Stream Habitat Needs for Brook Trout and Brown Trout in the Driftless Area

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1. Several conceptual frameworks have been proposed to organize and describe fish habitat needs.
2. The five-component framework recognizes that stream trout populations are regulated by hydrology, water quality, physical habitat/geomorphology, connectivity, and biotic interactions and management of only one component will be ineffective if a different component limits the population.
3. The thermal niche of both Brook Trout *Salvelinus fontinalis* and Brown Trout *Salmo trutta* has been well described.
4. Selected physical habitat characteristics such as pool depths and adult cover, have a long history of being manipulated in the Driftless Area leading to increased abundance of adult trout.
5. Most blue-ribbon trout streams in the Driftless Area probably provide sufficient habitat for year-round needs (e.g., spawning, feeding, and disturbance refugia) for most Brook Trout and Brown Trout life stages.

Life History | Age and Growth | Fecundity | Habitat Use and Selection | Biotic Interactions | Scale | Riverscape | Movement

Most streams in the Driftless Area of southwest Wisconsin, southeast Minnesota, northeast Iowa, and northwest Illinois were degraded by decades of poor land use practices in the late 19th and early 20th centuries (1, 2) (see Vondracek, page 8). Early settlers to the region removed trees from steep hillsides and valley bottoms and plowed upland prairies to promote settlement and agriculture. Loss of protective vegetation led to substantial erosion of hillsides and ravines and subsequent sediment deposition in stream valleys and stream channels. Formerly narrow and deep stream channels with deep pools and gravel riffles were filled with sediment, resulting in wide, shallow channels with few or no pools and riffle areas inundated with fine sand or silt sediments (Melchior, page 20). Originally abundant Brook Trout *Salvelinus fontinalis* were lost from many streams and reduced in abundance in others (1). Subsequent stocking efforts using Brook Trout, Brown Trout *Salmo trutta* and Rainbow Trout *Oncorhynchus mykiss* were deemed failures because instream habitat was considered insufficient to support them. Many studies were conducted between the 1930s and 1990s to identify important habitat needs of stream trout and to guide early fish habitat management practices (1, 3–5). More recently, public funding for restoring and enhancing these stream resources, principally for the salmonid fisheries they support, has increased. More than $2 million USD annually have been made available through federal (e.g., National Fish Habitat Partnerships) and state (e.g., Minnesota Outdoor Heritage Fund) sources.

To ensure stream restoration and enhancement activities include important habitat features for Brook Trout and Brown Trout, in this section we reviewed the biology of these species, as it pertains to the Driftless Area, and synthesize the habitat needs of both species as revealed from studies conducted in Driftless Area streams. **Our specific objectives were to: (1) summarize information on the basic biology of Brook Trout and Brown Trout in Driftless Area streams, (2) briefly review conceptual frameworks organizing fish habitat needs, (3) trace the historical evolution of studies designed to identify Brook Trout and Brown Trout habitat needs in the context of these conceptual frameworks, (4) review Brook Trout-Brown Trout interactions and (5) discuss lingering uncertainties in habitat management for these species.**

Brook Trout and Brown Trout Biology

Brook Trout. Brook Trout are native to North America, with their native range covering much of the northeastern portion of the continent. The Driftless Area lies at the western edge and a southern edge of their native range, which includes all of Wisconsin, eastern Minnesota, and northeastern Iowa (6). Brook Trout are also known as charr and are distinguished from trout such as Brown Trout and Rainbow Trout by the lack of black spots on their body. Brook Trout are characterized by small red spots surrounded by light blue halos scattered on their lateral sides with larger yellowish spots; yellowish vermiculate patterns on their dorsal surface and fin; and lower fins colored in various shades of orange-red with an anterior black border with a white edge. Their ventral surface can sometimes be a brilliant orange-red, particularly on mature males (Fig. 1).

Although mortality occurs throughout the Brook Trout life cycle, Brook Trout typically live to age 3 in streams and may be uncommon at older ages (7, 8). Brook Trout as old as 6 years have been observed in Driftless Area streams (M. G. Mitro, personal observation), and older ages can be attained in

Statement of Interest

All salmonid species, including Brook Trout and Brown Trout, are only native to the Northern Hemisphere. Brook Trout are the only salmonid native to the Driftless Area since the Pleistocene glaciation. Brown Trout are native to Europe, western Asia and northern Africa but all Brown Trout in North America originated from either Germany or Scotland. Both species provide excellent recreational fisheries in the Driftless Area that generate substantial economic and social benefits to the people of this region. Consequently, management of these species, especially habitat management, has important ecological, sociological, political, and economic implications.

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Fig. 1. A large mature male Brook Trout from a Driftless Area stream. Credit: J. Hoxmeier.

larger water bodies and colder environments. Annual survival rates are typically low and variable. McFadden (8) observed annual September-to-September survival rates of 0.21 (21%; age 0-1), 0.10 (age 1-2), 0.04 (age 2-3), and 0.09 (age 3-4) for Brook Trout in Lawrence Creek, Wisconsin (1953-1956). Hoxmeier, et al. (7) observed annual survival rates of 0.24 to 0.45 across ages 0 to 4 in six streams in southeastern Minnesota (2005-2010). The average October-to-October survival rate of age 1 and older Brook Trout in Ash Creek, Wisconsin was 0.16 (range: 0.10 to 0.28; 2004-2011; WDNR, unpublished data).

Brook Trout size-at-age will vary depending on stream size, productivity, thermal regime, and trout density. Brook Trout typically grow to lengths of 3 to 6-in (75 to 150-mm; all lengths reported as total length) in their first year (age 0), 6 to 10-in (150 to 250-mm) by their second year (age 1), and 8 to 13-in (200 to 330-mm) by their third year (age 2). Larger Brook Trout up to 18-in (460-mm) have been observed in Driftless Area streams but are uncommon.

Brook Trout spawn in autumn when water temperature declines and day length decreases. Spawning typically begins in early October and concludes in December, with peak spawning around mid-November (9)(WDNR, unpublished data). Brook Trout spawn in redds, in which eggs are buried in gravel in a nest-like pit in the stream. The gravel allows for stream flow to provide well-oxygenated water to the protected, developing eggs. If flows are insufficient and stream sediment load is high, redds may become buried by silt leading to egg suffocation and reproductive failure. Brook Trout may detect and spawn in areas with upwelling water, which helps keep eggs well oxygenated.

Male Brook Trout may mature as early as age 0 but typically begin spawning by age 1, whereas female Brook Trout may mature as early as age 1 but typically begin spawning by age 2. The average mature female Brook Trout may produce 300 to 400 eggs, with fecundity a function of size and varying from less than 100 eggs in a 5-in (125-mm) female to 1,200 eggs in a 14-in (350-mm) female (9). In a study in Lawrence Creek, Wisconsin, Brook Trout fecundity ranged from less than 100 eggs to about 700 in trout 4 to 10-in (100 to 250-mm) in length (8). In other Driftless Area streams, Brook Trout fecundity ranged from 130 to 1,645 eggs in trout 6 to 15-in (155 to 386-mm; WDNR, unpublished data).

Brown Trout. Brown Trout exhibit a wide range of colors, shapes, spot patterns and fin markings but most often the species is described as olive brown on its back shading to dark green on its sides and with a dark yellow or white belly (Fig. 2). Numerous red and black spots may be common across the body and on the dorsal and adipose fins.

Brown Trout in Driftless Area streams are short lived with few surviving past age 4 (10, 11). Brown Trout as old as 9 years have been observed in Wisconsin streams (M. G. Mitro, personal observation) and in southeast Minnesota, Brown Trout at least as old as age 7 have been identified (12) (D. J. Dieterman, personal observation). Annual survival rates in the 1980s and 1990s in Minnesota streams were estimated to be 0.59 (59%; age 0-1), 0.50 (age 1-2), 0.27 (age 2-3), 0.29 (age 3-4), 0.18 (age 4-5) (11). In a study in the mid-2000s, Brown Trout survival varied among seasons for age 0 and age 1-2 trout combined but did not vary among different reaches across an inter-connected group of streams. Survival across the three study streams was 0.26 for age 0 trout (September-May) and 0.36 to 0.46 (depending on year) for age 1 and 2 trout combined. Conversely, survival of age 3 and older trout varied by stream reach but not by season and was 0.28 to 0.63 depending on the reach the age 3 and older trout inhabited. Seasonal survival for age 0 and age 1-2 Brown Trout was always highest in winter and lowest during the spring-flood (age 0) or fall-spawning (age 1-2) seasons. The average apparent survival rate for adult Brown Trout in Timber Coulee Creek, Wisconsin, from 2004 to 2011 was 0.39 (M. G. Mitro, personal observation).

