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Assessing Trends and Challenges: Insights From 30 Years of Monitoring and Management of Threatened Southern Atlantic Salmon Populations

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ABSTRACT

The Atlantic salmon (*Salmo salar*) has suffered significant population declines worldwide, prompting urgent conservation efforts, especially in its southern distribution area. This study is aimed at characterising the population dynamics of Atlantic salmon in the Bidasoa River (Spain), by focusing on fluctuations and long-term trends in salmon returns, population characteristics and effects of angling and stocking activities. For this, monitoring data spanning three decades (1993–2023) from a salmon monitoring station and anglers' captures were used together with data on stocking activities provided by the Fish Management Section of the Navarre Government. Results reveal cyclical patterns driven by three distinctive wavelengths linked to the salmon life cycle, climatic variations and local habitat and connectivity improvements. The Bidasoa population was primarily dominated by one-sea-winter males returning during the autumn–winter season. Over the study period, a significant reduction in body size was observed, likely reflecting challenging marine conditions. Angling pressure was notably skewed towards multi-sea-winter females, which could influence natural recruitment dynamics. Despite the low mean stocking return rate of stocked salmon (0.13%), they contributed to one-third of the annual returns, underscoring their potential role in supporting population persistence albeit at the expense of reducing natural spawning, amid broader ecological challenges. This study provides valuable insights into the complex interplay of ecological and anthropogenic factors affecting Atlantic salmon populations in southern European rivers. These insights are crucial for developing and implementing effective conservation strategies aimed at preserving the Atlantic salmon, a species of significant cultural and ecological importance.

1 | Introduction

The Atlantic salmon (*Salmo salar*) is a remarkable fish species which displays considerable plasticity and variability in life history. Typically anadromous, Atlantic salmon expend most of their growth period in marine habitats, often for 1–4 years before attaining maturity, and return after to their home river for spawning (Fleming 1996; Klemetsen et al. 2003; Jonsson and Jonsson 2011). There are, however, landlocked populations, particularly in North America but also in Northern Europe, that complete their entire life cycle in freshwater (Berg 1985; Hutchings et al. 2019). Each river system hosts its unique stock or population of Atlantic salmon, specifically adapted to the environmental conditions of that particular river (King et al. 2001; Verspoor, Beardmore, and Consuegra 2005). Consequently, significant variations are expected related to migratory timing and routes, duration spent in both the river and ocean, adult size, population structure and survival rates.

The Atlantic salmon has suffered significant population declines worldwide over the last five decades (Parrish et al. 1998; Boisclair 2004; Chaput 2012; Dadswell et al. 2022), primarily due to threats such as habitat loss, river fragmentation and modification of river discharge (Aarestrup and Koed 2003; Lundqvist et al. 2008; Hvidsten et al. 2015; Lawrence, Kuparinen, and Hutchings 2016) together with the stressors derived from the climate change (increasing water temperature, water scarcity, food availability, etc.) (Renkawitz et al. 2015; Almodóvar et al. 2018; Thorstad et al. 2021; Strøm et al. 2023), among other impacts such as overfishing or hybridation (Scarnecchia, Ísaksson, and White 1991; Forseth et al. 2017; Keyser et al. 2018).

The socioeconomic significance of salmon together with its ecological importance, often considered a flagship umbrella species, an indicator of healthy rivers and a provider of important ecosystem services (Watz et al. 2022; Almeida et al. 2023), has prompted numerous countries to implement population recovery programs. These usually include habitat connectivity actions and stocking strategies (Lennox et al. 2021). While the first has been proved to be key for enhancing migratory fish populations (García de Leaniz 2008; Nyqvist et al. 2017; García-Vega et al. 2020), the latter has been questioned and growing debates are arising regarding the viability of stocking programs (Almodóvar et al. 2020; Saavedra-Nieves et al. 2021; Gabián et al. 2022). Any conservation effort should be followed by a monitoring study and the analysis of results, to assess the population status and to know if the applied measures are effective (Ham and Pearsons 2001; Bernhardt and Palmer 2011; Rodeles, Galicia, and Miranda 2017).

The southernmost distribution edge of Atlantic salmon in Europe is in the north of the Iberian Peninsula, where the Cantabrian Region (i.e. in rivers flowing to the Cantabrian Sea and the North Atlantic Ocean) supports small but stable Atlantic salmon populations (Álvarez et al. 2010). However, within this region, salmon has also experienced the global decline observed in other areas (García de Leániz and Martinez 1988; Horreo et al. 2011; Almodóvar et al. 2018; Nicola et al. 2018) and near-future climatic predictions raise additional concerns (Jonsson and Jonsson 2009; Valiente, Beall, and García-Vázquez 2010). While numerous studies have contributed valuable insights into the life-history variability and global decline of Atlantic salmon, there is a need for a comprehensive understanding of the dynamics specific to the southernmost distribution edge in the Cantabrian Region. This requires long-term monitoring studies which are essential for understanding broader ecological patterns and informing effective conservation strategies.

In response to these concerns, the regional government of Navarre (Spain) took the initiative with salmon stockings from mid-1980 and the establishment of a salmonid monitoring station in the early 1990s along one of these salmon-bearing rivers, the Bidasoa. The main aim of this station was to gather reliable data on Atlantic salmon status and trends to support effective management decisions.

In recent years, additional efforts have been made to improve river connectivity through obstacle removals and the construction and retrofitting of fishways across the Bidasoa Basin. These initiatives, part of projects such as Irekibai (LIFE14 NAT/ES/000186) and Kantauribai (LIFE21-NAT-ES-LIFE Ref. 101074197), have aimed at restoring migration pathways for salmon and other species. Moreover, fishing regulations have undergone several modifications to promote sustainable fishing practices. These include the introduction of more restrictive fishing quotas (even annual banning), a reduction in the fishing season and specific measures to protect multi-sea-winter salmon, such as catch quotas and the 'Salmon Sponsorship' program, where anglers voluntarily donate live-caught salmon for breeding and conservation purposes.

This paper focuses on the analysis of the data from the long-term (1993–2023) and full-year monitoring at the Bidasoa River monitoring station. These data were also combined with annual data from anglers' captures downstream of the monitoring station. The specific objectives were (1) to assess annual fluctuations and long-term trends (30 years) in adult salmon returns; (2) to analyse the population composition (sex, sea-winter age and origin) and biometric characteristics, identifying variations over time; (3) to identify possible effects of angling; and (4) to analyse the impact of stocking activities. Through these objectives, we aim to comprehensively understand Atlantic salmon trends in the Bidasoa Basin. This will offer valuable insights for conservation and sustainable management practices as well as contribute to broader ecological knowledge of this species, thereby informing future strategies for the enhancement and preservation of salmon populations, both locally and in similar ecosystems.

2 | Materials and Methods

2.1 | Study Area

The Bidasoa River has a total length of 69 km and a catchment area of 710 km^2 (Figure 1). The study site was located between the villages of Bera and Lesaka (ETRS89 43°16′ N, 1°41′ W; Navarre, Spain), 21.7 km upstream from the sea (11.6 km from the intertidal boundary), at an altitude of 40 m a.s.l. The mean annual discharge in the study reach was 25.7 m^3/s (MAPAMA 2023), and the mean annual water temperature was 15.2°C (Government of Navarre 2022). According to physical and chemical analyses (mean values: PO_4 = 0.064 mg/L, NH_4 = 0.06 mg/L, NO_3 = 3.0 mg/L, O_2 = 9.66 mg/L, pH = 8.0; Government of Navarre 2022), water quality was 'very good' (based on Spanish Act RD 817/2015).

The fish assemblage included diadromous species, such as Atlantic salmon, sea brown trout (*Salmo trutta*), European eel (*Anguilla anguilla*), sea lamprey (*Petromyzon marinus*) and Allis shad (*Alosa alosa*) as well as potamodromous species such as riverine brown trout, Ebro nase (*Parachondrostoma miegii*),

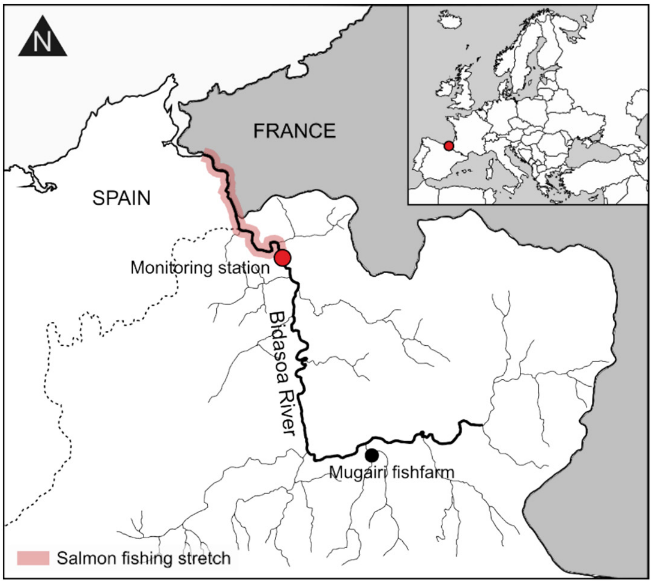

FIGURE 1 | Study area in the River Bidasoa Basin (Northern Iberian Peninsula). Location of the salmonid monitoring station and the designated salmon sport fishing stretch.

Pyrenean gudgeon (*Gobio lozanoi*), Pyrenean minnow (*Phoxinus bigerri*) and stone loach (*Barbatula quignardi*) (Government of Navarre 2016; SIBIC 2017).

2.2 | Salmon Data Collection

Data collected from 01/04/1993 to 29/02/2024 were utilised in the analyses. Two datasets were employed: one from the monitoring station and the other comprising information gathered by the Fish Management Section of the Navarre Government regarding capture data from anglers downstream of the monitoring station.

2.2.1 | Monitoring Station

A salmonid monitoring station was built in 1991 at a weir of a foundry in the village of Bera/Lesaka. The monitoring station comprises a stepped fishway of five pools and a fish lift. The cage of the lift works as a capture trap (it has a funnel in the entrance) and is located in the upper pool, lifted to transport the fish to the measuring room, where fish are identified, measured (fork length (FL), in centimetres: ±0.5 cm), weighed (W, in grams: ±1 g) and sex identified and observations are included (tags/marks, injuries, etc.). In autumn mature migrants clearly exhibit sexual dimorphism, allowing sex identification. Sex determination of the spring run migrants, when these differences were not visually clear, was done through blood analysis in the early years and DNA analysis of tissue samples later on (Yano et al. 2013). In addition, scales are collected for age estimation. The frequency of monitoring is two–three times per week during the whole year, increasing to once a day when high migration rates are observed. Data is gathered by the rangers of the Government of Navarre.

