State of Salmonid Streams Around the World:
A Multi-Scale Investigation of Habitat Quality, Restoration, and Abundance

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Abstract

State of Salmonid Streams Around the World: A Multi-Scale Investigation of Habitat Quality, Restoration, and Abundance.

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Many salmonid species are listed as threatened or endangered, despite over a hundred years of conservation efforts. Additionally, little is known about the spatial extent and abundance of salmonid populations around the world. This research combines ecological and hydrogeomorphological approaches to investigate salmonid abundance in streams. It uses a meta-analysis, field observations and a systematic review to assess restoration options for salmonid populations, determine if a morphological index is aligned with physical habitat and fish-based indices, and explore the range of salmonid abundance in streams around the world. Data from 100 stream restoration projects show that in-stream structures, a common restoration technique for salmonids, increase salmonid abundance. However, most projects are implemented at small spatial scales of a few hundred metres, and monitored for less than 5 years, which may be insufficient time for population changes to be apparent. Hence, it is unclear whether these projects provide a long-term solution. The Morphological Quality Index (MQI) considers fluvial processes at larger scales as well as channel forms, human impacts, and historical changes, but few studies have assessed its relevance for ecosystem health. A significant correlation was found between the MQI and habitat quality (using the Qualitative Habitat Evaluation Index, QHEI), in 26 salmonid streams, but establishing a strong correlation with fish metrics remains challenging. To describe the metrics of salmonid abundance at a broader spatial scale, a database was created using published material of over 1000 rivers with estimated salmonid biomass, covering 27 countries. This allowed detailed analyses of differences in biomass by species, region, period, and sampling techniques. Mean global biomass is 5.2 g/m^2, and while most streams are under 10 g/m^2, there is a large range (0-70.3 g/m^2). Salmonid production recorded for 194 rivers averaged 6.3 g/m^2/yr, and biomass and production were highly correlated (R = 0.82) with a mean production to biomass (P/B) ratio of 1.08. Expanding the list of variables in the database can help develop models to predict salmonid biomass, and determine conditions in high biomass streams. This knowledge will be useful for conservation and management authorities to design successful conservation programmes at a watershed scale.

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All manuscripts are directly linked to the primary purpose of this thesis. All authors contributed to the study conception and design. I performed the data collection, analysis, and material preparation, and wrote the first draft of each manuscript. All authors commented and edited subsequent versions of the manuscripts.

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1 **Introduction**

Biodiversity loss is a major concern, particularly for freshwater ecosystems (Cochran-Biederman et al., 2014; Dudgeon et al., 2006). Freshwater covers less than 1% of the Earth's surface and accounts for approximately 0.3% of global water supply but supports 40-50% of known fish species (G. M. Reid et al., 2013). However, due to a wide range of interacting pressures including habitat degradation, pollution, invasive species, over-exploitation of species, changes in flow regime, and changing climate regimes, the biological diversity and ecological health of freshwaters are in decline worldwide (Allan & Flecker, 1993; A. J. Reid et al., 2019; Strayer & Dudgeon, 2010; Vörösmarty et al., 2010). Freshwater fish are thought to be the most threatened group of vertebrates in the world (Freyhof & Brooks, 2011; G. M. Reid et al., 2013), and freshwater environments among the most threatened ecosystems in the world (Leidy & Moyle, 1998).

In many regions around the world, salmonid fish species are declining, with many populations listed as threatened or endangered (Dauwalter et al., 2020; Parrish et al., 1998). Habitat degradation is one of the major reasons for their decline. Information about what salmonid rivers look like, where populations might be threatened, and where populations are doing well, may be helpful to develop more effective restoration and conservation programs.

1.1 **Salmonid species**

The biological family Salmonidae (collectively known as the salmonids) consists of over 200 species in three sub-families: Salmoninae (including Pacific and Atlantic salmon, trout, and char species), Coregoninae (whitefishes and roundfishes), and Thymallinae (graylings). This thesis focuses on the genera *Oncorhynchus*, *Salmo* and *Salvelinus* of the Salmoninae sub-family, referred to as salmonids hereafter. The life cycles of salmonids are complex and highly variable between species and even between populations (Armstrong et al., 2003; Hutchings & Jones, 1998; Milner et al., 2003). Many salmonid species are anadromous, requiring the movement between freshwater and the sea to complete their lifecycles, although landlocked populations can occur in some species. The reproductive and juvenile phases typically occur in upper reaches of rivers, while growth phases occur in larger areas of lower rivers, lakes or the sea (Milner et al., 2003).

1.1.1 Distribution

Salmonids are found in most north temperate regions of the world (Leidy & Moyle, 1998). They have been deliberately introduced to every continent except Antarctic (Kershner et al., 2019) to promote sport fishing and have since become one of the main threats to many native populations in regions they have been introduced (Garcia de Leaniz et al., 2010). The native distribution of Pacific salmon (*Oncorhynchus* sp.) is centred around the west coast of North America and the east coast of Asia, while Atlantic salmon (*Salmo salar*) are located on the east coast of North America and throughout much of Europe. Major trout species (e.g. brown *Salmo trutta*, and brook *Salvelinus fontinalis*) are naturally located in Europe, or in eastern North America and the Great Lakes region.

1.1.2 Conservation status

Despite their importance, salmonid populations are declining in many regions around the world, with many populations and species listed as threatened or endangered (Jelks et al., 2008; Laramie et al., 2015; Yeakley & Hughes, 2014). In North America, 61% of described salmonid species are considered imperilled (Jelks et al., 2008), and 41% of salmonids in Europe are threatened (Freyhof & Brooks, 2011). In other regions, such as New Zealand and Australia, the introduction of salmonids has been implicated in the demise of native species (Cadwallader, 1996; McDowall, 2003, 2006; Townsend & Crowl, 1991) and can hamper conservation efforts for native fishes and water quality management (Townsend, 2003). However, trout remain an important economic and cultural part of these areas (Flecker & Townsend, 1994; Jackson et al., 2004; O'Connor, 1994), and even in places they are not native, deteriorating water quality, reduction in water quantity, and habitat degradation is raising concern for their viability (J. W. Hayes & Young, 2001; C. Stewart et al., 2019).

Many factors can impact the survival of anadromous species, including: barriers to migration such as dams, culverts, and weirs; pollution in their habitat range; habitat destruction and deterioration; and invasive species (McDowall, 1999; Rodeles et al., 2019; R. Saunders et al., 2011). While many of these variables will impact other species as well, anadromous species require adequate conditions throughout much of the catchment to the sea; they cannot always seek refuge in the upstream sections of rivers or in protected places. Thus, preserving and restoring whole watersheds will be important for the continued survival of these species as they occupy and move over several spatial scales (Katz et al., 2013; McDowall, 1999).

1.1.3 Measuring salmonid abundance

Knowing a species abundance is important for understanding population dynamics and for decision-making in species management and conservation (Yin & He, 2014). Population abundance can be expressed in several ways, for instance: density, biomass, or production. The type of abundance measure that should be used depends on what is being measured as they may produce different results about a species or population (Chiarucci et al., 1999). Population density, the number of organisms per unit area, is the standard measure for most species (Begon et al., 2014; Krebs, 1989). However, density may be inadequate for many populations. Firstly, it can be very difficult to count individuals of a population (Begon et al., 2014). Density also decreases with body size – larger organisms require more space (Grant et al., 1998; Grant & Kramer, 1990; Molles Jr., 2008; Steingrímsson & Grant, 1999). Fish vary greatly in size and require different habitat and food requirements (Grant et al., 1998; Grant & Kramer, 1990). Moreover, measuring numbers of individuals makes little sense in species with indeterminate growth, such as salmonid fish (Grant et al., 1998).

To address these problems, biomass (e.g. g/m^2) rather than density is commonly used by many fisheries biologists (Grant et al., 1998). Biomass may more accurately measure the 'size' of a population (D. B. Hayes et al., 2007) and can be a good approximation of productivity (Chiarucci et al., 1999). Average biomass can be calculated as the product of the number of individuals and the average weight of fish in the population (D. B. Hayes et al., 2007; Hunt, 1974). Biomass and density are static measures of populations – they provide a measure on the state of a population for only a single point in time (D. B. Hayes et al., 2007), which cannot consider the temporal variation (monthly and annually) that is known to exist (Hunt, 1974; Kratzer & Warren, 2012; Kwak & Waters, 1997).

Production is a more dynamic measurement of fish abundance because it describes populations over time, which is more meaningful for fish populations (D. B. Hayes et al., 2007), and it is responsive to environmental changes (Mann & Penczak, 1986). Production can be defined as the "total quantity of fish flesh elaborated in a year, regardless of whether or not all of it survives to the end of the year" (Ivlev 1945 cited in Mann & Penczak, 1986). Production is a rate, expressed as weight (or energy) per unit area per unit time and is commonly in g/m^2-y or kg/ha-y (Mann & Penczak, 1986). It can be measured in several ways, one being the Ricker (Ricker, 1946) method, that is production (P) is the product of mean biomass (B) of a cohort and mean instantaneous growth rate (G) of individuals within the cohort:

$$P = \bar{B}G$$

The annual production of salmonids has been studied since at least the 1950s (Allen, 1951; McKernan et al., 1950) and salmonids have also been the most widely studied group

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of fish in terms of production (Mann & Penczak, 1986), density, and biomass (Kwak & Waters, 1997). Determining biomass and production estimates of salmonids around the world and what characteristics are associated with high salmonid productivity could be important for salmonid conservation and restoration. Comprehensive appraisals of the global range of salmonid abundance have not been completed for several decades (i.e. since Mann & Penczak, 1986), thus the global state of salmonid populations is largely unknown.

1.2   Freshwater habitat

The viability of aquatic communities and species is dependent on habitat quality and quantity (Dyer et al., 1998), which together influence fish abundance and distribution (Armstrong et al., 2003; James et al., 2010; Kratzer & Warren, 2013). Habitat is roughly equivalent to the concept of the ecological niche, and encompasses a range of physical, chemical, and biological factors, all of which affect the growth and survival of a species or population (Armstrong et al., 2003; Jowett, 1997; Winger et al., 2005). Factors can act at a range of scales, from the immediate vicinity, through reach, river, oceanic and global extent (Armstrong et al., 2003). Physical patterns and processes acting at higher levels determine the habitat features present at lower levels in the system (Brierley & Fryirs, 2005; Frissell et al., 1986). Changes at a reach or watershed scale may cause habitat losses at a site, which may be left poorly understood if a larger scale is not considered (Imhof et al., 1996).

The habitat requirements of freshwater fishes are extremely variable (Heggenes et al., 1999). At the individual species level, the biological and geomorphological requirements of salmonid species have received a large amount of attention (Fukushima, 2001; Sear & DeVries, 2008; Wheaton et al., 2010). Habitat requirements are different for different salmonid species, populations, life-stages, and at different sites or streams (Armstrong et al., 2003; Bjornn & Reiser, 1991) and depend on the time of day (Mitchell et al., 1998) and season (Nickelson et al., 1992). Some species may adapt to suit local habitats and have wide tolerances in conditions (Armstrong et al., 2003; Milner et al., 2003). Variation between studies in types of habitat used may reflect differences between available conditions and ecology of the sites (Armstrong et al., 2003). Therefore, inferring habitat types between species should be done with caution (Greenberg, 1992).

1.2.1 Hydrogeomorphology

Hydrogeomorphology (also termed hydro-morphology, fluvial geomorphology and other similar terms) is the study of the interactions between the form of river channels, the processes that rivers carry out, and the landforms they create, at a range of spatial and temporal scales (Charlton, 2008; Newson & Sear, 1998). Spatial scales range from the drainage basin (whole catchment), through stream segments (e.g. series of meanders,

supply of water and sediment from upstream), channel reaches (e.g. a single meander, flow hydraulics within the bend), channel units or bedforms (e.g. pools and riffles), subunits (e.g. point bars), and individual particles (Charlton, 2008; Knighton, 1998; Newson & Sear, 1998). Time scales in geomorphological studies range from the formation of river channels over hundreds of thousands of years, through migration patterns of rivers over years or decades, annual flow patterns, to flow sediment interactions that occur within minutes (Charlton, 2008). Degradation of hydrogeomorphological conditions involves factors such as river straightening, flow regulation, sediment load alterations, and river disconnection from the floodplain, creating varying impacts in different river typologies (Campana et al., 2014).

Many authors have discussed the impact that geomorphological changes in rivers have on aquatic biota (Brierley et al., 2010; Poole, 2010; Vaughan et al., 2009). Concepts in hydrogeomorphology have influenced frameworks in stream ecology such as the River Continuum Concept (Vannote et al., 1980), Network Dynamics Hypothesis (Benda et al., 2004), and the Riverine Ecosystem Synthesis (Thorp et al., 2008). The European Water Framework Directive also considers that restoring hydrogeomorphology is essential to reach the 'good status' of rivers (European Commission, 2000). River management from a hydrogeomorphological perspective places the role of physical stream characteristics and processes at the centre (Newson & Large, 2006). Despite these frameworks, there is still little known about how morphological quality and its adjustments over time affects riverine biodiversity (Scorpio et al., 2016).

1.3 Restoration

Stream restoration has become an increasingly popular process in response to declining fish populations (Bash & Ryan, 2002; Kondolf & Micheli, 1995; G. B. Stewart et al., 2009; Whiteway et al., 2010). Bernhardt et al. (2005) estimated that between 1990 and 2003, in the United States alone, at least $14 to $15 billion was spent on river restoration, averaging around $1 billion per year. Analysis of river restoration projects across the United States (2005) found that common goals for restoration were to enhance water quality, manage riparian zones, improve in-stream habitat, provide fish passage, and stabilize banks; however, 20% of projects had no stated goals (Bernhardt et al., 2005).

Conservation and reintroduction efforts for freshwater fish are often unsuccessful because the causes of any initial decline remain in place or habitat is inadequate (Cochran-Biederman et al., 2014; Dunham et al., 2011; Nickelson et al., 1992; Rosenfeld & Hatfield, 2006; van Zyll de Jong & Cowx, 2016). Many projects fail to carry out habitat assessments prior to restoration, resulting in higher failure rates (Cochran-Biederman et al., 2014). Scientists have provided standards and information for successful river restoration (Palmer et al., 2005), but restoration is often carried out by managers and practitioners

who may not always follow scientific principles for environmental projects (Biron et al., 2018; Minns et al., 1996; Wohl et al., 2005). In Bernhardt et al.'s (2007) analysis of 317 projects across the USA nearly two-thirds of project managers determined their projects to be successful, but less than half of the projects set measurable objectives. In many cases, monitoring and evaluation of successful completion of goals is not carried out (Bash & Ryan, 2002; Bernhardt et al., 2005; Whiteway et al., 2010) and goals are not linked to any kind of success criteria (Bernhardt et al., 2007).

It is increasingly recognized that process-based principles are needed to restore river ecosystems, such as leaving more space around rivers for fluvial processes to operate (Biron et al., 2014; Buffin-Bélanger et al., 2015; Kline & Cahoon, 2010; Ollero, 2010; Piégay et al., 2005). However, most restoration actions continue to focus on the symptoms of degradation by adding structures or modifying channel forms that are perceived to provide good habitat for fish (i.e. in-stream restoration structures) (Beechie et al., 2010; Imhof et al., 1996; Roni et al., 2002).

1.3.1 In-stream structures

In-stream restoration structures were first developed on a large scale for trout in Wisconsin and Michigan in the 1930s (Nickelson et al., 1992; Thompson, 2006; White, 1996), to enhance habitat quality and quantity for increasing fish productivity. Few early studies measured the fish response to structure installation (Hale, 1969; Hartzler, 1983; Hunt, 1976; Latta, 1972), and previous meta-analyses (G. B. Stewart et al., 2009; Whiteway et al., 2010) on the effectiveness of in-stream structures on salmonid abundance gave contrasting results.

Installed structures are not always appropriate for the stream characteristics or cause the intended effects. In early restoration projects, failure was often attributed to applying techniques developed for low gradient streams (e.g. weirs and deflectors) to streams of high gradient and energy (Frissell & Nawa, 1992; Platts & Rinne, 1985). The move towards using more natural structures, such as large wood (LW or LWD (large woody debris[1])) and boulders, instead of more artificial structures, such as weirs and deflectors, in some ways attempts to limit structure failure (Roni et al., 2006) and buffer the effects of drought and flooding events (Sweka & Hartman, 2006). Few assessments of in-stream structures are greater than 5 years (Champoux et al., 2003; Roni et al., 2008). But

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[1] Recently the scientific community has been pushing to replace the term LWD with LW (large wood), as "debris" has negative perceptions (Ruiz-Villanueva et al. 2016), but Chapter 2 uses LWD to capture restoration papers that use the term since it takes time for habits like the use of "debris" to be widely accepted in the scientific community.

morphology changes required to create habitat may take years to occur (Roni et al., 2006; Roni & Quinn, 2001), and the response of fish populations to habitat changes will take even longer (Binns & Remmick, 1994; Luhta et al., 2012). Because of contrasting results of effectiveness, and that in-stream structures are still a common restoration technique, an updated detailed analysis on in-stream structure usefulness may be required.

For a longer-term solution, restoring natural processes is a better restoration approach. Unmodified streams with naturally dynamic hydrological regimes and processes are more resistant to the negative effects of flooding and drought (Elosegi et al., 2011; Poff et al., 1997), and if natural processes are restored, habitats that are limiting to native fish may more likely be created or restored (Beechie et al., 2010; Florsheim et al., 2008).

1.3.2 Process-based restoration

In recent years a much stronger emphasis on the importance of restoring natural fluvial processes at the watershed scale has occurred (Beechie et al., 2010; Biron et al., 2018; Roni et al., 2008), instead of focusing on manipulating in-stream habitats and specific morphologies that are targeted by in-stream structures (Roni et al., 2002). Allowing a river to move freely and maintaining a natural sedimentation regime is recognized as important for ensuring healthy river ecosystems (Choné & Biron, 2016; Florsheim et al., 2008; Williams et al., 2020). The ecological significance of erosion in providing riparian habitats and natural bank habitats providing large woody debris are becoming more obvious for river restoration practitioners (Benda et al., 2004; Florsheim et al., 2008; Piégay et al., 2005). A naturally moving river acts as a passive restoration approach, as a natural sedimentation regime creates habitats that many in-stream structures aim to replicate (Biron et al., 2018; Choné & Biron, 2016; Williams et al., 2020). Such passive restoration approaches are more likely to succeed in the long term (Mikuś et al., 2019).

Techniques where process-based principles have been employed in fish restoration include removing dams, which allow flow and sedimentation patterns to re-establish, the most notable probably being the Elwha dam in Washington State, USA (Pess et al., 2008; Shaffer et al., 2008); placing woody debris in streams to create fish habitat (Bisson et al., 2003; Pess et al., 2012; Roni et al., 2015); considering dynamics with the riparian zones and connection to the ocean to improve nutrient flows (Naiman et al., 2002); and considering beaver dams to restore geomorphic, hydrologic, and ecological functions of rivers (Bouwes et al., 2016; Conner et al., 2016; DeVries et al., 2012; Naiman et al., 1988; Pollock et al., 2012, 2017).

1.4 Indicators for assessing river conditions

Indices have been developed to assess stream habitat and ecological health and can incorporate biotic, physical, or chemical aspects of a stream (Gazendam et al., 2011). The type of index or assessment to use depends on the environmental objectives, for example, fish distribution, conservation, water management, or the assessment of ecosystem integrity or geomorphic condition (Raven et al., 2010). The European Water Framework Directive defines good ecological status of surface waters in terms of the quality of biologically, hydrogeomorphological, and chemical (water quality) characteristics (European Commission, 2000), stressing the importance of all of these components when considering ecological indicators.

1.4.1 Biological

Biological indices (or biomonitoring) are used to determine a stream's biological health, or biotic integrity. Biotic integrity has been defined as the ability to support and maintain "a balanced, integrated, adaptive community of organisms having a species composition, diversity, and functional organization" comparable to that of a similar natural habitat or ecoregion (i.e. a reference condition) (Karr & Dudley, 1981, p. 56). Periphyton, macro-invertebrates and fish are the most common indicators in river biomonitoring (Li et al., 2010). Macro-invertebrates and fish serve as indicators for degradation at local or regional scales, respectively, and are sensitive to habitat loss and effects from other environmental stressors (Souza & Vianna, 2020).

Biological indices can link water quality and habitat quality to the distribution and abundance of species (Golfieri et al., 2018). They are able to identify long-term pollution problems better than intermittent water quality sampling that only measures in-situ conditions at the time of testing (Gazendam et al., 2011). Thus, biotic indicators can be accurate in assessing stream conditions, but are unable to determine causes of problems if they are found (Gazendam et al., 2011). Relying only on biological indicators gives an incomplete ecological assessment of the entire river corridor as they do not describe hydrogeomorphological pressures or alterations (Belletti et al., 2018; Campana et al., 2014; Golfieri et al., 2018).

1.4.2 Physical

There are a range of physical methods to assess river conditions that focus on components of physical habitat, riparian habitat quality, morphological characteristics, and hydrological regime alteration. Belletti et al. (2014) concluded that most physical assessment methods inadequately considered physical processes, such as longitudinal and lateral connectivity, large scale sediment connectivity, channel adjustments, and vertical

connection with groundwater. There has also been a lack of a standardised methodology for mid- to long-term monitoring of river habitats, which would allow comparison of rivers among regions or at higher spatial levels (Fernández et al., 2011; Raven et al., 2010).

Methods to assess physical habitat generally only look at a small scale (site or reach that is a few hundred metres), current state of conditions (Belletti et al., 2014; Golfieri et al., 2018). A reach scale is inadequate to accurately analyse morphological alterations because processes and causes usually act on a wider scale (Golfieri et al., 2018; Imhof et al., 1996; Rinaldi et al., 2013). Changes at a segment or watershed scale, which are often responsible for habitat losses at a site, are left poorly understood (Imhof et al., 1996). Furthermore, channel processes and adjustments over time are often neglected due to the static nature of many habitat assessments (Rinaldi et al., 2013). Collection of data is also time-consuming with limited use of remote sensing and geomorphological methods (Belletti et al., 2014; Golfieri et al., 2018). However, physical habitat methods are useful for characterising the range and heterogeneity of physical habitats present and can help establish links between morphology and ecological conditions and communities (Belletti et al., 2014).

Incorporating hydrogeomorphological assessments into river monitoring and evaluation is now recognised as fundamental (Belletti et al., 2018). Since the introduction of the Water Framework Directive, which requires incorporating hydrogeomorphology into river management, numerous methodologies have been developed to do so (Belletti et al., 2014). Morphological assessments include a broader range of evaluations than physical habitat methods and they generally consider a larger spatial and temporal scale (Belletti et al., 2014; Golfieri et al., 2018). Often the entire river corridor is considered (i.e. channel banks, riparian zones, and floodplain) as well as channel patterns and physical variables, rather than in-stream habitats (Belletti et al., 2014). Some morphological assessments include river processes, such as sediment transport, bank erosion, and channel adjustments (Belletti et al., 2014). In contrast to physical habitat methods that often look at a site statically in time, morphological assessments often take account of recent and historical channel adjustments (Belletti et al., 2014; Golfieri et al., 2018; Rinaldi et al., 2013). The strengths of a morphological approach can also be its weaknesses or limitations. Several components may be difficult to assess, for example, physical processes and temporal elements (Belletti et al., 2014). Among morphological assessments there is also a lack of linkage with biological and water quality variables and little consideration of habitat for aquatic species (Belletti et al., 2014).

1.4.3 Metrics

Two indicators are used in this thesis to assess river quality: a physical habitat indicator (the Qualitative Habitat Evaluation Index (QHEI)), and a morphological index (the Morphological Quality Index (MQI)). The QHEI is a visual assessment that allows a rapid

evaluation of streams at a reach scale. It measures physical habitat quality, particularly aimed at factors that influence fish communities and other aquatic life, and considers: substrate, in-stream cover, channel morphology, riparian zone and bank erosion, pool and riffle quality, and stream gradient (Rankin, 1989; Taft & Koncelik, 2006). The QHEI can relate differences in physical habitat features to biological variation and determine habitat for stream organisms at individual sites (Gazendam et al., 2011). However, it is still focused on a small scale (comparative to a watershed), does not include processes or temporal adjustments, and requires field assessments to compute.

The MQI was developed to assess stream morphological quality in Italian rivers, designed for the Water Framework Directive (Rinaldi et al., 2013) and has been expanded and applied to other European countries (Rinaldi et al., 2015) as well as in other geomorphological contexts, for example Canadian lowland rivers (Lemay et al., 2021) or Eastern-Mediterranean ecosystems (Moshe et al., 2022). The procedure consists of 28 indicators, considered in terms of three components: channel forms and processes, artificiality or human impacts, and historical channel adjustments. Acknowledging that past stream conditions may be of little practical use for river management and restoration as the conditions may be very different from the present ones, the authors aim to identify a reference state that represents a dynamic river reach that is performing morphological functions expected for a specific typology, and shows no or only minor human impacts (Rinaldi et al., 2013). The method considers processes (i.e. is process-based), rather than only considering channel forms, and is aimed to assess morphological quality rather than just provide a quantification of processes or channel evolution (Rinaldi et al., 2016).

The ecological state of the rivers is not considered in the MQI – a high morphological quality is not necessarily related to a good ecological state, but it is commonly the case (Rinaldi et al., 2016). It is recognised that the presence of naturally dynamic physical processes encourages the creation and maintenance of habitats and help provide ecosystem integrity (Brierley & Fryirs, 2005; Florsheim et al., 2008; Wohl et al., 2005).

1.5   Synthesis and research gaps

While huge effort and money is being spent on salmonid restoration, many of the species continue to decline, implying that many restoration projects do not offer long-term, sustainable solutions. Owing to these declines, in-stream restoration structures have been used for over 80 years to increase abundance of fish. However, the relative effectiveness of these structures remains unclear for some species or regions, partly due to contrasting conclusions from previous studies.

Habitat degradation is one of the major reasons for freshwater species decline. Hydrogeomorphological processes (such as sediment transport, bank erosion, and

flooding) operate at the segment and catchment scale and determine habitat features in river reaches. However, habitat quality indices and restoration for freshwater fish species are often implemented at small spatial scales of a few hundred metres (i.e. in-stream structures). In contrast, the MQI considers fluvial processes at larger scales as well as channel forms, human impacts, and historical changes. Despite the theoretical link between hydrogeomorphology quality and stream biology, few studies have assessed the relevance of morphology quality indices to determine ecosystem health.

In many regions around the world many populations of salmonid species are listed as threatened or endangered. To our knowledge, comprehensive compilations on the global range of salmonid abundance have not been completed for several decades, so the global state of salmonid populations is largely unknown. There is evidence of local declines, but little is known on the spatial extent and abundance of populations and species in many parts of the world. Knowing the abundance of populations is important for understanding population dynamics and for decision-making in species management and conservation (Yin & He, 2014). It can tell us where populations might be threatened and help us determine where restoration should take place. Additionally, knowing areas with high salmonid abundance is useful to determine what environmental conditions may be ideal for populations to thrive.

There have been many attempts to estimate abundance of fish populations using models combining multiple variables. Stream width, flow stability, water temperature, stream cover, gradient, and water chemistry are among some of the environmental variables used to predict salmonid abundance and habitat. However, these models based on environmental variables are typically developed for a particular region, and haven't been as useful when applied to other areas of the world. Additionally, many of these variables are difficult to quantify for a large global dataset without field sampling. We currently don't have a global perspective on what abundance looks like around the world.

1.6 Research objectives

The overarching goal of this research is to combine ecological and hydrogeomorphological approaches to investigate salmonid abundance in streams. The specific objectives of this research are to:

1. Evaluate the effectiveness of artificial and more natural in-stream restoration structures to increase salmonid abundance (numbers and density) and biomass in rivers. This was assessed through a meta-analysis to obtain a current estimate of the effect of in-stream structures on salmonid abundance and biomass, to analyse the effects of different types of structures on various salmonid species and to examine any variation with time (Chapter 2).

2. Determine whether hydrogeomorphological quality (MQI), habitat quality (QHEI), and biotic indices for fishes (number of fish species, Index of Biological Integrity (IBI), and trout biomass) are related in salmonid streams. This was investigated through field observations in two different geographical regions of the world with differing river types: Ontario, Canada and Aotearoa New Zealand (Chapter 3).

3. Develop a database of salmonid biomass in streams around the world, with variables that may affect biomass in streams, in order to determine if there are differences in biomass by species, region, time period, and sampling techniques. This is addressed through a systematic review which allow the compilation of the largest database of published biomass and production studies for stream salmonids (Chapter 4).

Liaison paragraph

The first goal of this research was to determine if the implementation of in-stream structures, a common restoration technique for salmonids, was effective in increasing salmonid biomass and density in rivers. This involved reviewing two previous meta-analyses that used different methodologies and gave contrasting results. A meta-analytic approach was used to update these previous analyses and obtain a current estimate of the effect of in-stream structures on salmonid abundance. The findings are helpful for both researchers interested in fundamental knowledge on process-based and form-based differences in stream restoration as well as practitioners who need help in deciding whether in-stream structures are an effective long-term restoration technique, or if other approaches could be considered for long-term sustainability of salmonid species. Note that the following chapter, which details the investigation and results, was published in 2020 (in the Canadian Journal of Fisheries and Aquatic Sciences) and does therefore not include studies published after 2020.

2 Impact of in-stream restoration structures on salmonid abundance and biomass: an updated meta-analysis

Kyleisha J. Foote, **Pascale M. Biron** and **James W.A. Grant**

Abstract: Owing to declines in salmonid populations, in-stream restoration structures have been used for over 80 years to increase abundance of fish. However, the relative effectiveness of these structures remains unclear for some species or regions, partly due to contrasting conclusions from two previous meta-analyses. To update and reconcile these previous analyses, we conducted a meta-analysis using data available from 1969 to 2019 to estimate the effect of in-stream structures on salmonid abundance (number and density) and biomass. Data from 100 stream restoration projects showed a significant increase in salmonid abundance (effect size 0.636) and biomass (0.621), consistent with previous reviews and studies, and a stronger effect was found in adults than in juvenile fish. Despite a shift towards using more natural structures (wood and boulders) since the 1990s, structures have not become more effective. However, most projects monitor for less than 5 years, which may be insufficient time in some systems for channel morphology to adjust and population changes to be apparent. Process-based techniques, which give more space for the river, allow more long-term, self-sustaining restoration.

2.1 Introduction

Freshwater fish are in decline worldwide due to multiple factors including habitat degradation, overexploitation, pollution, climate change, and water extraction (Strayer & Dudgeon, 2010), making them the most threatened group of vertebrates in the world (G. M. Reid et al., 2013). In response to these declines, a wide range of approaches have been used over the past 100 years to increase fish populations and restore rivers to a more natural state (Bernhardt et al., 2007; Bernhardt & Palmer, 2011; Roni et al., 2008). It is increasingly recognized that process-based principles are needed to restore river ecosystems, such as leaving more space around rivers for fluvial processes to operate (Biron et al., 2014; Buffin-Bélanger et al., 2015; Kline & Cahoon, 2010; Ollero, 2010; Piégay et al., 2005). However, most restoration actions continue to focus on the symptoms of degradation by adding structures or modifying channel forms that are perceived to provide good habitat for fish (Beechie et al., 2010; Roni et al., 2002). The major target are stream salmonids, due to their economic and cultural importance, and the realisation that many are becoming threatened or endangered (Baldigo & Warren, 2008; Bash & Ryan, 2002; Rosi-Marshall et al., 2006).

Often, these restoration projects involve artificial structures (in-stream structures), first developed on a large scale for trout in Wisconsin and Michigan in the 1930s (Nickelson et al., 1992; Thompson, 2006; White, 1996). The structures used over the years have been based on early designs, despite little evidence in the pre-1980 literature that in-stream structures increased fish populations (Roni et al., 2002, 2008, 2015; Roni & Quinn, 2001; Thompson, 2006); few early studies measured salmonid abundance or biomass in response to structure installation (e.g. Hale, 1969; Hartzler, 1983; Hunt, 1976; Latta, 1972; Thompson, 2006; Ward & Slaney, 1981). The purpose of in-stream structures, both historically and currently, include enhancing habitat complexity and diversity (Bilby & Likens, 1980; Louhi et al., 2016; Swales, 1994; van Zyll de Jong & Cowx, 2016), increasing pool habitat (House & Boehne, 1985; Hunt, 1976; Keller & Swanson, 1979; Roni et al., 2010), providing spawning habitat, increasing cover (Gowan & Fausch, 1996; Hunt, 1976; Solazzi et al., 2000), increasing macroinvertebrate resources for fish (Kail et al., 2015), and particularly more recently, restoring channel morphology (Davidson & Eaton, 2013). The overarching aim is to increase the productive capacity of habitat for fish (Mitchell et al., 1998; Roni et al., 2010). Although few restoration projects evaluate their success (Bash & Ryan, 2002; Bernhardt et al., 2007; Bernhardt & Palmer, 2011), recent reviews have concluded that in-stream structures can lead to an increase in salmonid abundance (Roni, 2019; Roni et al., 2008).

Meta-analysis provides a statistical framework for comparing the results of multiple independent studies that test the same hypothesis (Harrison, 2011) and is particularly valuable in ecological studies where statistical power is often low, due to small sample sizes and high variability (Hillebrand, 2008; G. B. Stewart, 2010). Meta-analyses compute a

quantitative average estimate or effect across different studies and a measure of uncertainty for that effect (Harrison, 2011; Hillebrand, 2008). Furthermore, effect sizes can be calculated for different groups within the data (Hillebrand, 2008), for example by species.

Two previous meta-analyses (G. B. Stewart et al., 2009; Whiteway et al., 2010) on the effectiveness of in-stream structures to increase salmonid abundance used different methodologies and gave contrasting results. However, the conclusion by Stewart et al. (2009, p. 931) that "effectiveness of in-stream devices is equivocal" was based on data that included errors (Whiteway et al., 2010). These errors included reversing treatment and control reaches for one study and including projects that were outside of the scope of their review: did not use in-stream structures; used multiple restoration techniques; or combined data for species outside their target range. On the other hand, Whiteway et al. (2010) included more studies than Stewart et al. (2009), (51 vs 31), by relaxing the criteria for inclusion and omitting a variance estimate in each study. Variance is considered a 'hallmark' of meta-analysis, providing a weighting to average and compare effect sizes and minimise bias from studies with small sample sizes (Lajeunesse, 2011, 2015). Without it, erroneous conclusions may be drawn when pooling effect sizes (Lajeunesse, 2011).

In this study, we examined how the use of in-stream structures has varied over time and conducted a meta-analysis to obtain a current estimate of the effect of in-stream structures on salmonid abundance and biomass. We updated the previous meta-analyses both published a decade ago (G. B. Stewart et al., 2009; Whiteway et al., 2010) and applied a similar meta-analysis methodology as Stewart et al. (2009) whilst correcting their errors and adding biomass as a response variable. We measured whether effectiveness differed between the types of structures installed, different salmonid species and age classes, and seasons that fish were sampled. We also tested whether the effectiveness of restoration varied with the size of the stream restored. Additionally, we examined how the types of in-stream structures used (more artificial – deflectors and weirs, or more natural – boulders and large wood) varied over time, to test whether the theoretical paradigm shift towards process-based restoration since the 2000s is reflected in practice.

2.2 Methods

2.2.1 Search strategy and study selection

To obtain evidence and data for the meta-analysis, systematic review methodology was followed using guidelines from the Collaboration for Environmental Evidence (CEE 2018) (see Appendix A, Table A1 for further details on the methods used). Review questions were formulated among the authors and criteria required for data included in the meta-analysis was generated (Table 2.1). Our search strategy was focused to include

literature in peer-reviewed journals and grey literature (e.g. conference proceedings, government or organisation reports, and theses) published from 1969 to December 2019. First, studies used in the previous two meta-analyses (G. B. Stewart et al., 2009; Whiteway et al., 2010) and several reviews (Roni, 2019; Roni et al., 2002, 2008, 2015) were assessed for relevant criteria (Table 2.1). A literature search was then conducted in English for peer-reviewed articles and grey literature publications in electronic databases, online search engines, and library catalogues of relevant organisations. Electronic article databases included Web of Science, Google Scholar, Scopus, and ProQuest Dissertations & theses. The following key words were used wherever possible: (trout OR salmo*) AND (river OR stream OR channel OR reach OR watershed OR catchment) AND (restor* OR enhanc* OR improv* OR rehabilit* OR structure OR placement OR weir OR deflector OR cover OR boulder OR log OR wood OR LWD) AND (habitat OR population OR abundance OR densit* OR biomass), where * denotes a wildcard that can represent any collection of characters. Fifteen other databases and specialist organisations were searched using a simplified search string (see Table A1 for details). Searches were conducted in December 2018, April 2019 and March 2020.

Results from the searches were screened in three stages: (i) title, (ii) abstract, and (iii) full text. At each stage, publications were searched for inclusion criteria for the analysis (Table 2.1) and further references were found from the literature cited of included articles. The criteria for inclusion limited the number of suitable publications from the search to 63 (see Appendix A1 for a list of studies included). Some publications were compilations of multiple restoration projects that used different restoration techniques and were counted as different projects where monitoring data were reported separately, resulting in 100 projects overall. The number of publications used increased from the previous meta-analyses which included 51 (Whiteway et al., 2010) and 32 (G. B. Stewart et al., 2009) publications. Out of the 63 publications used in this analysis, 25 were not used in either of these previous analyses, 7 were used only by Stewart et al. (2009), 15 were used only by Whiteway et al. (2010), and 16 were used by both authors. The remaining publications in Whiteway et al. (2010) had no measure of standard deviation and/or sample size, and eight publications in Stewart et al. (2009) did not fit the assessment criteria (Table 2.1).

Table 2.1. Criteria for inclusion in the meta-analysis

Criteria	Include	Exclude
Ecosystem	River and streams, artificial channels that are connected to natural ones	Lakes and coastal waters
Species	Salmonid species	Non-salmonid species
Location	Global	None
Intervention	In-stream restoration structures: deflectors, weirs, cover structures, boulders, large woody debris. Examples of these structures are provided in Table 2.2.	Fish passage devices, comparison of degraded rivers to natural rivers, in-stream structures that were not used for restoration (e.g. for flood control or erosion control unless specifically for restoration purposes), spawning gravel
Monitoring design	Before/After, Control/Impact (BACI); control (or reference) and impact (or treatment, intervention, or experimental sections) (CI), also called extensive-post treatment; before and after treatment (BA)	No monitoring data, no appropriate control, modelled outcomes
Monitoring data	Mean, standard deviation, and sample size for at least a treatment group and control group	No quantitative data, inability to compute standard deviation
Time period	Any length of study published before 2019	Articles published outside of these limits
Measures	Total number, density and/or biomass for at least two comparable groups (i.e. impact and control, before and after). Any method of collection.	Survivability, condition, growth, movement of fish
Outcome	Irrespective of effects	None

In-stream structures were categorised into five types within two categories: artificial structures - weirs (including v-dams or wedge dams), deflectors, and cover; and, natural structures - boulders, and large wood (also referred to as large woody debris (LWD)). Structure types used followed Whiteway et al. (2010) and are common in-stream restoration techniques for salmonid rivers (Hunt, 1993). We defined artificial structures as those consisting of material, either naturally present or brought to the site, organised into a specific shape (e.g. V-shape or perpendicular) and can be made of boulders, wood or logs, metal, wire, or other artificial materials. Natural structures are boulders or woody material that have been placed in the stream to replicate natural accumulations of wood or rocks. Often, multiple structure types were used within a project. Projects were classified as Artificial if only artificial structures were used, Natural if only natural structures were used, and Both if both types were used. The types of structures in each category, the functions

they provide, and the number of projects that include each structure are listed in Table 2.2. Projects used three general types of monitoring design, with considerable variation within each: Before/After, Control Impact (BACI) designs (Stewart-Oaten et al., 1986; Stewart-Oaten & Bence, 2001); Before After (BA) designs tested differences between treatments (impact sites) before and after; and, Control Impact (CI) or extensive post-treatment designs compared treatments (or impacts) to adequate controls (Hicks et al., 1991; Roni et al., 2006; Roni & Quinn, 2001). Within these designs, controls were selected in multiple ways: upstream or downstream from impact sites, on different streams of similar characteristics in the region, or even next to impact sites (i.e. stream is divided into two and one side is treated and one is not).

Table 2.2. Structure types, functions, and use in projects included in the meta-analysis

Structure type (no. of projects)	Examples	Functions (references that describe function of structures)
Artificial structures		
Weirs (29)	Can be made from logs, boulders, and gabions; v-notch weirs, v-dams	• Creates pools (Gowan & Fausch, 1996; House & Boehne, 1985; Mitchell et al., 1998) • Reduces stream bed gradients (Klassen & Northcote, 1986) • Impounds beds with spawning gravel (House, 1996; Klassen & Northcote, 1986) • Restore incised streams (Conner et al., 2016) • Creates flow heterogeneity (Näslund, 1989) • Increase oxygen content in water by creating turbulent flow (Mitchell et al., 1998)
Deflectors (25)	Can be made from boulders, logs and gabions; bank deflectors, wing deflectors, vanes, groins, spur dikes, abutments	• Concentrates and accelerates stream current (Linløkken, 1997; Mitchell et al., 1998; J. W. Saunders & Smith, 1962) • Modifies flow and creates flow heterogeneity – important for fish development and spawning (Champoux et al., 2003) • Enhances scour to create pools (Pagliara & Kurdistani, 2017; Ward & Slaney, 1981) • Improves sinuosity (Hunt, 1976; Mitchell et al., 1998) • Narrows and deepens channels (Hunt, 1976), creating pools (Thompson, 2006)
Cover (30)	Bank cover structures, half-	• Provides protection from predators, competitors, or unfavourable conditions such as high velocities (Boss &

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Structure type (no. of projects)	Examples	Functions (references that describe function of structures)
	logs, cribs, single logs, can be made from artificial and natural material	Richardson, 2002; Hartzler, 1983) • Provides visually isolated shady areas (Dolloff, 1986; Fausch, 1993) • Creates good feeding position of low velocity adjacent to a switch current (Dolloff, 1986; Fausch, 1993; Inoue & Nakano, 1998)

Natural structures

Structure type (no. of projects)	Examples	Functions (references that describe function of structures)
Boulders (24)	Boulder groups and clusters, natural or placed boulders, cobble addition	• Creates shelter from current (Fausch, 1993; Giannico, 2000) • Provides cover (Bjornn et al., 1991; Dieterman et al., 2018; Fjellheim et al., 2003) • Increases turbulence and modifies flows (Miller, 1997; Näslund, 1989) • Creates habitat diversity (van Zyll De Jong et al., 1997)
LWD (43)	Natural and added large wood, structures, bundles, brush, fine woody debris, log dams (includes engineered if structured in a way to replicate natural placement), rootwads, beaver dam analogues (if made from natural materials)	• Facilitates gravel deposition for spawning (Antón et al., 2011; Sweka & Hartman, 2006) • Retains sediments, gravel, and organic matter (Bilby & Likens, 1980; Roni et al., 2015) - affects benthic invertebrate communities which are food for fish (Inoue & Nakano, 1998; Kratzer, 2018) • Creates and scours pools (Berg et al., 1998; Keller & Swanson, 1979) • Provides cover (Culp et al., 1996; Flebbe, 1999; Giannico & Hinch, 2003) • Increases nutrients through carcass retention (Johnson et al., 2005) • Increases bank stability (Keller & Swanson, 1979) • Provides shelter from current (Fausch, 1993), especially during floods (Lehane et al., 2002) • Increases structural complexity (Giannico, 2000; Zika & Peter, 2002) and diversity of habitats (Bilby & Likens, 1980; Lehane et al., 2002; Roni, 2001) • Raises water table and repairs incised streams (Pollock et al., 2014)

2.2.2 Data extraction and analysis

The location of restoration projects, year of restoration, project monitoring time, and use of different types of structures was recorded for each study. Change in the use of structures over time was tested with a chi-squared test. Five studies that did not report a single restoration year were excluded from this analysis, because either multiple projects were completed in different years that could not be extracted separately, or the year of restoration completion was not reported. The maximum monitoring time was calculated from the last year that data were extracted (seven projects that did not report monitoring time were excluded).

To obtain a measure for the effect of restoration structures on fish (termed effect size), we extracted the change in mean abundance (see below) at impact and control sites for BACI studies, and the mean for CI and BA studies. To calculate an effect size for a study i, a mean or change in mean (impact, m_{1i} and control, m_{2i}), standard deviation (SD_{1i} and SD_{2i}) and sample size were required for two groups (Deeks et al., 2001). The total sample size of a study i (N_i) is:

$$(2.1) \quad N_i = n_{1i} + n_{2i}$$

where and n_{1i} and n_{2i} are the samples sizes from the impact and control groups, respectively. The pooled SD of the two groups (S_i) is:

$$(2.2) \quad S_i = \sqrt{\frac{(n_{1i}-1)SD_{1i}^2 + (n_{2i}-1)SD_{2i}^2}{N_i - 2}}$$

When fish data were reported for multiple years before or after restoration, data were averaged across years. If multiple seasons were presented, data were extracted separately if possible, or averaged if less than 3 years of data were provided or no SD was given (at least three data points were needed to calculate SD). If SDs were not given, they were calculated from available data using methods recommended for meta-analyses (Higgins et al., 2019). Methods used to extract and calculate means and SDs were consistent for both groups within each project. Data from different restoration treatments, species, and age classes (if reported separately) within the same study were considered as independent data points, for which an effect size was calculated.

In each study, variables of salmonid abundance were measured in different units, such as total number in a reach, density (fish/m^2), or biomass (g/m^2). The method used was consistent within each project and should not bias the results, but was standardised using a common effect size (Deeks et al., 2001). Effect sizes were calculated for each species and age distribution reported, resulting in 198 individual effect sizes for number or density measures (termed abundance hereafter) and 52 for biomass measures. The Hedge's g

standardised mean difference method (Hedges, 1981) was used to calculate the effect size of each measure from the impact and control means, SDs, and sample sizes. In each measure, the size of the impact effect (difference in means) relative to the variability observed in that trial (pooled SD S_i) was assessed and an adjustment was included to correct for small sample bias (Deeks et al., 2001). Hedge's g is calculated as in (Deeks et al., 2001):

$$(2.3) \quad g_i = \frac{m_{1i} - m_{2i}}{s_i} \left(1 - \frac{3}{4N_i - 9} \right)$$

with standard error:

$$(2.4) \quad SE(g_i) = \sqrt{\frac{N_i}{n_{1i}n_{2i}} + \frac{g_i^2}{2(N_i - 3.94)}}$$

The small sample bias approaches zero when N_i is large (over 10) but can be substantial when N_i is small (Hedges, 1981), ensuring that studies with small sample sizes do not have equal weighting in the overall effect size. Individual effect sizes for abundance and biomass were each combined into a weighted average, termed an overall treatment effect, using the DerSimonian and Laird random effects model (DL) with a Hartung-Knapp adjustment (Deeks et al., 2001; DerSimonian & Laird, 1986). Analysis was conducted using the 'meta' package (Schwarzer, 2007) in R 3.5.1. (R Core Team, 2019). Abundance and biomass were also combined to obtain an overall effect size for all studies. We used a linear regression to test for a relationship between effect size and stream width before restoration. There was no differentiation made between different stream width measurements used (i.e. bank-full or wetted width), as it was reported inconsistently across studies or the type of width measured was not stated.

An overall effect size was calculated by structure type, species, age class, and season that fish were sampled. An effect size was calculated for each structure type whether or not other structures were present, and for projects that installed only one structure type at the restoration site (i.e. no other structure interventions were used) to test the effect of that particular structure type. The number of effect sizes calculated for each species and age class is reported in Table 2.3. Ages were grouped into adults (generally fish > 15 cm in length but may include older parr and pre-smolts), young juveniles (0+), older juveniles (1+ and some 2+), unspecified juveniles (age of juveniles not specified or fish < 15 cm where the juvenile stage was not identified), or population (all ages grouped together or age not specified). Because the majority of biomass effect sizes were for the whole population (42), biomass effect sizes were not described for different age classes. If fish were sampled in more than one season, effort was made to extract data separately, but this was not always possible if SDs were not provided. When fish data from more than one

season were combined, their effect size was calculated in a combined season category. Differences in effect sizes were tested with the Kruskal-Wallis nonparametric test (chi-squared values), Wilcoxon pairwise comparisons, or within the DL random effects model. Only species with four or more individual effect sizes were included in the analysis of species differences, and t tests were used to measure differences in the effectiveness of structures and in individual species responses between abundance and biomass measures.

