A LITERATURE REVIEW TO SUPPORT A LIMITING FACTOR ANALYSIS FOR STREAM BROWN TROUT POPULATIONS
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1. INTRODUCTION

In this document we provide a literature review to underpin a Bayesian Belief Network-based (BBN) limiting factor analysis (LFA) for stream brown trout fisheries. This document is not intended to be a stand-alone report. A detailed background, methodology and an example application of the BBN to the Horokiri Stream (Wellington, New Zealand) can be found in Holmes et al. (in review). For context, the methods section of that manuscript (included here as Appendix 1) should be read prior to reading the present document. A copy of the Netica BBN files (version 5.23, norsyes.com) are available from the lead author on request.

As well as supporting the BBN LFA, this literature review may also be useful for a variety of salmonid management applications. For example, it would allow determining environmental attribute limits that provide for the maintenance of brown trout fisheries in streams.

The literature review is structured as follows. For each potential limiting factor within the BBN we:

1. briefly explain why it was included (or excluded) from the BBN
2. list the key environmental-correlate nodes (parent nodes) that comprise the relevant sub-network branch of the BBN
3. suggest the form of data that should be used to populate the relevant parent nodes
4. explain how we determined environmental variable category-breakpoints for the relevant parent nodes
5. detail how the values in the conditional probability tables were determined for each limiting-factor child node.

Our suggestions for the data requirements to populate the BBN parent nodes are not intended to be fully prescriptive. Pre-existing data, collected using different protocols, may be useful if they are reinterpreted with respect to our input data suggestions. However, identical data collection methodologies should be used if comparing limiting-factor probabilities over time or between sites.

A table provided in Appendix 2 summarises our literature review. Based on our review, the key limiting factors that we chose to include in the BBN are shown in Table 1. Appendix 3 shows the Netica BBN structure.
Table 1. Key limiting factors for brown trout (*Salmo trutta*) in New Zealand wadeable lowland streams and their binary logic statement codes used in the BBN. Factors are ranked in a hypothetical order according to their likelihood of limiting trout production in a ‘typical’ New Zealand stream. Rankings are based on our interpretation of the literature.

<table>
<thead>
<tr>
<th>Key factors that limit stream brown trout fisheries</th>
<th>Binary logic statement codes used within the BBN</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Temperature</td>
<td>Too hot</td>
</tr>
<tr>
<td>2. Flow (flood flows, low flows)</td>
<td>Flood-limited, Low-flow-limited</td>
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</tbody>
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1.1. Temperature (‘Too hot’ limiting-factor child node)

The distribution of trout and the productivity of stream fisheries is determined by water temperature regimes, both within and between catchments (Jowett 1990; Hayes et al. 2000; Armstrong et al. 2003; Elliott & Elliott 2010). For example, in lowland New Zealand, the northern extent of brown trout occurrence is limited by high summer water temperatures (Scott & Poynter 1991). Accordingly, consideration of a stream’s temperature regime, in particular the upper temperature ranges that fish may experience, is a critical component of any LFA for a trout fishery.

To maintain simplicity within the BBN, we chose not to include a limiting-factor node to account for temperatures below optima for brown trout. The productivity of practically all brown trout streams is limited by low water temperatures during winter and spring-low temperatures (e.g. < 10°C), which maintain trout metabolic rates below optima for processing food. Lower-range temperatures are largely determined by latitude, altitude, topography, ground-surface water dynamics, stream channel aspect and riparian vegetation (Poole & Berman 2001). Other than riparian vegetation removal, which generally results in undesirable ecosystem outcomes (Slevers et al. 2017), there are no practical management levers to address these variables.

1.1.1. Parent node(s) and input data

The too-hot limiting-factor node has one immediate parent node that requires long-term stream temperature data to populate. Since the advent of inexpensive, continuous-temperature loggers, temperature is now a simple variable to measure within a river segment. We suggest using long-term stream-segment temperature
data, covering for example, at least five years of continuous records synthesised from 15-minute interval data. Various thermal regime summary metrics can be calculated from these data.

Davies-Colley et al. (2013) reviewed the ecosystem effects of temperature in New Zealand streams as part of the National Objectives Framework (NOF) initiative (MFE 2014). The NOF initiative is tasked with setting management objectives based on environmental attribute limits that maintain the ‘life supporting capacity’ of freshwater ecosystems. Davies-Colley et al. proposed that the Cox-Rutherford index calculated by:

\[
\frac{\text{Annual max temperature} + \text{mean temperature of the five hottest days of the year}}{2}
\]

was the most appropriate and ecologically relevant temperature summary statistic to define a river temperature ‘attribute’. It indicates sustained annual upper temperatures over a period of days. Consequently, this index is suited to indicate temperature conditions that may induce nonlethal effects on aquatic biota (e.g. modified behaviour). We chose the Cox-Rutherford index to inform our too-hot limiting-factor node based on Davies-Colley et al.’s rationale, and to align our model with data sets that are being generated to inform the NOF.

### 1.1.2. Data input categories

Brown trout can metabolise food at temperatures between 3.8 and 21.7°C (Elliott 1994; Elliott et al. 1995). However, food availability (both quantity and quality) dictate the optimum temperatures for growth. Trout experimentally fed on maximum invertebrate rations exhibit optimum growth rate at around 14°C. When feeding on a more energy-dense fish diet (such as smelt), the optimum temperature for growth is around 17°C. At temperatures above 17°C growth potential declines rapidly, and temperatures above 23°C cause chronic stress. Acute mortality occurs when temperature exceeds 27°C (Elliott 1994; Elliott & Hurley 1999). Based on these temperature thresholds, Cox-Rutherford index values below about 19°C would present a low risk of behavioural disturbance in trout for substantial periods of the year. Maximum Cox-Rutherford index values in the range 19–24°C would be tolerable but metabolism would be impaired and feeding behaviour would be disturbed (Elliott 1994).

The temperature attribute ‘bands’ recommended by Davies-Colley et al. (2013) for the NOF were largely set with reference to rainbow trout thermal tolerance values. These values are equivalent to the thresholds that cause behavioural disturbance or mortality for brown trout. Therefore, we chose the draft NOF stream temperature bands (> 19, 19–24, 24–27, > 27°C) to define the category breakpoints for the single too-hot limiting-factor parent node in our BBN. In addition, proposed breakpoint are also supported by initial analysis of data from the Cumulative Effects Programme (CEP) survey streams (see Appendix 1 for an explanation of these data), where juvenile trout
(< 200 mm) density (and biomass) showed a strong correlation with the Cox-Rutherford Index across relevant stream temperature bands.

1.2. Flow

Within rivers, flow is considered the ‘master variable’ because it is inextricably linked to all instream variables and processes (Poff et al. 1997). Fundamentally, a river’s flow regime, in combination with topography, defines the amount of space for fish (Jowett & Richardson 1989; Jowett 1997). Flow also dictates the rate of energy flux (organic sediment, debris and invertebrates) through a reach (Fausch 1984; Hayes et al. 2016; Naman et al. 2016). Simplistically, there are three key aspects of a flow regime that are relevant to trout habitat and invertebrate food supply. These include low flows for space, flushing flows to control algae and fine sediment and flood flows to define channel morphology (Jowett & Richardson 1989; Jowett et al. 2008; Crow et al. 2013; Fuller et al. 2013). Of particular relevance to our LFA are flood flows and extreme low flows which can be considered to represent disturbance events for a trout population.

1.3. Flood-limited node

Large floods displace and kill trout. Juvenile life history stages are particularly vulnerable (Harvey 1987; Strange et al. 1993; Hayes 1995; Holmes et al. 2013; George et al. 2015), although substantial floods can also severely impact adult trout populations (Allen 1951; Jowett & Richardson 1989; Young et al. 2001). The productivity of many fisheries in New Zealand rivers is likely to be limited by frequent flooding (Jowett 1990; Jowett & Duncan 1990). Nevertheless, it is hard to disentangle the direct effects of floods on trout populations from other potential limiting factors that are also linked to flooding. For instance, food resources may be poor in flood-prone rivers because invertebrate densities are low as a result of regular disturbance of stream substratum (Clausen & Biggs 1997; Matthei et al. 1999; Melo et al. 2003; Effenberger et al. 2006; Olsen et al. 2013). Moreover, some populations of juvenile trout appear remarkably resilient in their response to floods. For example, a juvenile trout population in the Rainy River (Nelson, New Zealand) achieved typical densities eight months after a channel-defining flood with a 1-in-50 year return period that severely reduced autumn abundance of young-of-the-year. This was a result of density-dependent loss to the yearling stage (Hayes et al. 2010).

