A field experiment to assess passage of juvenile salmonids across beaver dams during low flow conditions in a tributary to the Klamath River, California, USA.

Short Title: fish passage over beaver dams

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ABSTRACT

Across Eurasia and North America, beaver (*Castor* spp), their dams and their human-built analogues are becoming increasingly common restoration tools to facilitate recovery of streams and wetlands, providing a natural and cost-effective means of restoring dynamic fluvial ecosystems. Although the use of beaver ponds by numerous fish and wildlife species is well documented, debate continues as to the benefits of beaver dams, primarily because dams are perceived as barriers to the movement of fishes, particularly migratory species such as salmonids. In this study, through a series of field experiments, we tested the ability of juvenile salmonids to cross constructed beaver dams (aka beaver dam analogues). Two species, coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*O. mykiss*), were tracked using passive integrated transponder tags (PIT tags) as they crossed constructed beaver dams. We found that when we tagged and moved late-summer parr from immediately upstream of the dams to immediately downstream of them, most of them were detected upstream within 36 hours of displacement. By the end of a 21-day field experiment, 91% of the displaced juvenile coho and 54% of the juvenile steelhead trout were detected on antennas upstream of the dams while <1% of the coho and 15% of the steelhead trout were detected on antennas in the release pool below the dams. A similar but shorter 4-day pilot experiment with only steelhead trout produced similar results. In contrast, in a non-displacement experiment, juveniles of both species that were captured, tagged and released in a pool 50 m below the dams showed little inclination to move upstream. Finally by measuring hydraulic conditions at the major flowpaths over and around the

dams, we provide insight into conditions under which juvenile salmonids are able to cross these constructed beaver dams, which should help guide future restoration efforts.

INTRODUCTION

Human-constructed dams and other instream obstructions have become a ubiquitous feature across riverine landscapes and have altered many natural processes by reducing ecosystem connectivity. In the past five millennia, millions of dams have been constructed by humans, with over two million built in the USA alone [1, 2]. Currently, efforts are underway to remove many of these dams, with the primary objective of restoring stream connectivity, and more specifically, to improve fish passage [3, 4] .

While the number of dams built by humans is impressive, there are actually fewer dams in North America now than prior to European colonization, albeit of a different size and materials. Historic estimates of North American beaver (*Castor canadensis*) populations range from 60-400 million, suggesting that across their 1.5 x10^7 km^2 range, there was anywhere from 10-60 million beaver dams, mostly made of sticks and mud [5-7]. In addition, large wood formed millions of jams, dams and other obstructions that dammed and diverted sediment and water across streams, rivers and even entire valleys [8-10]. Historic accounts support the ubiquity of such biogenic dams. Walter and Merritts (2008) [11] in their comprehensive study of pre-European paleo-channels along mid-Atlantic seaboard of eastern North America, determined that many were so heavily impacted by beaver dams and vegetation, that there were few discernable channels. This description is consistent with the early depictions of valley bottoms as ubiquitous swampy meadows and marshes. On the other side of the continent, the Willamette Valley (13,700 km^2) in Oregon was described by some of the first Europeans to see it (e.g. beaver trappers) as full of wood jams and rafts that created ever shifting multiple channels and backwaters and extensive marshes across the valley, such that travel was limited to trails on edges [12]. Similarly, at our study site on the Scott River (area = 2.1x10^3 km^2) a major tributary to the Klamath River in California, the valley floor was described by trappers as "all one swamp, caused by the beaver dams, and full of (beaver) huts" [13].

Through commercial trapping for furs, and government-sponsored desnagging, stream cleaning and wildlife control, humans have removed most of these biogenic dams, jams and other obstructions, and most of this occurred prior to the 20th century [10, 14]. Because many scientific disciplines related to the study of rivers such as ecology, geology, and fluvial geomorphology emerged in the late 19th and early 20th centuries, and subsequent to the widespread removal of these obstructions to flow and sediment transport, this has profoundly influenced the perception among scientists and natural resource managers as to what is the natural condition of fluvial ecosystems. In combination with the obvious detrimental ecological impacts of modern dams, especially high-head dams, this has led to the widespread and largely incorrect perception that the natural and ideal condition of all streams is "free-flowing" and clear of dams and other obstructions [2, 10, 15].

However, such biogenic, wood-based dams are fundamentally different from modern concrete and rock dams in that they are small (very low-head), semi-permeable and ephemeral. Beaver dams in particular are usually small, not exceeding 2 m in height (mostly < 1 m high), and are transitory landscape features, with dam lives typically ranging from a few years to decades [14, 16-18]. Such dams have enormous beneficial ecosystem impacts, such as creating ponds, wetlands and other types of slow-water habitat, contributing to water storage and groundwater recharge across landscapes, altering sediment transport rates and stream morphology and changing the underlying geomorphic structure across entire valley floors [19-25].

Thus, throughout much of the northern hemisphere, beaver have been creating structurally complex and biologically diverse aquatic habitat for millions of years, and many anadromous and freshwater fishes have adapted to and evolved in such habitat [26, 27]. In addition to dams, beaver create complex habitat through the construction of lodges and caches made of wood from nearby trees that they fell, as well as the excavation of soil to build canals, channels, tunnels and burrows [5]. Such activities create an aquatic environment that is biologically, hydraulically, thermally and structurally diverse.

In North America, over 80 fishes are known to use beaver ponds, with 48 species commonly using them, inclusive of commercially, culturally and recreationally important species such as coho salmon (*Oncorhynchus kisutch*), steelhead trout (*O. mykiss*), Atlantic salmon (*Salmo salar*), cutthroat trout (*O. clarkii*) and brook trout (*Salvelinus fontinalus*) [6]. Many fishes utilize the structurally complex, deep, slow water and emergent wetlands created upstream of beaver dams [26, 28]. Beaver build dams typically ranging from 30-100 cm, but may be as high as 250 cm, and the height of such dams has raised concerns that they are barriers to fish passage, particularly for salmon and trout [28, 29]. In the United States, state and federal rules often require stream passage barriers to be no more than 15-20 cm in height, making most natural beaver dams non-conforming to existing guidelines [30, 31]. There are also concerns about steep stream gradients as fish passage barriers, and typically when constructing passage routes over barriers such as dams, a series of step-pools is created rather than a steep stream bed. Such rules are in place to ensure that human-built structures such as culverts, hydroelectric, water storage and diversion dams do not obstruct the natural movement of fishes. Globally, the rapid increase in large dam construction highlights the need to understand migratory behavior and passage needs for many fishes [28], and much effort has gone into designing and carefully engineering constructed fishways that ideally allow for fish passage over such structures [31].

At the same time, in Europe and North America natural resource policy guidance documents intended to facilitate recovery of fish and wildlife populations stress the need for more channel-spanning instream restoration structures such as beaver dam analogues (BDAs), log steps, boulder weirs, log jams and natural beaver dams, to create dynamic, structurally complex and spatially diverse aquatic, riparian and wetland habitat [32-37].

Fish passage rules designed for large dams, culverts and other obstructions are typically applied to restoration structures, even though their scale, purpose and function is quite different. In particular, restoration structures designed to be analogous to beaver dams (BDAs) in both form and function, are becoming an increasingly popular stream restoration technique [38-44].

In this study, we take advantage of a naturalistic situation to assess how salmonid species navigate past a beaver dam analogue constructed as part of a restoration project to help recover the Endangered Species Act (ESA)-listed Southern Oregon-Northern California Coast population of coho salmon [45]. The primary objective of this study was to evaluate whether juvenile coho salmon and steelhead trout can pass over beaver dam analogues and if so, identify a preferred flow path, e.g., do they prefer to jump over or swim around the BDAs?

Our second objective was to provide a basis for making a comparison between the number of fish that benefited from the habitat created upstream of the BDA and the number that may have been prevented from moving upstream because of the BDA. We hypothesized that because these salmonids have evolved in the presence of beaver dams for millions of years, that they have also evolved strategies for crossing them, and that by constructing dams similar to beaver dams in terms of size, location and materials, these fishes would also be able to cross these human-built structures. The results of this study are intended to guide future design considerations for fish passage at stream restoration structures.

SITE DESCRIPTION

The study took place in northern California on Sugar Creek, a tributary to the Scott River, which is itself a major tributary to the Klamath River (Fig 1). The Scott River watershed (HUC #18010208) encompasses 2,105 km^2 and is located in the Klamath and Marble Mountains of Western Siskiyou County in Northwest California (Fig 1).

Fig 1. Site Map of the Scott River, a tributary to the Klamath River, California, USA. Black lines indicate the current extent of coho salmon in California. Inset shows the topography of the Scott River watershed in greater and the location of Sugar Creek in the upper watershed. California is located on the western coast of the United States of America, north of Mexico and south of the state of Oregon.

When European trappers first arrived in the 1830s, the valley floor of the Scott River was so full of beaver dams and lodges that it was in essence one large swamp [13]. Because of this abundance, it was initially called the Beaver Valley, and trappers rapidly removed thousands of beavers [13, 46]. Today a small number of beaver persist in the watershed in a few streams, including Sugar Creek. The area also has a history of extensive gold mining and the study reach on Sugar Creek is in an area that has been dredged for gold as recently as the mid-twentieth century, and currently flows through large mounds of cobble-dominated mine tailings.

The bedrock in the area, dating from pre-Silurian to Late Jurassic and possibly Early Cretaceous time, consists of consolidated rocks whose fractures yield water to springs at the valley margins and in the surrounding upland areas [47]. The valley alluvial fill consists of a few isolated patches of older alluvium (Pleistocene) found along the valley margins and of younger alluvium which includes stream-channel, floodplain, and alluvial-fan deposits of recent age [47]. Recent alluvial deposits reach a maximum of more than 120 m thick in the wide central part of the valley. The average seasonal precipitation is 805 mm but may exceed 1780 mm annually in the western mountains, and exceed 760 mm in the eastern mountains. The average annual temperature in the valley is 10.2 °C. Streamflow in the Scott River is primarily driven by annual fluctuations in snowpack and the quality of the water year. Most of the watershed is forested with conifers, predominantly Ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*), transitioning into oak (*Quercus* spp) savannah on the lower foothills, and then to pasture and irrigated fields on the main valley floor, with cottonwood (*Populus trichocarpa*) and willow (*Salix* spp) lining the major streams in narrow bands between the channel and the frequently rip-rapped banks.

The winter of water year 2015 (October 1, 2014-September 30 2015) was the warmest in California's recorded history, causing most of the precipitation to fall as rain, and was the fourth consecutive year of drought (as defined by the U.S. Drought Monitor) in the Scott River watershed. With the exception of water year 2017, the drying trend has continued, and water year 2018 is the seventh year of drought or abnormally dry conditions in the Scott River watershed in the past eight years (US Drought Monitor at http://droughtmonitor.unl.edu).