To date, the Bera foundry weir is the second obstacle from the sea. The first obstacle, Las Nazas weir, located downstream of the monitoring station, had a new and better pool-type fishway constructed in 2008 (GAN-NIK 2017). Additionally, over the last decade, three other weirs downstream were removed (one in September 2014 and the other two in October 2016) as part of the Irekibai LIFE project (c.f. García-Vega et al. 2020).

The only possible way for upstream migration at Bera weir (6 m high) is through the monitoring station as the fishway is the unique route to pass the weir. Considering this, it can be deduced that salmon counts in the trap may not represent the entire population entering the river due to possible selectivity in finding and passing both fishways. Therefore, the salmon counts at the monitoring station represent the minimum estimated count of the population. The number of salmon that remain downstream is unknown, and all analyses are conducted under this premise. Downstream migrants cannot descend through the fishway (due to the configuration for fish trapping), and thus, they cannot be counted.

2.2.2 | Anglers' Captures

The salmon fishing regulations in the Bidasoa Basin allow for the 'catch and keep' modality. Historically, the fishing season extended from March to July, but over time, it has been gradually reduced. Until 2006, the season began in March; then, from 2007 to 2019, it started in April. Currently, the season runs from May to July, and in 2023, salmon fishing was entirely banned for the first time. The designated salmon fishing area extends from the Bera weir (upstream limit) to the northern boundary of the Navarre Region at Endarlatsa (downstream limit) (Figure 1). Thus, all angler's captures belong downstream of the monitoring station.

From 2008 onwards, fishing quotas are determined based on count records from the monitoring station over the previous 5 years, allowing for the capture of up to 15% of the mean number of salmon counted in the monitoring station during this period. Previously, a fixed quota of 75 captures was set for the period 1997–2005, which was lowered to 50 for 2006–2007. In 2015, a new measure was introduced to establish a catch quota specifically for salmon with a fork length of ≥70 cm, aimed at protecting multi-sea-winter salmon. Following the capture of salmon that reaches 80% of the quota, a 1-week fishing ban is enforced. After this period, salmon fishing is allowed to resume, although the quota for larger salmon is revoked.

Once an angler catches a salmon (max quota is one salmon per day and angler), it is required by fishing regulations to report it to the Environment Department. The rangers collect biological information about the angled salmon and provide the anglers with a seal for the legal possession and transportation of the captured specimen. In 2019, the Navarre Government initiated the "Salmon sponsorship" program, based on the voluntary donation of live-caught salmon by anglers. These salmon are used as broodstock for salmon stocking or marked and released back into the river for subsequent monitoring.

2.3 | Stocking Activities

Data on stocking activities was provided by the Fish Management Section of the Navarre Government. Stocking activities started in the mid-1980s with the goal of enhancing the population of salmon in the Bidasoa River. Initially (1983–1993), both direct egg utilization and juvenile stocking were attempted for population enhancement. However, the use of eggs was discarded by the Environment Department in 1993. This decision was based on the challenges associated with accurately evaluating the success of egg repopulations, as well as concerns regarding the impact that the origin of eggs (mixture from Bidasoa, Iceland and Scotland) and fry (from Iceland) could have on the genetic richness of the native population and possible genetic introgression (Campos, Posada, and Morán 2008).

Therefore, from 1993 onwards, only stocking with juveniles (both fry and parr) bred from Bidasoa broodstock was promoted as an alternative strategy. This strategy involves the extraction of wild broodstock from the river at the Bera monitoring station for captive breeding and cultivation at the governmental fish farm in Mugairi (Figure 1). The objective is to ensure the maximum possible survival during the most fragile stages of the life cycle (eggs and alevins), by stocking the fish in the river as soon as possible (most of them as fry), thereby allowing successful adaptation and feralization. As all juveniles are marked (adipose fin clipped), it is possible to monitor and evaluate the success of the measure. Adult salmon selected for extraction in the monitoring station are those that exhibit desirable breeding characteristics (i.e. representing the natural population structure as closely as possible, but aiming to reinforce the presence of multi-sea-winter salmon, which are in clear decline). Additionally, salmon tagged with coded wire tag (CWT) are also selected, as this allows tag recovery and fish identification after controlled spawning in the fish farm.

The juveniles raised at the fish farm are released only into sections of the upper–middle course of the Bidasoa River, where wild salmon typically do not access, resulting in limited or negligible natural salmon reproduction and thus avoiding intraspecific competition. Approximately 60% of the produced fish are released as fry (0+) in June and July after clipping the adipose fin. The remaining 40% were initially (1990–2006) released as smolts (1+) in February and March, and since 2007, they have been stocked as parr (0+) in October, with the adipose fin clipped and CWT for identification. In the rest of the river, downstream of the stoking sites, natural spawning is the origin of fish.

2.4 | Data Processing and Statistical Analysis

As no salmon returns were registered from February to April at the monitoring station and since counts in the trap during January may still be associated with the migration of the previous months, the 'migration years' were considered to start the first day of March and end the last day of February of the following year.

To fully define all the fish characteristics for the following analyses, firstly, each salmon was categorised by capture method (monitoring station vs. angling), sex (female vs. male) and origin (wild vs. stocked). In addition, they were classified by their river age as well as by their sea-winter age. In this sense, salmon can spend one or two years in the river before migrating to the sea and then spend one, two, threee and even four years in the sea before returning to the river again. Salmon with more than one-sea-winter (1SW) are referred to as multi-sea-winter (MSW).

To identify annual fluctuations and trends in salmon returns, first, fish were grouped (summed) by migration year. Then, fish were also grouped (summed) by month, to evaluate possible differences by season. Frequency analysis was used to evaluate the number of salmon by categories, and the test for equality of proportions (EP test) was used to find possible differences between groups. The dynamic of the total number of salmon returns over time was evaluated using sinusoidal regression together with fast Fourier transform (FFT) algorithm, which allows to transform a time-domain signal into a series of sine waves with different amplitudes and phases, thus decomposing the signal into its constituent sinusoidal components and identifying the most significant cyclic temporal patterns. In addition, the Mann–Whitney Wilcoxon (MW) test was used to detect significant differences in fork length and weight by categories. For size comparisons among months, post hoc Dunn's multiple comparison test with Bonferroni correction was performed. This nonparametric test was applied as variables were not normally distributed. The size evolution throughout the study period was evaluated via linear regression of the yearly mean FL together with sinusoidal regression considering the amplitudes that resulted significant for the study of the population size dynamics.

To evaluate the impact of stocking activities, the number of salmon of stocking origin counted at the monitoring station (i.e. those marked with adipose fin clipping or CWT) was compared to the releases of stocked fish by the Navarre Government. The year of stocking was estimated by determining the year of birth through scale analysis, which allowed to identify both sea-winter age and river age. For fish without sea-winter age information ($n = 10$), the age was estimated based on biometric characteristics (MSW if fork length > 70 cm and weight > 3000 g). For fish without river age information ($n = 553$), a river age of 1 was assumed (only for this analysis), given that 92.2% of identified fish fell into this category and no significant differences in fork length or weight between one-river-year and two-river-year fish across all sea-winter ages were found (all KW test p values > 0.05). These assumptions were only applied to the stocking return rate analysis.

For fish with a CWT, the year of stocking was considered the year of birth for those born from 2007 (released as parr) and the year of birth plus one if they were born before 2007 (released as smolt). For fish marked only with an adipose fin clip, those born from 2007 onwards had their year of stocking considered the year of birth (released as fry). For fish born before 2007, the year of release was the year of birth for one-river-year fish (released as fry) and the year of birth plus one for two-river-year fish (released as smolt).

Stoking return rates were calculated by dividing the number of salmon counted at the monitoring station that corresponded to a specific stocking year by the number of fish released in that year, both globally and by life stage (fry, parr and smolt).

Statistical analyses were performed using R version 4.3.0. (R Core Team 2023) and Python version 3.8.10 (Python Software Foundation 2021).

3 | Results

3.1 | Annual Fluctuations and Trends in Salmon Returns

From 1993 to 2023, a total of 9162 salmon were counted upon their return at the salmonid monitoring station during their upstream migration. The mean annual number was 296 ± 135, with a maximum of 623 (in 2014) and a minimum of 66 (in 2022) (Figure 2). Notably, the observed population counts (representing the minimum estimated population size due to monitoring limitations) displayed cyclical patterns of growth and decline of different magnitudes. The FFT analysis showed three recurrent periodicities of 3–4 years, 10 years and 15 years, together with another of 30 years that covers the whole study period (Figure 2).

Regarding the salmon captured by anglers during the period from 1993 to 2022 (2023 was banned), the total number amounted to 1316. This translated to a mean annual capture of 44 ± 14 salmon, with the highest recorded at 69 in 2001 and the lowest at 10 in 2009 (Figure 3). The relation between the number of captures by anglers and the number at the monitoring station varies through time, representing a mean of 17.3% of the counts at the monitoring station (a maximum of 34.9% in 2022 and a minimum of 4.3% in 2010) (Figure 3).

Most of the salmon counted at the monitoring station (59.1%) were male individuals (p value < 0.0001), resulting in a global male/female ratio of 1.5. This trend of males dominating held across all years (sex ratio ranged from 1.3 to 3.3 males per female), except for 3 out of the 31 years studied, where the proportion of females was higher, and 9 out of 31 years where no significant differences were found (Figure 4). In contrast, the sex ratio of angler's captures is inverted, with 1.5 females per males, indicating that, on average, significantly more females (57.7%; p value < 0.0001) were captured compared to males (39.1%), while the remaining 3.2% remained unidentified. This female dominance in angled salmon was observed in 11 out of 30 years (sex ratio ranged from 1.7 to 7.5 females per male), while no year males were prevalent.