Stream slope and the structural complexity of habitat interact with stream discharge to determine the power of floods to displace or kill fish. High-gradient streams concentrate flows and have intense flushing power. Conversely, in low-gradient streams, high flows dissipate over a wider channel cross section, reducing near-bed velocity and the potential for disturbance to trout populations and their food base.
(Jowett 1990; Poff et al. 1997). Structurally complex habitats (e.g., bedrock-lined pools) provide more diverse water velocities during floods and are refuges from high currents, flood debris and entrained sediment. Velocity refugia probably contribute to the resistance of trout populations to floods if extensively available in a stream (Penaluna et al. 2015).

1.3.1. Parent node(s) and input data

The ‘flood-limited’ child node has three parent input nodes: (1) flood-frequency, (2) segment-slope and (3) fish-cover (Appendix 2).

We used the mean annual frequency of flows that exceed 10 times the median flow (FRE10) as the index to represent the flood-frequency node. The FRE10 is commonly used to indicate flow stability. Clausen and Biggs (1997) showed that in most rivers a FRE10 event was enough to disturb a substantial portion of the substrate. Therefore, flows above this magnitude also have to potential to displace or kill trout, especially juveniles. Segment slope can be surveyed directly or estimated from the proximate segment(s) of interest from spatial mapping data bases; for instance, in New Zealand the River Environment Classification (REC) data base has modelled slope data for all stream segments (Snelder et al. 2004).

To approximate the degree of structural complexity within in a stream segment, we linked the fish-cover-limited node to the flood-limited node. The fish-cover-limited node is described in a subsequent section of this document (Section 1.9). It rates the probability-of-occurrence of structural fish security cover (e.g. woody debris), which is equivalent to flood refugia within a stream segment.

1.3.2. Data input categories

We determined category breakpoints for the flood-frequency node by quantile classification of the average frequency of FRE10 events within the CEP survey streams (see Appendix 1 for an explanation of these data). For the segment-slope node, we based the category breakpoints on inflection points in the empirical model by Kozel et al. (1989). This model showed that trout biomass is negatively correlated with stream segment slope. The fish-cover-limited node, which we assume substitutes for flood-refuge habitat, was linked to the flood-limited node as a continuous variable (i.e. with no category breakpoints). We weighted the parent nodes flood-frequency and segment-slope twice that of the fish-cover-limited node before calculating the conditional probabilities for the flood-limited node. We did this because we consider that the former two variables have an overriding influence on the ability for a population to resist floods relative to reach-scale flood-refuge features.
1.4. Flow variability (low-flow-limited)

Low flows, either naturally occurring or exacerbated by water abstraction, affect fish populations first through indirect mechanisms before directly limiting abundance through restricting space (Armstrong et al. 2003; Harvey et al. 2006). The potential consequences of a low-flow event include reduced food availability (resulting from diminished quantity and quality of benthic invertebrate habitat and invertebrate drift), or poor water quality because of increased temperatures and reduced dissolved oxygen concentrations (Armstrong et al. 2003). Stressful conditions for fish that occur during annually reoccurring low-flow events are accounted for in other parts of the BBN. This is because we require that input data for the fish cover- (including depths), food- and water quality-limitation sub-network nodes are collected during flows near the 7-day mean annual low flow (7d-MALF). However, extreme low flows (i.e. droughts) can be considered disturbance events in their own right (Crow et al. 2013). Droughts can depress a trout population so that in subsequent years, with higher base-flows, available resources will be underutilised (Armstrong et al. 2003; Harvey et al. 2006; Leprieur et al. 2006; Strange et al. 1993).

Channel morphology interacts with low flow to determine the degree of stress fish populations experience. Adverse effects of drought will be ameliorated when stream morphology is such that deep refuge habitats are available at low flow—provided that water quality is adequate (e.g. Jowett & Richardson 1989).

1.4.1. Parent node(s) and input data

The low-flow-limited child node has two parent nodes: (1) the coefficient of flow variation (flow-CV) and (2) the percentage of water deeper than 1 m at base flow (%-depth > 1 m).

We did not chose an absolute measure of low flow. We needed a transferable flow metric that indicates if a fish population is likely to be prevented from fully utilising habitat at typical flows because of a space squeeze occurring during extreme low flows. Habitat availability indices estimated with hydraulic-habitat models (Armour & Taylor 1991) would be informative, but we rejected this approach because it is too resource-demanding to be included in our LFA framework. Instead we opted for a measure of overall flow variability.

There are many potential indicators of flow variability for streams, all of which are highly correlated. We chose the coefficient of flow variation because it can be easily calculated from long-term flow statistics (e.g. > 10-year data sets).

We included a requirement to estimate the percentage of water depths > 1 m at flows close to the 7d-MALF. Water depths over a metre can be considered suitable refuge habitat for large brown trout (DeVore & White 1978; Raleigh et al. 1986; Bjornn &
Reiser 1991). Depths should be estimated within three randomly selected 100-m reaches within a target segment. Rapid-field-survey protocols for obtaining stream depth estimates can be found in Holmes & Hayes (2011), and an example application is provided in Holmes et al. (2016).

1.4.2. Data input categories

In general, rivers with a flow CV of < 1 can be considered to have a relatively stable flow regime, with a high proportion of base flow, whereas those with a flow CV of > 3 have highly variable flow regimes (MFE 1998; Jowett & Duncan 1990). We used these CV breakpoints to define the three categories (< 1, 1–3 and > 3) for the flow-CV parent node.

We determined three categories (< 10%, 10–50%, > 50%) to define the %-depth greater than 1 m node by visually identifying breakpoints within the frequency distribution of the depth data from the CEP streams. The lower depth category gives a crude estimation of the lower range of the percentage of ‘deep water’ available at MALF in New Zealand lowland wadeable trout streams (represented by the CEP data). Both the flow-CV and %-depth greater than 1 m nodes were weighted equally to calculate the conditional probabilities for the low-flow-limited child node.

1.5. Juvenile recruitment

Any LFA for a fishery must consider the supply of recruits. Within our BBN, recruitment is defined as the supply of juvenile trout less than three years of age. This incorporates the spawning, fry and juvenile rearing life history stages (briefly explained below).

Brown trout construct redds in coarse gravels and small cobbles in which to incubate their eggs. These are usually located in the tails of pools and the edges of runs where the bed slopes upward in the direction of the current. In these areas, downwelling forces oxygen-rich water through the gravels (Louhi et al. 2008). Fry require relatively slow water usually along the bank edges. Stream edge vegetation helps creates pockets of slow water and can produce good salmonid fry rearing habitat (Heggenes et al. 1999; Armstrong et al. 2003; Bardonnet et al. 2006). Juvenile trout tend to occupy cobble-boulder riffles and runs with a diverse range of velocity microhabitats (Armstrong et al. 2003). Commonly, spawning and juvenile rearing habitat may be located tens of kilometres upstream of lowland-stream segments in relatively low-gradient headwaters. Headwaters are less impacted by land use pressures, and critically, embryo incubation temperatures are more likely to remain below 10°C (Jowett 1990).
Recruitment of trout populations to a given stream segment depends on the amount of spawning and rearing habitat relative to the amount of adult habitat within the catchment. In addition, recruitment can be highly variable from year to year, even in streams where there is ample spawning and rearing habitat. Floods, particularly during the critical fry emergence period in early spring, are a common cause of poor recruitment years in rivers (Ottaway & Forrest 1983; Hayes 1995; Jensen & Johnsen 1999). If successive annual floods occur during fry emergence, this could create a negative feedback loop where recruitment is further reduced because of low numbers of returning adult spawners. On the other hand, the presence of a lake or large wetland in a catchment will ameliorate the negative effects of floods on recruitment (Jowett 1990). These provide productive refuge habitats for displaced trout and dampen the power of floods downstream.

### 1.5.1. Parent node(s) and input data

The recruitment-limited node has four parent nodes: (1) a subjective assessment of the adequacy of spawning and rearing habitat (rearing-habitat node), (2) floods during the fry emergence period (spring-floods), (3) maximum winter temperature in spawning areas (max-winter-temp) and (4) the presence (or absence) of a lake below rearing areas.

