

A Review of the Discovery, Research, and Conservation of the Formosan Landlocked Salmon (*Oncorhynchus masou formosanus*) in Taiwan

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ABSTRACT

First documented in Taiwan in 1919 as *Salmo formosanus*, the Formosan landlocked salmon (*Oncorhynchus masou formosanus*) holds the distinction of being one of the southernmost subspecies of Masu salmon (*Oncorhynchus masou*), and one of the most tropically distributed salmonids along with the Mexican golden trout and Mexican rainbow trout. Its morphology, ecology, and genetics have since been studied extensively, with particular focus on how factors like check dams impact its distribution. However, a sharp decline in wild numbers prompted the Taiwanese government to list the salmon as endangered under the Act on Wildlife Conservation in 1989. This critical designation led to a major conservation initiative: the establishment of an artificial propagation program within Shei-Pa National Park. The restoration team quickly found success, achieving complete artificial propagation by 2004, and establishing a sustainable breeding program using captive-bred fish. Starting in 2006, the release of artificially propagated fingerlings marked the beginning of a decades-long restoration effort. The results have been remarkable. Over 30 years (1994–2024), the population has exploded from an estimated 200 individuals in 1992 to a high of 18,630 in 2023, finishing at 16,897 in 2024. Habitats have similarly expanded, growing from a single stream to a total of nine major river basins. While the wild population is now considered stable, ongoing efforts are dedicated to identifying additional suitable habitats to fully reintroduce the Formosan landlocked salmon to its historical ranges.

Keywords: Formosan landlocked salmon, *Oncorhynchus masou formosanus*.

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1 THE DISCOVERY OF THE LAND-LOCKED SALMON IN TAIWAN

In 1919, Masamitsu Oshima, a Japanese graduate student, and his dissertation advisor, David Starr Jordan of Stanford University, published a paper titled "*Salmo formosanus*, a new trout from the mountain streams of Formosa" (Jordan & Oshima, 1919). The discovery of this new fish species in Taiwan, now known as Formosan landlocked salmon, generated worldwide excitement (Figure 1). This was because trout were believed to inhabit only temperate waters, and Taiwan is a subtropical island where trout were not expected to be found.



Figure 1. The landlocked salmon (*Oncorhynchus masou formosanus*) in its natural habitat (Scale bar = 200 mm).

Jordan and Oshima (1919) stated that "the specimen was a fish with a total length of 335 mm, collected from Taiko River at Saramao (currently Lishan), Nanto, Formosa. Saramao is located in the central part of Formosa, atop the Central Mountain Range. Prior to this, there had been no record of salmon or trout in Formosa, even in the midstream or estuary of Taiko River. However, it was noted that the indigenous people living near Saramao occasionally caught a trout-like fish, which they valued as food. Mr. Oshima received the specimen from Mr. Tomomatsu Tsusaki, a policeman at Shikikun, who stated it was caught by a native and forwarded to the Police Station at Shikikun in October 1918."

A thorough literature review, however, revealed that the Formosan landlocked salmon was first described by Takeo Aoki in 1917 (Aoki, 1917). In his paper titled "The trout of Taiwan," Aoki reported receiving a trout specimen from Taiwan on August 18. This specimen, measuring 33.9 cm in total length, was caught by local residents in the upper reaches of Dajia River, between Nan'ao and Yilan. In July of that year, Aoki visited the Yilan police station area for a freshwater fish survey. His patrol friend, Tomomatsu Tsusaki, informed him that local residents frequently caught this type of fish in mountainous areas thousands of meters above sea level and



in deep mountain valleys with heavy snow in the winter. Aoki requested Tsusaki to send him a specimen, which he received and confirmed to be a trout. He believed this trout was likely of the same nature as those from mainland Japan and had always lived in these high mountains, known only to some local residents. However, Aoki did not classify it as a new species, possibly due to his perception that it was indistinguishable from Japanese mainland trout.

In a separate paper, Oshima (1919) clarified that Aoki's 1917 specimen, along with those Oshima collected, had been identified by Dr. Jordan, confirming it was indeed a new species. Oshima further elaborated on the discovery processes: in July 1917, while Aoki was his assistant, Aoki visited the Yilan police station to collect freshwater fish. The local policeman, Tomomatsu Tsusaki, informed him that residents near the station often caught large mountain stream fish, with a local name as Yamasu, in the mountainous area where Yilan and Nan'ao meet, in the Central Mountain Range, which is also in the upper reaches of Dajia River. Oshima continued, stating that in March 1919, he traveled from Nan'ao to the trout's habitats (near the Wusher District Office) for joint capture efforts. The Wusher District manager told him that "Someone in the Wusher area is raising this type of fish." Oshima quickly arranged for fixatives to be sent and requested the preserved fish be sent back to him. This became the second specimen for research. Although it was a small, undeveloped fish, its body color and shape allowed for identification, and despite some differences from the first specimen, it was a better-preserved sample.

However, Oshima (1930) later proposed a radical idea regarding the scientific name of trout in Japan and Taiwan. He stated that a close examination of the species' scales revealed their structure to be identical to that of Amago trout. Furthermore, morphologically, the two were completely identical, leading him to conclude that the trout found in Taiwan were the same species as the Biwa trout. This raised the question of the new species name. Since the name *Oncorhynchus rhodurus*, given by Jordan and McGregor (in Jordan et al., 1925) to Biwa trout transplanted to Lake Ashi, had priority, therefore, Oshima proposed that both Biwa trout and Amago trout should henceforth be referred to as *Oncorhynchus formosanus*. Based on their scale structure, Oshima (1934) concluded there were no differences between *Oncorhynchus formosanus* of Formosa and the small landlocked salmon, *O. masou*, of southern Japan.

Behnke (1959) and Behnke et al. (1962) argued that all Formosan landlocked salmon possess basibranchial teeth, a characteristic absent in Japanese salmon, meaning they could not be considered identical. Therefore, it was suggested that *Oncorhynchus formosanus* should be placed within genus *Salmo* as originally proposed by Jordan and Oshima (1919)."

Watanabe and Lin (1985) proposed the official scientific name of the Formosan landlocked salmon should be *Oncorhynchus masou formosanus*, and since then this name has been used by academic and official publications.

Ho and Gwo (2010) submitted the Case #3526 application to the Commission on Zoological Nomenclature to change the scientific name of *Oncorhynchus formosanus* to *Salmo formosanus*. Their rationale was that "The older name *Salmo saramao* (Jordan & Oshima in Oshima, 1919), is a senior subjective synonym of *S. formosanus* but has not been catalogued or used since it was described. The suppression of *S. saramao* is therefore proposed to conserve the name *S. formosanus*". However, the International Commission on Zoological Nomenclature has yet to issue a formal decision. Governmental agencies, research institutions, and scientists in Taiwan continue to use *Oncorhynchus masou formosanus* as its official scientific name. Notably, Ho and Gwo's proposed name change aligns precisely with Behnke's suggestions in 1959 and 1962.