Three-quarters of the counts at the monitoring station (74.9%) were 1SW salmon, while the other quarter (24.8%) corresponded to MSW, with two (24.3%) and more rarely three (0.5%) winters (0.3% with no info), although with noticeable year-to-year variation (Figure 5a,c). Conversely, anglers extracted more MSW salmon (60.6%; 58.8% with two and 1.8% with three winters) than 1SW salmon (39.4%) (Figure 5b,c). In addition, 92.2% of the counts at the monitoring station were classified with one-river-year and 7.8% with two river-years (there were 2254 counts where the river-age information was not available). Similar values were observed in the angler's captures, with 89.6% one-river-year salmon and 10.4% with two river-years (163 captures with no river-age info).

While 1SW salmon skewed male (2.2 males per female; p value < 0.0001), MSW salmon had more females than males (2.2 females per male; p value < 0.0001) (Figure 5a,c). Similarly, the sex proportion of one-river-year salmon leans towards males (1.5 males per female; p value < 0.0001) whereas for two-river-years, it leans towards females (1.1 females per male; p value = 0.0442).

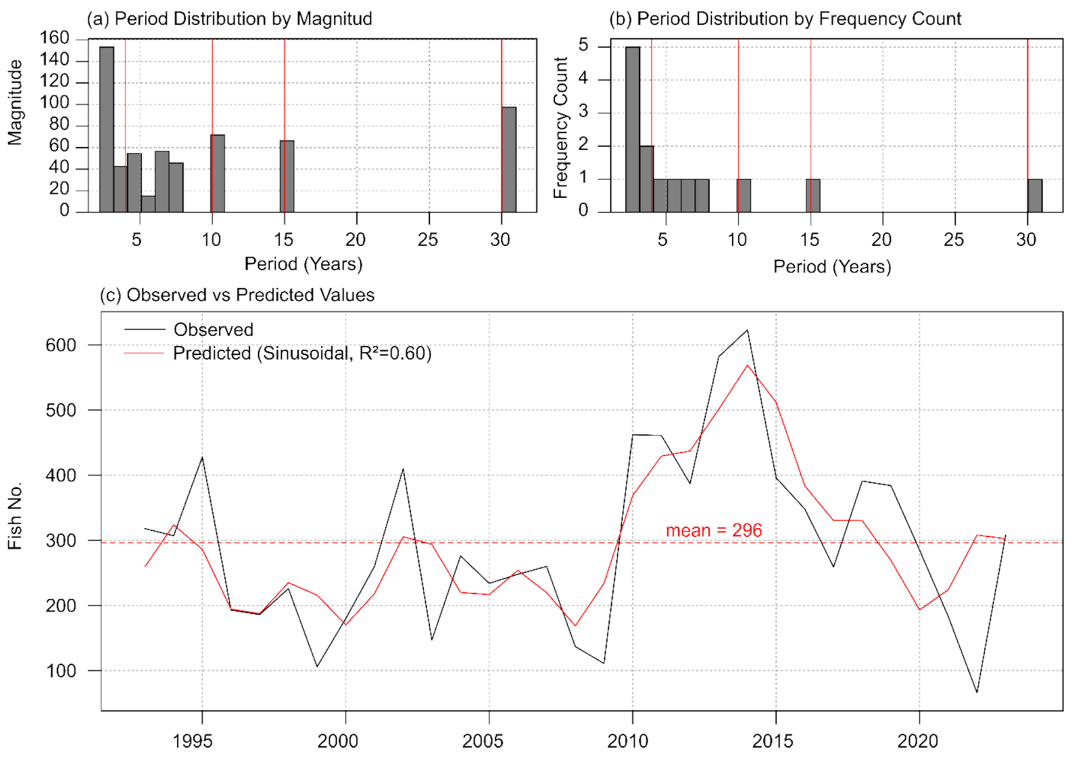

FIGURE 2 | Evolution and predictions of the number of salmon returns counted at the salmonid monitoring station. Period distribution by (a) magnitude and (b) frequency count of the decomposed signal of the sinusoidal regression. (c) Observed versus predicted fish number by the sinusoidal regression.

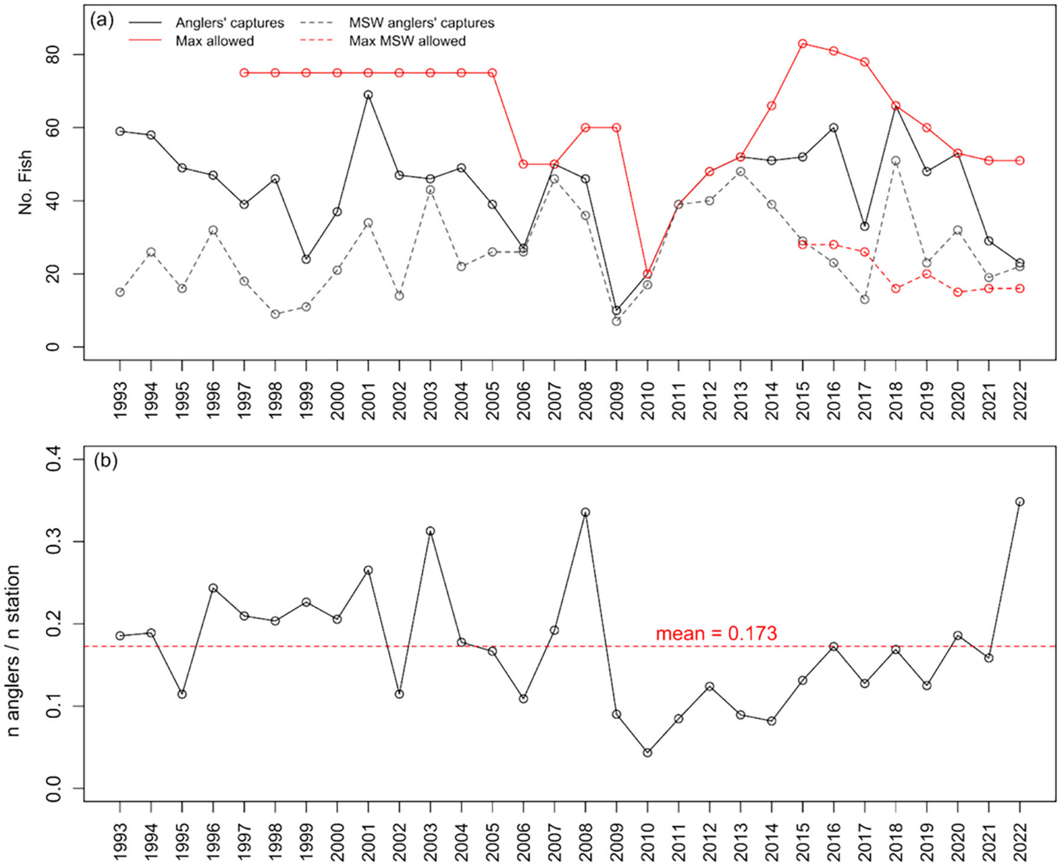

FIGURE 3 | (a) Evolution of the number of captures by anglers and max legal quotas (the multi-sea-winter (MSW) salmon quota is revoked after a one-week fishing ban when 80% of the quota is reached). (b) Relation of the captures by anglers and the counts at the monitoring station (2023 is not included since the angling was banned).

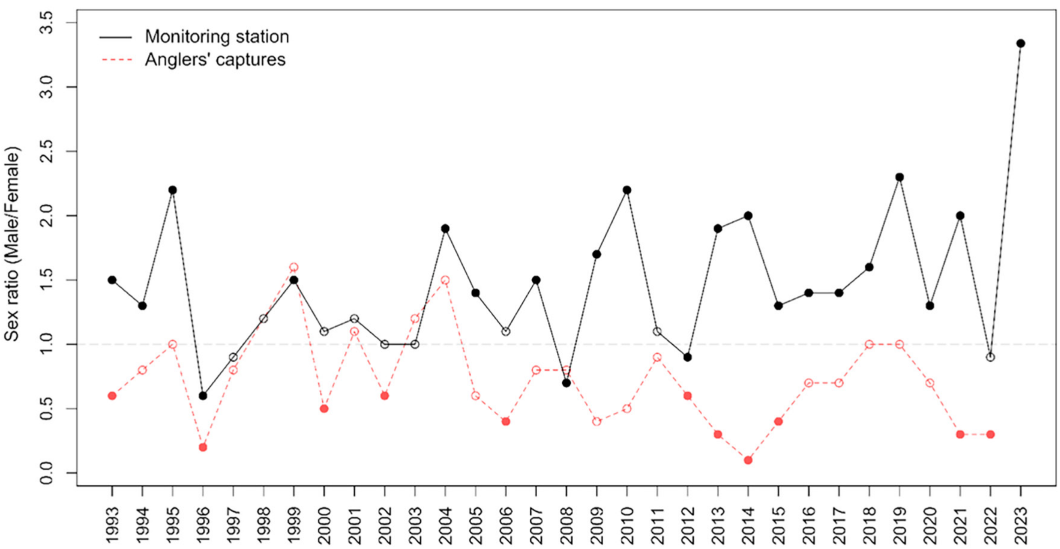

FIGURE 4 | Evolution of sex ratio of the salmon returns counted at the salmonid monitoring station and by anglers. Filled circles represent years with significant dominance in terms of sex proportion, and those without fill represent years without dominance.