METHODS

As part of an experimental stream restoration project intended to improve habitat for ESA-listed coho salmon, in 2015 we constructed two BDAs on Sugar Creek approximately 50 m and 200 m above its confluence with the Scott River, following the methods as described in [40, 48]. Such structures are intended to mimic the form and function of beaver dams, and under ideal conditions, they are eventually colonized by beaver. The structures were made by pounding a line of posts into the ground, approximately perpendicular to the direction of flow, then weaving willow between the posts. A downstream apron of cobbles was provided to minimize scour and an upstream berm of clay, organic material, sand and rock was constructed to create a semi-permeable structure with flow moving through, over and around the structure during most of the year, but with some side channel and side passage flow diminishing in the summer when flows decrease due to both natural causes and upstream water diversions. Although juvenile fish could likely wiggle through some of the pores within the structure, most of the flow was either over or around the structure and we thought that most fish would follow one of these major flow paths to cross the structures.

The lower BDA was constructed at the same location and height (approximately 1 m) as a naturally occurring beaver dam that had existed there a few years previous, and has a total linear width of 45 m. The upper BDA was constructed in a relatively constricted reach between piles of mine tailing cobbles. The crest elevation is approximately 30 cm above the downstream pool created by the lower BDA, and the total width is 15 m. In the summer of 2017, two smaller BDAs were constructed downstream of the lower BDA to provide additional stability of the structure and to address perceptions that the 1 m-high structure was a barrier to fish passage. As of summer, 2017, the BDAs have created approximately 7100 m^2 of slow water habitat and wetlands, and are actively being colonized by a family of beavers. Coho salmon spawn in Sugar Creek above the BDAs, and the ponds support juvenile coho salmon and steelhead trout throughout the year.

Experimental Captures and Releases

To assess the ability of juvenile salmonids to pass over the dams, we performed a series of three experiments in 2016 and 2017 by tagging and then displacing fishes from above to below a dam or dams, or by tagging fishes below dams and then monitoring to see if they moved upstream.

Experiment 1

During the summer and early fall of 2016, We tagged 758 juvenile coho salmon and 169 juvenile steelhead trout in the Sugar Creek beaver ponds with 12 mm full duplex Passive

Integrated Transponder (PIT) tags that resonate at 134.2 kHz (Biomark, Inc.) as part of a larger study to estimate the population size, seasonal survival and movement of these juveniles. Minimum allowable size of taggable salmonids was 65 mm, and almost all tagged fish were between 65-80 mm in length. As a pilot study to assess whether juvenile salmonids could cross BDAs, on September 30, 2016, we captured and tagged 32 juvenile *O. mykiss* and placed them in the pool below the single BDA that was installed at that time (Fig 2). The following day we captured and tagged another 16 *O. mykiss* juveniles and released them in the same pool. Below the release pool we placed a block net to minimize downstream movement. A series of temporary, 60 cm by 60 cm square portable PIT antennas attached to a Biomark RM301 reader board with a multiplexor that “sampled” each antenna for 100 mS every 900 mS, were placed in the release pool, just above the BDA in the pond, and downstream of the block net, to monitor the movement of tagged fish and maximize the potential for detecting any fish that moved upstream past the BDA and into the upstream Pond (Fig 2). Our arrays were not set up to detect fish that passed the dam by wiggling through the diffuse flow within the pores of the structure. PIT antenna were set up so that they covered approximately 90% of the total side channel area through which the fish could pass, and included the thalweg, which we assumed to be the most commonly used passage route.

Fig 2. Planview of fish passage experimental setups in 2016 and 2017.

The short red lines around BDAs indicate temporary PIT antennas, the long red lines indicate permanent PIT antennas; SC = side channel; RP = Release Pool, where tagged fish were released; BDA = Beaver Dam Analogue. Major flow paths are shown with blue arrows, though many minor flow paths exist throughout and between the BDAs. Blue shaded areas are places of BDA-influenced inundation.

There were numerous flow paths over, through and around the BDA, but the major flow path was a side channel that skirted the edge of the BDA on river left, with a discharge of approximately 0.03 m^3/s (about 1 cubic foot per second) or about half the total estimated discharge measured at a gage station approximately 1 km upstream (CA Dept. of Water Resources gage #F25890) at the time of the study (Fig 3). The side channel flowed over cobble and gravel for a distance of 8.3 m at a 10% slope, until it entered the pool immediately below the BDA.

Fig 3. Hydrograph of Sugar Creek during the period of study.

Coho outmigration occurs from March through May and is typically centered around peak flow events. Vertical arrows indicate when mark and release experiments to test for passage across BDAs occurred, which were all during low flow periods at the end of September-early October, 2016, late October-early November, 2017, and July, August and September, 2017.

Experiment 2

During the summer and fall of 2017, we tagged 1,078 juvenile coho and 363 juvenile steelhead trout in the Sugar Creek beaver ponds with 12 mm full duplex PIT tags. We also opportunistically tagged 16 juvenile Chinook salmon. By this time, two additional BDAs had been installed just below the original BDA to create a series of 3 pools intended to ease fish passage (Fig 2). The original BDA was labeled BDA 1.0 and the middle and downstream most

BDAs were labeled BDA 1.1 and BDA 1.2, respectively. To assess whether juvenile salmonids could cross BDAs, on October 24, we captured and tagged 154 juvenile *O. kisutch* and 39 juvenile *O. mykiss* and placed them in the pool below BDA #1.1 (Fig 2-bottom). Similar to Experiment #1, the portable PIT antennas were placed in the release pool, just above the upper BDA in the pond, and downstream of the block net (Fig 4). Flow during the experimental period is shown in Fig 3.

Fig 4. Experimental layout of the PIT antennas to detect fish passage across BDAs.

Layout of temporary antennas and block net in fall 2017 to monitor the movement of juvenile coho salmon and steelhead trout PIT-tagged and placed in the release pool below BDA 1.1. Drop over BDA 1.0 = 27 cm, drop over BDA 1.1 = 40 cm. Antennas A-09, A-06 and A-08 monitored the three primary jump routes on BDA 1.1, while Antenna A-00 monitored the single primary jump route available on BDA 1.0. Antenna A-05 monitored fish in the release pool, and Antenna A-03 was one of 3 antennas that monitored fish passage on the side channels (the other two are not pictured). Antenna A-90 and Antenna A-100 are approximately 30 and 40 m upstream of BDA 1.0, respectively. Just out of the picture on the right are antennas on side channels. Also not in view is another antenna below the block net, to detect for any downstream movement past the block net. Note the recently beaver-felled cottonwood (golden leaves) in upper left of photograph.

This arrangement allowed the monitoring of fish use of the release pool, four jumping routes and three side channel passage routes as well as any fish that made it into the lower large BDA pond or other parts of the restoration complex. We were not able to provide complete antenna coverage of all of the lesser flow paths and some fish may have passed undetected by wiggling through the pores of the BDAs. The temporary antennas were operational for approximately three weeks, from October 24 through November 11, at which point, few fish were detected in either the release pool or the passage routes and the threat of winter storms required removal of the small portable antennas. The larger permanent antennas upstream of the lower BDA (A-90 and A-100) collect data year-round. In 2017, for each major flowpath over or around a BDA, a longitudinal profile of bed and water surface elevation was mapped using a Trimble R8 Model 3 connected to Real-Time Kinematic Global Navigation Satellite System (RTK-GNSS). Velocities were measured at discrete points along the profile and at cross sections to approximate discharge for each of the flow paths, using a SonTek Flowtracker Handheld 2D ADV. Total stream discharge was measured at a California Department of Water Resources monitoring station on Sugar Creek, approximately 700 m upstream from the upper BDA (data available at https://cdec.water.ca.gov/).

There were numerous flow paths over, through and around the BDAs. On BDA 1.1 (the lower BDA that displaced fish had to cross) major flow paths were a side channel that skirted the edge of the BDA on river left, with a discharge of approximately 0.03 m^3/s, and three sections across the top of the BDA, each with a similar amount of discharge, where water flowed over the top to form waterfalls (Fig 4). The side channel flowed for 8 m over cobble and gravel at a slope of 11%, and entered into the pool below BDA 1.1 (i.e., the “Release Pool”, where displaced fish were released). The water surface elevation-to-water surface elevation drop at the falls flowing over the BDA ranged from 38-40 cm.

Major flow paths on BDA 1.0 (the upper BDA that fish displaced fish had to cross) were a side channel that flowed on the river left side of the main BDA section and a single section near the middle where water flowed over the top of the BDA. Flow out of BDA 1.0 was much more dispersed, flowed through dense vegetation, and there were numerous passage routes where we were unable to place PIT antennas (Fig 2). The side channel passage route that we were able to monitor flowed over cobble and gravel for a distance of 5 m at an 8% slope, until at the downstream end it entered the pool immediately above BDA 1.1. The water surface elevation-to-water surface elevation drop at the waterfall over BDA 1.0 was 27 cm.

In addition to the temporary portable antennas, we also placed two permanent antennas (A-90 and A-100) in BDA Pond 1 to monitor diurnal and seasonal movement of tagged fish (Fig 4). These antennas were large (6m x 1m) with each attached to a single Biomark IS1001 reader board. These antennas enabled us to detect fish that may have moved upstream after the initial study period was finished.

Experiment 3

During the summer and fall of 2017, we captured and tagged juvenile salmonids in the reach below the BDAs, at the confluence of Sugar Creek with a major side channel of the Scott River (Fig 2). We opportunistically captured and tagged juvenile salmonids on July 25 August 18 and September 19, 2017, for a total of 61 coho salmon, 126 steelhead trout and 12 Chinook salmon tagged during the three events (Experiments 3,4 and 5, respectively). Flow during those periods is noted in Fig 3. The purpose of this series of experiments was to assess whether fishes naturally summer-rearing in the relatively shallow pool-riffle environment below the BDAs moved past them and into the pond habitat above the BDAs.

Early fall population estimates upstream of the BDAs were made through a mark-recapture effort on 10/24-10/25/17. Populations of juvenile coho salmon and steelhead trout were estimated using the Lincoln-Petersen mark-recapture method (Chapman 1951). Juvenile coho salmon habitat capacity upstream of the BDAs was estimated using the method of Goodman et al. (2010) (see also Beechie et al. 2015). This method requires measuring the habitat parameters of velocity, depth and proximity to cover and then weighting their value to juvenile coho salmon based on the value of these parameters. We subsampled the habitat for these three metrics along six cross sections within the treated area at approximately equal intervals, then weighted for area based on the actual distance from the mid-points between cross-sections.

RESULTS

Experimental Capture and Releases

Experiment 1

This initial pilot experiment in 2016 showed that 43 of the 58 juvenile steelhead trout that were placed in the release pool were detected upstream of the single BDA (#1.0) within 3 days of release, and just a few individuals remained in the release pool 4 days after release (Fig 5). Most of the upstream movement occurred in the hours after sunset, from around 7 pm through midnight, with a smaller pulse near sunrise (Fig 6). There was little upstream movement during the daylight hours, with just 5 of 58 fish moving upstream between sunrise and sunset. Three fish exploited small openings in the block net and moved downstream. We also detected three tagged fish that were not part of the experimental displacement release below the BDA, suggesting volitional movement. Additionally, over the course of the 4-day experiment, several tagged fish moved upstream past the BDA, then back downstream and then back upstream again. One fish moved downstream below the block net, then back into the release pool, then upstream above the BDA.

