Movement patterns in inland cutthroat trout (Oncorhynchus clarki utah): management and conservation implications

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Abstract: Knowledge of movement patterns is critical to the management and conservation of inland salmonids. We studied the movements of Bonneville cutthroat trout (Oncorhynchus clarki utah) in a drainage in western Wyoming, USA. Our objectives were to (i) characterize the postspawning movement patterns of adult Bonneville cutthroat trout, (ii) contrast postspawning and summer movement patterns, and (iii) identify factors that disrupt the movements of Bonneville cutthroat trout. Our data showed that postspawning movements of Bonneville cutthroat trout formed a continuum, with fish moving from 0.5 to 82.0 km. Postspawning distance was positively related to fish length. Despite the wide range of movement observed during the spring, fish did not move more than 0.5 km during the summer. A road culvert and an irrigation diversion dam did not seem to pose barriers to the upstream movement of Bonneville cutthroat trout to headwater spawning areas in the spring. However, 23% of radio-tagged fish in 2000 moved into the irrigation diversion ditch as they moved downstream after spawning and subsequently died there. Maintaining drainage connectivity is an important conservation concern for trout populations such as this one, where fish move between complementary spawning and summer habitats.

Introduction

Movement is an integral part of the life history of many stream fishes. If most individuals in a population are sedentary (Gerking 1959; Hughes 2000), then a relatively small length of stream may provide sufficient habitat to meet all life-history needs. Preserving movement corridors and maintaining watershed connectivity may not be as critical for such species as it is for other species that undergo large-scale movements and utilize different habitats located in different parts of the watershed (Young 1994; Brown and Mackay 1995; Swanberg 1997). For such wide-ranging species, human-caused fragmentation of rivers can reduce population viability (Rieman and Dunham 2000). Fragmentation in streams causes declines in fish populations by interrupting movements to and from critical sites that fish must reach to complete their life history (Schlosser 1995). Consideration of the time scales over which movement occurs is also necessary. From the perspective of habitat selection and use, knowledge of movement within the lifetime of an individual is important, whereas from a metapopulation-dynamics perspective, understanding movement patterns...
over generations or even longer time scales is critical. Where stream-fish species fall along this continuum of movement has generated a lively debate among fisheries biologists (Gowan et al. 1994; Rodriguez 2002) because of the importance of movement patterns to management and conservation of stream fishes (Fausch et al. 2002; Webster et al. 2002).

The recent adoption of a landscape or “riverscape” perspective in stream ecology emphasizes the need to understand fish movement patterns in relation to the spatial arrangement of habitats in a drainage (Fausch et al. 2002). The spatial arrangement of habitats is important because the need for fish to move, and consequently the impacts of barriers to movement, depend on the degree of habitat complementation within stream reaches. Habitat complementation refers to the spatial proximity of different but non-substitutable habitats required by a species to complete its life cycle (Dunning et al. 1992; Schlosser 1995). When habitat complementation is low, critical habitats are located relatively long distances apart. Consequently, an individual must expend more energy to reach required habitat, perhaps exposing itself to increased risk of predation or other sources of mortality along the way (Dunning et al. 1992; Schlosser 1995). Furthermore, interruption of movement to and from complementary habitats will prevent individuals from completing their life cycle and ultimately cause declines in populations. Studying movement patterns can identify which portions of a stream are most critical for maintenance of a population (Rieman and Dunham 2000). The preservation of connectivity among habitats is especially critical to populations that face fragmentation from road crossings, reservoir development, water withdrawal, or introduction of non-native species.

In addition to knowing the extent of movement in a population, it is important to know how population demography affects movement patterns. There is evidence that larger fish move longer distances (Clapp et al. 1990; Young 1994). Long-distance movers may be larger as a result of greater growth potential in higher order reaches where they can become piscivorous (Behnke 1992; Bunnell et al. 1998; Colyer 2002). Or fish may be moving to find increased space, better physical habitat, or more tolerable thermal regimes (Kahler et al. 2001; Roni and Quinn 2001; Schrank et al. 2002). Because fecundity increases exponentially with body size, large fish that may spend most of their lives in main-stem areas potentially contribute more genetic material to the next generation than small fish that live in smaller tributaries. Examining reasons for variation in movement patterns related to fish size may help indicate how habitat requirements for individuals within a population vary and how conservation efforts can best target all portions of the population.

