikelihoodDrift_DF	Likelihood of entering drift, and being detected and captured (drift-feeding)
Movement_DF	Movement capability in drift (drift-feeding)
Emergence_DF	Emergence via drift (drift-feeding)
LikelihoodSubs_BB	Likelihood of being detected on substrate and captured (benthic-browsing)
Movement_BB	Movement capability on substrate (benthic-browsing)
TPI taxon scores	
Taxon_DF	Taxon scores for drift-feeding (based on multiplication of prey trait categories)
Taxon_BB	Taxon scores for benthic-browsing (based on multiplication of prey trait categories)
Taxon_combined	Taxon scores for general TPI (average of taxon drift-feeding and benthic-browsing scores)
Invertebrate indices/metrics	
InvertB	Invertebrate Biomass (mg/m^2)
InvertD	Invertebrate Density (no./m^2)
TPI_DF	Trout Prey Index (drift-feeding)
QTPI_DF	Quantitative Trout Prey Index(drift-feeding)
TPI_BB	Trout Prey Index (benthic-browsing)
QTPI_BB	Quantitative Trout Prey Index (benthic-browsing)
TPI_combined	Trout Prey Index (drift-feeding and benthic-browsing combined)
QTPI_combined	Quantitative Trout Prey Index (drift-feeding and benthic-browsing combined)
MCI	Macroinvertebrate Community Index
QMCI	Quantitative Macroinvertebrate Community Index
pEPT_taxa	Percentage of EPT taxa (by taxa)
pEPT_density	Percentage of EPT taxa (by density)
sEPT_taxa	Sum of EPT taxa (by taxa)
sEPT_density	Sum of EPT taxa (by density) (no./m^2)
DFS	Drift Feeding Score (Matheson et al. 2016)
BBS	Benthic Browsing Score (Matheson et al. 2016)
DC	Drift Count (Matheson et al. 2016)
BC	Benthic Count (Matheson et al. 2016)
Trout metrics	
TroutB	Trout Biomass (g/m^2)

5.1. Correlation of prey traits with trout biomass

TPI and QTPI scores for each prey trait were tested for correlation with trout biomass in the ‘100 rivers’ and CEP datasets (Table 4). Generally, the traits showed either a weak (*r* < 0.3) or very weak (*r* < 0.1) positive, or negative relationship with fish biomass in both datasets (Table 4). Of the traits which were positively related to trout biomass in the ‘100 rivers’ dataset, the strongest (but non-significant) correlation coefficients were obtained for taxon movement on the benthos (Movement_BB) (for the TPI but not QTPI) and emergence via the drift (Emergence_DF) (for the QTPI but not TPI). The strongest (but non-significant) positive correlation coefficients obtained for the CEP dataset were for taxon length and movement in the drift (Movement_DF) for the TPI but not QTPI (Table 4).

Table 4. Spearman’s rank correlation coefficients for the relationship between trout biomass for the ‘100 rivers’ and CEP datasets and invertebrate biomass and density and TPI (presence/absence) and QTPI (relative abundance) prey trait scores. Significant correlation coefficients (*P*<0.05) are italicised and shaded grey. See Table 3 for acronyms.

	“100 Rivers” dataset		**CEP dataset**	
	Correlation coefficient	***P* value**	**Correlation coefficient**	***P* value**
InvertB	*0.61*	*< 0.001*	0.12	0.585
InvertD	*0.49*	*0.002*	0.05	0.821
TPI prey traits				
Length	0.04	0.799	0.20	0.353
Digestibility	0.02	0.914	0.13	0.559
LikelihoodDrift_DF	-0.03	0.859	0.12	0.598
Movement_DF	-0.19	0.270	0.21	0.336
Emergence_DF	-0.12	0.468	0.01	0.983
LikelihoodSubs_BB	-0.09	0.615	0.02	0.936
Movement_BB	0.21	0.213	0.03	0.883
QTPI prey traits				
Length	-0.11	0.537	-0.10	0.650
Digestibility	0.09	0.601	-0.08	0.708
LikelihoodDrift_DF	-0.19	0.259	-0.07	0.746
Movement_DF	<-0.01	0.991	0.05	0.810
Emergence_DF	0.19	0.257	-0.07	0.739
LikelihoodSubs_BB	<-0.01	0.992	-0.01	0.971
Movement_BB	-0.24	0.189	-0.21	0.344

5.2. Correlation of TPI community scores and other invertebrate metrics, with trout biomass

Each invertebrate index/metric was tested for correlation with each other and trout biomass in the '100 rivers' and CEP datasets (Table 5). The correlation matrices of all of the invertebrate indices/metrics tested are displayed in Appendix 4 and 5.

5.2.1. Correlation of TPIs with other indices

In both datasets, the TPIs and QTPIs were generally positively, and often significantly, correlated with the EPT indices, the exception being sEPT_density for the CEP dataset (Appendix 4 and 5). Other significant positive correlations were found between the QTPIs for both drift feeding and benthic browsing and QMCI ('100 rivers' survey). The TPI for benthic browsing was also significantly correlated with invertebrate density ('100 rivers' survey), that but this has little biological relevance for trout other than indicating that biodiversity increased with density (the correlation coefficient for sEPT_taxa versus invertebrate density was also fairly high, but non-significant). The general (combined) TPI correlations reflected most closely those of the drift feeding TPI (Appendix 4 and 5).

The strength and direction of correlations between our TPIs and the Matheson et al. (2016) TPI variants differed between the two datasets. There were several positive significant correlations between our TPIs and QTPIs and the Matheson et al. TPI variants in the '100 rivers', but only two in the CEP dataset. The correlations between our QTPI for drift feeding (QTPI_DF) and Matheson et al.'s TPI variant drift count (DC), and between QTPI combined (QTPI_combined) and DC, were the only significant positive ones in common among both datasets (Appendix 4 and 5).

5.2.2. Correlation between TPIs, and other indices, with fish biomass

In the '100 rivers' dataset, five variables were significantly and positively correlated with trout biomass (Table 5). These were: the invertebrate metrics biomass and density, and the Matheson et al. (2016) TPI variants for drift feeding (DFS and DC) and benthic browsing (BBS) (Table 5). The Matheson et al. TPI variants combine aspects of the quality and quantity of invertebrate prey for trout. Importantly none of the invertebrate indices performed better than invertebrate biomass and density. Furthermore, all the indices that combined elements of prey quality with density reduced the strength of correlation with trout biomass relative to the correlations for invertebrate biomass and density, including: DFS, BBS, DC, BC and sEPT_density. By contrast with the '100 rivers' dataset, none of the invertebrate metrics or indices were significantly correlated with trout biomass in the CEP dataset (Table 5).