In total, 2814 salmon with stocking origin were counted at the monitoring station, with a mean annual number of counts of stocked salmon which was 91 ± 44, representing 30.7% of the total counted salmon (Figure 6a,c). Likewise, the percentages in the angler's captures showed similar proportions to those at the monitoring station (Figure 6b,c). Based on the monitoring station dataset, both wild and stocked salmon lean towards males (1.7 and 1.1 males per female respectively; p value < 0.0001 for

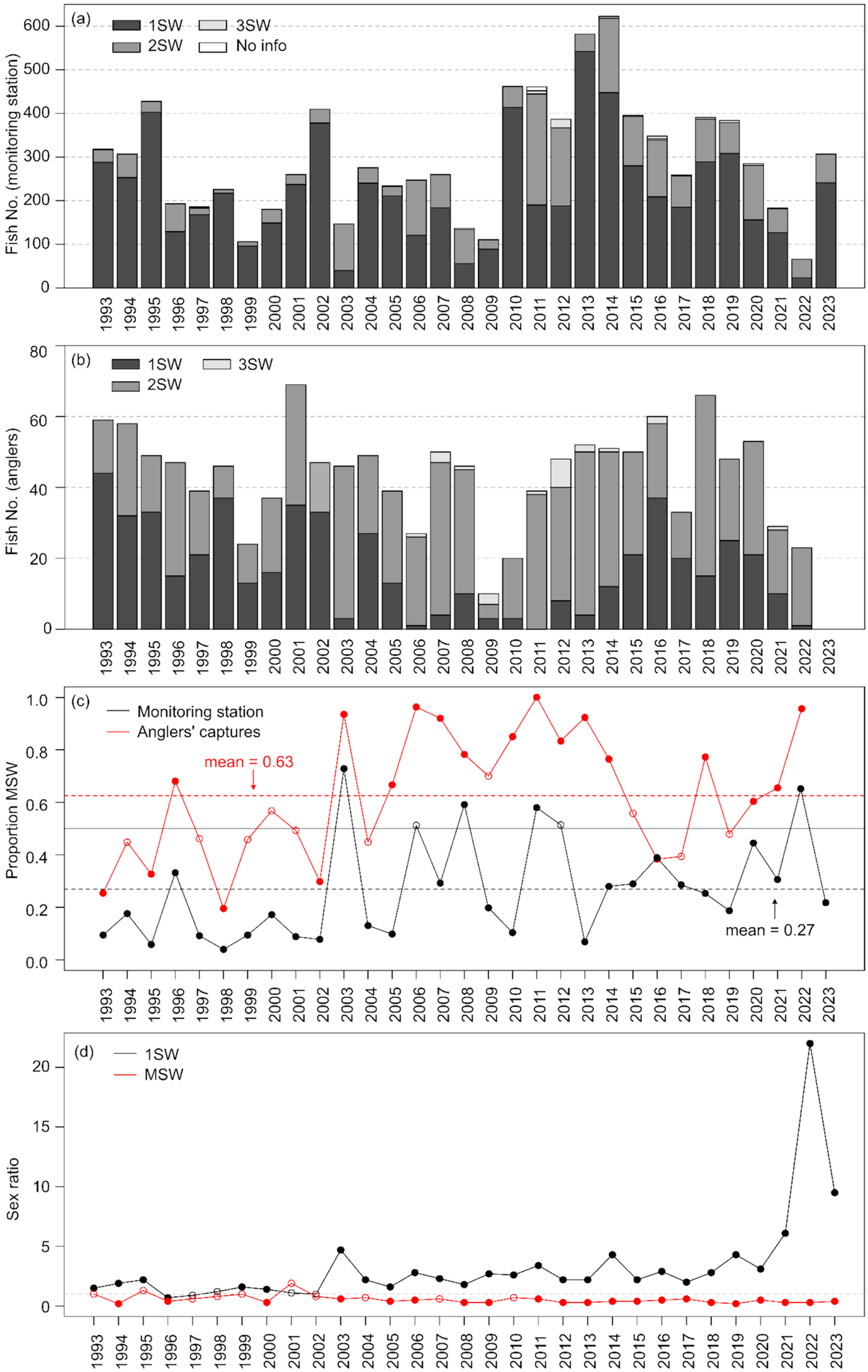

FIGURE 5 | Evolution of the number of salmon by sea winter (SW) age for (a) the salmonid monitoring station and (b) the anglers (1SW: one-sea winter; MSW: multi-sea-winter). (c) Comparison of proportion of MSW (salmon with two -2SW- or three sea-winters -3SW-) over the study period. (d) Sex ratio (male/female) evolution over time by sea winter age. Filled circles represent years with significant dominance in terms of sea-winter age (c) and sex proportion (d), and those without fill represent years without dominance.

wild and p value = 0.0051 for stocked) and the proportion of 1SW was greater for both origins (79.9% for wild and 64.3% for stocked; both p values < 0.0001).

3.2 | Biometric Characteristics and Trends

Salmon returns at the monitoring station ranged from 455 to 970 mm in fork length and from 660 to 9000 g in weight, with mean values of 662 ± 82 mm and 2585 ± 1157 g, respectively. Fork length–weight relation resulted in an allometric growth model following the equation $W = 2.457 \cdot 10^{-6} \cdot LF^{3.1881}$ ($R^2 = 0.9125$). For 1SW salmon, returned females were significantly shorter and heavier than males, while for 2SW salmon, females were also shorter and slightly heavier than males, though the weight difference was not statistically significant (Table 1a; Figure 7a,c). However, in 3SW salmon, females were significantly shorter and lighter than males. On the other hand, stocked salmon were generally larger than their wild counterparts in both 1SW and 2SW categories (Table 1b; Figure 7b, d) as well by sex (Table 1c), but no significant differences were found for 3SW salmon. Additionally, captures from anglers exhibited significantly heavier weights than those counted at the salmonid monitoring station for all three sea winter ages (no significant differences in fork length were detected) (Table 1d; Figure 7e,f).

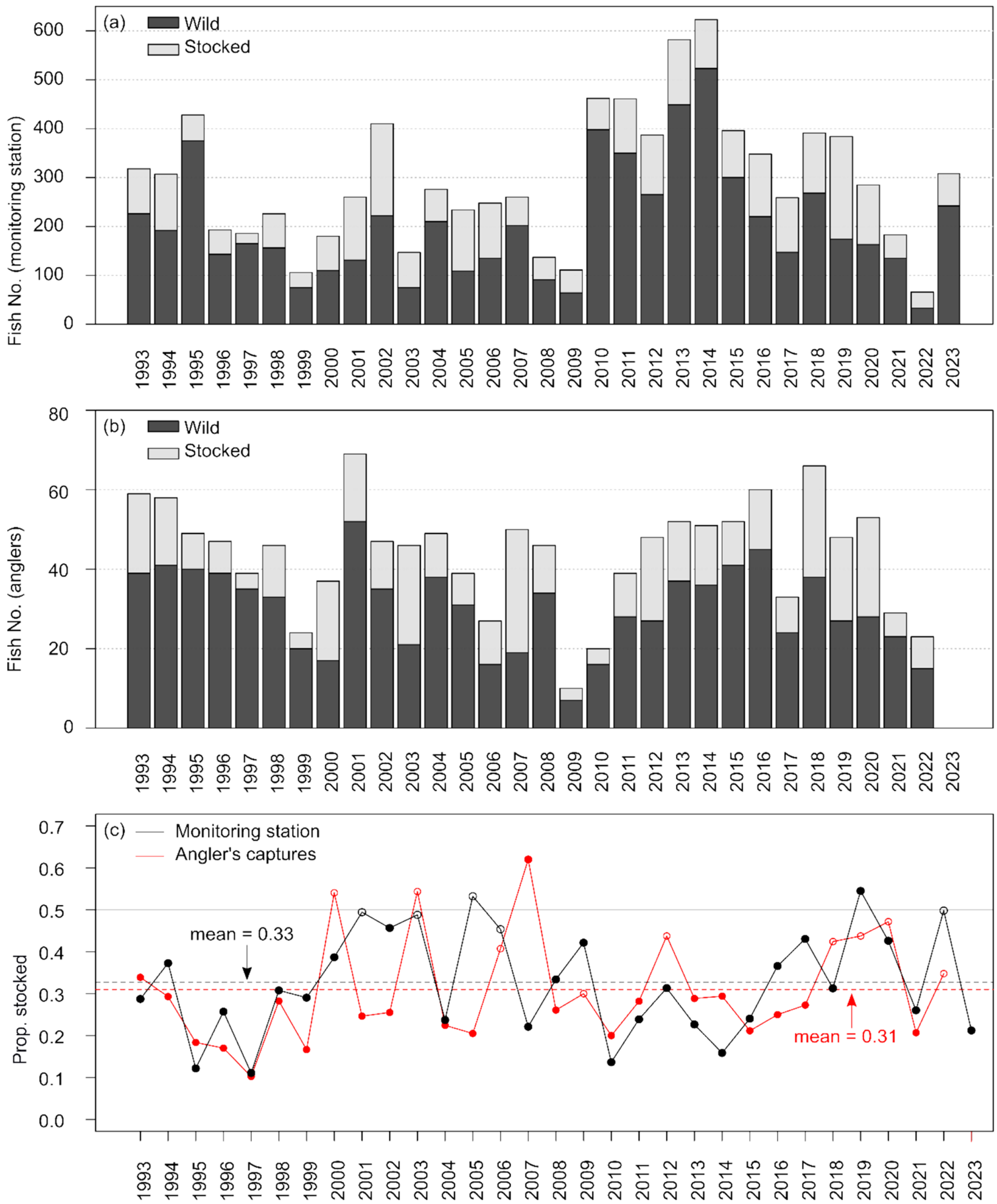

FIGURE 6 | Evolution of the number of salmon by origin (a, b) at the salmonid monitoring station. (c) Proportion of stocked salmon over the study period. Filled circles represent years with significant dominance in terms of origin proportion, and those without fill represent years without dominance.

TABLE 1 | Comparison of biometric characteristics by gender and origin of salmon counted at the monitoring station, as well as comparison between angler's captures and salmon counts at the monitoring station, classified by sea winter age (n = number of fish; salmon with no info in a category have been excluded; FL = fork length; W = weight).

a. Size comparison by sex based on winter age

Sea-winter age	Category	FL (mm) mean ± SD	W (g) mean ± SD	KW Test *p* value (FL)	KW test *p* value (W)
1SW	Female (n = 2160)	619 ± 42	2082 ± 484	< 0.0001	< 0.0001
	Male (n = 4694)	624 ± 45	1952 ± 463		
2SW	Female (n = 1544)	774 ± 38	4235 ± 725	< 0.0001	0.1663
	Male (n = 679)	793 ± 56	4183 ± 916		
3SW	Female (n = 21)	871 ± 41	5977 ± 1052	0.01904	0.1917
	Male (n = 26)	899 ± 36	6214 ± 902		

b. Size comparison by origin based on winter age

Sea-winter age	Category	FL (mm) mean ± SD	W (g) mean ± SD	KW test *p* value (FL)	KW test *p* value (W)
1SW	Stocked (n = 1803)	631 ± 46	2097 ± 522	< 0.0001	< 0.0001
	Wild (n = 5056)	619 ± 43	1956 ± 450		
2SW	Stocked (n = 979)	786 ± 44	4305 ± 773	< 0.0001	< 0.0001
	Wild (n = 1244)	775 ± 45	4151 ± 794		
3SW	Stocked (n = 22)	890 ± 43	6168 ± 1040	0.723	0.893

c. Size comparison by sex based on origin and winter age

Sea-winter age	Category		FL (mm) mean ± SD	W (g) mean ± SD	KW test *p* value (FL)	KW test *p* value (W)
1SW	Female (n = 2160)	Wild (n = 1498)	613 ± 40	2021 ± 452	< 0.0001	< 0.0001
		Stocked (n = 662)	630 ± 44	2226 ± 523		
	Male (n = 4694)	Wild (n = 3555)	622 ± 44	1929 ± 446	< 0.0001	< 0.0001
		Stocked (n = 1139)	635 ± 48	2024 ± 508		