Like Brook Trout, Brown Trout size at age varies depending on stream size, productivity, thermal regime, food quantity and quality, and trout density. Brown Trout can grow to lengths of 3 to 7-in (75 to 175-mm) in their first year (age 0), 6 to 10-in (150 to 250-mm) in their second year (age 1), 9 to 13-in (225 to 330-mm) in their third year (age-2) and 11 to 14-in (280 to 350-mm) in their fourth year (age 3). Male Brown Trout may grow slightly faster than females in some streams (10).

Brown Trout spawn in the fall with the female digging a redd, where she will deposit her eggs after being attended by one to several males. Brown Trout in the Driftless Area spawn between the first week of September and the first week of December (13, 14). Both sexes are mature by age 2, thus spawning during their third fall, but a few males may be

Fig. 2. Driftless Area Brown Trout. Credit: R. Binder.

mature and spawn at age 1 (10). In a Norwegian stream, larger male and female Brown Trout attracted and successfully bred with larger mates (15). Bigger males mated with only slightly bigger females but not the reverse. A female only needed to be 5-mm longer than another female to be selected, but males needed to be longer than each other by about 50-mm. Most males and females mated with 1 to 3 partners each year, but some males mated with up to 13 to 15 partners in a single spawning season.

In the Driftless Area in southeast Minnesota, female Brown Trout ovaries can represent up to 15% of their body weight and egg size and number (i.e., fecundity) are a function of female size (10). Fecundity is about 250 eggs in an 8-in (200-mm) female, 400 eggs in a 10-in (250-mm) female, 550 eggs in a 12-in (300-mm) female and 700 in a 14-in (350-mm) female (10). In central Wisconsin streams, fecundity estimates were reported to be higher with a 14-in female estimated to produce 1,200 eggs (16). Females typically bury eggs between 6 and 10-in (15 and 25-cm) below the stream bottom with bigger females burying eggs deeper in the substrate. Brown Trout redds are usually placed in riffles or glides but may be placed in pools and runs if depth, velocity and substrate conditions are adequate. Using the Rosgen (17) classification system, Zimmer and Power (18) found that Brown Trout in the Credit River, Ontario preferred C-channel pools and riffles for redd placement and avoided B-channel runs and glides. Although neither preferred nor avoided, redds were also found in C-channel runs and glides and B-channel pools and riffles.

Following fertilization and deposition, egg development within the redd is strongly influenced by water temperature. In southeast Minnesota streams, eggs can hatch anywhere between mid-December and mid-March (13). After hatching, young trout continue to reside within the redd feeding on their yolk-sac and are termed alevins. After the yolk-sac is used up, young trout emerge from the redd, begin feeding on external foods and are called fry. In the Driftless Area, alevins have been found to emerge from the redd between late February and mid-April (13). Flooding during or shortly after emergence can have a large effect on abundance of that year-class in subsequent time periods.

Fish-Habitat Relationships

Ecology at its most basic level is the study of how organisms relate to each other and to their physical surroundings (i.e., habitat). Thus, assessing habitat needs of a species cannot be fully understood without first considering several conceptual frameworks proposed in ecology. Perhaps the most unifying concept underpinning most other concepts is hierarchical scale, or more specifically spatial, temporal, and organismal scales. Ecological scaling acknowledges that larger-scale items are composed of a number of smaller-scale items nested within each larger-scale item. For example, Adams (19) identified several organismal scales representing the species of interest and three of these are useful for assessing habitat needs of species: population, life stage, and individual (Fig. 3). The larger-scale population is composed of multiple smaller-scale life stages (e.g., eggs, juveniles, adults). Each life stage in turn is composed of several individual fish. To quantify and describe the population-scale, three variables have been proposed: recruitment, growth and mortality (20). To describe fish life stages, several variables have been proposed, but five describe most freshwater, non-migratory salmonids: egg stage (fertilized egg deposited in a redd), alevin stage (hatched egg remaining in a redd), fry stage (individual that has emerged from the redd to early summer, about mid-June), immature juvenile (about mid-June in their first summer to development of mature gonads) and mature adult.

To determine habitat needs or more broadly, that is to describe the ecological niche of species, biologists commonly use statistical procedures to associate habitat features to either individuals representing each life stage or to one of the three population-level variables. These habitat associations mapped in environmental space have been termed the "Hutchinsonian Niche" of a species (21, 22). Important habitat features in a species' niche that are uncommon in a stream are often considered to be limiting factors, an old ecological concept (23). This implies that simply increasing the amount of the

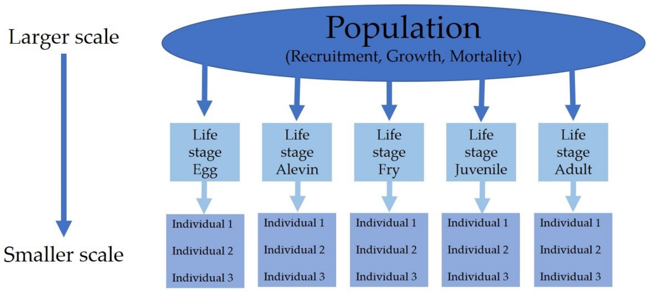

Fig. 3. Selected organismal scales of most freshwater salmonid species of importance to identifying habitat needs. Each larger scale item is composed of multiple smaller-scale items.

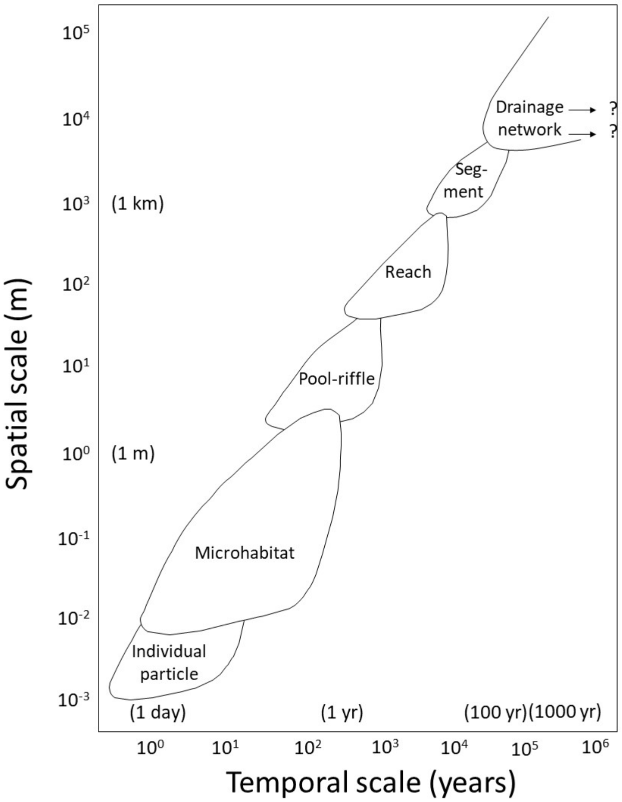

Fig. 4. Approximate spatial and temporal scales over which fish habitat changes in streams and rivers (from Allan (24)). The spatio-temporal linkage implies the time frame (e.g., minutes to hours to days to years) needed to detect meaningful changes at each spatial scale.

limiting factor will result in an increase in population abundance. However, understanding how those habitat features were created in the first place is equally important.

The creation and maintenance of physical habitat that stream fishes use is a result of distinct interactions between water and land over space and time at each habitat scale (24). For example, large spatial-scale features of streams, such as river valleys and floodplains, operate at long temporal scales, taking hundreds of years to form and change. Alternatively, very small-scale habitat features such as sand particles on the stream bed change every second (Fig. 4). In addition, larger spatio-temporal scale processes dictate the form and availability of smaller-scale habitat features that fish use as habitat (25). At very large spatio-temporal scales, processes such as minor glaciation or earthquakes can move entire stream channels at drainage basin or stream segment scales (Fig. 4; Table 1). These stream channel changes may then cause large inputs of sediment from erosion of new uplands or stream channel banks at the reach scale. Excess sediment can then fill pools or interstitial spaces in riffles at the pool-riffle scale. Microhabitats that fish use, such as deep water in pools are then lost at the microhabitat scale. **This illustrates a critical point of stream habitat management: habitat form follows ecological process.** If managers only address the form of habitat at one particular scale (e.g., re-digging out a pool at the pool-riffle scale that has been filled with sediment) without addressing the higher-scale processes that created and maintained that habitat (e.g., sediment movement in the stream channel from bank erosion at the reach-scale) then the habitat feature will return to its former degraded state following restoration actions.