The rest of the indices/metrics exhibited either a weak ($r < 0.3$) or very weak ($r < 0.1$) positive or negative correlation with trout biomass in both datasets (Table 5). Of the non-significant, positively correlated indices, TPI_DF, TPI_BB, sEPT_taxa and sEPT_density were the most strongly correlated with trout biomass. These are all indices of the quality of invertebrate taxa for trout prey. All indices which combined prey quality with relative abundance performed more poorly (QTPI, QMCI and pEPT_density) than indices that included only prey quality, or only density/biomass, or both prey quality and density.

Table 5. Spearman's rank correlation coefficients for the correlation between invertebrate metrics and fish biomass in the NIWA '100 rivers and Cawthron CEP datasets. Significant correlations ($p < 0.05$) are italicised and shaded grey. See Table 3 for acronyms.

	'100 Rivers' dataset (*n* = 37)		**CEP dataset (*n* = 23)**	
	Correlation coefficient	***P* value**	**Correlation coefficient**	***P* value**
InvertB	*0.60*	*<0.001*	0.12	0.585
InvertD	*0.49*	*0.002*	0.05	0.821
TPI_DF	-0.06	0.700	0.17	0.427
QTPI_DF	-0.09	0.616	-0.23	0.299
TPI_BB	0.15	0.368	0.30	0.166
QTPI_BB	-0.24	0.150	-0.12	0.556
TPI_combined	0.06	0.709	0.28	0.202
QTPI_combined	-0.17	0.304	-0.20	0.349
MCI	0.08	0.634	0.10	0.654
QMCI	-0.23	0.166	-0.01	0.952
pEPT_taxa	<-0.01	0.997	0.18	0.423
pEPT_density	-0.11	0.499	-0.21	0.339
sEPT_taxa	0.28	0.095	0.23	0.296
sEPT_density	0.23	0.177	-0.06	0.803
DFS	*0.38*	*0.020*	-0.04	0.861
BBS	*0.38*	*0.012*	0.03	0.908
DC	0.15	0.368	-0.13	0.562
BC	*0.42*	*0.010*	0.20	0.353

5.2.3. Relationship between invertebrate metrics/indices and trout biomass

A regression analysis was performed with trout biomass as the response variable and the most highly correlated invertebrate metrics/indices as predictor variables. The best predictors of trout biomass were invertebrate density and biomass (Figure 1). Invertebrate density explained about 20% and invertebrate biomass about 30% of the variation in trout biomass, respectively.

Biomass is not an invertebrate metric that is available in many quantitative datasets owing to the time taken to dry-weigh samples. For this reason, we were interested in determining whether adding a complementary predictor variable to invertebrate density would increase the predictive power over invertebrate density alone and explain an equivalent proportion of variance in trout biomass as invertebrate biomass.

Invertebrate taxon length was one of the prey traits better correlated with trout biomass (although not significant) and we considered it a surrogate of taxon biomass.

Apart from invertebrate length, we undertook regression analyses on no other invertebrate traits (or other indices) because others had either low correlative power, were negatively correlated with trout biomass, or were autocorrelated with density (e.g. the DFS and BBS scores for the '100 rivers' dataset, Table 5).

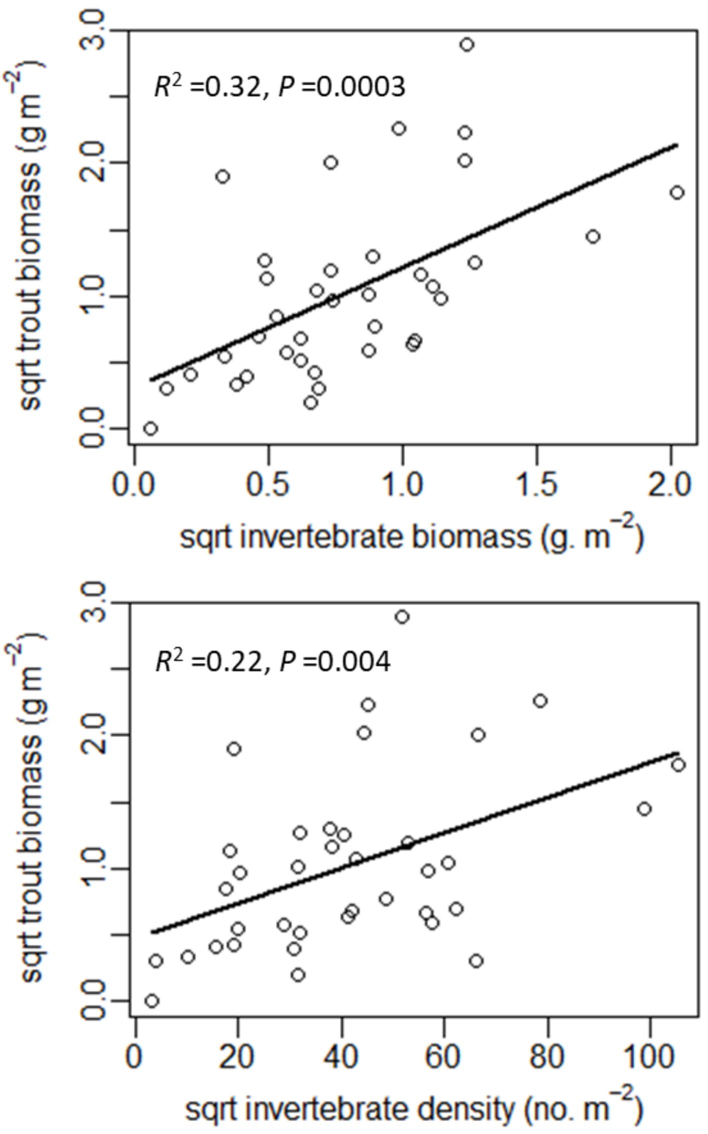

Figure 1. Regression plots of the relationship between trout biomass and two invertebrate metrics—invertebrate density (bottom) and biomass (top). The plots are based on the '100 rivers' dataset (n = 37).

Biomass is the total dry weight (g) of invertebrates per m². Given this, the inclusion of dry weight accounts for the 10% extra predictive power that invertebrate biomass has over density in explaining the variation in trout biomass.

The regression results in Table 6 show that the addition of invertebrate taxon length with abundance did not improve the fit to trout biomass or the proportion of variance explained.

Table 6. Statistical diagnostics for regression models predicting trout biomass from invertebrate density and biomass and density plus taxon length for the ‘100 rivers’ dataset.