(Continues)

c. Size comparison by sex based on origin and winter age

Sea-winter age	Category		FL (mm) mean ± SD	W (g) mean ± SD	KW test *p* value (FL)	KW test *p* value (W)
2SW	Female (n = 1544)	Wild (*n* = 864)	769 ± 38	4161 ± 728	< 0.0001	< 0.0001
		Stocked (*n* = 680)	780 ± 38	4329 ± 710		
	Male (n = 679)	Wild (*n* = 380)	787 ± 56	4127 ± 927	0.0068	0.0992
		Stocked (*n* = 299)	799 ± 55	4253 ± 898		
3SW	Female (n = 21)	Wild (n = 12)	857 ± 31	5760 ± 1112	0.1177	0.0754
		Stocked (n = 9)	890 ± 48	6267 ± 948		
	Male (n = 26)	Wild (*n* = 13)	908 ± 29	6328 ± 621	0.1819	0.2699
		Stocked (n = 13)	889 ± 41	6099 ± 1132		

d. Size comparison by capture method based on winter age

Sea-winter age	Category	FL (mm) mean ± SD	W (g) mean ± SD	KW test *p* value (FL)	KW test *p* value (W)
1SW	Monitoring (*n* = 6902)	623 ± 44	1992 ± 474	0.4133	< 0.0001
	Angler's (*n* = 517)	619 ± 42	2370 ± 538		
2SW	Monitoring (*n* = 2271)	780 ± 45	4229 ± 790	0.05681	< 0.0001
	Angler's (*n* = 774)	776 ± 40	4858 ± 852		
3SW	Monitoring (n = 55)	893 ± 49	6453 ± 1418	0.2752	0.02185
	Angler's (n = 23)	881 ± 49	7000 ± 1115		

Salmon returns at the monitoring station in April, May and June were significantly larger than those in the other months (Figure 7g), whereas returns in July and August were significantly shorter than those returning in the other months (Figure 7g).

Although a cyclical change in body size was observed through sinusoidal regression (Figure 8), this pattern was overshadowed by the significant decreasing trend in fork length observed for 1SW salmon over the study period (linear regression p value < 0.0001) (Figure 8a). This decreasing trend held true for both males and females (both p values < 0.0001), and it was also observed in the angler's captures (p value < 0.0001). In contrast, for MSW salmon, while a decreasing tendency was also noted, it only approached statistical significance (p value = 0.051), showing a more patent cyclical variation (Figure 8b). Further analysis by sex revealed that the decreasing trend was statistically significant for MSW females (p value = 0.0011) but not for males (p value = 0.6139). In the case of angler's captures, the decrease also was significant (p value = 0.0438).

3.3 | Extracted Fish From the River to the Fish Farm

A total of 1155 salmon were extracted from the river at the monitoring station for transportation to the Mugairi fish farm between 1993 and 2023. These extracted fish included those marked with CWTs and other selected salmon intended

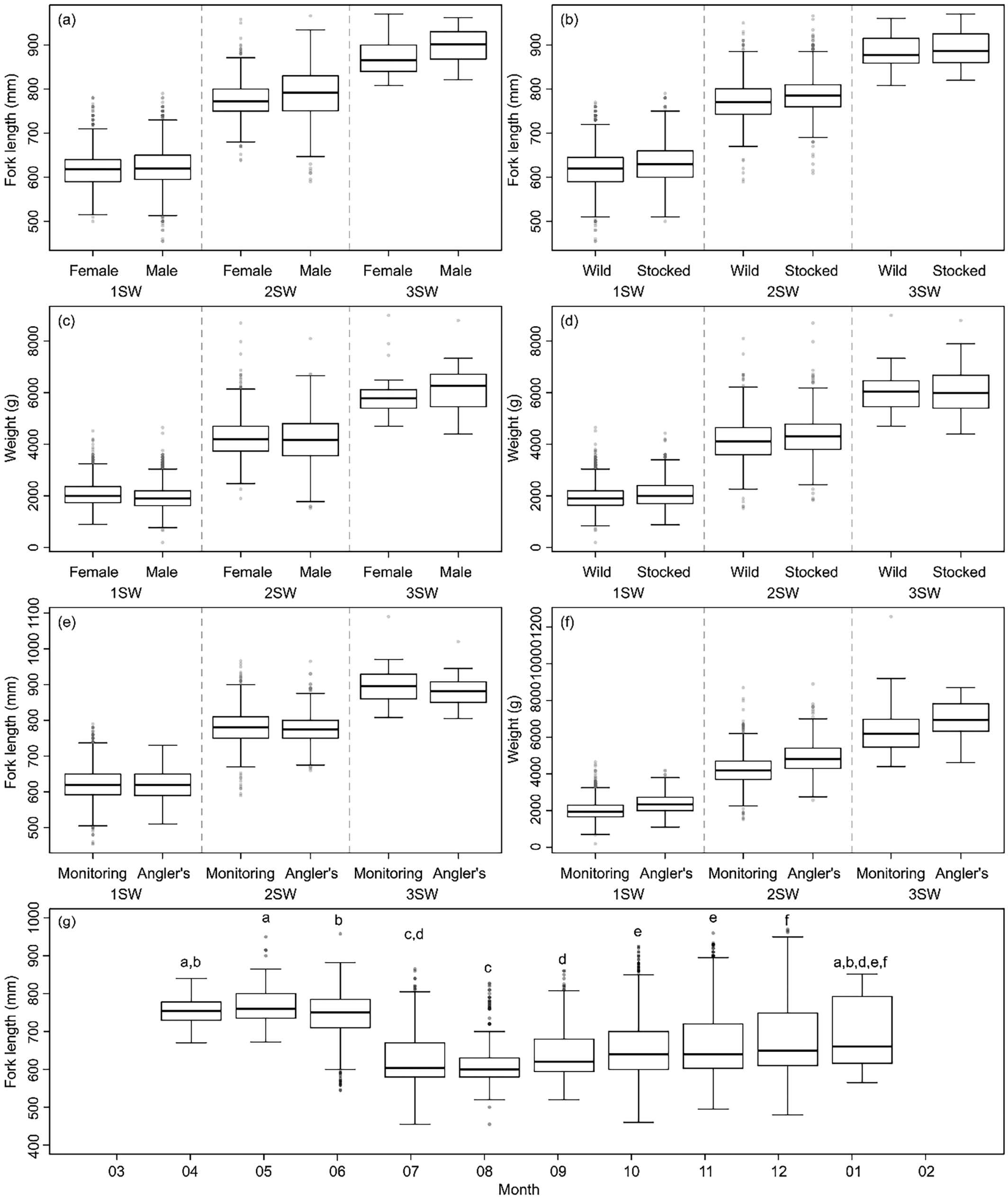

FIGURE 7 | Size of the returned salmon. Comparisons of fork length and weight by (a, b) sex, (c, d) origin at the monitoring station, and capture method (e, f) at the monitoring station depending on the sea winter (SW) age. (g) Size of the salmon returns at the monitoring station by month (the medians that do not share a letter are significantly different).

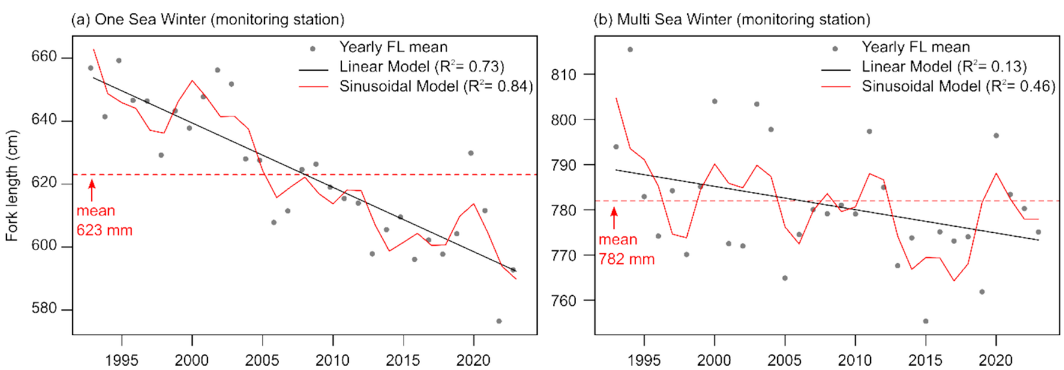

FIGURE 8 | Evolution in mean fork length (FL) over the study period for (a) one-sea-winter and (b) multi-sea-winter salmon at the monitoring station. Lines represent the tendency of linear and sinusoidal regressions.

for breeding and stocking purposes. Indeed, most of the extractions of fish (96.6%) occurred from October to December. In addition, as result of the "Salmon Sponsorship" program, a small number of salmon captured by anglers were donated alive to the fish farm during the angling seasons between 2019 and 2022 to be used as broodstock in the population recovery program.

The extracted fish represent the 12.6% of the total individuals counted at the monitoring station, with a mean annual number of 38 ± 18, a maximum of 103 (in 2002) and a minimum of 9 (in 2022). There were both males (n = 566) and females (n = 589). They also comprised MSW (n = 513) and 1SW (n = 641), and both origins were also selected, wild (n = 522) and stocked (n = 633).

From the extracted fish, an annual mean of fewer than two salmon per year did not reach sexual maturity at the fish farm before death. In addition, those extracted salmon marked with CWT (n = 474) were necessarily slaughtered to read the mark, although they were first used for breeding at the farm (except for 18 in total that did not reach sexual maturity before death), and consequently, they were not released back into the river. There were 74 additional CWT fish that were not extracted to the fish farm (n = 53), were released alive without reading the tag (n = 16) or were found dead at the fishway of the monitoring station (n = 5). In this regard, a total of 19 fish were found dead at the trap or in the vicinity of the fishway during the whole study period. On the other hand, from the extracted fish, nontagged males were released into the river after reproduction, while females were retained in the fish farm pools for up to 2 years for artificial reproduction.