2 RESEARCH ACTIVITIES

After Japanese colonial rule of Taiwan ended in 1945, the landlocked salmon no longer received legal protection, and its population was near the brink of extinction. Yuan-Ling Lin, an electrical engineer who was Director of the Lishan Power Supply Protection Station of TaiPower Company stationed near the salmon's main habitat, noticed the decline of the Formosan landlocked salmon population, so he initiated four years of personal efforts to save the fish from extinction (Watanabe & Lin, 1985; Wong, 1994). Another amateur naturalist, Ming-Neng Cheng (1919.2.12~2010.6.28) (Figure 2) (Tzeng, 2011), played a crucial role by establishing a privately funded artificial propagation program in 1974, and released fingerlings back into their home stream. His actions were pivotal in saving the fish from extinction.

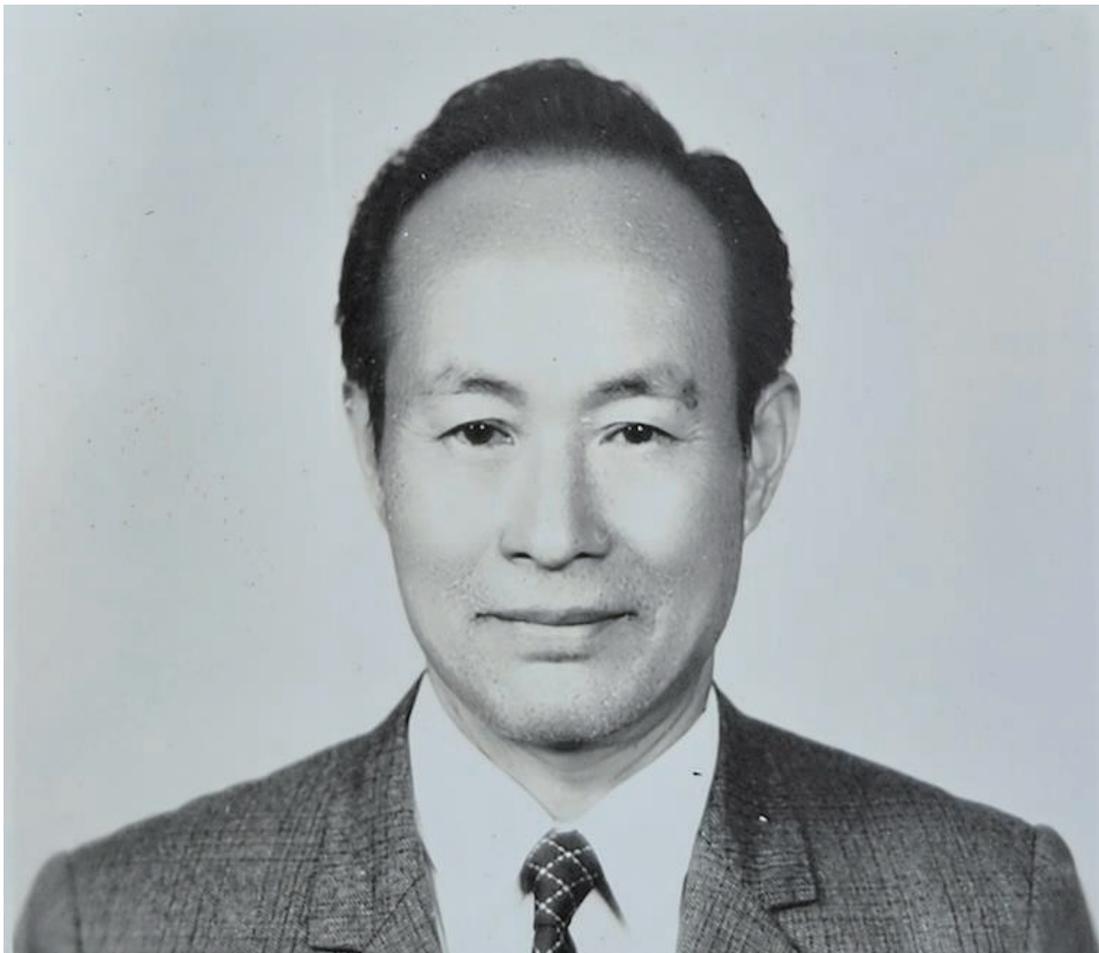


Figure 2. A portrait of Mr. Ming-Neng Cheng, one of the pioneers in in-captivity artificial propagation for the Formosan landlocked salmon. His efforts were crucial in saving the species from extinction.

The personal conservation efforts of both Lin and Cheng received extensive media coverage, which prompted government agencies to enact the Cultural Heritage Preservation Act in 1984. Since 1985, funding has been provided for scientists to research the status of landlocked salmon, their ecology, and habitat conditions. Furthermore, protective measures were introduced, a restoration program was initiated, and a public education program was launched (Day et al., 1993a). Major research outcomes from 1985 to 2024 are categorized and offered below.



2.1 Morphology

From October 1986 to December 1987, a total of 52 Formosan landlocked salmon specimens were collected from Qijiawan Creek, and their morphometric and meristic characteristics were measured (Jan et al., 1990). When compared with published data for this species, it was found that, except for the more variable dorsal and pectoral rays, meristic values were relatively consistent across various studies. The findings also indicated that this landlocked salmon is more closely related to *Oncorhynchus masou masou*, which is widely distributed in Japan.

The ultrastructure of the spermatozoa of Formosan landlocked salmon was examined by Gwo et al. (1996). The study found only minor differences between the mature spermatozoa of *O. masou* and rainbow trout (*O. mykiss*), particularly in the organization of the centriolar complex, the shape of the mitochondria, and the occurrence of intratubular differentiation (ITD) in the flagella. They concluded that the results on spermatozoan fine structure could not resolve the phylogeny of Salmoniformes. Subsequently, Gwo et al. (1999, 2008b) provided detailed protocols for cryopreservation of sperm from the Formosan landlocked salmon.

2.2 Ecology

During the Japanese colonial rule of Taiwan, the distribution range of the Formosan landlocked salmon was reported to extend over six streams of the Dajia (Taiko or Daiko) River system (Kano, 1940).

Tsao (1995) identified potential habitats for Formosan landlocked salmon, which included the presence of native sympatric species, a maximum summer water temperature of less than 18 °C, and an elevation higher than 1,600 m. Mesohabitat selection by the salmon was influenced by spatial, bioenergetic, and habitat factors, leading to varying salmon densities across six mesohabitat types. Pool habitats provided refuge from strong currents and for overwintering, riffle habitats were used for feeding; in addition, run habitats were important for spawning. These habitat relationships suggest that more than 25% of pool-run habitats within a stream section are crucial to maintaining a self-sustaining salmon population.

Tsao et al. (1998) found that newly emerged fry extensively used habitats with minimal current velocity and abundant instream cover. More than 50% of salmon between 5 and 9 cm in length moved into deeper water with moderate current (0.1 to 0.86 m/sec) and less instream cover. Adult salmon utilized slower (less than 0.2 m/sec), shallower sites with abundant instream cover for resting, and fast velocity (0.6 to 1.1 m/sec), deeper sites with less in stream cover for feeding. Spawning salmon preferred shallower waters (0.1 to 0.39 m), slower currents (0 to 0.3 m/sec), and small to moderate substrate sizes (<25.6 cm). The conclusion is that the microhabitat selection by Formosan landlocked salmon is related to fish size, water temperature, and life history activities.