Other scientists noted that the hierarchical scaling of stream habitat focused principally on the physical nature of habitat and failed to explicitly recognize other factors influencing stream biota. An alternative framework of five components was simultaneously proposed to organize the myriad factors influencing overall stream biological integrity: biotic interactions, flow regime, energy sources, water quality, and physical habitat (27). This framework was subsequently adapted to guide overall stream management and management of individual species with slight modifications (28, 29). The new five components were biotic interactions, hydrology, connectivity, water quality, and physical habitat/geomorphology (Fig. 5). Almost all variables regulating or limiting a fish population can be placed within one of these five components. Biotic interactions include predator-prey, competition and disease factors. Hydrology encompasses effects of floods and droughts whereas the water quality component includes dissolved oxygen, turbidity, agricultural chemicals, etc. The physical habitat/geomorphology component incorporates more traditional habitat features such as pool depths, water velocity, and fish cover as well as geomorphic processes that create, maintain or destroy these features. Energy sources, such as sunlight and microbial pathways in the original framework, was replaced by the broader connectivity component. The connectivity component retained the importance of energy movement in stream food webs but also incorporated the emerging importance of fish movements in streams as noted by Gowan, et al. (30). **An important implication of the five-component approach is that management emphasis on only one component, such as restoring physical habitat/geomorphology, may still fail to protect and enhance fish populations if other components, such as water quality or biotic interactions, are also limiting to a population.**

Schlosser and Angermeier (26) blended increasing knowledge of fish movements with landscape ecology and metapopulation concepts and proposed a dynamic landscape model for stream fish populations. Landscape ecology recognized that distinct habitat patches were present on the terrestrial landscape and that habitat patches differed in terms of size, juxtaposition and quality of habitat within them. The concept of metapopulations explicitly incorporated animal movements among these habitat patches. Schlosser and Angermeier (26) proposed that for fishes to complete their annual life cycle they may need to be able to move to different habitat patches in streams to complete critical life stages (Fig. 6). This included movement among habitat patches for spawning, feeding, and refugia from harsh conditions such as winter or drought. **An important implication is that if a single habitat patch does not provide all habitat features needed to complete the life cycle then movement corridors among patches will need to be identified and maintained.** This includes seasonal movements to and from spawning, feeding and winter habitat. **In addition, creation of new habitat features, as is common during instream restoration projects, will need to be cognizant of which part of the life cycle or life stage the**

Table 1. Events and associated processes controlling stream habitat at different spatiotemporal scales in the Driftless Area (adapted from Frissel, et al. (25)). Events in bold text are directly controlled by man.

System level	Linear spatial scale (m)	Evolutionary Events[a]	Developmental processes[b]	Time scale of persistence (years)
Drainage network	10^6-10^4	Glaciation; climatic shifts	Planation; denudation	1,000,000 to 100,000
Segment section	10^4-10^3	Minor glaciation; earthquakes; alluvial or colluvial valley infilling; **watershed land use changes**	Migration of bedrock nickpoints or channel head cuts; development of new first-order channels	10,000 to 1,000 (100 years due to poor landuse practices)
Reach section	10^3-10^2	Channel shifts; cutoffs; **channelization; damming by man; stream restoration activities; riparian land use practices**	Aggradation (from poor land use); degradation (large sediment storing structures (dams)); bank erosion; change in stream slope	100 to 10
Pool/riffle system	10^2-10^0	Bank failure; flood scour or deposition; **stream restoration activities**	Small-scale lateral erosion; elevational change in bed form; minor bedload sorting	10 to 1
Microhabitat	10^{-1}	Annual sediment delivery; organic matter transport; substrate scour	Seasonal depth, velocity changes; accumulation of fines; periphyton growth	1-yr to 1-mo

[a] Evolutionary events are extrinsic forces that create and destroy systems at that scale.

[b] Developmental processes are intrinsic and represent changes following an evolutionary event.

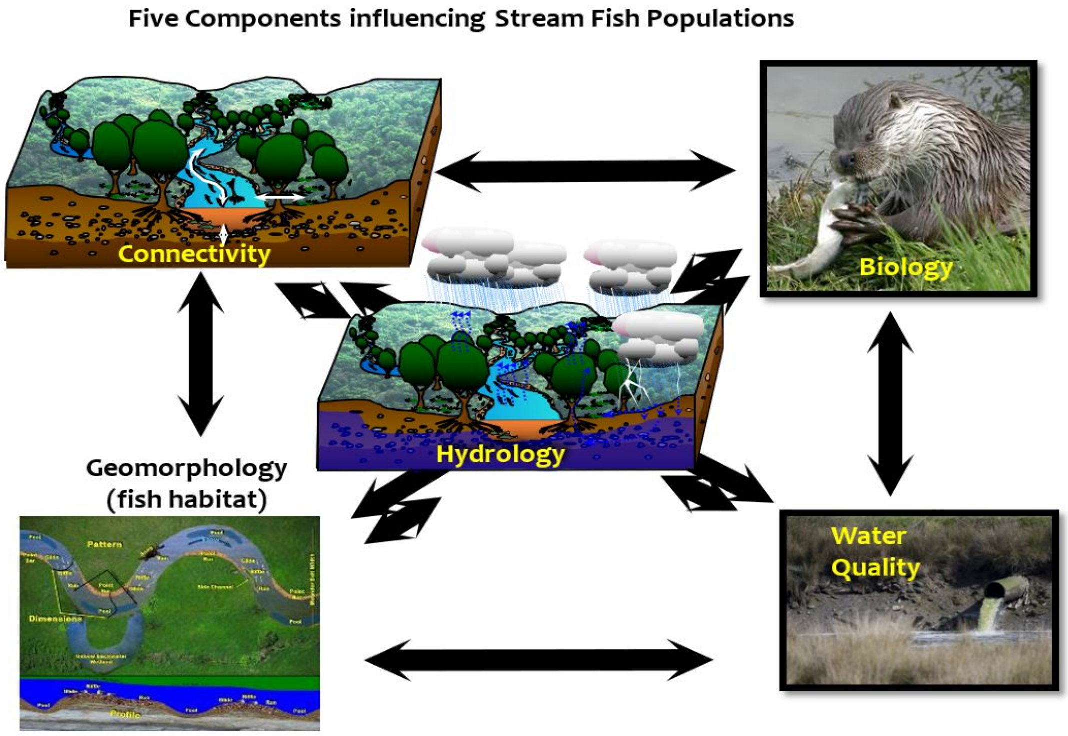

Fig. 5. Five components of streams influencing the health of streams and rivers and their associated fish populations (from L. Aadland, MNDNR).

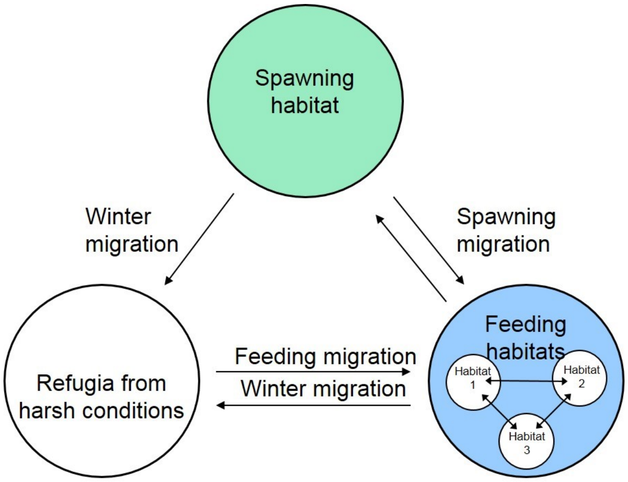

Fig. 6. Dynamic landscape model for stream fishes to complete their life cycle (modified from Schlosser and Angermeier (26) for fall-spawning salmonids).

restored habitat patch is providing habitat for and the distance between that restored habitat patch and other patches necessary for completion of other life stages. However, a corollary to this model is that fishes may not need to move if a single habitat patch fulfills the needs of all life-stages.

Finally, to provide a more holistic framework that incorporated all of the preceding concepts and models, Fausch, et al. (31) proposed the riverscape approach to guide management and conservation efforts for stream fishes. The riverscape approach expanded the dynamic landscape model to note, in part, that management and research efforts need to consider how fish movements among all heterogeneous habitat patches across the full extent of all spatial and temporal scales dictate the persistence and abundance of stream fishes in any particular habitat patch at a particular time. For example, their riverscape approach encouraged assessment of habitat requirements over longer-time scales than traditional within-season assessments (e.g., assessing summer habitat requirements of fishes because most fish sampling occurred during summer) and at much larger spatial scales than the 150 to 1,500-ft (50 to 500-m) sampling stations common to many previous fish-habitat studies. In particular, they noted the need to understand, sample, and manage fish populations at 0.5 to 50-mi (1 to 100-km) stream segment and 5 to 50-year scales. Collectively, each of these conceptual frameworks is important to describing the habitat requirements of stream fishes and incorporating that information in the implementation of stream habitat restoration projects (Table 2).