Knowledge of the adequacy of recruitment within a catchment will vary widely between fishery management staff or fishery researchers and catchments depending on staff experience and the availability of fish population data. To ensure the qualitative assessment component required to populate the rearing-habitat node is as robust as possible, as many independent assessments as feasible should be undertaken, with the results assessed for variation (see Marcot et al. 2006 and McDonald et al. 2015 for guidelines for incorporating expert assessments into BBNs). If there is inadequate knowledge available to populate this node, then when defining the BBN node settings, it should be held neutral and set to ‘OK’ to remove its influence on subsequent probability calculations within the BBN.

We chose to incorporate a parent node that represents the average occurrence of successive flood events in the spawning areas through August and September (New Zealand late winter–early spring). This node (spring-floods) accounts for floods during the critical fry emergence period. To populate the spring-floods node, we used the rolling-average number of spring FRE10 events within each three-year period of a flow record (ideally at least nine years). To account for the potential for lethal high temperatures during embryo incubation (i.e. in excess of 10°C), we included the max-winter-temp node. Finally, we included a parent node for the presence or absence of a substantial lake or wetland (e.g. > 10 hectares) within the catchment—to account for the positive effect that lakes or wetlands can have on trout survival (Appendix 1).
1.5.2. Data input categories

In any subjective assessment of spawning and rearing potential in a catchment, there is a large degree of inherent uncertainty. Accordingly, we used just three broad categories (good, OK and poor) to define the rearing-habitat node. The three categories that define the spring-floods node were based on the reasoning that if spring floods occurred annually throughout a cohort’s three-year life cycle this would result in very poor recruitment. This is because trout typically mature within 3 years in New Zealand streams (McDowall 1990). If spring floods occurred twice or ≤ once every three years, this would provide for adequate or good recruitment, respectively (all other factors held equal). We used two categories, < 10°C or ≥ 10°C during June, July or August to define the breakpoint for the max-winter-temp node. To define the node that represents the presence (or absence) of a lake or wetland below rearing areas in the catchment we used binary categories for the presence or absence of a lake or wetland in the system.

We weighted the parent nodes spring-floods, rearing-habitat, max-winter-temp and the ‘presence of a lake/wetland’ at 1, 0.5, 0.5 and 0.5, respectively, before calculating conditional probabilities. This reflects our opinion, backed by the literature cited above, that the occurrence of spring floods will be the dominant factor in determining recruitment potential in most catchments.

1.6. Food

Brown trout display varied feeding strategies to match their environment. Broadly, feeding strategies can be categorised into drift feeding (on aquatic and terrestrial invertebrates), benthic browsing and piscivory (Budy et al. 2013; Piccolo et al. 2014; Milardi et al. 2016). To some extent, food availability limits the production of trout in all wild fisheries. Taken to the extreme, this point is illustrated by the high biomass and large size of salmonids attainable in commercial trout farms that use energy-dense food (Piccolo et al. 2014). As a practical definition for our LFA, we consider food limitation as a food level that leads to growth rates below what can be achieved under maximum invertebrate rations, given typical temperature regimes in New Zealand rivers. Potential growth rate can be estimated with trout growth models (e.g. Elliott et al. 1995; Elliott & Hurley 1999, 2000; and also Hayes et al. 2000; Hayes 2013, which include Elliott’s equations).

If prey fish are plentiful and easy to obtain, they will be the preferred diet of trout (McCarter 1986; Keeley & Grant 2001). Trout feeding on fish diet can grow three times faster than on an invertebrate diet (Elliott & Hurley 2000) and therefore can obtain greater size and reproductive potential. Forage fish (including juvenile trout) are available as potential prey for larger trout in most rivers. However, in small wadeable streams, prey fish are assumed to be less important as food in comparison with
stream invertebrates because of their abundance and ease of capture (e.g. Bachman 1984; Kelly-Quinn & Bracken 1990; Cunjak & Power 1987; McLennan & MacMillan 1984; Glova & Sagar 1991). In New Zealand streams, opportunities for trout to exploit fish prey will increase closer to the coast because of the prevalence of diadromy in the native fish fauna. Diadromous, pelagic fish species, such as inanga (*Galaxias maculatus*) and common smelt (*Retropinnidae*), can be especially abundant, at least seasonally (McDowall 1990). In stream segments that are near to the coast, piscivory may compensate for poor invertebrate food resources.

Drift feeding on invertebrates is a common feeding strategy for stream trout (Hayes & Jowett 1994; Fausch et al. 1997). Drift-feeding trout conserve energy by holding station in ‘slow’ water whilst intercepting drifting invertebrates from adjacent fast water (Fausch 1984). With the potential exception of some heavily forested streams where terrestrial invertebrates can be important, benthic stream invertebrates are the primary food base that supports drift feeding. Jowett (1990) showed that benthic invertebrate density is strongly correlated with trout abundance in New Zealand rivers. In addition, Weber et al. (2014) found that steelhead (anadromous rainbow trout) consumption rates were correlated with total drift biomass in tributaries of the Columbia River, Oregon. The density of benthic invertebrates over 3 mm indicates the availability of invertebrate food for medium to large fish (i.e. > 200 mm) (Wankowski 1979; Hayes et al. 2000; Shearer et al. 2003).

If current speeds are too slow to support drift feeding, trout will browse for benthic invertebrates by picking them directly off the substratum, usually in pools or slow-flowing runs (Jonsson & Jonsson 2011). These habitats may be heavily silted and macrophytes, snails and chironomids can be abundant (Shupryt & Stelzer 2009). However, relative to drift feeding, benthic browsing is thought to be substantially less energy-efficient (Harvey & Railsback 2014). For example, Fausch et al. (1997) showed that numbers of Dolly Varden (*Salvelinus malma*) reduced by half (through emigration) when they were forced to benthic browse in a drift-blockage experiment in a natural stream.

We chose not to include a node that accounts for terrestrial-derived food for trout, because terrestrial insects provide only a small contribution to overall production in typical New Zealand lowland stream trout populations (McLennan & MacMillan 1984; Glova & Sagar 1991, Edwards & Huryn 1996). For example, Edwards & Huryn (1995) showed that terrestrial invertebrates contributed as little as 5% to annual brown trout production in a relatively unmodified native grassland-pasture catchment.

Temperature plays an important role in determining if a fishery is limited by food. As discussed in the temperature limitation section above, energy requirements increase exponentially as temperatures increase above 14°C. Therefore, if food quantity was held equal, trout populations in warmer streams are more likely to be limited by food.
Trout density is another major factor influencing the likelihood of a trout population being limited by food availability (Railsback & Harvey 2011). If a trout population is limited by recruitment, there is less chance that food availability will limit growth and abundance because there will be less pressure on available food resources. In contrast, at high population densities interspecific competition limits production. This has been demonstrated by numerous authors who reported density-dependent growth or loss rates in juvenile trout populations (e.g. Crisp 1993; Hayes 1995; Jenkins et al. 1999; Grant & Imre 2005; Lobón-Cerviá et al. 2011).

1.6.1. Parent node(s) and input data

We chose five parent nodes to inform the food-limited node. These include: (1) the probability of forage fish presence (prey-fish node), (2) the density of benthic invertebrates (invertebrate-density node), (3) drift-feeding-opportunity node (which required a separate BBN sub-network), (4) the too-hot-limiting-factor node and (5) the recruitment-limited node.

Leathwick et al. (2005) modelled diadromous fish distributions for stream and river segments based on presence-absence data from the extensive New Zealand freshwater fish data base. Leathwick et al.’s species probability-of-occurrence values can be considered a surrogate for abundance because both the likelihood of occurrence and abundance will be related to the strongest environmental predictors in the distribution model. These include distance from the sea, stream size, flow variation and summer temperatures. To maintain simplicity within our BBN, we have limited the prey-fish node to the likelihood of inanga and smelt being present in the stream segment of interest—based on Leathwick et al.’s model predictions. These two common pelagic fish are more vulnerable to trout predation than cryptic, obligate benthic species such as common bullies.

To account for the potential for drift feeding we created a ‘drift feeding opportunity metric’. This metric required its own BBN sub-network, the specifications for which are detailed in the next section. For the invertebrate-density node, we opted to use benthic invertebrate density data obtained using the Stark et al. (2001) quantitative Surber sampling method. To account for the synergistic effect of high temperatures on food limitation, we linked the too-hot-limiting-factor node to the food-limited node. Likewise, to account for the negative effect of high fish densities on food availability we linked the recruitment- and food-limited nodes.