Extensive habitat surveys revealed that the distribution of landlocked salmon was concentrated in the Qijiawan Creek area. Consequently, a series of studies were conducted to examine how the width and placement of riparian vegetated buffer strips could effectively control pollution by intercepting wastewater, surface runoff, and groundwater flow, thereby reducing pesticides, nutrients, and other organic pollutants before they entered the creek (Lin et al., 2002; Lin, Tsao et al., 2004). It was found that a potassium attenuation curve in the vegetable plot was widest due to easy potassium movement in the soil. A potassium safety soil depth of 8.81 m was calculated for the vegetable area.

An engineering project called the Qijiawan Creek Restoration Project (CCRP) was initiated in 1999 on Qijiawan Creek, which was designed to create a more desirable habitat for the Formosan landlocked salmon. The CCRP work began in the summer of 1999, and was completed in the fall of 2001. A shelter channel, 165 m long with an elevation drop from 1,686 m at the upper end to 1,679 m at the lower end, was built on Qijiawan

Creek near check dam number 1. The average slope of the channel was 4%, and its width varied from 1.0 to 6.0 m. Water depth ranged from 20 cm at the riffles to 1.5 m at the pools. A hydrodynamic modeling analysis was performed to provide design guidelines to maintain a maximum flow velocity of 1.0–1.5 m/s in the shelter channel during high flow events, such as typhoons (Lin, Lin et al., 2004).

To control erosion in Qijiawan Creek, a study was conducted to assess reforestation placement and its benefits. In accordance with the concepts of high sediment delivery ratio and vegetated buffer strips, 35.98 ha of reforestation placements were suggested in the study area. Sediment delivery ratio calculations were based on the concept of the probability density function of travel time, evaluated as a function of contributing area. From the analyzed sediment results, the suggested placement and overused farmland could reduce 15,544.01 and 6,339.61 t/year of sediments, respectively. The sediment retrieved ratio of the suggested placement was 2.41 times as high as that of the overused farmland. The results indicated that restoration sites implemented under related policies should be examined and reassessed afterwards (Lin et al., 2008).

To understand how landlocked salmon use microhabitats, several studies were conducted using nano-tag telemetry in the summer (typhoon season) of 2007; a major flood caused by a typhoon occurred during the tracking period, but it did not alter the positions or habitat use by adult salmon. Ten tagged fish predominantly used microhabitats near boulders and made frequent short movements of less than 200 m between habitats. The results suggest that adult salmon are generally sedentary in summer but undertake small-scale movements to secure food. The study provided useful information for Formosan landlocked salmon conservation by demonstrating that boulders in streams may serve as refuges from typhoon floods (Makiguchi et al., 2009).

Habitat use by Formosan salmon of different size classes varied slightly. Juvenile and subadult salmon inhabited sites with lower temperatures and current velocities, while adult salmon occurred more frequently with large-grain-sized substratum. A study showed that variations in the relative occurrence of fish in the Wuling basin were best explained by physicochemical parameters (38.8%), followed by substratum composition (11.4%). Variations exclusively explained by mesohabitat composition, seasonal effects, and biotic components were not significant (Hsu et al., 2010).

Nano-tag radio telemetries were attached to five individual fish (average length: 24.16 ± 4 cm) before being released into the main channel of Qijiawan Creek for a 36-day tracking experiment. The daily upstream and downstream movement distance of Taiwan landlocked salmon significantly decreased with time after release. Upstream movement distance was greater than downstream movement. The movement patterns of Formosan landlocked salmon exhibited two unique features: (1) strongly diurnal behavior, with daily movement starting near sunrise and ending at sunset, traveling to riffle areas during the day and returning to a specific deep pool at night; and (2) habitat preference behavior, where daily movement distance decreased with time after release for large fish, who tended to stay around their home pool, while non-competitive individuals moved frequently upstream and downstream between pools, remaining unstable while searching for a suitable habitat. This finding regarding habitat preference and local movement behavior of Taiwan landlocked salmon was informative for future release strategies and habitat restoration management (Liao et al., 2011).

With the aim of releasing artificially propagated landlocked salmon back into their original habitats, five historically inhabited streams with nine monitoring sites for cultivated breeds were selected. Three reference sites were chosen to represent various levels of habitat quality (best, mildly interfered, and worst circumstances for salmon) to evaluate the candidate sites. These three reference sites were located in streams where the Formosan salmon could naturally propagate. The results indicated that the overall habitat quality of Luoyewei Creek (potential releasing site Y#1) was superior to the other sites. The fish population in Luoyewei significantly increased, with a total of 1,269 fish in 2012, more than 2.5 times the 519 fish recorded in 2011. This significant boost in the salmon population in Luoyewei suggested that the strategy proposed in this study was feasible for salmon release (Kuan et al., 2019).



2.3 Population Changes

The estimated salmon population declined from approximately 1,798 in September 1987 (Tsao, 1988) to 918 in July 1990 (Day et al., 1993a). The abundance of Formosan landlocked salmon in Qijiawan Creek decreased and varied both spatially and temporally between September 1987 and January 1991. The abundance of young salmon changed over time, while adult abundance fluctuated less. Natural catastrophes (typhoons, floods) and human-made disturbances, such as check dams, contributed to the observed spatial and temporal variability in salmon abundance (Day et al., 1993b).

Census observations (Tzeng, 2003, 2004; Tzeng & Yang, 2003) from Qijiawan Creek over an 18-year period from 1987 to 2004 showed significant fluctuations in the population size of Formosan salmon. Numbers ranged from 253 to 4,221 individuals, with a mean of 1,343 individuals. There were two peaks in total numbers, one in the summer of 1996 and another in the summer of 2002. The 2002 summer peak could be attributed to a large increase in the number of juveniles. Consequently, the number of subadults peaked in the following summer. Similarly, in the tributary Kaoshan Stream, the number of juveniles also peaked in the summer of 2002 (Chung et al., 2007).

2.4 Feeding Habits

In July 1935, Masuzo Ueno accompanied Masamitsu Oshima to Dajia River, the home stream of the Formosan landlocked salmon, to study the stomach contents of the fish. He collected a total of 11 fish and sorted the stomach contents. Sand grains were found in 2 fish, and plant debris in 3 fish. Aquatic insects from 13 families comprised the majority of the contents, while terrestrial insects from 4 families were also found. Spiders were found in one fish, and isopod crustaceans in another. One fish was found to have an amphibian inside its stomach (Ueno, 1937).

Yang et al. (2012) reported that 92 fish samples were collected from five stations in Qijiawan Creek and Goshan Stream from 2006 to 2007. The ratio of aquatic to terrestrial insects in stomach contents was 7:3 in 2006 and 3:7 in 2007. The shift to a high proportion of terrestrial insects was likely due to 4 consecutive typhoons disturbing the area, which might have flushed away most aquatic insects.

