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A decision support system to diagnose factors limiting stream trout fisheries

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Abstract

Maintaining or restoring productive freshwater fisheries is a key challenge for resource managers. However, the inherent uncertainty and complexity of managing fisheries, often based on scant environmental data, make it difficult for managers and the public to reach consensus on appropriate actions. To help deal with this issue, we created a literature-based decision support system to diagnose limiting factors for stream brown trout fisheries. Once limiting factors are determined, appropriate management actions can be tailored to address them. Our Bayesian belief network (BBN)-based framework serves 2 functions: (a) It directs users to assemble a parsimonious environmental data set to inform stream fishery management, and (b) it integrates and interrogates these data to generate standardized and testable hypotheses about which environment factors are likely to limit trout productivity. The BBN has been trained on brown trout because among freshwater fish, this species has the richest literature base and is highly valued worldwide. However, the framework could be adapted for other stream fish. We applied our BBN to the Horokiri Stream, a data-rich catchment in Wellington, New Zealand. The BBN probability outputs were comparable with the conclusions of 5 experienced fishery biologists following their detailed investigation into the factors that led to the loss of the Horokiri brown trout fishery between 1951 and 1990.

KEYWORDS

Bayesian belief network, brown trout, fisheries management, habitat, limiting factor analysis, *Salmo trutta*

1 | INTRODUCTION

Improving fisheries is a common motivation for stream protection and rehabilitation initiatives (Beechie, Pess, & Roni, 2008). Yet effective fishery management is dependent on identifying and ranking the importance of environmental constraints on fish populations (Armstrong, Kemp, Kennedy, Ladle, & Milner, 2003; Lake, Bond, & Reich, 2007). If managers fail to identify limiting factors before acting they risk ecological surprises (King, 1995) or misdirecting resources (Beechie et al., 2008; Roni et al., 2002).

Underpinning the concept of limiting factor analysis (LFA) in fisheries biology is the Liebig–Sprengel "law of the minimum" (Figure 1)—where yield is proportional to the amount of the most limiting factor (Liebig, 1852; Sprengel, 1839). For example, improving salmonid spawning habitat, by adding spawning gravels, in a stream that lacks sufficient adult fish cover will not result in a better fishery—because additional recruits created through this action will encounter a population bottleneck later in their life history. More recent ecological theory states that environmental pressures can interact in complex ways to affect populations (Townsend, Uhlmann, & Matthaei, 2008). In addition, populations can experience "co-limitation" with multiple environmental factors (Sperfeld, Martin-Creuzbeurg, & Wacker, 2011). For example, two stressors (e.g., reduced food availability and elevated water temperatures) can act synergistically

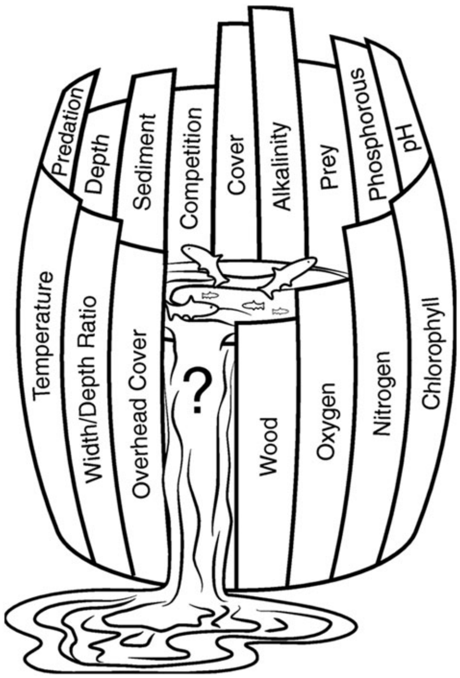

FIGURE 1 The Wurtsbaugh et al. (2015) version of a Liebig–Sprengel barrel for freshwater fish populations showing variables that can limit fish production (figure reproduced with lead author permission)

to negatively affect fish growth or survival (Bruder, Salis, Jones, & Matthaei, 2017). In this situation, alleviation of either stress on the population will result in increased density or biomass.