1.6.2. Data input categories

We suggest using the highest probability-of-occurrence for smelt or inanga predicted with Leathwick et al.’s (2015) model (for the nearest REC segment to the LFA segment of interest) to inform the prey-fish node. Within the BBN, this node was defined as a continuous variable (i.e. no category breakpoints). To define the three
categories within the invertebrate-density node, we used quantile classification of the Quinn and Hickey (1990) invertebrate data. We linked the drift-feeding-opportunity, too-hot and recruitment-limited nodes to the food-limited node as continuous variables.

To determine the conditional probabilities, we weighted the too-hot, recruitment-limited, prey-fish, drift-feeding-opportunity and invertebrate-density nodes 1, 1, 0.5, 0.5, and 0.5, respectively. We consider that high temperatures and high trout densities have an overriding positive influence on the probability that a trout population is limited by food relative to the other environmental-parent nodes.

1.7. Drift feeding opportunity

The opportunity for trout to drift feed in streams depends on invertebrate density and community composition. In general Ephemeroptera, Plecoptera and Trichoptera (EPT) taxa are larger and more prone to drift than other invertebrates. In particular, the mayfly Deleatidium spp. is common in the diets of drift-feeding New Zealand trout (Glova & Sagar 1991; McLennan & MacMillan 1984). Consequently, an invertebrate community with a high relative abundance of ETP taxa is thought to be more likely to support drift feeding (Shearer et al. 2003).

Identifying prey items in the drift is a cognitively demanding task for drift-feeding salmonids and the presence of algal fragments and other debris in the water column decrease feeding efficiency (O’Brien & Showalter 1993; Neuswanger et al. 2014). In addition, thick algal mats may make invertebrates less prone to enter the drift (Shearer et al. 2003; Jellyman & Harding 2016). Therefore, the presence of thick benthic algal mats should be considered when assessing drift-feeding potential.

As well as the biological factors influencing drift-feeding opportunity, water velocity and clarity factors also need to be considered. These factors required a separate sub-network to define which is described in the next section.

1.7.1. Parent node(s) and input data

Three parent nodes inform the drift-feeding-opportunity node including: (1) percentage abundance of EPT taxa (%EPT-abundance), (2) percentage algal cover (%-algal-cover) and (3) the physical-drift-feeding-conditions (which required its own BBN sub-network to calculate).

The %EPT taxa abundance index is commonly used to indicate stream ecosystem health (Stark et al. 2001). As such, it is routine to extract this information from quantitative invertebrate data. A version of the %EPT taxa abundance index that excludes percentage abundance of hydroptilid caddisflies is more relevant for
assessing invertebrate food potential for trout because it reduces the influence of small taxa (Collier 2009). A single benthic invertebrate sampling occasion following a stable flow period (of at least two weeks) during summer should be adequate to inform the %EPT-abundance node (Stark et al. 2001). However, the average values from longer-term invertebrate monitoring (e.g. 5 years of annual, summer sampling) would be preferable. We suggest visually estimating the combined percentage cover of filamentous algae and algal mats (> 3 mm) within a stream reach to inform the %-algal-cover node. This should be done after a stable flow period (of two weeks or more) during mid-late summer (Biggs & Kilroy 2000).

1.7.2. Data input categories

To determine the three categories that define the %EPT-abundance node, we visually assessed the frequency distribution of Quinn and Hickey’s (1990), data for break points. These invertebrate data were collected as part of the 100 rivers survey (Jowett 1990). To define the binary categories for the %-algal-cover node, we chose < 35% or ≥ 35 % composite algal mat (> 3 mm thick) and filamentous algal cover. Matheson et al. (2016) recommends 35% composite algal mat cover as a maximum cover limit to protect trout habitat values in New Zealand rivers. We linked the physical-drift-feeding-conditions node (described below) to the drift-feeding-opportunity node as a continuous variable.

To determine conditional probabilities, we weighted the physical-drift-feeding-conditions and %EPT-abundance nodes twice that of the %-algal-cover node. This was to account for the relatively strong influence of physical variables and the food-base on drift feeding potential relative to the indirect effects of benthic algae on drift food quality and quantity. In addition, in most streams, nuisance algal growths occur only intermittently following extended periods of stable flow (Biggs et al. 1998).

1.8. Physical drift feeding conditions

Drift feeding by trout is dependent on local current velocities that can keep invertebrates in suspension and deliver a high rate of drift. On the other hand, velocities must be moderate enough to constrain fish swimming costs within ranges that return a net-positive energy intake rate. The ‘sweet spot’ velocity range occurs because although drift flux through a cross-sectional foraging area increases with velocity, the foraging area contracts, prey capture success declines and swimming costs increase exponentially (Hill & Grossman 1993; Grossman et al. 2002).

Invertebrate production occurs mainly in riffles and shallow runs (Keup 1988; Jowett & Richardson 1989; Brown & Brussock 1991) and pools offer deeper water in which adult trout can feed and find cover (Keup 1988; Baran et al. 1997; Heggenes et al. 1999; Armstrong et al. 2003). The transition zone between riffle or a fast run and pool
(or a slow run) are preferred drift-feeding locations for trout, because they are close to the source of incoming drift and trout can find suitable feeding locations over the strong depth and velocity gradients. Therefore, the more riffle-pool sequences within a stream segment, the better the balance between food production and feeding areas for trout. The United States Environmental Protection Agency (USEPA) habitat assessment protocol for salmonids suggests that an ideal riffle to pool ratio is 1:1 (Barbour et al. 1999). This rule-of-thumb is thought to represent the ideal balance of adult trout habitat in the pools with food-producing and juvenile rearing habitat in the riffles.

Water clarity must also be sufficient for trout to see items in the drift. The maximum reaction distance for drift-feeding fish to detect prey is strongly affected by water clarity/turbidity (Sweka & Hartman 2001; Barrett et al. 1992; Hayes et al. 2016). When drift feeding, trout need enough time to react and intercept a prey item before it is carried downstream of their position (Hughes & Dill 1990; Railsback et al. 2009).

1.8.1. Parent node(s) and input data

The physical-variable drift feeding metric node has two parent nodes: (1) the relative percentage of riffles and/or fast runs to pools and/or slow runs (%-riffle-area) and (2) base-flow-turbidity.

The riffle and/or fast run: pool and/or slow run ratio for a river segment can be calculated mesohabitat mapping data. This should be collected following visual estimate protocols (e.g. Barbour et al. 1999). These estimates should be undertaken throughout the stream segment of interest during flows that are close to the 7d-MALF. The riffle-fast run to pool-slow run ratio metric will approximate velocity diversity and the frequency of steep velocity gradients within a stream segment. These are areas that provide drift-feeding opportunities for trout of a range of year classes. We accept that defining fast runs and slow runs can be ambiguous. However, Barbour et al. (1999) provide good narrative descriptions which are adequate for segment scale assessments.

Long-term average turbidity (NTU) values of monthly base-flow (e.g. at least a 2-year record) are sufficient to inform the data requirements of the base-flow-turbidity node. Base-flow NTU spot measurements are taken at most regional authorities’ routine stream monitoring locations in New Zealand.

1.8.2. Data input categories

We defined the binary categories for the %-riffle-area node as within or outside a 30-70% riffle or fast run-area range. This range includes the riffle or fast run to pool ratio or slow run ratio of 1:1 which is presumed to be optimum for small stream salmonids (Barbour et al. 1999). We deliberately chose a broad range of percentage
riffle or fast run areas to account for other factors that may influence the optimum amount of riffle (in relation to drift-feeding potential), such as the presence of instream structures creating patch-scale velocity gradients (Wheaton et al. 2017).

The prey reaction distance of drift-feeding salmonids reduces exponentially with increasing NTU values, reaching an asymptote at about 5 NTU (Gregory & Northcote 1993; Hayes et al. 2000; Railsback et al. 2009). We chose to interpret this continuous relationship according to the following three categories of NTU < 1, 1-5, > 5, as providing good, OK and poor water clarity for drift feeding, respectively. These NTU thresholds equate to approximate horizontal black-disk visual clarity readings of > 1.2 m, 1.2-0.8 m and < 0.8 m respectively—based on the NTU-visual range relationship presented in Davies-Colley & Close (1990).

1.9. **Fish cover**

Security cover is an essential component of fish habitat (Raleigh et al. 1986; Allouche 2002; Kratzer and Warren 2013). Any feature of a stream that obscures the bed from view can be considered fish cover. Common cover features include deep water (e.g. > 1 m), macrophytes, bedrock, boulders and large, loose cobbles, undercut banks, overhanging vegetation and woody debris. Consequently, the presence and amounts of these features are often included in standard stream and salmonid habitat assessment protocols (e.g. Barbour et al. 1999).