On August 23, 2010, a total of 48 salmon (11 large fish, 19-25.2 cm total length; 37 small fish, 8.0-14.8 cm total length) were collected by electrofishing from Yousheng Stream, a natural habitat of the fish. The fish underwent stomach pumping to remove their stomach contents for analysis. The main prey items found were aquatic and terrestrial insects. Large fish consumed 60.87% aquatic insects and 39.13% terrestrial insects, while small fish had 90.25% aquatic insects and only 9.75% terrestrial insects in their stomach contents. The proportion of the diet comprising terrestrial prey and its trophic diversity increased with salmon body size. It is clear that salmon rely on terrestrial resources for a significant part of their diet, particularly adult fish. For conservation and management purposes, Liao et al. (2012) urged that the restoration of forest vegetation, especially in riparian zones, be a top priority.

2.5 Genetics

As one of the southernmost distributed salmonids in the northern hemisphere, its genetic makeup was first investigated in 1990. By analyzing mitochondrial DNA, Numachi et al. (1990) reported that all 29 specimens of the Formosan salmonid showed the same single clonal genotype of mtDNA. This clonal genotype was very similar to one found in populations of the Masu salmon, *Oncorhynchus masou masou*, distributed in Japan. They concluded that the Formosan salmonid originated from Masu salmon distributed in the Sea of Japan, having passed through the Tsushima channel about 100,000 to 800,000 years ago. The unusual homogeneity of

mtDNA type found in the Formosan landlocked salmon population was attributed to a contracted stage of the population.

The complete mitochondrial genome sequence of *Oncorhynchus masou formosanus* was generated using next-generation sequencing. The circular genome (16,653 bp) has the typical vertebrate mitochondrial gene arrangement, consisting of 13 protein-coding genes, 22 tRNA genes, two rRNA genes, and a non-coding control region. The overall base composition of *O. m. formosanus* is 28.6% for A, 26.8% for T, 16.5% for G, and 28.1% for C, with a slight AT bias of 55.4%. Phylogenetic analysis showed that *O. masou formosanus* shared the same cluster with other *O. masou* subspecies. *Oncorhynchus masou formosanus* may have diverged earlier than *O. masou ishikawae* and *O. masou masou*, but later than *O. biwaensis*. It is expected that these results will help elucidate the taxonomic status of *O. masou formosanus* and contribute to its conservation (Ho et al., 2016).

When comparing it with Japanese populations, Tzeng et al. (2006) found that the genetic diversity of the Formosan landlocked salmon population is so small that population decline or a founder effect may have had a greater impact on it. Numachi et al. (1990) proposed that Formosan landlocked salmon evolved about 100,000 to 800,000 years ago. The shortest genetic distance between Taiwanese and Japanese populations is 0.1%. Applying a mutation rate of 0.25% to 0.45%/My, a divergence time of 110,000 to 200,000 years ago was suggested as the upper boundary, corresponding to the last glaciation period (Emery et al., 1971).

Using Amplified Fragment Length Polymorphism (AFLP) markers to examine the genetic diversity of 58 individuals of Formosan landlocked salmon, Hsu and Gwo (2007) found that the population has low genetic diversity ($H_e = 0.057$) with average values of 0.9692. They hypothesized that the diversity within and among salmon populations has been substantially reduced due to the extinction of many local populations, as well as a reduction in population size of most extant populations.

Gwo et al. (2008a) used AFLP markers in an attempt to sort out the phylogenetic relationship among four subspecies of cherry salmon: Amago (*O. masou ishikawae*), Biwa (*O. masou subspecies*), Masu (*O. masou masou*), and Formosa landlocked salmon (*O. masou formosanus*). However, their efforts failed to distinguish the differences and therefore concluded that the taxonomy and evolutionary relationships of the Formosa landlocked salmon with the other three species of the *O. masou* complex remain uncertain.

By comparing DNA sequences for the growth hormone 1 gene (GH1) from 11 species of *Oncorhynchus* subspecies, Chang et al. (2009) discovered that the Formosan landlocked salmon did not carry the 5-GCT genes within the sequence of primer F2. This suggests a more distant relationship to other *Oncorhynchus* subspecies, at least for *O. masou biwaensis*, *O. masou*, and *O. masou ishikawae*.

It is known that Formosan landlocked salmon can be genetically distinguished from other Masu salmon (Gwo et al., 2008a), but its genetic variation is extremely low, and genetic factors may now critically affect fitness (Hsu et al., 2015). Based on these two critical issues, Burridge (2019) proposed a bold idea: there appears to be clear merit for the genetic rescue of Formosan landlocked salmon, and test crosses involving other landlocked Masu salmon are urgently required. If these test crosses yield individuals of high fitness, guidelines will be provided for their introduction into the wild. Additionally, subpopulations above and below check dams must be connected through direct exchange of individuals to minimize further loss of genetic variation. Insurance populations with independent risk probabilities to the existing population should also be established, with continuing connectivity among populations through direct exchange of individuals. Academically, this suggestion seems sound and perhaps merits a small-scale experiment; however, many scientists objected to the idea of introducing genes from other *Oncorhynchus* subspecies into the gene pools of Formosan landlocked salmon.



2.6 Dam Removal

The Techí Dam was built in the upper stream of Dajia River in 1973. To protect it from siltation, numerous check dams were constructed along the upper tributaries leading to the Techí Dam. There are four such check dams in Qijiawan Creek, which inadvertently fragmented the original contiguous salmon populations into four separate subpopulations, preventing gene flow and resulting in inbreeding. The presence of check dams impeded natural hydraulic processes and hastened the downstream transport of sediment above the dam. Consequently, the upper reaches of the dams, previously suitable for salmon, gradually became monotonous, slate- and sandstone-bottomed shallow runs devoid of fish life. This may explain why more fish were observed below the dams than above them. The lack of adequate spawning and rearing grounds in both above and below the dams has contributed to the decline of the Formosan landlocked salmon in the past (Lin et al., 1990).

The call for the removal of check dams gained momentum (Yan, 2000), and the government approved the partial removal of four check dams starting from April 1999 until September 2001 (Yeh et al., 2002). After the dams were removed, fish were able to travel freely up and down the stream. Studies conducted by Chung et al. (2008) confirmed that partial dam removal might have improved the survival rate of the salmon population in response to floods.

A mid-size check dam, Qijiawan No.1 dam, was removed in 2011 to provide access to upstream habitat for the salmon. A three-phase radio telemetry tracking experiment was conducted to identify movement patterns before, during, and after dam removal. During the dam removal phase, fish below the dam moved very little when heavy machinery was in the stream, then made long-distance movements when the upstream habitat became accessible after dam removal. The rapid response of these salmon confirmed that the new habitat opened by the dam removal could be utilized almost immediately (Chen, 2012).