Predictors variables	R^2	*P*
sqrtInvertebrate biomass	0.32	0.0003
sqrtInvertebrate density	0.22	0.0036
sqrtInvertebrate density + length (presence/ absence)	0.22	0.0143
sqrtInvertebrate density + length (relative abundance)	0.22	0.0139

6. DISCUSSION

6.1. Partial test of Trout Prey Indices

The results from partial testing of TPIs against trout diet and biomass data do not provide strong support for the utility of TPIs as values-based indicators for trout. We failed to find any significant correlations between TPI scores, or the components of the TPIs, and trout biomass or trout diet. We did find some positive correlations which were encouraging but they were not statistically significant nor generally consistent among test data sets.

Fish biomass is one of the common metrics used to monitor fish populations, especially in a fisheries management context; yet our limited testing indicates that it is not sensitive to aquatic invertebrate community composition, which is a premise of fish prey quality indices. However, fish biomass is affected by many factors other than the composition of the available food resource. Fish diet ought to be more directly linked to invertebrate community composition. The results of our limited test of TPIs on diet data from one moderately-fast flowing river (Maruia River; *n* = 25 fish) were consistent with the trout predominantly drift feeding, taxon scores for drift feeding being consistently higher than those for benthic browsing, but the correlation coefficients were low to moderate strength (0.13–0.22) and not significant (Table 1).

We chose a traits-based approach, based on expert and existing knowledge/data, to develop the TPIs because it was the least expensive option. For the same reason we partially tested the TPIs using existing trout diet and paired invertebrate–trout biomass datasets. However, these shortcuts to development and testing imposed considerable limitations on the accuracy and precision of defining prey preference by trout and on testing TPIs and other indices.

Trout have relatively flexible foraging behaviours to make the best of spatial and temporal variation in the available food resource. Aquatic invertebrates are their staple diet in all inland flowing waters, and they feed predominately on the drifting component in moderately to fast-flowing rivers (Keup 1988; Stolz & Schnell 1991). Trout also take advantage of seasonal abundance of terrestrial invertebrates and small fish prey (native fish and juvenile trout). Moreover, they often exhibit optimal and selective foraging behaviour, the outcome of which is habituation to some prey, usually the most abundant taxa recently available. Foraging strategy (e.g. drift feeding or benthic browsing) and prey preference also varies between individuals, which contributes to strong disparity in the composition of diets in the same river or reach. Moreover, individual trout are not necessarily consistent in their foraging and prey preferences over time. All these factors will contribute to a mis-match between trout diet data and TPI component scores at a broad spatial and temporal scale.

Testing of FPIs and other indices/metrics against fish biomass data is also limited by some of the confounding factors mentioned above and others, especially partial tests such as ours based on limited, existing data sets. A key confounding factor is that fish biomass is the outcome of population processes acting on multiple age classes over temporal and spatial scales much different than those that have acted on the benthic invertebrate community; yet the tests are based on synoptic estimates of fish biomass and benthic invertebrate community structure/density/biomass. In respect to drift feeding in particular, another confounding factor is that drift community composition does not mirror benthic invertebrate composition. Benthic invertebrates have different propensities to drift, by intentional and accidental means. Moreover, the propensity to drift varies with flow and periphyton biomass (Shearer et al. 2003; Hayes et al. 2018). At a broad level drift biomass is correlated with benthic invertebrate biomass, and certain drift prone taxa are more common in the drift (e.g. leptophlebiid mayflies (Shearer et al. 2003; Hayes et al. 2018)), but strong, consistent correspondence between drifting and benthic community structure is unlikely.

Weak relationships between invertebrate community structure indices, trout diet composition and trout biomass are not unexpected given the wide scope for confounding factors, and limited data sets available for testing.

On a comparative basis, TPI component and community scores were more strongly, and more consistently positively, correlated with trout diet composition and trout biomass than those for the QTPI variants. In common with our test results for QMCI (see Section 6.2) expressing invertebrate community structure in terms of relative abundance in TPIs appears to decouple the indices from trout diet and biomass.

Matheson et al.’s (2016) TPI variants performed the best of TPI variants tested. However, they are influenced by invertebrate abundance—but importantly, not by relative abundance. Because they include taxon abundance Matheson et al.’s TPI variants are limited to quantitative samples (e.g. Surber samples). Moreover, they performed more poorly than total community density or biomass, so, for interpreting quantitative invertebrate data in respect of trout, it would be more parsimonious, and informative, to simply focus on total invertebrate density, or better still biomass. The same probably applies to native fish too.

Our traits-based approach to developing TPIs was based on expert knowledge of trout foraging behavior and subjective assessment of trout diet data (e.g. Appendix 3). There is potential to refine TPI scores through more quantitative assessment of trout diet data, especially when paired with benthic and drifting invertebrate data. Rader (1997) used a semi-selectivity analysis approach to develop a scoring system for North American invertebrates based on their propensity to drift and related vulnerability to predation by trout. His approach involved using extensive trout diet data as the foundation for developing his scoring system. In hindsight, a modification of Rader’s approach may be a better option for further development and testing of

FPIs for trout and native fish in New Zealand. Moreover, testing FPIs against fish diet data is likely to be more precise than testing against fish population biomass data, because diet composition is directly linked to prey preference.

Our progress to date provides a useful foundation for further research on FPIs. Two taxon prey traits have been identified as being the most relevant to trout, taxon length and movement—although relationships between even these and trout biomass were not consistent between test data sets and foraging modes (drift feeding versus benthic feeding) (Table 4).

6.2. Partial tests of other invertebrate indices/metrics

Our partial test results also do not provide strong support for the relevance of existing invertebrate community indices to trout, including the MCI, QMCI and some EPT index variants, but they do provide support for the relevance of total benthic invertebrate community density, and especially, biomass.

Other invertebrate indices such MCI and QMCI, EPT (by percent taxa and percent density) were generally poorly and/or negatively correlated with trout biomass. EPT (by sum of taxa or sum density) were the best performing indices, although still not significant (Table 5).

As mentioned at the beginning of Section 5, we expected that the MCI and EPT indices would negatively correlate with trout biomass because the latter increases with nitrogen concentration and invertebrate biomass (subsidy response,) whereas MCI and proportion of EPT taxa fall steeply as nitrogen concentration increases. The recent 2017 amendments to the National Policy Statement for Freshwater Management (NPS-FM, MfE 2014) require regional councils to use the MCI as a monitoring tool. Clapcott et al. (2017), who supported this inclusion, indicated that the MCI is a sensitive indicator of multiple stressor effects on macroinvertebrates resulting from dominant land uses in New Zealand and can be used to distinguish the ecosystem health of streams at a national scale. Clapcott et al. (2017) also cautioned that the MCI is only one indicator and cannot be used to identify specific stressors nor inform catchment and in-stream resource use.