1.9.1. **Parent nodes and input data**

The fish-cover limiting-factor node has five parent nodes, (1) the percentage of water deeper than 1 m at base flow (%-depth > 1 m), (2) %-overhanging-vegetation, (3) %-undercut-banks, (4) %-macrophyte-cover and (5) %-woody-debris and/or boulders.

With the exception of percentage depth data, we suggest that the input data for all of the cover features should be based on visual estimates of percentage aerial cover within three 100-m stream reaches randomly located within a stream segment of interest (Holmes et al. 2011). The percent estimates of water deeper than 1 m can be obtained through a combination of depth measurements and visual estimates following the protocol detailed in Holmes & Hayes (2011). Estimates should be undertaken during summer low-flows.

1.9.2. **Data input categories**

The %-woody-debris and/or boulder node has two categories to represent the presence or absence of a substantial amount of wood or boulder cover in a reach. To distinguish between the two categories, we chose the nominal breakpoint of < 5% or ≥ 5% of the wetted area of a stream segment. For the other fish-cover parent nodes,
we assigned three broad categories that were defined by visually assessing the frequency distributions of habitat survey data from the CEP streams for breakpoints.

We weighted the cover features %-deep-water, %-woody-debris or boulders, %-undercut-banks, %-overhanging-vegetation and %-macrophytes 1, 0.75, 0.75, 0.5 and 0.25, respectively, before calculating conditional probabilities. We assigned these weights by the ranked time-scale over which the cover features persist within a stream. We have assumed that relatively permanent cover features (e.g. undercut banks) are of more value to fish than features that can vary seasonally (e.g. macrophytes).

1.10. Water quality

Physicochemical water quality variables have the potential to limit trout production directly through physiological effects, or indirectly by altering ecosystem processes (e.g. high nitrate levels encouraging algal growth and causing subsequent changes in the invertebrate food web) (Quinn 2000). This section deals with direct effects of water quality on trout. Indirect effects on the food base are accounted for in separate sub-network branches of the BBN.

Trout need relatively good water quality to thrive in streams, particularly during the juvenile life history stages. Their temperature and dissolved oxygen (DO) requirements are well defined (Jonsson & Jonsson 2009). Nonetheless, determining the potential for adverse water quality effects is complicated by the fact that water quality variables interact in non-additive ways to create more (or less) stressful conditions for biota (ANZECC 2000).

We focused on basic water quality parameters that we consider most likely to limit trout production in New Zealand lowland streams. These include temperature, DO, pH and nitrate-nitrogen (NO\textsubscript{3}-N). In lowland macrophyte-dominated streams, DO and pH can fluctuate severely (Burrell et al. 2013), which can result in stressful condition for trout (Davies-Colley et al. 2013). Nitrate-nitrogen (NO\textsubscript{3}-N) is a pervasive non-point source pollutant in catchments dominated by intensive agriculture (Quinn 2000). Adult trout are relatively insensitive to NO\textsubscript{3}-N, however, levels present in some agricultural catchments may induce chronic effects on early life-history-stage rainbow trout. To our knowledge, there is no research available to determine NO\textsubscript{3}-N levels that could induce chronic effects brown trout eggs or alevins (Burdon & Taylor 2000).

Suspended sediment (SS) can also directly stress trout, for example by clogging gill membranes (Railsback et al. 2009). However, behavioural effects (e.g. impaired drift-feeding ability) can be expected to occur for salmonids at low suspended sediment levels relative to the levels required to cause acute effects (i.e. < 5 NTU vs. > 20 NTU) (Davies-Colley et al. 2015). Therefore, we did not include a SS node in the water quality BBN sub-net. Nevertheless, we do address the indirect effect of SS (using
turbidity as a surrogate) on feeding efficiency in the drift-feeding opportunity sub-network.

1.10.1. Parent nodes and input data

Four parent nodes are linked to the water-quality-limited node: (1) DO, (2) pH, (3) nitrate-nitrogen (NO₃-N) and 4) the too-hot limiting-factor node.

Dissolved oxygen and pH can be measured using standard water quality probes. Spot DO measurements should be taken in mid to late summer during base flows following at least a two-week period of stable flows to allow any algal growths to occur that may increase respiration and decrease DO at times (Davies-Colley et al. 2013). In addition, measurements should be taken close to dawn when DO concentration is lowest due to stream respiration and no photosynthesis overnight. Continuous oxygen loggers are becoming cheaper and more commonplace for routine monitoring. If deployed over a summer low-flow period, the minimum DO concentrations from these data should be used if available. By contrast, pH is best measured mid-afternoon during summer base-flow when photosynthesis peaks (Davies-Colley et al. 2011). Water samples for nitrate analysis should be taken in early spring near spawning and fry rearing habitat. This is where emerging fry will be most vulnerable to nitrate toxicity and nitrate levels are at their highest owing to saturated ground and winter-farming practices such as break-feeding (Quinn 2000).

1.10.2. Data input categories

Davies-Colley et al. (2013) provided a set of proposed DO condition bands to inform the NOF initiative. These condition bands are intended to provide DO limits which provide various degrees of protection for the ‘life supporting capacity’ of freshwater ecosystems. The more stringent DO condition bands were based on DO concentration tolerance of rainbow trout. These concentrations are likely to be equivalent to tolerance thresholds for brown trout. Accordingly, we chose Davies-Colley et al.’s four suggested DO ‘condition band’ ranges to define our DO node category breakpoints.

The longstanding ANZECC (2000) guidelines define the suitable pH range for salmonids as being between 6 and 9. We converted this range to a binary variable (within or outside 6-9 pH) to define the two pH node categories.

Research is required to determine accurate nitrate toxicity thresholds for brown trout. Hickey (2013) reviewed nitrate toxicity literature for freshwater fish and invertebrates and proposed NOF protection bands for New Zealand streams. These were based in part on estimated chronic NO₃-N toxicity thresholds for salmonids. The no-effect concentration (NOEC) of NO₃-N for rainbow trout is around 2.4 mg/l. This value was determined from the geometric mean of just two NOEC values derived from
experiments undertaken by Kincheloe et al. (1979). Subsequent long-term nitrate toxicity tests by Hickey (2013) found that a New Zealand strain of rainbow trout was nine times less susceptible to nitrate than the strain studied by Kincheloe et al. (1979). Nevertheless, to account for considerable uncertainty surrounding NO$_3$-N toxicity for salmonids, and the lack of direct NO$_3$-N chronic toxicity data for brown trout, we chose the (conservative) proposed NOF nitrate condition bands to inform our nitrate toxicity category thresholds (Hickey 2013). These are based on NOEC for lake trout (Salvelinus namaycush), which is the most nitrate-sensitive fish species present in New Zealand fresh waters.

We weighted all water quality variables equally when determining conditional probabilities. However, to account for the synergistic effect of high temperatures on water quality stress (see e.g. Bruder et al. 2017), we multiplied the DO, pH and nitrate variables by the too-hot limiting-factor node if it was with a range that would impair trout metabolism.

1.11. Social limitation to fishery usage

Humans are an essential component of a fishery. Consequently, poor aesthetic values or human health risk factors potentially limit angler usage. When selecting the parent nodes for this BBN sub-network, we chose to focus on instream values for which pre-existing numerical guidelines exist in relation to angling values.

Counts of the faecal bacteria *E. coli* in water samples are commonly used to indicate the health risk of undertaking ‘secondary contact’ recreational actives such as angling. In addition, percentage algal and macrophyte cover guidelines for trout angling aesthetics are available from Biggs and Kilroy 2000, recently modified by Matheson et al (2016).

1.11.1. Parent nodes and input data

The usage-limited child node has three parent nodes: (1) contact recreation status based on *E. coli* counts (rec-status), (2) %-algal-cover and (3) %-macrophyte-cover.