Chiou (2015) built a mathematical model based on more than 20 years of salmon movement data before and after dam removal to evaluate its effects. The results of statistical tests showed that the upstream population significantly increased after the destruction of dam #2, as the downstream population tended to move to cooler upstream areas, and sediments from the dam destruction persistently impacted the physical habitats downstream. For the comparison of three age-classes, small fish increased significantly, proving that dam #2 blocked the pathway for reproduction. Additionally, the results of the population-estimating model concerning the dam also showed that small fish increased when the dam did not exist. In contrast, the number of the other two age-classes decreased slightly due to competition from the increasing number of small fish. Nevertheless, the population structure became pyramid-shaped, indicating that dam removal benefits population renewal (Chiou, 2015).

3 SAVING THE ENDANGERED FORMOSAN LANDLOCKED SALMON: 30 YEARS OF CONSERVATION EFFORTS

In 1938, the Taiwan Governor-General's Office of Historical Sites and Natural Monuments Survey Committee, comprising Mr. Shinobu Koshigi and Mr. Hiroshi Nakamura identified Formosan landlocked salmon, (Jordan & Oshima, 1919), then referred to it as the 'cherry blossom trout', a living relic of the Ice Age in subtropical Taiwan, where cold-water fish are scarce and had been isolated by land for a long time. It was designated as a 'Natural Monument' for protection, possessing significant biogeographical importance.

During the Japanese colonial period, the Taiwan Governor-General's Office promptly formulated specific conservation measures for the Formosan landlocked salmon. These included prohibiting the release of other

fish species or fish eggs, banning fishing with nets and traps in some tributaries, prohibiting fishing in Qijiawan Creek during spawning season, and prohibiting logging and landform changes within 300 meters on both banks of the seven major streams.

When Taiwan was reclaimed by the Chinese authority in August 1945 after Japan's defeat by the Allied Forces, the landlocked salmon no longer received protection from the new government. After the Nationalist Government lost its civil war with Mao's Communist Force, they retreated to Taiwan in 1949. To settle discharged veterans who fled China to Taiwan, the government sent them to the Qijiawan Creek area to establish Wuling Farm for cultivating temperate zone fruits (apples, pears, peaches) and vegetables. Inevitably, the landscape underwent drastic changes. Original virgin forests were destroyed, and surface vegetation was removed. This caused erosion of riverbanks, and silts directly entered the salmon's home streams. Furthermore, the newly settled residents began consuming salmon without limitation. As a result, the salmon population was severely depleted and teetering toward extinction.

Four decades ago, the endemic Formosan landlocked salmon was on the brink of extinction. During Taiwan's rapid economic expansion, human development aggressively spread into mountainous regions. This led to a devastating combination of overfishing, water pollution, and habitat loss, shrinking the salmon's distribution by nearly 90% and leaving a mere 200 individuals scattered across five streams.

Astonishingly, these salmon inhabit the high mountains of subtropical Taiwan. Descended from Ice Age ancestors hundreds of thousands of years ago, they evolved in isolation due to geological transformations, becoming landlocked. The Formosan landlocked salmon is endemic to the mountainous regions of central Taiwan, representing the southernmost and highest-altitude population of temperate salmon globally. This remarkable creature is a living testament to glacial history.

Facing near-extinction by 1984, the Formosan landlocked salmon prompted a pivotal moment in the nation's environmental conservation history. Taiwan enacted the Act on Wildlife Conservation in 1989, a landmark piece of legislation that included listing the Formosan landlocked salmon as an endangered fish species.

3.1 With the Establishment of Shei-Pa National Park, an Artificial Propagation Program of Landlocked Salmon was Established

Recognizing the critical need for species conservation, Shei-Pa National Park was founded in 1992, incorporating the Formosa landlocked salmon's habitats in the Qijiawan Creek catchment. Five years later, in 1997, two significant milestone events occurred: the establishment of the Formosan landlocked salmon wildlife sanctuary and the creation of the Wuling Management Station within Shei-Pa National Park, specifically tasked with protecting the endangered Formosa landlocked salmon. It is important to note that although Shei-Pa National Park was established in 1992 with the mission of protecting the Formosan landlocked salmon and its natural habitat, the majority of funding and support for salmon conservation efforts—especially prior to the year 2000—came from the Council of Agriculture (COA) of the Taiwanese government.

Inspired by the concept of Noah's Ark, the Shei-Pa National Park Management Office started developing a breeding program to enhance Formosa landlocked salmon populations through artificial breeding. The initial strategy involved artificial breeding through wild-caught adults followed by releasing fingerlings into the wild. However, this method faced a key challenge: sustainable conservation practices dictated that only limited wild spawners could be captured for breeding, which inherently restricted the number of offspring that could be produced.



Recognizing the need for a comprehensive conservation approach, the Center for Endemic Biology convened an international collaboration workshop in 2000, hosting the "Formosan Landlocked Salmon International Conservation Symposium". Experts from the US, Canada, Japan, and other nations joined forces to develop a 30-year restoration plan for the upper Dajia River, focusing on the five key salmon streams. This plan outlined phased objectives and a dual strategy of *in-situ* and *ex-situ* conservation endeavors.

3.2 Complete in Captivity Breeding of the Formosan Landlocked Salmon (*Ex-Situ* Conservation)

Between 2001 and 2004, the restoration team successfully achieved complete artificial propagation of the Formosan landlocked salmon. By using captive-bred fish, they established a sustainable breeding program (Figure 3).