The importance of the effect size seems to be consistent among disciplines, with an effect size of 0.2 considered as small, 0.5 as moderate, and 0.8 as large (Bayliss et al., 2015; Cohen, 1988). Below zero, the effect would be negative. In impact and control studies, a negative effect size may not mean that abundance or biomass decreased, but that increases could have been larger in control reaches, indicating that structures had no effect on the increase. The significance level for all analyses was $p < 0.05$.

2.2.3 Assessment of bias

Publication bias (bias towards publishing papers with positive effects) could be the biggest potential source of type 1 error in a meta-analysis (Harrison, 2011; Hillebrand, 2008) and could overestimate the effectiveness of a treatment (G. B. Stewart et al., 2009). While the review methodology employed aimed to include grey literature and minimise bias (Collaboration for Environmental Evidence, 2018; Pullin & Stewart, 2006; G. B. Stewart, 2010), it is inevitable that literature will be missed. Bias was identified through a funnel plot of effect size versus standard error (Sterne & Egger, 2001). The effect sizes should be symmetrically distributed around the true effect size; asymmetry in the plot is suggestive of bias (Harrison, 2011; Sterne & Harbord, 2004). Studies with lower variance, and greater statistical power, will be centred around the top of the plot. Symmetry was tested by the Egger Test using a linear regression (Egger et al., 1997). If the Egger Test was significant (i.e. there was asymmetry), Duval and Tweedie's trim-and-fill method (Duval & Tweedie, 2000) was used to determine the number of unpublished studies needed to correct the bias and the true effect size without the bias was estimated using the R 'meta' package (Schwarzer, 2007). The presence of publication bias was only considered for the abundance and biomass grouped values and not for other groups (e.g. species, number of structures etc.).

Table 2.3. Number of effect sizes (ES) calculated by salmonid species (abundance and biomass) and age class (abundance)

Species	Abundance ES	Biomass ES	Number of abundance effect sizes by age-class				
			Adult	Young juvenile	Older juvenile	Unspecified juvenile	Population
Salmo trutta	67	21	25	15	10	8	9
S. salar	12	4		2	5	1	4
Oncorhynchus kisutch	36	-	1	19	3	13	
O. mykiss (steelhead)	30	-		3	16	10	1
O. mykiss (rainbow)	5	3		1			4
O. clarkii	10	3		1	5	1	3
O. tshawytscha	6	-		2		4	
Salvelinus fontinalis	17	9	4	2	1	3	7
Thymallus arcticus	-	1					
Salmonids (combined or unspecified)	15	11	4	6	1	3	1
Total	198	52	34	51	41	43	29

2.3 Results

2.3.1 Restoration projects

Most of the studies were carried out in North America (78 projects from 48 publications), with 22 projects from 15 publications in Europe (Fig. 2.1). Table A2 reports the species targeted from each study and the structure type installed, along with the number of projects and effect sizes extracted from those studies. The number of projects that reported sufficient data to be included in the meta-analysis has declined in the past decades (Table 2.4). Of the 100 total projects, 39 were BACI designs, 39 were CI, and 22 used a BA design. Of the 93 projects that reported the monitoring time after restoration, 78% monitored for less than 5 years and only 5 projects (from three publications) monitored for 15 years or more. The mean monitoring time was highest in the 1990s, while the median was higher in the previous and following decades (Table 2.4).
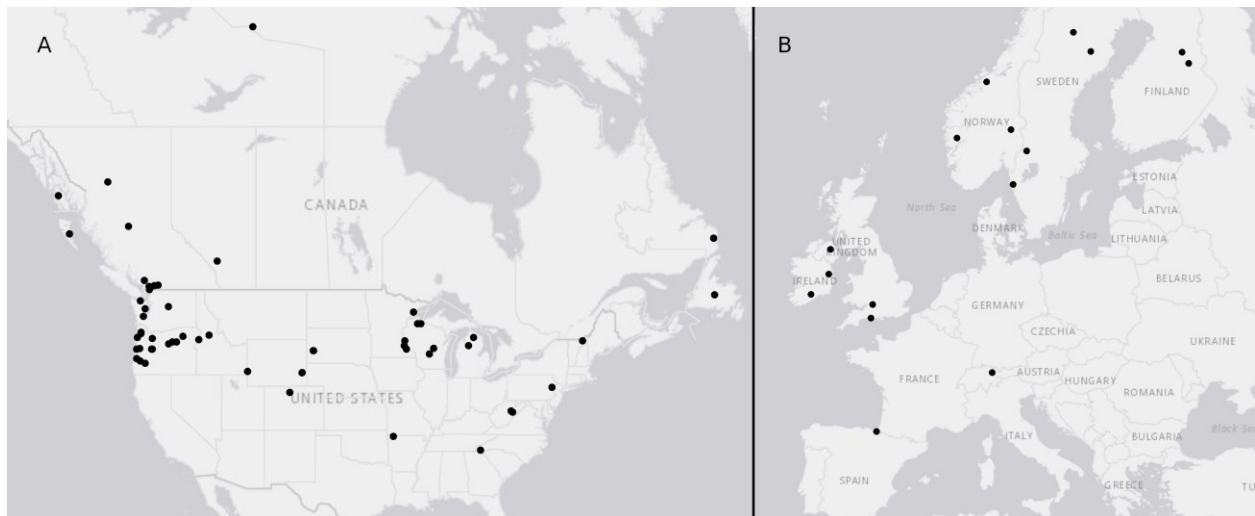
Fig. 2.1. Location of restoration studies included in the meta-analysis (black circles) in North America (A) and Europe (B). Maps made in ArcGIS 10.4. Sources: Baselayer for A and B: Esri (2011). State and province boundaries in (A): Esri (2009). Points: approximate locations of studies used in the meta-analysis were estimated from location data in each study.

Table 2.4. The number of projects completed over time and average monitoring times. Data is from abundance and biomass studies calculated from the maximum number of years that projects were monitored after installing structures

Time period	Mean (median) monitoring time (years)[1]	Number of projects completed[2]
Pre-1980	2.9 (2)	13
1980-1989	3.7 (3)	34
1990-1999	4.2 (2)	28
2000-2016	3.8 (3)	20
All years	3.7 (3)	95

[1]Projects that reported monitoring time after restoration (93 in total).
[2]Projects that reported a date for restoration completion (one project during 1980-1989 and two during 1990-1999 time periods did not report monitoring times).

The use of different types of restoration structures has changed over time (Fig. 2.2). Before 1990, weirs, deflectors, and cover structures were commonly used for habitat restoration (Fig. 2.2A). With time, a shift towards more natural structures was observed (Fig. 2.2B), and since the early 1990s, LWD clearly dominated with a marked declined in the use of deflectors and cover structures (Fig. 2.2A). Comparing the use of structures post-1990 with pre-1990, there was a significant increase in the number of projects that consisted only of natural structures and a decline in those that used only artificial structures (chi-square = 14.611, df = 2, p = < 0.001), while there was no significant difference in the number of projects that used both types (Fig. 2.2B).
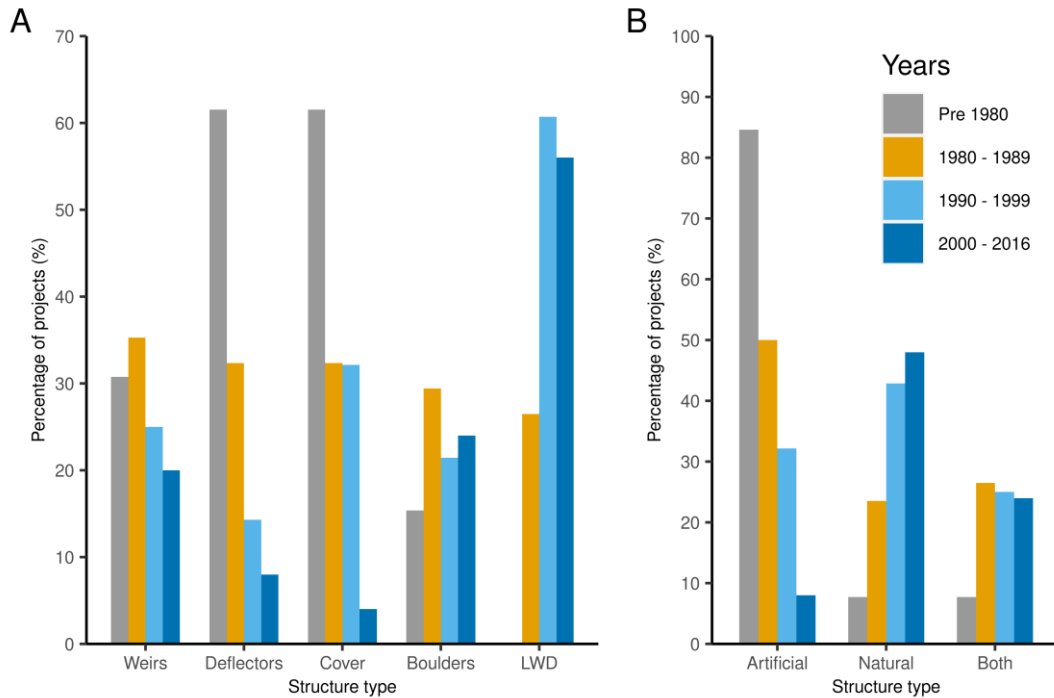
Fig. 2.2. Changes in the use of structure types over time. Proportions are calculated within each time period. (A) Proportion of projects that individual structures are used. Proportions do not add to 100%, as more than one structure could be used per project. (B) Proportion of projects that use artificial, natural, or a combination of both artificial and natural structures

2.3.2 Overall effect sizes

Both salmonid abundance (Fig. 2.3) and biomass (Fig. 2.4) significantly increased with in-stream structures (DerSimonian and Laird random effects model (DL) abundance = 0.636, 95% confidence interval (CI) (0.496, 0.776), $p < 0.001$, N = 198; biomass DL = 0.621 (0.395, 0.847), $p < 0.001$, N = 52). Combining abundance and biomass effect sizes resulted in an overall effect size of 0.637 (CI = 0.516, 0.757, $p < 0.001$, N = 250). Of the 198 abundance effect sizes, 158 were positive (an effect size greater than zero) of which 36 were significant, 40 were negative of which four were significantly negative, and 158 did not significantly differ from zero. Forty-two biomass effect sizes were positive, of which six were significant, ten were negative but none of these were significant, and 46 did not significantly differ from zero. There was no difference in abundance and biomass effect sizes (t test = 1.1485, df = 51.572, $p = 0.256$), nor were there differences in effect sizes by the time period installed for abundance, biomass, or both combined (Fig. 2.5) (all $p > 0.1$). Only three studies measured biomass in the years 2000-2016 and were not included in the analysis.
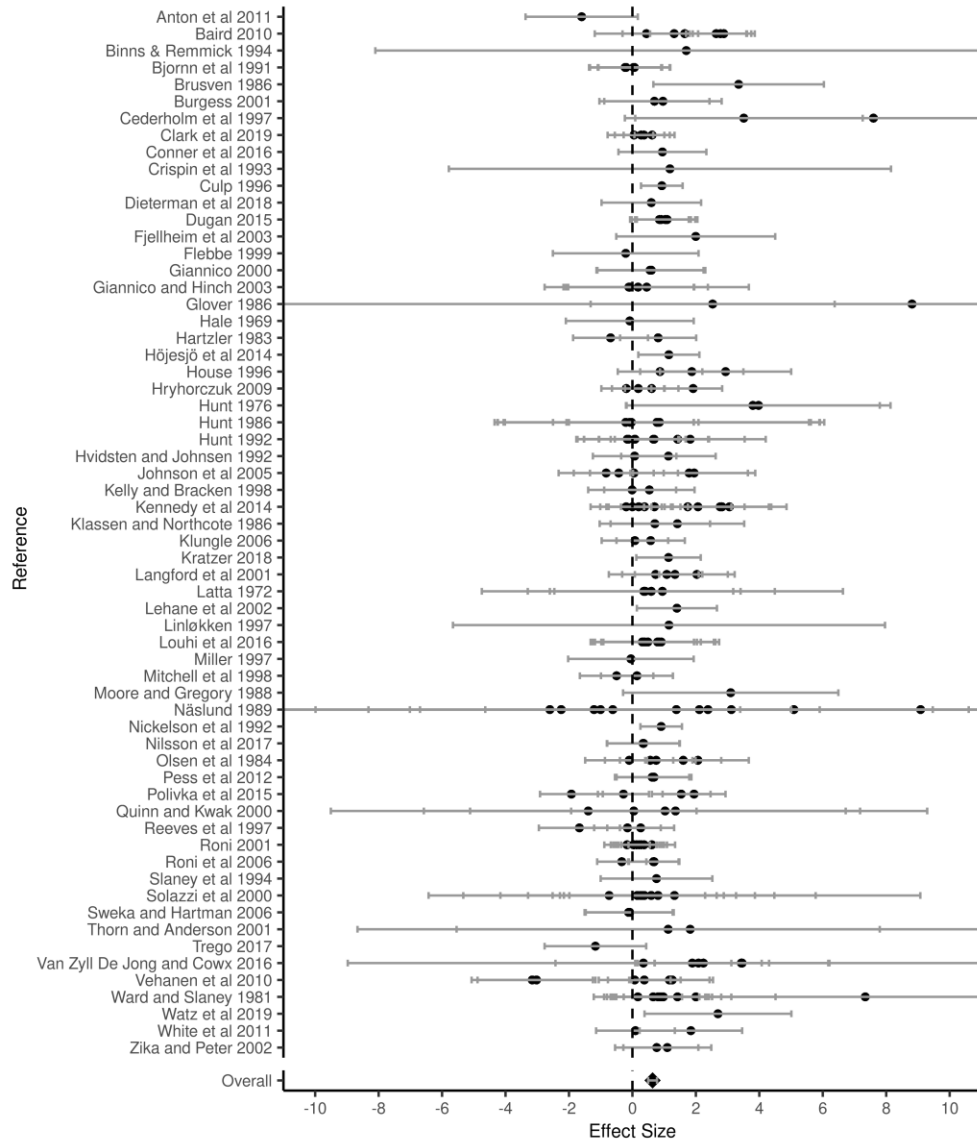
Fig. 2.3. Forest plot showing the effect of in-stream structures on salmonid abundance. Black circles represent the effect size of individual measures, and the black diamond at the bottom is the overall standardized effect size for all studies (0.636). Studies with multiple effect sizes calculated are shown on the same line. Grey error bars are 95% confidence intervals. Note that some confidence intervals extend beyond the axis
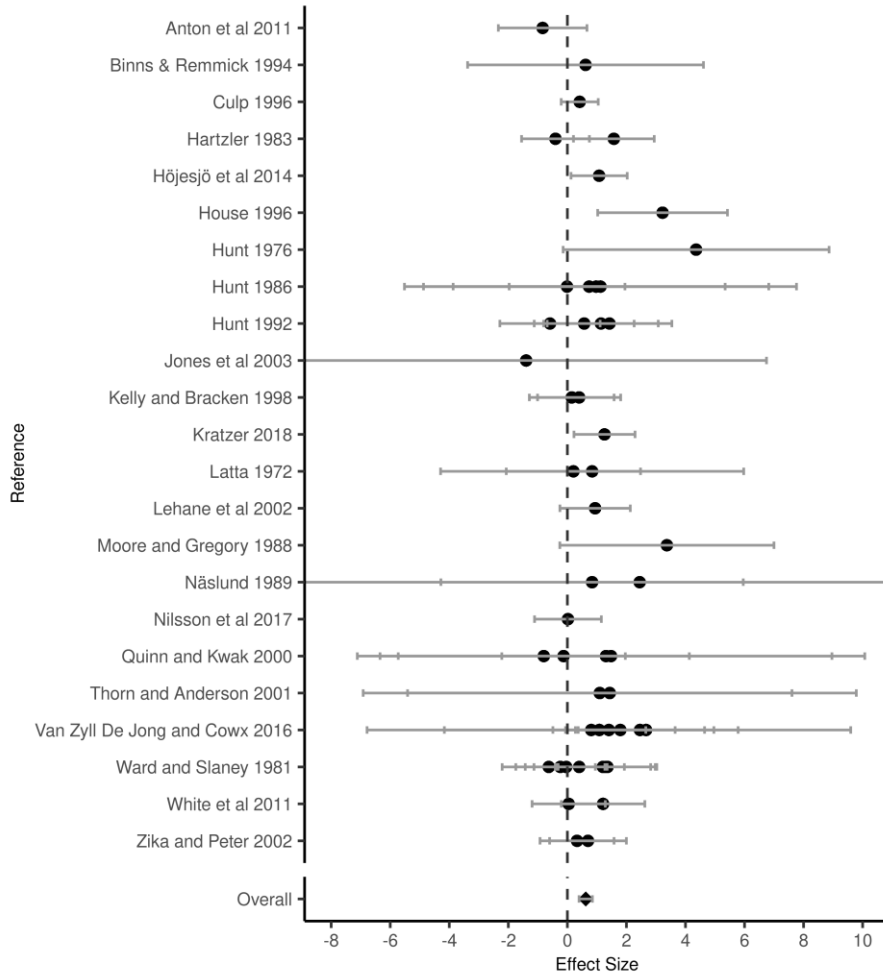
Fig. 2.4. Forest plot showing the effect of in-stream structures on salmonid biomass. Black circles represent the effect size of individual measures, and the black diamond is the overall standardized effect size (0.621) for all studies. Studies with multiple effect sizes calculated are shown on the same line. Grey error bars are 95% confidence intervals. Note that some confidence intervals extend beyond the axis

Stream size did not appear to influence the outcome of restoration projects, with no relationship between effect size and stream width (abundance: $R^2 = 0.011$, df = 119, $p = 0.247$; biomass: $R^2 = 0.0076$, df = 28, $p = 0.648$). Stream widths reported for 50 projects ranged from 2.5 m to 33 m (median = 5.7 m). However, most of the projects were carried out on small streams, with only three studies on streams larger than 10 m wide, and as mentioned previously different methods for measuring width were used across studies. Fish sampling was mostly conducted in the summer (Table 2.5). Projects that measured fish in the spring had the highest effect sizes among seasons, followed by summer, while projects that measured fish in autumn and winter had non-significant effect sizes (Table 2.5).
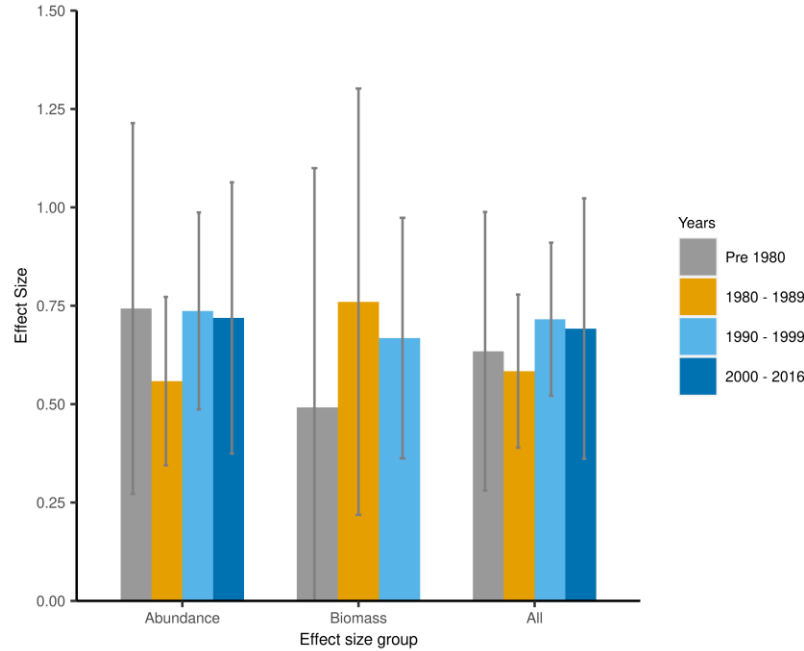
Fig. 2.5. Changes in the effect sizes by structure installation period for abundance, biomass, and both (All) effect size groups. Grey bars are 95% confidence intervals

Table 2.5. Effect sizes by the season of fish sampling (significant effect sizes in bold).

Season	Abundance effect size (95% CI)	N (p value)	Biomass effect size (95% CI)	N (p value)
Summer	**0.615 (0.441, 0.788)**	**105 (<0.001)**	**0.770 (0.369, 1.170)**	**25 (<0.001)**
Autumn	-0.232 (-0.769, 0.306)	23 (0.381)	0.402 (-0.287, 1.090)	8 (0.211)
Winter	1.393 (-0.085, 2.872)	5 (0.059)	-	-
Spring	**1.134 (0.816, 1.452)**	**14 (<0.001)**	**1.158 (0.237, 2.079)**	**6 (0.023)**
Combined (fish sampled in two or more seasons)	**0.676 (0.399, 0.953)**	**25 (<0.001)**	**0.466 (0.090, 0.841)**	**8 (0.022)**
Unspecified	**0.784 (0.406, 1.162)**	**26 (<0.001)**	0.381 (-0.628, 1.389)	5 (0.354)

2.3.3 Structure type

Projects often used a combination of structure types making it difficult to distinguish the effects of the individual structures. In-stream structures had a positive effect on salmonid abundance ($p < 0.001$) except when cover structures were the only intervention used ($p = 0.276$) (Fig. 2.6). In-stream structures also had a positive effect on salmonid biomass when multiple structure types were installed ($p < 0.05$), however, when considering studies with one structure type installed, only LWD had a positive effect ($p = 0.026$) (Fig. 2.7). Two structure types used alone (boulders and deflectors) were excluded in the biomass measures due to low sample sizes (N = 3). The type of structure installed did not make a significant difference to abundance or biomass effect sizes, whether only one type of structure was installed ($p > 0.1$) or multiple ($p > 0.05$). There was also no difference between projects classed as Artificial, Natural, or Both ($p > 0.1$) and effect sizes were significant for all these combinations for abundance and biomass ($p < 0.05$). The number of different types of structures installed did not significantly change the effectiveness of restoration on abundance or biomass ($p > 0.1$). While abundance effect sizes were all significant regardless of the number of different structures installed, there were no significant effects on biomass of projects with four types of structures (Table 2.6).

Table 2.6. Effect sizes by the number of different structure types installed at a site (significant results in bold).

No. of structure types	Abundance effect size (95% CI)	N (p value)	Biomass effect size (95% CI)	N (p value)
1	**0.693 (0.509 - 0.877)**	112 (< 0.001)	**0.650 (0.348 – 0.952)**	26 (0.001)
2	**0.493 (0.148 – 0.839)**	50 (0.006)	**0.776 (0.026 – 1.525)**	14 (0.044)
3	**0.675 (0.453 – 0.896)**	20 (<0.001)	**0.310 (0.077 – 0.543)**	6 (0.019)
4	**0.841 (0.500 – 1.183)**	16 (<0.001)	0.571 (-0.181 – 1.323)	6 (0.108)
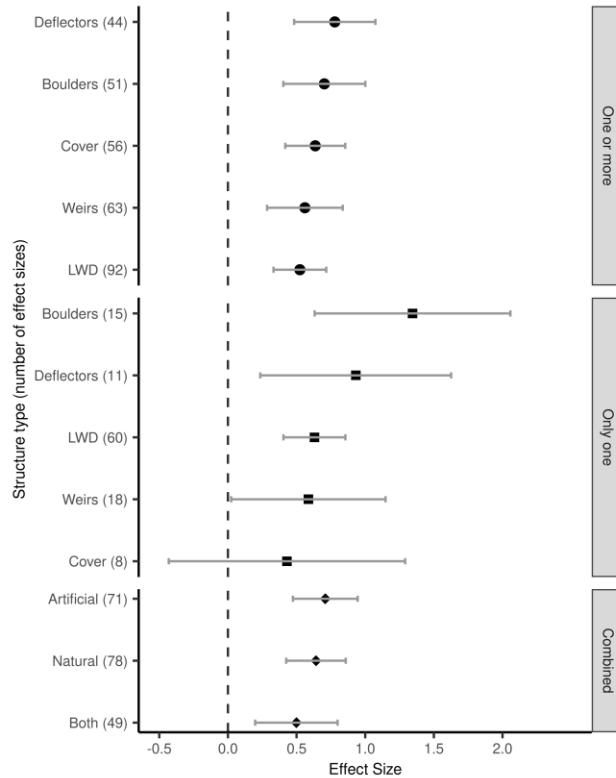
Fig. 2.6. Abundance effect sizes (mean ± 95% CI) by structure type. The top portion (One or more) shows the effect sizes for projects with each structure installed, whether or not another structure type is present; the middle portion (Only one) shows effect sizes for projects with just one structure type, and the bottom portion (Combined) shows effect sizes for projects with only artificial, only natural, or a combination of structures (both).

2.3.4 Species

The dominant species targeted in restoration was brown trout (*Salmo trutta*) (Table 2.3). Abundance increased for five species and salmonids combined ($p < 0.05$), but did not increase for cutthroat trout (*Oncorhynchus clarkii*; $p = 0.128$, N = 10), Chinook salmon (*Oncorhynchus tshawytscha*; $p = 0.067$, N = 5), or brook trout (*Salvelinus fontinalis; p = 0.110*, N = 17) (Fig. 2.8). There were no significant differences between species abundance effect sizes ($p = 0.352$), or between stream resident species (brown, brook, rainbow (*Oncorhynchus mykiss*) and cutthroat trout) and anadromous species (Atlantic (*Salmo salar*), coho (*Oncorhynchus kisutch*) and Chinook salmon and steelhead trout (*Oncorhynchus mykiss*)) (chi-squared = 0.0029, df = 1, $p = 0.957$). There were also no differences in biomass studies between species or anadromous vs. not ($p > 0.1$), even though only brook and brown trout showed increases in biomass ($p < 0.05$) (Fig. 2.8).

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There were no differences in effect sizes by species between abundance and biomass measures ($p > 0.1$ for all with sufficient data to compare).
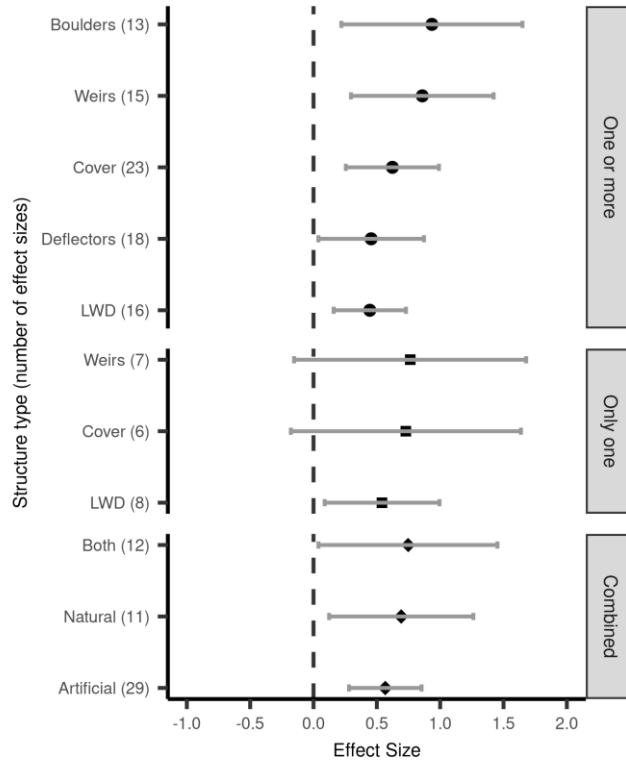
Fig. 2.7. Biomass effect sizes (mean ± 95% CI) by structure type. See Fig. 2.6 caption for further explanation.

2.3.5 Structures and species

When the effects of structures by species were considered, brown trout showed positive responses to the greatest variety of structures than other species, followed by coho salmon (Table A3). Brown trout abundance and (or) biomass increased with all structures and when artificial and natural structure types were used. There were no structures that appeared to benefit all species. However, many relationships between specific species and structures were not analysed due to small sample sizes (fewer than 4).
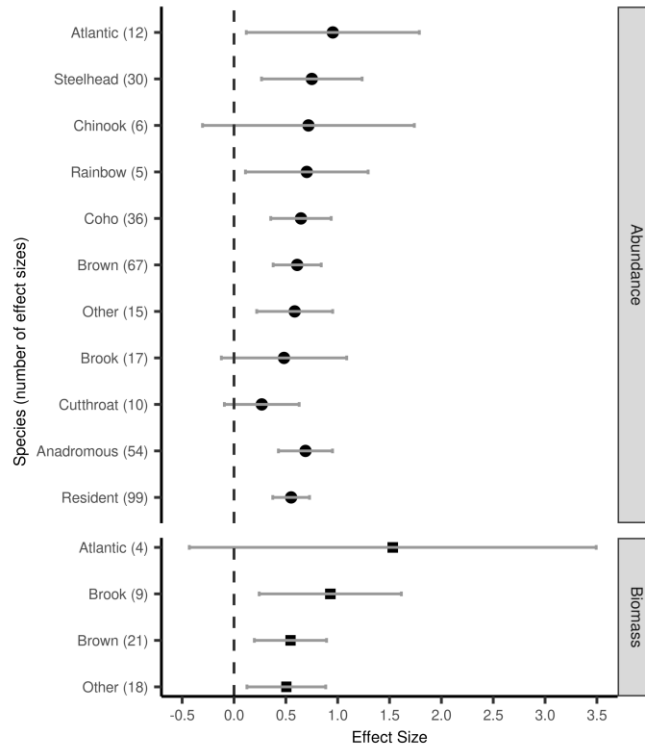
Fig. 2.8. Effect sizes (mean ± 95% CI) by species for abundance or biomass measures. "Other" included unspecified or combined trout or salmon or species that had fewer than four studies.

2.3.6 Age classes

Abundance increased in all age classes, with the largest increases found in adults (Fig. 2.9). There were significant differences in abundance effect sizes between adults and young juveniles and unspecified juveniles ($p < 0.05$), but not between other age classes. Analysis between age classes of each species could not be carried out due to small sample sizes in each group (Table 2.3). Most of the adults were brown trout (73%), while mostly juveniles were sampled for the majority of other species (Table 2.3).
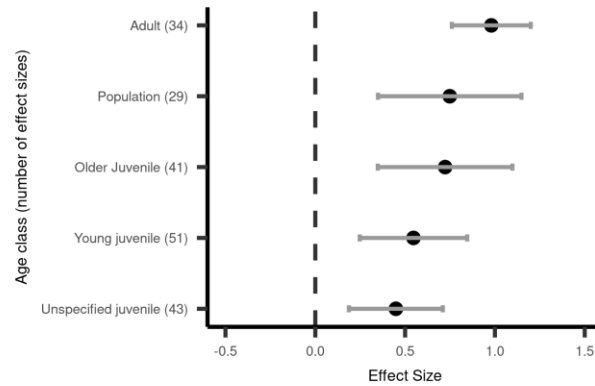
Fig. 2.9. Effect sizes (mean ± 95% CI) by age class for abundance measures. All species were combined.

2.3.7 Assessment of bias

The abundance effect sizes showed more than expected positive studies, shown in the asymmetry in the grey squares (original effect sizes plotted) in the funnel plot (Fig. 2.10; t = 2.198, df = 196, p = 0.029). This asymmetry indicates there is bias towards positive studies and should be corrected. Bias was corrected with Duval and Tweedie's trim-and-fill procedure (Duval and Tweedie 2000), where 39 dummy studies (black circles in Fig. 2.10) were added to the plot to compensate for the bias. The corrected effect size of 0.378 (95% CI: 0.210, 0.535; p < 0.001), indicated that in-stream structures still increased salmonid abundance, but the effect was small. The test for asymmetry for biomass meta-analysis showed no publication bias (t = 1.659, df = 50, p = 0.103; Fig. 2.11), so no correction was needed.
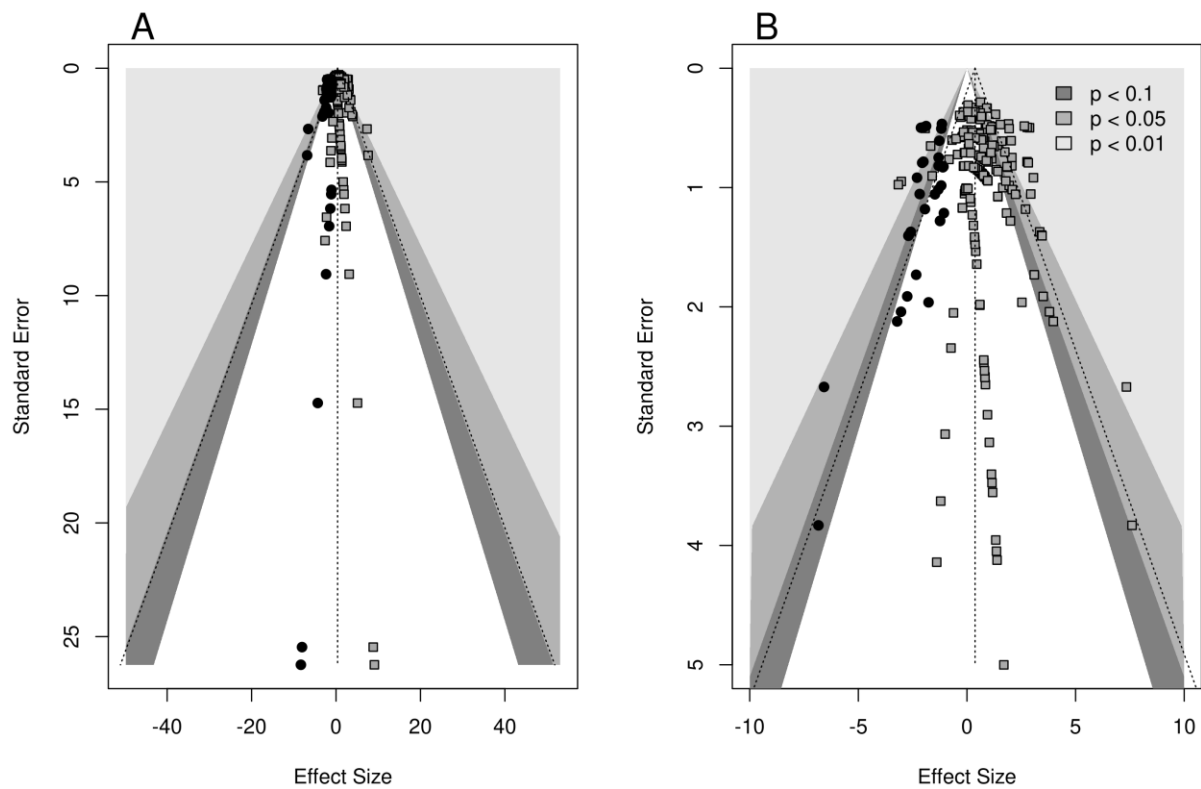
Fig. 2.10. Trim and fill funnel plot showing the abundance effect sizes against their standard errors (SEs). The original effect sizes in the meta-analysis are the grey squares, whereas the black circles are the added points to correct for the bias. Significance levels are shown (*p* values), with significant studies lying in the *p* < 0.05 and *p* < 0.01 areas. The dotted line is the pooled estimate of the effect size and SE for all abundance measures. (A) All effect sizes are shown. (B) Only the top of the plot (*y* axis 0 to 5) is plotted to show more detail. The large variance in SE of grey squares in A and asymmetry of studies (grey squares) around the mean (dotted vertical line) in B is indicative of bias.

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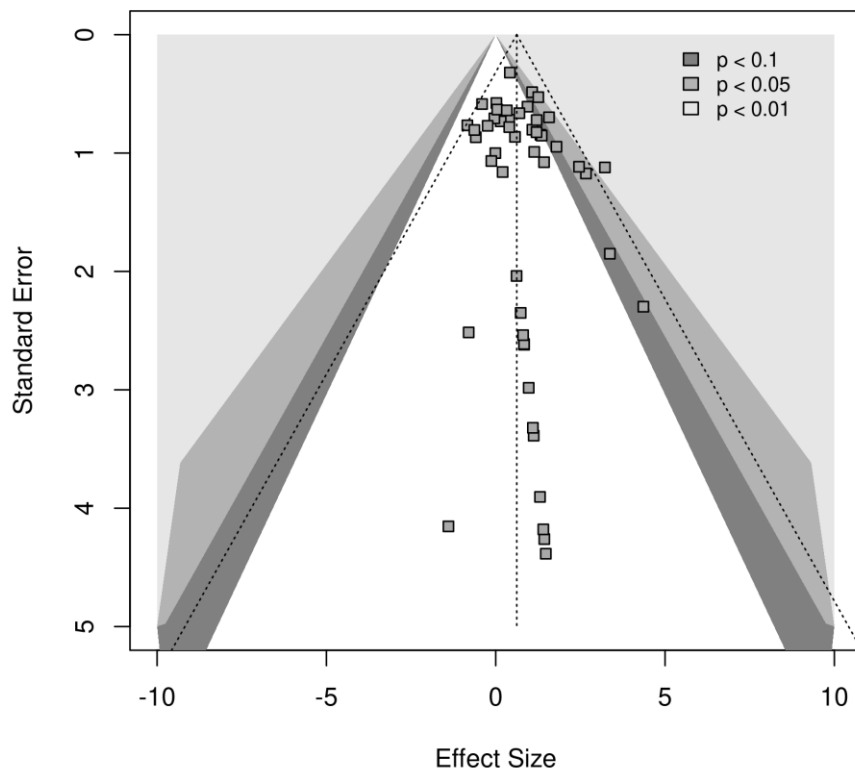
Fig. 2.11. Funnel plot for the biomass effect sizes against their standard error (SE). Significance levels are shown (p values), with significant studies lying in the $p < 0.05$ and $p < 0.01$ areas. The dotted line is the pooled estimate of the effect size and SE for all biomass measures.

2.4 Discussion

2.4.1 Overall effect sizes

Our meta-analysis showed that in-stream restoration structures increased both salmonid abundance (DL = 0.636) and biomass (DL = 0.621). With the exception of Stewart et al. (2009), these findings agree with most previous reviews and meta-analyses: that in-stream restoration structures increase fish abundance, although there is a large variation in responses (Roni, 2019; Roni et al., 2008; Whiteway et al., 2010). While there was publication bias towards positive studies for abundance measures in our analysis, the corrected effect size for this bias was still significantly positive (DL = 0.378), albeit at a lower level according to Cohen's (1988) criteria. This bias may indicate that significant

studies are more likely to be published (Harrison, 2011; Hillebrand, 2008; Kemp, 2010). Suspected publication bias led Stewart et al. (2009) to conclude that the effect of in-stream structures on salmonid abundance was equivocal, even though their meta-analysis did produce a statistically significant positive result. Our analysis did include a much higher proportion of grey literature than Stewart et al. (2009) (29% versus 9%), and there was no publication bias detected in our biomass effect size. Furthermore, there were very few significantly negative effect sizes in our analysis (four for abundance and none for biomass). For several studies in Stewart et al.'s (2009) analysis, we extracted data for longer time periods or from different experimental sections, including Brusven et al. (1986); Hvidsten and Johnsen (1992); Linløkken (1997); Mitchell et al. (1998); Giannico (2000); Zika and Peter (2002); Johnson et al. (2005); and Sweka and Hartman (2006). We found errors with data used by Stewart et al. (2009), including reversing treatment and control sections, using sites that had not used in-stream restoration structures, and overstating sample sizes. Given the extent of these errors, the results reported by Stewart et al. (2009) should be considered with caution. Whiteway et al. (2010) re-analysed Stewart et al.'s (2009) data using a log response ratio with some of the errors corrected and found a clear positive effect size of 1.1, larger than Whiteway et al.'s (2010) own effect size of 0.51. Additionally, in contrast with Whiteway et al. (2010), we examined study variance, resulting in a more robust estimate of effect size.

2.4.2 Structure type

The large variation in response to different in-stream structures in our study suggests that there are no broad guidelines for all salmonid species (Figs. 2.6 and 2.7). As suggested by previous reviews (Roni, 2019; Roni et al., 2002; Whiteway et al., 2010), we found no significant differences in effectiveness among structure types. This result may be due partly to insufficient sample sizes. Overall, cover structures on their own (when no other structures types were installed) appeared to have no significant effect on abundance or biomass; however, individual effectiveness of these structures was highly variable, and in some projects, they appeared to be very successful (e.g. Brusven et al., 1986; Höjesjö et al., 2014). Deflectors were often reported to be the most successful structures in fish rehabilitation projects (Mitchell et al., 1998; Thompson, 2002; Ward & Slaney, 1981). Deflectors had one of the highest effect sizes for salmonid abundance in our analysis, but had a very small effect on biomass. A higher response rate was detected for brook trout and Atlantic salmon numbers when boulder clusters and v-dams (classed as weirs in this study) were installed, compared with half log covers in a Newfoundland stream (van Zyll de Jong & Cowx, 2016), while a combination of LWD and cover structures resulted in a positive response to adult brown trout in Minnesota, compared with no significant effect with just cover structures (Thorn & Anderson, 2001). Our analysis suggested that boulders were highly effective for increasing both abundance and biomass. Boulder clusters or placements

are effective at creating habitat complexity and hiding places (Kennedy et al., 2014) and increasing pool volumes and instream cover (House, 1996; Näslund, 1989; van Zyll de Jong & Cowx, 2016). Several studies have documented the high stability of boulder structures (House, 1996; Kennedy et al., 2014), even after 20 years of placement (van Zyll de Jong & Cowx, 2016). In the right context, boulders can provide cost-effective (Kennedy et al. 2014) and sustainable long-term improvements in stream conditions (van Zyll de Jong & Cowx, 2016). Whether structures are artificial or natural, fish are responding to the effect of the structure, rather than the structure itself (Clark et al., 2019; Crispin et al., 1993; Floyd et al., 2009; House, 1996; Roni et al., 2008; Roni & Quinn, 2001). While artificial structures such as log weirs and deflectors can be effective creating habitat, and thus increasing fish numbers, often these effects do not last as long as more naturally placed structures such as LWD and boulders (Roni et al., 2002, 2015).

2.4.3 Species and age classes

Previous evidence suggests that in-stream structures may be more effective for stream-resident and larger fish than for juveniles of anadromous populations (Hicks & Reeves, 1994; Hunt, 1988; Whiteway et al., 2010). Other studies indicate that Pacific salmonid species and life stages that prefer pools, such as juvenile coho salmon, Chinook salmon, and cutthroat trout, may benefit more from in-stream restoration (Roni et al., 2008). Stream residents may prefer slower water velocity than migrants (Morinville & Rasmussen, 2008), and deeper habitats may be more preferred for larger fish (Armstrong et al., 2003; Fausch, 1993; Horan et al., 2000; Mäki-Petäys et al., 1997). For example, brown trout avoid shallow pools (<60 cm deep) and habitats that lack cover (Dieterman et al., 2018). The indication that species that prefer pool habitats do better after in-stream restoration is not surprising given that the purpose of many in-stream structures is to increase pool habitat and availability. Multiple studies document an increase in pool area, number of pools, and (or) increased depth with the addition of structures, particularly LWD (e.g. Antón et al., 2011; Cederholm et al., 1997; Gowan & Fausch, 1996; Näslund, 1989; O'Neal et al., 2016; Roni & Quinn, 2001). While our analysis does not suggest that structures were better for different species or migratory phenotypes, the sample sizes were probably not sufficient to detect differences between species. Furthermore, combining all life stages together may overlook important differences in habitat preferences at different life stages within species. Our analysis indicated that while salmonid abundance increased over all age classes, there were significant differences in effectiveness between adults and young juveniles ($p = 0.020$) and unspecified juveniles ($p = 0.002$). The effect size for adults was higher than for other life stages, agreeing with previous suggestions that in-stream restoration favours larger fish.

2.4.4 Reasons for structure or project failure

Previous research has suggested that many restoration projects fail to result in improvements in fish density or biomass because the habitat is inadequate (Nickelson et al., 1992; Rosenfeld & Hatfield, 2006) or the underlying causes of decline are not addressed (Cochran-Biederman et al., 2014; Roni et al., 2014; van Zyll de Jong & Cowx, 2016). Habitat requirements will be different at each site or stream, for species targeted, and at each life stage (Armstrong et al., 2003; Bjornn et al., 1991) and will depend on the time of day (Mitchell et al., 1998) and season (Nickelson et al., 1992; Roni & Quinn, 2001). Habitat requirements at each stage must be understood so that restoration can be targeted for the desired species (Armstrong et al., 2003; Nickelson et al., 1992). However, most salmonid restoration projects focus on providing summer habitat, even if habitat is more limiting in other seasons (Nickelson et al., 1992). For example, coho salmon smolt production is thought to be limited by the availability of winter habitat in many coastal Oregon streams (Nickelson et al., 1992). Of the projects included in our study, 53% sampled fish only in the summer, whereas several studies show high seasonal variability in habitat use (Bramblett et al., 2002; Cederholm et al., 1997; Mäki-Petäys et al., 1997; Mollenhauer et al., 2013; Nickelson et al., 1992; Polivka et al., 2015; Zika & Peter, 2002). If most restorations focus on summer habitat, then they will appear to be less effective if sampling is in the fall, when fish are beginning to move to over-wintering habitat. In our study, the highest effects on abundances and biomass were found in the spring, while the lowest were in autumn.

There are very few long-term (greater than 5 years) assessments of restoration outcomes (Champoux et al., 2003; Roni et al., 2008). Despite research suggesting that at least 4–8 years are needed postrestoration to determine the full fish population responses (Binns & Remmick, 1994; Hunt, 1976), monitoring time for projects in our analysis has not significantly increased over time (Table 2.4), and over three-quarters of all projects monitored for less than 5 years. In some catchments, years to decades may be needed to rebuild fish populations to sustainable levels (Luhta et al., 2012). More than a year or two is needed for populations to expand into existing and new habitats (Binns & Remmick, 1994; O'Neal et al., 2016), and multiple generations may be required to detect adult responses (Roni et al., 2002). First, adequate flows are required to change stream morphology to create the required habitat; fish then respond to this habitat change (Roni et al., 2006; Roni & Quinn, 2001). Monitoring for only 1 or 2 years may be confounded by natural variations in fish stocks (Binns & Remmick, 1994). Additionally, in some environments, morphological changes may not be apparent after only 2 years (Kondolf & Micheli, 1995). Therefore, it is recommended that 10 years or more of continuous monitoring is required to detect a sustained response to restoration (Bisson et al., 1992, 2003; Kondolf & Micheli, 1995; Reeves et al., 1997).

Installed structures are not always appropriate for the stream characteristics or cause the intended effects. In early restoration projects, failure was often attributed to applying techniques developed for low-gradient streams (weirs and deflectors) to streams of high gradient and energy (Frissell & Nawa, 1992; Platts & Rinne, 1985). The move towards using LWD instead of artificial structures in some ways attempts to limit structural failure (Bisson et al., 2003; Roni et al., 2006) and buffer the effects of drought and flooding events (Sweka & Hartman, 2006). Three of the projects with a significant negative effect size in our analysis were due to droughts and floods resulting in structural failure and decreased fish abundance (Reeves et al., 1997; Vehanen et al., 2010).

Many artificial structures are not built to last or last much less time than intended (Champoux et al., 2003). An early assessment of habitat structures in Oregon and Washington over a 20-year period found that woody debris and individual boulder placement were the only structures that did not fail in more than half the cases; many projects lasted less than 15 years because of washout from floods (Frissell & Nawa, 1992). Just 2 years after construction in Meadow Creek, Oregon, fewer than 20% of structures were still functioning (Miller, 1997), while in several Wisconsin streams, a lack of maintenance caused structures built to last up to a century deteriorate in 25 years (White, 1996). In other earlier projects, artificial structures had deteriorated or were no longer working almost 20 years after installation (Ehlers, 1956; White, 1972). Bank deflectors placed in Lawrence Creek, Wisconsin, failed in one area but were still mostly functioning in another 36 years later, highlighting the need for knowledge of the geomorphological context when placing structures (Champoux et al., 2003). For example, Champoux et al. (2003) postulated that deflectors were well adapted for narrow and sinuous channels, rather than wide, steep, and dynamic stretches with coarse sediments, resembling the area where they failed. Other studies have noted much lower failure rates (Roni et al., 2008, 2015; Roper et al., 1998; Schmetterling & Pierce, 1999). In an assessment of almost 4000 structures (logs, boulders, and gabions), Roper et al. (1998) found that more than 80% remained in place after floods with return intervals greater than 5 years; structures in larger streams and with higher magnitude floods were more likely to fail. Naturally placed structures seem to last longer than those anchored in place (Roni et al., 2008, 2015). In a stream in western Montana, 85% of rock and wood structures remained stable after a 50-year recurrence interval flood (Schmetterling & Pierce, 1999). Likewise, in a summary of natural and placed wood structures, Roni et al. (2015) reported that fewer than 20% failed.

