

# Stream inflows to lake deltas: A tributary junction that provides a unique habitat in lakes

John S. Richardson<sup>1</sup>  | Tracy Michalski<sup>2</sup> | Mariella Becu<sup>1</sup>

<sup>1</sup>Department of Forest and Conservation Sciences, The University of British Columbia, Vancouver, BC, Canada

<sup>2</sup>British Columbia Ministry of Forest, Land, Natural Resource Operations, and Rural Development, Nanaimo, BC, Canada

## Correspondence

John S. Richardson, Department of Forest and Conservation Sciences, The University of British Columbia, Vancouver, BC V6T 1Z4, Canada.

Email: john.richardson@ubc.ca

## Funding information

Natural Sciences and Engineering Research Council of Canada; BC Ministry of Forests, Lands, Natural Resource Operations and Rural Development; University of British Columbia

## Abstract

1. Tributary junctions in stream networks provide unique habitats within fluvial networks by contributing differently sized sediment and organic materials, providing temperature refuge, and other conditions distinct from the receiving stream. These same attributes at tributaries entering lakes (inflow streams) support special, within-lake locations that are used by several organisms at some times of year, which we call lake deltas.
2. Here we consider the evidence of these lake deltas as a special environment in terms of their physical, chemical, and biological characteristics. There are several potential contributions from tributary streams, and much of the emphasis has been on resource subsidies to lakes, but other factors may also contribute to the uniqueness of lake deltas.
3. The degree to which these deltas provide productivity and biodiversity hotspots is not well known, but we present evidence in support of this assertion. We also offer suggestions for a suite of hypotheses that can be tested. These junctions may also provide an excellent model system for testing the consequences of resource subsidies (organic matter, invertebrates) to recipient communities from small to mid-sized streams.
4. Consolidation of these ideas will allow testing for the uniqueness of these lake delta habitats and the mechanisms responsible, and perhaps promote greater efforts at protecting processes that sustain these areas in lakes.

## KEYWORDS

benthos, hot spots, meta-ecosystems, productivity, resource subsidies

## 1 | INTRODUCTION

Tributaries to rivers, lakes, and wetlands deliver materials to recipient ecosystems and there they create a special microenvironment. Tributary junctions of streams have been studied over the past 2 decades, and have established a paradigm that these are unique microhabitats within fluvial networks (Kiffney et al., 2006; Rice et al., 2001). These habitats often have different thermal regimes from most of the recipient waters (Tavernini & Richardson, 2020), and the tributaries can provide resources in the form of large

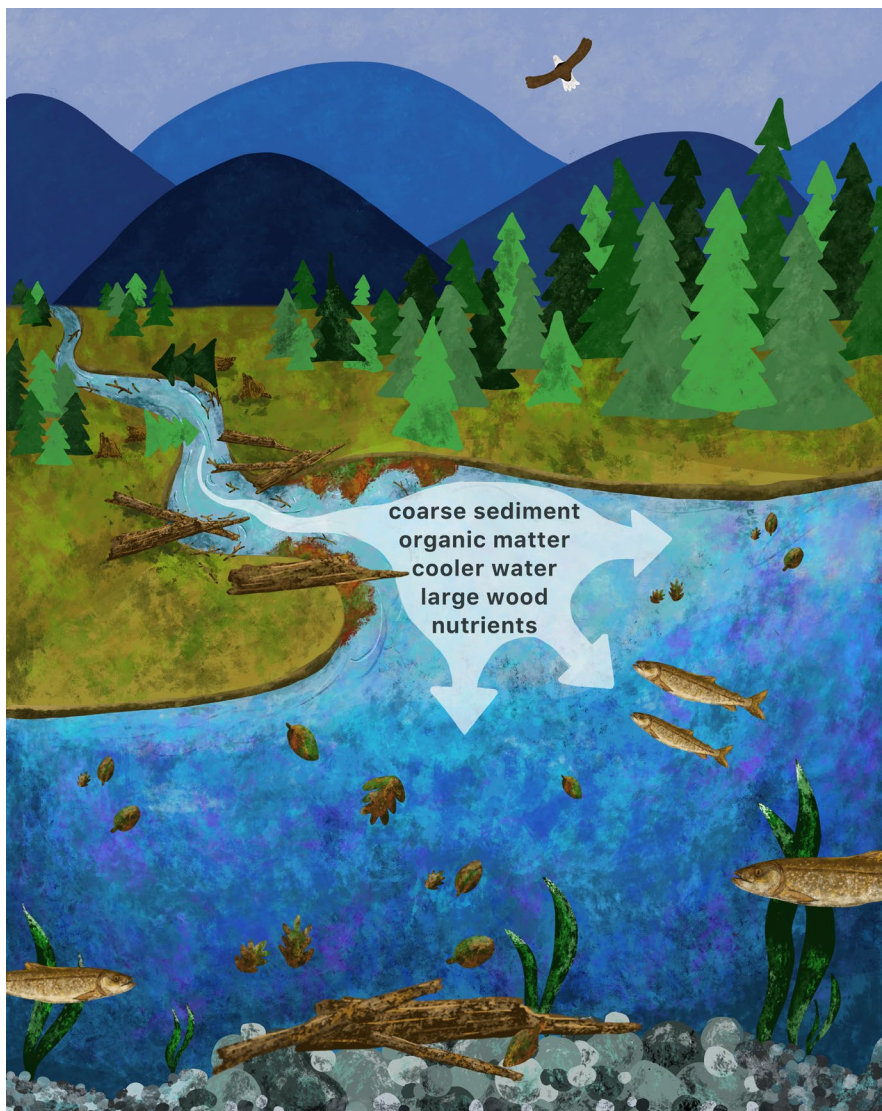
amounts of organic matter (OM) and drifting invertebrates (Wipfli & Gregovich, 2002). Moreover, these junctions can introduce sediment (including large wood) that provide greater habitat heterogeneity than elsewhere (Rice et al., 2001), and may contribute to fluvial channel development (Corenblit et al., 2007).