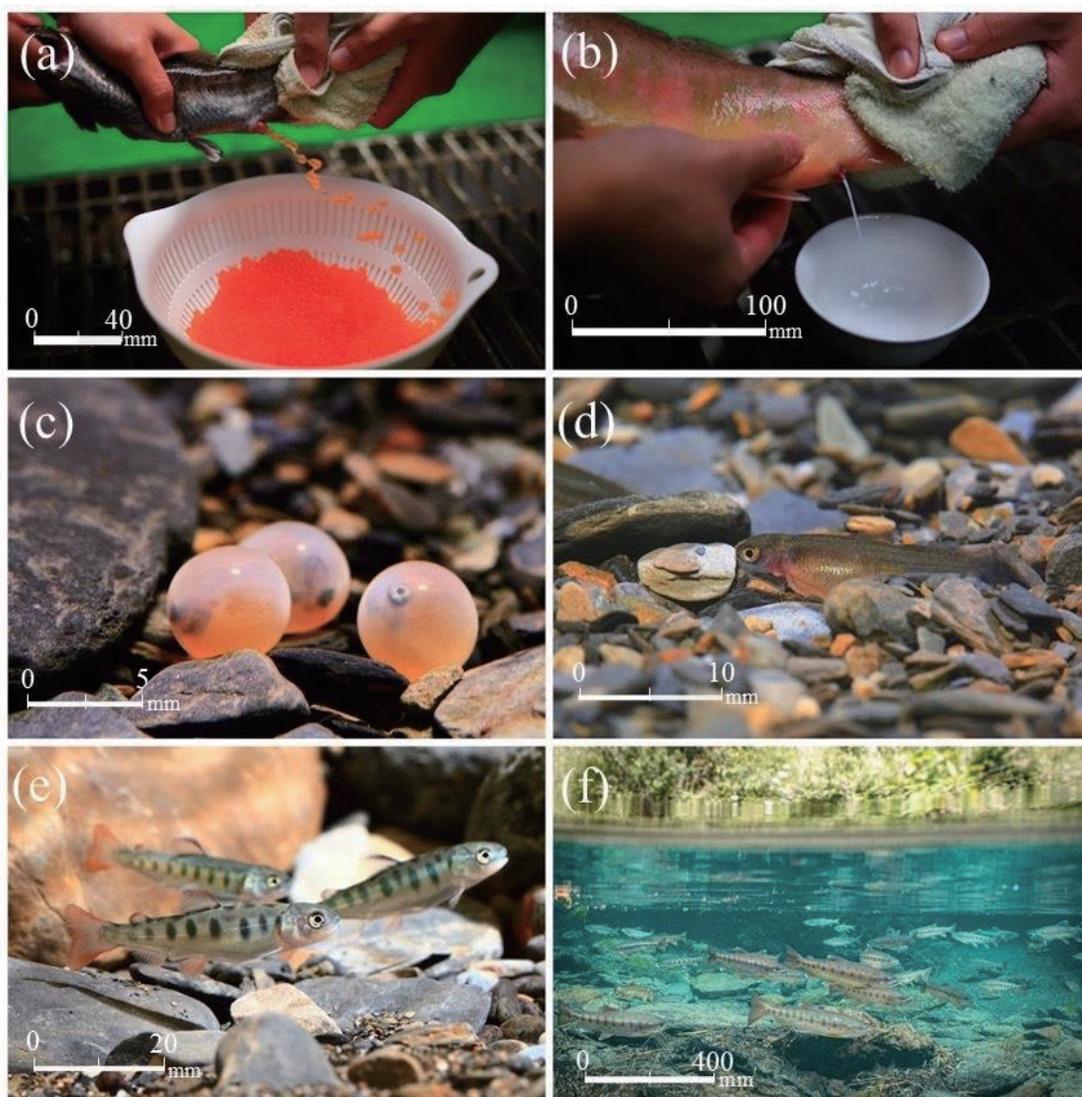


Figure 3. Artificial propagation of Formosan landlocked salmon in captivity and subsequent re-introduction into natural habitats: (a) collection of eggs; (b) collection of milt; (c) eye-stage embryos; (d) yolk-sac fingerling stage; (e) three-month-old juveniles; (f) re-introduced salmon observed in their natural habitat.

The releasing of artificially propagated fingerlings into the wild started as early as 2006, and has been an ongoing restoration effort (Table 1). The comprehensive biological profiles of the landlocked salmon, derived from life cycle studies, reveal several notable characteristics. Males mature at 0+ years, females at 1+ years, and about 90% of the population engages in reproduction. Both sexes can survive post-spawning, and the maximum lifespan is 3+ years. Early-maturing males (0+) exhibit significant size and growth advantages over same-age females. Interestingly, these traits share partial similarities with the life history patterns of Japanese mountain fish and migratory cherry salmon.

Table 1. The annual records of released artificially propagated *Oncorhynchus masou formosanus* fingerlings, including age and release sites.

Sampling Month	Release Stream	Count	Age
2006.10	Sijielan Creek	250	Age 1 ⁺
2006.10	Nanhu Creek	250	Age 0 ⁺
2007.10	Sijielan Creek	160	Age 1 ⁺
2007.10	Nanhu River	375	Age 0 ⁺
2008.03	Ika-wan Creek	300	Age 0 ⁺
2009.06	Luoyewei Creek	100	Age 1 ⁺
2009.06	Sijielan Creek ^{*1}	100	Age 1 ⁺
2010.05	Luoyewei Creek	350	Age 0 ⁺
2010.05	Sijielan Creek ^{*1}	180	Age 1 ⁺
2010.05	Sijielan Creek ^{*2}	180	Age 1 ⁺
2010.10	Luoyewei Creek	30	Age 1 ⁺
2010.10	Ika-wan Creek	30	Age 1 ⁺
2011.11	Ika-wan Creek	100	Age 1 ⁺
2011.11	Leshan Creek	100	Age 1 ⁺
2012.10	Leshan Creek	25	Age 1 ⁺
2013.10	Leshan Creek	25	Age 1 ⁺
2015.10	Zhile Creek	18	Age 1 ⁺
2017.10	Hehuan River ^{*3}	100	Age 0 ⁺
2017.10	Hehuan River ^{*4}	120	Age 0 ⁺
2017.10	Hehuan River ^{*5}	300	Age 0 ⁺
2018.06	Hehuan River ^{*6}	1,000	Age 0 ⁺
2018.09	Hehuan River ^{*5}	1,000	Age 0 ⁺
2018.10	Hehuan River ^{*3}	1,000	Age 0 ⁺



Sampling Month	Release Stream	Count	Age
2019.07	Hehuan River *6	1,000	Age 0+
2019.08	Hehuan River *5	1,000	Age 0+
2019.08	Hehuan River *3	1,000	Age 0+
2020.09	Sijielan Creek	1,000	Age 1+
2020.10	Nanhu River	1,000	Age 1+
2021.04	Nanhu River *7	1,000	Age 1+
2022.04	Nanhu River	300	Age 0+
2022.05	Yousheng Creek	500	Age 0+
2022.09	Sijielan Creek	300	Age 0+
2023.05	Yousheng Creek	500	Age 0+
2023.05	Sijielan Creek	1,000	Age 0+
2023.11	Zhongyangjian River	1,000	Eyed egg
2024.07	Sijielan Creek	1,000	Age 0+
*1 First Wild Stream Section of Sijielan Creek			
*2 Second Wild Stream Section of Sijielan Creek			
*3 Xiao Tansixi Bay, Hehuan River			
*4 Hehuan River Winter Training Center			
*5 Hehuan River Trail			
*6 Taiyangcheng, Hehuan River			
*7 Upper reaches of Nanhu River			

To improve hatching survival rates, the "Fish Egg Incubation and Fry Training System" was invented in 2008. This patented system controls water temperature, water quality, water intake, and light, increasing both hatching and survival rates up to 70%.

3.3 The Formosan Landlocked Salmon Back Home: Releasing Them into Their Historical Streams (*In-Situ* Conservation)

Typhoon Airy's destructive force in 2004, which brought torrential rains and landslides, completely destroyed the Qijiawan Creek hatchery. This catastrophic event undermined prior conservation work and disrupted off-site breeding initiatives.

The "Formosan Landlocked Salmon Ecological Center" was completed in 2005, setting the stage for further conservation efforts. In 2009 and 2010, a total of 550 cultured salmon were introduced into Luoyewei Creek, a historical stream outside Qijiawan Creek. This initiative successfully created a satellite population that now breeds independently and has stabilized at about 500 individuals. This achievement marked Luoyewei Creek as the second wild population stream that inspired the research team.

The artificial propagation program of landlocked salmon continued from 2018–2024 (detailed data are listed in Table 2). The number of spawners used from the broodstock ranged from 100 to 500 individuals. In order to maximize genetic diversity of the progenies produced, 20 wild-caught individuals were also used in the artificial propagation program.

Table 2. Summary of spawners (broodstock and wild-caught) used and the resulting number of fertilized eggs produced in the Formosan landlocked salmon artificial propagation project (2018–2024).