Water quality testing for *E. coli* is routinely undertaken by regional authorities at the network of sites associated with the New Zealand State of the Environment monitoring programme. However, if long-term *E. coli* data do not exist for a stream, then *E. coli* samples should be collected monthly during low-to-moderate flows when anglers are likely to be fishing (MFE 2002). To inform the %-algal-cover and %-macrophyte-cover nodes, we suggest obtaining visual estimates of percentage cover from three 100-m reaches that are randomly located within the focal stream segment (Holmes et al. 2016).
1.11.2. Data input categories

There is considerable ongoing debate over the appropriate level of health risk imparted by different concentrations of *E.coli* in waterway samples (McBride 2012). Therefore, rather than using counts to inform the category breakpoints for the rec-status node, we opted for the contact recreational status of the waterway as defined by contemporary risk profile calculation standards (e.g. MFE 2002). These include the categories ‘no contact’, ‘secondary contact’ (i.e. contact without submerging head, e.g. wading) through to primary contact (i.e. swimming / full immersion).

Matheson et al. (2016) provide an interim guideline of < 35% composite cover of filamentous algae and algal mats (> 3 mm thick) to protect angling aesthetic values. We converted this threshold to binary categories of < 35% or ≥ 35% to define the percent algal-cover node breakpoints.

We weighted contact recreational status, percent algal cover and percent macrophyte cover 1, 0.66 and 0.33, respectively, to reflect our expert opinion of anglers’ attitudes towards the severity of these potential issues within a fishery.
2. DIAGNOSTIC-TEST NODES

The limiting-factor nodes are the parent nodes to a set of fishery diagnostic metric nodes. These nodes include six standard metrics used by researchers and managers to monitor fisheries. We have selected metrics that vary in sophistication and expense to allow for different monitoring budgets. Our diagnostic metrics include:

1. January–March Relative Weight
2. Observed vs. expected growth rate
3. Young-of-the-year density (fish / m²)
4. Biomass (g / m²) of trout ≥ 200 mm
5. National Angler Survey (NAS) usage statistics
6. Enjoyment / importance survey scores.

The reasons for including these metrics, as well as the methods to determine the category breakpoints and conditional probabilities, are discussed below.

2.1. Relative weight (Wr)

One of the simplest and most widely used metrics for determining individual and fish population health is condition factor (K)—i.e. the length to weight ratio of a fish (Fulton 1902; Ricker 1975). However, more recently, relative weight (Wr) has been proposed as a more versatile measurement of fish condition (Murphy et al. 1991, Blackwell et al. 2000). This is because this metric does not assume isometric growth and therefore can be used to compare individuals with different lengths (Blackwell et al. 2000).

Relative weight is calculated using the following formula:

\[ Wr = \left( \frac{W}{Ws} \right) \times 100 \]

where \( W \) = actual fish weight, and \( Ws \) = a 'standard weight' for fish of the same length. Milewski and Brown (1994) determined \( Ws \) for stream brown trout from populations across the United States and Canada (n = 10,673) using the following formula:

\[ \log Ws = -5.422 + 3.194 \log TL \]

where \( Ws \) is in grams and TL (total length) is in millimetres. We see no reason why this formula will not be applicable to New Zealand trout populations.

The effects of spawning can substantially affect Wr, even in rivers with abundant food. Therefore, for the BBN, Wr should be estimated for fish sampled in mid-summer to early autumn (January–March in New Zealand) when fish ought to be in peak
condition. We suggest that an unbiased sample (i.e. not obtained by angling) of at least 20 fish is needed to generate average Wr input values (Blackwell et al. 2000). Preferably, sample collection should be undertaken over multiple years.

We linked the Wr node to the food-limited node because the most likely explanation for poor average condition in a population is food limitation. We determined two categories for the Wr node either above or below a Wr value of 85. Relative weight values below or above this value are considered to indicate poor or adequate condition, respectively (Blackwell et al. 2000).

2.2. Observed vs. expected growth rates

Bioenergetics growth models can be used to indicate whether fish populations are food limited by comparing observed growth rate with predicted growth rate assuming maximum rations (expected growth) (Hewett & Johnson 1992; Hansen et al. 1993; Railsback & Rose 1999). Predicted growth is varied until it matches observed growth and the resulting value (C/Cmax, where C = consumption and Cmax is maximum consumption based on invertebrate or fish diet or a combination of both) provides an indication of the degree of food limitation. For stream trout growth modelling, we suggest modelling an invertebrate diet. Observed growth rate can be estimated for multiple years from a size-at-age sample, with age being estimated from otoliths or, for juvenile fish, from scales. A sample of at least 20 fish is required for growth estimation. Detailed methods for applying bioenergetics trout growth modelling are given in Hayes (2013).

Because growth modelling relates directly to food limitation, we linked it with the food-limited node as a continuous variable in the BBN.

2.3. Biomass of brown trout over 200 mm

The maritime climate and temperate latitude of New Zealand streams provide close to ideal temperatures for trout growth. Growth is generally rapid in lowland-mid altitude streams and rivers, such that by the end of their second year brown trout usually reach about 200 mm (e.g. Hayes et al. 2000). Therefore, the biomass of fish > 200 mm is an indicator of the potential pool of mature fish approaching spawning age. We chose biomass and not density because it better represents the productivity of a fishery (Melstrom et al. 2015). Various methods are available for estimating medium to large trout biomasses, including electric fishing and visual surveys by snorkel divers (Johnson et al. 2007). However, water clarity is often insufficient to visually survey lowland streams. Therefore, we suggest using quantitative electric fishing (multiple pass depletion count method) to provide input data for this node. Standard protocols for quantitative electric fishing are given in Johnson et al. (2007).
We determined the categories for our biomass breakpoints (in g / m²) by visually assessing the frequency distribution of trout biomass for break points across the range present in the CEP data. The ‘trout > 200 mm biomass’ node was linked to the food-limited, water-quality-limited, low-flow-limited and fish-cover-limited nodes. We used the conceptual model (shown in Appendix 4, explained in Appendix 1) to determine the conditional probabilities for a given combination of limiting-factor probabilities within the parent nodes.

2.4. Young-of-the-year density

Recruitment potential can be measured directly from the density of young-of-the-year (YoY) trout estimated from quantitative electric fishing. Data should be gathered in mid-summer to autumn (January–March in New Zealand) to determine densities after the population bottleneck that occurs following spring emergence (Jensen & Johnsen 1999). Long-term annual sampling is recommended in order to account for environmental stochasticity (e.g. 10 years) (Frank et al. 2011).

We linked the YoY-density node to the flood-limited, recruitment-limited and water-quality-limited nodes. As discussed in Sections 1.2, 1.5 and 1.10 (respectively), these variables can have severe and disproportionate impacts on juvenile trout survival relative to adult trout. We determined the juvenile trout density category values by visually assessing the frequency distribution of YoY densities within the CEP data for breakpoints. We used the conceptual model (shown in Appendix 4, explained in Appendix 1) to determine the conditional probabilities for a given combination of limiting-factor parent node probabilities.

2.5. National angling usage survey statistics

The National Angling Usage Survey (NAS) has been undertaken approximately every five to seven years since 1994 (e.g. Unwin 2016). This resource gives a reliable estimate of the usage of more popular fisheries in New Zealand, and the survey results can inform whether a fishery is likely to be unpopular. Accordingly, we linked this node to the usage-limited node. We set the lower usage-breakpoint at < 100 angler days per year to indicate ‘unpopular fisheries’ based on the nominal value for ‘low-usage’ rivers suggested by Unwin (2013). We chose the upper categories of 100-500 and > 500 angler days based on the NAS usage rates in moderately popular and popular New Zealand wadeable-stream fisheries. To derive these values, we considered usage rates of ‘moderately popular’ and ‘popular’ New Zealand wadeable stream fisheries based on the lead authors’ expert opinion. This was guided by how often the streams assessed are mentioned in popular fishing documents and fishing guides (e.g. Kent 2009).
2.6. Enjoyment / importance score

As part of the 2011 / 2012 NAS, Unwin (2013) conducted an investigation of the "values of New Zealand angling rivers". He assessed the quality of rivers and streams by phone interviews of anglers, asking them to score nine attributes for each river they had fished. These attributes included: ‘close to home’, ‘close to holiday home’, ‘easy access to river’, ‘plenty of fishable water’, ‘scenic beauty’, ‘wilderness feeling’, ‘angling challenge’, 'expect good catch rate', and 'chance to catch trophy fish'. Unwin (2013) combined the attribute scores to generate overall average ‘enjoyment / importance’ scores that give a gross indication of the relative quality of the fisheries. We included an enjoyment / importance node in the set of diagnostic fishery metrics. The categories for this node were binary, ‘above or below’ the national overall mean enjoyment / importance score of 2.36 (out of a possible 5). We linked the enjoyment / importance node to the usage-limited node. If no data exist for a given catchment, anglers that are familiar with the waterway could be surveyed using Unwin's method.
3. REFERENCES


Jellyman PG, Harding JS 2016. Disentangling the stream community impacts of *Didymosphenia geminata*: how are higher trophic levels affected? Biological Invasions 18(12): 3419-3435.