In other projects, added material may not cause the intended effect (Flannery et al., 2017). For instance, LWD is often used to create pool habitats. In central Appalachian streams, however, LWD did not form pools in the highest gradient streams, and only 4% of the added LWD created pool habitat (Sweka & Hartman, 2006). Installing effective and long-lasting stream restoration structures likely requires skill and experience (Baril et al., 2019). However, restoration projects are managed by groups with a broad range of

expertise (but are often lacking hydrogeomorphological expertise; (Baril et al., 2019)), likely contributing to the high variability in responses and failure rates. For a longer-term solution, restoring natural processes is a better restoration approach. Unmodified streams with naturally dynamic hydrological regimes and processes are more resistant to the negative effects of flooding and drought (Elosegi et al., 2011; Poff et al., 1997), and if natural processes are restored, habitats that are limiting to native fish may more likely be created or restored (Beechie et al., 2010; Florsheim et al., 2008).

2.4.5 Process based restoration

In recent years, there has been a stronger emphasis on restoring natural fluvial processes at the watershed scale (Beechie et al., 2010; Biron et al., 2018; Roni et al., 2008), instead of focusing on manipulating in-stream habitats and specific morphologies that are targeted by in-stream structures (Roni et al., 2002) This shift in restoration approach has influenced the use of in-stream structures, reflected in the use of more large wood in restoration since the 1990s and an increase in projects that use only natural structures and a decrease in the use of artificial structures (Fig. 2.2). Restoration projects in western North America have also shown this trend, where the understanding of wood processes has led to more restoration projects using techniques that allow wood movement, rather than anchoring wood structures in place (Bisson et al., 2003). An added benefit of more natural wood structures is that they are often much cheaper than anchored techniques (Carah et al., 2014). This shift is also clear in the use of bank stabilization over time. Prior to 1995, several restoration projects incorporated bank stabilization structures such as riprap into restoration projects in an attempt to limit erosion and the lateral migration of channels (Hvidsten & Johnsen, 1992), as well as narrow channels to create pool habitat (Hunt, 1992). Bank erosion was perceived as a hazard and something that needed to be controlled (Piégay et al., 2005). Often riprap was employed for public safety or economic purposes, not for restoration benefits (Florsheim et al., 2008). More recently, allowing a river to move freely and maintaining a natural sedimentation regime is recognized as important for ensuring healthy river ecosystems (Choné & Biron, 2016; Florsheim et al., 2008; Williams et al., 2020). The ecological importance of erosion in providing riparian habitats and natural bank habitats providing LWD are becoming more obvious for river restoration practitioners (Benda et al., 2004; Florsheim et al., 2008; Piégay et al., 2005). A naturally moving river acts as a passive restoration approach, as a natural sedimentation regime creates habitats that many in-stream structures aim to replicate (Biron et al., 2018; Choné & Biron, 2016; Williams et al., 2020).

The shift in structure use was not associated with an increase in the effect size of in-stream structures over time (Fig. 2.5). This suggests that the type of in-stream structure is not important for generating overall positive benefits in fish response, also indicated by

other authors (Roni, 2019; Roni et al., 2008; Whiteway et al., 2010). However, for effective restoration it is suggested that in-stream enhancement techniques should only be used where short-term improvements are needed or used alongside process-based restoration (Roni et al., 2002; Roper et al., 1998) and that focus should instead be on protecting and connecting habitat and restoring habitat-forming processes (Cramer, 2012; Roni et al., 2008). This can be achieved by adopting river management approaches based on "erodible corridor" (Piégay et al., 2005), "fluvial territory" (Ollero, 2010), "river corridor" (Kline & Cahoon, 2010), or "freedom space" (Biron et al., 2014; Buffin-Bélanger et al., 2015; Choné & Biron, 2016). While these approaches are often aimed at larger watersheds, their principles of allowing natural erosion and hydrological processes to be restored can be implemented in smaller streams, where most restoration projects are carried out. Such passive restoration approaches are more likely to succeed in the long term, even if their impacts may be difficult to quantify in the short term.

Liaison paragraph

The previous chapter concluded that in-stream structures may be successful in the short term, but they often fail to provide a long-term solution (over 10 years). Often these restoration techniques, along with indices to evaluate habitat quality for fish, are implemented at small spatial extents of a few hundred metres. This is inadequate if fish move at large spatial scales. Hydrogeomorphology incorporates processes related to river mobility, flooding, and riparian connectivity, that operate at segment to catchment scales, and determine habitat features in smaller river reaches. The next chapter aims to assess whether an index that measures hydrogeomorphological quality can be used as an indicator for salmonid stream fish habitat quality and fish ecology. The Morphological Quality Index (MQI) considers fluvial processes at larger scales, but few studies have assessed its relevance for ecosystem health. In the next chapter we investigate relationships between the MQI, the Qualitative Habitat Evaluation Index (QHEI), land cover, and fish metrics in 26 salmonid streams in two different geographical regions.

3 Morphological and habitat quality of salmonid streams and their relationship with fish-based indices in Aotearoa New Zealand and Ontario (Canada)

Kyleisha J. Foote, **Pascale M. Biron** and **James W.A. Grant**

Abstract: Habitat degradation is one of the major reasons for freshwater species decline. Hydrogeomorphological processes (such as sediment transport, bank erosion, and flooding) operate at the catchment scale and determine habitat features in river reaches. However, habitat quality indices and restoration for freshwater fish species are often implemented at small spatial scales of a few hundred metres. The Morphological Quality Index (MQI) considers fluvial processes at larger scales as well as channel forms, human impacts, and historical changes, but few studies have assessed its relevance for ecosystem health. We investigated relationships between the MQI, habitat quality (using the Qualitative Habitat Evaluation Index, QHEI), land cover, and fish metrics (number of fish species, index of biotic integrity (IBI), and trout biomass) in 26 salmonid streams in Aotearoa New Zealand and Southern Ontario, Canada. We found a significant correlation between the MQI and QHEI, and both metrics were correlated with urban and native forest proportion in the catchment. However, we found no relation between the MQI and the proportion of agricultural land in the catchment, while the QHEI was correlated with agricultural land in the riparian zone, highlighting the importance of vegetated riparian buffers in providing fish habitat. Establishing a strong correlation with fish metrics remains challenging. Nevertheless, a modified MQI targeting ecological health could be used as an effective management tool for aquatic conservation.

3.1 Introduction

Freshwater environments are among the most threatened and damaged ecosystems in the world (Leidy and Moyle 1998) and freshwater fishes are thought to be the most threatened group of vertebrates (Freyhof and Brooks 2011; Reid et al. 2013; Collen et al. 2014) with the highest extinction rate among vertebrates in the 20th century (Burkhead 2012). Flow regulation and/or river fragmentation affects almost half of the world's rivers (Grill et al. 2015) and is a major threat to river integrity and fish populations, particularly diadromous species such as salmonids (Fullerton et al. 2010; Liermann et al. 2012; Rodeles et al. 2019; Hayes et al. 2022). Salmonid fishes are declining in multiple regions around the world, with many populations and species listed as threatened or endangered (Yeakley and Hughes 2014; Laramie et al. 2015). In North America, 61% of described salmonid species are considered imperilled (Jelks et al. 2008), and 41% of salmonids in Europe are threatened (Freyhof and Brooks 2011). Habitat degradation, due to practices such as river straightening, flow regulation, sediment load alternations, river disconnection from the floodplain, and loss of longitudinal connectivity (Muhar et al. 2000; Campana et al. 2014; Grill et al. 2019; Wohl 2019), is one of the major reasons for freshwater species decline (Dudgeon et al. 2006). Freshwater environments will be unable to recover without first removing the pressures that are causing degradation and then attempting to improve those degraded habitats (Roni et al. 2008; Reid et al. 2019).

Habitat quality is affected by processes at a range of scales, from micro-habitat scales, through site, reach, segments, river, watershed, and even global extents (Frissell et al. 1986; Imhof et al. 1996). Physical patterns and processes acting at higher scales largely determine the habitat features present at lower scales in the system (Frissell et al. 1986; Brierley and Fryirs 2005). At the reach scale (a few hundred metres long), habitat variables such as shelter, temperature, water velocity, depth, food, and water quality are important for riverine biodiversity (Shirvell and Dungey 1983; Heggenes 1990; Rabeni and Jacobson 1993; Vismara et al. 2001; Strakosh et al. 2003; Ayllon et al. 2009; Boets et al. 2018). Water quality can be affected by catchment land-use resulting in detrimental impacts on ecological communities (Carlson Mazur et al. 2022), with native fish declines and poor ecological state associated with agricultural and urban land-use (Čivas et al. 2016; Joy et al. 2018). Physical habitat indices such as the Qualitative Habitat Evaluation Index (QHEI), a visual assessment that allows a rapid evaluation of streams at the reach scale, are aimed at factors that influence fish communities and other aquatic life, and consider: substrate, in-stream cover, channel morphology, riparian zone and bank erosion, pool and riffle quality, and stream gradient (Rankin 1989; Taft and Koncelik 2006). The QHEI can identify habitat for stream organisms at individual sites and has been used as a predictive tool in design and restoration practices (Gazendam et al. 2011). However, it measures river conditions at

only one point in time (unless undertaken repeatedly at the same site over time) and is resource intensive as it requires field observations.

The reach scale is inadequate to accurately analyse morphological alterations because processes important for habitat availability and quality, such as sediment transport, flooding, connectivity through the fluvial system and mobility of the channel, usually act at the segment to catchment scales (Beechie et al. 2010; Biron et al. 2014; Choné and Biron 2016). Hydrogeomorphological assessments include a broader range of evaluations than physical habitat methods and generally consider larger spatial and temporal scales (Belletti et al. 2014; Golfieri et al. 2018). Often the entire river corridor is considered (including the channel banks, riparian zones, and floodplain) as well as channel patterns and physical variables, rather than just in-stream habitats (Belletti et al. 2014; Fuller et al. 2021). Additionally, morphological assessments often consider recent and historical channel adjustments (Rinaldi et al. 2013; Belletti et al. 2014; Golfieri et al. 2018; Fuller et al. 2021). The Morphological Quality Index (MQI) was developed to assess hydrogeomorphological quality in Italian rivers at the reach to segment scale, designed for the European Water Framework Directive (WFD) (Rinaldi et al. 2013). It has been expanded and applied to other European countries (Rinaldi et al. 2015) and recently tested successfully outside Europe (Lemay et al. 2021; Carvalho Carneiro de Mendonça et al. 2021; Müller et al. 2022; Moshe et al. 2022). The MQI comprises of 28 indicators that address functionality of river processes, artificiality or human impacts, and historical channel adjustments (Rinaldi et al. 2013). The method is process-based, rather than only considering channel forms, and is intended to assess morphological quality rather than just quantify processes or channel evolution (Rinaldi et al. 2016). The chemical or ecological state of rivers is not evaluated in the assessment, but a high morphological quality is often, but not necessarily, related to a good ecological state (Rinaldi et al. 2016), as the presence of naturally dynamic physical processes encourages the creation and maintenance of habitats and helps provide ecosystem integrity (Brierley and Fryirs 2005; Wohl et al. 2005; Florsheim et al. 2008). Moreover, the MQI is correlated with habitat quality indices such as QHEI (Golfieri et al. 2018; Lemay et al. 2021). Also, the MQI can be performed remotely (RMQI) with high accuracy (Lemay et al. 2021), a bonus for river managers carrying out assessments covering a large area or where access is limited. So far, there has been limited application of the MQI in North America or Aotearoa New Zealand, and few studies have assessed its relevance for biological and ecosystem health (Belletti et al. 2014; Scorpio et al. 2016; Golfieri et al. 2018). In fact, landscape scale indices that assess morphological quality and its changes over time are rarely aligned with biological indices or used to consider conservation measures for riverine biodiversity (Scorpio et al. 2016; Golfieri et al. 2018; Carvalho Carneiro de Mendonça et al. 2021).

Biological indices (or biomonitoring) are used to determine a stream's biological health, or biotic integrity. Biotic integrity has been defined as the ability to support and

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maintain "a balanced, integrated, adaptive community of organisms having a species composition, diversity, and functional organization" comparable to that of a similar natural habitat or ecoregion (i.e. a reference condition) (Karr and Dudley 1981, p. 56). Macro-invertebrates and fish serve as indicators for degradation at local or regional scales, respectively. The fish Index of Biotic Integrity (IBI) can rapidly assess the ecological health in a waterway (Karr 1981), as fish are sensitive to habitat loss and effects from other environmental stressors (Souza and Vianna 2020). A fish IBI varies across regions and depends on the local fish communities present. Generally, a fish IBI considers fish diversity, the number of intolerant species, and the number of certain types of species present, among other features. While biological indices can identify long-term pollution problems better than intermittent water quality sampling (Gazendam et al. 2011), they are unable to determine causes of problems. Furthermore, relying only on biological indicators gives an incomplete assessment of the entire river corridor as they poorly describe hydrogeomorphological pressures or alterations (Campana et al. 2014; Belletti et al. 2018; Golfieri et al. 2018). Additionally, long-term monitoring of biotic indices may be required to understand the health of a fish community.

The overarching goal of this study was to determine whether hydrogeomorphological quality, habitat quality, and biotic indices for fishes are related in salmonid streams. To answer this, we had several aims: (i) to investigate the relationship between the morphological quality (quantified using the MQI) and habitat quality (assessed with the QHEI); (ii) to investigate the relationship between the MQI, QHEI, and fish-based indices (i.e. number of fish species, IBI, and trout biomass); (iii) to investigate the link between land cover and the MQI, QHEI, and fish metrics); and (iv) to determine if other physical characteristics in the landscape are correlated with the MQI, QHEI, or fish metrics. Furthermore, we wanted to determine if differences existed in two different geographical regions of the world: Ontario, Canada and Aotearoa New Zealand.

3.2 Methods

3.2.1 Study sites

The study area comprises 14 sites located in 10 streams in Southern Ontario, Canada (ON) and 21 sites located in 16 streams in Aotearoa New Zealand (NZ) (Fig. 3.1, Table B1 in Appendix B). We selected streams in regions with a diversity of physical habitats and land cover to test the generality of the MQI in predicting fish habitat in cold-water streams in two different areas of the world. These sites historically supported native salmonid populations in Ontario and indigenous galaxiid populations in Aotearoa New Zealand. Exotic salmonid populations are now present in both stream communities.

Ontario sites were selected from the Flowing Waters Information System database (FWIS 2020) that contained salmonid populations. All drain into lakes: Lake Ontario, Lake Simcoe, or Georgian Bay on Lake Huron. In Aotearoa New Zealand, 18 of the sites (on 15 rivers) were selected in the South Island (Te Waipounamu) from past trout abundance surveys (Teirney and Jowett 1990; Jellyman and Graynoth 1994) and from expert opinion (personal communication with John Hayes and Robin Holmes, Cawthron Institute). The other three sites were surveyed on the Horokiri Stream in the lower North Island (Te Ika-a-Māui), which had one of the highest estimates of trout production globally (surveyed by Allen 1951), although trout abundance has subsequently declined to very low numbers (Jellyman et al. 2000). The ON sites are smaller (mean width and drainage area of 4.1 m and 41 km^2, respectively) than the NZ ones (mean width and drainage area of 14.4 m and 246 km^2, respectively). On average, ON sites are higher in elevation (286 m compared to 196 m for NZ) and closer to large downstream lakes (50 km) than NZ sites are to the coast (71 km).
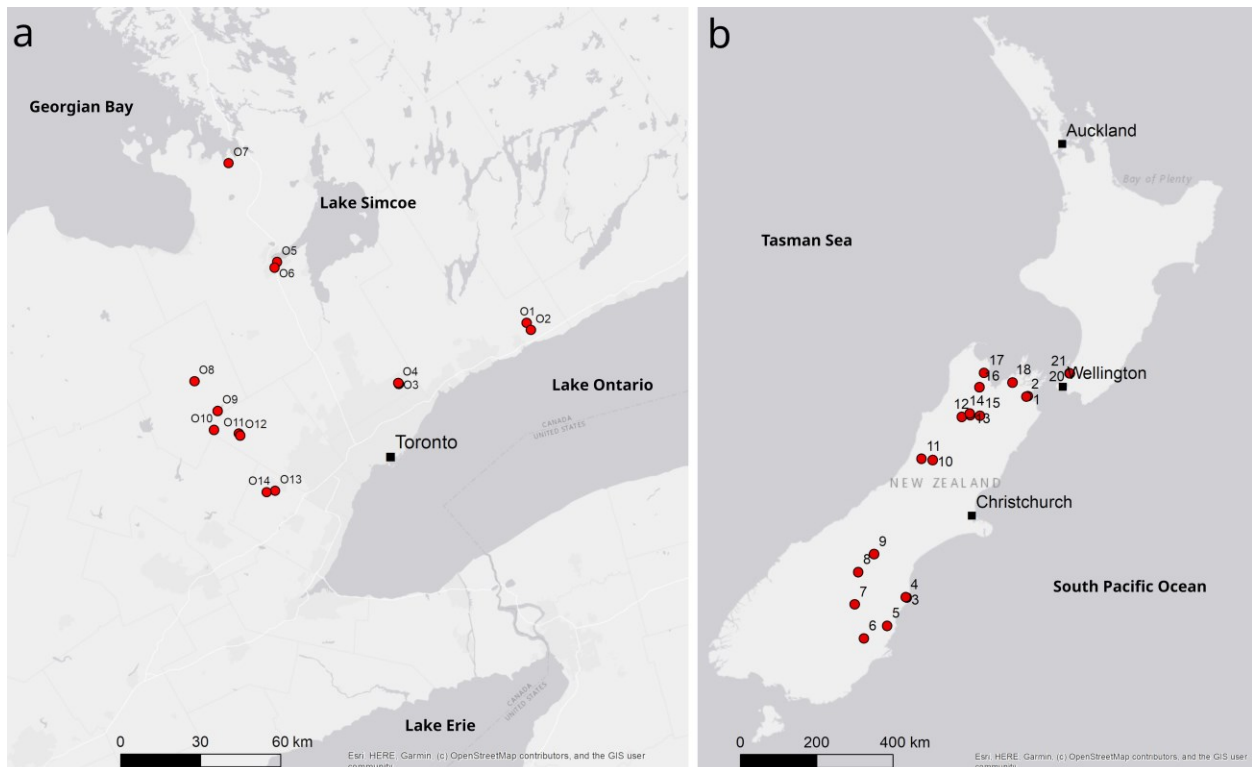
Fig. 3.1. Site locations in: a) Southern Ontario, Canada, and b) Aotearoa New Zealand. Site labels correspond to Site Numbers in Table B1 (Appendix B).

At each site, a range of indices and physical variables were measured at different spatial scales (Fig. 3.2). At the smallest scale (reach scale, generally 100 m or less), information for biotic indicators were obtained from databases or literature. The scale at which reach physical variables and the QHEI were measured at varied between 110 and

2420 m long (Table B1). These surveys were undertaken within the MQI segment; the length was based on accessibility in the field and they are thought to be representative of the whole MQI segment. The length of segments assessed for the MQI was a relatively homogeneous stretch in terms of river style and types of impacts and varied between 220 and 4750 m long (Table B1). Several variables were also measured at the catchment or sub catchment level (Fig. 3.2). Upstream and downstream variables were measured at the most downstream point of the reach. Aerial imagery, digital elevation models (DEMs), and GIS layers with stream interventions (dams and weirs) were used to determine whether there was a barrier to fish passage or a lake present in the catchment (Table 3.1).
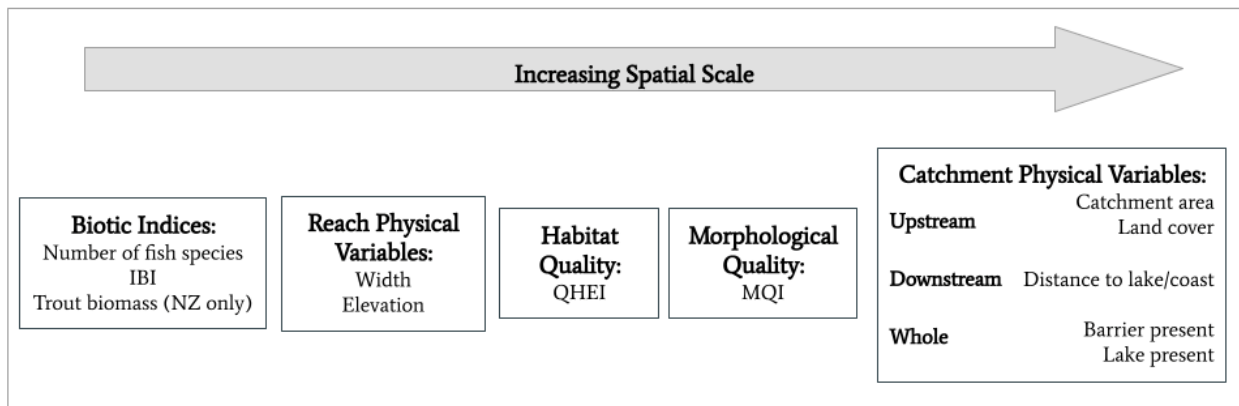
Fig. 3.2. Indices and physical variables measured at sampling sites with increasing spatial scale

Table 3.1. Percentage of study sites in each region with a barrier or lake present

	Barrier (% of sites)		Lake (% of sites)	
Region	*Upstream*	*Downstream*	*Upstream*	*Downstream*
Ontario	93	86	7	100
New Zealand	43	33	24	19

3.2.2 Assessment of habitat quality (QHEI)

To provide a general evaluation of physical macro-habitat quality, a QHEI assessment was carried out at each site following guidelines from the Ohio Environmental Protection Agency (Taft and Koncelik 2006). The QHEI involves six principal metrics (substrate, instream cover, channel morphology, riparian quality and bank erosion, pool and riffle quality, and gradient) that are important for stream fish habitat (see Appendix B, Table B2,

for details of the metrics) (Rankin, 1989; Taft & Koncelik 2006). Each metric is scored individually and summed to provide a maximum possible score of 100 (Fig. B1). Our assessment did not measure gradient so the total possible score was out of 90 and was then scaled to obtain a score out of 100. General narrative categories have been assigned to QHEI scores (Table 3.2).

3.2.3 Assessment of river morphological quality (MQI)

The MQI is applied at a river reach spatial scale, but the whole river corridor (active channel and adjacent floodplain) is considered. One or two reaches were selected on each stream for an MQI assessment (except the Horokiri Stream which had three), instead of following the first MQI phase of subdividing the network into homogeneous reaches (Rinaldi et al. 2016). Using a GIS (ArcGIS 10.7) database, which included Digital Elevation Models (DEMs), orthoimages, historical photos, and intervention layers (dams, weirs), along with field surveys, an MQI assessment of each site was conducted. For the MQI procedure, reaches were assessed as either confined, or partly confined and unconfined, based on the lateral confinement in the river valley (Rinaldi et al. 2016). In confined reaches, 22 out of 28 indicators are assessed, while partly confined and unconfined reaches use 26 indicators (see Appendix B, Table B3 for details of the metrics). Most of our study reaches were partly confined or unconfined, with the exception of two (WHY2 and MNG1).

The MQI evaluation procedures were followed to assess the morphological quality of river reaches (see Rinaldi et al. 2016 for information on the technique). Existing documentation was examined initially, including: (i) current or recent aerial imagery; (ii) remotely sensed images representing current river conditions; (iii) historical aerial photos; and (iv) information on interventions within the reach and catchment upstream from the reach. Field surveys were carried out to validate and assess some of the indices. To calculate the MQI score, a final analysis combined all aspects of the data.

The MQI evaluation uses a scoring system where each indicator falls into three degrees of alterations: 'A' corresponds to an undisturbed condition or negligible alterations; 'B' to intermediate alterations; and 'C' to highly altered conditions. To calculate an MQI score, a Morphological Alteration Index (MAI) is first calculated according to Rinaldi et al. (2016):

$$MAI = S_{tot}/S_{max}$$

where S_{tot} is the sum of the scores, and S_{max} is the maximum score that could occur when all possible indicators are in class C (the most degraded state). The MAI ranges from 0 (no alteration) to 1 (maximum alteration). The MQI is then defined as:

$$MQI = 1 - MAI$$

The final MQI score ranges from 0 to 1 and is related to morphological quality (Table 3.2). Some indicators may involve a degree of subjectivity during assessment due to lack of data or information. Therefore, a second choice in each indicator can be selected, so that a score contains a range of variability rather than a single value. Additionally, indicators can be left out of assessment if not enough data or information is available, and the overall score will be adjusted so that the maximum score for all assessed indicators is 1.

Table 3.2. General narrative ranges assigned to QHEI and MQI scores (from Taft and Koncelik 2006 and Rinaldi et al. 2013, respectively)

Narrative rating: QHEI / MQI	QHEI range		MQI score
	Headwaters	Larger streams	
Excellent / Very good or high	≥70	≥75	0.85 to 1
Good / Good	55 to 69	60 to 74	0.7 to 0.85
Fair / Moderate	43 to 54	45 to 59	0.5 to 0.7
Poor / Poor	30 to 42	30 to 44	0.3 to 0.5
Very poor / Very poor or bad	< 30	< 30	0 – 0.3

Computing an MQI remotely (RMQI), without a field assessment component, has been shown to be highly correlated to an overall MQI score (Lemay et al. 2021). We wanted to more closely relate the biological data with morphological conditions at the time of fish sampling. Because trout biomass was measured in the 1980s and the most recent fish data for several NZ sites was measured before the year 2000 (Table B5), we used the RMQI concept to evaluate a historical RMQI, using historical photos and information on reaches and interventions. Since several field metrics cannot be assessed in a RMQI, the overall score is adjusted. Additionally, there may be greater uncertainty surrounding a historical measure as less data are used to compute the indices. If fish data were measured before 2000, a historical RMQI was calculated as close as possible to this date (usually within a 10-year span, Table B5). Up to eight indices were removed from the assessment to compute a historical RMQI (see Appendix B, Table B4 for a list of omitted attributes). Four indices were removed for all assessments, and the other four depended on how much information was available for each site. A historical RMQI was computed for all NZ sites except one (SUT1) to determine if the MQI changed over time in these sites. A historical RQMI was not computed for ON sites because the fish data were more recent (2000-2019).

3.2.4 Biotic Indices

The number of fish species present at each site (or at a reach closest to the site) was assessed using the latest data recorded for each site from online databases: The Flowing Waters Information System (FWIS 2020) in Ontario and the NZ Freshwater Fish Database (NZFFD, Stoffels 2022) in Aotearoa New Zealand. The FWIS contains information on Ontario's streams about fishes, benthos, and habitat among other things to help conservation practitioners, and the NZFFD contains fish observations from across Aotearoa New Zealand from 1901 to the present. Years of fish data collection ranged from 2000 to 2019 and 1974 and 2019 for ON and NZ sites, respectively.

Different methods were used to calculate an Index of Biotic Integrity (IBI) for NZ and ON as the fish communities differ. Both methods were adapted from Karr's (1981) assessment of biotic integrity. For the NZ sites, the latest fish presence data from the NZFFD (Stoffels 2022) was used and an IBI was calculated based on Joy and Death's (2004) method, which does not include trout in the index (Table B6). Joy and Death (2004) assigned the following qualitative assessments for the NZ IBI: where no native fish were caught (0), low ecological quality (1-20), medium quality (20-40), and high quality (40-60). For the ON sites, electro-fishing data were obtained from the FWIS (2020) and fish were categorised using information about fishes in the area (Credit Valley Conservation 2002). The IBI was calculated using a method modified for use in Southern Ontario (Steedman 1988). Information on fish condition was not available in the FWIS (2020) database, so the fish condition indicator (% of sample with blackspot) was left out of the index for this study. Hence, our minimum and maximum possible IBI score for ON sites were 9 and 45, respectively, compared to 10 and 50 in the Steedman (1988) method. We categorised ON IBI scores between 9 and 21 as low, between 22 and 33 as medium, and 34 and 45 as good, to align with NZ IBI ratings. The IBI configuration and scoring criteria for NZ and ON are shown in Table B6 and B7, respectively (Appendix B).

For 12 NZ sites, salmonid biomass was obtained from trout drift diving assessments in the 1980s (Teirney and Jowett 1990; Jellyman and Graynoth 1994, Table B5). During the dive surveys, trout were identified by species, counted, and assigned a size class (large, medium or small). These were later converted to weight based on the mean weight of trout in each size class (for more information on dive methods see Teirney and Jowett, 1990). Not all sites had biomass data available and more recent public records of salmonid biomass for these rivers are not readily available. While map locations were given for trout biomass survey sites, there has been some reluctance to release location details to maintain secrecy about trout hot spots and not "betray the trout" (Jellyman and Graynoth 1994, p. 8), therefore exact locations are unknown. MQI and historical RMQI locations for sites with trout biomass were selected to encompass the map location given. Reliable salmonid biomass data was not available for the Ontario sites.

3.2.5 Field surveys

Field surveys were carried out during summer in Ontario (July 2019) and Aotearoa New Zealand (January and February 2020) to allow validation of some of the MQI indicators and carry out a QHEI assessment. Each metric in the QHEI was scored by walking the length of the reach to obtain a representative view of the site. We were unable to complete a QHEI assessment at one site (SUT1) due to lack of physical access to the stream. Many MQI metrics were validated in the field and several were assessed only using field surveys. Some sites were not accessible for their entire length (e.g. on private land, too far from an access point), and were assessed from nearby bridges or roads, as well as remotely using GIS.

Where possible, average wetted width was estimated at QHEI sites, by measuring 10 random wetted stream widths across the site. These were not carried out in sites that were too deep or swift to wade, or with bacterial or algal cover that presented health concerns[2]. In these streams an average width was calculated by measuring 10 random widths using satellite imagery.

3.2.6 Land cover

The proportion of different land cover types was assessed in the catchment from the downstream point of the reach surveyed upstream to the headwaters (Fig. 3.3). Land cover was classified into seven classes (Table 3.3) using land cover layers (Agriculture and Agri-Food Canada 2020; Landcare Research New Zealand 2020) and catchment boundaries were defined from DEMs and watershed boundary layers. Land cover types were also calculated in riparian areas: a 50 m wide riparian buffer was computed in GIS around each stream's river line in the reach and upstream to the headwaters (Fig. 3.3b). Buffer widths of 100-200 m are common in relating landscape variables to stream condition (Allan 2004), although fenced vegetated riparian widths of 5 m (Holmes et al. 2016) to over 30 m (Sweeney and Newbold 2014), are thought to be required for healthy stream ecosystems. The QHEI considers riparian quality 50 m from each bank (Taft and Koncelik 2006), and functional vegetation in the MQI is considered for 50 m of either bank (confined channels) or twice the channel width (unconfined or partly confined channels) (Rinaldi et al. 2016).

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[2] Many rivers in New Zealand contain cyanobacteria that can contain harmful toxins. In the South Island of New Zealand, *Didymosphenia geminate* (didymo) is also present (a diatom that can form large algal blooms, detrimental to aquatic life). There are strict bio-security rules to ensure it is not introduced to the North Island – all gear that has been in a stream, river or lake must be cleaned and dried before they enter another waterway. Therefore, extra care was taken to prevent contamination, and contact was avoided if there was a heavy presence of didymo or any presence of cyanobacteria.

We chose 50 m wide riparian buffers to align with the QHEI and MQI attributes. An example of land cover in the upstream hydrological networks at the catchment and buffer scale is shown in Fig. 3.3. Dominant land cover was classified as the one with the highest proportion in the upstream catchment or buffer (Table 3.4). Land covers were also then simplified into disturbed (agricultural, urban, and forestry land) and natural (native forest, shrub, wetland, gravel and rock) categories.

Table 3.3. Land cover categories and the types of land covers included in the ON and NZ sites

Land cover classification	Types of land cover included in each classification as described in the land cover layers	
	Ontario[a]	New Zealand[b]
Agriculture	Pasture/forages, fallow, barley, oats, rye, winter wheat, spring wheat, corn, canola/rapeseed, soybeans, orchards, peas, beans, potatoes, other vegetables, hemp, vineyards, greenhouses	High producing exotic grassland; low producing grassland; depleted grassland; orchard, vineyard, or other perennial crop; short-rotation cropland
Native forest	Coniferous, broadleaf, mixedwood	Broadleaved indigenous hardwoods, deciduous hardwoods, indigenous forest
Urban / developed	Urban/developed, exposed land / barren	Built-up (settlement), urban parkland/open space, transport infrastructure, surface mine or dump
Shrub	Shrubland, grassland	Alpine grassland/herbfield, fernland, flaxland, Gorse and/or broom, herbaceous freshwater vegetation, Manuka and/or Kanuka, Matagouri or grey scrub, mixed exotic shrubland, sub-alpine shrubland, tall-tussock grassland
Wetland (rivers, lands, and ponds)	Water, wetland	Lake or pond, river
Exotic forest	NA	Exotic forest, forest - harvested
Rock, gravel	NA	Gravel or rock, landslide

Land cover data: [a]2020 Annual Crop Inventory (Agriculture and Agri-Food Canada 2020); [b] 2018 Land Cover Database (LCDB) (Landcare Research New Zealand 2020).
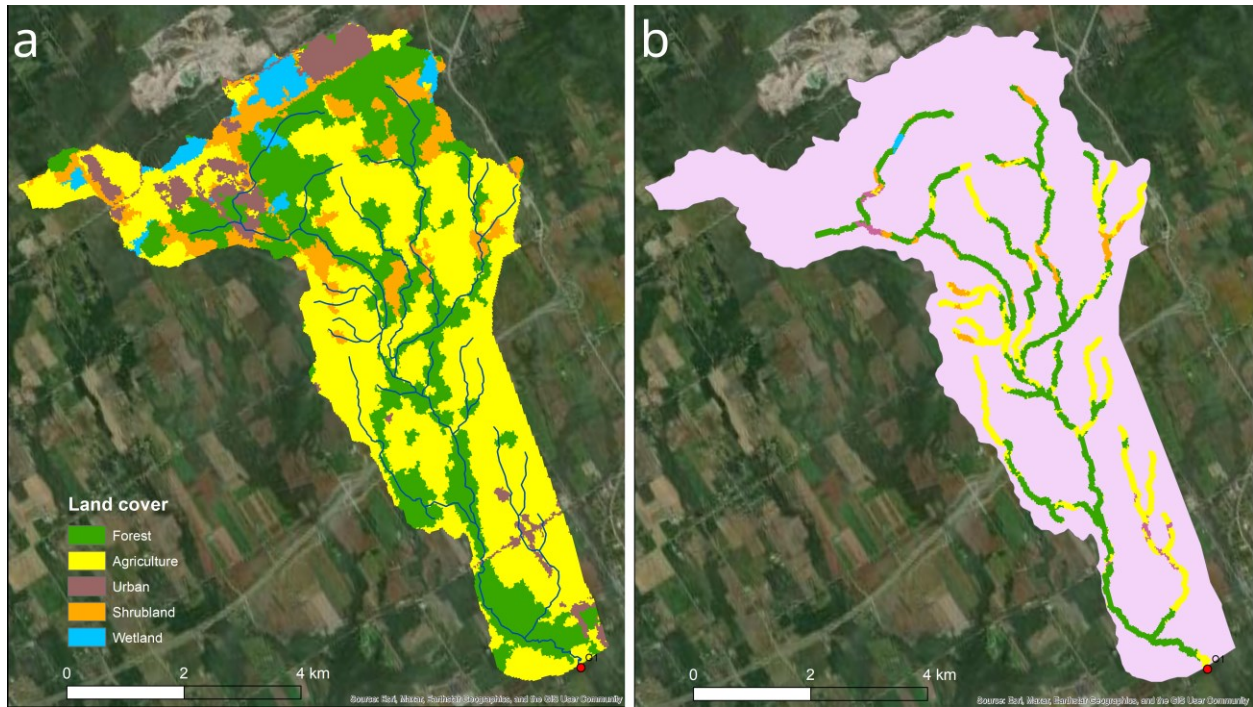
Fig. 3.3. Land cover in the Wilmot Creek catchment (site WIL1) for the whole catchment upstream of the site (a) and in the 50 m buffer zone (b)

Table 3.4. Percentage of ON or NZ sites and dominant land cover in the upstream catchment or buffer

Dominant land cover	Percentage of ON sites		Percentage of NZ sites	
	Catchment	Buffer	Catchment	Buffer
Agriculture	79	36	52	52
Native forest	0	36	43	43
Urban	21	21	0	0
Exotic Forest	0	0	5	5
Wetland	0	7	0	0

Note: There was no differentiation of native or exotic forest cover in Ontario so it was assumed all forest was native forest. Management of native and exotic forest in New Zealand is very different, so these land covers were separated.

3.2.7 Analysis

Statistical analyses were carried out using the stats package in R (R-core packages, 4.1.2). Relationships between variables were assessed with a linear regression. Differences between MQI and QHEI were explored using Welch's t tests, which is more reliable when the two samples have unequal sample sizes. Therefore, a modification to the degrees of freedom is used. For variables that did not meet the assumptions for a parametric test, we used Mann-Whitney tests. The significance level for all tests was $p < 0.05$.

3.3 Results

3.3.1 MQI and QHEI scores

Overall, MQI scores at studied streams revealed a relatively good hydrogeomorphological quality, with 8 sites in the very good category (23%), 10 in the good category (29%), 12 in the moderate category (34%), and 5 in the poor or very poor category (14%). There were no significant differences between the MQI scores in ON (mean = 0.686, SD = 0.25) or NZ (mean = 0.694, SD = 0.14), (t (df 18.7) = 0.12, p = 0.9). In Aotearoa New Zealand, there was no statistical difference between the current MQI (measured in 2020) and the historical RMQI (measured mostly in the 1980s) (t (38.9) = 0.78, p = 0.44) but the MQI declined in the majority of the sites (65%, 13 sites), increased at 6 sites (30%) and stayed the same at one site (5%) (Fig. 3.4). The current MQI and historical RMQI were also positively correlated (r = 0.85, p < 0.001; Fig. 3.4).

The QHEI scores showed that habitat quality in half of the reaches was also good, with 11 reaches (32%) in the excellent category, 6 in the good category (18%), 14 in the fair category (41%) and 3 in the poor or very poor category (9%). As with the MQI, we found no significant differences in QHEI scores in ON (mean 67.4, SD = 18.6) and NZ (mean 66.7, SD = 15.1), (t (df 24.3) = -0.13, p = 0.9).

3.3.2 MQI/QHEI relationship

Streams with a higher MQI also had a higher QHEI (r = 0.82, p < 0.001, Fig. 3.5). The range of MQI values (min, max, average) and the QHEI values for each site are presented in Fig. B2 (Appendix B). Photographs of some of the sites showing a good agreement between MQI and QHEI are provided in Appendix B1. Significant discrepancies between the MQI and QHEI occurred in two ON sites (BLK1 and NOT1, shown in Fig. 3.5). In BLK1, an alteration of longitudinal and lateral continuity due to a weir (Fig. 3.6b and c) contributed to a poor MQI score of 0.35, without markedly affecting habitat quality (good QHEI score of 71). The weir structure in Fig. 3.6b and c was located at the upstream boundary of BLK1 (Fig. 3.6a) and bank stabilisation structures (left side of Fig. 3.6d) were implemented throughout the

reach to protect nearby properties and roads from erosion (Fig. 3.6a, d). However, the reach included a diversity of habitat types and flows, riparian vegetation, and in-stream woody debris (Fig. 3.6e), all positive attributes in the QHEI scoring. The second discrepancy was a small upstream site (NOT1) that achieved a fair habitat quality (QHEI = 54) because of the lack of habitat diversity; NOT1 was a shallow stream with no riffle habitat and few shallow pools, heavy siltation (Fig. 3.7c), and extensive embedded substrate. However, upstream and in the reach, there were few artificial structures and geomorphological modifications (thus, a good MQI score of 0.81, Fig. 3.7a and 3.7b).
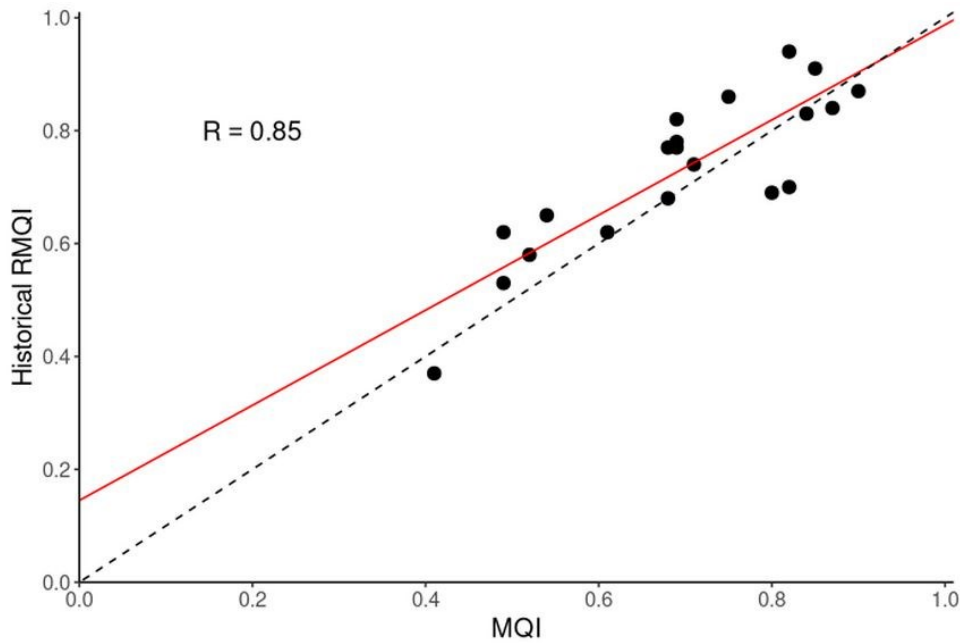
Fig. 3.4. Relationship between historical RMQI (measured in the 1980s) and the average MQI (measured in 2020) in the NZ sites. The regression (red solid) and 1:1 (black dotted) lines are shown
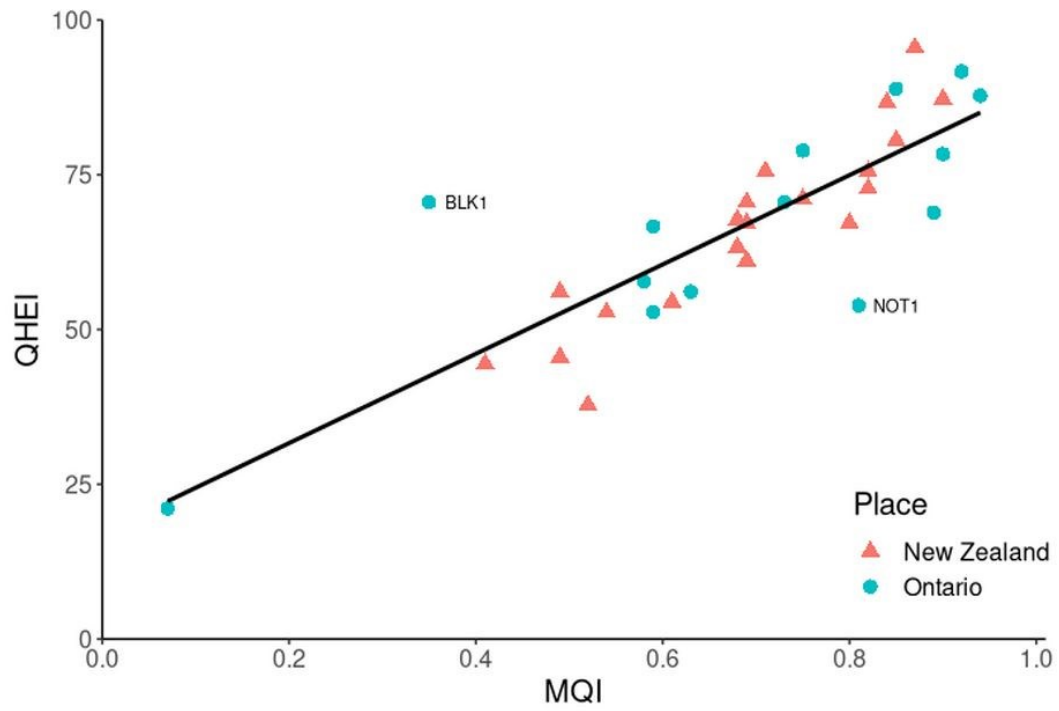
Fig. 3.5. Relationship between MQI and QHEI for Ontario (blue circles) and New Zealand (red triangles) site. Outliers are labelled (Black Creek: BLK1 and Nottawasga River: NOT1)

Fig. 3.6. BLK1 site (Black Creek, ON). a: the extent of the reach is shown by the red line. The orange triangle is the location of the weir in b and c. b and c: The weir spans the whole width of the reach, blocking the flow of wood and sediment. d: Large concrete slabs are used for bank stabilisation on the right side of the image. A house can be seen on the left. e: Woody debris are found at various points in the reach, considered a good attribute for the MQI and QHEI scores
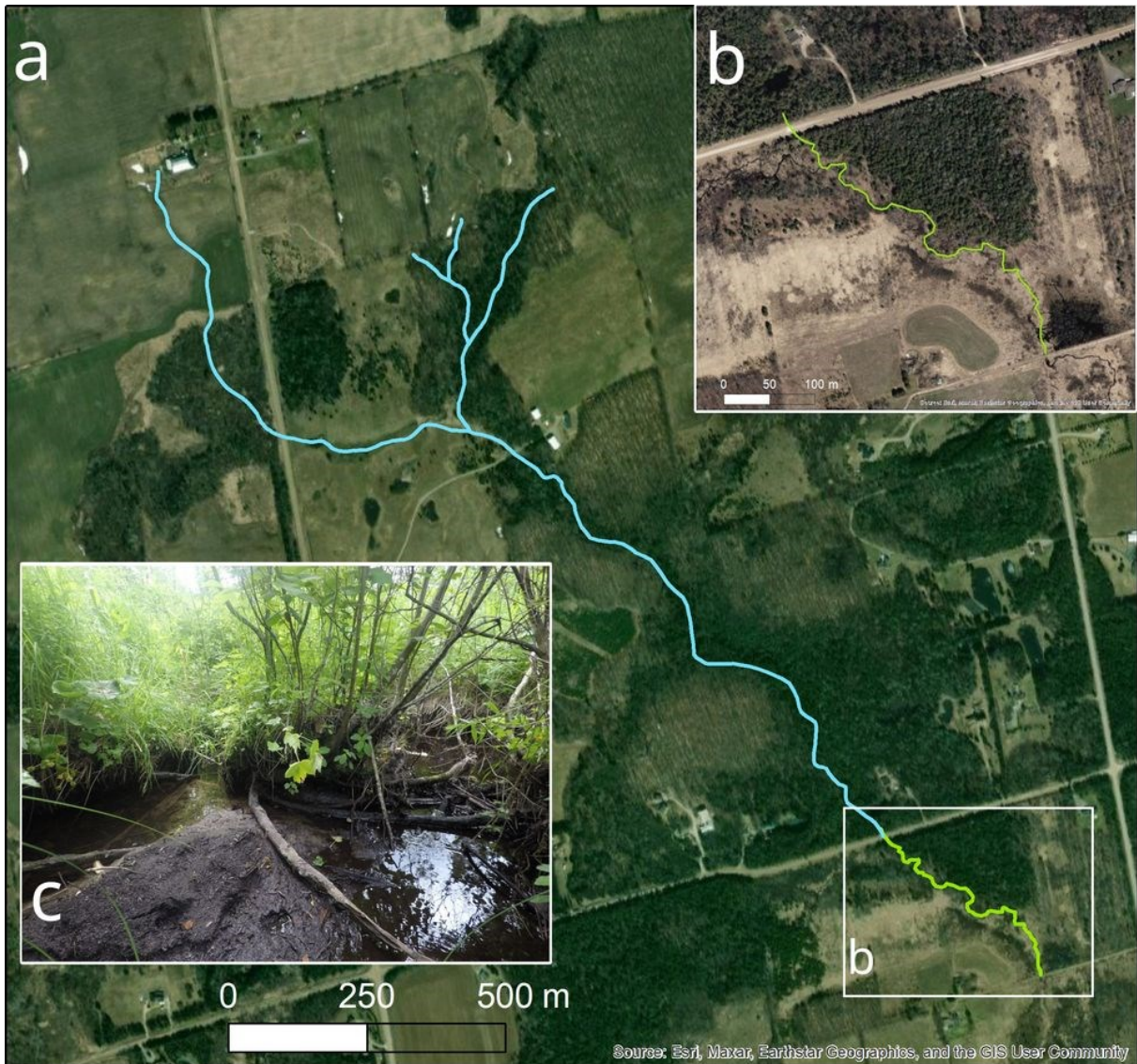
Fig. 3.7. NOT1 site and upstream (tributary in the upper Nottawasga River, ON). a: The green line in the white box is the extent of the reach, shown in b. The upstream extent of the river is shown by blue lines. b: The sampled reach is shown in green. Due to the mobile nature of the channel, the lines may not line up exactly with the stream at time of sampling. c: Typical nature of the stream – abundant vegetation and woody debris, fine sediment, shallow pools, and no riffles