The objectives of our study were to (i) characterize the postspawning movement patterns of adult Bonneville cutthroat trout (Oncorhynchus clarki utah), (ii) contrast postspawning and summer movement patterns, and (iii) identify factors that disrupt the movements of Bonneville cutthroat trout. Fausch et al. (2002) indicated the need for collecting spatially continuous data on stream fishes. By using radiotelemetry we were able to gain a continuous view of Bonneville cutthroat trout postspawning and summer movements throughout an entire watershed and position this population along the sedentary–migratory continuum. Angermeier et al. (2002) indicated that knowledge of spatiotemporal dynamics of fish movement is lacking. We examined movement patterns across spring and summer to describe some of the temporal variation that exists in movement patterns of individual fish. Finally, we sought to identify potential barriers to movement and the consequences of these barriers for the fish population. Fausch et al. (2002) indicated that rare features in a drainage such as a barrier can be disproportionately important to stream-fish populations. By tracking fish continuously through spring and summer we were able to determine if barriers prevented movement among complementary habitats in this watershed.

Methods

Study site

This study took place in the Thomas Fork drainage (584.2 km²) of the Bear River in Lincoln County, Wyoming, and Bear Lake County, Idaho, USA (Fig. 1). The climate in this drainage consists of cold snowy winters and hot dry summers. Huff, Little Muddy, and Coal creeks flow through land heavily impacted by livestock grazing. Consequently these creeks have little riparian vegetation to shade the stream. In recent years the Wyoming Game and Fish Department and the US Bureau of Land Management have been working to restore habitat conditions for Bonneville cutthroat trout in these tributaries (Binns and Remmick 1994). Water Canyon Creek flows through land that is not as heavily impacted by grazing, and it has a dense willow riparian area and numerous beaver dams along its length. The riparian area of the Thomas Fork main stem in Idaho is dominated by hay agriculture. During the summer, much of the Thomas Fork is diverted for irrigation, primarily through the Taylor Ditch (Fig. 1).

The Thomas Fork drainage contains native populations of Bonneville cutthroat trout and no non-native salmonids. The Bonneville cutthroat trout, along with other native subspecies of cutthroat trout throughout the western USA, has experienced severe declines as a result of hybridization with non-natives and habitat degradation and fragmentation, and is considered a species of concern by state and federal management agencies (Young 1995; US Fish and Wildlife Service 2001).

Objective I: to characterize the postspawning movement patterns of adult Bonneville cutthroat trout

We used radiotelemetry to determine the distribution of displacement distances as fish moved from spawning locations to summer locations. A total of 62 fish were implanted with radio transmitters during spawning (16 May – 8 June) in 1999, 2000, and 2001 in Coal, Huff, Little Muddy, and Water Canyon creeks (Table 1, Fig. 1). Fish were captured by electrofishing and anesthetized with clove oil (Anderson et al. 1997). Depending on fish weight, a transmitter with an external antenna weighing 2.9 or 3.6 g (Advanced Telemetry Systems Inc., Isanti, Minnesota, USA) or 8.9 g (Lotek Wireless Inc., Newmarket, Ontario, Canada) was surgically implanted into the ventral body cavity of each fish, just anterior to the pelvic girdle (Adams et al. 1998). In all fish the radio transmitter weight in air did not exceed 2% of the body weight of the fish (Adams et al. 1998). Fish were ground-
tracked with an Advanced Telemetry Systems R2000 receiver operating at frequencies of 150.000–151.999 MHz and a four-element Yagi antenna. During spring 2000 and 2001 fish were tracked both from the ground and using at least monthly aerial flights, but were ground-tracked only in 1999. When a fish was located its position was recorded using a Global Positioning System (GPS).

Adult fish captured on the spawning grounds in the spring were assumed to have spawned. Twelve of the 62 implanted fish died in the spawning tributaries before the end of June and were eliminated from the study. These fish were eliminated because it was impossible to determine how far they would have moved after spawning. The 50 fish that remained were tracked until death or late summer, whichever came first. In 1999 two fish were lost as they moved downstream after spawning. Because we were not using flights to relocate fish during 1999 and the Thomas Fork main stem was not easily accessible by foot, we assumed that these fish continued downstream beyond the area we could track on the ground. However, they could have been removed by predators, therefore we used the last known location of these fish to estimate their movement distance.