Of the invertebrate metrics we tested, invertebrate biomass and density were the two strongest predictors of fish biomass (at least in the '100 rivers' dataset). The weak correlation between invertebrate density/biomass and trout biomass for the CEP data may be due to differences in connection with the terrestrial landscape between the smaller CEP rivers and the larger '100 rivers' rivers. The trout in the CEP rivers may have had greater access to terrestrial invertebrates and fish prey, weakening the relationship between the aquatic food base and trout biomass (R. Holmes, Cawthon Institute—co-leader of the CEP trout study). Trout diet data were not available to test this hypothesis. The CEP data set was less robust than the ‘100 rivers’ dataset, another factor contributing to the poorer correlation between invertebrate density/biomass and trout biomass. The CEP dataset was less robust on two fronts: invertebrates were collected from an area of 0.3 m^2 for the CEP study compared to 0.7 m^2 in the ‘100 rivers’ study, and the CEP data set included fewer rivers (CEP n = 23 versus ‘100 rivers’ n = 37).

The significant correlations between the TPI and EPT metrics (and MCI and EPT) are not surprising. EPT taxa are known to be generally the most pollution sensitive of the aquatic invertebrates, and therefore score highly for MCI—an index based on the influence of organic pollution on invertebrates. EPT taxa are also important aquatic invertebrate prey for trout (as evidenced in the trout diet studies presented in this report), hence they also score highly in the TPI taxon scores (particularly for drift feeding). However, the correlations between the TPIs and MCI were generally weak. The main reason for the disjunct between TPIs and MCI is because some EPT taxa have a high MCI score but low TPI score e.g. the cased caddis *Olinga* has a high MCI score of 9, but relatively low TPI (drift feeding) score of 0.86. Also, the scoring system that Stark (1985) used resulted in a relatively even distribution of MCI invertebrate taxon scores, with slightly more animals scoring around the middle of the 1-10 scoring range, whereas the distribution of our TPI taxon scores was highly skewed to the left of the 1-10 range.

The difference between Matheson et al.’s (2016) drift feeding and benthic browsing scores and our respective TPIs is that the former include taxon density, whereas our TPI is based on presence absence and our QTPI is based on the relative abundance of taxa. This means the two indices will correlate well when the densities among invertebrate taxa are similar, but not when densities are highly variable—which is the norm.

Based on the data available, and considered in this report, there is no escaping the fact that it is the total invertebrate density/biomass that is the most important food resource factor for trout, and that invertebrate community structure is a secondary, much more minor, consideration. The EPT variants, sEPT_taxa and sEPT_density, also appear to have some utility, although less than total community density and biomass, for interpreting invertebrate community data with respect to trout. The same points may apply to native fish too.

An important caveat is that the above conclusion applies to the range of environmental conditions covered by the test rivers (‘100 rivers’ and CEP data sets, and Maruia River). Rivers in poor environmental condition supporting poor invertebrate species richness but high total biomass (e.g. dominated by worms and chironomids) are unlikely to support high adult trout biomass owing to such invertebrate communities comprising predominately small and unavailable prey.

However, for most New Zealand rivers, water quality parameters (e.g. low dissolved oxygen) are more likely to limit trout than the food supply.

6.3. Future role of invertebrate indices/metrics in a freshwater fisheries context

As mentioned above invertebrate biomass followed by density appear to be the strongest performing metrics/indices for assessments of the effect of changes in invertebrate communities on trout populations. A further limitation is that obtaining invertebrate density and biomass data requires quantitative sampling and traditional processing to estimate biomass, by drying and weighing samples, is time-consuming and results in destruction of the samples. However, the latter limitation can be overcome by estimating lengths of invertebrates during taxonomic processing and predicting biomass from published taxon length–weight relationships. Another advantage of processing invertebrate samples for size is that density and biomass can be size-structured for analysis to detect differences in average size and size structure between sites and sampling occasions. We encourage uptake of size structuring in invertebrate sample processing and analysis for extracting added value for fish impact assessment from invertebrate biomonitoring. However, some testing is required to define the relationship (i.e. error margins) between calculated estimates of biomass, based on size structured samples, and measured biomass.

Stark (1985) developed the MCI with a focus on the relationship between pollution (via nutrient enrichment) and invertebrates. By contrast, in developing our TPIs we have focused on a direct connection between invertebrates and trout i.e. using invertebrate traits that ought to elicit a feeding response and/or maximise net rate of energy intake. For traditional invertebrate indices, such as MCI, QMCI and EPT, and TPI variants, interpretation of what they are telling us requires consideration of many environmental factors that may be acting on the invertebrate communities prior to, and during, sampling (e.g. antecedent flows, periphyton and invertebrate community and biomass dynamics, temperature, degree of sedimentation, etc.)[9].

With further research, FPIs may be able to be advanced sufficiently to complement existing indices/metrics and allow better interpretation of invertebrate community data in respect of relevance to trout and other fish. Further research would need to be extensive, and include:

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[9] Relevant information on some of these environmental factors is relatively easy to collect, but can be overlooked when the invertebrate samples are collected by staff who are unaware of the context or purpose of the research or monitoring. An investigator then has to fall back on their own knowledge, or the memory of the field staff to provide context for interpretation of the behaviour of invertebrate indices. However, comprehensive effort in recording relevant environmental data will be unaffordable in many monitoring and effects assessment programmes.

- collection of concurrent invertebrate benthic, drift and trout diet data replicated in space and time
- revision of expert-derived prey taxon traits in light of more extensive testing on fish diet data than done for this report
- development of taxon prey traits based on quantitative selectivity analysis of fish diet (using paired fish diet and benthic and drifting invertebrate data).

In summary, our results support the use of aquatic invertebrate biomass (or abundance) as invertebrate indicators of trout biomass, whereas invertebrate metrics based on taxa presence–absence and/or relative community composition (such as the MCI and QMCI) appear to be unrelated to trout biomass. Our results do not support the utility of MCI and QMCI as ecosystem health indices relevant to trout. Of the existing invertebrate taxonomic composition indices, sEPT_taxa and sEPT_density appear most relevant to trout.