Likewise, regarding captures by anglers under the "Salmon Sponsorship" program, only 14 were transported to the fish farm (5 in 2019, 4 in 2020, 2 in 2021 and 3 in 2022). These included 2 males and 12 females; and all of them MSW; 4 from stocking and 10 wild.

3.4 | Monthly Fluctuations and Trends in Salmon Returns

A significant majority of salmon returns counted at the monitoring station (84.4%) took place between October and December, with November accounting for the highest percentage (47.2%) (Figure 9a). Notably, no salmon were recorded at the monitoring station in February and March throughout the study period. In the case of angler's captures, most occurred within the period from May to July, with the maximum in June (45.4%) (Figure 9e).

Based on the data from the monitoring station, in terms of sex proportions, a general trend emerged, where females dominated at the beginning of the migratory season (April, May and June), progressively changing the proportion towards males, which dominated from July to December (Figure 9b). Likewise, MSW salmon were significantly predominant in April, May and June whereas 1SW were from July to December (Figure 9c). As for wild versus stocked, the proportion of wild salmon was greater in all months (except in April, where it was greater but not significantly; p value = 0.1167) (Figure 9d).

The anglers' captures consisted mainly of MSW females of wild origin in all months except for July, where 1SW males dominated the proportion (Figure 9f–h).

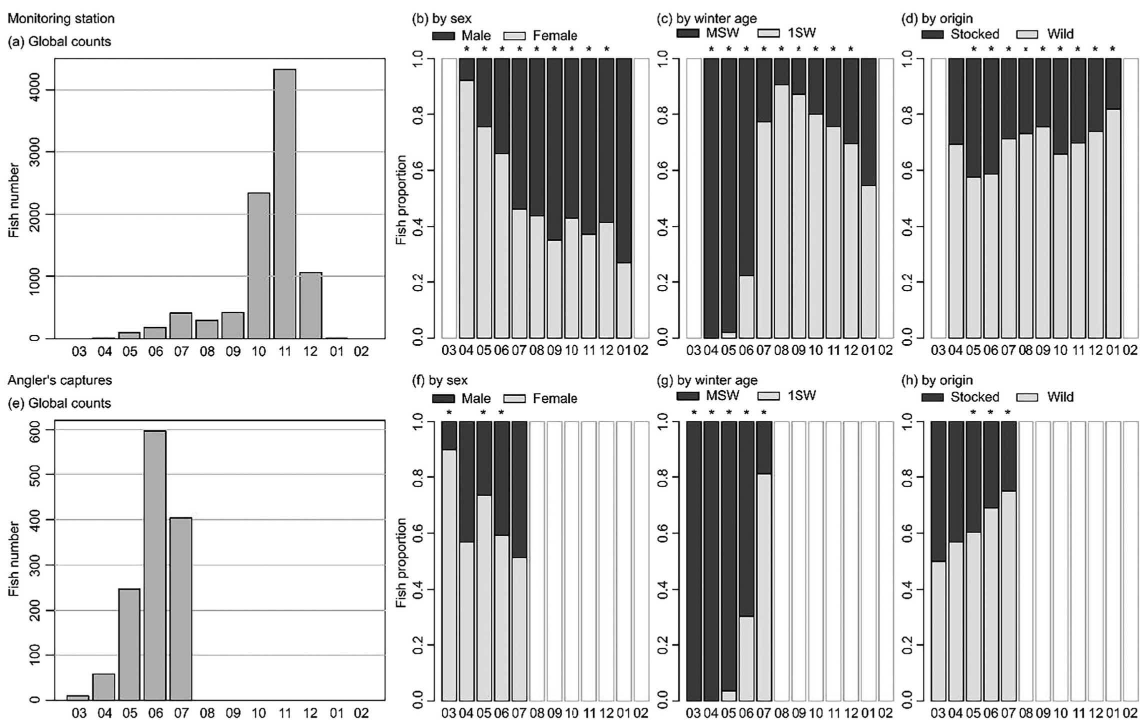

FIGURE 9 | Monthly frequency of the number of salmon returns counted at the salmonid monitoring station (a–d) and angler's captures (e–h). Results are presented in global (a, e), by sex (b, f), winter age (c, g) and origin (d, h) respectively. The asterisk stands for a significant p value (p < 0.05) in the test of equal proportions between the two studied groups/categories (1SW: one-sea-winter; MSW: multi-sea-winter).

3.5 | Released Fish From Stocking and Return Rates

The stocking activities were conducted over time using different life stages. Initially, eggs (from 1984 to 1993) and fry were used for stocking purposes. Additionally, smolts were stocked between 1990 and 2006, while parrs were stocked from 2007 to 2023. In 1996, only pre smolts ($n = 6650$) were released due to nursery complications caused by turbidity associated with the works on the Belate Tunnel (upstream of the Mugairi fish farm). In addition, in 2023, a group of 1904 presmolts were also released for downstream migration research purposes. Most of the stocked fish corresponded to fry (79.7%), followed by parr (14.1%), smolts (5.9%) and then presmolts (0.3%) (Figure 10a).

The mean stocking return rate was 0.1287%, representing one returned salmon per 777 released (Figure 10b,c). However, important variations among years were observed, with a stocking return rate of 0.4773% in the best year (1999; representing one returned salmon per 210 released) and 0.0094% in the worst year (1990; with one returned salmon per 10,603 released) (Figure 10c). Analysing the different life stages, the mean stocking return rate of those stocked as fry (0.1512%) was higher than those stocked as parr (0.0695%) or smolt (0.0268%), although there were variations among years (Figure 10c). The best return

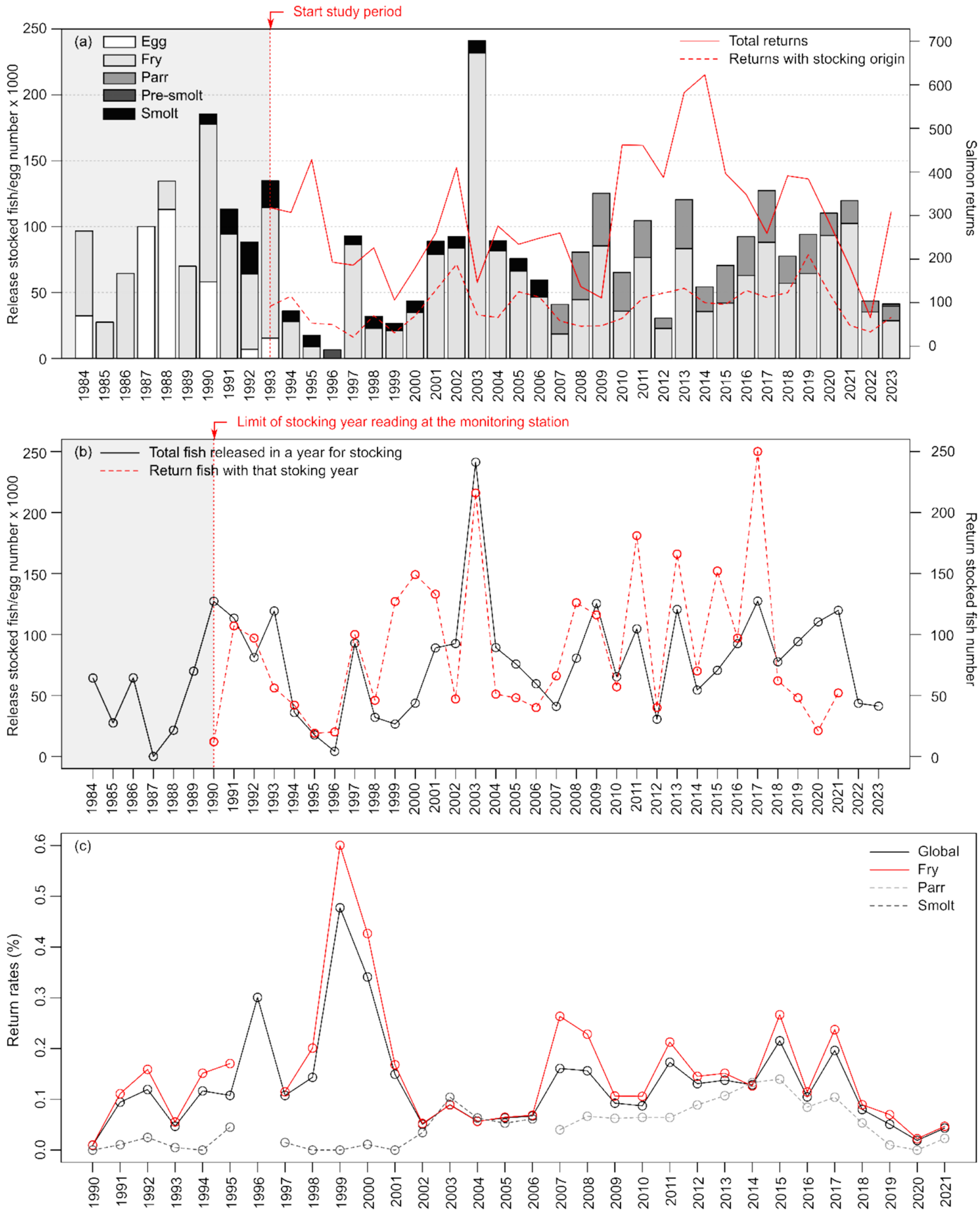

FIGURE 10 | (a) Number of stocked salmon by life stage per year and evolution of the total number of returning adults and returning adults with stocked origin. (b) Comparison of the total fish released (fry + parr + presmolts + smolts) and the returned adults considering the year of stoking. (c) Stocking return rates: global and by stocked life stage.

rate was observed for presmolts (0.3008%), although they were only used in 1996 (and then in 2023 but have not been recaptured since).

4 | Discussion

Atlantic salmon display significant variability and life history strategies aimed at optimising reproductive success across their wide distribution range (Fleming 1996). Some regions are characterised by populations dominated by fish maturing after one year at sea, while others are primarily composed of MSW salmon (Chaput 2012). This diversity is closely linked to factors such as growth rate and age at sexual maturity (Nicieza and Braña 1993; Friedland and Haas 1996; Jonsson and Jonsson 2007). Similarly, important regional differences in sex ratios have been reported along the natural distribution range of the Atlantic salmon (O'Connell, Dempson, and Chaput 2006) even with differences between mainstems and headwaters (Vähä et al. 2011).