Year	Broodstock	Wild-caught Fish	No. of Fertilized Eggs
2018	100	20	10,000
2019	100	20	10,000
2020	100	20	10,000
2021	200	20	10,000
2022	150	20	15,000
2023	400	20	15,000
2024	500	20	10,000

A collaborative effort with Hokkaido University led to the development of a button-sized radio transmitter, enabling researchers to study Formosan landlocked salmon behaviors. Implanted in young salmon since 2006, these transmitters have revealed several key daily migration patterns: diurnal movement with open water entry during the day and deep pool return at night, decreasing daily movement distance with release time, frequent exploration of adjacent pools for habitat selection, limited 563-meter daily activity range for sedentary individuals, and directional homing capabilities.

Utilizing transmitter data, researchers determined that Formosan landlocked salmon require suitable habitats with pools and slow-flow areas for optimal growth. The failure of releases in certain stream sections was directly attributed to a deficiency of deep pools. To address survival challenges, researchers examined the relationship between typhoons and population numbers. Diffusion studies in Nanhu and Sijielan Creeks, demonstrating limited dispersal (less than 10%), led to the recommendation for multiple release points to minimize risks from floods and droughts, thus improving the survival rate of the released population.

3.4 Dam Removal to Restore River Flow (*In-Situ* Conservation)

Habitat restoration is another key focus. Despite conservation efforts for Formosa landlocked salmon beginning in the 1980s, by the time Shei-Pa National Park was established in 1992, fewer than 200 individuals survived, and conservation was at one point declared a failure. Through data analysis, the research team identified the critical factor: check dams that limited the movement of the fish.

Taiwan's rivers have steep gradients and uneven rainfall distribution. To efficiently utilize water resources, various hydraulic facilities such as weirs and dams are distributed along Taiwanese rivers for flood control, sediment retention, irrigation, or hydropower. However, the construction of these structures alters the river's landscape, isolates upstream and downstream habitats, and impacts the original river ecosystem. Qijiawan Creek, located in the upstream catchment area of the reservoir, contained more than ten check dams spaced at intervals of less than 1 km, reflecting a very high density.



To provide migratory space for Formosa landlocked salmon and reduce habitat fragmentation, Shei-Pa National Park began feasibility studies for check dam removal in 1996. Between 1999 and 2001, over two and a half years, four check dams in Kaoshan Stream, a tributary of Qijiawan Creek, were successively removed.

After the removal of the check dams in Kaoshan Stream, the proportion of large stones on the riverbed increased, forming a more stable substrate, and the proportion of deep pool habitats also increased. The riverbed gradient upstream and downstream of the dam gradually flattened, allowing salmon to successfully migrate to upstream waters, where naturally bred juvenile salmon began to be found.

Since then, Shei-Pa National Park has continuously monitored the impact of check dam removal on the river channel and Formosan landlocked salmon habitat, and continued to evaluate improvements to other check dams within the habitat. They discovered that the 15-meter-high No. 1 check dam at the furthest downstream section of Qijiawan Creek was a critical bottleneck. After each typhoon, Formosan landlocked salmon washed downstream were unable to return upstream due to the dam's obstruction, and the downstream water temperature was too high for them to survive.

The tall check dam raised the riverbed, leading to habitat homogenization. During floods, it impacted roads and endangered road safety. Therefore, removing the No. 1 check dam in Qijiawan Creek not only provided a channel for salmon to move to cooler upstream waters but also ensured road safety. The No. 1 check dam was finally removed in 2011. Subsequently, even when typhoons struck, Formosan landlocked salmon washed downstream by floods could successfully move upstream to survive and reproduce. In 2012, the number of Formosan landlocked salmon in Qijiawan Creek significantly rebounded to 5,400 individuals, demonstrating the importance of restoring ecological corridors.

3.5 Converting Cultivated Land Back to Forest (*In-Situ* Conservation)

The ecological health of the upper Dajia River tributaries has been compromised by alpine agriculture in the Lishan area, leading to water quality degradation. This deterioration is the primary driver behind the near-extinction of the Taiwanese salmon. Given the crucial role of forests in water regulation, restoring these areas was an urgent task for safeguarding river ecosystems.

According to the restoration team, "A healthy forest ecosystem fulfills the three essential requirements of salmon: suitable temperature, food resources, and high-water quality". The cooling effect of tree shade results in waters 3 °C cooler than those without canopy cover. Forests also provide critical water regulation and purification services, and serve as a source of food for salmon through terrestrial insects and leaf litter. These interconnected functions could improve the environment's ability to withstand climate change impacts.

As a proactive measure to improve water quality in the Qijiawan Creek basin, Shei-Pa National Park commenced the planning and establishment of a sewage treatment system in 1997. This system was designed to mitigate sewage pollution from Wuling Farm and nearby recreational areas.

As a strategic measure, they pursued negotiations with Wuling Farm to accelerate its shift towards eco-tourism, simultaneously reducing farming operations and restoring farmland for reforestation. In partnership with the Taiwan Forestry Bureau, they implemented tree planting projects along Qijiawan Creek and on reclaimed agricultural land. Over the past 30 years, these efforts have resulted in the planting of more than 500,000 native trees.

Demonstrating a commitment to environmental protection, the Taiwanese government, for the first time, invoked the "Land Acquisition Law" to expropriate private vegetable land for reforestation, rather than development. The final 8.1 hectares of private land in the Wuling area were acquired in December 2006, directly benefiting the Formosan landlocked salmon in Qijiawan Creek by eliminating agricultural pollution.

Research into the dietary habits of the Formosan landlocked salmon demonstrates that terrestrial invertebrates play a larger nutritional role in larger fish compared to smaller ones. This dietary contribution is most pronounced during seasons with high terrestrial invertebrate abundance, typically coinciding with wet periods and a scarcity of aquatic insects, such as after typhoons. The forest's provision of terrestrial insects is critical for fulfilling the salmon's pre-breeding nutritional requirements, emphasizing the forest's importance to the species' survival.

3.6 Cross-Domain Collaboration to Increase Stream Water Releases

Improvements to the Qijiawan River habitat alone were not enough for the Formosan landlocked salmon conservation team. Dam removal causes temporary damage, and agricultural activities near the watershed remain frequent, with typhoons or heavy rains potentially destroying existing created habitats. To reduce the survival risk of the Formosan landlocked salmon and increase genetic diversity, releasing them into other streams was necessary.

Global warming was also a concern for the conservation team. Taiwan's temperature has increased by 1.3 °C over the past century, and the rate of temperature increase has accelerated during recent years, which is highly unfavorable for the low-temperature-dwelling Formosan landlocked salmon. Therefore, in addition to historically inhabited streams, releases have also been attempted in higher-altitude, lower-temperature streams.

Choosing different streams to release fingerlings could contribute to enhance the genetic diversity of the Taiwanese salmon. Different temperatures, food sources, and habitats may allow Formosan landlocked salmon to evolve. The 10,000 cultured individuals bred annually by the conservation center are specifically selected from broodstock with high genetic variations for pairing.