7. TROUT PREY INDICES: GENERAL QUERIES FROM REGIONAL COUNCILS

This section in the report was included to provide answers to questions that arose from a regional council workshop (held by MfE in Wellington on 22June 2018) where an outline of the TPI research to be undertaken for this report was presented.

Question: the relationship between benthic invertebrates and invertebrate drift is complex and difficult to define as it is dependent on environmental condition in a river (antecedent flow, algae biomass, competition for space/food). How then can we possibly expect an FPI calculated from benthic invertebrate data to have any meaning for drift-feeding fish?
Answer: It is true that antecedent flow and nutrient (and other environmental) conditions will affect benthic invertebrate community structure and biomass and all that will affect food intake by trout (by drift feeding and benthic feeding) and trout growth and population biomass. However, with respect to biomonitoring, and the frequency at which it is undertaken, benthic invertebrate data capture the outcome of those antecedent conditions. If relationships between benthic invertebrate metrics/indices and drift metrics/indices can be established, then these provide the link to drift feeding fish and adds value to routine benthic invertebrate biomonitoring. At a broad level benthos and drift are related. Significant relationships between total benthic invertebrate biomass and drift biomass have been reported in the literature (Weber et al. 2017).

Question: Piscivory and terrestrial food sources are also important components of fish (trout) diet that the TPIs do not account for. Why exclude them from the development of a prey index?
Answer: We partly address this point in Section 6.1. Benthic and drifting invertebrates are staple food resources in inland rivers. Fish prey are mainly important close to the coast, a result of the high contribution of diadromous species to the New Zealand freshwater fish fauna. Terrestrial invertebrates are seasonally available, but are not relevant for interpreting instream effects on fish.

8. CONCLUSIONS

Our results do not provide strong support for the utility of TPIs as values-based indicators for trout. We did not find any significant correlations between TPI scores, or the components of the TPIs, and trout biomass or trout diet. We did find some positive correlations which were encouraging but they were not statistically significant nor generally consistent among test data sets. However, our partial testing was limited by available datasets.

Our results also do not provide support for the relevance of existing invertebrate community indices to trout, including the MCI, QMCI and EPT index variants based on proportion. However, our results do provide support for the relevance of total benthic invertebrate community density, and especially, biomass to trout. The sum of EPT taxa and density appear to have some utility, although less than total community density and biomass.

Our progress to date provides a useful foundation for further research on FPIs. There is potential to refine TPI scores through more quantitative assessment of trout diet data, especially when paired with benthic and drifting invertebrate data.

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11. APPENDICES

Appendix 1. Invertebrate traits taken into consideration for developing drift-feeding and benthic-browsing individual invertebrate taxon prey scores.

Drift feeding traits				
Likelihood of entering drift and being detected and captured	**Maximum size (mm)**	**Invertebrate movement in drift**	**Emergence pathway**	**Relative proportion of digestible material**
0 = no - don't occur in water column or on surface	0 = ≤3	1 = low/feeble movement	1 = no - doesn't emerge through the water column	1 = low level of digestabiliy
1 = low - occasionally in water column or on surface	1 = >3 - ≤6	2 = low/med	2 = yes - does emerge through water column	2 = low/med
2 = low/med	2 = >6 - ≤9	3 = med		3 = medium
3 = med	3 = >9 - ≤12	4 = med/high		4 = med/high
4 = med/high	4 = >12 - ≤15	5 = active swimmers or erratic wriggler		5 = high level of digestabiliy
5 = high = often in water column or on water surface	5 = >15 - ≤18			
	6 = >18 - ≤21			
	7 = >21 - ≤24			
	8 = >24 - ≤27			
	9 = >27 - ≤30			
	10 = >30			

Benthic feeding traits			
Likelihood of being detected on substrate and captured	**Maximum size (mm)**	**Invertebrate movement on substrate**	**Relative proportion of digestible material**
0 = no - mainly not on substrate	0 = ≤3	1 = fast crawlers and swimmers	1 = low level of digestabiliy
1 = occasionally on substrate	1 = >3 - ≤6	2 = slow crawler/wriggler/glider	2 = low/med
2 = often on substrate	2 = >6 - ≤9	3 = medium crawler/wriggler	3 = medium
	3 = >9 - ≤12		4 = med/high
	4 = >12 - ≤15		5 = high level of digestabiliy
	5 = >15 - ≤18		
	6 = >18 - ≤21		
	7 = >21 - ≤24		
	8 = >24 - ≤27		
	9 = >27 - ≤30		
	10 = >30		

Appendix 2. List of adult Trout Prey Index (TPI) taxon prey scores (normalised and scaled) determined for drift-feeding (DF) and benthic browsing (BB) foraging strategies. The scores range from 0 (lowest value prey item) to 10 (highest value prey item).