Unwin 2016. Angler usage of New Zealand lake and river fisheries. NIWA technical report. No. 2016021CH.


Appendices

Appendix 1. Methods section excerpt from the accompanying manuscript: Holmes et al. (in review).

Methods

Model structure

We used Netica modeling software (version 5.23, Norsyes.com) to construct the BBN. Broadly, our network structure was modelled on medical diagnostic BBN-based decision support systems (Lucas et al. 2004).

Initially, we created an influence diagram to conceptualise cause and effect linkages between key environmental variables and stream fishery health. Key limiting factors for stream fisheries were then extracted from the linkage diagram (Table 1) to populate a Directed Acyclic Graph (DAG) which formed the BBN structure. Limiting factor nodes were phrased as a binary statement (e.g. ‘Too Hot’) and placed within the middle of the DAG. We then populated the DAG with causal environmental variable nodes (parent nodes) using the initial linkage diagram as a guide. The basic structure of the BBN is shown in Figure 2. Unlike some medical diagnostic BBNs, not all limiting factor variables were causally linked, meaning that the likelihood of occurrence for one limiting factor did not necessarily influence the likelihood of another.

Table 1. Key limiting factors for brown trout (Salmo trutta) in wadeable lowland streams and their binary BBN codes. Factors are ranked in hypothetical order according to their likelihood of limiting trout production in ‘typical’ lowland New Zealand streams. Rankings based on our interpretation of the literature and technical reports.

<table>
<thead>
<tr>
<th>Key factors that limit stream brown trout fisheries</th>
<th>Binary codes used within the BBN</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Temperature</td>
<td>Too Hot</td>
</tr>
<tr>
<td>2. Flow (flood flows, low flows)</td>
<td>Low flow limited, Flood limited</td>
</tr>
<tr>
<td>3. Recruitment</td>
<td>Recruitment limited</td>
</tr>
<tr>
<td>4. Food</td>
<td>Food limited</td>
</tr>
<tr>
<td>5. Instream fish cover</td>
<td>Cover limited</td>
</tr>
<tr>
<td>6. Water quality</td>
<td>Water quality limited</td>
</tr>
<tr>
<td>7. Socially limited usage</td>
<td>Usage limited</td>
</tr>
</tbody>
</table>
Figure 2. The basic structure of our BBN (left) and example (right). In the top row are the parent nodes, which contain environmental variable information. In the next row are causally linked nodes conditional on the parent nodes. Below these are horizontally listed limiting-factor probability nodes. In the bottom row are the diagnostic test nodes, which contain fishery population metrics. An example of a simplified sub-net for ‘Food Limitation’ is shown on the right.

We then undertook a review of the salmonid literature and relevant technical reports to inform the decisions inherent within the BBN. The structure of the DAG constrained the scope of our review, although refinement of the DAG and further review of the literature was an iterative process.

To simplify the BBN, where possible, we chose empirical data as input information rather than modelled proxies. For example, we require quantitative macroinvertebrate community composition data as an input variable in the Food-Limited sub-net branch. We did not attempt to model macroinvertebrate community composition based on causally linked variables - such as nitrate concentrations or deposited fine sediment. Our choice of parent node input variables was also filtered by environmental data that are practically obtainable, or potentially already exist, because they are extensively collected by water resource managers (e.g. physical habitat data collected by regional authorities for New Zealand’s State of the Environment monitoring programme).
Determining parent node environmental variable categories

Following the approach of Marcot et al. (2006), we discretised environmental variables into broad categories within each parent node. For a given environmental variable, our working definition of ‘not limiting’ was based on values that naturally occur in productive wild stream fisheries. We did not define the breakpoints for parent node categories relative to theoretical optima, which may not occur in natural streams. For example, continuous optimal water temperatures for salmonid metabolism occur only in controlled environments (e.g. hatcheries).

The environmental variable (parent node) category breakpoints were informed by either 1) linear interpolation, 2) literature-derived values in combination with author opinion, or 3) visual or quantile classification of data-distribution gradients (the former undertaken when breakpoints were obvious). For the latter method, we used two trout population and environmental spatial data sets from New Zealand. The first was from what is known as the ‘100 Rivers Study’, a nationwide multidisciplinary study in which trout abundance in 88 clear-water rivers was surveyed by snorkel divers (Jowett 1990, 1992). The second was a recent unpublished electrofishing study of 48 wadeable streams across a gradient of agricultural land-use intensity. This survey was undertaken as part of the Cumulative Effects Research Programme (CEP) (C01X1005) Fishery Quality Study. Finally, where possible, category breakpoints were aligned with attribute guidelines being developed as part of the New Zealand Government’s National Objectives Framework policy initiative (MFE 2014). This initiative seeks to set environmental attribute management limits that maintain ‘life supporting capacity’ in freshwater ecosystems.

Limiting factor nodes

A conditional probability matrix is the functional link between BBN child nodes and parent nodes (Marcot et al. 2006). When determining values for conditional probability tables (conditional probabilities), we first weighted the relative ‘strength of influence’ of the parent nodes - based on our literature review and/or author opinion. For example, the ‘flood-limited’ parent node variables ‘flood frequency’, ‘segment slope’ and ‘fish cover’ were weighted 1, 1 and 0.5, respectively. For each parent node variable category, we assigned a standardised weighted score according to its negative, neutral or positive influence on the child node. For
example, -4, -2, -1, 0 were used to score the four ‘flood frequency’ variable categories. Conditional probabilities (e.g. for flood limitation) were then calculated by summing all combinations of the parent node influence-weighted scores. The products were subsequently normalized to a 0–100 scale to represent the probability of the limiting factor child node’s logic statement being true.

In some instances, when supported by evidence, we accounted for potential synergistic or antagonistic interactions between parent node variables. For example, high temperatures are known to have a synergistic effect on dissolved oxygen (DO) stress in fish. Rather than adding influence-weighted standardised scores for the temperature and DO parent nodes, we multiplied the two if temperature and oxygen variable categories were above thresholds known to induce stress in brown trout.

**Diagnostic fish population metric nodes**

Generally, we used equal weighting for all parent nodes to determine values in the conditional probability tables that link the limiting-factor (parent) nodes with the diagnostic fish population metric (child) nodes. However, for the fish population metric nodes ‘trout biomass >200 mm’ and ‘young-of-the-year (YoY) density’, we developed intuitive conceptual models to represent the cumulative effect of multiple limiting factors that are acting on a population (Figure 3). The values from these conceptual models (on the y-axis) were used to populate the conditional probability tables. The models were based on the principal that fish populations can be resilient to a single stressor but decline exponentially as more stressors are added, before eventually crashing (i.e. a negative sinusoidal population response to cumulative multiple stressors). For example, a population with one acting limiting factor will have a 90% chance of having a high large-trout biomass, whereas, when two limiting factors are in effect (e.g. flood limited and food limited) there is a 75% chance of intermediate biomass and 25% chance of having high or low biomass. Three (or more) acting limiting factors would result in a very high chance of a low biomass (Figure 3). Young-of-the-year density and the biomass of trout >200 mm category breakpoints were determined with quantile classification of the CEP data.
Model testing
We tested our BBN using historical data from Horokiri Stream – recorded in Allen (1951) and more recently in Jellyman et al. (2000). The Horokiri fishery collapsed between 1951 and 1990, and Jellyman et al. (2000) presents a comprehensive expert-based analysis of potential causes.

We entered the ecological and trout population data from Horokiri Stream from its 1990 ‘impacted’ state into our LFA BBN. These data were supplemented with six years of flow and water temperature data, and monthly water quality spot measurements (2002–2008), from the Wellington Regional Council long-term monitoring site (mid-catchment, easting 1761804, northing 5450652). We could not find suitable reference-state temperature, flow and forage fish data, therefore, we supplemented these nodes with contemporary data.