Beyond being a type of stream junctions, tributaries flowing into lakes (possibly also wetlands and reservoirs) may provide unique features not found elsewhere in these lentic water bodies. Following other authors, we will use the term *lake deltas*. Other related terms used in the literature include stream inflow, lake inlet,

rivermouth, and tributary, but these refer more specifically to the input source or upstream of the depositional area, whereas a lake delta is the result of a variety of inputs. Tributaries obviously bring water that contributes to the water balance in lakes, and can deliver sediment particles of various sizes (e.g. fines that contribute to turbidity). However, there are additional ecosystem processes to consider beyond the volume and timing of water, sediment, or contaminant flows into lakes, as noted by Baker et al. (2016). As with tributary junctions in streams, there is a large contribution of allochthonous resources that can come from inflow streams, particularly invertebrates and OM (Richardson & Sato, 2015; Szokan-Emilson et al., 2011; Tanentzap et al., 2017; Wipfli & Gregovich, 2002). The importance of nutrient and particle inputs to the productivity of estuaries (Sakamaki et al., 2010) and shorelines of large lakes, such as the Laurentian Great Lakes, has been recognised for decades (e.g. review in Larson et al., 2016). However, here we extend the consideration of a broader spectrum of contributions from inflow streams to lakes of all sizes, at the resulting lake deltas (Szkokan-Emilson et al., 2011). Just as lake-outflow streams provide for a unique

freshwater environment (Richardson & Mackay, 1991), so too have lake deltas been noted as unique aquatic habitats (Jones, 2010; Szokan-Emilson et al., 2011; Willis & Magnuson, 2000). In this paper we will argue that these lake deltas formed from tributary inflows are productivity and biodiversity hotspots due to an array of putative mechanisms, and not solely for inputs of biological energy. This further integrates lakes into this concept of the importance of tributary junctions in fluvial networks (Benda et al., 2004; Kiffney et al., 2006; Rice et al., 2008).

Combined lake and stream systems have properties that emerge at the landscape scale, and modulate aspects of flows, temperatures, chemistry, and other attributes (Baker et al., 2016; Jones, 2010; Kling et al., 2000). For instance, when lakes are present in a fluvial network, densities of brook trout (*Salvelinus fontinalis*) tend to be higher than when there are no lakes (Pépin et al., 2017), so the combination of both habitats confers some advantage that needs to be parsed out into its respective contributions, as we will describe. Lakes are one of the features, along with reservoirs, that result in serial discontinuity in fluvial networks (Jones, 2010; Ward & Stanford, 1995).



**FIGURE 1** Schematic of a lake delta showing inputs from a contributing inflow stream. Drawing by Danielle H. Derrick (Simon Fraser University)

This serial discontinuity arises because lakes can trap materials from upstream and the water that leaves the lake is modified from that which arrives. This trapping of organic and inorganic materials at inflow points is what also makes these zones special, which we will elaborate upon below. We have not included reservoirs in our discussion as some are operated in ways that are quite distinct from lakes. Other linkages to terrestrial ecosystems occur that are integral to lakes around their perimeters (Nowlin et al., 2008), but here we are only concerned with the contributions of streams to receiving areas in lakes.

We know that lakes, particularly small lakes (which we arbitrarily define as lakes  $\leq 1 \text{ km}^2$ ), can receive a large amount of the fixed carbon that contributes to ecosystem productivity from terrestrial sources. There are estimates that in some small lakes 20%–85% of in-lake production may be terrestrially sourced (Carpenter et al., 2005; Karlsson et al., 2012; Pace et al., 2007). It is also clear that dissolved nutrients from their catchments affect the nutrient status of lakes. Moreover, fine sediments, such as glacial flour, contribute to the turbidity of lakes (Laird et al., 2021). There are several reviews of the roles of lakes within fluvial networks for providing habitats (Arostegui & Quinn, 2019; Lennox et al., 2021), modifying nutrient and flow regimes (Baker et al., 2016; Jones, 2010; Leach & Laudon, 2019), and altering thermal patterns. However, here we are focused on local characteristics of lake deltas, created by inputs from tributary streams along the edges of lakes, that we argue form a special habitat type within lakes.

We have several objectives in this paper. First, we summarise the potential for stream inflow contributions to productivity and biodiversity (especially fish production) in lake deltas, and provide a synthesis of the several non-exclusive hypotheses for uniqueness of these lake deltas (see Figure 1). Second, we provide suggestions on how to scale these contributions relative to tributary size and recipient lake attributes. Third, we address the effects of land use on streams with possible consequent impacts on lake deltas. Finally, we gather observations about the particular use of these patches by some organisms. In our review we will restrict our consideration

to relatively small lakes, although large lakes can also benefit from such inputs of materials and show the effects of catchment land use (Marcarelli et al., 2019).

## 2 | CONTRIBUTIONS OF TRIBUTARY STREAMS TO LAKES

Tributary inflows to lakes can contribute to productive habitats for aquatic biota, and they serve as an interface between terrestrial and aquatic systems via transport of terrestrial inputs and stream inputs from lake inflow streams to lake deltas (France et al., 1996; Vanni et al., 2006). Lake-inlet streams receive and transport allochthonous inputs that subsidise the lake trophic web and support biotic productivity (Curry et al., 1997; France et al., 1996). For instance, streams transport invertebrates, OM, and large wood into lakes (Wipfli et al., 2007), along with nutrients (Niswonger et al., 2017), at least locally at the inflow. The magnitude of OM inputs, based on the size of each delta's contributing catchment area has been used to compare the resulting productivity of some fishes and invertebrates for lakes of the Canadian Shield near Sudbury (Szkokan-Emilson et al., 2011; Tanentzap et al., 2014). Moreover, the size and characteristics of a tributary's catchment impacts hydrology, nutrient flux, sediment movements, water temperatures, and more, where they enter lakes. The water from streams may provide appropriate thermal (e.g. cooler in summer) and oxygen (better aerated) conditions that mobile species might use selectively to avoid warm epilimnetic areas (Curry et al., 1997). These characteristics differ from the overall lake environment and may provide unique microhabitats within lakes (Abell & Hamilton, 2015). Overall, tributary characteristics will have a large imprint on a lake's features resulting from the nature of their inputs. Most of these characteristics have been considered individually in various studies, but rarely as a potentially interacting set of mechanisms. Here we will review these potential contributions (Table 1), keeping in mind that some of these are still hypotheses, which we will expand upon further below.