Fig 5. Daily PIT antenna detections of juvenile steelhead trout above and below BDA in 2016.

The 2016 experimental release of juvenile steelhead trout below BDA 1 on two consecutive days showing the daily number of detections of individual steelhead trout for each release group in the release pool below BDA 1, in the Pond above BDA 1, and below the block net at the lower end of the release pool. Thirty two fish were released in the first cohort on 9/30/16 and 16 more in the second cohort on 10/1/16, for a total of 58 fish released. Day 1 refers to the day of release for each cohort, Day 2, the day after release, etc.

Fig 6. The hourly timing of movement of juvenile steelhead trout across the BDA in 2016.

The 2016 experimental release, showing the hourly timing of tagged juvenile steelhead trout detected moving past BDA 1 during the 4-day experiment (n = 38). Most of the fish moved during the late evening, after sunset (sunrise = 07:08 and sunset = 18:55 on 9/30/16).

Experiment 2

The majority (139 out of 155) of the tagged juvenile coho salmon that were placed in the release pool below BDA 1.1 left the pool within 36 hours of being released (Fig 7). The fish were released around 2 pm on October 25th, and by evening of the 26th, just 17 of 156 coho remained in the released pool, and a day later, just six remained. By November 8th, at the end of the experimental period, no coho salmon remained in the release pool. Overall, Ninety one percent (141/155) of the fish were eventually detected in BDA Pond 1. Twenty two of the 38 juvenile steelhead trout also moved up into the beaver pond after release, but not as rapidly as the coho (Fig 8). Seven of 38 steelhead were detected in the release pool 60 hours after release, and between five to nine steelhead trout were detected on a daily basis in the release pool throughout the rest of the experimental study period (through November 8th). Five of these fish were later detected by one of the permanent antennas in the BDA pond upstream sometime between November 9th 2017, and April 1, 2018, indicating that they had crossed the BDAs.

Fig 7. Daily PIT antenna detections of juvenile coho salmon above and below BDAs in 2017.

Daily detections in 2017 of the number of individual juvenile coho salmon in the release pool, jumping a BDA, using a side channel passage and in BDA Pond1, and above both BDAs (coho n=155). No individuals were detected below the block net on the downstream end of the release pool.

Fig 8. Daily PIT antenna detections of juvenile steelhead trout above and below BDAs in 2017.

Daily detections in 2017 of the number of individual steelhead trout in the release pool below BDA 1.1, jumping a BDA, using a side channel passage and in BDA Pond1, and above both BDAs (steelhead n = 39). No individuals were detected below the block net on the downstream end of the release pool.

Table 1 details the movement patterns, and flow path preferences of juvenile coho salmon and steelhead trout after they were released into the pool below BDA 1.1. The detection efficiency of the antenna network was quite good. During the initial study period, all (100%) of the tagged fish were detected at least once, somewhere in the antenna network: 93% were detected in the release pool, 94% were detected upstream of the first BDA (BDA 1.1), and 81% detected upstream of the second BDA (BDA 1.0). For juvenile coho salmon, 97% were detected upstream of the first BDA (BDA 1.1), and 89% detected upstream of the second BDA (BDA 1.0). Overall, the juvenile coho salmon had higher detection rates on the upstream PIT antenna network than the steelhead trout (89% v. 50% detection rates, respectively). No fish were detected on the antenna placed below the stop net to detect any potential downstream escapees.

Table 1. Summary of detection and movement of 196 juvenile coho salmon and steelhead trout (Stlhd) released below two beaver dam analogues in October, 2017.

Metric	Coho- N	Coho- (%)	Stlhd- N	Stlhd- (%)	Total- N	Total- (%)

Released	155	100%	39	100%	196	100%
Detected after release	155	100%	39	100%	196	100%
Detected in release pool	143	92%	39	100%	182	93%
Detected upstream of release pool	152	97%	32	80%	184	94%
Detected in BDA Pond 1	139	89%	20	50%	159	81%
Detected moving downstream	0	0%	0	0%	0	0%
BDA Passage Routes						
Detected using a side channel	93	60%	25	63%	118	60%
Detected jumping	77	49%	17	43%	94	48%
BDA-1.1 Passage Routes						
BDA1.1 Left Jump	66	42%	11	28%	77	39%
BDA1.1 Middle Jump	8	5%	13	33%	21	11%
BDA1.1 Right Jump	3	2%	4	10%	7	4%
All BDA1.1 Jump Passage	74	47%	17	43%	91	46%
BDA1.1 Side Channel Passage	61	39%	22	55%	83	42%
Total moving past BDA 1.1	129	83%	31	78%	160	82%
BDA 1.0- Passage Routes						

BDA 1.0 Jump	24	15%	0	0%	24	12%
BDA 1.0 small SC Passage	9	6%	4	10%	13	7%
BDA 1.0 main SC Passage	57	37%	14	35%	71	36%
All BDA 1.0 SC passage	63	40%	15	38%	78	40%
Total moving past BDA 1.0	83	53%	15	38%	98	50%

Sixty percent of the fish used at least one side channel passage to cross a BDA, but many fish chose to jump over at least one of the BDAs (49% for coho, 43% for steelhead), the jump heights of which were 38-40 cm and 27 cm for BDAs 1.1 and 1.0, respectively (Fig 9). The lower BDA (1.1) had three passageways for jumping and of the fish that jumped, there was a strong preference for the river left jump route, for reasons that are not entirely clear. Measurements of velocity profiles and jump heights suggest that the middle and left routes were similar (Fig 9). However 39% of all fish passing BDA 1.1 used the left jump route, while just 11% used the middle jump route and just 4% used the right jump route (the remainder used the side channel). The preferred route did have the deepest downstream pool (58 cm), while the right route, which was the least preferred, was in a shallower part of the release pool (23 cm), while the middle jump route had a pool depth of 37 cm. Discharge through the three falls on BDA 1.1 were approximately equal. Overall, 74/156 juvenile coho and 17/40 juvenile steelhead were detected making a 38-40 cm jump over the lower dam.

There were notable behavioral differences between coho and steelhead in term of the timing of passage and the mode of passage. Of the fish that jumped to cross a barrier, most of the coho jumped between sunrise and sunset, with most of the jumping occurring in the afternoon, while most of the steelhead jumped between sunset and sunrise, with a spike in activity in the hours before sunrise (Fig 10). In contrast, individuals of both species that used the side channel for passage crossed at all hours of the day and night, with spikes in activity for both species at sunrise and the hours after sunset (Fig 11).

Fig 10. The hourly timing of juvenile salmonids jumping over BDAs in 2017.

Hourly timing of jumping over BDAs by juvenile coho salmon (*O. kisutch*) and steelhead trout (*O. mykiss*) in 2017, as a percentage of tagged fish (coho n=155; steelhead n = 39). The data suggest that coho prefer to jump during the day, while the majority of steelhead jumping occurs at night. Sunrise = 07:34 and sunset = 18:17 on October 24th, 2017.

Fig 11. Hourly timing of side channel usage by juvenile salmonid to pass the BDAs in 2017.

Hourly timing of side channel passage of juvenile coho salmon (*O. kisutch*) and steelhead trout (*O. mykiss*) across BDAs in 2017, as a percentage of tagged fish (coho n=155; steelhead n = 39). In contrast to jumping, coho appear to prefer side channel passage at night, while the steelhead show no particular preference between day and night. Sunrise = 07:34 and sunset = 18:17 on October 24th, 2017.

Experiment 3

In contrast to the Experiment 2 fishes that were captured in the BDA Pond and then released below BDA 1.1, the fishes captured and released below in the confluence pool in the Scott River (below BDAs 1.0-1.2-see Fig 2) in July, August and September, 2017, showed little evidence of upstream movement above any of the BDAs (Table 2). Only 11 of 61 juvenile coho salmon, 1 of 126 tagged juvenile steelhead trout, and none of the 12 tagged juvenile Chinook salmon were detected upstream of the BDAs through May 31st, 2018. Overall, in total for these three experiments, 187/199 (94%) of the fish tagged in the Scott River, at the confluence with Sugar Creek, were never detected anywhere in the Sugar Creek PIT antenna network.

Table 2. Summary of 3 experimental releases of tagged juvenile steelhead trout and coho and Chinook salmon below Beaver Dam Analogues in 2016 and 2017. The data are summarized as both the number and percentage of a species detected or not detected above and below BDA 1.0. See Fig 2 for spatial configuration of the release site relative to BDAs.

Species	Total Released	Detected Below BDA1	Detected Above BDA1	Not Detected Above or Below BDA1
Expt-1, Sept. 2016: Capture in BDAP1, release in pool below BDA 1 w/dwnstrm block net				
O. mykiss	58 (100%)	58 (100%)	52 (90%)	0 (0%)
Expt-2, Oct., 2017: Capture in BDAP1, release in pool below BDA 1.1 w/dwnstrm block net				
O. kisutch	155 (100%)	152 (98%)	141 (91%)	0 (0%)
O. mykiss	39 (100%)	39 (100%)	22 (56%)	0 (0%)
Expt-3, July, 2017: Capture and release in Scott-Sugar confluence pool, no block net				
O. kisutch	12 (100%)	1 (8%)	4 (33%)	7 (58%)
O. mykiss	1 (100%)	0 (0%)	0 (0%)	1 (100%)
O. tshawytscha	1 (100%)	0 (0%)	0 (0%)	1 (100%)
Expt-3 Aug., 2017: Capture and release in Scott-Sugar confluence pool, no block net				
O. kisutch	6 (100%)	3 (50%)	1 (17%)	3 (50%)
O. mykiss	15 (100%)	3 (20%)	0 (0%)	12 (80%)
O. tshawytscha	5 (100%)	0 (0%)	0 (0%)	5 (100%)
Expt-3, Sept., 2017: Capture and release in Scott-Sugar confluence pool, no block net				
O. kisutch	43 (100%)	19 (44%)	6 (14%)	22 (51%)
O. mykiss	110 (100%)	13 (12%)	1 (%)	96 (87%)
O. tshawytscha	6 (100%)	0 (0%)	0 (0%)	6 (100%)

Population and habitat capacity estimates

As of fall, 2017, we estimated that the amount of habitat created upstream of the BDAs was 7,080 m^2 and of a quality sufficient to support 6,744 (SE=537) coho parr. From our fall, 2017 mark-recapture effort, we estimated a population of 2,517 (SE=1173) coho parr. We also estimated the coho survival from summer, 2017 through the 2018 spring outmigration to be 88%. This is based on detection of 863 tagged coho during the spring outmigration period, out of 1077 tagged the previous summer and fall (80.1%), multiplied by an estimated combined PIT antenna detection efficiency of 91% for juvenile coho salmon for the two antennas in the lower BDA pond during the spring outmigration period. We did not estimate steelhead abundance because of the relatively low densities observed, but we tagged 361 juveniles in the summer and fall and detected 152 during the spring outmigration period (42%), which multiplied by an 88% antenna detection efficiency (for juvenile steelhead trout) provides an overwintering "apparent" survival estimate of 48%.