We compared the limiting-factor probability outputs with Jellyman et al.’s (2000) narrative about the causes of the trout population decline. It is important to note that our BBN was not trained on the Horokiri Stream data. Therefore, this exercise represented a test of the BBN to generate limiting factor hypotheses (in the form of ranked probabilities) against the opinion of five experienced fishery scientists – who were informed by a targeted data collection exercise.
Appendix 2. Summary table for the decisions inherent within our Bayesian Belief Network (BBN) for undertaking a limiting factor analysis (LFA) on a stream brown trout population. For each limiting factor child node, the immediate environmental variable (parent) nodes are given along with a description of how the parent node were determined and their respective weightings used to calculate conditional probabilities. Also provided is our subjective assessment of how robust / adequate the available scientific knowledge base is that underpins the related decisions made for each BBN sub-net (very low, low, moderate or high).

<table>
<thead>
<tr>
<th>Limiting factor</th>
<th>Immediate parent nodes</th>
<th>Parent node discretisation thresholds</th>
<th>Knowledge source</th>
<th>Variable weight</th>
<th>Degree of confidence in knowledge base</th>
</tr>
</thead>
<tbody>
<tr>
<td>Recruitment limited</td>
<td>Rolling average number of August – November floods that exceed 10*median flow (FRE10) every three years</td>
<td>&lt; 1, 1 – 3, &gt; 3</td>
<td>Literature, logic</td>
<td>Weight 1</td>
<td>High</td>
</tr>
<tr>
<td></td>
<td>Catchment spawning and juvenile rearing habitat</td>
<td>Good, Ok, Poor</td>
<td>Expert opinion</td>
<td>Weight 0.5</td>
<td>Very low</td>
</tr>
<tr>
<td></td>
<td>Winter maximum temperature</td>
<td>≤ 10°C, &gt;10 °C</td>
<td>Literature</td>
<td>Weight 0.5</td>
<td>High</td>
</tr>
<tr>
<td></td>
<td>Large lake in the system</td>
<td>True or False</td>
<td>Literature, expert opinion, logic</td>
<td>Weight 0.5</td>
<td>Moderate</td>
</tr>
<tr>
<td>Food limited</td>
<td>Forage-fish supply</td>
<td>Present or absent</td>
<td>Literature, national spatial database,</td>
<td>Weight 0.5</td>
<td>Moderate</td>
</tr>
<tr>
<td></td>
<td>Macroinvertebrate (&gt; 3mm) density</td>
<td>750 / m², 750 – 3000 / m², &gt; 3000 /m²</td>
<td>Literature, expert opinion, quantile classification of data distributions</td>
<td>Weight 0.5</td>
<td>Low</td>
</tr>
<tr>
<td></td>
<td>Drift-feeding opportunity metric</td>
<td>High or Low (BBN sub-network)</td>
<td>Literature, expert opinion</td>
<td>Weight 0.5</td>
<td>Moderate</td>
</tr>
<tr>
<td></td>
<td>Temperature</td>
<td>Too hot or not too hot (BBN sub-net)</td>
<td>BBN network sub-branch (see below)</td>
<td>Weight 1</td>
<td>High</td>
</tr>
<tr>
<td>Recruitment</td>
<td>Recruitment limited Yes / No (BBN sub-net)</td>
<td></td>
<td>BBN network sub-branch (see below)</td>
<td>Weight 1</td>
<td>Low</td>
</tr>
<tr>
<td>Low-flow limited</td>
<td>Coefficient of flow variation</td>
<td>&lt; 1, 1 – 3, &gt; 3</td>
<td>Technical report</td>
<td>Weight 1</td>
<td>Moderate</td>
</tr>
<tr>
<td></td>
<td>Percentage of reach ≥ 1m deep at base flow</td>
<td>&lt; 10%, 10 – 50%, &gt; 50%</td>
<td>Literature, visual assessment of data distribution for break points</td>
<td>Weight 1</td>
<td>Moderate</td>
</tr>
<tr>
<td>Flood-flow limited</td>
<td>Average number of FRE10 floods per year</td>
<td>≤ 3.5, 3.6 – 4.7, 4.8-7.5, &gt; 7.5</td>
<td>Literature, expert opinion, unpublished data</td>
<td>Weight 1</td>
<td>Moderate</td>
</tr>
<tr>
<td></td>
<td>Segment gradient (%)</td>
<td>≤ 1.4, 1.5 – 4, greater than 4</td>
<td>Literature, expert opinion,</td>
<td>Weight 1</td>
<td>Moderate</td>
</tr>
<tr>
<td>Fish-cover limited</td>
<td>True, false</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fish-cover limited</td>
<td>Percentage of reach ≥ 1m deep at base flow</td>
<td>&lt; 10%, 10 – 50%, &gt; 50%</td>
<td>Literature, expert opinion, visual assessment of data distribution for break points</td>
<td>Weight 1</td>
<td>Moderate</td>
</tr>
<tr>
<td>Limiting factor</td>
<td>Immediate parent nodes</td>
<td>Parent node discretisation thresholds</td>
<td>Knowledge source</td>
<td>Variable weight</td>
<td>Degree of confidence in knowledge base</td>
</tr>
<tr>
<td>----------------</td>
<td>------------------------</td>
<td>----------------------------------------</td>
<td>-----------------</td>
<td>----------------</td>
<td>----------------------------------------</td>
</tr>
<tr>
<td>Undercut banks</td>
<td>0% of bank, &gt; 0 -50%, &gt; 50%</td>
<td>Literature, expert opinion, visual assessment of data distribution for break points</td>
<td>Weight 0.75</td>
<td>Low</td>
<td></td>
</tr>
<tr>
<td>Large wood</td>
<td>&lt; 5% of wetted area, ≥ 5%</td>
<td>Expert opinion, logic</td>
<td>Weight 0.75</td>
<td>Low</td>
<td></td>
</tr>
<tr>
<td>Overhanging vegetation</td>
<td>0% of bank, &gt;0 -50%, &gt; 50%</td>
<td>Literature, expert opinion, visual assessment of data distribution for break points</td>
<td>Weight 0.5</td>
<td>low</td>
<td></td>
</tr>
<tr>
<td>Macrophytes</td>
<td>&lt;10% cover, 10-35%, &gt;35%</td>
<td>Technical report</td>
<td>Weight 0.25</td>
<td>low</td>
<td></td>
</tr>
<tr>
<td>Water quality limited</td>
<td>Dissolved oxygen</td>
<td>0 – 4 mg/L, 4 – 6 mg/L, &gt;6 mg/L</td>
<td>Literature, technical report</td>
<td>Weight 1</td>
<td>High</td>
</tr>
<tr>
<td>NO3</td>
<td>&gt; 8 mg/L, 4 – 8 mg/L, 0 – 4 mg/L</td>
<td>Literature, technical report</td>
<td>Weight 1</td>
<td>High</td>
<td></td>
</tr>
<tr>
<td>pH</td>
<td>5.5 – 8.5 pH, outside this range</td>
<td>Literature, technical report</td>
<td>Weight 1</td>
<td>High</td>
<td></td>
</tr>
<tr>
<td>Underutilised fishery – social limitation</td>
<td>Algae % cover</td>
<td>&lt; 35% composite mat (&gt;3mm) and filamentous cover, ≥ 35%</td>
<td>Technical report</td>
<td>Weight 0.66</td>
<td>Moderate</td>
</tr>
<tr>
<td></td>
<td>Macrophyte % cover</td>
<td>&lt; 10% cover, 10 – 20%, &gt; 20%</td>
<td>Technical report</td>
<td>Weight 0.33</td>
<td>Low</td>
</tr>
<tr>
<td></td>
<td>Contact recreation status</td>
<td>Swimmable, secondary contact, no contact</td>
<td>NZ Government, Ministry for Environment derived values</td>
<td>Weight 1</td>
<td>Moderate</td>
</tr>
</tbody>
</table>
Appendix 3. The Bayesian Belief Network (version 5.23, Norsyes.com) directed acyclic graph for undertaking a limiting-factor analysis on stream brown trout fisheries. Limiting-factor nodes are located in the middle of the network, below the environmental parent nodes and above a set of fishery-population metrics (diagnostic nodes).
Appendix 4. Conceptual models (Figure 3) extracted from the accompanying manuscript: Holmes et al. (in review).

Figure 3 Conceptual models for determining the conditional probability table values for trout biomass > 200 mm and young-of-the-year trout densities (fish / m²). The models define, depending on the numbers of cumulative limiting factors, (A) the likelihood of the high biomass and intermediate biomass with varying densities, and (B) the likelihood of high density and low density with varying numbers of limiting factors.
occurrence of high, intermediate or low large trout biomass (>200 mm), and (B) the occurrence of high, intermediate or low young-of-the-year trout densities (fish / m²). All probabilities sum to 100.