Determining the environmental factors that limit highly mobile, long-lived, upper-trophic-level fish, such as brown trout (*Salmo trutta*), is challenging and resource-intensive. Consequently, managers are often faced with considerable uncertainty when assessing the potential outcomes of rehabilitation actions based on scant environmental data (Bash & Ryan, 2002). To avoid inaction in the face of uncertainty, pragmatic managers will assign management resources based largely on common sense or intuition (Walters, 2007). This issue is especially acute for small stream fisheries because investment of management resources is often unjustifiable given the relatively low fisheries value. Nevertheless, decision support tools are needed even for small-stream fisheries because collectively, they can receive considerable angler usage across management jurisdictions and can contribute recruits to main-stem fisheries.

In this paper, we present and trial a Bayesian belief network (BBN)-based LFA framework for lowland stream brown trout populations. BBNs are now widely used to support environmental decisions (Aguilera, Fernández, Fernández, Rumí, & Salmerón, 2011; Landuyt et al., 2013; O'Brien et al., 2018). For example, they have been used to predict the outcomes of different basin-scale fishery management plans, segment-scale river rehabilitation actions, and land-use effects over broad spatial scales (Borsuk, Reichert, Peter, Schager, & Burkhardt-Holm, 2006; Death, Death, Stubbington, Joy, & Belt, 2015; Marcot, Holthausen, Raphael, Rowland, & Wisdom, 2001; Quinn, Monaghan, Bidwell, & Harris, 2013). Our BBN differs from previous fishery management BBNs because by design, it has relatively low data requirements. It is intended as a "first step" to determine likely limiting factors and indicate the need and scope for further monitoring or management actions. The BBN formalizes the process of generating, integrating, and interrogating a parsimonious data set for undertaking an LFA on small stream brown trout fisheries. To our knowledge, this is the first time that BBN modelling has been applied in this context.

We tested our BBN on the Horokiri Stream (formally known as Horokiwi Stream), a data-rich catchment in Wellington, New Zealand. To do this, we entered existing environmental and brown trout population data into our BBN from before and after the well-documented decline of the stream's trout fishery (between 1951 and 1990). The BBN outputs were compared with a narrative by five experienced fishery biologists who discussed the likely reasons for the population decline after a detailed investigation of the stream (Jellyman, Glova, Bonnett, McKerchar, & Allen, 2000).

2 | METHODS

2.1 | Model structure

We used Netica modelling 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, van der Gaag, & Abu-Hanna, 2004). Initially, we created an influence diagram to conceptualize cause and effect linkages between key environmental variables and stream fishery health. Key limiting factors for stream fisheries, which were determined from our appraisal of the literature, were then extracted from the linkage diagram to populate a directed acyclic graph (DAG). Limiting factor nodes were phrased as a positive statement (e.g., "Too Hot" or "fish cover limited") 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. Subsequently, we undertook a broad review of the international 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 subnet 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.

2.2 | Determining parent node environmental variable categories

Following the approach of Marcot, Steventon, Sutherland, and McCann (2006), we discretized environmental variables into broad categories within each parent node. For a given environmental