Taxon	TPI_DF	TPI_BB
Ephemeroptera (mayflies)		
Acanthophlebia	4.29	1.60
Ameletopsis	5.71	2.13
Arachnocolus	2.86	1.07
Atalophlebioides	2.86	1.07
Austroclima	4.29	1.60
Austronella	2.86	1.07
Coloburiscus	2.57	2.40
Deleatidium	5.71	2.13
Ichthybotus	2.14	2.67
Isothraulus	2.86	1.07
Leptophlebiidae	4.29	1.60
Mauiulus	2.86	1.07
Neozephlebia	2.86	1.07
Nesameletus	5.71	2.13
Oniscigaster	5.36	2.00
Rallidens	5.71	2.13
Siphlaenigma	4.29	1.60
Tepakia	2.86	1.07
Zephlebia	5.71	2.13
Plecoptera (stoneflies)		
Acroperla	1.29	2.40
Austroperla	1.29	2.40
Cristaperla	0.64	1.20
Megaleptoperla	1.61	3.00
Spaniocerca	0.64	1.20
Stenoperla	2.25	4.20
Taraperla	1.29	2.40
Zelandobius	0.64	1.20
Zelandoperla	1.29	2.40
Trichoptera (caddisflies)		
Alloecentrella	0.64	0.80
Hydropsyche - Aoteapsyche	3.21	2.67
Beraeoptera	0.21	0.27
Confluens	0.43	0.53
Costachorema	10.00	7.00
Diplectrona	3.21	2.67
Edpercivalia	10.00	7.00
Helicopsyche	0.10	0.00
Hudsonema	1.71	2.13
Hydrobiosella	5.71	4.00
Hydrobiosidae	7.14	5.00
Hydrobiosis	8.57	6.00
Hydrochorema	4.29	3.00
Hydropsychidae	3.21	2.67
Hydroptilidae	0.00	0.00
Leptoceridae	1.07	1.33
Neurochorema	4.29	3.00
Oecetis	0.43	0.53
Oeconesus	1.07	1.33
Olinga	0.86	1.07
Hydropsyche - Orthopsyche	3.21	2.67
Oxyethira	0.00	0.00
Paroxyethira	0.00	0.00
Philorheithrus	1.07	1.33
Plectrocnemia	5.71	4.00
Polyplectropus	7.14	5.00
Psilochorema	4.29	3.00
Trichoptera (caddisflies)		
Pycnocentrella	0.64	0.80
Pycnocentria	0.86	1.07
Pycnocentrodes	0.64	0.80
Synchorema	4.29	3.00
Tiphobiosis	4.29	3.00
Triplectides	1.50	1.87
Triplectidina	0.64	0.80
Zelandopsyche	1.07	1.33
Zelandoptila	0.57	0.40
Zelolessica	0.43	0.53
Coleoptera (beetles)		
Antiporus (A)	0.29	0.60
Antiporus (L)	0.32	4.80
Berosus (A)	0.11	0.60
Berosus (L)	0.86	3.20
Elmidae (A)	0.32	0.60
Elmidae (L)	0.64	2.40
Enochrus (A)	0.11	0.60
Enochrus (L)	0.21	3.20
Homolaena	0.00	0.00
Hydora (A)	0.32	0.60
Hydora (L)	0.64	2.40
Hydraenidae (A)	0.00	0.00
Hydrophilidae (A)	0.32	1.20
Hydrophilidae (L)	0.32	4.80
Hyphydrus (A)	0.21	0.60
Hyphydrus (L)	0.21	3.20
Liodessus (A)	0.21	0.60
Liodessus (L)	0.11	1.60
Orchymontia	0.00	0.00
Ptilodactylidae (L)	0.86	4.80
Rhantus (A)	0.64	1.80
Rhantus (L)	0.32	4.80
Scirtidae (L)	0.43	2.40
Diptera (flies)		
Anthomyiidae	2.14	1.33
Aphrophila	3.21	2.00
Austrosimulium	0.54	1.33
Blephariceridae	0.21	0.80
?Brachydeutera	1.07	0.67
Ceratopogonidae	2.41	1.00
Chironomidae	1.43	0.67
Chironomini	1.43	0.67
Chironomus	2.14	2.00
Corynoneura	1.43	0.67
Cricotopus	1.43	0.67
Culex	1.61	0.67
Culicidae	1.61	0.67
Diamesinae	2.86	0.67
Dixidae	1.61	0.67
Dolichopodidae	1.07	0.67
Empididae	0.54	0.33
Ephydrella	1.07	0.67
Ephydridae	1.07	0.67
Eriopterini	3.21	1.33
Eukiefериella	1.43	0.67
Harrisius	1.43	0.67

Appendix 2 continued.

Taxon	TPI_DF	TPI_BB	Taxon	TPI_DF	TPI_BB
Diptera (flies)			**Megaloptera (dobsonflies)**		
Hexatomini	3.21	1.33	*Archichauliodes*	5.36	10.00
Limonia	1.61	1.00	**Mecoptera (scorpionflies)**		
Lobodiamesa	2.86	0.67	Nannochoristidae	1.79	3.33
Maoridiamesa	2.86	0.67	**Neuroptera (lacewings)**		
Mischoderus	2.68	1.67	Osmylidae	0.00	3.20
Molophilus	1.61	1.00	Sisyra	0.00	0.00
Muscidae	2.14	1.33	**Lepidoptera (moths)**		
Naonella	1.43	0.67	*Hygraula*	0.00	2.00
Neocurupira	0.21	0.80	**Crustacea (crustaceans)**		
Neolimnia	2.14	1.33	Amphipoda	0.05	0.60
Neoscatella	1.07	0.67	*Chiltonia*	0.05	0.60
Nothodixa	1.61	0.67	Cladocera	0.07	0.00
Orthocladiinae	1.43	0.67	Copepoda	0.00	0.00
Paradixa	1.61	0.67	Ostracoda	0.00	0.00
Paralimnophila	1.61	1.00	*Paracalliope*	0.05	0.60
Parochlus	1.43	0.67	*Paranephrops*	0.00	2.00
Paucispinigera	1.43	0.67	*Paratya*	0.00	1.60
Pelecorhynchidae	2.41	2.00	*Tanais*	0.05	0.00
Peritheates	0.21	0.80	**Mollusca (snails, limpets, bivalves)**		
Pirara	1.43	0.67	*Austropeplea*	0.05	0.80
Podonominae	1.43	0.67	*Glyptophysa* (formerly *Physastra*)	0.09	1.33
Polypedilum	1.43	0.67	*Gundlachia* (formerly *Ferrissia*)	0.00	0.00
Psychodidae	0.54	0.33	*Gyraulus*	0.02	0.27
Scatella	1.07	0.67	*Hydridella/Echyridella*	0.00	0.00
Sciomyzidae	2.14	1.33	*Latia*	0.00	0.53
Simuliidae	0.54	1.33	Lymnaeidae	0.18	2.67
Stictocladius	1.43	0.67	*Melanopsis*	0.00	2.40
Stratiomyidae	2.57	1.60	*Physa/Physella*	0.04	0.53
Tabanidae	4.82	6.00	*Potamopyrgus*	0.02	0.27
Tanyderidae	2.68	1.67	Sphaeriidae	0.00	0.00
Tanypodinae	1.43	0.33	**Hirudinea (leeches)**	0.00	2.00
Tanytarsini	1.43	0.67	**Nematoda (roundworms)**	0.80	0.00
Zelandotipula	4.82	3.00	**Nematomorpha (horse-hair worm)**	1.61	5.33
Hemiptera (bugs)			**Nemertea (proboscis worms)**	0.27	0.00
Anisops	0.21	0.00	**Oligochaeta (worms)**	0.94	0.00
Hydrometra	0.11	0.00	**Platyhelminthes (flatworms)**	0.27	1.00
Mesoveliidae	0.00	0.00	**Polychaeta (bristle worms)**	1.34	0.00
Microvelia	0.00	0.00	**Cnidaria (hydra)**		
Saldula	0.11	0.00	Hydra	0.00	0.00
Sigara	0.21	0.00	**Acarina (mites)**	0.00	0.00
Odonata (dragonflies, damselflies)			**Arachnida (spiders)**		
Aeschnidae	0.00	8.00	*Dolomedes*	0.67	0.00
Antipodochlora	0.00	5.60	**Collembola (springtails)**	0.00	0.00
Austrolestes	0.32	3.60			
Hemicordulia	0.00	4.80			
Ischnura	0.21	2.40			
Procordulia	0.00	5.60			
Uropetala	0.00	8.00			
Xanthocnemis	0.27	3.00			