3.3.3 Land cover relationships

For all sites, the MQI and QHEI decreased significantly with urban area (Fig. 3.8c and d, 3.9c and d). However, many catchments had less than 10% urban area, so this relationship could be largely influenced by streams with high proportions of urban cover. MQI and QHEI increased significantly with the proportion of native forest in the catchment both for the whole upstream catchment (Fig. 3.8e and f) and the 50 m buffer zone (Fig. 3.9e and f). There was no relationship with the proportion of agricultural land at the catchment or buffer level and the MQI (Figs. 3.8a, 3.9a). The QHEI was correlated with the proportion of land in agriculture at the buffer level (Fig. 3.9b), but not at the catchment level (Fig. 3.8b).
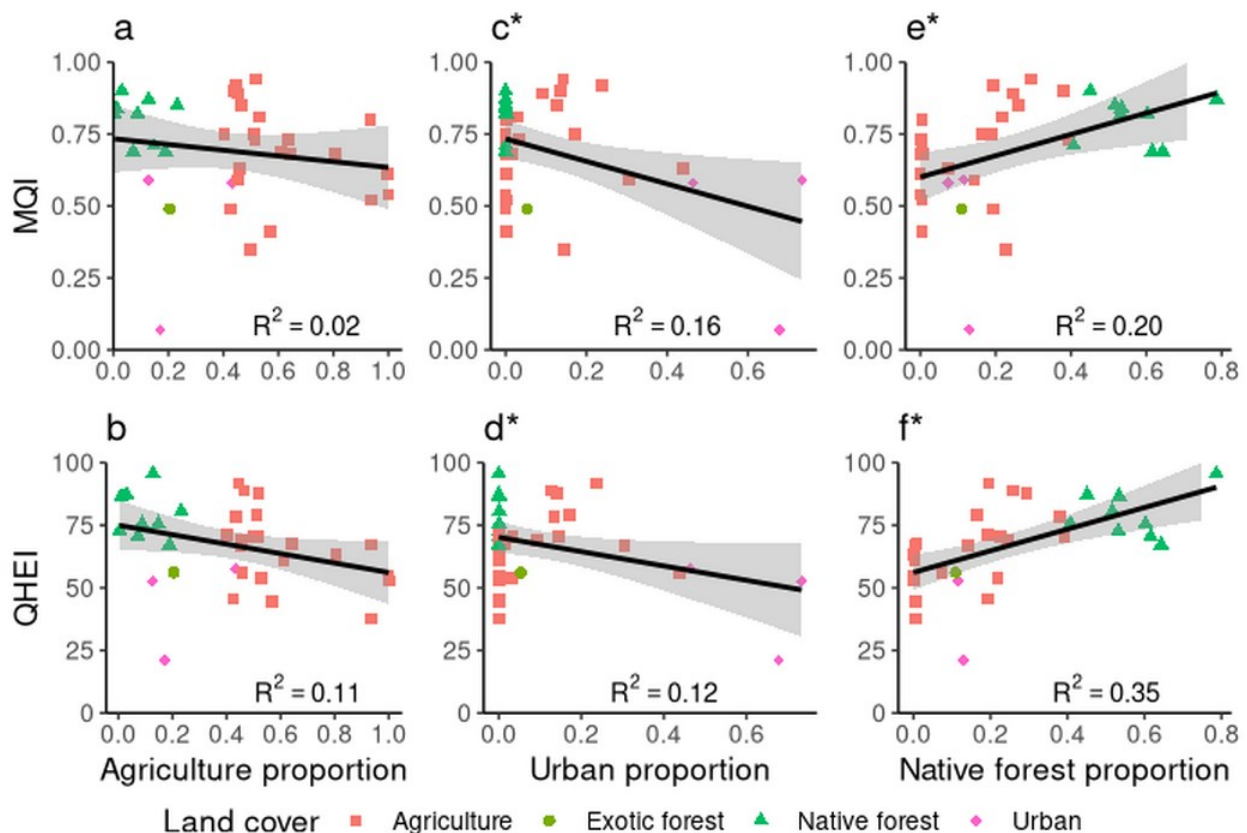
Fig. 3.8. MQI (top: a, c, e) and QHEI (bottom: b, d, f) plotted against the major land cover proportions in the catchment upstream from the reach sampled: agriculture (a and b), urban (c and d) and native forest (e and f). Sites are categorised by dominant land cover in the catchment upstream: red squares (agriculture), green circles (exotic forest), green triangles (native forest), and purple diamonds (urban). An asterisk (*) next to the plot letter indicates a statistically significant relationship exists (n = 35 for MQI and 34 for QHEI)
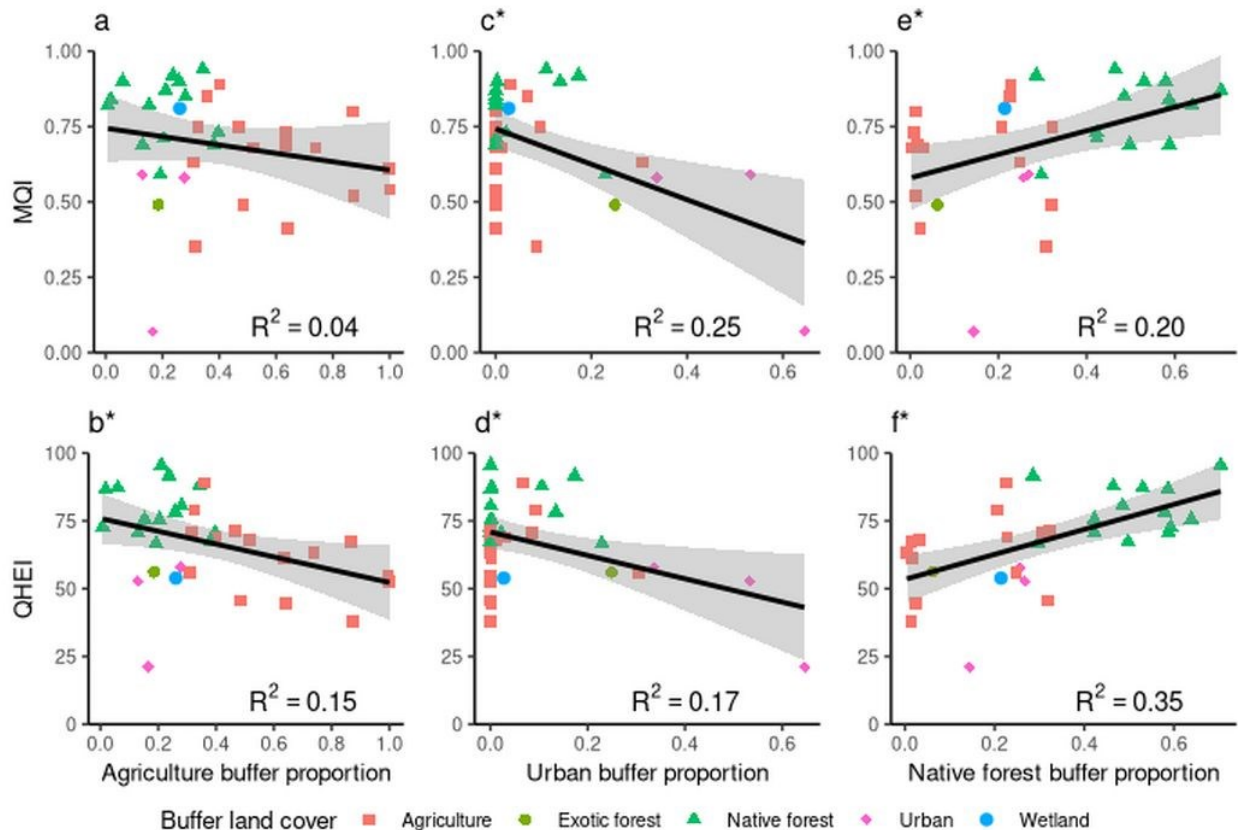
Fig. 3.9. MQI (top: a, c, e) and QHEI (bottom: b, d, f) plotted against the major land cover in the buffer zones upstream from the reach sampled: agriculture (a and b), urban (c and d) and native forest (e and f). Sites are categorised by dominant land cover in the buffer zone upstream: red squares (agriculture), green circles (exotic forest), green triangles (native forest), purple diamonds (urban), and blue circles (wetland). An asterisk (*) next to the plot letter indicates a statistically significant relationship exists (n = 35 for MQI and 34 for QHEI).

3.3.4 Biotic relationships

The sites were characterized with overall IBI scores of medium quality (23 sites), with some (4) in the high and 8 in the low categories. Trout biomass was available for 12 NZ sites, and ranged between 3.01 and 16.14 g/m². Mann-Whitney tests indicated there was no significant differences between the number of fish species in ON (median = 4.5) and NZ (median = 3), (p = 0.393), but that the IBI was greater for ON sites (median = 29) than for NZ sites (median = 20) (p = 0.001).

There was no significant relationship between the MQI (or historical RMQI) or QHEI and any of the biotic variables (number of fish species, IBI, trout biomass) (Fig. 3.10). Because there was no significant change in the MQI over time (Fig. 3.4), we assumed that the QHEI did not change significantly, and therefore the current QHEI scores are

reasonable to align to past fish surveys. Combining human disturbed land covers (urban, agriculture, exotic forest), we found stronger relationships between the proportion of disturbed land and the MQI and QHEI than with separate land uses, however, a relationship with the IBI and the proportion of disturbed land is lacking (Fig. 3.11). Likewise, the number of fish species and trout biomass did not have a relationship with any of the land cover categories. In the NZ streams, there was no significant relationship between trout biomass and the IBI ($r = 0.15$, $p = 0.29$).
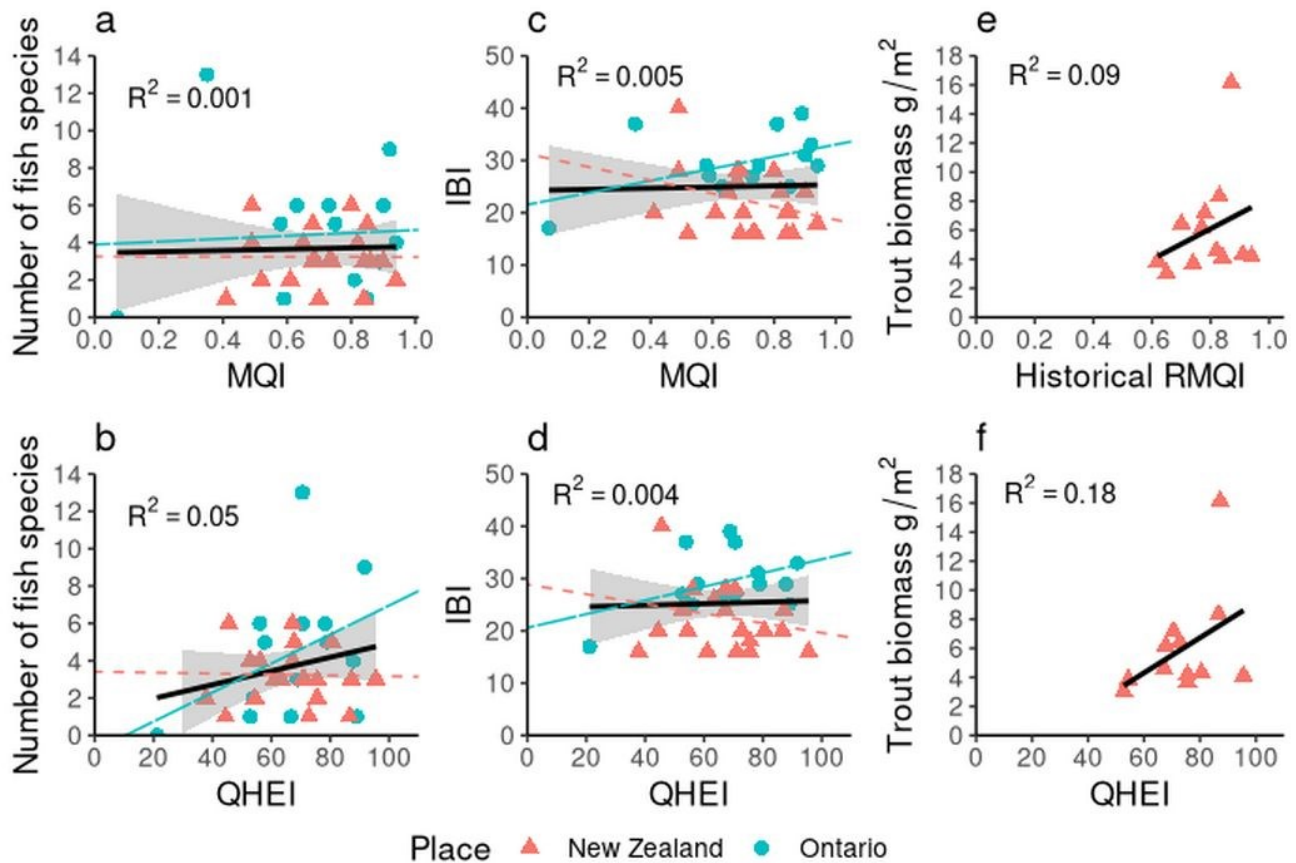
Fig. 3.10. Biotic indicators (number of fish species (a, b), IBI (c, d), and trout biomass (e, f)) plotted against MQI (or historical RMQI) (a, c, e) and QHEI (b, d, f). Black lines are the overall regression lines while the dashed lines are ON (blue, n=14) and NZ (red, n=21 or 12 for biomass) regressions between the MQI or QHEI and biotic variables
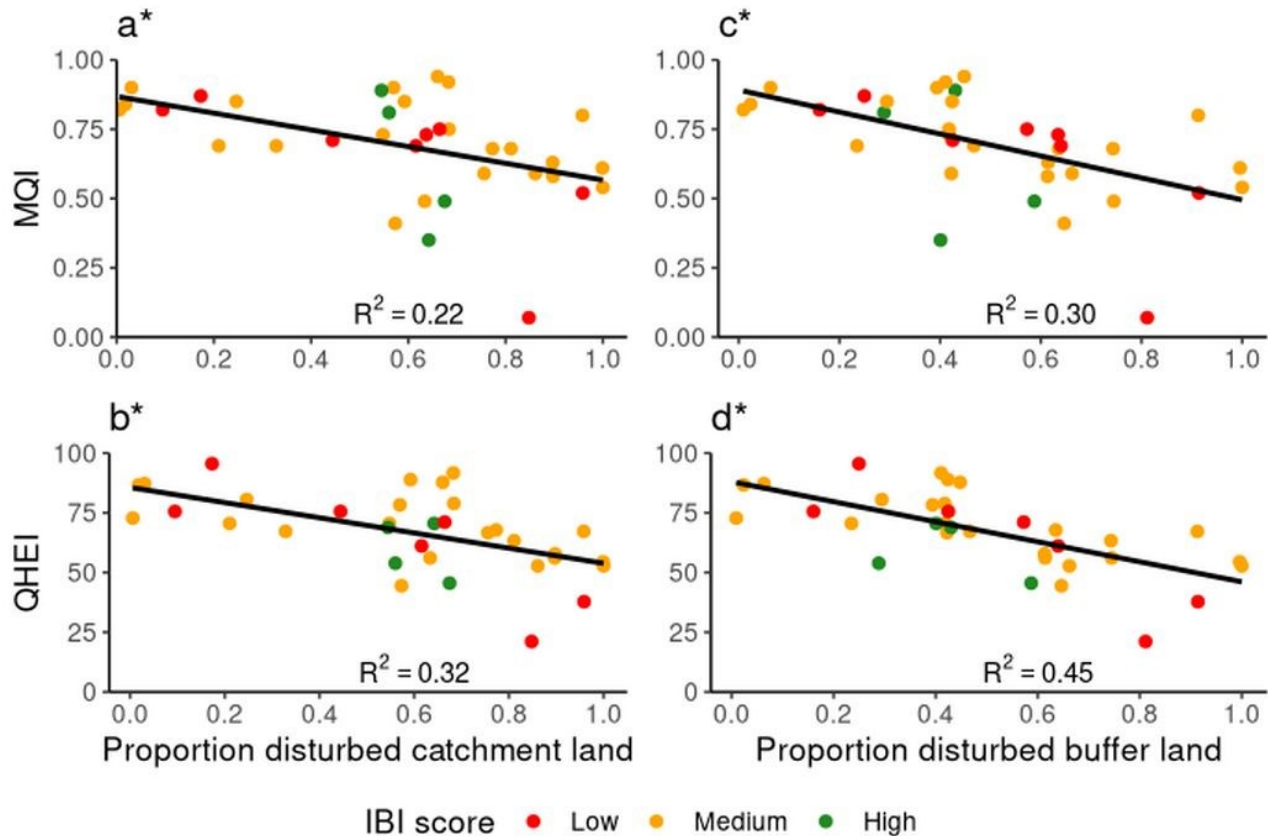
Fig. 3.11. Relationships between the MQI (a and c) and QHEI (b and d) and the proportion of disturbed land (sum of agriculture, urban and exotic forest) in the whole catchment (a and b) and 50m buffer zone (c and d). IBI scores are presented by low (red), medium (yellow), or high (green) values (n = 35 for MQI and 34 for QHEI

3.3.5 Other physical attributes

Relationships between each index (MQI, QHEI, number of species, IBI, trout biomass) and physical attributes in the reach or catchment were tested (Table 3.5). Not surprisingly, given the various metrics that penalize structures in the reach or upper catchment in the MQI, artificial barriers to longitudinal connection in the river had negative effects on the MQI scores (R^2 = 0.09, p = 0.04). For the QHEI, this effect was only seen if the barrier was upstream of the reach (R^2 = 0.1, p = 0.04), not downstream (R^2 = 0.002, p = 0.8). On average, sites with a lake upstream had higher MQI (R^2 = 0.09, p = 0.04) and QHEI scores (R^2 = 0.12, p = 0.03) and wider streams had a higher QHEI score (R^2 = 0.13, p = 0.02).

More fish species were found in sites that were closer to a large downstream lake (ON) or the coast (NZ) (R^2 = 0.09, p = 0.05). Given the migratory nature of many of New Zealand's freshwater fish, this is not surprising and is built into the NZ fish IBI (Joy and

Death 2004). On the contrary, trout biomass in Aotearoa New Zealand was higher in sites higher in elevation (R^2 = 0.59, p = 0.002) and further away from the coast (R^2 = 0.31, p = 0.035). Smaller streams had higher IBI scores (R^2 = 0.17, p = 0.007), and scores were also higher if there was a lake downstream (R^2 = 0.11, p = 0.03). These relationships could reflect the higher IBI scores found in ON streams compared to NZ streams (R^2 = 0.25, p = 0.001), which may be affected by the way the IBI is measured differently in the two regions.

Table 3.5. Response of index values with physical attributes in the reach or catchment (only statistically significant relationships are represented with arrows indicating the direction of the relationship)

	Index value				
Physical attribute	*MQI*	*QHEI*	*No. of species*	*IBI*	*Trout biomass*
Larger average width		↑		↓	
Higher elevation					↑
Closer to downstream lake or coast			↑		↓
Barrier present upstream	↓	↓			
Barrier present downstream	↓				
Lake present upstream	↑	↑			
Lake present downstream				↑	

3.4 Discussion

We had expected metrics of fish abundance to be positively related to two independent metrics of habitat quality. This expectation was even stronger given a strong positive relationship between hydrogeomorphological quality and fish habitat quality in both Ontario and NZ salmonid streams. Therefore, further analysis of the relationship between morphological and habitat quality to biological variables is likely warranted.

3.4.1 MQI and QHEI relationship

The correlation between the MQI and QHEI (r = 0.82) in our study sites is similar to the correlation of 0.81 in Lemay et al. (2021) for lowland rivers in Canada, showing that hydrogeomorphological quality is strongly related to fish habitat quality. This concept is not new, and the link has been postulated by many authors (Brierley and Fryirs 2005; Wohl et al. 2005; Florsheim et al. 2008; Rinaldi et al. 2013), but few studies show a statistical association between the two.

A deviation in the indices occurred where longitudinal and lateral connectivity had been altered by artificial structures and modifications (thereby lowering the MQI score), without severely affecting habitat quality (BLK1, Figs. 3.5 and 3.6). The weir in BLK1 (Fig. 3.6b and c) blocked the flow of sediment and debris and restricted water flow at times, and bank stabilisation (Fig. 3.6d) restricted connectivity with the floodplain. Connectivity and flow variability are required for many hydrogeomorphological processes to occur, such as the movement and sorting of sediment and wood, erosion and deposition, floodplain inundation, and bed mobility (Frissell et al. 1986; Allan 2004; Rinaldi et al. 2013). Attributes in the MQI put a large emphasis on connectivity and disturbance from artificial structures, whereas the QHEI focuses on in-stream habitat and substrate; the physical formations and structures present are considered, not the processes that create these formations, and anything beyond the reach and riparian area is disregarded. These processes are important for the formation of in-stream fish habitat (Brierley and Fryirs 2005; Beechie et al. 2010; Biron et al. 2014; Choné and Biron 2016), including the formation and maintenance of pools, riffles, bars, and side channels (Allan 2004; Williams et al. 2020). Riparian zones, sediment, and debris transported from upstream contribute to woody debris, gravel patches, and a diverse range of sediment sizes (Frissell et al. 1986), which provide numerous benefits: shelter (Bjornn et al. 1991; Culp et al. 1996; Dieterman et al. 2018), areas for spawning (Sweka and Hartman 2006) and fish food (source of invertebrates) (Inoue and Nakano 1998; Kratzer 2018); create pools (Berg et al. 1998) and habitat diversity (Bilby and Likens 1980; Roni 2001); and, increase bank stability (Keller and Swanson 1979) and nutrient input (Johnson et al. 2005).

It is increasingly recognized that process-based principles are needed to restore river ecosystems, such as leaving more space around rivers for fluvial processes to operate (Piégay et al. 2005; Ollero 2010; Biron et al. 2014). However, many restoration actions continue to focus on the symptoms of degradation by adding in-stream structures or modifying channel forms that are perceived to provide good habitat for fish (Imhof et al. 1996; Roni et al. 2002; Beechie et al. 2010), even though connectivity is seen as extremely important (Seliger and Zeiringer 2018). Where these processes have been reduced, adding structural habitat (such as woody debris, and boulders) can be beneficial for fish populations (Roni et al. 2006; Whiteway et al. 2010; Foote et al. 2020), as has been implemented at many places at the BLK1 site (Fig. 3.6e). The addition of structures may create the illusion of a healthy stream, at a site scale, even if larger scale hydrogeomorphological processes have been disturbed. But structures usually require regular maintenance (Champoux et al. 2003) and are limited in the spatial scale they are implemented; therefore, they may not be viable for long-term restoration solutions (Roni et al. 2002, 2008; Foote et al. 2020). Furthermore, migratory movement through the catchment and downstream to a lake or sea is essential for diadromous species, of which New Zealand has a high proportion of (McDowall 1999; McDowall and Taylor 2000). Likewise, many Ontario fish use both lake and stream habitats throughout their life cycles (Dolinsek et al. 2014), so connectivity between these places is important.

3.4.2 Land cover

A high MQI score accompanied by a lower QHEI score could be the result of the effects of agriculture not being fully incorporated into the MQI. Lemay et al. (2021) found that the lack of dams in agricultural areas may artificially boost MQI scores. While several attributes in the MQI indirectly account for agricultural effects (sedimentation, excessive erosion, river straightening, riparian vegetation removal), these attributes play a smaller role in the overall MQI score than do artificial structures and disruption of connection, shown in our sites with lower MQI scores when upstream and downstream barriers are present (Table 3.5). Conversely, substrate quality, pool/riffle quality, and instream cover are key components of a QHEI score.

Human disturbances from land use cause problems to waterways such as sedimentation, nutrient enrichment, contaminant pollution, hydrologic alterations, riparian clearing and canopy opening, and loss of large woody debris (Allan 2004). Not surprisingly, given the presence of artificial structures (e.g. weirs, culverts, bridges, bank stabilisation) is incorporated into many of the MQI attributes, lower MQI (and QHEI) scores were found in sites with more urban land (which very likely contains more artificial structures and impervious surfaces than other types of land cover (Allan 2004)). Conversely, the more forested land, the better the MQI and QHEI scores in our sites.

Correlations with the proportion of agricultural land and the MQI or any of the biotic variables in our study did not follow the same association with urban and forested land and the MQI and QHEI, contrary to what other authors have found. Increases in agricultural land area have occurred alongside declines in water quality, habitat quantity and quality, and biological assemblages (Wang et al. 2002; Allan 2004; Julian et al. 2017). Lower IBI scores are found in urban and agricultural land in Aotearoa New Zealand and Ontario (Steedman 1988; Joy and Death 2004), and New Zealand native fish are declining at faster rates in these land uses compared to native forest (Joy et al. 2018). Likewise, habitat quality and IBI scores were highly correlated in Michigan agricultural streams, along with the proportion of agricultural area at the catchment scale (Roth et al. 1996). In fact, stream conditions at these Michigan sites were mainly determined by regional land use (Roth et al. 1996).

Along with good physical habitat, water quality is extremely important for fish communities. Water pollution, from nutrients, suspended matter, or chemicals, is a major threat to freshwater biodiversity (Dudgeon et al. 2006; Lee et al. 2011; Reid et al. 2019). An over-abundance of nutrients is not only toxic to animals, but can cause eutrophication, which in turn can lead to lower dissolved oxygen (DO) concentrations detrimental to aquatic life (Shields Jr. et al. 2013; Joy 2015). Pastoral land cover has been related to increased nutrients and chlorophyll-a concentrations (Julian et al. 2017; Carlson Mazur et al. 2022), and higher water temperature (Jackson et al. 2022) in watersheds. In Korean watersheds, QHEI values were significantly correlated with nitrogen and phosphorus concentrations (Lee et al. 2011), and a study in Southern Ontario found significant correlations between biotic indices and the QHEI, water quality, and land use (Gazendam et al. 2011). The correlation between the proportion of agricultural land in the 50 m buffer zone and the QHEI (Fig. 3.9b) shows that the QHEI might be better at detecting agricultural impacts than the MQI. This also highlights the importance of a vegetated riparian buffer in providing good fish habitat. The QHEI could be an important index for agricultural land managers to determine habitat quality on their land and how they can improve it (i.e. by increasing riparian vegetation). A lack of connection between the MQI and agricultural land in our study areas could be because factors affecting water quality are not highly weighted in the overall scoring. A greater proportion of urban landscape in Europe where the MQI was developed may have contributed to this weighting decision. Therefore, adjusting weightings in the MQI scoring to better capture the effect of agriculture could help make the MQI a more effective tool for ecological monitoring in less urban regions.

3.4.3 Biotic indices

Several reasons may explain the lack of significant relationships for the three biotic variables and either the MQI or the QHEI. Firstly, average MQI and QHEI scores were high

in our streams – so it is possible that a stronger relationship with biotic variables would have appeared if our sampled streams had included poorer morphological and habitat quality watercourses. Indeed, Steedman (1988) found that land-use in a watershed was less able to predict IBI changes in the upper range, so this could be the case for the MQI and QHEI as well. In the literature there has been mixed results when relating hydrogeomorphological quality with biotic indices, although most indicate that poor hydrogeomorphological conditions have an impact on aquatic ecology (Scorpio et al. 2016; Golfieri et al. 2018; Hayes et al. 2022). A decline of the range and biomass of cyprinid fishes in Austria were linked with hydrogeomorphological disturbance from barriers (Hayes et al. 2022). Scorpio et al. (2016) show the MQI was positively correlated to the presence of Eurasian otters (*Lutra lutra*) in streams in southern Italy, particularly to sub-indices of river continuity and channel adjustments. In Northern Italian rivers Golfieri et al. (2018) found a significant relationship between the MQI and the Odonata River Index, a biotic index that incorporates the whole river corridor when evaluating ecological integrity, but a relationship was not found with organisms that are considered to be good indicators of water quality (biological quality elements, BQE). This is postulated to be because of the different spatial scales that the indices consider (Golfieri et al. 2018). Fish are BQE, which could explain why a correlation with fish metrics was not found in this study – the organism studied is mostly confined to the wetted river channel. However, other studies have found that hydrogeomorphological conditions affect fishes at larger spatial scales of river reaches and river segments, rather than smaller scales that fish are usually sampled at (Carvalho Carneiro de Mendonça et al. 2021; Knehtl et al. 2021). The spatial scale of investigation may be important depending on the species studied, but the complexity of habitat needs of biota throughout their life-cycle, the lack of relationship found in this study, and the contrasting results found in the literature, may be indicative of the shortcomings of the MQI as an ecological health index. However, the MQI and QHEI may be more useful at predicting biological responses if they are applied at multiple sites throughout the catchment, instead of a single reach or segment as in the case of this study.

The IBI is a common measure for ecological condition in streams, but may not be entirely indicative of healthy conditions in salmonid streams, especially in trout dominated streams of Aotearoa New Zealand. All salmonids' species are exotic in Aotearoa New Zealand; thus, they are penalised in the New Zealand fish IBI used in this study. This could be why the NZ IBI scores are significantly lower than the ON IBI scores, where salmonids are positively incorporated into the index. In fact, Steedman (1988) found that the best predictor of the IBI developed for Ontario was the presence of brook trout, particularly in small streams. Smaller streams in our study had higher IBI scores (Table 3.5), which could also be reflective of the difference between ON and NZ sites (as ON sites were smaller in size, Table B1).

Given trout abundance is affected by many variables at multiple scales (Fausch et al. 1988; Armstrong et al. 2003), the lack of correlation between trout biomass and the MQI or QHEI is probably not surprising. This could be because trout biomass was high in the NZ sites (median = 4.43 g/m^2, minimum = 3.01 g/m^2), when compared to a global database of salmonid biomass in 550 rivers (median = 3.17 g/m^2, Foote et al. in prep). If we were to include streams with a low biomass and low MQI, our data might show stronger relationships with biotic variables. Secondly, the lack of data limited the possibility of finding a statistically significant relationship. Only 12 sites with biomass data were included, which greatly limited our power to detect a relationship. Unfortunately, the lack of reliable salmonid biomass data for Ontario streams precluded the inclusion of these sites in the analysis.

Physical habitat is only one facet of the equation. Fish abundance and biodiversity in rivers is highly complex and depends on a multitude of factors, including flood disturbances, fishing pressure, migration, and biotic variables (Armstrong et al. 2003; Dudgeon et al. 2006; Reid et al. 2019). Stability of flow is thought to be important for sustaining trout populations (Binns and Eiserman 1979; Fausch et al. 1988); therefore, recent floods could impact trout abundance, irrespective of habitat quality. Furthermore, poor habitat in other areas of the catchment may contribute to low fish biomass or biodiversity, and may be affecting recruitment to parts of the stream that do have 'good' habitat.

3.4.4 Conclusion

Morphological (MQI) and physical habitat (QHEI) quality was strongly correlated in 26 salmonid streams in Ontario and Aotearoa New Zealand. However, both of the indices fell short in one area or another that are important for fish biology (land use/water quality, and connectivity), resulting in no significant relationship with the number of fish species, IBI or trout biomass. A combination of indices may be required to accurately predict ecological health in streams – one component does not give us a complete picture. Incorporating metrics from the QHEI and increasing their weighting in the MQI, as well as sampling at multiple segments throughout a catchment or river, may increase the usefulness of these metrics for ecological monitoring.

Vegetated riparian zones tended to buffer streams from morphological alterations and land-use practices affecting habitat, so even in agricultural catchments, fencing off streams from stock, and allowing vegetation to grow would be highly beneficial for overall stream health. However, water quality concerns in agricultural catchments still poses concerns for ecological health.

The MQI can nevertheless be a useful index for understanding ecosystem health at a larger scale (segment to catchment) than habitat or biotic indices (reach scale). While hydrogeomorphological-based management is not yet highly practiced in Aotearoa New Zealand (Brierley et al. 2022), or Canada (Biron et al. 2018), it would likely have ecological benefits. Because the MQI can also be calculated remotely and widely applied throughout a catchment, a modified MQI targeting ecological health could be used as an effective management tool for aquatic conservation.

Liaison paragraph

Chapter 3 concluded that both the MQI and the QHEI may need adapting to be used as a predictor for fish-based indices in salmonid streams. However, it also indicated that small sample sizes and the limited spatial range used may result in low statistical power. This is a difficult problem in ecological systems, where time and resource limitations often do not permit extensive fieldwork in hundreds of locations. Therefore, we need to explore other methodologies to increase the sample size of salmonid rivers and further explore salmonid abundance. The following chapter describes a systematic review of published literature on salmonid biomass to create a database of salmonid rivers. This chapter further explores the spatial extent and abundance of salmonid populations and details analyses of differences in biomass by species, region, period, and sampling technique. With such a large database of rivers (over 1000 rivers), it was not feasible to explore extensive environmental variables, but there is scope to expand the list of variables in the database and continue to add data. A brief exploration of top biomass sites in the database is presented in Appendix D.

4 Salmonid biomass in streams around the world: A quantitative synthesis

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Abstract: Salmonid species are one of the most studied freshwater fish, but little is known about the spatial extent and abundance of populations in many parts of the world. We created a database using published material of over 1000 rivers with estimated salmonid biomass, covering 27 countries and 11 species. To our knowledge, the database is the largest known compilation of studies on salmonid biomass, allowing detailed analyses of differences in biomass by species, region, period, and sampling techniques. Mean global biomass is 5.2 g/m², and while most streams are under 10 g/m², there is a large range (0-70.3 g/m²). Salmonid production recorded for 194 rivers averaged 6.3 g/m²/yr, and biomass and production were highly correlated (R = 0.82) with a mean production to biomass (P/B) ratio of 1.08. Biomass in New Zealand and France is significantly lower and higher, respectively, than at least five other countries. Brown trout (*Salmo trutta*) have a higher proportion of biomass estimates over 10 g/m² than many other species. Additionally, native brown trout populations have a higher biomass than exotic brown trout, while native brook trout (*Salvelinus fontinalis*) biomass is significantly lower than their exotic counterparts. Biomass is overall higher in small streams (less than 10 m wide) and where smaller spatial extent is surveyed, perhaps because the proportion of available habitat is higher. A slight decrease in biomass over time is observed. Expanding the list of variables in the database would be useful for developing models to predict salmonid biomass, and determining potential conditions for high biomass streams.

4.1 Introduction

In many regions around the world, salmonid species are declining in abundance, with many populations listed as threatened or endangered (Dauwalter et al., 2020; Jelks et al., 2008; Laramie et al., 2015; Parrish et al., 1998). To our knowledge, comprehensive compilations on the global range of salmonid abundance have not been completed for several decades (i.e. since Mann & Penczak, 1986). Therefore, the global state of salmonid populations is largely unknown. There is evidence of local declines (Ayllón et al., 2013; Budy et al., 2008), but little is known on the spatial extent and abundance of populations and species in many parts of the world. Knowing the abundance of populations is important for understanding population dynamics and for decision-making in species management and conservation (Yin & He, 2014) - e.g. where populations might be threatened and where restoration should take place. Additionally, knowing areas with high salmonid abundance is useful in identifying the environmental conditions that are ideal for populations to thrive.

Salmonid biomass and production have been estimated since at least the 1950s for many rivers around the world in areas where they are both native and exotic (Allen, 1951; McKernan et al., 1950). While production is a more accurate reflection of population growth and change than biomass (Chapman, 1965; Cote, 2007; Kwak & Waters, 1997), estimating production rates in the wild is costly and time-consuming (Lobón-Cerviá et al., 2011) compared to measuring biomass (Hopkins, 1971). Hence, production is measured less frequently than biomass (Hayes et al., 2007). Furthermore, if salmonid production is limited by social factors, such as territoriality, then it is easier to predict the carrying capacity of a stream based on density or biomass, rather than production, per se (e.g. Grant & Kramer, 1990).

Biomass and production estimates for stream salmonids can vary widely (Kwak & Waters, 1997; McFadden & Cooper, 1962; Platts & Nelson, 1988), depending on species sampled, life-stage, the number of species present, fish sampling methods (Dauwalter et al., 2020; Korman & Yard, 2017; Riley & Fausch, 1992), and many environmental conditions (Almodóvar et al., 2006; Bowlby & Roff, 1986; Hayes et al., 1996). There have been many attempts to predict salmonid abundance using models combining multiple variables (Fausch et al., 1988; Milner et al., 1993; See et al., 2021), including stream width, flow stability, water temperature, stream cover, gradient, and water chemistry (Almodóvar et al., 2006; Binns & Eiserman, 1979; Bowlby & Roff, 1986; Milner et al., 1993). However, these models are typically developed for a particular region (Binns & Eiserman, 1979; Fausch et al., 1988; Milner et al., 1993), and haven't been as useful when applied to other areas of the world (Bowlby & Roff, 1986; Leiner, 1996). Additionally, many of the variables included in these models are difficult to quantify for a large global dataset without field sampling. Gallagher et al. (2022) found that latitude and elevation were key variables in a

global database that determined climate effect patterns and therefore effects on future salmonid productivity. Latitude and elevation can be measured remotely on a global scale, so can be easily integrated in a global database.

To synthesize the published biomass estimates of stream salmonids around the world, we conducted a systematic review focusing on the genera *Salmo, Oncorhynchus and Salvelinus*. Production was also included if it was reported in the biomass studies. To the best of our knowledge, this is the largest database of published biomass and production studies for stream salmonids. We will first focus on general descriptions of the biomass data from this unique dataset and then use the data set to test the predictions (see below and Table 4.1) based on current knowledge of salmonid ecology, general ecological theory, and variables that are easy to quantify for most streams.

Biologists have long speculated about what limits salmonid abundance in streams, focussing on food availability, habitat quantity and quality, and social behaviour (see Rosenfeld et al. 2024). Le Cren's (1969) suggestion of an upper limit to production of 12 $g/m^2/yr$ was subsequently shown to be too low; current estimates suggest 30-40 $g/m^2/yr$ (Elliott, 1993; Lobón-Cerviá et al., 2011; Mann & Penczak, 1986). An upper limit to biomass is estimated to be 30 g/m^2 based on territorial behaviour (Grant & Kramer, 1990). We test whether these upper limits are accurate for a global database; see Question/prediction 1, hereafter QP1, and QP2 (Table 4.1).

Biomass and production are linked both theoretically and empirically by the ratio of production to mean biomass (P/B), also known as the turnover ratio (Hayes et al., 2007; Kwak & Waters, 1997; Lobón-Cerviá et al., 2011). If biomass is known, then P/B ratios for a species can be used to estimate production (Randall, 2002). However, biomass may not always be an accurate predictor of production (Allen, 1971; Cote, 2007); P/B ratios can vary significantly among species and age classes, within species (Elliott, 1993; Hayes et al., 2007; Kwak & Waters, 1997; Mann & Penczak, 1986; Waters, 1999), and even temporally (Lobón-Cerviá et al., 2011). For instance, previous studies found mean P/B ratios for salmonid species of 1.06 and 1.30 but ranges between 0.48 and 3.00 are reported for individual species in different rivers (Kwak & Waters, 1997; Mann & Penczak, 1986; Randall, 2002; Waters et al., 1990). Because we anticipated more biomass than production estimates in the literature, we first tested whether biomass can be used to predict production in salmonid streams (QP 3, Table 4.1). We then tested whether biomass and P/B ratios vary by species (QP4 and QP5, Table 4.1).

According to the niche complementarity hypothesis (Fargione et al., 2007; Mason et al., 2008), total salmonid biomass will be higher if there are more species present (Bailey et al., 2018; Bisson et al., 1988; Ruggerone & Irvine, 2018). For instance, for species with different habitat preferences (e.g. pools versus riffles), biomass may be higher in sympatry, as habitats can be exploited more efficiently (Bisson et al., 1988; Glova, 1986; Young, 2001).

In other cases, the presence of one species may benefit others, by providing resources such as eggs and fry (Bailey et al., 2018; Ruggerone & Irvine, 2018). We tested whether biomass increases with more species present (QP6, Table 4.1).

Biomass estimates are also likely to be higher for stream resident than anadromous populations of salmonids. Because of the fast growth at sea, spawning anadromous fish are likely to be larger than spawning resident fish (Jonsson & Jonsson, 2007; Kendall et al., 2015). However, anadromous salmonid species only use the stream environment for juvenile life stages before they migrate to sea, compared to resident species that use it throughout their life-cycle. We tested whether stream-resident species have higher biomass estimates than anadromous species (QP7, Table 4.1).

The introduction of salmonids outside of their native range can have negative impacts on native salmonids as invasive species often outcompete native species (Carlson et al., 2007; Fausch, 2007; Harig et al., 2000). For example, Benjamin and Baxter (2010) found that non-native brook trout (*Salvelinus fontinalis*) had a higher biomass than the native cutthroat trout (*Oncorhynchus clarkii*) that they replaced, and in a small Massachusetts stream, non-native brown trout grew faster than native brook trout (Carlson et al., 2007). However, it is unclear whether exotic populations have a higher abundance than native populations of the same species in different locations. Estimates of brown trout (*Salmo trutta*) production and biomass are high in areas where they are both exotic (Allen, 1951; Cooper & Scherer, 1967) and native (Mortensen, 1982). We tested whether exotic salmonid biomass is higher than native biomass with a larger database of studies (QP8, Table 4.1).

Abundance estimates can depend on the extent of sampling in space and time (Begon et al., 2014). Less extensive sampling in space and time may not affect the mean but will lead to an increase in the variance in abundance measured. However, sampling small areas of a stream often target preferred habitats for a particular species or age class sampled (i.e. pool versus riffle) resulting in a higher biomass estimate (Macnaughton et al., 2015). Stream width has often been used to predict salmonid populations (Cote, 2007), with many suggesting that smaller streams have higher abundance or production (Kozel & Hubert, 1989; Rosenfeld et al., 2000; Scruton & Gibson, 1993), as the area may have a high proportion of available habitat (Naiman et al., 1987; Rosenfeld et al., 2002). We tested whether there are regional differences in biomass and differences in biomass in space and time (QP9-12, Table 4.1). Because of reported declines in some regions due in part to habitat degradation, we also tested whether biomass estimates have changed over time (QP13, Table 4.1).

Fish sampling methods can bias abundance estimates. Multi-pass sampling (depletion) methods can reduce this bias (Riley & Fausch, 1992), but other potential factors remain, such as the target species, age of fish, habitat types surveyed, and the number of fish removals (Peterson et al., 2004). Certain fishing methods, such as electrofishing or

snorkelling, may affect biomass estimates, with suggestions that snorkel surveys may underestimate biomass (Cunjak et al., 1988; Hayes & Baird, 1994; Macnaughton et al., 2015; Young & Hayes, 2001). We tested whether biomass estimates are significantly lower for snorkel surveys compared to other fish sampling methods (QP14, Table 4.1), as predicted in many studies. In addition to sampling methods, most fish surveys are carried out in summer (Foote et al., 2020; Nickelson et al., 1992), when it is easier to sample quantitatively, and perhaps safer when flows are low and temperatures high; but abundance has temporal variation (from month to month and annually) (Hunt, 1974; Kwak & Waters, 1997; Lobón-Cerviá et al., 2011). Season, and even time of day, may be crucial for obtaining reliable estimates (Barrett & Munkittrick, 2010; Pope & Willis, 1996). Sampling in only one season may not provide an accurate estimate of stream biomass (Tremain & Adams, 1995), and sampling when anadromous populations are migrating, for instance, may result in very low numbers or no fish at all (Weitkamp et al., 2012). The time of year that sampling occurs may depend on the sampling goal and target species. We tested whether there are differences in biomass depending on the season when sampling occurred (QP15, Table 4.1).

We formulated predictions and questions based on key variables and mechanisms that fish biologists speculate affect salmonid abundance in rivers, summarised in Table 4.1. While many other variables exist that affect salmonid biomass, we chose ones that are easy to quantify for most rivers and samples.

Table 4.1. Questions/predictions on salmonid ecological theory tested in this study and mechanisms the affect predictions

Question/prediction (QP)	Mechanism
1. Upper limit to biomass is 30 g/m^2	Territoriality limits density and biomass
2. Upper limit to production is 30-40 g/m^2/yr	Observations; limited by biotic and abiotic factors – e.g. food availability, habitat quantity and quality, social behaviour
3. Biomass is a good predictor of production	Biomass and production linked theoretically; overall observations of average P/B ratios vary within a narrow range
4. Biomass varies by species	Fish species differ in growth rate, habitat use and life history
5. P/B ratios vary by species	Growth varies by species, affecting the ratio; P/B ratios vary among species

Question/prediction (QP)	Mechanism
6. Rivers with more salmonid species have a higher overall biomass	Niche complementarity
7. Resident species have a higher biomass than anadromous species	Anadromous species only spend the juvenile phase in freshwater ecosystems, when their biomass will be lower. Spawning populations are not measured in this study, so adult anadromous biomass is not included
8. Exotic populations have a higher biomass than native populations	Exotic species often out-compete native populations, sometimes grow faster
9. There are regional (country) differences in biomass	Countries near the latitudinal range for salmonids will likely experience temperatures that are either too cold or warm for optimal growth and production
10. Variability of biomass and production estimates is greater when the spatial extent of the river is smaller	Samples at fish survey sites will include very high and low estimates, compared to an average estimate of all samples
11. Biomass is higher in smaller streams (< 10 m wide)	Smaller streams are likely to have a higher proportion of bank side habitat available for fish, hence they are able to support more fish
12. Biomass is higher when surveying smaller spatial areas (e.g. a pool versus a 200 m reach).	Sampling small areas often targets preferred habitats, resulted in a higher biomass estimate
13. Biomass has decreased over time	Degradation of freshwater by human activities has led to declines of many freshwater fish
14. Fish sampling by snorkelling under-estimates biomass	Visual surveys (i.e. by snorkelling) may underestimate biomass as fish seek cover and hide. Cover availability and temperature can affect whether fish will be seen
15. Biomass is higher in summer	Most growth and sampling easier in summer

4.2 Methods

4.2.1 Literature search

We compiled published biomass estimates of salmonids in rivers and streams around the world, focusing on the genera *Salmo*, *Oncorhynchus* and *Salvelinus*. To obtain the data, systematic methodology (Collaboration for Environmental Evidence, 2018) was followed to conduct a systematic review of peer-reviewed articles and grey literature (see Table C2 in Appendix C1 for full details of the review). Criteria were applied to incorporate relevant studies from the literature (Table 4.2). A Review Team conducted the search in English from two main sources: 1) Web of Science (WOS) database using keywords; and 2) reference lists and cited data from included articles and known studies. A total of 240 studies, on 1063 different rivers, were included in our database. Due to time constraints only one article database (Web of Science) was searched in full. The comprehensiveness of the final search was tested by determining if key benchmark articles appeared in the database search (see Table C2 in Appendix C1).

Search terms were identified and tests were run on different combinations of search strings (see Appendix C1 for details on the initial search). The following keywords were used in a final WOS database search for the date range 1979 to 1 December 2021: (salmonid OR salmon OR trout OR Salvelinus OR Oncorhynchus) AND (biomass) AND (river OR stream), with 957 results. The search was later updated to include studies published between 1 December 2021 and 31 July 2023, producing 45 studies, resulting in the total of 1002 studies in the WOS search. The entire result list of the final search was screened (see below). To ensure a comprehensive inclusion of grey literature and older literature not included in the WOS search, reference lists from included articles were searched for possible inclusion. Search results were screened for inclusion criteria (Table 4.2) in four stages: (i) title, (ii) abstract, (iii) partial article, and (iv) full text. Results at each stage of screening were recorded (Table C2).