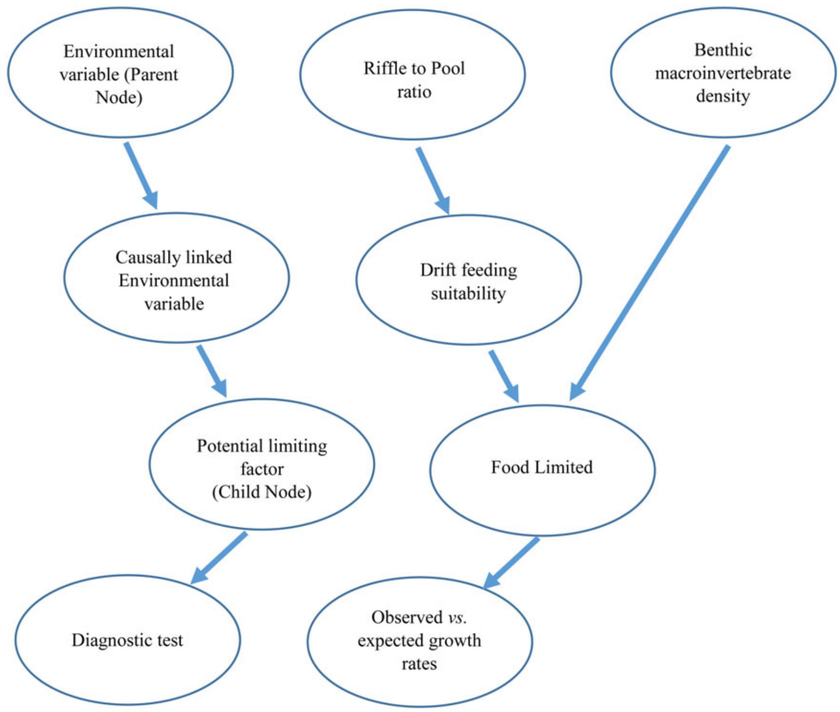

FIGURE 2 The basic structure of our BBN (left) and example (right). In the top row are the parent nodes, which contain environmental variable information. In the next row are causally linked nodes conditional on the parent nodes. Below these are horizontally listed limiting factor probability nodes. In the bottom row are the diagnostic test nodes, which contain fishery population metrics. An example of a simplified subnet for "food limitation" is shown on the right [Colour figure can be viewed at wileyonlinelibrary.com]

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 (a) linear interpolation, (b) literature-derived values in combination with author opinion, or (c) 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 clearwater 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 Fishery Quality Study (C01X1005). The methods used to define the various category breakpoints are listed in Table 2.

2.3 | 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. In this instance, fish cover was down-weighted because we suggest that the presence of structural cover (from floods) in a stream is less important than the occurrence and severity of large floods when determining a population response. For each parent node variable category, we assigned a standardized weighted score according to its negative, neutral, or positive influence on the child node. For example, −4, −2, −1, and 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 results 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 stress in fish. Rather than adding influence-weighted standardized scores for the temperature and dissolved oxygen parent nodes, we multiplied the two if temperature and oxygen variable categories were above thresholds known to induce stress in brown trout.

2.4 | Diagnostic fish population metric nodes

Generally, we used equal weighting for all parent nodes to determine the conditional probability table values 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 estimate the cumulative effect of multiple limiting factors, or stressors, 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 conceptual models are based on the principal that a proportion of a population will be resilient to a single stressor but the population will decline logistically as more stressors are added (Liess, Foit, Knillmann, Schäfer, & Liess, 2016). For example, our conceptual model assumes