**TABLE 1** Potential hypotheses for the contributions of tributary streams to lakes that influence lake deltas and create a special environment there

| Property                        | Contribution to lakes and lake organisms  | Example                                 |
|---------------------------------|---|---|
| Food inputs from streams        | Flux of stream invertebrates and organic matter   | Wipfli and Gregovich (2002)             |
| Addition of nutrient-rich water | Higher productivity of phytoplankton and benthic biofilms   | Finlay et al. (2011)                    |
| Thermal refuge                  | Cooler in summer, warmer in winter  | Curry et al. (1997)                     |
| Higher oxygen concentrations    | Turbulent flow adds oxygen  | ...                                     |
| Cooler and oxygen-rich water    | Preferred spawning and rearing areas for certain species, especially during warm summers                      | Interaction of the two mechanisms above |
| Addition of coarse sediments    | A unique physical habitat with more interstitial spaces   | Rice et al. (2001)                      |
| Large wood cover                | Lake delta might provide good cover from predation if there is a lot of wood deposited                        | Czarnecka (2016)                        |
| Flushing of fine sediments      | Clearing of interstitial spaces and more benthic productivity   | Carlson et al. (2018)                   |
| In stream as a refuge           | Some fish spawn in upstream areas or escape predation there due to the restriction of larger-bodied predators | Arostegui and Quinn (2019)              |

## 2.1 | Resource subsidies

Streams can transport large amounts of fixed carbon in the form of particulate or dissolved OM, and invertebrates, which can provide a large subsidy of resources to lakes. Most of this flux occurs during high flows (Babler et al., 2011; Wipfli & Gregovich, 2002; Wipfli et al., 2007), but this OM settles out near the stream inflow, potentially creating a particularly resource-rich patch. Wipfli and Gregovich (2002) estimated that small streams flowing into a larger stream in Alaska could support the production of 100–2,000 juvenile salmonids per km of receiving stream. However, the actual fate of such flows is difficult to estimate directly in receiving streams, whereas measuring this is more tractable in lakes as the tractive force of stream flow diminishes (Klemmer & Richardson, 2013). France (1995a) found that shoreline contributions of particulate OM accounted for 6% of allochthonous inputs to a series of lakes, with the implication that 94% of these inputs are stream-derived. Moreover, accumulations of detritus accounted for greater lake-wide production of littoral zone benthos than did macrophytes (France, 1995b). Young-of-the-year yellow perch in a boreal lake had a nearly 4-fold higher individual biomass, reflecting higher growth rates, within distinct deltas (bays) that had greater OM inputs than at non-inflow littoral areas (Tanentzap et al., 2014). Brook trout in lake deltas likewise had higher growth and survival than in other parts of a lake, putatively due to food resources there (Curry et al., 1997).

Productivity of lakes can be largely supported by terrestrially fixed carbon, but most studies have looked generally at the whole lake ecosystem. Our intent is not to address whether terrestrial sources versus autochthony is more important overall to lake productivity, only the localisation at deltas relative to other parts of lakes. One study of the stream inflow deltas of lakes showed that organic materials from streams contributed specifically to increased growth and biomass of zooplankton and fishes, and was positively related to input amounts from particular streams (Tanentzap et al., 2014). The quantity and quality of dissolved organic carbon flowing from tributary streams into Lake Superior following high rates of precipitation created a nearshore plume of heightened productivity (Marcarelli et al., 2019); however, our discussion is primarily for small lakes. The proportional contribution of terrestrially derived OM from inflow streams to lake productivity also depends on the nutrient status of a lake and the autochthonous production available relative to those inputs (Marczak et al., 2007). Experimental additions of particulate organic carbon to littoral communities demonstrated that this particulate organic carbon was used and contributed to increased benthic productivity (Bartels et al., 2012), although this was not linked directly to inflows.

## 2.2 | Nutrient-rich water

Streams may deliver nutrient-rich water, or at least may have higher concentrations of some elements (Nowlin et al., 2008), and if these nutrients are limiting may be rapidly taken up within the delta. In particular, oligotrophic lakes may receive inputs from tributaries, particularly those with higher nutrient loads as a consequence of land. It

is also possible that inflow streams may not have any higher concentration of nutrients, or could be lower, than the receiving delta, but this varies spatially, seasonally, and with land use. The potential nutrient subsidies from catchments could be substantial through transport from inflow streams (Finlay et al., 2011; Rice et al., 2008). We hypothesise that communities within lake deltas will be capable of rapidly sequestering nutrients that are limiting. Stoichiometry or the form of those nutrients might also be an important consideration.

## 2.3 | Thermal refuge

As many temperate lakes stratify in summer and winter, water from the streams entering lake deltas might be cooler than other littoral areas in summer, and perhaps warmer in winter. Several studies show that fish exhibit seasonal use of stream inflow areas within lakes. For instance, Curry et al. (1997) observed most of a brook trout population migrating to and inhabiting a small inflow stream of a lake in Ontario for the summer months, presumably using the stream for a cooler and more stable habitat. Brook trout show selection for sites with suitable temperatures, moving seasonally to groundwater upwellings, in a fashion similar to the use of inflow streams (Biro, 1998). Prickly sculpins appeared to use stream inflows in a Washington state lake primarily for its temperature regime and not for food inputs, but there was still some small effect of stream-supplied food, as well as some age-structured interactions within the populations (Polivka et al., 2013).

In winter, tributary streams may be warmer than epilimnial water, and also provide patches of earlier ice-off in spring for ice-covered lakes. Some fish species, e.g. some salmonids, may use lakes over winter only, perhaps to avoid extreme conditions in streams from near super-cooled water, ice flows, or high flows associated with freshet or rain-on-snow events (Arostegui & Quinn, 2019; Heim et al., 2019). There are few studies of this sort, so this could provide a set of ideas for testing whether differential seasonal use of these zones occurs at times other than summer. The limited amount of published work addresses fish in temperate lakes; however, it is likely that organisms in lakes in other regions with thermal regimes different from temperate lakes may still take advantage of selection of water from stream inflows to occupy better thermal conditions in lake deltas.

## 2.4 | Oxygen concentrations

As lakes can become oxygen depleted at times with limited epilimnetic mixing and high biological demand, it is possible that inflow streams may provide water that is better oxygenated from the turbulent flow. This would be difficult to distinguish from the effects of cooler water. To date, we have found no evidence to suggest that stream water flowing into a lake delta is better oxygenated than water in the remainder of a recipient lake, but we include it here as a hypothesis to be tested.