Movement distances of each radio-tagged fish were calculated from GPS locations using a geographic information system with ArcView® 3.2 and ArcInfo® 8.1 software (Environmental Systems Research Institute, Inc., Redlands, California, USA). Total postspawning displacement distance was recorded from the most upstream location of a fish (where it was assumed to have spawned) to the location to which it had moved as of 30 days after the spawning season ended each year. We chose 30 days because all fish that left their spawning tributary had done so by then. All postspawning movement distances reported refer to total displacement distance.

In addition to examining the distribution of displacement distances, we examined the relationship between postspawning movement patterns and fish total length. We used simple linear regression to examine the relationship between post-
spawning movement distance (in kilometres) and fish total length (in millimetres). To eliminate fish that may have died before reaching summer locations, we only used fish that were alive on 1 July in this analysis (N = 17).

Objective II: to contrast postspawning and summer movement patterns

To address objective II we examined mobility patterns across seasons using two approaches. First, we compared histograms of spring versus summer displacement distances for 12 of the 50 fish originally tagged in the spring that we were able to monitor through the subsequent summer. These 12 fish were tracked between 3 and 21 times during the summer. Second, in addition to the 50 fish radio-tagged in the tributaries in the spring, 11 other fish were radio-tagged in Coal, Huff, and Little Muddy creeks during the summer (Fig. 5). Between 4 August 1998 and 2 July 2001, 1235 fish were implanted with VI tags below the large highway culvert on Salt Creek. These included 403 fish that were implanted with VI tags below the Taylor Ditch diversion dam (Fig. 1). Reaches upstream of these barriers were sampled from May 1999 through September 2001 to determine if any fish tagged below these structures were able to pass them successfully.

Results

Objective I: to characterize the postspawning movement patterns of adult Bonneville cutthroat trout

Movement distances ranged from less than 0.5 km to 82.0 km downstream from spawning locations (Fig. 2). No fish moved upstream. Postspawning movement distances formed a continuum, with two fish even leaving the Thomas Fork and entering the Bear River system (Fig. 3). There was a significant positive linear relationship between postspawning movement distance moved and fish length (N = 17, r² = 0.38, P = 0.009, df = 16, α = 0.05, Fig. 4).

Objective II: to contrast postspawning and summer movement patterns

Movement patterns of 12 fish radio-tagged during spawning in spring of 1999, 2000, or 2001 were monitored throughout the subsequent summer. Despite the range of movement observed after spawning (up to 82.0 km), the same fish showed little movement during the summer at a scale larger than 0.5 km (Figs. 5a and 5b). Because some of these fish were located only a few times, we also examined summer movement data for the group of 11 fish radio-tagged between 24 June and 10 July 1999 and located every other day until at least 10 September 1999. None of these 11 fish had a displacement distance of more than 0.3 km throughout the summer (Fig. 5c).

Objective III: to identify factors that interrupt fish movement

One VI-tagged fish and one radio-tagged fish moved above both the Salt Creek highway culvert and the Taylor Ditch diversion dam (Table 2, Fig. 6). An additional VI-tagged fish was observed to have moved successfully upstream through
Fig. 2. Postspawning movement distances varied from 0.5 to 82.0 km (N = 50). The large peak at 16 km represents 21 fish that moved to lower Salt Creek and subsequently died there.

the Salt Creek highway culvert. Finally, seven VI-tagged fish and two radio-tagged fish moved upstream past the Taylor Ditch diversion dam. The maximum water velocity through the Salt Creek highway culvert was at least 1.5 m s\(^{-1}\) during the spring.

In addition to monitoring barriers to upstream movements, we also monitored disruption of downstream movement. No radio-tagged fish entered the Taylor Ditch in 1999 (N = 7) or 2001 (N = 15). However, in 2000, 9 of 40 (23%) fish that were radio-tagged on the spawning grounds eventually moved downstream into the Taylor Ditch and subsequently died there when irrigation flows ceased in late summer (Fig. 3).