In the Bidasoa River, the population structure observed over the last 30 years has been dominated by 1SW males returning primarily in autumn–winter (October to December), which agrees with populations of other Cantabrian rivers (García de Leaniz et al. 2002). In contrast, MSW salmon—representing only a quarter of the migrants—are predominantly females that return during the spring–summer (May–July). This structure reflects broader trends in Atlantic Salmon populations, where spring-run returning fish are typically dominated by large MSW females, while late-summer and autumn runs tend to be dominated by male-biassed, 1SW salmon (Jonsson, Jonsson, and Hansen 1990; Trépanier, Rodriguez, and Magnan 1996; Jokikokko, Kallio-Nyberg, and Jutila 2004; Harvey et al. 2017).

The variability in sea-age composition and run timing in the Bidasoa may be partly influenced by genetic factors, as traits such as sea age at maturity and timing of river entry are partially inherited and likely adaptive (Gardner 1976; Fleming 1996; Stewart, Smith, and Youngson 2002). Furthermore, selective exploitation by anglers, particularly of large early-running MSW fish, may have influenced the population structure. This pressure can lead to a reduction in size and age at maturation, as the removal of large MSW fish favours smaller, late-running individuals in subsequent generations (Consuegra et al. 2005; Garcia de Leaniz et al. 2007; Kuparinen et al. 2009).

Early migrants (spring–summer) have been found significantly larger than those arriving closer to the spawning season (autumn–winter). Usually, female salmon are typically observed entering and ascending the river earlier than males (Niemelä et al. 2006), potentially to ensure the location of adequate spawning grounds (Fleming 1996). An early entry results in a prolonged residence in freshwater without feeding, as salmon stop feeding before they enter freshwater (Kadri et al. 1995). This may give an advantage to older and larger individuals (i.e. MSW), due to the larger energy reserves of bigger fish (Jonsson 1997; Mobley et al. 2021). On the other hand, the reproductive fitness of female salmon—predominantly found at the beginning of the season—is enhanced by increased body size, which is associated with older age at maturity and an increased egg number and egg size per female, whereas the fitness of males—predominant later in the season—can be optimised at smaller body sizes (Dickerson et al. 2005; Mobley et al. 2020).

In addition, a short time spent in freshwater by juveniles has been identified in the Bidasoa salmon population, as indicated by the predominance of one-river-year individuals. Southern European rivers present one of the lowest egg-to-smolt survival rates (Hutchings and Jones 1998) which seemed to be partly compensated by one of the highest growth rates for the species and a growth strategy, which involves shortening the time spent by juveniles in freshwater (Dumas and Prouzet 2003). Age at seaward migration is regulated by growth (Økland et al. 1993). Within populations, fast growers often migrate at a younger age and smaller size than slow growers (Refstie and Steine 1978; Jonsson, Jonsson, and Jonsson 2016b). This indicates an inherited association between migration and growth rate, where fast-growing Atlantic salmon parr may require more energy and therefore seek richer feeding opportunities sooner than their slower-growing counterparts (Metcalfe, Wright, and Thorpe 1992; Forseth et al. 1999).

Atlantic salmon typically follows a characteristic natural cycle of annual returns, with periodic fluctuations in abundance (Lajus et al. 2007; Dadswell et al. 2022). Historical records from the Bidasoa River monitoring station reveal distinct cyclical patterns of growth and decline, with varying magnitudes and periodicities. A notable short-term wavelength of 3–4 years has been depicted, closely linked to the salmon's life cycle, which involves 1–2 years in freshwater and several years at sea. This cycle reflects the biological rhythms of the species and its responses to environmental conditions (Webb et al. 2007; Jonsson and Jonsson 2011).

In addition to this short-term cycle, two longer wavelengths have been detected: one of 10 and the other one of 15 years. The 15-year wavelength represents the midpoint of the study period, as clearly depicted in Figure 2: 1993–2009 (mean $n = 237$) and 2010–2023 (mean $n = 367$). This may relate to significant habitat changes, such as the construction of a new and better fishway in Las Nazas weir in 2008—the single obstacle below the monitoring station—along with changes in fishing management practices that have influenced annual catch limits based on population assessments.

At this regard, a major change occurred from 2009 in the management of the species in the Bidasoa Basin, as the Environmental and Water Authorities began a determined commitment to the elimination of obsolete obstacles (23 dams were removed between 2009 and 2023), increasing the permeability of the basin to a much greater extent than the fish ladders that had been built up to that date. Indeed, the connectivity improvement projects implemented in the basin (e.g. Irekibai and its successor, the ongoing Kantauribai project) have demonstrated improvements in habitat and river continuity, leading to clear positive impacts on the population dynamics of the Bidasoa River fish species (Rodeles et al. 2019; García-Vega et al. 2020).

Notably, the observed 10-year cycle in the Bidasoa aligns with patterns documented in salmon populations globally (Dadswell et al. 2022), as well as in Spanish rivers (Almodóvar et al. 2018)—with a decline in overall abundance—and attributed to the variations of the North Atlantic Oscillation Index (Dickson and Turrell 1999; Condron et al. 2005; Drinkwater et al. 2014). Climatic variations also influence the dynamics of many species populations (Post and Forchhammer 2002; Vázquez et al. 2017). Likewise, environmental conditions can affect the return rates by narrowing or favouring migration opportunities (García-Vega et al. 2018, 2022), as well as survival during the different life stages (Jonsson and Jonsson 2011; Honkanen et al. 2019).

The early development of salmon is strongly influenced by water temperature, with higher temperatures speeding up incubation and juvenile growth but also increasing mortality above 25°C (Elliott and Elliott 2010). Fluctuating water flows further exacerbate survival challenges, especially during emergence and early life stages (Jensen and Johnsen 1999). Smolts rely on seasonal changes in temperature and flow to trigger downstream migration (Otero et al. 2014), and their survival at sea is highly dependent on their size at migration (Jonsson, Jonsson, and Jonsson 2017) and is affected by variable sea surface temperatures and food availability, both of which are increasingly unpredictable due to climate change (Friedland and Todd 2012; Strøm et al. 2023).

As adult salmon return to freshwater, they encounter further challenges, especially during summer droughts in European southern rivers. Low river flows and elevated water temperatures create stressful and often lethal conditions, forcing salmon to seek refuge in deeper, cooler areas to survive the harsh summer months (Riley et al. 2009; Corey, Linnansaari, and Cunjak 2023). Prolonged droughts can severely disrupt migration, limiting access to suitable spawning grounds and reducing overall survival rates. In the Bidasoa River, radio-tracking studies from 2018 revealed that, on average, 53.7% of tagged salmon died due to natural causes during the summer low-flow period, with mortality rates varying significantly across years depending on annual conditions (Elso 2024). The exceptionally low salmon numbers recorded in 2022 exemplify these climate-related impacts. That year saw one of the warmest and driest periods on record in the Bidasoa Basin, with above-average temperatures and reduced rainfall throughout spring, summer and autumn. In fact, all radio-tracked salmon in 2022 perished during the summer. The late arrival of rains in November, combined with their scarcity, further compounded the difficulties faced by the salmon population, restricting migration and reducing their chances of successful spawning.

In recent decades, this natural cyclic abundance has ceased in both Europe and North America, leading to an unexplained and widespread decline in annual adult returns (Parrish et al. 1998; Fay et al. 2006; Chaput 2012; Dadswell et al. 2022), particularly at the southern limit of its distribution range (Horreo et al. 2011; Mota, Rochard, and Antunes 2016; Almodóvar et al. 2018; Nicola et al. 2018), with some populations nearing extirpation or extinction in the most severe cases (Jonsson, Waples, and Friedland 1999; Limburg and Waldman 2009; Nunn et al. 2023; van Rijssel et al. 2024). In the Bidasoa River, natural spawning has been reported at 31% below the critical conservation limit and 47% below the recommended favourable conservation limit set by ICES and NASCO (García de Leániz 2021).

Over the past 15 years, the Navarre Government has tried to protect and preserve salmon populations through restoration programs and projects (e.g. Irekibai, Kantauribai). These efforts are mainly focused on habitat restoration and full connectivity from the sea to the monitoring station (as well as in other locations upstream) by means of fishway constructions and dam removals. However, these efforts, while proven to greatly benefit salmon (and other fish species) by providing access to previously restricted higher-quality upstream habitat (Rodeles et al. 2019; García-Vega et al. 2020), seem to not completely solve the problem, at least in terms of fish abundance and recruitment, with other underlying issues preventing the species' recovery (Parrish et al. 1998).

Furthermore, additional work is needed. For instance, the effectiveness of the fishways at Las Nazas and Bera weirs, the first two obstacles in the Bidasoa River, is estimated to be less than 25% and 50%, respectively, for brown trout (GAN-NIK 2017; Bravo-Córdoba et al. 2024a). However, the effectiveness for salmon remains unknown due to the lack of available studies to date. Moreover, there are five hydroelectric power plants along the mainstem of the Bidasoa River upstream from Bera, each equipped with similar fishway types. Unfortunately, these facilities face significant maintenance problems, resulting in unfavourable conditions for upstream migration (Bravo-Córdoba et al. 2024b). Moreover, none of these facilities have mechanisms to prevent small fish from entering the channels and/or turbines during the downstream migration, which may impact salmon survival and return rates. Currently, the only escape route for fish trapped in these channels is the occasional emptying of the channels, accompanied by rescue surveys conducted when high concentrations of smolts are detected.

The observed decline in salmon abundance in the Bidasoa River from 2015 onwards, reaching its lowest number in 2022 (66 in the trap and 23 angled), forced the Navarre Government to a complete angling closure in the basin during 2023 and 2024. This measure has proved to be effective for the brown trout in the past within the same basin (García-Vega et al. 2020). However, it is a measure that stirred significant controversy, with many angler's collectives expressing strong reluctance while others supporting the decision. The study's results have revealed that, even with the controlled quotas of fishing by the Navarre Government, the actual extractions by anglers (averaging one angled salmon for every eight counted at the monitoring station) could also potentially pose a threat to the population's overall health. Furthermore, the characteristics of the extracted fish, the majority being MSW females, might suppose a severe impact on the population due to possible decreases in the breeding stock and overall egg production, and thus, natural recruitment may become insufficient for supporting fisheries and even for salmon conservation (Almodóvar and Nicola 2004). For instance, of the 23 salmon angled in 2022 (the worst year), 22 were MSW and 18 of them were females. Intensive fishing and selective practices based on species, size classes or gender can result in decreased fish populations and disrupt the functioning of aquatic ecosystems (Daupagne et al. 2021). Moreover, recreational angling in wild Atlantic salmon populations can exert selective pressure leading to size and length reductions, especially when the angling season aligns with the return of the largest sea-age fish class (Thorley, Youngson, and Laughton 2007; Saura et al. 2010; Harvey et al. 2017; Miettinen et al. 2024).