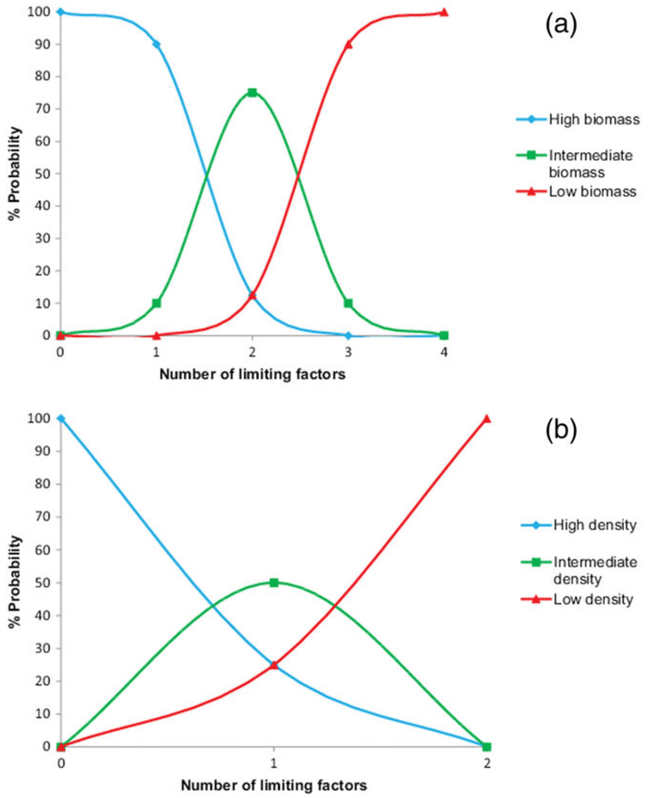

FIGURE 3 Conceptual models used to determine conditional probability table values that link fish population metric nodes to limiting factor nodes. The models define, depending on the numbers of cumulative limiting factors, (a) the likelihood of the occurrence of high, intermediate, or low biomass of trout >200 mm and (b) the occurrence of high, intermediate, or low young-of-the-year trout densities (trout/m^2). All probabilities sum to 100 [Colour figure can be viewed at wileyonlinelibrary.com]

that 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 high or low biomass. Three (or more) acting limiting factors will result in a very high chance of low biomass (Figure 3a). Breakpoints for YoY density and biomass of trout >200 mm categories were determined with quantile classification of the Cumulative Effects Research Programme data.

2.5 | Model application

We assessed our BBN using historical data from Horokiri Stream—recorded in Allen (1951) and more recently in Jellyman et al. (2000). The Horokiri brown trout 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 6 years of flow and water temperature data and monthly water quality spot measurements (2002–2008), from the Wellington Regional Council long-term monitoring site (midcatchment, easting 1761804, northing 5450652). We could not find suitable reference-state temperature, flow, and forage-fish data, so we supplemented these nodes with present-day (impact state) 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 an independent assessment of the BBN's ability 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.

3 | RESULTS

3.1 | Literature review

The key limiting factors included in the BBN are presented in Table 1. The literature review underpinning our BBN is provided in a companion report (Holmes, Gabrielsson, Matthaei, & Closs, 2017). In this report, we detail the network structure, give the rationale for including or excluding each potential limiting factor, suggest data requirements to populate BBN parent nodes, and cite the literature used to define breakpoints for parent node categories. This information is summarized in Table 2.

3.2 | Application of the LFA

The narrative in Jellyman et al. (2000) suggests that the decline of the Horokiri fishery was due to the stream becoming wider and shallower, in combination with reduced riffle area, undercut banks, and residual pool depths. These changes reduced macroinvertebrate production and the fish cover. In addition, increased benthic algae altered the macroinvertebrate community to one dominated by low food-value taxa (relative to the pre-1951 community). Jellyman et al. (2000) contend that the trout population became severely limited by food and cover. Allen (1951) comprehensively studied the Horokiri fishery prior to its decline and co-authored the Jellyman et al. (2000) report. In the latter, he suggests that the decline was due to "the apparent dramatic reduction in pool depth and undercut bank cover."

TABLE 1 Key limiting factors for brown trout (*Salmo trutta*) in wadeable lowland streams and their binary Bayesian belief network (BBN) codes

Key factors that limit stream brown trout fisheries	Binary codes used within the BBN
1. Temperature	Too Hot
2. Flow (flood flows, low flows)	Low flow limited, Flood limited
3. Recruitment	Recruitment limited
4. Food	Food limited
5. Instream cover	Cover limited
6. Water quality	Water quality limited
7. Socially limited usage	Usage limited

Note. Factors 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 2 Summary of the decisions within our limiting factor analysis Bayesian belief network (BBN)