Discussion

Understanding the movement patterns of inland salmonids is critical to preserving and managing populations. However, there has been much debate about where inland salmonids fall on the migratory–resident continuum (Gowan et al. 1994). A classic example of migration involves cutthroat trout that live in Yellowstone Lake most of the year, migrate up into tributaries in the spring to spawn, and return to the lake immediately after spawning (Varley and Gresswell 1988). At the other extreme are populations of salmonids in streams where fish are considered to be highly sedentary throughout their lives (Miller 1954; Young 1998). However, even salmonids living in small streams may move farther upstream to find spawning sites on relatively small scales, indicating that many salmonids are migratory at some level (Soloman and Templeton 1976; Young 1994, 1996). Our data showed that Bonneville cutthroat trout that moved extensively after spawning moved over a much smaller range during the summer. Other researchers have also noted this pattern (Swanberg 1997; Hilderbrand and Kershner 2000; Schmertlering 2001), and therefore characterizing movements of salmonids during one season will not necessarily allow movement patterns during other seasons to be predicted.

The extent of migratory behavior within a population appears to depend on the degree of habitat complementation that exists in a drainage (Dunning et al. 1992; Schlosser 1995). If all the habitats fish need to complete their life history are in close proximity, then movement will be minimal. However, if spawning, feeding, and overwintering habitats are located far apart, then movement distances will be high (Schlosser 1995). In the Thomas Fork drainage, we never observed spawning activity in the main stem; however, spawners were frequently observed in the tributaries. Furthermore, White (2003) found many young-of-the-year Bonneville cutthroat trout in the tributaries but few in the main stem of the Thomas Fork. Our data showed that of 50 fish radio-tagged on the spawning grounds, 75% moved out of the tributaries within 30 days of spawning. Clearly, fish in the Thomas Fork need the combination of main-stem habitat for feeding and overwintering and tributary habitat for spawning. Furthermore, for some fish these habitats are located a long distance apart, requiring a high degree of movement. Rather than focusing on the proportion of mobile or sedentary fish in a population (Hegggenes et al. 1991; Hughes 2000; Rodriguez 2002), determining the range of movement and why movement occurs will offer more insight into which habitats are critical for population persistence.

Often, researchers model fish movement by assuming that fish move randomly through the environment following a model of passive diffusion (Rodriguez 2002). Data from our study indicate that cutthroat trout postspawning movements do not follow a negative exponential function suggestive of passive diffusion. Hilderbrand and Kershner (2000) also noted that movement of Bonneville cutthroat trout in their study stream did not fit a model of passive diffusion. This suggests that cutthroat trout in these streams are exhibiting ranging behavior (Dingle 1996) in which they move downstream after spawning and stop when they reach suitable summer habitats. In our case, the movement data have a peak at 16 km representing a large number of fish that moved downstream to lower Salt Creek. These fish resided in a reach with an exceptionally deep pool and extensive overhanging vegetation that was rare in upstream reaches or in tributary streams. Interestingly, despite the apparent high quality of the habitat, most of the fish in this reach died during the remainder of the summer. We suspect that this mortality was caused by river otters (Lutra canadensis) because we saw otter scat and tracks in the area and located some of the radio transmitters in heavy brush far away from the stream. Thus, although we usually consider that movement to downstream deep-water habitat reduces the exposure of trout to predators, there may be localized situations where predation remains a significant source of mortality.

One of the patterns apparent in this study was that larger fish tended to move farther after spawning than smaller fish. Several researchers have found that movement distances increase with fish length for brown trout (Salmo trutta) (Clapp et al. 1990; Young 1994; Bunnell et al. 1998). In contrast, Hilderbrand and Kershner (2000) found no relationship between distance moved and fish length in their study of Bonneville cutthroat trout in a headwater stream in Idaho. This discrepancy with our results is probably due to the absence of large fish in the Idaho study, where the maximum length of fish captured (300 mm total length) was less than in our study (503 mm total length). It has been suggested that fish move downstream after spawning because of greater...
growth potential in higher order stream reaches, including the opportunity to become piscivorous (Clapp et al. 1990; Behnke 1992; Bunnell et al. 1998). In the Thomas Fork, piscivory by large trout would require movement to the farthest downstream reaches, where small prey fishes, especially cyprinids, become abundant (Colyer 2002).