To address these challenges, the Navarre Government has implemented several angling measures for the protection of MSW salmon (e.g. delaying the opening of the fishing season and establishing a catch quota for those salmon with fork length ≥ 70 cm) as well as the “Salmon sponsorship” program, based on the voluntary donation of live-caught salmon by anglers. However, only 14 salmon were donated during the 4 years of the existence of this measure, out of a total of 153 salmon angled during that period. Although these measures suppose a starting point, one primary action to prevent overfishing and secure long-term sustainability of salmon populations while still pleasing anglers should involve implementing more restrictive angling regulations, like catch and release (Lennox et al. 2015) and/or a later opening of the fishing season (Jokikokko, Kallio-Nyberg, and Jutila 2004; Pérez et al. 2005; Borgstrøm et al. 2010; Harvey et al. 2017). These measures may help maintain the abundance of MSW females and improve natural recruitment in populations, while allowing the angling practice. However, it is important to note the need for a study of postrelease effects (mortality, reproduction behaviour, etc.) (Havn et al. 2015; Lennox et al. 2015) together with angler's awareness to prevent reluctance towards the adopted measures (Stensland, Aas, and Mehmetoglu 2013; Olaussen 2016). Moreover, these measures, along with the study of population trends during several years of fishing closure, appear to be a reasonable short-term decision. In this regard, a new Fisheries Management Law of Navarre was implemented in 2023, which changes the model and prioritises catch and release, leaving only 20% of the sections for extractive fishing. In the Bidasoa River, this equates to a river length of only 1.5 km. However, due to the salmon fishing ban in 2024, the effects of this law have not yet been observed. Moreover, the IUCN recently upgraded Atlantic salmon to “vulnerable” from “least concern” (Soto et al. 2023) and, in 2022, a coalition of associations, fishing collective and conservationists, supported by nationally recognised scientists, requested Spain's Ministry of Environment to classify salmon as an endangered species.

One of the main strategies traditionally employed to restore salmon populations, which is strongly advocated by angling collectives across Cantabrian rivers, is stocking (Cowx 1994; Welcomme and Bartley 1998). The marine survival of salmon smolts from stocking is known to be inferior to that of wild smolts (Jonsson, Jonsson, and Hansen 1991; Larocque, Johnson, and Fisk 2020), although the larger size of smolts from stocking assures a higher survival in freshwater and may compensate for their lower sea performance compared to wild smolts (Saloniemi et al. 2004). Results showed that a third of the counts from the monitoring station and angling corresponded with salmon from stocking origin. These fish, grown in controlled conditions with a stable food supply, exhibited larger body size, which at first could potentially contribute to a higher marine survival (Armstrong et al. 2018; Gregory et al. 2019; Simmons et al. 2022), but with hatchery–induced deficits in behaviour such as reduced predator-avoidance capabilities, lower feeding abilities and genetic diversity (Olla, Davis, and Ryer 1998). Stocking returning rates of fish from stocking consistently remained much below 1%, which may suppose an overall low survival rate in the marine environment. This implies a significant effort and economic investment for the recovery of only a small number of salmon, although it is important to note that a third of the counts at the monitoring station in the Bidasoa had stocking origin. Jonsson, Jonsson, and Hansen (2003) reported annual recapture rates of wild adult Atlantic salmon higher than in hatchery-reared fish (8.9% of the wild vs. 3.3% and 2.9% for hatchery-reared fish released as 1- and 2-year-old smolts respectively) in the Imsa River (Norway). Meanwhile, Chaput, Douglas, and Hayward (2016) reported return rates of smolts to maiden spawners (sum of 1SW and 2SW returns from a smolt class) between 0.6% and 7.6% for the Northwest Miramichi River system and between 1.7% and 11.9% for the Southwest Miramichi River system (New Brunswick, Canada).

Two associated impacts to the stocking activities have been identified. First is the extraction of fish from the river for captive breeding at the fish farm, avoiding natural spawn and recruitment in the river. Since these fish do not reproduce in nature, the extractions limit the river's natural recruitment. In addition, the stocked fish come from the 12.75% adult salmon extracted to the fish farm as breeders, which may also lead to unfavourable effects on the genetic composition of wild populations, with the reduction in genetic diversity as a small number of fish become responsible for an entire cohort. In this regard, genetic variability studies conducted in the Bidasoa in order to account for the possible effect (Morán Martínez 2005, 2020) have not shown a measurable impact on genetic diversity in this case. The periodical genetic studies during stocking actions are vital, moreover considering the synergistic effects of a warming climate, river water detraction and the homogenizing effect of human-mediated introgression, which may drive the genetic erosion of native population structure (Almodóvar et al. 2023).

Secondly, the tagging system with CWTs can have certain effects on the salmon's abundance. These fish require also to be removed from the river and slaughtered for reading the tags, which contradicts the efforts to recover the population. To minimise this impact, in the Bidasoa, these fish are used for captive breeding to produce new cohorts for stocking. Nonetheless, this practice still removes individuals from the river that could have reproduced naturally. Alternative tagging procedures, such as passive integrated transponders (PIT), could be considered. However, it is important to conduct an economic assessment to determine whether the cost of the tag outweighs its contribution to the assessment of the success of the stoking programs. Fish stocking is a fishery management tool that particularly requires risk assessment and cost-effectiveness evaluation, due to its common application, possible ecological risks and heavy investment, both economically and socially (Ham and Pearsons 2001; Hunt et al. 2017). In this regard, a controlled cessation of stocking over a few consecutive years could provide valuable insights into the population's ability to sustain itself naturally, provided that the population is above critical conservation limits (García de Leániz 2021). In fact, this is contemplated in the Salmon Management Plan of the Bidasoa River, which foresees to end stocking when the population has reached its favourable conservation status, that is, when 1.3 million eggs are reached in the basin. This would be crucial in evaluating both the necessity and long-term effectiveness of the stocking program.

Marine mortality is currently considered a key driver of the observed population declines in recent decades (Chaput 2012; Olmos et al. 2019; Thorstad et al. 2021; Gillson et al. 2022). Adult salmon are now tending to return to rivers in fewer numbers and in poorer conditions (Jonsson, Jonsson, and Albretsen 2016a; Bal et al. 2017; Gillson et al. 2022). In this regard, an increase in marine mortality has been observed in recent decades (Olmos et al. 2020; Gillson et al. 2022) and a reduction in body size and sea-winter age has been reported (Saura et al. 2010; Adams et al. 2022; Long et al. 2023; Tréhin et al. 2024). This trend is corroborated by the observations in the Bidasoa River, where the mean fork length of returning 1SW salmon has declined from 657 mm in 1993 to just 593 mm in 2023, while MSW females saw a reduction from 812 to 765 mm in the same period. Similar declines in salmon body size—approximately 1 cm per decade—have been documented in other regions such as Scotland, Ireland, Norway and France (Jonsson, Jonsson, and Albretsen 2016a; Bal et al. 2017).

This reduction in body size suggests not only potential environmental stressors but also decreased energy reserves, which may impact the fish's reproductive success, recruitment and overall fitness and increase the probability of predation (Todd et al. 2008; Jonsson, Jonsson, and Albretsen 2016a). Changes in the distribution of ocean thermal conditions may be affecting salmon directly by eliciting physiological and behavioural compensations that in turn affect growth (Friedland and Todd 2012; Jonsson, Jonsson, and Albretsen 2016a; Olmos et al. 2020). Additionally, the decrease in zooplankton biomass, the lower availability of feeding areas, their northward shift and increased competition with other species (Almodóvar et al. 2018; Vollset et al. 2022; Strøm et al. 2023) pose significant constraints on salmon growth and maturation potential.

In this situation, the actions to take may be challenging. While freshwater habitats have shown overall improvement through habitat restoration and connectivity projects, the persistent global decline of Atlantic salmon populations, despite a relatively stable trend in the Bidasoa River, underscores the necessity of implementing more rigorous conservation measures. Promoting angling practices that do not result in fish death, such as catch and release, along with nonlethal tagging methods for population monitoring, and employing adaptive management strategies—involving close cooperation between local communities, anglers, scientists and authorities—will be crucial for the conservation and sustainable management of salmon populations. Additionally, enhancing public awareness and angler education programs will help foster a greater understanding of the ecological importance of salmon, ensuring angler participation in conservation efforts and increasing compliance with sustainable practices. Furthermore, assessing the effectiveness of existing fishways and retrofitting them, if necessary, along with implementing a mandatory maintenance program—overseen by water authorities—to ensure fishways remain functional, should be prioritised. Improved downstream fish passage and the installation of turbine safeguards are also critical to reducing the risk of juvenile salmon mortality during downstream migrations and preventing delays in diversion channels. These measures should be continuously refined based on ongoing monitoring and scientific research to effectively address the multifaceted challenges posed by both anthropogenic impacts and natural environmental changes.

Author Contributions

Conceptualization: A.G.-V. and F.J.S.-R. Developing methods: J.E. and J.A.-G. Conducting the research: A.G.-V., J.F.F.-P. and J.E. Data analysis: A.G.-V. and J.F.F.-P. Data interpretation: A.G.-V., J.F.F.-P., J.E., F.J.S.-R. and F.J.B.-C. Preparation of figures and tables: A.G.-V. and J.F.F.-P. Writing—original draft: A.G.-V. Writing—review and editing: J.F.F.-P., F.J.S.-R., F.J.B.-C. and J.E.

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Ethics Statement

All procedures and experiments carried out in the monitoring station and fish farm were performed following European Union ethical guidelines (Directive 2010/63/UE) and Spanish Acts ECC/566/2015 and RD 118/2021 (by which it is modified RD 53/2013), with the approval of the competent authorities (Regional Government on Natural Resources and Water Management Authority).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the Government of Navarre but restrictions apply to the availability of these data, which were used under license for the current study, and so are not publicly available.

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