## 2.5 | Spawning and rearing areas with cooler, oxygen-rich water

Fish in lakes may differentially use lake inflow (lacustrine-adfluvial life history) or outflow streams for spawning and rearing. For salmonids, the adfluvial life history with spawning in well-oxygenated streams and residence in lakes is common to populations of many species in the genera *Oncorhynchus*, *Salmo*, and *Salvelinus* (Arostegui & Quinn, 2019; Heim et al., 2019; Lennox et al., 2021). For example, brown trout in Ireland may show philopatry to particular inflow streams (Finlay et al., 2020). Brook trout also use lake-inlet stream areas for spawning (Curry & Devito, 1996). White suckers, Lahontan cutthroat trout and others have been observed to use inflow streams for spawning, and then the adults return to their lakes. Sockeye salmon (*Oncorhynchus nerka*) represent this strategy well, where eggs typically are laid in streams, and newly emerged larvae move to lakes to rear for a year or more (e.g. Arostegui & Quinn, 2019). Some species of fish lay their eggs in littoral areas, and newly emerged larvae move into tributary streams to rear (Arostegui & Quinn, 2019). While use of littoral areas by fishes is common (Winfield, 2004), there are few studies that distinguish deltas from other littoral areas. Most fish entering lakes after hatching in streams are not restricted to the deltas of their tributaries, e.g., sockeye, so it is the lake more generally that provides the alternate habitat.

## 2.6 | Sediment size composition

Streams also can provide sediments of different calibre from those in the lake (Rice et al., 2008), creating additional substrate heterogeneity or increased turbidity that may favour some species. The supply of grain sizes from the stream that potentially differ from the rest of the littoral zone can create important differences and variation in terms of particle size distributions of benthic environments. High flows may rework delta sediments (Carlson et al., 2018), perhaps flushing finer sediments away from the inflow area (fining), again providing a different physical environment, and contributing to a gradient of diminishing mean sizes of particles away from the inflow. These differences are readily seen at tributary junctions between streams, but there are few assessments of this in lake deltas, so there are ample opportunities to test this hypothesis about sediment sizes as another mechanism that may contribute to uniqueness of lake deltas.

## 2.7 | Wood and complex structure in deltas

Inflow deltas can provide hiding places, i.e. security cover, if there is a lot of wood or other features that provide structures where small individuals can hide from predators (Kiffney et al., 2006). The complexity might also offer other structural habitat features not found elsewhere in the littoral zone, in addition to the mineral sediments discussed in the previous paragraph. Wood can also provide important

habitats for invertebrates and microbes, again providing a habitat and trophic feature (Czarnecka, 2016). While mobile organisms could select cooler, hypolimnetic water, the foraging and predation-risk environment there might be unsuitable (Winfield, 2004). Littoral areas may provide more structural complexity, such as large wood flushed in from streams, which can provide cover from predation. While lake deltas may offer greater complexity than the remainder of the littoral zone, this hypothesis remains to be tested.

Depending on the size of tributary stream and its riparian areas, there may be considerable supplies of large wood that come to rest at the lake delta, potentially creating a more complex physical environment that may contribute to suitable spawning or rearing sites, independently of temperature or oxygen. This mass wasting of wood and sediment, and channelised flow events through tributary streams are rare, but can deliver a large pulse of large wood and coarse sediments when they occur (Benda et al., 2003; Swanson et al., 1998). However, the distribution of wood around littoral zones may be more dependent on wind and wave action than the actual source (Czarnecka, 2016), suggesting that more work is needed to address whether deltas are more complex than the remainder of the shoreline.

## 2.8 | Escape habitat

Small fishes (young age classes or small-bodied species) may use inflow streams as escape habitat. Many small tributary streams are too small or steep for piscivorous fish to occupy, or streams may contain more cover from other predators (Richardson, 2019), thus streams near lake deltas may provide a refuge for small fishes. The lake or stream habitat adjacent to each other can also provide escape (refuge) from other adverse conditions (beyond temperatures), such as drying or flooding of streams, or wave action in lakes (Willis & Magnuson, 2000).

## 3 | SCALING OF THE CONTRIBUTIONS OF TRIBUTARIES TO LAKE DELTAS

In studying the connections between tributaries and their lake deltas, it is useful to consider some potential variables that might serve as predictors of the effect sizes on the deltas. The specific variables considered will be influenced by the nature of inquiry, whether the questions are essentially chemical, physical, or ecological. The relative influence of a tributary stream on a lake delta will depend on the tributary's size (catchment area) relative to that of a given lake, i.e. larger streams will probably result in bigger or more dynamic deltas, or both (Jones, 2010). The number of tributaries entering a lake may scale with lake size, with smaller lakes having proportionally more tributaries relative to their size, which could affect the relative magnitude of the influence on deltas (Seekell et al., 2021). Some inputs to lakes will have lake-wide influences, e.g. transported nutrients, suspended sediments, and dissolved OM (Squires & Lesack, 2002),

but here we are focussed on the scale of the lake delta. For instance, the Laurentian Great Lakes show local impacts of inflow streams on turbidity, nutrient regimes, and OM inputs, although some of this is spatially measured more broadly than just at the delta (Larson et al., 2016; Marcarelli et al., 2019). In general, a delta's features will scale with the size of a tributary's discharge, sediment loads and calibre, and gradient (Syvitski, 2008).

Within stream networks, some tributary effects can be scaled based on the flow difference of the tributary relative to the larger receiving stream (Rice et al., 2001; Tavernini & Richardson, 2020). For tributary junctions, this scaling is known as the basin area ratio, based on relative catchment areas, and it could be based on instantaneous flow differences for processes that respond quickly, or average annual flows for processes that occur over longer time scales. Scaling of OM inputs to individual deltas within a lake on the basis of contributing area was used to compare productivity by Tanentzap et al. (2017). Likewise, Babler et al. (2011) used the ratio of catchment area:lake area as a way to scale relative contributions of stream-derived OM to detritivorous fish in their lakes (not restricted to the delta). This ratio might also be scaled relative to annual peak flows in the case of some geomorphic processes, including moving coarse sediment clasts or large wood. Peak flows do two things: (1) transport larger materials; and (2) rework materials at the delta. Materials (inorganic sediment and OM, including large wood) accumulated at the delta can be pushed further into a lake, and perhaps even relatively long distances away from the inflow. The geomorphology of deltas will evolve through time by subsidence, sediment inputs, progradation, and fluvial reworking (Carlson et al., 2018). This scaling might also consider water residence time (Baker et al., 2016). However, while this kind of scaling is necessary, it will not be sufficient as predictor variables.