DISCUSSION

This study lends support to the hypothesis that because salmonids have evolved with beaver dams, they have developed behavioral and physical adaptations that allow them to cross such dams at important life-history stages. The two relocation experiments suggest that both coho salmon and steelhead trout parr have little difficulty crossing the BDAs, whether by jumping over a 40-cm waterfall or swimming up a short side channel with an 8-11% slope, the former being somewhat analogous to an engineered pool-weir passage structure and the latter being somewhat analogous to an engineered embedded rock ramp [49]. The fish appeared to time their movements according to light conditions and the majority of them moved upstream within the first or second favorable opportunity. In Experiment #2, a small number of juvenile steelhead trout remained in the release pool throughout the first few weeks of the study, but the majority of those were detected upstream at a later date by the permanent antennas. The upstream antennas had a much higher efficiency in detecting coho salmon relative to steelhead trout, probably in part due to the antenna locations, which were placed in deep slow water habitat favored by coho salmon, as opposed to the faster and more turbulent water preferred by steelhead. Juvenile coho salmon reliably move to pools with cover (which is where the upstream antennas were placed), whereas juvenile steelhead trout occupied a variety of habitats. We also note that the habitat in the release pool was not poor quality, with good depth, cover and aeration (Figs 4 and 9), and the initial lack of upstream movement by some individuals may have been due to the fact that they found the release pool to be suitable habitat.

There are surprisingly few studies of specific conditions under which juvenile salmonid (or other species) crossed instream barriers, whether natural or artificial, and even fewer studies documenting the hydraulic and hydrologic conditions under which juvenile fishes cross beaver dams, and especially during low-flow conditions. Guidelines for adult fish passage suggest that the pool depth in pool-weir passage routes be at least twice the length of the fish, and for ramps that the depth be at least as much as the body height of the fish, conditions that were easily met for our juvenile fish in our experimental conditions [50] [51]. Guidelines for jump heights at pool-weir fish passage facilities (i.e. the difference in water surface elevations between two consecutive pools) generally ranges between 15-20 cm, conditions that were not met under our "pool-weir" passage option [30] [31].

That close to half of the juveniles in Experiment #2 crossed a 40-cm (4-5 body lengths) jump, even when a much gentler sloping cobble ramp was available a few meters away suggests that for beaver dams or naturalistic beaver dam-like structures, current jump height guidelines, which generally try to keep jump heights to ≤ 15 cm, may need revising. Such jump height guidelines were generally developed to ensure that fish (primarily salmonids) can pass culverts, diversion dams, hydropower dams and other human-built instream obstructions. However, the hydraulics of such structures are quite different from those of beaver dams. Consider culverts for example, which fish may have an initial jump to get into, and then face a long swim through high velocity water to reach the upstream end of the culvert. Such a challenge potentially exceeds the swimming capabilities of juvenile or even adult salmonids. In contrast, the hydraulic conditions at the preferred jump passage route at the BDAs require a fish to begin at a pool with a depth of 5-6 body lengths, and then jump or swim up a waterfall that has a high velocity segment extending no more than 15 cm swim distance (about 2 body lengths) followed by a deep (> 6 body lengths), low velocity pool with cover immediately upstream (Fig 9). Thus, not unexpectedly, experiments of fish passage through culverts (usually with hatchery fish) have observed much lower successful jump heights that the results we observed with wild fish jumping over beaver dams [52].

Alternatively, the side channel passage consisted of a short, high gradient (8-11%) flow path, but with extensive channel roughness in the form of cobbles that dissipate energy. For a juvenile salmonid, this flow path appears as a series of small chutes and pools with the roughness creating turbulent flow and relatively low velocity conditions (Fig 9). These hydraulic conditions are significantly different than a culvert or cement flume angled to a 8-11% slope, which would tend to have more laminar and uniform flow. We did not find specific guidelines for the acceptable length and slope of embedded rock ramps that is thought to ensure fish passage, but recommendations for culverts are generally that the slope should be close to zero or at least consistent with the upstream and downstream stream slope [30] [31]. For adult salmonids, we found examples of sloped flow-ways that provided passage, but the physical characteristics were not well described [53]. For our study, we provided the equivalent of an embedded rock ramp that was generally at least a juvenile fish height deep, with an 8-11% slope, a total distance ranging from about 50-250 juvenile fish lengths and a discharge of about 0.03 m^3/s. To the best of our knowledge, this study provides the first quantitative data for hydraulic conditions (velocity and depth) in the field under which juvenile salmonids cross natural or naturalistic instream barriers such as beaver dams or BDAs both by jumping and through the use of short but steep side channels.

Because our study also showed dense concentrations of juvenile coho salmon and steelhead trout in the ponds upstream of the beaver dams (consistent with other studies), it raises a larger philosophical question as to how to weigh the benefit of the habitat created upstream of a barrier such as a beaver dam against the cost that it might not be passable to all species at all their different life-history stages and under all flow conditions. Upon review we found that most studies suggest that fishes, and in particular salmonids, benefit from natural obstructions such as beaver dams [6, 26, 38], while studies suggesting that beaver dams are detrimental to fish are uncommon, and typically indicate a temporally intermittent negative impact, with no indication of a population-level effect [28].

For example, over a period of 12 years in Nova Scotia, it was observed that in years with low flow, adult Atlantic salmon were unable to pass over some beaver dams and thus spawned lower in the system, but in most years, beaver dams had no detectable effect on the distribution of spawning redds [54]. In Utah it was observed that beaver dams appeared to impede the movement of invasive brown trout (*Salmo trutta*), but not native brook or cutthroat trout [29], whereas in California it was observed that brook, brown and rainbow trout regularly crossed beaver dams in both an upstream and downstream direction, but that the loss of beaver dams after severe flooding decreased the brown trout population [55]. In a Midwestern stream it was observed that fish movement of multiple species was linked to flow, with more downstream movement occurring during periods of elevated discharge [56].

None of these studies considered whether there were any population-level effects, nor did they examine similar habitat without beaver as a comparison, or consider that it might be advantageous for fishes not to cross beaver dams. For example, in the Nova Scotia study, it was left undiscussed the possibility that the Atlantic salmon may have found it more advantageous in drought years to spawn in the lower reaches of a stream, and below beaver dams, because of improved flow conditions downstream, potentially a result of water stored behind the upstream beaver dams[54]. As another example, in Washington, a telemetry study of the rare Salish sucker (*Catostomus catostomus*) indicated that they rarely crossed beaver dams, but then a later study at the same site indicated that the highest number of suckers were in the beaver pond complexes, and that the habitat was consistent with habitat descriptions of “good” sucker habitat [57].

At our study site, we demonstrated that the ponds upstream of the dams produced thousands of fishes, from a reach that formerly ran dry during the summer. This indicates that breaching the dams (and thus draining the ponds) to ensure fish passage would have likely resulted in a net loss of benefit. Because we also demonstrated juvenile fish passage, a decision to breach the dam (to comply with 15 cm fish passage jump heights) would clearly have been detrimental to the species. However in other situations, where there are not data to assist with decision-making and where flow conditions may be different, the decision of whether to remove or modify an obstruction so that it complies with fish passage guidelines, or to require a proposed restoration structure to comply with fish passage guidelines, may be less clear. The data from our study provide some general guidance, which suggests that knowledge of how fish use a particular stream system and the relative abundance of different habitat types within the system is key to understanding how to manage instream obstructions such as beaver dams.

For coho salmon, the target species of the restoration project, the data suggest that if adult fish are spawning above the dams, then the offspring of such adults will have access to the ponds and upstream fish passage for these juveniles is less important. We think that because outmigrating juveniles time their downstream movements to coincide with high flows, concerns over passability at this life-history stage are less warranted. For adult salmon, an assessment of hydraulic conditions at a time when adults are trying to move past the structure is essential to assess whether or not the structure may be blocking movement, but even then, a consideration of the juvenile overwintering habitat that will be lost if the dam is breached needs to be weighed against the potential benefits to having an increased number of fish spawning upstream.

Overall, we suggest that unless there is clear and compelling evidence that a beaver dam or BDAs are preventing the movement of fishes *and* that this is likely to have a population-level effect, such structures should not be removed. Options such as temporarily notching may be an alternative under some conditions, such as the presence of adult salmon stacking up below a dam, but guidelines need developing. For human-built structures such as BDAs and other weirs, we suggest that our data provide some guidance as to what constitutes a passable structure, but that more examples from the field are needed under a wider range of flow conditions.

Studies that assess the costs and benefits of a structure to a fish population are essential. Because beaver dams and similar structures can provide extensive habitat upstream, the cost of impaired fish passage needs to be weighed against the upstream habitat benefits accrued. In general the benefits of increased connectivity, that is access to habitat, needs to be weighed against the quality of the habitat that is available to use. We speculate that in the case of coho salmon, decades of emphasizing habitat connectivity over habitat quality by removing perceived obstructions to fish passage is a significant contributing factor to their widespread decline..

Studies from Alaska to California suggest that where abundant instream obstructions that create deep slow-water habitat, coho salmon thrive, and that conversely, where such habitat is rare or absent, coho salmon are typically rare or absent [45, 58]. While connectivity in fluvial systems is in general an important goal, the pursuit of that goal needs to be tempered against the need for creating habitat of a type and quality to which species have adapted. Species have adapted to and evolved in the presence of instream obstructions such as beaver dams and wood jams. Numerous species utilize the complex and dynamic pool, pond and wetland habitat created by such obstructions and some of those species are in steep population decline. In addition to coho salmon, other rare or endangered species that benefit from beaver ponds include the willow fly catcher and yellow-legged frog [59-63]. We suggest the need for a more nuanced approach to fluvial ecosystem management, an approach that recognizes that a dynamic tension exists between the need for habitat connectivity and habitat quality, between the need for fast-water habitat and slow-water habitat. We suggest that different species, life-history stages within a species and even different life-history strategies within a cohort of the same species have differing, and at times competing aquatic habitat needs, and that management strategies that more explicitly recognize that such variation exists would lead to more successful recovery of a number of aquatic and riparian-dependent species in decline, including coho salmon.