Limiting factor	Immediate parent nodes	Parent node discretization thresholds	Knowledge source	Variable weight	Degree of confidence in knowledge base
Recruitment limited	Rolling average Number of August–November floods that exceed 10*median flow (FRE10) every 3 years	<1, 1–3, >3	Literature, logic	Weight 1	High
	Catchment spawning and juvenile rearing habitat	Good, Ok, Poor	Expert opinion	Weight 0.5	Very low
	Winter maximum temperature	≤10 °C, >10 °C	Literature	Weight 0.5	High
	Large lake in the system	True or False	Literature, expert opinion, logic	Weight 0.5	Moderate
Temperature too hot	Cox-Rutherford index Temperature	≤18 °C, 18.1–20 °C, 20.1–24 °C, >24 °C	Technical report, literature	No weighting	High
Food limited	Forage-fish supply	Present or absent	Literature, national spatial database,	Weight 0.5	Moderate
	Macroinvertebrate (>3 mm) density	<750/m^2, 750–3,000/m^2, >3,000/m^2	Literature, expert opinion, quantile classification of data distributions	Weight 0.5	Low
	Drift-feeding opportunity metric	High or low (BBN subnetwork)	Literature, expert opinion	Weight 0.5	Moderate
	Temperature	Too hot or not too hot (BBN subnet)	BBN network sub-branch (see below)	Weight 1	High
	Recruitment	Recruitment limited Yes/No (BBN subnet)	BBN network sub-branch (see below)	Weight 1	Low
Low-flow limited	Coefficient of flow variation	<1, 1–3, >3	Technical report	Weight 1	Moderate
	Percentage of reach ≥1 m deep at base flow	<10%, 10–50%, >50%	Literature, visual assessment of data distribution for break points	Weight 1	Moderate
Flood-flow limited	Average number of FRE10 floods per year	≤3.5, 3.6–4.7, 4.8–7.5, >7.5	Literature, expert opinion, unpublished data	Weight 1	Moderate
	Segment gradient (%)	≤1.4, 1.5–4, >4	Literature, expert opinion	Weight 1	Moderate
	Fish cover limited	True, false			Moderate
Fish cover limited	Percentage of reach ≥1 m deep at base flow	<10%, 10–50%, >50%	Literature, expert opinion, visual assessment of data distribution for break points	Weight 1	Moderate
	Undercut banks	0% of bank, >0–50%, >50%	Literature, expert opinion, visual assessment of data distribution for break points	Weight 0.75	Low
	Large wood	<5% of wetted area, ≥5%	Expert opinion, logic	Weight 0.75	Low
	Overhanging vegetation	0% of bank, >0–50%, >50%	Literature, expert opinion, visual assessment of data distribution for break points	Weight 0.5	Low
	Macrophytes	<10% cover, 10–35%, >35%	Technical report	Weight 0.25	Low
Water quality limited	Dissolved oxygen	0–4 mg/L, 4–6 mg/L, >6 mg/L	Literature, technical report	Weight 1	High
	NO_3	>8 mg/L, 4–8 mg/L, 0–4 mg/L	Literature, technical report	Weight 1	High
	pH	5.5–8.5 pH, outside this range	Literature, technical report	Weight 1	High
Underutilized fishery—social limitation	Algae % cover	<35% composite mat (>3 mm) and filamentous cover, ≥35%	Technical report	Weight 0.66	Moderate
	Macrophyte % cover	<10% cover, 10–20%, >20%	Technical report	Weight 0.33	Low
	Contact recreation status	Swimmable, secondary contact, no contact	NZ Government, Ministry for Environment derived values	Weight 1	Moderate

Note. For each limiting factor (child) node, the immediate parent nodes are given along with a description of the parent node discretization thresholds and the respective weightings used to calculate conditional probabilities. Also provided is our subjective assessment of how robust/adequate the available scientific knowledge is that underpins related decisions made for each BBN subnet (very low–high). See Holmes et al. (2017) for more details.

On the basis of the Jellyman et al. (2000) electric fishing data, we estimated that postdecline YoY trout densities were 0.06 trout/m^2 and biomass of trout >200 mm was 0.22 g/m^2. This contrasts with the exceptionally high total trout biomass of 26.5 g/m^2 reported by Allen (1951) for the fishery in its reference state.

Based on postdecline environmental data alone (from Jellyman et al., 2000), the BBN ranked a lack of cover as the most likely limiting factor (81% chance of occurrence), followed by low flow, recruitment, and food limitation (Table 3). Limiting factors were ranked similarly when the BBN was rerun with the inclusion of the Jellyman et al. (2000) trout population data (Table 3). Based on Allen's (1951) predecline environmental data, the BBN identified low flows as the most likely limiting factor (50% chance of occurrence). After adding the reference-state trout population data, recruitment limitation became the most limiting factor (18%; Table 3).