Appendix 3. Trout diet data from six rivers collected by Cawthron (unpublished data) and from the Mataura River (Witherow & Scott 1984). "–" indicates taxon not found in diet. Grey and black shading = taxon found in diet, black also indicates the taxon was very common in the diet. NR = not recorded

	Cawthron unpublished data						**Witherow and Scott (1984)**					
	South Island					**North Island**	**Mataura River system (South Island)**					
Taxon	**Ettrick Burn**	**Pomahaka**	**Waikaia**	**Maruia**	**Travers**	**Rangitikei**	**Otamita**	**Reids**	**Tophams**	**Crumps**	**Shands**	**Russel**
Ephemeroptera												
Ameletopsis	-	-	-	░	-	-	-	-	-	-	-	-
Austroclima	-	-	-	░	░	░	-	-	-	-	-	-
Deleatidium	█	█	█	█	█	█	█	█	█	█	█	█
Coloburiscus	-	░	░	░	-	░	-	-	░	-	-	░
Nesameletus	-	-	░	░	-	░	░	░	░	░	-	-
Zephlebia	-	-	-	-	-	-	░	░	░	░	░	░
Plecoptera	-	-	-	-	-	-	-	-	-	-	-	-
Austroperla	░	-	░	-	-	░	-	-	-	-	-	-
Megaloptera	-	░	░	-	-	-	-	-	-	-	-	-
Stenoperla	░	-	░	░	-	-	-	-	-	-	-	-
Zelandobius	-	-	░	-	-	-	-	-	-	-	-	-
Zelandoperla	░	-	░	░	░	░	-	-	-	-	-	-
Trichoptera												
Aoteapsyche	-	█	░	░	-	-	░	░	░	░	█	░
Beraeoptera	-	-	-	░	-	-	░	░	░	░	░	-
Confluens	-	-	░	█	-	-	-	-	-	-	-	-
Costachorema	░	░	-	░	░	░	-	-	-	-	-	-
Helicopsyche	-	-	-	░	-	-	-	-	-	-	-	-
Hudsonema	-	█	░	░	-	-	░	░	░	-	░	░
Hydrobiosella	░	-	-	-	-	-	-	-	-	-	-	-
Hydrobiosis	░	░	░	█	░	░	░	░	░	░	░	░
Hydrochorema	░	-	-	-	-	-	-	-	-	-	-	-
Neurochorema	-	▒	-	█	-	-	-	-	-	-	-	-
Olinga	-	█	█	░	░	-	░	█	░	░	░	░
Oxyethira	-	-	-	-	-	-	-	-	-	░	-	░
Philorheithrus	-	-	-	░	-	-	-	-	-	-	-	-
Plectrocnemia	░	-	-	░	-	░	-	-	-	-	-	-
Polyplectropus	-	-	░	-	-	-	-	-	-	-	-	-
Psilochorema	-	░	░	█	░	░	-	-	-	-	-	-
Pycnocentria	-	█	█	░	-	-	█	█	█	░	░	░
Pycnocentrodes	-	█	░	█	-	-	░	░	█	░	░	░
Synchorema	░	-	-	-	-	-	-	-	-	-	-	-
Triplectides	-	░	-	░	-	-	-	░	-	-	-	-

Appendix 3 continued…

	Cawthron unpublished data						Witherow and Scott (1984)					
	South Island					North Island	Mataura River system (South Island)					
Taxon	**Ettrick Burn**	**Pomahaka**	**Waikaia**	**Maruia**	**Travers**	**Rangitikei**	**Otamita**	**Reids**	**Tophams**	**Crumps**	**Shands**	**Russel**
Diptera												
Anthomyiidae	-	-	▒	-	-	-	-	-	-	-	-	-
Austrosimulium	-	-	-	-	-	-	▒	▒	▒	▒	-	▒
Maoridiamesa	-	▒	-	▒	-	-	-	-	-	-	-	-
Neocurupira	-	-	-	▒	-	-	-	-	-	-	-	-
Chironomidae	-	-	-	-	-	-	▒	▒	▒	▒	▒	■
Hexatomini	-		▒	-	-	-	-	-	-	-	-	-
Orthocladiinae	▒	▒	-	▒	-	-	-	-	-	-	-	-
Tanyderidae	▒	-	▒	▒	-	-	-	-	-	-	-	-
Tanypodinae	-	-	▒	-	-	-	-	-	-	-	-	-
Tanytarsus	-	-	-	▒	-	-	-	-	-	-	-	-
Zelandotipula	-	▒	▒	-	-	-	-	-	-	-	-	-
Odonata	-	▒	-	-	-	-	-	-	-	-	-	-
Uropetala	-	-	-	▒	-	-	-	-	-	-	-	-
Megloptera												
Archichauliodes	-	-	▒	▒	▒	-	-	-	-	-	-	-
Neuroptera	-	▒	▒	-	-	-	-	-	-	-	-	-
Coloeptera												
Antiporus	-	▒	-	-	-	-	-	-	-	-	-	-
Elmidae	▒	■	▒	-	-	-	▒	▒	▒	▒	▒	▒
Scirtidae	-	-	▒		-	-	-	-	-	-	-	-
Hemiptera												
Anisops	-	-	▒	-	-	-	-	-	-	-	-	-
Corixidae	-	-	▒	-	-	-	-	-	-	-	-	-
Sigara	-	▒	▒	-	-	-	-	▒	▒	-	▒	-
Mollusca												
Physa	-	■	-	-	-	-	▒	▒	▒	▒	▒	▒
Potamopyrgus	-	■	▒	-	-	-	▒	▒	▒	▒	▒	■
Planorbarius	-	-	-	-	-	-	-	-	-	-	-	▒
Sphaeriidae	-	-	■	-	-	-	-	-	▒	▒	-	▒

Appendix 3 continued…

	Cawthron unpublished data						**Witherow and Scott (1984)**					
	South Island					**North Island**	**Mataura River system (South Island)**					
Taxon	**Ettrick Burn**	**Pomahaka**	**Waikaia**	**Maruia**	**Travers**	**Rangitikei**	**Otamita**	**Reids**	**Tophams**	**Crumps**	**Shands**	**Russel**
Crustacea												
Amphipoda	-	-	▨	-	-	-	-	-	-	-	-	-
Paracalliope	-	-	-	-	-	-	■	▨	▨	▨	▨	▨
Cladocera	-	-	-	-	-	-	-	-	▨	-	-	▨
Oastracoda	-	-	-	-	-	-	-	-	-	-	-	▨
Paranephrops	-	▨ (claws)	-	-	-	-	-	-	-	-	-	-
Nematomorpha	▨	-	▨	▨	-	-	-	-	-	-	-	-
Oligochaeta	-	-	-	-	-	-	▨	▨	▨	▨	▨	▨
Number of stomachs	3	42	16	25	8	1	35	72	62	53	69	68
Fish size range (mm)	315-550	260-730	192-620	350-635	540-650	NR	NR	NR	NR	NR	NR	NR

Appendix 4. Spearman's rank correlation coefficients for correlation between invertebrate indices/metrics and trout biomass for the '100 rivers' dataset. Significant differences ($p < 0.05$) are italicised and shaded grey. See Table 3 for acronyms.