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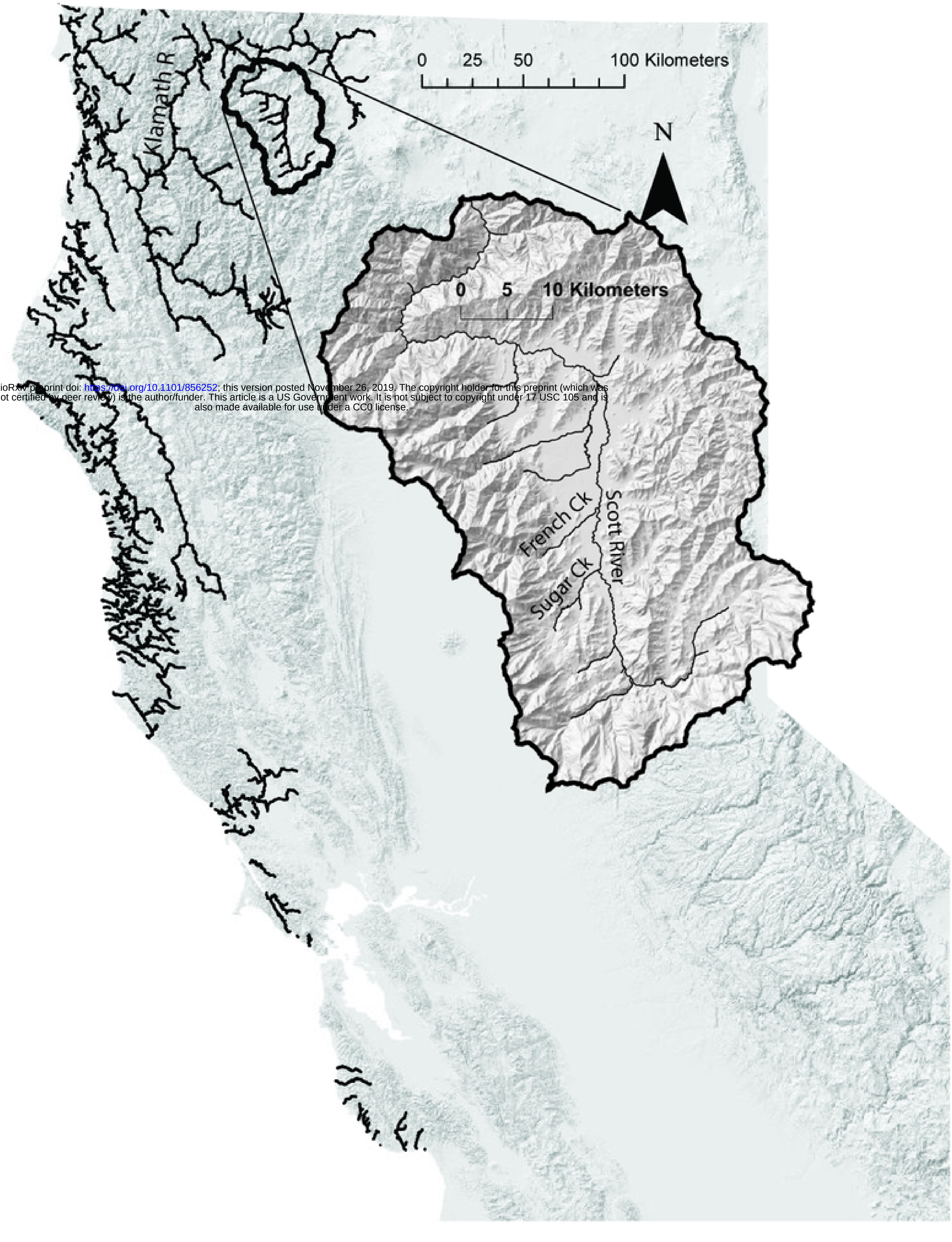
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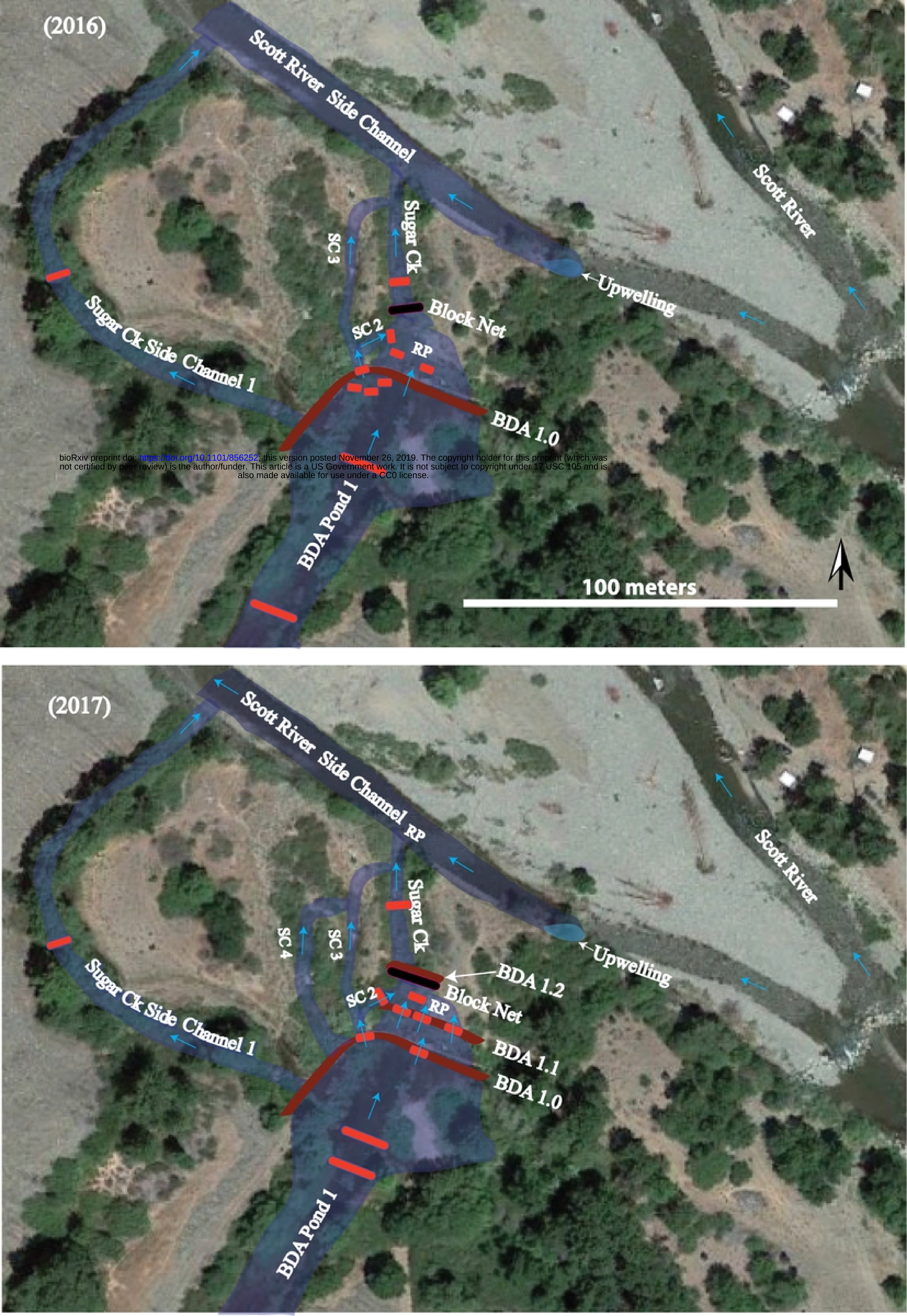
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Scott River Side Channel
RP
Scott River
Sugar Ck
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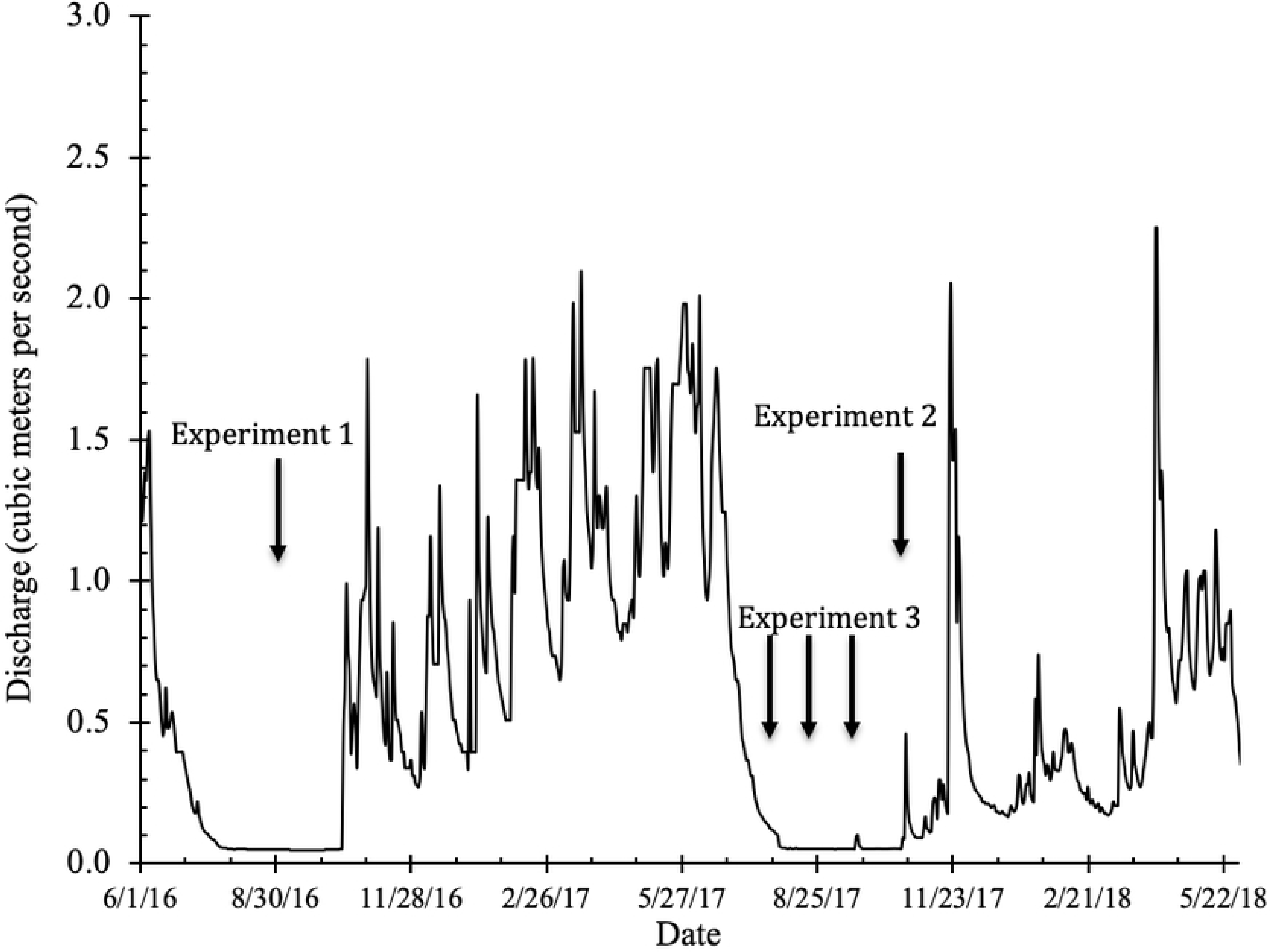