In 2017, Shei-Pa National Park collaborated with Taroko National Park to release Formosan landlocked salmon into Hehuan River and Nanhu River within its borders. The selected stream sections are at an altitude of approximately 2,200 m, higher than Qijiawan Creek (1,750 m). The release into Hehuan River was successful in 2018, and it has now become the largest satellite population outside Qijiawan Creek.

In 2022, the wild population of Formosan landlocked salmon reached 15,374 individuals, 60 times the number at the beginning of the conservation effort. In October 2023, the Formosa landlocked salmon conservation team achieved a major breakthrough in rearing techniques, successfully overcoming the long-standing challenge of long-distance transport and ensuring fish survival in their new habitats.

Through a waterless transportation method, thousands of eyed Taiwanese salmon eggs were transported over mountains and rivers for 48 hours in a humid environment maintained at 2° Celsius, reaching Zhongyangjian River, a tributary of Nanhu River, at an altitude of 2,200 meters. They were released using the *in-situ* burial method. In the summer of 2024, the conservation team surveyed the released Formosan landlocked salmon population and found 19 individuals. The conservation team stated that the presence of Formosan landlocked salmon in Zhongyangjian River, from none to 19, should be considered as a significant breakthrough.



3.7 Collaboration with Local Indigenous Communities in Patrolling Habitats

Tracking and management are necessary after fingerling releases. Shei-Pa National Park chose to collaborate with indigenous communities and local residential communities.

In the early 20th century, the slopes of the various tributaries in the upper Dajia River were originally covered with dense virgin forests, and Formosan landlocked salmon were abundant in the streams. They served as an important food source for the local Atayal indigenous people, establishing deep historical and cultural ties between people and fish. As a result, the Atayal people have a deep understanding of the Taiwanese salmon's ecosystem. To protect the Formosan landlocked salmon within their traditional territories, the Hsinchu and Nanshan tribes reached an internal consensus in 2000 and formed informal fish protection teams.

Indigenous people are familiar with the local terrain and possess rich traditional ecological knowledge, enabling them to identify threats from invasive species or abnormalities in the ecosystem. Collaborating with indigenous communities for co-management can more effectively promote conservation efforts, provide employment opportunities for indigenous people, alleviate economic pressure caused by reduced traditional hunting or farming activities, and reduce potential conflicts such as poaching or other illegal activities.

Shei-Pa National Park decided to cooperate with indigenous communities and officially established conservation patrol teams. In 2004, they partnered with the Hsinchu tribe to assist in patrolling Yousheng Creek, Yikawan River, Sijielan Creek, and Nanhu River. In 2009, they partnered with the Nanshan tribe to assist in patrolling Luoyewei Stream. In 2011, they partnered with the Songmao tribe to assist in patrolling Leshan Stream. In 2017, they partnered with the Cuihua community to assist in patrolling Hehuan River within Taroko National Park.

3.8 Environmental Education within Habitats

In a span of 30 years (1994~2024), restoration initiatives have yielded significant results: the salmon population surged from a mere 200 to 16,897 in 2024 with a record historical high in 2023 of 18,630 individuals; in addition, their habitats grew from a single stream, i.e., Qijiawan Creek, to encompass nine additional major river basins including Luoyewei Creek, Yousheng Creek, Nanhu River, Zhongyangjian River, Ewu Creek, Bilu Creek, Hehuan River, Leshan Creek, and Sijielan Creek (Figure 4). The ambitious three-stage objectives established in 2000 were surpassed ahead of schedule, marking a truly inspiring success story.

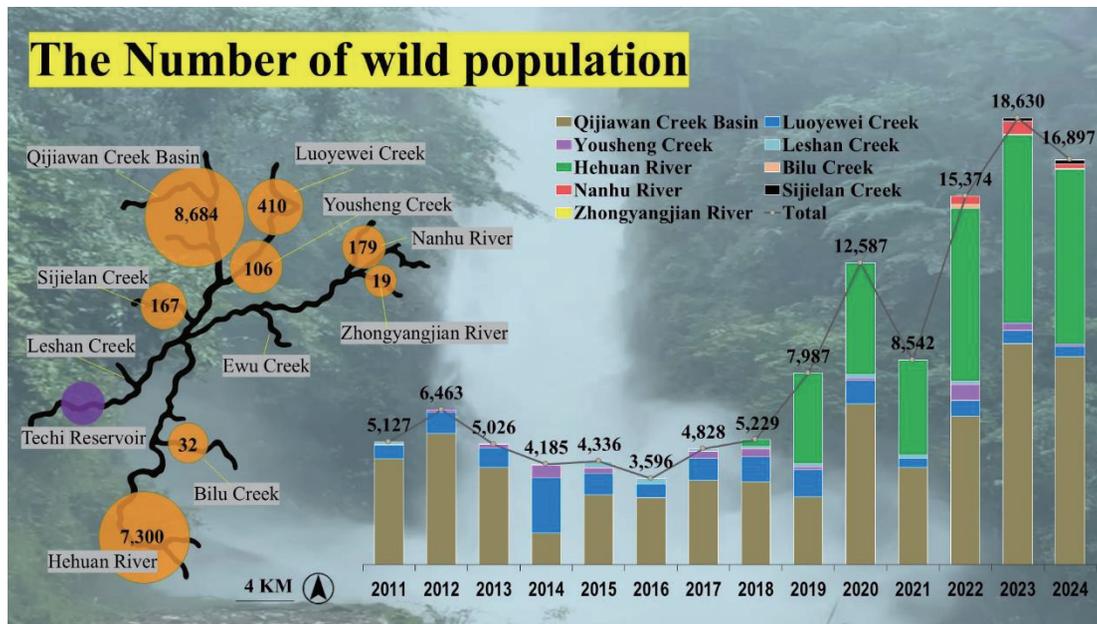


Figure 4. Field counts showing the fluctuation in the number of Formosan landlocked salmon individuals in their natural habitats from 2011 to 2024. The lowest number was recorded in 2016 with 3,596 individuals while the historical highest number of 18,630 fish was registered in 2023. Prior to 2018, the Qijiawan Creek basin was the major habitat. However, the number of fish residing in Hehuan River has increased significantly since 2019, highlighting the considerable success of the project's re-introduction efforts.

The restoration team stressed that the conservation of Formosa landlocked salmon is fundamentally about safeguarding the entire ecosystem, rather than focusing solely on a "star species". The integrated conservation approach requires addressing the health of the stream's origin. Recognizing the salmon as a vital indicator of stream environmental quality, the team underscores the critical importance of a healthy forest ecosystem.

Employing a comprehensive approach to environmental education, the restoration team provides interpretation services and guided tours at Qijiawan Creek, implements community and tribal education programs, collaborates with local schools to develop conservation courses and ecological camps, and actively recruits volunteers for conservation efforts.

With the goal of fostering a deeper connection to the environment, plans are underway to create an immersive salmon experience classroom. This initiative will allow tourists to directly witness Formosan landlocked salmon in their stream habitat, equipped with wetsuits, thereby promoting understanding, concern, and active participation in safeguarding stream ecosystems and water resources.

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