From the 1002 results in the WOS search, 145 met the acceptance criteria (14.5% acceptance rate). A further 95 publications were sourced from the reference lists of included studies, of which 35 were published before 1979 (the start year of the WOS database). The majority (87%) of the 240 studies included in the database were published as journal articles. Searches were conducted in English, but automated translators and fluent speakers were used where necessary for studies found in other languages. Only 4.1% of accepted publications were in languages other than English and included: French (5 studies), Czech (3), Slovak (1), and Spanish (1), while 2.1% (21) of publications in the total WOS search were not in English. For full results of the literature search see Table C2.

Table 4.2. Criteria for inclusion in the systematic search

Field	Include	Exclude
Ecosystem	River and streams, artificial channels that are connected to natural ones	Lakes, marine and coastal environment, lab experiments.
Species	Salmonid genera *Salmo*, *Oncorhynchus* and *Salvelinus*	Non-salmonid species. Salmonid species from other genera. Estimates that include salmonids and non-salmonids
Location	Global	
Abundance data	A measure of biomass per unit area (g/m^2) – mean and variance if provided. Production and density data recorded if reported	No quantitative data. If target fish were stocked as part of an experiment before sampling
Time period	Any time before 31 July 2023. Note that the Web of Science database starts from 1979 but earlier studies were included by searching the literature cited of papers included in the analysis	Studies published after 31 July 2023
Publication format	Published data in articles, reports, books, conference proceedings and theses	Online databases, unpublished surveys, data from presentations, personal communications.

4.2.2 Database creation and data extraction

To test the predictions listed in Table 4.1, data extracted from studies that met the inclusion criteria (Table 4.2) were recorded at multiple scales in a SQL (Structured Query Language) database (Fig. 4.1, Table 4.3). Tables were related to each other with common ID numbers (see Appendix C2 for more details). Tables can be specific to each project (records were related to only one project), place specific (the same place can be attached to many different projects), or can relate to all projects (Fig. 4.1).

The smallest scale is the fish sampling site (fish site and fish survey, Fig, 4.1, Table 4.3). Estimated biomass was recorded in the database at the smallest scale it is reported by species (fish survey). Biomass for all salmonid species can then be summed at the fish survey scale, and further averaged at larger scales (e.g. river scale). Multiple fishing sites that had similar conditions were combined into a river section and study section. Data across projects and sections can then be averaged at a river scale. If studies reported one

biomass estimate over several rivers, it was only included in the database if environmental conditions were very similar among rivers and rivers were close together (i.e. in the same catchment); in most cases these studies were not included.
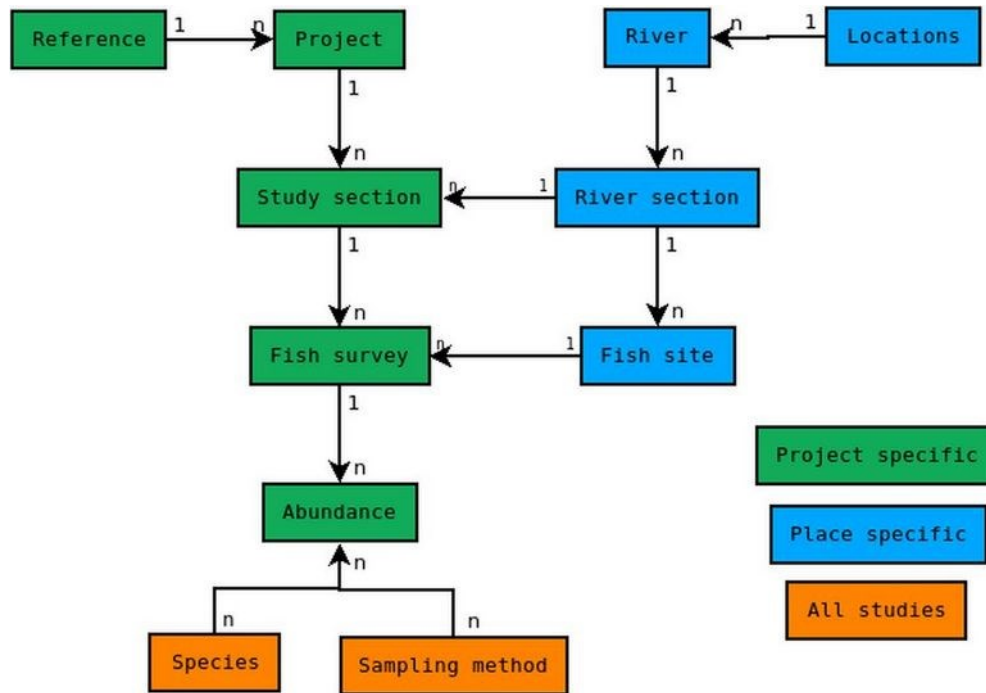
Fig. 4.1. SQL database overview. Boxes represent separate tables in the database and are related with a common ID by either a one-to-many (1-n) or many-to-many (n-n) relationship (see Appendix C2 for more details).

Table 4.3. Description of tables in the database and data extracted if reported

Table name	Description	Items included
Reference	Reference information and identification for each study	Reference id, author, publication year, publication type (e.g. article, report, book chapter, conference proceedings)
Project	Project details for each study. Most references have one project, but some have multiple projects	Reference id, project id, project start and end date, number of years the project spans, number of streams/rivers that have biomass measures, project type (i.e. population study, restoration study)

Table name	Description	Items included
Locations	General location details for the study.	Location id, region, province (or state), country, continent
River	River, stream, or creek sampled for fish. Can be shared over different studies.	Location id, river id, river name, drainage area (of whole river), river length, watershed name (name of basin that river drains in to)
River section	Section of the river studied. May have several river sections where obvious changes occurred. Can be shared over different studies.	River id, river section id, latitude, longitude, elevation
Study section	Section of the river that is specific to the study. May have several sections where obvious changes occurred. Study sections are not shared among studies.	River section id, project id, study section id, study length, number of treatments (if restoration or intended modifications occurred at the site)
Fish site	Site where fish sampling occurred. Can be shared over different studies	River section id, site id, site name, stream order
Fish survey	Site details where fish sampling occurred, specific to each study.	Study section id, site id, fish survey id, length fished, sections fished, mean width and depth, start and end dates of fishing, number of years that were fished (1 if 1 or less), season fished
Abundance	Details about fish catch, specific to each study. Separated by species and age class if reported separately in the study.	Fish survey id, abundance id, species id, age id, fishing id, number of species included in measure, biomass, density and production (mean, SD and N for all), PB ratio, exotic (true or false)
Species	Species details for all studies	Species id, common name, scientific name, migratory strategy (resident, anadromous, or semi-anadromous (mixture of both or may or may not be anadromous)
Sampling method	Method of fish sampling for the study for all studies	Fishing id, fishing type, number of removals, fishing methods, reference

4.2.3 Life history

Migratory strategies for species were recorded in the species table (Table 4.3), and included simplified categories of stream residents, anadromous, and anadromous and/or residents. Migratory status was recorded at the species level rather than the population level. While some species listed in the resident category do have anadromous and potamodromous life histories, we separated species into general stream resident and anadromous species, with a mix being where two or more species are present belonging to both categories, or with species that are often semi-anadromous (i.e. cutthroat trout). Stream resident species included: brown trout, brook trout, rainbow trout (*Oncorhynchus mykiss*), bull trout (*Salvelinus confluentus*), and some sub-species of cutthroat trout. Anadromous populations included: Atlantic salmon (*Salmo salar*) steelhead trout (*Oncorhynchus mykiss*), Chinook salmon (*Oncorhynchus tshawytscha*), and coho salmon (*Oncorhynchus kisutch*). In the mixed category were: rainbow/steelhead (where no differentiation was given between them), cutthroat trout, masu salmon (*Oncorhynchus masou*), Arctic char (*Salvelinus alpinus*), and Dolly Varden trout (*Salvelinus malma*). No other salmonid species were included in the database.

4.2.4 Data analysis

All data were analysed in R (version 4.1.2) using the base 'stats' package and the significance level for all analyses was $p < 0.05$. For questions and predictions where characteristics didn't change for each river (QP 1, 2, 3, 6, 9, 10, 13), a river scale (Fig. 4.1) was a datum in our analyses (n = 1063). The fish survey (n=2018) or river section (n = 1226) (Fig. 4.1) was the datum for the rest of the QP (4, 5, 7, 8, 10, 11, 12, 14, 15), as characteristics were likely different for each site or section on the river. Because of the nature of our data set, we first tested QP in a univariate way, and then considered multiple variables in a single model (see below).

The relationship between production and biomass (for studies that measured both) was tested with a linear regression. Differences in biomass in studies that did or did not measure production were tested with a Welch's F test. We used non-parametric (Kruskal-Wallis and Wilcoxon) tests to determine whether biomass differed among species and a chi-squared test to test whether the proportion of high biomass (10 g/m^2 and over) rivers differed between species. Only species that had more than 50 estimates were included. Since there were no significant differences in biomass between rainbow (n = 157) and steelhead (n = 51) trout (Wilcoxon test = 4295, p = 0.44), these were combined. Kruskal-Wallis and Wilcoxon tests were also used to test whether biomass was higher: with more species present, in resident populations compared with anadromous, and exotic populations compared with native populations.

Differences in biomass by country were tested with a Kruskal-Wallis rank sum test and post-hoc Wilcoxon rank sum test. We used a chi-squared test to determine whether there were differences between Europe and North America in the proportion of biomass estimates that were either native or exotic species (or a combination of both). Differences in average and variance of biomass and production by the spatial extent of the study were tested with a Welch's F test (average) and Levene's test (variance). Biomass versus width and area fished were tested with a linear regression. Additionally, data were divided into three stream width groups (< 5 m wide, 5 – 10 m, and > 10 m) and differences between them were tested with a Wilcoxon test.

To test whether there has been a decline in biomass over time we performed a linear regression on biomass and the year of surveying. For studies that sampled over multiple years, the last year of fish sampling was used and biomass was averaged over the entire period. Data were then grouped into three time periods based on the sampling year, and differences were tested with a Kruskal-Wallis test. The sampling methods tested were the type of fishing method used, the season during which the fish were sampled (Kruskal-Wallis), and the number of years of fishing (linear regression).

Finally, we performed a stepwise AIC to find the best generalised linear model (GLM) for predicting stream salmonid biomass using variables in the database. Variables were first tested for collinearity and closely related variables were removed. Variables considered include: species, country, latitude, last year of fishing, season, stream width, elevation, number of species, species status (exotic or native), sampling method, area fished, migratory status, number of years of sampling, and area fished (see Appendix C4, Table C7 for more information on variables).

4.3 Results

The spatial extent of the studies included 27 countries, the majority in the Northern Hemisphere (Fig. 4.2). Out of the total 426 defined freshwater ecoregions, 51 had rivers in the database within their area (26 with at least 10 rivers). Freshwater Ecoregions are defined as areas of similar distinct freshwater species, dynamics and environmental conditions (Abell et al. 2008). Over half of the studies (58%) were from just three countries (United States, Canada and New Zealand, Fig. 4.2), representing 67% of the 1063 rivers in the database. Fish sampling spanned 84 years, from 1937 to 2021.
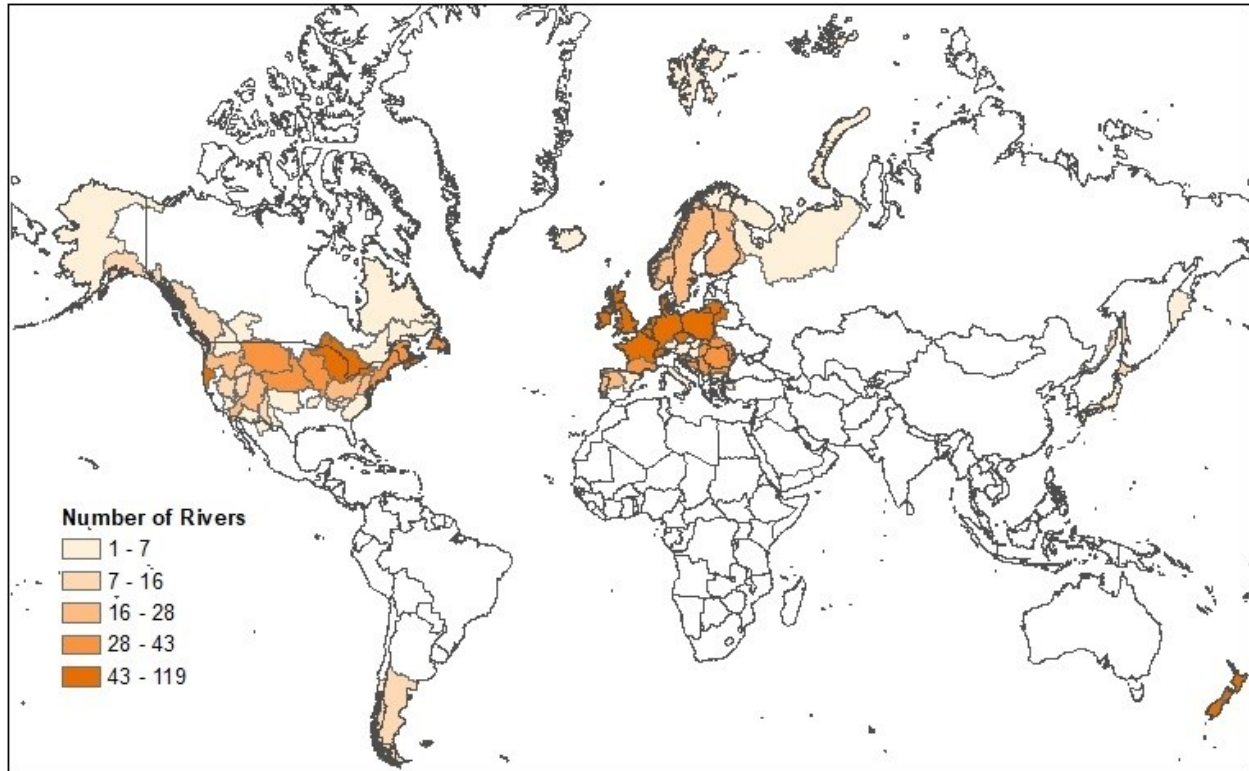
Fig. 4.2. Number of rivers in the database per Freshwater Ecoregions (FEOW, 2019).

4.3.1 Biomass and production

Distributions of biomass and production at the river scale are shown in Fig. 4.3. The biomass distribution was skewed strongly to the right and clearly was significantly different from both a normal (Shaprio-Wilk W = 0.619, p < 0.001) and a log-normal (w = 0.739, p<0.001) distribution. Most biomass values were very low, less than 5 g/m^2, with a mean of 5.2 g/m^2 and a median of 3.1 g/m^2. Out of the 240 publications in the database, 68 reported production estimates for 194 rivers (Fig. 4.3b). Production and biomass were significantly correlated (production = 0.36 + 0.92(biomass), R^2 = 0.68, p < 0.001, Fig. 4.4; QP3), and the mean P/B ratio at the river scale was 1.08.

Only 1.3% (14 rivers) had estimated biomass over 30 g/m^2 (Fig. 4.3a, QP1), a predicted upper limit for biomass (Grant & Kramer, 1990). Only two rivers (1.0%) reported average production over 30 g/m^2/yr (Horokiri Stream in New Zealand and Big Spring Creek in Pennsylvania, USA[3]) and 11.3% were greater than 12 g/m^2/yr, the

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3   This only includes estimates that also report biomass.

theoretical limit proposed by Le Cren (1969) (Fig. 4.3b, QP2). Similarly, 11.2% of rivers had a biomass greater than 11.1 g/m^2, the biomass equivalent to 12 g/m^2/yr, assuming our mean P/B ratio of 1.08. Mean biomass in rivers was significantly higher (Welch's F test = 8.49, p = 0.004) for studies that also estimated production (biomass = 6.28 g/m^2), compared to studies that did not estimate production (biomass = 4.96 g/m^2), alluding to a focus on 'good' salmonid rivers when measuring production. Fish survey sites that estimated biomass higher than 30 g/m^2 were investigated in more detail (Appendix D).
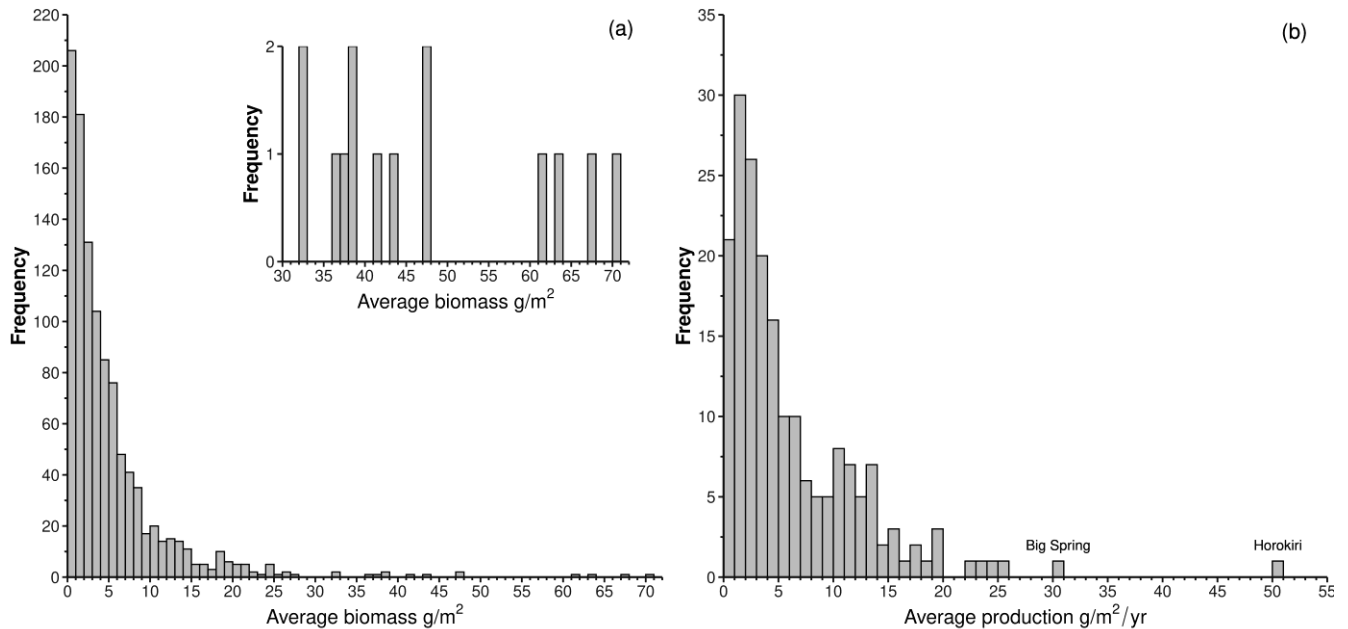
Fig. 4.3. Histogram of mean biomass (a, n=1063) and mean annual production (b, n=198) by river with a bin size of 1 g/m^2 and 1 g/m^2/yr respectively. Insert in (a) shows estimates with an average biomass greater than 30 g/m^2, and rivers with production over 30 g/m^2/yr are labelled in (b).
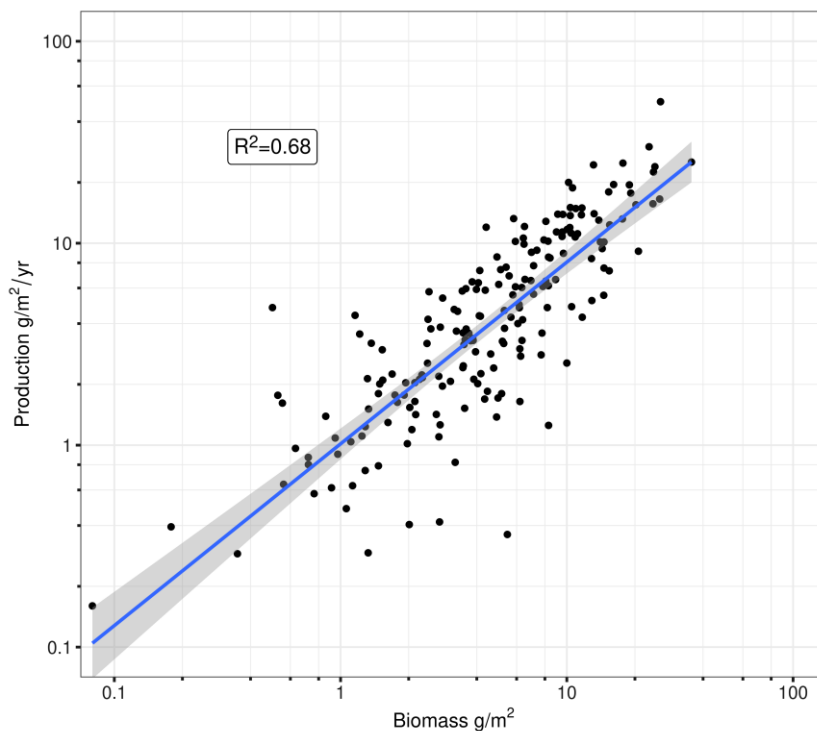
Fig. 4.4. Relationship between production and biomass (both axes are plotted on a log scale). Blue line and grey shaded area are the linear regression relationship and standard error (SE), respectively.

4.3.2 Species biomass

Many species showed a large variability of biomass estimates (Fig. C1). Coho salmon had the highest mean biomass (12.4 g/m^2, median = 2.2) and Chinook salmon had the lowest (0.12 g/m^2, median = 0.09). For estimates with one species (see Appendix C4, Fig. C1), significant differences in biomass were found between species (Wilcoxon test, Table C4, QP4). Chinook salmon had a significantly lower biomass than all species with 8 or more estimates, and brown trout biomass was significantly higher than five other species (Table C4). For the six individual species that had more than 50 biomass estimates, three species (brown trout, brook trout, and coho salmon) had estimates over 20 g/m^2 (Fig. 4.5). The proportion of biomass estimates over 10 g/m^2 were significantly different between some of the species presented in Fig. 4.5. Brown trout had a significantly greater proportion of estimates over 10 g/m^2 (23.5%) than all other species except coho salmon (13.4%, Fig. 4.5). P/B ratios were calculated for studies that reported both production and biomass and ranged between 0.24 for Dolly Varden trout and 2.75 for steelhead trout (mean = 1.18 at the fish survey scale, Table C5, QP5).
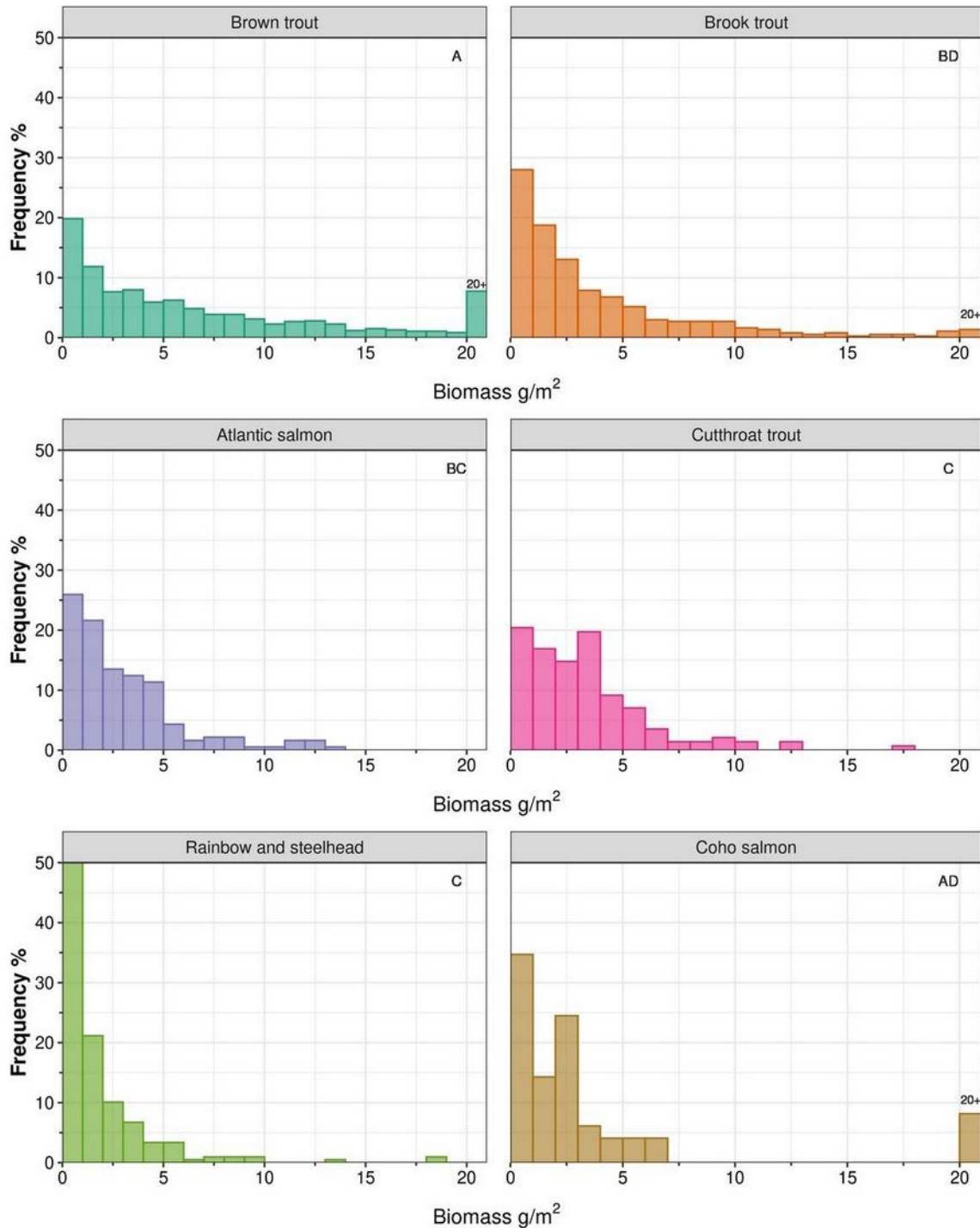
Fig. 4.5. Percent frequencies of biomass ranges within each species that had 50 estimates or more. Bins are 1 g/m^2 except the last bin for brown trout, brook trout and coho salmon, which includes all estimates over 20 g/m^2. Species in figures that share the same capital letters (ABCD) do not have significant differences in the proportion of biomass estimates over 10 g/m^2.

The maximum number of salmonid species measured in a fish survey reach was four, however, most reaches had only one species (Fig. 4.6a). Contrary to predictions (QP6), biomass at fish survey sections where only one salmonid species was present were higher than when two species were present (Wilcoxon test p = 0.005), but there were no differences between other numbers of species (Fig. 4.6a).

While some of the species classed as 'stream residents' in this analysis do have anadromous or potamodromous life-cycles, these species had higher biomass estimates than species that mostly have anadromous migratory strategies (Wilcoxon test p < 0.01, Fig. 4.6b, QP7).

Biomass was higher for native species compared to exotic or combined native or exotic (Wilcoxon test p = 0.003, Fig. 4.6c), opposed to predictions (QP8). However, this pattern did not hold for all species. Looking at just brook and brown trout species separately, exotic brook trout had higher biomass than native brook trout, but the opposite was found for brown trout (native were higher) (Wilcoxon test p < 0.001 for both brown and brook trout, Fig. 4.7).
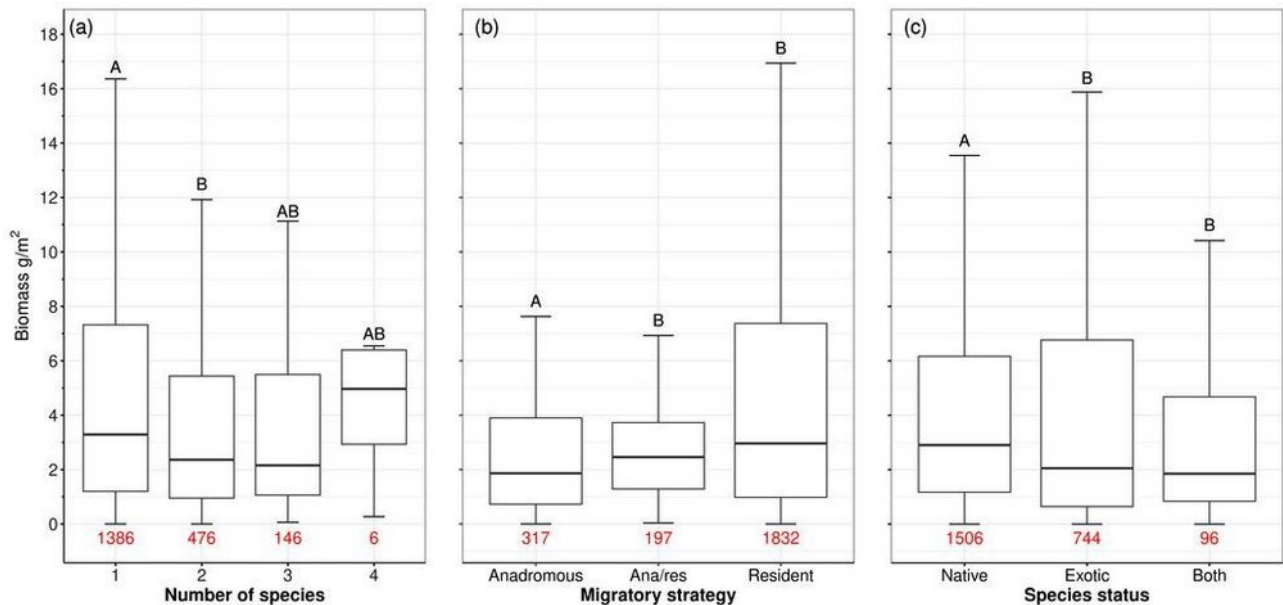
Fig. 4.6. Average biomass by: (a) number of species in a fish survey section; (b) migratory strategy, where Ana/res = Anadromous and/or resident species; and (c) the species status in the watershed (native, exotic, and both (containing two or more species that are native and exotic)). Boxes that share a letter within each panel are not significantly different from each other. Values in red at the bottom of the box plots are the number of biomass estimates at fish survey sites.
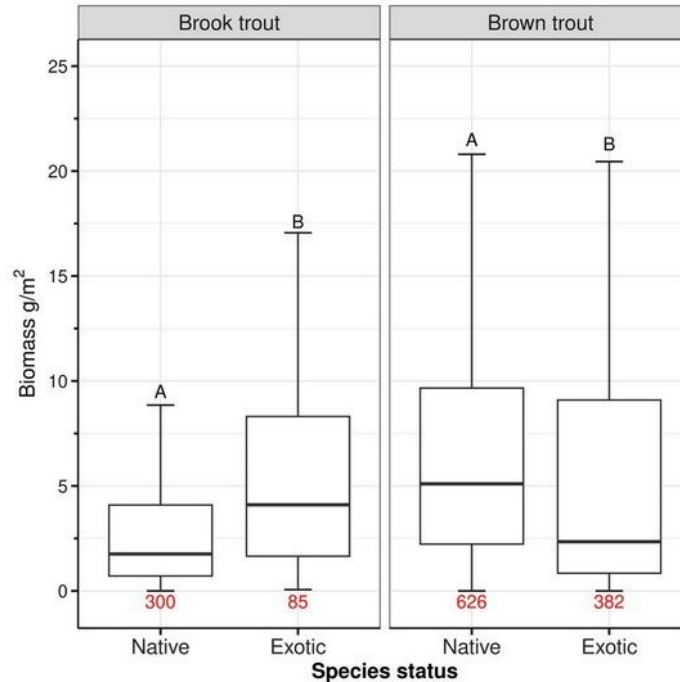
Fig. 4.7. Brook and brown trout biomass as exotic and native populations. Boxes that share a letter within each panel are not significantly different from each other. Values in red at the bottom of the box plots are the number of estimates at fish survey sites.

4.3.3 Biomass by Freshwater Ecoregions and country

Freshwater ecoregions of high biomass included the mid-western United States (upper and middle Missouri and upper Mississippi), Central and Western Europe, Iceland, Western Iberia, and the Cantabrian Coast (Fig 4.8). There was a difference in biomass between ecoregions (chi-squared = 297, p < 0.001). While not as meaningful in terms of freshwater habitat, differences in biomass between countries was also assessed. Rivers in Denmark had the highest mean biomass by country (14.8 g/m^2), but only two rivers were included in the estimate (Fig. 4.9), whereas Finland had the lowest mean biomass (1.1 g/m^2). At the fish survey scale, biomass followed a similar pattern (Fig. C2). Significant differences in biomass were tested between 14 countries with data for 10 or more rivers (Countries with n>10 in Fig. 4.9). Biomass in New Zealand rivers was significantly lower (Wilcoxon test p < 0.01) than most countries (Fig. 4.9, Table C6). Rivers in France had a significantly higher biomass than rivers in five countries, including New Zealand (Wilcoxon test p < 0.05) and Spanish rivers had a higher biomass than Canadian and New Zealand rivers (p < 0.05) (Fig. 4.9, Table C6). Biomass estimates included a higher percentage of native populations in Europe (98%) than in North America (60%, Pearson's chi-squared 43.52, df = 1, p < 0.01); all estimates in the Southern hemisphere were of exotic populations (Fig. 4.8).
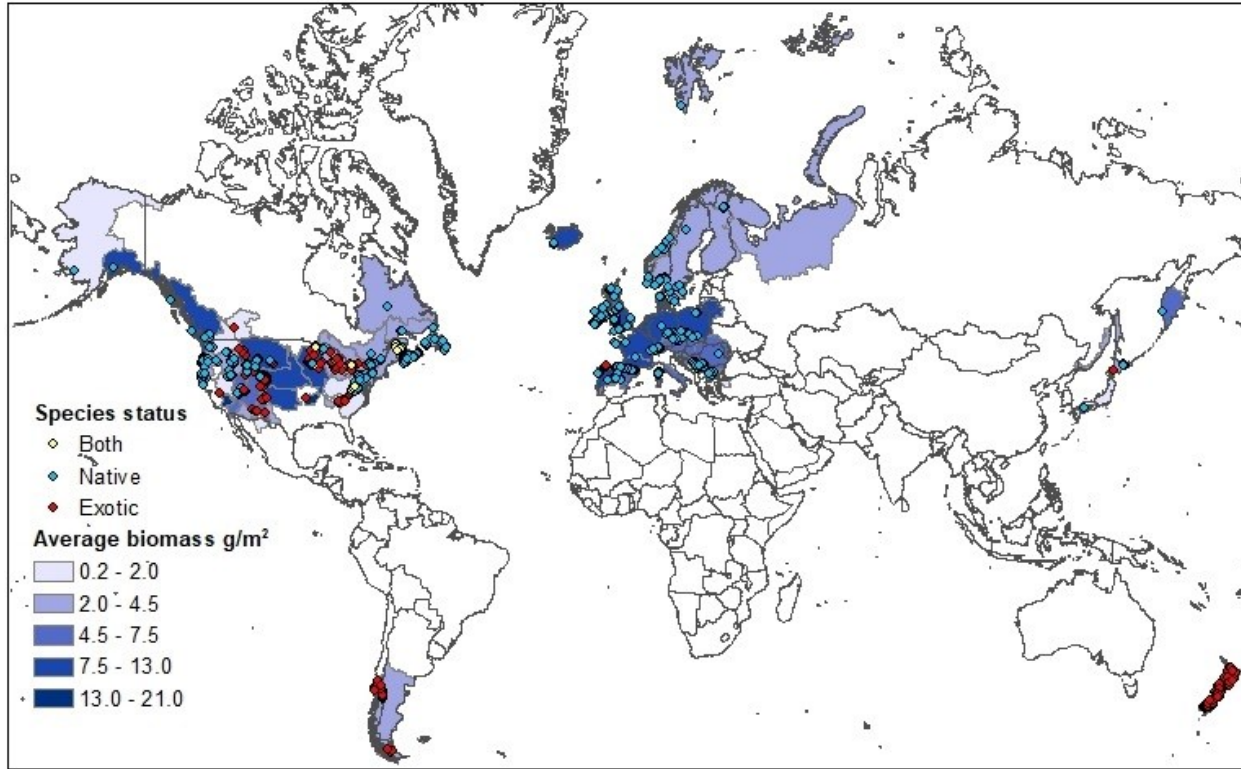
Fig. 4.8. Average biomass at the river scale per Freshwater Ecoregion (FEOW, 2019).
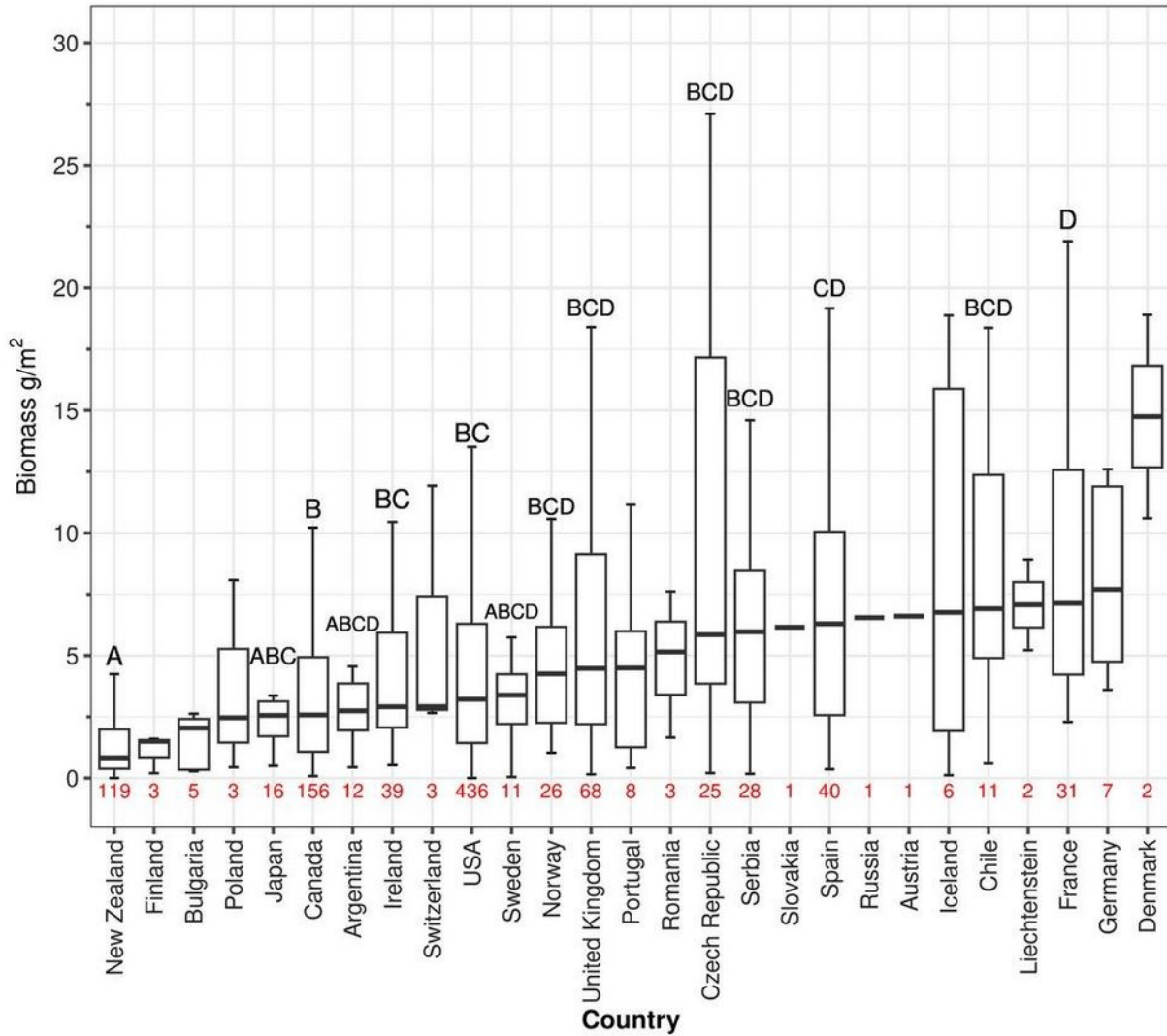
Fig. 4.9. Range of biomass (g/m^2) in each country calculated at the river scale (outliers are not plotted). Bottom values in red are the number of rivers (N) for each country. Boxes that share a letter are not significantly different from each other.

4.3.4 Space and time

The mean biomass was higher at the fish survey scale than at the river scale (Welch's F test = 9.72, p = 0.002, Table 4.4). In contrast, variance in biomass was higher at the smallest scale (fish survey) compared to the river scale (Levene's F value = 9.76, p = 0.002, Table 4.4, QP10). Mean production at the fish survey scale (7.4 $g/m^2/yr$) was not significantly different to production at the river scale (6.3 $g/m^2/yr$) (Welch's F test, p = 0.1).

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Table 4.4. Summary of biomass at different scales in the database.

Scale (from largest to smallest)	N	Biomass g/m^2			
		Mean	Median	Range	Standard deviation
River	1063	5.2	3.1	0-70.3	6.98
River section	1226	5.2	3.0	0-70.3	6.99
Fish survey	2018	6.1	3.4	0-169.4	9.14

The mean width for fish surveys was 8.4 m (median = 5.0 m). The mean area fished for all surveys with data available was 7945 m^2, however, the median was much lower (548 m^2). Biomass slightly decreased with increasing width (QP11, R^2 = 0.02, p < 0.01) and area fished (QP12, R^2 = 0.01, p < 0.01 Fig. 4.10). Average biomass of streams greater than 10 m wide (4.3 g/m^2) was lower than streams less than 10 m wide (7.1 g/m^2; Wilcoxon test p < 0.001, Fig. 4.10a). There was no difference between streams that were less than 5 m and 5 to 10 m (Wilcoxon test p = 0.61). When accounting for life-history, biomass decreased with increasing width and area for stream residents (R^2 = 0.02, p < 0.01, for both), but no relationship was found for anadromous species (Fig. 4.10b). When looking at individual species, a significant correlation between width and biomass was only found for brown trout (R^2 = 0.03, p <0.01), with biomass decreasing with increasing stream width.
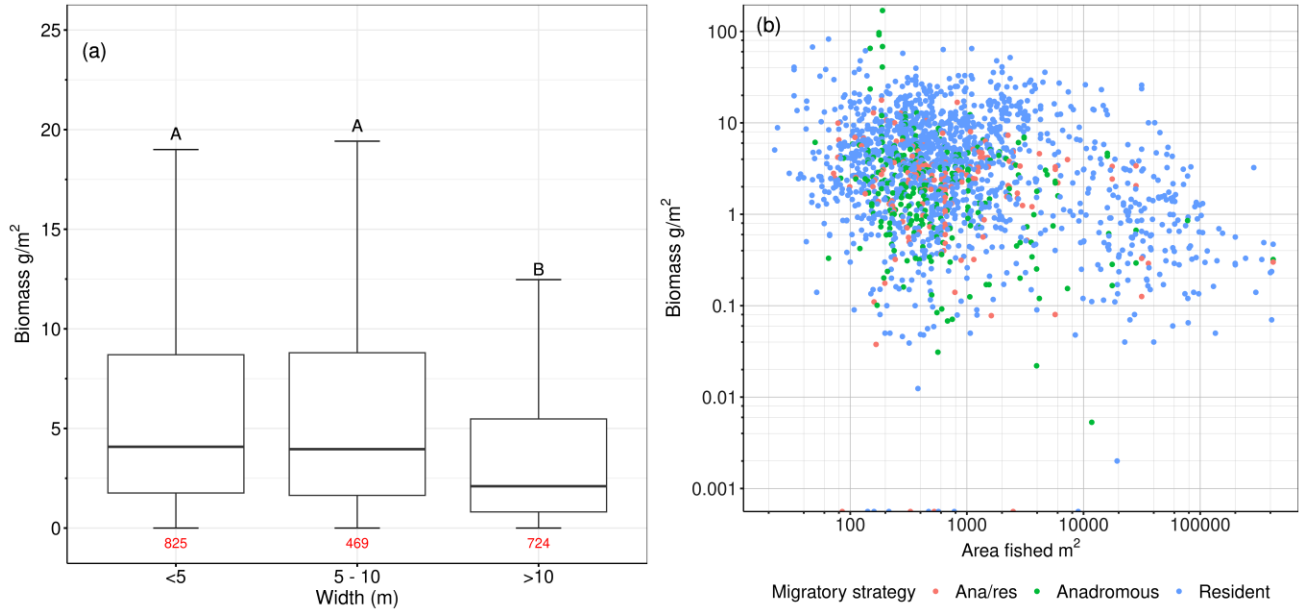
Fig. 4.10. Estimated biomass at the fish survey scale by average stream width (a), and total area fished at the site (b). Migratory strategies of species are shown in colour, Ana/res = anadromous and/or resident species.

There seems to be a small population biomass decrease over time (p <0.01, QP13), although the R^2 value is small (0.01), and this is mainly due to high biomass values in the early part of the 20th century (Fig. C3). When combining biomass estimates into three time periods based on the last year of fishing, surveys before 1980 had a higher biomass than those after 1980, and surveys in the 1980s and 1990s were higher than those after 2000 (Wilcoxon test p <0.01, Fig. 4.11).
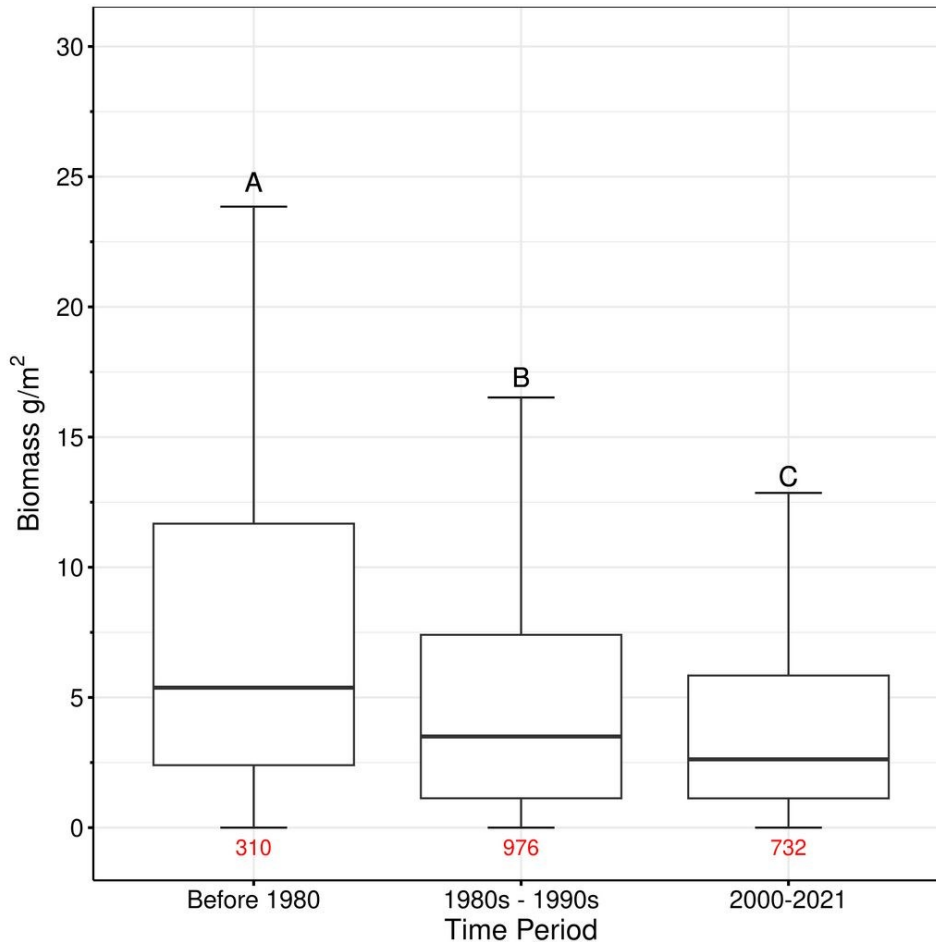
Fig. 4.11. Biomass of salmonids by time period. Different letters above boxplots indicate significant differences. Values in red at the bottom of the box plots are the number of estimates at fish survey sites for each time period.