If fish are not moving downstream to find food it is possible that they are simply searching for increased habitat space (Kahler et al. 2001; Roni and Quinn 2001). Headwater tributaries of the Thomas Fork tend to be shallow, with few deep pools (Binns and Remmick 1994). Large fish that return from spawning later may have to continue downstream until they encounter suitable habitat space lower in the drainage. Gowan and Fausch (1996) showed that salmonids will move relatively long distances (>500 m) until they encounter suitable habitat and then will tend to remain in these areas. If fish are moving to find better habitat, this suggests that habitat restoration would increase fish abundance in the tributaries by increasing habitat complementation. For example, Binns and Remmick (1994) examined Bonneville cutthroat trout populations before and after habitat improvement on
Huff Creek. Large cutthroat trout (>15 cm total length) increased from 22 km\(^{-1}\) before habitat improvement to 106 km\(^{-1}\) 11 years after habitat improvement, suggesting that habitat limited the abundance of large fish in the tributaries. Habitat restoration has been historically concentrated in the tributaries in the Thomas Fork drainage, but could include improvement of spawning substrates in lower portions of the drainage. Habitat improvement is likely an effective strategy for increasing habitat complementation and thus increasing the carrying capacity for large trout in this drainage.

In addition to understanding the temporal variation in movement patterns, determining if there are barriers to movement is critical to maintaining inland salmonid populations. Although we thought that the Salt Creek highway culvert and the Taylor Ditch diversion dam had the potential to be major barriers to upstream movement in the Thomas Fork,

Fig. 5. Frequency histograms of movement distances for postspawning movements of 12 fish radio-tagged during spawning (16 May through 8 June 1999–2001) (a); summer movements (1 July through 31 August 1999–2001) of the same 12 fish (b); and summer movements (1 July – 31 August 1999) of 11 additional fish radio-tagged during summer 1999 (c).
Table 2. Summary of fish recorded moving past the Salt Creek highway culvert and (or) the Taylor Ditch diversion dam.

<table>
<thead>
<tr>
<th>ID No. and tag type</th>
<th>Date implanted</th>
<th>Total length (mm)</th>
<th>Weight (g)</th>
<th>Date recaptured</th>
<th>Total length (mm)</th>
<th>Weight (g)</th>
<th>Structure passed</th>
</tr>
</thead>
<tbody>
<tr>
<td>1, VI</td>
<td>9 June 1999</td>
<td>372</td>
<td>508</td>
<td>3 Aug. 1999</td>
<td>368</td>
<td>451</td>
<td>Culvert</td>
</tr>
<tr>
<td>2, VI</td>
<td>6 Oct. 1999</td>
<td>400</td>
<td>646</td>
<td>27 May 2000</td>
<td>402</td>
<td>529</td>
<td>Both</td>
</tr>
<tr>
<td>3, VI</td>
<td>6 Oct. 1999</td>
<td>352</td>
<td>412</td>
<td>18 May 2000</td>
<td>356</td>
<td>404</td>
<td>Dam</td>
</tr>
<tr>
<td>4, VI</td>
<td>6 Oct. 1999</td>
<td>360</td>
<td>510</td>
<td>18 May 2000</td>
<td>361</td>
<td>454</td>
<td>Dam</td>
</tr>
<tr>
<td>5, VI</td>
<td>6 Oct. 1999</td>
<td>212</td>
<td>93</td>
<td>2 July 2001</td>
<td>263</td>
<td>154</td>
<td>Dam</td>
</tr>
<tr>
<td>6, VI</td>
<td>27 Apr. 2000</td>
<td>160</td>
<td>32</td>
<td>14 Aug. 2000</td>
<td>200</td>
<td>73</td>
<td>Dam</td>
</tr>
<tr>
<td>7, VI</td>
<td>27 Apr. 2000</td>
<td>246</td>
<td>120</td>
<td>14 Aug. 2000</td>
<td>266</td>
<td>160</td>
<td>Dam</td>
</tr>
<tr>
<td>8, VI</td>
<td>27 Apr. 2000</td>
<td>204</td>
<td>70</td>
<td>14 Aug. 2000</td>
<td>232</td>
<td>108</td>
<td>Dam</td>
</tr>
<tr>
<td>9, VI</td>
<td>8 May 2000</td>
<td>240</td>
<td>114</td>
<td>14 Aug. 2000</td>
<td>264</td>
<td>140</td>
<td>Dam</td>
</tr>
<tr>
<td>10, radio</td>
<td>8 May 2000</td>
<td>369</td>
<td>435</td>
<td>24 May 2000</td>
<td>×</td>
<td>×</td>
<td>Both</td>
</tr>
<tr>
<td>11, radio</td>
<td>8 May 2000</td>
<td>418</td>
<td>614</td>
<td>9 May 2000</td>
<td>×</td>
<td>×</td>
<td>Dam</td>
</tr>
</tbody>
</table>

aVI, visual implant tag; radio, radio transmitter.