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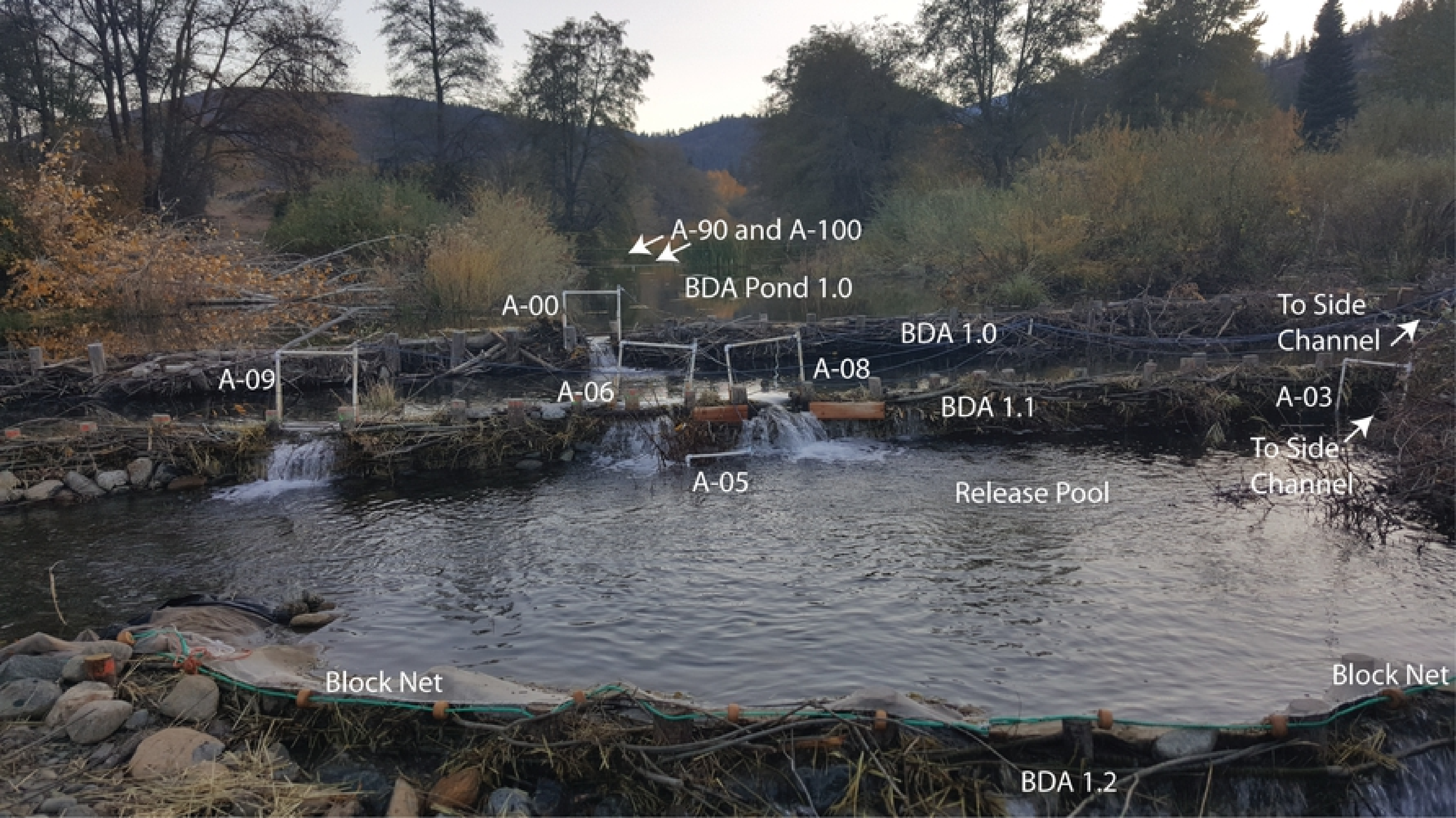
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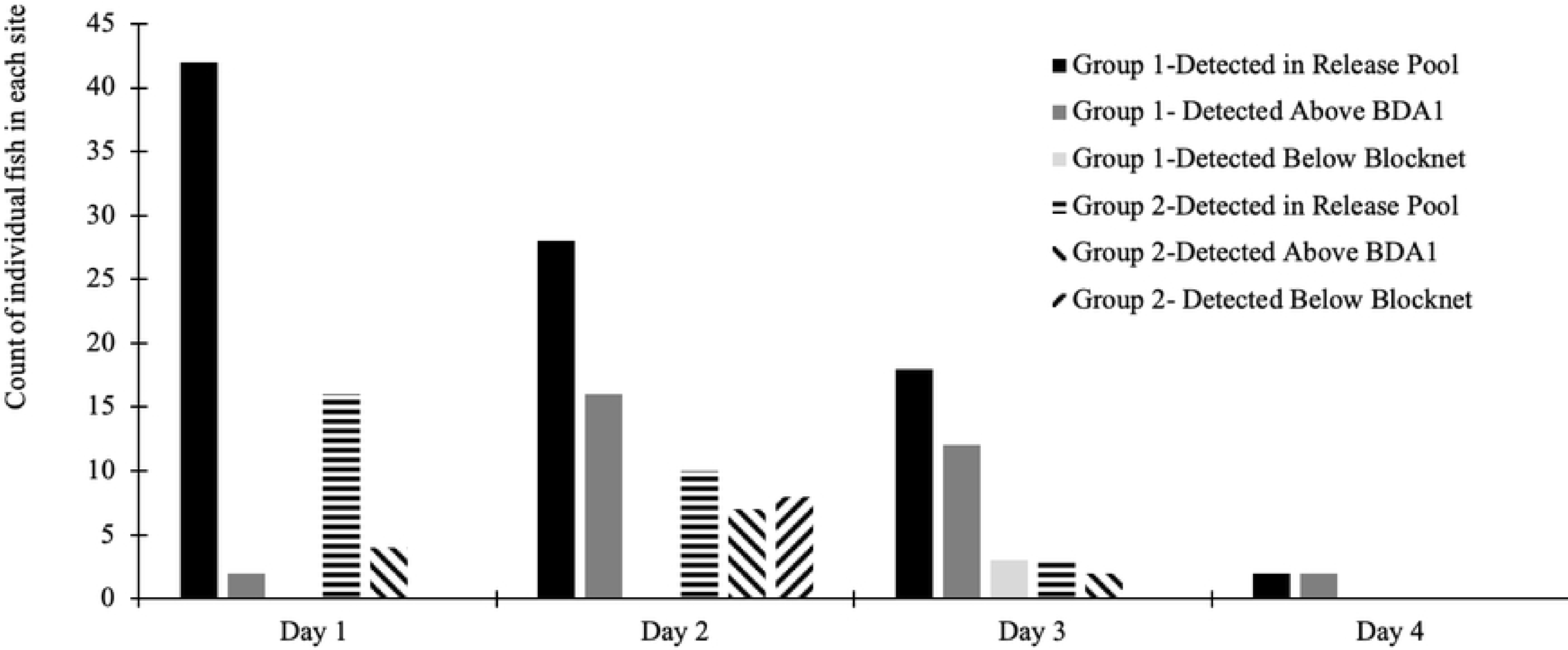
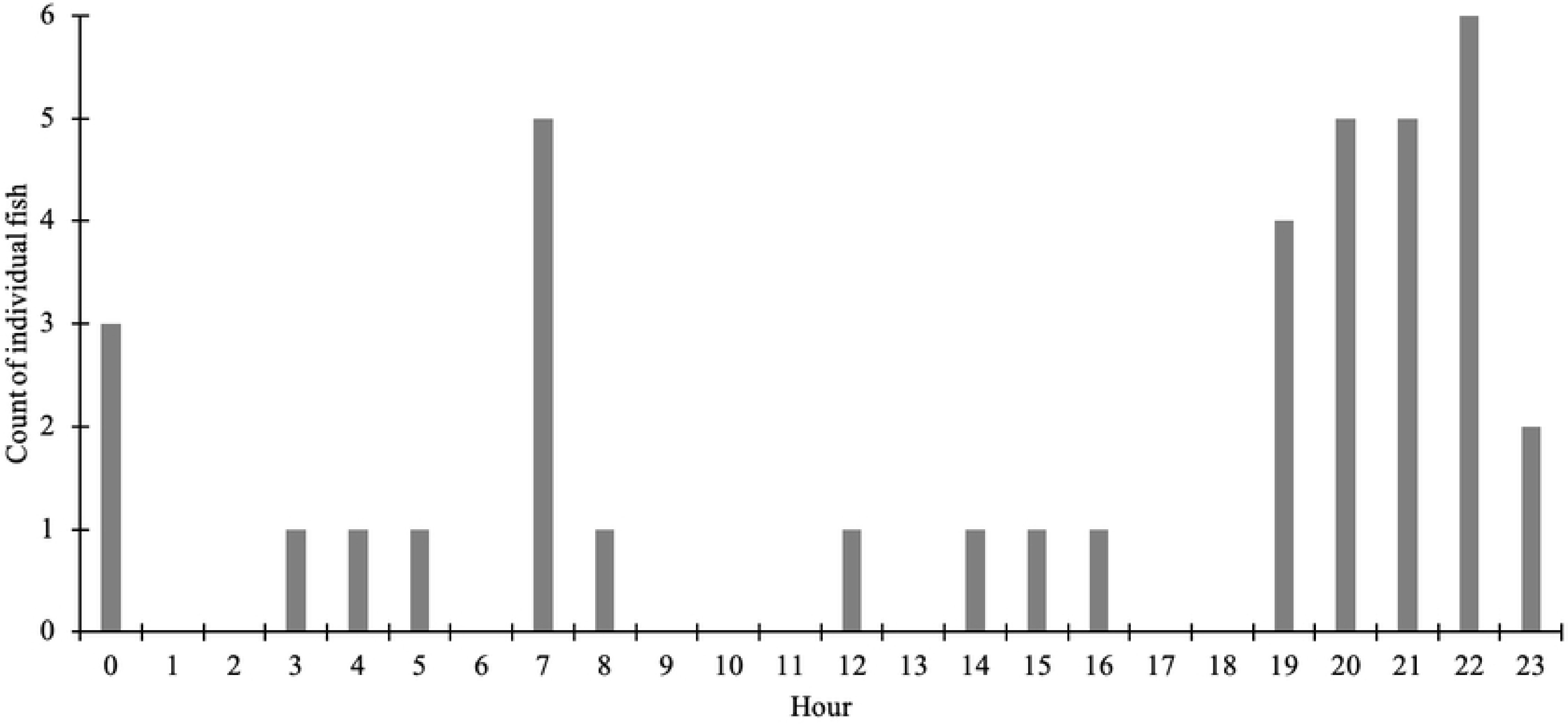
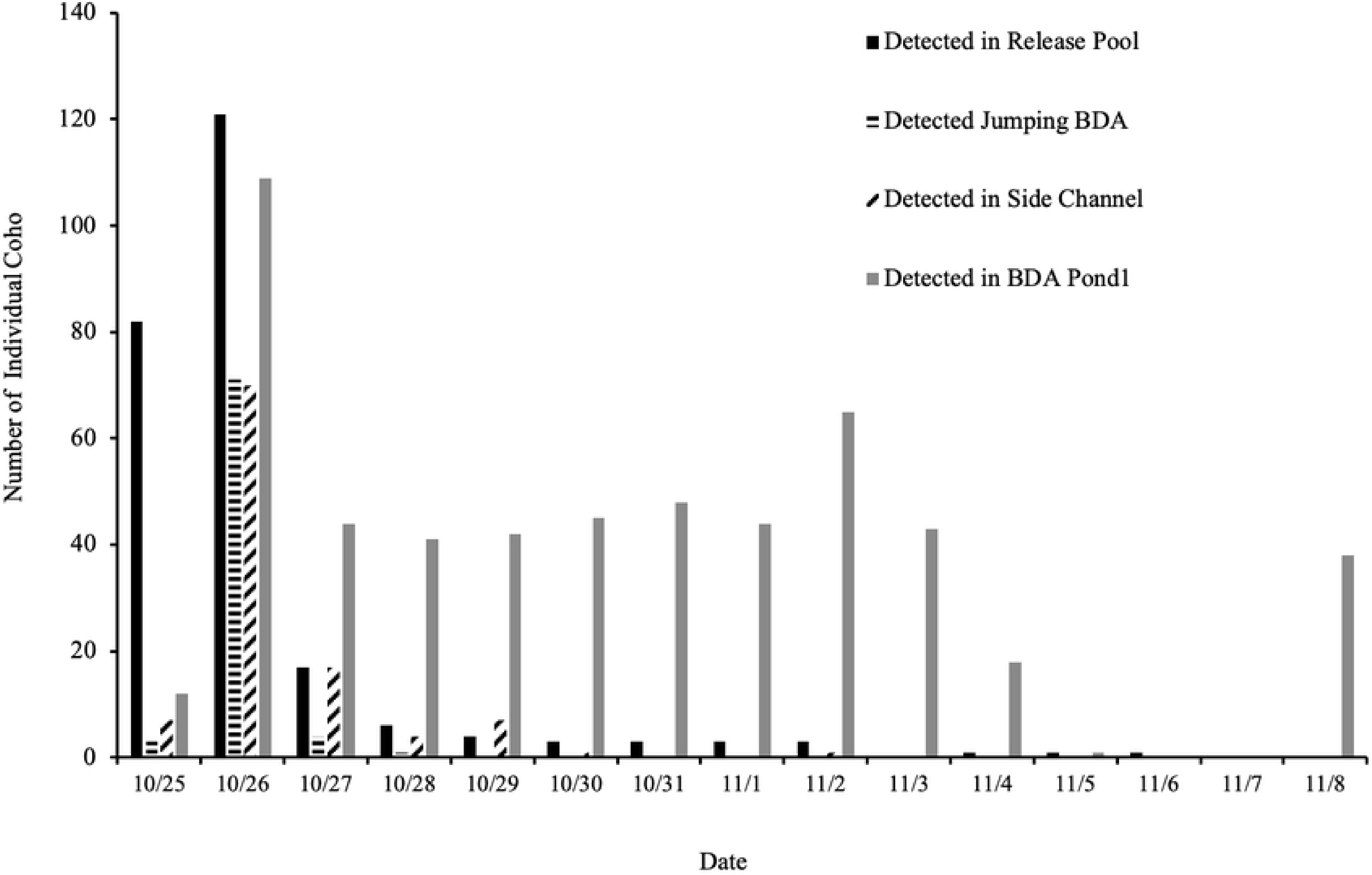
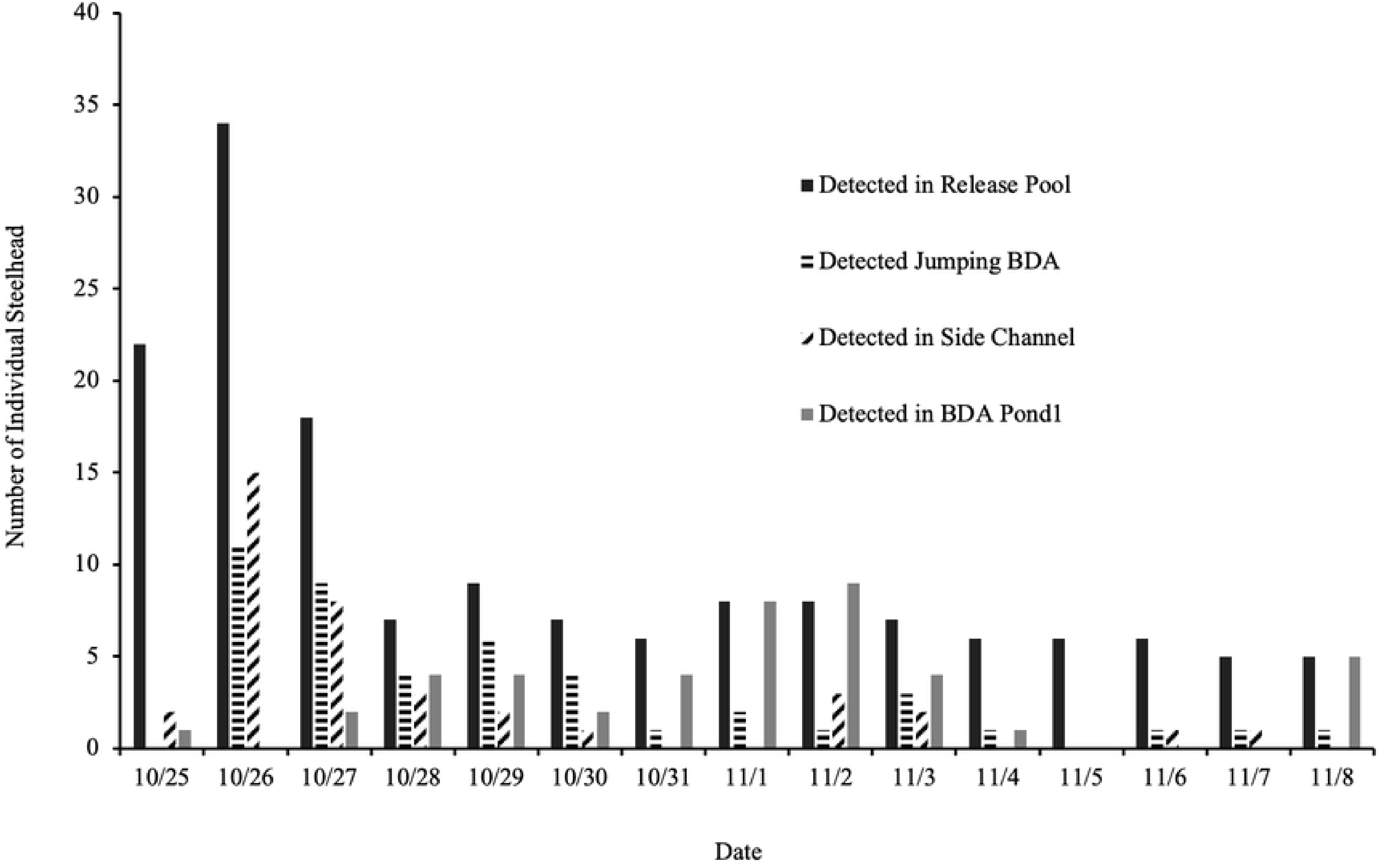
Release Pool
Block Net
Block Net
BDA 1.2