Brook Trout and Brown Trout Habitat Needs

Brook Trout. Brook Trout are a sportfish uniquely suited for living in Driftless Area streams and many aspects of the Hutchinsonian niche, especially the thermal niche, have been described. Brook Trout are typically associated with cold, clear streams, which are abundant across the karst topography of the Driftless Area (Splinter, page 5). Brook Trout can be found in small headwater streams or larger, higher-order streams with suitable thermal regimes and physical habitat that support the trout life cycle.

Brook Trout share similar thermal tolerance limits with Brown Trout and Rainbow Trout (32). Thermal tolerance limits can be defined by water temperatures in which trout have been observed over a defined duration of time. For example, the maximum 3-day mean temperature for a Wisconsin or Michigan stream in which Brook Trout or Brown Trout were found was 75.6°F (24.2°C) (32). This temperature was found for a stream by taking the highest 3-day moving average for every 3-day interval during the June-August period of record. The maximum n-day daily mean temperature decreased rapidly from 77.5 to 72.5°F (25.3 to 22.5°C) for exposure periods ranging from 1 to 14-days and declined more gradually from 71.8 to 69.8°F (22.1 to 21.0°C) for 21 to 63-day exposure periods (32). Brook Trout can survive short-term spikes in water temperature, such as those associated with surface runoff from precipitation events during summer, provided it does not exceed the upper incipient lethal temperature, which may vary depending on the acclimation temperature for the fish (33). But chronic exposure to elevated water temperatures can be limiting, with the limiting temperature decreasing as exposure time increases.

Within thermal tolerance limits for trout are a series of decreasing temperature ranges preferred for functions such as feeding and growth. Behnke (6) noted that species of the genus *Salvelinus*, which are often referred to as charr and include Brook Trout, can be distinguished from species of *Salmo* such as Brown Trout or species of *Oncorhynchus* such as Rainbow Trout by their adaptation to, and preference for, colder water within thermal tolerance limits. Charr, which also include Lake Trout *S. namaycush*, Bull Trout *S. confluentus*, Arctic Charr *S. alpinus*, and Dolly Varden *S. malma*, have an optimal temperature range of 10 to 14°C versus 14 to 18°C for trout and salmon. However, among the charr, Brook Trout are more tolerant of warmer water and are more comparable to Brown Trout and Rainbow Trout (6). Different studies have reported different thermal preferences for trout, which vary due to acclimation temperatures. In a summary of thermal preference data for fish, the optimum growth temperature was reported as 55, 57, and 61°F (13, 14, and 16.1°C) for Brook Trout and 50, 53.5, 55, and 60°F (10, 12, 12.8, and 15.5°C) for Brown Trout, and the final preference temperature was reported as 52, 57, 64, and 66.5°F (11.3, 14, 18, and 19.2°C) for Brook Trout and 54, 57.7, and 63.7°F (12.2, 14.3, and 17.6°C) for Brown Trout (34). The take-home messages on thermal conditions supporting Brook Trout and Brown Trout may therefore be: (1) acclimation temperature (i.e., prior temperature experience) is important in identifying thermal optima, preference, or tolerance; (2) each species may thrive under similar thermal conditions; and (3) factors other than temperature may be important in determining which species thrives best in a coldwater stream.

As outlined in Schlosser and Angermeier's dynamic landscape model and the broader riverscape approach, Brook Trout require different habitats during the various stages of their life history. These include habitat for spawning, habitat for rearing during early life stages, habitat for adults, and overwintering habitat. Habitat characteristics including physical habitat, water quality, and hydrology have been well described for Brook Trout. Brook Trout usually spawn in gravel riffle areas as described above and eggs develop overwinter until hatching sometime between mid-winter and early spring.

Brook Trout fry may emerge from spawning redds from January through April depending on when spawning occurred and conditions during incubation, such as temperature. Brook Trout fry need rearing habitat with low water velocity and protective cover during their first month or two following emergence from spawning redds. During spring, Brook Trout fry can often be seen along stream margins. Brook Trout are vulnerable during spring flood events that may wash young trout out of streams. Year-class abundance has been positively associated with flows lower than normal and negatively associated with flows higher than normal (35), which can result in regional trends in recruitment (36). Year-class defining flood events can occur any time following emergence through their first summer depending on the magnitude of the flood event. However, stage-based population models also show that Brook Trout population growth rates are sensitive to survival from late in their first growing season (age 0 in autumn) to early in their second growing season (age 1 in spring) (37, 38).

As Brook Trout grow and relocate to other stream areas, they begin to establish and defend territories. Defending a territory allows a fish to sequester resources such as access to food and protection from predators or strong flows. Defending a territory is advantageous to the fish when energy obtained by feeding exceeds energy expenditures in holding and defending the territory. Such habitat for adults becomes limiting in degraded streams, and stream habitat development projects have been used to increase adult trout biomass.

Stream habitat development (aka, habitat improvement, restoration) in Wisconsin streams is predicated on the idea that in some streams adequate spawning and rearing habitat and an abundant food supply would support more trout if more adult habitat were available. Hunt (39) demonstrated how stream habitat development could increase brook trout biomass, numbers, and production in a long-term project on Lawrence Creek, Wisconsin. The development project narrowed and deepened the stream channel, increased pool area and streambank cover for trout, and used paired bank covers and current deflectors to increase stream sinuosity. Stream habitat development today is a widely used approach by state management agencies and conservation organizations like Trout Unlimited to rehabilitate or restore degraded streams and to improve trout fisheries therein.

Overwintering habitat is also very important to Brook Trout and often overlooked in trout habitat evaluations (35). Winter is a dynamic and stressful time for fishes in streams, requiring changes in fish behavior to survive (40). Brook Trout winter habitat typically includes deeper stream areas with slower water velocity and greater overhead cover, with Brook Trout sometimes aggregating in pools near areas of groundwater discharge (41). Age 1 and older trout generally occupy positions in water deeper and faster compared to age 0 trout, the latter of which may use interstitial spaces along stream margins (41, 42).

At the largest spatial scales, such as the drainage network scale, the karst topography of soluble limestone and dolomite in the Driftless Area provide an abundance of coldwater springs feeding the smaller-scale productive coldwater stream segments and reaches that support Brook Trout. The density of Brook

Table 2. Selected conceptual frameworks of ecological importance to describing, organizing, quantifying and managing habitat requirements of stream fishes.

Concept	Key aspects	Implications
Ecological scaling (19, 24, 25)	Ecological scales are hierarchically nested; Populations are composed of distinct life cycle stages each of which are composed of individuals; Larger-scale items and processes influence smaller-scale processes; Space and time interact at each scale	Management of a habitat feature without regard for larger-scale processes creating and maintaining it will be ineffective
Hutchinsonian niche (21, 22)	The needs of any species can be organized and quantified along an axis and there are many axes that describe where and how a species lives; For example, there are axes for habitat needs (e.g., water depth, velocity), prey source needs (prey size, prey type), etc.	Various habitat features (e.g., water depth) can be quantified and plotted along axes to identify a fish's niche or habitat needs that might be created in habitat projects; A fish population may be at low abundance because one or two key axes are missing. These few axes are considered to be limiting the population and increasing those will result in a population increase
Five components of streams (27, 28)	Hydrology, water quality, connectivity, biotic interactions and physical habitat/ geomorphology regulate fish population abundance in streams	Management of only one component will be ineffective if another component limits the population
Dynamic landscape model (26)	Streams provide a heterogeneous mosaic of distinct habitat patches; Fish may need to move among patches to complete critical life cycle stages of recruitment, growth, and survival during harsh environmental conditions	If a single habitat patch doesn't provide all features to complete a life cycle, movement corridors among patches will need to be maintained; Stream restoration projects may need to provide habitat diversity to ensure all life cycle needs are met
Riverscape approach (31)	Synthesized previous conceptual models; Need to understand complete spatial and temporal arrangement of all habitat patches at all scales; Fish life history facets, from genetics to populations, may require 1 to 100-km stream segments and 5 to 50-years to complete	Stream restoration projects may need to be scattered across much larger spatial scales and may need to persist in a functional state for at least 50-years