Scaling of the relative influence of a tributary on a lake delta would be specific to particular biomes. We hypothesise that the difference of deltas from the remaining littoral areas will vary depending on climate patterns (e.g. intensity and duration of discharge), sediment types, nutrient limitation, thermal regimes, etc. Another metric to scale contributions would need to consider the relative productivity of the tributaries versus the lake deltas (Marczak et al., 2007). Geomorphic aspects, such as bathymetric and shape differences of lake basins, particularly depth, rate of drop-off to depth, or some other attribute may need to be included, as these affect development and localisation of deltas (Carlson et al., 2018; Jones, 2010). The spatial configuration of inflow streams will also be relevant to development of deltas, as inflows very close to outflows are unlikely to facilitate the longer-term storage needed for the mechanisms described above (Jones, 2010). Moreover, multiple inflows in close proximity might be synergistic in providing a unique habitat. We have not tried to develop such a scaling metric, as there are no doubt other elements that limnologists would want to include.

Larger streams differ from smaller streams in having a different composition and concentration of contributions (e.g. leaves or wood) that affect what is received in lakes (Salvo et al., 2020). For

instance, Babler et al. (2011) found that the proportional contribution of stream inputs to detritivorous fish declined as catchment size increased, perhaps because larger streams have disproportionately less particulate OM (per unit discharge) than smaller streams. Some kind of mixing model might serve to compare tributary contributions relative to resources already available in deltas. Some accounting for stream properties themselves is needed in any kind of a scaling metric. These scaling issues are a topic that would benefit from further research to determine how delta configuration and use varies spatially, seasonally, according to peak flows, and other scaling attributes.

## 4 | IMPACTS OF LAND USE AND APPLICATIONS

Throughout the world there has been a large-scale historic impact of forest harvesting and other land uses (e.g., agriculture, urbanisation, mining) on freshwaters, and these effects on streams are well known (Dudgeon et al., 2006). These impacts include alteration to hydrologic regimes (Moore & Wondzell, 2005), sediment flows, nutrient concentrations and stoichiometry (Feller, 2005), OM and invertebrate fluxes (Wipfli et al., 2007), thermal regimes, and other impacts. Land-use, such as forest harvesting in riparian areas or at the catchment scale can have impacts on biotic and abiotic components of lakes and streams (e.g. see review by Prepas et al., 2001). However, our focus here is on the specific changes from land use on the contributions of stream inflows into lake deltas. Many of these land uses noted above tend to increase flux of fine (inorganic) sediments, nutrients, and pesticides, and decrease OM inputs due to disturbed riparian areas. The magnitude and direction of the impact of upstream land use on formation and dynamics of lake deltas needs additional study.

There are relatively few studies of land-use impacts on lake deltas. However, Tanentzap et al. (2014) found a positive relationship between the productivity of lake deltas and the amount of forest cover in the contributing catchment, indicating that forest harvest and other land uses (i.e. removal of terrestrial biomass) have downstream impacts on deltas. However, the effects that land use has on downstream lake deltas via tributary inflows have been under-studied in comparison to the direct effects on streams. For instance, we could hypothesise that increased sediment transport and higher peak flows resulting from impacts of forest harvesting, could alter and expand delta areas. Moreover, one might be able to link specific types of forestry caused changes in the physical and biological characteristics of streams, to ecosystem alterations as one way to test the influence of land use on deltas. If these deltas turn out to be distinct and critical habitats within receiving lakes, then more attention to protection of contributing waters would be warranted. There is a need to test the generality of our assertion that these are distinct habitats, which requires a broader evaluation, but our focus here is to draw attention to this need for further study.

## 5 | EVIDENCE FOR UNIQUE COMMUNITIES OR SEASONAL USE BY SPECIES

In the examples above, we discussed evidence for seasonal use of lake deltas by species such as brook trout. There is less evidence that other lacustrine species use these areas seasonally or as a special habitat. However, determining differential use of lake deltas versus other littoral areas requires a particular study design that probably has not been applied to many species (see Willis & Magnuson, 2000). We hypothesise that these small habitats are likely to be used as seasonal refuges and as productivity hotspots within lakes by many species. There is abundant evidence of the value of tributary junctions in fluvial networks (Benda et al., 2004; Kiffney et al., 2006; Rice et al., 2008), and we hope our review will focus efforts on collecting similar data for lake deltas.

Some species in lakes seem to be particularly associated with lake deltas. For instance, Willis and Magnuson (2000) found a taxonomically diverse subset of fish species most commonly found in the transitional areas of lake inflows and deltas. Another example comes from a small lake (c. 13 ha) in British Columbia, where the larvae of a number of caddisfly species were mostly found on the coarse OM of the lake delta (Winterbourn, 1971). Winterbourn (1971) also noted the large amount of organic material there, the coarser nature of the substrate, and that the stream inflow was the only ice-free section during winter (Winterbourn, 1971). The caddisflies found in that delta were rarely found in other parts of the lake. Brook trout are well known for frequenting cool inflow areas in summer (Curry et al., 1997). There are undoubtedly many other examples, and distinguishing these lake deltas as a special habitat will help focus on which species use these sites and why.

Tributary stream inflows and the deltas within lakes may provide a model system for looking at the fate of resource subsidies from inflow streams. These sites may also offer a test location to evaluate the fate of all the OM and invertebrates flowing from small streams (Wipfli & Gregovich, 2002). Measuring the consequences of such inputs could contribute to our quantitative understanding of resource subsidies (Marczak et al., 2007). In this way, inflow deltas provide a convenient unit for such studies, as was done in Tanentzap et al. (2014).

## 6 | CONCLUSIONS

Recognition of deltas in lakes as a special habitat should also note that stream organisms upstream from lakes might benefit from features of refuge within lakes (Pépin et al., 2017) and that stream-lake linkages occur at many scales (Jones, 2010). Despite this, there have been few assessments (but see Polivka et al., 2013) of how the mechanisms might interact with each other at a local spatial scale within lakes or vary temporally as physical and biological conditions change. Most studies have focused on single hypotheses, such as food or temperature, rather than trying to study how different processes might interact. It is our hope to advance consideration of

hypotheses as we have outlined that address multiple, interacting mechanisms (Table 1), and which may result in lake deltas providing a unique environment within lakes, rather than each process in isolation.