4.3.5 Sampling methods

Electrofishing was the most common method for sampling fish (Fig. 4.12). Biomass estimates were lower when fish were sampled by snorkel surveys than electrofishing, netting and trapping, and other methods (Kruskal-Wallis chi-squared = 189, p < 0.01, Fig. 4.12, QP14). Most fish surveys were carried out in summer and there were many significant differences between seasons (Fig. 4.13, QP15), most notably, biomass was higher in spring than in summer, autumn and winter and biomass in autumn was significantly lower than all other groups except winter (Kruskal-Wallis chi-squared = 104.85, p < 0.01). No relationship was found between biomass and the number of years that sites were fished (R^2 = 0.07, p = 0.3).
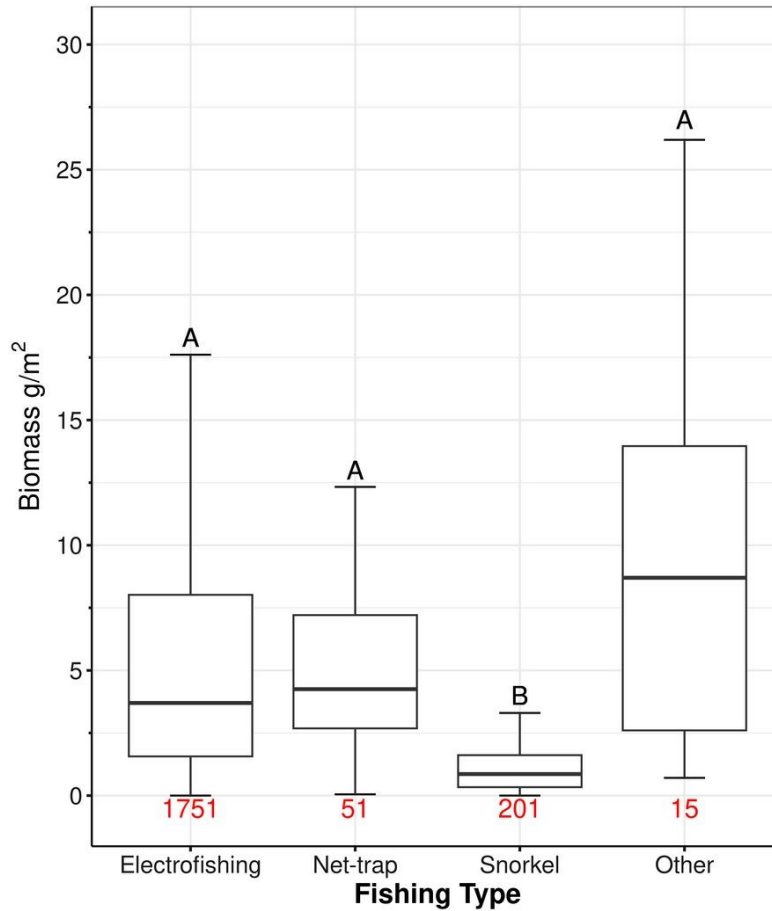
Fig. 4.12. Biomass ranges for different fishing methods (outliers are not shown). Net-trap = netting and trapping, other = all other methods. Boxes that share a letter are not significantly different from each other. Values in red at the bottom of the box plots are the number of biomass estimates for each method.
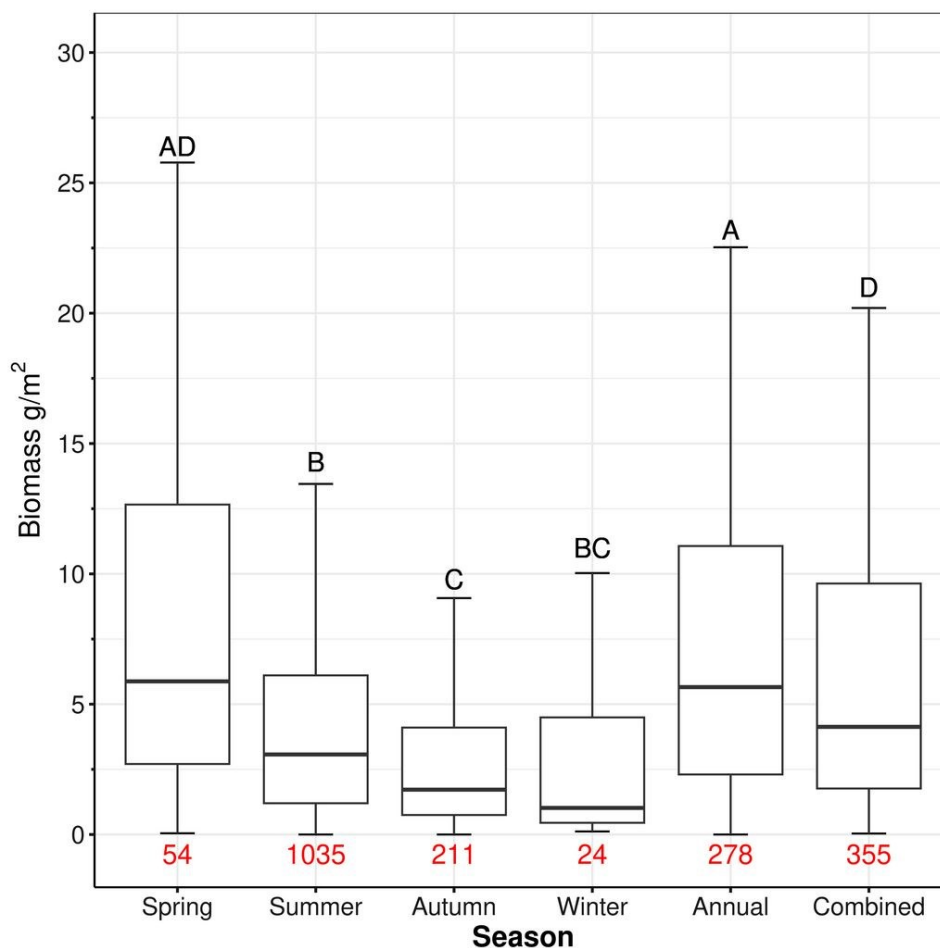
Fig. 4.13. Biomass ranges by the season fish were sampled (outliers not shown). Annual surveys were carried out in at least three seasons and Combined includes two seasons. Boxes that share a letter are not significantly different from each other. Values in red at the bottom of the box plots are the number of biomass estimates for each season.

4.3.6 Predictors of salmonid biomass

Before testing variables in an AIC for a generalised linear model (GLM), the following considered variables were tested for collinearity: species, country, latitude, river ID, last year of fishing, season, stream width, length of stream fished, area fished, elevation, number of species, species status (exotic or native), sampling method, migratory status, and number of years of sampling. Where collinearity was found, only one variable was used in the AIC (area, length of stream fished, and country were removed). Out of the variables tested in the stepwise AIC (Table C7), the GLM model (with Poisson distribution) with the lowest AIC included the following variables: species, season, elevation, year surveyed, sampling method, stream width, whether the population was native or exotic, latitude and

migratory strategy. Adding or subtracting variables produced poorer models (Table 4.5). Fitting the best model to a linear regression produced a weak but significant correlation (R^2 = 0.198, p <0.001).

Table 4.5. Summary analysis of biomass predictors for the generalised linear model (GLM). AIC$_c$ is the Akaike information criterion corrected for sample size, and ΔAIC$_c$ is the difference between given model and the best model (indicated in bold). +/- indicates when a variable is added or subtracted to the best model. Models are arranged by increasing AIC$_c$

GLM model (first row) and variables added (+) or subtracted (-) to model	AIC$_c$	Δ AIC$_c$
Species + season + elevation + year surveyed + sampling method + stream width + status (exotic or native) + latitude + migratory strategy	25924	0
+ Number of years of fishing	25925	1
+ Number of Species	25926	2
+ River ID	25926	2
- Migratory strategy	25928	4
- Latitude	25929	5
- Status – exotic or native	25930	6
- Mean stream width	25933	9
- Sampling method	25953	29
- Year surveyed	25956	32
- Elevation	25961	37
- Season	25978	54
- Species	26097	173
Intercept only	26502	578

4.4 Discussion

The unique dataset provided by this systematic review of published studies on stream salmonids biomass and production in over 1000 rivers revealed that, overall, many of results corroborated the predictions in Table 4.1, albeit with a few unexpected findings (Table 4.6).

Table 4.6. Summary of tested questions/predictions (QP) in this study. Outcomes in blue agree with our predictions, while we did not find support for outcomes in orange.

Outcomes of QP (from Table 4.1)

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1. Average biomass exceed the predicted limit of 30 g/m^2 in 1.3% of rivers, with some estimates as high as 70 g/m^2. If we define excellent and outstanding salmonid rivers as the top 10% and 1% of biomass, respectively, then our data suggests threshold biomasses of 11.9 and 36.5 g/m^2.

2. No strong evidence that production was higher than the predicted limit of 40 g/m^2/yr. Only one river exceeded the limit (Horokiri Stream, NZ). If we define excellent and outstanding salmonid rivers as the top 10% and 1% of production, respectively, then our data suggests threshold production 13.9 and 25.6 g/m^2/yr.

3. Biomass was positively correlated with production and explained 68% of the variability of the latter.

4. Brown trout had a higher average biomass and a higher proportion of estimates over 10 g/m^2 than many other species. Chinook salmon had a significantly lower average biomass than all species with 8 or more estimates.

5. P/B ratios ranged from 0.24 for Dolly Varden trout to 2.75 for steelhead trout.

6. Biomass was not higher with more salmonid species present. Biomass estimates were higher for 1 salmonid species compared to 2 species.

7. Average biomass was higher for species that tend to have resident life-histories compared to species than are usually anadromous.

8. Native salmonid populations tended to have a higher biomass than exotic populations. However, exotic brook trout had higher biomass than native brook trout streams, and vice-versa for brown trout.

9. Biomass differed among countries, tending to be low in NZ and high in France.

10. Variance in biomass was higher at the fish survey scale, compared to the river scale.

11. Biomass was higher in streams that were <10 m wide compared to streams >10 m.

12. Biomass declined as the area sampled increased.

13. Biomass decreased slightly over time. Biomass estimates were higher in studies before 1980 compared to studies completed after 1980.

14. Fish sampling by snorkel surveys appeared to under-estimate biomass, compared to electrofishing or netting/trapping.

15. Biomass was the highest in spring compared to other seasons (but not in studies that measured in two or more seasons).

4.4.1 Biomass

This study highlighted the large variability in salmonid biomass around the world, and the multitude of factors that can influence biomass estimates. We found reported biomass estimates that clearly exceeded previously predicted limits of 30 g/m^2 for biomass (Grant & Kramer 1990). The highest biomass for a fish survey site was 169 g/m^2 for coho salmon (Martin et al., 2010), but this occurred directly after large wood had been placed at the site, which was also was extremely small (average 63 m^2). Nevertheless, average biomass for all sites before and after restoration on this river (Resurrection Creek in Alaska) was 70.3 g/m^2, the highest in the database. Other high values at the river scale included 67.6 g.m^2 for brook trout in Patterson Brook, Nova Scotia (MacMillan et al., 2008), 63.4 g/m^2 for brown and rainbow trout combined (Sand Creek, Wyoming) (Binns & Eiserman, 1979) and 61.5 g/m^2 for brown trout (Mušlov, Czechia) (Lojkásek et al., 2000). Since these high values were all from one sampling day, it is unclear if the population is maintained at those levels over longer periods of time. Long-term studies (10 or more years), show that biomass and production vary considerably over time (Ayllón et al., 2016; Crisp & Beaumont, 1996; Elliott, 1988; Grossman et al., 2017; Lobón-Cerviá et al., 2011; Platts & Nelson, 1988; Waters, 1999; Zorn & Nuhfer, 2007), so point samples may not give a good indication of stream carrying capacity or production dynamics (Binns & Remmick, 1994).

The upper limit for production is quite variable, with Le Cren (1969) estimating it at 12 g/m^2/yr and others (Elliott, 1993; Lobón-Cerviá et al., 2011) at 30-40 g/m^2/yr. Our database does suggest some rules of thumb for excellent (top 10%), and outstanding (top 1%) salmonid rivers based on biomass and production estimates from around the world. The top 10% and 1% of rivers in our data set correspond closely to 12 and 36 g/m^2 for biomass and 13 and 25 g/m^2/yr for production. This suggests that predicted upper limits are at or near the top 1% of salmonid river productivity seen in our database. Thus, it is very likely that the upper limit is indeed 40 g/m^2/yr.

It is unclear what limits salmonid carrying capacity in streams. Some authors suggest nutrient enrichment and acidification may lower stream productivity (Baldigo et al., 2007; Baldigo & Lawrence, 2001; Lacoul et al., 2011; Murdoch et al., 2021), whereas others find high salmonid biomass and high productivity with nutrient enriched streams (Gibson & Colbo, 2000; Jenkins & Keeley, 2010). Temperature and flow stability tend to be highly important for many salmonid species (Binns & Eiserman, 1979). It is likely carrying capacity is linked to a combination of biotic and abiotic factors (Armstrong et al., 2003; Clarke & Scruton, 1999), and perhaps explains the skewed distributions for both biomass and production. The complexity of these relationships and resource limitations for study make it difficult to determine all the factors contributing to abundance limits.

4.4.2 P/B ratios

The average P/B ratio of 1.08 from our database at the river scale is similar to the 1.06 for Minnesota Streams (Kwak and Waters (1997), but lower than the average of 1.30 from multiple earlier studies (1951-1983) around the world (Mann and Penczak 1986, all included in our database). In line with other studies (Kwak & Waters, 1997; Mann & Penczak, 1986; Randall, 2002), we found P/B ratios differed among species, hence, using an average P/B ratio to estimate production of a population may lead to over- or under-estimation of production. Even within species, P/B ratios can differ for different age classes (Randall, 2002), and spatially and temporally in the same region (Lobón-Cerviá et al., 2011). Caution should therefore be exercised when using general P/B ratios to estimate population production (Cote, 2007). Nevertheless, biomass predicted 68% of the variation in production. Adding species and age class to the model would likely improve this prediction. P/B ratios for individual species could be used for more accuracy (Table C5).

4.4.3 Differences in species

As expected, significant differences were found between species, with a markedly higher biomass for brown trout than most other species. Higher biomasses were also found for resident species compared to anadromous species. Given biomass estimates for all life stages are included for resident species, versus only juvenile stages for anadromous species, this was predicted.

Surprisingly, biomass did not significantly increase with more species present, as anticipated. Sites with only one species had a significantly higher biomass than sites with two species present. This could indicate that many streams with two or more species were in competition, rather than complementarity. Bergheim and Hesthagen (1990) found allopatric trout had a higher production than sympatric trout in the Kvassheimasana River, indicating interspecific competition may be responsible.

In contrast to what others have reported (e.g. Baxter et al., 2007; Benjamin & Baxter, 2010; Harig et al., 2000), we found higher biomass estimates for native populations than exotic populations. However, differences between exotic and native species are not the same for all species; exotic brook trout had higher biomass estimates than native brook trout, while native brown trout have higher biomass than their exotic counterparts. A focus on 'good' salmonid rivers in Europe reporting almost exclusively on native populations, coupled with the large number of studies of exotic salmonids in New Zealand (with a significantly lower biomass than many countries), could contribute to the pattern of biomass in our data set.

4.4.4 Temporal trends

Concern about the viability of salmonid populations (Dauwalter et al., 2020; Jelks et al., 2008) is justified given the significant decline we found since the 1980s. A shift in focus away from reporting high productivity streams towards focusing on restoration and water quality could be one reason for the decline. However, it is more likely that this shift in study focus has been prompted by the decline. Wilson et al. (2022) recorded a decline in productivity for several Pacific salmon species since 2010, driven in large part by logging. It is likely that declines are driven by a cumulation of factors in both freshwater and marine ecosystems that are not fully understood (Wilson et al., 2022). Looking at a range of spatial scales across environments is likely to give us more information on the processes that are driving the changes. In many cases, it's likely that multiple factors are causing general habitat degradation, rather than one event, as is postulated for the Horokiri Stream where brown trout biomass went from 26 g/m^2 in 1941 to 0.9 g/m^2 in the late 1990s (Jellyman et al. 2000).

4.4.5 Stream size

The inverse relationship between stream width and biomass that many authors have observed (Cote, 2007; Hubert et al., 1996; Jonsson et al., 2011; Kozel & Hubert, 1989; Scarnecchia & Bergersen, 1987), was not as strong as expected, even at the level of individual species. We found a weak relationship with brown trout biomass and decreasing width (R^2 = 0.03), but no relationship with other species which may indicate a more complex relationship. For all species, biomass decreased for streams over 10 m, with no significant differences between the very small (< 5 m) and small (5 - 10 m) streams. Binns and Eiserman (1979) found a similar relationship in Wyoming streams: biomass increased as wetted stream width increased between 0.6 and 6.6 m, but then decreased as width increased past 6.6 m, showing streams with widths between 5.4 and 6.6 had the highest biomasses. Other studies have found no relationship with width for certain species (Bowlby & Roff, 1986; Cote, 2007; Stichert et al., 2001). Smaller streams may be more important for species that are dependent on bankside cover as they tend to have a higher proportion of edge habitat, associated with bankside cover (Rosenfeld et al., 2000).

4.4.6 Fishing methods

Fishing methods may affect biomass estimates (Dauphin et al., 2018). Snorkelling (or drift diving, visual assessment) is often used in larger rivers where electrofishing is not possible (Teirney & Jowett, 1990). It is quicker and requires fewer resources than other methods (Teirney & Jowett, 1990), but may underestimate fish populations compared to electrofishing (Cunjak et al., 1988; Macnaughton et al., 2015). Our study found significantly

lower biomass estimates with snorkelling than electrofishing and netting and trapping, but other studies have found the contrary (Chamberland et al., 2014; Kajgrová et al., 2023). For certain species, age classes, and habitats, snorkelling or spotlighting had higher populations estimates than electrofishing (Hickey & Closs, 2006; Macnaughton et al., 2015), while others suggest that electrofishing underestimates some populations (Pope et al., 2010). It appears there is no clear consensus on which method is more accurate; regardless, certain fishing methods will be better suited to certain conditions. For instance, fish capture by electrofishing can be inefficient in deep and slow flowing water (Glova, 1988). The number of fish passes could also bias results. While many studies find two passes are sufficient to produce an estimate of fish abundance (Hicks, 2003), biases can still exist by fish species and size, the statistical estimator, and the characteristics of the area sampled (Peterson et al., 2004).

Targeting preferred habitats can lead to overestimating biomass in a river. For instance, only measuring small areas such as pools could lead to high biomass estimates that do not reflect the rest of the reach (Elso & Giller, 2001). For example, Gibson and Colbo (2000) reported a biomass around 80 g/m^2 in a single pool in Newfoundland, while riffles in the same river had biomasses less than 25 g/m^2. Sampling more often, over several seasons, and over a larger spatial area may reduce bias in estimates, and be better able to assess trends and variations in populations.

4.4.7 Biases and gaps

A large representation of rivers from three countries (USA, Canada and New Zealand), could indicate a possible bias in the search. Given the search was conducted in English, and many salmonids species' native range is in North America, it was not surprising that representation was in favour of this area. While many European countries were represented, the number of projects and rivers may have been higher if the search was completed in languages other than English. A language bias is a common bias in systematic reviews (Harrison, 2011; Hillebrand, 2008). One method to address this for the future could be to target areas with gaps in the literature, focusing on local languages. Gaps in the literature in our database were from exotic populations in Europe and the Southern Hemisphere, New Zealand being the exception. Salmonids have been introduced to every continent except Antarctica (Kershner et al., 2019; Rahel, 2002) and most of these areas are not represented in the database.

The lack of studies in areas outside of North America, Europe, and New Zealand could be due to several reasons: exotic salmonid populations are not a priority, particularly for biomass and production estimations, so they are not measured; there is a lack of published research in these areas or it only exists in the grey literature, making it more difficult to find; or there is simply no interest or lack of resources to publish data. It is also possible

that studies may have been missed in our search – if salmonids were not the target species. Studies published before the start of the Web of Science database in 1979, or published in languages other than English, were also more likely to be missed. In Europe, where exotic salmonid populations have become invaders (Fausch, 2007), very few studies reported biomass estimates for exotics, instead focusing on native salmonid species. This was in contrast to North America where around 40 percent of estimates were for exotic populations.

We found multiple variables were important for predicting salmonid biomass. The variables that we included (species, country, season, latitude, elevation, stream width, the year surveyed, native or exotic populations, sampling method, and how many years were sampled) only explained 20% of the biomass variance, so more information is needed to be able to develop a predictive model of salmonid biomass. Expanding the list of variables in the database, and in particular including environmental variables such as water temperature, land cover, water chemistry, or geology, would be useful to determine if there are specific conditions that we find in higher biomass streams or specific differences between species. Aligning past conditions to the time of fish sampling may be difficult for many variables, particularly ones measured at small spatial ranges and that change frequently. Air temperature could be added to the database using the ERA5 database which dates from 1940 to present (Hersbach et al. 2023); hence, temperature from the time of fish sampling could be added.

Separating species, age classes, or regions (either spatially or by environmental conditions) will be a useful next step to find potential trends in the database. Additionally, sampling at a range of extents, from stream reaches of 100 m, segments of a few kilometres, and whole river catchments, would help identify habitat characteristics and limitations at all levels of the system (Foote et al. 2024; Maddock, 1999).

4.4.8 Conclusion

The database presented in this study is, to our knowledge, the largest compilation of biomass studies for salmonid fish, representing over 1000 rivers worldwide. Results from this analysis generally agree with the literature in showing a reduction in biomass over time, a bias in sampling methods and locations, and a large variation in the P/B ratio by species (Table 4.6). However, we found published biomass estimates that far exceeded theorised limits of 30 g/m^2 (1.3%, or 14 rivers), which could be due to a bias from sampling methods. We may find more reliability in long-term studies that measure both biomass and production. However, our analysis shows studies that measure production had a higher biomass than those that did not. Given that production is costlier and more labour-intensive to measure, researchers may focus their attention on 'good' salmonid streams, though what constitutes a 'good' salmonid stream is still contested. A fuller picture of the

state of salmonids in the world requires more long-term productivity studies in a wide range of environments and habitat quality. Reporting biomass more systematically would help detect patterns more easily. This could include using the same fishing method; including multiple habitat types in the survey (e.g. pools, riffles, and runs); surveying in multiple sites across the river; and surveying over all seasons. Ideally, sampling should also occur over multiple consecutive years, to determine if there are annual changes in populations. Systematic reporting may help determine if there is indeed a decline of salmonid populations over time.

5 Conclusion

The overarching goal of this research was to combine ecological and hydrogeomorphological approaches to investigate salmonid abundance in streams. This involved investigating restoration techniques and habitat quality at a range of scales in salmonid streams around the world. Steps taken to achieve the research objectives were to determine the effectiveness of a common restoration technique for salmonids (in-stream structures) using a meta-analysis methodology; link habitat quality, hydrogeomophological quality, and fish indices through field observations; and link salmonid abundance to variables at a range of scales in a river catchment by conducting a systematic review and developing a database of salmonid biomass that will be shared (Foote et al. in prep for Scientific Data and Dryad) and can be expanded upon for future research. This research provided insight into the range of salmonid abundance around the world, different techniques to assess habitat quality, and gaps in research for future focus on restoring salmonid streams.

5.1 Findings

A meta-analysis approach was used to determine the effectiveness of in-stream structures on salmonid abundance (Chapter 2). Data from 100 restoration projects showed a significant increase in salmonid abundance, consistent with previous reviews and studies (Roni, 2019; Roni et al., 2008; Whiteway et al., 2010). Overall, structures did improve habitat, and despite a shift since the 1990s in using more natural structures (wood and boulders), compared to artificial structures (weirs and deflectors), structures have not become more effective over time. However, short-term monitoring (i.e. less than 5 years), makes it difficult to determine long-term sustainability of this restoration technique. At least 10 years of monitoring is required to detect a sustained response to restoration (Bisson et al., 1992, 2003; Kondolf & Micheli, 1995; Reeves et al., 1997), but most projects monitor for less than 5 years. Some structures fail (i.e. fall apart or do not have the intended effect) in just a few years, especially if they are inappropriate for the stream characteristics (Champoux et al., 2003; Frissell & Nawa, 1992; Miller, 1997; White, 1996). Furthermore, the small spatial extent at which structures are usually implemented at (typically ~50-500m), ignores habitat limitations in the rest of the catchment. Processes that occur at bigger scales (i.e. segment to the catchment) are not recognised. Process-based techniques, which give more space for the river, allow more long-term, self-sustaining restoration. Process based techniques could involve restoring natural flow and sediment regimes (Poff et al. 1997), allowing rivers to erode – so limiting bank stabilization

(Williams et al. 2020), removing dams or other barriers (Bednarek 2001), reconnecting rivers with their floodplain (Mant & Janes 2006), and re-introducing beaver dams to regions they were historically present (Kemp et al. 2012). While there has been recent paradigm shifts towards process-based restoration, there are still few long-term restoration projects that measure biological or physical effects of this type of restoration (Roni et al. 2008; Rogosch et al. 2023), limiting the potential for testing these projects using meta-analyses. However, process-based techniques could still be assessed using case studies (e.g. dam removals (Bellmore et al. 2017)), until more long-term studies become available.

A promising metric to assess hydrogeomorphological quality and processes is the Morphological Quality Index (MQI), originally developed in the Italian Alps context to comply with the European Water Framework Directive. Links were found between the MQI, that is assessed at larger spatial scales (i.e. river segment and catchment), and fish habitat quality (using the QHEI) at reach scales (Chapter 3). The benefits of the MQI over the QHEI are that it can be applied over larger extents, so more of the river catchment can be assessed, and it can be calculated remotely with high accuracy (Lemay et al., 2021). The lack of a relationship between the MQI or QHEI and any of the biotic variables make it difficult to determine if these indices can be used as adequate ecological indicators. It is unclear whether this is due to the performance of the indices themselves, the methodology of the study, or because the system is too complex to capture in one index. Such a lack of relationship was also noted by Hughes et al. (2010) in agricultural watersheds because they are likely impacted by chemical stresses. Effects from land-use, particularly agriculture, are not fully captured in the indices, and water quality measures are not incorporated (Hughes et al., 2010). Applying the MQI and QHEI at multiple sites through the catchment, and increasing the number of streams in the study, may make the indices more useful at predicting biological responses.

To increase the number of sample sites, and further link salmonid abundance with a range of variables and habitat characteristics, a global database was created to record salmonid biomass from published literature (Chapter 4). This allowed detailed analyses of differences in biomass by species, region, period, and sampling techniques. Mean global biomass from over 1000 rivers is 5.2 g/m^2, and mean production from 164 rivers is 6.3 g/m^2/yr. The high correlation of biomass to production (R = 0.82) allows researchers to use the average production to biomass (P/B) ratio of 1.08 to predict production from biomass with some confidence. However, for more accuracy for single salmonid species, individual species P/B ratios should be used. Adding other variables to the model would also improve this prediction. Because stream residents spend their life cycle in rivers, and hence more age classes are included in biomass estimates than anadromous species (where only juvenile phases are included), residents have a higher biomass than anadromous species. Brown trout (*Salmo trutta*) have a higher proportion of biomass estimates over 10

g/m^2 than many other species. Additionally, native brown trout populations have a higher biomass than exotic brown trout, while native brook trout (*Salvelinus fontinalis*) biomass is significantly lower than their exotic counterparts. Small streams (less than 10 m wide) and smaller spatial extents had a higher biomass, perhaps because the proportion of available habitat is higher.

5.2 Future directions

While is it clear that improving stream habitat using in-stream structures is beneficial for the aquatic organisms living there, more long-term solutions are needed. Future restoration should focus on restoring hydrogeomorphological processes, such as natural flow and sediment regimes, lateral and longitudinal connectivity, and erosion (Beechie et al., 2010; Biron et al., 2018; Roni et al., 2002, 2008). In-stream structures should only be used as a short-term temporary measure or used alongside process-based restoration (Cramer, 2012; Roni et al., 2002). If in-stream structures must be used, continuous monitoring of at least 10 years should be undertaken, to correspond with time scales at which hydrogeomorphological and ecological changes occur. For longer lived species, longer time scales may be needed.

Criteria for designing process-based restoration of fluvial systems has been outlined by many authors (Biron et al., 2014; Ciotti et al., 2021; Piégay et al., 2005; Williams et al., 2020). Future fluvial restoration research should focus on monitoring the effectiveness of process-based restoration techniques for morphological quality and increasing habitat capacity for aquatic life. This will require monitoring before and after implementation of techniques. Long-term monitoring (at least 10 years) after implementation is ideal to test if techniques are self-sustaining.

An improved assessment of habitat quality for fish could include aspects of the MQI and QHEI. Since agricultural land-use is associated with fish declines and poor ecological state (Čivas et al., 2016; Joy et al., 2018), adaptation of the indices should better reflect the impacts of agriculture. This could include a greater weighting on vegetative bank cover and excessive erosion, or the incorporation of water quality indices. While water quality attributes such as nutrient concentrations and water temperature require long-term records to be meaningful (Canning et al., 2021; Julian et al., 2017), measuring water clarity using a secchi disc and algae cover can be done with a quick visual assessment. Applying the MQI and QHEI at multiple segments throughout a catchment or river will also give a better indication of conditions, and may increase the usefulness of the metrics for ecological monitoring. It could also indicate where restoration should be focused. Increasing the number of rivers and habitat quality range, as well as more recent biological monitoring, may improve the statistical power to detect relationships.

This research resulted in the largest known (to my knowledge) global database of published salmonid biomass estimates. In itself, the database could be used to test numerous ecological questions. Expanding the list of variables in the database would be useful for developing models to predict salmonid biomass. Flow stability, water temperature, stream cover, gradient, and water chemistry are some of the variables used in models to predict salmonid abundance (Fausch et al., 1988; Milner et al., 2003; See et al., 2021), but have mostly been used in a limited spatial region. Applying these on a global scale would provide a test of applicability of local scale studies to general fish ecology. The database could also be used to determine potential conditions for high biomass streams. Looking deeper into the high biomass streams (top 10% of streams – see Appendix D) might give us more insight into what to strive for when restoring streams for salmonid species. The database includes a large number of production estimates (for 194 rivers), which could be explored in the same detail as biomass. Production/biomass relationships could also be examined more closely.

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Appendix A

Supplementary Material: Impact of in-stream restoration structures on salmonid abundance and biomass: an updated meta-analysis

Kyleisha J. Foote, **Pascale M. Biron** and **James W.A. Grant**

Table A1. Our systematic review methodology, following some of the guidelines from the Collaboration for Environmental Evidence (2018)

Steps in systematic review	Our methods
1. Conducting a search	
Including peer-reviewed and grey literature	Our analysis included 45 (71%) journal articles and 18 (29%) grey literature items (reports, theses, book chapters, and conference proceedings).
Test comprehensiveness of search	Our search terms captured 64% of the studies used in Whiteway et al. (2010) and 91% used in Stewart et al. (2009). All journal articles except one from these two studies were captured. Twenty-one grey literature items from the studies were not captured using our search terms, of which 11 were published before 1980. All the items not found in the search except one were obtained from the authors of Whiteway et al. (2010).
All search terms provided	For article databases, the following terms were used where possible: (trout OR salmo*) AND (river OR stream OR channel OR reach OR watershed OR catchment) AND (restor* OR enhanc* OR improv* OR rehabilit* OR structure OR placement OR weir OR deflector OR cover OR boulder OR log OR wood OR LWD) AND (habitat OR population OR abundance OR densit* OR biomass), where * denotes a wildcard. Search terms were simplified for grey literature searches to 'trout OR salmon AND restoration OR instream OR structure, and if more than 200 results were produced more search terms were added.
Databases, search engines and search dates reported	Databases searched include Web of Science, Google Scholar, Scopus, and ProQuest Dissertations and theses. Searches were performed in December 2018 and repeated in April 2019.
Updates to searches	In response to reviewers, an updated search was conducted in February 2020 to capture recently published articles and broaden the search terms.
Description of grey literature searches reported	Publication searches of: Canadian Wildlife Federation; Google; Fisheries and Oceans Canada; Salmon Watersheds Program; Atlantic Salmon Federation; Food and Agricultural Organisation of the United Nations; Nature England; United States Environmental Protection Agency; Agricola; US National Park Service; Pacific Salmon Foundation; Society for Ecological

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Restoration; Environment and Climate Change Canada; Joint Nature Conservancy Council; Agris. Of the 18 grey literature items included 9 were reports, 5 were theses, 3 were conference proceedings, and one was a book chapter.

Limitations	Many studies in the grey literature did not have formal replication (so we could not extract an SD or N), thus, we have a lower percentage of grey literature (29%) than Whiteway et al. (2010), with 42% but higher than Stewart et al. (2009), with 9%.
	Searches were only conducted in English.
	Many assessments of in-stream restoration structures on salmonid species were excluded because of the data required for a meta-analysis. While it is impossible to capture all the literature, our study included 25 additional studies to the previous two meta-analyses (Stewart et al. 2009; Whiteway et al. 2010) and provides a more comprehensive statistical analysis.

2. Eligibility screening

Eligibility criteria defined	See Table 2.1.
Stages of screening literature	Search results were screened in three stages: (*i*) title - search results were ordered by relevance and the titles of the first 200 outputs were scanned for eligibility; (*ii*) abstract - abstracts or summaries of those that seemed relevant or were unclear were scanned for eligibility criteria; and (*iii*) full text - if deemed relevant or it was unclear, the full text was searched for inclusion criteria. All the studies included in the previous meta-analyses and reviews (Roni et al. 2002, 2008, 2015; Stewart et al. 2009; Whiteway et al. 2010; Roni 2019) were screened at the full-text stage and further references from included articles were screened.
Eligibility discussed among authors	The types of in-stream restoration projects to be included in the analysis was discussed. It was decided that engineered log jams and beaver dam analogues (if made of natural materials) would be included and classed as 'natural' types of structures because they aim to mimic natural structures of LWD and beaver dams.
	It was decided that bank stabilisation structures and spawning gravels would not be included as a restoration structure, although stabilisation was used in many earlier projects to control

erosion, and spawning gravels are used in many projects. We did not exclude studies that used either of these techniques (unless it was the only intervention used) but did not analyse their effects separately.

Numbers of articles found in search and number excluded	Number of results from articles databases: Google Scholar (472,000), Web of Science (6,443), Scopus (4,555), ProQuest (819). A total of 405 publications from article databases and grey literature searches were scanned at stages *ii* and *iii* and excluded from the analysis. A further 190 printed grey materials were scanned, of which 170 were excluded. Duplicate studies were removed at this point.
Reasons for exclusion	The main reasons for projects being excluded were: not enough replicates to calculate a standard deviation (SD) (if multiple years of data were presented for one replicate then a SD could have been calculated); no adequate control; other restoration interventions used so that the effect of in-stream structures could not be independently assessed; or other criteria in Table 2.1 not met. Due to the large number of projects assessed during the eligibility screening, excluded projects are not listed.
List of studies included in the meta-analysis	See Appendix A1.

3. Data coding and data extraction

Data extracted to estimate effect size	See methodology section. If no SD was presented, it was calculated from standard errors, confidence intervals, or calculated from the data presented if able (Higgins et al. 2019). If projects were not replicated, studies were not used unless two or more years of data were provided (if SD could be calculated). For these studies, the treatment and control n were 2 so the study was not over-weighted.
	If multiple years of data were presented, data were averaged across years where possible, but before and after data were not combined (i.e. before years were averaged together and after years were averaged together). Generally, seasonal data was combined as it was often not possible to extract independently.
	Where possible, species and age classes were extracted separately.
	Within each study, the data were treated the same (i.e. the two groups that were compared

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were extracted in the same way).

Information extracted	Year of restoration; number of years since restoration was completed and fish data were extracted; location information (river name, region, country, and lat, long); type of restoration structure (classed as weirs, deflector, cover, boulders LWD); if bank stabilisation or gravel input was used; if the project had artificial, natural, or both types of structures; season fished; species; age class of fish; outcome units (e.g. density or biomass units, if it is change in numbers); type of methodology used (BACI, BA, CI); and stream width (before restoration if provided, otherwise width after is used).
Additional information recorded (not included in the analysis due to low number of studies that report data)	Project cost, stream order, stream gradient, basin area, elevation, depth, change in width, average temperature, dominant substrate, canopy cover, pool volume or %, and in-stream cover area or %.

4. Critical appraisal of study validity

Identify sources of bias and correct or preform sensitivity analysis	Small sample bias (studies with a low number of replicates weighted the same as other studies) – corrected with the Hedge's g adjustment for small sample bias (Deeks et al. 2001) (see methods).
	Publication bias (statistically significant results are more prone to be published than non-significant ones) – assessed with Egger test (Egger et al. 1997) (see Assessment of bias in methods).
	Language bias (only including literature in English may result in an over-representation of statistically significant results) – also captured with Egger test (Egger et al. 1997)
	Availability bias (only easily available studies are included) – obtained grey literature from previous studies and performed extensive grey literature searches
	Duplication bias (studies may be published more than once) – studies were checked when included and duplicates were removed. Two studies included in the previous meta-analyses (Stewart et al. 2009; Whiteway et al. 2010) had been updated so our study included the most recent publication and excluded the earlier studies.

5. Data synthesis

Results of meta-analysis	See results
Study weighting and sensitivity analysis	Correction for small sample bias included and publication bias assessed
Effects modifiers – subgroups	Effect sizes by structure type, number of structure types installed, species, and age classes were estimated. Differences between groups were assessed. See methods and results for full details.
Information on eligible studies	A simplified table on species targeted, number of projects and effect sizes is provided in Table A2. Contact authors for further study information.

Table A2. The species targeted, number of projects, structure type installed, effect sizes (ES), and sample sizes (*n*) for ES extracted from each study included in the meta-analysis

Author	Species[1]	Number of projects[2]	Structure type[3]	Number of abundance / biomass ES	n for each treatment and control group[4]	
					Abundance	Biomass
Anton et al. 2011	*St*	1	LWD	1/1	4	4
Baird 2010	*Omy*, *Ok*	2	LWD	6	6 treatment and 2 control (2 ES), and 25 or 26 treatment and 12 or 11 control (4 ES)	
Binns & Remmick 1994	*Oc*	1	W, D	1/1	2	2
Bjornn et al. 1991	*Ok*	4	C, B, LWD	4	6	
Brusven 1986	*Ot*	1	C	1	4	
Burgess 2001	*Oc* and *Om* combined	1	LWD	2	3	
Cederholm et al. 1997	*Ok*	2	LWD	2	3	
Clark et al. 2019	*Ot, Ok, Oc, Omy*	1	LWD	4	7, 19, 21, 26 for each ES	
Conner et al 2016	*Omy*	1	LWD	1	9 treatment, 3 control	
Crispin et al. 1993	*Ok*	1	D, C	1	2	
Culp 1996	*Om*	1	LWD	1/1	20	20
Dieterman et al. 2018	*St*	1	C, B, LWD	1	4 treatment, 3 control	
Dugan 2015	*St*	2	C, B, LWD	4	10	
Fjellheim et al. 2003	*St*	1	LWD	1	3	

Flebbe 1999	*Om*	1	LWD	1	2	
Giannico 2000	*Ok*	2	LWD	2	3	
Giannico and Hinch 2003	*Ok*	2	LWD	4	2	
Glover 1986	*St*	2	D, C, B	2	2	
Hale 1969	*Sf*	1	W, D, C	1	2	
Hartzler 1983	*St*	1	C	2/2	6	6
Höjesjö et al. 2014	*St*	1	C	1/1	10	10
House 1996	*Ok, Ot, Omy, S*	1	W, B	3/1	5	5
Hryhorczuk 2009	*Omy, Ok*	1	LWD	4	28 treatment, 8 or 7 control	
Hunt 1976	*Of*	1	D, C	2/1	3	3
Hunt 1986	*St*	4	C, LWD	8/4	2	2
Hunt 1992	*St, Sf*	2	W, D, C	8/4	3	3
Hvidsten and Johnsen 1992	*St, Ss*	1	W	2	4 treatment, 5 control	
Johnson et al. 2005	*Ok, Oc, Omy*	1	LWD	5	4	
Jones et al. 2003	*Ta*	1	W, D	1		2
Kelly and Bracken 1998	*Ss, St*	1	D, B	2	6 treatment, 3 control	5 and 6 treatment, 3 control
Kennedy et al. 2014	*Ss, St*	2	D, B	10	5 or 7 treatment, 8 control	
Klassen and Northcote 1986	*Ok, Omy*	1	W	2	3	
Klungle 2006	*St, Om*	1		2	7	

Kratzer 2018	*Sf*	1	LWD	1/1	9	9
Langford et al. 2001	*Ss, tr*	2	W, D, C, B	4	4 (for 2 ES), 9 (for 2 ES)	
Latta 1972	*St, Sf*	1	W, D, C	4/2	2	2
Lehane et al. 2002	*St*	1	LWD	1/1	4 treatment, 12 control	4 treatment, 12 control
Linløkken 1997	*St*	1	W, D	1	2	
Louhi et al. 2016	*St*	2	W, B	6	3	
Miller 1997	*Omy*	1	W, C, LWD	1	**2**	
Mitchell et al. 1998	*Ss*	2	W, D, C, B	2	6	
Moore and Gregory 1988	*Oc*	1	D, B	1/1	3	3
Näslund 1989	*St*	4	W, D, B	11/4	2	2
Nickelson et al. 1992	*Oc*	1	LWD	1	24 treatment, 17 control	
Nilsson et al. 2017	*St, Ss*	1	B, LWD	2/1	6	6
Olsen et al. 1984	*Omy*	5	W, D, B	5	Treatments (3, 4, 5, 7, 10), controls (6 for 4 ES, 4 for 1 ES)	
Pess et al 2012	*Ot, Ok, Omy and Oc* combined	1	LWD	4	6	
Polivka et al. 2015	*Ot, Omy*	1	W, LWD	4	10 treatment, 15 control	
Quinn and Kwak 2000	*St, Sf, Oc, Om*	1	C, B, LWD	4/4	2	2
Reeves et al. 1997	*Ok, Omy*	1	B, LWD	3	7	
Roni 2001	*Ok, Oc, Omy, tr*	2	LWD	8	15	

Study	Species		Structures			
Roni et al. 2006	*Ok, Omy and Oc* combined	1	W	3	13	
Slaney et al. 1994	*Ot*	1	C, LWD	1	3	
Solazzi et al. 2000	*Ok, Omy, Oc*	2	W, C, LWD	8	2	
Sweka and Hartman 2006	*Sf*	1	LWD	2	4	
Thorn and Anderson 2001	*St*	2	C, LWD	2/2	2	2
Trego 2017	*Sf*	1	D, LWD	1	4	
Van Zyll De Jong and Cowx 2016	*Ss, Sf*	3	W, B, C	6/6	2 (for 2 ES), 4 (for 4 ES)	2 (for 2 ES), 4 (for 4 ES)
Vehanen et al. 2010	*St*	2	W, B	6	6	
Ward and Slaney 1981	*Ok, Omy, S*	8	W, D, C, B	10/7	3 (for 2 ES), 4 (for 8 ES)	Treatments (3 for 3 ES, 4 for 4 ES), control 4
Watz et al. 2019	*St*	1	LWD	1	4	
White et al. 2011	*tr*	1	W	2/2	5	5
Zika and Peter 2002	*St, Om*	1	LWD	2/2	5	5
Total		100		198/52		

[1]Species names: *St* = brown trout; *Ss* = Atlantic salmon; *Sf* = brook trout; *Ok* = coho salmon; *Omy* = steelhead; *Om* = rainbow trout; *Oc* = cutthroat trout; *Ot* = Chinook salmon; *Ta* = Arctic grayling; *S* = unspecified or combined salmonids; *tr* = unspecified or combined trout.

[2]Some publications were compilations of multiple restoration projects that used different restoration techniques. Where monitoring data were reported separately, they were counted as separate projects.

[3]Structures were classed as weirs (W), deflectors (D), cover (C), boulders (B), or large woody debris (LWD).

[4]Where *n* was different between the treatment and control groups or different effect sizes from each study, it is specified.

Table A3. Effect size of in-stream structures on individual salmonid species (significant effects are in bold). Effect sizes were only estimated for species with four or more studies in each structure category.

Structure type	Species (number of effect sizes)	Effect size (95% CI)	p value
	Abundance measures		
Weirs	Brown trout (23)	0.221 (-0.311, 0.752)	0.399
	Brook trout (6)	0.536 (-0.400, 1.471)	0.201
	Coho salmon (6)	**0.855 (0.113, 1.598)**	**0.032**
	Cutthroat trout (4)	**0.742 (0.229, 1.255)**	**0.019**
	Steelhead trout (11)	0.642 (-0.214, 1.499)	0.126
Deflectors	**Brown trout (20)**	**0.927 (0.610, 1.245)**	**<0.001**
	Brook trout (10)	0.114 (-0.667, 0.895)	0.750
	Atlantic salmon (4)	0.730 (-1.473, 2.938)	0.369
Cover	**Brown trout (21)**	**0.700 (0.398, 1.002)**	**<0.001**
	Brook trout (11)	0.334 (-0.298, 0.966)	0.266
	Coho salmon (7)	0.241 (-0.209, 0.691)	0.238
	Steelhead trout (5)	0.851 (-1.857, 3.559)	0.432
Boulders	**Brown trout (27)**	**0.658 (0.331, 0.985)**	**<0.001**
	Coho salmon (5)	0.625 (-0.727, 1.978)	0.285
	Steelhead trout (6)	0.777 (-0.771, 2.324)	0.253
	Atlantic salmon (6)	0.900 (-0.622, 2.422)	0.189
LWD	**Brown trout (20)**	**0.632 (0.302, 0.962)**	**<0.001**
	Coho salmon (24)	**0.652 (0.245, 1.058)**	**0.003**
	Cutthroat trout (7)	0.186 (-0.157, 0.529)	0.232
	Steelhead trout (18)	0.498 (-0.166, 1.162)	0.132
Artificial	**Brown trout (26)**	**0.567 (0.098, 1.036)**	**0.020**
	Brook trout (11)	0.507 (-0.214, 1.227)	0.148
	Coho salmon (9)	**0.513 (0.024, 1.002)**	**0.042**
	Steelhead trout (8)	0.902 (-0.023, 1.827)	0.054
	Atlantic salmon (7)	0.970 (-0.114, 2.053)	0.071
Natural	**Brown trout (18)**	**0.705 (0.210, 1.201)**	**0.008**
	Brook trout (4)	0.754 (-1.386, 2.894)	0.344
	Coho salmon (23)	**0.626 (0.248, 1.005)**	**0.002**
	Cutthroat trout (4)	0.195 (-0.477, 0.866)	0.424
	Steelhead trout (15)	**0.761 (0.066, 1.456)**	**0.034**
Both	**Brown trout (23)**	**0.623 (0.293, 0.954)**	**<0.001**
	Coho salmon (4)	1.177 (-0.887, 3.241)	0.167
	Cutthroat trout (5)	0.756 (-0.309, 1.821)	0.120
	Steelhead trout (7)	0.418 (-0.948, 1.784)	0.482

Biomass measures

Weirs	**Brown trout (4)**	**1.369 (0.631, 2.109)**	**0.010**
Deflectors	**Brown trout (6)**	**0.725 (0.037, 1.412)**	**0.042**
	Brook trout (4)	0.371 (-1.907, 2.649)	0.640
Cover	**Brown trout (11)**	**0.734 (0.199, 1.269)**	**0.001**
	Brook trout (6)	0.305 (-0.925, 1.536)	0.552
LWD	Brown trout (9)	0.260 (-0.288, 0.807)	0.306
Artificial	**Brown trout (10)**	**0.818 (0.247 1.389)**	**0.010**
	Brook trout (6)	0.520 (-0.597, 1.637)	0.285
Natural	Brown trout (6)	0.312 (-0.478, 1.013)	0.356
Both	Brown trout (5)	0.099 (-0.351, 0.550)	0.574

A1. Meta-analysis References

The following references were included in the meta-analysis:

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Appendix B

Supplementary Material: Morphological and habitat quality of salmonid streams and their relationship with fish-based indices in Aotearoa New Zealand and Ontario (Canada)

Kyleisha J. Foote, **Pascale M. Biron** and **James W.A. Grant**

Table B1. Site location characteristics

Site Number on map / Site Code	Stream name	Length of reach (m)		Average width (m)	Elevation (m)[a]	Distance downstream to lake or coast[b] (km)	Upstream catchment area (km²)
		MQI	QHEI				
Ontario Sites							
O1 / WIL1	Wilmot Creek	1510	600	5.0	133	11	39.3
O2 / WIL2	Wilmot Creek	1220	500	5.0	112	8.2	60.5
O3 / ROB1	Robinson Creek	220	220	3.1	186	28	12.9
O4 / ROB2	Robinson Creek	890	890	4.1	189	29	12.2
O5 / WHY1	Whiskey Creek	1300	600	1.8	252	2.0	6.0
O6 / WHY2	Whiskey Creek	1200	700	3.0	272	3.5	3.7
O7 / HOG1	Hog Creek	530	530	3.1	201	4.6	60.1
O8 / NOT1	Upper Nottawasaga tributary	240	110	1.8	482	155	1.7
O9 / MON1	Monora Creek	620	390	3.9	416	100	11.2
O10 / SHW1	Shaw's Creek tributary	800	110	2.5	448	98	1.5
O11 / CAL1	Caledon Creek	280	280	2.3	391	82	49.4
O12 / CRT1	Credit River	1340	1340	11.6	382	81	204.0
O13 / BLK1	Black Creek	420	420	6.2	241	55	80.6
O14 / BLK2	Black Creek	1530	400	4.4	300	98	34.2
Average ON Sites		864	506	4.1	286	50	41.2
Aotearoa New Zealand Sites							
1 / SPR1	Spring Creek	1460	920	8.4	5	17	10.6
2 / SPR2	Spring Creek	1210	480	5.7	10	22	2.1

3 / WAK1	Waikakahi Stream	740	740	5.1	22	5	136.3
4 / WAK2	Waikakahi Stream	2250	280	2.5	33	8	135.6
5 / SHG1	Waihemo / Shag River	1740	580	7.5	46	27	340.5
6 / SUT1	Sutton Stream	640	NA	5.2	216	98	153.5
7 / IDA1	Ida Burn	4750	500	7.8	465	217	203.7
8 / OMA1	Omarama Stream	2250	1120	6.7	430	128	305.8
9 / MRY1	Mary Burn	3980	1970	6.7	512	157	151.6
10 / HAU1	Haupiri River	2490	560	32.3	189	98	169.7
11 / ARN1	Arnold River	4360	240	29.9	94	46	538.8
12 / MNG1	Mangles River	2930	330	21.9	214	113	368.9
13 / GOW1	Te Kauparenui / Gowan River	2370	640	24.5	456	147	370.7
14 / GOW2	Te Kauparenui / Gowan River	2260	200	24.0	415	143	385.6
15 / BUL1	Buller River (Kawatiri)	2420	2420	21.4	620	165	200.5
16 / MOT1	Motueka River	3770	980	56.6	88	40	1441.0
17 / RIU1	Riuwaka River	1230	660	9.1	59	11	62.9
18 / RAI1	Rai River	1240	650	19.0	40	33	152.7
19 / HOR1	Horokiri Stream West	600	600	3.20	73	6.7	11.7
20 / HOR2	Horokiri Stream West	1000	380	3.2	58	6	13.1
21 / HOR3	Horokiri Stream East	540	200	2.0	72	5.7	8.9
Average NZ streams		2106	723	14.4	196	71	246
Average all streams		1609	634	10.3	232	62.8	164

Notes: [a] Elevation measured in the middle of the QHEI reach. [b] Ontario sites = distance to downstream lake; New Zealand sites = distance to coast.