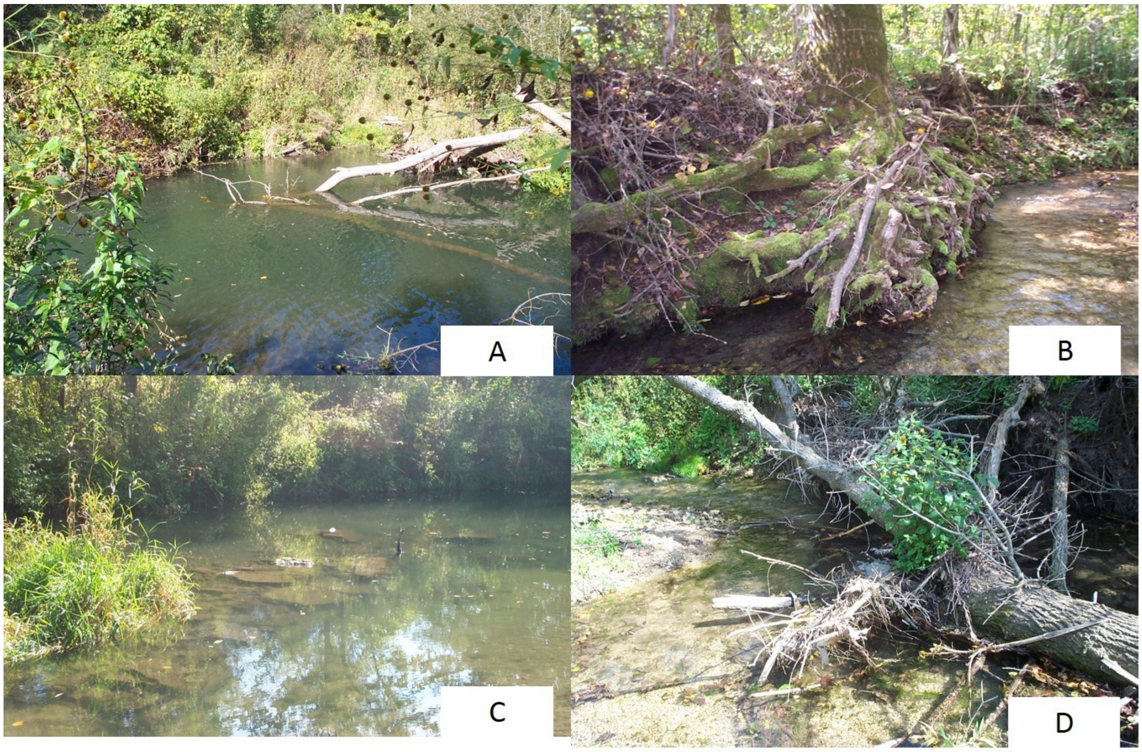

Fig. 7. Important instream cover for large Brown Trout in Driftless Area streams includes pools with depths exceeding 3-ft (A), overhead bank cover such as natural undercut banks with root wads (B), large instream rocks (C) and woody debris (D). Credit: D. Dieterman.

Trout that can be supported in these streams is positively related to stream discharge (7). Higher levels of baseflow support more physical habitat for trout, provided stream conditions have not been degraded. Changes in climate and land management over the past century have led to improvements in Driftless Area stream baseflow, which has coincided with improvements in trout fisheries. Juckem, et al. (43), in a study of the Kickapoo River Watershed in Wisconsin, showed that the timing of an increase in baseflow followed an increase in precipitation after 1970, with higher infiltration rates of precipitation, associated with less intensive agricultural land use, responsible for increasing the magnitude of the change in baseflow. A combination of agricultural lands protected in the Conservation Reserve Program and minimal impervious surfaces in a watershed support groundwater recharge and provide for cold water in Driftless Area streams (44, 45). As recently as the 1970s, Driftless Area streams in Wisconsin were largely devoid of wild trout populations (9, 46). Today, Driftless Area streams boast some of the most productive trout fisheries in the world (47), which can be attributed to a combination of improved land use, a favorable climate, a dedicated stream habitat development program, and improved genetics of trout stocked to restore extirpated populations (48).

Brown Trout. Although native to Europe, and extreme western Asia and northern Africa, Brown Trout have been introduced around the world and the subsequent literature on this species is vast. Because of this, many aspects of the Hutchinsonian niche of Brown Trout have been described previously but most by studies conducted outside of the Driftless Area. Much of this literature has been summarized in several review papers (33, 49–51). Most reviews presented niche information for selected Brown Trout life stages at microhabitat and pool/riffle spatio-temporal scales. These niche axes can be organized into four of the five stream components (Table 3). The oxy-thermal niche axes have been the most studied (33, 52) but other water quality and physical habitat/geomorphology parameters have been studied as well.

Because of the preponderance of information from other areas, relatively few niche axes have been directly examined in the Driftless Area. Wehrly, et al. (32) examined the thermal niche in upper Midwestern streams that included several Driftless Area streams. They developed thermal tolerance criteria for Brown Trout based on field observations. Most observations indicated a weekly thermal tolerance limit of about 75.2 to 77.9°F (24.0 to 25.5°C) and a daily maximum of 81.7°F (27.6°C). Grant (53) quantified the microhabitat feeding niche in one stream on the northern extent of the Driftless Area. Drift-feeding sites for 6 to 12-in (150 to 300-mm) Brown Trout were from 1 to 3-ft (30 to 100-cm) deep with column velocities from 0.6 to 0.9-ft/s (0.2 to 0.3-m/s). For larger Brown Trout (>12-in, or 300-mm) drift-feeding sites were 2 to 3-ft (60 to 100-cm) deep with velocities from 0.46 to 0.88-ft/s (0.15 to 0.29-m/s). Although not specifically quantifying Brown Trout niche axes, several other studies have examined Brown Trout associations with other parameters in the Driftless Area. These include biotic interactions of predation, diet and intra- and inter-specific interactions (54–57) (see later section in this review); water quality parameters including stream productivity (47), sediment (58), dissolved oxygen (13); and hydrology, principally flooding effects (13, 59). However, the physical habitat component has been perhaps the most studied aspect of the Brown Trout's niche in southeast Minnesota.

Many Driftless Area studies examined Brown Trout associations with physical habitat features at multiple spatial scales in large part because this component has been amenable to stream habitat management programs. Most studies quan-

Table 3. Summary of selected aspects of the Brown Trout niche at microhabitat and pool/riffle spatio-temporal scales based on published information outside of the Driftless Area. Data are organized by life stage for each of the five components of streams. Overall maximum-minimum values, representing niche boundaries, are presented here. See references in text for more detailed information.

		Life Stage				
Component	Parameter	Egg[1]	Alevin	Fry	Juvenile	Adult
Hydrology	Flooding	No winter floods, variously defined (e.g., >75th-percentile flows)	No flooding during spring emergence (flooding variously defined)	Intermediate flows best (variously defined)	undefined	Intermediate flows best (variously defined)
Water quality	Oxygen	≥7.0 mg/L	≥7.0 mg/L, ≥80% saturation	≥3 mg/L		
	Temperature (survival)	0-8°C	0-22°C	0-25°C	0-29°C	0-29°C
	Temperature (growth)			7-19°C		4-19.5°C
	pH			5.0-9.5	5.0-9.5	5.0-9.5
	Suspended sediment				≤59,800 mg/L (1 hr) ≤400 mg/L (1 week)	≤59,800 mg/L (1 hr) ≤400 mg/L (1 week)
Physical habitat	Depth	6-82 cm	6-82 cm	5-35 cm	14-122 cm (50-65 cm preferred)	≥60 cm
	Column velocity	11-80 cm/s		0-20 cm/s	0-70 cm/s	
	Focal velocity	0.03 cm/s		0.1-4 cm/s	<20 cm/s	<27 cm/s
	Substrate	8-128 mm	8-128 mm	10-90 mm	8-128 mm	
	Cover	Woody debris		≥15% stream surface area composed of small branches, cobble substrate, instream vegetation	≥15% stream surface area composed of small branches, cobble substrate, instream vegetation	Woody debris, instream rocks, instream vegetation, undercut banks, overhanging vegetation
Biotic interactions	Intra-cohort Brown Trout density			≤10 fry/m^2	≤1.5 juveniles/m^2	≤0.50/m^2

[1] Physical habitat for the egg stage describes characteristics associated with locations of spawning redds where eggs were deposited.

tified Brown Trout population responses, usually changes in abundance or biomass, following manipulation of fish cover, at pool/riffle and stream-reach scales (3, 4, 60, 61). Such manipulations have variously been termed instream habitat improvement, enhancement, or restoration. These studies showed positive increases in Brown Trout abundance or biomass following addition of overhead bank cover, current deflectors, instream rocks, or large wood (1, 3, 5). Many projects also observed increasing Brown Trout abundance in association with increasing pool depths (generally depths >2-ft, or 60-cm) following stream narrowing (1, 3). Authors speculated that abundance increases were due to increased natural recruitment and higher adult survival. Collectively, these studies demonstrated that adult cover was a primary factor limiting adult Brown Trout abundance in Driftless Area streams as concluded by Thorn, et al. (1). Based on these studies, Thorn, et al. (1) provided a table of recommended amounts of cover to be maintained or added in stream habitat projects at pool-riffle and stream reach scales (Table 4).