Based on postdecline environmental data, the BBN predicted a 37% chance of low YoY trout density (<0.1 trout/m^2) and a 20% chance of moderate density (0.1–1 trout/m^2). The model also predicted a high (79%) probability of biomass of trout >200 mm being below 0.4 g/m^2. The model predicted that prior to 1951 (reference state), there was a 54% chance of YoY density exceeding >1 fish/m^2 (the highest density category), whereas there was a low (16%) chance of the biomass of trout >200 mm exceeding 4 g/m^2.

Using all available data, the relative changes in limiting factor probabilities from predecline to postdecline (i.e., impacted-state minus reference-state probabilities) were as follows: Fish cover, low flow, recruitment, and food limitation increased by 80%, 70%, 47%, and 35%, respectively. There was <25% change in all other limiting factor probabilities.

4 | DISCUSSION

4.1 | The BBN

Our model is underpinned by a substantial review of salmonid literature and relevant technical reports (Holmes et al., 2017). By consolidating this literature within a BBN, we created a novel and systematic framework for undertaking an LFA. The BBN approach allowed different types of information to be blended in a transparent manner. The result was a flexible weight-of-evidence approach to assess factors potentially limiting a fishery.

Our approach has advantages over previous expert assessment-based LFA. The LFA-BBN output probabilities indicate the severity of limitation by key environmental factors, and when ranked, these probabilities specify the order in which limiting factors should be mitigated. Applying the BBN modelling process required limited input from fishery specialists. In addition, LFA-BBNs produce standardized numerical outputs, which change in a consistent way with varying environmental parameters. This ought to substantially reduce subjectivity inherent within repeat expert appraisals of potential fishery problems.

Our BBN is targeted at the segment scale (i.e., 1-km stream segments). We anticipate that the assessment could be scaled up by applying the process to multiple stream segments distributed within a catchment using a stratified randomized approach (e.g., Stevens & Olsen, 2004). Used this way, the BBN could indicate how limiting factors vary in intensity within a catchment, allowing spatial targeting of appropriate management actions.

Creating our BBN was as much about deciding what to exclude from the modelling process as to what to include. Our goal was to create a tool to aid managers and community groups that are resource limited. Consequently, we have attempted to strike a balance between precision and practicality. Users are required to collect what we consider to be a parsimonious environmental data set for undertaking a meaningful LFA to underpin stream and fishery management. We did not include an exhaustive list of limiting factors within the BBN.

We omitted some potential limiting factors because they will be self-evident or occur relatively infrequently. These include abiotic factors such as metal pollution or discrete catastrophic events (e.g., chemical spills). We also excluded two biotic factors—harvest and predation. With respect to harvest as a potential limiting factor, angling usage data (such as collected by New Zealand's National Angler Survey; e.g., Unwin, 2016) will provide some indication of fishing pressure. If fish abundance is relatively low in the face of substantial fishing pressure, and other potential limiting factors are considered unlikely (e.g., <25% probability), then overfishing could be considered the primary limiting factor through a process of elimination.

TABLE 3 Bayesian belief network percent probability outputs for potential limiting factors in the Horokiri Stream brown trout fishery in its pre-1951 “reference state” and recent “impacted state” (based on data from 2000)

	Probability (%)			
	Environmental data		Environmental and fish population data	
Limiting factor	Reference state	Impact state	Reference state	Impact state
Cover limited	44	81	7	87
Low flow limited	50	75	10	80
Recruitment limited	38	50	18	65
Food limited	37	45	8	43
Too hot	20	20	0	65
Flood limited	35	44	0.3	30
Water quality limited	6	6	0	19
Socially limited	0	25	0	25

Note. Two sets of predictions are given for both states: (a) probabilities based on environmental data alone (i.e., leaving fishery population metrics undefined) and (b) probabilities based on environmental and fish population data.