A × denotes missing data.

“Culvert” indicates that a fish moved upstream past the Salt Creek highway culvert, “dam” indicates that a fish moved upstream past the Taylor Ditch diversion dam, and “both” indicates that a fish moved upstream past both structures.

Fig. 6. Map showing locations of fish implanted with visual implant (VI) and radio tags below the Salt Creek highway culvert and (or) the Taylor Ditch diversion dam and the locations to which these fish moved upstream of these structures. Squares indicate locations below potential barriers at which fish were radio- and VI-tagged and subsequently relocated upstream of these structures (N = 12). An asterisk denotes a radio-tagged fish. Numbers inside or pointing to squares indicate the identification number(s) of the fish tagged there. Ovals indicate recapture locations of fish originally tagged downstream of barriers. Numbers inside or pointing to circles indicate the identification number(s) of the fish recaptured there.
some fish were able to navigate these structures. Belford and Gould (1989) modeled the ability of rainbow trout (Oncorhynchus mykiss) to swim through highway culverts and predicted that the maximum current speed passable by trout (161–393 mm total length) would be 1.32 m·s⁻¹ for a 10 m long culvert. However, fish that passed through the Salt Creek highway culvert swam against velocities of at least 1.5 m·s⁻¹ over a distance of 16 m. This discrepancy likely reflects the fact that fish in our study were generally longer (369–400 total length) than those used to develop the models of Belford and Gould (1989). The fish that moved above the Thomas Fork irrigation diversion dam had to leap a maximum of 1.1 m during spring runoff, which is within the leaping ability of salmonids (Bjornn and Reiser 1991). Although some fish made it past each of the potential migration barriers in the Thomas Fork, we do not know what proportion of the population may have been unable to get past them.

Surprisingly, disruption of downstream movement was more of an issue than disruption of upstream movement. Upstream migration of Bonneville cutthroat trout coincides with high spring flows that facilitate jumping over or circumventing potential barriers (Bjornn and Reiser 1991). Downstream migration occurs during lower flows, when water withdrawal increases the likelihood of fish following major currents and being diverted into dead-end canals. When the timing of irrigation along the lower Thomas Fork coincides with the time fish are returning from spawning, as it did during the spring of 2000, fish are vulnerable to being trapped in the Taylor Ditch diversion. There is no screen or other device on this ditch to prevent fish access, and fish moving downstream may be directed into the ditch rather than down the actual river channel. Of the 40 fish implanted with radio transmitters during the spring of 2000, 23% were trapped in the Taylor Ditch and subsequently died there. Given that estimates of mortality after spawning range from a minimum of 38% for westslope cutthroat trout (Oncorhynchus clarki lewisi) (Schmetterling 2001) to 89% for Lahontan cutthroat trout, Oncorhynchus clarki henshawi (Vinyard and Winzeler 2000), an additional 23% mortality could have severe consequences for cutthroat trout populations. This supports the contention of Fausch et al. (2002) that a rare feature in the environment such as a barrier can have a disproportionate effect on a stream fish population.

Extensive movements such as those observed in cutthroat trout have important implications for both management and conservation of fish. From a management perspective, vulnerability to harvest may vary among habitats. For example, large trout can be highly vulnerable to angling during the period they spend in shallow tributary streams and thus, seasonal closures, increased size limits, or reduced creel limits may be needed to reduce harvest. Management activities that increase habitat complementation, such as restoration of pool habitat in shallow tributary streams or creation of spawning areas lower in the drainage, can increase local population size by reducing the need for fish to emigrate to upstream or downstream reaches. From a conservation perspective, maintaining connectivity between complementary habitats such as spawning, summer, and overwintering areas will ensure that fish have access to all habitats necessary to sustain the population. Furthermore, it is important to note that movement pathways can be disrupted not only by blocking upstream spawning movements but also by connecting to sink habitats, such as irrigation canals, as fish return downstream.

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