Table B2. Description of QHEI metrics and method of assessment (from Taft & Koncelik, 2006, Rankin 1989)

Metric and components	Description	Assessment method
1. Substrate (maximum 20). Substrate type, origin and quality	Type: Bed substrate is identified from best types (boulder/slabs, boulder, cobble, gravel, sand, bedrock) and other types (hardpan, detritus, muck, silt, artificial). Origin: The parent material from which the substrate originates is identified (limestone, tills, wetlands, hardpan, sandstone, rip rap, lacustrine, shale, coal fines). Quality: Substrate embeddedness and silt cover	Type: Visual assessment and Wolman zigzag pebble count where possible. The two most common substrate types are selected – if one predominates (greater than 75-80% of the bottom area) that type is checked twice. Other types present are noted. The number of best types is indicated. Origin: Visual assessment, geological material map. The most common substrate origin is selected (can be double-checked if two are common). Quality: Visual assessment, wading stream, digging below surface material
2. Instream cover (maximum 20) Presence and extent	Presence of functional instream cover types (undercut banks, overhanging vegetation, shallows (in slow water), rootmats, pools > 70 cm, rootwads, boulders, oxbows or backwaters, aquatic macrophytes, logs or woody debris) and amount of overall instream cover (extensive, moderate, sparse, nearly absent). Cover types are not counted if in areas with insufficient depth (< 20 cm) or cannot be used by fish.	Visual assessment
3. Channel morphology (maximum 20) Channel sinuosity,	Quality of the stream channel that relates to the creation and stability of macrohabitat. Level of sinuosity, channel development (pool/riffle	Visual assessment, validate with aerial photographs (sinuosity and development) or documented information

channel development, channelization, stability	complexes), extent of channelization, and channel stability are assessed according to guidelines.	(channelization) if needed
4. Riparian zone and bank erosion (maximum 10) Bank erosion, riparian width, floodplain quality	Quality of the riparian buffer zone and floodplain vegetation. Includes extent of bank erosion, riparian zone width, and floodplain quality (forest or swamp, shrub or old field, residential park or new field, fenced pasture, open pasture or rowcrop, conservation tillage, urban or industrial, mining or construction).	Visual assessment, validate with aerial photographs (riparian width, floodplain type quality), estimate or measure riparian width with tape. Average of left and right banks.
5. Pool/glide and riffle-run quality (maximum 20) Pool/glide depth, channel width morphology, current velocity, riffle depth, run depth, riffle/run substrate and embeddedness	Quality of pool, glide, and/or riffle-run habitats. Pool depth, overall diversity of current velocities in pools and riffles, pool morphology, and riffle-run depth, substrate and quality (embeddedness)	Visual assessment, digging in substrate, measuring with tape measure or metre ruler

Table B3. Definition, assessment parameters, assessment methods, and ranges of application of each indicator (from Rinaldi et al. 2016)

Indicators and assessment parameters	Assessment methods	Range of application
Functionality		
F1 – Longitudinal continuity in sediment and wood flux Presence of crossing structures that may alter the natural flux	GIS and/or intervention information: identification of crossing structures; field survey: visual assessment of level of interception	All river types
F2 – Presence of a modern floodplain Width and length	GIS: measurement of width and longitudinal length; field survey: identification of modern floodplain	PC-U; not evaluated in mountain streams along steep (>3% slope) alluvial fans
F3 – Hillslope – river corridor connectivity Presence and extent of disconnection within a 50-m width each side of the river	GIS: identification and measurement of width of disconnecting elements; field survey: checking disconnecting elements	C
F4 – Processes of bank retreat Presence/absence of retreating banks	GIS and/or field survey: identification of eroding banks	PC-U; not evaluated in some low-energy river types (see Rinaldi et al 2016)
F5 – Presence of a potentially erodible corridor Width and longitudinal length of an erodible corridor – without structures or structures, e.g. bank protections, levees, houses, roads	GIS: width and longitudinal length measurements	PC-U
F6 – Bed configuration – valley slope Identification of bed configuration in comparison with the expected bed configuration	Topographical maps and GIS: mean valley slope; field survey: identification of bed configuration	Single-thread, alluvial, except in the case of deep streams where observation of the bed is not possible
F7 – Planform pattern Percentage of the reach length with altered planform and geomorphic units	GIS: identification and measurement of length of altered portions; field survey: identification/verification	PC-U; some confined types (see Table 1.8 Rinaldi et al 2016)
F8 – Presence of typical fluvial landforms in the floodplain Presence/absence of appropriate landforms in the	GIS and/or field survey: identification and checking of fluvial forms	PC-U

floodplain

F9 – Variability of the cross section Percentage of reach length with alteration of the natural heterogeneity of the cross section that is expected for that river type and is caused by human factors	Field survey: identification/checking; GIS: identification and measurement of length of altered portions	All types
F10 – Structure of the channel bed Presence/absence of alterations of bed sediment (armouring, bedrock outcrops, bed revetments)	Field survey: visual assessment	All types; except the case of deep channels when observation of the bed is not possible
F11 – Presence of in-channel large wood Presence/absence of large wood	Field survey: visual assessment	All types; not evaluated above the tree-line and in streams with a natural absence of woody riparian vegetation
F12 – Width of functional vegetation Mean width of functional riparian vegetation in the fluvial corridor potentially connected to channel processes	GIS: identification and measurement of mean width of functional vegetation	All types; not evaluated above the tree-line and in streams with a natural absence of riparian vegetation
F13 – Linear extension of functional vegetation Longitudinal length of functional riparian vegetation along the banks with direct connection to the channel	GIS: identification and measurement of longitudinal length of functional vegetation	All types; not evaluated above the tree-line and in streams with a natural absence of riparian vegetation

Artificiality

A1 – Upstream alteration of flows Changes in discharges caused by interventions upstream (dams, diversions, spillways, retention basins, etc)	Hydrological data: evaluation of reduced/increased discharge caused by interventions. In the absence of available data, the assessment is based on the presence of flow intervention and its use	All types
A2 – Upstream alteration of sediment discharges Presence, type, and location (drainage area) of relevant structures responsible for bedload interception (dams, check-dams, weirs)	GIS and/or database of interventions: identification of structures and relative drainage area	All types

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A3 – Alteration of flows in the reach Amount of alterations of discharge caused by interventions within the reach	See A1	All types
A4 – Alteration of sediment discharge in the reach Type and spatial density of structures intercepting bedload (check dams, weirs) along the reach	GIS and/or database of interventions: identification and number of structures	All types
A5 – Crossing structures Spatial density of crossing structures (bridges, fords, culverts)	GIS and/or database of interventions: identification and number of structures	All types
A6 – Bank protections Length of protected banks (walls, rip-raps, gabions, groynes, bioengineering measures)	GIS and/or database of interventions: length of structures	All types
A7 – Artificial levees Length and distance from the channel	GIS and/or database of interventions: length and distance of structures	PC-U
A8 – Artificial changes of river course Percentage of the reach length with documented artificial modifications of the river course (meander cutoff, relocation of river channel, etc.)	Historical/bibliographic information and/or database of interventions	PC-U
A9 – Other bed stabilization structures Presence, spatial density and typology of other bed-stabilizing structures (sills, ramps) and revetments	GIS and/or database of interventions: identification, number or length of structures	All types
A10 – Sediment removal Existence and relative intensity of past sediment mining activity (over the last 100 years, with a particular focus on the last 20 years)	Database of interventions and/or information available by public agencies; field survey and/or GIS: indirect evidence	All types; not evaluated in strongly confined and highly stable streams that are sediment supply-limited with no continuous alluvial bed
A11 – Wood removal Existence and relative intensity (partial or total) of in-channel wood removal during the last 20 years	Database of interventions and/or information available by public agencies; field survey: additional evidence	All types; not evaluated above the tree-line and in streams with natural absence of riparian vegetation
A12 – Vegetation management	Database of interventions and/or information	All types; not evaluated above the tree-

Existence and relative intensity (selective or total) of vegetation cuts during the last 20 years	available by public agencies; field survey: additional evidence	line and in streams with natural absence of riparian vegetation

Channel adjustments

CA1 – Adjustments in channel pattern Changes in channel patterns from 1930s to 1960s based on changes in sinuosity, braiding, and anastomosing indices	GIS	All types; evaluated only for sufficiently large channels
CA2 – Adjustments in channel width Changes in channel width from 1930s to 1960s	GIS	All types; evaluated only for sufficiently large channels
CA3 – Bed-level adjustments Bed-level changes over the last 100 years	Cross sections / longitudinal profiles (if available); field survey: evidence of incision or aggradation	All types; evaluated in case field evidence or information is available

Table B4. MQI metrics that were omitted from the Historical RMQI assessment

Historical RMQI omission	MQI metric
Attributes left out of all assessments	F9 – variability of the cross-section
	F 10 – structure of the channel bed
	F11 – presence of in-channel large wood
	A9 – bed stabilization structures[1]
Attributes possibly left out of assessment	F4 – bank retreat[1]
	F6 – bed configuration[2]
	A6 – bank protections
	A10 – sediment removal
	A11 – wood removal

Notes: [1]Only assessed in partially confined and unconfined channels. [2]Only assessed in confined channels. See Rinaldi et al. (2016) for full explanation of MQI metrics.

Table B5. Survey dates of trout biomass, fish data to calculate the IBI, and historical photos used to calculate a historical RMQI score for NZ sites.

NZ site code	Survey dates		
	Trout biomass[1] (DD/MM/YYYY)	IBI[2] (MM/YYYY)	RMQI – historical photo[3] (DD/MM/YYYY)
SPR1	19/02/1986	07/2002	07/03/1983
SPR2	19/02/1986	12/1999	07/03/1983
WAK1		02/2014	24/02/1984
WAK2		02/2014	24/02/1984
SHG1	13/02/1986	01/2006	19/03/1981
SUT1		03/2015	na
IDA1		01/2019	27/02/2003
OMA1		03/2006	02/02/1986
MRY1		02/2016	13/02/1984
HAU1	01/03/1987	01/2002	13/03/1973
ARN1	01/03/1987	07/2003	15/03/1982
MNG1	07/01/1988	02/1993	15/11/1983
GOW1	07/01/1988	05/1974	31/01/1980
GOW2	18/02/1986	09/2004	31/01/1980
BUL1	05/01/1989	11/1991	16/02/1982
MOT1	26/02/1985	02/1987	07/12/1986
RIU1	06/01/1988	12/2012	31/01/1980
RAI1	23/02/1987	03/1996	20/11/1983
HOR1		02/1997	02/01/1988
HOR2		12/2007	02/01/1988
HOR3		11/2007	02/01/1988

[1]Trout biomass data from Teirney and Jowett (1990) and Jellyman and Graynoth (1994); [2]fish data for IBI from the NZFFD (Stoffels 2022); [3]Historical photos sourced from http://retrolens.nz

Table B6. IBI configuration for New Zealand fish communities (from Table 3, Joy and Death 2004).

Metric	Scoring criteria		
	5	3	1
(1) Number of native species			
(2) Number of riffle dwelling species			
(3) Number of benthic pool species	> 67% MSRL	33-67% MSRL	< 33% MSRL
(4) Number of pelagic species			
(5) Number of intolerant species			
(6) The proportion of native species	> 67%	33-67%	<33%

Note: MSRL is the maximum species richness line and is based on elevation and distance from the coast (see Joy and Death 2004 for more information).

Table B7. *IBI configuration for Ontario fish communities (from Table 3, Steedman 1988).*

Category	Metric	Score and scoring criteria		
		5 (best)	*3*	*1 (worst)*
A. Species richness	No. of native fish species			
	No. of darter or sculpin species	0.67 MSRL* or higher	0.33 to 0.67 MSRL*	Less than 0.33 MSRL*
	No. of sunfish or trout species			
	No. of sucker or catfish species			
B. Local indicator species	Presence/absence of brook trout	Present	-	Absent
	% of sample as *Rhinichthys* spp.	<50%	-	>50%
C. Tropic composition	% of sample as omnivores	<20%	20-40%	>40%
	% of sample as large piscivores	>2%	-	<2%
D. Fish abundance	Catch per minute of sampling (CPUE)	4-25	>25	<4

*Maximum species-richness lines (MSRL) for species richness metrics were as follows: native species richness = 8.24 LGWSAR - 0.47, darter/sculpin species richness = 3.33 LGWSAR - 0.25, sunfish/trout species richness = 2.06 LGWSAR + 0.48, and sucker/catfish species richness = % 1.45 LGWSAR + 0.42, where LGWSAR = $\log_{10}$ (watershed area in km^2).

Fig. B1. QHEI assessment field sheet (from Taft and Koncelik, 2006)

OhioEPA Qualitative Habitat Evaluation Index Field Sheet QHEI Score: [ ]

River Code: _____ RM: _____ Stream: _____

Date: _____ Location: _____

Scorers Full Name: _____ Affiliation: _____

1] SUBSTRATE (Check ONLY Two SubstrateTYPE BOXES; Estimate % present

TYPE	POOL RIFFLE		POOL RIFFLE	SUBSTRATE ORIGIN Check ONE (OR 2 & AVERAGE)	SUBSTRATE QUALITY Check ONE (OR 2 & AVERAGE)
□□-BLDR /SLBS[10]	____ ____	□□-GRAVEL [7]	____ ____	□ -LIMESTONE [1] SILT:	□- SILT HEAVY [-2]
□□-BOULDER [9]	____ ____	□□-SAND [6]	____ ____	□ -TILLS [1]	□-SILT MODERATE [-1]
□□-COBBLE [8]	____ ____	□□-BEDROCK[5]	____ ____	□ -WETLANDS[0]	□-SILT NORMAL [0]
□□-HARDPAN [4]	____ ____	□□-DETRITUS[3]	____ ____	□-HARDPAN [0]	□-SILT FREE [1]
□□-MUCK [2]	____ ____	□□-ARTIFICIAL[0]	____ ____	□ -SANDSTONE [0] EMBEDDED	□-EXTENSIVE [-2]
□□-SILT [2]	____ ____	NOTE: Ignore Sludge Originating From Point Sources		□ -RIP/RAP [0] NESS:	□-MODERATE [-1]

Substrate [ ] Max 20

NUMBER OF SUBSTRATE TYPES: (High Quality Only, Score 5 or >) □-4 or More [2] □-3 or Less [0] □-LACUSTRINE [0] □-NORMAL [0]
  □-SHALE [-1] □-NONE [1]
COMMENTS_____ □-COAL FINES [-2]_____

2] INSTREAM COVER (Give each cover type a score of 0 to 3; see back for instructions)   AMOUNT: (Check ONLY One or check 2 and AVERAGE)   Cover [ ] Max 20

(Structure) **TYPE:** Score All That Occur

___UNDERCUT BANKS [1]	___POOLS> 70 cm [2]	___OXBOWS, BACKWATERS [1]	□ - EXTENSIVE > 75% [11]
___OVERHANGING VEGETATION [1]	___ROOTWADS [1]	___AQUATIC MACROPHYTES [1]	□ - MODERATE 25-75% [7]
___SHALLOWS (IN SLOW WATER) [1]	___BOULDERS [1]	___LOGS OR WOODY DEBRIS [1]	□ - SPARSE 5-25% [3]
___ROOTMATS [1] COMMENTS:_____			□ - NEARLY ABSENT < 5%[1]

3] CHANNEL MORPHOLOGY: (Check ONLY One PER Category OR check 2 and AVERAGE)   Channel [ ] Max 20

SINUOSITY	DEVELOPMENT	CHANNELIZATION	STABILITY	MODIFICATIONS/OTHER	
□- HIGH [4]	□- EXCELLENT [7]	□- NONE [6]	□- HIGH [3]	□- SNAGGING	□- IMPOUND.
□- MODERATE [3]	□- GOOD [5]	□- RECOVERED [4]	□- MODERATE [2]	□- RELOCATION	□- ISLANDS
□- LOW [2]	□- FAIR [3]	□- RECOVERING [3]	□- LOW [1]	□- CANOPY REMOVAL	□- LEVEED
□- NONE [1]	□- POOR [1]	□- RECENT OR NO RECOVERY [1]		□- DREDGING	□- BANK SHAPING
				□- ONE SIDE CHANNEL MODIFICATIONS	

COMMENTS:_____

4]. RIPARIAN ZONE AND BANK EROSION (check ONE box per bank or check 2 and AVERAGE per bank) River Right Looking Downstream   Riparian [ ] Max 10

RIPARIAN WIDTH L R (Per Bank)	FLOOD PLAIN QUALITY (PAST 100 Meter RIPARIAN) L R (Most Predominant Per Bank)	L R	BANK EROSION L R (Per Bank)
□□- WIDE > 50m [4]	□ □-FOREST, SWAMP [3]	□ □-CONSERVATION TILLAGE [1]	□ □-NONE/LITTLE [3]
□□- MODERATE 10-50m [3]	□ □-SHRUB OR OLD FIELD [2]	□ □-URBAN OR INDUSTRIAL [0]	□ □-MODERATE [2]
□□- NARROW 5-10 m [2]	□ □-RESIDENTIAL,PARK,NEW FIELD [1]	□ □-OPEN PASTURE,ROWCROP [0]	□ □-HEAVY/SEVERE[1]
□□- VERY NARROW <5 m[1]	□ □-FENCED PASTURE [1]	□ □-MINING/CONSTRUCTION [0]	
□□- NONE [0]			

COMMENTS: _____

5.]POOL/GLIDE AND RIFFLE/RUN QUALITY   Pool/ Current [ ] Max 12

MAX. DEPTH (Check 1 ONLY!)	MORPHOLOGY (Check 1 or 2 & AVERAGE)	CURRENT VELOCITY [POOLS & RIFFLES!] (Check All That Apply)	
□- >1m [6]	□-POOL WIDTH > RIFFLE WIDTH [2]	□-EDDIES[1]	□-TORRENTIAL[-1]
□- 0.7-1m [4]	□-POOL WIDTH = RIFFLE WIDTH [1]	□-FAST[1]	□-INTERSTITIAL[-1]
□- 0.4-0.7m [2]	□-POOL WIDTH < RIFFLE W. [0]	□-MODERATE [1]	□-INTERMITTENT[-2]
□- 0.2- 0.4m [1]		□-SLOW [1]	□-VERY FAST[1]
□- < 0.2m [POOL=0]	COMMENTS:_____		

CHECK ONE OR CHECK 2 AND AVERAGE   Riffle/Run [ ] Max 8

RIFFLE DEPTH	RUN DEPTH	RIFFLE/RUN SUBSTRATE	RIFFLE/RUN EMBEDDEDNESS
□- Best Areas >10 cm [2]	□- MAX > 50 [2]	□-STABLE (e.g.,Cobble, Boulder) [2]	□- NONE [2]
□- Best Areas 5-10 cm[1]	□- MAX < 50[1]	□-MOD. STABLE (e.g.,Large Gravel) [1]	□- LOW [1]
□- Best Areas < 5 cm [RIFFLE=0]		□-UNSTABLE (Fine Gravel,Sand) [0]	□- MODERATE [0]
			□- EXTENSIVE [-1]

COMMENTS:_____ □- NO RIFFLE [Metric=0]

Gradient [ ] Max 10

6] GRADIENT (ft/mi): _____ DRAINAGE AREA (sq.mi.) : _____

%POOL: [ ]   %GLIDE: [ ]
%RIFFLE: [ ]   %RUN: [ ]

* Best areas must be large enough to support a population of riffle-obligate species

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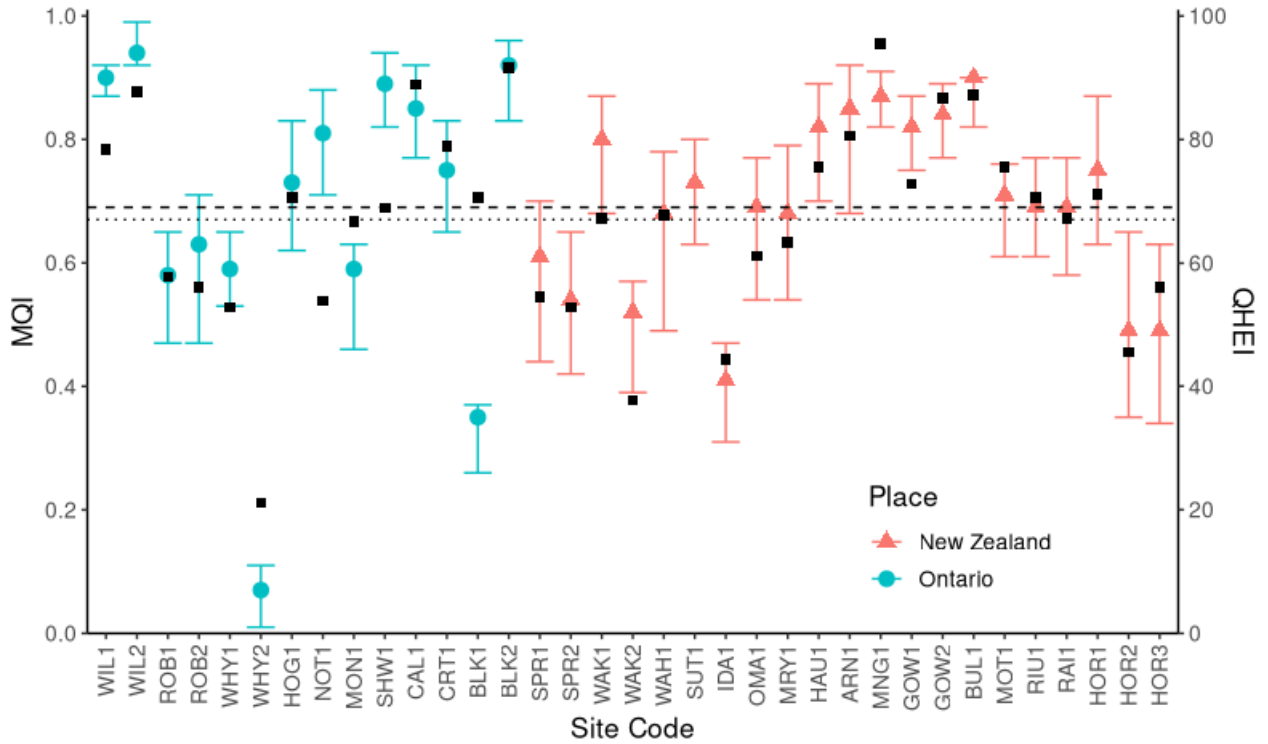
Fig. B2. Range of MQI values and uncertainty (min, max, and average). Average MQI scores are blue circles (ON) and red triangles (NZ). The black squares are QHEI scores. The grey dashed line and the dotted line are the average MQI and QHEI score for all sites, respectively.

B1. Photographs of some of the sites showing a good agreement between MQI and QHEI scores.

For a description of MQI and QHEI metrics and method of assessment see Rinaldi et al (2016), and Taft and Koncelik (2006) and Rankin (1989), respectively.

Colors relating to MQI scores in the maps below

MQI scores	
Very good	———
Good	———
Moderate	———
Poor and very poor	———
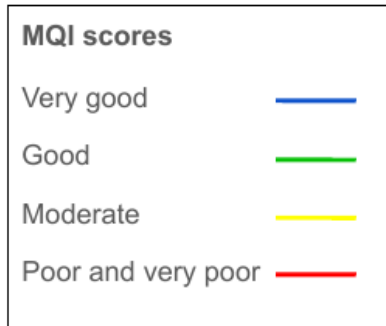
Wilmot Creek (Site WIL1, Fig. B3) in Ontario and Buller River (BUL1, Fig. B4) in New Zealand both scored very good and excellent on the MQI and QHEI, respectively, the highest value categories possible. The Buller River is a high elevation lake-fed river and the site (BUL1) is located directly below the lake outlet (Fig. B4A). Most of the catchment area is in native forest (45%) and scrub or alpine tussock (28%), with only 3% disturbed land. On the other hand, the catchment upstream of WIL1 is covered in 43% agriculture and 38% native forest, with 57% disturbed land. However, the land management practices have ensured that the riparian zone is largely protected from farming, with 58% of the 50 m buffer zone upstream in native forest, and 26% in agriculture. This appears to have proven important for maintaining a good hydrogeomorphological and habitat status.

Both of these reaches have very few artificial structures in the reach, high widths of riparian vegetation that extended more than 90% of the reaches, and hydrogeomorphological processes were largely undisturbed (Fig. B3A and B4A). There was a slight alteration of longitudinal continuity of sediment and wood upstream of WIL1 due to bridges and bed structures, but the reach had plentiful in-stream woody debris and a wide diversity of flow and sediment types (Fig. B3B, C and D). Substrate at BUL1 is dominated by boulders and cobble (scoring highly in the QHEI) (Fig. B4B). The reach has a wide diversity of flow types, and cover from boulders, undercut banks, and rootwads, although little in-stream woody debris. BUL1 had the highest trout biomass (16.14 g/m^2) of the NZ sites.
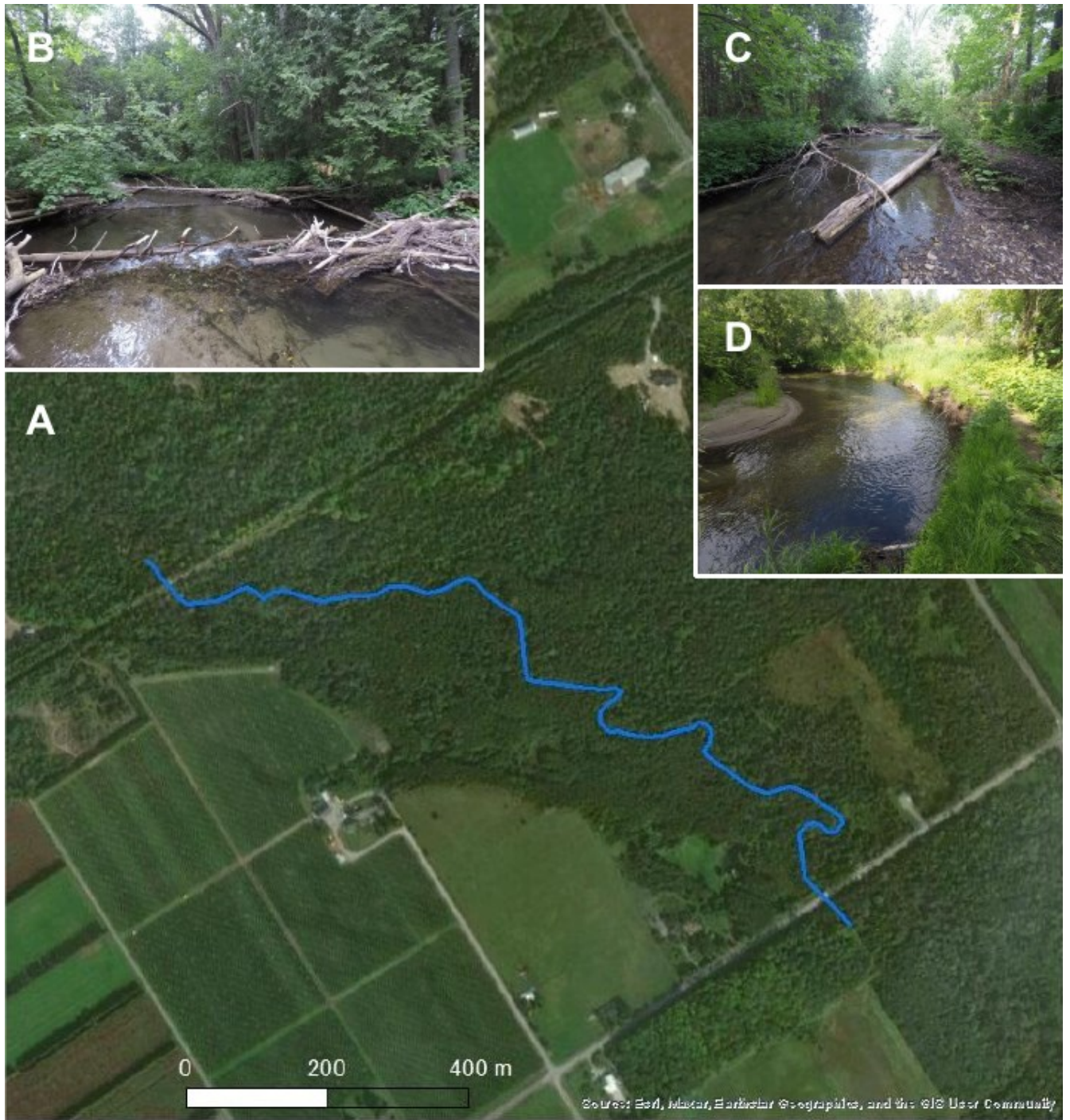
Fig. B3. A: Map of reach WIL1 (Wilmot Creek) – Very good MQI (0.9) and Excellent QHEI (78). B and C: Woody debris placed in the reach. D: Bend with undercut banks, riparian vegetation, and variability of substrate.

Fig. B4. A: Buller River (BUL1) reach – Very good MQI (0.9) and excellent QHEI (87). B: Typical characteristics of reach with boulders and riparian forest vegetation.

Spring Creek (SPR1, Fig. B5) had a moderate MQI and fair QHEI score. Spring Creek is a spring-fed lowland creek located entirely in agricultural land use. It was once a highly valued trout stream due to stable flows and temperatures, but in recent decades water quality and the ecological condition of the stream has declined, resulting in a perceived decline in the trout fishery (Young et al. 2000). While extensive river straightening has not occurred since at least the 1940s (first historical photos), levees in the lower catchment have narrowed the active floodplain, and roads have been built alongside the stream (Fig.

B5A and B). Side and secondary channels have been largely cut off from the main channel, and there is little evidence of fluvial landforms in the floodplain (Fig. B5A). Historically, the stream had a secondary channel where the holiday park now sits (White box in Fig. B5), and there was more riparian vegetation along the main stem and tributary channels in 1948 than currently (Fig. B5A and D). Riparian vegetation is present over much of the linear extension of the channel, but it is very narrow and often only on one side of the bank (Fig. B5A and B). There is very little in-stream woody debris. Vegetation removal and stable flows has led to sedimentation problems in the stream (Fig. B5C).
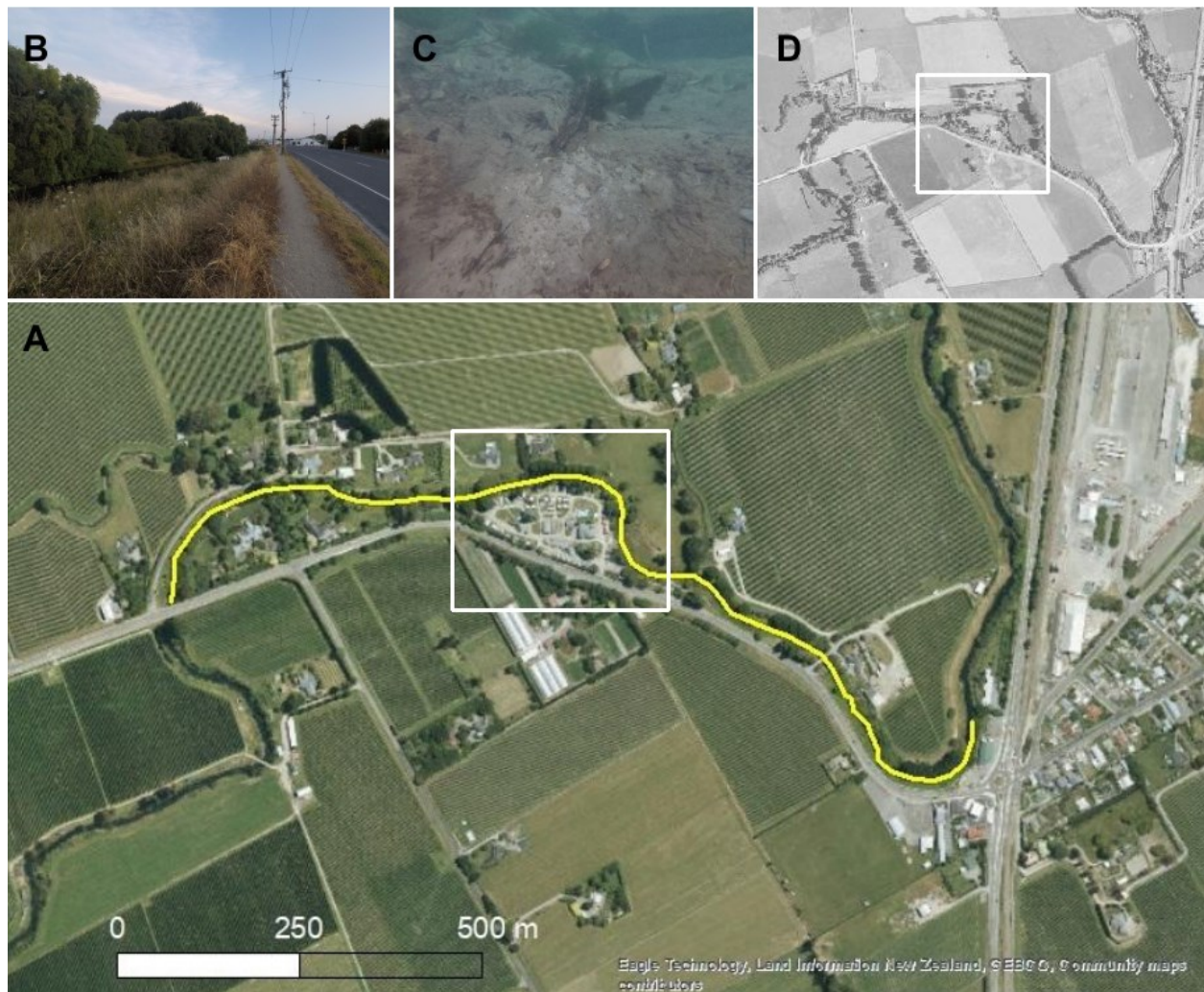
Fig. B5. A: Reach SPR1 in Spring Creek – Moderate MQI (0.61) and Fair QHEI (54). White box is location of the holiday park. B: The road and footpath follow the reach. Riparian vegetation on left side of the bank. C: Thick fine sediment covers most of the stream bed. D: Historical photo (1948) showing current site of the holiday park (white box), where two channels were present.

Two consecutively sampled sites on the western side of the Horokiri Stream (HOR1 and HOR2) had very different MQI and QHEI scores (Fig. B6). The sites are located in Battle Hill Farm Forest Park. The upper site (HOR1) is located in a native forest reserve (Fig. B7A), although 40% and 26% of the upstream catchment is in agricultural and forestry land, respectively. This reach had good MQI and QHEI scores. Reach substrate is dominated by cobble and gravel (Fig. B7D), although it did have moderate siltation and embeddness. There was a large range of in-stream cover types, with most types in the QHEI assessment present (woody debris, pools, undercut banks, overhanging vegetation, shallows, boulders, backwaters, and rootmats) (Fig. B7A-D). A road ran alongside the length of most of the reach, approximately 20-50 m away, and bank stabilisation consisted of a mix of wooden grids that allowed vegetation to grow through, and concrete slabs (Fig. B7E). There were few artificial structures in the reach, but upstream of the forest reserve, agricultural and rural housing meant that there was less room for the stream to move along its natural floodplain. Bridges and culverts upstream alter the movement of sediment and debris into the reach, but do not obstruct it altogether.

In the downstream reach (HOR2), there is little riparian vegetation and in-stream woody debris (Fig. B8A). Parts of the stream are deep, with ample undercut banks, root mats, and shade (Fig. B8E), but other parts lack in-stream cover (Fig. B8A, B, D). Concrete bank stabilisation was used to prevent bank erosion (Fig. B8D), and the multiple crossing structures allowed vehicle access across the stream (Fig. B8B). The reach was less mobile than HOR1. This reach is used as a recreational reserve (camp ground), so the stream is frequently disturbed. Boulders have been placed in the stream to create pools and flow diversity (Fig B8A), but the reach was largely used for human swimming. Despite the poor and fair MQI and QHEI scores, respectively, the IBI in a section close to the HOR2 was high (40) and there is an abundant population of longfin eels in the reach (Fig. B8C).

Fig. B6. Horokiri Stream sites. Green is HOR1 – good MQI (0.75) and Good QHEI (71). Red is HOR2 Poor MQI (0.49) and Fair QHEI (56).
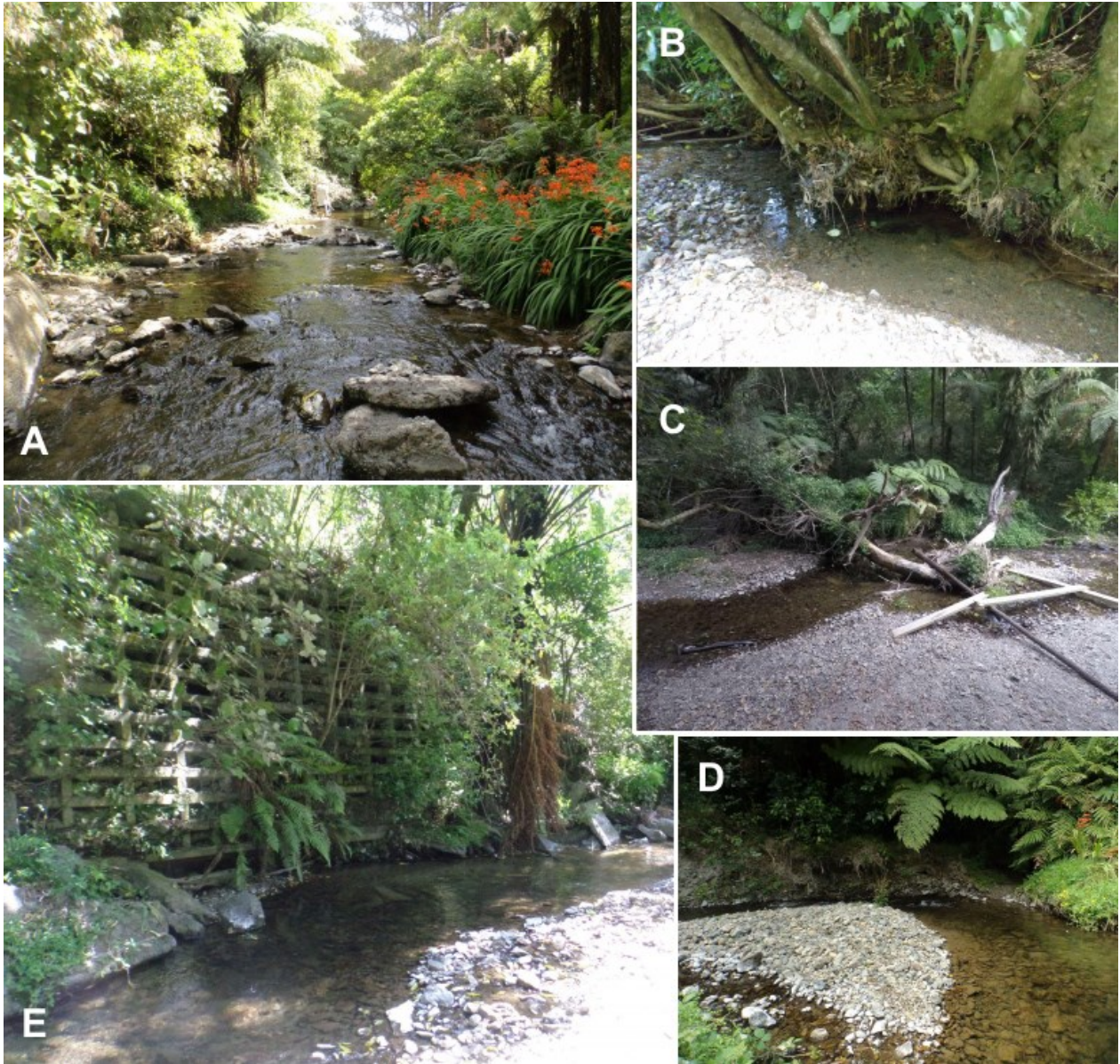
Fig. B7. HOR1 site. Photos show diversity of habitat in the stream, including riparian vegetation and small boulders (A), undercut banks (B), woody debris (C) and diversity of sediment types (D). E: wooden and concrete slab bank stabilisation.
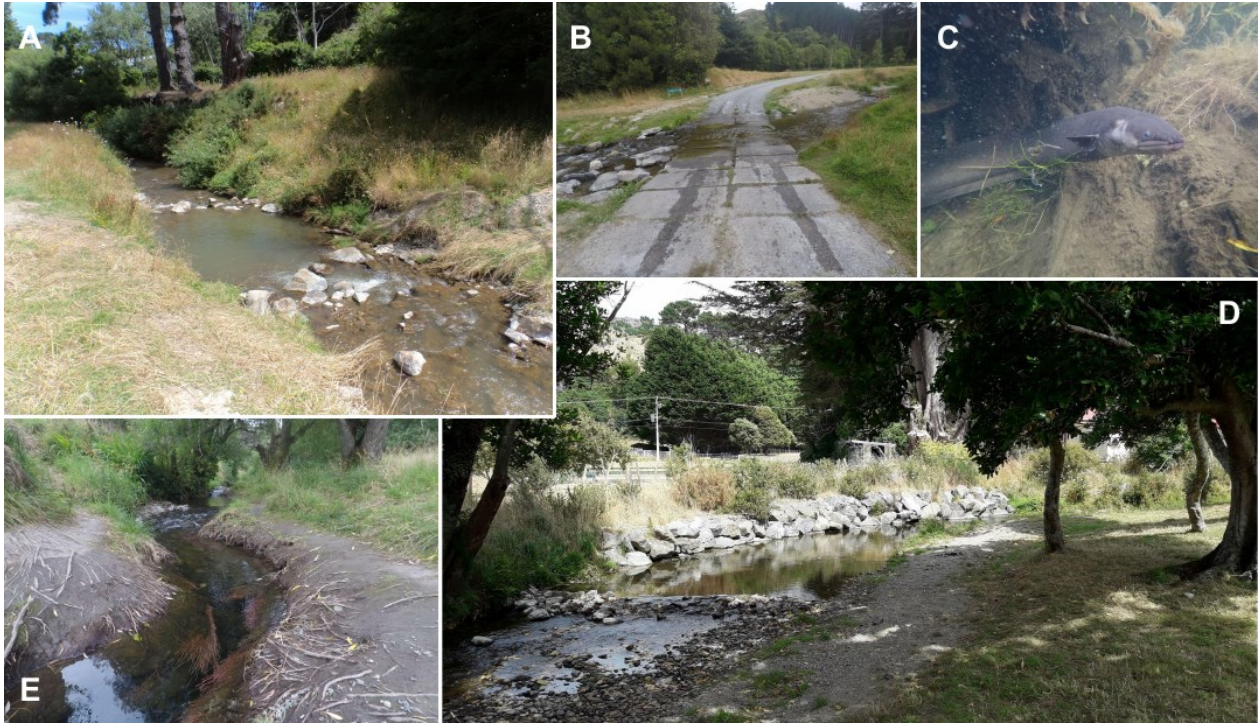
Fig. B8. HOR2 site. A: Boulders have been placed in the reach to create pools. B: Ford crossing over the stream. C: Eel in the reach. D: Concrete bank stabilization and minimal riparian vegetation characteristic of most of the reach. E: Deep section of the reach which had root mats and undercut banks.

Whiskey Creek is a small tributary of Lake Simcoe in Ontario. Two sites were assessed on the creek, one around 2 km from the lake outlet (WHY1), and the other directly upstream of WHY1 (WHY2) (Fig. B9). Around 70% of Whiskey Creek is in urban land use. WHY1 has a wide vegetated riparian buffer for the size of the stream (Fig. B9B). Woody debris structures had been placed in the stream to create cover and flow diversity (Fig. B9C). The substrate did consist of some cobbles and gravel (Fig. B9B), but was mainly fine silt and sand (Fig. B9C). The stream banks were mobile and the floodplain was free from artificial structures stuck in place. The stream could have acted as a refuge; the area was very urbanised (Fig. B9A), and the reach was one of the few in the catchment that contained forested riparian areas.

Upstream of the reserve, in WHY2, the stream had been straightened and modified to flow around a building (Fig. B9A, D). The reach contained very little water and substrate had been placed on the bed and banks of the channel (Fig. B9D), so movement in the stream was limited. Vegetation was growing in much of the reach due to the lack of water flow (Fig. B9D). Culverts in the upstream portion of the reach severed the reach from further upstream and part of the stream flowed underground due to the presence of roads.

The flow of sediment, debris and water was cut off. No fish were found in surveys in WHY2 carried out in 2007.

Fig. B9. A: Whiskey Creek (WHY1 and WHY2) – Yellow is Moderate MQI (0.59) and Fair QHEI (53); Red is Very Poor MQI (0.07) and Poor QHEI (21). B: Reach section showing cobble and gravel substrate and riparian vegetation. C: Woody debris placed in reach against the bank. Substrate mainly silt and sand. D: Substrate covering the bed of the reach and grass growing in the middle and side of the reach.