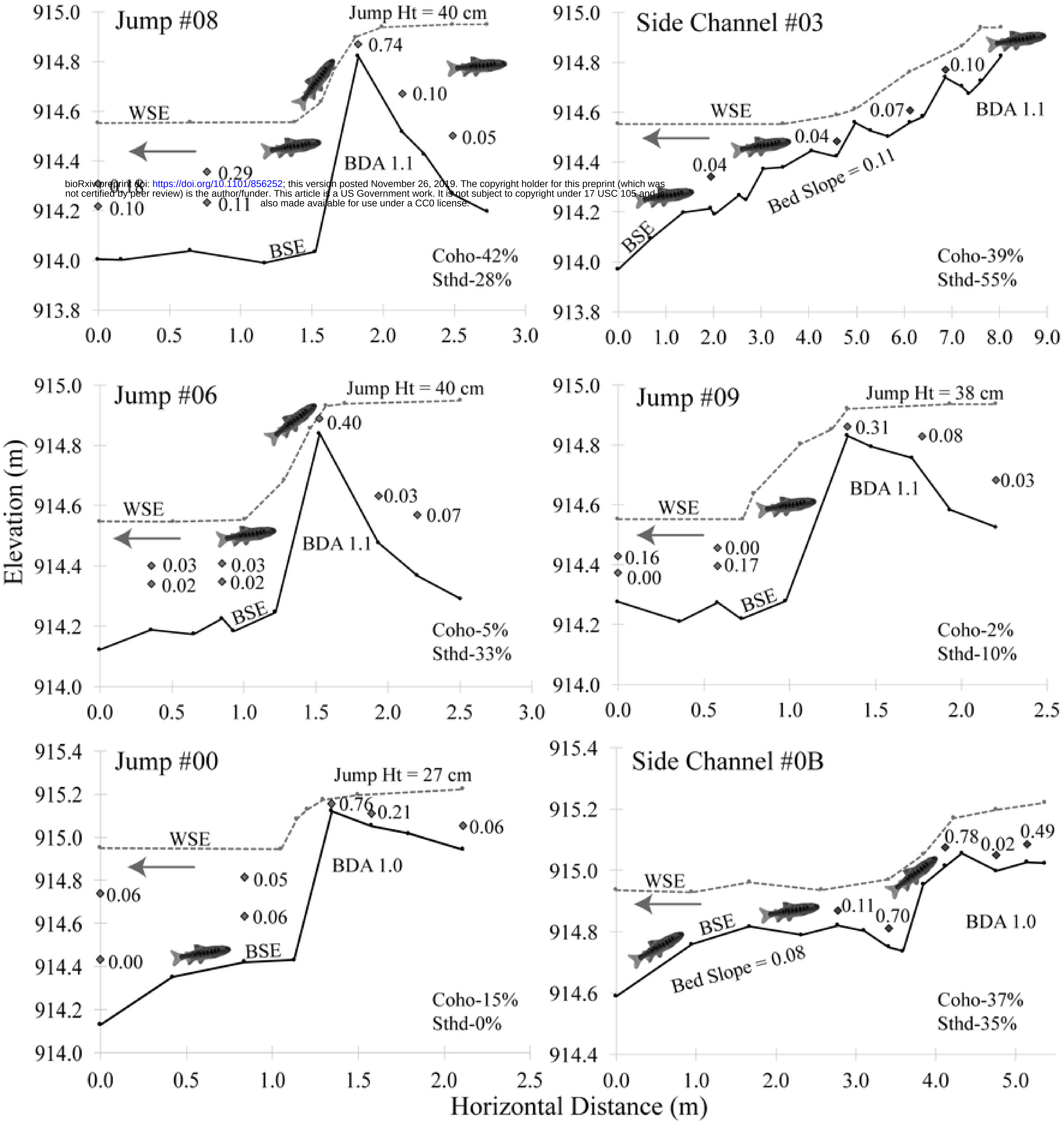

Count of individual fish in each site
45
40
35
30
25
20
15
10
5
0
Day 1
Day 2
Day 3
Day 4
Group 1-Detected in Release Pool
Group 1- Detected Above BDA1
Group 1-Detected Below Blocknet
Group 2-Detected in Release Pool
Group 2-Detected Above BDA1
Group 2- Detected Below Blocknet