	TroutB	InvertB	InvertD	MCI	QMCI	pEPT_ taxa	pEPT_ density	sEPT_ taxa	sEPT_ density	TPI_ DF	QTPI_ DF	TPI_ BB	QTPI_ BB	TPI_ combined	QTPI_ combined	DFS	BBS	DC
InvertB	*0.61*																	
InvertD	*0.49*	*0.69*																
MCI	0.08	0.06	0.10															
QMCI	-0.23	-0.07	0.09	*0.38*														
pEPT_taxa	0.00	0.07	-0.01	*0.74*	0.27													
pEPT_density	-0.11	0.04	0.04	*0.44*	*0.79*	*0.38*												
sEPT_taxa	0.28	*0.33*	0.28	*0.75*	0.30	*0.73*	0.38											
sEPT_density	0.23	*0.44*	*0.61*	*0.56*	*0.63*	*0.42*	*0.68*	*0.60*										
TPI_DF	-0.07	-0.13	0.00	0.18	0.09	*0.35*	0.24	0.14	0.17									
QTPI_DF	-0.09	-0.08	-0.09	0.29	*0.66*	0.27	*0.74*	0.24	*0.42*	*0.44*								
TPI_BB	0.15	0.16	*0.34*	0.30	0.17	0.25	0.25	0.32	*0.43*	*0.80*	*0.38*							
QTPI_BB	-0.24	-0.15	-0.10	0.19	*0.70*	0.15	*0.49*	0.15	*0.36*	0.04	*0.55*	0.05						
TPI_combined	0.06	0.03	0.19	0.25	0.12	0.31	0.24	0.24	0.32	*0.94*	*0.41*	*0.94*	0.03					
QTPI_combined	-0.17	-0.14	-0.12	0.27	*0.75*	0.23	*0.74*	0.19	*0.42*	*0.34*	*0.95*	0.28	*0.75*	0.31				
DFS	*0.38*	*0.53*	*0.82*	*0.42*	*0.36*	0.26	*0.36*	*0.50*	*0.80*	0.22	*0.33*	*0.55*	0.19	*0.40*	0.28			
BBS	*0.38*	*0.63*	*0.90*	0.31	*0.34*	0.20	0.29	*0.42*	*0.81*	0.05	0.14	*0.40*	0.21	0.24	0.15	*0.93*		
DC	0.15	*0.34*	*0.58*	*0.52*	*0.67*	*0.36*	*0.65*	*0.53*	*0.91*	0.26	*0.58*	*0.50*	*0.49*	*0.39*	*0.60*	*0.84*	*0.78*	
BC	*0.42*	*0.54*	*0.48*	0.10	-0.06	0.09	0.05	*0.44*	*0.38*	*0.33*	0.07	*0.58*	-0.18	*0.48*	-0.04	*0.48*	*0.42*	*0.33*

Appendix 5. Spearman’s rank correlation coefficients for correlation between invertebrate indices/metrics and trout biomass for the Cawthron CEP rivers dataset. Significant differences ($p < 0.05$) are italicised and shaded grey. See Table 3 for acronyms.

	TroutB	InvertB	InvertD	MCI	QMCI	pEPT_taxa	pEPT_density	sEPT_taxa	sEPT_density	TPI_DF	QTPI_DF	TPI_BB	QTPI_BB	TPI_combined	QTPI_combined	DFS	BBS	DC
InvertB	0.12																	
InvertD	0.05	*0.68*																
MCI	0.10	-0.33	-0.25															
QMCI	-0.01	-0.29	-0.27	*0.47*														
pEPT_taxa	0.18	-0.09	-0.26	*0.76*	0.32													
pEPT_density	-0.21	-0.14	-0.15	0.39	*0.61*	0.41												
sEPT_taxa	0.23	-0.06	0.06	*0.77*	0.17	*0.64*	0.19											
sEPT_density	-0.06	*0.45*	*0.62*	0.15	0.18	0.13	*0.54*	0.25										
TPI_DF	0.17	-0.26	-0.27	0.34	-0.25	*0.44*	0.01	*0.44*	-0.10									
QTPI_DF	-0.23	-0.21	*-0.42*	0.21	0.20	0.35	0.32	0.13	0.00	*0.42*								
TPI_BB	0.30	-0.29	-0.30	0.39	-0.10	0.29	0.05	*0.50*	-0.12	*0.79*	0.16							
QTPI_BB	-0.13	-0.27	*-0.42*	0.37	0.27	0.38	0.38	0.28	0.04	*0.50*	*0.88*	0.26						
TPI_combined	0.28	-0.26	-0.31	0.39	-0.22	*0.44*	-0.02	*0.50*	-0.15	*0.95*	0.31	*0.92*	0.37					
QTPI_combined	-0.20	-0.23	*-0.45*	0.26	0.21	0.33	0.33	0.17	-0.01	*0.47*	*0.97*	0.21	*0.96*	0.34				
DFS	-0.04	*0.49*	*0.75*	-0.08	-0.17	-0.05	0.04	0.22	*0.75*	0.08	0.18	-0.10	0.14	-0.03	0.16			
BBS	0.03	*0.63*	*0.89*	-0.19	-0.27	-0.22	-0.10	0.09	*0.63*	-0.12	-0.07	-0.28	-0.05	-0.22	-0.07	*0.87*		
DC	-0.13	0.04	0.31	0.16	0.30	0.20	0.32	0.19	*0.59*	0.15	*0.53*	-0.03	0.38	0.06	*0.43*	*0.70*	*0.46*	
BC	0.20	0.30	*0.42*	0.18	-0.25	0.14	-0.01	*0.55*	*0.53*	0.38	0.14	0.26	0.31	0.31	0.23	*0.72*	*0.56*	0.31