Several early studies (1970s-1990s) found that abundances of larger Brown Trout, those 14-in or longer (≥356-mm), did not respond to management actions, such as more restrictive angling regulations or instream habitat improvement. This led to recommendations to investigate habitat requirements of these larger individuals (62, 63). Studies were subsequently conducted that investigated summer and winter habitat needs of larger Brown Trout, but again at stream reach and pool/riffle scales (12, 59, 64). Important reach-scale features were larger streams (summer baseflows >15.2-ft^3/s, or 0.43-m^3/s) with abundant cover in pools. Important cover types were water depths >35.4-in (>90-cm), overhead bank cover, instream rocks and woody debris (Fig. 7). Cumulatively, all four cover types should be present in a pool and the latter three, (overhead bank cover, instream rocks, and woody debris) should exceed 10-m^2 of pool surface area. Dieterman, et al. (64) investigated the microhabitat niche of wintering large Brown Trout during daylight and found selection for depths from 23.9 to 46.9-in (60 to 119-cm) near woody debris and with water column velocities ≤4-in/s (≤10-cm/s). They also concluded that artificially placed habitat structures were used similarly to natural cover, such as undercut banks, in streams that had been rehabilitated.

At larger stream segment and drainage network scales, Brown Trout populations in Driftless Area streams have been associated with land use patterns, soil types and underlying geology. For example, higher Brown Trout abundance and improved trout growth have been associated with larger drainage basins with increasing percentages of forested lands and bedrock with greater porosity (65–70). More specifically, Blann (66) found that adult Brown Trout abundance was positively associated with the Jordan sandstone geologic layer, a layer known for its many springs. Conversely, stream segments with fewer adult Brown Trout have upstream drainage basins with more urban (>11%) or agricultural (69% on average)

Table 4. Recommended amounts (percent of total stream area except as indicated) of instream habitat in pools and stream reaches for juvenile and adult Brown Trout in the Driftless Area (adapted from Thorn (1))

Variable	Abbreviation	Recommended amount or range
Overhead bank cover (%)[a]	OBC	2-12
Instream rock cover (%)	IR	2-3
Debris cover (%)[b]	DEB	5
Total cover (%)[c]	TC	20
Length of OBC/thalweg length (%)	LOBC/T	20
Area of water deeper than 60 cm (%)	D60	25
Pool bank shade (%)	PBS	75
Pool length / reach length (%)	PL	75
Gradient (m/km)	GRAD	5-7
Velocity (cm/s)	VEL	15-25

[a] Includes undercut banks, artificial structures, overhanging grass. [b] Usually woody debris but can be other debris items (e.g., old farm machinery in the stream). [c] Sum of OBC, IR, DEB.

landscapes with soils with high runoff potential (45, 66). However, most Driftless Area studies have noted that large-scale drainage basin features usually explained only modest amounts of variation (<40%) for specific Brown Trout variables, that is, land use is only part of the picture. This is probably because the trout are responding to proximate instream habitat features, such as pool depth and cover (60, 66), rather than the larger-scale drainage basin features directly. However, as noted previously, larger-scale drainage network and stream segment processes are important regulators of proximate instream habitat features, patterns confirmed for Driftless Area watersheds in southeast Minnesota (69).

Almost all Driftless Area studies on Brown Trout habitat needs focused on physical habitat components with identification of cover as a primary limiting factor for adult life stages and at pool/riffle and stream-reach scales. However, individual pools and stream reaches only represent single habitat patches scattered across the entire stream system. Earlier we discussed the importance of also considering all the other habitat patches that exist throughout a riverscape and potential importance of fish movements among those patches to complete seasonal life cycle needs (e.g., seasonal movements to/from summer-feeding areas and overwintering habitats) or critical life stages (e.g., juvenile feeding areas in summer or fall spawning areas in headwater reaches). Although, no studies have examined the importance of a complete Driftless Area riverscape to Brown Trout populations, one study examined the importance of 3.5 or more mi (>6-km) of riverscape to juvenile and adult life stages in southeast Minnesota (59, 71). In that study, six geomorphically similar reaches were identified and represented six habitat patches differing in terms of habitat features. Three were shallow reaches with abundant riffle habitat for spawning and two of these reaches were headwater sites near spring inputs with colder summer water temperatures (59). The other three patches had more deep-water pool habitat with adult cover that could provide winter and spring-flood refugia. One of the tenets of the dynamic landscape model is that fishes may need to move seasonally among spawning, feeding, and refugia habitat patches to complete critical life stage needs. However, no large-scale seasonal movement patterns among these habitat patches were documented for either juvenile or adult Brown Trout suggesting that each habitat patch had adequate habitat to fulfill annual life cycle needs (i.e., each patch had habitat to support spawning, rearing, wintering and adequate growth). The primary pattern observed was an ontogenetic shift of smaller and younger trout in shallow habitat patches transitioning to adjacent patches with more deep pools as they grew into larger adults. In particular, one stream reach with extensive instream habitat improvement did not conform to earlier predictions that habitat improvement project areas produce excess individual trout that emigrate into adjacent reaches (i.e., increased fish production in adjacent reaches). Instead, smaller and younger Brown Trout (ages-0, -1, and -2) immigrated into the reach with habitat improvement as they grew older and increased trout abundance there. The authors speculated that as the trout grew in size, they sought deeper pool habitat with good cover, stream features provided by the habitat improvement project. More deep-water pool habitat and instream cover likely increased Brown Trout immigration and subsequent survival.

Brook Trout and Brown Trout Interactions

Competition. Biotic interactions is one of the five components that regulate the abundance of stream fishes and several studies have examined the interactions between Brook Trout and Brown Trout. The only salmonid to historically populate Driftless Area streams was the native Brook Trout. Following the 19th century introduction of nonnative Brown Trout to midwestern streams, the distribution of Brown Trout has increased and distribution of Brook Trout has decreased. It should be noted that Brown Trout were not simply added to streams populated by Brook Trout. Poor land use during the late 19th and early 20th centuries led to extirpation of trout from many Driftless Area streams (9, 46), and late 20th century improvements in land use and stream conditions were often followed by stocking of Brown Trout rather than Brook trout. The native ranges of Brook Trout and Brown Trout do not overlap, and these species do not naturally co-occur. Plots of Brown Trout versus Brook Trout catch per effort for adult trout surveyed in Wisconsin streams show that while co-occurring populations of Brook Trout and Brown Trout now exist, rarely do these species occur together at or near equal abundances (Fig. 8). Rather, streams tend to be dominated by one species or the other.

The mechanisms for change in species dominance are varied and may have included, following introduction of Brown Trout, biotic interactions that favored reproductive success or stage-specific survival of one trout species over another and net immigration or emigration (72). Such interactions between individuals of the same or different species, in which one or more individuals experience a net loss and none experience a net gain, is termed competition. For salmonid species that do not naturally co-occur, there is a greater likelihood that interspecific competition will affect one of the species (73). Stream habitat and environmental conditions also may affect the outcome of biotic interactions of Brook Trout and Brown Trout such that different trout species succeed in some streams and not in others (Johnson, page 70).

The evidence for interspecific competition between Brook Trout and Brown Trout is varied. The segregation of Brook

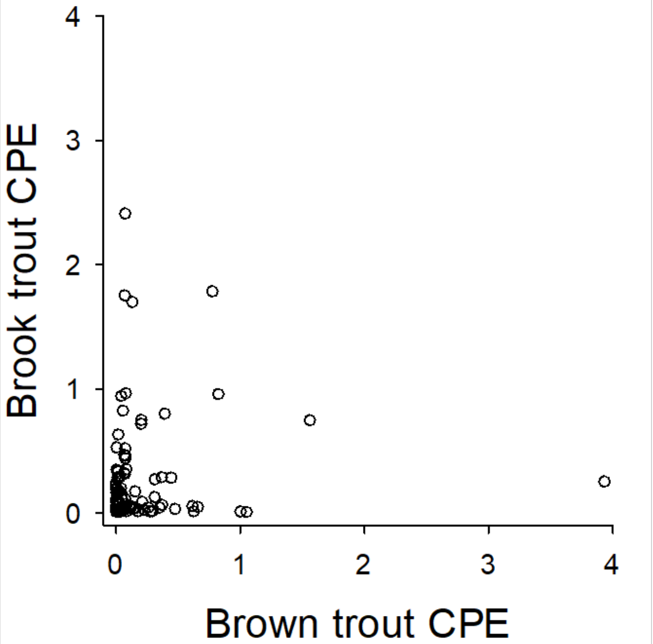

Fig. 8. Catch per effort (CPE) of Brown Trout versus Brook Trout in 345 Wisconsin streams in which only Brown Trout (n=126), only Brook Trout (n=134), or both Brown Trout and Brook Trout are present (n=85). Data from WDNR.