Lake deltas formed by inflow streams provide patches of resources and unique physio-chemical conditions within lake ecosystems. The extent to which these localised environments are special and the magnitude of their contributions is not well known. Moreover, there may be different mechanisms determining the use of these deltas by particular species and different age classes, and it will be helpful to consider the alternative hypotheses as we have outlined. Some of the reasons for use of these sites may appear obvious; however, interactions among mechanisms, including food-web effects should be considered. Our intent is to focus on this particular environment such that the conservation value of these sites might be considered. If lake deltas indeed are productivity and biodiversity hotspots within lakes, then landscape-scale protection might provide greater emphasis on these habitats and the inflow stream reaches sustaining these functions.

### ACKNOWLEDGEMENTS

We appreciate funding from the Natural Sciences and Engineering Research Council (Canada), the BC Ministry of Forests, Lands, Natural Resource Operations and Rural Development, and the University of British Columbia. All authors contributed to the development of the ideas and the writing of the manuscript. We thank Dr Peter Kiffney, US-NOAA for comments on a draft of this work, and we are grateful for the thorough and thoughtful comments from two reviewers.

### DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analysed in this study.

### ORCID

John S. Richardson  <https://orcid.org/0000-0001-8135-7447>

### REFERENCES

- Abell, J. M., & Hamilton, D. P. (2015). Biogeochemical processes and phytoplankton nutrient limitation in the inflow transition zone of a large eutrophic lake during a summer rain event. *Ecohydrology*, 8(2), 243–262. <https://doi.org/10.1002/eco.1503>
- Arostegui, M. C., & Quinn, T. P. (2019). Reliance on lakes by salmon, trout and charr (*Oncorhynchus*, *Salmo* and *Salvelinus*): An evaluation of spawning habitats, rearing strategies and trophic polymorphisms. *Fish and Fisheries*, 20, 775–794.
- Babler, A. L., Pilati, A., & Vanni, M. J. (2011). Terrestrial support of detritivorous fish populations decreases with watershed size. *Ecosphere*, 2(7), art76. <https://doi.org/10.1890/ES11-00043.1>
- Baker, M. A., Arp, C. D., Goodman, K. J., Marcarelli, A. M., & Wurtsbaugh, W. A. (2016). Chapter 7. Stream-lake interaction: Understanding coupled hydro-ecological systems. In J. B. Jones, & E. J. Stanley (Eds.), *Stream ecosystems in a changing environment* (pp. 321–348). Elsevier Inc. <https://doi.org/10.1016/B978-0-12-405890-3.00007-5>
- Bartels, P., Cucherousset, J., Gudas, C., Jansson, M., Karlsson, J., Persson, L., ... Eklöv, P. (2012). Terrestrial subsidies to lake food