In New Zealand's lowland streams, cormorants, longfin eels, and adult trout are the main potential natural trout predators (Hayes & Hill, 2005; McDowall, 1994). Despite the ubiquitous presence of these predators, New Zealand's lowland fisheries have remained productive by global standards for over a century. Furthermore, no management options are available to ameliorate the effects of natural predators, other than adding structural fish cover, which we account for within the "fish cover limited" BBN subnet. Therefore, we excluded predation as a limiting factor within our model and argue that predation must be accepted within a fishery as a natural self-limiting constraint (Berryman, 1992), much like the occurrence of temperatures below optima for trout metabolism.

4.2 | BBN application

The initial application of our BBN shows that it can generate results that are consistent with expert opinion in degraded stream fisheries. The probability outputs were comparable with the expert narrative in Jellyman et al. (2000), explaining the decline in the Horokiri Stream brown trout fishery. They suggested that, post decline, the Horokiri trout population was severely food and cover limited. Likewise, our BBN suggests that the Horokiri fishery is probably limited by a lack of cover (87% probability) and habitat availability at low flow (80% probability)—primarily because of scarce deep water at base flow. Food limitation was also ranked highly (43%), fifth among the eight potential limiting factors. In addition, based on environmental data alone, the BBN predicted a 79% chance of biomass of trout >200 mm being <0.4 g/m^2 (the lowest biomass category). The observed biomass of trout >200 mm estimated from the Jellyman et al. (2000) data fell in the middle of this range (approximately 0.22 g/m^2).

The BBN performed less convincingly when predicting limiting factors for the Horokiri's reference state (pre-1951)—although some key environmental data were missing. Allen (1951) determined that the trout population was food limited at this time, whereas the BBN gave just an 8% chance of food limitation and ranked recruitment limitation highest (18% probability). The inconsistency of the BBN outputs with Allen's findings are largely due to our working definition of "food limitation." Where Allen framed food limitation in terms of production, we define food limitation "relative" to food levels present in New Zealand stream fisheries with high trout biomasses. Predecline, the Horokiri Stream supported a very productive fishery. Moreover, trout biomass apparently exceeded the productive capacity of the invertebrate food base—leading to the "Allen Paradox," which was a source of a lengthy scientific debate (Huryn, 1996). Therefore, based on our definition, the low chance of food limitation given by the BBN is consistent with the high trout biomass observed in the stream pre-1951. Interestingly, a subsequent investigation by Allen (1985) showed that Horokiri trout appeared to exceed maximum expected growth rates based on the stream's temperature regime and assuming maximum invertebrate rations. This suggests that invertebrate food limitation may not have been as strong a constraint on productivity as originally assumed by Allen (1951).

Based on the reference-state environmental data, the BBN correctly predicted a high chance of high juvenile trout density (54%) but incorrectly predicted a relatively low chance (16%) of high biomass of trout >200 mm. We did not have a complete environmental data set for Horokiri Stream before 1951. Compatible temperature, flow, and pelagic forage-fish abundance estimates were not available. These environmental variables may have been more favourable for trout production at the time. Nevertheless, on the basis of the above results, we suggest that our BBN will provide more accurate limiting factor probability outputs when applied to degraded streams.

The weakest component of our BBN is the subjective expert assessment of recruitment potential within the "recruitment-limited" subnet. We suggest that a BBN at least as complex as ours would be required to model recruitment limitation effectively. There are guidelines provided in Armstrong et al. (2003) for assessing the adequacy of spawning and juvenile rearing habitat within a catchment. We recommend that these are followed. However, if there is little information available to assess the recruitment capacity of a stream, we suggest that this node should be held neutral (at "OK") to reduce its potential to influence probability calculations within the BBN (as we did for Horokiri Stream). Developing a literature-based BBN to determine trout recruitment potential in stream catchments would be a useful way to consolidate the vast body of research available on this subject.

Despite its limitations, we have demonstrated that our BBN can generate sensible and objective hypotheses about limiting factors for trout in streams. Importantly, it does this with pragmatic data requirements to improve the management of data-poor fisheries. More broadly, our BBN is useful globally because it provides a flexible LFA template that can be tailored for any stream fish species. Adapting this template to other fish will make existing research directly applicable to species management and expose fundamental knowledge gaps.

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