Ida Burn is a high elevation stream with 57% of the upstream catchment in agriculture and 38% in alpine shrubs and tussock. The main disturbance was the presence of an irrigation dam upstream of IDA1 (Fig. B10A), altering flows and sediment movement in the reach. Much of the reach was devoid of water because of the dam (Fig. B10B, C). Due to reduced flows, erosion and depositional processes had been largely cut off. Riparian vegetation was sparse in most of the reach (Fig. B10) with the lower reach only containing pastoral grasses (Fig. B10D and E). Some of the stream was fenced off but cows had access to the stream bed in the lower reach, where there were no trees (Fig. B10D and E). Here, bank erosion seemed to be mainly caused by cattle. In parts of the stream intermittent pools were present (Fig. B10C). Good habitat for fish, including rootwads, rootmats, and undercut banks, were present where there were trees, but due to the lack of water they were largely inaccessible to fish (at least at the time of the survey).
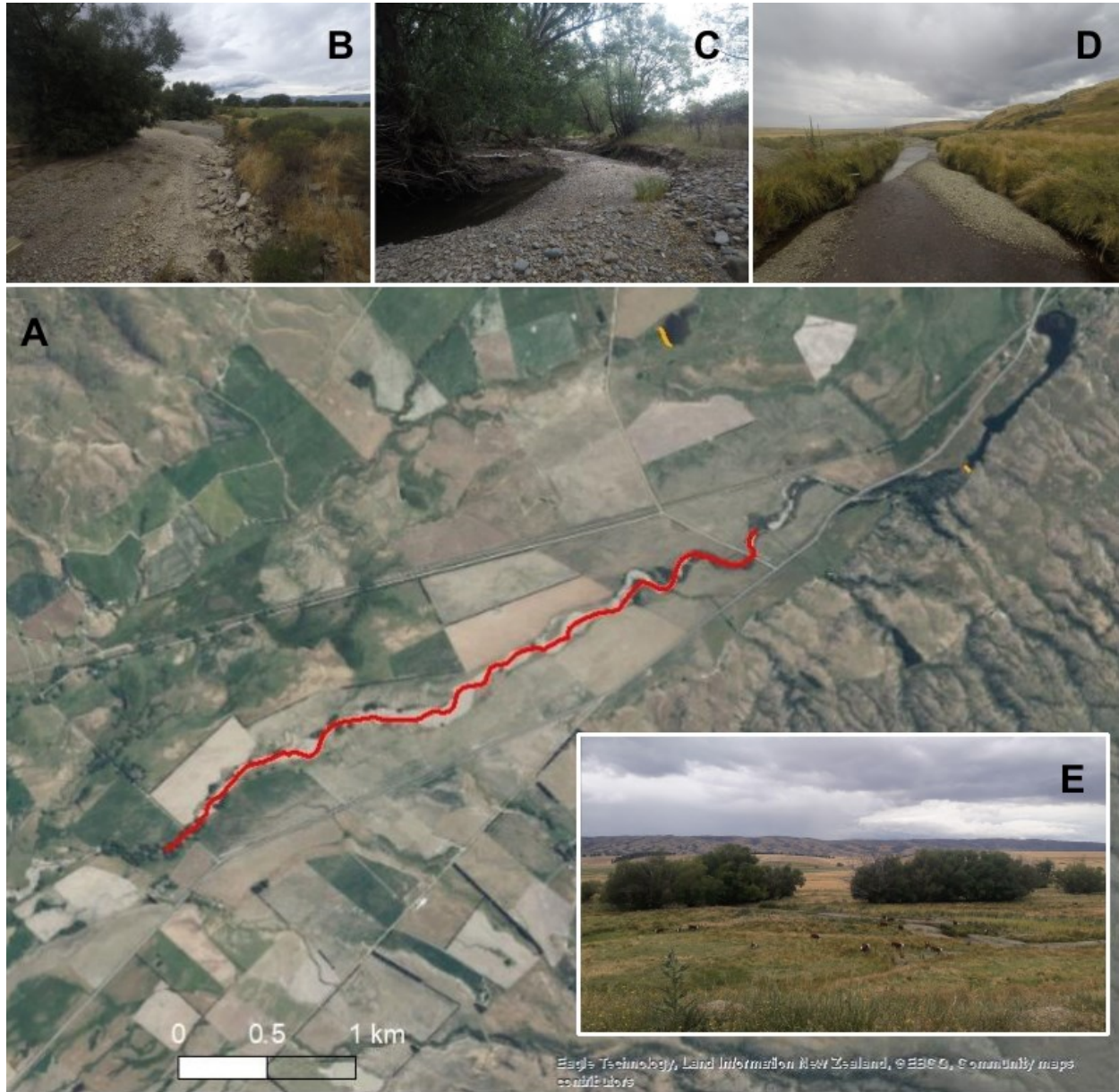
Fig. B10. A: Ida Burn IDA1 – Poor MQI (0.41) and Poor QHEI (44). B: Dry stream bed representative of around one third of the reach. C: Disconnected intermittent pools were present in part of the reach. D: More water was present in the lower part of the reach, but the riparian zone only contained pastoral grasses. E: Lower portion of reach showing cattle surrounding stream.

Appendix C

Supplementary Material: Salmonid biomass in streams around the world: A quantitative synthesis

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In preparation for submission to Fish and Fisheries

C1. Methods

C1.1. Initial search

Search terms were identified and tests were run on different combinations of search strings. Initially, density was included as an additional criterion for inclusion in the database. During the initial search, the following keywords were used in the Web of Science search for the date range 1979 to 1 July 2021: TOPIC: (salmonid OR salmon OR trout OR *salvelinus* OR *oncorhynchus*) AND TOPIC: (biomass OR abundance OR product* OR 'standing stock' OR densit*) AND TOPIC (river OR stream), where an asterisk (*) denotes a wildcard that can represent any collection of characters. This produced 7,564 results. The results were sorted by relevance and then the first 500 papers were screened (see Table C2). The acceptance rate for biomass studies was 9.2%. Due to the large scope of studies that report density, it was decided that density would only be included in the database if biomass was also reported. Hence, the initial search string was modified. A preliminary search conducted in 2019 on different pairings of abundance measures (Table C1) also emphasized the search should be focused on biomass with other search terms added.

Table C1. Results of search string in Web of Science in December 2019 for different abundance measures.

Search string	Paired with	Results
	AND densit*	7,260
Salmonid OR salmon OR trout	AND biomass	2,148
	AND production	10,402

Table C2. Our systematic review methodology, following some of the guidelines from the Collaboration for Environmental Evidence (2018)

Steps in systematic review	Our methods
1. Conducting a search	
Including peer-reviewed and grey literature	Our analysis included 208 (87%) journal articles and 32 (13%) grey literature items (reports, theses, book chapters, and conference proceedings).
Test comprehensiveness of search	All of the items that met the acceptance criteria (Table 4.2 in main text) in the initial search (most relevant 500 of 7,564 studies) were present in the final Web of Science (WOS) search. Out of the total 240 publications in the database, 145 were sourced in the WOS search. For items not included in the WOS search (95 total publications), 33 were published before 1979 (the start date of the WOS database), 2 were published in 1979 (may have missed being included in the WOS database), 24 were grey literature, 19 were focused on production or growth rather than biomass (but still reported biomass), 7 were restoration studies that may not have mentioned biomass in the abstract, 2 were not in English, and the remaining 8 were published in obscure small journals that may not be included in the WOS database.
All search terms provided	During the initial search, the following keywords were used in the Web of Science search for the date range 1979 to 1 July 2021: TOPIC: (salmonid OR salmon OR trout OR *salvelinus* OR *oncorhynchus*) AND TOPIC: (biomass OR abundance OR product* OR 'standing stock') AND TOPIC (river OR stream), where an asterisk (*) denotes a wildcard that can represent any collection of characters. Search terms were updated to: (salmonid OR salmon OR trout OR *salvelinus* OR *Oncorhynchus*) AND (biomass) AND (river OR stream).
Databases, search engines and search dates reported	The only database that a comprehensive search was conducted was the Web of Science. The initial search was conducted in July 2021 with the updated search terms used in December 2021 and repeated in August 2023.
Updates to searches	An updated search was conducted in August 2023 to capture recently published

articles.

Description of grey literature searches reported	References lists of review articles and accepted articles that mentioned biomass studies were searched. Salmonid researchers and experts were contacted to find published reports and hard to find literature. Of the 32 grey literature items included, 14 were reports, 12 proceedings (mostly from conferences), 2 book chapters, 1 book, 2 special publications, and 1 thesis.
Limitations	Search strings were only conducted in English, however, publications that were in other languages were scanned and included if they met the acceptance criteria data. The database only included studies that were reported, or could be converted to g/m^2. Many studies reported biomass in weight only or by linear stream length and did not include width measures to convert it to an area measurement. Many studies that focused on production also reported biomass but did not get picked up using the key words. Due to time constraints, a further search was not conducted. Publications were overwhelming focused in three countries (United States, Canada, and New Zealand). This could have been because the authors were situated in these areas or from these areas (KF is from New Zealand), so were familiar with the research.

2. Eligibility screening

Eligibility criteria defined	See Table 4.2 in Chapter 4
Stages of screening literature	Search results were screened in four stages: (*i*) title - the titles were first scanned for eligibility; (*ii*) abstract - abstracts or summaries of those that seemed relevant or were unclear were scanned for eligibility criteria; (iii) partial article – the text was scanned for inclusion criteria but if deemed very irrelevant the whole text was not scanned and (*iv*) full text - if deemed relevant or it was unclear, the full text was searched for inclusion criteria. References from included articles were screened in these stages.
Eligibility discussed among authors	Due to the large amount of search results in the initial search where density was

included, it was decided that only biomass would be included as a criterion. Density and production would only be recorded if the publication reported biomass.

Salmonid species were narrowed down to three main genera due to most of the literature focused on these genera.

Studies that were assessing the effects of fish stocking were not included, as the results could be short lived, but streams that had been stocked in the past were included, as it assumed that populations had reached a stable state, and it was not always reported if stocking had taken place or not.

Spawning anadromous fish were not included due to most of the growth being undertaken at sea.

Only published data was included to limit the scope of the study and exclude data that may not have been rigorously sampled.

Numbers of articles found in search and number excluded	Number of results from Web of Science search: Initial (7,564) – sorted by relevance and first 500 were scanned. Updated search terms December 2021 (957), then July 2023 (45). From the updated search (1002 publications), 747 were scanned at stage *iv*, 237 at *iii*, 10 at *ii*, and 8 at *i*. Due to the large amount of extra material searched (not in the WOS search) and overlapping of studies, the numbers searched and excluded were not counted.
Reasons for exclusion	The main reasons for publications that reported biomass being excluded were: biomass not reported in the right units (and no way to convert it), only lakes or coastal areas were surveyed, biomass was for spawning anadromous fish, or fish were stocked directly before sampling (so the effect of stocked was being tested).
List of studies included in the meta-analysis	See Table C3 and Appendix C3

3. Data coding and data extraction

Data extracted	See Table 4.3 of the main text for data that was extracted from each study (if reported). If latitude and longitude were not given by the study authors, they were estimated based on study descriptions. There may be some inaccuracy here as exact

	locations were not always given.
Scale reported	Data was extracted and reported at multiple scales. Biomass was recorded at the fish survey scale for all studies, even if the biomass reported was averaged over many sites (these were classed as the fish survey scale in our database). Data can then be average for reaches, river sections or whole rivers (see methodology section of main text for more details).

4. Critical appraisal of study validity

Identify sources of bias and correct or preform sensitivity analysis	Publication bias (rivers that have high known biomass and production are more likely to be studied and reported on). Language bias (only conducted the search in English will result in English speaking countries being overly represented). Availability bias (only easily available studies are included) – searched reference lists of included studies, and obtained grey literature from salmonid researchers. Duplication bias (studies may be published more than once) – studies were checked when included and duplicates were removed. Where studies had been updated, only the most recent data was included or data were included in separate time periods (so study years do not overlap).

5. Data synthesis

Results of systematic review	See results in Chapter 4
Information on eligible studies	A simplified table on articles included, species targeted, and number of rivers included is provided in Table C3. Full references are in Appendix C3.

Table C3. The species and number of rivers included from each publication in the systematic review

Author	Number of streams	Number of species
Alexander & MacCrimmon 1974	1	1
Allen 1951	1	1
Almodóvar & Nicola 1998	1	1
Almodovar & Nicola 1999	1	1
Almodóvar et al. 2006	10	1
Anton et al. 2011	4	1
Avery & Hunt 1981	4	1
Ayllon et al. 2016	1	1
Bagliniere 1981	1	1
Bagliniere & Arribe-Moutounet 1985	1	2
Baker et al. 1996	13	1
Baldigo et al. 2015	10	3
Baldigo et al. 2017	40	1
Baldigo et al. 2019	5	1
Baldigo et al. 2021	3	4
Baldigo & Lawrence 2001	3	2
Baldigo & Warren 2008	3	1
Baran et al. 1995	15	1
Baran et al. 1993a	4	1
Baran et al. 1993b	1	1
Bateman et al. 2016	2	2
Bateman et al. 2018	2	2
Bellmore et al. 2012	1	2
Benjamin & Baxter 2010	10	2
Bergheim & Hesthagen 1990	1	2
Bernthal et al. 2023	3	1
Biggs et al. 2000	3	1
Binns 1994	1	1
Binns 1986	2	1
Binns & Eiserman 1979	34	4
Binns & Remmick 1994	1	1
Bohlin et al. 2002	2	1
Boussu 1954	1	3
Bowlby & Roff 1986	6	2
Bremset & Berg 1997	2	2
Brynildson & Brynildson 1984	1	1
Burgess 1985	1	1
Burns 1971	7	3
Chadwick & Green 1985	1	1

Chalupa et al. 2013	1	3
Champkin et al. 2018	1	1
Chapman 1965	3	1
Chappaz et al. 1996	6	1
Clarke & Scruton 1999	3	1
Connolly & Hall 1999	16	1
Cooper 1952	1	3
Cooper & Scherer 1967	2	1
Cote 2007	18	2
Crisp & Beaumont 1995	1	1
Crisp & Beaumont 1996	1	1
Crisp & Cubby 1978	2	1
Crisp et al. 1975	4	1
Crisp et al. 1974	6	1
Culp et al. 1996	1	1
de Billy et al. 2002	1	1
Dębowski 1991	2	1
Dineen et al. 2007	8	1
Di Prinzio et al. 2009	12	3
Dolloff 1984	4	2
Dunham & Vinyard 1997	7	1
Eggleton & Morgan 2000	2	1
Egglishaw & Shackley 1977	1	2
Elliott 1988	2	1
Ellis & Gowing 1957	1	1
Elso & Giller 2001	1	1
Ensign et al. 1990	1	2
Evans et al. 2015	2	3
Everest et al. 1987	1	3
Farag et al. 2003	3	2
Fausch & Northcote 1992	1	2
Fleituch & Amirowicz 2005	1	1
Foldvik et al. 2017	9	2
Formigo & Penczak 1999	2	1
Frazey & Wilzbach 2007	22	3
Gee et al. 1978	6	1
Geist et al. 2006	12	1
George et al. 2015	6	2
Gibson b et al. 1993	3	2
Gibson & Colbo 2000	1	3
Gibson et al. 1987	6	2
Glova 1988	1	1
Glova & Sagar 1994	3	1

Gordon & MacCrimmon 1982	1	3
Grant et al. 1986	10	3
Grossman et al. 2017	1	1
Hanel & Lohnisky 1995	1	2
Hannesdottir et al. 2013	6	1
Harrison et al. 2014	64	2
Harvey et al. 2014	1	1
Hayes et al. 2010	1	1
Hepworth et al. 1997	16	1
Hepworth et al. 2001	5	3
Herdrich et al. 2018	7	1
Hicks 2003	1	1
Hocking et al. 2021	4	1
Höjesjö et al. 2014	1	1
Hopkins 1971	2	1
Horton 1961	1	1
House 1996	1	3
House et al. 1989	3	3
Hunt 1974	1	1
Hunt 1986	2	1
Hunt 1992	3	2
Inoue et al. 2013	1	1
James et al. 2010	2	1
Jellyman et al. 2000	1	1
Jellyman & Graynoth 1994	10	1
Jellyman & Harding 2016	12	1
Jenkins & Keeley 2010	1	1
Johnson 1980	1	3
Jones 1970	6	2
Jones & Stanfield 1993	1	4
Jonsson et al. 1998	1	1
Jonsson et al. 2011	12	2
Kaspersson & Höjesjö 2009	1	1
Kawai et al. 2014	1	4
Kaylor & Warren 2017	5	1
Kelly & Dick 2005	1	1
Kelly & Bracken 1998	1	2
Kelly-Quinn & Bracken 1988	1	1
Kelly-Quinn et al. 1996	14	1
Kennedy et al. 1983	1	2
Kennedy et al. 2012	1	2
Kennedy & Strange 1986	1	2
Kiffney et al. 2023	1	2

Kolden et al. 2016	1	2
Kolev 2010	4	1
Kratzer 2018	6	1
Kratzer & Warren 2013	33	1
Kubečka & Matena 1991	3	1
Kwak & Waters 1997	12	3
Lagarrigue et al. 2002	1	1
Lance & Baxter 2011	1	4
Lane 1964	1	1
Larsen & Hesthagen 1995	1	2
Larson & Moore 1985	4	2
Lavelle et al. 2021	1	1
Le Cren 1969	10	2
Leclerc & Power 1980	1	2
Lehane et al. 2004	18	1
Lehane et al. 2002	1	1
Leiner 1996	15	2
Li et al. 1994	5	1
Libosvársky & Lusk 1970	1	1
Lobón-Cerviá 2003	1	1
Lobón-Cerviá et al. 2011	4	1
Lobón-Cerviá et al. 1986	4	1
Lobón-Cerviá & Penczak 1984	1	1
Lohnisky 1993	1	1
Lojkasek et al. 2000	4	2
Lojkasek et al. 2004	3	2
Long & Medina 2006	1	3
Lowry 1966	3	1
MacMillan et al. 2008	69	1
Maia & Valente 1999	6	1
Malison et al. 2016	2	2
Mann 1971	4	2
Mann et al. 1989	2	1
Maridet & Souchon 1995	3	1
Martin et al. 2010	1	1
McClurg et al. 2007	20	3
McFadden 1961	1	2
McFadden & Cooper 1962	6	3
McIntosh et al. 2002	5	1
Milner et al. 1978	4	1
Moore & Gregory 1988	1	1
Morante et al. 2012	14	1
Moreau 1984	1	1

Morrison 1989	1	2
Mortensen 1977	1	1
Mortensen 1982	1	1
Munshaw et al. 2013	1	1
Muzik 1995	1	1
Myers et al. 2017	6	2
Myrvold & Kennedy 2017	4	1
Näslund 1989	1	1
Needham et al. 1945	1	1
Neophitou & O'Hara 1986	2	1
Neves et al. 1985	1	1
Neves & Pardue 1983	1	1
Newman & Waters 1989	1	1
Nystrom et al. 2006	11	1
O'Connor & Power 1976	4	1
Oscoz et al. 2005	1	2
Overton et al. 1981	1	1
Pearsons & Temple 2010	1	2
Penczak et al. 1985	1	1
Pierce et al. 2015	1	2
Pivnička et al. 1996	8	1
Platts & Nelson 1988	10	5
Polednik et al. 2004	3	1
Preston et al. 2021	3	1
Quinn & Kwak 2000	1	4
Randall et al. 2017	17	3
Randall et al. 1989	1	3
Randall & Paim 1982	2	1
Richer et al. 2022	1	1
Riley & Fausch 1995	6	3
Rosenfeld et al. 2008	1	1
Sahashi et al. 2015	12	1
Sanchez-Hernandez et al. 2015	8	1
Scarnecchia & Bergersen 1987	10	4
Schuck 1945	1	1
Scruton 1996	1	2
Scruton et al. 2005	1	2
Scruton et al. 1998	1	2
Shetter & Hazzard 1939	3	3
Shetter & Leonard 1943	1	1
Simon et al. 2004	1	1
Simonović et al. 2020	14	1
Simonović et al. 2021	6	1

Simonović & Nikolić 2007	9	1
Sittenthaler et al. 2015	1	1
Smith & Atkinson 1999	2	1
Smith et al. 1949	24	3
Soto et al. 2006	10	4
Stefanich 1952	1	2
Stichert et al. 2001	16	3
Strange et al. 2000	1	1
Sweka et al. 2012	7	1
Teirney & Jowett 1990	93	2
Thomas et al. 2015	18	2
Thorn & Anderson 2001	1	1
Urabe & Nakano 1998	2	1
Ureche et al. 2012	3	1
VanDusen et al. 2005	9	1
Vila et al. 1999	4	2
Vlach et al. 2005	1	1
Ward & Slaney 1981	1	2
Waters 1999	1	3
Waters et al. 1990	2	3
White & Harvey 2017	6	3
Whitworth & Strange 1983	1	2
Williams et al. 2009	12	1
Wills 2006	6	1
Witkowski et al. 2008	1	1
Zika & Peter 2002	1	2
Zimmerli et al. 2007	4	1
Zoellick 2004	2	1
Zorn & Nuhfer 2007	3	1

C2. Database overview

Tables are related to each other with common ID numbers. Two types of relationships between tables existed in our database: One-to-many and Many-to-many. The most common was the one-to-many relationship, where one record in a table is related to one or more records in another table. For example, one location id can have many rivers, but one river can only have one location id. The many-to-many relationship exists where multiple records in one table are related to multiple records in another table. For example, a fish survey site may have many species, and fishing methods recorded, and likewise, species and fishing methods can be recorded over many fish surveys. Usually these require a third table to record them, in this case the abundance table.

C3. Database references

Alexander, D. R., & MacCrimmon, H. R. (1974). Production and Movement of Juvenile Rainbow Trout (Salmo gairdneri) in a Headwater of Bothwell's Creek, Georgian Bay, Canada. *Journal of the Fisheries Research Board of Canada*, *31*(1), 117–121. https://doi.org/10.1139/f74-021

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C4. Results

Table C4. Wilcox test p values for significant differences between species with one species estimated. Rows show species with a higher biomass and columns are species with a lower biomass (where p values are present). Empty boxes are non-significant.

Species with higher biomass	Species with significantly lower biomass – Wilcox test p value[a]				
	Atlantic	Brook	Chinook	Cutthroat	Rainbow & Steelhead
Atlantic	-		< 0.001		< 0.001
Brook	< 0.001	-	< 0.001		< 0.001
Brown	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Coho			< 0.001		
Cutthroat			< 0.001	-	<0.001
Dolly Varden			< 0.001		
Masu			< 0.001		
Rainbow & steelhead			< 0.001		-

[a]Only *p* values for significant tests are shown

Table C5. Mean biomass, production and P/B ratios at the fish survey scale for species that reported both production and biomass.

Species	N^a	Mean biomass $(g/m^2)^b$	Mean production $(g/m^2/yr)$	Mean P/B
Atlantic salmon	48	2.45	3.47	1.36
Brook trout	56	3.72	3.77	1.10
Brown trout	187	8.16	8.94	1.20
Chinook salmon	4	0.12	0.23	1.92
Coho salmon	12	2.41	3.09	1.18
Cutthroat trout	14	3.23	1.97	0.98
Dolly Varden trout	8	2.21	0.50	0.24
Rainbow trout	13	2.71	1.71	0.74
Steelhead trout	6	2.02	4.70	2.75

[a]N is the number of fish survey sites that have both a biomass and production estimate to calculate a P/B ratio. [b]Mean biomass is calculated only for studies that reported production as well, not all studies in the database.

Table C6. Wilcox test P values for significant differences between countries with data for 10 or more rivers. Rows show countries with a higher biomass and columns are countries with a lower biomass (where p values are present). Empty boxes are non-significant.

Countries with significantly higher biomass	Countries with significantly lower biomass – p values				
	New Zealand	Canada	USA	Ireland	Japan
Argentina					
Canada	< 0.001				
Chile	0.008				
Czech Republic	< 0.001				
France	< 0.001	< 0.001	0.002	0.03	0.03
Ireland	< 0.001				
Japan					
Norway	< 0.001				
Serbia	< 0.001				
Spain	< 0.001	0.03			
Sweden					
UK	< 0.001				
USA	< 0.001				

Table C7. Description of variables included in the stepwise AIC

| Variable	Description	Groups included or unit of variable
Species	Species sampled	Individual species, two species, three species
Country	Country	One of 27 countries
Latitude	Latitude of site	Decimal degrees
Year	Last year of fish sampling	Year (date)
Season	Season fished	Spring, summer, autumn, winter, combined (2 seasons), annual (3 or more seasons)
Stream width	Mean stream wetted width	m
Elevation	Elevation of site	m
Number of species	Number of species included in biomass estimate	1-4
Status	Whether population is exotic or native	Exotic, native, both
Sampling method	Fish sampling method	Electrofishing, snorkeling, netting and trapping, another method
Migratory	Migratory status	Resident, anadromous, resident and/or anadromous
Number of years	The number of years that were fished	Years (number)
River	River id – to differentiate different rivers	Individual rivers
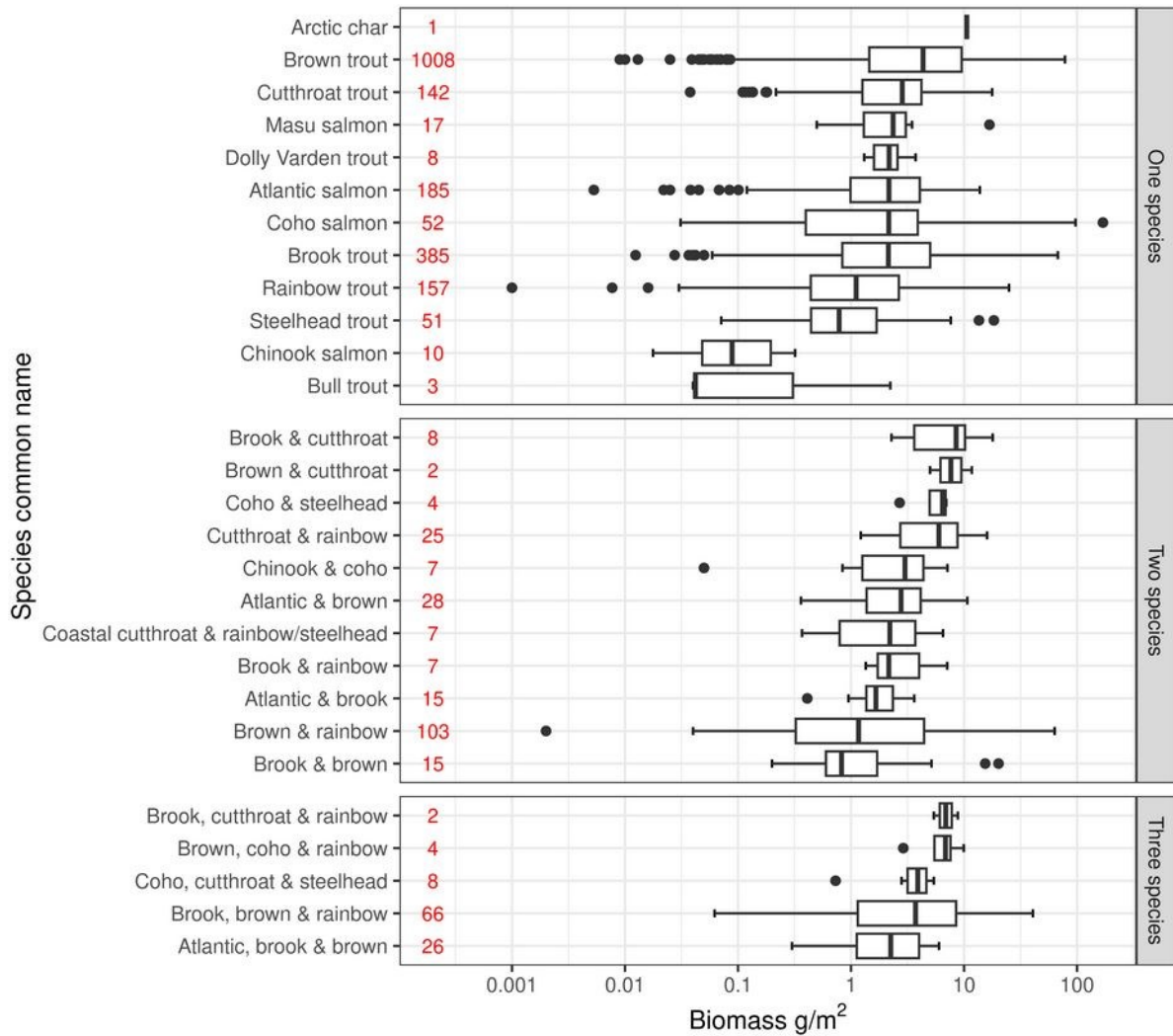
Fig. C1. Boxplots of biomass (log scale) by species with one, two, or three species included in the estimate. Estimates with two or three species are where species were reported together in one estimate, so could not be separated by species. Estimates are not summed at the fish survey scale, so one fish survey site could have several species counted separately.
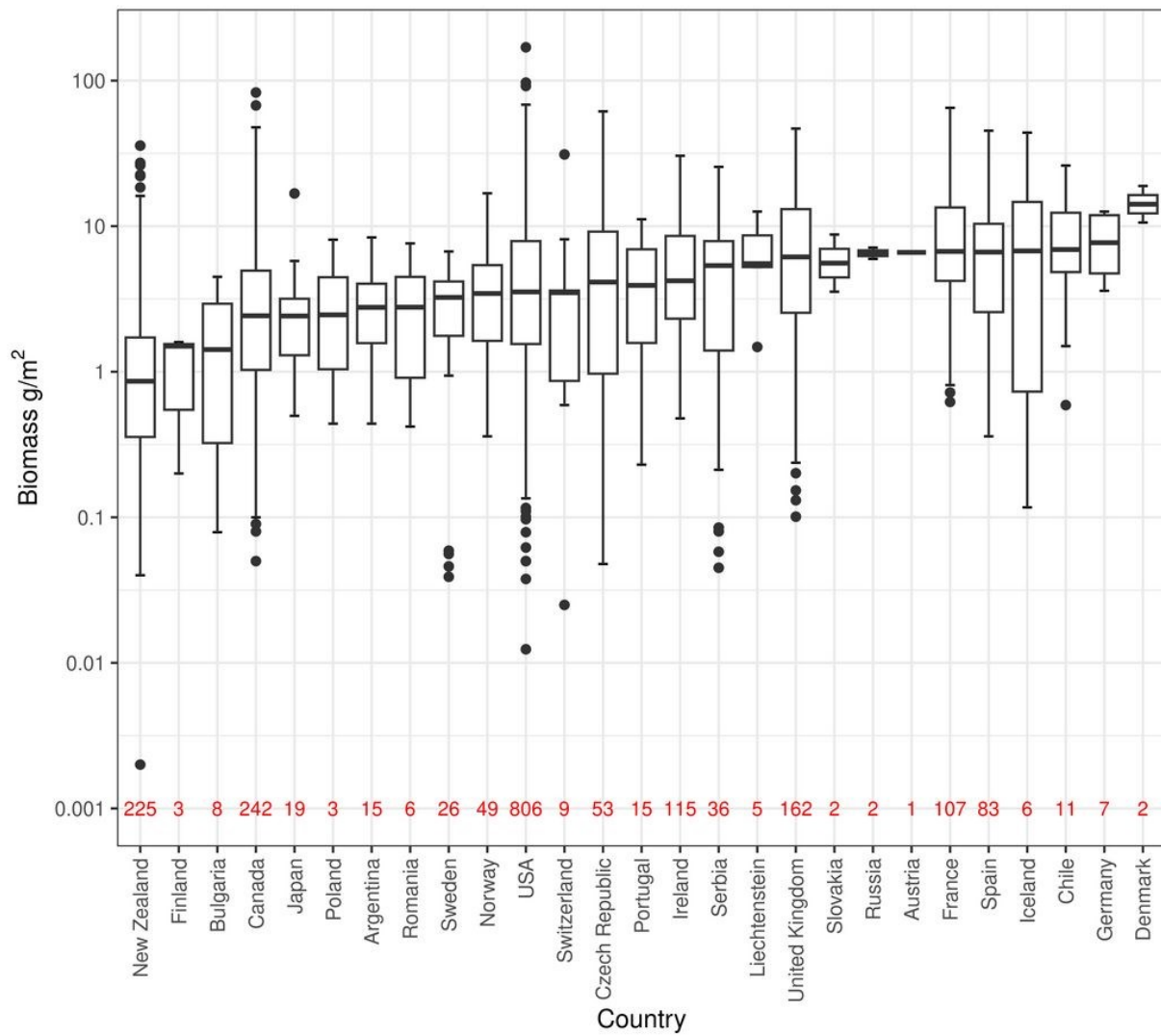
Fig. C2. Range of biomass (g/m^2) in each country calculated at fish survey scale (biomass is plotted on a log scale). Red numbers are the number of fish survey sections in each country.
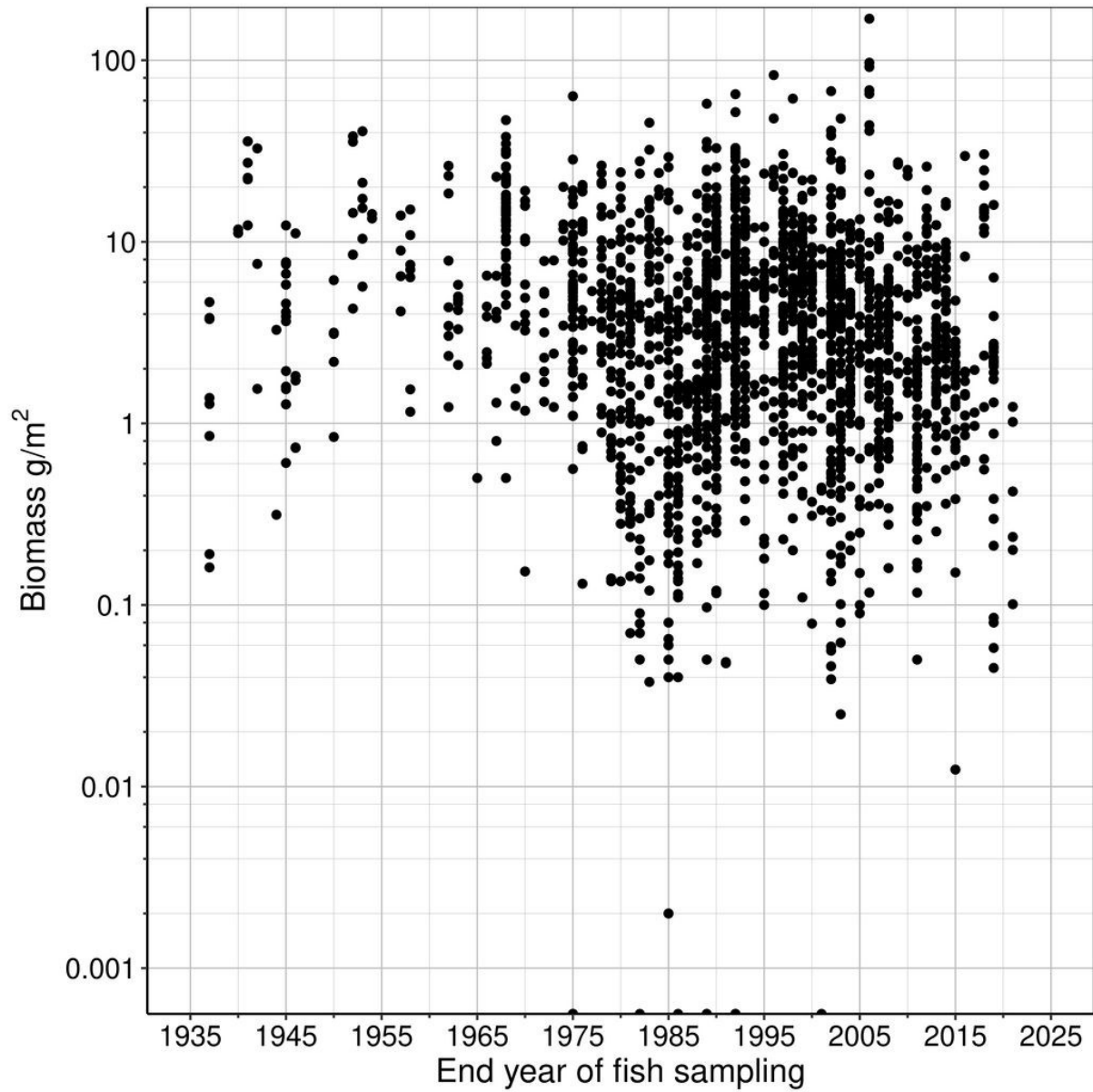
Fig. C3. Biomass of salmonids over time by last year of fish sampling. Biomass is presented on a log scale.

Appendix D

The best salmonid streams in the world?

A preliminary peek into streams with the highest recorded salmonid biomass

Forty-four sites that had an estimated biomass of 30 g/m^2 or over (named the 'top sites' hereafter) from the salmonid database discussed in Chapter 4 were investigated in more detail. This section explains further methodology for analyses of these sites. One site with a biomass of 169 g/m^2 is included in analyses but not shown in graphs. All other sites were under 100 g/m^2.

D1. Methodology

For full methods on the systematic review, database creation, and data extraction see Chapter 4. Most studies did not report precise locations of survey sites; therefore, site locations were estimated based on descriptions given in each study. Elevation and upstream catchment area were either estimated from approximate locations (using Google Earth and ArcGIS respectively) or reported from each study. Width and area fished was taken directly from each study (except for four sites where data was not given).

The biomass at each site was averaged for the total years sampled. If more than one year was sampled, the last year that fish were surveyed was attributed the 'end year of fish survey'. To test whether biomass changed over time, we tested a linear regression between average biomass and the end year of fish survey. Dominant catchment land use for each site was either obtained from site details in the literature, or estimated from satellite imagery or historical imagery taken as close as possible to sampling years.

D2. Results

Half of the sites were in North America (22), 46% in Europe (20), and two sites (5%) in New Zealand (Fig. D1). On average, sites were small, high elevation streams, but there was a large variability in most of the site characteristics (Table D1, Fig. D2). Only three sites were wider than 10 meters. Biomass was slightly higher streams with smaller upstream

catchment areas (Fig. D2c). In contrast to the whole dataset of over 1000 rivers (Chapter 4), biomass estimates of the top sites increased slightly over time (Fig. D3). The most dominant land-use in the catchments was agriculture (41% of catchments), followed by forest (25%) (Fig. D4). There were no differences in biomass for different land uses.

Table D1. Characteristics of the top sites.

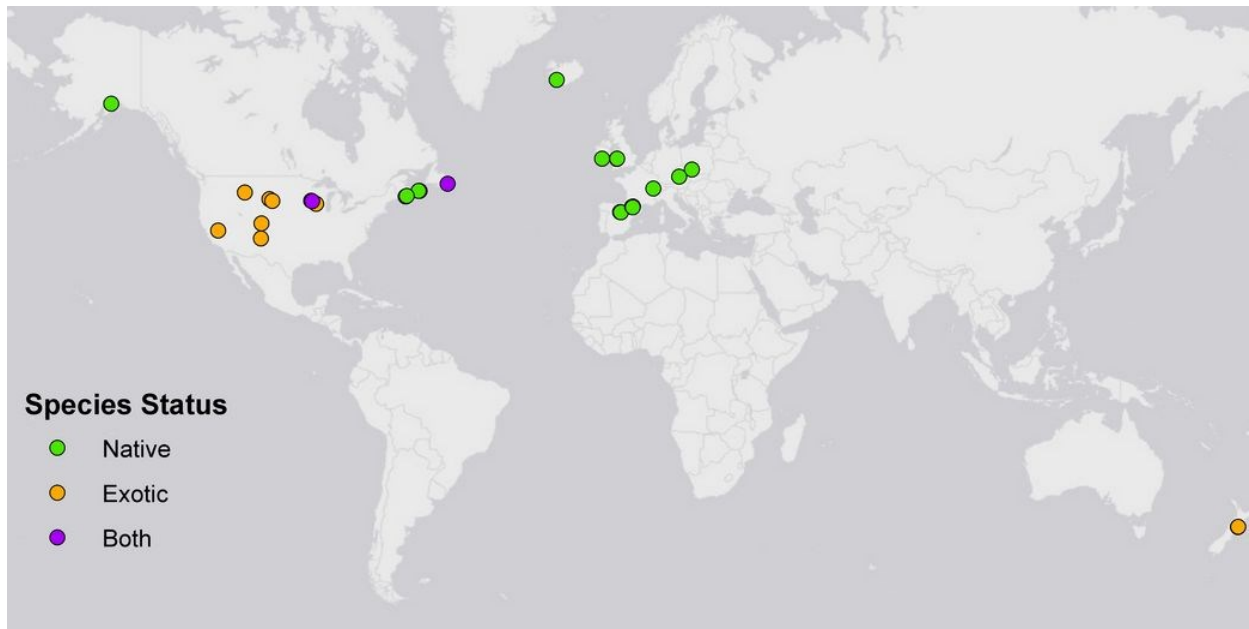| Variable	Mean	Median	Standard Deviation (SD)
Wetted stream width (m)	5.2	4.1	4.8
Total area fished (m^2)	705	303	940
Elevation (m)	581	223	698
Upstream drainage area (km^2)	145	27	224

Fig. D1. Location of all the top sites with species status (native, exotic or both).
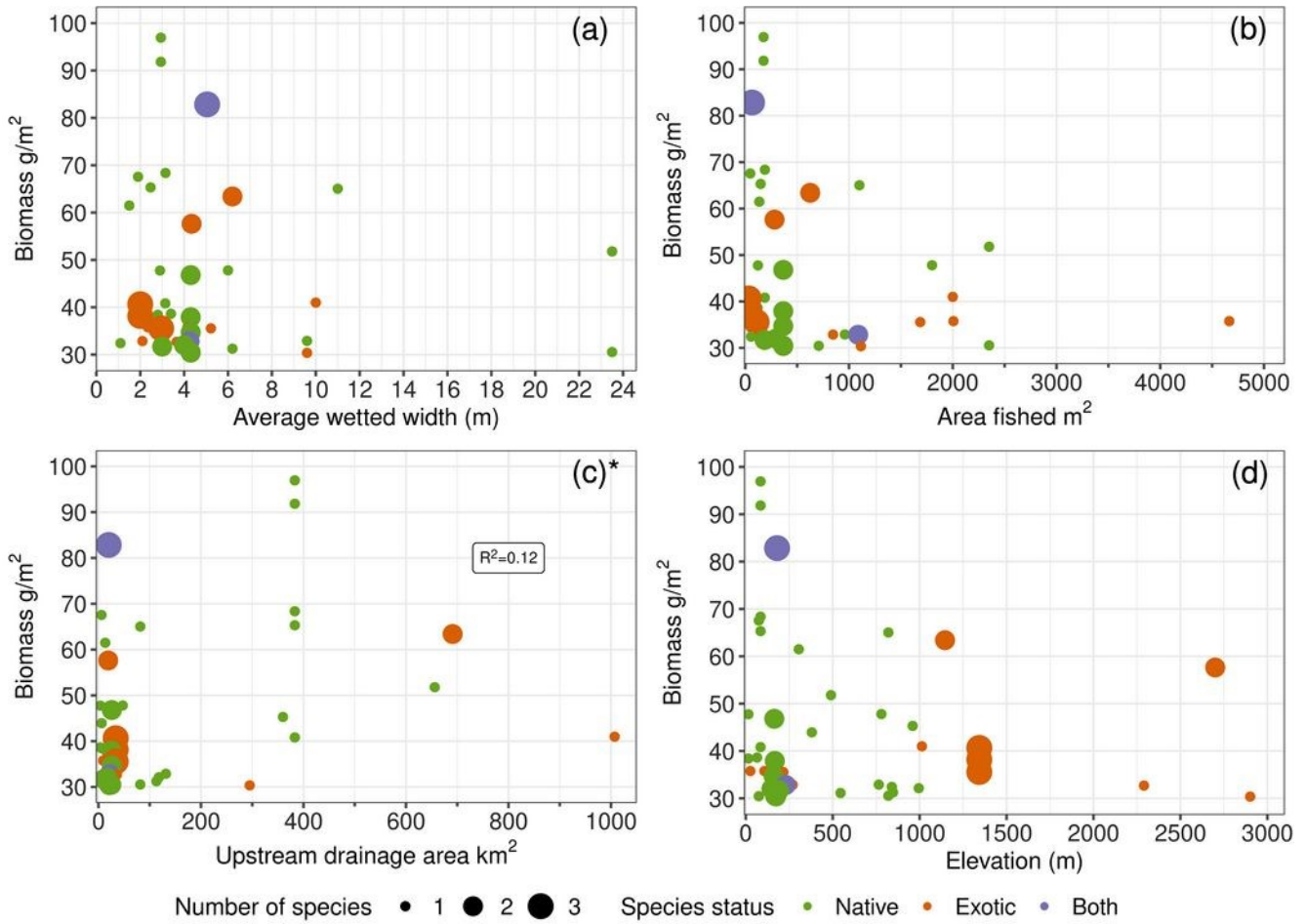
Fig. D2. Biomass of sites showing species status and the number of salmonid species recorded at the site for average wetted stream width (a), area fished (b), the drainage area upstream of the site (c), and approximate elevation at the site (d). Significant results denoted by an asterisk (*) and R^2 value.
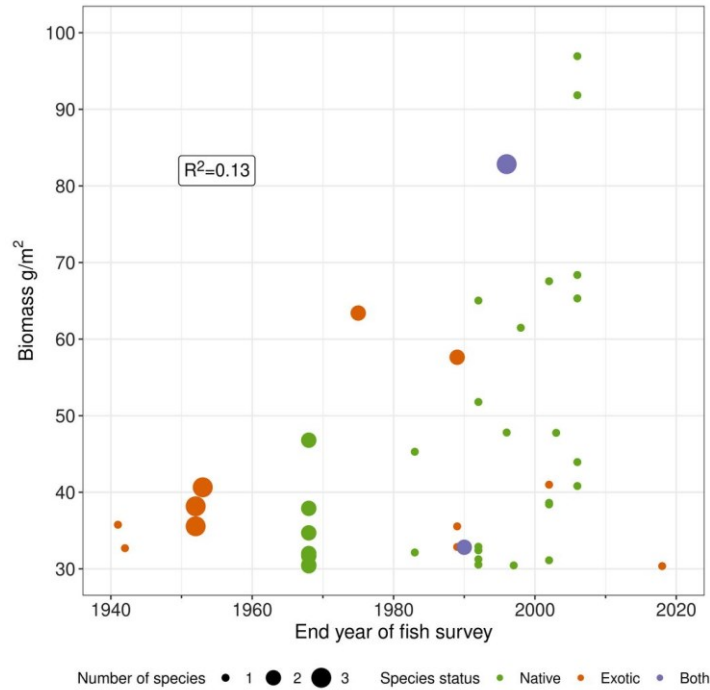
Fig. D3. Biomass of top sites over time by the last year that sites were surveyed, showing species status and the number of salmonid species recorded at the site.
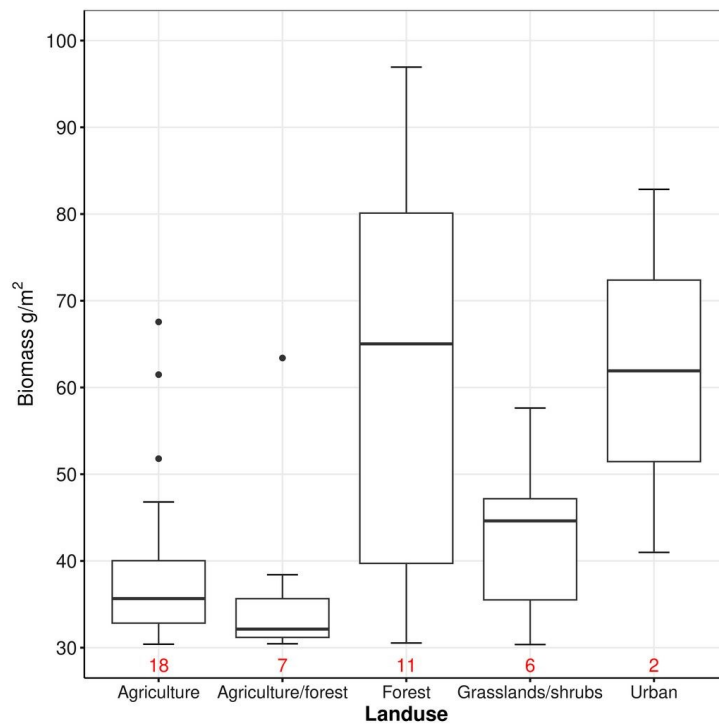

Fig. D4. Biomass of top sites by dominant land-use in the upstream catchment.