- webs: An experimental approach. *Oecologia*, 168, 807–818. <https://doi.org/10.1007/s00442-011-2141-7>
- Benda, L., Poff, N. L., Miller, D., Dunne, T., Reeves, G., Pess, G., & Pollock, M. (2004). The network dynamics hypothesis: How channel networks structure riverine habitats. *BioScience*, 54, 413–427.
- Benda, L., Veldhuisen, C., & Black, J. (2003). Debris flows as agents of morphological heterogeneity at low-order confluences, Olympic Mountains, Washington. *Geological Society of America Bulletin*, 115, 1110–1121. <https://doi.org/10.1130/B25265.1>
- Biro, P. A. (1998). Staying cool: Behavioral thermoregulation during summer by young-of-year Brook Trout in a lake. *Transactions of the American Fisheries Society*, 127, 212–222.
- Carlson, B., Piliouras, A., Muto, T., & Kim, W. (2018). Control of basin water depth on channel morphology and autogenic timescales in deltaic systems. *Journal of Sedimentary Research*, 88, 1026–1039. <https://doi.org/10.2110/jsr.2018.52>
- Carpenter, S. R., Cole, J. J., Pace, M. L., Van de Bogert, M., Bade, D. L., Bastviken, D., ... Kritzberg, E. S. (2005). Ecosystem subsidies: Terrestrial support of aquatic food webs from <sup>13</sup>C addition to contrasting lakes. *Ecology*, 86, 2737–2750.
- Corenblit, D., Tabacchi, E., Steiger, J., & Gurnell, A. M. (2007). Reciprocal interactions and adjustments between fluvial landforms and vegetation dynamics in river corridors: A review of complementary approaches. *Earth-Science Reviews*, 84, 56–86. <https://doi.org/10.1016/j.earscirev.2007.05.004>
- Curry, R. A., Brady, C., Noakes, D. L. G., & Danzmann, R. G. (1997). Use of small streams by young brook trout spawned in a lake. *Transactions of the American Fisheries Society*, 126, 77–83. [https://doi.org/10.1577/1548-8659\(1997\)126<0077:UOSSBY>2.3.CO;2](https://doi.org/10.1577/1548-8659(1997)126<0077:UOSSBY>2.3.CO;2)
- Curry, R. A., & Devito, K. J. (1996). Hydrogeology of brook trout (*Salvelinus fontinalis*) spawning and incubation habitats: Implications for forestry and land use development. *Canadian Journal of Forest Research*, 26, 767–772.
- Czarnecka, M. (2016). Coarse woody debris in temperate littoral zones: Implications for biodiversity, food webs and lake management. *Hydrobiologia*, 767, 13–25. <https://doi.org/10.1007/s10750-015-2502-z>
- Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z.-I., Knowler, D. J., L ev eque, C., ... Sullivan, C. A. (2006). Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews*, 81, 163–182. <https://doi.org/10.1017/S1464793105006950>
- Feller, M. C. (2005). Forest harvesting and streamwater inorganic chemistry in western North America: A review. *Journal of the American Water Resources Association*, 41, 785–811. <https://doi.org/10.1111/j.1752-1688.2005.tb04464.x>
- Finlay, J. C., Hood, J. M., Limm, M. P., Power, M. E., Schade, J. D., & Welter, J. R. (2011). Light-mediated thresholds in stream-water nutrient composition in a river network. *Ecology*, 92, 140–150. <https://doi.org/10.1890/09-2243.1>
- Finlay, R., Poole, R., Coughlan, J., Phillips, K. P., Prod ohl, P., Cotter, D., ... Reed, T. E. (2020). Telemetry and genetics reveal asymmetric dispersal of a lake-feeding salmonid between inflow and outflow spawning streams at a microgeographic scale. *Ecology and Evolution*, 10, 1762–1783. <https://doi.org/10.1002/ece3.5937>
- France, R. L. (1995a). Empirically estimating the lateral transport of riparian leaf litter to lakes. *Freshwater Biology*, 34, 495–499. <https://doi.org/10.1111/j.1365-2427.1995.tb00907.x>
- France, R. L. (1995b). Macroinvertebrate standing crop in littoral regions of allochthonous detritus accumulation: Implications for riparian forest management. *Biological Conservation*, 71, 35–39.
- France, R., Culbert, H., & Peters, R. (1996). Decreased carbon and nutrient input to boreal lakes from particulate organic matter following riparian clear-cutting. *Environmental Management*, 20, 579–583. <https://doi.org/10.1007/BF01474657>
- Heim, K. C., Arp, C. D., Whitman, M. S., & Wipfli, M. S. (2019). The complementary role of lentic and lotic habitats for Arctic grayling in a complex stream-lake network in Arctic Alaska. *Ecology of Freshwater Fish*, 28(2), 209–221. <https://doi.org/10.1111/eff.12444>
- Jones, N. E. (2010). Incorporating lakes within the river discontinuum: Longitudinal changes in ecological characteristics in stream-lake networks. *Canadian Journal of Fisheries and Aquatic Sciences*, 67, 1350–1362. <https://doi.org/10.1139/F10-069>
- Karlsson, J., Berggren, M., Ask, J., P ar, B., Jonsson, A., Laudon, H., & Jansson, M. (2012). Terrestrial organic matter support of lake food webs: Evidence from lake metabolism and stable hydrogen isotopes of consumers. *Limnology and Oceanography*, 57, 1042–1048. <https://doi.org/10.4319/lo.2012.57.4.1042>
- Kiffney, P. M., Greene, C. M., Hall, J. E., & Davies, J. R. (2006). Tributary streams create spatial discontinuities in habitat, biological productivity, and diversity in mainstem rivers. *Canadian Journal of Fisheries and Aquatic Sciences*, 63, 2518–2530. <https://doi.org/10.1139/f06-138>
- Klemmer, A. J., & Richardson, J. S. (2013). Quantitative gradient of subsidies reveals a threshold in community-level trophic cascades. *Ecology*, 94, 1920–1926. <https://doi.org/10.1890/12-1444.1>
- Kling, G. W., Kipphut, G. W., Miller, M. M., & O'Brien, W. J. (2000). Integration of lakes and streams in a landscape perspective: The importance of material processing on spatial patterns and temporal coherence. *Freshwater Biology*, 43, 477–497. <https://doi.org/10.1046/j.1365-2427.2000.00515.x>
- Laird, K. R., Barouillet, C., Cumming, B. F., Perrin, C. J., & Selbie, D. T. (2021). Influence of glacial turbidity and climate on diatom communities in two Fjord Lakes (British Columbia, Canada). *Aquatic Sciences*, 83, 13. <https://doi.org/10.1007/s00027-020-00767-3>
- Larson, J. H., Frost, P. C., Vallazza, J. M., Nelson, J. C., & Richardson, W. B. (2016). Do rivermouths alter nutrient and seston delivery to the nearshore? *Freshwater Biology*, 61, 1935–1949. <https://doi.org/10.1111/fwb.12827>
- Leach, J. A., & Laudon, H. (2019). Headwater lakes and their influence on downstream discharge. *Limnology and Oceanography Letters*, 4(4), 105–112. <https://doi.org/10.1002/lo12.10110>
- Lennox, R. J., Pulg, U., Malley, B., Gabrielsen, S.-E., Hanssen, E. M., Cooke, S. J., ... Vollset, K. W. (2021). The various ways that anadromous salmonids use lake habitats to complete their life history. *Canadian Journal of Fisheries and Aquatic Sciences*, 78, 90–100.
- Marcarelli, A. M., Coble, A. A., Meingast, K. M., Kane, E. S., Brooks, C. N., Buffam, I., ... Stottleyer, R. (2019). Of small streams and Great lakes: Integrating tributaries to understand the ecology and biogeochemistry of Lake Superior. *Journal of the American Water Resources Association*, 55, 442–458. <https://doi.org/10.1111/1752-1688.12695>
- Marczak, L. B., Thompson, R. M., & Richardson, J. S. (2007). A meta-analysis of the role of trophic position, habitat type and habitat productivity in determining the food web effects of resource subsidies. *Ecology*, 88, 140–148.
- Moore, R. D., & Wondzell, S. M. (2005). Physical hydrology and the effects of forest harvesting in the Pacific Northwest: A review. *Journal of the American Water Resources Association*, 41, 763–784. <https://doi.org/10.1111/j.1752-1688.2005.tb04463.x>
- Niswonger, R., Naranjo, R., Smith, D., Constantz, J., Allander, K., Rosenberry, D., ... Stonestrom, D. (2017). Nutrient processes at the stream-lake interface for a channelized versus unmodified stream mouth. *Water Resources Research*, 53, 237–256. <https://doi.org/10.1002/2016WR019538>
- Nowlin, W. H., Vanni, M. J., & Yang, L. H. (2008). Comparing resource pulses in aquatic and terrestrial ecosystems. *Ecology*, 89, 647–659. <https://doi.org/10.1890/07-0303.1>
- Pace, M. L., Carpenter, S. R., Cole, J. J., Coloso, J. J., Kitchell, J. F., Hodgson, J. R., ... Weidel, B. C. (2007). Does terrestrial organic carbon subsidize the planktonic food web in a clear-water lake? *Limnology*