Trout and Brown Trout observed in streams (74) may be selective or interactive, with interactive segregation a result of interference competition. Interference competition may be observed when co-occurring species differ in resource use, in contrast to similar resource use when they are not co-occurring. Interference competition may occur when behavior of one individual interferes with the ability of another to acquire a resource. A good example is the territorial behavior by trout in streams that may result in interference competition in which the superior competitor occupies the most profitable stream habitat measured in terms of net energy gain while drift feeding (e.g., growth).

Fig. 9. A Brook Trout x Brown Trout hybrid from a Driftless Area stream often called a Tiger Trout.

Fig. 10. A gill louse *Salmincola edwardsii* from a Brook Trout captured in Maple Creek, Fillmore County, Minnesota in 2008. Credit: J. Hoxmeier.

Observations of changes in abundance of one species following introduction of another can also serve as evidence of interspecific competition (75). A limitation of such observations, however, is the potential confounding of other factors such as predation of one species on another. Controlled experiments have been used to separate such factors and have provided evidence to show that Brown Trout can be competitively superior to Brook Trout. For example, Fausch and White (76) conducted field experiments in a Michigan stream to show that introduced Brown Trout can aggressively exclude Brook Trout from preferred resting places. Following release of competition from Brown Trout, Brook Trout shifted resting positions. Fausch and White (76) also noted that declines in Brook Trout populations while Brown Trout populations expanded may have been attributable to the combined effects of interspecific competition, predation on juvenile Brook Trout by Brown Trout, and a differential response to environmental factors. In laboratory studies of native Brook Trout and hatchery Brown Trout, DeWald and Wilzbach (77) found that Brown Trout presence resulted in changes in Brook Trout behavior. Brook Trout shifted location, initiated fewer aggressive interactions towards other Brook Trout, lost weight, and were more susceptible to disease in the presence of Brown Trout. The authors suggested that if these changes in behavior and growth rates extended to co-occurring populations in streams, they may help explain observed declines in native Brook Trout populations.

Competition for spawning habitat in streams may also be important in displacement of Brook Trout by Brown Trout. Brook Trout and Brown Trout spawning seasons consistently overlapped by two to four weeks in Valley Creek, a small Minnesota stream, during a three-year study in which Sorensen, et al. (78) observed attempts at hybridization (Fig. 9) and superimposition of spawning redds (i.e., building a new redd on top of an existing redd). About 10% of sexually active females were courted by males of both species. There was evidence of redd superimposition, particularly by later-spawning and larger Brown Trout. The authors concluded that reproductive interactions may be partially responsible for displacement of Brook Trout by Brown Trout because Brook Trout spawn earlier in the season, are smaller in size, and rarely survive long enough to spawn in subsequent years. A subsequent study by

Essington, et al. (79) found that frequency of superimposition of redds was greater than expected by chance, with females exhibiting a behavioral preference to spawn on existing redds. Grant, et al. (80) also showed that reproductive interactions between Brook Trout and Brown Trout may play a role in displacement of native Brook Trout by introduced Brown Trout.

Life history differences between Brook Trout and Brown Trout favor Brown Trout population growth. Although female Brown Trout begin to mature at age 2 (versus age 1 in Brook Trout), they live longer, grow larger and become more fecund than Brook Trout. Brown Trout commonly live to age 4 or 5 in streams and may live to age 9 or older (M. G. Mitro, personal observation) and commonly grow to 12 to 20-in (300 to 500-mm) in length (16). A 14-in (350-mm) Brown Trout can produce about 1,200 eggs, a 16-in (400-mm) Brown Trout can produce 1,500 eggs, and a 20-in (500-mm) Brown Trout can produce over 2,700 eggs. Over time, these demographic differences will favor population growth rates in Brown Trout over Brook Trout.

The infection of Brook Trout with the gill louse *Salmincola edwardsii* (Fig. 10) also favors Brown Trout in streams where the two trout species co-occur (56). *S. edwardsii* is an ectoparasitic copepod that infects the gills of Brook Trout but not Brown Trout. Brown Trout in Wisconsin have been observed to not have any parasites typically found in Brown Trout where they are native (R. White, personal communication). An epizootic of the *S. edwardsii* in Ash Creek, Wisconsin in 2012-2014, for example, led to a 77 to 89% decline in age 0 Brook Trout recruitment. Brown Trout are also present in Ash Creek and did not experience such a decline in age 0 recruitment. The inspection of Brook Trout for *S. edwardsii* in 283 streams across Wisconsin in 2013-2017 showed that the epizootic that occurred in Ash Creek was not common. However, *S. edwardsii* were found to be present in 79% of streams inspected with prevalence of infection (percent of fish infected) ranging from 0.4 to 100%, and maximum intensity of infection was 15 or more *S. edwardsii* in a Brook Trout for 34% of streams where the parasite was present. In the Driftless Area of southeast Minnesota, *S. edwardsii* were present on Brook Trout in 24 of 60 streams (40%) examined from 2006 to 2009 (81). Changing environmental conditions such as warming stream temperatures and drought conditions may favor the *S. edwardsii* life cycle and potentially lead to further epizootics and the potential extirpation of Brook Trout where Brown Trout co-occur (56).

Trout Habitat Needs in the Driftless Area: Lingering Uncertainties

For Brook Trout, there is a continuing need to determine if there are habitat features that could be incorporated into habitat development projects that may favor Brook Trout over Brown Trout when those species co-exist in the same stream. Although Hunt (39) documented an increase in Brook Trout following common stream habitat development techniques, such as narrowing and deepening a stream, Brown Trout were not present in his study stream, Lawrence Creek, Wisconsin (though some Rainbow Trout were present). Do habitats used by Brook Trout differ when they are the only salmonid species present versus when co-occurring with Brown Trout? Several studies have suggested that when co-occurring with Brown Trout, Brook Trout prefer headwater areas (74), but Hoxmeier and Dieterman (82) demonstrated that when Brown Trout are removed from larger downstream areas, Brook Trout from headwaters will emigrate and reproduce in the downstream reaches. In another study, Hoxmeier and Dieterman (83) documented a natural decrease in Brown Trout abundance coincident with an increase in Brook Trout in East Indian Creek, Minnesota. This suggests that some natural environmental changes may enhance Brook Trout abundance at the expense of Brown Trout. Identification of these environmental factors may help promote management efforts that benefit Brook Trout. Limited data from East Indian Creek suggested that baseflows increased and summer water temperatures decreased from the 1970s to the mid-2010s, but a more rigorous testing of these and other factors, including changing habitat features, is needed.

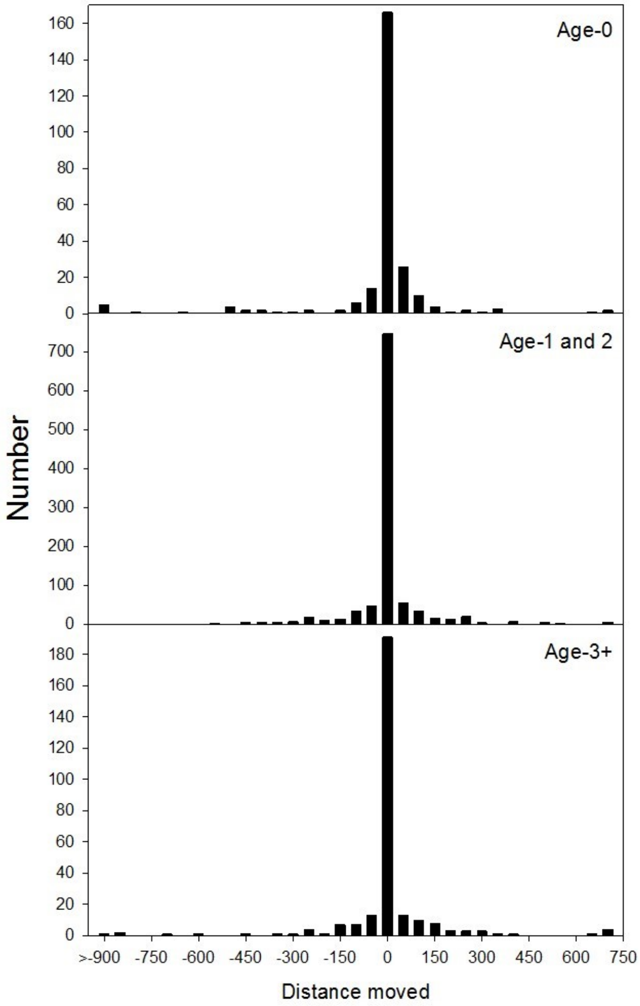

Fig. 11. Frequency of distance moved (in meters) by individual Brown Trout of three age groups in nine consecutive sampling events spaced three months apart from September 2006 to September 2008 in three inter-connected southeast Minnesota streams. Negative numbers are downstream movements. Similar movements were observed for Brook Trout (84).