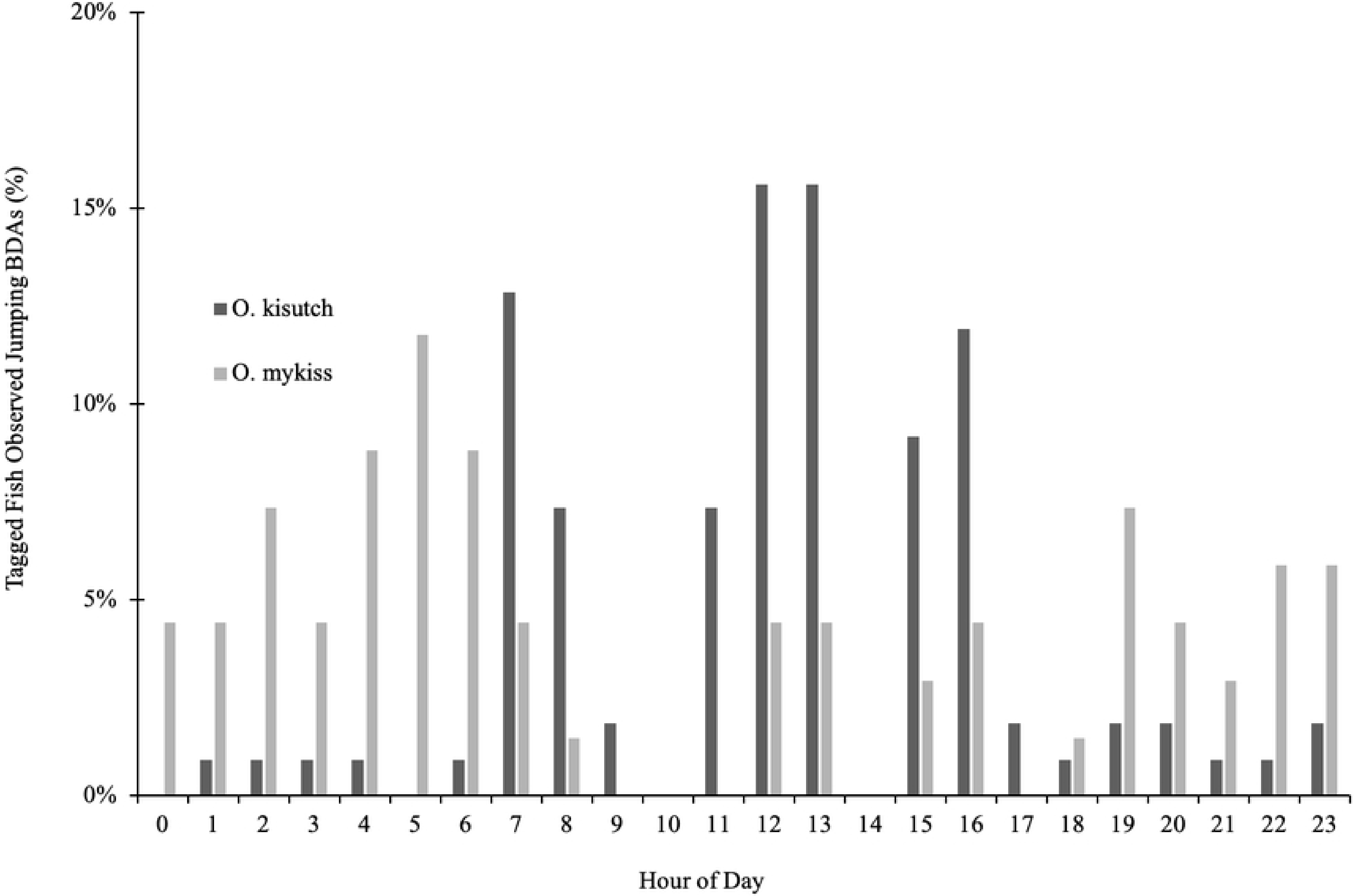

Count of individual fish
0
1
2
3
4
5
6
Hour
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23

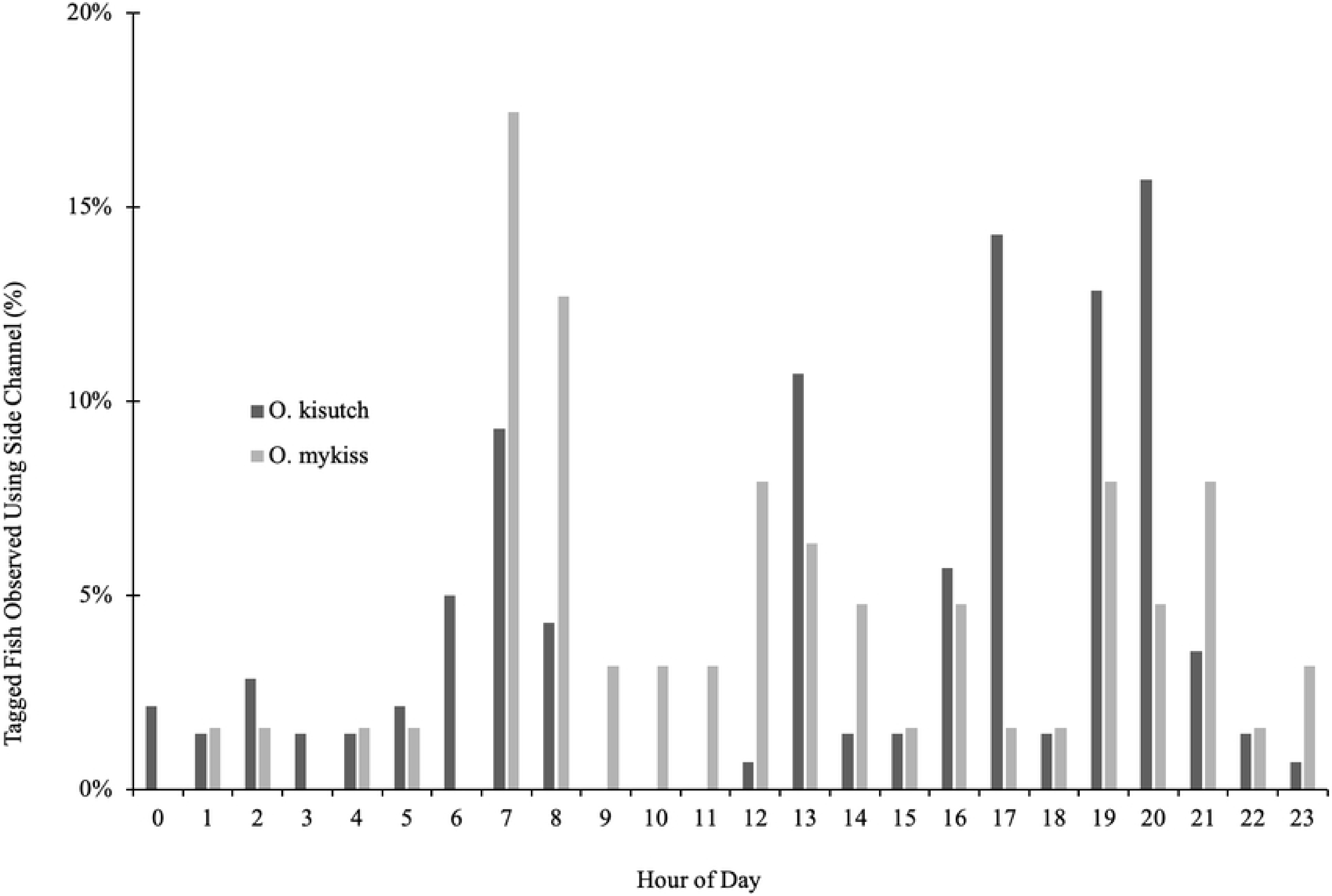

140
120
100
80
60
40
20
0
Number of Individual Coho
Detected in Release Pool
Detected Jumping BDA
Detected in Side Channel
Detected in BDA Pond1
10/25
10/26
10/27
10/28
10/29
10/30
10/31
11/1
11/2
11/3
11/4
11/5
11/6
11/7
11/8
Date



Number of Individual Steelhead
40
35
30
25
20
15
10
5
0
Detected in Release Pool
Detected Jumping BDA
Detected in Side Channel
Detected in BDA Pond1
10/25
10/26
10/27
10/28
10/29
10/30
10/31
11/1
11/2
11/3
11/4
11/5
11/6
11/7
11/8
Date


Jump #08
Jump Ht = 40 cm
WSE
BSE
BDA 1.1
0.74
0.10
0.05
0.29
0.11
0.18
0.10
Coho-42%
Sthd-28%
Side Channel #03
WSE
BSE
BDA 1.1
Bed Slope = 0.11
0.10
0.07
0.04
0.04
Coho-39%
Sthd-55%
Jump #06
Jump Ht = 40 cm
WSE
BSE
BDA 1.1
0.40
0.03
0.07
0.03
0.02
0.03
0.02
Coho-5%
Sthd-33%
Jump #09
Jump Ht = 38 cm
WSE
BSE
BDA 1.1
0.31
0.08
0.03
0.16
0.00
0.00
0.17
Coho-2%
Sthd-10%
Jump #00
Jump Ht = 27 cm
WSE
BSE
BDA 1.0
0.76
0.21
0.06
0.05
0.06
0.06
0.00
Coho-15%
Sthd-0%
Side Channel #0B
WSE
BSE
BDA 1.0
Bed Slope = 0.08
0.78
0.02
0.49
0.11
0.70
Coho-37%
Sthd-35%
Elevation (m)
Horizontal Distance (m)
915.4
915.2
915.0
914.8
914.6
914.4
914.2
914.0
913.8
0.0
0.5
1.0
1.5
2.0
2.5
3.0
4.0
5.0
6.0
7.0
8.0
9.0
]


20%
15%
10%
5%
0%
Tagged Fish Observed Jumping BDAs (%)
O. kisutch
O. mykiss
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
Hour of Day


20%
15%
10%
5%
0%
Tagged Fish Observed Using Side Channel (%)
O. kisutch
O. mykiss
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
Hour of Day