- and *Oceanography*, 52, 2177–2189. <https://doi.org/10.4319/lo.2007.52.5.2177>
- Pépin, M., Rodríguez, M. A., & Magnan, P. (2017). Incorporating lakes in stream fish habitat models: Are we missing a key landscape attribute? *Canadian Journal of Fisheries and Aquatic Sciences*, 74, 629–635. <https://doi.org/10.1139/cjfas-2016-0221>
- Polivka, K. M., Friedli, L. M., & Green, E. C. (2013). Stream inflow and predation risk affect littoral habitat selection by benthic fish: Resource matching and predation risk in lakes. *Freshwater Biology*, 58, 986–994. <https://doi.org/10.1111/fwb.12101>
- Prepas, E. E., Pinel-Alloul, B., Planas, D., Methot, G., Paquet, S., & Reedyk, S. (2001). Forest harvest impacts on water quality and aquatic biota on the Boreal Plain: Introduction to the TROLS lake program. *Canadian Journal of Fisheries and Aquatic Sciences*, 58, 421–436. <https://doi.org/10.1139/f00-259>
- Rice, S. P., Greenwood, M. T., & Joyce, C. B. (2001). Tributaries, sediment sources, and the longitudinal organisation of macroinvertebrate fauna along river systems. *Canadian Journal of Fisheries and Aquatic Sciences*, 58, 824–840. <https://doi.org/10.1139/f01-022>
- Rice, S. P., Kiffney, P., Greene, C., & Pess, G. R. (2008). The ecological importance of tributaries and confluences. In S. P. Rice, A. G. Roy, & B. L. Rhoads (Eds.), *River confluences, tributaries and the fluvial network* (pp. 209–242). John Wiley & Sons.
- Richardson, J. S. (2019). Biological diversity in headwater streams. *Water*, 11. Article number: 366.
- Richardson, J. S., & Mackay, R. J. (1991). Lake outlets and the distribution of filter feeders: An assessment of hypotheses. *Oikos*, 62, 370–380. <https://doi.org/10.2307/3545503>
- Richardson, J. S., & Sato, T. (2015). Resource flows across freshwater-terrestrial boundaries and influence on processes linking adjacent ecosystems. *Ecohydrology*, 8, 406–415.
- Sakamaki, T., Shum, J. Y. T., & Richardson, J. S. (2010). Watershed effects on chemical properties of sediment and primary consumption in estuarine tidal flats: Importance of watershed size and food selectivity by macrobenthos. *Ecosystems*, 13, 328–337. <https://doi.org/10.1007/s10021-010-9321-x>
- Salvo, J., Valdovinos, C., & Fierro, P. (2020). Benthic macroinvertebrate assemblages of a stream-lake network in the upper zone of the trans-Andean basin of the Valdivia River (Chile). *New Zealand Journal of Marine and Freshwater Research*, 55(2), 375–392. <https://doi.org/10.1080/00288330.2020.1784239>
- Seekell, D., Cael, B., Lindmark, E., & Byström, P. (2021). The fractal scaling relationship for river inlets to lakes. *Geophysical Research Letters*, 48, e2021GL093366. <https://doi.org/10.1029/2021GL093366>
- Squires, M. M., & Lesack, L. F. W. (2002). Water transparency and nutrients as controls on phytoplankton along a flood-frequency gradient among lakes of the Mackenzie Delta, western Canadian Arctic. *Canadian Journal of Fisheries and Aquatic Sciences*, 59, 1339–1349. <https://doi.org/10.1139/f02-085>
- Swanson, F. J., Johnson, S. L., Gregory, S. V., & Acker, S. A. (1998). Flood disturbance in a forested mountain landscape. *BioScience*, 48, 681–689. <https://doi.org/10.2307/1313331>
- Syvitski, J. P. M. (2008). Deltas at risk. *Sustainability Science*, 3, 23–32. <https://doi.org/10.1007/s11625-008-0043-3>
- Szkokan-Emilson, E. J., Wesolek, B. E., & Gunn, J. M. (2011). Terrestrial organic matter as subsidies that aid in the recovery of macroinvertebrates in industrially damaged lakes. *Ecological Applications*, 21(6), 2082–2093.
- Tanentzap, A. J., Kielstra, B. W., Wilkinson, G. M., Berggren, M., Craig, N., del Giorgio, P. A., ... Pace, M. L. (2017). Terrestrial support of lake food webs: Synthesis reveals controls over cross-ecosystem resource use. *Science Advances*, 3, e1601765. <https://doi.org/10.1126/sciadv.1601765>
- Tanentzap, A. J., Szkokan-Emilson, E. J., Kielstra, B. W., Arts, M. T., Yan, N. D., & Gunn, J. M. (2014). Forests fuel fish growth in freshwater deltas. *Nature Communications*, 5, 1–9. <https://doi.org/10.1038/ncomms5077>
- Tavernini, D. A., & Richardson, J. S. (2020). Effects of tributary size on the resource supply and physical habitat at tributary junctions along two mainstem rivers. *Canadian Journal of Fisheries and Aquatic Sciences*, 77(8), 1393–1408. <https://doi.org/10.1139/cjfas-2019-0435>
- Vanni, M. J., Andrews, J. S., Renwick, W. H., Gonzalez, M. J., & Noble, S. J. (2006). Nutrient and light limitation of reservoir phytoplankton in relation to storm-mediated pulses in stream discharge. *Archiv für Hydrobiologie*, 167, 421–445.
- Ward, J. V., & Stanford, J. A. (1995). The serial discontinuity concept: Extending the model to floodplain rivers. *River Research and Applications*, 10, 159–168. <https://doi.org/10.1002/rrr.3450100211>
- Willis, T. V., & Magnuson, J. J. (2000). Patterns in fish species composition across the interface between streams and lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, 57, 1042–1052. <https://doi.org/10.1139/f00-028>
- Winfield, I. J. (2004). Fish in the littoral zone: Ecology, threats and management. *Limnologia*, 34, 124–131. [https://doi.org/10.1016/S0075-9511\(04\)80031-8](https://doi.org/10.1016/S0075-9511(04)80031-8)
- Winterbourn, M. J. (1971). The life histories and trophic relationships of the Trichoptera of Marion Lake, British Columbia. *Canadian Journal of Zoology*, 49, 623–635. <https://doi.org/10.1139/z71-100>
- Wipfli, M. S., & Gregovich, D. P. (2002). Export of invertebrates and detritus from fishless headwater streams in southeastern Alaska: Implications for downstream salmonid production. *Freshwater Biology*, 47, 957–969. <https://doi.org/10.1046/j.1365-2427.2002.00826.x>
- Wipfli, M. S., Richardson, J. S., & Naiman, R. J. (2007). Ecological linkages between headwaters and downstream ecosystems: Transport of organic matter, invertebrates, and wood down headwater channels. *Journal of the American Water Resources Association*, 43, 72–85.

**How to cite this article:** Richardson, J. S., Michalski, T., & Becu, M. (2021). Stream inflows to lake deltas: A tributary junction that provides a unique habitat in lakes. *Freshw Biol.*, 00, 1–9. <https://doi.org/10.1111/fwb.13816>