Although much is known about the habitat needs of Brook Trout and Brown Trout based mostly on studies outside the

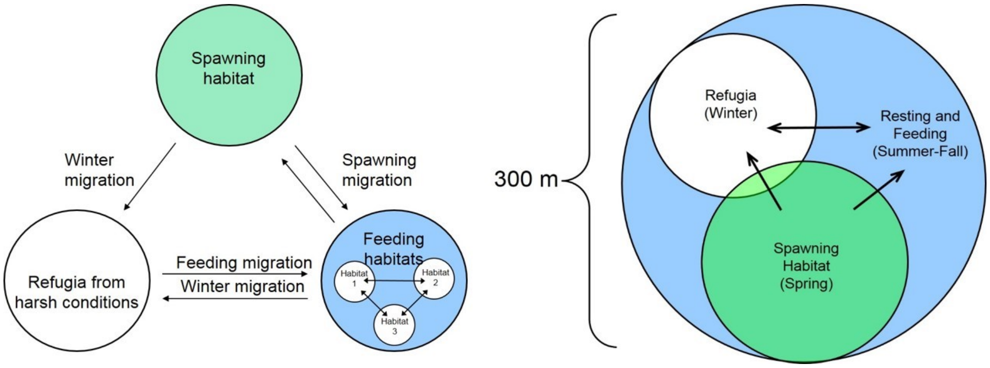

Fig. 12. Riverscape conceptual figures contrasting the need for fish movement in differing stream systems. The figure on the left is the traditional riverscape concept, emblematic of northeastern Wisconsin trout fisheries, where trout need to move to different stream reaches to fulfill key life history needs (e.g., spawning or overwintering habitat). The figure on the right likely exemplifies most Driftless Area streams where trout are able to fulfill all their habitat needs within a short stretch of stream (e.g., within one or two pool/riffle sequences).

Fig. 13. A downstream reach of a Driftless Area stream in southeast Minnesota. These reaches often have abundant sand and silt substrate limiting trout spawning and often become thermally stressful during warm summers, yet can still provide excellent recreational fisheries in some seasons and years. The inset picture shows a 14-in Brown Trout caught at this site. Credit: D. Dieterman.

Driftless Area, there are still several lingering questions that could influence the prioritization, placement, design and management of instream habitat. In particular, how does the full riverscape approach apply to trout management and research in the Driftless Area? Past management and research have confirmed that cover is often a limiting physical habitat feature in Driftless Area streams and Dieterman and Hoxmeier (59) demonstrated that improvement of such habitat in typical "blue ribbon" trout streams (i.e., streams with existing optimal water temperatures and dissolved oxygen levels for supporting wild trout) will fulfill most of the niche needs of juvenile and adult Brown Trout life stages. This is probably due to the abundance of groundwater springs to most streams which provide ample water flows with moderate, almost ideal thermal regimes for trout. Thus, when physical habitat conditions that fulfill the year-round needs of trout are present or enhanced in habitat improvement projects (e.g., deep pools with log jams for overwintering, gravel riffles for spawning, etc.), Driftless Area trout probably do not need to move much. Dieterman and Hoxmeier (59) and Hoxmeier and Dieterman (84) found that most juvenile and adult Brown Trout and Brook Trout stayed within one or two pool/riffle sequences (<900-ft, or <300-m) in Driftless Area streams in southeast Minnesota (Fig. 11). In contrast, trout in other stream systems, such as in northeastern Wisconsin, may need to move greater distances to find appropriate habitat conditions to fulfill life cycle needs (Fig. 12).

Less certain are other applications of the riverscape concept including application to some stream reaches with seasonally-poor habitat and importance for early life history stages and genetics. Some Driftless Area stream reaches have excellent trout fisheries at certain times of the year. Most often these reaches are at the most downstream end of streams with an abundance of sand and silt substrate and are believed to become thermally stressful during summer months (Fig. 13). Such reaches are also believed to provide a variety of abundant fish prey such as Creek Chub *Semotilus atromaculatus* and White Sucker *Catostomus commersonii*. Large adult trout are known to inhabit these reaches because angling for them can be excellent during some seasons and years. Knowing where, when and how long these larger adult trout inhabit these areas (and their movements to and from them) is less well known, making justification for, and design of, instream habitat projects less certain for these areas.

Dieterman and Hoxmeier (59) were unable to examine other aspects of a complete Driftless Area riverscape including dispersal of younger Brown Trout life stages (eggs, alevins, fry) and the larger spatial (>3.7-mi, or >6-km, they studied) and longer time periods (5 to 50-years; Dieterman and Hoxmeier's study was three years) recommended by Fausch, et al. (31). In particular, the importance of even a small number of fish moving throughout a riverscape may be important to aiding population recovery following disturbance or to maintaining genetic diversity (85). Although most Brook Trout and Brown Trout appeared to move little in the Driftless Area streams examined by Dieterman and Hoxmeier (59) (Fig. 11), a few individuals did move longer distances (>2,700-ft, or 900-m) and some disappeared entirely indicating that they either died or moved completely out of the 3.7-mi (6-km) study area. These few individual dispersers may play an important role in maintaining the genetic integrity of the broader trout population in the riverscape. Thus barriers, such as improperly designed road crossings or perched culverts (Fig. 14), could still be problematic.

Examination of habitat needs over longer time periods are important for identifying other key factors, such as hydrology, water quality, and biotic interactions, that may be limiting Brook Trout and Brown Trout in Driftless Area streams. For example, Mundahl (86), used a 25-year dataset for Brown Trout in a 610-ft (200-m) section of Gilmore Creek, a Driftless Area stream in Minnesota, to document that Brown Trout population dynamics were related to hydrology and biotic

Fig. 14. Perched culverts, such as this culvert on Trout Brook in Dakota County, Minnesota, may prohibit trout movements during most stream flow conditions, except large floods. Credit: D. Dieterman.

interactions, such as intraspecific competition. Implementation of such long-term studies is imperative but requires long-term commitments in resources (staff time and money) to maintain study integrity. Such long-term monitoring programs can help evaluate system resistance and resilience to rare events (e.g., floods, fish kills), time lagged responses, true changes in highly variable systems, and effects of management actions (87).

There is also lingering debate about the appropriateness of various stream restoration designs for bolstering Driftless Area trout populations and how long those artificially placed habitat structures will persist (or should persist). Much of the lingering debate is fueled by a poor understanding of stream restoration terminology and lack of robust long-term data to assess persistence of artificially-placed structures. In overly simple terms, the debate contrasts the use of traditional techniques of using rock to narrow streams and "stabilize" them in a permanent position versus using less rock and more geomorphic principles to design a geomorphically-stable stream channel (i.e., a channel that may move but that retains its width, depth, gradient, and meander pattern (Fig. 15; Melchior, page 20). The geomorphic approach is sometimes call natural channel design (NCD) and may include instream wood for additional fish cover. Even though several studies reviewed in this chapter noted the importance of instream wood as habitat for Brook Trout and Brown Trout, there continues to be debate about the importance of wood as fish cover in Driftless Area streams. In addition, many traditional habitat projects that used wood have been incorrectly labeled NCD, leading to suggestions that NCD projects do not provide cover for trout. The paucity of true NCD projects and the fact that this is a relatively new approach means that there have not been many comprehensive, long-term evaluations completed and certainly none that have simultaneously contrasted NCD with more traditional designs. Thus, the debate over these two broad approaches will likely continue until more data are collected.

Finally, there is a lack of verification of the importance of selected habitat features for large Brook Trout and Brown Trout. For example, several studies documented in this review identified important physical habitat aspects of the niche of large Brown Trout including the importance of deeper pools ($>$25-in, or $>$90-cm) with woody debris, instream rocks, and overhead bank cover. However, very few instream habitat projects have specifically incorporated these items in projects with a stated goal to increase large Brown Trout abundance. Implementation of a number of such projects is needed, in conjunction with adequate long-term monitoring, to verify the importance of these features to bolstering large trout abundance for anglers as has been documented for adult trout in several agency review reports (3).

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Fig. 15. Examples of two broad approaches to enhancing or restoring stream habitat. The figure on the left is a more traditional approach that uses a lot of rock to stabilize a stream channel and provide fish habitat (note the substantial amount of rock on both sides of the stream). The figure on the right represents a natural channel design approach that constructs a stable stream channel using geomorphology principles. Some natural channel design projects use woody debris, in addition to limited amounts of rock, for channel stabilization and fish cover (note the presence of root wads along the left bank in the photograph).

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